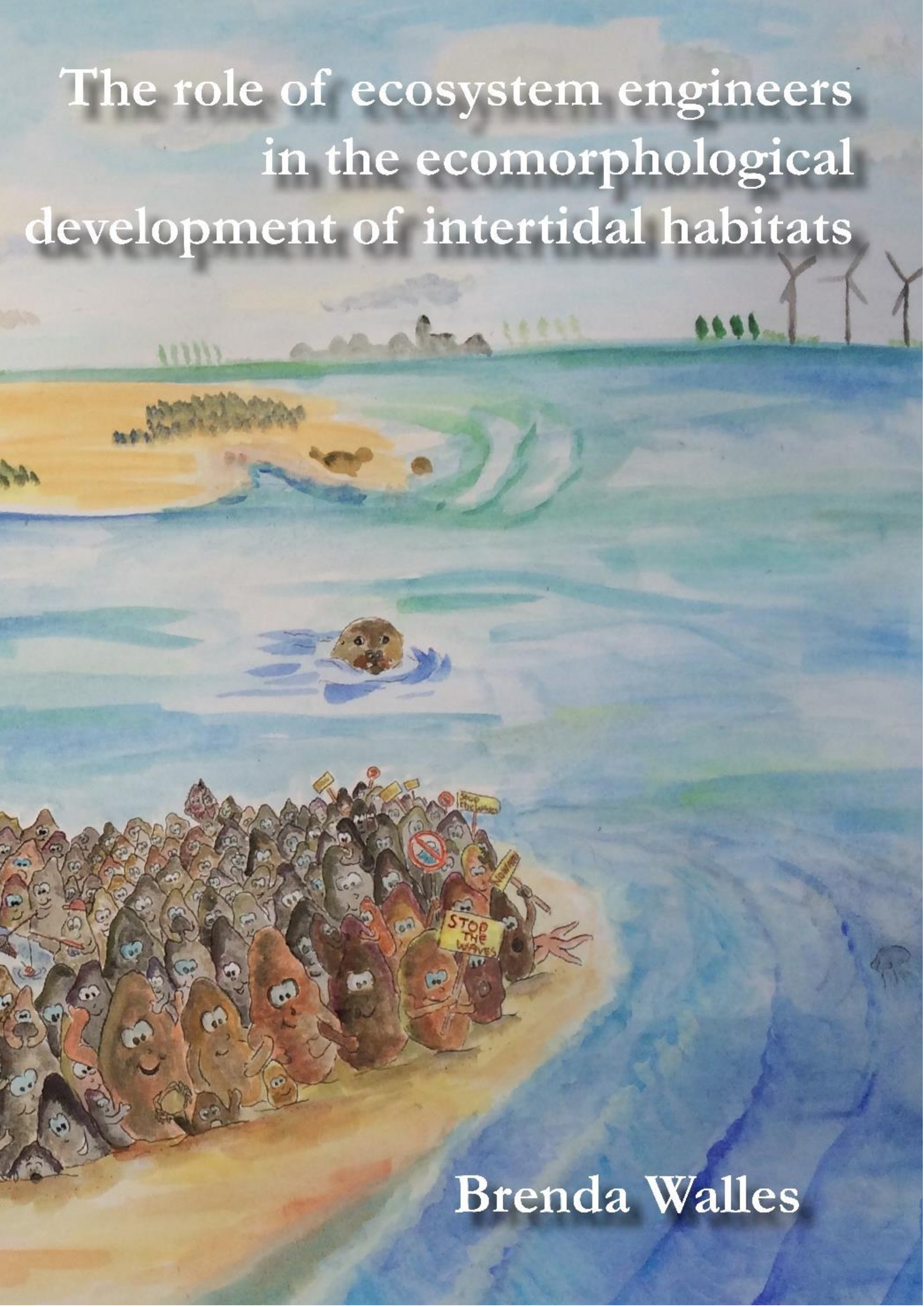
The role of ecosystem engineers in the ecomorphological development of intertidal habitats



Brenda Walles

The role of ecosystem engineers in the ecomorphological development of intertidal habitats

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Brenda Walles

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For my three true loves: Bart, Milou and Thijs Verhaeghe de Naeyer

Vannacht heeft zij haar grenzen weer verlegd.
De vloedlijn weer een stuk vooruitgeschoven.
En ik blijf maar steeds geloven
dat wij met onze dammen, onze dijken
minder veilig zullen blijken dan we lijken.

Want zeeën worden hoger
en spannen elementen samen tegen ons stukje land,
houden dan onze mensenwerken stand?

En lopend op het strand
hoop ik op mijn ongelijk
en wandel terug
over de dijk

Johanna W.
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Chapter 1

The role of ecosystem engineers in the ecomorphological development of intertidal habitats:

General introduction & outline of the thesis

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General introduction & outline of the thesis

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1.1 Coastal ecosystems and ecosystem engineers

Coastal zones are amongst the most extreme, dynamic and complex ecosystems. At the same time coastal ecosystems are some of the most productive systems in the world. A wide range of different habitats can be found in the coastal zone, such as sandy and rocky shores, mangroves and salt marshes, coastal wetlands, intertidal areas, sand and mudflats, biogenic reefs (corals, oysters, etc.), shallow inlets and bays. These habitats provide a wide variety of ecosystem services, such as shoreline stabilization, nutrient cycling, carbon sequestration, detoxification of polluted waters and the supply of food and energy resources. Coral reefs, for example, provide many ecosystem services as they maintain fisheries by providing shelter and substrate for a large variety of species. They also play an important role in the nutrient cycling, and provide coastal protection by attenuating waves (Ferrario et al., 2014). Seagrass beds and mangrove forests provide coastal protection, erosion control, water purification, carbon sequestration and maintenance of fisheries (Garrard and Beaumont, 2014; Lee et al., 2014).

Coastal habitats can be modified by certain key species inhabiting these areas. These species are known as ecosystem engineers (see Box 1.1). Ecosystem engineering organisms can temper extreme environments, creating favourable conditions by modifying their direct biotic and abiotic environment. Seagrass beds for example, can purify the water by nutrient uptake and deposition of suspended particles within their canopy (Koch et al., 2006). Furthermore, their presence changes abiotic factors, such as water residence time, hydrodynamic conditions, light availability, and provision of habitat for other species. Coral reefs, for example, provide structural complexity which creates habitat for other species.

1.2 Human pressure

Coastal ecosystems have always been important for humans as they guaranteed food resources (through fishing, shellfish harvesting and bird-hunting) and are accessible from both land and water, which makes them interesting trading locations. It is therefore no coincidence that 22 of the 32 largest cities in the world are situated on estuaries (Ross, 1995). Globally, 80% of the human population lives in coastal areas. While coastal areas facilitated the rapid increase in human population (McGranahan et al., 2007), ironically, human activities (overfishing, eutrophication, coastal development, dredging, sedimentation, biological invasions) put these areas under constant and increasing pressure. Furthermore, global-scale climate change threatens coastal ecosystems through global warming, diseases, ocean acidification, increased storminess and sea level rise.

Box 1.1
Ecosystem engineers

The concept of ecosystem engineers was first introduced by Jones et al. (1994), who felt the need for a systematic identification for the role of organisms in modifying, creating and maintaining habitats. An ecosystem engineer is defined as "an organism that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials" (Jones et al., 1994). Two different types of ecosystem engineers are identified by Jones et al. (1994). Ecosystem engineers can affect the availability of resources to other organisms either as a direct consequence of the structure created by them (autogenic engineers) or by the modulation of biotic or abiotic forces by its structure or their biological activity (allogenic engineers) (Commito and Boncavage, 1989; Gutiérrez et al., 2003; Jones et al., 1994). Ecosystem engineering is demonstrated by many different types and sizes of organisms in different environments (terrestrial, freshwater and marine systems).

A good example of an allogenic engineer is the beaver. By creating dams they alter the landscape, forming extensive wetland habitat in which some native plants and species are banned, while new plants and species can thrive. Overall, beavers increase the heterogeneity of the landscape which results in an increase of the biodiversity (Wright et al., 2002). Trees, on the other hand, are autogenic engineers which create habitat for other organisms while they grow.

Many examples of both autogenic and allogenic ecosystem engineers are found in coastal ecosystems. An example of an allogenic engineer is the Australasian isopod *Sphaeroma quoyanum* which increases salt marsh erosion in California, due to its burrowing and filter feeding activity (Talley et al., 2001). Arenicola marina is an allogenic engineer as it destabilise the sediment by bioturbation (Montserrat et al., 2011). Coastal vegetation, such as kelp forest, mangroves, marsh plants and sea grasses, are known as autogenic ecosystem engineers, as they reduce water flow within their canopy or root system, promoting sedimentation within the vegetation and provide substrate for both sessile as mobile organisms (Bos et al., 2007; Bouma et al., 2014; Bouma et al., 2005b; de Vries et al., 2007; Steneck et al., 2002). In temperate climate zones, sea grasses trap sediment between their leaves during summer, whereas in winter no leaves are present to fix the trapped sediment (Paul and Amos, 2011). In the tropics sea grasses do not show this seasonal effect as they are present year round. Although marsh plant also die off during winter, increased elevation by remaining plant parts as well as increased surface roughness increases wave attenuation (Callaghan et al., 2010). Coral reefs and bivalve reefs are also autogenic engineers as they provide structure and complexity on bare sediment (Ruesink et al., 2005). Species are not exclusive autogenic of allogenic ecosystem engineers. Besides providing habitat for other species, filter feeding bivalves filter the water in lakes and estuaries, increasing the light penetration which affects benthic macroalgal communities.

Furthermore, ecosystem engineers can facilitate other species. Changes in the physical environment caused by corals for example, affect the entire ecosystem as other coastal ecosystems, such as seagrass beds and mangrove forests can develop at the reduced hydrodynamic conditions.

Consequently, coastal ecosystems, and especially many of the ecosystem engineers, are world-wide degrading. Globally 29% of the seagrass beds, 30% of coral reefs, 35% of mangroves, 50% of salt marshes, and 85% of oyster reefs are either lost or degraded (Barbier et al., 2010 and references therein; Beck et al., 2011). Regardless of the cause of loss of these coastal habitats, this deterioration has adverse impacts on the provision of ecosystem services upon which humans and other species depend. Worm et al. (2006) showed that a loss in marine biodiversity resulted in 33% decline in the number of sustainable fisheries; 69% decline of nursery habitats, such as oyster reefs, seagrass beds, and wetlands; and 63% decline of filtering and detoxification services provided by wetlands, submerged vegetation and filter feeders.

Another threat to coastal ecosystems is coastal erosion. This global problem is expected to become even more serious in the next decades due to ongoing human-induced changes in estuarine and coastal landscapes combined with an accelerated sea-level rise (Govarets and Lauwerts, 2009; Nicholls, 2011; Nicholls and Cazenave, 2010). In Europe alone, more than 5 million people live in areas threatened by coastal erosion and flooding. As humans extensively use the coastal zone, coastal erosion in no longer a natural phenomenon but became an important problem for societies, as it causes loss of land of ecological, economical and societal value. One quarter of the European coastline is currently affected by coastal erosion, partly due to human activities in the coastal zone. Figure 1.1 shows the pattern of erosion and accretion in Europe, including percentages for all European seas. The Mediterranean and North Seas have the largest percentage of eroding coasts. Protection of the coastal habitats against erosion is expensive. In the Netherlands for example, 40 million euro is spent each year for beach nourishment (Sistermans and Nieuwenhuis).

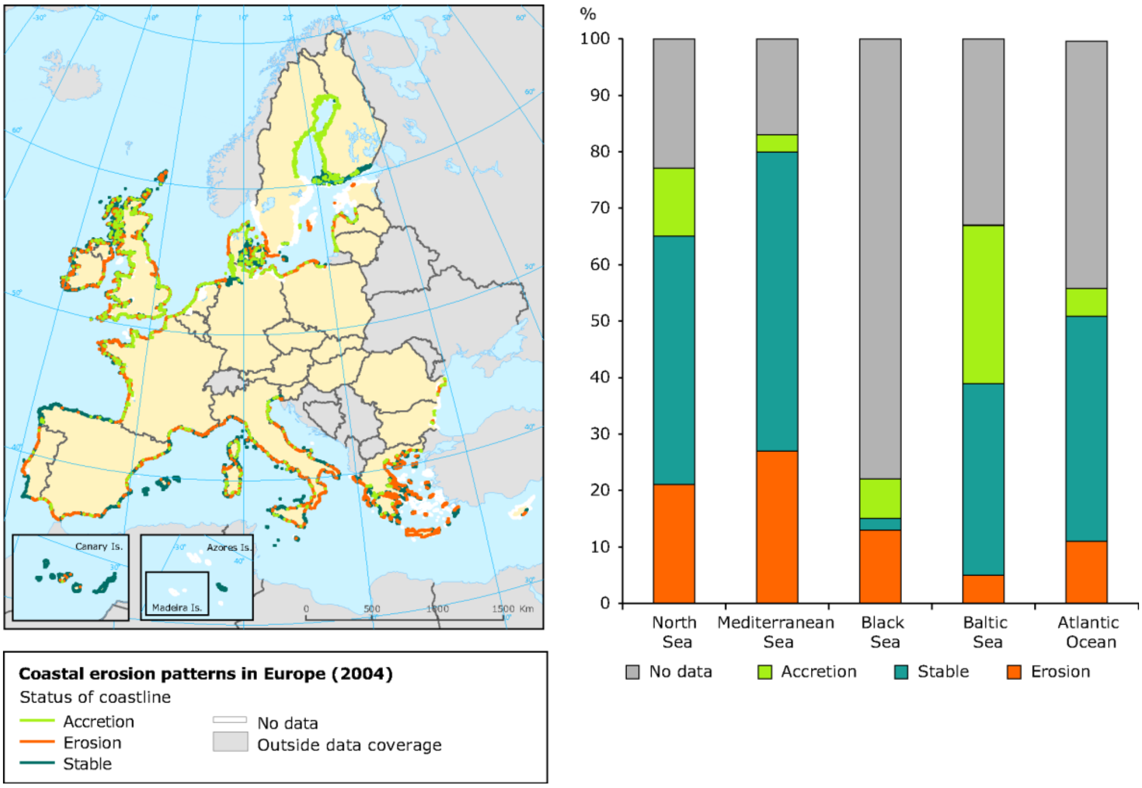

Figure 1.1 Coastal erosion patterns in Europe (European Environment Agency (EEA)).

One striking example of human induced coastal erosion is found in the Oosterschelde estuary (the Netherlands, Figure 1.2), where intertidal areas are eroding and disappearing as a consequence of coastal defence infrastructures, constructed after a devastating flooding in 1953. A storm surge barrier, completed in 1986, separates the estuary from the North Sea. The barrier still permits tides going in and out, and can be closed in the event of a storm surge. The basin area of the Oosterschelde, the tidal prism, the tidal range, and the tidal currents decreased as a consequence of these measures. Due to the reduction of tidal volume and flow, the Oosterschelde basin is presently not in morphological equilibrium and the oversized channels are in need of sediment. Sediment erodes from the tidal flats into the channels during storms (so-called "sediment starvation" see box 1.2); whereas tidal forces are too small to redistribute the sediment back to the tidal flats (Mulder and Louters, 1994). On average, a net erosion rate of 10 mm year^{-1} on the tidal flats has been observed (Santinelli and De Ronde, 2012). Reduction in tidal flat area and elevation result in a loss of valuable habitats, impacting biodiversity including bird populations and seals. It also poses threats to coastal defence as dikes become less protected from waves and currents when tidal flats and salt marshes in front of dikes are lost. The scale of erosion currently encountered in the Oosterschelde, makes this ecosystem a suitable model system to study ecosystem-based coastal defence methods.

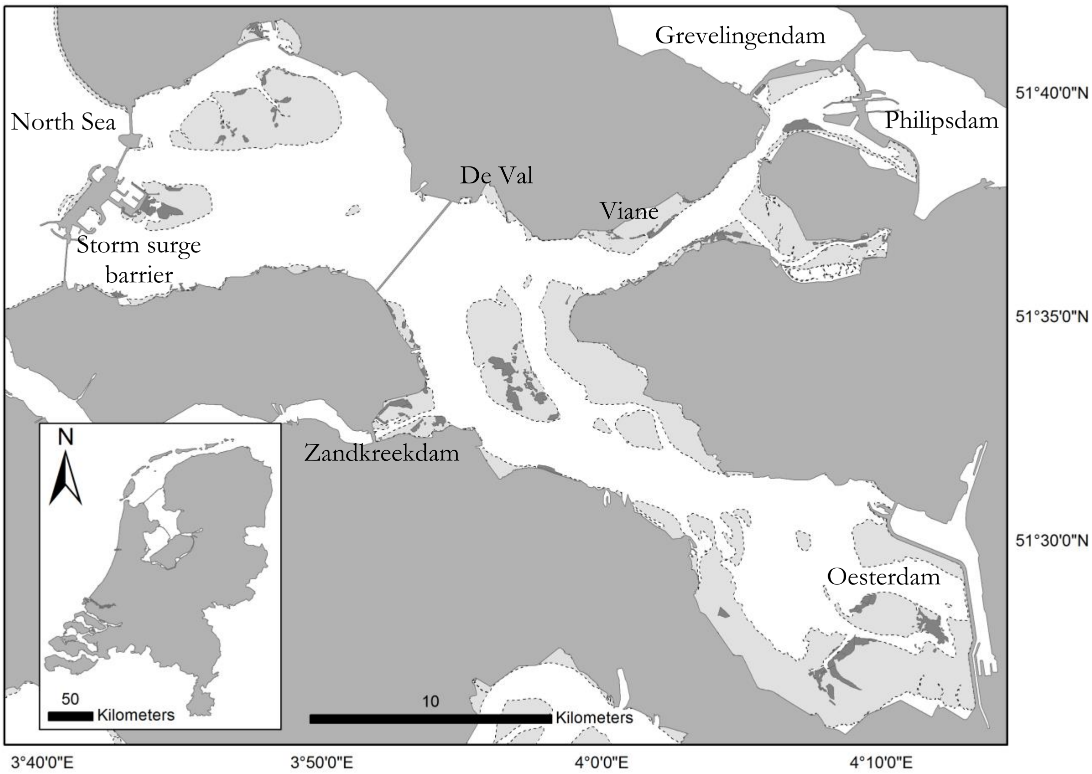

Figure 1.2 Overview of the coastal defense works (Storm surge barrier, Zandkreekdam, Grevelingendam, Philipsdam and Oesterdam) in the Oosterschelde estuary (the Netherlands). The estuary is separated from the North Sea by the storm surge barrier in the west. Tidal flats are indicated with light grey, dotted lines indicate the mean low tide level. Intertidal areas covered with oysters in 2011 are indicated in dark grey. The artificial reefs are located at two intertidal flats: De Val and Viane.

1.3 Paradigm shift: Ecological engineering for coastal protection

The traditional approach to protect the coastline has been to 'harden' shorelines by building dikes, breakwaters, revetments, floodgates, barriers etc. Although engineered solutions are needed and essential in some context, they can be costly to build and maintain (Hillen et al., 2010). These structures may also have negative side-effects (Cheong et al., 2013). Shoreline constructions for instance, causes degradation of coastal fish reproduction habitats (Sundblad and Bergstrom, 2014) and fragmentation of populations (Major et al., 2014). Furthermore, shoreline construction reduces the ability of the shoreline to respond to natural forces needed to build up the shoreline, often enhance erosion in other parts, degrade water quality, impair recreation, fragment habitats and reduce the production of fisheries (Defeo et al., 2009; Govarets and Lauwerts, 2009; Peterson and Lowe, 2009).

Box 1.2
Sediment starvation in the Oosterschelde estuary as a result of the Delta Works

On the 1st of February 1953 the South-western part of the Netherlands experienced a large flood due to a severe storm surge. The combination of springtide with a severe north-westerly storm in the North Sea basin induced tides up to 3 meters above normal tidal levels. More than eighteen-hundred people drowned, 100.000 people lost their houses and belongings.

To prevent future flooding, compartmentalization dams where designed to shorten the coastline of the South-West delta (the Delta Plan) closing off several tidal basins, such as the Grevelingen, Haringvliet and the Oosterschelde. Between 1961 and 1987 dams were constructed (the Delta Works) to achieve this plan. The dam, which would close off the Oosterschelde estuary from the North Sea, creating a large freshwater basin, was last in line. But around 1973 several environmental organizations and the shellfish sector protested against the disappearance of valuable, unique estuarine habitat as well as an important mussel and oyster cultivation area. Instead of a closed dam, a storm surge barrier was built, which could be closed during storm conditions, while allowing exchange with the North Sea during normal conditions.

The intertidal areas are one of the most important areas for the ecosystem of the Oosterschelde. They are rich in benthic fauna, which serves as food for (migrating) wading birds and other organisms. The intertidal habitat comprises 118 km^2, about 34% of the total surface. The Delta Works however, have a major impact on this valuable habitat, and without any intervention the intertidal habitats will eventually disappear.

Due to the Delta Works the tidal volume decreased, which resulted in lower current velocities (Brinke et al., 1994; Smaal and Nienhuis, 1992; Vroon, 1994). Due to this reduction of tidal volume and flow, the Oosterschelde basin is presently not in morphological equilibrium and the oversized channels are in need of sediment. Reduction of tidal volume and current has resulted in a concentration of wave energy dissipation in a smaller vertical zone of the intertidal area, which causes resuspension of the deposited material and an increase in erosion of the tidal flats (Mulder and Louters, 1994; Vroon, 1994). Sediments that are eroding from shoals, tidal flats and salt marshes end up being deposited in channels and gullies (Figure B1.2.1), whereas tidal forces are too small to redistribute the sediment back to the tidal flats (Mulder and Louters, 1994). This process is currently referred to as "sediment starvation". It might take several hundreds of years before the Oosterschelde estuary is adapted to the current tidal volume and current velocities (Kohsiek et al., 1987; Mulder and Louters, 1994). Calculating the required sediment to stop this process results in a range of 400-600 million m^3 of sand. Because there is barely any import of sand from the North Sea through the storm-surge barrier, the only source for sediment is the intertidal area within the basin itself. Calculations show that degradation of the total intertidal area can provide only 160 million m^3 of sand. Therefore the intertidal areas are bound to disappear. Recent observations show an average net erosion of 10 mm year^{-1} (Santinelli and De Ronde, 2012), resulting in a loss of 50 ha of intertidal area per year (Zanten and Adriaanse, 2008), and a decrease in emersion of 0.3 % per year (Ronde et al., 2013).

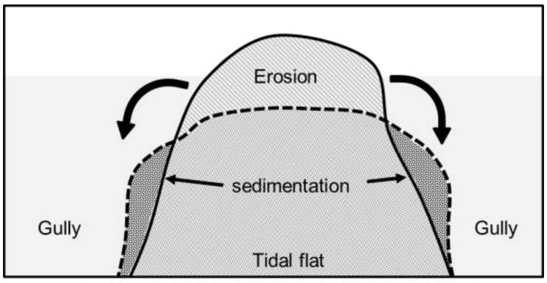

Figure B1.2.1 Sediments that are eroding from the tidal flat end up being deposited in the gullies.

Global climate change will magnify the risk of flooding and erosion in coastal areas as the sea level rises, and storms will increase in frequency and intensity. By 2080 the number of people affected by flooding is expected to increase more than five-fold (Gedan et al., 2011). Traditional defence structures will not be sufficient in many places (Cheong et al., 2013). There is a need for coastal defence structures which can adapt to shifting conditions through growth and self-maintenance. Over the past decade a shift to a more ecosystem-based coastal protection occurred, incorporating 'soft' defence structures (i.e. coastal ecosystems) such as dunes, mangroves, tidal wetlands, marshes, seagrass beds, kelp forests, and bivalve and coral reefs (Bouma et al., 2014; Duarte et al., 2013; Temmerman et al., 2013). This ecological engineering aims at restoring or developing ecosystems, for the benefit of both humans and nature, by optimising ecosystem services provided by these ecosystems. These 'soft' defence structures have the natural capacity to temper wave action and prevent shoreline erosion (Barbier et al., 2008; Gedan et al., 2011). Ecosystem-based coastal protection using ecosystem engineers, such as mangroves, seagrasses, and reefs is especially interesting for developing countries as it may offer greater opportunities for those countries to achieve coastal protection using limited financial resources (Duarte et al., 2013). Approaches and tools for evaluating potential role and context-dependent aspects of natural defence mechanisms, however, are lagging behind those for shoreline hardening (Gedan et al., 2011; Jones et al., 2012). Incorporating 'soft' defence structures requires knowledge on how and where habitats reduce exposure to erosion and provide protection, as well as ecological data to identify where these ecosystems and species can be implemented sustainably.

The research presented in this thesis is driven by the Building with Nature philosophy (De Vriend and Van Koningsveld, 2012). The aim of Building with Nature is to make use of natural processes in coastal engineering schemes, while providing opportunities for nature. With natural processes doing part of the work, building with nature solutions could provide innovative, cost-efficient alternatives in the realisation of coastal infrastructures. This thesis investigates the potential role of oyster reefs in ecosystem-based coastal protection. Results presented in this thesis contribute to a better understanding of the ecosystem engineering capacity of the oyster *Crassostrea gigas*.

1.4 Building with Nature

This thesis is part of the innovation programme Building with Nature, and fits within the case 'SouthWest Delta', where the environmental impact due to "sediment starvation" (see Box 1.2) of the Oosterschelde has been chosen as main issue (www.ecoshape.nl). Building with Nature aims at developing new design concepts for the layout and sustainable exploitation of river, coastal and delta areas. To adequately deal with large scale coastal erosion problems, such as found in the Oosterschelde as well as in other ecosystems, innovative, cost-efficient and sustainable methods are required for conservation of estuarine tidal habitats and thereby maintaining both ecological values as well as a good coastal defence. Ecosystem engineering has been shown to be an important mechanism in shaping estuarine and marine ecosystems. Preservation of the tidal flats by means of stabilization measures with ecosystem engineers looks promising, but more research is needed to understand underlying mechanisms and processes and predict their impact on the morphology and ecology of the system. Ecosystem engineers can locally shift an area dominated by erosion into an area where sediment accumulates. As engineers have a catalyzing effect, human effort required to introduce the engineer might be small compared with the magnitude of change required to shift the system in their absence. Ecosystem engineers can reduce the threshold of human effort needed to obtain the desired state (Byers et al., 2006). To apply ecosystem engineers successfully in coastal protection, oyster reefs need to become self-sustainable, three-dimensional structures that stabilize the tidal flats at locations were erosion is severe.

1.5 Bivalve reefs for ecosystem-based coastal protection

Reef building suspension feeding bivalves, such as mussels and oysters, are both allogenic and autogenic ecosystem engineers. As allogenic engineer they remove large quantities of suspended material from the water column by filter feeding and producing fecal and pseudofecal biodeposits that accumulate in the reef and its surroundings (Newell, 2004; Ostroumov, 2005; Ulanowicz and Tuttle, 1992; van Leeuwen et al., 2010). As autogenic engineers, their three-dimensional reef structure increases habitat heterogeneity and complexity in soft-sediment environments, increasing species diversity and abundance (Gutiérrez et al., 2003; Meyer and Townsend, 2000; Peterson et al., 2003). Furthermore, water flow and wave action are altered due to their physical structure (Donker et al., 2013; Lenihan, 1999; Piazza et al., 2005; Ruesink et al., 2005; van Leeuwen et al., 2010), resulting in a change of the sediment deposition, consolidation and stabilization (Dame and Patten, 1981).

The rate at which reef building suspension feeding bivalves change the local soft-sediment environment differs between species. Mussels form a bed by attaching themselves to each other by byssal threads. They organize themselves at different spatial scales, in order to increase the resilience of mussel beds (Liu et al., 2014). Young mussels can detach themselves, which enables them to climb on top of deposited material protecting the sediment against erosion, whereas older mussels are less mobile resulting in stabilizing the sediment which has already been deposited underneath (van Leeuwen et al., 2010). Most of this captured sediment however resuspends in winter and often the mussel bed itself disappears due to storms (Dankers et al., 2006). Oysters form reefs by cementing themselves permanently on conspecifics during the metamorphose from larval stage into benthic juvenile stage (Arakawa, 1990). As sediment and biodeposits settle between the shells, they become (partly) buried forming a strong shell-mud matrix for next generations to settle on. Oyster reefs are more robust then mussel beds due to the different way oysters and mussels are attached to conspecific. The cemented oysters stay in the reef structure, whether dead or alive, whereas dead mussel shells can flush out of the bed structure when they are not secured by byssal threads of live conspecifics. The heavier weight of the oysters cemented together also prevents them from being flushed away by waves and currents. Oyster reefs are, however, more vulnerable to sedimentation then mussels beds, due to their sessile lifestyle.

The role of the ecosystem engineering Pacific oyster (*Crassostrea gigas* (Thunberg, 1973)) on the eco-morphological evolution of tidal flat habitats and their possible role for coastal protection and protection against erosion is investigated in this thesis. *C. gigas* was initially introduced in the Oosterschelde estuary in 1964, when the shellfish industry seeded the area with spat originating from British Columbia (Drinkwaard, 1998, 1999; Shatkin et al., 1997), after mass mortality of the native European flat oyster, *Ostrea edulis*. More introductions of both spat and adult oysters soon followed (Drinkwaard, 1998). Introduction of the Pacific oyster was acceptable as water temperatures in the Netherlands were assumed to be too low for reproduction (Drinkwaard, 1999). Additionally, plans for closing off the Oosterschelde estuary from the North Sea had already been made. According to plan, this would have resulted in a stagnant freshwater lake, unsuitable for oyster growth and reproduction. But plans changed and the Oosterschelde estuary remained a marine tidal system (Nienhuis and Smaal, 1994; Smies and Huiskies, 1981), see Box 1.2. Oysters were, against expectations, able to reproduce in the cold Dutch waters. The first natural recruitment event after introduction was recorded in 1975 (Drinkwaard, 1998). After this the oysters spread rapidly (Smaal et al., 2009), presently occupying 9 km^2 of the (lower) intertidal (i.e. about 8%) with large dense oyster reefs, Figure 1.3. The ecosystem engineering capacity of the species may help explain the success of its invasion; engineers may make novel habitat suitable for themselves, enhancing conditions for their spread while altering the environment for present species (Cuddington and Hastings, 2004). Oysters change the environment via their own physical structure (autogenic engineering), which tends to constitute in a positive feedback on conspecifics (Figure 1.4). The spread of this introduced species represents an opportunity to learn about their impact on the existing ecosystem (Crooks, 2002), since it can be a potential threat to the existing ecosystem, although it has the opportunity to be used for shellfish farming and for coastal protection.

Figure 1.3 Natural *Crassostrea gigas* reef at the intertidal flat Viane in the Oosterschelde estuary (SW Netherlands).

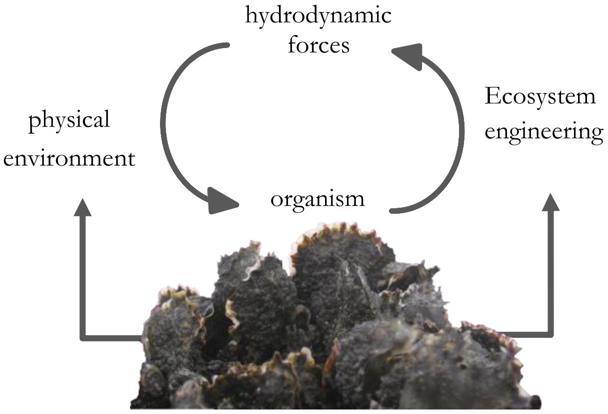

Figure 1.4 Schematic overview on how oysters modify their surroundings to their needs (positive feedback loop). The organism change the hydrodynamic forces due to its physical structure (autogenic ecosystem engineering), which affects the surrounding physical environment. The traits of the organism and the environmental context will determine the extent of this positive feedback loop.

The ecosystem engineering capacity of *C. gigas* and its potential use for the protection of tidal flats against erosion in the Oosterschelde was experimentally tested within the project Building with Nature. Five artificial oyster reefs (Figure 1.5) were constructed in the Oosterschelde estuary (The Netherlands, Figure 1.2) on eroding tidal flats. The aim was to investigate their impact on tidal flat morphology and their ability to grow out into a living oyster reef that can maintain their own habitat. The reefs were constructed by filling 25 cm high gabions with Pacific oyster shells, to provide substrate and encourage settlement of new oyster recruits (Arakawa, 1990; Tamburri et al., 2008). In the summer of 2009, two small artificial oyster reefs (called Pilot reefs) were constructed on the tidal flat Viane. In the autumn of 2010, three large artificial oyster reefs (called VianeEast, VianeWest and De Val) were constructed on two tidal flats: Viane and De Val. These biogenic reefs will be studied to obtain knowledge on the biological development over time.

Figure 1.5 Aerial photograph of the intertidal artificial oyster reefs in the Oosterschelde estuary. Picture was taken during the construction of one of the large artificial oyster reefs (VianeWest) in 2010. In the right corner, one of the small Pilot reefs constructed in the summer of 2009 is visible. Photo credits: L. Adriaanse

1.6 Outline of this thesis

The aim of this thesis is to investigate the ecosystem engineering capacity of the oyster *Crassostrea gigas*. More specifically, this thesis aims at revealing the mechanisms by which ecosystem engineers affect morphological development and ecological functioning of estuarine tidal flats by using (natural and designed) biogenic bivalve reefs in the Oosterschelde estuary as 'model' engineers. It is expected that the application of biogenic reefs can be very beneficial in preventing coastal erosion. It is still unknown under which conditions such reefs can thrive; also the effects (extent, magnitude) on sediment dynamics need to be analysed.

In this thesis three main research topics can be distinguished. Firstly, I will focus on the effect oyster reefs have on tidal flat morphology and the surrounding soft-sediment environment (Chapter 2). Secondly, I will study the boundary conditions for reef persistence (Chapter 3 and 4). And in the end oyster reefs as ecosystem-based coastal defence structures will be evaluated using data from natural as well as artificial reefs (Chapter 5 and 6).

In Chapter 2 the scale at which existing natural reefs influence sedimentation/erosion patterns is explored. Ecosystem engineers that inhabit coastal and estuarine environments, such as reef building oysters, do not only stabilise the sediment within their own footprint, but their influence might also extend far outside their reefs, affecting tidal flat morphology and protecting the surrounding soft-sediment environment against erosion. However, quantitative information is largely missing, and the spatially extended ecosystem engineering effects on the surrounding soft-sediment unknown. In this chapter the relationship between reef characteristics (dimensions, orientation, location, etc.) of eleven natural *C. gigas* reefs and the scale of morphological (i.e. elevation) changes in intertidal soft sediment environments is investigated. Knowledge showing the scale at which an oyster reef affects the surrounding soft-sediment environment can help to optimize the application of oyster reefs in shoreline protection and tidal flat conservation.

In Chapter 3 the persistence of reefs is being investigated and calculated. Can an oyster reef form a persistent structure with sufficient vertical accretion to keep up with sea level rise? Based on the population demography of long-existing natural *C. gigas* reefs (>30 years old) in the Oosterschelde, vertical reef accretion rates and carbonate production are calculated. This chapter provides a framework to predict reef accretion and population persistence under varying recruitment, growth and mortality scenarios, which can provide insight in the vertical development of an artificial reef.

In order to achieve long-term, persistent structures (Chapter 3) oysters need to settle, survive and grow. Providing a suitable substrate for oysters to settle on offers a kick start to enhance establishment at places where they were lost or are desirable as part of a coastal defence scheme. Chapter 4 investigates if reef development is limited by establishment, growth and survival thresholds. Knowledge about these thresholds is necessary to identify potential areas for successful implementation of oyster reefs for coastal defence.

In Chapter 5, data on oyster settlement, growth and survival, obtained from the artificial oyster reefs are discussed and compared with natural oyster reefs. What did we learn from natural reefs, and how can we incorporate this knowledge into the design of artificial reefs.

The final chapter contains a summary and a discussion of the main outcomes of this thesis. The discussion provides insights in the ecosystem engineering capacity of the oyster *Crassostrea gigas*, and evaluates their use as ecosystem-based coastal defence structures.

Chapter 2

The ecosystem engineer *Crassostrea gigas* affects tidal flat morphology beyond the boundary of their reef structures

Published as

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Abstract

Ecosystem engineers that inhabit coastal and estuarine environments, such as reef building oysters, do not only stabilise the sediment within their reefs, but their influence might also extend far outside their reefs, affecting tidal flat morphology and protecting the surrounding soft-sediment environment against erosion. However, quantitative information is largely missing, and the spatially extended ecosystem engineering effects on the surrounding soft-sediment largely unstudied.

To quantify this, we measured elevations around eleven natural *Crassostrea gigas* reefs occurring on tidal flats in the Oosterschelde estuary (the Netherlands). These tidal flats experience strong erosion as a consequence of human interventions in the system. Various reef sizes were chosen to test the proportional effects of reefs on tidal flat morphology. Measurements were used to create 3-dimensional surface maps to obtain properties of the reefs and the surrounding soft-sediment environment.

The area of the oyster reefs ranged from 2 m^2 to 1908 m^2. Reef length varied between 1 and 61 m, reef width between 1 and 45 m, and reef height between 0.20 and 1.08 m. Reefs varied in shape, going from round shape structures to more elongated ones. We observed elevated areas (>5 cm elevation from the background intertidal slope) on the lee side of all reefs, caused by the interaction between the reef's structure and locally prevailing wave conditions. The elevated area (i.e. the spatially extended ecosystem engineering effect) affected by the reef was of the same order of magnitude as the reef area. The elevated area was related to reef properties such as reef length, width, and height. Reef length; however, appeared to be the best predictor.

These findings contribute to management solutions for coastal adaptation and protection. Our study clearly showed that oyster reefs not only protect the tidal flat under their footprint, but as well an area beyond the boundary of the reef.

The ecosystem engineer *Crassostrea gigas* affects tidal flat morphology beyond the boundary of their reef structures

Brenda Walles, João Salvador de Paiva, Bram van Prooijen, Tom Ysebaert, Aad Smaal

2.1 Introduction

In terrestrial, freshwater and marine ecosystems, organisms are present which create, modify or maintain the habitats in which they live. These organisms are known as ecosystem engineers (Jones et al., 1994). Ecosystem engineering appears to be very common in nature, and in shallow estuarine and coastal areas, a number of distinct ecosystem engineers are present (e.g. coral reefs (Lugo-Fernández et al., 1998), reef forming bivalves (Dame and Patten, 1981; Lenihan, 1999; Piazza et al., 2005; Ruesink et al., 2005; van Leeuwen et al., 2010), dense vegetation of kelps and sea grasses (Bos et al., 2007; Bouma et al., 2005a; Jones et al., 1994), marsh vegetation (Bouma et al., 2010; Bouma et al., 2005b; Ysebaert et al., 2011) and mangroves (Danielsen et al., 2005; Mazda et al., 1997; Sanford, 2009)). These organisms typically reduce flow and dampen wave energy through their physical structures (i.e. autogenic engineering), thereby promoting sedimentation and reducing sediment resuspension (Bouma et al., 2005a; Commito and Boncavage, 1989; Duarte et al., 2013; Gutiérrez et al., 2003; Jones et al., 1994; Koch and Gust, 1999). The ability of these organisms to engineer the coastal environment through positive interactions is increasingly applied in ecological conservation and restoration, and offers an alternative, ecosystem-based solution for coastal protection (Borsje et al., 2011; Crain and Bertness, 2006; Gutiérrez et al., 2011; Widdows and Brinsley, 2002). This emerging field of ecological engineering for coastal protection and adaptation is gaining increased attention. It aims at creating ecosystems with a natural capacity to temper storm surges and prevent shoreline erosion (Cheong et al., 2013; Temmerman et al., 2013). To become common practice; however, more quantitative proof of the concept and its effectiveness for coastal protection is required (Cheong et al., 2013; Temmerman et al., 2013).

This paper focuses on the potential role of oyster reefs as ecosystem-based coastal protection and conservation structures in soft sediment environments. Oyster reefs are valued for the many ecosystem services they generate, such as stabilization of shorelines (Meyer et al., 1997), improvement of water quality (Dame et al., 2005; Grizzle et al., 2006b; Newell et al., 2002), and creation of habitat for other organisms (Meyer and Townsend, 2000; Peterson et al., 2003; Scyphers et al., 2011; Shervette and Gelwick, 2008). At the local scale, the oyster reefs form complex three-dimensional hard substrates, influencing hydrodynamics, stabilizing the bottom, and modifying sediment composition within their reef structures through the deposition of large amounts of fine particles, faeces and pseudofaeces (Grabowski and Peterson, 2007; Gutiérrez et al., 2011). Moreover, in soft-sediment environments, their effects may extend beyond the direct surroundings of the reefs and can be detectable up to several hundreds of meters affecting morphological and ecological processes in these soft sediment environments (Donadi et al., 2013; Zee et al., 2012).

Although the capacity of oyster reefs in enhancing sedimentation and reducing sediment resuspension is frequently stated (Borsje et al., 2011; Dame and Patten, 1981; Grabowski et al., 2012; Meyer et al., 1997; Piazza et al., 2005), quantitative information is largely missing, and especially the spatially extended ecosystem engineering effects on the surrounding soft-sediment environment, remain largely unstudied. Meyer et al. (1997) observed sedimentation behind artificially constructed oyster reefs, whereas nearby unprotected shorelines showed erosion. Recently, van der Zee et al. (2012) observed strong spatial gradients in sediment properties in the surrounding area of Pacific oyster (*Crassostrea gigas*) reefs, indicating large scale (100s of m) engineering effects. The scale at which reefs influence sedimentation/erosion patterns has; however, not been quantified by previous studies. Knowledge showing the scale at which an oyster reef affects the surrounding (soft sediment) environment can help to optimize the application of oyster reefs in shoreline protection and tidal flat conservation.

We investigate the relationship between reef characteristics (dimensions, orientation, location, etc.) of natural *Crassostrea gigas* reefs and the scale of morphological changes in intertidal soft sediment environments (Oosterschelde estuary, the Netherlands). We hypothesize that reef characteristics such as length, width and height determine the scale of the morphological response. As reefs reduce wave energy and tidal currents, an elevated area on the lee side of the reefs is expected, seen from the dominant wave direction.

2.2 Methods

2.2.1 Study area

The Oosterschelde estuary (the Netherlands) is a 351 km^2 tidal basin with tidal flats (118 km^2), artificial rocky shore habitats (dikes), deep gullies and shallow water areas. In response to a devastating flooding in 1953, a storm surge barrier was constructed at the sea side (finished 1986) that separates the estuary from the North Sea; in the same period the eastern part of the estuary was closed off by two dams. The basin area of the Oosterschelde, the tidal prism, the tidal range and the tidal currents decreased as a consequence of these measures. At present, the estuary has a mean tidal amplitude ranging from 2.47 m near the storm surge barrier to 2.98 m in the northern branch and 3.39 m at the southeast end (Troost et al., 2009). The maximum current velocity is about 1.0 m s^{-1}. Salinity throughout the estuary is high, generally > 30 psu (Troost et al., 2009). Due to the reduction of tidal volume and flow, the Oosterschelde basin is presently not in morphological equilibrium and the oversized channels are in need of sediment. Sediment erodes from the tidal flats into the channels during storms, whereas tidal forces are too small to redistribute the sediment back to the tidal flats (Mulder and Louters, 1994). On average a net erosion rate of 10 mm year^{-1} on the tidal flats has been observed (Santinelli and De Ronde, 2012). This study focuses on natural reefs of the Pacific oyster (*Crassostrea gigas*) located on three different tidal flats (Galgeplaat, St. Annaland and Viane) in the Oosterschelde estuary (Figure 2.1). The Galgeplaat is a tidal flat in the middle of the estuary, whereas St. Annaland and Viane are tidal flats connected to dikes in the northern branch. The dominant wave's direction depends on the wind's direction and the fetch length of each direction. Local wind conditions were obtained from wind measurements at Stavenisse, the Netherlands (www.hmcz.nl). In the Netherlands, mainly south-westerly winds prevail and north-westerly storms. Reefs at Viane mainly experience waves in the northeast direction, whereas at St. Annaland and Galgeplaat southeast waves predominate.

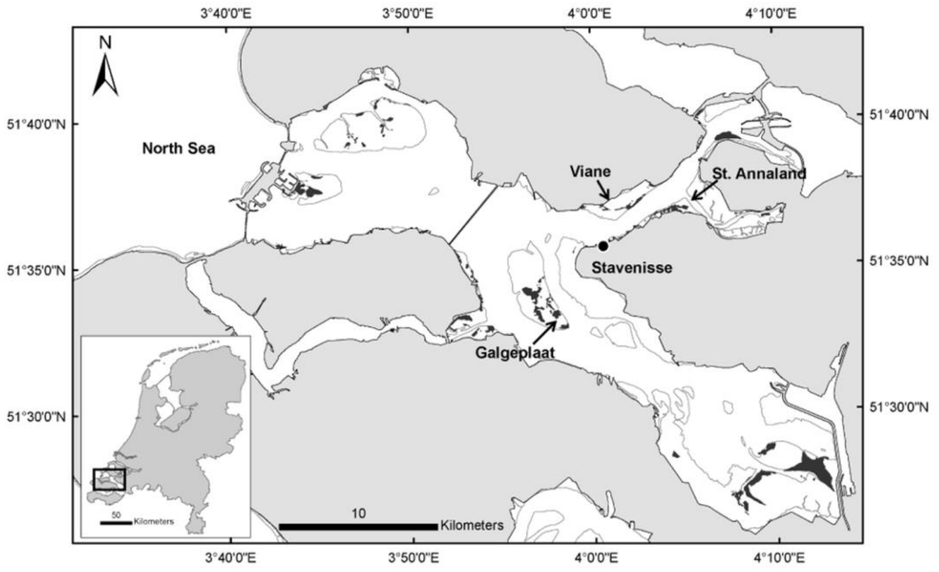

Figure 2.1 The Oosterschelde estuary (the Netherlands). Oyster reefs were studied on three tidal flats (Galgeplaat, St. Annaland and Viane). The estuary is separated from the North Sea by a storm surge barrier. Grey lines indicate the mean low tide level. Intertidal areas covered with oysters are indicated in black. The measuring station for wind (Stavenisse) is indicated with a black dot.

2.2.2 Studied species

The Pacific oyster *Crassostrea gigas* (Thunberg, 1793) was introduced by the shellfish industry in the Oosterschelde estuary in 1964, after mass mortality of the native European flat oyster *Ostrea edulis* (Drinkwaard, 1998). After its introduction, *C. gigas* spread rapidly through the estuary following natural spatfall events in the 1970s. At present *C. gigas* covers more than 9 km^2 (8%) of the intertidal habitat (Smaal et al., 2009), typically forming dense reefs of different sizes. These dense reefs persist longer than the lifespan of an individual oyster. In the Oosterschelde estuary reefs older than 30 years, with oysters above 7 years of age can be found (Walles, pers. observ.). Nine of the studied reefs were over 17 years of age as they were clearly observed on aerial photos from 1996. Only the two small reefs at St. Annaland (reefs 8 and 9) can be considered as relatively young, immature reefs.

2.2.3 Data collection

The morphology around a reef is the result of the interaction between the reef's structure and the prevailing hydrodynamic forcing by waves and tides. Incoming wave energy is reduced by the reefs, and enhances accretion or reduces erosion at the lee side of the reef. This potentially translates into an elevated area compared to the non-affected surroundings. To quantify this, elevation measurements were done at eleven isolated oyster reefs, of varying sizes, at the three study locations (Galgeplaat, St. Annaland and Viane). We selected isolated reefs to ensure we only measured the effect caused by the presence of that particular reef. The reefs chosen also had relatively sharp outer boundaries, meaning that they were not surrounded by a diffuse area consisting of scattered smaller oyster patches. Different reef sizes were chosen to test the effect of reef size on the surrounding tidal flat morphology. Reefs larger than those measured within this study were present in the Oosterschelde estuary, but as these were influenced by other nearby reefs, they were excluded from this study.

Elevation measurements of the reefs and their surroundings were conducted using two differential GPS devices with a horizontal and vertical measure accuracy of 8 and 13 mm respectively (Thales Z-Max, Thales Navigation, France, correction signal: 06-GPS, the Netherlands; and Leica GS12, Leica Geosystems AG, Switzerland, correction signal: SmartNet, Leica Geosystems, the Netherlands). Reef height was estimated by measuring the oyster's uppermost point. The perimeter of the reef was measured on the sediment directly adjacent to the reef. Measurements were done every 2 to 4 m, except in close proximity of the reefs and when special features such as depressions were present, smaller intervals were used. Data were imported to MATLAB to perform data analyses.

2.2.4 Data analysis

Based on the measured elevations, 3-dimensional surface maps were created for the surrounding morphology of each reef using linear interpolation on a Cartesian grid. In order to correctly evaluate sedimentation and erosion patterns, the slope of the tidal flat (background slope) needs to be suppressed. For each tidal flat 2 dimensional polynomial regression detrending curves of the background slope were generated using the Curve Fitting Toolbox of Matlab. Detrending curves were subtracted to obtain 3-dimensional surface maps which showed a deviation from the background slopes (Figure 2.2). On the surface maps, the perimeter of the reefs were indicated. To investigate the area influenced by the reefs (influenced zone), contour lines were drawn at 2 and 5 cm elevation. Reef areas (A_r) and the area of the influenced zones (A_i) were obtained by the number of 1 m^2 grid cells within the perimeter of the reefs and the contours of the 5 cm elevated areas. For reefs 8 and 9 we used an elevation of 3 cm, as these reefs (oyster patches) were too small to measure an influenced zone when using an elevation of 5 cm. The area of the influenced zone is expected to change proportional to reef characteristics such as reef length (L), width (W) and height (H). In this study, we define reef length as the maximum distance of the reef contour perpendicular to the dominant wave direction. Reef height was determined as the maximum elevation from the background slope. To obtain a measure for the maximum distance (D), perpendicular to the reef length, over which a reef elevates the surrounding sediment, we measured the maximum distance between the reef contour and the 5 cm elevated contour line.

2.2.5 Statistical analysis

Linear regression models were used to test which reef characteristic (reef length, width, height) was the most important determinant for the area and maximum distance of the influenced zone. A stepwise linear regression, with forward and backward substitution, was performed to find the most parsimonious model using the Akaike Information Criterion (AIC). All analyses were performed using "*R*" statistical software (R Development Core Team). Statistical significance was set at $p \leq 0.05$.

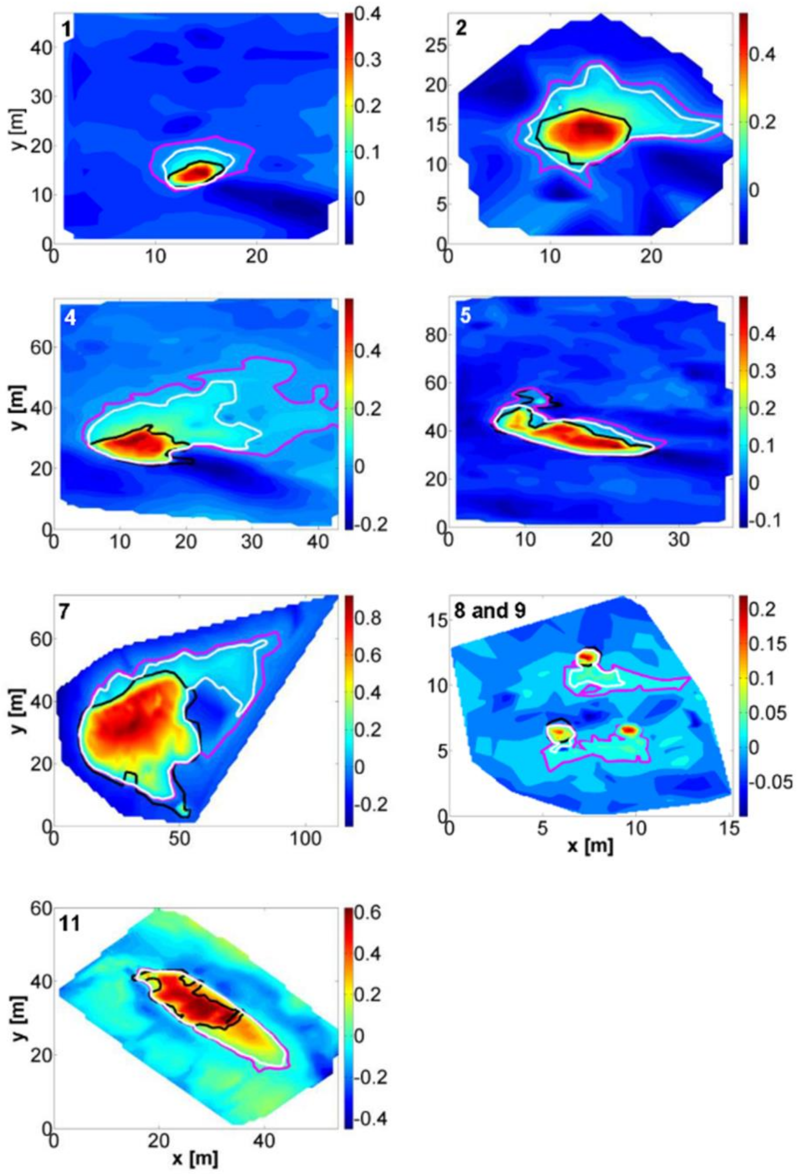

Figure 2.2 Elevated areas around Pacific oyster reefs in the Oosterschelde. 3-dimenisional surface maps of the morphology around Pacific oyster reefs minus the slope of the tidal flat. Deviation from the background slope are indicated in meters (Note the different scales per reef). Reefs are indicated with a black solid line. Areas elevated by 2 cm (pink solid line) and 5 cm (white solid line) are indicated. For reefs 8 and 9 the white line indicates the areas elevated by 3 cm. Reefs 1 to 7 are located at Viane, reef 8 to 10 at St. Annaland and reef 11 at the Galgeplaat.

2.3 Results

The area of the oyster reefs ranged from 2 m^2 to 1908 m^2. Reef length varied between 1 and 61 m, reef width between 1 and 45 m, and reef height between 0.20 and 1.08 m (Table 2.1). Reefs varied in shape, going from round shaped structures to more elongated ones (Figure 2.2). The reefs appeared to be clearly elevated structures on the tidal flats (Figure 2.3). The top of the reefs was on average 0.72 ± 0.16 m below Mean Sea Level (MSL) (excluding the two smallest reefs (8 and 9) which are presently considered immature), Figure 2.3. This corresponds on average with an exposure time of 4 hours (33%) per low tide within the semi-diurnal tidal cycle of the Oosterschelde. Vertical reef growth seems to be limited up to this point. In line with this finding, reef heights vary at different locations in the intertidal zone. Reef height was linearly related to the elevation at which the reef was located (R^2 = 0.74); reefs located lower in the intertidal zone were taller than reefs located higher.

Table 2.1 Characteristics of eleven oyster reefs and the area influenced by these reefs in the Oosterschelde estuary, the Netherlands

		Reef characteristics					Influenced zone			
Location	reef	Area (m^2)	Length (m)	Width (m)	Height (m)	Reef top below MSL (m)	Area (m^2)	Maximum distance (m)	Maximum sediment height (m)	Direction
Viane	1	19	5	6	0.40	-0.84	21	5	0.14	NE
	2	44	7	7	0.52	-1.02	54	8	0.24	
	3	70	13	7	0.52	-0.74	16	2	0.16	
	4	116	12	12	0.58	-0.72	279	20	0.28	
	5	195	26	11	0.50	-0.66	44	4	0.16	
	6	747	35	32	1.08	-0.78	684	23	0.32	
	7	1,409	54	45	0.92	-0.66	514	32	0.24	
St. Annaland	8	2	2	1	0.20	-1.68	3	2	0.10	SE
	9	4	1	2	0.20	-1.66	3	2	0.08	
	10	1,908	61	41	0.98	-0.44	5,174	75	0.60	
Galgeplaat	11	138	9	19	0.64	-0.66	103	15	0.34	SE

The studied reefs showed an elevated area (>5 cm elevation from the background intertidal slope) connected to each reef. Elevated areas were located northeast of reefs at Viane and southeast of those at St. Annaland and Galgeplaat (Figure 2.2). Most reefs at Viane (reef 1 to 6) showed a small depression southeast of the reef, which was not observed for the reefs on the other tidal flats. Seen from the dominant wave direction, elevated areas were always on the lee side of the reef. The maximum sediment height was measured directly next to the reef and was approximately 40% of the reef height itself (Table 2.1). Contour lines indicating an elevated area of 2 and 5 cm were close to each other at most reefs, showing a relatively sharp increase in height near the boundary of the influenced zone (Figure 2.2). Only at reef 4 and 6 the distance between the two contour lines was greater, showing a more gentle increase in height near the boundary of the influenced zone. The area of the influenced zone ranged from 3 m^2 to 5174 m^2. Reef area and the area of the influenced zone showed a linear relationship ($A_i = A_r$; R^2=0.97, p<0.00). The elevated area (i.e. the spatially extended ecosystem engineering effect) affected by the reef was of the same order of magnitude as the reef area (Table 2.1).

All reef parameters (length, width and height) showed significant correlations with the area and distance of the influenced zone (Table 2.2). Using stepwise linear regression, with forward and backward substitution, we found that reef length was the better predictor for both the area (p=0.01) and maximum distance (p=0.00) of the influenced zone, see Table 2.3.

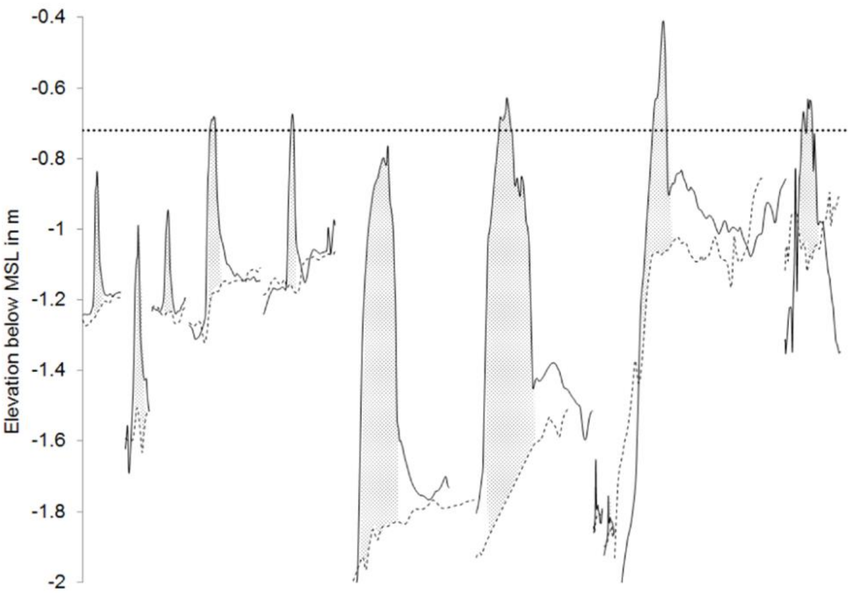

Figure 2.3 Cross-sections of parallel transects crossing reefs (solid line) or bare sediment (reference: dashed line). Cross-sections from the wave dominate side (left) towards the lee side (right). The grey shade indicates the reef. The total length of the line transects differs per reef (from left to right: reef 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11): 35 m, 23 m, 31 m, 67 m, 67 m, 104 m, 109 m, 8 m, 9 m, 160 m, and 52 m respectively. The black dotted line indicates the average reef height (0.72 m below MSL).

Table 2.2 Relation between reef parameters and the influenced zone.

Formula	R^2
$A_i = 0.96\ A_r^{0.97}$	0.87
$A_i = 1.78\ L^{1.55}$	0.77
$A_i = 1.26\ W^{1.78}$	0.86
$A_i = 861.7\ H^{3.77}$	0.85
$D = 0.85\ L$	0.72
$D = 1.08\ W^{0.91}$	0.76
$D = 29.31\ H^{1.87}$	0.72

A_i is the area of the influenced zone in m^2, A_r the area of the reef in m^2, L the length of the reef in m, W the width of the reef in m, H the height of the reef in m, and D the maximum distance of the influenced zone in m.

Table 2.3 Stepwise linear regression with forward and backward substitution.

Linear model	AIC
$A_i = L + W + H$	159.3
$A_i = L + W$	157.3
$A_i = L$	156.0
$D = L + W + H$	60.5
$D = L + W$	58.5
$D = L$	56.8

A_i is the area of the influenced zone in m^2, L the length of the reef in m, W the width of the reef in m, H the height of the reef in m, and D the maximum distance of the influenced zone in m.

2.4 Discussion

Although ecosystem engineers can affect their surrounding environment far beyond their local presence, so far these spatially extended ecosystem engineering effects have rarely been quantified. Here we demonstrate the effect oyster reefs have on the surrounding morphology (i.e. elevation) of tidal flats that experience strong erosion. We observed an elevated area at the lee side of all reefs, which indicated that the observed patterns were caused by the interaction between the reef's structure and the locally prevailing wave conditions. We hypothesized that reef size would determine the size of the area at which morphological (i.e. elevation) changes occur. Our results showed that the spatially extended influence of the ecosystem engineer *Crassostrea gigas* on the tidal flat morphology is of the same order of magnitude as the reef area. Increase in length, width, and height, of the reef resulted in an increase of the influenced area. Reef length however, appeared to be the best predictor for the area influenced by the studied reefs. We found the highest reefs low in the intertidal as reef height was limited up to a certain exposure time (33%). This limitation could be influenced by factors such as temperature and food availability (Child and Laing, 1998; Ren and Ross, 2001). While exposed, oysters are vulnerable for heat and cold stress which could limit reef height through direct mortality.

Several mechanisms, related to the interaction between hydrodynamics (i.e. waves) and the reef's structure, are important in explaining the observed relation between the reef dimensions and the influenced area: wave dissipation, wave diffraction, and directional spreading. Wave dissipation by breakwaters is discussed in several studies, see e.g. d'Angremond et al. (1996) or Van der Meer et al. (2005). These studies indicate wave dissipation when wave heights exceed the water depth above the breakwater. For smaller wave over water depth ratios, waves pass the breakwater without losing energy. Consequently, reef height influences the period in which waves are dissipated, broken or blocked by the reef. Hence, taller reefs will result in a longer period of reduced wave heights and therefore more calm conditions behind the reef. Reef width can be important for wave penetration through the reef and wave dissipation by bed friction. As we deal with large reef width over reef height ratios, it is unlikely that wave penetration through the reef is significant. This follows directly from the empirical formulations for breakwaters of Van der Meer et al. (2005). Wave dissipation on the reef by bed friction is expected to be small, as the width is only a few wave lengths. Wave breaking is considered to be the dominating mechanism. The width of the reef is therefore expected to play a minor role. Correlations between reef width and the influenced area are most likely the consequence of the correlation between reef length and width. Only for very wide reefs, like mussel beds, bed friction is expected to play a role (Donker et al., 2013).

Waves not only travel over the reef, but also penetrate the area behind the reef by going around the reef due to diffraction, similar to the development of waves around breakwaters in harbour entrances. For simplicity, we consider the situation with a horizontal bed and an emerged reef. The wave pattern can then be determined with the Sommerfeld equation, see textbooks like Holthuijsen (2007) for further details. Figure 2.4. shows a sketch of the Sommerfeld solution for waves perpendicular to the reef, based on Holthuijsen (2007). The figure illustrates the contours of wave heights in the lee side of a reef. In the lee side, far from the tip, all waves are dissipated. Some influence is present for a distance of five wave lengths from the tip (x=5L). 20% of the wave height is still present at two to three times the wave length from the tip (x=2L). Note that the wave height is slightly increased for small negative values for distance x. It can be stated, as rule of thumb, that edge effects by diffraction occur at x<3L. Wave lengths in our study area were 2-3 m. Wave diffraction is therefore occurring up to a distances of 6 to 9 m from the tip. This implies that especially small reefs will be highly affected by diffraction.

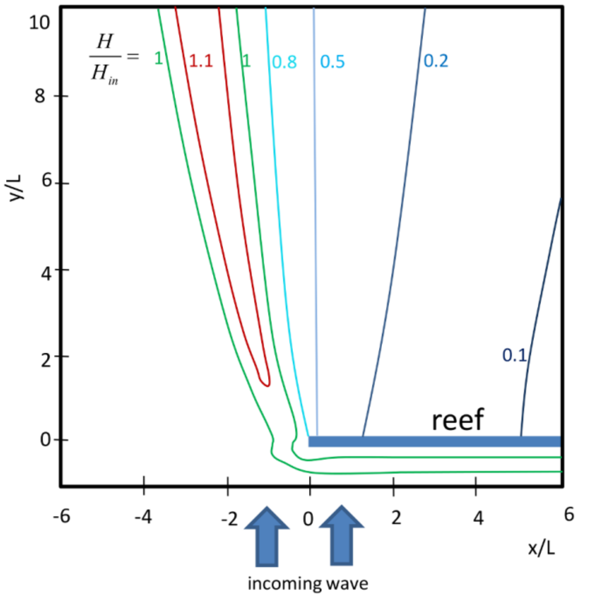

Figure 2.4 Sketch of the contours of the relative wave heights in the lee side of a reef (Drawn after Holthuijsen 2007, Fig 7.13). The waves come from below, the reef is located at y=0 and x>0. The contours indicate the ratio between the local wave height (H) and the height of the incoming wave (H_{in}).

Waves can also reach the lee side by variation in wave's direction, relative to the reef. As waves come from different angles due to changing wind directions, the lee side of the reef is changing position, making the effect more diffuse. This directional spreading is illustrated in Figure 2.5. Note that effects of diffraction are not considered in this illustration. Figure 2.5.a represents the situation without directional spreading, i.e. waves come from the south only. Figure 2.5.b depicts the influence of directional spreading. There is a core area (triangular in this case) that has the same level of influence, as found in the case with unidirectional waves. The reef protects this core area from waves of all directions. Additionally, an area can be identified that is influenced by waves from a specific direction only. The effect in that region is smaller. Decreasing the length of the reef, results in a quadratic reduction of the total influenced area, as not only the base of the triangle decreases, but also the triangle's altitude. To determine the combined effect of diffraction and directional spreading, numerical modelling is required. It is preferred to apply a wave-resolving model like SWASH (Zijlema et al., 2011). It is noted that directional spreading affects the influenced area for small and large reefs, whereas diffraction is mainly an edge effect and therefore only important for small reefs.

Some reefs showed an area of depression on the wave dominate side (Figure 2.2 and 2.3), but overall this depression was limited and did not undermine the reef structure. Waves are reflected less by the shape and permeability of reefs, resulting in only a small area of scouring. This in contrast to breakwaters, where wave reflection causes scouring and undermining of the structure (Sumer et al., 2002).

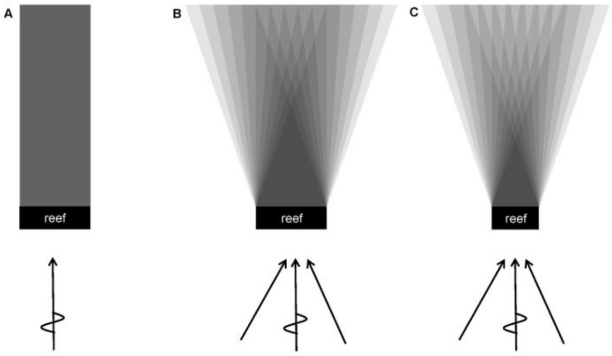

Figure 2.5 Graphical illustration of directional wave spreading behind a reef. A) The effect of the reef for unidirectional waves from the south; B) The effect of a reef for waves from different directions southwest till southeast; C) Similar as B, but with a shorter reef. Note that in reality the lines will not be straight, but curved inwards due to wave diffraction.

2.4.1 Implementation

The fact that oyster reefs have an effect that spatially extends beyond their direct surroundings can be beneficial to their use for coastal protection. In the Oosterschelde estuary, 8% of the intertidal area is covered with natural oyster reefs, protecting this area under their footprint directly against erosion, and in addition sediment accumulation and stabilization in the lee side of these reefs (i.e. the spatially extended ecosystem engineering effect as estimated in this study) essentially double this influence. Several coastal engineering projects use oyster reefs as breakwaters within a few meters from the shore to reduce wave impact on salt marsh edges (Meyer et al., 1997; Piazza et al., 2005; Scyphers et al., 2011). When placed somewhat more seawards, oyster reefs can potentially influence and protect a much larger area, following the above described findings. As a result, shoreline growth can be promoted and valuable shallow habitat (e.g. seagrass beds) created between the reef structure and the shoreline. Field studies using artificial oyster reefs at various distances from the shoreline are necessary to test these hypotheses. Additionally, site-specific conditions such as the slope of the tidal flat, exposure time, depth, substrate type, recruitment, growth rates, predation risk, salinity, and the local hydrodynamic forces should be taken into account, as these will determine the scale and magnitude of the morphological response. A similar idea has been demonstrated with a breakwater of 60 m in front of a mangrove habitat (Kamali and Hashim, 2011). The breakwater enhanced sediment deposition behind the structure, increasing the bed level and creating calm conditions, allowing natural mangrove outgrow without planting (Kamali and Hashim, 2011; Kamali et al., 2010).

Although our study focused on the abiotic effect oyster reefs have on their surrounding environment, other studies stress the biotic effect of oyster reefs. As *C. gigas* is a non-native species in many parts of the world, many studies focus on the impact this invasive species has on the environment. *C. gigas* has a large filtration capacity and could compete with native bivalves for food, resulting in a shift in the benthic population (Diederich, 2006; Smaal et al., 2005). Kochmann et al. (2008) shows that a change from native mussel beds to invasive oyster reefs in the Wadden Sea does not pose a threat to species diversity, but results in a shift in abundance of the dominant species. A shift in the benthic population may have consequences for the food availability for bird populations (Smaal et al., 2005). These consequences are not necessarily negative. Van der Zee et al. (2012) show the positive effect of the presence of oyster reefs on feeding grounds for birds. Reefs not only protect the feeding grounds of protected bird species from erosion, they also have a positive effect on the food source birds feed upon. Donadi et al. (2013) indicate the importance of understanding the interaction between reef-forming ecosystem engineers (mussels) and surrounding benthic communities (cockles), for conservation and restoration of soft-bottom intertidal communities. These studies and our observations suggest that removal or creation of reef builders can cascade through the ecosystem and have much larger effects on both the abiotic and biotic environment, at a scale exceeding the size of the reefs.

2.5 Conclusions

Ecological engineering is increasingly recognized as a new, ecosystem based approach to coastal protection that is more sustainable and cost-efficient than conventional coastal engineering (Cheong et al., 2013; Temmerman et al., 2013). Mangroves, salt marshes, and oyster reefs are examples of ecosystem engineers that have the natural capacity to reduce flow and dampen wave energy through their physical structures, and can keep pace with sea-level rise by natural accretion (Cheong et al., 2013; Duarte et al., 2013; Gutiérrez et al., 2011; Temmerman et al., 2013). However, quantitative studies are needed to support their effectiveness in coastal protection. Our study clearly shows that oyster reefs protect the tidal flat under their footprint, as well as an area beyond the boundary of the reef itself.

Chapter 3

Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence

Adapted from

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Abstract

Marine species characterized as structure building, autogenic ecosystem engineers are recognized worldwide as potential tools for coastal adaptation efforts in the face of sea level rise. Successful employment of ecosystem engineers in coastal protection largely depends on long-term persistence of their structure, which is in turn dependent on the population dynamics of the individual species. Oysters, such as the Pacific oyster (*Crassostrea gigas*), are recognized as ecosystem engineers with potential for use in coastal protection. Persistence of oyster reefs is strongly determined by recruitment and shell production (growth), processes facilitated by gregarious settlement on extant shell substrate. Although the Pacific oyster has been introduced world-wide, and has formed dense reefs in the receiving coastal waters, the population biology of live oysters and the quantitative mechanisms maintaining these reefs has rarely been studied, hence the aim of the present work. This study had two objectives: (1) to describe the demographics of extant *Crassostrea gigas* reefs, and (2) to estimate vertical reef accretion rates and carbonate production in these oyster reefs. Three long-living oyster reefs (>30 years old), which have not been exploited since their first occurrence, were examined in the Oosterschelde estuary in the Netherlands. A positive reef accretion rate (7.0-16.9 mm year^{-1} shell material) was observed, consistent with self-maintenance and persistent structure. We provide a framework to predict reef accretion and population persistence under varying recruitment, growth and mortality scenarios.

Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence

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3.1 Introduction

Epibenthic bivalve reefs are abundant, persistent structures of marine and estuarine ecosystems and deliver many ecosystem services (Grabowski et al., 2012; Grabowski and Peterson, 2007). Epibenthic bivalves (oysters, mussels) are both allogenic and autogenic ecosystem engineers according to the definitions of Jones et al. (1994). As individuals they act as allogenic engineers enhancing benthic-pelagic coupling by their strong filter feeding capacity, removing large quantities of suspended material from the water column and producing fecal and pseudofecal biodeposits that accumulate in the reef and its surroundings (Newell, 2004; Ostroumov, 2005; Ulanowicz and Tuttle, 1992; van Leeuwen et al., 2010). In high densities epibenthic bivalves are autogenic engineers, creating three-dimensional reef structures that increases habitat heterogeneity and complexity in soft-sediment environments, that promote both species diversity and abundance (Gutiérrez et al., 2003; Meyer and Townsend, 2000; Peterson et al., 2003; Zee et al., 2012). The reef structure changes water flow patterns and attenuates waves (Borsje et al., 2011), while trapping and stabilizing sediment (van Leeuwen et al., 2010; Walles et al., 2014). Furthermore, bivalve shells are a sink for calcium carbonate (Waldbusser et al., 2011; Waldbusser et al., 2013) which alter the chemical conditions in the sediment and provide a buffer against low pH (Green et al., 2009; Lee et al., 2008). Over time oyster reefs build significant biogenic carbonate masses in shallow water estuaries (Rodriguez et al., 2014; Waldbusser et al., 2011). These biogenic carbonate masses can be critical for colonization of species with carbonate shells (Green et al., 2009). While the allogenic engineering effect is limited to the lifespan of the individual bivalve, the autogenic engineering effects depends largely on shell production and taphonomic loss, and post-mortem ecosystem engineering effects of the shells (Guo and Pennings, 2012; Jones et al., 1994; Jones et al., 1997; Powell et al., 2012).

Structure building autogenic ecosystem engineers like oysters are increasingly recognized as a potential tool in support of coastal protection and adaptation (Arkema et al., 2013; Borsje et al., 2011; Rodriguez et al., 2014; Scyphers et al., 2011) and are thus increasingly developed or restored for that purpose. Ecosystem engineers can provide coastal protection, maintain or increase biodiversity, and accrete in concert with sea level rise through recruitment and growth (Reed, 1995; Rodriguez et al., 2014). The selection and introduction of an ecosystem engineer for coastal protection purposes not only requires knowledge about the coastal defence value of the ecosystem engineer under study, but equally requires prior knowledge on the species' habitat requirements, life cycle, population dynamics and long-term persistence once established. If an ecosystem engineer cannot maintain its structure, it will undergo structural decay, like all physical structures (Jones et al., 2010; Raynaud et al., 2013).

The Pacific oyster *Crassostrea gigas* is an example of an ecosystem engineer that (re)introduces structural complexity in NW European coastal waters (see Troost 2010), where it was intentionally introduced for mariculture purposes (see contributions in Mann 1979a). *Crassostrea* *gigas* became established (naturalized) and its range expanded rapidly, forming dense reefs in intertidal and shallow subtidal habitats (Troost, 2010). In the Oosterschelde (SW Netherlands) *C. gigas* reefs cover about 8 % of the intertidal habitat (Smaal et al., 2009) and most of these reefs are not fished and remained undisturbed since their first mapped occurrence in the 1980s (Kater and Baars, 2004). This is in contrast to many oyster reef systems worldwide that have been disturbed by fishing or habitat destruction (Airoldi and Beck, 2007; Beck et al., 2011; Kirby, 2004).

Recently, the use of oyster reefs for coastal protection, and more specifically for mitigating erosion of tidal flats, has been studied in the Oosterschelde estuary (Ysebaert et al., 2012), see also www.ecoshape.nl. The Eastern oyster *Crassostrea virginica*, has been used for the same purpose along the Atlantic coast of the USA (Piazza et al., 2005; Scyphers et al., 2011). Both oyster species are sessile and highly dependent on a hard substrate for settlement, metamorphosis and survival (Arakawa, 1990; Markert et al., 2010). Changes in population demography (e.g. increase in mortality due to new predators or diseases) interact with the engineered structure (Mann and Powell, 2007) and can be considered as engineering feedback (Jones et al., 2010). The gregarious settlement behaviour of oysters (Arakawa, 1990; Tamburri et al., 2007) and production of shell substrate (positive engineering feedback) are keys to the long-term persistence of oyster reefs (Powell et al., 2012). At small spatial scales, bivalve reefs show a high degree of temporal variation in reef growth and persistence; however, shell material can persist for hundreds and even thousands of years over larger spatial scales (Gutiérrez et al., 2011). Knowledge of shell production and loss rates (taphonomic loss, Davies et al 1989) can be used to predict the ecosystem engineering impacts in space (e.g. reef height determines wave dampening) and time (related to persistence).

The present study aimed to interrogate and quantify the ecosystem engineering role of *Crassostrea gigas* using two objectives. The first objective was to determine the population structure of *C. gigas* in existing natural reefs in an area with low mortality due to the restriction of fisheries and absence of diseases, bio-eroders and co-evolved predators with a significant effect on mortality rates in the Oosterschelde population of *C. gigas*. Three reefs were studied in Oosterschelde estuary. Oyster growth and mortality rates were estimated through cohort analyses. The second objective was to estimate rates of vertical reef accretion and carbonate production. This was accomplished using a 'model population' based on field observations and observed vital rates. The estimated accretion rates were then validated in the field by excavating the entire vertical profile of the three oyster reefs.

3.2 Methods

3.2.1 Study area

The Oosterschelde estuary, located in the Southwest of the Netherlands (Figure 3.1), is a 351 km^2 tidal basin with tidal flats (118 km^2), artificial rocky shore habitats (dikes), deep gullies, and shallow water areas. A storm surge barrier, completed in 1986, separates the estuary from the North Sea. The barrier still permits tides going in and out, and can be closed in the event of a storm surge. The estuary has a mean tidal amplitude ranging from 2.47 m near the storm surge barrier to 2.98 m in the northern branch and 3.39 m at the southeast end (Nienhuis and Smaal, 1994). The maximum current velocity is about 1.0 m s^{-1}. Salinity throughout the estuary is high, generally >30 psu (Nienhuis and Smaal, 1994).

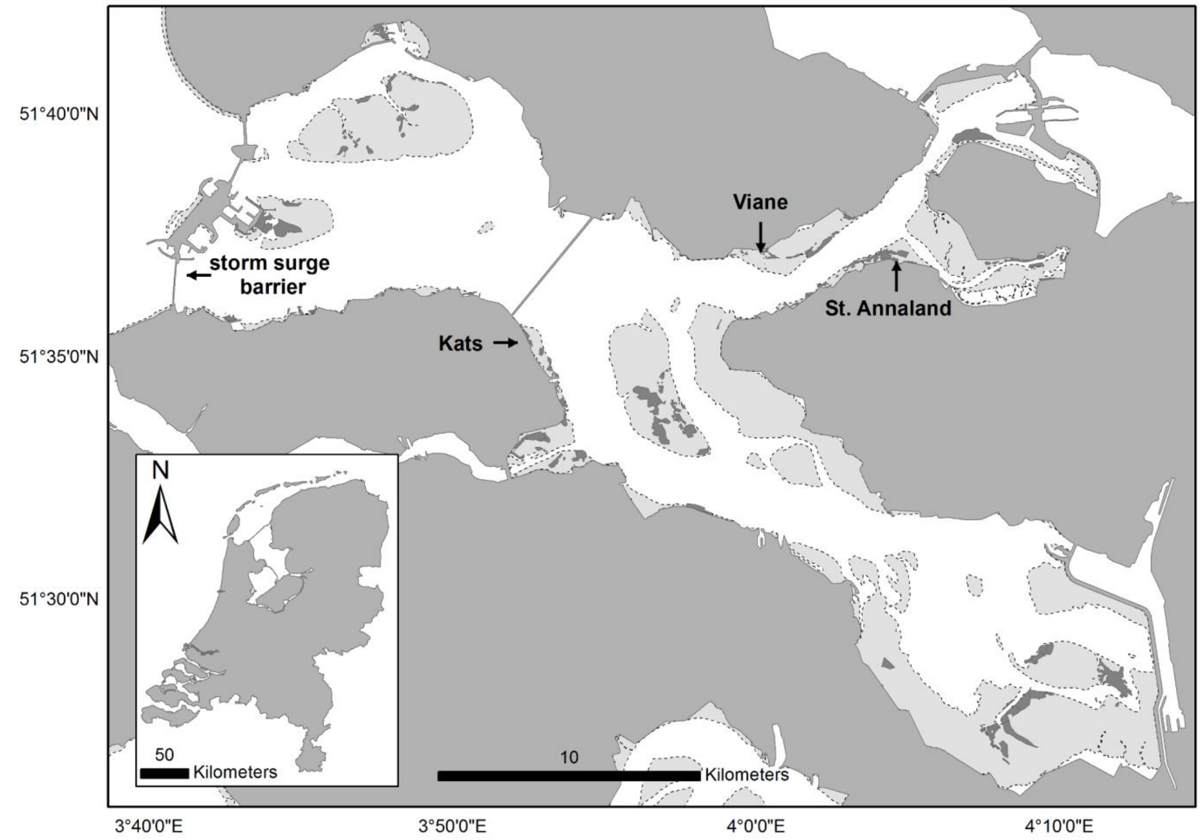

Figure 3.1 Locations of three intertidal oyster reefs (Viane, St. Annaland and Kats) in the Oosterschelde estuary (The Netherlands). The estuary is separated from the North Sea by a storm surge barrier in the west. Tidal flats are indicated with light grey, dotted lines indicate the mean low tide level. Intertidal areas covered with oysters in 2011 are indicated in dark grey.

This study focuses on naturally established reefs of the Pacific oyster (*Crassostrea gigas*) located on three different tidal flats: Viane (1265 m^2 surface area), St. Annaland (41951 m^2) and Kats (25240 m^2), see Figure 3.1. Reefs were selected based on their history. *C. gigas* was initially introduced in the Oosterschelde estuary in 1964, when the shellfish industry seeded the area with spat originating from British Columbia (Drinkwaard, 1998, 1999; Shatkin et al., 1997). More introductions of both spat and adult oysters soon followed (Drinkwaard, 1998). The first natural recruitment event after introduction was recorded in 1975 (Drinkwaard, 1998). After this the oysters spread rapidly (Smaal et al., 2009), presently occupying 9 km^2 of the (lower) intertidal (i.e. about 8%). The reefs at Kats and St. Annaland are at least 30 years of age as they were observed on aerial pictures taken in 1980 (Kater and Baars, 2004). The reef at Viane was first photographed in 1983, showing the typical contours of a patchy oyster reef that must have been there for several years already (Walles, pers. unpublished obs.). These reefs are the only reefs found in 1980s that are still present today. The three reefs differ in their exposure to waves, due to a different orientation and location within the Oosterschelde. As mainly southwesterly winds and northwesterly storms prevail in the Netherlands, the reef at Viane is most exposed to waves, followed by the reef at St. Annaland and the reef at Kats (Figure 3.1).

3.2.2 Data collection

The three intertidal *Crassostrea gigas* reefs were sampled at low tide in the winter of 2011-2012 (Viane: 1 November 2011; Kats: 7 February 2012; St. Annaland: 9 February 2012). Sampling locations were randomly selected within each of the reefs. At each location all live oysters (from the taphonomically active zone, TAZ (Davies et al., 1989)) were removed within a number of quadrants and transported to the laboratory for analysis. Sampling at Viane started with a 1 m^2 quadrant (n=2), but due to the high oyster density quadrant size was reduced to 0.25 m^2 (n=6) resulting in a total sampled area of 3.5 m^2 at Viane. At St. Annaland and Kats 10 quadrants of 0.25 m^2 were sampled (n=10, total sampled area=2.5 m^2). Shell length (*L*, longest dimension from hinge to growing edge) of all live oysters collected was measured to the nearest mm. From each reef a subsample of the live oysters, covering the entire size ranges (Viane *L* 16-210 mm, n = 54; St. Annaland *L* 16-222 mm, n = 41; Kats *L* 14-225 mm, n = 49), was used to estimate the relationship between shell length (*L*) and dry shell weight (*W*, g). Additional measurements are provided in Box 3.1. Dry shell weight was determined after dissecting the oyster, separating the tissues from the shell, and air-drying the shell at room temperature for 2 days (Mann et al., 2009; Power et al., 2006).

3.2.3 Population structure

Length frequency distributions were plotted and age structure estimated using the method of Bhattacharya (1967) (see Box 3.2). This method dissociates the length demographic into Gaussian distributions that were assumed to be normally distributed and correspond to cohorts. Each cohort was assumed to correspond to a separate year class since *Crassostrea gigas* only spawns once a year in this location (Diederich et al., 2005). Using the 1st of July as recruitment date, lengths in November represent ages of $a + 0.33$ (a in years, first year $a = 0$) and lengths in February represent ages of $a + 0.58$. Ages <1 are termed "0 years", ages between 1 and <2 years as 1 years, and so on. Obtained cohorts were compared with five years of cohort data from oysters growing on artificial constructed *C. gigas* reefs in the Oosterschelde estuary (Walles, unpublished results). Cohort data at the artificial *C. gigas* reefs was obtained by annually measuring the shell lengths of all oysters settled, within fixed quadrants (0.25 m^2, n=57), after the construction of the reef (2009) up till 2013. The length versus age estimates were fitted to a Von Bertalanffy growth model (1938) using the method described by Haddon (2001).
Growth and mortality rates were estimated from the length-at-age structure using the following relationships:

$$\text{Growth rate (g year}^{-1}) = W_{(a+1)} - W_{(a)} \qquad \text{Eq. 3.1}$$

$$\text{Mortality rate (fraction dead year}^{-1}) = (N_{(a)} - N_{(a+1)}) / N_{(a)} \qquad \text{Eq. 3.2}$$

in which $W_{(a)}$ equals the average dry shell weight (*W*) at age *a* (years) and $N_{(a)}$ equals the number of live oysters at age *a*. For mortality a possible error is inherent in this static life table approach, as we compared the number of live oysters of age *a* with oysters of age *a+1* within the same year, comparing different cohorts. In some instances (e.g. high recruitment event in previous year) $N_{(a+1)} > N_{(a)}$, resulting in nonsense negative or very high positive mortality values.

Box 3.1.
Oyster characteristics

Methods. Live oysters in a certain size range (Viane L 16-210 mm, n = 54; St. Annaland L 16-222 mm, n = 41; Kats L 14-225 mm, n = 49) were used to estimate oyster characteristics. The oysters were weighed to obtain the total weight per oyster in g (TW). The oysters were dissected, separating the tissue from the shell. The flesh was weighed (wet weight in g, *ww*) prior to drying and incinerating the flesh to determine the ash-free dry weight. The flesh was dried (dry weight in g, *dw*) at 70 ºC until weight constancy was achieved (4 days) and incinerated at 540 ºC for 4 hours (ash-free dry weight in g, *afdw*). Dry shell weight (W) was determined after air drying the shells at room temperature for 2 days.

Results. Oyster's shell length showed a power function with the other oyster characteristics, Table B3.1.1.

Table B3.1.1 Power functions ($y=\alpha x^{\beta}$) between oysters characteristics of the three sampled reefs (Viane, St. Annaland and Kats), in which W is the shell weight in gram, and L the shell length in mm, TW the total weight of the oyster in g, *ww* the wet weight in g, *dw* the dry weight in g and *afdw* the ash free dry weight in g.

Reef	Power function	R^2	p-value	5% quantile	95% quantile
Viane	W=4.40e-04$L^{2.55}$	0.93	P<0.00	W=1.92e-04$L^{2.56}$	W=1.69e-03$L^{2.37}$
	TW=5.41e-04$L^{2.56}$	0.94	P<0.00	TW=2.80e-04$L^{2.57}$	TW=1.27e-03$L^{2.50}$
	ww=1.17e-04$L^{2.52}$	0.95	P<0.00	ww=7.03e-05$L^{2.52}$	ww=2.80e-03$L^{1.90}$
	dw=6.00e-06$L^{2.67}$	0.92	P<0.00	dw=1.15e-06$L^{2.88}$	dw=2.36e-05$L^{2.50}$
	$afdw$=4.10e-06$L^{2.70}$	0.90	P<0.00	$afdw$=8.06e-07$L^{2.29}$	$afdw$=2.19e-06$L^{2.48}$
St. Annaland	W=2.62e-04$L^{2.56}$	0.97	P<0.00	W=1.81e-04$L^{2.50}$	W=3.55e-04$L^{2.58}$
	TW=5.55e-04$L^{2.50}$	0.97	P<0.00	TW=1.84e-04$L^{2.59}$	TW=7.46e-04$L^{2.53}$
	ww=4.15e-05$L^{2.66}$	0.95	P<0.00	ww=1.43e-05$L^{2.73}$	ww=2.67e-05$L^{2.97}$
	dw=5.50e-06$L^{2.66}$	0.95	P<0.00	dw=1.23e-05$L^{2.69}$	dw=6.62e-06$L^{2.81}$
	$afdw$=1.58e-06$L^{2.85}$	0.95	P<0.00	$afdw$=6.87e-07$L^{2.84}$	$afdw$=1.35e-06$L^{3.09}$
Kats	W=1.26e-03$L^{2.16}$	0.98	P<0.00	W=6.76e-04$L^{2.20}$	W=4.326e-03$L^{2.01}$
	TW=2.24e-03$L^{2.13}$	0.97	P<0.00	TW=1.08e-03$L^{2.19}$	TW=1.364e-02$L^{1.84}$
	ww=3.16e-04$L^{2.13}$	0.91	P<0.00	ww=3.52e-04$L^{1.85}$	ww=1.97e-03$L^{1.88}$
	dw=6.48e-05$L^{1.98}$	0.95	P<0.00	dw=4.83e-05$L^{1.89}$	dw=1.69e-04$L^{1.91}$
	$afdw$=4.97e-05$L^{1.92}$	0.92	P<0.00	$afdw$=8.95e-01$L^{1.98}$	$afdw$=1.03e-04$L^{1.92}$

3.2.4 Mortality rates

To calculate mortality rates the non-linear least-squares fit of the logarithmic transformed observed age-specific survival was fitted to a survivorship curve, using the complementary cumulative Weibull frequency distribution (Pinder et al., 1978). Based on the Weibull frequency, the probability that an individual lives at least to age a was calculated using the following equation:

$N_{(a)} = N'_{(0)}\, e^{-(a/\lambda)^{\wedge}k}$ for age > 0 Eq. 3.3

in which $N'_{(0)}$ is the back-transformed density from logarithmic to arithmetic units, λ is a scale parameter that is inversely related to the mortality rate, and k is a shape parameter that allows the model to produce a survival distribution of different forms, from exponential to an extreme inverted S-shape. Values of the shape parameter $k>1$, $k=1$ or $k<1$ correspond to type I, II or III survival curves, respectively (Pinder et al., 1978). Different models were tested to estimate the Weibull parameters and coefficient of determination: constant N_0 and k for all reefs; variable recruitment (N_0) between reefs, with constant k; and reef specific N_0 and k. All models were tested using a fixed scale parameter ($\lambda=1$), as the algorithm could not estimate all parameters at the same time due to the large variety of N_0, λ and k combinations producing approximately the same curves. Test, using different λ's, shows that λ did not change the results, even over a wide range (0.001-10). Using Akaike information criterion (AIC) the best model was found. Weibull parameters were used to calculate a "model population" for each reef. Estimates of Weibull parameters and coefficient of determination were obtained using "R" statistical software (R Development Core Team).

3.2.5 Reef accretion rate

Accretion of oyster reefs is determined by the addition of shell material (through recruitment, growth and mortality) to the reef structure. Since older and therefore, larger oysters contribute more shell material to the reef structure, the age at which oysters die strongly determines the accretion rate. Reef accretion rate (in kg shell added to the reef by mortality or growth) was calculated using the following equation:

$$\text{Reef accretion by mortality (kg year}^{-1}) = \int_0^\infty W \frac{dN}{dt}\, dt \qquad \text{Eq. 3.4}$$

in which W equals the dry shell weight (*W*) at time *t*, using the relationship between shell length (*L*) and dry shell weight (*W*). Continuous shell lengths were derived from the Von Bertalanffy growth model. N equals the number of live oysters at time *t*, based on the "model population". Mass of shell addition per unit area was converted to volumetric addition using the relationship 0.731 kg shell = 1 L added reef volume. This conversion function was estimated as follows. Calcium carbonate has a specific gravity of 2.7; however, a conversion wherein 2.7 kg of shell results in 1 L of volumetric addition could only occur when the shell is pure and totally crushed. An oyster reef contains an open pore structure of live and dead oysters with sediment and biodeposit filled spaces between the shells, thus volume added per unit shell addition is increased and shell mass per unit volume is decreased. The volumetric conversion was estimated by the shell weight within 12 L buckets (n=3) collected from the taphonomically active zone, 1 L shell = 0.731 kg ± 0.006 kg (mean ± sd). An addition of 1 L in volume corresponds to a layer of 1 mm shell accretion when spread over 1 m^2. Thus we estimated vertical reef accretion using the conversion function of 1 mm $year^{-1}$ per a 0.731 kg of shell addition.

3.2.6 Field validation of estimated accretion rates

Given that the dates of introduction and first spawning of the invading oysters were known, excavating the entire vertical profile of a reef offers the opportunity to obtain an integrated estimate of total reef accretion since its first establishment. We examined reef accretion since their first existence (assumed to be between 1975, corresponding to the first natural recruitment event after introduction (Drinkwaard, 1998), and 1980 when they were observed on aerial pictures) by excavating holes using a shovel (Viane, n=3; St. Annaland, n=3; Kats, n=1), in the part of the reef known to be present in the 1980s, to the depth where no shell material was encountered.

3.2.7 Carbonate production

Oysters are among the largest, if not the largest producers of biogenic carbonate in temperate estuaries. Carbonate is critical in the alkalinity budgets of estuaries (Waldbusser et al., 2013). The current study allows estimation of the magnitude of carbonate production by *Crassostrea gigas* in the Oosterschelde. The obtained relation between shell length (L) and dry shell weight (W) was used to convert the density of live oyster into kg oyster shell m^{-2}. Based on the proportion of shell weight of live oysters per m^{2} in the taphonomically active zone (71%, Walles, unpublished results) the total shell weight (live and dead oysters) could be calculated. Ignoring the protein matrix within the shell structure and assuming that shell is pure calcium carbonate, we could calculate annual production of calcium carbonate per m^{2} using the following equation:

$$\text{Calcium carbonate production (kg m}^{-2}\text{ year}^{-1}) = \int_0^\infty \mathrm{N}\frac{dW}{dt}dt \qquad \text{Eq. 3.5}$$

in which N equals the number of live oysters at time t, based on the 'model population'; and W equals the dry shell weight (W) at time t, using the relationship between shell length (L) and dry shell weight (W). Continuous shell lengths were derived from the Von Bertalanffy growth model. Results were extrapolated to reef and system scale (assuming 9 km^{2} intertidal oyster reefs (Smaal et al., 2009) covered with 22.5 kg live and dead oyster shells m^{-2}). Based on the calcium carbonate present and produced in the taphonomically active zone the production to biomass ratio ($\mathrm{P}:\overline{\mathrm{B}}$) was calculated per reef.

The cumulative decades of reef accretion dictate that even higher quantities of carbonate are buried within the reef structure. As reefs consist of both shells and deposited sediments, we estimated the proportion of shell in the shell-sediment matrix below the taphonomically active zone. This was used to estimate the carbonate buried under the taphonomically active zone.

3.3 Results

3.3.1 Population structure

In total 2640 live oysters were measured at Viane, 1341 at St. Annaland and 990 at Kats, corresponding to a density of 782 ± 276, 536 ± 85 and 396 ± 95 live oysters m^{-2} respectively. The relation between shell length (L, mm) and dry shell weight (W, g) was described using a power fit (Figure 3.2; Viane: W=4.40e-04$L^{2.55}$ (R^2=0.93); St. Annaland: W=2.62e-04$L^{2.56}$ (R^2=0.97); Kats: W=1.26e-03$L^{2.16}$ (R^2=0.98)). The coefficient values in the power equation were different for each of the three reefs, with Kats differing the most from the other reefs. Oysters from Viane and St. Annaland had relatively short, wide shells resembling a more spherical shape, whereas oysters from Kats were long and narrow resembling a more cylinder-like shape.

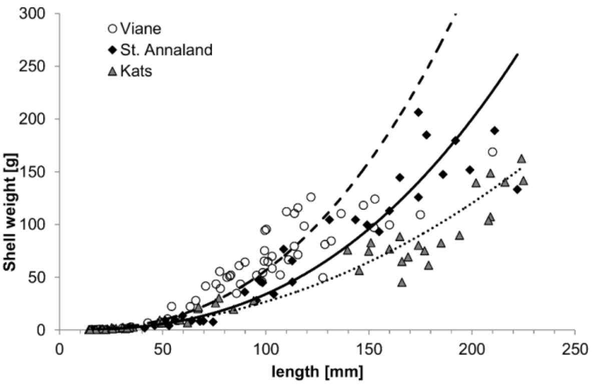

Figure 3.2 Length versus shell weight of oyster (open circle: Viane (R^2=0.93, P<0.00, n=54); closed triangle: Kats (R^2=0.98, P<0.00, n=49); closed diamond: St. Annaland (R^2=0.97, P<0.00, n=41)). The relation between length and shell weight was described using a power fit (Viane: dashed line; Kats: dotted line; St. Annaland: solid line).

The length frequency distributions of all three reefs showed high abundance of oysters between 0 and 35 mm *L* with continuing presence of oysters to 225 mm *L* at Viane, 221 mm *L* at St. Annaland, and 270 mm *L* at Kats (Figure 3.3). Based on the method of Bhattacharya (see Box 3.2) a length-at-age structure for the three oyster reefs was estimated (Table 3.1), mean shell lengths are indicated in Figure 3.3. The length-at-age structure fitted a Von Bertalanffy curve (Figure 3.4).

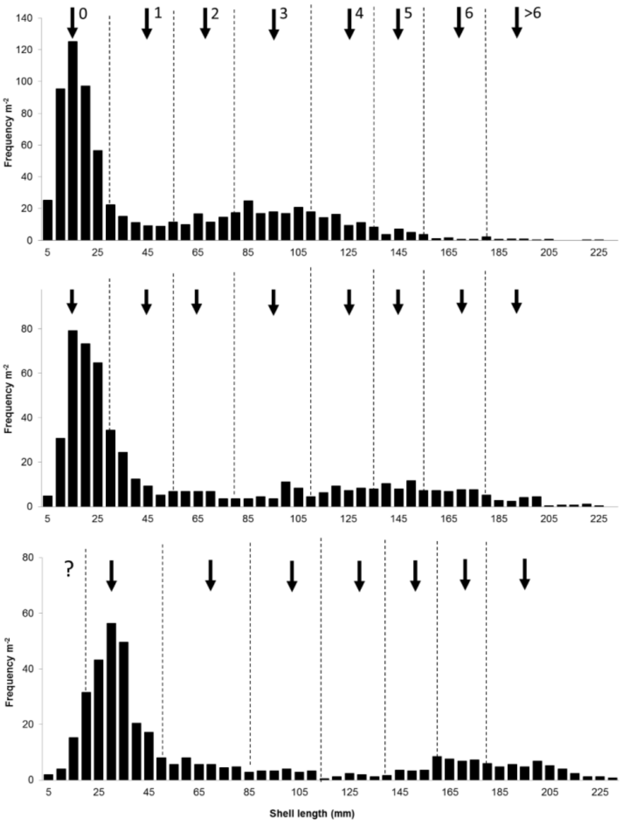

Figure 3.3 Length frequency distribution of oysters, pooled in 5 mm sizes bins, collected in 0.25 m^2 quadrants (n=10) on three intertidal oyster reefs in the Oosterschelde estuary (The Netherlands): Viane, sampled November 1st 2011 (n=2640); St. Annaland, sampled February 9th 2012 (n=1341); Kats, sampled February 7th 2012 (n=990). Year classes are separated by dashed lines. The arrows indicate the mean shell length for each year class.

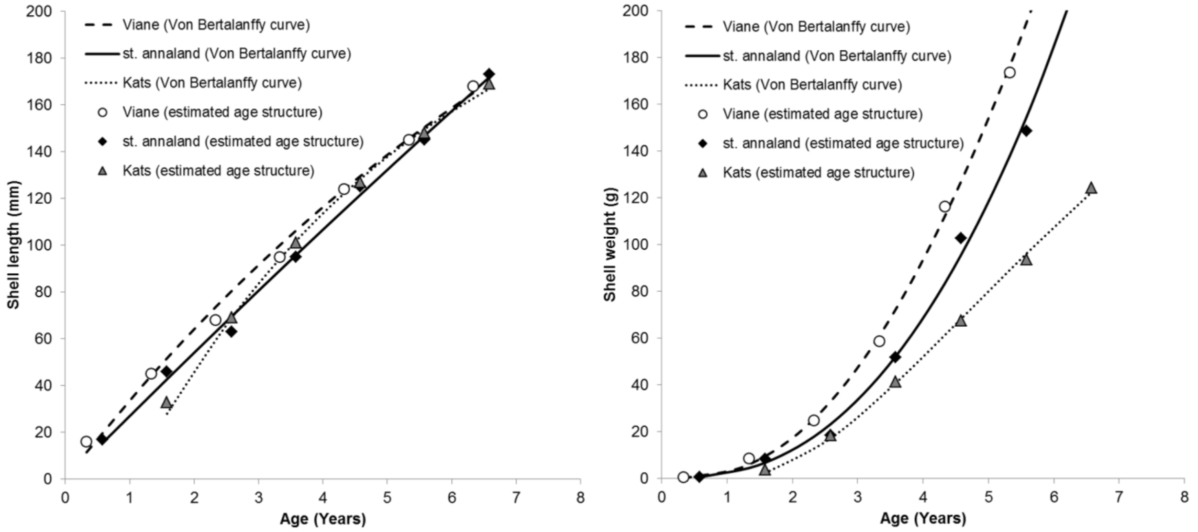

Figure 3.4 Estimated age structure versus shell length (left) and shell weight (right) plotted as a Von Bertalanffy curve for each sampled oyster reef: Viane (L_∞ =345 mm, *k*=0.10, *b*=2.83); St. Annaland (L_∞ =1525 mm, *k*=0.02, *b*=2.53); Kats (L_∞ =238 mm, *k*=0.22, *b*=2.22). L_∞ is the estimated maximum length of the oysters, *k* is the proportion of surviving animals, and *b* is the allometric growth parameter.

Growth rates expressed as shell length (*L*) decreased with increasing age, whereas growth rates expressed as shell weight (*W*) increased slightly with increasing age (Figure 3.4). Overall the mortality rate decreased with increasing age in the observed population (Figure 3.3), with an exponential decline of the first year classes followed by a period of low to no mortality between 2 and 6 years, after which mortality increased again.

Box 3.2.
Properties of the Gaussian distribution

Methods. One challenge when fitting Gaussian distributions within a demographic is that of resolution of the individual (year class) distributions. The method of Bhattacharya (1967) has been widely used to determine age structure in fish populations. Demographic frequency distributions can be skewed and polymodal. Identifying the individual age classes requires identification of the modes (means of each age class). The method of Bhattacharya (1967) considers the density within a class to be a cubic approximation and approximates the logarithm of class frequency by a quadratic function. This introduces some corrections for grouping. The assumption is that each Gaussian distribution equals one year class. A simple plotting approach using length data wherein the logarithmic difference of class frequency is plotted versus the midpoint of the class provides an estimate of the mean length of the year class. The graph shows a number of points through which a line with a negative slope can be drawn, indicating a number of distinct components (year classes). The point at which the line crosses y=0 corresponds with the mean length (in mm) per year class. In the present study the length data was examined using different aggregation intervals (1, 3, 4, 5, 6 & 7mm) as the analysis is sensitive to aggregation. Some length interval will be too small to observe clear modes, whereas in larger intervals the possibility exists that modes will be missed. Assuming that the Gaussian inflexion points will be present in the majority of the plots, the modes were combined to estimate a length versus age structure of each reef.

Results. The logarithmic values for the length data were plotted at several intervals (1, 3, 4, 5, 6 and 7 mm) in an attempt to identify the modes of the year classes (Figure B3.2.1). The Gaussian plots of 1 mm are too scattered to obtain clear modes. The 3, 4 and 5mm intervals give a reasonable number of modes, whereas the 6 and 7mm intervals clearly miss some modes. Examination of all modes for each Gaussian distributions combined indicates that certain length classes are always present. These are assumed to correspond to a mode of a year class. The values for the length classes for each location were averaged to provide a general age length structure (Table B3.2.1).

Table B3.2.1 Gaussian distributions for different length intervals (3.4.5.6. and 7mm).

Reef	Modes per mm interval					Average length	Age class
	3	4	5	6	7		
Viane	14	15	16		17	16	0
	44	47	45			45	1
	61	61				68	2
	66		66				
	74	73		72	70		
	84	84	85	86	85	95	3
	89	94	95				
	102						
	111	110	109				
	119		119	118		124	4
	125				125		
	133	131					
	146		144	147	143	145	5
			166		169	168	6
					183		>6
St. Annaland	15	16	17	19	20	17	0
	40					46	1
	51						
	61	60		60	64	63	2
				69			
	89	91	90	92	94	95	3
	101	100	102				
	111					125	4
	119	119		120			
	132	132	131	132	128		
	141	139	140		143	145	5
	147	150		148			
	154						
	171	173		174		173	6
	175						
	195				197		>6
Kats						missing	0
	29	32		30	33	33	1
			40				
	60	60		59	62	69	2
	71	71	74	71			
	78	80					
	91					101	3
	98	98	98				
	105	108		106			
	123	120	120	128	128	127	4
	134	132	134				
	141	140				148	5
	147	149	155	153	148		
	164	161	165	164	164	169	6
	172	173	175	173	174		
	176						
	185		185				>6
	192	192		192	198		

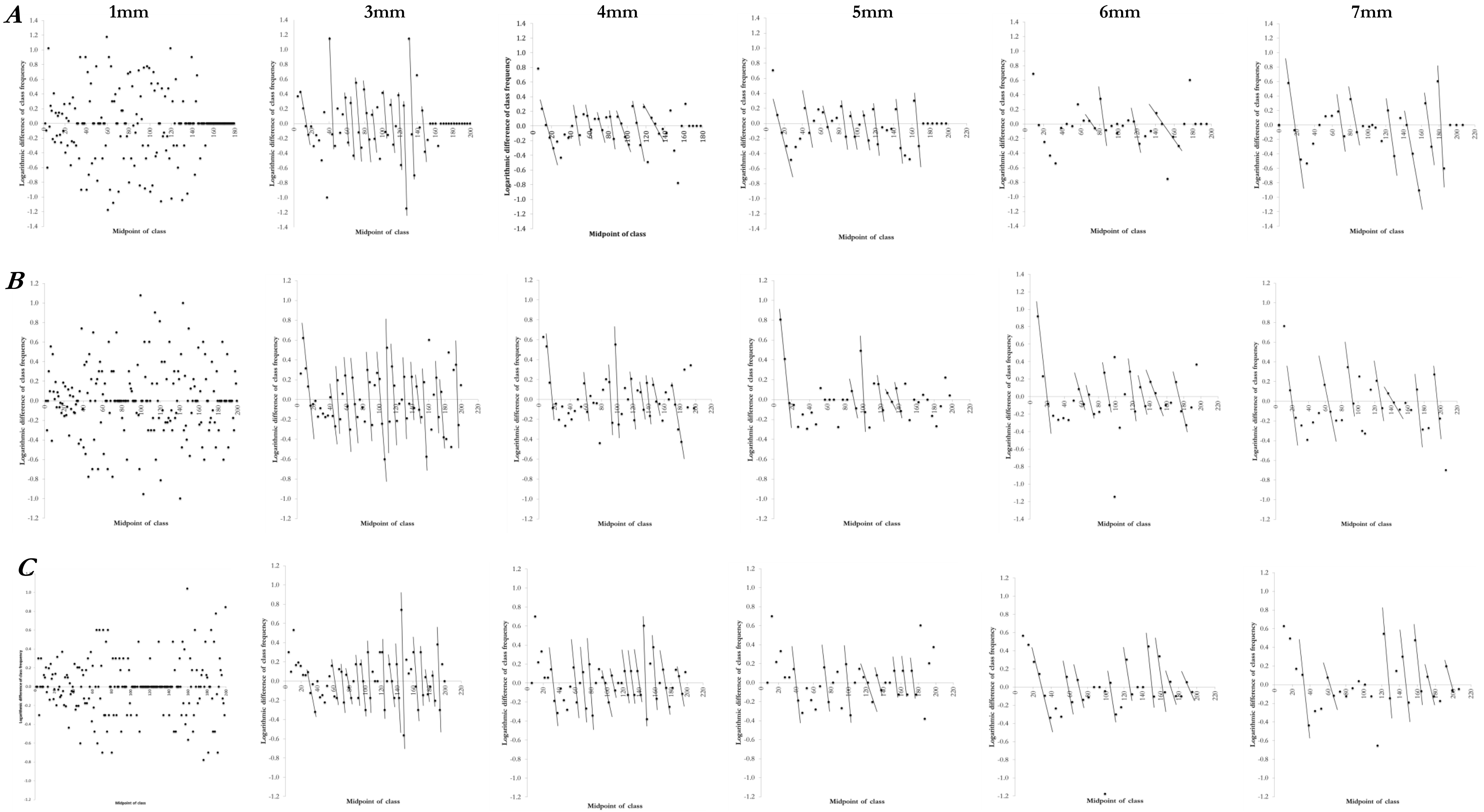

Figure B3.2.1 Gaussian plots for the length data plotted at several intervals (1, 3, 4, 5, 6 and 7 mm) for each oyster reef: ***A***, Viane; ***B***, St.Annaland; ***C***, Kats. The graphs show a number of points through which a line with a negative slope can be drawn, indicating a number of distinct components (year classes). The point at which the line crosses y=0 correspond with the mean length (in mm) per year class.

Table 3.1 Length-at-age structure (mean ± standard error) for the three oyster reefs, based on the method of Bhattacharya (see box 3.2). Observed oyster density per year class and the obtained "model population" per year.

	Age	Shell length (mm)	observed population	'model population'[b]	Mortality[c] %
Viane	**0**	16±1	422	289	
	1	45±2	57	106	63
	2	68±5	70	66	38
	3	95±11	104	46	31
	4	124±6	65	33	28
	5	145±2	26	25	25
	6	168±2	6	19	23
	7		4[a]		100
St. Annaland	**0**	17±2	294	289	
	1	46±8	50	106	63
	2	63±4	28	66	38
	3	95±5	37	46	31
	4	125±8	39	33	28
	5	145±5	42	25	25
	6	173±2	30	19	23
	7		17[a]		100
Kats	**0**		85	289	
	1	33±4	164	106	63
	2	69±8	35	66	38
	3	101±6	17	46	31
	4	127±6	7	33	28
	5	148±6	15	25	25
	6	169±6	31	19	23
	7		42[a]		100

[a] In all reefs oysters older than 6 years were found (Viane: 4; St. Annaland: 17; Kats: 42). As their exact age is unknown we assume they all die at an age of 7.

[b] Derived from the Weibull distribution ($N_0=289$, $\lambda=1$, $k=0.6$).

[c] From the "model population".

3.2 Mortality rate

The observed age-specific survival of the three reefs was best summarized using one single model for all reefs, $N_{(a)} = N'_{(0)}\, e^{-(a/1)^{0.6}}$ (in which $N'_{(0)} = 289$ oysters), Table 3.2. Distribution of the age-specific survival rate of the three reefs around the Weibull frequency distribution is presented in Figure 3.5.

Table 3.2 Model comparison. All models were tested using a fixed scale parameter ($\lambda=1$)

Model	df	AIC
Constant N_0 and k	3	59.3
Reef specific N_0, with constant k	5	62.6
Reef specific N_0 and k	7	59.8

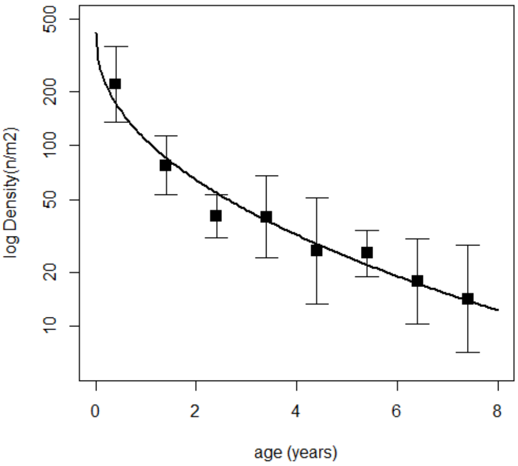

Figure 3.5 Weibull distribution (*λ*=1, *k*=0.6) fitted to survivorship data (mean ± se) of three oyster populations (Viane, St. Annaland and Kats) in the Oosterschelde estuary.

3.3.3 Reef accretion rate

Shell addition to the reef matrix by mortality was calculated using the "model population" described in Table 3.1. In total a shell addition of 10.7 kg m^{-2} $year^{-1}$ was estimated for the reef at Viane, 12.3 kg m^{-2} $year^{-1}$ at St. Annaland, and 5.1 kg m^{-2} $year^{-1}$ at Kats. This corresponds to volumetric additions of 14.6 L m^{-2} (or mm $year^{-1}$ vertical accretion) at Viane, 16.9 L m^{-2} at St. Annaland and 7.0 L m^{-2} at Kats.

3.3.4 Field validation of estimated accretion rates

At Viane oyster shells were detected to a depth of 65 cm below the reef surface before reaching only sand and stones. The layer with oyster shells was 40 cm thick at St. Annaland and 75 cm at Kats. At St. Annaland and Kats mussel shell fragments were observed deep in the excavated holes, indicating these reefs started on former mussel beds. The observed shell layer corresponded with the reef height above the tidal flat, with only a small fraction (~5 cm) of the reef subsided below the tidal flat surface, see Figure 3.6. As noted earlier, the reefs were first observed in 1980 and assumed to be related to the 1975 natural recruitment in the Oosterschelde estuary (Drinkwaard, 1998). Based on the "model population" 31 up to 36 years of reef growth (1975-1980 through 2011) resulted in a shell accretion in the range of 45-53 cm at Viane, 52-61 cm at St. Annaland, and 22-25 cm at Kats. Estimated accretion at Viane and St. Annaland are in the same order as the observed shell layer thickness in the field, whereas the estimated accretion at Kats is lower.

3.3.5 Carbonate production

In the TAZ Viane, St. Annaland and Kats had a density of 782 ± 276, 536 ± 85 and 396 ± 95 live oysters m^{-2}, which correspond with 20 ± 9, 17 ± 3 and 11 ± 3 kg live oyster shells m^{-2}, respectively. This corresponds with a total shell weight (live and dead oysters) of 28, 24 and 15 kg shells m^{-2} at Viane, St. Annaland and Kats, respectively, corresponding to 39 mm thickness m^{-2} (or litres m^{-2}) shell material at Viane, 33 mm m^{-2} at St. Annaland, and 21 mm m^{-2} at Kats. At reef scale the total standing stock is 36 x 10^3 kg shell at Viane (1265 m^2), 1024 x 10^3 kg at St. Annaland (41951 m^2), and 379 x 10^3 kg at Kats (25240 m^2).

Annually 11.2 kg $CaCO_3$ m^{-2} is produced at Viane, 14.2 kg $CaCO_3$ m^{-2} year^{-1} at St. Annaland, and 5.2 kg $CaCO_3$ m^{-2} year^{-1} at Kats, the resulting $P:\overline{B}$ ratio is 0.40 at Viane, 0.58 at St. Annaland and 0.35 at Kats. On the scale of the entire Oosterschelde estuary 176 x 10^6 kg of biogenic carbonate is present in the TAZ and 80 x 10^6 kg of biogenic carbonate is produced annually, resulting in an average production $P:\overline{B}$ ratio of 0.45.

A range of small to large shell fragments and even intact oyster shells were found deep in the excavated holes. The proportion of shell in the shell-sediment matrix decreased by depth from 35% (± 1%) shell material by weight in the upper 25 cm (below the taphonomically active zone) to 17% (± 3%) shell material deeper in the reef. At Viane 64 kg shells m^{-2} is estimated to be present in the upper 25 cm of the reef matrix and 50 kg m^{-2} deeper in the reef, resulting in a total of 114 kg shells m^{-2} buried in the reef structure at Viane. At St. Annaland and Kats totals of 83 and 131 kg m^{-2} of buried shells was estimated respectively.

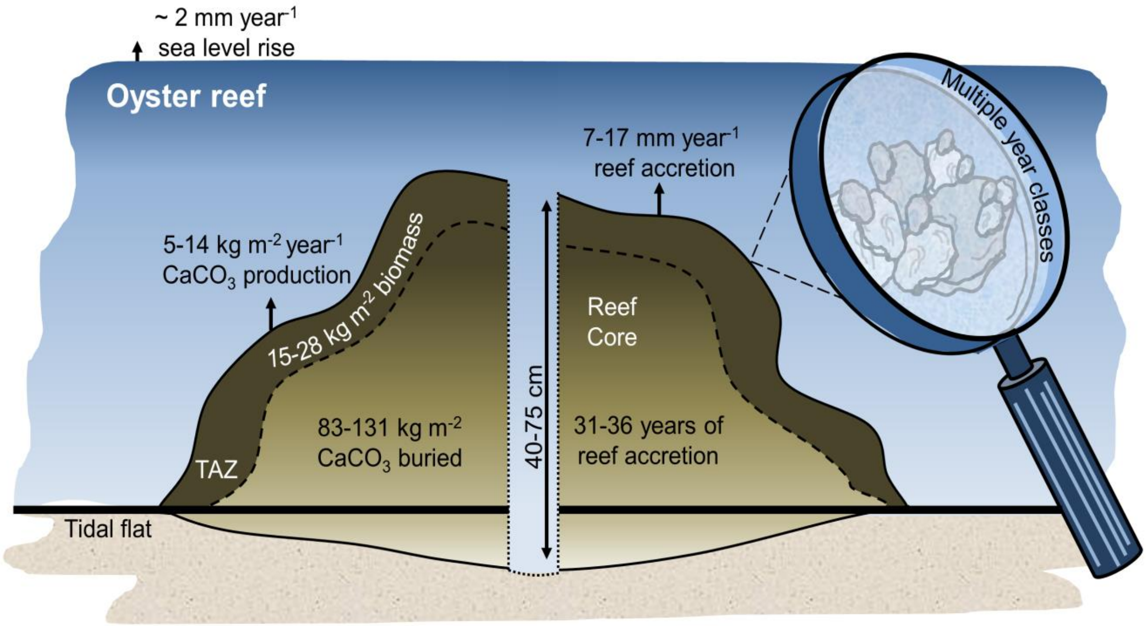

Figure 3.6 Summary of vertical reef accretion and calcium carbonate biomass and production of three intertidal *C. gigas* reefs in the Oosterschelde estuary (the Netherlands). Vertical reef accretion is in the order of 7-17 mm year^{-1}, well in excess of sea level rise. These reefs increased 40 to 75 cm in 31-36 years' time. Annually 5-14 kg m^{-2} $CaCO_3$ is produced by shell growth in the taphonomically active zone (TAZ). Het TAZ consist of 15-28 kg m^{-2} $CaCO_3$ and 83-131 28 kg m^{-2} $CaCO_3$ is buried within the reef core, indicating that these reefs are among the largest, if not the largest producers of biogenic carbonate in temperate estuaries.

3.4 Discussion

This is the first study that describes the population demography of natural *Crassostrea gigas* reefs, and addresses the patterns influencing reef maintenance and persistence. The results from our modelling approach, subsequently validated by field observations, provide the basis for a better understanding of growth and mortality processes contributing to vertical reef accretion and reef persistence in bivalve reefs in general. In a larger context, the results also provide a framework to predict reef accretion and population persistence in the future under varying recruitment, growth and mortality scenarios.

The present study required the estimation of age versus shell length in the population of *Crassostrea gigas*. The obtained length-at-age structure provide results that compare well with published values and our own unpublished data (Table 3.3). We observed an average shell growth increment of 26 ± 3 mm year^{-1} across all ages. This is comparable to mean growth rates observed in the German Wadden Sea (Schmidt et al., 2008).

Table 3.3 Shell lengths in mm (mean ± standard error) at different ages of *Crassostrea gigas* within European estuaries.

					age				
Location		0	1	2	3	4	5	6	reference
Denmark	Limfjord		53±9	79±9	102±10	119±13	134±8		(Christensen and Elmedal, 2007)
	Isefjord	32	67±11	87±14	109±18	113±16	140±12	151±71	(Wang et al., 2007)
Germany	Wadden Sea		44±6	75±1					(Diederich, 2006)
Netherlands	Wadden Sea (Texel)	10±2	27±8	70±6	97±7	140±10			(Cardoso et al., 2007)
	Oosterschelde (Yerseke)	10±1	28±12	58±7	77±6	119±7	142±30	140±42	(Cardoso et al., 2007)
	Oosterschelde (Artificial reefs, Viane)	5±1	34±5	65±3	96.5±6	133			(Chapter 5 of this thesis)
	Oosterschelde **(Viane)**	**16**±1	**45**±2	**68**±5	**95**±11	**124**±6	**145**±2	**168**±2	**“Current study”**
	Oosterschelde **(St. Annaland)**	**17**±2	**46**±8	**63**±4	**95**±5	**125**±8	**145**±5	**173**±2	**“Current study”**
	Oosterschelde **(Kats)**		**33**±4	**69**±8	**101**±6	**127**±6	**148**±6	**169**±6	**“Current study”**
France	La Rochelle	9±1	43±16	61±10	63±9	65±13			(Cardoso et al., 2007)

The age-specific survival curves fitted a complementary cumulative Weibull frequency distribution with a $k<1$, indicating that all three populations examined had a survival curve type III, which has a significant "infant mortality". This high infant mortality is probably the result of predation. Eggleston (1990) shows that the Eastern oyster, *Crassostrea virginica*, suffers from crab predation until it reaches a prey refuge size at 45-50 mm shell length. This is comparable to the size demographic observed in the current study (Figure 3.3). Oysters larger than refuge size appear to suffer very low or no mortality until senescence. The observed low mortality among larger oysters could be explained by the absence of diseases, bioeroders and co-evolved predators with a significant effect on mortality rates in the Oosterschelde population of *Crassostrea gigas*. In contrast, *C. virginica* populations in the Chesapeake Bay, suffer continuing mortality in the assumed refuge range associated with the diseases *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX), and exhibit truncated length and age population structure with oysters rarely exceeding 4 years of age (Harding et al., 2010; Mann et al., 2009; Southworth et al., 2010). The period of no or very low mortality above refuge size has important implications for both the evolutionary success of oysters as pioneer species in estuaries with rising sea level over geological time scales (DeAlteris, 1988) and in terms of shell carbonate addition budgets over annual to decadal time scales. The low mortality rate preceding a terminal senescent phase dictates a disproportionate or enhanced contribution per individual to the shell base when large, old animals die, more so than if the population exhibited constant mortality. Accretion rate is thus enhanced, generally exceeding that of sea level rise (Rodriguez et al., 2014), facilitating the invasion of new estuaries with sea level rise with the subsequent creation of complex habitat and a benthic alkalinity reservoir. The creation of a complex habitat contributes to the establishment and maintenance of rich estuarine communities that support apex predators and the nursery regions of estuarine dependent species (Pierson and Eggleston, 2014). The provided benthic alkalinity reservoir insures a benthic environment moderated at pH ranges supportive of metamorphosis of invertebrate larvae to sessile benthic adult forms (Green et al., 2009). The importance of old individual oysters is illustrated by the abundance of larger shells in reef deposits at archaeological sites (Kent, 1992; Kidwell and Jablonski, 1983; Kirby, 2001).

A positive accretion rate was observed for the oyster reefs in the Oosterschelde, indicating that reefs are able to grow and maintain themselves. We found accretion rates in the order of 7.0 to 16.9 mm year^{-1}. These reef accretion rates are comparable with accretion rates observed by Rodriguez et al. (2014) for Eastern oyster reefs located at their “growth ceiling”. The reefs at Viane and St. Annaland are located around -0.6 m MSL, slightly above the growth ceiling (-0.72±0.16 m MSL) found by Walles et al. (2014), whereas Kats, located around -1 m MSL, did not reach this growth ceiling at present. Relative mean sea level rise (inclusive of both eustatic sea level rise and land subsidence) at Vlissingen, a harbour at the North Sea outside the Oosterschelde estuary, is reported at 2.1 ± 0.1 mm year^{-1} for the period 1900 through 2011 (Wahl et al., 2013), although within this time frame the rate has been increasing (1950-2011: 1.8 ± 0.3 mm year^{-1}; 1980-2011: 2.5 ± 0.7 mm year^{-1}; 1993-2011: 4.1 ± 1.5 mm year^{-1}). The observed reef accretion rates are well in excess of these relative mean sea level rise values.

Estimated reef accretion by shell addition was in the same order as the observed shell layer thickness in the field at Viane and St. Annaland, whereas estimated reef accretion at Kats was significantly lower. When taking the proportion of shell in the shell-sediment matrix (below the TAZ) into account, 31 to 36 years of accretion results in a shell plus sediment accretion in the order of 62-67 cm, which is in the order of the observed reef accretion in the field (75cm). The reef at Kats differs from Viane and St. Annaland as it is less exposed to wave action, resulting in a muddy environment at Kats versus a sandy environment at Viane and St. Annaland. The differences between these locations might also explain the more elongated shapes of the oysters at Kats. Within the Oosterschelde estuary there has been a marked increase in erosion of sediments on tidal flats since the completion of the storm surge barrier (see Figure 3.1 for location) in 1986 (Mulder and Louters, 1994). Recent transect data in the estuary show an average erosion rate of 10 mm year^{-1} on the tidal flats (Santinelli and De Ronde, 2012). In this erosive system, reef accretion at locations exposed to wave action (Viane and St. Annaland) is determined by the addition of shell material, whereas the accretion rate at a sheltered location (Kats) is determined by both the addition of shell material and the deposition of sediments.

Oyster reefs produce large amounts of biogenic carbonate. In total (in and below the TAZ) 142, 107 and 146 kg shells m^{-2} was present at Viane, St. Annaland and Kats, respectively. We estimate an annual production of 11.2, 14.2 and 5.2 kg $CaCO_3$ m^{-2} year^{-1} at Viane, St. Annaland and Kats, respectively. This is comparable to carbonate production of coral reefs: Perry et al. (2013) report values between -2.29 and 16.68 kg $CaCO_3$ m^{-2} year^{-1}, from which only 5% of the 19 studied reefs exceeded 5 kg $CaCO_3$ m^{-2} year^{-1} production. The observed $P:\overline{B}$ ratios (Viane: 0.40; St. Annaland: 0.58; Kats 0:35) are in the order of P:B ratios found for other intertidal macrozoobenthic communities: *Littorina* sp.: 0.30; *Mytilus edulis*: 0.30; *Crassostrea gigas*: 0.38 (Hily et al., 2013). In the light of ocean acidification trends, these carbonate masses can be critical as a buffer for colonization of sessile benthic species in shallow water estuaries.

Future scenarios

The obtained model provide a framework to predict reef accretion and population persistence under varying recruitment, growth and mortality scenarios.

Scenario I - diseases: Low mortality of large oysters observed in the *C. gigas* population in the Oosterschelde, could increase in the future by diseases, bio-eroders or co-evolved predators. If oysters, in the studied population, rarely exceed 4 years of age (e.g. comparable to that observed in *C. virginica* populations with disease in the Chesapeake Bay (Harding et al., 2010; Mann et al., 2009; Southworth et al., 2010)), reef accretion would limited to the shell addition by growth up to this age. This scenario reduces reef accretion to 7.4 mm shell material year^{-1} at Viane, 4.6 mm year^{-1} at St. Annaland and 5.5 mm year^{-1} at Kats, see Table 3.4.

Scenario II - harvesting: By harvesting oysters above the age of 5, reef accretion is limited to the mortality of oysters younger than 5 years. This scenario results in an accretion of 3.4 mm shell material year^{-1} at Viane, 1.9 mm year^{-1} at St. Annaland and 3.0 mm year^{-1} at Kats, see Table 3.4.

Table 3.4 Reef accretion in mm year^{-1} under Future scenarios: Scenario I: natural mortality ≥5; Scenario II: harvesting ≥5.

Scenario	Viane	St. Annaland	Kats
	Reef accretion in mm year^{-1}		
Studied population	14.6	16.9	7.0
Scenario I: $\int_0^{<5} \mathrm{N} \frac{dW}{dt} dt$	7.4	4.6	5.5
Scenario II: $\int_0^{<5} W \frac{dN}{dt} dt$	3.4	1.9	3.0

The observed accretion rates for *Crassostrea gigas* oyster reefs in the Oosterschelde indicate that these reefs are able to both grow and persist over time periods of decades, making them suitable for ecosystem-based coastal protection structures. The framework to predict reef accretion under varying scenarios has important implications for practical management of oyster reefs. Harvesting of oysters above the age of 5 reduces the current accretion rate by 77, 89 and 57% at Viane, St. Annaland and Kats, respectively. This indicates that harvest of only certain year classes already has significant effects on the rate at which reefs accrete. Oyster reefs targeted as ecosystem-based coastal protection structures should remain untouched from harvest in order to accrete at the pass of sea level rise.

Chapter 4

Spatial distribution and niche dimension of different life stages of Pacific oysters (*Crassostrea gigas*) in intertidal environments

Brenda Walles, Tom Ysebaert, Peter M.J. Herman and Aad C. Smaal

Abstract

Coastal ecosystems inhabited by marine species characterized as structure building, autogenic ecosystem engineers (e.g. oysters) are recognized worldwide as potential tools for coastal adaptation efforts in the face of sea level rise. Successful application of ecosystem engineers in coastal protection largely depends on the long-term sustainability and persistence of their structures. Therefore knowledge is needed about the fundamental niche organisms occupy in relation to prevailing biotic and abiotic conditions. In this study response curves of different life-history stages (larvae, juvenile and adult) of oysters are investigated along an exposure gradient during a manipulative field study. Knowledge on recruitment, growth, oyster performance and survival rates at various intertidal levels defines the area where optimum growth can be obtained, which can be used to predict where ecosystem engineering oyster reefs can develop and form persistent structures which can be implemented in coastal defence schemes. The number of juvenile oysters showed an optimum around 36% exposure time. Shell growth (mm) of both juvenile and adult oysters, CI (g/ml) of adult oysters as well as mortality (%) among adult oysters is negatively related with exposure time (%). Mortality (%) among juvenile oysters is positively related to exposure time (%). Overall, adult and juvenile oysters differ in their response to the same response variable. This study provides valuable insights in the thresholds for oyster reefs establishment and development, which adds to a better mechanistic understanding of these communities in space and time. Exposure time has a strong structuring effect on reef development. Reef development is limited up to 55% exposure time. Understanding the response of (different life stages of) species to environmental factors is critical in predicting how species occurrence might be altered in the future, especially under influence of climate change.

CHAPTER 4

Spatial distribution and niche dimension of different life stages of Pacific oysters (*Crassostrea gigas*) in intertidal environments

Brenda Walles, Tom Ysebaert, Peter M.J. Herman and Aad C. Smaal

4.1 Introduction

Marine habitats, such as oyster reefs, mangroves and salt marshes are recognized for their ecological engineering potential for coastal adaptation and hazard mitigation, as they have the natural capacity to reduce flow and dampen wave energy through their physical structures, and can keep pace with sea-level rise by natural accretion (Cheong et al., 2013; Duarte et al., 2013; Gutiérrez et al., 2011; Temmerman et al., 2013; Walles et al., 2015). Epibenthic bivalve reefs, such as oyster reefs and mussel beds, deliver many ecosystem services and are abundant, persistent structures of marine and estuarine ecosystems (Grabowski et al., 2012; Grabowski and Peterson, 2007). In areas characterised by extensive intertidal mud flats, primarily mussels and oysters provide hard bottom substrate (Diederich, 2005). Hard substrate is essential for many organisms as it provides a habitat in coastal environments on which complex food webs are based (Scyphers et al., 2011; Spalding et al., 2014; Tolley and Volety, 2005), and offers a refuge and protection against predation, waves, sedimentation and desiccation for many species (Commito et al., 2008; Gutiérrez et al., 2003). Three-dimensional bivalve structures also alter water flow and reduce wave action (Borsje et al., 2011; Donker et al., 2013), while trapping and stabilizing sediment (van Leeuwen et al., 2010; Walles et al., 2014). Epibenthic bivalve reefs are therefore increasingly restored or constructed for shoreline protection and habitat restoration (Byers et al., 2006). Successful application of epibenthic bivalve reefs for coastal protection and habitat restoration does not only depend on the coastal defence value, but also on the long term persistence and sustainability of their structures.

Natural epibenthic bivalves do not occur randomly over the tidal flats, nor do they cover the entire area. Physical processes at local scale and food availability limit the total intertidal area available to bivalves to only a fraction actually occupied by bivalves (Heip et al., 1995). For example, in mussel beds, self-organization generates spatial patterns at different spatial scales, resulting in small-scale net-shaped patterns due to behavioural aggregation of individuals, and large-scale banded patterns due to the interplay of between-mussel facilitation and resource depletion (Liu et al., 2014).

Within estuarine environments biotic and abiotic factors affect species demographic. Predation, diseases, hypoxia, salinity, hydrodynamics, food availability and exposure gradients alter demographic rates and may affect the development and persistence of marine populations. Establishment of many marine populations depend on supply and success of larvae settlement (Knights and Walters, 2010). Many marine species have a life cycle which includes a planktonic larval stage prior to metamorphosis into a mobile or sessile benthic juvenile and adult stage (Ayata et al., 2009; Thorson, 1950; Troost, 2010). A planktonic larval stage allows marine species to disperse over great distances. Patterns of wind, currents and other hydrodynamic processes are important for regulating larvae supply to potential settlement sites (Alexander and Roughgarden, 1996; Ayata et al., 2009; Knights and Walters, 2010; Roughgarden et al., 1988). Potential settlement sites often contain conspecifics that attract larvae by high concentrations of chemical attractants (Diederich, 2006; Tamburri et al., 2007; Troost, 2009; Troost et al., 2009). This results in local high densities and even reef formation for some organisms. Examples of reef forming organisms are corals (Rogers, 1990), worms (Ayata et al., 2009), mussels and oysters (Troost, 2010). The spatial and temporal distribution of occurrence and abundance of a species is determined by the species optimum response surfaces and their local population dynamics. The fundamental niche for a species along one dimension is often conceptualized as a single response curve, with an optimum and thresholds beyond which individuals cannot survive (Jackson et al., 2009). Response curves, however, may differ among life-history stages, with adults often having wider niches than juveniles (Jackson et al., 2009). For sessile organisms, such as oysters, establishment highly depends on colonization and survival during the first life stages (i.e. first years). Adult individuals are important for the supply of off-spring and in the case of oysters, for the supply of settlement substrate for next generations (Schulte et al., 2009; Walles et al., 2015). Mortality among adult oysters is generally low as they have a type III survivorship curve (Walles et al. 2015). Understanding the response of (different life stages of) species to environmental factors is critical in predicting how species occurrence might be altered in the future, especially under influence of climate change.

This study focuses on the reef forming Pacific oyster, *Crassostrea gigas* (Thunberg, 1793), in the Oosterschelde estuary. In this estuary tidal flats are disappearing due to human induced changes (Zanten and Adriaanse, 2008). These tidal flats not only provide foreshore protection by reducing wave energy to the dikes, they also provide foraging grounds for internationally important migrating water birds. *C. gigas* reefs locally protect the tidal flats against erosion in the Oosterschelde estuary (Walles et al., 2014). To mitigate erosion, artificial reefs can be constructed at places were erosion is most severe. These reefs provide a stable structure which offers a kick-off for reef development (de Vries et al., 2007). As oysters are sessile organisms, reef development depends on recruitment events followed by growth and survival at the prevailing circumstances. Reef development might be hampered by factors such as local hydrodynamic conditions and sediment dynamics, insufficient larval supply and predation, causing a failure in one or multiple life-history stages of the oyster. Larval supply is important in the first years of reef development due to large year-to-year variation in recruitment. This becomes less important after a reef has formed, since oysters are long-lived (type III survivorship curve, Walles et al., 2015) and their structure can last longer than the life span of the oyster itself. To understand oyster growth and reef development, response curves of different life-history stages (larvae, juvenile and adults) are investigated along an exposure gradient during a manipulative field study on two intertidal flats in the Oosterschelde estuary. Recruitment, growth, oyster performance and survival rates were studied at various intertidal levels to determine the area where optimum growth can be obtained. This understanding is critical in order to predict where ecosystem engineering oyster reefs can develop and form persistent structures which can be implemented in coastal defence schemes. The aim of this study is to provide valuable insights in oyster establishment and development, which adds to a better mechanistic understanding of these communities in space and time.

4.2 Methods

4.2.1 Study area

The Oosterschelde estuary, located in the southwest of the Netherlands, is a 351 km^2 semidiurnal tidal basin with tidal flats (118 km^2), artificial rocky shore habitats (dikes), deep gullies and shallow water areas. In response to a devastating flooding in 1953, a storm surge barrier was constructed at the sea side (finished 1986) separating the estuary from the North Sea; in the same period the eastern part of the estuary was closed off by two compartmentalization dams. The basin area of the Oosterschelde, the tidal prism, the tidal range and the tidal currents decreased as a consequence of these measures. At present, the estuary has a mean tidal amplitude ranging from 2.47 m near the storm surge barrier to 2.98 m in the northern branch and 3.39 m at the southeast end (Nienhuis and Smaal, 1994). The maximum current velocity is about 1.0 m s^{-1}. Salinity throughout the estuary is high, generally > 30 psu (Nienhuis and Smaal, 1994). Due to the reduction of tidal volume and flow, the Oosterschelde basin is presently not in morphological equilibrium and the oversized channels are in need of sediment. Sediment erodes from the tidal flats into the channels during storms, whereas tidal forces are too small to redistribute the sediment back to the tidal flats (Mulder and Louters, 1994). On average, a net erosion rate of 10 mm year^{-1} on the tidal flats has been observed (Santinelli and De Ronde, 2012). Reduction in tidal flat area and elevation result in a loss of valuable habitats, impacting biodiversity including bird populations and seals. It also poses threats to coastal defence as dikes become less protected from waves and currents because of loss of tidal flats and salt marshes in front of dikes. The scale of erosion currently encountered in the Oosterschelde, make this ecosystem a suitable model system to study ecosystem-based coastal defence methods to combat coastal erosion.

4.2.2 Studied species

The Pacific oyster *C. gigas* (Thunberg, 1973) is a bivalve species with persistent, long-lived individuals which increases the population by colonization and growth (Walles et al., 2015). *C. gigas* was initially introduced in the Oosterschelde estuary in 1964, when the shellfish industry seeded the area with spat originating from British Columbia (Drinkwaard, 1998, 1999; Shatkin et al., 1997). More introductions of both spat and adult oysters soon followed (Drinkwaard, 1998). The first natural recruitment event after introduction was recorded in 1975 (Drinkwaard, 1998). After this the oysters spread rapidly (Smaal et al., 2009), presently occupying 9 km^2 of the (lower) intertidal (i.e. about 8%), forming dense reefs. Most of the dense reefs in the Oosterschelde estuary are located in the low intertidal up to 55% exposure time, Figure 4.1. This is comparable with the occurrence of oyster reefs from the low intertidal up to 40-50% exposure time in the Wadden Sea, Figure 4.1. In the Wadden Sea, both oyster reefs as well as mixed reefs containing mussels and oysters can be found. These mixed reefs have a wider range which can be ascribed to the niche occupied by mussels in the Wadden Sea (Sil Nieuwhof, pers. comm.).

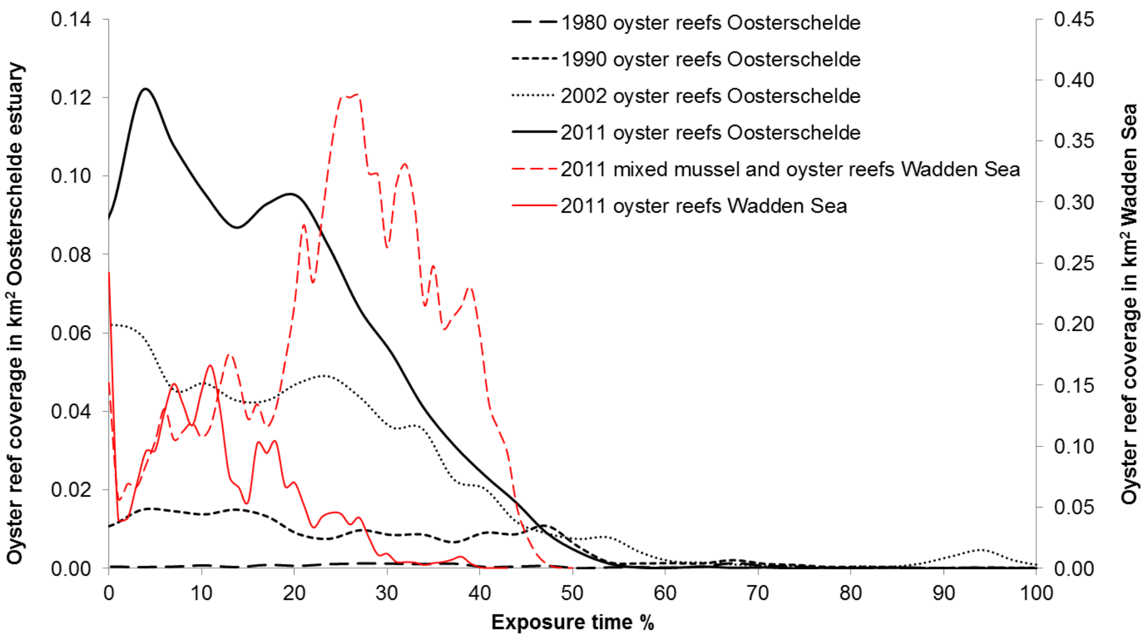

Figure 4.1 Oyster reef coverage in km² at different exposure times in the intertidal of the Oosterschelde estuary and the Wadden Sea. Most oyster reefs occupy the intertidal zone between 0 and 55 % exposure time. The distribution of oyster reefs in the intertidal zone of the Oosterschelde was analysed using detailed bathymetry maps of the Oosterschelde estuary combined with cover maps of littoral oyster reefs. Oyster maps of 1980, 1990, 2002, 2005 and 2011 were combined with bathymetry maps of 1983, 1990, 2001, 2007 and 2010 respectively.
The distribution of oyster reefs along an exposure gradient in the intertidal zone of the Wadden Sea was based on annual stock assessment and mapping of intertidal mussel (*Mytilus edulis*) and Pacific oyster (*C. gigas*) beds commissioned by the Dutch Ministry of Economic Affairs carried out by IMARES (van den Ende et al., 2014) in combination with a bathymetry map of the Wadden Sea.

4.2.3 Data collection

To investigate larvae occurrence, recruitment, growth rate, oyster performance and survival along an intertidal exposure gradient, manipulative field experiments were conducted at two tidal flats (Viane and St. Annaland) in the Oosterschelde estuary (Figure 4.2). Both tidal flats are connected to dikes in the northern branch. These tidal flats were selected, as both tidal flats contain natural oyster reefs and have areas unoccupied by oysters between the dike and the natural reef and between the low water line and the natural reef. Both tidal flats also differ in elevation and therefore exposure time, with St. Annaland being lower situated compared to Viane. Several field sites were selected above mean low water covering a range of 0-70% exposure time; eight sites at Viane (ranging from 36 – 69 % exposure time), six sites at St. Annaland (ranging from 2 – 42 % exposure time) (Figure 4.2). Plankton nets were placed at each site during the main spawning season of *C. gigas* (August) to investigate larvae occurrence in the water column. At each site 3 replicated cages were placed, each containing 16 wild-cultured oysters and 2 settlement plates, enclosed with 5 mm plastic mesh, to investigate recruitment, growth rate and oyster performance. The wild-cultured oysters (*C. gigas*, 4 years old, 76 ± 11 mm shell length) were collected at bottom culture plots from the Yerseke bank in the Oosterschelde. The settlement plates were made from rough Plexiglas plates of 20 x 18 cm, covered with a thin layer of chalk. Settlement plates were placed vertical in the cages to mimic the natural position of oysters (Bushek, 1988). Cages were placed in the field from July until November 2010.

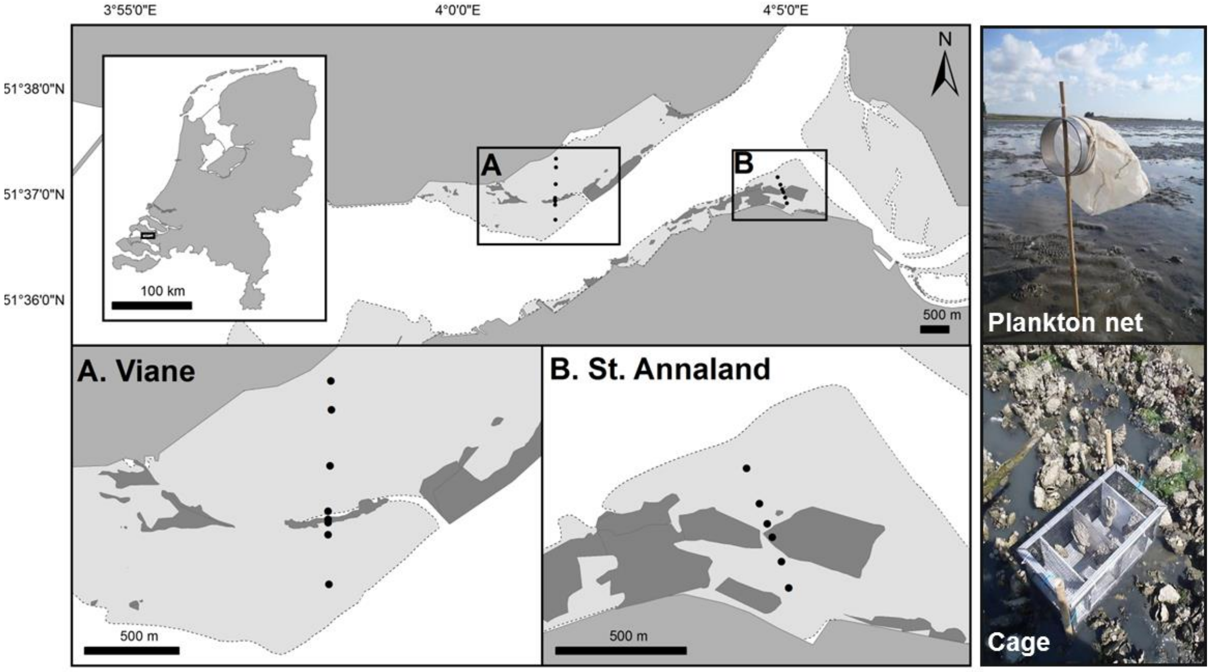

Figure 4.2 Location of the two experimental sites (Viane and St. Annaland) in the Oosterschelde estuary (the Netherlands). Dotted lines indicate the mean low tide level. Intertidal areas (light grey) covered with oysters in 2013 are indicated in dark grey. Black dots indicate the position of the field sites at which plankton nets and cages were located in which larvae occurrence, recruitment, growth rate and oyster performance was measured. The exposure time of the field sites at Viane were 36, 47, 36, 38 (on top of natural reef), 41, 57, 66 and 69 from the gully to the dike, and at St. Annaland 2, 2, 4, 16 (on top of natural reef), 28 and 42 from the gully to the dike.

4.2.4 Larvae occurrence

Pacific oysters spawn between July and September in the Oosterschelde estuary (Troost et al., 2009). The larvae stay approximately 3 weeks in the water column where they undergo a series of changes before they are competent to settle on a suitable substrate and metamorphose into the benthic juvenile stage (Troost, 2010). As spawning occurs within a relatively large time frame of several months, oyster larvae abundance and shell length was monitored on a daily basis from the 15th of July till the 10th of August 2010, to observe the moment oysters become competent to settle. At five locations along the platform of Wageningen IMARES (Yerseke, the Netherlands) samples of 20 litres surface water were taken with a bucket (in total 100 litres), and filtered over a 100 μm mesh. The residue was flushed into a bottle and brought to the lab. Samples were analysed within the same day. Bivalve larvae were counted using a universal camera microscope (Reichert Me-F2, 52.6x). Length of the larvae was measured as longest distance form anterior to posterior. In hatcheries, oyster larvae ready to settle reach a settlement size of 320 to 340 μm (Helm and Bourne, 2004). When larvae of this size were observed in the samples (beginning of August 2010), planktonic nets (Troost et al., 2009) were placed along an exposure gradient at the two study areas (Figure 4.2) to investigate the occurrence of oyster larvae in the intertidal. The opening of the nets (opening diameter 10.0 cm; mesh size 60 μm) were always oriented towards the current as nets could freely rotate around bamboo poles (Armonies, 1994). Nets were placed during low tide, with the centre of the opening 30 cm above the sediment. For logistic reasons nets were deployed on two different dates at the two tidal flats (Viane: 11th of August 2010; St. Annaland: 13th of August 2010), during the main spawning season of *C. gigas* (July – September) and collected after two tidal cycles. Moist nets were transported in plastic bags to the laboratory, where their content was flushed into plastic containers and fixed with lugol after which bivalve larvae were counted.

4.2.5 Recruitment

As settlement plates were already in the field from the beginning of July, the settlement plates were cleaned from outgrowth (mainly micro-organisms like algae and barnacles) at the beginning of August, when settlement of oyster larvae started, to present a clean settlement surface. Settlement of juvenile oysters (spat) was monitored on a monthly basis till the end of November. All live spats (larvae which survive the post-settlement period and reach detectable size >1 mm (Keough and Downes, 1982)) were counted. From each settlement plate pictures were taken to measure shell lengths (measured as longest distance from anterior to posterior, parallel to the hinge) and individual growth rate. Pictures were georeferenced in ArcGIS, after which the length of individual spats could be measured to the nearest mm.
Spat could suffer from high winter mortality resulting in a failure of reef development. To investigate winter mortality, cages were left in the field throughout the winter months. In March cages were brought to the lab where all live spats were counted and measured.

4.2.6 Growth, condition index and mortality of adult oysters

Growth of the wild-cultured oysters was measured as shell length and width increment between the start and end of the experiment, which lasted from the beginning of July to November 2010. At the end of the experiment, survivors at each exposure level were cleaned free of encrusting organisms and brought to the laboratory to determine their condition index (CI), to give an indication of their overall health. Initial condition of the wild-cultured oysters were obtained using a batch of 100 oysters at the start of the experiment. Condition index was calculated as follows:

$$\text{Condition index (g/ml)} = afdw/icv \qquad \text{(Lawrence and Scott, 1982)}$$

in which $afdw$ is the ash-free dry weight in g and icv the internal cavity volume in ml. The oysters were dissected, separating the tissue from the shell, after which the flesh was dried at 70 ºC until weight constancy was achieved (4 days). Subsequently they were incinerated at 540 ºC for 4 hours, to determine their ash-free dry weight. Internal cavity volume was determined by submerging the empty oyster shell in water, pushing the two valves tightly together, creating a water-retaining oyster shell. The weight of the water in grams corresponds with the internal cavity volume of the oyster in millilitres. During the monthly visits, the number of dead oysters per cage was recorded and the dead oysters removed. Mortality was estimated as follows:

$$M\ (\text{day}^{-1}) = 1/t\ \ln(N_t/N_0) \qquad \text{(Diederich, 2006)}$$

in which N_0 is the number of live oysters at the start of the experiment (t_0) and N_t the number of live oysters at time t. The total time of the experiment (t) was 146 days.

4.2.7 Statistical analyses

Trends in larvae occurrence, number of recruits, shell length of recruits, shell growth, oyster performance and survival along a exposure gradient were tested using linear, polynomial and exponential regression. Trends were tested for data from both tidal flats combined, covering a range of 0-70% exposure time. Data obtained from cages on top of the reef were excluded from the regression as oysters at these locations were clearly affected by the conspecifics from the reef. All analyses were performed using the SPSS Statistics software version 21. Statistical significance was set at $\alpha=0.05$.

4.3 Results

4.3.1 Larvae occurrence

Larvae competent to settle were observed in the beginning of August. Larvae were present along the whole exposure gradient at the two study areas and highly variable (8514 ± 7391 larvae). No trend between larvae occurrence and exposure level was observed.

4.3.2 Recruitment

At Viane (exposure gradient from 36 to 69 %) highest number of *Crassostrea gigas* recruits m^{-2} were observed at 36 and 38 % exposure times (Table 4.1). No recruitment was observed at an exposure time of 69 % over the whole course of the experiment. At St. Annaland (exposure gradient from 2 to 42 %) recruits showed small variation at different exposure times. Variation in recruitment numbers between months is caused by mortality of the recruits settled in previous months and recruitment of new oyster spat.

The shell length (mm) of spat and their growth rate (mm d^{-1}, Figure 4.3) were negatively correlated with the exposure time (Figure 4.4), this negative trend was highly significant in all months (Table 4.2). Almost no growth between August and November was observed for oyster spat at high exposure times, whereas spats under low exposure times almost doubled in size during the first month. At the end of the experiment, in November, oysters were grown to maximum size of 56 mm at St. Annaland and 43 mm at Viane. Recruits located on a natural reef had smaller shell lengths per month (Figure 4.4, indicated by the arrows), indicating that they experience a lower growth rate than recruits located on bare sediment.

Winter mortality among the settled oyster spat was significant positively correlated with the exposure time (exponential regression: $F_{1,10}=6.1$, $R^2=0.38$, $p=0.034$, $\text{mortality}=5.827e^{0.034\text{exposure time}}$). Highest percentage of mortality was observed at high exposure times.

Table 4.1 Number of live *Crassostrea gigas* recruits m^{-2} per month observed on settlement plates in cages, located at two experiment sites (Viane and St. Annaland). Data are ordered by exposure time, which differs from the order of the sites from mean low water line towards the dikes, see Figure 4.2.

Location	Exposure time (%)	Number of *C. gigas* recruits m^{-2}			
		August	September	October	November
St. Annaland	2	$	$	88	79
	2	162	194	181	130
	4	245	250	241	269
	16*	111	130	153	162
	28	227	181	194	190
	42	116	42	65	37
Viane	36	597	532	394	551
	36	134	755	301	310
	38*	315	361	319	264
	41	56	60	32	51
	47	5	65	60	65
	57	5	0	14	19
	66	0	56	51	56
	69	0	0	0	0

* Cages located on top of natural reefs

$ Cages submerged during the whole tidal cycle.

Figure 4.3 Left: settlement plate with oyster spat photographed after cages were brought back to the lab in early spring. Right: individual growth (indicated by the different colours) obtained from the monthly analysis of the photographed settlement plates. As temperatures already rose in March oyster spat started to grow after winter.

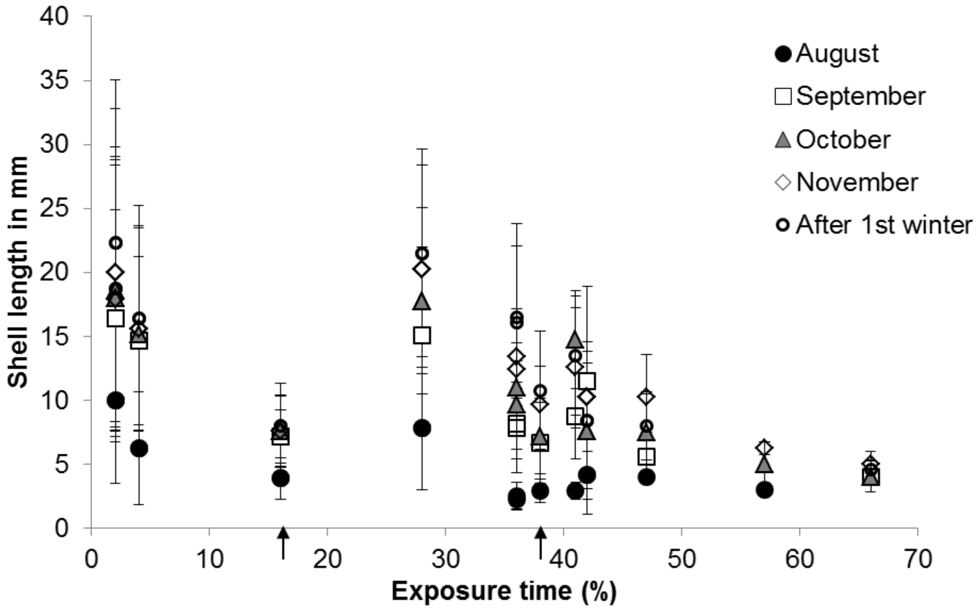

Figure 4.4 Shell length (mean ± se) of *C. gigas* recruits in mm along an intertidal exposure gradient at monthly intervals. Data obtained from cages located on top of natural reefs are indicated by the arrow.

Table 4.2 Results of linear and polynomial regression analysis of shell length (mm) and growth (mm d^{-1}) along an exposure gradient (x) at monthly intervals.

dependent	time	constant	x	x²	x³	R²	*df*	F	*p*
Shell length (mm)	August	8.231	-0.114			0.55	9	10.8	0.009
	September	13.992	0.089	-0.009	7.0E-5	0.86	3, 6	12.1	0.006
	October	15.689	0.238	-0.014	0.000	0.80	3, 8	10.7	0.004
	November	17.562	0.136	-0.008	4.6E-5	0.85	3, 8	15.1	0.001
Growth (mm d^{-1})	August	0.276	-0.004			0.55	8	9.9	0.014
	September	0.312	-0.005			0.52	7	7.7	0.027
	October	0.149	0.001	-7.8E-5	4.2E-7	0.77	3, 7	7.7	0.013
	November					0.15	11	1.9	0.198

4.3.3 Growth, condition index and mortality of adult oysters

Shell length and width increment of the adult oysters between July and November were negatively correlated with exposure time (Table 4.3). Oysters located in cages on top of the natural oyster reef showed a lower increment in shell length compared to the negative trend observed in the cages located on bare sediment.

At the start of the experiment wild-cultured oysters had an average afdw of 0.72 ± 0.24 g (mean ± se) and internal shell cavity of 14.8 ± 4.9 ml (mean ± se), which corresponded with an average CI of 49.9 ± 13.0 g/ml (mean ± se). At the end of the experiment CI was negatively correlated with exposure time, with an optimum around 20% exposure time. CI of oysters located in cages on top of natural reefs deviated from this trend with lower CI's. Below 50 % exposure time CI increased over the course of the experiment, whereas the overall health of oysters located above 50 % exposure time decreases, when oysters on top of the natural reefs were excluded. When the oysters located on natural reefs are included, this tipping point occurs around 40 % exposure time. Although afdw and internal cavity volume increased over the course of the experiment a negative trend with exposure time was also observed for both of these parameters (Table 4.3). The change observed in internal volume corresponds with the different growth rates of the length and width of shells along the exposure gradient.

The estimated daily instantaneous mortality rate (M; d^{-1}) during the period from July to November was 0.0022 ± 0.0018 d^{-1} (mean ± se). Mortality was also negatively correlated with exposure time (Table 4.3), with highest mortality (56%) among the oysters located at low exposure times. Mortality of oysters located on top of natural reefs did not deviate from the trend observed along the whole exposure gradient.

Table 4.3 Results of linear and polynomial regression analysis of shell growth, changes in oyster performance and mortality of adult oysters along a exposure gradient (x) for cages located on bare sediment. Oysters located in cages on top of the natural reefs were excluded from this analysis as the natural reef affects growth rates and oyster performance of these oysters.

dependent	constant	x	x^2	x^3	R^2	*df*	F	*P*
shell length	20.499	-0.121			0.41	10	6.9	0.025
shell width	14.564	-0.214	0.005	-6.2E-5	0.75	3, 8	7.9	0.009
icv	16.148	-0.073	0.000	-8.2E-6	0.72	3, 8	7.1	0.012
afdw	1.163	-0.008	0.000	-6.2E-6	0.89	3, 8	21.7	0.000
CI	12.871	-0.610	0.028	0.000	0.82	3, 8	11.8	0.003
Mortality	54.517	-1.506	0.020	0.000	0.90	3, 8	32.3	0.000

4.4 Discussion

The aim of this study was to investigate the response of different life stages (larvae, spat and adults) of the Pacific oyster (*Crassostrea gigas*) to environmental factors, focusing on the role of exposure time to predict where ecosystem engineering oyster reefs can develop and form persistent structures which can be implemented in coastal defence schemes. Recruitment, growth rates and oyster performance are limited by exposure time in the upper intertidal, thus limiting reef development whereas highest recruitment, growth rates and oyster performance was observed in the lower intertidal.

4.4.1 Larvae distribution

We observed a large variability in larvae numbers over the intertidal zone, but without any trend. As the Oosterschelde estuary is a well-mixed system with a high residence time (Nienhuis and Smaal, 1994), larvae are well dispersed throughout the water column in this system (Troost, 2010). Examples from other areas show that larvae dispersion can be limited by several factors such as, low residence time, small tidal movement, low salinity events reducing larval development (Narvaez et al., 2012), and hydrodynamic paths of dispersal (Haase et al., 2012; Roughgarden et al., 1988).

4.4.2 Recruitment success

The number of recruits was highest around 36 % exposure time. There seems to be an optimum around this point. The decrease in number of spat from this point was highest towards the longer exposed locations. According to Rodríguez et al. (1993), larvae dispersion in the water column is responsible for spatial variation in recruitment. This probably is the case when looking at recruitment on a large scale, but not when looking at a small scale such as a tidal flat as larvae were observed over the whole exposure gradient. No recruitment was observed on settlement plates located at 69 % exposure time, whereas larvae were observed in the planktonic nets at this location. The absence of recruits on these settlement plates does not mean larvae did not settled on these plates. Mortality of oyster larvae, just after settlement is difficult to measure, but could be a first factor responsible for the observed spatial variation. Winter mortality among juveniles exponentially increased towards the longer exposed locations. Locally a variety of factors could be responsible for spatial variation in recruitment. Recruited oysters can experience too high stress caused by limited inundation (Rodriguez et al., 2014) or temperature, which could explain the observed decline in the number of recruited oysters towards the more exposed areas. Predation pressure could explain the observed decline towards the less exposed areas. In Corpus Christi Bay (TX, USA), oyster mortality is significantly greater in the subtidal due to predation pressure, limiting the Eastern oyster (*Crassostrea virginica*) to the intertidal habitat, while they thrive subtidally in adjacent estuaries (Johnson and Smee, 2014). Knowledge on predation of *C. gigas* in the Oosterschelde estuary is however largely missing.

Slightly more oysters recruited onto the settlement plates located in cages on top of the natural oyster reefs, compared to the recruitment in cages located at bare sediment in close proximity of these reefs. Oysters are gregarious settlers which are attracted to conspecifics (Diederich, 2006; Tamburri et al., 2007; Troost, 2009), which could explain the higher recruitment in the cages located on top of natural reefs (positive feedback). At this location however, spat experience a lower growth rate than recruits located on bare sediment. Food could be limited at this location due to competition caused by high density of conspecific (negative feedback), resulting in less energy available for oyster growth. Cages located on bare sediment nearby the reef with lower recruitment, but doubled growth rates, confirm this positive and negative feedback mechanism.

4.4.3 Adult oyster performance

Overall health of adult oysters is highest around 20% exposure time. Above 40 – 50 % exposure time overall health of oysters decreased compared to their condition at the start of the study. Spencer et al. (1978) observed that Pacific oysters did not grow around 36 % exposure time at Menai Straits and 47 % at R. Roach in England. Although the CI decreased with increasing exposure time and showed a decline compared to the initial condition when located above 50 % exposure time, oysters still show shell growth above 50 % exposure time. Both shell growth and changes in meat content were negatively correlated with exposure time. This was also observed by Spencer et al. (1978). The fact that shell growth and meat content were both lower at long exposure times indicate that oysters had reallocated energy away from growth under these environmental conditions. This did not result in an increase in mortality during the course of the experiment. Mortality increased towards the less exposed sites. Mortality was not affected by the overall health of the oysters as oyster performance was highest at these locations. Factors such as predation or sedimentation could explain the high mortality at short exposure times, however indication for both factors influencing mortality were not found during this study. At one location, 2 % exposure time, cages did however experience colonization with sponges.

4.4.4 Implications for reef development

Local environmental conditions affect the development of the different life stages (larvae, juvenile and adult) of a species. A constraint for one life stage, is not necessarily a constraint for another life stage. Lack of reef development at some locations in the intertidal zone could be a result of failure in one life-history stage. During the pelagic larval stage, supply of larvae does not seem to be limiting in the intertidal zone of a well-mixed systems like the Oosterschelde, as larvae in the pediveliger stage are found throughout the intertidal zone during high tide. The juvenile stage (i.e. spat) does show limitations, with low recruitment at long exposure times and low growth rates at those locations (Figure 4.5). The adult stage also shows limitations, as shell length increment is negatively correlated with exposure time and oysters above 40 % exposure time show a decrease in their condition (Figure 4.5). Furthermore, mortality of adult oysters is positively correlated with exposure time, whereas mortality among the juveniles is negatively correlated (Figure 4.5). If oysters survive past the juvenile stage, mortality is low at high exposure times. This could explain the absence of oyster reefs in the high intertidal zone (due to a lack of sufficient recruitment), whereas sporadic oysters are present in this zone on debris (low numbers of recruits do survive at this location, but insufficient for reef development). According to recruitment, growth rates and oyster performance, reefs can develop in the lower intertidal (Figure 4.5). Offering stable substrate in the form of artificial reefs, could kick-off reef development at such locations.

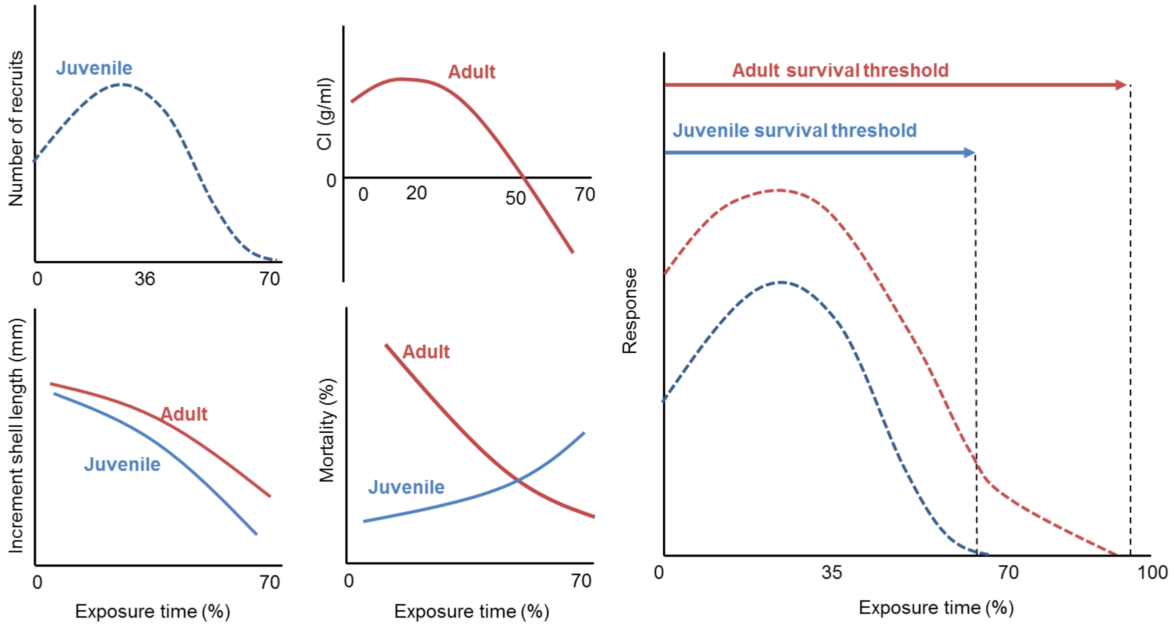

Figure 4.5 Summary of the observed response curves of juvenile and adult oysters along the exposure time gradient. The number of juvenile oysters showed an optimum around 36% exposure time. Shell growth (mm) of both juvenile and adult oysters, changes in CI (g/ml) of adult oysters as well as mortality (%) among adult oysters is negatively related with exposure time (%). Mortality (%) among juvenile oysters is positively related to exposure time (%). Overall, adult and juvenile oysters differ in their response to the same response variable.

This study provides valuable insights in the thresholds for oyster establishment and reef development, which adds to a better mechanistic understanding of the distribution of these ecosystem engineers in space and time. Exposure time has a strong structuring effect on reef development. Reef development is limited up to 55% exposure time. Above this point sporadically oysters do survive, but not at densities resulting in oyster reefs. Understanding the response of different life stages of a species to environmental factors is critical in predicting how species occurrence might be altered in the future.

CHAPTER 4

Chapter 5

From artificial structures to self-sustaining oyster (*Crassostrea gigas*) reefs for coastal adaptation

Submitted to Journal of Sea Research

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Abstract

Coastal ecosystems are increasingly recognized as essential elements within coastal defence schemes and coastal adaptation. The capacity of coastal ecosystems, like marshes and biogenic reefs, to maintain their own habitat and grow with sea-level rise via biophysical feedbacks is seen as an important advantage of such systems compared to man-made hard engineering structures.

Providing a suitable substrate for oysters to settle on offers a kick-start for establishment at places where they were lost or are desirable for coastal protection. Reef building is essential to the maintenance of oyster populations as the accumulation of shell material, through recruitment and growth, provides substrate for new generations (positive feedback loop), forming a self-sustainable structure. Insight in establishment, survival and growth thresholds and knowledge about the population dynamics are necessary to successfully implement oyster reefs in coastal defence schemes.

In this study we tested under which conditions artificial constructed Pacific oyster reefs have the potential to become long-persisting, self-sustaining structures. Artificial reefs were constructed for mitigating the erosion of tidal flats in the Oosterschelde estuary (SW Netherlands). A comparison was made of recruitment, survival and growth rates of oysters on the artificial reefs with natural Pacific oyster reefs. The results of this study show that sustainability is dependent on the local environmental conditions where the reefs are constructed, with tidal exposure and sediment dynamics governing oyster recruitment, survival and growth dynamics. Under appropriate conditions, self-sustaining reefs can develop and add to coastal defence schemes.

CHAPTER 5

From artificial structures to self-sustaining oyster (*Crassostrea gigas*) reefs for coastal adaptation

Brenda Walles, Karin Troost, Douwe van den Ende, Sil Nieuwhof,
Aad C. Smaal and Tom Ysebaert

5.1 Introduction

The integration of coastal ecosystems within coastal defence schemes is increasingly being proposed (Cheong et al., 2013; Duarte et al., 2013; Spalding et al., 2014; Temmerman et al., 2013). Particularly intertidal wetlands (salt marshes, mangroves) and reefs (shellfish, corals) provide coastal defence through enhanced wave attenuation, sediment capture, erosion reduction and vertical accretion (Gedan et al., 2011; Kench and Brander, 2006; Meyer et al., 1997; Rodriguez et al., 2014; Scyphers et al., 2011; Shepard et al., 2011; Temmerman et al., 2012; Walles et al., 2014; Wamsley et al., 2010; Zhang et al., 2012). The ability to maintain their own habitat through biophysical feedbacks (D'Alpaos et al., 2012; Kirwan and Megonigal, 2013; McKee et al., 2007) secures the long-term sustainability of ecosystem-based coastal protection, especially in case of accelerating sea level rise (Temmerman et al., 2013). Many studies focus on relatively short-term (1-2 years) influences of ecosystem engineers on the local environment, but long-term sustainability of the engineered structure is not always considered. Long-term sustainability is dependent on the ability of the ecosystem engineer to grow and maintain its own structure at the designated place. Ecosystem-based coastal protection incorporating ecosystem engineering species (e.g. salt marsh plants, corals, oysters) requires knowledge about the life history, population dynamics and habitat requirements of the species under consideration, in order to predict the sustainability of the engineered structure.

Epibenthic bivalve reefs deliver many ecosystem services and are abundant, persistent structures of marine and estuarine ecosystems (Grabowski et al., 2012; Grabowski and Peterson, 2007). Oysters form dense three-dimensional reef structures which can alter water flow and reduce wave action (Borsje et al., 2011), while trapping and stabilizing sediment (Walles et al., 2014). They also provide other ecosystem services as they are keystone species which create a habitat in coastal environments on which complex food webs are based (Scyphers et al., 2011; Spalding et al., 2014; Tolley and Volety, 2005). Oyster reefs are increasingly constructed for shoreline protection and erosion control. The construction of artificial reefs and restoration of natural reefs is often complicated by several factors, including sedimentation, substrate limitation, degraded water quality and diseases. Burial by sediment causes significant loss of reef habitat (Powers et al., 2009; Rodriguez et al., 2014). To escape sedimentation, reef height needs to exceed a certain threshold (Jordan-Cooley et al., 2011; Schulte et al., 2009). Substrate limitation can be attributed to a variety of factors, including the choice of construction/restoration material (Nestlerode et al., 2007), and a lack of addition of substrate by natural recruitment and growth. Reef building is essential to the maintenance of oyster populations as the accumulation of shell material, through recruitment and growth, provides substrate for new generations (positive feedback loop), forming a self-sustainable structure that can persist for decades (Mann and Powell, 2007; Walles et al., 2015). A reef consisting of multiple year classes can buffer for annual recruitment variability, as long-lived oysters disproportionally add shell material to the reef structure (Schulte et al., 2009; Walles et al., 2015). In absence of continued growth, a reduction in shell substrate is expected to affect the available settlement space, which in turn will decrease the shell accumulation. Since most dead shell material remains in the reef (resulting from the way oysters are cemented together), natural mortality sustains the structure on which the living oyster population depends (Mann and Powell, 2007). Diseases, parasitism, predation, and harvesting can affect population demography, which is of importance for reef formation (Walles et al., 2015).

Whether oyster reefs can be incorporated into coastal defence and coastal adaptation schemes depends not only on their coastal defence value, but also on the long-term persistence or self-sustaining character of the reef over a specific time-frame. Providing a suitable substrate for oysters to settle on offers a kick-start for establishment at places where they were lost or are desirable as part of a coastal defence scheme (Bouma et al., 2014). But subsequently oysters need to settle, survive and grow at the designated place in order to achieve long-term, persistent structures. Insight in establishment, survival and growth thresholds and knowledge about the population dynamics are necessary to successfully implement oyster reefs in coastal defence schemes.

Within the Dutch innovation program “Building with Nature” three-dimensional artificial reefs, consisting of gabions filled with Pacific oyster (*Crassostrea gigas*) shells, were constructed on eroding tidal flats in the Oosterschelde estuary (The Netherlands). The aim of these experimental, large-scale artificial oyster reefs was to investigate their potential in erosion mitigation of the tidal flats in the Oosterschelde (De Vriend and Van Koningsveld, 2012). These tidal flats do not only provide foraging grounds for migrating water birds, they also provide foreshore protection by reducing wave energy to the dikes. The artificial oyster reefs were constructed at sites that differ in exposure time, orientation, and erosive nature of the surrounding tidal flat. The effect of these reefs on tidal flat morphology (sedimentation/erosion) (Ysebaert et al., in prep) and the development of the reefs were monitored over a five year period. This paper particularly focuses on the development of these artificial Pacific oyster reefs by studying the recruitment, survival and growth rates of oysters on the constructed reefs in comparison with natural Pacific oyster reefs. The ability of the artificial structures to maintain their own structure through oyster growth in relation to the prevailing environmental conditions is evaluated and the preconditions for successful long term persistence of oyster reef structures are discussed. Understanding the development of the reef structure and its consequences on reef sustainability will allow maximizing the long-term ecological function of oyster reefs within restoration and ecosystem-based coastal defence schemes.

5.2 Method

5.2.1 Study area

The Oosterschelde estuary is a 351 km^2 tidal basin with tidal flats (118 km^2), artificial rocky shore habitats (dikes), deep gullies, and shallow water areas, located in the Southwest of the Netherlands (Figure 5.1). A storm surge barrier, completed in 1986, separates the estuary from the North Sea. Under normal operation the open barrier still allows the tide going in and out, but can be closed completely in the event of a storm surge. The estuary has a mean tidal amplitude ranging from 2.47 m near the storm surge barrier to 2.98 m in the northern branch and 3.39 m at the southeast end (Nienhuis and Smaal, 1994). The maximum current velocity is about 1.0 m s^{-1}.

Salinity throughout the estuary is high, generally >30 psu (Nienhuis and Smaal, 1994). The Pacific oyster *Crassostrea gigas* was initially introduced in the Oosterschelde estuary in 1964, when the area was seeded with spat originating from British Columbia (Drinkwaard, 1998, 1999; Shatkin et al., 1997). More introductions of both spat and adult oysters soon followed (Drinkwaard, 1998). The first natural recruitment event after introduction was recorded in 1975 (Drinkwaard, 1998). After this the oysters spread rapidly (Smaal et al., 2009), presently occupying 9 km^2 of the (lower) intertidal (i.e. about 8%). The Pacific oyster reproduces in late summer (July – September) in the Oosterschelde estuary, and the population is presently little affected by diseases and predation. Natural oyster reefs of >35 years old are found in the Oosterschelde estuary (Walles et al., 2015).

5.2.2 Artificial reefs

Five artificial oyster reefs were constructed in the Oosterschelde estuary (The Netherlands) on eroding tidal flats. The aim was to investigate their impact on tidal flat morphology and their ability to maintain their own habitat. The reefs were constructed by filling 25 cm high gabions with Pacific oyster shells, to provide substrate and encourage settlement of new oyster recruits (Arakawa, 1990; Tamburri et al., 2008). In the summer of 2009, two small reefs (hereafter called Pilot reefs) were constructed on the tidal flat Viane (Figure 5.1). Both reefs had a surface area of 40 m^2 and consisted of 10 m^3 oyster shell material, but the layout differed (Figure 5.1). In the autumn of 2010, three large reefs (hereafter called VianeWest, VianeEast and De Val) were constructed on two tidal flats: Viane and De Val (Figure 5.1). VianeEast and VianeWest were constructed in the period July - October, during the reproductive season of the Pacific oyster. For both reefs the western part was constructed in the beginning of the reproductive season, whereas the eastern part was constructed at the end of this season. De Val was constructed from September till November, at the end of the reproductive season. VianeWest has a surface area of 1728 m^2 and consisted of 432 m^3 shell material, VianeEast is 1650 m^2 and consist of 413 m^3 shell material and De Val is 1560 m^2 with 390 m^3 shell material. The three reef locations differed in prevailing abiotic conditions. First of all, the reefs were located at different heights in the intertidal zone (Pilot reefs: -0.72 ± 0.03 m MSL (Mean Sea Level); VianeWest: -0.96 ± 0.03 m MSL; VianeEast: -0.13 ± 0.08 m MSL; De Val: -0.59 ± 0.05 m MSL, measured on top of the reefs). Secondly, the reefs differed in their exposure to waves and their position on the tidal flat. VianeWest was located nearby the Pilot Reefs (Figure 5.1), exposed to north-westerly waves, on a mudflat area that is showing strong erosion (3 cm $year^{-1}$). VianeEast is situated more to the east on the same Viane mudflat, exposed to north-easterly waves. The reef De Val is situated on a less exposed mudflat, showing only slight erosion.

Recruitment numbers and growth of the recruited oysters was measured within fixed quadrants of 0.25 m^2. On the two pilot reefs, 6 quadrants were randomly distributed over the reef structure (Figure 5.1). On the three large reefs, 15 quadrants were distributed over the reef in 5 groups of 3 quadrants. Distance between the five groups was approximately 30 meters apart (Figure 5.1). Within each group the 3 quadrants were aligned perpendicular to the long edge (Front (most southern quadrant), Middle, Back), to test if recruitment and growth of the recruited oysters differed at different positions within the reef.

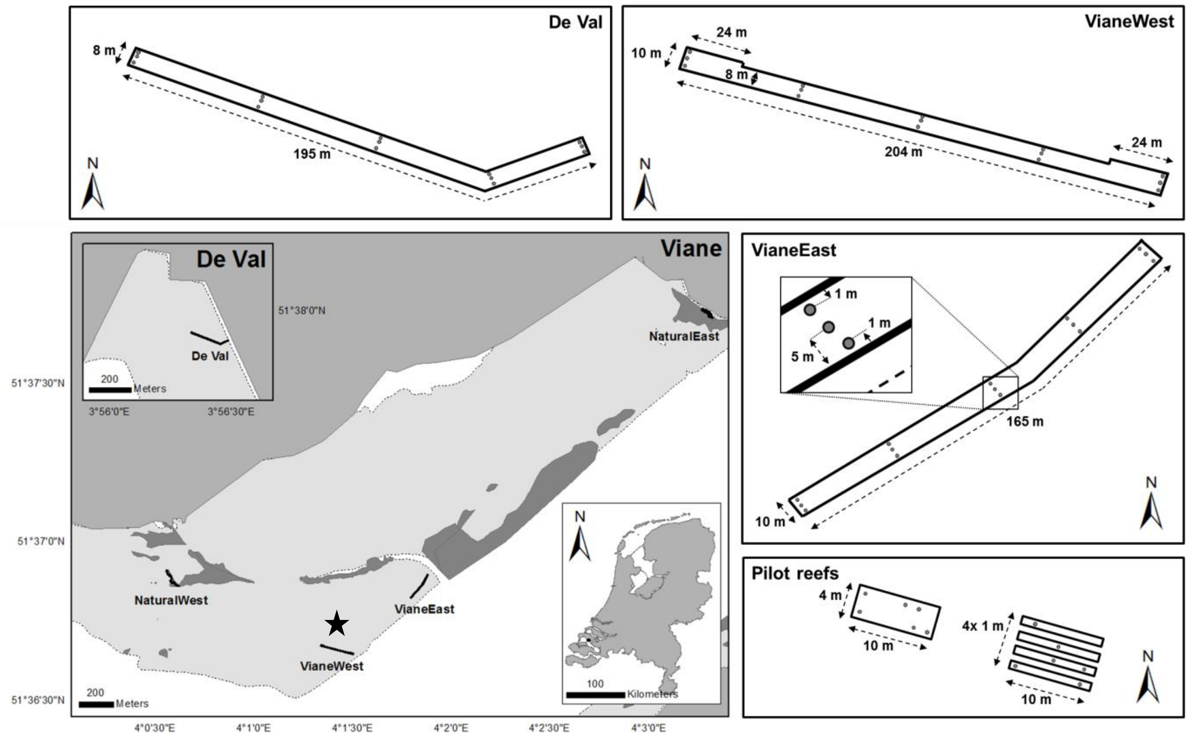

Figure 5.1 Location of the five artificial Pacific oyster reefs (two Pilot reefs (indicated by the star), VianeEast, VianeWest and De Val) and two natural reefs (NaturalWest and NaturalEast) at two intertidal flats (Viane and De Val) in the Oosterschelde estuary (SW, The Netherlands). Dotted lines indicate the mean low tide level. Intertidal areas (light grey) covered with oysters in 2011 are indicated in dark grey. The height of the artificial reefs is 25 cm. Grey circles within the reefs indicate the position of fixed quadrant (0.25 m^2) in which recruitment and growth rates were measured.

5.2.3 Natural reefs

The recruitment and growth rate of the recruited oysters observed at the artificial reefs were compared to two nearby natural oyster reefs located at the tidal flat Viane (NaturalEast and NaturalWest, Figure 5.1). NaturalEast located near the dike is sheltered from waves, whereas NaturalWest is more exposed to north-westerly waves. Recruitment was measured in 2011 by randomly selecting 30 sampling locations at each reef at which all oysters were removed from the taphonomically active zone, TAZ (Davies et al., 1989), within a quadrant of 25 x 25 cm. For all sampling locations the height on the reef with respect to the MSL (NaturalEast: -0.60 ± 0.06 MSL; NaturalWest: -0.78 ± 0.15 MSL) was measured using a Differential Global Positioning System (DGPS).

5.2.4 Recruitment

Recruitment rates were monitored annually (during the winter months: December and January), within the fixed quadrants of 0.25 m^2 on the five artificial oyster reefs, Figure 5.1. Recruitment was defined as the number of living juvenile oysters (> 1 mm in shell length) present in winter that had settled during the preceding summer season. Only the settled oysters visible from above were counted and their shell length measured to the nearest mm, leaving the gabions intact. These measurements were performed from the first winter after the construction of the reefs up to December 2013.

In 2011 recruitment rates at the two nearby natural oyster reefs were studied by counting and measuring all newly settled oysters found in the quadrants.

5.2.5 Growth rates

To determine annual shell growth rates, shell length was measured, as the longest dimension from the hinge to growing edge, of all newly settled oysters after construction of the artificial reefs. The maximum shell length observed in the first year after construction was used to identify the range of shell lengths for the 0 year old oysters. This was assumed to be the minimum shell length for the oysters in the next year up to the maximum obtained shell length within that year (1 year old oysters). The ranges (up to 3 year old oysters) were used to calculate the average shell length per year class, from which annual shell growth was calculated. Due to partial sedimentation within the reef, it was not possible to measure the full length of the largest (4 year old) oysters on the two pilot reefs in 2013 without destroying the reef structure. Therefore, all oysters (233 ± 36 live oysters) within 3 new quadrants of 0.25 m^2 on the pilot reefs were removed and brought to the lab for length measurements. The shell length data were used to construct a length frequency distribution, which was used to dissociate the length demographic into Gaussian distributions to estimate year classes using the method of Bhattacharya (1967). The Gaussian distributions were combined with the yearly maximum observed shell length to obtain the mean shell lengths of 5 year classes and the range of these year classes.

Growth rates for natural reefs was obtain uses the method of Bhattacharya at NaturalWest in 2011 (Walles et al., 2015). At NaturalWest all live oysters (from the TAZ) were removed within 8 quadrants (1 m^2, n=2 and 0.25 m^2, n=6; corresponding to a total sampled area of 3.5 m^2) and brought to the lab for length measurements.

5.2.6 Survival

Measuring all oysters settled on the artificial reefs within fixed quadrants allowed for survival estimates per quadrant. Survival was studied by calculating the number of oysters which survived from year class a at time t ($N_{a,t}$) into the next year class a year later ($N_{a+1,t+1}$) per quadrant. As sedimentation could affect survival, percentage covered with sediment was estimated per quadrant.

5.2.7 Manipulative study

Although oyster shells were used to construct the artificial reefs, they differ significantly in settlement substrate from natural reefs. Shells were mainly positioned horizontally, rather than vertically as observed in natural reefs growing on tidal flats. By counting recruits from above only (since the gabions needed to remain intact), recruitment rates at the artificial reefs were probably underestimated, because oysters that settle in the cavities underneath shells are easily missed. Contrary to the natural reefs, the densities of live oysters in the constructed reefs were low which minimize food competition and thereby stimulate recruitment success and growth of the recruits. To account for a bias in settlement substrate recruitment, growth and oyster performance was measured under controlled conditions in cages located on top of the reefs.

Fifty cages were placed on top of the natural reefs (NaturalWest, n=25; NaturalEast, n=25) and thirty-six cages on top of the three large artificial reefs (VianeEast, n=12, VianeWest, n=12 and

De Val, n=12). For all cages the height on the reef with respect to the MSL was measured using a DGPS. Shell growth and oyster performance (condition index) at the different reef locations was studied from mid-April (natural reefs) and the end of June (artificial reefs) till mid November 2011, using 9 wild-bottom-cultured oysters per cage. The oysters were collected from the location "Yerseke bank" in the Oosterschelde (Natural reefs: 91 ± 15 mm shell length, Artificial reefs: 85 ± 16 mm shell length). Shell length, width and height in mm, and total oyster weight in g were measured at the beginning and end of the study (natural reefs: 207 days; artificial reefs: 116 days). Since the cages at the natural reefs stayed in the field for a longer period of time, we calculated daily growth rates to be able to compare growth rates observed on the artificial reefs with those observed on the natural reefs. In November all oysters were brought to the lab to determine their condition index (CI), to give an indication of their overall health. Condition index was calculated as follows:

$$\text{Condition index (g/ml)} = \frac{afdw}{icv} \qquad \text{(Lawrence and Scott, 1982)}$$

in which *afdw* is the ash-free dry weight in g and *icv* the internal cavity volume in ml. The oysters were dissected, separating the tissue from the shell, after which the flesh was dried at 70 ºC until weight constancy was achieved (4 days). Subsequently they were incinerated at 540 ºC for 4 hours, to determine their ash-free dry weight. Internal cavity volume was determined by submerging the empty oyster shell in water, pushing the two valves tightly together, creating a water-retaining oyster shell. The weight of the water in grams corresponds with the internal cavity volume of the oyster in millilitres. Changes in shell growth over the course of the study, as well as the CI at the end of the study, were used for statistical analysis.

At the end of June two vertically placed Plexiglas settlement plates (0.20 x 0.18 m) were added to the cages to count and measure all settled oysters in November 2011. Unfortunately, no recruitment information was obtained from the artificial reefs as these settlement plates were lost during a storm event.

5.2.8 Statistical analyses

Differences between reefs were tested using one-way analyses of variance. Before analyses of variance, Levene's test for homogeneity of variance was applied and data were transformed in case of heterogeneity. After analysis, significant terms were analysed using Fisher's Least Significant Difference (LSD) procedure. Differences along a height gradient were tested using linear regression. All analyses were performed using the SPSS Statistics software version 21. Statistical significance was set at $\alpha=0.05$.

5.3 Results

5.3.1 Recruitment

The number of recruits differed between the artificial reefs, with the highest number of recruits at VianeWest, followed by De Val and VianeEast, Table 5.1. This difference was consistent from year to year and statistically significant (2011: $F_{2,42}=10.3$, $p=0.000$; 2012: $F_{2,42}=3.5$, $p=0.041$; 2013: $F_{2,42}=6.9$, $p=0.003$). Recruitment varied from year to year with the highest observed number of recruits in 2013 (Table 5.1). The reef at De Val was constructed from September till November in 2010, at the end of the reproductive season, and therefore showed an overall low recruitment in 2010, with only 6 ± 7 recruits m^{-2}. VianeEast was covered by a layer of sediment and cockle shells each year, deposited on top of the reef by autumn storms, resulting in low recruitment rates from 2011 onwards (Table 5.1). The two Pilot reefs constructed in 2009 differed in their reef design, see Figure 5.1. Only in 2010 a significant difference ($F_{1,10}$=8.8, p=0.014) was observed between the two reefs, with more recruits on the open structured reef (93 ± 37 recruits m^{-2}), compared to the solid reef (42 ± 21 recruits m^{-2}). Shell lengths differed significantly between the artificial reefs in 2010 ($F_{2,29}$=13.1, p=0.000) with larger recruits at VianeWest compared to VianeEast and De Val, and in 2013 ($F_{2,22}$=6.0, p=0.010) with smaller recruits at VianeEast compared to VianeWest and De Val.

Recruitment at NaturalWest was significantly higher than recruitment at NaturalEast ($F_{1,58}$=5.9, p=0.018). Likewise shell length differed significantly between the natural reefs ($F_{1,58}$=11.1, p=0.002), with an average shell length of 10 ± 3 mm at NaturalWest and 8 ± 2 mm at NaturalEast.

Recruitment was highly variable within the artificial and natural reefs, as can be seen in Figure 5.2 where numbers of recruits per quadrant are plotted. No effect of the distance to the front edge of the reef (p>0.05) could be detected. Shell length however did not differ within the artificial reefs. In 2010 a significant difference in number of recruits between the east and west part of the reefs VianeEast ($F_{1,13}$=16.5, p=0.001) and VianeWest ($F_{1,13}$=8.2, p=0.013) was observed. Since no significant difference between the east and west part of the reef was observed during the succeeding years, this difference observed in 2010 is likely due to the timing of the reef construction. At VianeEast on average 140 ± 99 recruits m^{-2} were counted at the west part of the reef, whereas only 8 ± 8 recruits m^{-2} were counted at the east part. This difference was also observed at VianeWest (192 ± 190 recruits m^{-2} at the west part of the reef, versus 12 ± 19 recruits m^{-2} at the east part).

At the natural reefs, recruitment was also highly variable between quadrants (Figure 5.2 and Table 5.1). Despite this high variability, the number of recruits showed a significant increase towards the lower part of the reef at NaturalWest (linear regression: R^2=0.19, p=0.017), but not at NaturalEast (Table 5.2). This trends was also observed for the natural reefs together. If height determines the number of recruits, highest number of recruits are expected at VianeWest, followed by De Val and VianeEast. An indication for a negatively correlated recruitment with height in the intertidal zone was indeed found on the artificial reefs in 2011, 2012 and 2013 (Table 5.2). At the natural reefs, shell length was not negatively correlated with height in the intertidal zone, whereas shell length at the artificial was negatively correlated with the height in the intertidal in 2010 and 2013 (Table 5.2).

Table 5.1 Number of oyster recruits m^{-2} (mean ± se). Reefs are ranked by their average height in the intertidal zone. Oysters recruits on natural reefs (NaturalWest and NaturalEast) were only counted in 2011. Values for VianeWest, VianeEast and De Val show average number of recruits for the whole reef, although recruitment significantly differed between the east and west part of the VianeWest and VianeEast reefs in the year of construction (2010) (see text). The pilot reefs were constructed in 2009.

Reef	Height in m MSL	2009	2010	2011	2012	2013
VianeWest	-0.96 ± 0.03		84 ± 146	81 ± 86	72 ± 46	237 ± 189
NaturalWest	-0.78 ± 0.15			488 ± 300		
Pilot	-0.72 ± 0.03	22 ± 14	68 ± 39	26 ± 23	58 ± 27	147 ± 107
NaturalEast	-0.60 ± 0.06			316 ±245		
De Val	-0.59 ± 0.05		6 ± 7	17 ± 21	44 ± 42	152 ± 202
VianeEast	-0.13 ± 0.08		61 ± 89	1 ± 2	28 ± 50	19 ± 40

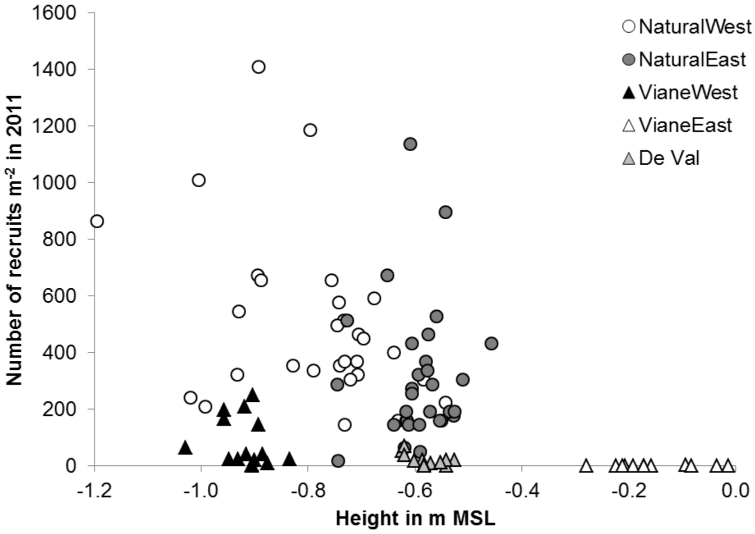

Figure 5.2 Number of oyster recruits m^{-2} in 2011 relative to the height in the intertidal zone. Data are shown from the natural reefs (dots) as well as the artificial reefs (triangles).

Table 5.2 Results of linear regression analysis of number of recruits and shell length (in mm) of recruits along a height (in m MSL) gradient. For the significant linear regression lines slopes are given.

dependent	reef	intercept	slope	R^2	*df*	F	*p*
Number of recruits	NaturalWest 2011	-198.390	-876.242	0.19	28	6.5	0.017
	NaturalEast 2011				28	0.2	0.667
	Natural reefs 2011	-139.122	-784.617	0.16	58	11.4	0.001
	Artificial reefs 2011	-16.097	-91.453	0.27	43	16.1	0.000
	Artificial reefs 2012	20.979	-50.704	0.13	43	6.4	0.015
	Artificial reefs 2013	11.348	-232.807	0.20	43	10.5	0.002
Shell length in mm	NaturalWest 2011				28	0.4	0.536
	NaturalEast 2011				28	1.6	0.212
	Natural reefs 2011				58	3.3	0.077
	Artificial reefs 2010	3.890	-2.459	0.33	30	14.8	0.001
	Artificial reefs 2011				24	0.2	0.637
	Artificial reefs 2012				34	2.2	0.145
	Artificial reefs 2013	2.642	-1.118	0.25	23	7.6	0.011

5.3.2 Growth rates

Based on the mean shell lengths per year class (Table 5.3), an average shell growth rate of 29 ± 4 mm per year was calculated. Using the method of Bhattacharya, shell lengths of 5 year classes were estimated for the Pilot reefs. These estimated shell lengths correspond with mean shell lengths observed during the annual monitoring (Table 5.3). A clear difference in the number of oysters per year class can be observed (Figure 5.3). This seems to be related to the number of recruits observed during the annual monitoring in those years (Pilot, Table 5.1).

Mean shell lengths observed at NaturalWest (Table 5.4) were within the range of shell lengths observed at the artificial reefs for oysters of 2 year and older. Shell lengths of the 0 and 1 year old oysters were, however, smaller at the artificial reefs compared to the natural reef.

Table 5.3 Average shell length in mm (mean ± standard error) per year class at the artificial reefs. Data from VianeEast, VianeWest and De Val was obtained during the annual monitoring from 2010 till 2013. Data from the Pilot reefs was obtained during the annual monitoring from 2009 till 2013, method A. Using the method of Bhattacharya, average shell lengths of 5 year classes was obtained at the Pilot reef in 2013, method B.

Year class	**VianeEast**	**VianeWest**	**De Val**	**Pilot reefs**	
				Method A	Method B
0	4±2 (n=230)	5±2 (n=1497)	4±1 (n=808)	6±2 (n=527)	6±4 (n=166)
1	28±8 (n=49)	39±6 (n=585)	34±6 (n=347)	34±2 (n=1013)	35±8 (n=213)
2	65±15 (n=9)	65±6 (n=311)	61±6 (n=105)	61±6 (n=318)	69±12 (n=140)
3	*missing*	92±1 (n=35)	*missing*	91±4 (n=62)	101±7 (n=217)
4				*immeasurable*	133±10 (n=73)

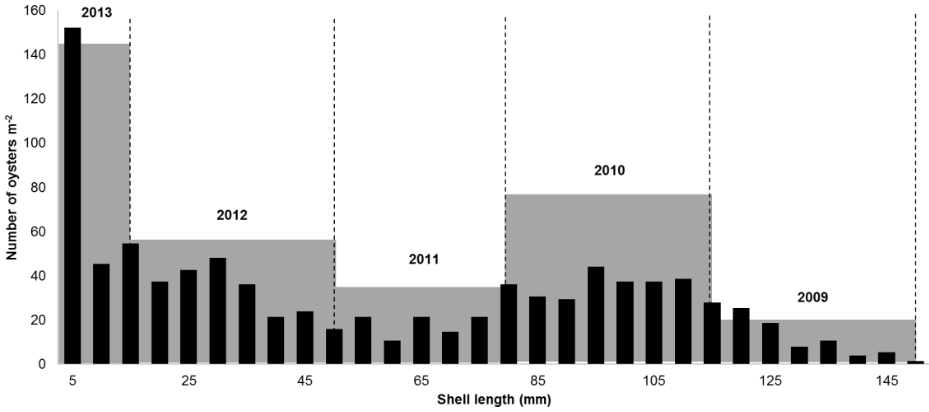

Figure 5.3 Number of oysters m^{-2} per shell length (mm), pooled in 5 mm bins, collected in 0.25 m^2 quadrants (n=3) at the Pilot reefs in the Oosterschelde estuary (The Netherlands). Year classes are separated by dashed lines. The height of the shaded areas show the amount of recruits in the different year classes (Table 5.1) with the year in which those oysters recruited onto the reef.

Table 5.4 Average shell length in mm (mean ± se) per year class at a natural reef, NaturalWest. Adapted from Walles et al. (2015).

Year class	**NaturalWest**
0	16±1 (n=1476)
1	45±2 (n=199)
2	68±5 (n=245)
3	95±11 (n=365)
4	124±6 (n=229)
5	145±2 (n=92)
6	168±2 (n=20)

5.3.3 Survival

Multiple year classes were observed during the annual monitoring, showing the survival of oysters from one year class into the next year class, Figure 5.4. At VianeEast and De Val no 3 year old oysters were observed. Only a small number of oysters was expected to be 3 years old at De Val because at the time of construction in 2010 the oyster reproduction period of that year was nearly ended. This explains the absence of this group in 2013. Yearly deposition of sediment and cockle shells on top of the VianeEast could explain the absence of 3 year olds for this reef, as oysters suffocate under this deposition. Unfortunately, survival could not be calculated at quadrant scale as the number of oysters that grew and survived till year t+1 ($N_{a+1,t+1}$) was often larger than the number of oysters observed in the previous year t ($N_{a,t}$). At most quadrants sediment deposition took place, however no relation between sediment deposition and the number of oysters was observed.

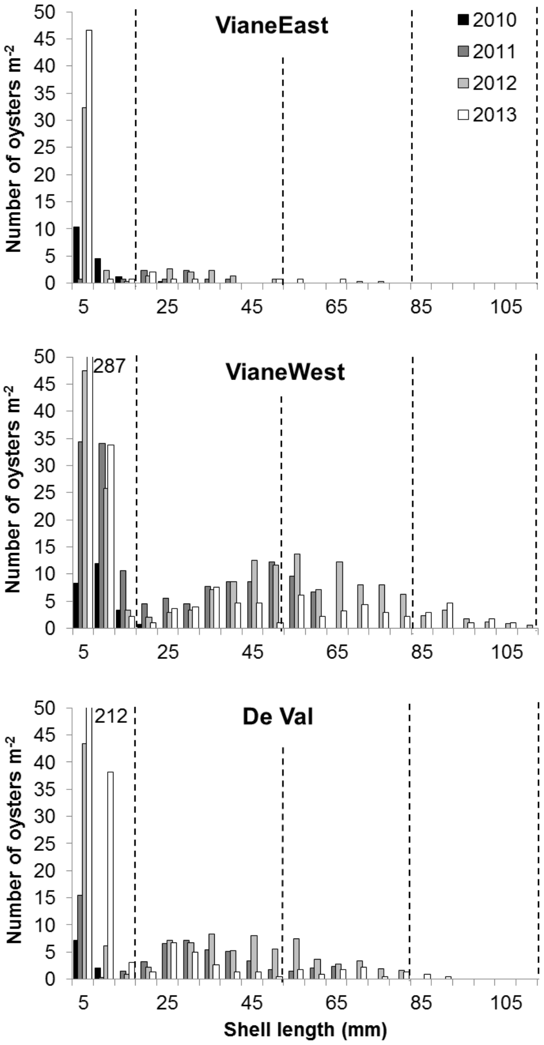

Figure 5.4 Number of oysters m^{-2} per shell length (mm), pooled in 5 mm sizes bins, collected in fixed 0.25 m^2 quadrants (n=15 per reef) at artificial reefs in the Oosterschelde estuary (The Netherlands) from 2010 till 2013. Year classes are separated by dashed lines. Annual monitoring shows growth of oysters from one year class into the next year class.

5.3.4 Manipulative study

Shell growth (in mm d^{-1}) and oyster performance (g ml^{-1}) was significantly different between the two natural reefs. Oysters at NaturalWest increased significantly more in shell length (One-way ANOVA: $F_{1,45}$=13.3, p=0.001), width (One-way ANOVA: $F_{1,45}$=13.6, p=0.001), height (One-way ANOVA: $F_{1,45}$=30.7, p=0.000) and total body weight (One-way ANOVA: $F_{1,45}$=18.0, p=0.000) than oysters at NaturalEast. Also CI of the oysters at NaturalWest was higher than CI observed at NaturalEast (One-way ANOVA: $F_{1,44}$=6.2, p=0.017). Differences between these reefs could be caused by the difference in their location in the tidal height. Shell growth and oyster performance (CI) were indeed both negatively correlated with height in the intertidal zone (Table 5.5): an increase in both parameters was observed towards the lower parts of the reefs (Figure 5.5).

Table 5.5 Results of linear regression analysis of shell growth (in mm d^{-1}), oyster performance (g ml^{-1}), number of recruits and shell length (in mm) of recruits at the natural reefs along a height (in m MSL) gradient (independent).

dependent	**intercept**	**slope**	**R^2**	***df***	**F**	***p***
length	0.027	-0.046	0.33	45	21.8	0.000
width	0.034	-0.018	0.20	45	11.3	0.002
height	0.009	-0.046	0.34	45	22.8	0.000
total weight	0.032	-0.096	0.51	45	47.3	0.000
CI	52.103	-17.365	0.20	44	11.2	0.002
number of recruits	-113.228	-251.880	0.30	48	20.8	0.000
shell length of recruits	-1.028	-7.623	0.48	25	25.3	0.000

Shell growth (length: $F_{2,32}$=16.5, p=0.000; width: $F_{2,32}$=31.2, p=0.000; height: $F_{2,32}$=8.7, p=0.001; and total body weight: $F_{2,32}$=22.6, p=0.000) and oyster performance (One-way ANOVA: $F_{2,32}$=63.5, p=0.000) were significantly different between the artificial reefs but did not show a negative correlation with height in the intertidal zone. Oyster's shell growth and performance were higher at VianeWest compared to VianeEast and De Val (Figure 5.5). This corresponds with the observation that at VianeWest the total body weight of the oysters increased during the course of the 5 month experiment, whereas the oysters at VianeEast and De Val lost body weight. In line with this finding, highest CI's were observed at VianeWest (Figure 5.5). Oysters at VianeWest and De Val show a comparable increase in shell length and width with oysters at the natural reefs located at the same height in the intertidal, despite the differences in experiment period (Natural reefs: 8 months; Artificial reefs: 5 months). The CI of the oysters at De Val was within the range of the CI's observed on the natural reefs at the same height in the intertidal zone. The CI at VianeWest was higher than CI's at the natural reefs at the same height in the intertidal, whereas the CI at VianeEast was comparable to CI's of oysters located in the high parts of the natural reefs (~0.5 m below MSL, Figure 5.5). Values of shell growth and oyster performance found at the artificial reefs are in line with values found at the natural reefs. Growth conditions were comparable.

Recruitment on the settlement plates differed significantly ($F_{1,48}$=17.2, p=0.000) between the natural reefs, with more recruits at NaturalWest (137 ± 140 recruits m^{-2}), compared to NaturalEast (19 ± 23 recruits m^{-2}). Recruitment was negatively correlated with height in the intertidal zone (Figure 5.6) when combining the data of both natural reefs (Table 5.5), but not within the reefs (NaturalWest: $F_{1,23}$=2.2, p=0.154; NaturalEast: $F_{1,23}$=0.2, p=0.699). This is consistent with the observations within quadrants at these natural reefs (Table 5.2, Figure 5.2). Shell length of recruits also shows a negative correlation with height in the intertidal (Table 5.5, Figure 5.6).

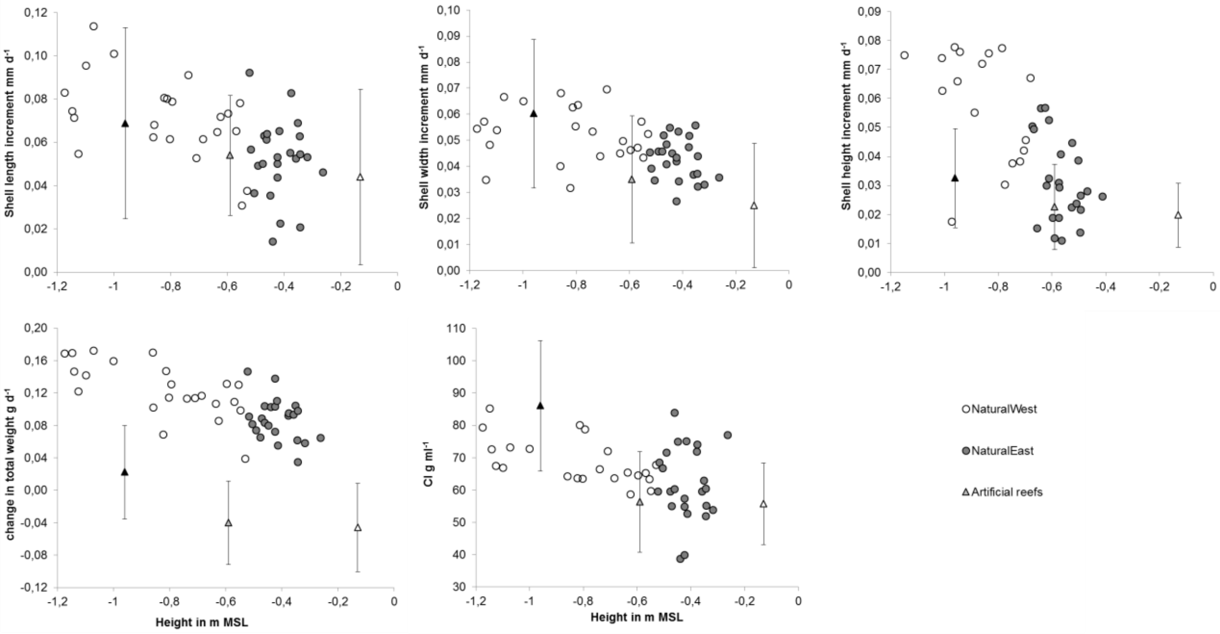

Figure 5.5 Daily shell growth: length, width and height (mm d^{-1}); changes in total weight (g d^{-1}); and CI (g ml^{-1}), at different heights in the intertidal zone, measured in cages on natural and artificial Pacific oyster reefs in 2011. Natural reefs are indicated by the white (NaturalWest) and grey (NaturalEast) circles. Artificial reefs (mean ± standard error) are indicated by the black (VianeWest), white (VianeEast) and grey (De Val) triangles.

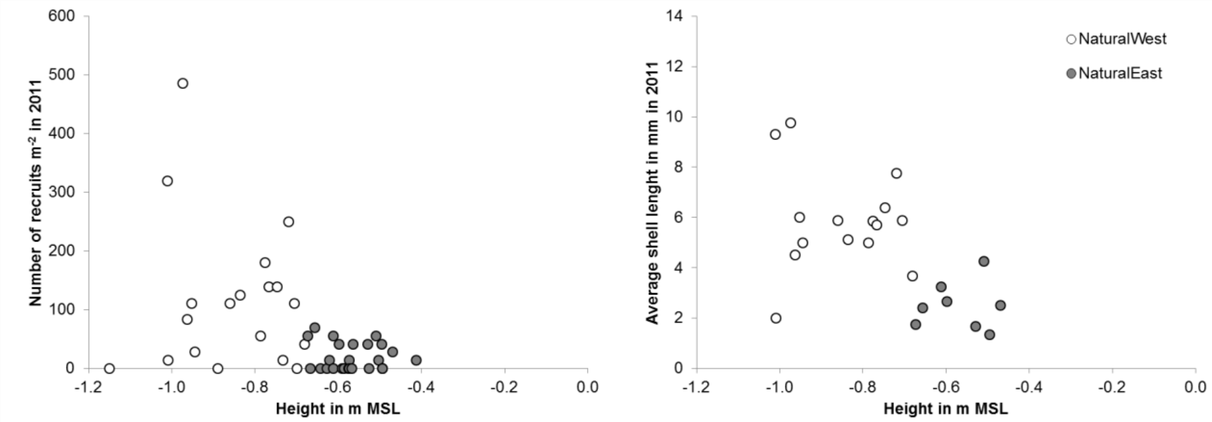

Figure 5.6 Number of oyster recruits m^{-2} and average shell length in mm on settlement plates at different heights in the intertidal zone. Newly settled oysters on the natural reefs in 2011 (quadrants) are indicated by the white (NaturalWest) and grey (NaturalEast) circles.

5.4 Discussion

As many projects fail to monitor the development of oyster reef construction for coastal adaptation on relevant spatial and temporal scales, it is difficult to assess failure or success (La Peyre et al., 2014a; La Peyre et al., 2014b). Our study shows that oysters settled, grew and survived on artificially constructed reefs, creating a multiple year class structure which buffers for annual recruitment variation and provide settlement substrate for next generations (Schulte et al., 2009), and as such facilitating self-sustainability of the reef structure. We identified several environmental constraints that need to be taken into account for successful oyster reef growth.

5.4.1 Tidal exposure

Recruitment as well as the shell length of recruits, shell growth and oyster performance was negatively correlated with the height in the intertidal zone. A study by Lenihan (1999) explains differences in recruitment, growth, survival and condition of oysters by variation in water flow speed. Due to the increased surface roughness, caused by the oysters, water flow speed at the back of a reef is lower than at the front of a reef. In this light recruitment, growth and survival is expected to differ between the front and back of the reefs, but no such differences were observed in this study. Rodriguez et al. (2014) showed that reefs have an upper limit of the tidal range, a so called growth ceiling above which oysters cannot grow as stress from limited inundation is too high. In the Oosterschelde this growth ceiling occurs around -0.72 ± 0.16 m MSL, which corresponds with an exposure time of 4 h (33 %) per low tide within the semidiurnal tidal cycle of the Oosterschelde (Walles et al., 2014). VianeEast (-0.13 ± 0.08 m MSL) is located above this growth ceiling, De Val (-0.59 ± 0.05 m MSL), NaturalEast (-0.60 ± 0.06 m MSL), the Pilot reefs (-0.72 ± 0.03 m MSL) and NaturalWest (-0.78 ± 0.15 m MSL) at this growth ceiling, whereas VianeWest (-0.96 ± 0.03 m MSL) did not reach this growth ceiling yet. Oysters located at VianeEast and de Val showed a decrease in total weight and had significant lower CI compared to oysters located at VianeWest. Since the internal cavity of the oysters at VianeEast and de Val did not differ from oysters at VianeWest, this low CI reflects a low meat content, which could be a result of starvation. Height in the intertidal zone, in other words, the inundation period, is an important factor which needs to be taken into consideration when constructing an artificial oyster reef with the potential to become a self-sustainable structure.

5.4.2 Sediment dynamics

Burial by sediment is commonly observed in reef restoration projects and causes significant loss of reef habitat (Powers et al., 2009; Rodriguez et al., 2014; Schulte et al., 2009). To escape sedimentation, the initial reef height needs to exceed a certain threshold (Jordan-Cooley et al., 2011). In an erosive system, such as the Oosterschelde estuary, low-relief reefs (0.25 m reef height) experience some sedimentation but mainly exceed this threshold. One reef (VianeEast), however, became buried by sediment. Tidal flat morphodynamics are complex, especially at the tidal flat of Viane. A sand ridge is moving in northeasterly direction towards the shore and moved over the reef structure of VianeEast, suffocating the oysters at this reef with sand and shell debris. VianeEast can be considered as an artificial reef on which recruitment starts each year from scratch. The observed deposition of sediment and shells affected the survival rates of oysters at VianeEast, making this location less suitable for reef development.

5.4.3 Substrate

Although recruitment rates were highly variable, recruitment rates were higher on the natural reefs compared to the artificial reefs in 2011. Low recruitment rates at the artificial reefs could be a lack of attractors which guide larvae to the reefs. Several studies show that larvae are able to detect a reef by chemical cues of conspecifics (Tamburri et al., 2008; Tamburri et al., 2007; Troost, 2009) or by the sound of the reef (Lillis et al., 2013). As the artificial reefs did not have time to develop yet, and could still be considered as dead structures in 2011, these attractors were most likely less present on these reefs at that time. Over time, one expects to observe an increase in recruitment rate. At VianeWest a positive correlation between the adults density and recruitment density ($R^2=0.7$) was found in 2012, which supports this theory, but due to the large annual variation it is difficult to draw conclusions from this observation.

At the natural reefs, we observed lower recruitment rates on the settlement plates than on the shell material from the quadrants.

5.4.4 Growth rates

The annual shell length measurements in fixed quadrants at the artificial reefs show growth of oysters throughout the entire experimental duration. Comparable mean shell lengths per year classes were obtained from the annual monitoring at the artificial reefs and based on analysis of the length frequency distribution using the method of Bhattacharya at the Pilot reefs. Shell lengths per year class observed on the artificial oyster reefs were compared to shell lengths found in a population structure study carried out on NaturalWest in 2011. Although shell lengths of the 0 and 1 year old oysters were larger at natural reefs, compared to the artificial reefs, similar shell lengths were observed for 2, 3 and 4 year old oysters. The difference observed for the first two year classes could not be explained by the timing of monitoring as both studies took place during the winter months. We only counted and measured oysters from above, missing the oysters that settle in the cavities underneath shells. These oysters could be larger in size due to more stable microclimatic properties (Amat-Valero et al., 2014) in such cavities. Smaller shell lengths in the first year classes, appear not to cascade through the older year classes.

As shell length of oysters on the artificial reefs are comparable to shell lengths observed on natural reefs, a vertical accretion rate in the order of 7.0 to 16.9 mm year^{-1} is expected, indicating that reefs are able to grow and maintain themselves (Walles et al., 2015). From this it is expected that De Val needs 8 years to grow 13 cm before reaching the growth ceiling whereas VianeWest needs 16 years to grow 37 cm. Diseases and harvesting are however a potential threat which could reduce vertical accretion rates (Walles et al., 2015).

Although oysters in the experimental cages show comparable shell length and width increment at the artificial and natural reefs, total weight was lower at the artificial reef (Figure 5.5). This difference could be a result of differences in the period the oysters were located in the field. Oysters at the natural reefs were placed in the field a few months earlier than the oysters at the artificial reefs.

5.4.5 Survival

Oysters are gregarious settlers, which was observed in some quadrants as all measured oysters were attached to only a small number of shells (Walles, personal observation). Although quadrants are fixed on the gabions from which the artificial reefs are made, shells can still move around by wave action. Relocation of shells with high number of recruited oysters in- and outside the sample quadrant, by waves action, could explain why ($N_{a+1,t+1}$) was often larger than ($N_{a,t}$).

5.5 Conclusion

Coastal ecosystems are increasingly recognized as essential elements within coastal defence schemes and coastal adaptation (Spalding et al., 2014; Temmerman et al., 2013). The capacity of coastal ecosystems, like marshes and biogenic reefs, to maintain their own habitat and to actively resist and grow with sea-level rise via biophysical feedbacks is seen as an important advantage of such systems compared to man-made hard engineering structures (Bouma et al., 2014). Many of these coastal ecosystems have declined tremendously over the past decades due to anthropogenic activities (Wilkinson and Salvat, 2012). Globally 29% of the seagrass beds, 30% of coral reefs, 35% of mangroves, 50% of salt marshes, and 85% of oyster reefs are either lost or degraded (Barbier et al., 2010 and references therein; Beck et al., 2011). In recent years, restoration of these coastal ecosystems became a common mitigation option. Successful application of these coastal ecosystems for coastal protection does not only depend on the coastal defence value of the ecosystem, but also on the long term persistence and sustainability of these ecosystems. In this study we showed that persistence and sustainability of artificial constructed oyster reefs is strongly dependent on the local environmental conditions where the reefs are constructed, with tidal exposure and sediment dynamics governing oyster recruitment, survival and growth dynamics. Our study provides valuable insights in the thresholds for establishment and long-term resilience of oyster reefs and adds to a better mechanistic understanding of these ecosystems in space and time. Regular monitoring and evaluation are necessary to measure their effectiveness.

Chapter 6

The role of ecosystem engineers in the ecomorphological development of intertidal habitats:

General discussion

The role of ecosystem engineers in the ecomorphological development of intertidal habitat:

General discussion

Brenda Walles

6.1 Main findings of this thesis

The results of this thesis show that oysters are physical ecosystem engineers which interact with their environment. This was demonstrated using natural and artificially constructed oyster reefs in the Oosterschelde, a coastal bay in the Southwest of the Netherlands. This bay is characterised by fast eroding tidal flats, as a consequence of infrastructural works in the 1980's to increase the safety of the area against flooding. The oyster *Crassostrea gigas*, introduced by fishermen in the 1960's, nowadays occupy about 9 km^2 (8 %) of the tidal flats in the Oosterschelde, and within the innovation programme Building with Nature, experiments with artificial oyster reefs are carried out to evaluate the application of oyster reefs for erosion reduction of the tidal flats. I used these natural and artificial oyster reefs to study the ecosystem engineering effect of the oyster reefs on tidal flat morphology, as well as the biology of the oysters to better understand reef development and reef persistence. Knowledge on both aspects is crucial for use of these organisms for coastal protection.

First of all, I showed that these reef forming organisms can locally affect tidal flat morphology as they protect the area under their footprint directly against erosion, and in addition they have a spatially extended engineering effect on sediment accumulation and stabilization in the lee side of the reefs, due to wave attenuation (Chapter 2). The scale of this spatially extended engineering effect depends on reef length and reef height, as well as on the directional spreading of the incoming waves and diffraction of the waves (Chapter 2).

Secondly, oyster reefs in the Oosterschelde have a positive vertical accretion rate in the order of 7.0 to 16.9 mm year^{-1}, indicating that reefs are able to grow and maintain themselves (Chapter 3). Natural oyster reefs in the Oosterschelde occurred up to an exposure time of 6 hours (50%) per low tide within the semi-diurnal tidal cycle of the Oosterschelde. Vertical reef growth seems to be limited up to this ceiling point. In line with this finding, reef heights vary at different locations in the intertidal zone; reefs located lower in the intertidal zone were taller than reefs located higher (Chapter 2).

Thirdly, reef development is hampered by exposure time, as recruitment numbers, growth rate and oyster performance decrease with increasing exposure time (Chapter 4 and 5). In line with this, persistence and sustainability of artificially constructed oyster reefs is strongly dependent on the local environmental conditions where the reefs are constructed, with tidal exposure and sediment dynamics governing oyster recruitment, survival and growth dynamics (Chapter 5). Successful application of oyster reefs for coastal protection does not only depend on the coastal defence value of the ecosystem, but also on the long term persistence and sustainability of these ecosystems, which depends among others on tidal exposure and sediment dynamics.

6.2 Spatially extended ecosystem engineering effect

Ecosystem engineering effects of reef building oysters are not limited to the boundaries of the reef structure. As autogenic ecosystem engineers, oyster reefs change the local environment via their own physical structure, affecting the local hydrodynamics which influence deposition patterns. Although the capacity of oyster reefs in enhancing sedimentation and reducing sediment resuspension is frequently stated (Borsje et al., 2011; Dame and Patten, 1981; Grabowski et al., 2012; Meyer et al., 1997; Piazza et al., 2005), quantitative information is largely missing, and especially the spatially extended ecosystem engineering effects on the surrounding soft-sediment environment, remain largely unstudied. Meyer et al. (1997), who measured elevations along transects, observed sedimentation behind artificially constructed oyster reefs, whereas nearby unprotected shorelines showed erosion. It is common to use transect measurements to investigate sediment patterns behind engineered structures. This provides one-dimensional information on changes in sediment patterns. Two dimensional information on sediment patterns provide additional information on the scale and direction of the spatially extended engineering effect of oyster reefs. In this thesis elevations were measured spatially around natural occurring oyster reefs using 2 to 4 m intervals to obtain a three-dimensional surface area in which the scale of the spatially extended ecosystem engineering effect of reef building oysters could be examined. The Pacific oyster reefs studied in this thesis protect the area under their footprint directly against erosion, whereas sediment accumulation and stabilization in the lee side of these reefs affect an area of the same magnitude, essentially doubling the influence of oyster reefs on soft-sediment environment (Chapter 2). Reef length was the best predictor for the area in which sediment accumulation and stabilization took place. Directional spreading and diffraction of incoming waves were the mechanisms identified shaping the deposition area behind these reefs. Directional spreading is important for small and large reefs, whereas diffraction is mainly an edge effect and therefore only important for small reefs. For longer reefs, wave dissipation, in combination with the slope of tidal flat is expected to determine the scale of the influenced area, in which case reef height will become the best predictor for the size of the influenced area, as reef height influences the period in which waves are dissipated (van Prooijen et al. in prep). With incoming tides, waves are completely blocked by the reef structure up to the point where the water levels exceeds the height of the reef. Above reef height waves are dissipated up to the point where waves over water depth ratios are so small that waves pass the reef without losing energy (Figure 6.1). For tidal flats with a steeper slope, the area of influence will be less.

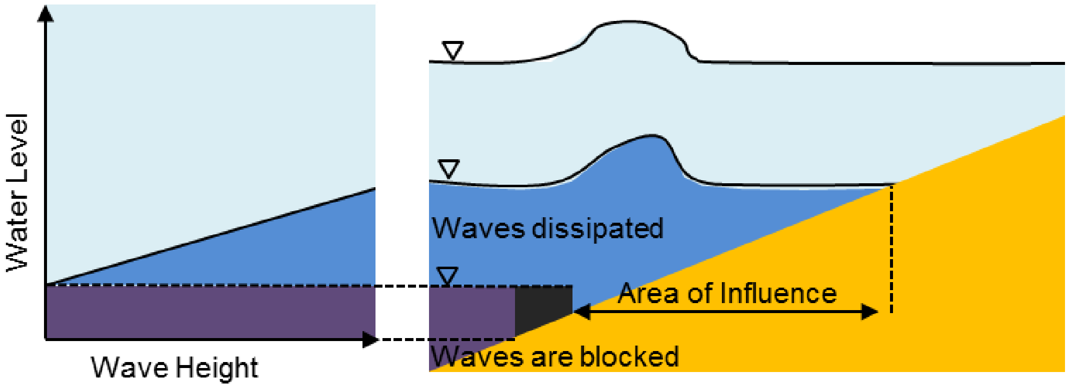

Figure 6.1. Water level, wave height and reef height influences the period in which waves are dissipated or blocked by a reef. For small wave over water depth ratios, waves pass the reef without losing energy (Bram van Prooijen pers. comm).

Although our study focused on the abiotic spatially extended ecosystem engineering effect oyster reefs have on their surrounding environment, other studies stress the biotic spatially extended effect of oyster reefs. Habitat modifications, such as sediment accumulation and stabilisation at the lee side of the reefs result in changes in the sediment composition, affecting local communities. Modifications can result in a change of the local and/or regional biodiversity; a shift in abundance of dominant species; a change in distribution patterns of local species; and changes in the ecosystem functions. Van der Zee et al. (2012) shows a positive effect of the presence of oyster reefs on feeding grounds for birds. At the lee side of the reef, sediment contained more organic matter, altering the benthic community which affected feeding behaviour of higher trophic levels.

6.3 Reef dynamics

The Pacific oyster is a sessile organism which is highly dependent on a hard substrate for settlement, metamorphosis and survival (Arakawa, 1990; Markert et al., 2010). Reef building is therefore essential to the maintenance of oyster populations in soft-sediment environments as the accumulation of shell material, through recruitment and growth, provides substrate for new generations (positive feedback loop), forming a self-sustainable structure that can persist for decades (Mann and Powell, 2007; Walles et al., 2015).

6.3.1 Recruitment

Recruitment of Pacific oysters is not a regular phenomenon (Diederich et al., 2005). The number of recruited oysters, differ from year to year (Chapter 5). This yearly variation could be temperature dependent, as high late-summer water temperatures facilitate higher recruitment events (Diederich et al., 2005). At the scale of an intertidal flat, spatial variation in recruitment success was observed, with the highest number of recruits observed around 36 % exposure time and the highest growth rates low in the intertidal (Chapter 4). According to Rodríguez et al. (1993), larval dispersion in the water column can be responsible for spatial variation in recruitment. Larval dispersal can be limited by several factors, such as low residence time, small tidal movement, low salinity events reducing larval development (Narvaez et al., 2012), and hydrodynamic paths of dispersal (Haase et al., 2012; Roughgarden et al., 1988). As the Oosterschelde estuary is a well-mixed system with a high residence time of 10 – 150 days (Nienhuis and Smaal, 1994), it is expected that larvae are relatively homogeneously dispersed throughout the water column. Local factors most likely are responsible for the observed spatial variation in recruitment. Recruited oysters can experience too high stress caused by limited inundation (Rodriguez et al., 2014) or extreme temperature variations, which could explain the observed decline in the number of recruited oysters, as well as the increased mortality towards the longer exposed areas. Predation pressure is another factor that could explain the observed decline towards the shorter exposed areas. Predation pressure can limit reef development to the intertidal, as observed in Corpus Christi Bay (TX, USA), where reefs thrives subtidally in adjacent estuaries in absence of predation pressure (Johnson and Smee, 2014). Although recruitment in the Oosterschelde estuary seems not to limit reef development (so far), recruitment can limit reef development in other areas when larvae settle in insufficient densities to result in reef development (Geraldi et al., 2013).

6.3.2 Growth

Shell growth is important for the growth and persistence of a reef. In absence of continued shell growth, a reduction in shell substrate is expected to affect the available settlement space, which in turn will decrease the shell accumulation. To obtain shell growth estimates, oysters need to be aged to obtain demographics of extant *C. gigas* reefs. For a number of shellfish species, growth lines visible on the shell can be counted to estimate yearly growth. Lines visible in oysters however, do not represent annual lines. To determine age of oysters part of the hinge need to be investigated on its chemical composition. There are a number of methods available. Lartaud *et al.* (1994) and Cardoso *et al.* (2007) determined the age of *C. gigas* analysing the fluctuations in cathodoluminescense of manganese ions in the shell hinge. Most methods are expensive and time consuming which restricts age determination to a small subsample. In Chapter 3 we determined age of oysters based on analysing the occurrence of cohorts in length frequency data. The obtained length-at-age structure provided results that compare well with published values (Cardoso et al., 2007; Christensen and Elmedal, 2007; Diederich, 2006; Wang et al., 2007) and with five years of cohort data from oysters growing on the artificial constructed *C. gigas* reefs in the Oosterschelde estuary (Chapter 5). Determining the age of oysters based on analysing the occurrence of cohorts in length frequency data provides an easy and cheap method of gaining knowledge on population structure of oyster reefs (Chapter 3).

Shell growth of both juvenile and adult oysters differs along an exposure gradient. For adult oysters a tipping point around 40 – 50 % exposure time in overall health was observed. Spencer et al. (1978) observed that Pacific oysters did not grow around 36 % exposure time at Menai Straits and 47 % at R. Roach in England. Although the CI decreased with increasing exposure time and showed a decline compared to the initial condition when located above 50 % exposure time, oysters still show shell growth above 50 % exposure time. Both shell growth and changes in meat content were negatively correlated with exposure time. This was also observed by Spencer et al. (1978). The fact that shell growth and changes in meat content were both lower at long exposure times indicate that oysters had reallocated energy away from growth under these environmental conditions. Although oysters can be found throughout the whole intertidal (even high on dikes) reef development is restricted to the areas were shell growth does not experience stress from exposure time. This is at areas with less than 50% exposure time in the Oosterschelde and Wadden Sea (Figure 4.1).

6.3.3 Reef accretion

Demographics of *C. gigas* reefs were used to estimate vertical accretion rates of oyster reefs (Chapter 3). The positive accretion rate, in the order of 7.0 to 16.9 mm year^{-1}, indicates that the studied reefs are able to grow and maintain themselves. These accretion rates were in the same order as accretion rates observed by Rodriguez et al. (2014) for the Eastern oysters (*Crassostrea virginica*). The reefs in the Oosterschelde estuary consist of multiple year classes which buffer for annual recruitment variability, as long-lived oysters disproportionally add shell material to the reef structure compared to shell material provided by juvenile oysters (Schulte et al., 2009; Walles et al., 2015).

6.3.4 Reef persistence

Changes in demography (e.g. increase in mortality due to new predators, diseases or harvesting; or decline in recruitment) interact with the engineered structure (Mann and Powell, 2007) and can be considered as engineering feedback (Jones et al., 2010). Within estuarine environments oyster demographic rates are affected by biotic and abiotic factors. Predation, diseases, hypoxia, (variation in) salinity and temperature, and exposure gradients alter oyster demographic rates and may affect reef development and persistence. In Chapter 4 and 5 we showed that exposure time influence recruitment, growth and oyster performance. Recruitment, growth rates and oyster performance (overall health) increased with decreasing exposure time (Chapter 4 and 5). Also within a reef, exposure time affects recruitment rates. Geraldi et al. (2013) and Lenihan (1999) likewise found higher recruitment at deeper depths in a reef structure. Mortality of juvenile oysters increased with exposure time, whereas mortality diseased with exposure time for adult oysters. Salinity throughout the Oosterschelde estuary is high, generally >30 psu (Nienhuis and Smaal, 1994), hence oyster demographic within this system is not affected by salinity. In other areas salinity does affect oysters demography. In Maryland (Beaven, 1954), Pamlico Sound (Ortega and Sutherland, 1992) and the Gulf of Mexico (Butler, 1954) for example, oyster recruitment is higher in high-salinity areas. The oyster industry moves oysters from low-salinity to high-salinity areas to improve oyster growth and meat quality (Kraeuter et al., 2003). Salinity can also provide a refuge against predation and diseases. In the Delaware Bay, oysters experience significant mortality in the high-salinity areas due to the disease MSX (Kraeuter et al., 2003). In the Delaware Bay, Chesapeake Bay, and other areas, the diseases MSX (*Haplosporidium nelsoni*), followed by Dermo (*Perkinsus marinus*) caused large-scale mortality to oysters (Harding et al., 2010; Kraeuter et al., 2003; Mann et al., 2009; Southworth et al., 2010), with oysters rarely exceeding 4 years of age. This affects the growth and persistence of reefs in these areas. Recruitment on a regular basis is essential for reef development. When a reef is not recruited anymore and completely dies off the half-life of oyster shells determines how long the reef structure will persist. Based on shell half-life in the Delaware Bay (3 to 10 years (Powell et al., 2006)) and the Oosterschelde estuary (3 to 7 years, Chapter 3) it is expected that reefs will be completely gone after a few decades without recruitment.

6.4 Management

Many coastal ecosystem engineers are world-wide degrading. Globally 29% of the seagrass beds, 30% of coral reefs, 35% of mangroves, 50% of salt marshes, and 85% of oyster reefs are either lost or degraded (Barbier et al., 2010 and references therein; Beck et al., 2011). Regardless of the cause of loss of these coastal habitats, deterioration of these habitats has adverse impacts on their provision of ecosystem services upon which humans and other species depend.

6.4.1 Goods and services

Since oysters provide many different ecosystem services, oyster reefs are restored or constructed for many different reasons. They can be restored to improve the overall water quality, as they enhance benthic-pelagic coupling by their strong filter feeding capacity, contributing to water purification (Newell, 2004; Ostroumov, 2005; Ulanowicz and Tuttle, 1992; van Leeuwen et al., 2010). As their three-dimensional reef structure increases habitat heterogeneity and complexity in soft-sediment environments (Gutiérrez et al., 2003; Meyer and Townsend, 2000; Peterson et al., 2003; Zee et al., 2012), reefs can be used to increase local biodiversity and act as a nursery area for fish and crustaceans. Furthermore, structure building autogenic ecosystem engineers like oysters are increasingly recognized as a potential tool in support of coastal protection and climate change adaptation (Arkema et al., 2013; Borsje et al., 2011; Rodriguez et al., 2014; Scyphers et al., 2011) and are thus increasingly developed or restored for that purpose. By changing water flow patterns and attenuation of waves (Borsje et al., 2011) they trap and stabilize sediment (van Leeuwen et al., 2010; Walles et al., 2014), contributing to coastal protection and adaptation. An interesting, but largely overlooked ecosystem service provided by oyster reefs is their potential buffering capacity in perspective of ocean acidification. By creating reef structures oysters produce significant amount of biogenic carbonate (Rodriguez et al., 2014; Waldbusser et al., 2011). These significant biogenic carbonate masses can act as a buffer against acidification. In the light of ocean acidification trends, these carbonate masses can be critical as a buffer for colonization of sessile benthic species in shallow water estuaries(Green et al., 2009). Furthermore, oysters are also restored or reconstructed for harvesting purposes.

As the economic value of the ecosystem services provided by undisturbed oyster reefs can be greater than the value obtained from harvesting them (Coen et al., 2007; Grabowski and Peterson, 2007; Peterson et al., 2003), management should be reef specific addressing the desired outcome. For example, oyster reefs targeted as ecosystem-based coastal protection structures should be protected from destructive harvest in order to maintain their structure and accrete at the pass of sea level rise. As harvesting of only certain year classes already has significant effects on the rate at which reefs accrete (Walles et al., 2015), harvesting activities should be restricted to a certain level at which the reef structure can still accretes at a desire pace, leaving the structure of the reef intact for coastal protection.

6.4.2 Oyster reefs for coastal mitigation

The capacity of salt marshes and biogenic reefs to maintain their own habitat and grow with sea-level rise via biophysical feedbacks (D'Alpaos et al., 2012; Kirwan and Megonigal, 2013; McKee et al., 2007) is seen as an important advantage of such systems compared to man-made hard engineering structures (Bouma et al., 2014). Therefore it is important to understand the mechanism behind habitat maintenance to optimize the use of biogenic reefs in coastal defence schemes. In this thesis we showed that oyster reefs can be used as coastal defence structure in the Oosterschelde estuary. They can locally protect tidal flats against erosion (Chapter 2), and at the right conditions (Chapter 3 and 4), self-sustaining reefs can develop (Table 6.1). Providing a stable settlement substrate, in the form of artificial reefs, offers a kick-off for the establishment of a reef (Chapter 5). When located at the right exposure time (Chapter 4 and 5), reefs can rapidly accrete.

Table 6.1. Criteria for reef development

Establishment	stable settlement substrate gregarious behaviour larval dispersion
Accretion	rapid growth frequent settlement trapping sediment
Persistence	sufficient height (escape sedimentation) accretion (exceeding the rate of sedimentation) lack of predators, parasites and diseases

In the Oosterschelde estuary reef developments is not recruitment limited, but in other areas reef development may be limited by oyster recruitment. Where reef development is thought to be limited by recruitment, seeding with juvenile oysters can be used to overcome this limitation. This is a common practice for the Eastern oyster (Brumbaugh and Coen, 2009; Grizzle et al., 2006a; Rodney and Paynter, 2006). Seeding consists of adding hatchery raised juvenile oysters to the reef. As oysters have a pelagic larval stage of 2 to 3 weeks, larvae may not recruit to the same reef on which they spawned, in which cases multiple seeding events are necessary. Reef development may also be limited by high mortality among recruited oysters for example caused by predation (Eggleston, 1990). This could result in few oysters reaching maturity (Kraeuter et al., 2003). In this cases, seeding with oysters above the prey refuge size could overcome this predation pressure. Due to the lack of predators, parasites and diseases with significant impact on the oyster demographics during our study, reefs can persist in the Oosterschelde estuary (Table 6.1). Predators and diseases however are of concern as in the last years recruitment at spat collectors has declined dramatically due to the Herpes virus (pers. comm A. Cornelisse). Furthermore, oyster drills (*Ocinebrellus inornatus* and *Urosalpinx cinerea*) have increased in numbers and are effecting the subtidal culture plots in the Oosterschelde (pers. comm A. Cornelisse). These predatory snails are however, scarcely observed in the intertidal. In the future, their impact on reef persistence might increase due to the ongoing increase in sea water temperatures. Furthermore, with increasing sea water temperatures new predators and diseases can be introduced by the continuous transport of shellfish between areas. Although the herpes virus as well as the predators are effecting commercially cultured oysters subtidally, little is known about their impact on reef persistence at the intertidal.

6.4.3 Invasive oysters

C. gigas is a non-native species to many parts of the world. The spread of this species can have both positive as well as negative effects on the receiving environment (Table 6.2). In soft-sediment environments, the three-dimensional reef structure of *C. gigas* increases habitat heterogeneity and complexity, increasing species diversity and abundance and add to shoreline stabilization (Dame and Patten, 1981; Walles et al., 2014). As *C. gigas* has a large filtration capacity and therefore it competes with native bivalves for food, resulting in a possible shift in the benthic community (Diederich, 2006; Smaal et al., 2005). In an area near carrying capacity, like the Oosterschelde estuary, expansion of the *C. gigas* population may induce the risk of overexploitation (Smaal et al., 2013). A shift in one trophic level can cascade through the whole food chain. A shift in the benthic community may have consequences for the food availability for bird populations (Smaal et al., 2005). In the Wadden Sea *C. gigas*, transformed a large percentage of the native mussel, *Mytilus edulis*, beds into oyster reefs. As mussel beds are important foraging habitats for migratory birds on the East Atlantic flyway, this has led to concern that birds might lose feeding opportunities in the Wadden Sea. Especially birds dependent on mussels as food resource (i.e. Common Eiders) were expected to lose their foraging habitat. Intertidal mussel beds are important foraging sites due to their high biomass and productivity (Nehls et al., 1997). Birds not only used mussel beds to feed on mussels, but many species feed on the associated fauna living on and between the mussels. Kochmann et al. (2008) shows that a change from native mussel beds to invasive oyster reefs in the Wadden Sea does not pose a threat to species diversity, but results in a shift in abundance of the dominant species. These consequences are not necessarily negative. Markert et al. (2013) observed that bird species which feed on associated fauna experience a positive differences. The engineered reef structure promoted the presence of shore crabs (*Carcinus maenas*) on which the Eurasian curlew (*Numenius arquata*) feed extensively. For birds feeding on mussels, both negative and positive changes were observed. The European herring gulls (*Larus argentatus*) was negatively affected by the habitat change. In contrast, the Eurasian oystercatcher (*Haematopus ostralegus*) learned to adapt its foraging strategy and was able to attain sustainable intake rates by foraging on the food supply offered by *Crassostrea* reefs (Markert et al., 2013).

Table 6.2 Positive and negative effects of the invasive Pacific oyster *Crassostrea gigas*.

	Effect	Reference
Increased habitat heterogeneity	+	(Gutiérrez et al., 2003)
Shoreline stabilization	+	(Dame and Patten, 1981; Walles et al., 2014)
Increased species diversity and abundance	+/-	(Meyer and Townsend, 2000; Peterson et al., 2003)
Filtering	-	(Smaal et al., 2013)
Shift in benthic community	+/-	(Diederich, 2006; Smaal et al., 2005)
Food availability to higher tropic levels	+/-	(Kochmann et al., 2008; Markert et al., 2013; Zee et al., 2012)

6.4.4 Practical implications

Oyster reefs can locally protect tidal flats and shorelines against erosion. However, taking the optimal niche of the oyster *C. gigas* into account, i.e. low in the intertidal zone (Chapter 4), as well as the size of the area protected by oyster reefs (Chapter 2), reefs do not have a direct effect on the dikes in the Oosterschelde. The presence of oyster reefs on tidal flats will therefore not impact the design of dikes. They can however be used to locally limit coastal erosion by protecting intertidal flats and salt marshes. The placement of reefs in the intertidal area is important. When placed low in the intertidal, oyster reefs can potentially influence and protect a much larger area at their lee side compared to reefs high in the intertidal. As a result, shoreline growth can be promoted and valuable shallow habitat (e.g. seagrass beds) created between the reef structure and the shoreline (Figure 6.1). A similar idea has been demonstrated with a breakwater of 60 m in front of a mangrove habitat (Kamali and Hashim, 2011). The breakwater enhanced sediment deposition behind the structure, increasing the bed level and creating calm conditions, allowing natural mangrove outgrow without planting (Kamali and Hashim, 2011; Kamali et al., 2010).

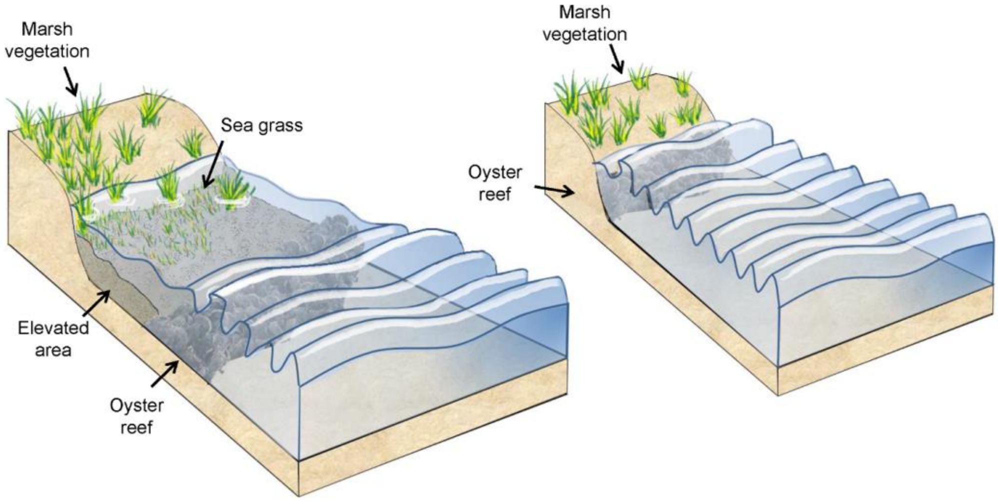

Figure 6.1. Oyster reefs placed somewhat more seawards to promote shoreline growth. Left: Oyster reef placed at some distance from the shoreline. The reef enhances sediment deposition, increasing the bed level. Changing the bed level could create a zone between the reef and the shoreline, where shoreline growth is promoted and valuable shallow habitat is created (e.g. seagrasses). Right: Oyster reef at the edge of marsh vegetation as breakwater to prevent shoreline erosion.

When using *C. gigas* reefs for coastal mitigation, the receiving ecosystem should be taken into account. As *C. gigas* is already cultivated at a large scale in the Oosterschelde estuary addition of a few hectares of oyster reefs for coastal defence does not have large impacts on the ecology of this estuary. Carrying capacity of this estuary however, should be taken into account when determining the amount of reefs which can be used for coastal defence. Shells used for the construction of these reefs can be harvested from locations were they form a plague at present, such as beaches used for recreation. As no native mussel beds exist anymore in the Oosterschelde estuary oyster reefs increased habitat heterogeneity in the intertidal. The use of *C. gigas* reefs for coastal mitigation in the Wadden Sea however, is a different story. In the Wadden Sea *C. gigas* reefs are present in the intertidal, but the species is not cultured here. When oyster reefs are constructed here, the effect of the receiving ecosystem should be evaluated, e.g. the possible effect on the native mussel beds through increased recruitment events of the oysters. This, in turn, can impact higher trophic levels (e.g. birds) which are dependent on mussel beds as a food source. When constructing oyster reefs in the Wadden Sea, shell material should come from the Wadden Sea and not from other areas, to avoid introduction of new species, new diseases and/or predators into this system.

6.5 Main conclusions

Reef building is essential to the maintenance of oyster populations. Accumulation of shell material, through recruitment and growth, provides substrate for new generations (positive feedback loop), contributing to the self-sustainability of a reef structure. Reef accretion rates in the Oosterschelde indicate that oyster reefs in this system are able to both grow and persist over time periods of decades. Reef development is however strongly dependent on the local environmental conditions with tidal exposure governing oyster recruitment, survival and growth dynamics. Providing a suitable substrate for oysters to settle on (below 50% exposure time) offers a kick-start for establishment at places where they were lost or are desirable for coastal protection. At the right conditions, artificial oyster reefs developed into self-sustaining, natural reefs, making them suitable ecosystem-based coastal protection structures. Furthermore, as ecosystem engineer, *Crassostrea gigas* affects tidal flat morphology under its footprint as well as beyond the boundary of their reef structures. This spatially extended ecosystem engineering effect contribute to the protection of tidal flats which add to coastal defence schemes.

CHAPTER 6

Summary

English - Dutch

Summary

Coastal zones are amongst the most extreme, dynamic and complex ecosystems. A wide range of different habitats can be found in the coastal zone, such as sandy and rocky shores, mangroves and salt marshes, coastal wetlands, intertidal areas, sand and mudflats, biogenic reefs (corals, oysters, etc.), shallow inlets and bays. Many of the species inhabiting coastal habitats are considered ecosystem engineers, as they modify their environment and often determine spatial structuring in ecosystems. Autogenic structuring ecosystem engineers, such as salt marsh plants and oyster reefs, typically reduce wave energy and tidal currents, and by doing so reduce erosion, maintaining or increasing the surface elevation of the substrate. These habitats and species provide a wide variety of ecosystem services, such as shoreline stabilization, nutrient cycling, carbon sequestration, detoxification of polluted waters and the supply for food and energy resources.

Coastal areas are rapidly degrading under pressure caused by humans. Global-scale climate changes threaten coastal ecosystems even further through global warming, diseases, ocean acidification, increased storminess and sea level rise. Addressing the additional stress of climate change may require new approaches to managing land, water, waste, and ecosystems. Coastal protection traditionally consists of man-made structures armouring the land-water interface by building dikes, breakwaters, revetments, floodgates, etc. Although engineered solutions are needed and essential in some context, they can be costly to build and maintain. These structures may also have negative side-effect, such as reducing the ability of the shoreline to respond to natural forces needed to build up the shoreline, enhanced erosion, degraded water quality, etc. Over the past decade a paradigm shift to a more ecosystem-based coastal protection occurred, incorporating ‘soft’ defence structures such as dunes, mangroves, marshes, seagrass beds, and bivalve and coral reefs. These species are known as ecosystem engineers. Ecosystem engineering organisms can temper extreme environments, as they attenuate waves and reduce coastal erosion. Approaches and tools for evaluating potential role and context-dependent aspects of natural defence mechanisms however, are lagging behind those for hardenings shorelines. Incorporating ‘soft’ defence structures requires knowledge on where habitats reduce exposure to erosion and provide protection, as well as ecological data, such as species’ habitat requirements, life cycle, population dynamics and long-term persistence to identify where habitats can be successfully implemented. Bivalve reefs and salt marsh plants are ecosystem engineers who are increasingly recognized as ecosystem-based coastal protection and conservation structures in soft sediment environments. The use of ecosystem engineers is based on the natural capacity of the organisms to temper wave action and prevent shoreline erosion, combined with the potential to maintain their own habitat. This adaptive capacity secures the long-term sustainability of ecosystem-based coastal protection, especially in light of accelerating sea level rise. Results presented in this thesis aim at a better understanding of the ecosystem engineering capacity of the oyster *Crassostrea gigas* in soft-sediment environments.

As a model system, tidal flats and oyster reefs are studied in the Oosterschelde (SW Netherlands). This system is experiencing rapid erosion of tidal flats due to significant modifications to the Oosterschelde basin by the so-called Delta works. These modifications resulted in a decrease in the tidal prism, the tidal range and the tidal currents resulting in a reduction of the deposition processes at the intertidal flats, while the eroding processes by locally generated waves were not

changed. Sediment erodes from the tidal flats into the channels during storms, whereas tidal forces are too small to redistribute the sediment back to the tidal flats. On average a net erosion rate of 10 mm year^{-1} on the tidal flats has been observed. The oyster *Crassostrea gigas* was introduced by fishermen in the Oosterschelde in 1964, after which the species rapidly spread throughout the estuary and is occupying nowadays about 8% of the tidal flats (9 km^2). Until recently, C. gigas populations in the Oosterschelde were experiencing low pressure from bioeroders, predators and diseases. Within the framework of the innovation programme Building with Nature (BwN, www.ecoshape.nl), large scale experiments with constructed oyster reefs were executed to evaluate their contribution to mitigate the erosion of tidal flats in the Oosterschelde. This thesis is part of the BwN programme and focuses both on natural and artificially constructed oyster reefs in the Oosterschelde. Oyster performance, reef development, as well as the ecosystem engineering effect of the oyster on tidal flat morphology were studied in an integrated way. In this way this thesis aims to provide fundamental insights in the conditions under which oyster reefs may be valuable for coastal protection, including long-term dynamics (i.e. reef persistence).

Ecosystem engineers that inhabit coastal and estuarine environments, such as reef building oysters, do not only stabilise the sediment within their reefs, but their influence might also extend far outside their reefs, affecting tidal flat morphology and protecting the surrounding soft-sediment environment against erosion. In **Chapter 2**, the elevation around eleven natural *Crassostrea gigas* reefs was measured in the Oosterschelde to quantify the spatially extended ecosystem engineering effect of Pacific oyster reefs on tidal flat morphology. Measurements were used to create 3-dimensional surface maps to obtain properties of the reefs and the surrounding soft-sediment environment. Various reef sizes were chosen to test the proportional effects of reefs on tidal flat morphology. The area of the oyster reefs ranged from 2 m^2 to 1908 m^2. Reef length varied between 1 and 61 m, reef width between 1 and 45 m, and reef height between 0.20 and 1.08 m. Elevated areas (>5 cm elevation from the background intertidal slope) were observed on the lee side of all reefs, caused by the interaction between the reef's structure and locally prevailing wave conditions. The elevated area (i.e. the spatially extended ecosystem engineering effect) affected by the reef was of the same order of magnitude as the reef area, extending to 75 m behind a 61 m long reef. The elevated area was related to reef properties such as reef length, width, and height. Reef length however, appeared to be the best predictor. Directional spreading and diffraction of waves were the mechanisms identified shaping the deposition area behind these reefs. Directional spreading is important for small and large reefs, whereas diffraction is mainly an edge effect and therefore only important for small reefs. For longer reefs, wave dissipation is expected to determine the scale of the influenced area, in which case reef height will become the best predictor for the size of the influenced area, as reef height influences the period in which waves are dissipated. Oyster reefs not only protect the tidal flat under their footprint, but as well an area beyond the boundary of the reef.

The gregarious settlement behaviour of oysters and production of shell substrate (positive engineering feedback) are keys to the long-term persistence of oyster reefs. In **Chapter 3** the population demography of *Crassostrea gigas* is described based upon three long-living *C. gigas* reefs (>30 years old), which have not been exploited or disturbed since their first occurrence in the Oosterschelde estuary. Oysters in the Oosterschelde estuary reach at least an age of 6 years, in which they grow to an average shell length of 170 mm. The demography study was used to estimate vertical reef accretion rates and carbonate production in these oyster reefs. The estimated accretion rates were validated in the field by excavating the entire vertical profile of the three oyster reefs. The observed accretion rates (7.0-16.9 mm year^{-1} shell material) indicate that these reefs are able to both grow and persist over time periods of decades, making them suitable for ecosystem-based coastal protection structures. Oysters in the Chesapeake Bay for comparison, rarely exceeding 4 years of age due to diseases affecting reef dynamics, which affects the growth and persistence of reefs in these areas. The results from the modelling approach, subsequently validated by field observations, provide the basis for a better understanding of growth and mortality processes contributing to vertical reef accretion and reef persistence in bivalve reefs in general. In a larger context, the results provide a framework to predict reef accretion and population persistence in the future under varying recruitment, growth and mortality scenarios (e.g. as a result of increased predation or diseases). The framework to predict reef accretion under varying scenarios has important implications for practical management of oyster reefs. Oyster reefs targeted as ecosystem-based coastal protection structures should be protected from destructive harvest in order to maintain their structure and accrete at the pass of sea level rise. As harvesting of only certain year classes already has significant effects on the rate at which reefs accrete harvesting activities should be restricted to a certain level at which the reef structure can still accretes at a desire pace, leaving the structure of the reef intact for coastal protection.

Chapter 4 investigates if reef development is limited by establishment, growth and survival thresholds. Knowledge about these thresholds at various intertidal levels (i.e. along the exposure time gradient) defines the area where optimum growth can be obtained, which can be used to predict where ecosystem engineering oyster reefs can develop and form persistent structures which can be implemented in coastal defence schemes. Natural epibenthic bivalves by nature do not occur randomly over the tidal flats, nor do they cover the entire area. Within estuarine environments biotic and abiotic factors alter demographic rates and may affect the development and persistence of marine populations. To understand reef development, the response of different life-history stages was investigated along an exposure gradient during a manipulative field study. The number of juvenile oysters showed an optimum around 36 % exposure time. Shell growth of both juvenile and adult oysters was negatively related with exposure time. Overall condition index of adult oysters was highest around 20 % exposure time. Above 40 – 50 % exposure time condition index of oysters decreased compared to their condition at the start of the study. Oysters still show shell growth above 50 % exposure time, but shell growth and meat content were both lower at long exposure times indicating that oysters had reallocated energy away from growth under these environmental conditions. This did not result in an increase in mortality during the course of the experiment as mortality increased towards the less exposed sites. In contrast, winter mortality among juvenile oysters exponentially increased towards the longer exposed locations. Overall, adult and juvenile oysters differ in their response to the same response variable. According to recruitment, growth rates and condition index of oysters, reefs could develop in the lower intertidal. Providing a suitable substrate for oysters to settle on offers a kick-start for establishment at places where they were lost or are desirable for coastal protection.

Reef building is essential to the maintenance of oyster populations as the accumulation of shell material, through recruitment and growth, provides substrate for new generations (positive feedback loop), forming a self-sustainable structure. In **Chapter 5** it was tested under which conditions artificially constructed oyster reefs have the potential to become long-persisting, self-sustaining structures. Within the innovation program Building with Nature three-dimensional artificial oyster reefs were constructed for mitigating the erosion and for the conservation of ecological services of eroding tidal flats in the Oosterschelde estuary (the Netherlands). Recruitment, survival, growth rates and conditions index of oysters on the artificial reefs were compared to recruitment, survival, growth rates and condition index at natural Pacific oyster reefs. The results of this study showed that persistence of the reef was strongly dependent on the local environmental conditions where the reefs were constructed, with tidal exposure and sediment dynamics governing oyster recruitment, survival and growth dynamics. More recruitment was observed on the natural reefs, compared to the artificial reefs. Recruitment as well as the shell length of recruits, shell growth of adult oysters and condition index was negatively correlated with the height in the intertidal zone. Oysters on artificial reefs located above and around 33 % exposure time show a lower condition index compared to oysters on the artificial reef below 33 % exposure time. Shell length of oysters on the artificial reefs are comparable to shell lengths observed on natural reefs. Therefore a vertical accretion rate in the order of 7.0 to 16.9 mm year^{-1} is expected, indicating that reefs are able to grow and maintain themselves. Sedimentation, diseases and predation are however a potential threat which could reduce vertical accretion rates. At the right conditions, artificial oyster reefs can develop into self-sustaining, natural reefs and add to coastal defence schemes. At other sites, smothering with sediment due to local sediment dynamics or a too long emersion time hamper the development of persistent oyster reefs. This study provides insights in the thresholds for establishment and long-term resilience of oyster reefs and adds to a better mechanistic understanding of these ecosystems in space and time. Regular monitoring and evaluation are necessary to measure their effectiveness.

Although oyster reefs can stabilize intertidal areas against erosion, as was demonstrated for the Oosterschelde case, they will not have a direct effect on protecting the dikes due to their location in the low intertidal as well as the size of the area protected by oyster reefs. They can however be used to limit coastal erosion by protecting intertidal flats and salt marshes, which in turn act as buffering habitats for the hinterland. When used for coastal protection, the exact placement of reefs in the intertidal area is important. Oyster reefs can potentially influence and protect a much larger area at their lee side due to their spatially extended ecosystem engineering effect. By doing so, they can facilitate or support the growth of other structuring ecosystem engineers (seagrasses, salt marsh plants) higher up in the intertidal zone. The spatially extended ecosystem engineering effect should be taken into account to optimize their use in coastal protection. As *C. gigas* is a non-native species to many ecosystems world-wide the ecological impact of *C. gigas* should be taken into account before implementing them in coastal defence schemes (**Chapter 6**).

Samenvatting

Kustzones behoren tot één van de meest extreme, dynamische en complexe ecosystemen. De kustzone bestaat uit een grote verscheidenheid aan habitats, zoals zand- en rotskusten, mangroves, schorren, wetlands, intergetijdengebieden, zand- en slikplaten, riffen (koraal, oesters, etc.), ondiepe inhammen, kreken en baaien. Een groot aantal soorten, levend in kusthabitats, kunnen beschouwd worden als biobouwers, omdat ze hun omgeving veranderen en vaak de ruimtelijke structuur van het ecosysteem beïnvloeden. Fysische biobouwers, zoals schorreplanten en oesterriffen, reduceren golfenergie en de stroomsnelheid, wat leidt tot een verminderde erosie. Dit resulteert in het behoud of zelfs een verhoging van het omliggende substraat. Deze habitats en diersoorten dragen bij aan diverse ecosysteemdiensten, zoals stabilisatie van de kustlijn, nutriëntcyclering, vastleggen van koolstof, zuiveren van afvalwater en voedsel- en energievoorziening.

Kustgebieden degraderen in een snel tempo door de toenemende druk van de mens. Wereldwijde klimaatveranderingen versterken de degradatie van deze kustgebieden door het broeikaseffect, ziektes, verzuring van de oceaan, toenemende stormintensiteit en zeespiegelstijging. Wanneer de toenemende stress door klimaatsveranderingen in acht genomen wordt, vraagt het managen van land, water, afval en ecosystemen om nieuwe benaderingen. Kustverdediging bestaat traditioneel uit het kunstmatig beschermen van de kustlijn door het bouwen van dijken, golfbrekers, revetments, dammen, enz. Hoewel deze oplossingen in sommige situaties essentieel zijn, is de aanleg en onderhoudt duur. Daarnaast kunnen deze verdedigingswerken ook negatieve neveneffecten hebben, zoals een afname van natuurlijke processen welke nodig zijn voor de opbouw van de kustlijn, versterkte erosie, verslechterde waterkwaliteit, enz. In het afgelopen decennium is er een verschuiving gaande naar een meer ecosysteem gebaseerde kustverdediging met integratie van natuurlijke verdedigingsstructuren zoals duinen, mangroves, schorren, zeegras bedden, schelpdier- en koraalriffen. Deze soorten staan bekend als biobouwers. Biobouwers kunnen extreme omgevingen temperen door bijvoorbeeld golven te remmen en kusterosie te verminderen. De evaluatie van de potentiële rol en context-afhankelijke aspecten van natuurlijke verdedigingsstructuren lopen echter achter op die van kunstmatige verdedigingswerken. Het toepassen van natuurlijke verdedigingsstructuren vereist kennis over: waar deze habitats erosie verminderen en bescherming bieden; evenals ecologische gegevens, zoals soortafhankelijke habitatseisen, levenscyclus, populatiedynamiek en lange-termijn persistentie. Dit laatste kan gebruikt worden om plaatsen te identificeren waar habitats succesvol geïmplementeerd kunnen worden. Schelpdierriffen en schorreplanten zijn biobouwers die steeds meer erkend worden als structuren die bijdragen aan kustbescherming en het behoud van estuarien intergetijdesediment. Het gebruik van deze biobouwers is gebaseerd op hun natuurlijke capaciteit om de impact van golven te minderen en kustlijnerosie te voorkomen, in combinatie met de potentie om hun eigen habitat te onderhouden. Deze aanpassingscapaciteiten verzekeren de duurzaamheid van deze ecosysteem gebaseerde kustbescherming op lange termijn. Vooral onder druk van versnellende zeespiegelstijging. Resultaten in deze thesis dragen bij aan kennis over de biobouwerscapaciteit van de oester *Crassostrea gigas* in estuarien intergetijdesediment.

Intergetijdengebieden en oesterriffen zijn bestudeerd in de Oosterschelde (SW Nederland), welke dient als modelsysteem. In dit systeem eroderen getijdengebieden in een rap tempo als gevolg van significante wijzigingen aan het Oosterschelde bekken door de Deltawerken. Deze wijzigingen resulteerden in een daling van het getijdeprisma, het getijdeverschil en de getijdestroming, wat resulteert in een vermindering van depositieprocessen in de intergetijdengebieden, terwijl de eroderende processen door lokaal gegenereerde golven niet gewijzigd zijn. Tijdens stormen erodeerd sediment van de intergetijdengebieden richting de geulen, terwijl getijdenkrachten te klein zijn om het sediment terug te verplaatsen van de geulen naar de getijdengebieden. Gemiddeld is er een netto erosie van 10 mm per jaar geobserveerd op de getijdenplaten. In 1964 introduceerde vissers de oester *Crassostrea gigas* in de Oosterschelde. Hierna vond een snelle verspreiding plaats. Momenteel wordt ongeveer 8 procent van de intergetijdengebieden (9 km^2) bedekt met natuurlijke oesterriffen. Tot voor kort ondervond de *C. gigas* populaties weinig stress in de Oosterschelde door bio-eroders, predators en ziekten. Binnen het kader van het innovatie programma Building with Nature (BwN, www.ecoshape.nl) zijn grootschalige experimenten uitgevoerd met kunstmatige oesterriffen om te evalueren wat hun bijdrage is in het beperken van de erosie van intergetijdengebieden in de Oosterschelde. Dit proefschrift is onderdeel van het BwN programma en richt zich zowel op natuurlijke als kunstmatig oesterriffen in de Oosterschelde. De conditie van de oesters, rifontwikkeling, evenals het effect van de oester als biobouwer op de morfologie van intergetijdengebieden is op een geïntegreerde wijze bestudeerd. Op deze manier draagt dit proefschrift bij aan fundamentele inzichten in de voorwaarden waaronder oesterriffen een waardevol bijdrage kunnen leveren voor kustbescherming, inclusief inzicht in lange-termijn dynamieken (rif persistentie).

Biobouwers in kustgebieden en estuaria, zoals rifvormende oesters, stabiliseren niet alleen het sediment binnenin het rif, maar kunnen ook ver buiten het rif de morfologie van de intergetijdengebieden beïnvloeden en bescherming bieden tegen erosie. In **Hoofdstuk 2** is de topografie rondom elf natuurlijke *C. gigas* riffen in de Oosterschelde gemeten om het ruimtelijk effect van oesterriffen op de morfologie van intergetijdengebieden te kwantificeren. Deze metingen werden gebruikt om 3-dimensionale oppervlaktekaarten te maken waaruit rifeigenschappen en informatie over de omringende morfologie was verkregen. Riffen van verschillende afmetingen waren gekozen voor het bestuderen van proportionele effecten van de riffen op de morfologie. Het oppervlak van de oesterriffen varieerde van 2 m^2 tot 1908 m^2. Riflengte varieerde tussen de 1 en 61 m, rifbreedte tussen 1 en 45 m, en rifhoogte tussen 0.20 en 1,08 m. Aan de lijkant van alle riffen werd een verhoogd gebied (> 5 cm verhoogt ten opzichte van de helling van de intergetijdenplaat, achtergrondwaarde) waargenomen als gevolg van de interactie tussen de structuur van het rif en lokaal golfcondities. Het oppervlak van het verhoogde gebied was in dezelfde orde van grootte als het oppervlak van het rif en reikte tot een afstand van 75 m achter een 61 m lang rif. Het verhoogde oppervlak was gerelateerd aan rifeigenschappen zoals riflengte, breedte en hoogte. Riflengte bleek echter de beste voorspeller van het beïnvloede gebied te zijn. Directionele verspreiding en diffractie van golven waren geïdentificeerd als de mechanismen die de vorm van het depositiegebied achter deze riffen beïnvloeden. Directionele verspreiding is belangrijk voor kleine en grote riffen, terwijl diffractie voornamelijk een randeffect is en daarom alleen belangrijk bij kleine riffen. Voor langere riffen is het verwacht dat golfdissipatie de grootte van het beïnvloede gebied bepaalt, in welk geval rif hoogte de beste voorspeller zal zijn, omdat rifhoogte de periode bepaalde waarover golven dissipatie ondervinden. Oesterriffen beschermen niet allen het intergetijdengebied onder hun voetafdruk, maar ook een gebied ver buiten de grenzen van het rif.

Het vestigen in groepen evenals de productie van schelpsubstraat (positieve engineeringsfeedback) zijn belangrijk voor de persistentie van oesterriffen op lange termijn. In

Hoofdstuk 3 wordt de populatie dynamiek van *C. gigas* beschreven aan de hand van drie oude riffen (ouder dan 30 jaar), welke niet bevist of verstoord zijn sinds hun ontstaan in de Oosterschelde. Oesters in de Oosterschelde bereiken ten minste een leeftijd van 6 jaar, waarin ze tot een gemiddeld schelplengte van 170 mm uitgroeien. Aan de hand van een demografie studie zijn verticale groeisnelheden en carbonaat productie van riffen geschat. De geschatte groeisnelheden ware gevalideerd in het veld door het hele verticale profiel van 3 oesterriffen uit te graven. De geobserveerde groeisnelheden (7.0-16.9 mm jaar^{-1} schelpmateriaal) geven aan dat deze riffen in staat zijn om te groeien en persistent zijn over decennia's. Dit maakt ze geschikt als ecologische kustbeschermingsstructuren. Oesters in de Chesapeake Bay ter vergelijking, worden zelden ouder dan 4 jaar door ziektes. Dit beïnvloed de rifdynamiek, welke de groei en persistentie van riffen in dit gebied reduceren. De resultaten van deze modelbenadering, gevalideerd door veldobservaties vormen een basis voor het beter begrijpen van de bijdrage van groei- en mortaliteitsprocessen aan verticale rif groei en persistentie van schelpdierriffen in het algemeen. In een bredere context bieden de resultaten een kader om rifgroei en populatie persistentie te voorspellen in de toekomst onder verschillende vestigings-, groei- en mortaliteitscenario's (bijvoorbeeld als gevolg toenemende predatie of ziekten). De mogelijkheid om rifgroei onder verschillende scenario's te voorspellen is belangrijk voor het managen van oesterriffen. Oesterriffen bedoeld als natuurlijke kustverdediging moeten beschermd worden tegen destructieve oogst zodat hun structuur behouden blijft en ze mee kunnen groeien met zeespiegelstijging. Omdat oogst van een bepaalde leeftijd al significant effect heeft op de groeisnelheid van een rif moet er een restrictie zijn op het aantal te oogsten oesters zodat de rifstructuur kan groeien en behouden blijven voor kustverdediging.

In **Hoofdstuk 4** is bestudeerd of rifontwikkeling gelimiteerd is door vestiging-, groei- en overleving. Kennis van deze processen over een intergetijdengradient (droogvalduurgradient) draagt bij aan het definiëren van het gebied van optimale groei. Aan de hand hiervan kan voorspelt worden waar oesterriffen zich ontwikkelen tot persistente structuren die bijdragen aan kustbescherming. Schelpdierriffen komen van naturen niet random voor op intergetijdengebieden, noch bedekken ze het hele gebied. Biotische en abiotische factoren binnen een estuaria veranderen demografische waarden, welke de ontwikkeling en persistentie van marine populaties beïnvloeden. Om meer inzicht te krijgen in rifontwikkeling is de reactie van verschillende levensstadiums over een droogvalduurgradient bestudeerd tijdens een manipulatieve studie. Vestiging van juveniele oesters heeft een optimum rond 36 % droogvalduur. Schelpgroei van juveniele en volwassen oester was negatieve gerelateerd aan droogvalduur. De conditie index van volwassen oesters was het hoogst rond 20 % droogvalduur. Boven een droogvalduur van 40 – 50 % name de conditie index van oesters af in vergelijking met de conditie aan het begin van het experiment. Oesters laten echter nog steeds schelpgroei zien boven 50 % droogvalduur. Schelpgroei en vleesinhoud waren beiden lager bij een langere droogvalduur wat aangeeft dat energie voor andere doeleinden dan groei gebruikt werd onder deze omstandigheden. Dit resulteerde niet tot een toename van mortaliteit tijdens het experiment. Mortaliteit onder volwassen oesters nam toe met afnemende droogvalduur. Wintermortaliteit onder juveniele oester in tegenstelling, nam exponentieel toe bij toenemende droogvalduur. Volwassen en juveniele oesters verschillen in hun reactie op dezelfde omgevingsvariabelen. Vestiging, groeisnelheden en de conditie index van oesters laten zien dat riffen kunnen ontwikkelen laag in het intergetijdengebied. Het aanleggen van geschrikt substraat voor oesters werkt als een kick-start voor rifontwikkeling op plaatsen waar ze waren verdwenen of gewenst zijn voor kustverdediging.

Rifopbouw is essentieel voor het behoud van oesterpopulaties, omdat de accumulatie van schelpmateriaal door vestiging en groei, substraat creëert voor nieuwe generaties (positieve feedback) wat resulteert in een zelfonderhoudende structuur. In **Hoofdstuk 5** werd getest onder welke omstandigheden kunstmatige oesterrriffen de potentie hebben om persistente, zelfonderhoudende structuren te worden. Binnen het innovatie project Building with Nature zijn driedimensionale kunstmatige oesterriffen aangelegd om erosie te beperken en de ecologische functie van de intergetijdengebieden in de Oosterschelde te behouden. Vestiging, overleving, groei en de conditie index van oesters op kunstmatige riffen werden vergeleken met de vestiging, overleving, groei en de conditie index van oesters op natuurlijke Japanse oesterriffen. Resultaten van deze studie laten zien dat persistentie van riffen sterk afhankelijk is van lokale condities. Droogvalduur en sediment dynamiek beïnvloeden vestiging, overleving en groei dynamieken. Een hogere vestiging was geobserveerd op de natuurlijke riffen vergeleken met de kunstmatige riffen. Vestiging van de juveniele oesters en hun schelplengte, evenals schelpgroei en conditie index van volwassen oesters was negatief gecorreleerd met de hoogte in het intergetij. Oesters op de kunstmatige riffen lieten een lagere conditie zien bij een droogvalduur van 33% of hoger vergeleken met oesters bij een droogvalduur lager dan 33%. Schelplengtes van oesters op de kunstmatige riffen waren vergelijkbaar met schelplengtes geobserveerd op de natuurlijke riffen. Hierdoor is de verticale groei in de orde van 7.0 tot 16.9 mm per jaar geschat, wat laat zien dat de riffen in staat zijn te groeien en zich zelf te onderhouden. Sedimentatie, ziekten en predatie zijn echter een potentiele bedreiging en kunnen verticale rifgroei reduceren. Onder de juiste omstandigheden kunnen kunstmatige riffen zich ontwikkelen in zelfvoorzienende riffen die bijdrage aan kustverdediging. Rifontwikkeling en persistentie kan belemmerd worden door te lange droogvalduur of door verstikking als gevolg van lokale sediment dynamieken. Deze studie biedt waardevolle inzichten in de vestiging van oesterriffen en de veerkracht van oesterriffen op lange-termijn. Dit draagt bij aan het beter begrijpen van de mechanismen achter dit ecosysteem in ruimte en tijd. Regelmatige monitoring en evalueren is echter wel nodig om hun effectiviteit te meten.

Hoewel oesterriffen intergetijdengebieden kunnen stabiliseren en beschermen tegen erosie, zoals gedemonstreerd in de Oosterschelde, bieden ze geen bescherming voor dijken. Door hun lage ligging in het intergetij beïnvloeden ze maar een beperkt gebied. Ze kunnen echter wel gebruikt worden om kusterosie te reduceren door intergetijdengebieden en schorren te beschermen, die op hun beurt een buffer vormen voor het achterland. Bij het gebruik van oesterriffen voor kustverdediging is de exacte plaats op het intergetij belangrijk. Oesterriffen kunnen een groter gebied beschermen en beïnvloeden aan de lijzijde van het rif. Hierdoor kunnen ze groei van andere structuur vormende biobouwers (zeegrassen, schorreplanten) hoger in het intergetij faciliteren. Om optimaal gebruik te maken van biobouwers voor kustbescherming moet rekening gehouden worden met hun ruimtelijke effect. Omdat *C. gigas* voor vele ecosystemen in de wereld een invasieve soort is, moet rekening gehouden worden met de ecologische impact van *C. gigas* voordat ze geïmplementeerd kunnen worden voor kustverdediging (**Hoofdstuk 6**).

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About the author

Brenda Walles was born in Emmen, the Netherlands, on January 19th, 1985. Her scientific career began in 2004, when she started with the bachelor Soil, Water and Atmosphere at Wageningen University (the Netherlands), followed by the Master Hydrology and Water Quality, both with the specialization Aquatic Ecology and Water Quality Management. Driven by her enthusiasm for the marine environment, she performed her MSc-internship at New Zealand's Institute of Water and Atmospheric Research (NIWA) in Hamilton (New Zealand), studying genetic variation in tolerance and resilience to the stressor anoxia in the cockle *Austrovenus stutchburyi*. She finished her studies with a MSc-thesis at the Centre for Estuarine and Marine Ecology of the Netherlands Institute of Ecology (NIOO-CEME) in Yerseke (the Netherlands) studying predator induced differences in byssal thread production and cluster formation of the blue mussel, *Mytilus edulis*. She graduated in 2009, after which she directly started in a PhD position. The PhD study was carried out at the Institute for Marine Resources and Ecosystem Studies (IMARES) in Yerseke. The PhD is part of the innovative program Building with Nature. The practical goal of this project was to investigate the role of the ecosystem engineering oyster *Crassostrea gigas* in coastal protection. During this time, she successfully presented her research at international conferences, and published in peer-reviewed journals. She was awarded with the 1st place in the student competition at the Deltas in time of climate change II conference in 2014 (Rotterdam, the Netherlands), with her presentation on the role of biogenic reefs for coastal adaptation and conservation; the 3th place in the student competition at the European Marine Biology Symposium in 2013 (Galway, Ireland), with her presentation on scale-dependent effect of the ecosystem engineer *Crassostrea gigas* on tidal flat morphology; and the 1st place at the IMARES PhD day in 2011 (Texel, the Netherlands) with her presentation on controlling algal fouling on intertidal artificial oyster reefs using periwinkles (*Littorina littorea,* Gastropoda). During the PhD she visit Virginias Institute of Marine Science (VIMS) in the USA. The current thesis is the result of this PhD project.

From the 1st of July, 2015 Brenda will start working as post-doctoral researcher within the project EMERGO (Eco-morphological functioning and management of tidal flats) stationed at the NIOZ in Yerseke.

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WIAS Training & Supervision Plan

Education and training	**ECTS**
The basic package	**3.0**
WIAS introduction course	
Ethics & philosophy in aquatic life science	
Scientific exposure	**15.8**
BwN workshop: Physical scale interactions 2009, Dordrecht, the Netherlands	
BwN launching event 2010, Dordrecht, the Netherlands	
NCK-days 2010, West Kapelle, the Netherlands (poster presentation)	
WIAS science day 2011, Wageningen, the Netherlands (poster presentation)	
Vliz young scientists' day 2011, Gent, Belgium (oral presentation)	
Benthic Ecology Meeting 2011, Mobile, USA (oral & poster presentation)	
BwN midterm conference 2011, Dordrecht, the Netherlands (oral presentation)	
International Conference on Shellfish Restoration 2011, Stirling, Scotland (oral presentation)	
IMARES PhD day 2011, Texel, the Netherlands (oral presentation)	
Benthic Ecology Meeting 2012, Norfolk, USA (oral presentation)	
IMARES PhD day 2012, Texel, the Netherlands (oral presentation)	
European Marine Biology Symposium 2013, Galway, Ireland (oral presentation)	
NCK-Thema day: Een veranderde Oosterschelde 2013, the Netherlands (oral presentation)	
96th Dies natalis WUR 2014, Wageningen, the Netherlands (oral presentation)	
In-depth studies	**5.5**
Estuarine ecology 2010, Yerseke, the Netherlands	
Spatial ecology 2011, Elst, the Netherlands	
Design of experiments 2010, Wageningen, the Netherlands	
Dicussion group Yerseke	
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Writing and presenting scientific papers	
Conversation skills in one-to-one guidance	
Job assessment	
Teaching and supervising Thesis students	
Lecturing	
Theatre skills and oral presentation	
Didactic & research skills training	**16.1**
Preparing own research proposal	
External training period 2012 at VIMS, USA	
Introduction into R	
Guest lectures & field excursions for HZ, HAS and WUR	
BwN course, supervising field practical	
Supervising 2 MSc major students	
Supervising 6 BSc minor students	
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NOTES

NOTES

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