# Changing interactions in the Wadden Sea

***A literature study on the dynamics of the Wadden Sea ecosystem***

*Mussel bed near the island of Schiermonnikoog, the Netherlands, 2009  Foto: R. Fokkema*


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# Summary

The Wadden Sea is one of the largest intertidal ecosystems on earth. Situated along the coasts of the Netherlands, Germany and Denmark the area has shared a unique connection with early human development. Anthropogenic influences as exploitation and habitat change have started to affect ecological processes and species composition within the Wadden Sea from very early on. These effects especially intensified during the last half of the previous century. Resulting in the loss of many indigenous species of which several ecosystem engineers.

Ecosystem engineers create suitable living conditions for many associated species and are associated with unique ecological processes. Before 1900 four types of habitat could be distinguished in the Wadden Sea. The bare tidal flat and habitat provided by three ecosystem engineers. European flat oyster beds (*Ostrea edulis*), Seagrass beds consisting of *Z. noltii* and *Z. marina* and reefs built by colonies of the polychaete *Sabellaria spinulosa*. After the 1900s Oyster beds vanished from the Wadden Sea due to overexploitation. This was followed around the 1920s/1930s by the disappearance of most *Sabellaria* reefs and almost all *Z. marina* based seagrass beds. Both of which could be related to human influences as habitat change by coastal engineering and overexploitation.

The oyster beds were taken over by the Blue mussel (*Mytilus edulis*) that from then on assumed the role as dominant ecosystem engineer. Associated species with Oyster beds, *Sabellaria* reefs and Seagrass beds were lost. Species associated with mussel beds increased in abundance. History repeated itself around the 1990s when a year of low spatfall led to an increase in mussel fishery on intertidal mussel beds resulting in a dramatic decrease in the area of stable littoral mussel beds. Restrictions to mussel fishery on littoral mussel beds have caused fishery to be limited or absent in most parts of the Wadden Sea. This has however not yet resulted in the recovery of stable littoral mussel beds. To determine the causes for this lack of recovery and to find a way to successfully aid in the restoration of mussel beds a large scale project is to be conducted in the Dutch part of the Wadden Sea. The restoration of mussel beds is expected to aid in bringing the whole ecosystem back to a more 'natural' ecological state.

The future of the Wadden Sea area might however not be so bright. It might prove impossible to get the ecosystem in a stable state associated with high biodiversity under the strain of upcoming changes caused by factors like climate change and invading species. One of these invading species the Pacific oyster (*Crassostrea gigas*) is likely to become a dominant ecosystem engineer in the Wadden Sea and might outcompete the Blue mussel (*Mytilus edulis).*

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# Introduction

Situated along the coasts of Denmark, Germany and the Netherlands lies the Wadden Sea, one of earths largest intertidal ecosystems. The Wadden Sea has always been of great national and international importance. In previous times it was mostly valued in an economical sense as a shipping, fishery and recreation area. During the last decades however the area has been increasingly recognized as and area of great ecological importance (Ramsar Convention, Natura 2000, World Herritage Site Status) (Wolff 2000; Olff et al. 2008; Piersma 2007).

Soft sediment systems like the Wadden Sea belong to the most productive natural ecosystems, even compared with those in terrestrial habitats (Piersma 2007). The main cause for this wealth is the continuous supply of nutrients, which makes the water and sediment extremely fertile. Nutrients are provided in two ways. By inflow from the rivers and the surrounding North Sea and secondly by the primary producers. Sunlight can easily reach the phytoplankton and the microphytobenthos in the shallow waters ensuring a high primary productivity. This productivity sustains high biomasses and large numbers of benthic invertebrates. That on their turn serve as an important food-source for species of fish, crustaceans and many breeding and migrating birds (Wolff 2000).

The development of the Wadden Sea cannot be discussed without taking human development into account. Human exploitation of the area has started from very early on and especially in the last few 100 years exploitation has grown to overexploitation in many cases. This together with habitat change and destruction by humans has severely affected the dynamics of the complex ecosystem of the Wadden Sea (Haartsen et al 2001, Piersma 2007, Wolff 2000).

The strong connection between a complex and highly productive ecosystem with human development is what most probably has resulted in the Wadden Sea being one of the most intensively studied areas in the world. At present the number of biological publications on the Wadden Sea area including the terrestrial habitats on the islands and the main coast is close to 10.000. The oldest publications date back to the $18^{th}$ century (Wolff 2000). All the data collected throughout the years and the scientific findings connected to these data has shown us that the dynamics of the Wadden Sea area are indeed very complex.

Throughout the decades several changes in the community composition of the Wadden Sea area have been observed. One of the most prominent changes is the disappearance of many types of ecosystem engineers. Ecosystem engineers are species that create suitable living conditions for themselves and for an often large and diverse amount of associated species. Several of these prominent members of the Wadden Sea ecosystem have now largely vanished in most parts of the area. Including Seagrass beds, European oyster beds, Mussel beds and *Sabellaria* reefs. Resulting in a loss of habitat for many associated species. At present many once indigenous species have vanished and several invading species have settled. Only a handful of species seem to dominate the system. Direct and indirect influences of human activities as exploitation, habitat change, eutrophication, pollution and climate change have shown to be involved in the changing dynamics in the Wadden Sea (Weijerman 2005; Essink 2005; de Vlas et al. 2005; Reise et al. 2005; Vorberg 2005 ).

In recent years actions have been taken in order to restore the biodiversity and natural conditions of the Wadden Sea. For example, detrimental practices like mussel fishery and cockle fishery were restricted or completely banned. These actions have however not yet shown to be effective. It has been hypothesized that this lack of recovery is because the system has collapsed to such an extent that present conditions do not allow the system to return to it's previous state. In order to aid in the recovery of the ecosystem, future actions will be aimed more directly at the restoration of ecosystem engineers like mussel- and seagrass beds. Restoration of such vital parts of the ecosystem is expected to bring the whole ecosystem back to a more 'natural' state. Conditions created by these ecosystem engineers are expected to promote the survival chance and recovery of many species and to restore ecological processes that have vanished (de Vlas et al. 2005; Olff et al. 2008).

In an area of changing dynamics like the Wadden Sea however it remains the question what exactly constitutes as the 'natural' situation. Mussel beds for instance are now seen as an important component of the natural Wadden Sea, but did not occur before the 1900s. The European flat oyster filled in the role of ecosystem engineer at that time. These Oyster beds vanished due to overexploitation around the 1900s and the Blue Mussel took over (Riesen & Reise 1982). Illustrating that what is now regarded as the natural situation in the Wadden Sea has not always been the natural situation. Knowledge of the history of the Wadden Sea and insight in the changing dynamics of the Wadden Sea ecosystem is essential for conservation of the area.

This literature study is aimed at providing an overview of the knowledge gathered about the Wadden Sea during the last 100 years. To answer the question; what are the causes and consequences of changing dynamics in the Wadden Sea ecosystem? Travelling from the natural situation to the current situation and eventually providing a glimpse of what the future situation might be like.

We start with a closer look at the Geological and Cultural history of the Wadden Sea area in chapter 1.1 and 1.2. Followed by a further exploration of the connection between anthropogenic effects and the dynamics of the Wadden Sea ecosystem in chapter 1.3 and 1.4.

Chapter 2 will focus more directly at the ecology of the Wadden Sea. Starting with a general overview of the different functional groups that exist in the Wadden Sea in chapter 2.1. Followed by a more detailed look in chapter 2.2 at the 'natural' situation of the Wadden Sea. Describing four different types of habitat that once existed in the Wadden Sea. The littoral mudflat and habitat created by the presence of three ecosystem engineers. Seagrass beds, *Sabellaria* reefs, and European flat oyster beds. Presenting a detailed description of associated communities and ecological functions. Furthermore the causes and consequences of the disappearance of these ecosystem engineers are discussed.

Chapter 2.3. will discuss the transition of the 'natural' situation to a situation in which Mussel beds dominate the system. Describing the habitat in terms of ecological functions and associated species. Furthermore the causes and consequences of the dramatic decrease of the mussel beds are discussed. In chapter 2.4 the question if the Pacific Oyster will take over the role of the Blue mussel as ecosystem engineer is discussed.

Chapter 3 will focus on the future of the Wadden Sea combining the knowledge about the history and changing dynamics of the Wadden Sea as presented in the previous chapters with existing and upcoming conservation management in the area. To assess the chances for a bright future for the Wadden Sea.

# History of the Wadden Sea area

### 1.1. Recent geological history

In order to fully understand the ecology of the Wadden Sea an exploration of its geological and cultural past is crucial. After the last Ice age the North Sea level rose by around 100m. This caused a rise in the level of fresh groundwater and a zone of peat developed parallel to the coast. Around 5000 BC the straits of Dover flooded. The currents of the North Sea changed and began to run more parallel to the coast. Offshore bars were created which were divided by later breaches by the sea into islands. Between the islands and the peat lands on the main coast an area with gullies, sand bars and salt marshes arose. For the characteristic plant and animal species of the Wadden Sea suitable living conditions have been present since this time (Haartsen & van Marrewijk 2001; Wolff 2000).

### 1.2. Cultural history: urban civilization in the Wadden Sea area

It is not surprising that in this area teeming with life, human settlers found a good place for habitation. Remains of Neolithic settlements(5000-2000 BC) can be found. Settlers adapted to the coastal environment and lived mainly by catching fish and gathering shellfish, but evidence for agricultural settlement has been found as well. Human habitation increased in the period between 500-700BC. In the Roman period(50BC-275AD) the island of Texel and the marsh area along the mainland coast were the most densely populated parts of the Netherlands. The cultural heritage of the Wadden Sea area around that time can be compared with other centres of civilization around that era (Haartsen & van Marrewijk 2001).

Thus in contrast to other wetland areas the impact of urban culture in the Wadden Sea area has always been considerable. Two main anthropogenic effects can be described, exploitation of natural resources and habitat change and destruction (Wolff 2000). These two effects share a strong connection with each other.

### 1.3. From exploitation to overexploitation

As previously mentioned human exploitation of the tidal flat started relatively non-intrusive consisting of small-scale fishing and gathering shellfish by hand. In the 19$^{th}$ century however fishery intensified to such an extent that large top predators as sharks, rays and harbour porpoise started to disappear from the system (Olff et al. 2008; Piersma 2007; Haartsen et al. 2001). Around 1870 this was followed by a dramatic decrease in the yield of the oyster fishery for the European flat oyster (*Ostrea edulis*). The oyster beds never recovered and since the 1920s oyster fishery has been abandoned (Riesen & Reise 1982).

In the second half of the 20$^{th}$ century exploitation further intensified due to an increase in motor power and the use of larger nets and mechanical harvesting techniques. Drediging for cockles(*Cerastoderma edule*) and lugworms(*Arenicola marina*) became a veritable industry around the 1970s/1980s (Olff et al. 2008; Piersma 2007). Around the 1960s a new practice of mussel culture also came into use. Artificial sub tidal mussel beds were created, stocked with seed mussels and dredged out. Around 1990 a shortage of seed mussels, led to an increase in fishery for seed mussels on natural littoral mussel beds and wiped out most of them (de Vlas et al. 2005; Olff et al. 2008; Piersma 2007).

Together with many scientific publications, the demise of littoral mussel beds led to an increased recognition of the detrimental effect of overexploitation. This added to the already increased responsibility to preserve an restore the Wadden Sea by national and international agreements and led to several actions (Olff et al. 2008). Mussel fishery on intertidal beds has been limited or absent due to restrictions since 1990 in the entire Wadden Sea (de Vlas et al. 2005). Followed in 2004 by a ban on Cockle fishery using mechanical harvesting techniques in the Dutch part of the Wadden Sea. Cockle fishery using non-mechanical methods is still allowed. Other fishery for pelagic and demersal fish and shrimp is also still taking place (Olff et al. 2008, de Vlas et al. 2005).

**1.4. Habitat change and destruction**

In the Carolingian era(AD 780-900) people started to open up the peat bogs situated between the marshlands and the higher sandy ground to bring the land into use. Drainage of the peat bogs caused the surface to sink and water became a problem. During heavy storms the sea could penetrate, damaging the area and large areas of the original peat bog were claimed by the sea. Human settlers also made use of dykes to protect themselves from- and to capture land from the sea. The first enclosures of larger areas with dykes date from the 11th century. As in the case with the peat bogs the sea claimed land as well. Poorly maintained dykes and salt mining using salty peat layers were often the cause of large marine incursions. These marine incursions for instance led to the formation of the Zuiderzee and the Dollard in the Netherlands (Haartsen et al. 2001). At the end of the twelfth century most of the mainland was separated from the tidal Wadden Sea by a system of dykes. The large salt marsh areas outside these dykes were gradually turned into farmland.

In recent times entire tidal inlets have been separated from the Wadden Sea, one example is the closure of the Zuiderzee by the Afsluitdijk in 1932. This caused important abiotic changes in the Wadden Sea area. The Zuiderzee is believed to have acted as a major sedimentation area, and the closure of the Zuiderzee must have led to more turbid waters. This increased turbidity is believed to have had an important impact on the failure of eelgrass(*Zostera marina)* to re-establish itself after it had disappeared due to a so called wasting disease in the 1930s. Another effect of the closure of the Zuiderzee lies in changing chemical conditions. The gradual transition between the sea and the land became much more abrupt and the ecological conditions of these different types of waters vanished. Brackish water species were lost (Wolff 2000).

Chemical conditions of the Wadden Sea were also changed due to an intensification in agriculture from the 1950s onwards. The water was increasingly contaminated with nitrogen and phosphate. Probably the entire Wadden Sea has been in an early state of eutrophication since the last two decades. Since the 1990s the water quality has improved. The present eutrophication status of the Wadden Sea is however still about five times higher than the early 1930s (van Beusekom et al. 2005; Olff et al 2008). Other pollutants like heavy metals have also caused significant problems in the twentieth century. Most heavy metals have decreased after a peak around 1970 (Wolff 2000).

Habitat change can also be related to (over)exploitation. The intensification of fishery since the 1950s has had a severe effect on the Wadden Sea. Intrusive techniques like dredging and trawling have caused major disturbance of the sea floor. Causing immediate disturbance of the intertidal biota and increasing the turbidity of the water (Olff et al. 2008; Piersma 2007) The loss and decline of ecosystem engineers as the European flat oyster (*Ostrea edulis)* and the Blue mussel (*Mytilus edulis*) are strongly related to overexploitation. Ecosystem engineers create conditions that are otherwise not found in the ecosystem of the Wadden Sea. Some species are exclusively found on the habitat an ecosystem engineer provides. Exploitation leading to the loss of ecosystem engineers can therefore be regarded as habitat loss (Riesen & Reise 1982; Wolff 2000).

Other changes in ecosystem dynamics due to anthropogenic influences can be related to invading species. Research has shown that for the Dutch Wadden Sea at least 40 species have been introduced. Some of these species were deliberately introduced, like the Pacific oyster (*Crassostrea gigas*). The Pacific oyster was introduced to replace the European flat oyster (*Ostrea edulis*) for oyster farming in 1986 and has drastically increased in the entire Wadden Sea since then (Wolff 2000; Nehls & Büttger 2007). Some researchers believe *Crassostrea gigas* is set to take over the role of the Blue mussel (*Mytilus edulis*) as an ecosystem engineer (Büttger et al 2007).

To summarize human development has had a strong influence on the current condition of the Wadden Sea. The geomorphology of the area has been altered by creating hard instead of gradual transitions between the tidal Wadden Sea and the non titdal land and fresh water areas as well as changing the hydrographical conditions (Wolff 2000). Eutrophication, pollution, overexploitation and the introduction of species contributed most to the chemical and biological changes within the Wadden Sea.

The consequences of these changes on the species composition and ecological functioning of the Wadden Sea will be discussed more in depth in the next chapter. Describing how the Wadden Sea ecosystem has deteriorated during the past century due to mostly human influences.

# 2. Ecology of the Wadden Sea

### 2.1. Functional groups within the Wadden Sea

Several functional groups can be distinguished in the ecosystem of the Wadden Sea. (Fig.1) Primary production is provided by the macrophytobenthos, microphytobenthos and the phytoplankton. The latter two being the main producers. The main consumers of this primary production are the benthic consumers and the zooplankton. Some birds however also feed directly on the macrophytobenthos.

The benthic consumers can be divided into four different feeding groups:

- Suspension feeders that feed by filtering water through their siphons extracting phytoplankton and to a lesser extent zooplankton.
- Detritus feeders that feed on organic material that is deposited on the seafloor.
- Grazers that feed on microphytobenthos and macrophytobenthos.
- Invertebrate predators like crab and shrimp that prey on other benthic consumers, zooplankton and other invertebrate predators.

Besides predation by invertebrate predators, benthic consumers are also preyed upon by fish(pelagic and demersal) and birds(breeding and migratory) Bird species feeding on the tidal flats show a preference for crustaceans, while fish species show a preference for worms (Beukema 1976). The group of fish species once consisted of larger predatory fish like rays and sharks, these vanished from the system however due to overexploitation around 1800 (Olff et al 2008). Other so called top predators that once existed in the ecosystem of the Wadden Sea are large marine mammals. Seals are still present but Harbour porpoises also vanished from the

Wadden Sea around the 1800s. In the last few years however Harbour porpoises are increasingly sighted in the Wadden Sea (Reijnders et al. 2005).

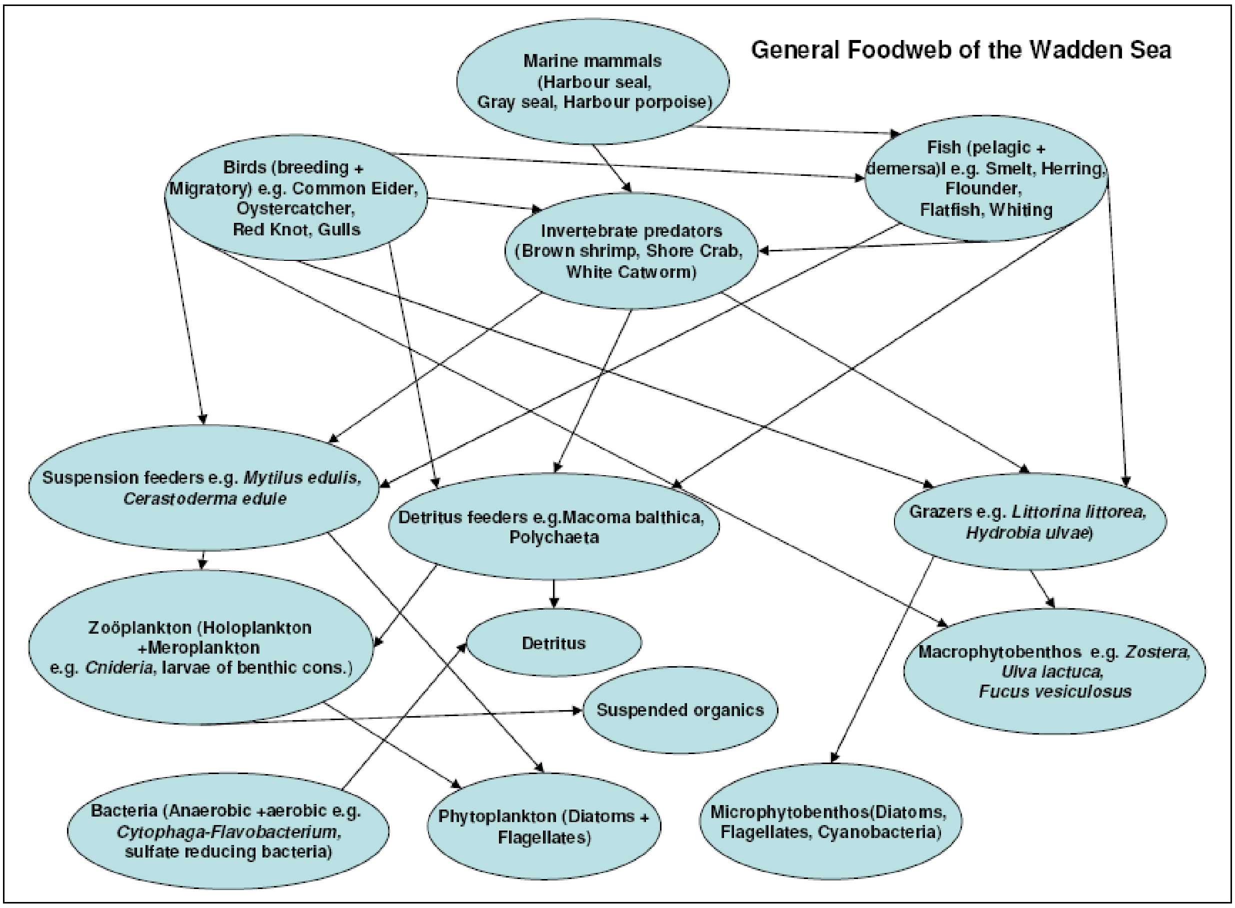



*Figure 1: The boxes show the different functional components of the food web of the Wadden Sea . Consumer-resource interactions are depicted by the direction of the black arrows.*

Top predators like sharks, rays and harbour porpoises might have played an important role in providing the connection between a variety of habitats that once existed in the Wadden Sea. The bare mud flat and habitats created by ecosystem engineers. Ecosystem engineers provide conditions like hard substrate, shelter and refuge for many associated species. These different habitats are spatially separated within the ecosystem, creating a sort of compartmentalisation within the ecosystem. Large predators travel from habitat to habitat in search of food, thereby linking the different compartments of the ecosystem. This might have played an important role in stabilizing the spatially dispersed food web (Rooney et al. 2006).

After the loss of top predators around the 1800s several other transitions and shifts in species composition took place in the ecosystem of the Wadden Sea. The next paragraphs will describe how the species composition of the Wadden Sea has changed. Starting with a description of the 'natural' situation of the Wadden Sea and its most prominent members.

### 2.2. 'Natural' situation

Some of the earliest scientific publications on the Wadden Sea show a remarkably different community composition around the 1900s. Vast areas of Oyster beds composed of the European flat oyster (*Ostrea edulis*) covered the tidal flats. Seagrass beds were found throughout the Wadden Sea and in the German part of the Wadden Sea the tube-living polychaete *Sabellaria spinulosa* formed extensive reefs (Riesen & Reise 1982). Each ecosystem engineer had its own associated community of species that relied on certain conditions the ecosystem engineer could provide. These conditions and associated species will be discussed more in depth in the next paragraphs. Causes for the demise of each ecosystem engineer will also be discussed.

#### 2.2.1. Seagrass beds

Seagrasses are a group of aquatic angiosperms. In the Wadden Sea they are represented by two species of the genus *Zostera*. *Z. noltii* and *Z. marina*. Both species prefer a different habitat. *Z. noltii* is most common and prefers to grow in the intertidal zone. *Z. marina* prefers to grow in puddles in the shallow sub tidal and the lower intertidal and seems to be less adapted to desiccation stress (Reise et al. 2005; Reise & Kohlus 2008). Seagrass beds have drastically declined during the last century. A wasting disease in the 1930s wiped out all the sub tidal *Zostera marina* beds. Since the 1950s intertidal beds of *Z. noltii* and *Z. marina* have started to decline as well (Van Katwijk et al. 1999; Reise et al 2005). This decline in seagrass beds mostly happened in the Southern and Central Wadden Sea. In the Northern Wadden Sea no general decline in seagrass beds has been observed. Around 80 percent of all seagrass beds are now located in the Northern Wadden Sea and mostly consist of *Z. noltii*. (Reise et al. 2005) The decline and lack of recovery of seagrass beds can be more closely linked to human activities. Around the time of the outbreak of the wasting disease two large scale engineering works were built. The Afsluitdijk was constructed in the Dutch part of the Wadden Sea and the Hindenburg dam in the German part of the Wadden Sea. Especially the construction of the Afsluitdijk has caused markable changes in the hydrographical conditions of the area. This combined with other practices as bottom disturbance by fishing activities, has led to an increased turbidity of the water. This increased turbidity led to light limitation and deteriorated living conditions for seagrass. (Van Katwijk et al. 1999; Wolff 2000). Light limitation might have also been influenced by eutrophication, causing increased algal growth and therefore more turbid waters (Phillipart 1994).

Seagrass beds provide a suitable substratum for several associated species. Acting as refuge to avoid predation and as an area of reduced wave velocity and currents. Due to this less turbid waters in the vicinity of seagrass beds, more nutrients and particulate organic matter are able to settle. Acting as a sort of sink. This potentially increases food availability for endobenthic and epibenthic organisms (Polte et al. 2004; Reise & Kohlus 2008; Olff et al. 2008). Furthermore a study by Polte et al (2004) showed that the presence of *Z. noltii* beds significantly increases abundances and production of juvenile epifauna on the tidal flats. Additionally it was shown that the residual water layer within dense *Z. noltii* beds provides extended ebb-tide refuges for dominant epifaunal species by retaining water trapped under their leaves (Polte et al 2004).

Apart from it's functions as shelter and nursery area, seagrass beds are grazed upon as well. This is done mainly by geese and duck, because the leaves of seagrass are not easily digested. *Zostera marina* for instance was an important component of the diet of the Brent geese before the wasting disease wiped out most of the seagrass beds. Sea snails like the periwinkle and the mud snail are found in large densities on the seagrass beds as well, but mostly graze on algae attached to the leaves and rhizomes (Jones et al. 2000).

The associated species with Seagrass beds are comprised of dense populations of amphipods, snails and juvenile epifauna like starfish, shore crab and shrimps. Polychaetes and Cniderians are also found. Fish seek shelter among the leaves and some species of fish lay their eggs in the seagrass beds. Species like seahorse are sometimes found in seagrass beds and are characteristic for a well functioning seagrass bed (Fig. 2) (Jones et al. 2000).

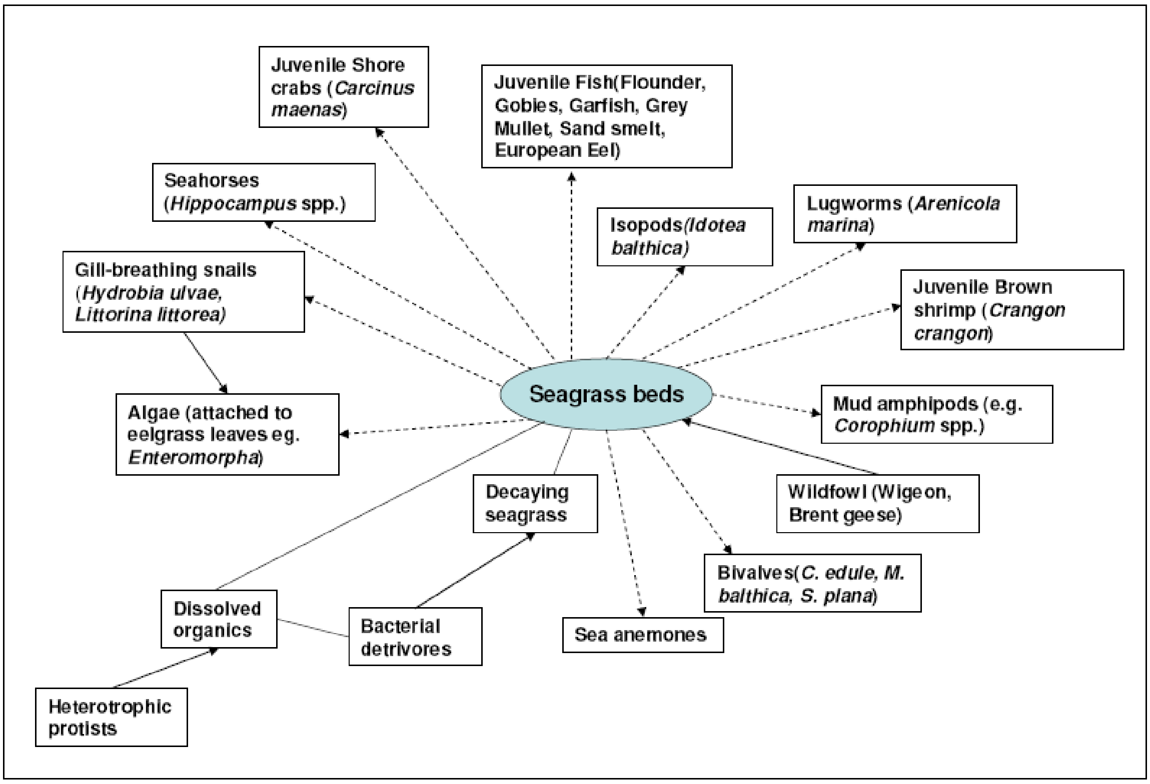



***Figure 2: Associated species with seagrass beds****. The dotted arrows are interactions, the direction of the arrow shows the species that have an interaction with conditions the seagrass bed provides. The black arrows are consumer-resource interactions. The black lines depict connections. For example seagrass beds contribute to the level of dissolved organics and decaying seagrass.*

### 2.2.2. Sabellaria Reefs

Polychaetes of the species *Sabellaria spinulosa* are common and widespread and single worm-tubes are frequently found on hard substrates like mussel shells in the entire Wadden Sea. Under certain circumstances *Sabellaria spinulosa* colonies are built, resulting in massive reef-like structures. Reef communities only occur in very turbid areas where sand is placed into suspension by water movement. *Sabellaria spinulosa* needs this sand to built its tubes. A single reef can extend over several hectares. *Sabellaria* reefs have occurred for more than a century in the German part of the Wadden Sea, forming extensive reefs. The reefs were a common sub tidal structure in the area. Around the 1920s a net decrease of *Sabellaria* reefs was observed. At the present only three viable reefs exist. There are no records of *Sabellaria* reefs ever being present in the Danish and Dutch part of the Wadden Sea (Vorberg 2005; Nehring 1999; Jones et al. 2000).

Possible causes for the decline of *Sabellaria* reefs might be found in changes in the hydrodynamics of the area. Coastal engineering and Blue mussel farming in sub tidal areas are likely to have contributed to these changes and the dramatic decrease in *Sabellaria* reefs. The most physical disturbance upon the reefs was caused by bottom trawling by shrimp fishery and is also implicated as cause for the decline in *Sabellaria* reefs (Vorberg 2005; Nehring 1999) *Sabellaria* reefs have been placed on the IUCN Red list of Biotopes and are classified as threatened with complete destruction (Jones et al. 2000).

Sabellaria reefs are characterized as areas with a high diversity. Twice as many species and almost three times as many individuals were found at *Sabellaria* reefs compared to sites with very few, or no *Sabellaria* reefs (Jones et al 2000). The associated species with *Sabellaria* reefs are mainly polychaetes, amphipods, sponges and bivalves like White furrow shell *Abra alba* (Fig.3) (Riesen & Reise 1982; Jones et al. 2000).

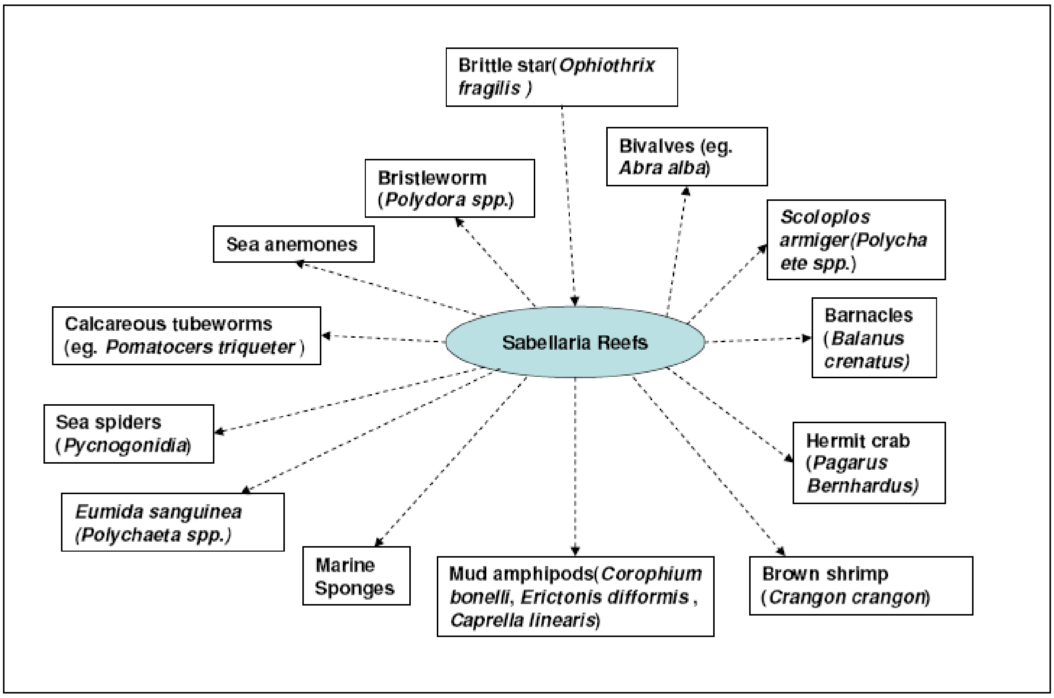



***Figure 3: Associated species with Sabellaria reefs.*** *The dotted arrows are interactions, the direction of the arrow shows the species that have an interaction with conditions the Sabellaria reef provides. The Brittle star has a negative effect on Sabellaria reefs.*

### 2.2.3. Oyster beds: *Ostrea edulis*

The European flat oyster (*Ostrea edulis*) was once an important ecosystem engineer in the Wadden Sea. It represented a structurally complex and diverse marine habitat (Saier 2002). One of the earliest publications on the Wadden Sea was written in 1877 by a German naturalist called Karl Moebius and describes several topics regarding the European oyster. In one chapter Moebius describes the community of species associated with the Oyster beds, which in his opinion constituted as the most diverse part of the tidal flat.

Moebius describes 24 species encountered while dredging for Oysters and mentions that not all species present in the Wadden Sea area at that time were encountered during the dredging. Several polychaete species and quite a lot of sponges were encountered. Also several bivalves including the Blue mussel and the Cockle were already associated with the oyster bed. Furthermore invertebrate predators like hermit crab, shore crab and starfish were encountered.

(Moebius 1877) What is interesting is that some of the species he encountered have severely declined or have disappeared completely. Like the sponge *Clione Celata*, the polychaete *Dodecaceria concharum*, the bryozoan *Alcyonidium gelatinosum,* the common Whelk *Buccinum undatum* and the Thornback ray *Raja clavata* (Fig.4) (Saier 2002; Moebius 1877).

Moebius also issued a warning that the Oyster beds should not be overexploited like they did in France, because then the Blue mussel *Mytilus edulis* and the Cockle *Cerastoderma edule* would take over (Moebius 1877). Around the same time of his publication his fear was justified as the yields of the oyster fishery suddenly dropped, remaining low over a period of 50 years. Since 1925 oyster fishery was abandoned and since 1950 no live specimen of *Ostrea edulis* had been seen. In 1992 however a small number of living *Ostrea edulis* have been found in the German part of the Wadden Sea. Living in the shallow sub tidal and on the edges of littoral mussel beds. Mussels had taken over the role of ecosystem engineer and most of the remains of the former oyster beds were covered by *Mytilus edulis* (Nehring 1999).

The transition of a 'natural' situation with oyster beds, *Sabellaria* reefs and seagrass beds abundantly present in the Wadden Sea to a situation in which vast areas of Blue mussel beds covered the tidal flats had massive consequences on the species composition of the Wadden Sea. The consequences of this transition will be further discussed in the next paragraph.

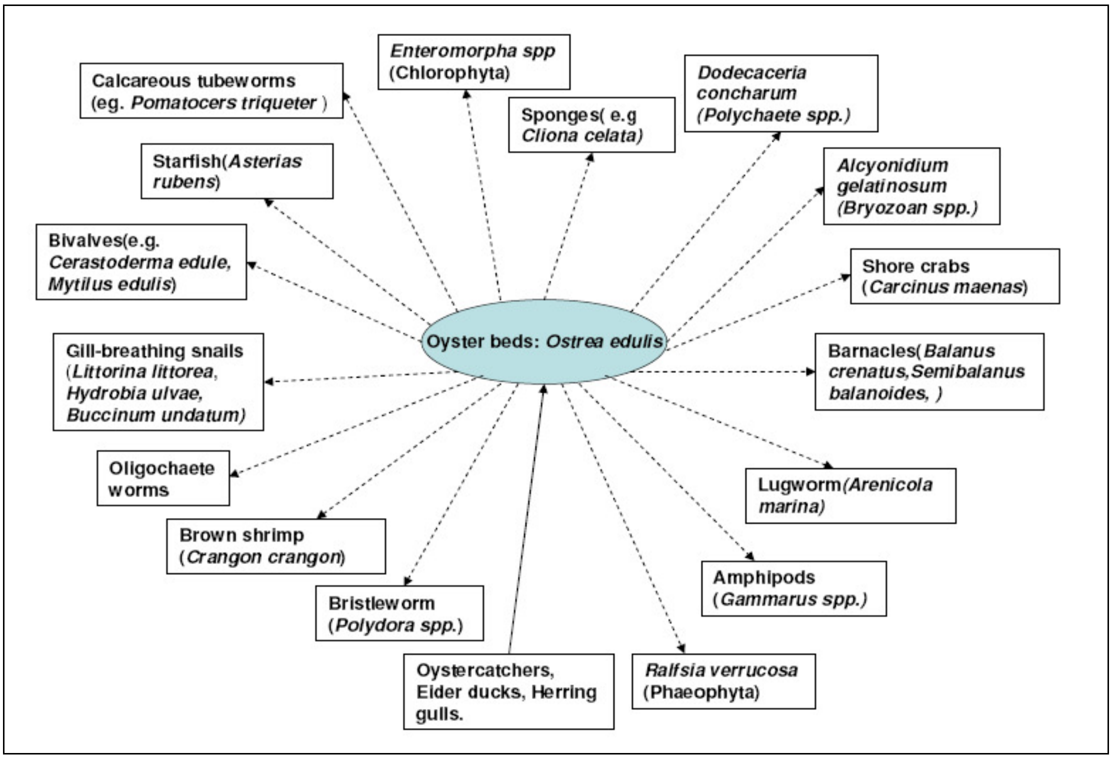



**Figure 4: Associated species with European flat oyster beds.** *The dotted arrows are interactions, the direction of the arrow shows the species that have an interaction with conditions the oyster bed provides. The black arrows are consumer-resource interactions.*

## 2.3. Transitions in the ecosystem of the Wadden Sea

The effect of the disappearance of oyster beds and most of the *Sabellaria* reefs and seagrass beds in the beginning of the twentieth century is most evidently shown in a study conducted in 1980 by Riese & Reise. Areas close to the island of Sylt in the German Wadden Sea that were sampled to determine the macrofauna in the years 1923-1926 were reinvestigated in the 1980s. The benthic assemblage of species had completely changed. Were there still were some European oysters (*Ostrea edulis*) present in the years 1923-1926, none were encountered in the 1980s. *Sabellaria* reefs that stood in the way of shrimp trawling had been destroyed and a subtidal *Zostera marina* bed was wiped out due to the wasting disease. The Blue mussel (*Mytilus edulis)* had spread in the entire region and achieved dominance (Fig.5) .

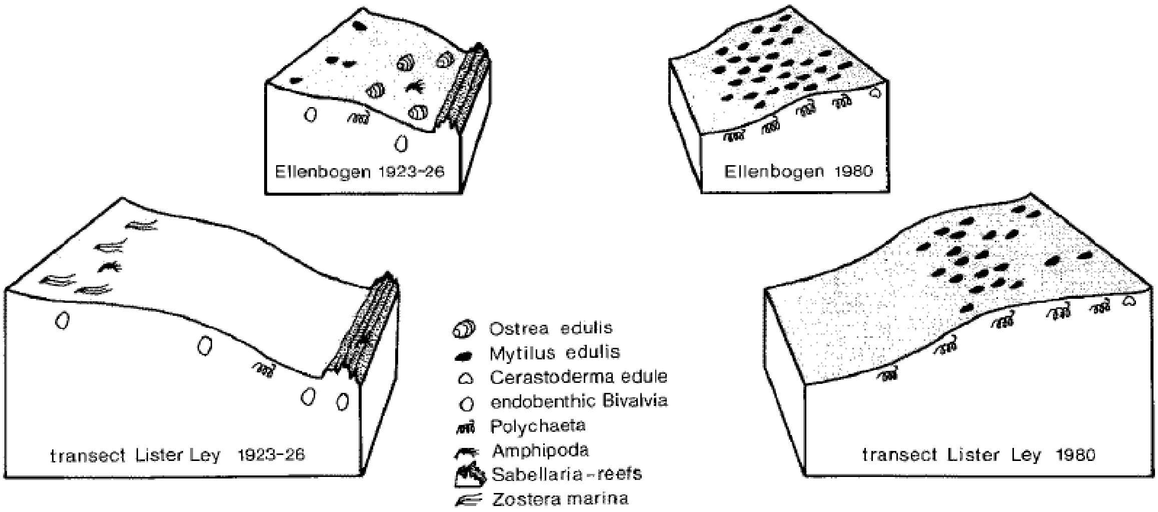



*Figure 5: Mussel dominance in the areas investigated by Riese & Reise in 1980 compared to earlier research in the same areas in the years 1923-1926 (Riesen & Reise 1982).*

Associated species with mussel beds particulary barnacles and many polychaetes seemed to benefit from the expansion of the mussel beds. Overal abundances increased and based on species density the Blue mussel (*Mytilus edulis*), the cockle (*Cerastoderma edule*), the polychaete (*Scoloplos armiger*) and the barnacle *Balanus crenatus* seemed to dominate the system. Only *Balanus Crenatus* was already abundant during the years 1923-1926 (Table 1).

| 1923–1926 | N | 1980 | N |
|---|---|---|---|
| *Balanus crenatus* | 520 | *Balanus crenatus* | 2300 |
| *Sabellaria spinulosa* | 250 | *Mytilus edulis* | 1988 |
| *Corophium bonelli* | 105 | *Scoloplos armiger* | 226 |
| *Scoloplos armiger* | 29 | *Cerastoderma edule* | 164 |
| *Abra alba* | 17 | *Heteromastus filiformis* | 116 |
| *Eumida sanguinea* | 17 | *Nereis virens* | 62 |
| *Ericthonius difformis* | 14 | *Pholoe minuta* | 58 |
| *Caprella linearis* | 10 | *Capitella capitata* | 30 |

*Table 1: 8 most abundant species in the study during the years 1923-1926 and in 1980. Showing Sabellaria dominance in 1923-1926 and mussel dominance in 1980. Abundance is based on species density (Individuals*$m^{-2}$ ) (Riesen & Reise 1982).*

Species associated with *Sabellaria* reefs and Seagrass beds like the amphipods *Corophium bonelli*, *Erichtonius difformis* and *Caprella linearis* that were once abundant, showed a dramatic decrease in species density (Table 1). Several species of Molluscs were lost. This was compensated by a diversification in polychaetes and the species richness remained about the same. Invertebrate predators like crabs and starfish were able to hold their position (Riese & Reise 1982).

Research by Beukema in 1976 on tidal flats in the Dutch Wadden Sea found that according to biomass only six species made up 90% of the macrozoobenthic biomass. The Blue mussel (*Mytilus edulis*) being most important followed by the Lugworm(*Arenicola marina*), the Sand Gaper (*Mya arenaria*), the Cockle (*Cerastoderma edule*) and the Balthic Tellin (*Macoma balthica*). Suspension feeders like the mussel and the cockle dominated the system with 55 percent of the total biomass and were found mostly strongly aggregated. Deposit feeders like polychaetes were found to be more evenly distributed and made up 40 percent of the total biomass (Beukema 1976).

The research by Riesen & Reise (1982) and Beukema (1976) were conducted in different parts of the Wadden Sea around the same time and show that over the whole area mussel beds achieved dominance. Former oyster beds, seagrass beds and *Sabellaria* reefs were seriously declined ore had disappeared. The resulting situation in the Wadden Sea is further discussed in the next paragraph. Describing the characteristics, ecological functions and associated species accompanying this new habitat of mussel beds.

### 2.3.1. Blue Mussel beds

Blue Mussel beds are important biogenic structures in the Wadden Sea area and may form very stable and long-lived structures. Mussel beds can be found in the littoral and the sub littoral part of the Wadden Sea and are ecologically not the same. The differ in biogenic structure, species interactions and associated organisms. Mussel beds provide many important ecological functions. Many species of birds feed directly on the littoral mussel beds or on the many associated species that use the mussel bed as feeding and breeding ground. Mussel beds also act as a place of refuge for predators and provide shelter against the wave velocity and the currents. Another important function relies on the fact that mussels are filter feeders, they filter the phytoplankton and suspended sediments digesting the part that can be eaten and excreting the rest as pseudofaeces around the mussel bed. By doing this they decrease the amount of suspended sediments and phytoplankton. This results in a decreased turbidity of the water and could have a positive effect on the development of seagrass beds. By increasing the amount of available nutrients for seagrasses that else would have been used by the phytoplankton and because sunlight can reach the seagrass more easily (de Vlas et al. 2005; Olff et al. 2008).

Several species are associated with mussel beds. *Fucus vesiculosus* is often found attached to the mussel bed and can occur in high abundances. Organisms like the sea snail *Littorina littorea*, the hopper *Gammarus locusta* and juvenile shore crabs are also common amongst the species found upon the mussel beds. Barncacles like *Balanus crenatus* are attached to the mussels. The soft sediment provided by the excretion of pseudofaeces by the mussels is inhabited by polychaetes as *Arenicola marina* and *Lanice conchilega* and the bivalve *Cerastoderma edule* (Cockle) (Fig. 6) (Riese & Reise 1982; Büttger et al. 2007; Jones et al 2000).

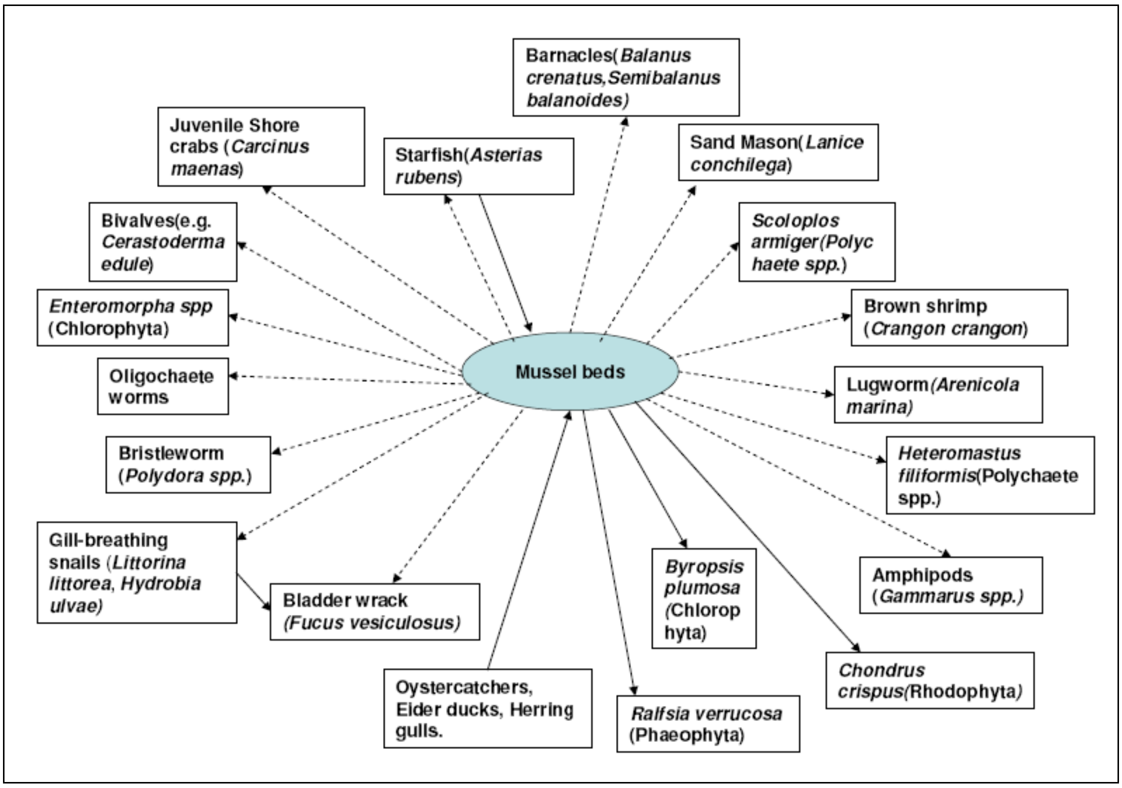



**Figure 6: Associated species with Blue mussel beds.** *The dotted arrows are interactions, the direction of the arrow shows the species that have an interaction with conditions the mussel bed provides. The black arrows are consumer-resource interactions. Starfish have a negative effect on mussel beds.*

### 2.3.2. History repeats: the demise of Blue Mussel beds

Mussel fishery started from very early on and especially intensified when the practice of mussel farming came into use in the 1960s. This involved the creation of artificial subtidal mussel beds that were stocked with seed mussels and dredged out. During the 1980s/1990s a combination of several years of low spatfall combined with an intensified fishing pressure on littoral mussel beds led to a dramatic decrease in the total area of stable littoral mussel beds. Since then several actions to preserve and restore mussel beds have been taken. Mussel fishery on littoral mussel beds is largely restricted and has been absent in most parts of the Wadden Sea since the last few years. Furthermore environmental conditions have improved. Musselbeds have however not recovered and are unstable at most sites. (Olff et al. 2008; de Vlas et al. 2005)

The loss of large areas of littoral mussel beds has led to situation in which bare mudflat now dominates in most of the Wadden Sea. The mudflat is characterized by detritus feeding species like polychaetes and shrimp. These species now seem to dominate the system with the species of fish(eg. Flatfish) and birds that prey on them (Fig.7) (Olff et al. 2008).

The period of relative absence of ecosystem engineers in the Wadden Sea seems to be short however. The Pacific oyster (*Crassostrea gigas*) has shown a drastic increase during the last few years and has settled on top of the remaining musselbeds and on the bare mudflat. Raising the question if history will repeat itself and *Crassostrea gigas* will take over the role of the Blue mussel as dominant ecosystem engineer in the Wadden Sea (Büttger et al 2007). The next paragraph will discuss the spread and settlement of the Pacific oyster in the Wadden Sea in more detail.

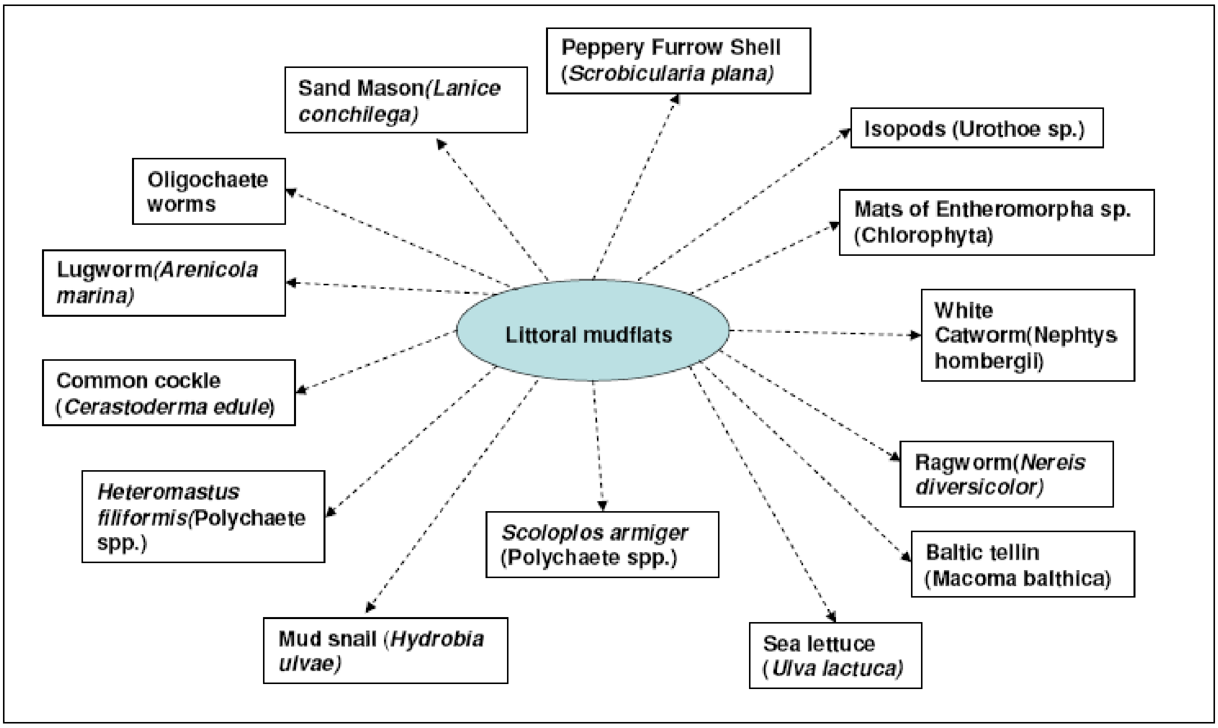



**Figure 7: Associated species with the littoral mudflat.** *The dotted arrows are interactions, the direction of the arrow shows the species that have an interaction with conditions the mudflat provides.*

### 2.3.3. Pacific Oysters: Invasion of the Wadden Sea

After the loss of the European flat oyster *Ostrea edulis* and the profits that could be gained from it's fishery several attempts have been made to introduce other oysters. In 1964 Dutch oyster farmers imported spat from the pacific oyster *Crassostrea gigas* to use for aquaculture activities in the Oosterschelde estuary. In the years 1975 and 1976 exceptionally warm summers caused natural spatfalls contributing to an explosive development in the Pacific oyster abundances. From the 1980s other estuaries started to be colonized and in 1983 the first specimens of *Crassostrea gigas* were observed near the Island of Texel in the Dutch Wadden Sea. Whether this colonization was fully natural is doubted. The species really started to increase in numbers since the 1990s and in 1996 the Pacific oyster also settled in the German part of the Wadden Sea. Dispersal might have taken place from the Netherlands. In 1999 the first free living Pacific oysters were observed in the Danish part of the Wadden Sea. Dispersion might have taken place from the Northern German Wadden Sea. Especially in the last few years the pacific oyster has drastically increased in the entire Wadden Sea (Nehls & Büttger 2007).

This drastic increase has caused many to worry. Invading species are known to have had great impact on ecosystems causing the loss of many endemic species (Wolff 2000). To determine the effect of the Pacific oyster in the Wadden Sea several comparisons were made. The next paragraph will discuss the outcome of these comparisons.

### 2.3.4. Is the Pacific oyster a threat?

The Pacific oyster uses the substrate of  mussel beds or remains of mussel beds for settlement. Resulting in mixed beds with both Blue mussels and Pacific oysters. By first glance the Blue mussels and Pacific oysters seem to coexist. Both species are filter feeders however and compete for the same food sources. To determine what the effects of a possible shift towards dominance of Pacific oysters would be, several comparisons have been made.

A comparison of the associated species of Pacific oyster beds with the adjacent bare mudflat showed that the diversity and abundances of organisms on Pacific oyster beds were higher. Showing that several species benefit from the conditions the Pacific oyster provides (Fig. 8). Comparisons between the associated species of  Pacific oyster beds and mussel beds have also been made. One thing that was noticed was that the seaweed *Fucus vesiculosis* can not establish itself on oyster beds. This is because it depends on Blue mussels which attach it with so called byssus threads. This might affect the occurrence of some epibenthic species.
Other findings were that species richness did not seem to differ between Pacific oyster and Blue mussel beds. Species did however differ in abundances. For example densities of the barnacle *Semibalanus balanoides* and juvenile shore crabs were higher on mussel beds. While densities of the sea snail *Littorina littorea* and the polychaete *Polydora ciliate* were higher on oyster beds. These differences in abundance could lead to a different dominance structure of the associated community between Pacific oyster beds and mussel beds. Therefore functional relationships in the ecosystem might change if oyster beds take over.

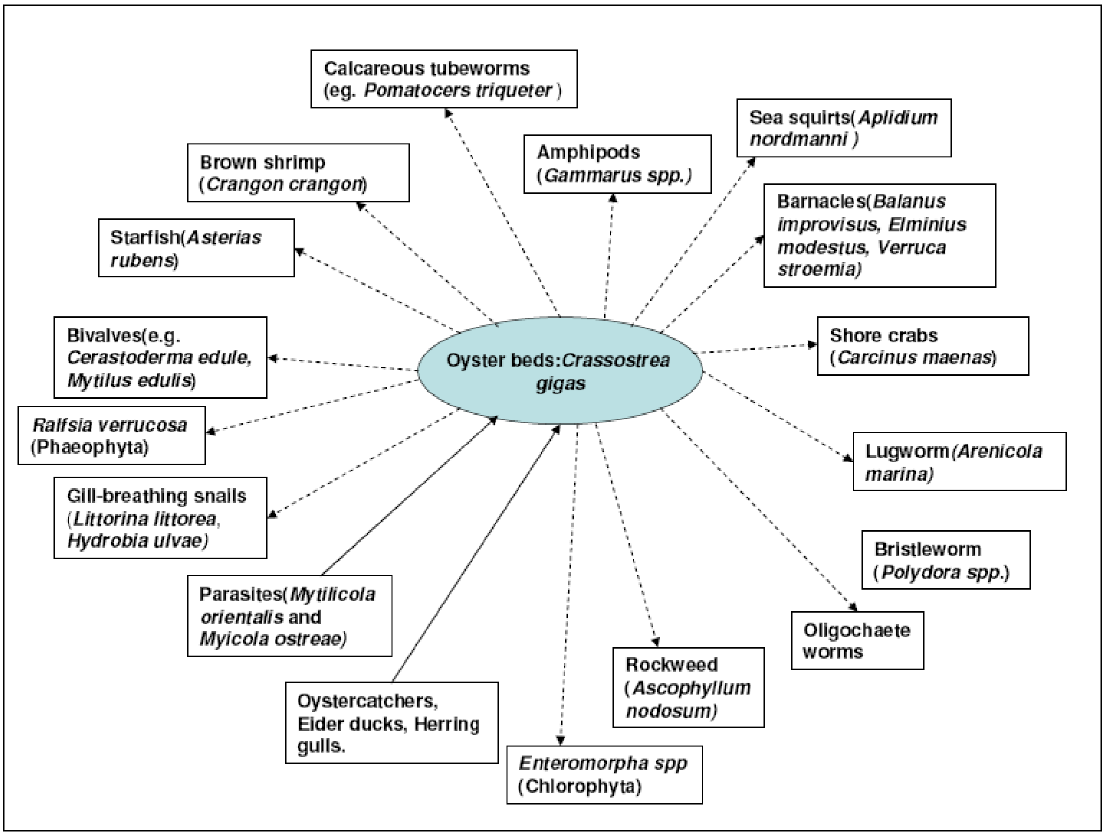



**Figure 8: Associated species with Pacific oyster beds.** *The dotted arrows are interactions, the direction of the arrow shows the species that have an interaction with conditions the mussel bed provides. The black arrows are consumer-resource interactions. Predation on Pacific Oysters is limited in the Wadden Sea.*

Overall these first comparisons between the associated species of oyster beds versus mussel beds have not yet shown any loss of species. The Blue mussel seems to be able to coexist with the Pacific oyster. The increase of the Pacific oyster is however still taking place and the effects on the ecosystem might not be visible right now.

Another remark is that the Pacific oyster is hardly predated in the Wadden Sea. From other areas it is known for species like the shore crab, eider ducks, wading birds and polychaetes that they predate on Pacific oysters. Predators in the Wadden Sea seem to need time to adapt to this new food source.

Whether ore not the Pacific oyster will take over the mussel beds thus remains to be seen. Two scenarios are possible. The mussels and the oysters are able to live together in a new sort of reef like structure in the Wadden Sea. Species loss will be minimal and oyster beds will offer an extra dimension to the habitat that already existed in the form of mussel beds. A second scenario is that the Pacific oysters do have a negative effect on the mussel beds. By overgrowing and outcompeting the mussels, mussel beds will further disappear from the Wadden Sea ecosystem. Associated species might find alternative habitat in the form of the Oyster beds. Several species like *Fucus vesiculosus* that can not settle on oyster beds might however seriously decrease in abundance. The most pronounced effect in the loss of mussels from the system however might lie in the lack of predation on the Pacific oyster in the Wadden Sea. The loss of the mussel as a major food source for migrating and breeding birds like the Red Knot, the Oystercatcher and the Eider duck, will seriously affect population sizes of these species. Unless these species shift their diet from mussels to Pacific oysters, production and biomass of the oysters will be hardly available for higher trophic levels. The energy flow will be redirected into the storage compartment and microbial decomposition (Nehls & Büttger 2007).

In contrast to the disappearance of the European flat oyster *Ostrea edulis* however that happened without intervention. Actions to conserve and restore mussel beds have- and will be taken. Mussel fishery has been limited or absent during the last few years on intertidal mussel beds and is increasingly restricted in the sub tidal area. This however has not led to a recovery of the mussel beds. To determine what causes this lack of recovery and to find ways to aid mussel bed recovery are large scale project is planned in the Netherlands. The next chapter will further clarify the goals of this project and how this is part of a future perspective on the Wadden Sea. Whether or not this future is certain, remains to be seen.

# 3. Future of the Wadden Sea

The previous chapters have shown a large scale deterioration of the ecosystem of the Wadden Sea. Large transitions have taken place and most ecosystem engineers are now classified as threatened with complete destruction (Jones 2000). This resulted in a loss of a variety of habitats and associated species. Detritus feeding organisms like polychaetes and shrimp now dominate the system. The most important cause cited for the deterioration of the ecosystem are anthropogenic influences as overexploitation and habitat change and destruction (Olff et al. 2008; Wolff 2000).

### 3.1. Conservation management of the Wadden Sea

In the last three decades and especially the last few years the ecological importance of the Wadden Sea area has been increasingly recognized. Conservation of ecological values has become the main priority. One of the reasons for this assumed responsibility are international agreements like the Ramsar Convention in 1971 and the recent recognition of the Wadden Sea as a World Herritage Site. A second reason lies in scientific findings that almost all show the detrimental consequences of human impact on the Wadden Sea. However this change of policy was not gradual. It took many scientists and protesters to stress the need to stop overexploiting and polluting the Wadden Sea area before any changes were made (Olff et al 2008, Piersma 2007).

Only in the last few years real efforts have been made to turn the tide. Mussel fishery on intertidal mussel beds has been limited or absent during the last few years in most parts of the Wadden Sea and is increasingly restricted in the sub tidal area. Furthermore mechanical dredging for cockles has been banned in the Dutch part of the Wadden Sea since 2004. These restrictions have not yet proven to be effective. No return of lost species or ecological processes has been observed. This might be due to the fact that these restrictions are not sufficient enough. Fishery for cockles using less intrusive techniques is for instance still allowed and fishery for shrimp and pelagic and demersal fish was never restricted. The ecosystem might only be able to recover if all human exploitation in the area is restricted. Other theories indicate that an approach aimed directly at the restoration of ecosystem engineers might aid in the recovery of the ecosystem. By restoring ecosystem engineers to abundances previously known in the Wadden Sea, key processes and associated species are expected to return as well (Olff et al. 2008; Piersma 2007; de Vlas et al. 2005; Vorberg et al. 2005).

### 3.2. Restoration of the ecosystem: Future perspectives

Based on this theory a large scale project has been designed in the Dutch part of the Wadden Sea. For the upcoming five years several Dutch conservation organizations, researchers from the university of Groningen and several other research institutions will be working together in an effort to restore mussel beds. Two sets of hypothesis about the lack of recovery of stable mussel beds in the Wadden Sea will be investigated. Hypotheses that have to do with reproduction, dispersion and settlement and hypotheses that have to do with maintaining already settled mussel beds.

The aim of this project is to gain more insight in the causes of the lack of recovery of stable mussel beds in the Wadden Sea and to gain knowledge on the way mussel beds function within the ecosystem of the Wadden Sea. The goal for the year 2030 is to restore littoral mussel beds at a large scale to abundances known to be present in 1975. The restored mussel beds are expected to act as a sort of leverage for other species and ecological processes to recover. This effect will be immediate with a re-establishment of associated species and ecological processes on- and within the habitat mussel beds provide. Furthermore during the development of mussel beds conditions are expected to enhance as such that seagrass beds can re-establish. The goal for 2030 is to reach at least half of the amount of sub tidal seagrass beds that were present during the 1930s (Olff et al. 2008).

If all goes to plan this would mean a bright future for the Wadden Sea. In a system of seemingly constant changing dynamics like the Wadden Sea however it seems unlikely that a stable situation can ever be reached. Several factors might intervene and the outcome might not be as expected. Some scientists believe that the Wadden Sea has changed beyond return. (Reise et al. 2007)

### 3.3. Future perspectives: can the goals be reached?

It can be questioned whether a restoration of mussel beds will immediately lead to the return of associated species and accompanying ecological processes. Most benthic species start out as planktonic larvae and are able to detect suitable substrate for settlement (Beukema 1976). For settlement of associated species on the newly formed mussel beds to take place, larvae need to be present. Some once associated species might not be able to disperse to the Wadden Sea and re-establish that easily because they have completely vanished from the area.

Mussel beds and associated fauna might also be limited in their recovery because mussel beds are increasingly overgrown by the Pacific oyster. Early research has not yet shown any detrimental effect of the presence of Pacific oysters on Blue mussel beds and associated species. However this could be because the number of Pacific oysters is still growing. An increase in the area of mussel beds would also mean an increase of hard substrate for Pacific oysters to settle upon. Pacific oysters and Blue mussels are both filter feeders and competition for phytoplankton might prove eminent when larger numbers of Pacific oysters are present. This competition might influence attempts to restore mussel beds (Nehls & Büttger 2007). Other invading species that have already settled or are still to come might also cause future changes to the community composition of the Wadden Sea ecosystem (Reise et al. 2007).

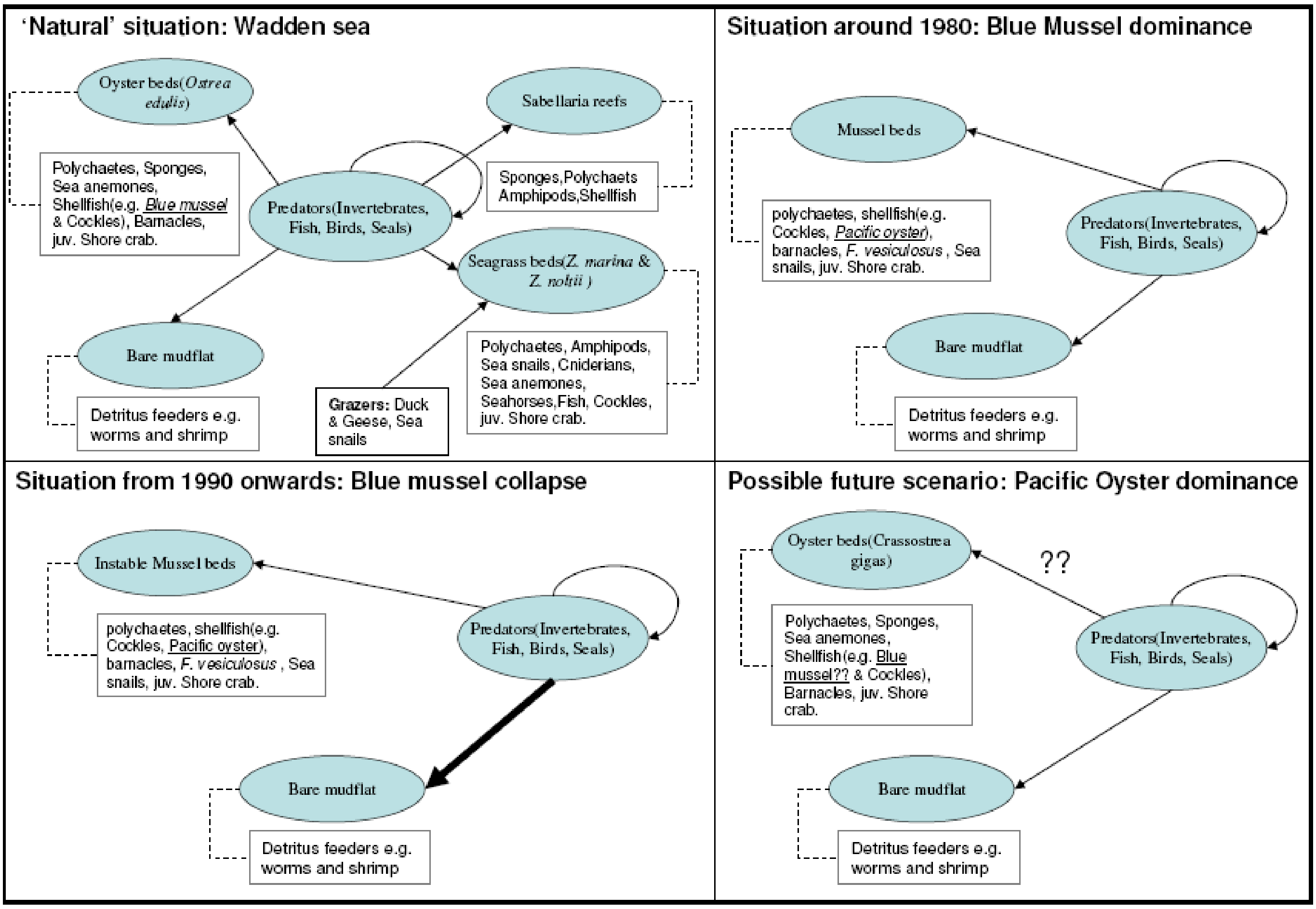
The disappearance of top predators in the ecosystem of the Wadden Sea might also be more important than previously thought. Top predators like rays, sharks and harbour porpoises have largely vanished in the Wadden Sea due to overexploitation from the 1800s onwards (Olff et al. 2008). Large predators might have been essential in providing connections between the different habitats and associated species that existed in the Wadden Sea (Rooney et al. 2006). Most conservation management has however been aimed at the restoration of the bottom of the food chain. Fishery for pelagic and demersal fish and shrimp has never been restricted ignoring the important ecological role of these species in the ecosystem of the Wadden Sea. This ongoing fishery might also be the cause for the lack of recovery of larger predators like rays and sharks. In the last few years however Harbour porpoises have been increasingly sighted in the Wadden Sea area indicating that conditions might have improved (Vorberg et al 2005; Reijnders et al. 2005)

One of the largest uncertainties in the future of the Wadden Sea is climate change. Changes in the average water temperature and rise in sea level will alter conditions within the Wadden Sea ecosystem. For example an increase in storminess, wave action and river discharge are expected due to climate change. An increase in sea level might also result in changing sea currents in front of the mainland causing less sedimentation and an increase in sandiness of the mudflat in these areas. Sea level rise could further lead to 'drowning' of the tidal flat, salt marshes and the pioneer zone. Tidal flats are most at risk from drowning, but are believed to keep up with sea level rise due to faster sedimentation. Apart from these changes to the geomorphology of the Wadden Sea area several effects of changing temperature on the ecological functioning of the Wadden Sea are expected. Changes in species composition, growth rates and overall ecological functioning of the Wadden Sea might occur (Oost et al. 2005; Reise et al. 2007). For example climate change might facilitate the spread of the Pacific oyster. The Pacific oyster (*Crassostrea gigas)* needs an average water temperature of more than 20 degrees Celsius to reproduce. This was for instance the case in the Oosterschelde in 1975 and 1976 in which very warm summers ensured the first natural spatfalls of the Pacific oyster. These spatfalls were the beginning of an explosive development of the Pacific oyster (Nehls & Büttger 2007). The Blue mussel on the other hand seems to suffer from high winter temperatures. After a mild winter annual spatfall by blue mussels will have dramatically decreased. Hypotheses about this phenomenon relate to the fact that species like shrimp and shore crabs survive the less cold winters. Resulting in higher abundances of species that predate on the mussels and especially on the mussel larvae. Decreasing annual recruitment of mussels (Essink et al. 2005).

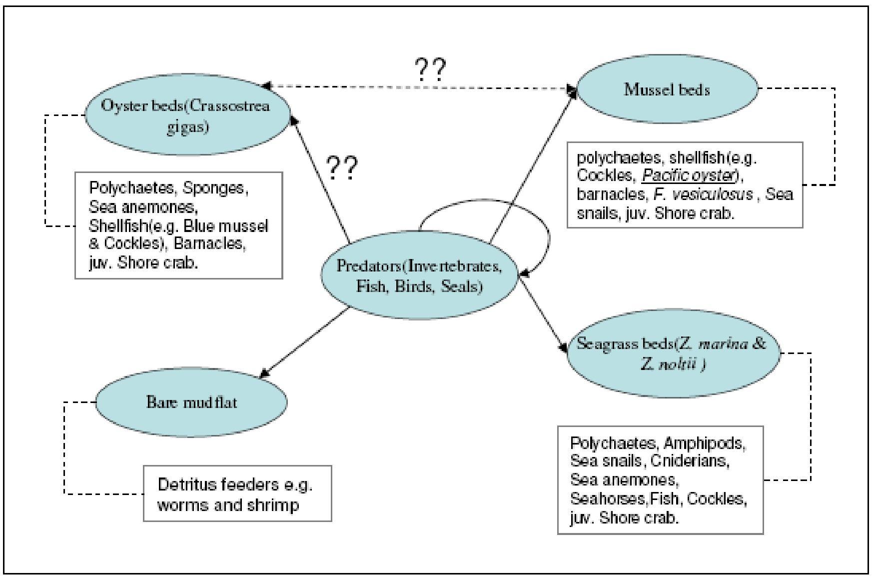
### 3.4. Bright future for the Wadden Sea?

All in all one cannot predict the future, especially in the case of a complex and highly dynamic area as the Wadden Sea. Whether or not the goals to have restored mussel- and seagrass beds around 2030 can be realised remains to be seen. Factors like climate change and invading species are likely to cause further changes in the ecosystem of the Wadden Sea. It might prove impossible to maintain the ecosystem of the Wadden Sea in a stable state of high biodiversity under the strain of these changes. The upcoming Pacific oyster might present a problem in the upcoming years. In the case of a shift towards dominance of the Pacific oyster in the Wadden Sea ecosystem. Decisions will have to be made as to whether the spread of the Pacific oyster should be counteracted or 'nature' should be left to run it's course.

## Appendix: Graphic overview of transitions in the ecosystem of the Wadden Sea




**Transitions in the ecosystem of the Wadden Sea.** *The different habitats that could be found in each different situation are shown along with the characteristic associated species. Predators provide the connection between the different habitats. The black arrows show consumer-resource interactions. The thickness of the arrow shows the importance of the habitat for the consumers. The circular arrow indicates that the predators also feed on each other. Question marks indicate the uncertainty if predators will feed on the Pacific oyster(Crassostrea gigas).*




**Possible future scenario: outcome of conservation management**
If restoration of seagrass- and mussel beds succeeds and the pacific oyster establishes itself without outcompeting mussel beds this might be a possible future scenario. Question marks indicate the uncertainty as to how mussel beds and Pacific oyster beds will interact and if predators in the Wadden Sea will feed on the Pacific oyster.

# References


Beukema, J. (1976). Dierlijk leven in en op de bodem. *Waddenzee*, 125-133.

Beukema, J. (1976). Biomass and species richness of the Macro-Benthic animals living on the tidal flats of the Dutch Wadden Sea. *Neth. J. Sea Res*, 12, 236-261

Büttger, H., Asmus, H., Asmus, R., Buschbaum, C., Dittman, S., Nehls, G. (2007) Community dynamics of intertidal soft-bottom mussel beds over two decades. *Helgol. Mar. Res.*

Beusekom, J., Bot, P., Göbel, J., Hanslik, M., Lenhart, H.J., Pätsch, J., Peperzak, L., Petenati, T., Reise, K. (2005) Eutrophication. *Quality status Report. Wadden Sea Ecosystem*, 19, 141-153.

de Vlas, J., Brinkman, B., Bushbaum, C., Dankers, N., Herlyn, M., Kristensen, P., Millat, G., Nehls, G., Ruth, M., Steenbergen., J., Wehrman, A. (2005). Intertidal Blue Mussel Beds. *Quality Status Report. Wadden Sea Ecosystem,* 19, 190-200.

Essink, K. (2005). Macrozoobnethos. *Quality Status Report. Wadden Sea Ecosystem*, 19, 184-189.

Haartsen, A., van Marrewijk, D. The Dutch Wadden Sea Region. *Wadden Sea Ecosystem*, 12, 225-256.

Jones, L.A., Hiscock, K, & Connor, D.W. 2000. *Marine habitat reviews. A summary of ecological requirements and sensitivity characteristics for the conservation and management of marine SACs*. Peterborough, Joint Nature Conservation Committee. (UK Marine SACs Project report.)

Moebius, K. (1877). Auster und die Austerwirtschaft. *Wiegandt, Hempel & Parey*.

Nehring, S. (1999). Oyster beds and Sabellaria reefs. *Quality Status Report. Wadden Sea Ecosystem* No. 9: 146-147.

Nehls, G., Büttger, H. (2007). Spread of the Pacific Oyster *Crassostrea gigas* in the Wadden Sea. *HARBASINS Report*.

Olff, H. (2008). Waddensleutels*. Projectplan herstel sleutelprocessen in the intergetijdegebied van de Waddenzee.*

Phillipart, C. (1994). Effects of shading on growth, biomass and population maintenance of the intertidal seagrass *Zostera noltii* Hornem.in the Dutch Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, 188, 199-213.

Piersma, T. (2007). Why do Molluscivorous shorebirds have such a hard time in the Wadden Sea right now? *Wadden Sea Ecosystem*, 23, 53-63.

Polte, P., Schanz, A., Asmus, H. (2004). The contribution of seagrass beds (Zostera noltii ) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. *Marine Biology, 147, 813-822.*

Riesen, W., Reise, K. (1982). Marobenthos of the subtidal Wadden Sea: revisited after 55 years*. Helgoländer Meresunters*, 35, 409-423.

Reise, K., Herre, E., Sturm, E. (2008). Mudflat biota since the 1930s: change beyond return? *Helgol. Mar. Res*, 63, 13-22.

Reise, K., Kohlus, J. (2007). Seagrass recovery in the Northern Wadden Sea? *Helgol Mar. Res*., 62, 77-84.

Reise, K., Jager, Z., de Jong, D., van Katwijk, M., Schanz, A. (2005). Seagrass. *Quality Status Report*. *Wadden Sea Ecosystem,* 19, 201- 207.

Reijnders, P, Abt, K.F., Brasseur, S., Camphuysen, K., Reineking, B., Scheidat, M., Siebert, U., Stede, M., Tougaard, J., Tougaard, S. (2005) Marine Mammals. *Quality Status Report. Wadden Sea Ecosystem*, 19, 305-318.

Rooney, N., McCann, K., Gellner, G., Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature,* 442, 265-269.

Saier, B. (2002). Subtidal Mussel Beds in the Wadden Sea: Threatened Oases of Biodiversity. *Wadden Sea Newsletter-1*.

van Katwijk M.M., Hermus D.C.R., de Jong D.J., Asmus R.M. & de Jonge V.N. (2000). Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds. *Helgoland Mar. Res.*, 54, 117-128.

Vorberg, R. (2005). Subtidal Habitat Structures. Quality *Status Report. Wadden Sea Ecosystem*, 19, 208-218.

Vorberg, R., Bolle, L., Jager, Z., Neudecker, T. (2005). Fish. *Quality Status Report. Wadden Sea Ecosystem*, 19, 219-318.

Weijerman, M., Lindenboom, H., Zuur, A. (2005). Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar Ecol Prog Ser,* 298, 21-39.

Wolff, W.J. (2000). Causes of extirpations in the Wadden Sea, an estuarine area in the Netherlands. *Conserv. Biol.*, 14, 876-885.