Photo: CWSS/ Bostelmann. Pacific oysters and blue mussel.

Wadden Sea Quality Status Report

Beds of blue mussels and Pacific oysters

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1. Introduction

1.1 Biology and occurrence

In the northern hemisphere, three taxa of blue mussels (*Mytilus edulis* complex) occur along the coasts of the North Atlantic and North Pacific. On the soft sediments in the Wadden Sea individual blue mussels aggregate and form beds (Figure 1). Pacific oysters (*Crassostrea gigas*) were introduced to several locations along the North Sea coast within NW Europe for aquaculture purposes in the 1960s and to the western Dutch Wadden Sea in the late 1970s (Troost, 2010) (see report "Alien species"). Wild Pacific oysters were first observed in the western Dutch Wadden Sea near Texel in 1983 (Fey et al., 2010; Troost, 2010). Pacific oysters naturally spread eastwards reaching the central Wadden Sea in 1998 (Wehrmann et al., 2000). Oysters were introduced in the northern Wadden Sea in the 1970s and the first Pacific oyster outside culture plots was observed in 1991 (Reise, 1998). Pacific oysters need hard substrates for larval settlement and shortly after their introduction they were found on shells of blue mussels. Mussels also colonize oyster beds (Troost et al., 2012; Van Stralen et al., 2012); mussels and Pacific oysters may co-exist in mixed beds with compositions ranging from almost 100 % blue mussels to almost 100 % Pacific oysters. Dense oyster beds are reef-like structures that often contain blue mussels (Kochmann et al., 2008; Markert et al., 2010; Figures 2 and 3).

Intertidal beds/reefs of blue mussels and Pacific oysters are important for community composition and ecological functioning in the Wadden Sea (Folmer et al., 2014; van der Zee et al., 2012; Markert et al., 2010). Blue mussels and Pacific oysters are an important link between the pelagic and benthic zones. They provide structural heterogeneity and serve as habitat and food source for a large number of species and thus increase biodiversity (Kochmann et al., 2008; Troost, 2010; Markert et al., 2010, 2013). Blue mussels and Pacific oysters have high filtration rates and compete with each other and other suspension feeders by consuming phytoplankton (Kamermans, 1994; Cadée & Hegeman, 2002; Diederich, 2006; Troost, 2010). Blue mussels and Pacific oysters also promote primary production by accelerating nutrient cycling and by deposition of nutrient-rich feces and pseudofeces (Asmus & Asmus, 1991). They can also influence local sediment properties by reducing hydrodynamic forces and are considered important ecosystem engineers in the Wadden Sea (Widdows & Brinsley, 2002; Markert et al., 2010; van der Zee et al., 2012; Walles et al., 2014).

Distribution and dynamics of blue mussel beds and Pacific oyster reefs are determined by larval supply, settlement and various post-settlement processes (Brandt et al., 2008; Schmidt et al., 2008, 2010; Markert et al., 2010; Folmer et al., 2014; Dankers & Fey-Hofstede, 2015). The densities of pelagic blue mussel larvae are highest in spring and the densities of Pacific oyster larvae are highest in late summer (Bayne, 1976; Pulfrich, 1996; Philippart et al., 2014). The main intertidal settling substrata for mussels are blue mussel beds and Pacific oyster reefs, beds of dead shells, tubes of the sand mason worm (*Lanice conchilega*), macroalgae and seagrass stems (Pulfrich, 1996; Herlyn et al., 2008; wa Kangeri et al., 2014). In years with large quantities of settlers, settlement of blue mussels may also occur on bare mudflats. The most important settling substrata for Pacific oysters on intertidal flats are mussel and oyster beds/reefs, shells and hard substrates in harbours and embankments.

Important natural loss processes shortly after settlement are predation by shrimp, starfish and crabs (van der Veer et al., 1998; Andresen & van der Meer, 2010; Weerman et al., 2014). Currents and waves during storms (Nehls and Thiel, 1993; Brinkman et al., 2002; Hammond and Griffiths, 2004; Herlyn et al., 2008; Donker et al., 2013) and ice-scouring during cold winters (Strasser et al., 2001; Büttger et al., 2011) are important during all life stages of blue mussels and Pacific oysters.

Figure 1. Blue mussel (Mytilus edulis) bed on the intertidal flats south of Norderney (Lütetsburger Plate) in the Lower Saxon Wadden Sea (photo: Marc Herlyn, 22 April 2013).

Figure 2. Reefs of Pacific oyster (Crassostrea gigas) on the tidal flats south of Mellum (Robbenplate) in Lower Saxony. The picture illustrates the dramatic ecosystem engineering effects oyster reefs may have on the morphology of tidal flats (Photo: Alexandra Markert, 06 July 2011).

Figure 3. Co-existence of blue mussels (Mytilus edulis) and Pacific oysters (Crassostrea gigas) at an oyster dominated reef south of Baltrum (Dornumer Nacken) in Lower Saxony. The blue mussels mainly occur in the interspace of the oysters (Photo: Alexandra Markert, 12 July 2011).

1.2 Fishery and management

Decreases in blue mussel bed area due to mussel fisheries in the 1980s and 1990s led to fierce societal debate. In Lower Saxony, fishery caused a strong decline or even complete loss of intertidal young blue mussel beds that were open to fishery (Herlyn & Millat, 2000). At the same time, the surface area of protected (unfished) beds also declined. In the Dutch Wadden Sea, most intertidal mussel beds disappeared in the period 1988-1991 due to fishery and lack of spatfall (CWSS, 2009). Consequently, protection measures were established. Trilateral targets for intertidal blue mussels were formulated in 1994 and a policy and management plan for blue mussel fishery was included in the Wadden Sea Plan 1997 (CWSS, 2010 (updated)). Blue mussel fishery is presently not allowed in the entire intertidal area of the Dutch Wadden Sea. Since 2014, part of the subtidal area of the Dutch Wadden Sea has been closed for mussel fisheries. In the subtidal areas fishery still takes place in autumn and spring. In autumn fisheries are allowed on beds in areas designated as "unstable" and in spring also in areas designated as "stable". Definition of stable and unstable areas is based on historical observations on winter survival of mussel beds by researchers and fishermen. The main differences between the stable and unstable areas are due to the impact of storms on mussel beds and the intensity of predation by starfish (Smaal et al., 2014). In Lower Saxony, fishery of seed mussels is allowed in the subtidal and in defined parts of the intertidal. In Schleswig-Holstein, mussel fishery is not allowed in the intertidal area but has been permitted in the subtidal area except in the national park core zones since 1997. About 50 % of the Danish Wadden Sea has been closed for mussel fishery since 1992. Since 2008 mussel fishery has not been allowed in the entire Natura 2000 area in the Danish Wadden Sea.

Section 2.1 presents the status and trends of the area covered by mussel and oyster beds/reefs and the biomass of both species; section 2.2 shows the spatial coverage of mussel and oyster beds/reefs per tidal basin through time; section 2.3 presents the spatial distributin of mussel and oyster beds/reefs between 1999 and 2013 by means of a map with the frequency of occurrence; section 3 is the assessment and Wadden Sea

Plan Target Evaluation; recommendations for management and monitoring are provided in section 4 and a summary is given in section 5. An overview about methods and data is given in the annex.

Box 1: Classification and denomination of mussel beds and oyster reefs and mixed structures

Due to the invasion and expansion of Pacific oysters, pure mussel beds have become less abundant and the structure of mussel and Pacific oyster aggregations has changed and has become increasingly "reef-like" (Figures 1.2 and 1.4). The following classification rules of mussel, oyster and mixed structures have been used:

1. Biomass based: The species with the highest biomass (live wet weight) determines the denomination (CWSS, 2009).
2. If biomass samples are not taken, the classification is based on relative coverage of Pacific oyster (judged visually) (CWSS, 2009):
    - Mussel bed: <30 % oysters
    - Pacific oyster bed: >60 % oysters
    - Mixed bed: 30-60 % oysters
3. Based on coverage of mussels and Pacific oysters (judged visually):
    - Mussel bed: mussel cover >=5 %, oyster cover < 5 %
    - Oyster bed: oyster cover >= 5 %, mussel cover < 5 %
    - Mixed bed: mussel cover >=5 % and oyster cover >= 5 %

In Schleswig-Holstein classification was usually based on biomass (where biomass was calculated on the basis of the shell length of individual blue mussels and Pacific oysters). In years without sample collection, the classification was based on relative coverage (2).

In the Netherlands classification is based on the rules under point 3.

The assessment of the total area by aerial photography in Lower Saxony does not yield measures of the proportion of blue mussels and Pacific oysters. The species are monitored in separate programs and the classification was reconstructed based on their biomass in the total area.

Figure 4. Left: Mussels (Mytilus edulis); right: Pacific oysters (Crassostrea gigas) with blue mussels in interspaces (Photos: Alexandra Markert).

2. Status and Trends

Box 2: Interactions between blue mussels and Pacific oysters

The invasion of Pacific oysters into blue mussel beds has raised questions about interactions between both species. Particularly, questions concerned the effects of competition and coexistence mechanisms.

In beds with only few Pacific oysters the oysters tend to lay flat on top of the mussel bed, or they may grow upright and anchored into the sediment (Figure 5). In beds with a higher oyster density the oysters grow upright and mussels tend to live in the interspace (Buschbaum et al., 2016). Mussels sitting in the interspace of the oysters have lower food intake rates due to interspecific competition. Consequently, growth rates and body condition of these mussels are lower than of mussels growing at the top of a reef (Eschweiler & Christensen, 2011). Experiments have shown that the presence of predators induced mussels to migrate downwards towards the bottom of reefs. Eschweiler and Christensen (2011) concluded that downward migration was the result of a trade-off between growth and predation risk. Possible consequences of reduced growth and body condition are lower fecundity and survival with implications for the entire populations. Whether the long-term impact of competition and facilitation via refuge on the population of mussels will turn out positive or negative depends on a complex interplay of various factors such as larviphagy (Troost, 2009), predation (Markert et al., 2013) and parasitism (Thieltges, 2006; Goedknegt et al., 2016).

Both, blue mussel beds and Pacific oyster reefs provide substrate for sessile species and habitat or refuge for mobile species. Whether the Pacific oyster invasion has affected the native mussel communities has been investigated in detail (see Kochmann et al., 2008; Markert et al., 2010). Markert et al. (2010) did not find a suppression of indigenous species but rather found an increased species richness, abundance and biomass across taxa in Pacific oyster reefs.

Figure 5. A blue mussel (Mytilus edulis) and Pacific oyster (Crassostrea gigas) bed/reef after a storm. What remained was a mix of dead and alive oysters anchored upright in the sediment (Photo: Karin Troost).

2.1 Development of surface area and biomass of blue mussels and Pacific oysters

Yearly monitoring of blue mussels and Pacific oysters takes place in the German and Dutch Wadden Sea. In the Danish Wadden Sea, monitoring of mussels and Pacific oysters ended in 2008, as blue mussel fisheries were no longer allowed. In Schleswig-Holstein monitoring of blue mussels and Pacific oysters is combined. In Lower Saxony blue mussel monitoring is still ongoing. Monitoring of Pacific oysters, however, took place as part of research projects between 2003 and 2013, but is not implemented in the long term. The Pacific oyster monitoring was carried out at selected sites of the blue mussel monitoring. In the Dutch Wadden Sea, the monitoring of blue mussels and Pacific oysters is combined; the method consists of a combination of aerial and field surveys.

The development of the area of blue mussel and Pacific oyster beds/reefs show distinct patterns (Figure 6). The area of beds and reefs in the Schleswig-Holstein Wadden Sea was relatively high (1,000 ha) around the year 2,000 and consisted of only blue mussels. Due to low recruitment, the area of blue mussel beds decreased in Schleswig-Holstein between 2001 and 2005 after which it remained constant, but low. The area of Pacific oyster reefs increased strongly after 2005 and since 2008 more than half of the beds/reefs were classified as Pacific oyster reefs. The biomass of blue mussels decreased between 1999 and 2005 after which it showed a slight increase until 2013. The biomass of Pacific oysters strongly increased in Schleswig-Holstein between 2004 and 2009. After the cold winter of 2009/2010 the biomass of Pacific oyster decreased to similar levels as blue mussels (Büttger et al., 2011).

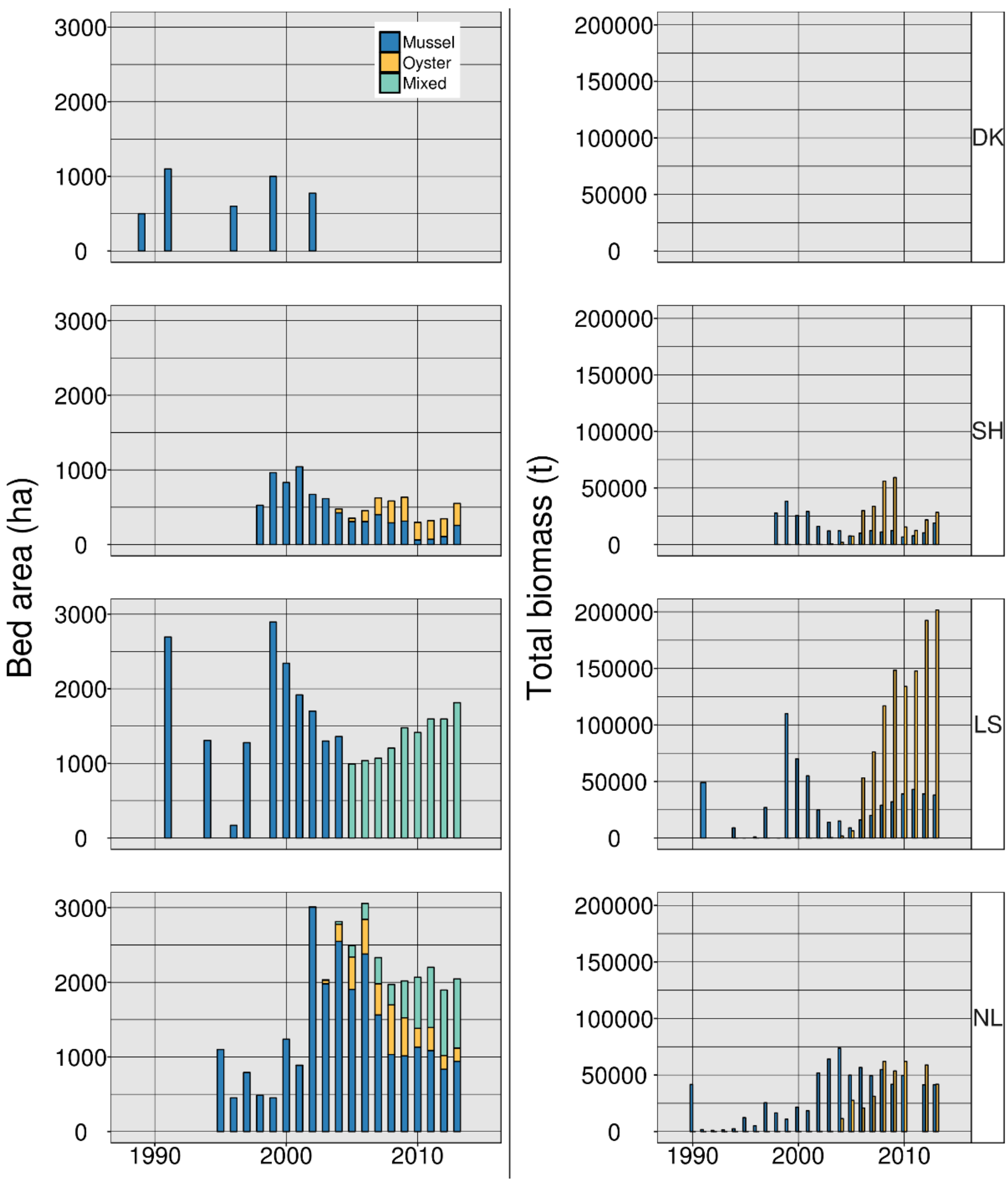

Figure 6. Development of the total area (ha) and biomass of blue mussels (Mytilus edulis) and Pacific oysters (Crassostrea gigas) in Denmark (DK), Schleswig-Holstein (SH), Lower Saxony (LS) and the Netherlands (NL), between 1988 and 2013. The biomass is given as total live wet weight in tons (t). Biomass data for Denmark are lacking. In Lower Saxony, the biomass for mussels and oysters was surveyed on a selected number of sites (see Box 1).

Blue mussel biomass in Lower Saxony decreased from 110,000 tons live wet mass and a total area of almost 3000 ha in 1999 to 9,000 tons and 1,000 ha in 2005. The biomass of Pacific oysters remained very low until 2004 but increased rapidly from 2005 through 2007 (Millat et al., 2009, 2012). Thereafter, biomass of Pacific oysters and also of blue mussels has increased in the total area, while Pacific oysters dominate with 80 % of the total biomass. In 2013, a total of almost 250,000 tons live wet mass of both species was determined for Lower Saxony (Figure 6).

The area of blue mussel beds in the Dutch Wadden Sea was relatively low until 2002 when the recruitment event in summer 2001 resulted in a strong increase. The total area of beds was variable but remained relatively high after 2002. Since 2008, the total area of blue mussel and Pacific oyster beds/reefs has remained relatively constant at around 2,000 ha. The proportion of Pacific oyster and mixed beds/reefs has increased since 2003 and has remained relatively constant at ca 50 % since 2008. The biomass of blue mussels shows a similar pattern as the area of blue mussel beds, i.e., an increase until 2005 and a slight decline after which it remains relatively constant between 2005 and 2013. The biomass of Pacific oysters has steadily increased after invasion but has remained relatively constant since 2008.

2.2 Spatial coverage per tidal basin

Figure 7 shows the average spatial coverage of the intertidal area by blue mussel and Pacific oyster beds/reefs per tidal basin for the periods 1999-2002, 2003-2006, 2007-2010 and 2011-2013. Because most of the bed/reef structures consist of both, blue mussels and Pacific oysters, species are not distinguished. The percentage coverage of the intertidal area per tidal basin varies between 0 and 6 %. The high average coverage of 6 % is observed in one small tidal basin in the eastern Dutch Wadden Sea only (Eilanderbalg). The highest coverages occur in the eastern Dutch and the western Lower-Saxon Wadden Sea where the intertidal flats are sheltered from strong hydrodynamics (Folmer et al., 2014). The coverages are low in the western Dutch Wadden Sea and the Dithmarschen area which are highly exposed to currents and waves (southern part of Schleswig-Holstein).

The largest changes are observed in the southwestern part of the Lower-Saxon Wadden Sea where the coverage decreased in the period 1999-2006 and slightly increased in the period 2007-2013 due to the invasion of the Pacific oyster. The mussel and oyster bed/reef area in the northern half of the Wadden Sea decreased between 1999-2002 and 2003-2006 after which the coverage remained stable.

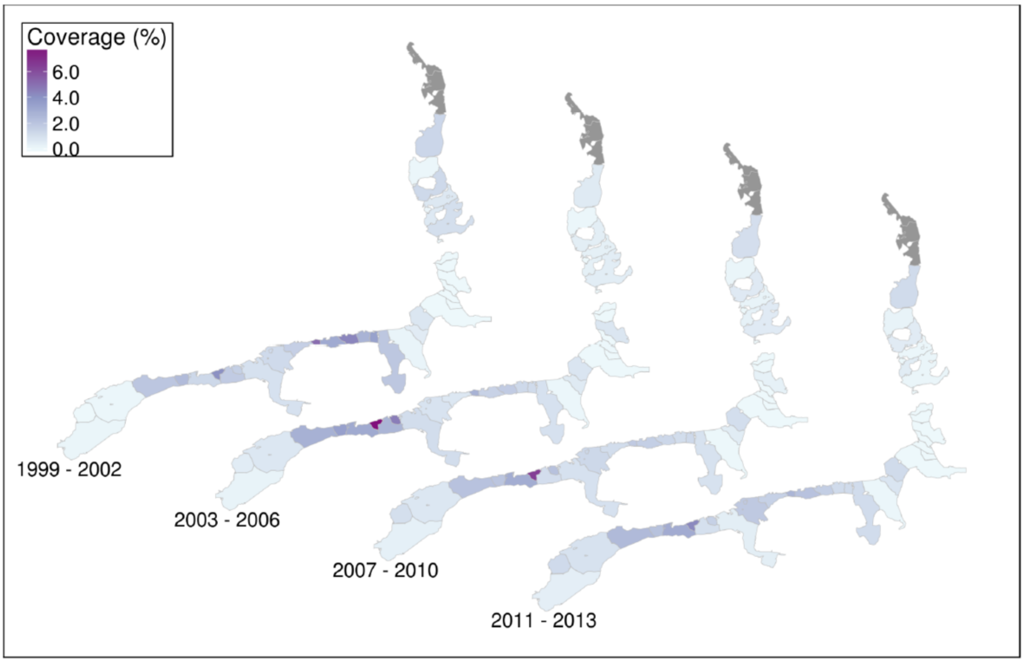

Figure 7. Average coverage per tidal basin for the periods 1999-2002, 2003-2006, 2007-2010 and 2011-2013. Coverage is the percentage of intertidal flat that is covered by blue mussel beds, Pacific oyster reefs or mixed beds. Data for Denmark is lacking and denoted in grey.

2.3 Spatial distribution between 1999 and 2013

The map in Figure 8 shows for each 200 × 200 m pixel of the intertidal Wadden Sea how often it was covered by blue mussel beds or Pacific oyster reefs in the period 1999-2013. It illustrates the locations on the intertidal flats where mussel and oyster beds/reefs tend to occur. The majority of the intertidal flat area was never occupied during 1999-2013 and beds/reefs occur at rather specific locations. Particularly, they occurred on sheltered intertidal flats in the intermediate elevation zones where the inundation time is not too low (inundation is required for filter feeding) and where the impact of currents and waves is not too high (as is the case in the lower intertidal zone).

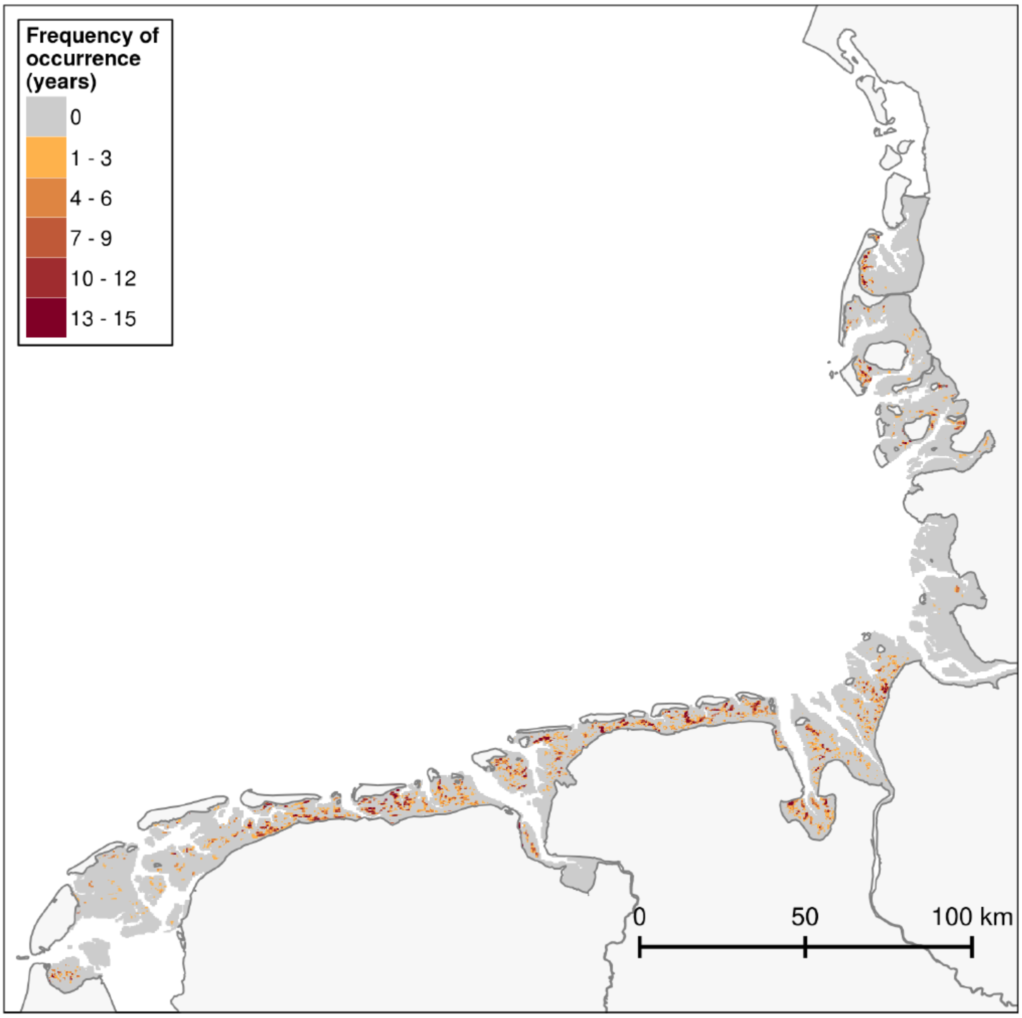

Figure 8. Frequency of occurrence of blue mussel, Pacific oyster and mixed beds/reefs. The value of each pixel represents the number of times it was occupied in the period 1999-2013. A pixel is considered to be occupied if part of it contained beds/reefs.

2.4 Relationship between occurrence of blue mussel and Pacific oyster beds/reefs and environmental conditions

In this section the relationships between the occurrence of beds/reefs and the abiotic environmental conditions at the seafloor are presented. These types of relationships are important to understand and model future distributions when conditions change (for example due to sea level rise). Abiotic variables describing the hydrodynamics at the seafloor (mean shear stress and exposure time) were simulated with the General Estuarine Transport Model (Burchard & Bolding, 2002), which is designed for coastal ocean simulations with drying and flooding of intertidal flats. A bathymetry with resolution 200 × 200 m for the entire Wadden Sea was used as a basis for the hydrodynamic model (Gräwe et al., 2016, Folmer et al., 2016). The bathymetry was also used to calculate the slope. Slopes are steep at tidal channels where tidal currents are strong and shallow slopes occur in calmer areas. The slope can be used as a proxy for past and present hydrodynamics and is thus related to mussel and oyster bed distributions.

The points in Figure 9 represent the fraction of cells in which beds/reefs were present per environmental variable interval during the period 1999-2013. The fraction of occupied cells is high for the classes with shallow slopes and decreases quickly when the slopes increase. Particularly, the fraction of occupied cells is about 0.13 for the class with the smallest slopes. It is virtually zero for slopes beyond the 9th class (0.024-0.027). The fraction of occupied cells is high for the classes of low bottom shear stress. Interestingly, the curve peaks at a shear level that is greater than the minimum shear class. This may be explained by the fact that some current is required for the replenishment of food resources (mainly phytoplankton and suspended microphytobenthos). Mussel and Pacific oyster beds/reefs do not occur at locations where bottom shear stress is too high. The fraction of occupied cells is related to exposure time in a hump-shaped fashion. The habitat characteristics of cells that are exposed to air about 20-35 % of the time are best. Below these levels, the exposure time may be too low so that there is too little time for filter feeding. Above these optimal exposure time levels, which is low in the intertidal, the hydrodynamic stress may limit the occurrence of mussel beds and oyster reefs. Analyzing regional differences in these relationships may help explain regional differences in mussel bed cover as observed in Figures 7 and 8.

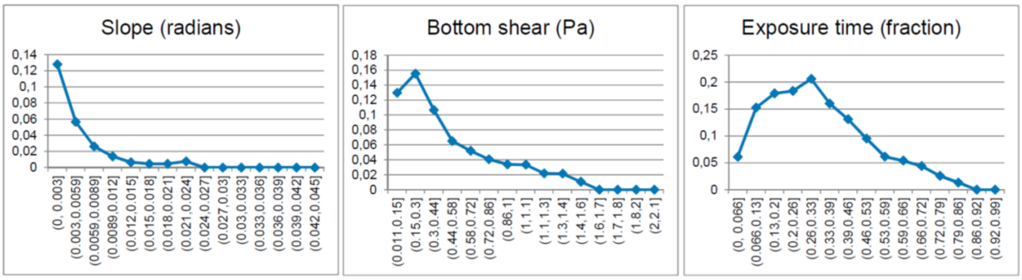

Figure 9. Relationships between the fraction of occupied cells and the environmental variables describing the abiotic conditions at the seafloor: slope, bottom shear and exposure time. The continuous environmental variables are classified into intervals of equal size.

3. Assessment

3.1 Overview of targets and management

In the late 1980s and early 1990s the total area of intertidal blue mussel beds strongly declined in all parts of the Wadden Sea. As a result, protection measures and trilateral targets for intertidal blue mussels were established. The Wadden Sea Plan 1997 contained a trilateral policy and management plan for mussel fishery aiming for a trilateral increase of the total area and a more natural development and distribution of natural intertidal mussel beds. The following related targets were defined in relation to intertidal mussel beds and habitat (Essink et al., 2005, CWSS, 2009 (QSR 2009)):

- A natural dynamic situation in the tidal area;
- An increased area of geomorphologically and biologically undisturbed tidal flats and subtidal areas;
- An increased area of, and a more natural distribution and development of natural blue mussel beds.

To protect and obtain an increase in the area of intertidal blue mussel beds, the entire intertidal area in the Dutch Wadden Sea was permanently closed for blue mussel fisheries in 2004, after partial closures of 25 % in 1993 and another 10 % in 1999 (Steenbergenet al., 2006). Currently, blue mussel fishery in autumn is restricted to parts of the subtidal considered to be unstable, and in spring stable areas can also be fished (Smaalet al., 2013). In Lower Saxony, fishery of seed mussels is allowed in the subtidal and defined parts of the intertidal. Fishery takes place in accordance with the (regularly revised) management plan. In Schleswig-Holstein, mussel fishery has not been allowed in the intertidal area, but in the subtidal, except for the national park core zones since 1997. About 50 % of the Danish Wadden Sea has been closed for mussel fishery since 1992. Since 2008, mussel fishery has not been allowed in the entire Natura 2000 area in the Danish Wadden Sea.

The prohibition of mussel fishery in the intertidal areas should allow a natural development of blue mussel beds. However there are two developments which may be considered unnatural, depending on ones perspective. The first is the spread of the Pacific oyster after its introduction by humans in the 1970s; it has affected morphology and ecological functioning (Troost, 2010; Markert et al., 2010). Secondly, since 2010, intertidal Pacific oysters are being hand-picked by a limited group of licensed fishermen. Hand-picking of Pacific oysters is also accepted on intertidal flats near the island of Sylt. Hand-picking mainly occurs on beds that are predominantly occupied by Pacific oysters but also on mixed beds. Blue mussels and Pacific oysters co-exist and mussels may find shelter in the interspace of oyster reefs (Eschweiler & Christensen, 2011; Buschbaum et al., 2016). It is therefore possible that the spread of the Pacific oyster led to an increase in the area covered by mussel beds/oyster reefs. However, due to competition, the growth and biomass of individual mussels is likely to be hampered by the presence of Pacific oysters (Eschweiler & Christensen, 2011), which may in turn affect birds that are dependent on blue mussels (Markert et al., 2013). It remains unknown how mussel beds would have developed without the presence of Pacific oysters.

3.2 Overview of threats

The Wadden Sea emerged in its current form 8000 years ago. Since then, the Wadden Sea has continuously gone through significant changes in environmental conditions and community composition; changes resulted from both natural and anthropogenic causes (Reise, 2013). Environmental conditions will continue to change. The most prominent expected upcoming changes with respect to blue mussel beds and Pacific oyster reefs are related to global warming, sea-level rise and de-eutrophication (see reports eutrophication, climate ecosystems, climate change, geomorphology).

1. Due to global warming the phenology of the resources of bivalves (pico-plankton for bivalve larvae) and of predators (shrimps and crabs) will change (Beukema & Dekker, 2005). It is likely that temporal shifts in trophic dynamics cause changes in recruitment of bivalve populations (Philippart et al., 2014). Furthermore, the development rate of larvae also depends on water temperature which influences the duration of the pelagic phase and thus dispersal distances. How these environmental changes will play out and influence net recruitment and adult mussel and oyster populations is an important research question which requires a substantial monitoring effort and targeted research.

2. Sea level rise and geomorphology: Sea-level rise and the mining of gas and salt (especially relevant in the Netherlands) may cause (relative) seafloor subsidence and change the geomorphology and result in shifting habitats. Relative seafloor subsidence can, however, be compensated by sediment accretion (Oost et al., 1998, Wiersma et al., 2009 (QSR 2009)). Whether accretion rates are sufficient to fully compensate for future sea-level rise and seafloor subsidence is unknown and presumably site specific. Either way, due to anthropogenic impacts from the past (dikes, dams, groynes) and

present (mining), the intertidal geomorphological situation can not be considered to be entirely natural. The changing geomorphology affects the habitat suitability and thus the distribution of mussel and oyster beds/reefs.

3. De-eutrophication: Nutrient loading (most importantly phosphate) in the Wadden Sea has decreased since the 1980s which has led to lower levels of eutrophication and phytoplankton biomass (Van Beusekom et al., 2009 (QSR 2009)). It is possible that de-eutrophication reduces phytoplankton densities while growing Pacific oyster populations may increase the competition for food. It should be noted, however, that there are many other factors that also influence the populations of mussels.

4. Recommendations

Recommendations for monitoring and research

- More systematic and trilateral harmonized monitoring of coverage, biomass and proportion of blue mussels and Pacific oysters is required (see Box 2). In addition to improving comparability between regions, it is important to maintain comparability within series. Comparability can be improved by the application of innovative techniques, such as remote sensing by means of satellites and drones. These techniques have the potential to provide large scale and frequent measures of coverage. Harmonized monitoring will help to compare regions, provide better insight into the determinants of the coverage and evaluate ecosystem engineering effects. Trilateral harmonization of biomass monitoring would lead to better understanding of trophic dynamics. Field surveys will remain necessary as long as there is no established methodology for estimating surface area and biomass by means of remote sensing only;
- The current monitoring programs lack systematic measurements on productivity of blue mussels and Pacific oysters. This is a shortcoming, as productivity is crucial to understanding the provision rates of food for consumers. In a similar vein, recruitment is an important determinant of populations and systematic monitoring of larvae and spat is required to understand population variability. Additional monitoring in late summer or autumn is required to meet these shortcomings;
- Whether the area of mussel beds are at natural and targeted levels is hard to answer because these levels are impossible to define for naturally fluctuating populations. Furthermore, the invasion of Pacific oysters has changed the environmental conditions for mussels. Insight into how mussel and oyster beds/reefs will develop under constant or changing environmental conditions requires targeted and integrated research into factors such as recruitment, hydrodynamics and ice-scouring. These factors are highly stochastic and variable in space and time which asks for harmonized and intensified monitoring integrated with models;
- Pacific oyster reefs and mussel beds affect the physical environment (van der Zee et al., 2012) and they provide habitat and resources for many species (Markert et al., 2010, 2013). Although oysters and mussels have similar kinds of effects on the environment, it is important to understand the differences. Further changes in the development and composition of beds/reefs is expected which may influence hydrodynamics, morphology, habitat supply and the associated communities. We recommend targeted large-scale research into differences in ecosystem functioning in and in the vicinity of mussel beds, oyster reefs and mixed beds/reefs of variable composition;

- Further surveys, research and integration of the distribution and structure of subtidal natural mussel beds so that subtidal and intertidal populations can be considered jointly (see report subtidal habitats);
- Pacific oyster reefs are hot-spots for non-native species which may become invasive. Establishments, developments and interactions of non-native species with Pacific oysters and mussels should be monitored regularly to understand the spread of these species.

Recommendations for management

- Nature conservation targets should be clarified and evaluated against the background of changing environmental conditions in the Wadden Sea;
- Maintain current protection measures to allow natural development of intertidal and subtidal mussel beds and oyster reefs. To understand the effectivity of protection, the measures should be combined with systematic monitoring.

5. Summary

Until the Pacific oyster invaded the Wadden Sea, the blue mussel was the most abundant bed-forming intertidal, epibenthic species. Mussel fisheries in Lower-Saxony and the Dutch Wadden Sea in the 1980s and 1990s caused dramatic decreases in blue mussel bed area. Protection measures were established which enabled more natural development of mussel beds and more recently Pacific oyster reefs. Although the invasive Pacific oyster was already introduced to the Wadden Sea in the early 1970s, it took until 2005 before the exponential increase set in. Currently, blue mussels and Pacific oysters are important in terms of biomass, community composition, ecological functioning, ecosystem engineering and biodiversity.

Distribution and dynamics of blue mussel beds and Pacific oyster reefs are determined by larval supply, settlement and various post-settlement processes. Predation by shrimp, starfish and crabs is important shortly after settlement. Currents, waves and ice-scouring during cold winters may be important limiting factors during all life stages. Beds and reefs of mussels and Pacific oysters mostly occur between the main land and islands where they are protected from strong onshore winds and waves. During the period 1999-2013, the highest abundances were found in the eastern Dutch Wadden Sea and in Lower-Saxony.

Global warming is likely to affect the phenology and development of adult mussels and oysters, of their larvae and of their resources and predators. Shifts in phenology in combination with changing trophic dynamics are expected to cause changes in recruitment of bivalve populations with consequences for the populations. Sea-level rise may cause (relative) seafloor subsidence and change the geomorphology and hydrodynamics leading to shifting habitats and in changing distributions of mussel and oyster beds/reefs. Finally, it is likely that de-eutrophication in combination with increasing Pacific oyster populations (competition for food) will reduce food availability for native blue mussels. The way in which these (and other) changing environmental conditions will interact and affect mussel and oyster distributions is hard to predict.

More systematic and trilateral harmonized monitoring of blue mussels and Pacific oysters is recommended, so that understanding and modeling of population dynamics and spatial distributions can be improved. Harmonization may be supported by the

application of innovative techniques such as remote sensing by means of satellites and drones. In addition to improved monitoring of adult populations it will be important to include systematic monitoring of larvae and spat of blue mussels and Pacific oysters so that population variability and future response to climate change can be modeled. Improved knowledge of the interplay of the intertidal and subtidal populations are expected to help understand the development of both intertidal and subtidal populations. Finally, the development of blue mussels and Pacific oysters lead to (new) interactions with native and non-native species (including diseases and parasites (Goedknegt et al., 2016). To understand the consequences of these interactions it will be important to adapt the data collection of mussel beds and oyster reefs such that it fits in the context of their current and future communities.

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