Different ecosystem engineering by alien oysters and

native mussels – a field experiment in the Wadden Sea

Master Thesis

University of Southern Denmark

Institute of Biology

Odense

by

Judith Kochmann

Written at Alfred Wegener Institute for Polar and Marine Research,

Wadden Sea Station Sylt

December 2007

Declaration

I herby confirm that this thesis is my own work and has been carried out only with the mentioned forces and help. It has not been submitted to any study board either at this or another university before.

List, 18th of December 2007

Judith Kochmann

Acknowledgements

Contents

Chapter 1

Chapter 2

Chapter 1

1 Theory and Background

First, an introduction is given to the concepts of ecosystem engineers and bioinvasion in the marine environment. Then, the two habitat-generating ecosystem-engineers in the Wadden Sea are introduced, the invasive oyster *Crassostrea gigas* and the resident mussel *Mytilus edulis*, together with comments on the associated benthic assemblages. Finally, purpose and design of the field experiment are explained.

1.1 Biogenic habitat engineering

1.1.1 The concept of ecosystem engineering

Intra- and interspecific competition for abiotic and biotic resources, predation, parasitism and mutualism are key processes of interactions between organisms and determine the distribution and abundance of species (Krebs 1985, Begon at al. 1990). The concept of 'Ecosystem engineering' was introduced by Jones et al. (1994) adding the role of creation, modification and maintenance of habitats by organisms as non-trophic interactions. This has become a major focus of recent research.

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species. The direct provision of resources, feeding and assimilation by the engineers are not included and thus, separate engineering from other ecological processes. Ecosystem engineers cause physical changes in the state of biotic and abiotic materials. Two essential terms given by Jones et al. (1994) are 'autogenic' and 'allogenic' engineering. Autogenic engineering describes the 'change in the environment by the structure of the organism itself, mainly dead or living tissues'. One example is phytoplankton scattering and absorbing light in the water column (Townsend et al. 1992). Allogenic engineering means a 'change of the environment by transformation of living or non-living materials from one physical state to another'. It changes the quality, quantity or distribution of resources utilised by other taxa. Marine burrowing macrofauna, such as the lugworm *Arenicola marina*, are typical examples of allogenic engineers. They actively change the sediments by particle reworking and burrow ventilation (Kristensen 2001, Volkenborn and Reise 2006). An overview of organisms acting as ecosystem engineers is given by Hastings et al. (2007).

In conclusion, an organism might influence a set of target abiotic variables through altered structure and these altered abiotic variables then influence a set of target biological traits (Hastings et al. 2007).

1.1.2 Molluscs as ecosystem engineers

Molluscs are important ecosystem engineers in aquatic habitats by producing a large amount of shells. Shells introduce complexity and heterogeneity in the benthic environment. These shells persist over long geological times although this calcimass and its distribution can be changed by human activities. Individual shells differing in size and texture can be used as substratum for fouling organisms. Aggregates of dead or living mollusk shells provide refuges for organisms. Further, the characteristic physical structure of shells and their arrangement in biogenic reef habitats modify physical conditions, especially the flow of water above the bottom which in turn explains a majority of the variation in the performance of a resident organism (Lenihan 1999, Gutiérrez et al. 2003).

Soniat et al. (2004) showed that shell orientation plays a major role in mediating development and influencing community dynamics. Experiments with different orientation of oysters were undertaken and differences in larval responses depending on surface orientation could be shown. Sedimentation rates might also depend on shell orientation as it was revealed in a study by Castel et al. (1989). The sediment of Pacific oyster beds was compared to oyster-free sediment in Arcachon Bay, France. Even though the beds were more structurally complex compared to oyster-free sediments the deposition of organic-rich material decreased the oxygen levels and macrofaunal density.

Ecosystem engineering is also relevant in ecosystems where biological invasions take place and it is important to ask whether novel species assemblages function in the same way as native assemblages (Sax et al. 2007).

1.2 Marine bioinvasion

1.2.1 Terms

Biological invasions refer to range and expansions of species into new areas. Today, natural ecosystems constrained by biogeographic barriers such as oceans have become functionally connected by humans through global transport and trade. This results in an increasing number of species in areas where they have not been recorded in historical times and leads to a homogenisation on a global scale (Reise et al. 2006).

Many different terms are linked and commonly used with regard to bioinvasion. 'Native' or 'resident' species occur or have arrived in a region independent of humans whereas 'non-native', 'exotic', 'alien' or 'invasive' species have been introduced by humans. The term 'introduction' refers to a release of organisms into natural ecosystems by human activities across natural barriers of dispersal. 'Invasion' means any process of colonization and establishment. It is more an ecological occupation process with community and habitat interactions regardless of evolutionary history (Falk-Petersen et al. 2006, Reise et al. 2006).

1.2.2   Facilitation of invasion

Among ecosystems, coastal areas and estuarine environments are particularly vulnerable to invasions due to numerous introduction vectors and activities facilitating invasions. In the North Sea about 80 non-indigenous species have been established and occur in self-sustaining populations. In estuaries, exotics account for about 20 % of the macrobenthic species, mainly invertebrates (Reise et al. 1999).

Human mediated transports allow a much wider and faster distribution of species to new habitats. Intercontinental shipping leads to an increase of exotic species in coastal environments mainly through the transport of spores, larvae or resting stages in ballast waters and fouling organisms attached to ship hulls. Inadvertent or even intentional introductions associated with mariculture are also some of the gateways for enhanced number of non-native species (Hedgpeth 1993, Carlton 1996, Wolff and Reise 2002). A detailed list of factors promoting aquatic species transmissions is given by Minchin (2007).

In addition to human vectors, certain characteristics of successful invaders have been discussed. These often cited features include: early sexual maturity, asexual reproduction, ability to colonize a wide range of habitat types, gregarious behaviour, high reproductive capacity and high dispersal rates. Species possessing more of these characteristics are likely to be successful invaders (van der Velde et al. 2006). A changing environment such as rising temperatures often cause physiological stress and failures in recruitment of native species and might facilitate invasive species to occupy empty habitats (Occhipinti-Ambrogi 2007). Recently, Sax et al. (2007) hypothesized that frequency distribution and variations in patterns of specialization of (1) predators and pathogens and (2) mutualists and facilitators might influence the invasibility of an ecosystem.

A successful invasion seems therefore to be less predictable than any explanatory model for invasion suggests. In fact, it depends on viable propagules which must arrive in

the novel habitat, physical factors and positive or negative biological interactions but also on the recipient community and current habitat conditions (Crawley 1987, Lodge 1993, van der Velde et al. 2006, Occhipinti-Ambrogi 2007).

1.2.3   Impacts and consequences of invasion

When species function as ecosystem engineers they are affecting functional diversity and food web structure of communities and ecosystems. In coastal systems, studies are mainly focused on ecological and evolutionary impacts. Ecological consequences include single-species impacts, multiple trophic impacts, recipient community impacts as well as pathogens and the spread of diseases. The term 'evolutionary impact' refers to invasive species removing or lifting natural dispersal and reproduction barriers that prevented hybridization between closely related invading and native species. It is more directed towards invasion pathways, hybridization and physiological adaptation. Details are given by Grosholz (2002).

Negative effects of invasive species have been widely discussed and a philosophy of 'guilty until proven innocent' has been suggested by Simberloff (2003). Beside land-based sources of marine pollution, overexploitation of living marine resources and physical alteration and destruction of marine habitats, invasive species constitute one major threat to oceans (Streftaris et al. 2005). They have been also termed 'biological pollutants' which negatively affect communities and habitats by structural shifts and modification of physical and chemical conditions (Elliot 2003, Olenin et al. 2007).

In contrast, non-natives can also be a complementary contribution to the functional diversity of the recipient ecosystem and facilitate native species (Reise et al. 2006). Habitat complexity might be increased and habitat modification and the creation of novel habitats might provide a limited or even new exploitable resource that can be utilized by native biota (Rodriguez 2006).
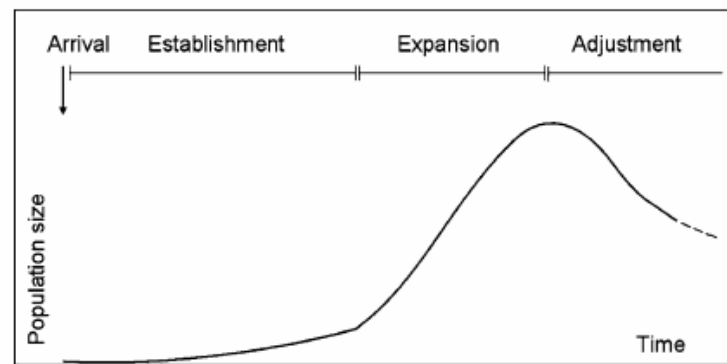
Fig. 1. Phases of invasion (Figure from Reise et al. 2006)

In general, studies on invasive species need to be species specific and regarded at different scales before an overall effect on recipient ecosystems can be evaluated. Many communities are not saturated at local and regional spatial scales and an increase in total species richness will be the net consequence of invasion (Sax et al. 2007). The invasion stage needs to be under observation as each invasion can be portioned into different phases: The arrival of the invader, the establishment of successfully reproducing individuals, an expansion phase and finally a phase of adjustment (Fig. 1). At each stage the effects might be different. As short-term assessments often fail to describe the role and impact of invasive species, a focus on long-term effects is strongly recommended because important processes as e.g. shifts of species composition, native biodiversity and interaction with abiotic variables can change over time (Strayer et al. 2006). Exotic species are unlikely to cause extinctions and the role of predation and disease and other biotic interactions as e.g. facilitation should be emphasized rather than competition (Sax et al. 2007). Overall, ecological effects, human-relevant impacts and ethical norms and values should be distinguished (Thieltges et al. 2006). Considering both, negative and positive effects of an introduced species, this might help to evaluate the overall effect of an invasion on recipient ecosystems.

1.2.4   Invaders as ecosystem engineers –examples

Habitat complexity can be decreased by invasive species when they replace more heterogeneous native species or assemblages. This has been shown in a comparative study of cordgrass in San Francisco Bay. There, the native cordgrass *Spartina foliosa* provides a moderate level of structural complexity compared to the hybrid *Spartina* (*S. alterniflora* x *S. foliosa*) which is excluding invertebrates due to its greater belowground biomass.

However, both species act as ecosystem engineers transforming open mudflats into vegetated habitats but with opposing effects on invertebrate communities (Brusati and Grosholz 2006).

Another example is the American slipper limpet *Crepidula fornicata*. For mussel beds in the Wadden Sea it was shown that the epigrowth by the slipper limpet reduces growth of *Mytilus edulis*. Due to an increased drag, the mussel has to invest more energy in its byssal production which reduces overall fitness. But, as revealed experimentally, starfish predation on mussels is decreased due to difficulties in handling fouled mussels and thus, the survival of mussels is enhanced. *C. fornicata* is also beneficial for its basibiont in acting as a sink for infectious trematode parasites. At the coast of France, it can also cause a shift of phytoplankton blooms from toxic flagellates to diatoms due to its faster silicate mineralization (Thieltges et al. 2006).

The Pacific oyster *Crassostrea gigas* in the Wadden Sea is another example of an invasive ecosystem engineer with ecological consequences for the ecosystem which need further exploration.
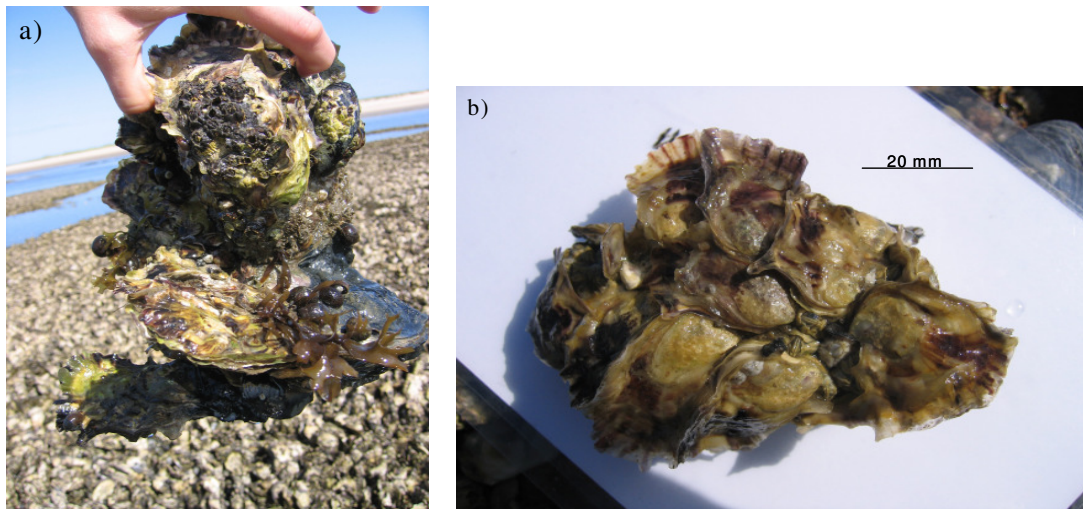
1.3 Beds of Pacific oysters in the Wadden Sea

1.3.1 Characteristics

Crassostrea gigas originates from Japan and has been introduced into various coastal areas around the world, mainly for aquaculture purposes (Wolff and Reise 2002). Its shape is irregular and depends on the type of substratum it is growing on. Individuals are often found attached to each other and forming huge clumps (Fig. 2). The external surface is mostly rippled with many cracks and crevices. Their filtering capacity is up to $19 \, l \, h^{-1} \, ind^{-1}$ (Walne 1972, Dame et al. 1984). *C. gigas* discharges eggs into the water where fertilization and all subsequent development take place. Egg spawning (50-100 million eggs) occurs mainly in late summer and larvae have a free-swimming period of up to 4 weeks where they are widely broadcasted before juveniles settle on hard substratum. Optimum temperature for development is about 23°C (Quayle 1988).

Oyster colonization of sediments plays an important role in the ecology of soft-substratum communities. They stabilize their substratum against erosion, stimulate further sedimentation and provide food resources for the organisms that live within the oyster matrix. Oysters also provide refuge to fish and invertebrates from consumers and physical stresses (Bertness 2007). Increased flow on oyster reefs elevated above the bottom,

however, has also been shown to increase the delivery of larvae and particulate food to filter feeders, reduce sedimentation and decrease hypoxic events (Lenihan 1999).

Fig. 2. Clump of a) adult oysters b) juvenile oysters

1.3.2   Occurrence of oyster beds in the Wadden Sea

The Pacific oyster *Crassostrea gigas* is an invasive species in the Wadden Sea. It was regularly introduced for aquaculture farming on the island of Sylt in 1986 and first record of natural spread from larvae dates from 1991 (Reise 1998, Fig. 3). On the island of Texel the oyster was first recorded in 1983 as a result from direct releases; a strong western current could have drifted larvae into the German Wadden Sea (Wehrmann et al. 2006).
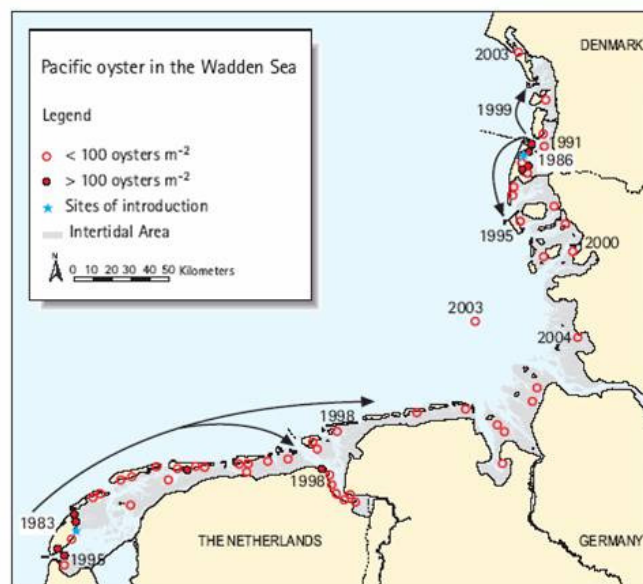
Fig. 3. Distribution of *C. gigas* in the Wadden Sea. Shown are years of introduction on Texel (1983) and Sylt (1986) and first records of settlement by larvae. Circles show mean abundance in 2003. Map from Reise et al. 2005.

The settlement period of *C. gigas* in the Wadden Sea is confined to a short period in summer from August to mid September. The larvae settle on all kind of hard substratum as mollusc shells, living mussels and periwinkles, stones, wood and concrete panels whereas *C. gigas* was mainly found attached to *M. edulis* in its beginning of spreading (Reise 1998). *C. gigas* primarily lives in the intertidal areas, in the same zone as *M. edulis*. With a mean growth rate of 7 mm per month juvenile oysters may reach a shell length of 35 - 53 mm after one year and a shell length of 70-80 mm after the 2nd year (Diederich 2006). Adult oysters can reach a shell length of 300-400 mm with individual live wet weight of 1 kg.

Anomalous high water temperatures in years 2001-2003 facilitated the development of the *C. gigas* population in the Northern Wadden Sea and the strong spatfalls occurring subsequently led to a high recruitment success in 2004 (Diederich et al. 2005). But there are other factors which probably enhanced the spread of *C. gigas*. The Pacific oyster is highly tolerant against cold winter temperatures (Reise 1998, Diederich et al. 2005). Survival of spat in the first winter depends on temperature whereas adult oysters seem to be less affected when ice covers tidal flats (Diederich 2006). No viral diseases are known to impact populations and predation rate is very low (Diederich et al. 2005). They are increasingly overgrowing blue mussels and so far, blue mussel beds are the most important location for the establishment of Pacific oyster reefs (Fig. 4). Nearly all existing intertidal blue mussel beds have turned into oyster reefs in the List tidal basin and mean densities increased from > 100 ind. / m² in 2003 to > 1000 ind. / m² in 2006 (Nehls and Büttger 2007). A positive feedback in settlement was also revealed; it is suggested that oysters will aggregate in more compact oyster reefs and more recruits are to be expected on already established aggregations in the future (Diederich 2005).
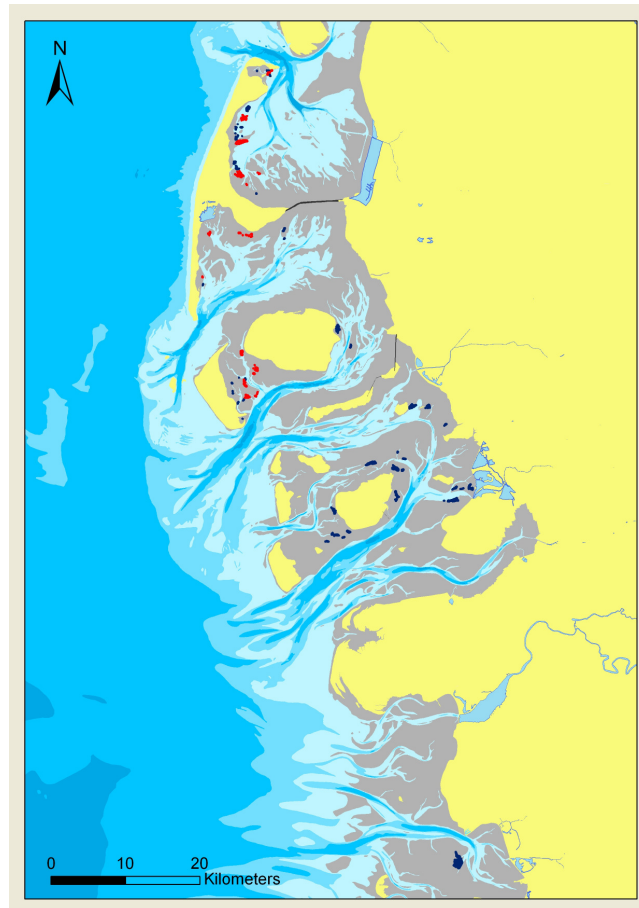
Fig. 4. Occurrence of blue mussel beds in the North Frisian Wadden Sea. Blue mussels (blue), mussels associated with oysters (red). Data provided by Nehls and Büttger from 2005 and 2006.

Species associated with oysters in the Wadden Sea have been investigated by Diederich (2005). Adult oysters can be overgrown by barnacles and juvenile oysters also use barnacles as substratum for settlement. The brown algae, *Fucus vesiculosus* can be found on oyster reefs but is not supposed to overgrow these as much as mussel beds. On intertidal mussel beds the presence of *F. vesiculosus* decreases oyster recruitment and lowers overall oyster abundance. Predation is of minor importance in the Wadden Sea due to a temporal mismatch between predator abundance and oyster recruitment (Nehls et al. 2006). The Oystercatcher *Haematopus ostralegus* and the Herring Gull *Larus argentatus* may adapt to new species and learn to handle at least small individuals of oysters whereas the Common Eider *Somateria mollissima* is neither able to crush the hard-shelled oysters nor to swallow large-sized individuals.

1.4   Beds of Blue mussels in the Wadden Sea

### 1.4.1   Characteristics and occurrence of mussel beds in the Wadden Sea

The blue mussel *Mytilus edulis* is widely distributed along the coasts of Europe. It secretes byssal threads for attachment and thus, can be found on rocky shores and soft-bottoms. Blue mussels produce very large numbers of gametes (5 – 12 million eggs) and larvae undergo a planktonic life of several weeks depending on temperature, food supply and the availability of suitable settlement substratum (Saurel at al. 2004). Postlarvae attach themselves with secreted byssus threads and after 3-4 years individuals may attain sizes of 40-70 mm in the Wadden Sea (Nehls 2003). Peak settlement occurs from May to September (Strasser & Günther 2001).

Spatfall is very variable and often shows annual variations which can be partly related to variations in winter temperature. After mild winters the main predators such as shore crabs appear earlier on the tidal flats. This seriously affects the survival of young benthic bivalve stages. Therefore, *M. edulis* often shows a higher recruitment success after strong winters than after mild winters (Beukema 1991, Strasser and Günther 2001). Mussels are particularly gregarious at settlement, the attraction of larvae to adult beds essentially being a thigmotactic response which is aided by their ability to attach and detach until favourable situations are encountered. Settlement is also favoured by roughened, scarred or pitted surfaces and distribution patterns can partly be attributed both to the surface texture and the topography of mussel beds (Seed 1969).

In the Wadden Sea, the blue mussel *Mytilus edulis* is forming extensive stable and permanent beds which are known as 'hotspots' of epibenthic biodiversity (Saier et al. 2002, Buschbaum 2006, Fig. 5). They are found in the subtidal as well as on intertidal sites and are commercially valuable. Persistent mussel beds generally occur on sheltered areas, e.g. in the 'Königshafen' which is a protected embayment at the island of Sylt.

Today, the area of blue mussel beds and blue mussel biomass are strongly decreasing in most places of the Wadden Sea; total biomass of blue mussels in the List tidal basin decreased from 1400 tons in 1999 to 200 tons in 2006 (Nehls & Büttger 2007). Primarily, the occurrence of the invasive Pacific oyster is believed to cause the decline in mussels. But it appears that blue mussel biomass and area started to decrease independently long before the Pacific oyster reached significant densities. It is likely that the annual variation in predation rate and recruitment success relates to winter temperatures (Strasser and Günther 2001, Beukema and Dekker 2005). Thus, the long

period of mild winters since 1995/96 led to a low recruitment of blue mussels on existing beds with no further establishment of new beds (Nehls et al. 2006).
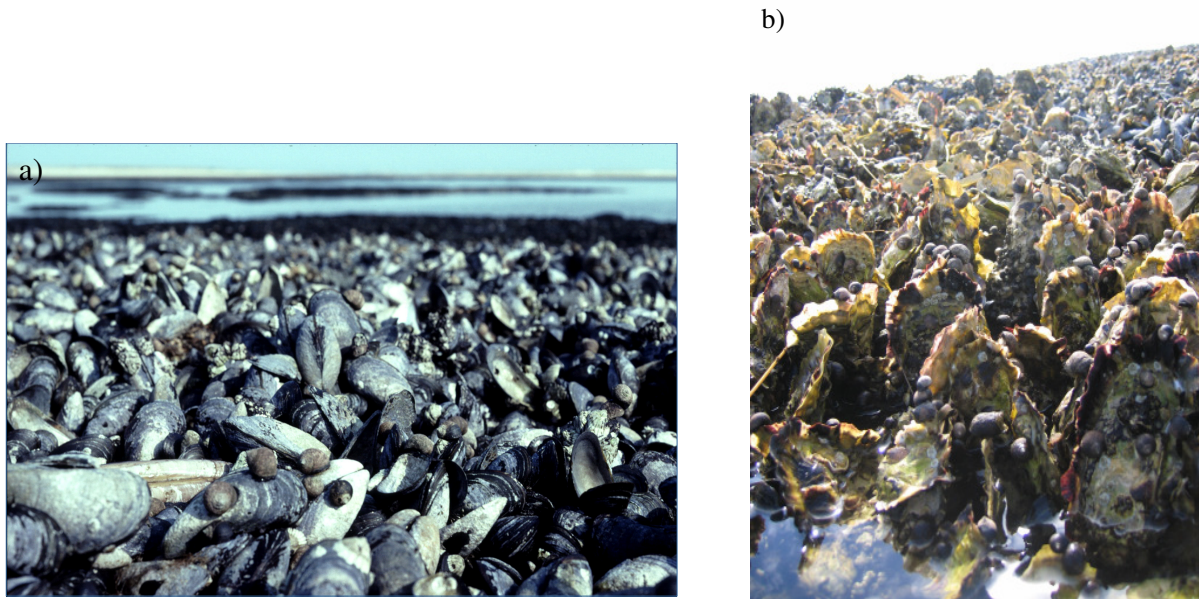
Fig. 5. a) Mussel bed in 1995 b) Oyster reef in 2006 in the Wadden Sea

1.4.2 Role of blue mussel beds in the ecosystem

Blue mussels provide one of the main biogenic hard structures in soft-sediments and are important ecosystem engineers in marine benthic systems; they aggregate into beds and modify the nature and complexity of the substratum. Major processes of mussel beds are altered flow regime by a raised bottom layer, enrichment by biodeposits (faeces and pseudofaeces), accumulation of sediment and irregular surface topography, which influences the rates of dislodgement, predation, larval recruitment and growth (Commito and Dankers 2001, Reise 2002). Mussel beds are also important for the material flux in shallow water habitats; they have a strong filtering capacity of up to 9 l h^{-1}ind^{-1} (Walne 1972). They act as processors of estuarine materials and accelerate the cycle of production and breakdown of organic matter (Dame and Dankers 1988, Dankers and Zuidema 1995). A high areal coverage by mussel beds increases the energy flow which is based on phytoplankton production and depends upon input from offshore waters (Asmus 1994).

Mussel beds also serve important functions for a range of organisms either directly or indirectly by providing shelter and creating space for associated organisms (Asmus 1987, Commito and Boncavage 1989; Dittmann 1990). Thus, many associated species are more abundant in mussel beds than in surrounding habitats e.g. juvenile shore crabs (*Carcinus maenas*) and periwinkles (*Littorina littorea*).

1.4.3   Associated species of mussel beds

Mussel beds and their dense byssus matrix support a rich benthic community. With increasing size and age of the mussel beds the diversity of the associated community, mainly invertebrate species, increases, because the structural complexity and thickness of the bed is linked to age (Tsuchiya and Nishihira 1986). Conversely, diversity decreases with increasing tidal elevation (Seed 1969, Saier 2002).

The infaunal community structure is often affected by the strong filtering capacity of the blue mussels, the production of faeces and pseudofaeces, low oxygen and high sulfide levels (Commito and Dankers 2001). Therefore, the abundance of oligochaetes and polychaetes with non-planktonic larvae is often high inside mussel beds whereas other polychaetes are less abundant. Deposit-feeding worms profit from the organic matter that is deposited as pseudofaeces (Dittmann 1990, Commito and Boncavage 1989).

Diversity of epifauna differs between subtidal and intertidal mussel beds mainly due to a higher abundance of a few dominant species such as juveniles of *L. littorea* and *C. maenas* in the intertidal and higher number of less dominant species in subtidal mussel beds (Saier 2002). Grazing and bulldozing effects of *L. littorea* depend on tidal emergence of the mussel beds. As recruitment is restricted to the intertidal zone juvenile periwinkles are more abundant on intertidal mussel beds where they can significantly reduce barnacle abundance (Buschbaum 2000). Barnacle epibionts and tidal emergence have strong effects on growth of mussels. On subtidal beds, mussels are larger and less overgrown by barnacles (Buschbaum and Saier 2001). It is suggested that a heavy barnacle cover can increase mussel recruitment as epibionts provide additional structure for settlement. In contrast, individual mussels may suffer reduced growth from the presence of balanid epibionts. They need to invest more energy in byssal production due to the increased drag imposed by the epibiont. Another species often found on mussel beds is the shore crab *C maenas*. It is one of the main predators on the intertidal flats in the Wadden Sea and studies on predation pressure have revealed that the early benthic stages prey on microfauna and juvenile macrofauna (Scherer and Reise 1981). During winter juveniles stay in the subtidal channels whereas in October they bury on tidal flats and use mussel beds as refuge against predation (Thiel and Dernedde 1994). The epiphyte *Fucus vesiculosus* is also often associated with mussel beds. It partly covers mussel beds, reduces current velocities, enhances sedimentation and supports overall macrobenthic diversity (Albrecht and Reise 1994).

Blue mussels serve as important food item for the seastar *Asterias rubens*. Experiments on the feeding behaviour of *A. rubens* by Saier (2001) showed that clean subtidal mussels are preferred above barnacle-overgrown intertidal mussels. But abundance patterns reveal that seastars are too scarce in subtidal areas to reduce the number of mussels. On the other hand, it is suggested that juvenile seastars may indirectly reduce mussel recruitment in the subtidal zone by preying upon barnacles that usually enhance mussel recruitment. While epibenthic predators such as *A. rubens* and *C. maenas* increase the mortality for juvenile mussels, the most important predators consuming adult mussels are the Common Eider *Somateria mollissima* and the Oystercatcher *Ostralegus haematopus* (Obert and Michaelis 1991, Dankers and Zuidema 1995, Nehls et al. 1997).

The buffering effect of the associated macrofauna on predation of mussels may be important for young mussels to succeed in growth. So despite their relative low biomass and production the associated macrofauna has a key function in the development of intertidal mussel beds which in turn have an important impact on the whole tidal flat ecosystem (Asmus 1987).

1.5   Experimental design and purpose of the work

Consequences of the facilitation or inhibition of other organisms that have responded to the availability of resources caused by the ecosystem engineers are 'organism-mediated feedbacks' (Gutiérrez et al. 2003). A field experiment was designed to test the role of the invasive species Pacific oyster *Crassostrea gigas* and the native blue mussel *Mytilus edulis* (Fig. 6). Both act as ecosystem engineers in the Wadden Sea and with their shell provide a resource which is not provided in the non-engineered environment.

Effects of suspension feeders on each other and on the ecosystem are expected to change systematically with scale, where introduced species may represent novelties on small scale but may be redundant at larger scales. Thus, a large-scale experimental approach was applied in this study. A closer look at their specific characteristics may reveal quite different effects on other organisms that are responding to the biogenic habitat change.

Hastings et al. (2007) suggested that studies on physical ecosystem engineers should be directed towards various questions, i) How does engineer abundance and type of physical activity influence the spatial distribution and temporal persistence? ii) How do physical processes then influence persistence of structure and its effects in the landscape?

iii) How does structural change influence the target abiotic variables and biological traits? In our study we tried to focus on these questions.

The experimental design allowed testing effects of both bivalves on the associated benthic community. This study focused on effects on sediment composition, infaunal and epibenthic invertebrates associated with changes in the suspension feeder guild. The main questions of this study are:

1. What are the differences (number of species and individuals) between mussel, oyster, mixed and control plots with regard to:

    a) the associated endobenthic macrofauna?

    b) recruitment of the mussels, oysters and barnacles?

    c) the most abundant predator (shore crab *Carcinus maenas*) and most abundant grazer (periwinkle *Littorina littorea*)?

2. Does the composition of the surface sediment differ between the treatments?

We hypothesized that the physical differences between the two ecosystem engineers, *C. gigas* and *M. edulis*, would be reflected in differences in density, diversity and taxonomic composition of the invertebrate communities.

1.6 References

Albrecht, A. and Reise, K., 1994. Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. Helgol. Mar. Res. 48, 243-256.

Asmus, H., 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. Mar. Ecol. Prog. Ser. 39, 251-266.

Asmus, H., 1994. Benthic grazers and suspension feeders: which one assumes the energetic dominance in Königshafen? Helgoländer Meeresunters. 48, 217-231.

Begon, M., Harper, J.L. and Townsend, C.R., 2006. Ecology. Fourth ed. – Blackwell Publishers, Boston, 738 pp.

Bertness, M.B., 2007. Atlantic shorelines. Natural History and Ecology. Princeton University Press, New Jersey, 446 pp.

Beukema, J.J., 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. J. Exp. Mar. Ecol. 153, 97-113.

Beukema, J.J. and Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar. Ecol. Prog. Ser. 287, 149-167.

Brusati, E.D. and Grosholz, E.D., 2006. Native and introduced ecosystem engineers produce contrasting effects on estuarine infaunal communities. Biological Invasions 8, 683-695.

Buschbaum, C., 2000. Direct and indirect effects of *L. littorea* (L.) on barnacles growing on mussel beds in the Wadden Sea. Hydrobiologia 440, 119-128.

Buschbaum, C., 2006. Muschelbänke als Lebensgemeinschaften. In: Hempel, G., Hempel, I. und Schiel, S. (Hrsg.). Faszination Meeresforschung: ein ökologisches Lesebuch. Bremen. Seiten, 210-215.

Buschbaum, C. and Saier, B., 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. J. Sea. Res. 45, 27-36.

Carlton, J.T., 1996. Marine bioinvasions: the alteration of marineecosystems by nonindigenous species. Oceanography 9, 233-247.

Castel, J., Labourg, P.J., Escaravage, V., Auby, I. and Garcia, M.E., 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. Estuar. Coast. Shelf. Sci. 28, 71-85.

Commito, J.A. and Boncavage, E.M., 1989. Suspension-feeders and coexisting infauna an enhancement counterexample. J. Exp. Mar. Biol. Ecol. 125, 33-42.

Commito, J.A. and Dankers, N.M.J.A., 2001. Dynamics of spatial and temporal complexity in European and North American soft-bottom mussel beds. In: Reise, K. (Ed.), Ecological Comparisons of Sedimentary Shores. Springer, Berlin, pp. 39-59.

Crawley, M.J., 1987. What makes a community invasible? Gray, A.J. and Crawley, M.J. Colonization, sucession and stability: the 26th symposium of the British ecological Society. Oxford: Blackwell Sci. Publ., pp. 429-453.

Dame, R.F. and Dankers, N., 1988. Uptake and release of materials by a Wadden Sea mussel bed. J. Exp. Mar. Biol. Ecol. 118, 207-216.

Dame, R.F., Zincmark, R.G. and Haskin, E., 1984. Oyster reefs as processors of estuarine materials. J. Exp. Mar. Biol. Ecol. 83, 239-247.

Dankers, N. and Zuidema, D.R., 1995. The role of the Mussel (*Mytilus edulis* L.) and Mussel culture in the Dutch Wadden Sea. Estuaries 18, 71-80.

Diederich, S., 2006. High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. J. Exp. Mar. Biol. Ecol. 328, 211-227.

Diederich, S., Nehls, G., Beusekom, J.E.E. van and Reise, K., 2005. Introduced Pacific oysters (*Crassostrea gigas*) in the Northern Wadden Sea: Invasion accelerated by warm summers? Helgol. Mar. Res. 59, 97-106.

Dittmann, S., 1990. Mussel beds – amensalism or amelioration for intertidal fauna? Helgol. Mar. Res. 44, 335-352.

Elliott, M., 2003. Biological pollutants and biological pollution – an increasing cause for concern. Marine Pollution Bulletin 46, 275-280.

Falk-Petersen, J., Bøhn, T. and Sandlund, O.T., 2006. On the numerous concepts in invasion biology. Biological Invasions 8, 1409–1424.

Grosholz, E., 2002. Ecological and evolutionary consequences of coastal invasions. Trends in Ecology and Evolution 17 (1), 22-27.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L. and Iribarne, O.O., 2003. Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. Oikos 101, 79-90.

Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G., Talley, T.S. and Wilson, W.G., 2007. Ecosystem engineering in space and time. Ecology Letters 10, 153-164.

Hedgpeth, J.W., 1993. Foreign invaders. Science 261, 34-35.

Jones, C.G., Lawton, J.H. and Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373-386.

Krebs, C.J., 1985. Ecology. The experimental analysis of distribution and abundance. Third ed. – Harper and Row, New York, 800 pp.

Kristensen, E., 2001. Impact of polychaetes (*Nereis spp.* and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediements. Geochem. Trans. 12, 1-12.

Lenihan, H.S., 1999. Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. Ecological Monographs 69 (3), 251-275.

Lodge, D.M., 1993. Biological Invasions: Lessons for Ecology. Tree 8 (4), 133-137.

Minchin, D., 2007. Aquaculture and transport ina changing envrionment: Overlap and links in the spread of alien biota. Mar. Poll. Bull. 55, 302-313.

Nehls, G., 2003. Miesmuschelmonitoring 1998-2002 im Nationalpark Schleswig-Holsteinisches Wattenmeer. (Unpubl. Report to Regional Office fort he Wadden Sea National Park of Schleswig-Holstein) Bio Consult SH, Hockensbüll, Germany.

Nehls, G. and Büttger, H., 2007. Spread of the Pacific Oyster *Crassostrea gigas* in the Wadden Sea. Causes and consequences of a successful invasion, 55 pages.

Nehls, G., Hertzler, I. and Scheiffarth, G., 1997. Stable mussel *Mytilus edulis* beds in the Wadden Sea - They`re just for the birds. Helgol. Mar. Res. 51, 361-372.

Nehls, G., Diederich, S., Thieltges, D. and Strasser, M., 2006. Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? Helgol. Mar. Res. 60, 135-143.

Obert, B. and Michaelis, H., 1991. History and ecology of the mussel beds (*Mytilus edulis* L.) in the catchment area of a Wadden Sea tidal inlet. In: Elliot, M. and Ducrotoy, J.-P., eds. Estuaries and Coasts: Spatial and temporal intercomparisons. Fredensborg. Olsen and Olsen, pp. 185-194.

Occhipinti-Ambrogi, A., 2007. Global change and marine communities. Alien species and climate change. Mar. Poll Bull. 55, 342-352.

Olenin, S., Minchin, D. and Daunys, D., 2007. Assessment of biopollution in aquatic ecosystems. Marine Pollution Bulletin 55, 379-394.

Quayle, D.B., 1988. Pacific oyster culture in British Columbia. Canadian Bulletin of Fisheries and Aquatic Science 218, 1-241.

Reise, K., 1998. Pacific oysters invade mussel beds in the European Wadden Sea. Senckenbergiana maritime 28, 167-175.

Reise, K., 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48, 127-141.

Reise, K. Dankers, N. and Essink, K., 2005. Introduced species. Wadden Sea Quality Status Report. Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Reise, K., Gollasch, S. and Wolff, W.J., 1999. Introduced marine species of the North Sea coasts. Helgol. Mar. Res. 52, 219-243.

Reise, K., Olenin, S. and Thieltges, D.W., 2006. Are aliens threatening European aquatic coastal ecosystems? Helgol. Mar. Res. 60 (2), 106-112.

Rodriguez, L.F., 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions 8, 927-939.

Saier, B., 2001. Direct and indirect effects of seastars *Asterias rubens* on mussel beds (*Mytilus edulis*) in the Wadden Sea. J. Sea Res. 46, 29-42.

Saier, B., 2002. Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. Helgol. Mar. Res. 56, 44-50.

Saier, B., Buschbaum, B. and Reise, K., 2002. Subtidal mussel beds in the Wadden Sea. Threatened Oases of Biodiversity. Wadden Sea Newsletter 2002 (1).

Saurel, C., Gascoigne, J. and Kaiser, M.J., 2004. The Ecology of Seed Mussel Beds - Literature Review. Project code FC1015.

Sax, D.F., Stachowicz, J.J., Brwon, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D. Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I. and Rice, W.R., 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology and Evolution 22, 465-471.

Scherer, B. and Reise, K., 1981. Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. Kieler Meeresforsch., Sonderh. 5, 490-500.

Seed, R., 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores: I. Breeding and settlement. Oecologia 3, 277-316.

Simberloff, D., 2003. Confronting introduced species: a form of xenophobia? Biological Invasions 5, 179-192.

Soniat, T.M., Finelli, C.M. and Ruiz, J.T., 2004. Vertical structure and predator refuge mediate oyster reef development and community dynamics. J. Exp. Mar. Biol. Ecol. 310, 163-182.

Strasser, M. and Günther, C.P., 2001. Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. J. Sea Res. 46, 57-67.

Strayer, D.L., Eviner, V.T., Jeschke, J.M. and Pace, M.L., 2006. Understanding the long-term effects of species invasions. TRENDS in Ecology and Evolution 21(11), 645-651.

Streftaris, N., Zenetos, A. and Papathanassiou, E., 2005. Globalisation in marine ecosystems: The story of non-indigenous marine species across European Seas. Oceanography and Marine Biology: An Annual Review 43, 419-453.

Thiel, M. and Dernedde, T., 1994. Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. Helgol. Mar. Res. 48, 321-332.

Thieltges, D.W., Strasser, M. and Reise, K., 2006. How bad are invaders in coastal waters? The case of the American slipper limpet *Crepiduala fornicata* in western Europe. Biological Invasions 8, 1673-1680.

Townsend, D.W., Keller, M.D., Sieracki, M.E. and Ackleson, S.G., 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. Nature 360, 59-62.

Tsuchiya, M. and Nishihira M., 1986. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. Mar. Ecol. Prog. Ser. 31, 171-178.

Van der Velde, G., Rajagopal, S., Kuyper-Kollenaar, M., Bij de Vaate, A., Thieltges, D.W., MacIsaac, H.J., 2006. Biological invasions – concepts to understand and predict a global threat, In: Bobbink, R., Beltman, B., Verhoeven, J.T.A., Whigham, D.F. (eds.) Wetlands as natural resource. Volume 2. Wetlands: functioning, biodiversity, conservation and restoration. Ecological Studies, Springer Verlag, Berlin.

Volkenborn, N. and Reise, K., 2006. Lugworm exclusion experiment: Responses by deposit-feeding worms to biogenic habitat transformations. J. Exp. Mar. Biol. Ecol. 330, 169-179.

Walne, P.R., 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. J. Mar. Biol. Ass. UK 52, 345-374.

Wehrmann, A., Markert, A., May, P., Schiek, P. and Schmidt, A., 2006. Gefährdungspotential der eulitoralen Miesmuschelbänke im Niedersächsischen Wattenmeer durch die Bioinvasion der Pazifischen Austern *Crassostrea gigas*. Abschlussbericht Projekt 7/02 der Niedersächsischen Wattenmeer-Stiftung.

Wolff, W. J. and Reise, K., 2002. Oyster imports as a vector for the introduction of alien species into northern and western European coastal waters. In: Leppäkoski, E., Gollasch, S., Olenin, S. (Eds), Invasive aquatic species of Europe. Kluwer Academic Publ, Dordrecht, 193-205.

Chapter 2

2 Ecosystem engineering in the Wadden Sea: Alien oysters versus native mussels

Abstract

Blue mussel (*Mytilus edulis*) beds in the intertidal Wadden Sea are replaced by introduced Pacific oysters (*Crassostrea gigas*), which has been facilitated by anomalous warm summers and mild winters. To test for effects of a switch in dominance of these habitat-generating suspension feeders on the associated macrozoobenthic community, a field experiment was designed. Circular plots ('rings') were composed either of oysters, mussels, both together or none at all. These four treatments were arranged in June 2006 in 5 blocks along low tide line. Rings enclose 3m² of bare muddy sand surrounded by a 1-m-wide belt (10 m²) of the densely packed epibenthic suspension feeders. Sediment, infauna and mobile and recruiting epibenthic macrofauna was sampled on the belts four and eight months later. Mussels caused a fining of sediment grain compared to bare sediment. This did not occur among oysters but both bivalves increased organic content. The presence of mussels and oysters increased the abundance of infaunal and epibenthic mobile species differently. The polychaete *Lanice conchilega* was more abundant on oyster rings and the oligochate *Tubificoides benedeni* on mussel rings. Juvenile shore crabs *Carcinus maenas* and young periwinkles *Littorina littorea* (< 10 mm) preferred mussel rings, while *L littorea* $\geq$ 10 mm preferred oyster rings. Juveniles of the barnacle *Elminius modestus* and of mussels showed no preference while oyster spat preferentially settled on conspecifics. We conclude that a shift in dominance from mussels to oysters alters habitat structures which entail differential abundances of associated organisms. This exchange of suspension feeder species is not neutral to community structure because resident mussels and alien oysters function differently as ecosystem engineers.

2.1 Introduction

Introduced by Jones et al. (1994), the concept of ecosystem engineers focuses on habitat structuring organisms. They are affecting biological traits by profound architectural changes in the environment. In marine soft-sediments this has been described for e.g. lugworms (Volkenborn and Reise 2006), sand masons (Rabaut et al. 2007), mussels (Ragnarsson and Raffaelli 1999) and oysters (Lenihan 1999). Such engineers may differentially inhibit and facilitate other organisms, provide opportunities for novel niches and the differentiation of existing ones, and may alter the structure of food webs (Buschbaum et al. 2006, Diederich 2006, Volkenborn and Reise 2006). Habitat modifications are also essential when evaluating the role of alien species with their effects on resident populations (Crooks 2002, Cuddington 2004, Buschbaum et al. 2006, Thieltges et al. 2006, Wallentinus and Nyberg 2007).

In the Northern Wadden Sea, the Pacific oyster *Crassostrea gigas* plays a fundamental role as an invasive ecosystem engineer. Near the island of Sylt regular introductions of this oyster commenced in 1986 for oyster farming, and natural spread by larvae to mussel beds was observed subsequently (Reise 1998). Anomalously high water temperatures, high recruitment success and positive feedback in settlement facilitated the development of the feral *C. gigas* population (Diederich et al. 2005, Nehls et al. 2006). Mussels are increasingly overgrown and almost all existing intertidal mussel beds adjacent to the oyster farm have turned into oyster reefs since 2005. It is expected that mussels and oysters will coexist in dense aggregations forming compact reefs (Diederich 2005). However, their relative proportions over a range of habitats cannot yet be foreseen.

This shift in dominance from mussels to oysters could have (a) top-down effects on phytoplankton, (b) bottom-up effects on shellfish predators and parasites, and (c) habitat effects on organisms dwelling within beds of mussels or reefs of oysters. To investigate the habitat effects, a large-scale field experiment was designed to mimic effects of mussel beds, mixed beds and oyster reefs on associated organisms. Against the null-hypothesis that a reversal of roles in dominant suspension feeders will be neutral to other macrozoobenthos, we test for abundant taxa of the infauna, mobile epifauna and settling sessile epifauna whether there are losers or winners when dominance shifts from mussels to oysters.

2.2 Materials and Methods

2.2.1 Study site

A large-scale field experiment was set up in the lower intertidal zone of the outer Königshafen, which is a tidal embayment at the northern end of the island of Sylt (North Sea, Germany, 55°01' N; 08°26'E; Fig. 6). This embayment is part of the List tidal basin which covers an area of 401 km² and is connected to the North Sea through a narrow tidal inlet of 2.8 km width. Intertidal flats are dominated by sand and make up 159 km² of the area. Epibenthic mussel beds covered 1 % of the intertidal flats in the past but have been largely overgrown by Pacific oysters during the last decade (Diederich et al. 2005, Nehls et al. 2006). Presently, 0.1 km² of the Königshafen are covered by mixed mussel and oysters beds (personal comm. by T. Dolch).

Sediment at the experimental site (Oddewatt) mainly consists of medium sand (mean grain size 254 µm) and shell gravel (Austen 1994). Mussel beds occurred along low tide line (Reise et al. 1994) but have been scoured away by ice floes in the winter 1995/96 and subsequent storms. Tides are semi-diurnal and mean tidal range is 1.8 m. Salinity ranges between 31 in summer and 28 in winter. Mean monthly water temperature varies between 19.5°C in August and 3.5°C in February. Further details on the List tidal basin are given in Gätje and Reise (1998).
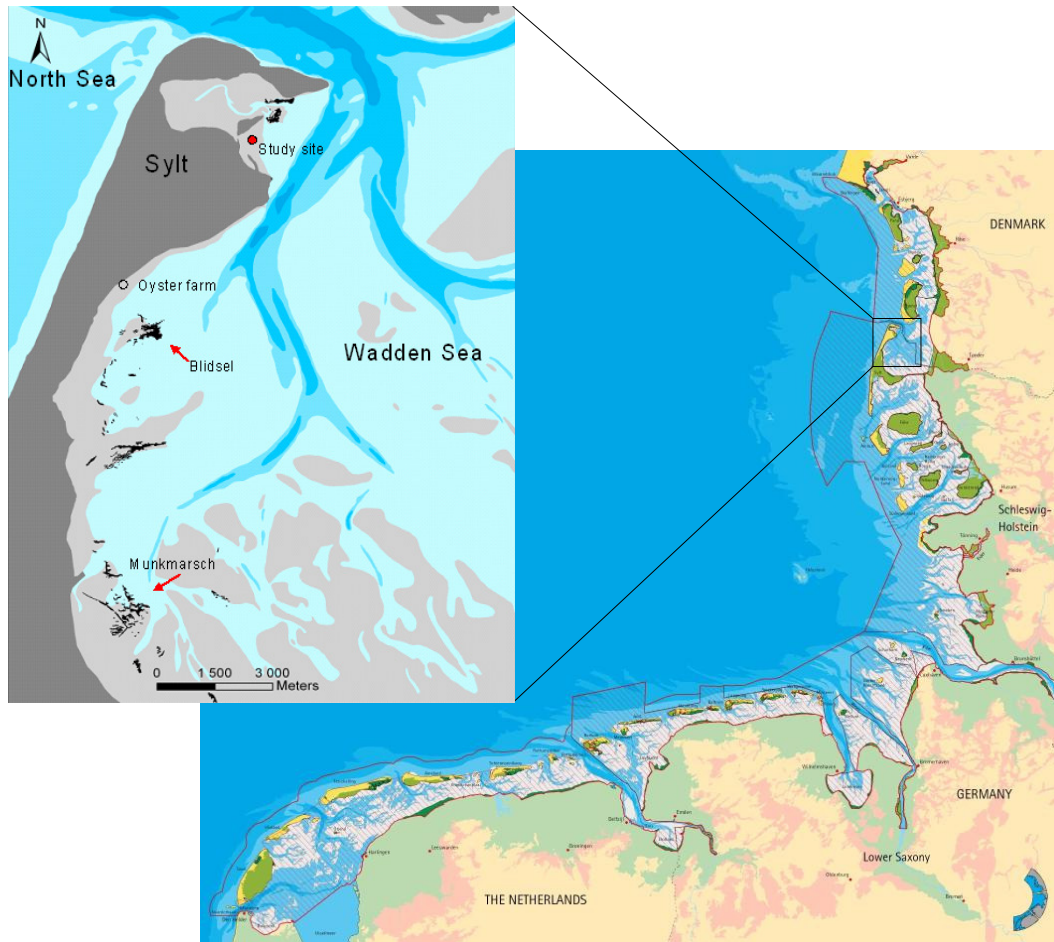
Fig. 6. Wadden Sea coast in the eastern North Sea with study site and the occurrence of intertidal mussels beds/oyster reefs at the leeside of northern Sylt. Arrows point to source areas of mussels (Munkmarsch) and oysters (Blidsel).

2.2.2   Experimental design

During May/June 2006, Pacific oysters (*Crassostrea gigas)* and blue mussels (*Mytilus edulis)* from natural beds (arrows in Fig. 6) have been arranged parallel to low tide line in Oddewatt (Fig. 7). This site was chosen because mussel beds were abundant in this area until ice scoured them away in the winter 1995/96 (Strasser et al. 2001), indicating potentially suitable conditions for dense aggregations of suspension feeders at this site. Emersion time was 0 - 3 h per tidal cycle.

The experimental set-up was a randomized block-design, consisting of 5 blocks over a distance of 110 m (Fig. 7). Each block consisted of 4 experimental plots differing in treatment: plot covered with oysters (C), plot covered with mussels (M), plot covered with oysters and mussels (CM) and bare sediment (S). Plots were designed as rings enclosing 3 m² of bare sediment surrounded by a 1 m wide belt (10 m²) of the densely packed

epibenthic suspension feeders. On each plot the biovolume as a measure of autogenic ecosystem engineering sensu Jones et al. (1994) for oysters and mussels was approximated to natural mussel and feral oyster beds, with 10000 to 30000 cm³ of biovolume (bivalves with shells closed) per 1 m² of sediment surface (Fig. 8). Cover of epibenthic suspension feeders was absent on bare sediment plots. The experimental design allowed for testing the effects of mussels and oysters on the associated benthic community and on test organisms placed into the centre of the rings. Results of the latter are reported by Buschbaum et al. (in prep.) and Thieltges et al. (submitted). We here focus on sediment change and associated species at the belts of the suspension feeder rings compared to bare sediment rings.
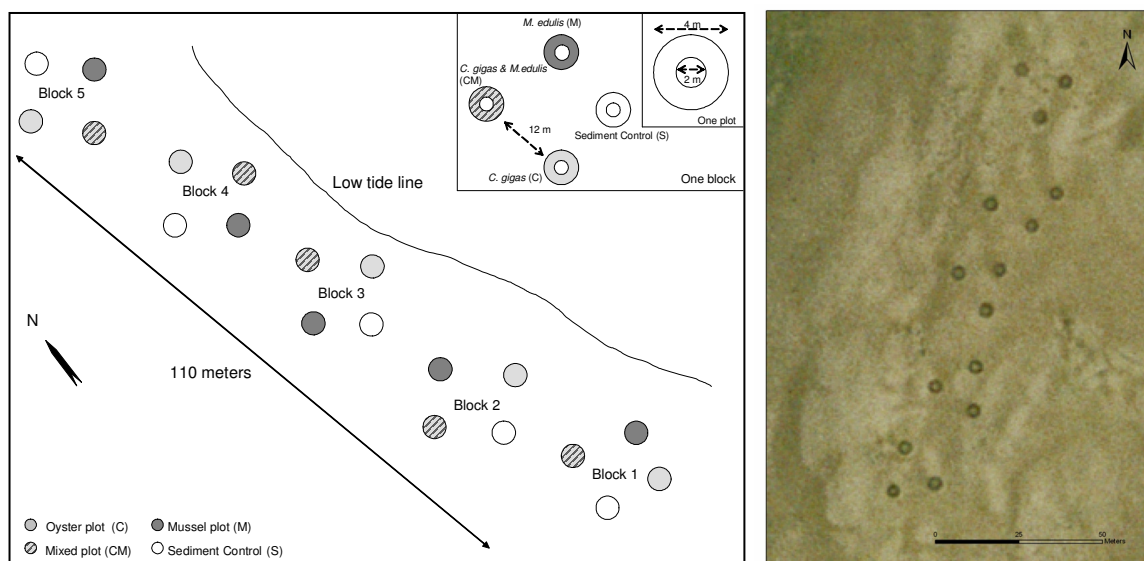
Fig.7. Experimental set-up positioned just above mean low water tide line as randomized block-design. Inset shows design of individual treatments and their distance to each other. Aerial photograph shows the suspension feeder rings contrasting with bare sediment; dark colour in the upper left is caused by mats of green algae (June 2006).
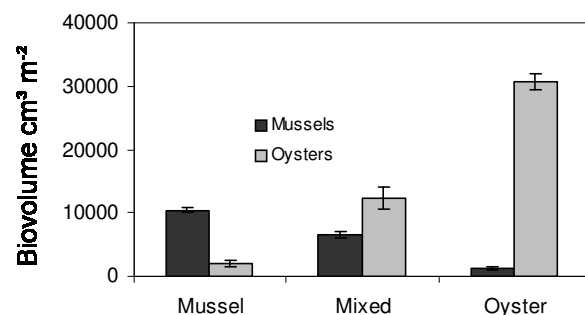
Fig. 8. Experimental plot and shellfish volume on experimental plots with epibenthic suspension feeders in June 2006. Shown are means ± SE.

2.2.3 Sampling of sediment, infauna and mobile and recruiting epibenthic macrofauna

Samples were taken at random from belts of epibenthic suspension feeders and bare sediment plots but excluding positions < 20 cm from edges. To facilitate comparison of abundances, we extrapolated individual numbers of infauna, mobile and recruiting species to m² although this may not be appropriate for the Standard Error.

Sediment analysis

To analyze particulate organic matter (POM), 5 samples of 10 cm³ of surface sediment (upper 5 cm) were taken from each plot, dried at 60°C for 5 d, combusted at 520 °C for 8 h and organic content was calculated as weight loss from dried to ash weight of the sediment. Further, 5 surface sediment samples (upper 2 cm) were taken from each plot to analyze grain size composition. Subsamples of 8 – 10 g were taken from each sediment sample and treated with acetic acid and hydrogen peroxide H_2O_2 (6 %) to remove organic components. Grain size was measured with CILAS 1180 Laser particle analyzer and the results were further evaluated with the statistic package GRADISTAT (Version 4.0 Blott and Pye 2001).

Infauna

To analyze effects of mussels and oysters on the endobenthic community, experimental rings were sampled in Autumn (October 2006) and Spring (March 2007). Autumn sampling was focused on small and large macrofauna (> 250 µm), while Spring sampling was focused only on large macrofauna (>1000 µm). The former was chosen to include potential summer recruitment after the experiment had commenced, and the latter to address differential survival or choice to stay in adult specimen.

In October 2006 sediment samples of 10 cm² and 5 cm depth were randomly taken between suspension feeders to analyze infaunal assemblages. To level out small-scale patchiness 5 replicate samples were pooled to 250cm³ in total for each experimental plot. Species retained on a 250 µm mesh were identified to species and counted. In March 2007 a box corer of 200 cm² and a sampling depth of approximately 15 cm were used and specimen retained on a 1 mm mesh were identified and counted. Additionally, numbers of tube caps of *Lanice conchilega* (after Hoey et al. 2006) were recorded on 4 randomly chosen squares of 625 cm² on each experimental plot.

Epifauna

Sessile epifauna, i.e. *Semibalanus balanoides, Balanus crenatus, Lepidochitona cinerea, Crepidula fornicata, Polydora ciliata* and encrusting algae, was co-transplanted when the experiment was set up. Therefore we focused on abundance of new recruits during the experimental period and on mobile epifauna assumed to have immigrated in the course of the experiment. In particular, we counted recruitment of oysters and mussels, and the barnacle *Elminius modestus* which had settled in summer 2006. Mobile epifauna sufficiently abundant for analysis were the periwinkle *Littorina littorea* and the shore crab *Carcinus maenas*, both of which were present on the ambient tidal flat.

In October 2006 mobile epibenthic macrofauna (> 1 mm) was sampled by randomly placing a frame of 25 x 25 cm (625 cm²) on the belt once within each ring covered by suspension feeders or on bare sediment respectively. All organisms encountered above sediment surface were collected. The following size classes were recognized: *Carcinus maenas* 5 - 10 mm carapax width, *Littorina littorea* < 10 mm and $\geq$ 10 mm shell height, *Mytilus edulis* $\leq$ 25 mm and > 25 mm shell length, *Crassostrea gigas* $\leq$ 30 mm and > 30 mm of max. shell length.

In March 2007 a smaller frame of 14 x 14 cm (~ 200 cm²) was used. Sampling procedure was similar to October but oysters and mussels were not counted again. The density of *Elminius modestus* on any kind of hard substratum found inside the frame of 200 cm² was assessed.

2.2.4   Statistical analysis

All univariate response variables were analysed using generalized linear models (GLM). The maximum models included the factor 'treatment' comprising of 4 levels and the experimental block (unreplicated) that accounted for spatial heterogeneity. For abundance data errors followed in principal a poisson distribution; marginal overdispersion was accounted for by using a quasi-poisson error structure. Proportional response variables such as mud, sand and POM content followed a binomial error-distribution. When overdispersion occurred, again models were fitted using a quasi-binomial error function. All models were simplified to the minimum adequate model (after Crawley 2005). Resulting significant differences are reported as such and denoted by letters. Data are given as arithmetic means with standard error (SE). The free software R ('R' Development Core Team 2006) was used to compute generalised linear models.

For studying infaunal species assemblages we applied multi-dimensional scaling (MDS) based upon Bray-Curtis similarity matrices. Prior to analysis data were 4th-root transformed to prevent down weighting of rare species. To detect single species contribution to average Bray-Curtis similarity we used SIMPER procedure within treatments and non-parametric ANOSIM procedure allowed testing of treatments effects on species community structure. The oligochaete *Tubificoides benedeni* outnumbered all others in abundance and strongly affected community structure. Thus, it was excluded from this analysis and only univariate effects were tested. We used PRIMER software (Plymouth Marine Laboratory) for this analysis.

2.3 Results

### 2.3.1 Experimental plots and sediment characteristics

Mussel rings maintained their shape better than mixed and oyster rings over the observation period from June 2006 to April 2007. Mussels readily became tossed again with their byssal threads after transplantation and thus formed a coherent mat of interconnected mussels. At oyster rings, some individual oysters were found scattered inside or adjacent to rings after rough tides. Oysters had been taken from dense reefs where most were in vertical position with approximately one third of their length anchored in the sediment and stabilized in this position by their neighbors. We were unable to restore original positioning of oysters in the experimental rings. However, after 5 month a vertical positioning of oysters in block 2 to 4 re-emerged, and all rings were still intact after 8 months. Mixed rings performance was intermediate. At the seaward edge of rings, most exposed to wave action more oysters and mussels became dislodged than at other sites. The bare sediment areas enclosed by the rings of epibenthic suspension feeders were subject to erosion on the seaward side. Part of this eroded sediment became deposited inside the rings on the landward side. Because of this erosion puddles covered by residual water throughout low tide phase developed inside rings. Mean water depths (n = 4 at each ring) inside oyster belts was 46 mm and significantly different from mixed and mussel belts with 73 and 74 mm respectively (p = 3.1e-05, Table 1). This suggests differential effects of mussels and oysters on near-bottom hydrodynamics.

Table 1. Sediment characteristics of experimental plots. Shown are means from 5 plots ± SE.

	Bare sediment (S)	Mussel (M)	Mixed (CM)	Oyster (C)
mean of grain size (µm)	283.12 ± 10.70	146.41 ± 17.59	88.25 ± 15.24	213.24 ± 36.25
mud fraction < 63 µm (%)	3.48 ± 0.91	16.65 ± 2.37	28.66 ± 6.09	13.52 ± 4.18
POM (%)	0.66 ± 0.06	1.14 ± 0.07	1.44 ± 0.20	1.22 ± 0.15
water depth (mm)	0	74.1 ± 5.5	72.9 ± 6.1	45.5 ± 5.1
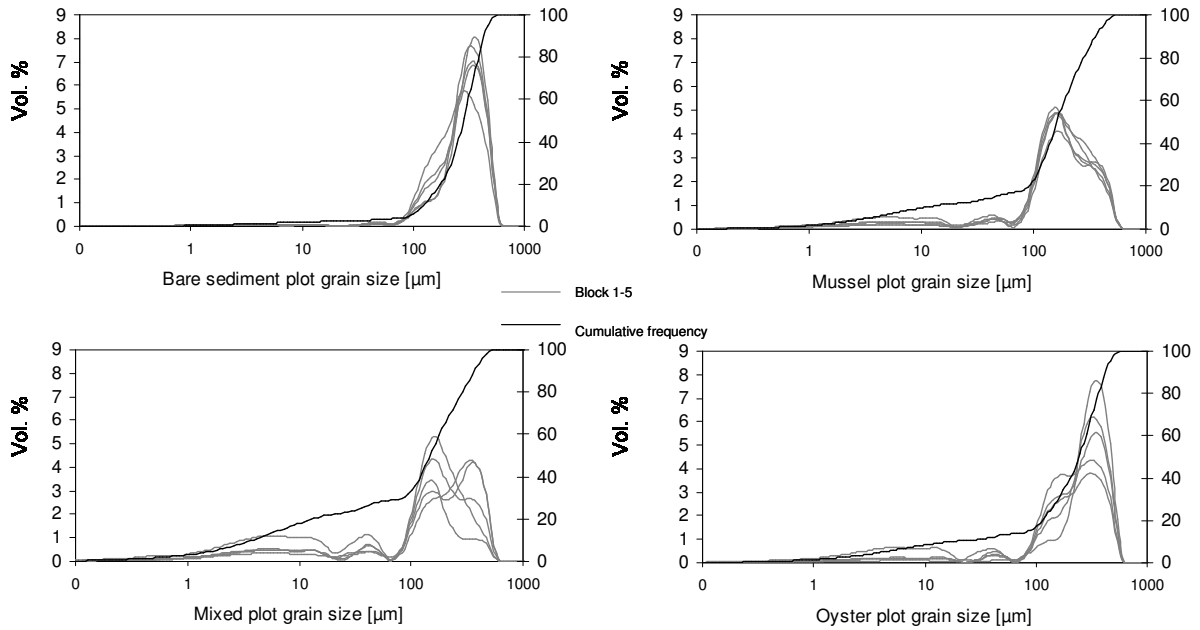
Fig. 9. Frequency distribution of grain sizes expressed in volume percentages analyzed from samples taken within belts of suspension feeder rings and bare sediment plots. Shown are grain size distributions for each treatment from each block (grey) and the cumulative frequency (black).
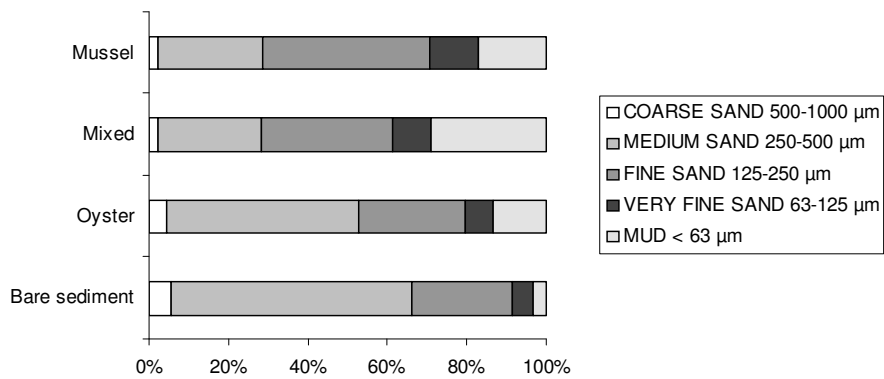
Fig. 10. Grain size distribution (%) on experimental plots, grain size scale after Wentworth 1922.

In the upper 2 cm, mean sediment grain size distribution ranged from very fine sand to medium sand with lowest value on mixed plots (88 µm) and highest on bare sediment plots (283 µm, Table 1). On mixed plots most grain sizes (40%, Fig. 9) were below 100 µm and explain the lowest mean grain size.

Considering the mode of grain size the trend was slightly different, indicating highest value on bare sediment plots (348 µm) and lowest value on mussel plots (166 µm). The sorting of grain sizes (according to Blott and Pye 2001) showed that most of the sediment was poorly sorted and mixed plots visibly showed the most polymodal grain size

distribution (Fig. 9) with a high SE of the first mode. The first modi of mussel and oyster plots were both represented on mixed plots. Bare sediment plots were mainly dominated by medium sand and contained less than 5% of finer particles < 63µm (Table 1, Fig. 10). On mussel treatments fine sand contributed highest percentage (40%). On mixed treatments mud fraction was highest with 29 % and significantly different from mussel and oyster plots ($p = 0.0162$, Table 1). Organic content was about 1 % and did not differ significantly between suspension feeder treatments but was significantly lower on bare sediment plots with < 1 % ($p = 0.0003$, Table 3).

2.3.2 Infauna

In total 18 infauna taxa were found at experimental plots in October 2006 and 16 species in March 2007, most were polychaetes (Table 2). The polychaete worms *Pygospio elegans*, *Spio martinensis*, *Phyllodoce mucosa, Nereis virens* and *Nephtys* sp. preferentially occurred on bare sediment with 1 - 6 individuals and *Scoloplos cf. armiger* with 1 - 8 individuals per sample. However, treatments did not have significant effects on species richness.

Table 2. Infaunal taxa encountered on bare sediment and belts of mussels and oysters October 2006 and March 2007.

|	October `06				March `07			
	Bare sediment	Mussel	Mixed	Oyster	Bare sediment	Mussel	Mixed	Oyster
Nemertea								
Anopla								
Lineus ruber	.	.	x	.	.	.	.	.
Lineus viridis	x	.	x	.	.	x	x	x
Annelida								
Oligochaeta								
Tubificoides benedenii	x	x	x	x	.	.	.	.
Tubificoides sp	x	x	x	x	.	.	.	.
Polychaeta								
Arenicola marina	.	.	.	.	.	x	x	.
Aricidea sp	x	x	.	.	.	.	.	.
Capitella capitata	x	x	x	x	.	x	x	x
Eumida sanguinea	.	.	.	.	.	.	.	x
Heteromastus filiformis	.	x	.	x	.	x	x	.
Lanice conchilega	x	x	x	x	x	x	x	x
Malacoceros fuliginosus	x	x	x	x	.	x	x	x
Nepthys sp	x	x	.	.	x	.	.	.
Nereis diversicolor	.	.	.	.	.	.	.	x
Nereis virens	x	x	.	x	x	.	.	.
Phyllodoce mucosa	.	.	x	x	x	.	.	.
Polydora cornuta	x	x	x	x	.	.	.	x
Pygospio elegans	x	.	.	.	.	.	.	.
Scoloplos cf. *armiger*	x	.	.	x	x	x	.	x
Spio martinensis	x	.	.	.	x	.	.	.
Tharyx killariensis	.	x	x	.	.	.	.	.
Mollusca								
Pelecypoda								
Cerastoderma edule	x	.	x	x	x	x	.	.
Macoma balthica	x	.	x	x	x	x	x	x

Even with different mesh size used during sampling species mainly (> 20 %) contributing to average similarity did not change (Table 3).

Malacoceros fuliginosus and *Lanice conchilega* always showed the highest contribution to average similarity. *M. fuliginosus* accounted for more similarity (28 - 67 % contribution to average similarity) than *L. conchilega* (23 - 43 % contribution to average similarity). In bare sediment, *Scoloplos* cf. *armiger* and *Spio martinensis* were also contributing to average similarities.

Table 3. SIMPER analysis of species assemblages sampled on experimental plots. Shown are species with major contributions to average Bray-Curtis similarity within treatments and different samplings. Data are based on 4th-root transformation. *Tubificoides benedeni* excluded from analysis.

	Bare sediment		Mussel		Mixed		Oyster	
	Infauna `06	Infauna `07	Infauna `06	Infauna `07	Infauna `06	Infauna `07	Infauna `06	Infauna `07
Lanice conchilega	.	42.55	22.89	.	36.51	35.23	30.76	33.56
Malacoceros fuliginosus	28.23	.	57.86	66.55	51.99	44.19	55.03	46.99
Scoloplos cf. *armiger*	25.39	50.63	.	.	.	.	.	.
Spio martinensis	22.18	.	.	.	..	.	.	.

ANOSIM procedure shows that the bare sediment assemblage differed in community structure from those on belts composed of suspension feeders. In March differences were stronger (R = 0.436, *p* = 0.001) compared to October (R = 0.205, *p* = 0.006) and this is also indicated by MDS plots (Fig. 11). ANOSIM suggests a low differentiation of treatments in October (R = 0.064, *p* = 0.265) and March (R = -0.102, *p* = 0.879) and the effect of different suspension feeders on infaunal assemblages was not consistent as revealed below by univariate effects on single species.
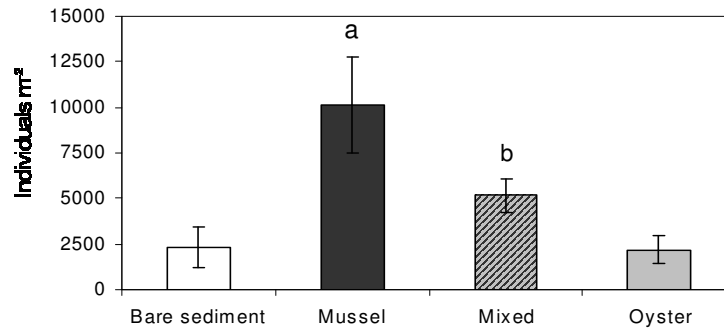
October 2006   March 2007
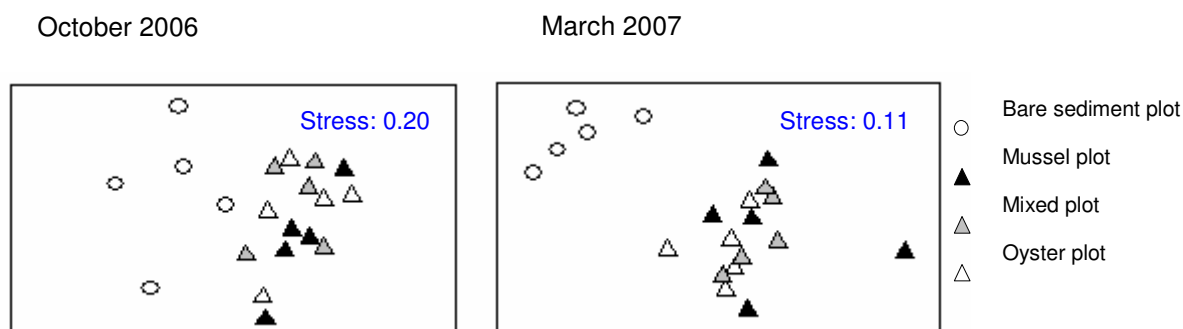
Fig. 11. MDS plots of species assemblages based upon Bray-Curtis similarity matrices of 4th-root transformed data. Triangles indicate suspension feeder plots. *Tubificoides benedeni* excluded from analysis.

Total number of individuals differed among treatments (Fig. 12). The total number of individuals, including the dominant *T. benedeni,* was highest on mussel plots (mussels > mixed > oysters > bare sediment). However, oyster belts yield most individuals when the oligochaete was excluded and were significantly different from other treatments (Fig. 12). Lowest numbers always occurred on bare sediment. In October 2006, bare sediment, mussel and mixed treatments did not differ significantly but had 42 % less individuals than the oyster treatment ($p = 0.0080$). In March 2007, number of individuals on mussel and mixed treatments was 44 % lower than on oyster plots ($p = 0.0128$) and 52 % higher than on bare sediment ($p = 0.0383$).
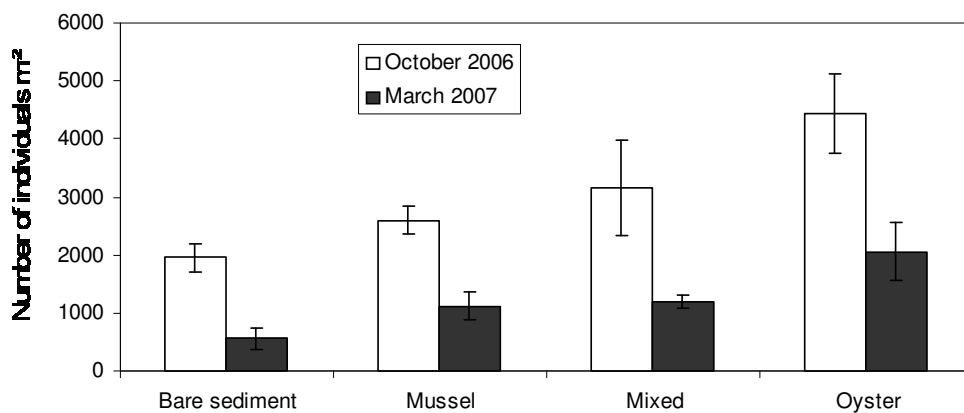
**Fig. 12.** Number of infaunal individuals (N) on experimental plots. *Tubificoides benedeni* excluded from analysis. Shown are means from 5 plots ± SE. Notice different mesh sizes used (October 0.25 mm, March 1 mm).

To show species responses to treatments, univariate analysis was applied to the oligochaete *T. benedenii* (Fig. 13) and the two polychaete species, *M. fuliginosus* and *L. conchilega* (Fig. 14). The abundance of the oligochaete *T. benedeni* was 78 % higher in mussel plots (10120 ± 2638) than in bare sediment and oyster plots ($p = 0.0001$, Fig. 13). Mixed plots (5160 ± 900) had 57 % more individuals than oyster plots and bare sediment ($p = 0.0225$).

Fig. 13. Abundance of *Tubificoides benedeni* on experimental plots in October 2006, n = 5. Shown are means ± SE. Significant differences are denoted by letters.

The spionid polychaete *M. fuliginosus* was absent from the bare sediment in March 2007, and its abundance in suspension feeder belts did not differ significantly (Fig. 14). Tube cap abundance of *L. conchilega* was significantly higher on oyster plots (572 ± 89) than on bare sediment, mussel and mixed plots in March ($p = 0.0015$, Fig. 14).
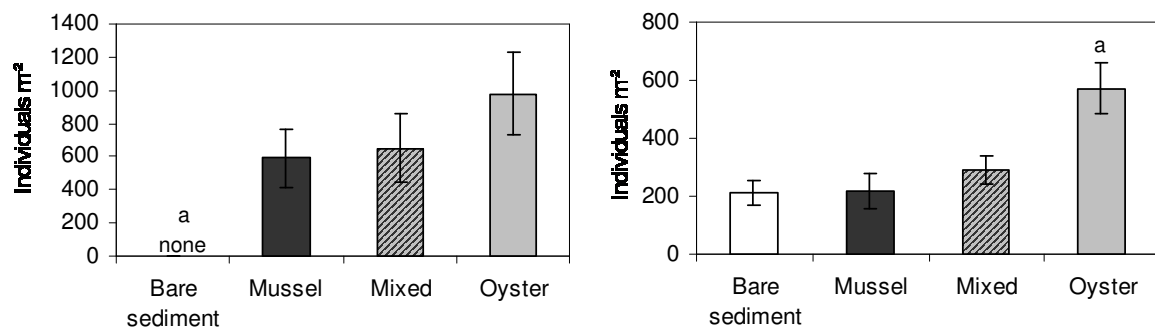

Fig. 14. Abundances of *Malacoceros fuliginosus* (left; n = 5) and *Lanice conchilega* tube caps (right; n = 20) on experimental plots in March 2007. Shown are means ± SE. Significant differences are denoted by letters.

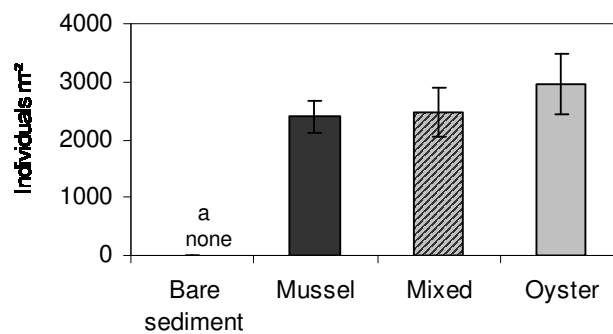### 2.3.3   Epifauna

Recruitment by oysters, mussels and barnacles

Oyster recruitment showed a preference for conspecifics. Individuals ≤ 30 mm were significantly less abundant on mussel plots (1580 ± 259) compared to mixed and oyster plots with 2614 ± 217 individuals ($p = 0.0078$, Fig. 15). On mixed plots the young oysters were mainly attached to adult oysters. On bare sediment the few scattered aggregates of oysters and some shell gravel provided scarcely any substratum for attachment. *M. edulis* ≤ 25 mm showed no preference for any epibenthic treatment and a significant difference occurred only towards bare sediment ($p = 0.0042$, Fig. 15). Highest number of mussel recruits was considerably lower with only 1020 ± 196 individuals compared to 2627 ± 349 oyster recruits in congeneric treatments respectively.
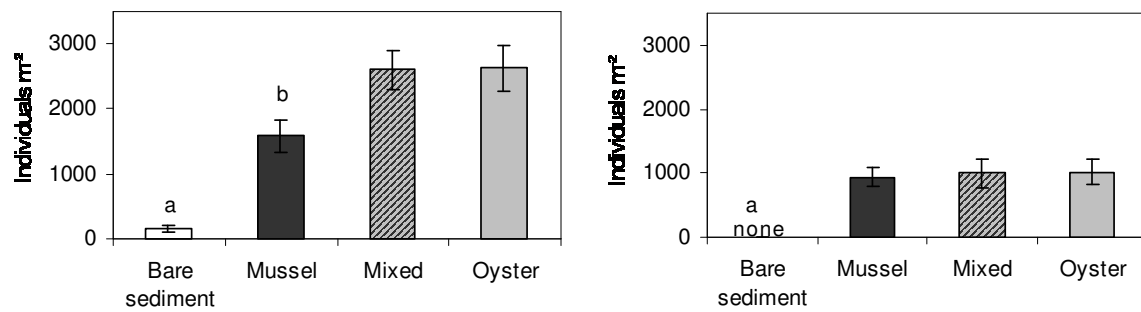
Fig. 15. Abundance of recruits of *Crassostrea gigas* (≤ 30 mm; left) and *Mytilus edulis* (≤ 25 mm; right) on experimental plots in October 2006, n = 5. Shown are means ± SE. Significant differences are denoted by letters.

Density of the barnacle *Elminius modestus* recruits revealed no significant differences between mussel, mixed and oyster plots, but were absent on bare sediment where attachment of recruits was limited by scarcity of substratum ($p = 0.0013$, Fig. 16).

Fig. 16. Abundance of *Elminius modestus* on experimental plots in March 2007, n = 5. Shown are means ± SE. Significant differences are denoted by letters.

Abundance of mobile epifauna

Mobile epifauna preferred epibenthic treatments over bare sediment in all cases. GLM`s revealed different preferences depending on bivalve identity. In October, the presence of *Mytilus edulis* explained the highest abundance of juvenile shore crabs *Carcinus maenas* (742 ± 127, Fig. 17). Oyster plots (365 ± 70) were significantly different from mussel and mixed plots ($p = 0.0098$), while *C. maenas* was absent from the bare sediment. In March, juvenile *C. maenas* showed no preference for any treatment and was almost absent from bare sediment plots with 96 % difference in means ($p = 0.0018$). Fewer numbers occurred on all plots compared to October 2006 (Fig. 17).
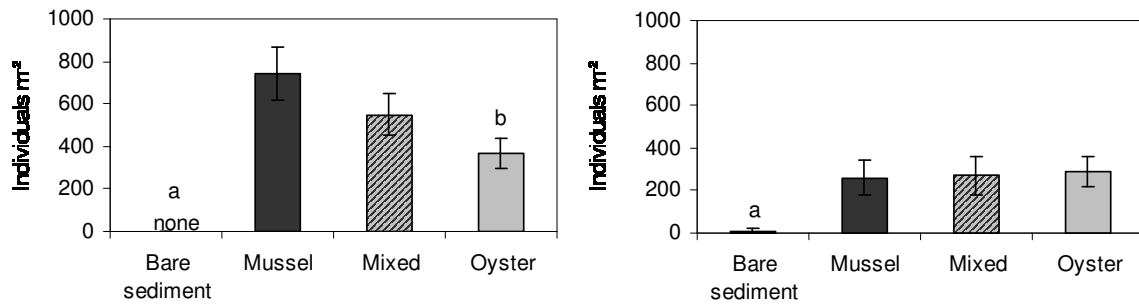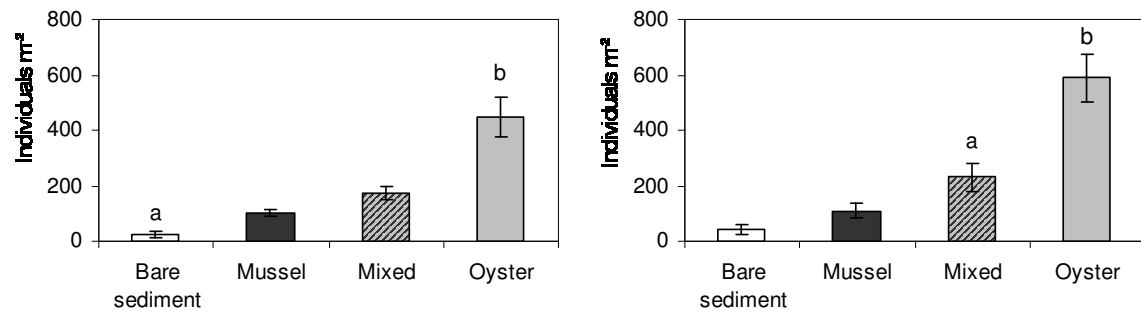
Fig. 17. Abundance of juvenile *Carcinus maenas* (5-10 mm carapax width) on experimental plots in October 2006 (left) and March 2007 (right), n = 5. Shown are means ± SE. Significant differences are denoted by letters.

Only few juveniles of *Littorina littorea* were found on bare sediment in October and March (Fig. 18). In October 2006, juvenile *L. littorea* < 10 mm shell height were significantly more abundant on mussel plots (3152 ± 382) compared to the other epibenthic treatments (*p* = 0.0203). In March 2007, abundance of small periwinkles differed significantly between all treatments (oysters > mixed > mussels > bare sediment; *p* = 1.698e-19) with highest numbers occurring on oyster plots (3940 ± 459, Fig. 18).
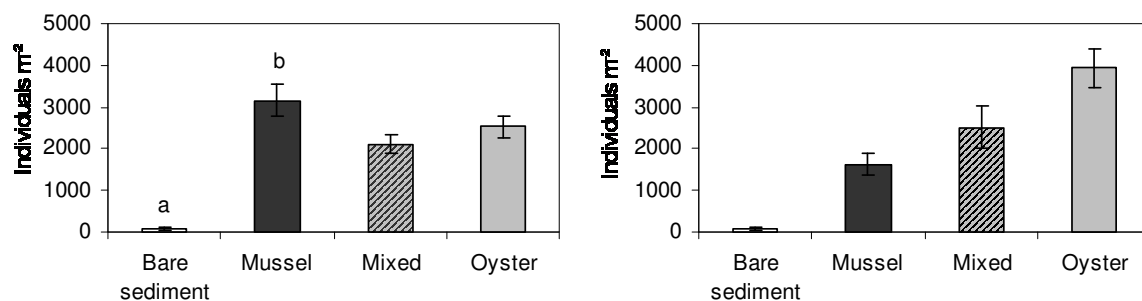
Fig. 18. Abundance of small *Littorina littorea* (< 10 mm shell height) on experimental plots in October 2006 (left) and March 2007 (right), n = 5. Shown are means ± SE. Significant differences are denoted by letters.

The latter pattern was also adapted by larger periwinkles (*L. littorea* ≥ 10 mm shell height) which preferred oyster plots in both sampling periods (448 ± 73 in October, 590 ± 87 in March; Fig. 19). Oyster plots were significantly different from mussel and mixed plots in October 2006 (*p* = 1.75e-06, 69 % difference in means) and also from bare sediment (*p* = 0.0009, 81 % difference in means). Large periwinkles on mussel and bare sediment plots were significantly less abundant than on oyster plots in March 2007 (*p* = 0.9.13e-06) with 87 % difference in means.

Fig. 19. Abundance of large *Littorina littorea* (≥ 10 mm shell height) on experimental plots in October 2006 (left) and March 2007 (right), n = 5. Shown are means ± SE. Significant differences are denoted by letters.

2.4   Discussion

In this study, the two ecosystem engineers *C. gigas* and *M. edulis* were tested for their effects on the associated macrozoobenthic community in an attempt to elucidate the ecosystem impact of the ongoing displacement of mussel beds by Pacific oyster reefs in the Wadden Sea. We approached this subject with a large-scale field experiment. Biogenic structures of the epibenthic suspension feeders altered sediment composition, infauna, recruitment patterns of oysters, mussels and barnacles, and mobile epifauna.

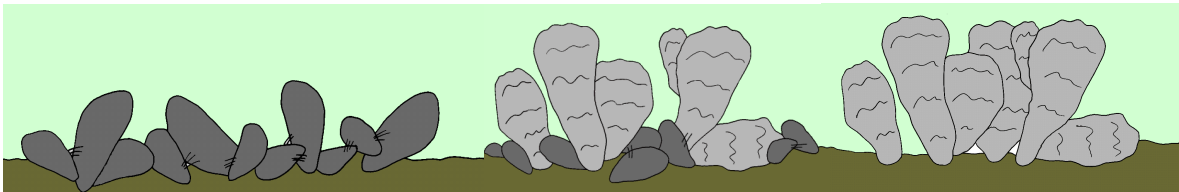### 2.4.1   Experimental plots and biogenic habitat structure

The circular arrangement of belts of suspension feeders was chosen to simulate environments composed of resident mussels, invading oysters or both. Although ring shaped beds do not occur naturally, their effects on sediment, associated species and recruitment within the belts are assumed to be representative also for other shapes and sizes of beds or reefs, at least near the edges. It is obvious that central parts of extensive mussel beds may show characteristics of their own (Tsuchiya and Nishihira 1986, Ragnarsson and Raffaelli 1999). However, we rarely observe extensive coherent beds in the Wadden Sea. Most are elongated and show bare patches similar to the central areas enclosed by our experimental rings.

Mussels are better suited than oysters for transplanting because they quickly reestablish their previous matrix by new byssal connection (Commito and Dankers 2001). The matrix of oyster beds arises in part by solid attachment of new generations to the shells of previous ones and by adopting an elongated shape with upright positioning in crowded assemblages (own observation). This kind of structure cannot easily be reconstructed by transplanted oysters. Thus, our experimental oyster belts were less dense than natural beds although crowding was the same. This was probably a minor artifact as rings of oysters as well as the mixed and mussel rings basically maintained their shape over a year in spite of a particularly stormy winter.

Nevertheless, the microtopography of mussel, mixed and oyster rings was distinctly different (Fig. 20). Oysters within belts were patchier than mussels and with their larger individual sizes and generally upright position they generate more surface roughness than mussels. We hypothesize that surface roughness in particular is crucial for the differential effects of these ecosystem engineers on sediment properties and associated fauna. The dense matrix of mussels, on the other hand, may explain why more fine sediment particles accumulate there compared to the belts of oysters where the sediment remained more

similar to that of the bare sediment plots. This interpretation is supported by the observation that less erosion occurred in central areas of oyster rings compared to mixed and mussel rings. Belts of oysters are more permeable to the flow of water than the other belts.

The experiment also indicates that there is no linear relationship for the effects of mussels and oysters on their surrounding when arranged in different proportions. The mixed treatment did not always show an intermediate effect. Mussels positioned between the larger oysters may retain more biodeposits of oysters than if oysters occur alone. This is highly important for the Wadden Sea we may expect continued coexistence in mixed beds (Diederich 2005). More investigations are needed to determine the exact production, fate and quality of faeces and pseudofaeces generated by oysters and mussels and how they are retained in monocultures and mixed assemblages.

Fig. 20. Illustration of biogenic habitat structures on experimental plots differentially dominated by mussels and oysters; from left to right: mussel plot, mixed plot, oyster plot.

2.4.2 Differential effects on infauna

As expected from the observed differences in sediment composition, there was a strong effect on infauna by the experimentally arranged suspension feeder belts. In addition to the differences relative to the bare sediment plots, the effects of epibenthic suspension feeders differed in the species composition of attracted infauna, while species richness did not differ. Two mechanisms may explain this phenomenon: (1) differentiated alteration of sediment by the respective epibenthic suspension feeders and (2) differential protection from predation from above or mitigating physical disturbance resulting from wave action caused by the epibenthic structures.

Predation is assumed to be a key factor. Intertidal flats of the Wadden Sea are nurseries for young epibenthic predators such as flatfish, shrimp and crabs that are capable of significantly reducing infaunal abundances (i.e. Reise 1985, Strasser 2002, Beukema and Dekker 2005). The series of mild winters proceeding the time of our experimental period may facilitate these predators and their effects on macrozoobenthic recruitment in particular by a temporal match between juveniles of predator and prey. A better accessibility to prey in bare sediment compared to sediment covered with suspension

feeders might explain higher infaunal abundances among mussels and oysters. In the same way, accumulation of biodeposits and suspended material as potential food for infaunal species will be facilitated by the epibenthic structures (Crooks 1998, Commito and Dankers 2001). On the other hand, the subsurface feeder *Scoloplos* cf. *armiger*, which is highly abundant on sandy intertidal flats in Königshafen outside mussel beds (Reise et al. 1994), is known to be susceptible to hydrogen sulfide enrichment and decreasing sediment permeability (Kruse et al. 2004, Volkenborn and Reise 2006). In this study, *Scoloplos* cf. *armiger* preferentially occurred in bare sediment plots.

While ANOSIM analysis revealed that the bare sediment assemblage deviated from the other environments, the more subtle differences between mussel, mixed and oyster treatments are particularly apparent by single species analysis. Ecosystem engineering by mussels and oysters facilitated *Malacoceros fuliginosus*, *Lanice conchilega* and *Tubificoides benedeni*. The surface deposit-feeding spionid *M. fuliginosus* preferred epibenthic structure but was indifferent towards bivalve identity. For mussel beds this was previously shown by Dittmann (1990) who observed an increase in abundance of deposit-feeders from bare sandflats to mussel beds. The mainly suspension-feeding *L. conchilega* was most abundant on oyster plots. It might benefit from oyster belts which keep fine particles resuspended near the bottom. Mussels may occasionally be a problematic neighbor because tube caps of *L. conchilega* become entangled in the byssal matrix (own observation). Highest densities of the oligochaete *Tubificoides benedeni* occurred underneath mussel plots. This might be due to a combination of food enrichment and tolerance to anoxic conditions. This species often thrives well under low oxygen conditions and dominates the fauna of sulfide-rich deoxygenated sediment such as in mussel beds (Commito and Boncavage 1989).

The singularity of oysters and mussels seem to play an important role affecting infaunal species by various combinations of habitat modifications. The mixed treatment usually exhibited intermediate effects on infauna.

2.4.3   Differential effects on epifauna

The enrichment by shells as a secondary hard substratum and the provision of refugial interspaces was a common feature of the experimental belts of epibenthic suspension feeders. However, the effects on recruiting oysters, mussels and barnacles as well as on mobile epifauna differed between suspension feeder species and sampling periods.

As previously shown by Diederich (2005), juvenile *M. edulis* showed no preference for mussels or oysters, while oyster spat preferentially settled on conspecifics. Similarly, preference of conspecifics was confirmed on mixed plots where most oyster spat settled on adult *C. gigas* rather than on mussels (own observation).

The high recruitment success of oysters in summer 2006 and the positive feedback in settlement will lead to further reef formation in the Wadden Sea. The lack of specificity in mussel recruitment will secure a coexistence of *M. edulis* with the dominant *C. gigas*. Thus, the ring experiment does support the conjecture of Diederich (2005) that resident mussels will not be excluded completely by the invading oysters. Mussels are able to use oyster reefs as a new habitat, and the relative shares of oysters and mussels in these densily packed suspension feeder reefs is likely to depend on the climate regime with differential effects on recruitment (Diederich et al. 2005, Nehls et al. 2006).

Although recruitment of the Australian barnacle *Elminius modestus* did not differ between the suspension feeder treatments there might be a tendency to prefer oysters. Barnacles preferentially settle on surfaces with cracks and pits (Chabot and Bourget 1988). Due to their shell structure oysters might provide better available substratum for sessile organisms compared to mussels with smooth and unruffled shells. Barnacle epigrowth is also known to enhance the recruitment of oysters on less favoured mussels and they also increase mussel recruitment on oyster and mussel shells (Buschbaum and Saier 2001, Diederich 2005). Thus, barnacle epigrowth may influence recruitment patterns of both bivalve species. As it was not feasible to brush off epibionts of the transferred oysters and mussels composing the 150 m² of experimental belts, we cannot extend our results to the entire community of sessile epibiota. This needs a different experimental approach.

The distribution patterns of adult *L. littorea* and *C. maenas* found in this study resemble the situation on natural mussel and feral oyster beds in the List tidal basin of 2005 (S. Görlitz, unpubl.). There were no significant differences in species richness of mobile epibenthos between sites dominated by oyster and mussels beds but abundances of *C. maenas* and *L. littorea* changed.

In October, the highest abundance of juvenile shore crabs *C. maenas* (5-10 mm carapax width) occurred on *M. edulis* plots, while in March these juveniles were spread in equally but at lower numbers across the different suspension feeder plots. Mussel clumps are known to constitute a spatial refuge against predation for juvenile shore crabs which might benefit from the dense mussel matrix during their first months of benthic life (Thiel and Dernedde 1994). We can only speculate why the preference of young shore crabs for

belts with mussels compared to belts of oysters was lost from autumn to spring. Additional experiments are needed to reveal whether this is caused by changing food availability or a different predation pressure on the crabs. However, oyster reefs seem to constitute an alternative habitat for juvenile shore crabs.

The experimental results on small and large periwinkles seem to reveal ontogenetic and/or seasonal shifts in habitat preference between rings of mussels and oysters. Large shore crabs preferentially attack small periwinkles (Hadlock 1980, Buschbaum et al. 2007) but leave the tidal zone of Königshafen to overwinter subtidally (Reise 1985, Thiel and Dernedde 1994). A more intricate matrix of interconnected mussels is suggested to provide a better refuge from adult crabs in October as compared to a coarser matrix of the large oysters. In March adult crabs have not yet returned from their overwintering sites, and small and large periwinkles distribute more according to food availability rather than predator refuge. Thus, we further suggest that oyster belts with their large biovolume (Fig. 3) supply more surface area to feed on microbial films than do mussels. This could explain why in autumn only the larger *L. littorea* were more abundant on oysters, while in March both, small and large periwinkles were taking advantage of the oyster habitat. More experiments are required to explore the subtle roles of habitat structures with respect to bottom-up and top-down effects on periwinkles.

2.5 Conclusion

The ring experiment has shown that biogenic habitat change from resident mussel beds to novel oyster reefs does not constitute a threat to species diversity but causes a shift in abundance of dominant associated species. Mussels and oysters may be functionally equivalent as consumers. However, the epibenthic biogenic structures they generate seem unfold subtle differences in habitat properties. Their community effects can only be explained in the context of the ecological web of species interactions. The differences in infauna and epifauna on mussel, mixed and oyster belts will have implications on foraging birds as well as on the relative proportions between mussels and oysters in the intertidal Wadden Sea in the years to come.

2.6 References

Austen, I., 1994. The surficial sediments of Königshafen – variations over the past 50 years. Helgol. Meeresunters. 48, 163-171.

Beukema, J.J. and Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar. Ecol. Prog. Ser. 287, 149-167.

Blott, S.J. and Pye, K., 2001. GRADISTAT 4.0: A grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Process. Landforms 26, 1237-1248.

Buschbaum et al. (in prep.)

Buschbaum, C. and Saier, B., 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. J. Sea. Res. 45, 27-36.

Buschbaum, C., Chapman, A.S. and Saier, B., 2006. How an introduced seaweed can affect epibiota diversity in different coastal systems. Mar. Biol.148, 743-754.

Buschbaum, C., Buschbaum, N., Schrey, I. and Thieltges, D.W., 2007. Shell-boring polychaetes affect gastropod shell strength and crab predation. Mar. Ecol. Prog. Ser. 329, 123-130.

Chabot, R. and Bourget, E., 1988. Influence of substratum heterogeneity and settled barnacle density on the settlement of cypris larvae. Mar. Biol. 97, 45-56.

Clarke, K.R. and Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed., PRIMER-E: Plymouth.

Commito, J.A. and Boncavage, E.M., 1989. Suspension-feeders and coexisting infauna an enhancement counterexample. J. Exp. Mar. Biol. Ecol. 125, 33-42.

Commito, J.A. and Dankers, N.M.J.A., 2001. Dynamics of spatial and temporal complexity in European and North American soft-bottom mussel beds. In: Reise, K. (Ed.), Ecological Comparisons of Sedimentary Shores. Springer, Berlin, pp. 39-59.

Crawley, M.J., 2005. Statistics. An introduction using R. John Wiley, New York. 342 pp.

Crooks, J.A., 1998. Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. Mar. Ecol. Prog. Ser. 162, 137-152.

Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97, 153-166.

Cuddington, K. and Hastings, A., 2004. Invasive engineers. Ecological Modelling 178 (3–4), 335–347.

Diederich, S., 2005. Differential recruitment of introduced Pacific oysters and native mussels at the North Sea coast: coexistence possible? J. Sea. Res. 53, 269-281.

Diederich, S. 2006. High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. J. Exp. Mar. Biol. Ecol. 328, 211-227.

Diederich, S., Nehls, G., Beusekom, J.E.E. van and Reise, K., 2005. Introduced Pacific oysters (*Crassostrea gigas*) in the Northern Wadden Sea: Invasion accelerated by warm summers? Helgol. Mar. Res. 59, 97-106.

Dittmann, S. 1990. Mussel beds – amensalism or amelioration for intertidal fauna? Helgol. Meeresunters. 44, 335-352.

Gätje, C. and Reise, K., 1998. Ökosystem Wattenmeer, Austausch-, Transport-, und Stoffumwandlungsprozesse. Springer, Berlin.

Görlitz, S., 2005. Neue Riffe im Wattenmeer: Die Pazifische Auster *Crassostrea gigas* und ihre assoziierte Lebensgemeinschaft. Diplomarbeit Kiel.

Hadlock, R.P., 1980. Alarm response of the intertidal snail *Littorina littorea* (L.) to predation by the crab *Carcinus maenas* (L.). Biol. Bull. 159, 269-279.

Hoey, van G., Vincx, M. and Degraer, S., 2006. Some recommendations for an accurate estimation of *Lanice conchilega* density based on tube counts. Springer-Verlag and AWI in the Wadden Sea: diversity differences of associated epifauna. Helgol. Mar. Res. 56, 44-50.

Jones, C.G., Lawton, J.H. and Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373-386.

Kruse, I., Strasser, M., Thiermann, F., 2004. The role of ecological divergence in speciation between intertidal and subtidal Scoloplos armiger (Polychaeta, Orbiniidae). J. Sea. Res. 51, 53-62.

Lenihan, H.S., 1999. Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. Ecological Monographs 69 (3), 251-275.

Nehls, G., Diederich, S., Thieltges, D. and Strasser, M., 2006. Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? Helgol. Mar. Res. 60, 135-143.

Rabaut, M. et al., A bio-engineered soft-bottom environment: The impact of Lanice conchilega on the benthic species-specific densities and community structure, Estuar. Coast. Shelf Sci. (2007), doi:10.1016/j.ecss.2007.05.041

Ragnarsson, S.A. and Raffaelli, D., 1999. Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments. J. Exp. Mar. Biol. Ecol. 241, 31-43.

R Development Core Team, 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org

Reise, K., 1985. Tidal Flat Ecology. Springer, Berlin, 191 pp.

Reise, K., 1998. Pacific oysters invade mussel beds in the European Wadden Sea. Senckenbergiana maritime 28, 167-175.

Reise, K., Herre, E. and Sturm, M., 1994. Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. Helgol. Meeresunters. 48, 201-215.

Strasser, M., 2002. Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. Mar. Ecol. Prog. Ser. 241, 113-123.

Strasser, M., Reinwald, T. and Reise, K., 2001. Differential effects of the severe winter of 1995/96 on the intertidal bivalves *Mytilus edulis*, *Cerastoderma edule* and *Mya arenaria* in the Northern Wadden Sea. Helgol. Mar. Res. 55, 190-197.

Thiel, M. and Dernedde, T., 1994. Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. Helgol. Mar. Res. 48, 321-332.

Thieltges, D.W., Strasser, M. and Reise, K., 2006. How bad are invaders in coastal waters? The case of the American slipper limpet *Crepiduala fornicata* in western Europe. Biological Invasions 8, 1673-1680.

Thieltges, D., Prinz, K., Reise, K. and Jensen, K.T., 2008. Oecologia (submitted)

Tsuchiya, M. and Nishihira M., 1986. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. Mar. Ecol. Prog. Ser. 31, 171-178.

Volkenborn, N. and Reise, K., 2006. Lugworm exclusion experiment: Responses by deposit-feeding worms to biogenic habitat transformations. J. Exp. Mar. Biol. Ecol. 330, 169-179.

Wallentinus, I. and Nyberg, C.D., 2007. Introduced marine organisms as habitat modifiers. Mar. Poll. Bull. 55, 323-332.

Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30, 377-392.