Invasion of Pacific oysters (*Crassostrea gigas*) in the Wadden Sea: competitive advantage over native mussels

Eingeführte Pazifische Austern (*Crassostrea gigas*) im Wattenmeer:
Konkurrenzvorteil gegenüber heimischen Miesmuscheln

DISSERTATION

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Oyster reef *Crassostrea gigas* in the northern Wadden Sea, Germany
Austernriff *Crassostrea gigas* im nordfriesischen Wattenmeer bei Sylt

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Contents

Summary

Pacific oysters (*Crassostrea gigas* Thunberg 1793) have been introduced into the Wadden Sea (North Sea) by aquaculture in the 1980s. Subsequently, natural spatfalls occurred and wild oyster populations became established. For settlement, oyster larvae need hard substrates to which they attach themselves permanently. By settling on top of each other, they may create massive biogenic reefs. On the sedimentary tidal flats of the Wadden Sea, epibenthic mussel beds (*Mytilus edulis* L.) represent the main insular hard substrates, wherefore the oysters attached themselves mainly to the shells of living and dead blue mussels.

Resident mussel beds became more and more overgrown by *C. gigas* and the question arose, whether they all might soon be replaced by oyster reefs. In this context, the objective was to assess the impact of *C. gigas* on the native ecosystem by investigating the population development in the northern Wadden Sea, and by evaluating the scope for coexistence with resident mussels. In general, this may be a test case whether an introduced species is capable of displacing a native analogue in a sedimentary shore environment.

The invasion of *C. gigas* in the northern Wadden Sea started in 1991 when the first wild oysters had settled on an intertidal mussel bed in the vicinity of an oyster farm that has started its business in 1986 in the List tidal basin (island of Sylt, Germany). At first, abundances on intertidal mussel beds remained low and patchy (1995: 3.56 ± 3.21 individuals m^{-2}; 1999: 3.71 ± 3.79 individuals m^{-2}). The population slowly expanded its range from intertidal to subtidal locations as well as from Sylt north- and southwards along the coastline. However, a succession of three summers (2001 – 2003) with anomalous high water temperatures led to a massive increase in oyster abundances (2003: 125.80 ± 119.47 individuals m^{-2}, 2004: 244.44 ± 172.84 individuals m^{-2}). It is assumed that the further invasion of *C. gigas* in the northern Wadden Sea will benefit from high late-summer water temperatures when these oysters reproduce. However, length frequency distributions revealed that successful cohorts survived for at least 5 years, allowing for population persistence even when warm summers are rare.

Studies on recruitment showed differential settlement of oysters and mussels that may lead to niche separation and coexistence of both species. As oysters settle preferentially on conspecifics, a positive feedback of adults on recruitment may facilitate rapid reef formation. Mussels may find a refuge underneath a cover of the brown macroalga *Fucus vesiculosus*. Potentially, mussels may overgrow oyster reefs in high recruitment years especially if a facilitating barnacle cover is high. However, biotic interactions with *C. gigas* that reaches about three to four times the size of mussels may prevent *M. edulis* to become abundant on oyster reefs.

Growth experiments revealed a faster growth of *C. gigas* compared to *M. edulis* in intertidal and subtidal habitats. Whereas oyster growth is not hampered by the presence of oysters, mussels, and barnacle epigrowth, the growth of mussels is reduced in the presence of these species, thus suggesting competitive inferiority.

In field experiments, a high survival rate of juvenile oysters was found and presumably caused by very low predation pressure. About 70% of juvenile *C. gigas* survived the first three months on an intertidal mussel bed and about 40% reached their first reproductive period one year after settlement. Only early recruitment in the subtidal zone was reduced due to predation. Laboratory feeding preference experiments confirmed that the main benthic predators, shore crabs (*Carcinus maenas* L.) and starfish (*Asterias rubens* L.), strongly prefer mussels to oysters. Size selective feeding by the main mussel predators together with an early size refuge from predation due to faster growth and larger size may facilitate a competitive advantage of *C. gigas* over *M. edulis*.

As *C. gigas* is well adapted to the Wadden Sea ecosystem and competitive superior to their native congeners, a further increase of the oyster population in the Wadden Sea is expected. The development of massive intertidal and possibly also subtidal oyster reefs that may contain a variable amount of mussel epigrowth depending on recruitment success in different years is considered as a likely future scenario. As oyster recruitment depends on high summer water temperatures whereas high mussel recruitment usually follows severe winters, a possible climate change leading to warmer summers and milder winters will further support the displacement of *M. edulis* by *C. gigas*. This regime shift is expected to have profound impacts on the Wadden Sea ecosystem, mainly because oysters are less integrated in the basic food web. A massive increase of the oyster population may lead to food limitation of other suspension feeders, especially in the wake of decreasing eutrophication, and to a decline of benthic predators. However, in which way the resident community will adapt to this new invader will be a future task to tackle. I conclude that the invasion of *C. gigas* in the Wadden Sea is facilitated by a high efficiency of using space and food resources and by low predation pressure by resident predators.

Zusammenfassung

Die Pazifische Auster (*Crassostrea gigas* Thunberg 1793) wurde Mitte der 1980er Jahre zu Aquakulturzwecken ins Wattenmeer eingeführt und hat sich seitdem durch natürliche Larvenfälle an der gesamten Wattenmeerküste etabliert. Austernlarven benötigen zur erfolgreichen Ansiedlung Hartsubstrate, an denen sie sich festzementieren können. Auf den sandigen Böden des Wattenmeeres beschränken sich solche Hartsubstrate jedoch größtenteils auf epibenthische Miesmuschelbänke (*Mytilus edulis* L.), die einer Vielzahl sessiler Arten als Siedlungsraum dienen.

Da sich die Austern auf die Schalen der Miesmuscheln heften, wurden die heimischen Muschelbänke zunehmend von den etwa drei- bis viermal größeren Austern überwachsen und es stellte sich die Frage, ob die Miesmuscheln bald verdrängt werden könnten. Das Ziel dieser Studie war es daher, die Ausbreitung und Einnischung von *C. gigas* im Wattenmeer zu untersuchen und zu einer Prognose zu gelangen, ob eine Koexistenz von Miesmuscheln und Austern in Zukunft möglich sein wird. Damit leistet die vorliegende Arbeit einen Beitrag zum Verständnis der möglichen Auswirkungen eingeschleppter Arten auf die Lebensgemeinschaften der Sedimentküsten.

Nachdem 1991 die ersten freilebenden Austern auf einer eulitoralen Muschelbank in der Nähe der Austernfarm im Lister Tidebecken (Sylt, nordfriesisches Wattenmeer) gefunden wurden, fand zunächst eine regionale Verbreitung statt, die mittleren Dichten nahmen hingegen kaum zu. So zeigten die ersten Kartierungen aus den Jahren 1995 (3.56 ± 3.21 Individuen m^{-2}) und 1999 (3.71 ± 3.79 Individuen m^{-2}) noch keinen nennenswerten Abundanzzuwachs, aber die Austern hatten sich allmählich sowohl nord- und südwärts entlang der Küste als auch vom Gezeitenbereich ins Sublitoral ausgebreitet. Erst eine Folge von drei Sommern (2001 – 2003) mit überdurchschnittlich hohen Wassertemperaturen führten zu einer dramatischen Zunahme des Austernbestandes (2003: 125.80 ± 119.47 Individuen m^{-2}; 2004: 244.44 ± 172.84 Individuen m^{-2}). Da in allen Jahren mit hohem Rekrutierungserfolg besonders hohe Wassertemperaturen im Spätsommer herrschten, wird vermutet, dass die weitere Bestandsentwicklung der Austern im nördlichen Wattenmeer vom Auftreten warmer Sommer abhängt. Da Längenhäufigkeitsverteilungen jedoch zeigen, dass bestandsbildende Kohorten mindestens 5 Jahre lang überleben, wird auch eine Periode mit kalten Sommern nicht zum Verschwinden der Austern führen.

Untersuchungen zur Rekrutierung von Austern und Miesmuscheln haben artspezifische Unterschiede ergeben, die eine Koexistenz von beiden Arten ermöglichen könnten. Während sich Austern bevorzugt auf Artgenossen ansiedeln, zeigen Miesmuscheln keine Präferenz für Austern- oder Miesmuschelsubstrate, sie bevorzugen vielmehr mit Seepocken bewachsene Schalen vor unbewachsenen. Die positive Verstärkung des Rekrutierungserfolges durch die Anwesenheit adulter Austern wird die Ausbildung von Austernriffen beschleunigen. Da die Rekrutierung von *C. gigas* jedoch durch das Vorhandensein der Braunalge *Fucus vesiculosus* stark behindert wird, könnten Miesmuscheln unter *Fucus* einen Rückzugsraum finden und in Jahren mit hohem Rekrutierungserfolg, wie sie meist auf kalte Winter folgen, die neuen Austernriffe überwachsen. Dies wird jedoch unter anderem davon abhängen, inwieweit die Miesmuscheln mit den Austern um potentiell limitierende Ressourcen konkurrieren können.

Wachstumsexperimente haben gezeigt, dass Austern schneller wachsen als Miesmuscheln. Weder die Überdeckung mit der Braunalge *F. vesiculosus*, noch der Aufwuchs von Seepocken oder die Anwesenheit von Miesmuscheln und Austern haben einen negativen Einfluss auf die Wachstumsrate von *C. gigas*. Das Wachstum von Miesmuscheln wird hingegen durch die Anwesenheit dieser Arten verlangsamt, was vermuten lässt, das *M. edulis* konkurrenzschwächer ist.

Freilandexperimente haben ergeben, dass juvenile Austern sehr hohe Überlebensraten auf eu- und sublitoralen Miesmuschelbänken aufweisen. In Räuberausschlussexperimenten und Nahrungswahlversuchen konnte gezeigt werden, dass geringer Prädationsdruck für die niedrige Mortalität verantwortlich sein könnte. Sowohl Strandkrabben (*Carcinus maenas* L.) als auch Seesterne (*Asterias rubens* L.) haben die heimischen Miesmuscheln den Austern vorgezogen. Da die Austern schneller wachsen und größer werden als die heimischen Miesmuscheln, wachsen sie zudem schneller aus dem Nahrungsspektrum von möglichen Räubern heraus, was Ihnen einen weiteren Konkurrenzvorteil verschafft.

Da *C. gigas* sehr gut an den Lebensraum Wattenmeer angepasst und konkurrenzstärker ist als *M. edulis*, ist zu erwarten, dass ihre Dichte weiter zunehmen wird und es zur Ausbildung von großflächigen eu- und sublitoralen Austernriffen kommen kann. Die Miesmuscheln werden wahrscheinlich weiter abnehmen und könnten zu einer Existenz als eine unter vielen Aufwuchsarten auf Austernriffen zurückgedrängt werden. Diese Vorhersage wird durch Klimaprognosen gestützt, die wärmere Sommer und mildere Winter vorhersagen. Falls die Austern sehr stark zunehmen und abnehmende Eutrophierung in Zukunft zu Nahrungslimitierung im Wattenmeer führen wird, könnten die Austern auch andere

Muschelarten zurückdrängen. Da die Austern zumindest gegenwärtig noch schlecht ins Nahrungsnetz integriert sind, wird Ihre Zunahme auf Kosten anderer Arten auch deutliche Auswirkungen auf höhere trophische Stufen wie benthische Prädatoren und Vögel haben. Inwieweit sich jedoch das heimische Ökosystem an die eingeschleppte Art anpassen kann, muss einer weiteren Untersuchung vorbehalten bleiben.

1 General Introduction

This study discusses an invasive species that may have profound impacts on ecosystem dynamics in the Wadden Sea (North Sea). The spread and niche occupation of introduced Pacific oysters (*Crassostrea gigas*) was investigated in field surveys as well as in field and laboratory experiments. As the oysters are settling on top of native epibenthic mussel beds (*Mytilus edulis*), the scope of coexistence for both species was assessed. The first section of this introduction deals with general aspects of marine bioinvasions, whereas the second section is focussed on the invasion history of *C. gigas*. The third section illustrates possible effects of *C. gigas* on the benthic ecosystem and especially on the ecology of mussel beds. Finally, the main questions of this study are presented.

1.1 Marine bioinvasions

Non-native species accumulating in marine ecosystems are a significant component of human induced environmental change, leading to a homogenisation of the earth's biota (Lodge 1993, Lövei 1997, Vitousek et al. 1997, Occhipinti-Ambrogi & Savini 2003). Even though changes in species compositions and interactions due to climatic and geographic variations have occurred throughout evolutionary time, human mediated transport vectors are allowing a much wider and faster distribution to new habitats. Especially the improvement of intercontinental ship traffic largely enhanced the number of non-native species that were transported in ballast water or attached to ship hulls and survived even long distance journeys (Carlton 1985, Carlton & Geller 1993, Ruiz et al. 2000, Minchin & Gollasch 2003). The deliberate or accidental release of aquaculture products is another important gateway, not only for target species, but also for organisms associated with them, such as epifauna and -flora as well as parasites and pathogens (Chew 1990, Naylor et al. 2001, Wolff & Reise 2002). Aquarium trade and plastic debris drifting on the sea surface are other anthropogenic vectors with increasing significance (Barnes 2002, Semmens et al. 2004).

However, even though enormous amounts of organisms are transported beyond their native ranges every day, only few of them are able to establish themselves in recipient habitats and even less become invasive and develop an immense population growth (Lodge 1993, Williamson & Fitter 1996a). Nevertheless, there are numerous examples of invasive species that have profound direct and indirect effects on the native community, ranging from species-level consequences to impacts on food-web properties and ecosystem processes (Grosholz 2002). One example for an invasion that has caused changes at ecosystem level is the introduction of the estuarine Asian clam *Potamocorbula amurensis* into San Francisco Bay. The bivalve interrupted the basic food chain by transferring most of the primary production from the pelagic to the benthic food web, thereby enhancing benthic invertebrates and bottom-feeding fishes on the expense of zooplankton and larval fish (Carlton et al. 1990, Nichols et al. 1990, Kimmerer et al. 1994). Another example is the comb jelly *Mnemiopsis leidyi* that was introduced into the Black Sea via ballast water in the early 1980s. The voracious zooplanktonic predator devastated the food chain of the entire Black Sea basin and caused a huge economic damage to the fishing industry by feeding on the food supply and on the eggs and larvae of resident pelagic fish (Kideys 2002). However, eutrophication may have played an important role in this process, thus supporting a theory that states that disturbed habitats are more susceptible to invasions than undisturbed ones (Occhipinti-Ambrogi & Savini 2003, Marvier et al. 2004). Assuming that successful invaders are habitat generalists and that generalists are competitive inferior to habitat specialists because of a trade-off between competitive ability and habitat breadth, habitat destruction and short-term disturbances should favour invasion by habitat generalists despite their inferior competitive ability (Marvier et al. 2004).

In order to predict or prevent further introductions, many studies have focussed on characteristics of successful invaders (di Castri 1990, Lodge 1993, Kolar & Lodge 2001, McMahon 2002) and on habitat characteristics (Crawley 1987, Case 1991) that may determine susceptibility to invasion. Species with r-selected life history traits (rapid growth, early maturity, short life spans, high fecundity, and extensive dispersal capacity) are generally considered to be successful invaders because they are able to achieve massive population densities soon after introduction to a new habitat (Lodge 1993, Williamson & Fitter 1996b, McMahon 2002). The term ‘niche opportunity’ was employed to describe conditions that promote invasions in terms of resources, natural enemies, the physical environment, and interactions between these factors varying in time and space (Shea & Chesson 2002). How a species responds to these conditions determines its ability to invade a certain habitat. In this context, high species richness has been proposed as a prerequisite for a low susceptibility to invasion – or low niche opportunity – because of a more complete utilization of resources by resident species (Elton 1958, Stachowics et al. 1999). However, characteristics that may facilitate invasion or invasibility are controversially discussed, because many successful invasions are not following any of the general rules (Crawley 1987, Lodge 1993).

Climate change leading to changing maximum and minimum temperatures has frequently been discussed as supporting biological invasions (Stachowicz et al. 2002). For example, higher winter temperatures are promoting the spread of slipper limpets *Crepidula fornicata*, and higher spring temperatures facilitate the expansion of the cord grass *Spartina anglica* in the northern Wadden Sea (Thieltges et al. 2004, Loebl et al. submitted).

The spread and niche occupation of an introduced species offers opportunities to study basic processes in population biology (Sakai et al. 2001). Assuming that an invasive species encounters suitable environmental conditions in its new habitat, its population development will depend on whether it is consumed by native predators (Robinson & Wellborn 1988, Trowbridge 1995) or outcompetet by resident species (Moulton & Pimm 1983, Case 1991). Exploitative competition between an introduced and a native species may occur if one species has a more efficient way of using limiting resources (Byers 2000). Various case studies have compared the ability to compete for space and/or food between exotic species and their native congeners in order to explain or assess future invasion success (e.g. Byers 2000, Talman & Keough 2001, Kotta & Ólaffson 2003, Cope & Winterbourn 2004). In addition, home and away comparisons, that is, comparisons of species in their native and invaded ranges, are considered to be important for the understanding of invasion processes (Lohrer et al. 2000). Recently, the enemy release hypothesis has been widely discussed in invasion literature. It states that the success of invaders is related to the scarcity of natural enemies such as predators, parasites and pathogens, in the introduced range compared to the native habitat (Torchin et al. 2001, 2003, Keane & Crawley 2002, Shea & Chesson 2002, Clay 2003, Drake 2003, Mitchell & Power 2003, Colautti et al. 2004). However, phenotypic plasticity may enable native species to react to the invaders (Cox 2004). For example, in New England the native periwinkle *Littorina obtusata* developed thicker shells in response to the introduction of a new predator, the European green crab *Carcinus maenas* (Trussel 2000).

At the North Sea coast, about 80 non-native species became established, with ship traffic and aquaculture being the most important introduction vectors (Reise et al. 2002). Most of these species remained insignificant additions to the native biota, but there are some species that may alter ecosystem functioning (Reise et al. 2005). Examples are the cord grass *Spartina anglica* (Loebl et al. submitted), the Japanese seaweed *Sargassum muticum* (Buschbaum in press), the American slipper limpet *Crepidula fornicata* (Thieltges et al. 2004), and the Pacific oyster *Crassostrea gigas* (Reise 1998).

As *C. gigas* is an ecosystem engineer that alters habitat characteristics by forming massive epibenthic reefs, its introduction may have community-level effects proportional to its abundance (Reusch & Williams 1999, Jones et al. 1994). Possible impacts of *C. gigas* on the Wadden Sea ecosystem, and how competition with native mussels and predation by resident predators may influence the invasion success, will be discussed in chapter 6 (General Discussion).

1. 2 Invasion history of *Crassostrea gigas*

1.2.1 Global distribution

The Pacific oyster originates from Japan and has been introduced to various coastal areas due to aquaculture activities (Korringa 1976, Andrews 1980, Chew 1990; Fig. 1). In many regions, natural spatfalls occurred and wild oyster populations established: e.g. British Columbia (Quayle 1988), California (Span 1978), South Africa (C. Griffith, pers. comm.), Australia (Ayres 1991), New Zealand (Dinamani 1991), France (Grizel & Héral 1991), The Netherlands (Drinkwaard 1999), and Germany (Reise 1998). It is important to note that according to genetic studies the Portuguese oyster *Crassostrea angulata* is a strain of *C. gigas* originating from Taiwan (Boudry et al. 1998, Huvet et al. 2002). *C. angulata* was accidentally introduced to Portugal sometime between the early 16th and the late 18th century and was later imported into France (1860s) and The Netherlands (19th century) for aquaculture (Wolff & Reise 2002). However, gill disease and viral pathogens led to a severe decline of the Portuguese oyster in the 1960s and 1970s, and stocks never recovered thereafter (Goulletquer & Héral 1991).

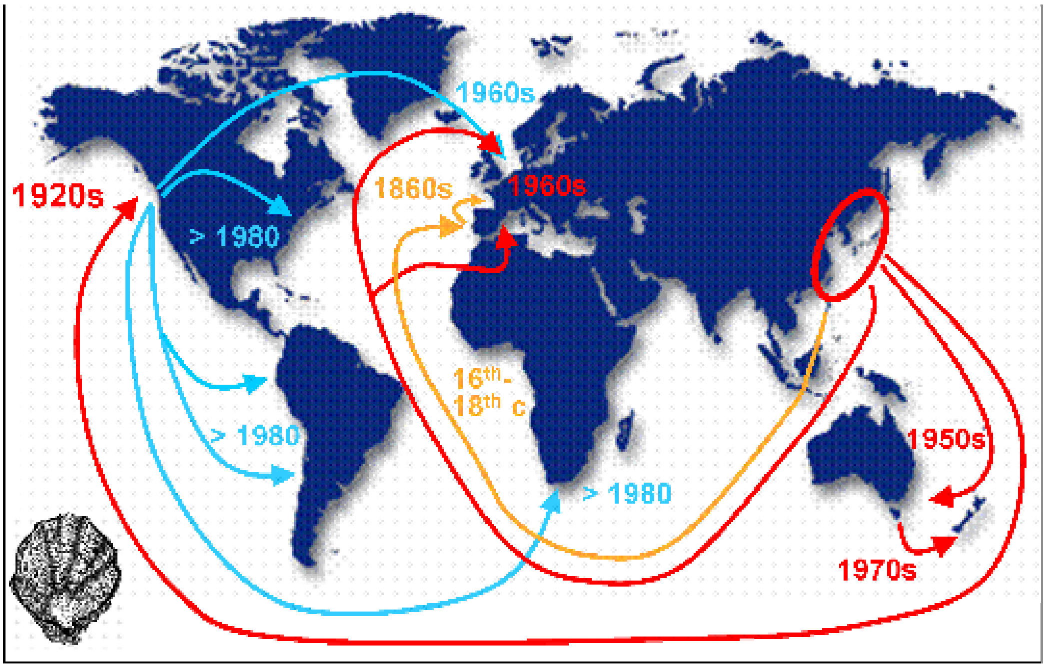

Fig. 1 Worldwide distribution of *C. gigas* respectively *C. angulata*. Given is native range (encircled; Japan and Korea for *C. gigas*, Taiwan for *C. angulata*), and years of first introductions. Yellow: *C. angulata*; red: *C. gigas* from Japan; blue: *C. gigas* from the west coast of the U.S. Map after Chew (1990) and Wolff & Reise (2002)

In Europe, imports of *C. gigas* started in 1964 with spat oysters from British Columbia that were released in the Oosterschelde (The Netherlands) for aquaculture purposes (Drinkwaard 1999). The first natural spatfalls occurred during two exceptionally warm summers in 1975 and 1976 and subsequently a wild population established. From then on, the oyster population increased enormously, from 15 - 35 ha oyster reef area in 1980 to 210 - 370 ha in 1990 and to 640 ha in 2002 (Kater & Baars 2003). The introduction of *C. gigas* to France, which started in 1966 with imports of spat from Japan, led to a similar population increase (Le Borgne et al. 1973, Grizel & Héral 1988). However, in Great Britain, where *C. gigas* is cultured since 1965, only sporadic natural spatfalls occurred in some estuaries (Spencer et al. 1994, Child et al. 1995).

In the Wadden Sea, which is a 500 km long coastal stretch between Den Helder in The Netherlands and Esbjerg in Denmark (Fig. 2), the invasion of *C. gigas* started from two locations: from the island of Texel (The Netherlands) in 1983 and from the island of Sylt (Germany) in 1991 (Bruins 1983, Reise 1998). The oysters near Texel in the Dutch Wadden Sea are considered to have been accidentally introduced with mussel transports from the Oosterschelde (Bruins 1983), whereas the oysters in the northern German and Danish Wadden

Sea sprang from an oyster culture near Sylt (Reise 1998). From Texel, the oysters spread eastwards along the coast and reached the German Wadden Sea in 1998 (Wehrmann et al. 2000). Meanwhile, extensive intertidal oyster reefs have developed near the islands of Texel and Rottum in The Netherlands (Dankers et al. 2004), and also in the western German Wadden Sea the formation of oyster reefs has recently begun (A. Schmidt, pers. comm.).

Near Sylt, the first wild oyster that had dispersed as a larva was found in 1991 on an intertidal mussel bed *Mytilus edulis* in the vicinity of an oyster farm that started its business in 1986. The wild oyster population slowly expanded its range from Sylt north- and southwards along the coastline. However, abundances remained on a low level until a succession of three consecutive summers (2001 - 2003) with anomalous high water temperatures led to an immense increase in oyster densities and to the formation of oyster reefs in some locations by 2004.

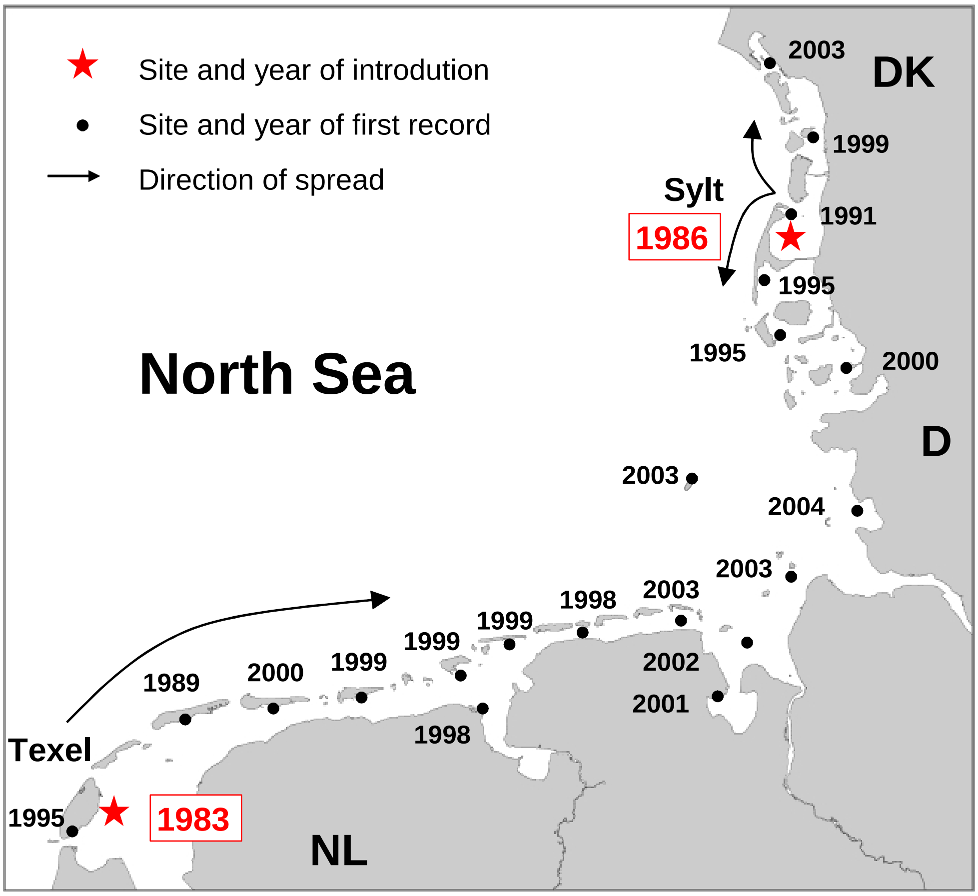

Fig. 2 Distribution of *C. gigas* in the Wadden Sea. Given are years and sites of introduction (red; asterisks) and years of first records (black, dots). Map after Reise et al. 2005

1.2.2 History of oyster fishery in the northern Wadden Sea

Until the end of the 19th century the Wadden Sea was famous for a thriving oyster industry based on extensive subtidal beds of the native European oyster *Ostrea edulis*. However, overexploitation and diseases resulted in dramatic decline of the oyster population (Hagmeier & Kändler 1927, Hagmeier 1941, Reise 1982, 1990). Karl Möbius came up with the concept of an ecological community – or biocoenosis – by studying the declining oyster reefs (Möbius 1877). However, neither fishing regulations nor the import of seed oysters from France and The Netherlands could prevent that *O. edulis* became extinct in the Wadden Sea in the 1940s or 1950s (Reise 1990). To compensate for the loss of *O. edulis*, exotic oyster species were introduced for aquaculture, but only the Pacific oyster *Crassostrea gigas* turned out to be profitable. After some preliminary attempts to cultivate *C. gigas* in the north and east Frisian Wadden Sea in the 1970s, the only commercial oyster farm started its business in 1986 off the coast of Sylt in the List tidal basin (Fig. 3, 4).

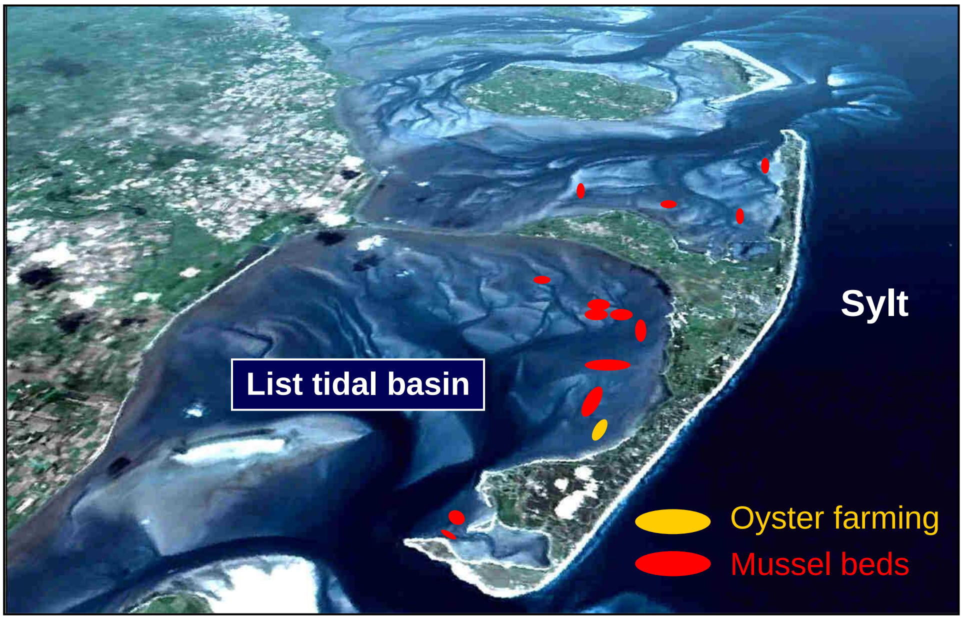

Fig. 3 Study site (List tidal basin; 54°50’ - 55°10’ N, 0 8°20 ’- 08°40’ E). Marked are intertidal mussel beds and the location of the oyster farm. Satellite picture from GAF / Euromap

Spat oysters from hatcheries in Great Britain and Ireland are regularly imported and placed in mesh bags that are deployed on trestles close to the low water line. It takes about 2 years until the oysters reach marketable size and the annual production is about 2 million individuals.

Fig. 4 Farming of *C. gigas* in the northern Wadden Sea. The oysters are kept in mesh bags on trestles in the low intertidal zone

1.3 *C. gigas* and the ecology of mussel beds

Shortly after oyster farming had commenced, natural spatfalls occurred and wild *C. gigas* were found in the vicinity of the culture plot. In order to metamorphose, oyster larvae need hard substrates to which they attach themselves by releasing cement drops from a foot gland (Quayle 1988). From then on, the young oyster will be attached for life. However, hard surfaces are scarce on the extensive mud and sand flats of the Wadden Sea. Only dead shell material and epibenthic mussel beds *Mytilus edulis* provide secondary hard substrata for sessile species. Therefore, the oysters are mainly found as epibionts on mussel beds, attached to the shells of living and dead mussels (Fig. 5). Mussels generate epibenthic bed structures by attaching themselves to each other and to other hard material via byssal threads, which are protein fibres generated by certain foot glands (Fig. 6). This creates a three dimensional matrix of connected living and dead mussels that provides a habitat for a diverse associated flora and fauna (Riesen & Reise 1982, Tsuchiya & Nishihira 1986, Dittmann 1990, Matsumasa & Nishihira 1994). This high species richness and biomass renders mussel beds important food resources for various benthic predators, fish, birds, and humans (Seed 1969, Dankers & Zuidema 1995, Nehls et al. 1997, Saier 2001). Mussel beds are also very important for the material flux in shallow water habitats, because they exchange

Fig. 5 Juvenile *C. gigas* attached to a living mussel

high amounts of particulate matter, nutrients, and oxygen with the water column (Asmus 1987, Dankers et al. 1989, Asmus & Asmus 1990, 1991, Prins & Smaal 1994).

Fig. 6 Intertidal mussel bed *Mytilus edulis*.
Inset:
M. edulis attached to each other with byssal threads

The densely packed communities are now overgrown by *C. gigas*, a reef-building invader that reaches about three to four times the size of native mussels. In comparison to the dynamic mussel beds where mussels are able to move to a certain extend using their foot and byssal threads, oyster reefs are more massive and fixed because the individuals are cemented to each other (Fig. 7).

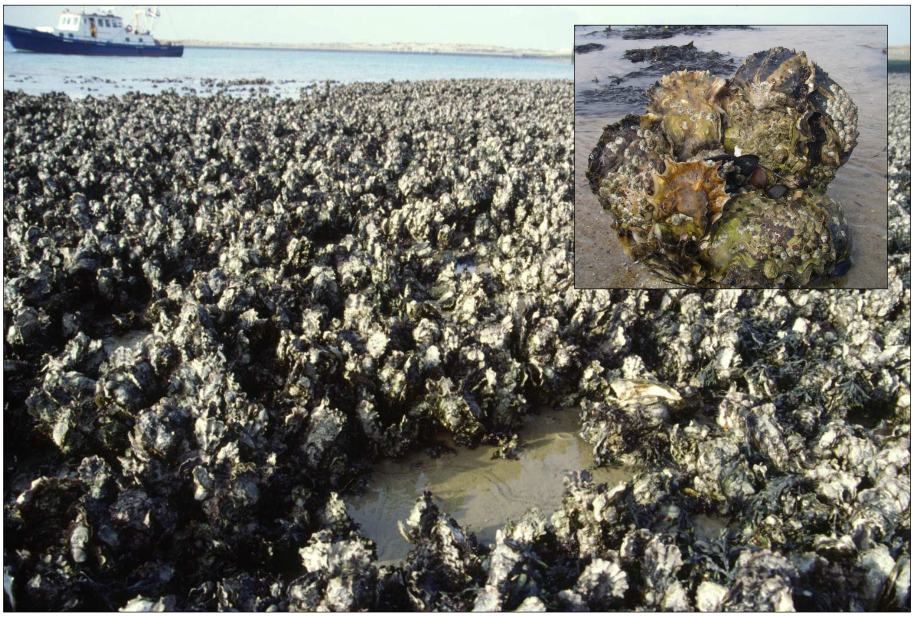

Fig. 7 Intertidal oyster reef *Crassostrea gigas* in the Oosterschelde, The Netherlands.
Inset:
start of an oyster reef with about 20 oysters attached to each other

In order to assess the future population development of *C. gigas* and the scope of coexistence with native mussels, different aspects of biotic interactions between oysters and their recipient habitat were studied. Firstly, population parameters like abundances and length-frequency distributions were recorded in different locations and years. Secondly, field experiments were conducted to compare recruitment, survival, and growth of *C. gigas* with native mussels, thereby taking important biological interactions on mussel beds into account. For example, mussel beds may be partly covered with a thick layer of the brown macroalga *Fucus vesiculosus* forma *mytili* (Fig. 8). *Fucus*-cover reduces current velocities above the mussel bed, enhances sedimentation, and has negative impacts on abundances of mussels and their epibionts, but supports various herbivores and increases overall macrobenthic diversity (Albrecht & Reise 1994). Another important factor for mussel bed dynamics is epibiosis (Albrecht & Reise 1994, Wahl et al. 1997, Laudien & Wahl 1999, Buschbaum & Saier 2001, Buschbaum 2002). In the Wadden Sea, the barnacles *Semibalanus balanoides* and *Balanus crenatus* are the most abundant epibiont species on mussels (Fig. 8). Their impacts on mussels are two sided: they reduce the growth rate of their basibiont, but enhance mussel recruitment (Grant 1977, Saier 2001, Buschbaum 2002).

Fig. 8 *Fucus*-cover on mussel bed (left); Barnacle overgrowth on mussel shells (right)

As mussel populations are often limited by predation, field and laboratory experiments were carried out in order to assess whether low predation pressure by the main benthic predators, the shore crab *Carcinus maenas* and the starfish *Asterias rubens*, may facilitate a competitive advantage of *C. gigas* over *M. edulis* (Fig. 9).

Fig. 9 Shore crab *Carcinus maenas* (left) and starfish *Asterias rubens* (right). Starfish photo by C. Buschbaum

1.4 Outline of the study

This study is divided into four separate manuscripts each dealing with a different aspect of the life history of *C. gigas*: population development (chapter 2), recruitment (chapter 3), survival and growth (chapter 4), and predation (chapter 5). In chapter 6 results are summarised and the impact of a possible regime shift with mussel beds being largely replaced by oyster reefs is discussed on species and ecosystem level.

- **Chapter 2** describes the population development of *C. gigas* in the northern Wadden Sea and links the recent massive increase in abundances to high recruitment success in years with abnormally high summer water temperatures.
- In **chapter 3**, recruitment patterns of *C. gigas* and *M. edulis* are compared in order to assess whether habitat preferences may facilitate niche separation and coexistence of both species.
- **Chapter 4** deals with survival and growth of *C. gigas* and *M. edulis* in relation to tide level, substrate, barnacle epigrowth and algal cover. In field experiments it was investigated whether habitat requirements of both species are similar or whether there are species-specific refuges from potential competition.
- In **chapter 5**, the hypothesis that low predation pressure by resident predators may facilitate a competitive advantage of *C. gigas* over *M. edulis* was tested. Therefore, predator exclusion experiments and laboratory feeding preference experiments with shore crabs *Carcinus maenas* and starfish *Asterias rubens* as predators were conducted.
- In **chapter 6** it is concluded that most mussel beds will become replaced by oyster reefs which may be overgrown with varying numbers of *M. edulis*. This will have consequences on the food web and other ecosystem properties.

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Chapter 2

Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers?

Abstract

Among the increasing number of species introduced to coastal regions by man, only a few are able to establish themselves and spread in their new environments. We will show that the Pacific oyster (*Crassostrea gigas*) took 17 years before a large population of several million oysters became established on natural mussel beds in the vicinity of an oyster farm near the island of Sylt (northern Wadden Sea, eastern North Sea). The first oyster, which had dispersed as a larva and settled on a mussel bed, was discovered 5 years after oyster farming had commenced. Data on abundance and size frequency distribution of oysters on intertidal mussel beds around the island indicate that recruitment was patchy and occurred only in 6 out of 18 years. Significant proportions of these cohorts survived for at least 5 years. The population slowly expanded its range from intertidal to subtidal locations as well as from Sylt north- and southwards along the coastline. Abundances of more than 300 oysters m^{-2} on mussel beds were observed in 2003, only after two consecutive spatfalls in 2001 and 2002. Analyses of mean monthly water temperatures indicate that recruitment coincided with above-average temperatures in July and August when spawning and planktonic dispersal occurs. We conclude that the further invasion of *C. gigas* in the northern Wadden Sea will depend on high late summer water temperatures.

Keywords

Crassostrea gigas, Introduced species, Recruitment, Water temperature, Wadden Sea

1 Introduction

Marine ecosystems have always been subject to changes in species composition and interactions, but natural migration of organisms due to climatic and geographic variations is becoming superimposed by anthropogenic vectors facilitating a much faster and wider distribution into new habitats. Important vectors are intercontinental shipping and the commercial transport of aquaculture products from one coast to another (Chew 1990, Carlton & Geller 1993, Carlton 1996, Reise et al. 1999, Gollasch et al. 2000, Ruiz et al. 2000, Naylor et al. 2001, Wolff & Reise 2002). However, only about ten percent of these introduced species are expected to become established and to spread in their new environments, and only a small fraction may furthermore induce changes to the recipient ecosystem (Williamson & Fitter 1996).

In the North Sea, at least 80 non-indigenous species have established themselves in historical time and most of them inhabit the coastal and estuarine zones (Reise et al. 1999, Wolff 1999). Approximately 50% of these species were introduced through aquaculture, that is, either the imported target species was released into the wild or associated organisms were unintentionally co-introduced. Examples of species that were introduced with shellfish are the American slipper limpet *Crepidula fornicata* (Hagmeier 1941, Werner 1948, Thieltges et al. 2003) and various parasites such as the copepods *Mytilicola orientalis* and *M. ostreae* (Stock 1993).

The oyster fishery industry and accompanying shellfish imports have a long tradition in the North Sea. Until the end of the nineteenth century, the extensive subtidal beds of the European oyster *Ostrea edulis* supported a thriving fishing business. Overfishing, however, resulted in a dramatic decline in the native oyster population as the demand for fresh oysters grew (Hagmeier & Kändler 1927, Hagmeier 1941, Reise 1982, 1990). Fishermen thereupon started to import large numbers of seed oysters to restock the local oyster grounds but with no success (Möbius 1877, Hagmeier 1941, Korringa 1976, Utting & Spencer 1992). Only the cultivation of the Pacific oyster *Crassostrea giga*s turned out to be commercially successful. This oyster originates from Japan and has been distributed in oyster cultures all over the world since the early twentieth century (Andrews 1980, Quayle 1988, Arakawa 1990, Chew 1990). In most regions, the Pacific oysters did not remain restricted to their culture plots, but reproduced and dispersed successfully in the new environments (e.g. British Columbia: Qualye 1988, Australia: Ayres 1991, and New Zealand: Dinamani 1991). In the North Sea imports of *C. gigas* started in 1964 in the Netherlands (Drinkwaard 1999), followed by transports to England (Walne & Helm 1979, Utting & Spencer 1992, Spencer et al. 1994), France (Maurin & LeDantec 1979, Grizel & Héral 1991) and Germany (Neudecker 1985). Whereas only sporadic natural spatfalls occurred in Great Britain (Spencer et al. 1994, Smith 1994, Eno et al. 1997), wild oyster populations are growing fast in France (Grizel & Héral 1991) as well as in the Netherlands (Drinkwaard 1999, Dankers et al. 2004). The success of natural recruitment and the rate of spread are different in these locations and seem to depend on abiotic factors such as water temperature and salinity (Quayle 1988, Ayres 1991, Spencer et al. 1994).

The spread of the Pacific oyster in the northern Wadden Sea began 5 years after the first German oyster farm had started its business off the island of Sylt in 1986 (Reise 1998). The first oyster that had dispersed as a larva was found on an intertidal mussel bed (*Mytilus edulis*) about 6.5 km north of the oyster farm. Oysters are found mainly as epibionts on natural mussel beds because they need hard substrates to settle on. Oyster larvae use the shells of living and dead mussels as attachment surface because mussel beds represent one of a limited number of secondary hard substrata available on the extensive mud and sand flats in the Wadden Sea. In this article, we describe the slow expansion of a wild *C. gigas* population since the first settlement of spat in 1990 and suggest that the increase in population size may be retarded by irregular recruitment, which we assume is limited by late-summer water temperatures.

2 Methods

2.1 Study site

The Wadden Sea is a large intertidal area in the south-east part of the North Sea, characterized by extensive mud and sand flats. First records of *Crassostrea gigas* on intertidal mussel beds, revetments, and harbour constructions are given for the northern Wadden Sea, which extends from Esbjerg (Denmark) in the north to the Elbe estuary (Germany) in the south (Fig. 1). The quantitative surveys of *C. gigas* abundances and size distributions were carried out on intertidal mussel beds close to the island of Sylt (North Frisian Wadden Sea, Germany; Fig. 2). Sylt is adjacent to two tidal basins: the List basin in the northeast and the Hörnum basin in the southeast. The List tidal basin (54°50’ - 55°10’N and 08°20’ - 08°40’E) is largely closed by dams to the north and south and covers an area of about 404 km². It is connected to the North Sea through a narrow tidal inlet of only 2.8 km in width (Reise & Riethmüller 1998). Tides are semidiurnal and the mean tidal range is 2 m; the average salinity is close to 30 psu. Long term mean water temperatures (based on monthly mean temperatures) range from 18.2°C in August to 2.3°C in February. Intertidal flats, which are mostly sandy, make up 33% of the area (Reise & Lackschewitz 1998), and intertidal mussel beds cover 1.5 km^2 (Nehls 2003, Stoddard 2003). The Hörnum tidal basin in the south of Sylt is widely open to the North Sea. It covers 290.2 km² (Spiegel 1997) and contains at present only five small mussel beds that cover about 0.04 km² of the intertidal zone (Nehls 2003, Stoddard 2003).

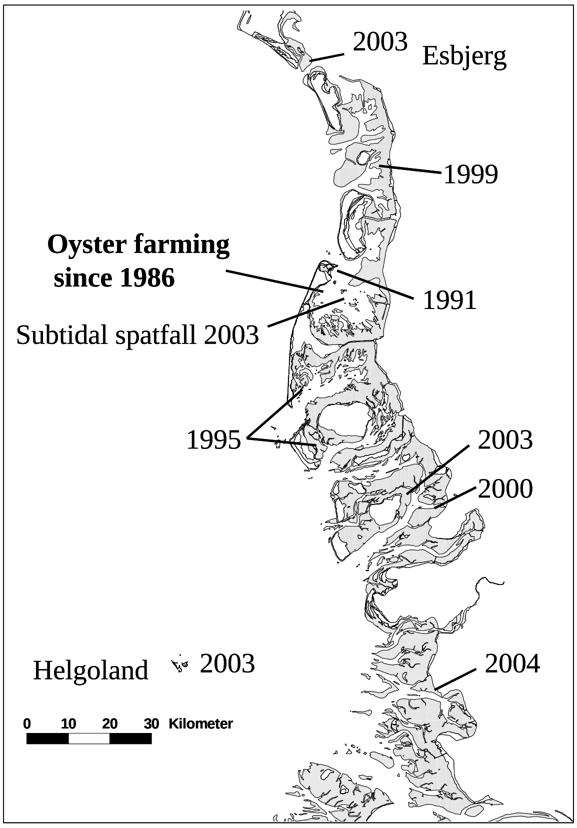


Fig. 1 Northern Wadden Sea from Esbjerg (Denmark) to Elbe estuary (Germany) with first records of *Crassostrea gigas*. Grey areas represent intertidal mud and sand flats

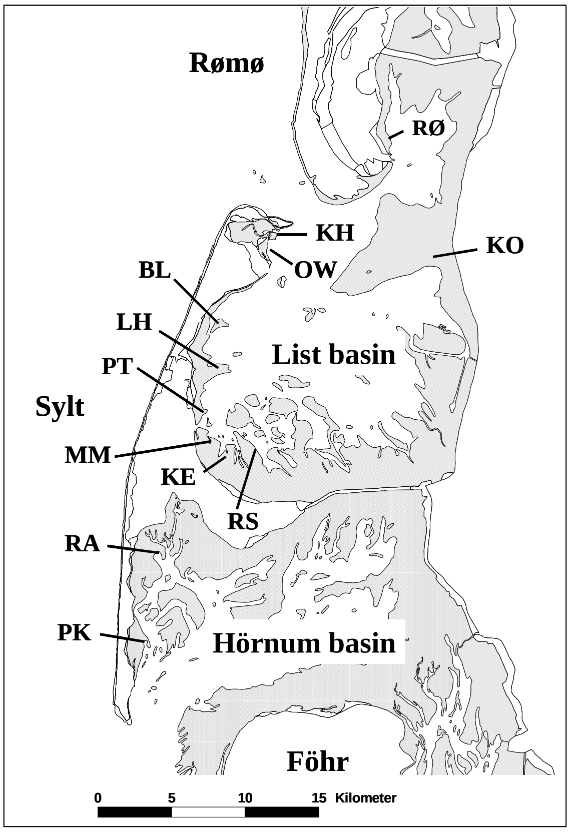


Fig. 2 Map of Wadden Sea near Sylt (List and Hörnum tidal basin) with labelled intertidal mussel beds (for abbreviations see Table 1)

2.2 Abundance and size of *C. gigas* on intertidal mussel beds

Comprehensive field surveys on the abundance of *C. gigas* were carried out twice near the island of Sylt. The first survey took place from March to May and from September to October 1999 on 12 intertidal mussel beds: 11 in the List tidal basin and 1 in the Hörnum tidal basin (Fig. 2). The second survey was conducted in July and August 2003 on 10 intertidal mussel beds: 8 in the List basin and 2 in the Hörnum basin. Two mussel beds were also visited in spring and autumn 2001 and 2002 to detect changes in abundance on a smaller time scale. The data are compared with those from a survey that was done in the same area and in the same way in 1995 by Reise (1998).

The abundance of *C. gigas* on intertidal mussel beds was determined by randomly placing a frame of 50 × 50 cm (0.25 m²) within the area covered by mussels. During the 2003 survey we used a smaller frame (25 × 25 cm) on the mussel beds Munkmarsch and Königshafen because of the very high oyster abundances. The oysters inside the frame were counted. If the mussel bed patch was covered with fucoid algae, these were lifted and the oysters beneath the algal canopy were counted. The number of replicates varied with the amount of time available due to the turning tide and the size of the mussel bed (11 - 238 per site). Field surveys were carried out before the recruitment of the same year took place or before the recruits were large enough to be counted. The recorded abundances, therefore, did not include the 0-group of the respective year and the spring and fall data from 1999 can be compared with those of July and August in 1995 and 2003. The total amount of *C. gigas* in the List basin in 2003 was calculated by multiplying the overall mean abundance of *C. gigas* by the total area within the basin that was covered with mussel beds in 2003: 1.54 km² mussel bed area, mussel coverage 31%, i.e. 0.48 km² mussel ground. These data are derived from a regular monitoring program that surveys the size of mussel beds with aerial views and ground inspection with a global positioning system (GPS). Mussel coverage is determined by walking in linear transects across the mussel beds and counting the amount of steps that hit areas covered with mussels and steps that hit areas with no living mussels (Nehls 2003 and more recent data).

The length-frequency distribution of *C. gigas* was investigated by measuring the shell length (largest diameter of the shell) of oysters that were randomly encountered on the mussel bed. Shell length was measured with vernier callipers to the nearest millimetre.

Results are given as arithmetic means with standard deviations (SDs). Data of abundance were analysed with non-parametric tests because of the heterogeneity of variances despite transformation. We used Kruskal-Wallis analysis of variance (ANOVA) followed by Mann-

Whitney *U*-tests (software STATISTICA 1999 by StatSoft). Differences were considered significant at $P < 0.05$.

2.3 Biomass

Biomass of *C. gigas* on different mussel beds in 2003 was estimated by using an exponential relation between dry weight (meat and shells) and length of 83 oysters collected on two mussel beds ($y = 0.0002x^{2.8072}$, $R^2 = 0.9122$). With this equation we determined the biomass of *C. gigas* on each mussel bed by converting the length of the oysters into dry weight data.

2.4 Abundance and size of *C. gigas* on subtidal habitats

Abundance of *C. gigas* on subtidal mussel beds in tidal channels around Sylt was estimated by taking hauls with a traditional oyster dredge (see Reise et al. 1989). These dredge hauls were carried out in 1999 (20 hauls at two locations), 2001 (22 hauls at two locations), 2002 (10 hauls at one location), and 2004 (30 hauls at three locations). The distance dredged and the geographic position was noted for each haul. Furthermore, we counted the number of *C. gigas* in each haul and measured the shell length as longest diameter of the oyster shell.

2.5 Water temperature

Since 1984, surface water temperatures are regularly measured (about twice weekly) in the main tidal channel near List and at the entrance of Königshafen bay. Temperature data presented in this paper are based on mean monthly values from 1987 to 2003. Results are given as arithmetic means with standard deviations and analysed with *t*-tests for independent variables. All data were tested for homogeneity of variances using the Levene test. Deviations from the monthly mean water temperatures for the months July and August were calculated by subtracting the mean water temperature in each year from the long-term average (1987 - 2003).

3 Results

3.1 Distribution of *C. gigas* in the North Frisian Wadden Sea

Since 1986, the oyster farm located on the tidal flats east of the island of Sylt (List tidal basin) produces about 2 million oysters per annum (Fig. 1). A wild oyster population developed in the area due to larval dispersal and the first wild oysters were found in Königshafen bay in 1991. A quantitative survey in 1995 revealed that 14 out of 17 mussel beds in the List tidal basin were colonised with *C. gigas*. In the Danish Wadden Sea north of the List basin, adult *C. gigas* were found in the Juvre tidal basin near the island Mandø (1999) and at the northern end of the Wadden Sea near Esbjerg (2003: 6.8 individuals m^{-2}). South of Sylt, Pacific oysters were found in Hörnum tidal basin (first record in 1995), east of the island of Amrum (1995), at Nordstrand (2000), near the island of Pellworm (2003) and near Büsum (2004). On the offshore island of Helgoland, wild *C. gigas* were found from 2003 onwards. Oyster densities in the northern Wadden Sea outside the List basin are, however, still much lower than inside. Abundances stayed below 1 m^{-2} in 2003 on all mussel beds in the North Frisian Wadden Sea south of the List basin (except one mussel bed in Hörnum basin which contained 1.8 indiviudals m^{-2}).

3.2 Abundance of *C. gigas* on intertidal mussel beds near Sylt

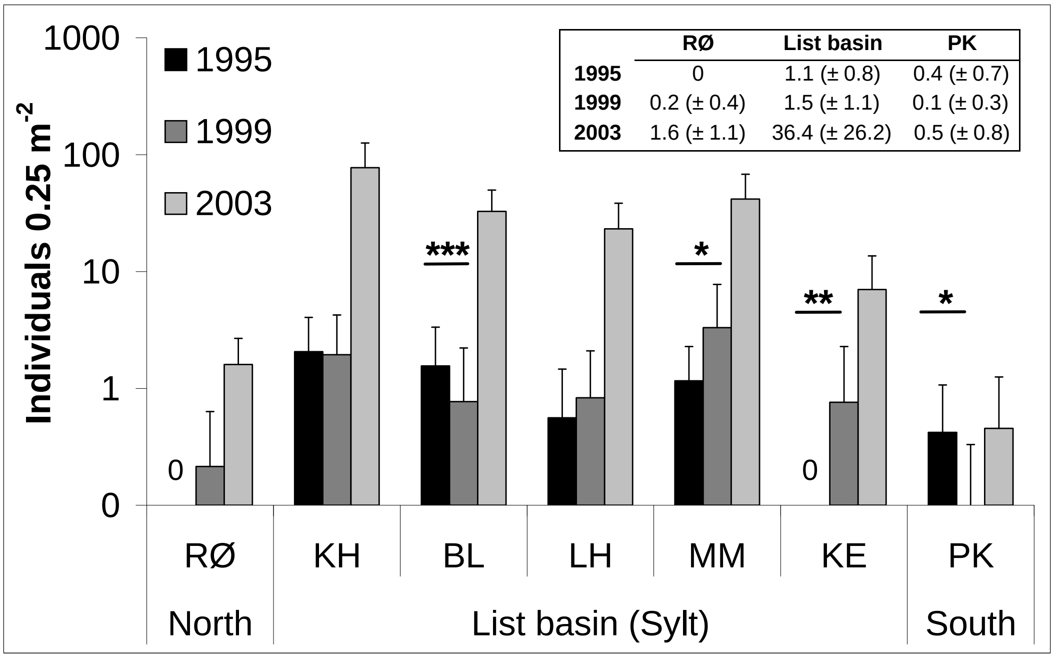
In 1995, some mussel beds on the tidal flats near Sylt and Rømø were still without oysters, but by 1999 living *C. gigas* were found on all investigated intertidal mussel beds (Fig. 2, Table 1). The mean abundance of oysters in the List tidal basin, however, did not increase. In 1995, Reise (1998) counted 3.6 individuals m^{-2}, and in 1999, we found 3.7 m^{-2}. This changed profoundly by 2003, when the mean abundance of *C. gigas* reached 125.8 oysters m^{-2} on intertidal mussel beds. This is equivalent to about 2,100 g dry weight (including shell and meat) m^{-2}.

Using the data of mean abundance (125.8 m^{-2}) and the total area of intertidal mussel beds (0.48 km^2), we estimate for the List tidal basin a number of 60.4 million oysters in 2003 (i.e. approximately 1,000 t dry weight). The population development of *C. gigas* stagnated in the tidal basin in the south of Sylt (Hörnum basin). Abundances stayed on a low level throughout the entire period from 1995 to 2003.

Table 1 Abundance (individuals / 0.25 m² ± SD), number of samples, and biomass (grams dry weight per square metre) of *Crassostrea gigas* on 15 intertidal mussel beds in the Sylt area: 13 in the List tidal basin and 2 in Hörnum tidal basin. *Blank cells*: no data available. *Asterisks* indicate that mussel beds no longer exist. For location of sites see Fig. 2. Data for 1995 from Reise (1998).

Site		**Abundance**						**Number of samples**			**Individuals / m²**			**Grams / m²**
		Individuals / 0.25 m^2			**SD**									
		1995	**1999**	**2003**	**1995**	**1999**	**2003**	**1995**	**1999**	**2003**	**1995**	**1999**	**2003**	**2003**
List basin														
RØ	Rømø	0	0.2	1.6		0.4	1.1	40	29	25	0	0.9	6.4	30.2
KO	Koldby	0		0.4			0.7	32		21	0		1.6	31.7
KH	Königshafen	2.1	1.9	77.2	2.0	2.3	48.4	48	238	23	8.2	7.8	308.9	1967.1
KH1	Mövenbergwatt	0.9	0.4	*	1.1		*	32	65	*	3.6	1.5	*	*
KH2	Ostfeuerwatt		0.8	*			*		89	*		3.4	*	*
KH3	Uth. Außenwatt		1.0	61.3		1.5	33.3		54	15		3.9	245.3	1232.0
OW	Oddewatt	0.6	0.1	*	0.8		*	70	80	*	2.4	0.5	*	*
BL	Blidsel	1.6	0.8	32.8	1.8	1.4	16.9	80	165	14	6.2	3.1	131.1	1381.7
LH	Leghörn	0.6	0.8	23.2	0.9	1.3	15.2	48	236	18	2.2	3.3	92.9	793.9
PT	Pander Tief	2.1		69.3	2.0		57.6	40		75	8.2		277.0	11386.1
MM	Munkmarsch	1.2	3.3	41.7	1.1	4.4	26.4	44	126	29	4.6	13.2	166.6	4168.5
KE	Keitum	0	0.8	7.0		1.5	6.6	36	82	24	0	3.0	27.8	469.2
RS	Rauling-Sand		0.1	0.1					58	11		0.3	0.4	0
	Mean										**3.6**	**3.7**	**125.8**	**2146.0**
Hörnum basin														
RA	Rantum	0.1		0.1				32		38	0.5		0.2	27.8
PK	Puan Klent	0.4	0.1	0.5	0.7	0.3	0.8	48	20	22	1.7	0.3	1.8	148.0
	Mean										**1.1**	**0.3**	**1.0**	**87.9**

We focus on seven mussel beds, one at the northern end of the List basin (RØ), five adjacent to the island of Sylt in the List basin (KH, BL, LH, MM, KE) and one in the southern basin (PK) in order to describe the population development of *C. gigas* in more detail (Fig. 3). By comparing the oyster densities in 1995 and 1999, it turns out that a significant increase in abundance only occurred on two mussel beds in the List basin, MM (Kruskal-Wallis ANOVA, $P < 0.0001$; Mann-Whitney *U*-test, $P = 0.011$) and KE (Kruskal-Wallis ANOVA, $P < 0.0001$; Mann-Whitney *U*-test, p = 0.009), whereas on two other mussel beds, BL (Kruskal-Wallis ANOVA, $P < 0.0001$; Mann-Whitney *U*-test, $P < 0.001$) and PK (Kruskal-Wallis ANOVA, $P = 0.001$; Mann-Whitney *U*-test, $P = 0.014$), a significant decrease in numbers occurred. Four years later, in 2003, abundances of *C. gigas* were significantly higher on all mussel beds in the List basin, with Königshafen containing over 300 oysters m^{-2}. It is remarkable that the mussel bed in the north of the List basin (RØ) and the one in the southern basin (PK) still showed comparatively low oyster densities (6.4 m^{-2} for Rømø, and 1.8 m^{-2} for Puan Klent). The mean values of oyster abundance on the five mussel beds adjacent to Sylt in the List basin increased from 4.3 m^{-2} in 1995 and 6.1 m^{-2} in 1999 to 145.5 m^{-2} in 2003.



	RØ	List basin	PK
1995	0	1.1 (± 0.8)	0.4 (± 0.7)
1999	0.2 (± 0.4)	1.5 (± 1.1)	0.1 (± 0.3)
2003	1.6 (± 1.1)	36.4 (± 26.2)	0.5 (± 0.8)

Fig. 3 Mean abundance (individuals per 0.25 m² + SD; logarithmic scale) of *C. gigas* on 7 intertidal mussel beds (RØ, KH, BL, LH, MM, KE, PK) near Sylt surveyed in 1995, 1999, and 2003. Sample size varied between *n* = 14 and *n* = 238. *Asterisks* mark significant differences between 1995 and 1999 data sets (Mann-Whitney *U*-test): * 0.05 > *P* ≥ 0.01, ** 0.01 > *P* ≥ 0.001, *** P < 0.001. *Inset*: mean abundance of *C. gig*as (individuals per 0.25 m^{-2} ± SD) on mussel bed RØ, over all five mussel beds in List basin (Sylt) and on mussel bed PK

3.3 Length-frequency distribution of *C. gigas*

In Fig. 4, we present length-frequency distributions of *C. gigas* on two mussel beds (KH and MM) from 1999 to 2004. Based on these frequency distributions the age structure of the population is described by distinguishing different year classes and calculating their length increments. By growth experiments we verified that peaks in these graphs indicated year-classes: juvenile oysters reach 20 - 33 mm shell length in the first spring after settlement in the previous summer. They will continue to grow to 40 - 60 mm by the end of the growing season in November and will remain this size until the next growing period starts in April (own unpublished data). In spring 1999, oysters at the Königshafen site were represented by a distinct year class between 25 and 65 mm shell length (cohort of 1997) and some older individuals. The cohort of 1997 represented 53% of all oysters in this area. The distribution looked similar at Munkmarsch, but with a higher proportion of oysters of the year class 1997 (86%). Until fall 1999, the 1997-year class grew by 20 to 30 mm in shell length to approximately 50 to 100 mm.

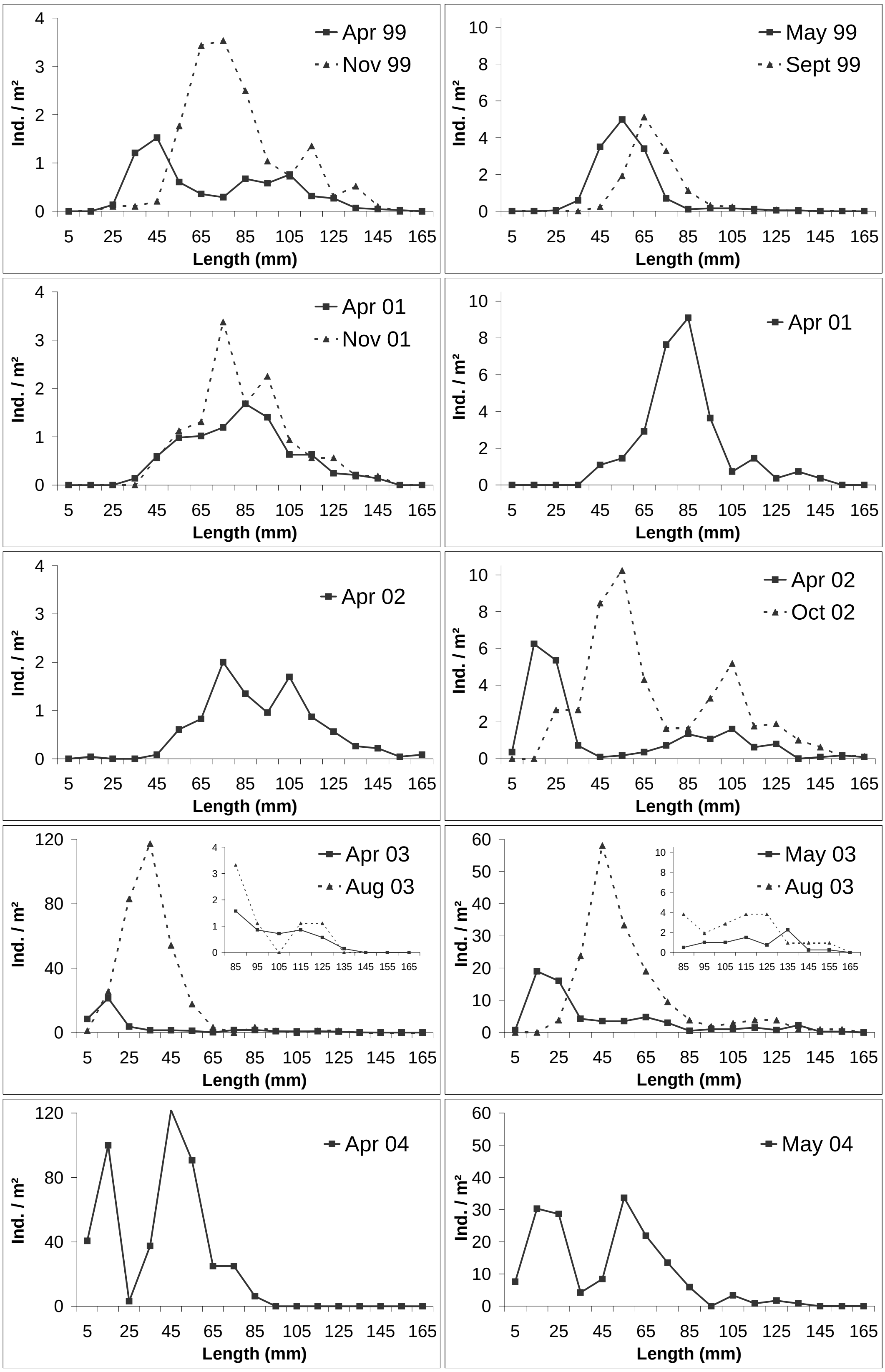


Fig. 4 Length-frequency distribution of *C. gigas* on two intertidal mussel beds near Sylt (*left* Königshafen; *right* Munkmarsch) from 1999 to 2004. Number of individuals measured varied between *n* = 68 and *n* = 307. *Insets* in 2003 graphs depict large size classes on a lower scale to show survival of adults

It is important to note that we did not consider oyster spat in the fall monitoring because these oysters were still too small to be counted. The offspring of the summer of a certain year is, therefore, first represented in the spring graphs of the following year. The spring graphs, however, still show a lower abundance of juvenile oysters than the subsequent autumn graphs, because the recruits of the previous summer were still too small to be included adequately in the spring monitoring. By autumn, however, the oysters had grown to a larger size and were more adequately represented. This is especially the case in the Königshafen 1999 and in the Königshafen and Munkmarsch 2003 graphs.

The data set from April 2001 shows a much older population than in April 1999 for both Königshafen and Munkmarsch. There were no signs of any significant recruitment or mortality in 1999 and 2000. The size distribution of *C. gigas* in Königshafen for April 2002 was similar to that for 2001, but a strong recruitment was apparent at Munkmarsch with 60% of the oysters measuring less than 30 mm. This 2001 cohort grew approximately 30 mm by October 2002. In spring 2003, recruitment on both mussel beds was evident: the majority of oysters belonged to the year class of 2002. This cohort grew by about 20 mm until August 2003 and represented 97% of the Königshafen population and 76% of the Munkmarsch population. In April/May 2004, oyster recruitment from the previous summer was evident on both mussel beds.

It is important to note that the 1997 cohort was still present in 2002 in almost the same numbers as in the years before, that is, no detectable mortality occurred from 1999 to 2002, suggesting a high survival rate of 2- to 5-year-old oysters. Even in 2003, the 1997 cohort was still present (see insets in Fig. 4).

3.4 Mean water temperatures and *C. gigas* recruitment

The comparison of monthly mean water temperatures during years with notable *C. gigas* recruitment (1991, 1994, 1997, 2001, 2002, 2003) and years with no measurable recruitment (1987 - 1990, 1992, 1993, 1995, 1996, 1998 - 2000) revealed significantly higher water temperatures in July and August in recruitment years (Fig. 5). No significant differences in water temperatures occurred for all other months. Deviations of water temperatures from the long-term mean (1987 - 2003) in July and August show that successful recruitment only occurred in relatively warm summers (Fig. 6).

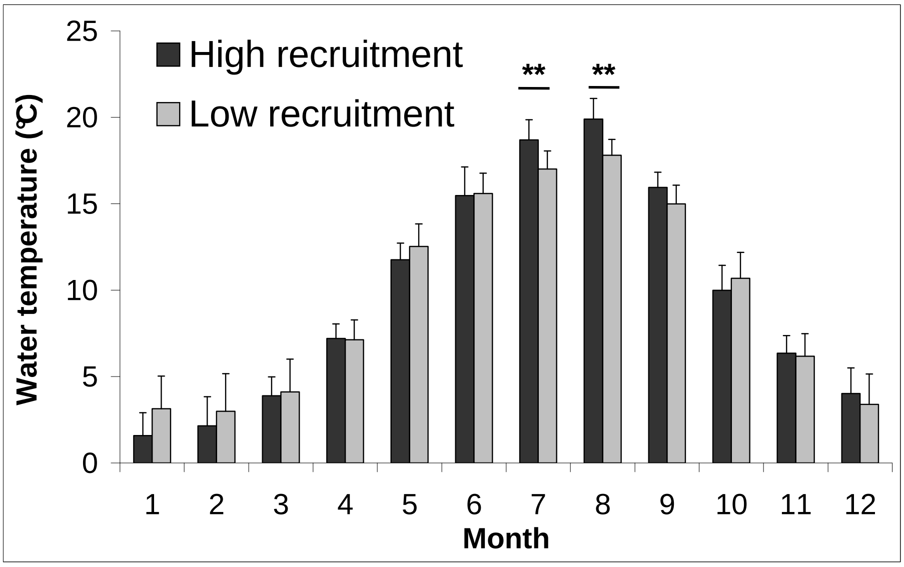


Fig. 5 Monthly means of water temperature (℃) during years with notable or high *C. gigas* recruitment (1991, 1994, 1997, 2001, 2002, 2003) and years with no or very low recruitment (1987-1990, 1992, 1993, 1995, 1996, 1998-2000). Significant differences in water temperature occurred in July (7) and August (8; ** *P* = 0.008 and *P* = 0.001, respectively; *t*-test for independent variables)

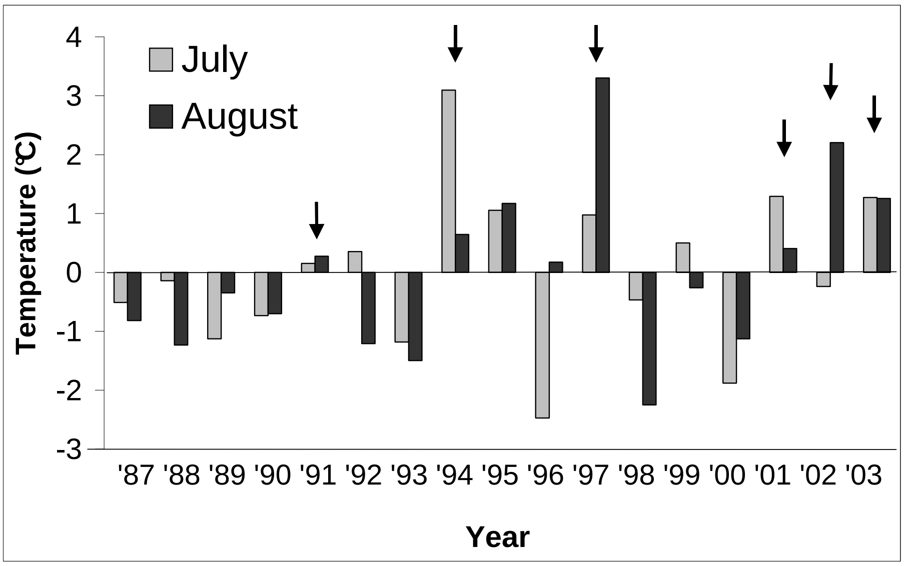


Fig. 6 Deviations of mean monthly water temperatures in July and August from the long-term mean (1987 - 2003). *Arrows* mark years with high *C. gigas* recruitment (1991, 1994, 1997, 2001, 2002, 2003)

3.5 Abundance and size of *C. gigas* in the subtidal zone near Sylt

Dredge hauls in subtidal channels around the island of Sylt in the time period from 1992 to 1996 did not yield any living *C. gigas* (Reise 1998). In 1999, we fished at two locations (Munkmarsch and Königshafen) of subtidal mussel stocks and found only one and three adult oysters, respectively (Table 2). The Munkmarsch site was again investigated in 2001 and 2002 and we still only caught four and two oysters, respectively. In 2004, however, we found 95 oysters at Munkmarsch and 25 at Königshafen. There was a noticeably high proportion of juvenile oysters present. Another 10 dredge hauls in the middle of the tidal basin yielded 428 living oysters of which 33% belonged to the 2003 year class.

Table 2 Dredge hauls in subtidal channels in the List tidal basin. Given are locations, number of hauls, and area fished. The distance dredged varied between 150 and 470 m. Also total number and length of *C. gigas* for each location are shown. Data for 1992 - 1996 from Reise (1998)

	1992 - 1996	**1999**		**2001**		**2002**	**2004**		
Location	**Sylt area**	**MM**	**KH**	**MM**	**KO**	**MM**	**MM**	**KH**	**Bay**
No. of hauls	216	10	10	10	12	10	10	10	10
Area (m²)	108,000	4,000	2,000	4,000	3,000	3,000	3,700	2,100	3,000
No. of *C. gigas*	0	1	3	4	12	2	95	25	428
Length (mm)	-								
Min - max		108	70 - 109	75 - 137	28 - 144	5; 120	5 - 134	8 - 146	2 - 97
Mean (±SD)				99.8 (±26.5)	94.5 (±31.9)		56.7 (±28.7)	59.6 (±29.5)	38.5 (±23.4)

4 Discussion

Since 1986, a potential spawning population of *Crassostrea gigas* has been cultured for commercial purposes at Sylt. Significant recruitment in the area only took place in 1991, 1994, 1997, 2001, 2002 and 2003 (i.e. in 6 out of 18 years). This indicates that the reproductive success of *C. gigas* in the northern Wadden Sea is not a regular phenomenon but occurred only in about one-third of the years since the local introduction of the species.

The expansion of Pacific oysters in the Wadden Sea near Sylt started off slowly with the colonisation of certain intertidal mussel beds near the oyster farm. Successful recruitment did not occur in all suitable habitats, and it was not before 1999 that all mussel beds in the List tidal basin contained wild *C. gigas*. Nevertheless, strong recruitment was still confined to certain locations within the basin. By 2003, some mussel beds in the area still had very low oyster densities, whereas a massive population increase took place in other areas. In 2001, for example, recruitment occurred on mussel beds in the southern part of the List basin but not in the northern part (approximately 15 km apart).

The spread towards areas outside the List tidal basin also occurred slowly. Abundances of *C. gigas* on mussel beds in the Hörnum basin in the south of Sylt remained at a low level until 2003, although living *C. gigas* had been found from 1995 onwards. Also near the islands further south (Föhr, Amrum, Pellworm) abundances are still low in comparison to northern Sylt. The same is true for the Danish Wadden Sea, where *C. gigas* is now present although still in low numbers. The origin of the oysters south of the island of Sylt is not clear, as natural transport against the south-north current is unlikely and may only occur on rare occasions. Transport from the List basin due to mussel farming activities is possible, as well as further introductions from several experimental cultures in the North Frisian Wadden Sea. Larval drift from the Oosterschelde or the Dutch Wadden Sea, however, seems to be rather unlikely. Transport times between Texel and the North Frisian Wadden Sea amount to about 150 days (de Ruijter et al. 1988) and are, therefore, longer than the mean lifetime (3 - 4 weeks) of pelagic larvae (Neudecker 1985, Quayle 1988). The extended planktonic larval period nevertheless allows a high dispersal by currents as has been described for *C. gigas* in British Columbia, where settlement of wild oysters occurred 60 km away from the next oyster farm (Elsey & Qualye 1939).

Larval retention in the List tidal basin, however, should be high as it is practically enclosed and is only connected to the North Sea by a 2.8-km-wide channel. This is very favourable to the oyster larvae because they remain on suitable sites close to their origin, and this certainly facilitates population growth when adult stocks are still low. Larvae in more open areas may be widely distributed and are, therefore, less likely to find suitable settling substrates and subsequently perish. The List tidal basin thus offers ideal conditions for the spread of species with planktonic larvae due to the continuous input of larvae from the local oyster farm and the closed bay environment.

The fast development of oysters in the closed Oosterschelde and the much later spread into the Dutch and western German Wadden Sea followed the same pattern (Wehrmann et al. 2000, Dankers et al. 2004). Within the bay, the slow and patchy expansion presumably does not result from a lack of dispersal but from limited larval supply or poor initial survival after settlement. This might also explain the slow colonisation of subtidal habitats. It is important to note that the site where we found juvenile *C. gigas* used to be an important subtidal spatfall area of blue mussels (Ruth 1994) and is located about 7 km from the nearest intertidal mussel bed. These findings are thus the first clear indications of subtidal spatfall in Pacific oysters in the Northern Wadden Sea. Even though *C. gigas* is considered to be more an intertidal species, it has the capability to colonise subtidal habitats (Buroker 1985). In the Oosterschelde (The Netherlands), where Pacific oysters have been introduced in the 1960s, *C. gigas* is now a dominant species in intertidal and subtidal benthic communities (de Kluijver & Leewis 1994, Leewis et al. 1994, Meijer & Waardenburg 1994, Drinkwaard 1999). In British Columbia, *C. gigas* is found only in intertidal habitats, presumably because low temperatures in deeper waters limit the survival of larvae and juveniles (Quayle 1988).

The irregular recruitment of *C. gigas* in the northern Wadden Sea is apparently no threat to the population because of the high survival rate after 1-year-old cohorts have become established. As the cohort of 1997 showed high persistence during the subsequent 5 years, a failure in reproductive success during 4 consecutive years is not expected to threaten population maintenance. The long persistence of *C. gigas* populations has also been reported from Great Britain, where adult oysters were still present 9 years after the closure of an oyster farm (Smith 1994).

What could be the reason for this irregular recruitment success? We compared water temperature regimes in years with notable or high oyster recruitment and those with no or low reproductive success and found that high recruitment corresponded with higher than average water temperatures in late summer. This is an important time period in the oyster life cycle: spawning occurs, larvae are dispersed and juveniles settle on hard substrates. In the Wadden Sea, *C. gigas* spawns in late July and August. After fertilisation, pelagic larvae develop and will stay in the water column for 21-30 days before settlement occurs (Neudecker 1985, Quayle 1988). The importance of temperature for oyster spawning and recruitment has been described by various authors. In Japan, 23-25°C is considered as the optimum water temperature for successful recruitment (Korringa 1976, Kobayashi et al. 1997), and even though spawning has been observed in British Columbia (Canada) at 15°C, the optimal temperature for larval development is considered to be 23°C (Quayle 1988). In Great Britain, *C. gigas* has been observed to spawn from 18°C onwards but natural recruitment is sporadic and occurred only in exceptionally warm summers (Mann 1979, Spencer et al. 1994). In the Oosterschelde (The Netherlands), *C. gigas* was introduced in 1964 and the first natural recruitment was observed in 1975 and 1976 during exceptionally warm summers with water temperatures above 20°C in July and August of 1976 (Drinkwaard 1999). The next major larval outbursts occurred in 1982, 1986, and 1989 (Drinkwaard 1999). The oyster population increased dramatically from then onwards. Monitoring of the area expansion of oyster reefs in the Oosterschelde revealed an increase from 0 ha in 1976 to 15-35 ha in 1980, 210-370 ha in 1990, and 640 ha in 2002 (Kater & Baars 2003). In France, *C. gigas* expanded much faster. Since the introduction of broodstock from British Columbia and Japan in 1971, spat recruitment was successful with the exception of three specific years (1972, 1981, and 1986) where abnormally low temperatures were held responsible for low spatfalls (Grizel & Héral 1991). A similar rapid rise in oyster densities occurred in New Zealand, where the first naturally dispersed oysters were found in 1971 and a strong increase in spat abundance has been observed ever since. A marked rise in temperature during the main spatting period was held responsible for the dramatic increase of *C. gigas* spatfalls, which superseded those of the native rock oyster *Saccostrea glomerata* in 1978 (Dinamani 1978, 1991). In Tasmania and New South Wales (Australia), however, only erratic spatfalls occurred after the introduction of *C. gigas* and low water temperature and high salinity were considered to be major limiting factors (Ayres 1991). Nevertheless, large oyster reefs were formed about 9 years after the first oyster spat was observed in Tasmania and a rapid spread was documented in some estuaries in New South Wales. Comparing the spread and recruitment success of *C. gigas* in the Wadden Sea with that in other areas, it can be assumed that Pacific oysters here are at the edge of their physiological range and are expected to rely on high late summer water temperatures occurring at least once every 5 years.

It is well known that the spread of exotic species may depend on temperature regimes and may profit from climate change (Lodge 1993, Nehring 1998, Franke et al. 1999, Stachowicz et al. 2002, Walther et al. 2002). In the Wadden Sea, the American slipper limpet (*Crepidula fornicata*) is limited by cold winter temperatures and is expected to increase in abundance if climate change should lead to milder winters (Thieltges et al. 2004). Another example is the introduced cord-grass, *Spartina anglica*, which is increasing in the northern Wadden Sea presumably as a result of warmer spring seasons (M. Loebl, J.E.E. van Beusekom, and K. Reise, submitted). Regarding the Pacific oyster, a possible climate change involving warmer late-summer water temperatures or a higher frequency of hot summers could have a profound impact on its abundance in the northern Wadden Sea.

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Chapter 3

Differential recruitment of introduced Pacific oysters and native mussels at the North Sea coast: coexistence possible?

Abstract

Pacific oysters (*Crassostrea gigas* Thunberg 1793) have been introduced into the Wadden Sea (North Sea) where they settle on native mussel beds (*Mytilus edulis* L.), which represent the only extensive insular hard substrata in this soft sediment environment. As abundances of *C. gigas* rose, some mussel beds became increasingly overgrown with oysters, whereas others did not. Field experiments revealed that recruitment of *C. gigas* was higher in the lower intertidal than in the upper subtidal zone, that it was higher on conspecifics than on mussels, and that it was not affected by barnacle epigrowth except when settling on mussels. Mussel recruitment is known from inter- and subtidal zones. It occurred equally on oyster and mussel shells but showed a clear preference for barnacle epigrowth over clean shells. Assuming that settlement and recruitment are key processes for species abundances on the North Sea coast, it is predicted that the positive feedback in oyster settlement will lead to rapid reef formation of this invader at the expense of mussel beds. Mussels, however, may escape competitive exclusion by settling between or on the larger oysters especially when barnacles are abundant. Experimental patches with mussels were more often covered by fucoid algae (*Fucus vesiculosus* forma *mytili* Nienburg) than patches with oysters, and oyster recruitment was poor underneath such algal canopies. Thus, fucoids may provide mussels with a refuge from the invading oysters and the two bivalves may coexist, provided food is not limiting.

Keywords

Crassostrea gigas, Settlement, *Mytilus edulis*, Introduced species, Niche partitioning, North Sea

1 Introduction

Invasive Pacific oysters (*Crassostrea gigas*) and resident mussels (*Mytilus edulis*) are both gregarious epibenthic suspension feeders that colonise coastal soft-sediment environments in the North Sea. Both species require living or dead shells as substrate for attachment when settling on mudflats. This brings the invading oysters potentially into competition with the native mussels. Recruitment patterns were investigated in order to explore whether overlap in spatial niches is complete or whether some spatial partitioning and co-existence may be expected.

Pacific oysters originate from Japan, and have been cultivated in the northern Wadden Sea since 1986. The cultured oysters have reproduced naturally and are now firmly established in the wild, still spreading in abundance and range (Reise 1998, Diederich et al. in press). Oyster larvae attach mainly onto clean, hard surfaces with a slight unevenness or groove by releasing a cement drop from a foot gland and placing the left valve into the cement (Korringa 1976, Quayle 1988, Arakawa 1990a). The Wadden Sea, which is characterised by its extensive intertidal mud and sand flats, lacks primary hard substrata for sessile organisms. Dikes, groins, and especially beds of empty shells and mussel beds (*Mytilus edulis*) are the only major secondary hard substrate available as attachment surface for oyster larvae. Some mussel beds in the Wadden Sea are already heavily overgrown by Pacific oysters (Reise 1998, Dankers et al. 2004).

Mussel beds consist of a three-dimensional matrix of connected living and dead mussels on an organo-rich bottom sediment layer (Seed & Suchanek 1992). In the Wadden Sea, mussel beds may persist over many decades (Reise et al. 1989, Obert & Michaelis 1991, Hertweck & Liebezeit 2002). Besides fishing activities (Dankers & Zuidema 1995, Herlyn & Millat 2000), ice scour (Bahr 1950, Obert & Michaelis 1991, Strasser et al. 2001) and storms (Nehls & Thiel 1993) may severely damage or dislodge mussel beds. Regeneration of mussel beds is facilitated by a high dispersal capability and site-specific and gregarious settlement of mussel larvae (Seed 1969, Petersen 1984), the latter caused by the structure of the substratum (Chipperfield 1953, Seed 1969, Menge 1976, Grant 1977), biofilms (Dobretsov & Railkin 1994) and chemical cues exuded from macroorganisms (Dobretsov & Wahl 2001) or as a result of passive entanglement of mussel larvae in filamentous structures such as algae or byssus threads (Caceres-Martinez et al. 1994).

Recruitment patterns can also be affected by epibionts already present on the settlement surfaces. In the Wadden Sea, the most abundant epibiont species on mussels are the barnacles *Semibalanus balanoides* (L.) and *Balanus crenatus* (Bruguière) (Albrecht & Reise 1994, Buschbaum & Saier 2001). Barnacles can cover almost 100% of mussel surface area but abundances show high interannual and seasonal fluctuations (Buschbaum 2000). Nevertheless, the presence of barnacles increases mussel recruitment (Grant 1977, Saier 2001).

Another important structure on North Sea intertidal mussel beds is the brown alga *Fucus vesiculosus* forma *mytili* (Nienburg) Nienhuis (Nienburg 1925, Nienhuis 1970, Albrecht & Reise 1994, Albrecht 1998). This perennial seaweed can cover intertidal mussel beds either partly or completely in a thick layer. In association with mussels, this brown alga lacks a holdfast and gas vesicles and is fastened by the mussels' byssal threads. Reproduction is vegetative by means of drifting thalli that are "captured" by mussels and attached to the bed. On intertidal mussel beds in the Wadden Sea, dense *Fucus* patches reduce current velocities and enhance sedimentation (Albrecht & Reise 1994). This has a negative influence on abundances of mussels and their epibionts, but supports various herbivores and increases overall macrobenthic diversity (Albrecht & Reise 1994).

This complex mussel bed biocoenosis is now invaded by the Pacific oyster. The question arose of whether the oysters may outcompete the local mussels by invading their niche, or whether niche partitioning would allow coexistence of the two bivalves. In the Wadden Sea, stable and mature mussel beds are confined to sheltered parts behind the islands, because storms and ice shear readily destroy young mussel beds on more exposed locations (Nehls & Thiel 1993, Dankers et al. 2001). Spatial displacement to less favourable habitats may therefore lead to short-lived, young mussel beds and this may pose a threat to mussel populations. Recruitment of introduced Pacific oysters and native mussels in different microhabitats was studied in an attempt to predict the further development of the oyster and mussel populations in the Wadden Sea. Thus, the focus of this study is not the settlement process (largely defined as the larval search for a suitable substratum, attachment and finally metamorphosis), but the combined effects of settlement and subsequent post-settlement survival.

2 Material and methods

2.1 Experimental sites

Field experiments were carried out at two locations: the List tidal basin in the northern Wadden Sea (Germany) and the Oosterschelde estuary (The Netherlands). The List tidal basin, which is located between the islands of Sylt and Rømø (54°50’ - 55°10’N and 08°20’ - 08°40’E) covers an area of about 404 km² and is closed by dams to the north and south (Fig. 1). A tidal inlet of 2.8 km width is the only connection to the North Sea. This inlet branches into three main channels (maximum depth 40.5 m) that are responsible for the current and transport regimes within the bay. Intertidal flats, which are mostly sandy, comprise 33% (134 km²) of the total area (Backhaus et al. 1998). Tides are semidiurnal and the mean tidal range is 2 m. The average salinity is close to 30 psu. Monthly mean water temperatures range from 18.2°C in August to 2.3°C in February. Detailed information on hydrography, geology, sediments and biota of the bay is given in Gätje and Reise (1998). Within the List tidal basin, intertidal mussel beds cover 1.5 km^2 (Nehls 2003) and are partly covered by the brown macroalgae *Fucus vesiculosus* forma *mytili* (Albrecht 1998). Investigations were carried out on two mussel beds, one at the northern end of the bay in Königshafen (KH), and one close to the southern end of the bight south east of Munkmarsch harbour (MM). Experiments took place in the intertidal near the low water line and in the shallow subtidal. Sites referred to as intertidal had an exposure time of about 2 h per tide and subtidal sites were located 0.5 - 1 m below low water level.

One recruitment experiment was carried out in the Oosterschelde estuary (The Netherlands), a tidal bay of 351 km² surface area which was partly closed from the sea by a storm-surge barrier in 1987. Tidal flats cover 118 km² and mean tidal range is 3.3 m (Nienhuis & Smaal 1994). Here, Pacific oysters were introduced for cultivation in 1964 and first natural spatfalls occurred in 1975 and 1976 (Drinkwaard 1999). From 1982 onwards abundances of wild *C. gigas* increased strongly (Wolff & Reise 2002) and in 2002 the area covered with oysters amounted to 640 ha in the intertidal and about 700 ha in the subtidal zone (Geurts van Kessel et al. 2003). Wild mussel stocks do not exist in this area, but mussels are kept in subtidal culture plots that comprise an area of about 3000 ha (Kater & Kesteloo 2003).

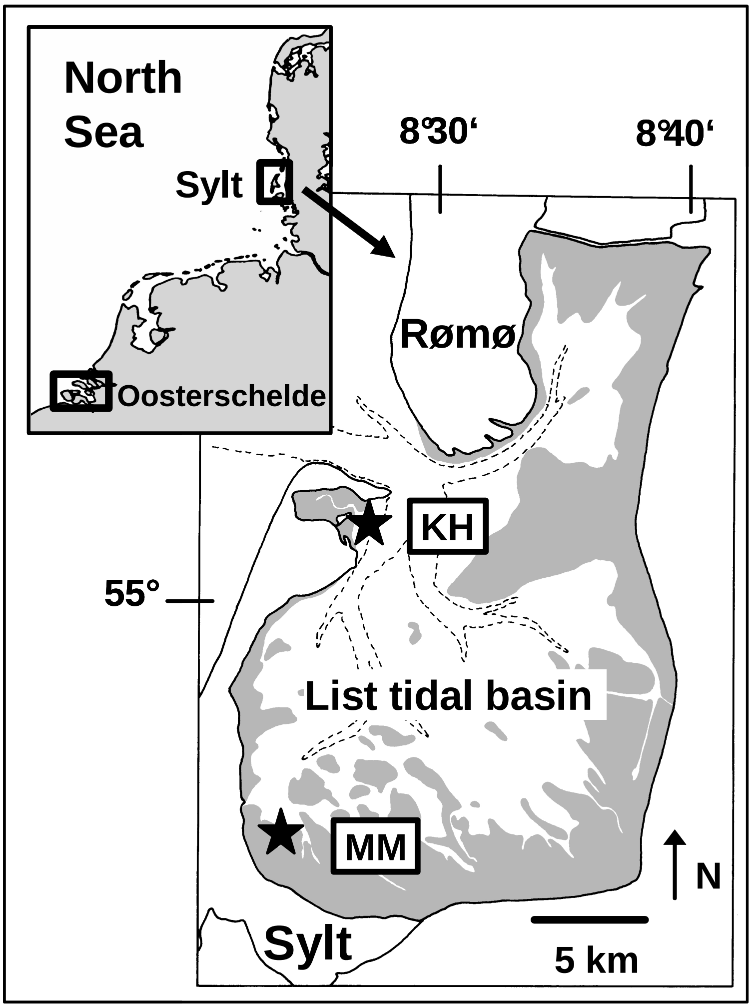

Fig. 1 Location of experimental sites: two in the List tidal basin (KH and MM, asterisks) in the northern Wadden Sea (Germany) and one in the Oosterschelde (The Netherlands). Map of List tidal basin after Bayerl et al. (1998)

2.2 Effect of tidal height on recruitment (*C. gigas*)

Recruitment of *C. gigas* was studied in the intertidal and adjacent shallow subtidal of KH and MM in August 2002 and 2003 using shell collectors. Each shell collector was constructed from 10 clean oyster shells that had a hole drilled in the middle so that they could be strung on a plastic covered clothesline. These lines were 30 - 40 cm long and were pinned with iron bars horizontally on the mussel beds so that the shells touched the mussels underneath. In 2002, collectors were installed in the field from 10 to 30 August and in 2003 from 30 July to15 September. This time frame was chosen because it covered the main settlement period and also allowed conclusions to be drawn about early recruitment patterns. At the end of periods, the strings were brought back to the laboratory and attached juvenile oysters were counted with a stereomicroscope.

2.3 Substrate specificity of recruitment near Sylt (*C. gigas* and *M. edulis*)

Experimental oyster and mussel plots were built next to a natural intertidal mussel bed (MM) in July 2001. Oyster plots were created by collecting wild oysters from a nearby mussel bed, removing any attached mussels, and placing the oysters in four 2 × 2 m plots. The oysters were densely packed, resulting in a three-layered aggregation with a density of about 500 oysters m^{-2}. Mussel plots were built by collecting *M. edulis* clumps from a nearby mussel bed and placing them on four 2 × 2 m areas. Mussel density in these plots was about 3400 ind m^{-2}. These oyster and mussel plots were randomly distributed along the edge of an existing mussel bed (distance from the bed 10 - 20 m) on sand covered with dead mussel shells. As the mussels attached themselves with byssal threads and most of the oysters were large and heavy individuals, they remained on the plots without the aid of a fence. Samples from these experimental plots and from the nearby mussel bed were taken in November 2001 (initial abundance of *C. gigas* and *M. edulis* in the plots), in October 2002 and May 2003. October 2002 was chosen as the first sampling date, because oyster spatfall in this area occurs during late summer and by October juveniles are large enough to be counted with the naked eye (about 2 - 20 mm shell length). Two sub-samples were taken from each of the four experimental oyster plots by placing a 25 × 25 cm frame randomly in the area and removing all living bivalves and dead shells. On mussel plots (two sub-samples taken from each of the four plots) and on the mussel bed (eight samples taken in 2002 and twelve in 2003) samples were taken using a 14.5 × 14.5 cm box corer instead of a frame. This corer could not be used on the oyster plots, because some oysters were up to 20 cm long. All material inside the frame or box corer was sieved with a 5 mm mesh sieve. In the laboratory, all mussels and oysters were measured with electronic vernier callipers to the nearest 0.01 mm. Also dead shell material was searched for attached juvenile oysters. Percent coverage of the experimental plots with *Fucus vesiculosus* was estimated visually to the nearest 5% at all three sampling dates.

In a similar way, experimental *Crassostrea* and *Mytilus* plots were constructed in the adjacent shallow subtidal, but these plots were 1 × 1 m in size. The smaller size was necessary because of the difficulties in transporting the bivalves over longer distances. This was considered legitimate because not absolute recruitment but recruitment differences dependent on the type of substrate were tested. Samples were taken in the same way as described for the intertidal area in October 2003 during an extreme spring low tide when plots were exposed.

2.4 Substrate specificity of recruitment in the Oosterschelde (*C. gigas*)

This experiment was conducted on a tidal flat near Yerseke in August 2001. Four substrate types for oyster settlement were placed on 35 × 50 cm plots (six replicates for each substrate) that were randomly distributed in a 100 × 100 m area on an intertidal sand flat close to the low water line. A fence 8 cm high and made of plastic-coated wire netting (mesh opening: 1 cm) surrounded each plot and prevented the substrates being washed away. The following substrates for oyster attachment were used: (1) living adult *C. gigas* (mean shell length: 103.2 ± 9.4 mm), (2) dead *C. gigas* shells (mean shell length: 96.6 ± 10.6 mm), (3) living adult *M. edulis* (mean shell length: 59.8 ± 2.5 mm), (4) dead *M. edulis* shells (mean shell length: 62.7 ± 2.6 mm). It was estimated visually that the plots contained the same volume of substrate material, which was freed from epigrowth with an iron brush. Plots were installed in the field on 2 August 2001 and settlement of oyster spat occurred from 9 August 2001 onwards. On 20 August 2001 the substrates were removed and brought to the laboratory. From each plot 8 items (i.e. oysters, mussels or dead shells) were randomly chosen and searched for oyster spat. On living oysters and mussels a mean was calculated from left and right valve so that number of spat per valve is given. On dead shells the outer and inner surfaces of shells were investigated separately. In this way the amount of spat on the outer surface of dead shells could be compared with the number of spat on the shells of living bivalves.

2.5 Effect of barnacle epigrowth on recruitment (*C. gigas* and *M. edulis*)

This experiment was conducted on an intertidal mussel bed (MM) in summer 2003. Four substrate types for oyster attachment were tested: living adult *C. gigas* with and without a dense barnacle cover and living adult *M. edulis* with and without barnacles (Table 1). These substrates were placed separately in plastic mesh cages (cages open at the top; diameter: 10 cm; height: 8 cm; mesh opening: 5 mm; 16 replicates) that were fixed onto the mussel bed with iron bars. This experiment was done twice, once for mussel recruitment (10 July - 18 August 2003) and once for oyster recruitment (29 July - 12 September 2003) because mussel settlement occurred earlier in the year than oyster settlement. As mussel substrate two mussels were used together in one cage whereas as oyster substrate only one oyster was used in order to outbalance the size difference. Caged mussels and oysters were measured with vernier callipers to the nearest millimetre and their volume was estimated by placing the content of each cage (two mussels and one oyster respectively) in a calibrated cylinder to calculate the volume of water displaced upon submergence. At the end of experimental time all attached juvenile oysters and mussels were counted with a stereomicroscope.

Table 1 Size of mussels and oysters used as substrate in the experiment on the effect of barnacle cover on recruitment of *Crassostrea gigas* and *Mytilus edulis*. Length, width and height are mean values for individuals, but volume data are based on cage content, i.e. two mussels and one oyster respectively

	Exp. 1 (Mussel recruitment)				**Exp. 2 (Oyster recruitment)**			
	Length (mm)	Width (mm)	Height (mm)	Volume (ml)	Length (mm)	Width (mm)	Height (mm)	Volume (ml)
M. edulis without barnacles	59.6	26.4	26.1	39.3	58.9	27.	26.4	39.0
M. edulis with barnacles	57.3	27.8	30.2	52.3	60.5	34.3	40.1	61.5
C. gigas without barnacles	89.2	59.4	38.6	71.9	100.3	63.6	39.7	86.3
C. gigas with barnacles	92.4	59.9	45.1	106.9	101.2	63.7	46.9	112.5

2.6 Effect of *Fucus* cover on recruitment (*C. gig*as)

Adult *C. gigas* (110 - 120 mm shell length) were collected from an intertidal mussel bed (KH), cleaned from epigrowth with an iron brush, and placed as attachment surfaces for oyster larvae back on the same mussel bed. Twenty oysters were placed on top of a dense mussel layer with no *Fucus* overgrowth and another 20 oysters were placed on nearby mussel bed patches with a dense *Fucus* cover. The algal thalli were carefully lifted and the oysters were placed underneath. Oysters were marked individually with an iron bar that was labelled and placed next to them. The experiment started on 5 August 2003 and ended 30 days later when all oysters were brought back to the laboratory and searched for oyster spat.

2.7 Statistical analysis

Results are given as arithmetic means with standard error (SE). Data on abundance of juveniles were subjected to analysis of variance (ANOVA) or to Repeated Measures ANOVA if data sets contained two or three time periods. The Levene test was used to test for homogeneity of variances and data were log (x + 1)- or square root-transformed if variances were heterogeneous. Data on recruitment of *M. edulis* in relation to barnacle overgrowth were subjected to non-parametric tests (Kruskal-Wallis-ANOVA followed by Mann-Whitney U-Tests) because of the heterogeneity of variances despite transformation. Effects were considered to be statistically significant if p-value was < 0.05.

3 Results

3.1 Effect of tidal height on recruitment (*C. gigas*)

The abundance of *Crassostrea gigas* spat was significantly higher on intertidal shell collectors than on subtidal ones (Fig. 2; Table 2). This pattern was consistent over sites (KH and MM) and years (2002 and 2003).

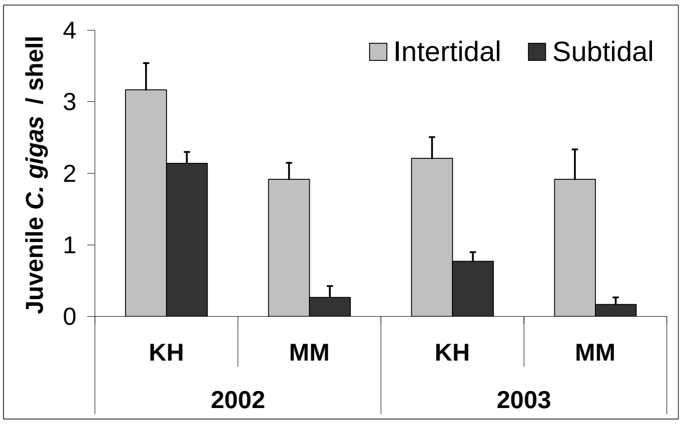

Fig. 2 Effect of tidal height on recruitment of *Crassostrea gigas* (mean ± 1 SE, n = 6) on oyster shells placed on two mussel beds (KH and MM) in intertidal and subtidal locations during August 2002 and 2003

Table 2 Effect of tidal height, substrate and barnacle epigrowth on recruitment of *Crassostrea gigas*. Results of Repeated Measures ANOVA (effect of tidal height and substrate) and ANOVA (barnacle epigrowth)

Source of variation	SS	df	MS	F	p
Tidal height					
Site	11.14	1	11.14	31.00	0.000
Tidal height	25.16	1	25.16	70.04	0.000
Site x tidal height	0.53	1	0.53	1.49	0.238
Error	6.83	19	0.36		
Time	4.46	1	4.46	9.64	0.006
Time x site	3.77	1	3.77	8.16	0.010
Time x tidal height	0.24	1	0.24	0.52	0.479
Time x site x tidal height	0.10	1	0.10	0.23	0.641
Error	8.79	19	0.46		
Substrate specificity intertidal: *Crassostrea* plot, *Mytilus* plot, mussel bed					
Substrate	366.33	2	183.16	8.68	0.010
Error	168.90	8	21.11		
Time	651.88	1	651.88	23.35	0.001
Time x substrate	39.26	2	19.63	0.70	0.523
Error	223.35	8	27.92		
Barnacle epigrowth					
Substrate (*C. gigas* – *M. edulis*)	0.69	1	0.69	14.68	0.000
Barnacle cover (yes – no)	0.06	1	0.06	1.24	0.270
Substrate x barnacle cover	0.36	1	0.36	7.71	0.008
Error	2.38	51	0.05		

3.2 Substrate specificity of recruitment near Sylt (*C. gigas* and *M. edulis*)

Substrate (*Crassostrea* plots, *Mytilus* plots or mussel bed) significantly influenced abundances of juvenile *C. gigas* in October 2002 and in May 2003 (Fig. 3; Table 2). In October 2002, i.e. about 2 months after settlement took place, abundance of 0-group juvenile oysters was about three times higher on intertidal *Crassostrea* plots (804.0 m^{-2}) than on *Mytilus* plots (231.9 m^{-2}) and on the natural mussel bed (285.4 m^{-2}). In May 2003 abundance on all three substrate types was about 75% lower, indicating that winter mortality did not differ between substrates (no substrate × time interaction). Recruited *M. edulis* (< 25 mm shell length) were equally abundant on *Crassostrea*, *Mytilus* and mussel bed sites in October 2002 (ANOVA, F = 0.53, df = 9, p = 0.604, i.e. no significant difference between plots). In May 2003 densities were reduced by 50% on all three substrate types, again indicating mortality to be independent of substrate.

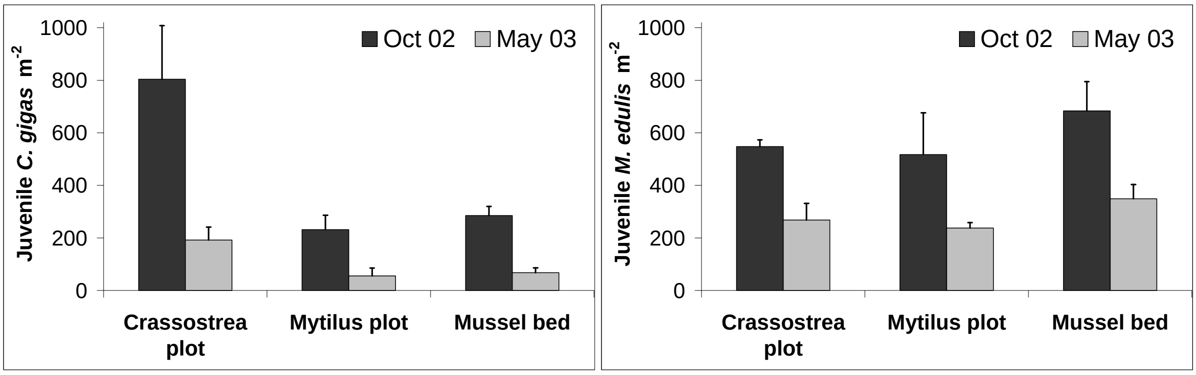

Fig. 3 Substrate-specific recruitment in the intertidal. Mean abundance (± 1 SE) of *Crassostrea gigas* (< 20 mm in October, < 33 mm in May) and *Mytilus edulis* (< 25 mm in October and May) on experimental *Crassostrea* plots (4 m^2, n = 4), *Mytilus* plots (4 m^2, n = 4), and on control mussel bed areas (n = 8; n = 12) in October 2002 and May 2003

In the subtidal (Fig. 4), recruitment of *C. gigas* was about twelve times higher on *Crassostrea* than on *Mytilus* plots (ANOVA, F = 39.70, df = 6, p < 0.001) while mussel recruitment showed no difference (ANOVA, F = 0.03, df = 6, p = 0.869).

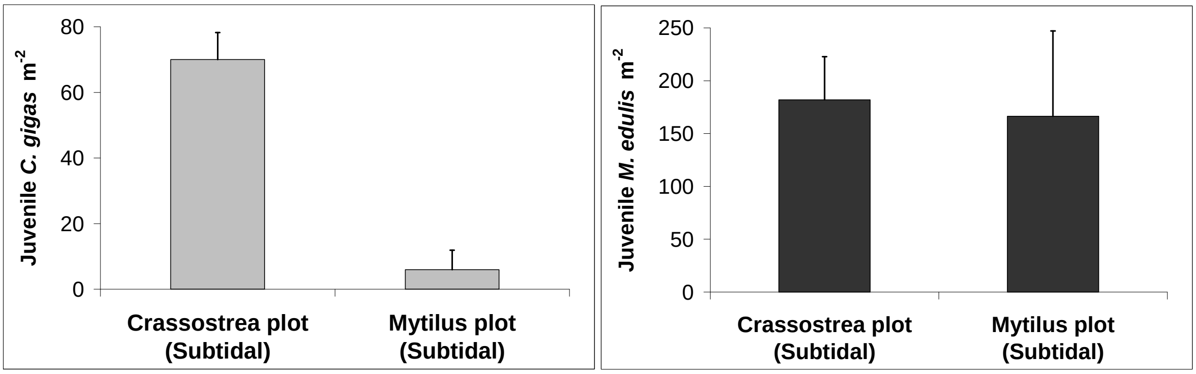

Fig. 4 Substrate-specific recruitment in the subtidal. Mean abundance (± 1 SE, n = 4) of *Crassostrea gigas* (< 20 mm) and *Mytilus edulis* (< 25 mm) on experimental *Crassostrea* plots (1 m²) and *Mytilus* plots (1 m²) in October 2003

3.3 Substrate specificity of recruitment in the Oosterschelde (*C. gigas*)

Recruitment of *C. gigas* was much higher on living oysters (100.6 juveniles/shell valve) than on living mussels (1.1 juveniles/shell valve; Fig. 5). Taking into account that oysters used as substrate were about twice as long and wide as the mussels, the amount of spat on *M. edulis* should be multiplied by 4 to balance for the size difference. In addition, the undulated, grooved surface of oyster shells has a much higher surface area than the smooth mussel shells. This difference is roughly estimated to be about threefold. Thus, in this experiment, shell surface area of living oysters is considered to be 7 times higher than the shell area of mussels. But as the amount of spat on oysters was 100 times higher than on mussels, there is still a difference by an order of magnitude.

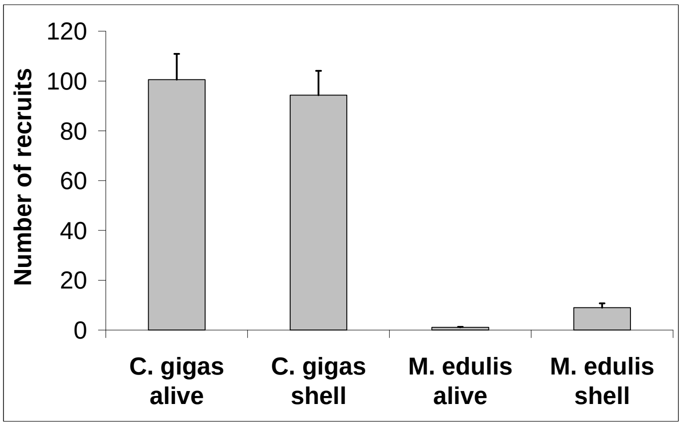

Fig. 5 Substrate-specific recruitment of *Crassostrea gigas* on an intertidal area in the Oosterschelde (The Netherlands). Mean number (± 1 SE, n = 6) of spat per shell valve of living bivalves and per outer surface of dead shell valves

Comparing oyster recruitment on living substrates and dead shells showed no difference between living and dead oysters, whereas there was a significantly higher recruitment on dead mussel shells than on living mussels (ANOVA, F = 40.62, df = 10, p < 0.001). Recruitment of

C. gigas was significantly higher on the rougher outer surface of oyster shells than on the smooth inner surface (ANOVA, F = 5.51, df = 20, p = 0.029).

3.4 Effect of barnacle epigrowth on recruitment (*C. gigas* and *M. edulis*)

C. gigas or *M. edulis* as substrates had a significant influence on oyster recruitment; it explained 19.7% of the variance (Fig. 6; Table 2). Barnacle cover on the other hand had no significant effect; however, the interaction between substrate species and barnacles was significant, showing that barnacles had an effect on recruitment on the less favoured substrate, *M. edulis*.

Mussel recruitment was strongly affected by the presence of barnacles (Kruskal-Wallis-ANOVA, $p < 0.001$); significantly more recruits were found on oysters and mussels with barnacle overgrowth than on those without barnacles (Mann-Whitney U-Test, $p < 0.001$ and $p = 0.005$ respectively). Even though slightly more recruits were found on mussels than on oysters, the difference was not significant. In summary, recruitment of oysters largely depends on the type of substrate while mussel recruitment is influenced by the presence of barnacles.

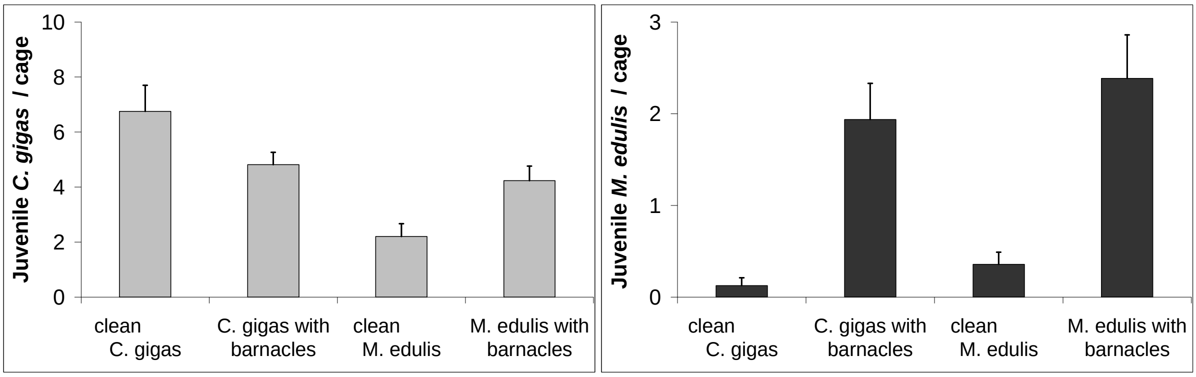

Fig. 6 Effect of barnacle epigrowth on shells for recruitment of *Crassostrea gigas* (left) and *Mytilus edulis* (right). Substrates were placed in open cages on a mussel bed near Munkmarsch; for *C. gigas* recruitment from 29 July to 12 September 2003; for *M. edulis* recruitment from 10 July to 18 August 2003. Mean number of juveniles (± 1 SE, n = 16) per cage (each cage containing 1 *C. gigas* or 2 *M. edulis*)

3.5 Effect of *Fucus* cover on recruitment (*C. gigas*)

Recruitment of *C. gigas* was significantly reduced underneath *Fucus* cover (ANOVA, df = 32, F = 42.46, $p < 0.001$). On *Fucus*-free adult oysters about 4 times more juvenile *C. gigas* (7.6 ± 1.0) were found than on *Fucus*-covered oysters (1.7 ± 0.4).

3.6 *Fucus* coverage on *Crassostrea* and *Mytilus* plots

Fucus cover varied during the investigation period but was always higher on experimental *Mytilus* plots than on *Crassostrea* plots (Fig. 7; Table 3). Repeated Measures ANOVA revealed significant effects of substrate, time and interaction of substrate and time; however, substrate explained 45% of the variance, compared to a lower time (16%) and interaction (15%) effect.

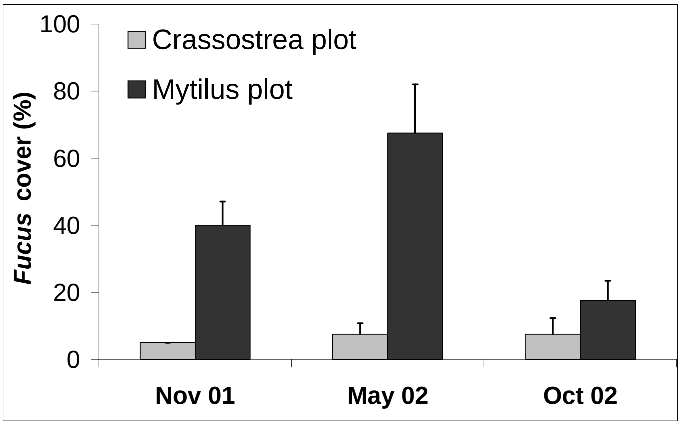

Fig. 7 Variability of *Fucus* cover (% ± 1 SE, n = 4) on experimental intertidal *Crassostrea* plots (4 m²) and *Mytilus* plots (4 m²) in November 2001, May 2002 and October 2002

Table 3 Repeated Measures ANOVA on effect of substrate (experimental *Crassostrea* and *Mytilus* plots) on *Fucus* cover.

Source of variation	SS	df	MS	F	p
***Fucus* cover**					
Substrate	7350.00	1	7350.00	15.94	0.007
Error	2766.67	6	461.11		
Time	2533.33	2	1266.67	12.85	0.001
Time x substrate	2500.00	2	1250.00	12.68	0.001
Error	1183.33	12	98.61		

4 Discussion

This study showed differences and similarities in recruitment patterns of introduced oysters and native mussels that may lead to niche separation and coexistence of the two species (Fig. 8). Recruitment of *C. gigas* and *M. edulis* occurred mainly in the intertidal zone (this study and Buschbaum, unpubl. data). While oyster recruitment was highest on conspecifics, mussels showed no preference for either oyster or mussel substrate. Barnacles, the most abundant fouling organisms on both mussel and oyster shells, had a positive influence on mussel but not on oyster recruitment. *Fucus vesiculosus*, which can cover mussel beds with a dense canopy, led to reduced abundances of juvenile oysters (this study) and mussels (Buschbaum, unpubl. data). Recruitment patterns in relation to the different factors are discussed in the corresponding order.

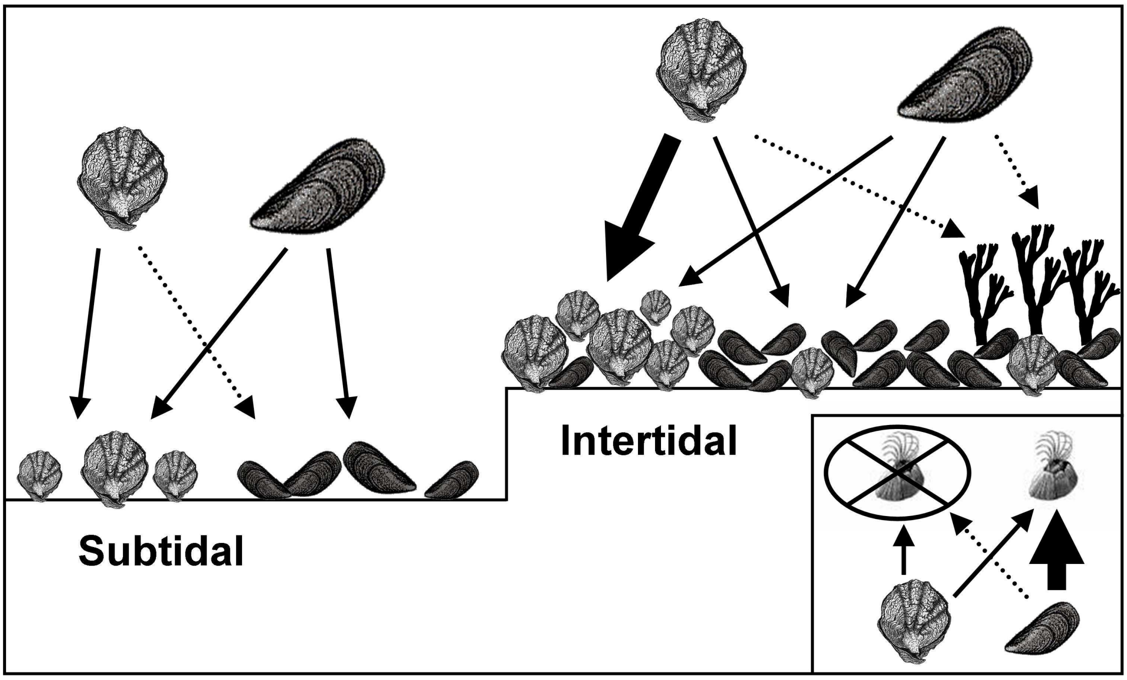

Fig. 8 Differential recruitment patterns of *Crassostrea gigas* and *Mytilus edulis* on intertidal and subtidal habitats and in relation to *Fucus* and barnacle cover as revealed by experiments in the northern Wadden Sea. Arrows indicate high (thick arrow), medium (thin arrow) or low (dotted arrow) recruitment of oysters and mussels. Some arrows for mussels are based on Buschbaum, unpubl. data

4.1 Tidal height

Crassostrea gigas has been described as an intertidal species that only occasionally occurs in subtidal locations (Buroker 1985). Presumably, this is due to reduced recruitment success because of sediment deposition on the settlement surfaces (MacKenzie 1970, Keck et al. 1973, Rothschild et al. 1994) or water temperatures being too low for larval or spat survival in the subtidal zone (Quayle 1988). Also high current velocities could lead to oyster larvae having difficulties in attaching to the substrate (Arakawa 1990b). In this study recruitment of *C. gigas* was significantly higher on shell collectors in the intertidal than in the adjacent shallow subtidal zone. Even though deposition of sediment on the settlement surfaces was higher in the subtidal compared to the intertidal zone, on average only 10 - 20% of the surface area was covered with sediment. As the temperature difference between surface water and deep water in the gullies is very small (less than 1°C; van Beusekom, pers. comm., 2004), water temperature is not a very likely reason for the lower recruitment in the subtidal zone. High current velocities might be a cause of lower oyster abundances in the subtidal, but *C. gigas* has settled successfully in tidal gullies with relatively high current speeds in the Dutch Wadden Sea near Texel (Dankers, pers. comm., 2004). However, a comparison of the performance of *C. gigas* in the Dutch and northern German Wadden Sea should take into account that the oysters originate from different introductions. The oysters in the Dutch Wadden Sea most likely originate from the Oosterschelde (Bruins 1983) whereas the oysters in the northern German Wadden Sea sprang from an oyster culture near Sylt (Reise 1998). Therefore, the populations could be genetically different. Another aspect could be higher early post-settlement mortality due to predation in the subitdal zone: when shell collectors were protected with mesh cover, recruitment of juveniles was similar on intertidal and subtidal habitats (own unpubl. data).

Mytilus edulis is widespread from high intertidal to subtidal locations because it withstands high fluctuations of salinity, desiccation, temperature and oxygen tension (Seed & Suchanek 1992). In the subtidal, however, it is limited by high predation pressure and competition (Ebling et al. 1964, Kitching & Ebling 1967, Paine 1974). In the study area, *M. edulis* recruitment in the subtidal also seems to be limited by predation (Buschbaum, unpubl. data; Saier 2001). Thus, both oyster and mussel recruits may find a refuge from predation in the intertidal.

4.2 Substrate specificity

Recruitment of *C. gigas* was higher on conspecifics than on mussels. Oyster larvae tend to settle gregariously triggered by adult conspecifics (Bayne 1969, Keck et al. 1971, Hidu et al. 1978). The preference of oyster larvae for rough surfaces has been described before (Korringa 1976, Quayle 1988) and has been confirmed in this study, because the smooth mussel shells caught much less oyster spat than the rough oyster shells and also the smooth inner surface of the oyster shells received fewer recruits than the rougher outer surface. Protection from predation in the shell crevices is considered to be a reason for high recruitment success on rough shells (O’Beirn et al. 2000). The higher recruitment of oysters on conspecifics than on mussels suggests that the oysters will aggregate and that the more oysters are present, the more recruits are to be expected on these aggregations in future years. This positive feedback may soon generate compact oyster reefs like the ones already present in the Dutch Wadden Sea near Texel (Dankers et al. 2004).

Mussel recruits were equally abundant on *Crassostrea*, *Mytilus* and mussel bed plots and suffered the same winter mortality of about 50% on all three sites. This contradicts other findings of gregarious behaviour of mussels and the avoidance of competition due to site-selective settlement (Suchanek 1981, Petersen 1984). Irregular, grooved and rough surfaces have also been described to be especially suited for mussel settlement (Chipperfield 1953, Seed 1969, Menge 1976, Grant 1977) and mussel fouling on oyster cultures is a common phenomenon (Quayle 1988, Arakawa 1990b). Therefore the oyster shell is likely to be a good settling substrate for mussels, which may even provide protection from predation in the crevices of the shell.

4.3 Barnacle epigrowth

Barnacles had little influence on oyster recruitment: only on the less favoured mussel substrate did barnacle cover increase oyster spat abundance. Presumably the rougher surface structure due to the barnacle shells enhanced settlement and early post-settlement survival of juvenile oysters. A similar effect was observed for *C. virginica* (Osman et al. 1989). On the other hand, there may also be space and/or food competition between oysters and barnacles (MacKenzie 1970, Abbe 1986, Arakawa 1990b) that could lead to differential settlement and horizontal zonation (Bushek 1988). In this study, recruitment was measured after about one month, and hence did not include post-settlement events over a longer period of time. For example, oysters settling on barnacles instead of on living bivalves may have a greater risk of dislodgement, because the barnacles may fall off the substrate as the oyster grows. The juvenile oyster could then easily be washed away to unfavourable habitats. Juvenile oysters attached to the remains of dead barnacles were indeed frequently found scattered on the tidal flats in the study area (own obs.). On the other hand, this may as well be regarded as a way of dispersal and may give rise to oyster reefs outside the mussel beds. In turn, massive settlement of barnacles on juvenile *C. gigas* was not observed, while adult oysters may be as heavily overgrown as mussels (own obs. and Görlitz, pers. comm., 2004). The reason for this might be the smoother shell surface of juvenile compared to adult oysters, because barnacles settle gregariously and preferentially on surfaces with cracks, crevices and pits (Chabot & Bourget 1988, Berntsson et al. 2004).

In contrast to the effects on oysters, barnacles strongly increased mussel recruitment, regardless of whether the barnacles were attached to oyster or mussel shells. This is attributed to protection from predation and from unfavourable environmental conditions such as desiccation and heat (Seed 1969, Navarette & Castilla 1990, Barnes 2000, Saier 2001). It can be concluded that barnacles may have an influence on the further development of mussel beds and oyster reefs in the area.

4.4 *Fucus* cover

The presence of *Fucus vesiculosus* on intertidal mussel beds reduced recruitment of *C. gigas*. This corresponds with lower overall oyster abundances on *Fucus*-covered mussel bed patches compared to *Fucus*-free areas (Reise 1998, own unpubl. data). Densities of juvenile mussels are also reduced underneath *Fucus* cover (Buschbaum, unpubl. data). Total mussel biomass, however, is only slightly lower and more persistent on *Fucus*-covered mussel bed areas compared to *Fucus*-free patches, which leads to the conclusion that *Fucus* cover is not a major factor for mussel bed dynamics (Nehls 2003). It is important to note that *Fucus* on mussel beds lacks a holdfast and is attached to the mussel bed only by the byssus threads of the mussels. This is the reason why oyster reefs will not be overgrown by *Fucus*, while mussel beds can be almost completely covered (Nehls 2003). The *Fucus* cover varies considerably over time, but some mussel bed areas are more often covered than others (Nehls 2003). These densely covered mussel beds will catch less oyster spat than bare ones resulting in a very slow increase in oyster abundance. Thus, oyster recruits will accumulate in areas free of *Fucus* overgrowth where abundances of adult oysters are already high. Once the proportion of mussels and oysters is in favour of oysters, these areas may stay free from *Fucus* overgrowth and attract still more oyster spat. However, during years with high mussel recruitment, the mussels may settle on top of the oysters and subsequently *Fucus* overgrowth could occur. Thus, fucoids may give rise to a mosaic of oysters and mussels, which may show patch dynamics as recruitment of the two species as well as of *Fucus* varies over the years.

5 Conclusion

The further development of the oyster population in the Wadden Sea and especially the spatial distribution on existing mussel beds will depend on recruitment success in different habitats.

Oyster reproduction in the northern Wadden Sea is confined to a short period in summer (July to September) when spawning and settlement occurs. Recruitment success depends on high water temperatures during this time and is therefore erratic: it occurred only in 6 out of 18 years since the first introduction of *C. gigas* in this area (Diederich et al. in press). Mussel spawning and settlement, on the other hand, is extended and occurs throughout the year with peaks in early summer and autumn (Pulfrich 1996). Strong year classes that lead to a rejuvenation of mussel beds, however, are rare and usually follow severe winters (Beukema 1992, Beukema et al. 2001, Strasser et al. 2001). In the study area, the last mass recruitment event occurred in 1996 (Nehls 2003) when oysters were still rare. Temperature may thus play a key role in determining the balance between the two bivalves: hot summers will favour oyster reproduction, while cold winters will lead to high mussel recruitment in the following summer.

The experiments revealed sufficient differences in settlement and/or recruitment patterns between oysters and mussels to predict that both species are likely to co-occur in mixed and mosaic beds, provided other processes such as food competition do not overrule the studied fine-scale performance with regard to substrate.

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Chapter 4

High survival and growth rates of introduced Pacific oysters may facilitate displacement of native mussels in the Wadden Sea

Abstract

Pacific oysters (*Crassostrea gigas* Thunberg 1793) were introduced to the northern Wadden Sea (North Sea, Germany) by aquaculture in 1986 and finally became established. Even though at first recruitment success was rare, three consecutive warm summers led to a massive increase in oyster abundances and to the overgrowth of native mussel beds (*Mytilus edulis* L.). These mussels constitute biogenic reefs on the sand and mud flats in this area. Survival and growth of the invading *C. gigas* were investigated and compared with the resident mussels in order to predict the further development of the oyster population and the scope of coexistence for both species. Field experiments revealed a high survival of juvenile *C. gigas* (approximately 70%) during the first three months after settlement. Survival during the first winter varied between > 90% during a mild and 25% during a cold winter and was independent of substrate (i.e. mussels or oysters) and tide level. Within their first year *C. gigas* reached a mean length of 35 - 53 mm, and within two years grew to 68 - 82 mm, which is about twice the size native mussels would attain during that time. Growth of juvenile oysters was not affected by substrate (i.e. sand, mussels, other oysters), barnacle epigrowth and tide level, but was facilitated by fucoid algae. By contrast, growth of juvenile mussels was significantly higher on sand flats than on mussel or oyster beds and higher in the subtidal compared to intertidal locations. Cover with fucoid algae increased mussel growth but decreased their condition expressed as dry flesh weight versus shell weight. High survival and growth rates may compensate for years with low recruitment, and may give *C. gigas* a competitive advantage that may lead to the permanent displacement of native mussels to less favourable habitats.

Keywords

Crassostrea gigas, Growth, Introduced species, Mussel bed, *Mytilus edulis*, Survival, Wadden Sea

1 Introduction

The accidental or deliberate release of ‘exotic’ (non-native) species into new habitats by shipping and aquaculture activities is an increasing phenomenon in coastal ecosystems all over the world (Carlton & Geller 1993, Reise et al. 1999, Ruiz et al. 2000, Naylor et al. 2001). Most introductions fail to produce self-sustaining populations or develop only a limited population growth (Williamson & Fitter 1996). Nevertheless, there are numerous examples of invasive exotics that profoundly changed the recipient ecosystem (Nichols et al. 1990, Grosholz & Ruiz 1996, Kideys 2002). The Pacific or Japanese oyster (*Crassostrea gigas*) is an example of an invasive species that has been introduced to various coastal areas through aquaculture activities and subsequently established in the wild (Andrews 1980, Chew 1990). Examples include introduced oyster populations in British Columbia (Quayle 1988), California (Span 1978), South Africa (C. Griffith, pers. comm.), Australia (Ayres 1991), New Zealand (Dinamani 1991), France (Grizel & Héral 1991), The Netherlands (Drinkwaard 1999), and Germany (Reise 1998).

Recently a dramatic increase in oyster abundances has been observed in the Dutch and German Wadden Sea (Dankers et al. 2004, Diederich et al. in press). As this area is characterised by extensive intertidal mud and sand flats, it lacks primary hard substrata for oyster settlement. However, epibenthic mussel beds (*Mytilus edulis*) and dead shell material provide secondary hard substrata, which the oysters use as settlement surfaces. In the German Wadden Sea, oysters are therefore mainly found as epibionts on intertidal mussel beds and are at present turning some mussel beds into oyster reefs (Diederich et al. in press). Since mussel beds take a prominent position in the Wadden Sea and generally constitute hot spots with respect to productivity and filtering-capacity (Asmus 1987, Asmus et al. 1992, Dankers & Zuidema 1995), biodiversity (Riesen & Reise 1982, Tsuchiya & Nishihira 1986, Dittmann 1990), and as a food resource for various crustaceans, fish, birds and man (Seed & Suchanek 1992, Nehls et al. 1997, Saier 2001), their overgrowth or possible displacement by oysters might profoundly change the entire ecosystem. Up to now, recruitment of *C. gigas* in the northern Wadden Sea was sporadic depending on years with high summer water temperatures. However, three consecutive warm summers (2001-2003) and a positive feedback of adult oysters on recruitment of juveniles, strongly increased oyster abundance and expansion of the population (Diederich in press, Diederich et al. in press). Thus, abundance may be high enough, by now, to ensure some recruitment even during ‘cool’ summers. Provided these recruits suffer a low mortality and adults achieve high longevity, this might guarantee population persistence and facilitate a further increase in the Wadden Sea. As a consequence, oysters might permanently restrict the local mussels to less favourable habitats, especially if they show higher growth and survival rates than the natives. However, no information is available on survival and growth of *C. gigas* in the Wadden Sea. The present study aims to fill that gap and attempts to find out whether oyster reefs may be regarded as a temporary phenomenon or are likely to be habitat structures superseding mussel beds in the Wadden Sea.

Generally, survival or mortality of benthic bivalves is described as a change in abundance of individuals or year classes present in a population over some period of time. In addition to physical stress, competition and desease, predation is often a major cause of natural mortality in bivalves (Walne & Davies 1977, Reise 1985, McGrorty et al. 1990, Strasser 2002). As predation is especially effective on juveniles and under conditions of extended submersion, survival largely depends on size and tide level (Theisen 1968, Seed 1969, 1993). Fast growing species may rapidly outgrow predation pressure. Therefore, it is assumed that Pacific oysters, which grow to about 30 cm in their native habitat as well as in the Dutch Wadden Sea (Korringa 1976, Dankers et al. 2004) might have an advantage over the much smaller native mussels (*Mytilus edulis*), which attain a maximum size of about 7 cm in the northern Wadden Sea (Nehls 2003). The growth rates of both, mussels and oysters may depend on various factors, including tidal exposure (Quayle 1988, Buschbaum & Saier 2001), interspecific competition (Bertness & Grosholz 1985, Okamura 1986), and epibionts on the shells like algae or barnacles (Arakawa 1990, Dittman & Robles 1991, Buschbaum & Saier 2001).

In the study at hand, survival of *C. gigas* and growth of both, *C. gigas* and *M. edulis,* were investigated in relation to tide level, substrate, barnacle epigrowth and algal cover, in order to assess whether habitat requirements are the same or whether there might be species specific refuges from potential competition. Information on mussel survival and growth rates was taken from literature but for a comparison of growth performance in different microhabitats oyster and mussel growth was investigated simultaneously.

2 Material and Methods

2.1 Study area

The study was conducted in the List tidal basin in the northern Wadden Sea (North Sea, Germany, 54°50’ - 55°10’N and 08°20’ - 08°40’E). This basin (404 km² area) is surrounded by the mainland and by two islands (Sylt and Rømø) that are connected to the mainland by dams (Fig. 1).

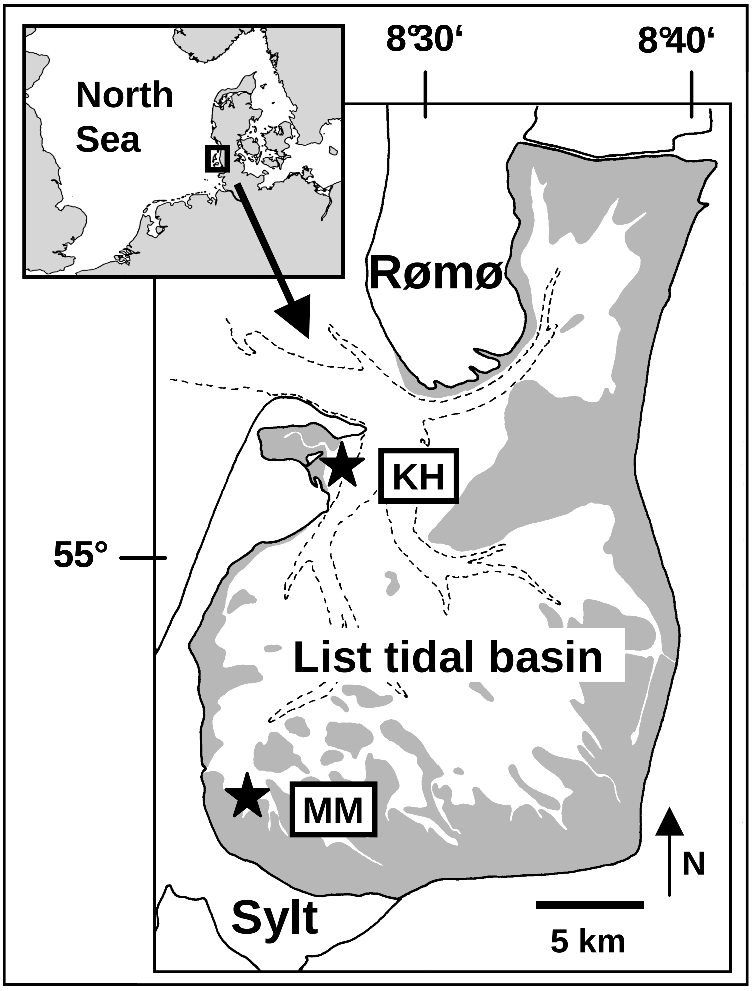


Fig. 1 Study area in the northern Wadden Sea (Germany) and location of experimental sites (KH and MM, asterisks). Shaded areas indicate intertidal sediment flats

A narrow tidal inlet of 2.8 km in width is the only connection to the North Sea. This inlet branches out into three main water channels (maximum depth 40.5 m; maximum current velocity 1.2 m s^{-1}), which govern the current and transport regimes within the lagoon. Intertidal flats, which are mostly sandy, comprise 33% (134 km²) of the total area. Tides are semidiurnal and the mean tidal range is 2 m; the average salinity is close to 30 psu. Monthly mean water temperatures range from 18.2°C in August to 2.3°C in February. Primary production is about 300 g C m^{-2} $year^{-1}$. Detailed information on hydrography, geology, sediments and biota of the bay is given in Gätje and Reise (1998). Within the List tidal basin, natural intertidal mussel beds cover about 1.5 km^2 (Nehls 2003) and are partly covered by the brown macroalgae *Fucus vesiculosus* forma *mytili* (Nienburg) Nienhuis. Some of these mussel beds extend into the shallow subtidal zone. A commercial oyster farm has been in operation in this basin since 1986 and produces about 2 million oysters per annum. Experiments were carried out in Königshafen (KH), a tidal bay at the northern end of the island of Sylt, and in Munkmarsch (MM) approximately 15 km further south.

2.2 Survival of *C. gigas*

Survival of *C. gigas* was investigated via three experiments on different time scales (during the first three months, the first winter, and the first year after settlement) and in relation to tide level (intertidal and subtidal) and substrate (mussel and oyster bed).

To quantify the survival of early recruits on an intertidal mussel bed during the first three months after settlement, six unglazed ceramic tiles (29 × 29 cm) were fixed on mussel bed MM on 16 August 2002 as settlement surfaces for oyster larvae. Settlement onto the tiles followed shortly thereafter with the main settlement period ending at the end of August, but light settlement occurring until late September. As the tiles had an imprinted grid, the position of each attached oyster could be exactly determined. The survival of juveniles was calculated from the difference in numbers of oysters that were present at the first examination on 29 August and the subsequent sampling dates. Sampling occurred seven times in irregular intervals until 26 November 2002.

To investigate the survival of oysters during their first year after settlement in relation to tide level, I counted numbers of juveniles that were attached to shell collectors placed on two mussel beds (KH and MM), at each site on intertidal and subtidal locations. Each collector was made from 30 clean (i.e. with no epibionts), dead oyster shells (mean shell length ± SD: 101.0 ± 14.1 mm) that had a hole drilled in the middle so that they could be strung on a plastic covered clothesline. These lines were about 1m long and were pinned with iron bars horizontally on the mussel bed so that the shells touched the mussels underneath. The collectors (6 at each location) were deployed in the field on 9 and 10 August 2002. Settlement occurred shortly thereafter and the number and length (largest diameter of the shell) of juveniles on the shell surfaces was recorded first on 29 and 30 August 2002 by removing 10 oyster shells from the clothesline and searching them for oyster spat with a stereomicroscope in the laboratory. On 27 and 28 November another 10 shells were removed from the string and searched for living oyster spat. On 21 February and 4 March 2003 the remaining 10 shells were returned to the laboratory and juvenile oysters were counted and measured.

The latter set of shells were kept in an indoor tank with continuous seawater flow for 1 to 2 days and then brought back to the field and installed on the same spot on the mussel beds to follow their survival for another few months. On 7 and 16 May 2003 and finally on 7 and 10 July 2003 the oyster shells were again returned to the laboratory and the attached juveniles were counted and measured. As significant settlement on the collectors exposed on site MM occurred later than 29 August 2002, the numbers of juveniles present in November 2002 were taken as starting value for mortality quantification, because there was no more settlement after that date.

Two calculations were made: survival of juveniles from November 2002 to February 2003 to determine survival over winter, and survival during the “first year” after settlement, that is from November 2002 to July 2003. As the collectors on the subtidal MM site were lost before the end of the experiment, the comparison of abundances from November 2002 with July 2003 could only be done for intertidal locations. 2-factor (site and tide level) analysis of covariance was used to compare abundances of juveniles in November 2002 and February 2003. The percentage survival at the different sites and tide levels was analysed using 2-factor (site and tide level) analysis of variance. Abundance data were log(x+1) transformed and percentages were arcsine square-root transformed to achieve homogeneity of variances (Levene test).

To quantify the dependence of survival on substrate quality, survival of juvenile *C. gigas* was analysed during two consecutive winters on experimental intertidal *Crassostrea* plots, *Mytilus* plots and on a nearby natural mussel bed (MM). Experimental *Crassostrea* and *Mytilus* plots ($n = 4$) were randomly distributed along the edge of a mussel bed (MM) on sand covered with dead mussel shells in July 2001. ‘Oyster plots’ were created by collecting live wild oysters from the nearby mussel bed, removing all attached mussels, and placing the oysters on four 2 × 2 m plots. The oysters were densely packed, resulting in a three-layered aggregation with a density of about 500 oysters m^{-2}. ‘Mussel plots’ were constructed by collecting live *M. edulis* clumps with no attached oysters from the adjoining mussel bed and placing them on four 2 × 2 m areas. Mussel density on these plots was about 3400 m^{-2}.

Samples were taken on each of the plots and on the adjoining mussel bed in November 2001, May 2002, October 2002 and May 2003. Two sub-samples were taken from each of the four experimental oyster plots by randomly placing a 25 × 25 cm frame on the plot area and removing all living bivalves and dead shells underneath. On mussel plots (two sub-samples taken from each of the four plots) and on the natural mussel bed (eight samples taken in 2002 and twelve in 2003) samples were collected using a 14.5 × 14.5 cm box corer instead of a frame. The different sampling devices were used because of substantial size differences between oysters that were forming solid aggregations often exceeding 15 cm in diameter and the much smaller mussels. Therefore, the corer could not be used for oysters and the frame would have been too time-consuming to use for mussel sampling. All material inside the frame or box corer was sieved over a 5 mm mesh sieve. In the laboratory, all mussels and oysters were measured with electronic vernier callipers to the nearest 0.01 mm. Dead shell material was searched for attached juvenile oysters as well. Oysters were considered as 0-group juveniles if their shell length was < 20 mm in the fall samples and < 33 mm in the spring samples. These size cutoffs were chosen after an analysis of length-frequency data. Numbers of juveniles in November 2001 were compared with numbers in the following spring (May 2002) using a non-parametric test (Kruskal-Wallis ANOVA) because of heterogeneity of variances despite transformation. Abundances in October 2002 and May 2003 were compared using Repeated Measures ANOVA.

2.3 Size and growth of *C. gigas*

Length frequency data of *C. gigas* were obtained at two mussel beds (KH and MM) by measuring the shell length (largest diameter) of randomly encountered oysters (n = 68 - 307 for each sampling) with vernier callipers to the nearest millimetre (see Diederich et al. in press). Sampling was conducted in 1999 (April/May and September/October), 2001 (April and November), 2002 (April and October), 2003 (May and August), and 2004 (April/May and September). The mean length of cohorts was determined by using Bhattacharya's Method (1967) with the program FISAT II (Version 1.1.2, FAO-ICLARM Fish Assessment Tools). A von Bertalanffy growth function was established using electronic length-frequency analysis (ELEFAN; Gayanilo et al. 1989, Pauly & David 1981) to calculate growth parameters. As larger animals were poorly represented, the parameter L_∞ was not determined iteratively, but set to 180 mm according to the maximum length observed during this survey. As the oysters did not grow during winter in this area (approximately November to February; own unpublished data and Fig. 6), the winter point was set to WP = 1. The calculation was run with the starting point May 2003 for KH and May 2004 for MM, because of clearly defined cohorts in these data sets. To verify these calculations I used the growth of 0-group juvenile *C. gigas* that were attached to shell collectors described above.

2.4 Growth experiments with *C. gigas* and *M. edulis*

2.4.1 Substrate and tide level

A field experiment was carried out to investigate growth of juvenile *C. gigas* and *M. edulis* in relation to substrate (sand flat, mussel bed, and oyster reef) and tide level. It is important to note that this experiment was not designed to investigate differences in absolute growth between oysters and mussels, but to find out how oysters and mussels perform in different habitats. Therefore it was not essential to use oysters and mussels of the same age. Juvenile oysters (mean shell length ± SD: 27.7 ± 1.0 mm) and mussels (mean shell length ± SD: 30.4 ± 1.8 mm) were collected from mussel bed MM in April 2002 and cleaned from all epigrowth with an iron scraper and brush. Only oysters that were attached to dead shell material were used to avoid possible interactions between basibiont and epibiont. The shell length (largest diameter) of each oyster and mussel was measured with vernier callipers to the nearest millimetre. Afterwards the oysters and mussels were placed separately (that is one bivalve per cage) in cylindrical cages made from plastic covered wire netting (∅ 5 - 6 cm, length 8 - 9 cm, mesh opening 11 mm). 280 cages (20 containing oysters and 20 containing mussels for each of 7 locations) were installed in the field in May and June 2002 by fixing each cage with an iron bar to the ground. Seven different locations were chosen: (1) intertidal sand flat (northern Sylt), (2) shallow subtidal sand (northern Sylt), (3) intertidal mussel bed (KH), (4) subtidal mussel bed (KH), (5) intertidal mussel bed (MM), (6) experimental intertidal *Crassostrea* plot (MM), (7) experimental intertidal *Mytilus* plot (MM). Subtidal habitats are referred to as areas remaining submerged during spring low tides and comprise depths of about 1 m at mean low tide. Intertidal sites had a mean exposure time of 2 - 3 hours per tide. Experimental *Crassostrea* and *Mytilus* plots (n = 4) were built next to a natural mussel bed (MM) in July 2001 (see above). The cages were randomly distributed on these plots but only on areas without *Fucus* cover. The length of each individual oyster and mussel was measured in the field in June, July, August, September and November 2002. Unfortunately, the cages at the subtidal sand flat location were lost after August 2002. Daily growth rates were calculated for a two months (49 - 64 days) period from June to August 2002 for all seven locations. The daily growth rates on the 5 intertidal locations were compared using analysis of variance (ANOVA). In a separate ANOVA the effect of tidal height was analysed for the sand flat and mussel bed (KH) locations. Tukey’s HSD test for unbalanced data sets was used to compare single sites. All data were square root transformed to obtain homogeneity of variances (Levene test). Effects were considered to be statistically significant if p-value was < 0.05.

2.4.2 *Fucus* cover

A second set of field experiments was designed to study the effect of a dense fucoid cover on intertidal mussel beds with respect to growth and condition of juvenile *C. gigas* and *M. edulis*. This experiment was conducted three times, each time using a different intertidal mussel bed in “Königshafen” in the north of Sylt: KH I (30 May to 28 August 1999), KH II (23 July to 20 September 1999), KH III (3 May to 8 August 2001). For each experimental site 40 juvenile oysters (mean shell length ± SD: KH I: 51.3 ± 5.7 mm; KH II: 45.8 ± 2.8 mm; KH III: 40.6 ± 5.6 mm) were collected a few days prior to the experiments on intertidal mussel beds and cleaned from all epigrowth with an iron scraper and brush. Only oysters attached to dead shell material were used. Shell length and at site KH I also shell width of oysters was measured with vernier callipers to the nearest millimetre and all oysters were marked individually. For experiments KH I and KH II oysters were marked with bee numbers (2 mm in diameter) that were glued to the upper shell valve. For experiment KH III the oysters were placed separately in pouches made from plastic covered wire netting (240 × 180 mm; mesh opening 10 mm). After marking the oysters, they were brought to the respective mussel beds. On each mussel bed 20 oysters were placed on fucoid-free patches and 20 oysters on patches with a dense *Fucus* canopy. In experiments KH I and KH II the oysters were placed between the byssus threads of the mussels to prevent them from getting washed away. On algal covered areas the oysters were placed between the mussels underneath the *Fucus* thalli. In experiment KH III the cages were fixed to the mussel bed with iron bars. Over the following 2 - 3 months, fucoid algae were removed several times from *Fucus*-free patches as necessary. At the end of this period, the oysters were collected and length increment (on site KH I also width increment) was measured in the laboratory. On location KH III also the growth of juvenile *M. edulis* was investigated. Mussels (mean initial shell length ± SD: 36.5 ± 2.4 mm) were treated the same way as described above for *C. gigas*.

To test whether the fucoid cover had an effect on the condition of *C. gigas* and *M. edulis*, the condition index (CI) of the oysters and mussels was determined in experiment KH III. The condition index used here is among the most accurate ones that involve easily measured parameters (Davenport & Chen 1987): CI = Dry meat weight / Dry shell weight × 100. For dry weight determination, the oysters and mussels were stored in a deep freezer at –20°C for several days. Then the bivalves were cooked in seawater for 4 minutes. Afterwards meat and shell of the individuals were separated and dried to constant weight at 80°C (6-7 days). After cooling in a desiccator, meat and shell were weighed on a torsion balance (± 0.01 g). Data on growth and condition were subjected to ANOVA (see above).

2.4.3 Barnacle epigrowth

The effect of barnacle cover on the growth of juvenile and adult oysters was experimentally tested during the growing season of 2003. 32 juvenile oysters (mean shell length ± SD: 20.25 ± 3.96 mm) and 32 adult oysters (mean shell length ± SD: 50.32 ± 12.72 mm) which were attached to living mussels were collected on mussel bed MM on 30 May 2003. 16 juvenile and 16 adult oysters with their attached mussels were cleaned from barnacles with an iron scraper and brush, whereas the other oysters with attached mussels were not cleaned and > 50% of their shell surfaces were covered with barnacles. The shell length of the oysters was measured with electronic vernier callipers to the nearest 0.01 mm and afterwards the oysters were placed separately in cages made from plastic covered wire netting (mesh opening 11 mm). The cages were fixed with iron bars on an intertidal mussel bed (KH) on 1 June 2003. On 8 October 2003 the cages were returned to the laboratory and all oysters were measured again. The growth of the oysters was determined by subtracting the initial length of each oyster from the final length and data were analysed using ANOVA.

3 Results

3.1 Survival of *C. gigas*

On 29 August 2002 there were 11.0 ± 2.2 (mean ± SE) juvenile oysters attached to the tiles that had been fixed on an intertidal mussel bed. From these 70.0% survived their first three months until 26 November 2002 (Fig. 2). The decrease in abundance was estimated according to $M = 1/t \ln(N_t/N_0)$ with N_0 = density at t_0 and N_t = density at $t = 89$ days. The estimated daily instantaneous mortality rate (M; d^{-1}) during the period from late August to late November was 0.004 ± 0.001 (mean ± SE).

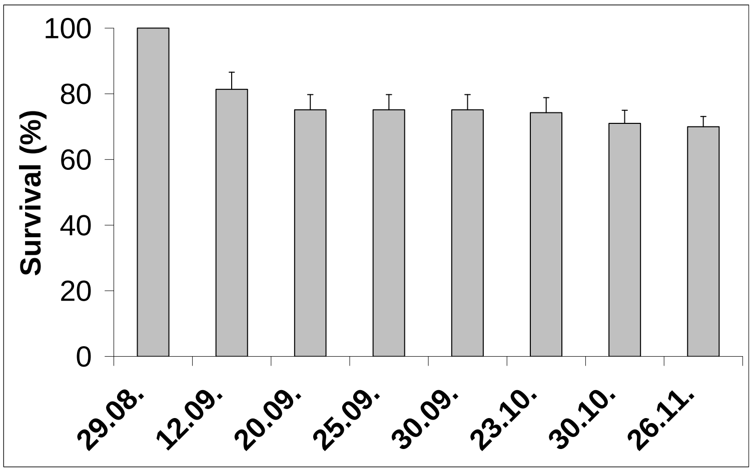


Fig. 2 Survival (% + SE) of juvenile *C. gigas* on tiles (n = 6 tiles with 5-19 attached oysters each) that were fixed on an intertidal mussel bed (MM) from August to November 2002

Abundance decreases of juvenile *C. gigas* on shell collectors were independent of site (mussel beds KH or MM) and tidal height (Fig. 3, Table 1). The over winter survival rate (November 2002 to February 2003) amounted to 63.7 ± 7.1% (mean ± SE) and the daily mortality rate for the same period was M = 0.005 ± 0.001 d^{-1}. First year survival of juveniles (November 2002 to July 2003) was independent of site as well and averaged 42.6 ± 3.9%. The daily mortality rate for this period was 0.004 ± 0.0004 d^{-1}.

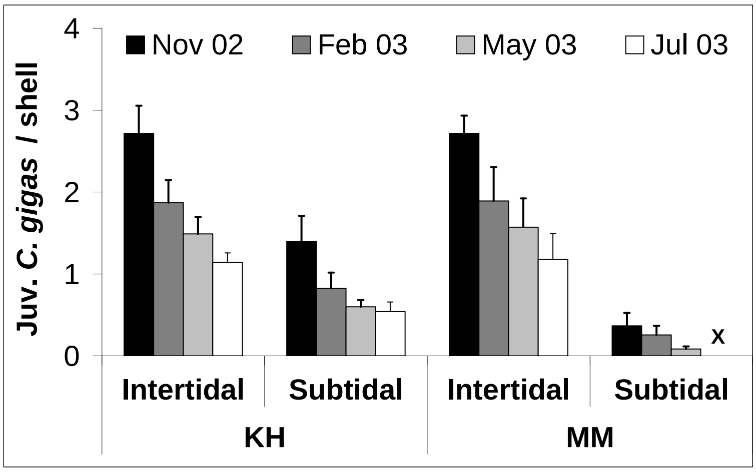


Fig. 3 Abundance of juvenile *C. gigas* on shell collectors (mean + SE, n = 4-6 collectors on each location) on two mussel beds (KH and MM) in intertidal and subtidal locations from November 2002 to July 2003. X = no data

Table 1 Analysis of covariance of abundance of juvenile *C. gigas* (log transformed) and analysis of variance of survival (%) of juvenile *C. gigas* (arcsine square-root transformed). Bold face values: $p < 0.05$

Source of variation	SS	df	MS	F	p
Abundance Nov 02 - Feb 03					
Site (KH – MM)	0.002	1	0.001	0.203	0.658
Tide level (intertidal – subtidal)	0.017	1	0.017	1.985	0.178
Site x Tide level	0.001	1	0.001	0.107	0.748
Abundance Nov 02	0.044	1	0.044	5.295	**0.035**
Error	0.133	16	0.008		
Survival Nov 02 – Feb 03					
Site (KH – MM)	0.082	1	0.082	0.485	0.497
Tide level (intertidal – subtidal)	0.255	1	0.255	1.506	0.239
Site x Tide level	0.003	1	0.003	0.019	0.893
Error	2.543	15	0.170		
Survival Nov – July 03					
Site (KH – MM)	0.001	1	0.001	0.049	0.831
Error	0.260	9	0.029		

Following a strong recruitment event in the summer of 2002 abundances of 0-group *C. gigas* were six to eight-folds higher in October 2002 than in November 2001 in all three locations (Fig. 4). A decrease in numbers of juveniles could not be detected during the winter of 2001/2002 suggesting high survival (*Crassostrea* plot: 94.1% survival from November 2001 to May 2002). In the following winter (2002/2003) abundances decreased significantly (Repeated Measures ANOVA, Factor Substrate: MS = 183.16, F = 8.68, p = 0.010, Factor Time: MS = 651.88, F = 23.35, p = 0.001). The interaction between substrate and time was not significant (MS = 19.63, F = 0.70, p = 0.523) showing that survival did not differ between substrates (*Crassostrea* plot: 23.9%, *Mytilus* plot: 23.9%, mussel bed: 23.6%).

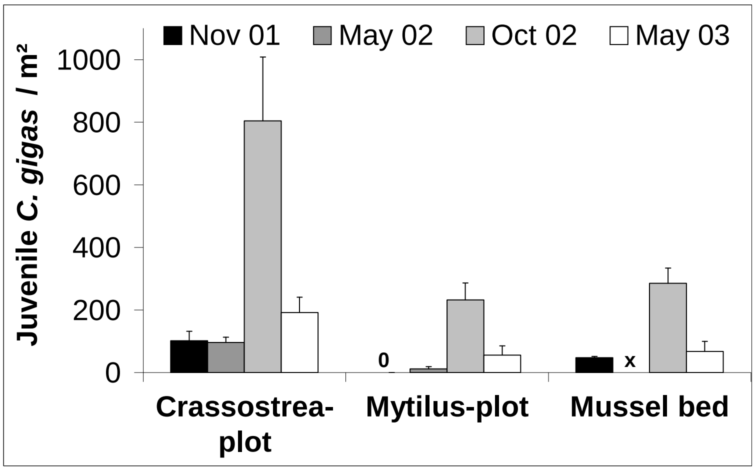


Fig. 4 Mean abundance (+ SE) of juvenile *C. gigas* (< 20 mm in fall, < 33 mm in spring) on experimental intertidal *Crassostrea* and *Mytilus* plots (4m², n = 4) and on control mussel bed areas (n = 8-12) in November 2001, May 2002, October 2002 and May 2003. X = no data

3.2 Size and growth of *C. gigas*

Analysis of length-frequency data revealed that 0-group juvenile *C. gigas* reached a mean shell length of 12.0 mm on site KH and 20.0 mm on site MM about eight to nine months after settlement which occurred in August and September (Fig. 5). Within one year post settlement they reached 39.6 mm (KH) and 48.1 mm (MM) and after two years they had grown to 74.2 mm (KH) and 75.4 mm (MM). Von Bertalanffy growth functions were fitted to both data sets (sites KH and MM) with fixed L_∞ = 180.00 mm and calculated growth constants of K(KH) = 0.26 and K(MM) = 0.30. Growth rates of *C. gigas* cohorts were slightly higher on site MM than on site KH (Table 2) and lower in the winter half year than during the growing season from spring to fall.

Table 2 *C. gigas* cohort length increment (in mm month^{-1}) in two locations (KH, MM) during the first winter after settlement (fall - spring), the first growing season (spring - fall), the second winter and the second growing season, respectively. Data derived from length-frequency distributions and cohorts were separated using Bhattacharya's method

	Cohort of 1997		**Cohort of 2001**		**Cohort of 2002**		**Cohort of 2003**	
	KH	MM	KH	MM	KH	MM	KH	MM
1st winter				2.7	1.5	2.1	1.5	2.1
1st growing season				4.8	7.2	9.3	6.3	7.2
2nd winter				0.3	1.5	2.7		
2nd growing season	4.2	2.7			5.7	3.9		

The growth experiment with newly settled *C. gigas* revealed that juveniles grew from 1.7 ± 0.3 (mean ± SE) mm in August 2002 to 12.3 ± 2.5 mm in May 2003 and reached 31.5 ± 7.0 mm in July 2003 (Fig. 6). During the 2 months from 11 May 2003 to 10 July 2003 they reached a mean growth rate of 9.6 ± 2.3 mm month^{-1}. No growth occurred during winter from November to February.

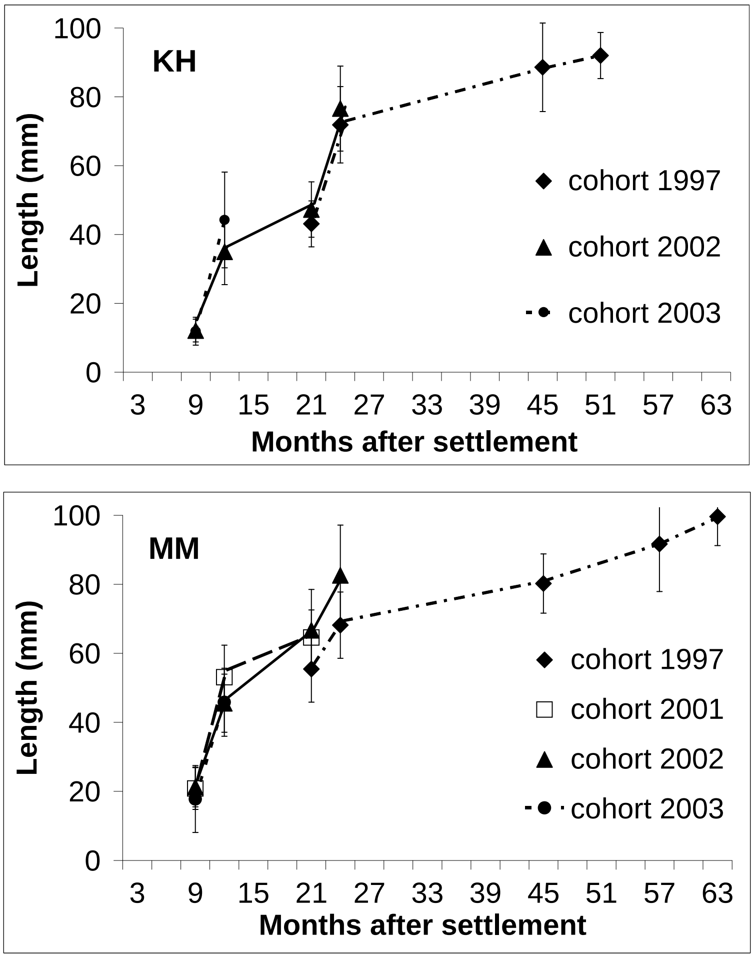


Fig. 5 Mean cohort shell length (± SD) of *C. gigas* at two locations (KH, MM) during the first 5 years after settlement

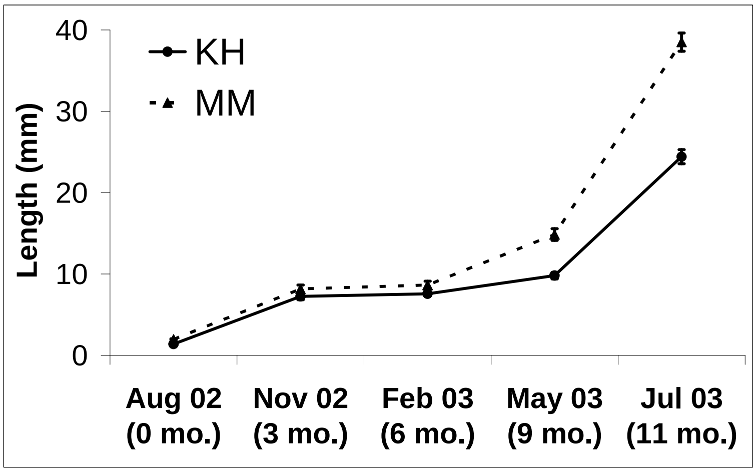


Fig. 6 Mean shell length of juvenile *C. gigas* (± SE; n = 5-6 collectors on each location) that had attached to shell collectors on two intertidal mussel beds (KH and MM) from August 2002 (settlement) to July 2003 (11 months after settlement). mo. = months after settlement

3.3 Growth experiments with *C. gigas* and *M. edulis*

3.3.1 Substrate and tide level

The length of individually marked juvenile *C. gigas* increased similarly on all intertidal sites from 27.8 ± 0.6 mm (mean ± SE) in June to 45.9 ± 0.6 mm in November 2002 (Fig. 7; left). For *M. edulis* there was a higher length increase on the sand flat than on all other intertidal locations (Fig. 7; right). The mean daily growth rates of *C. gigas* on intertidal locations were independent of site (Sand, mussel bed KH, mussel bed MM, experimental *Mytilus* plot and experimental *Crassostrea* plot; Fig. 8, Table 3). However, comparing growth on the 2 intertidal and 2 subtidal sites (sand flat and mussel bed KH) tide level showed a significant effect on growth on the sand flat (Tukey's HSD test for unbalanced data, MS = 0.02, df = 63, p = 0.001), but not on the mussel bed.

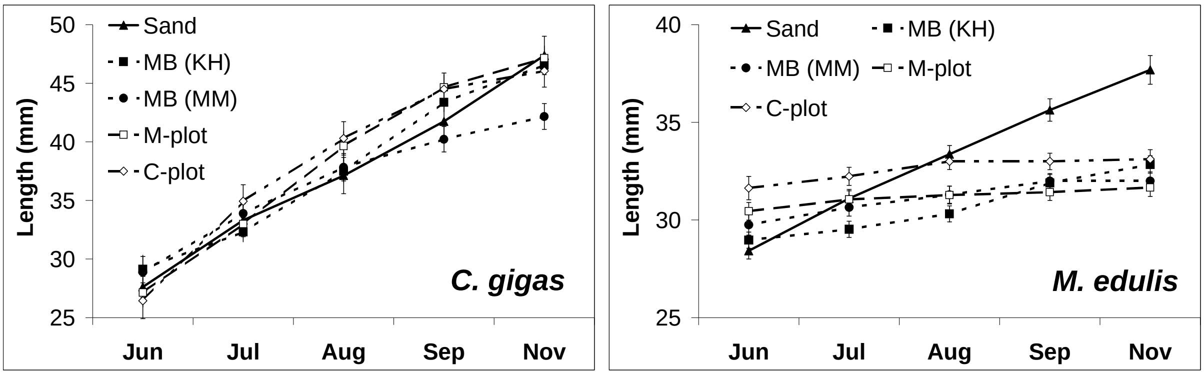


Fig. 7 Length (mean ± SE) of individually marked juvenile *C. gigas* (left, n = 16-20) and *M. edulis* (right, n = 16-19) on 5 intertidal locations in the List tidal basin from June to November 2002

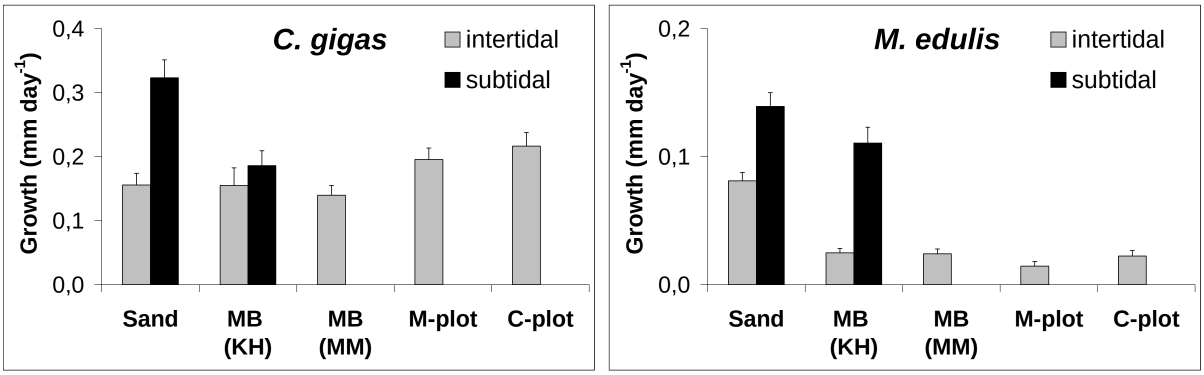


Fig. 8 Daily growth rate (mean + SE) of juvenile *C. gigas* (n = 16-20) and *M. edulis* (n = 16-19) calculated from length increment from June to August 2002 on 5 intertidal and 2 subtidal locations. Sand: sand flat; MB (KH): mussel bed KH; MB (MM): mussel bed MM; M-plot: experimental *Mytilus* plot; C-plot: experimental *Crassostrea* plot

The daily growth rate of juvenile *M. edulis* in the intertidal was significantly higher on the sand flat than on mussel bed or oyster plot locations (Tukey's HSD test for unbalanced data, MS = 0.00, df = 82, p = 0.000). Tide level affected growth of *M. edulis* on both sand flat and mussel bed, explaining 40.4% of the variation (Tukey's HSD test for unbalanced data, MS = 0.00, df = 65, p(Sand) = 0.002, p(MB) = 0.000).

Table 3 Analysis of variance on daily growth rate of *C. gigas* and *M. edulis* (square-root transformed). Bold face values: $p < 0.05$

Source of variation	SS	df	MS	F	p
Daily growth rate *C. gigas* intertidal					
Site (Sand - MB(KH) - MB(MM) - M-plot - C-plot)	0.110	4	0.028	2.398	0.057
Error	0.930	81	0.011		
Daily growth rate *C. gigas* intertidal - subtidal					
Site (Sand – MB(KH))	0.110	1	0.110	7.000	**0.010**
Tide level (intertidal – subtidal)	0.217	1	0.217	13.834	**0.000**
Site x Tide level	0.058	1	0.058	3.691	0.059
Error	0.989	63	0.016		
Daily growth rate *M. edulis* intertidal					
Site (Sand - MB(KH) - MB(MM) - M-plot - C-plot)	0.293	4	0.073	26.314	**0.000**
Error	0.228	82	0.003		
Daily growth rate *M. edulis* intertidal - subtidal					
Site (Sand – MB(KH))	0.135	1	0.135	33.468	**0.000**
Tide level (intertidal – subtidal)	0.290	1	0.290	71.730	**0.000**
Site x Tide level	0.029	1	0.029	7.287	**0.009**
Error	0.263	65	0.004		

3.3.2 *Fucus* cover

Growth of juvenile *C. gigas* was significantly higher on *Fucus* covered mussel bed patches than on uncovered ones (Fig. 9, Table 4).

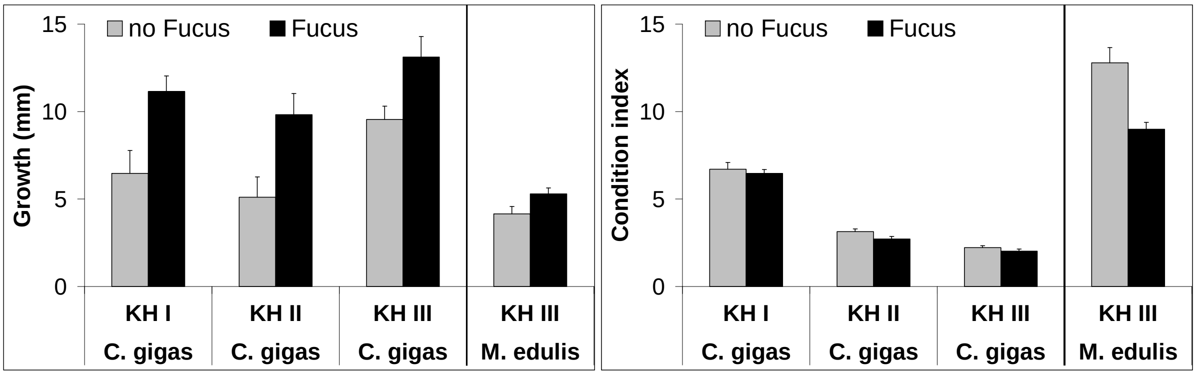


Fig. 9 Growth (left; mean + SE, n = 17-20) and condition index (right; mean + SE, n = 17-20) of individually marked juvenile *C. gigas* on three intertidal mussel beds (KH I, KH II, KH III) and of juvenile *M. edulis* on one intertidal mussel bed (KH III) on patches without and with *Fucus* cover

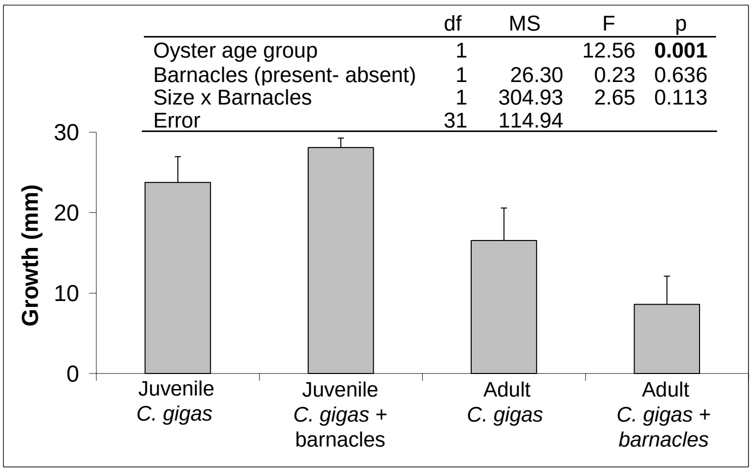
This pattern was consistent over all three sites. On site KH I also width increment was measured and was significantly higher on *Fucus*-patches (ANOVA, MS = 250.82, F = 9.32, p = 0.004). Even though the condition of *C. gigas* on all three sites was lower on *Fucus* covered patches than on uncovered ones, ANOVA revealed neither a significant effect of *Fucus* cover on a 5% probability level nor a significant interaction between *Fucus* and site on condition index. Juvenile *M. edulis* also showed a significantly higher growth rate when covered with *Fucus*, but their condition was significantly reduced in the presence of algal canopy.

Table 4 Analysis of variance on effect of site (KH I, KH II, KH III) and *Fucus* cover on growth and condition index of *C. gigas* and on effect of *Fucus* cover on growth and condition index of *M. edulis*. Bold face values: p < 0.05

Source of variation	SS	df	MS	F	p
Growth *C. gigas*					
Site (KH I, KH II, KH III)	286.38	2	143.19	6.46	**0.002**
Fucus cover (present - absent)	526.425	1	526.43	23.74	**0.000**
Site x *Fucus* cover	7.89	2	3.94	0.18	0.837
Error	2372.25	107	22.17		
Growth *M. edulis*					
Fucus cover (present - absent)	12.34	1	12.34	4.47	**0.04**
Error	96.74	35	2.76		
Condition index *C. gigas*					
Site (KH I, KH II, KH III)	4.97	2	2.49	256.62	**0.000**
Fucus cover (present - absent)	0.03	1	0.03	3.53	0.063
Site x *Fucus* cover	0.02	2	0.01	0.82	0.441
Error	1.04	107	0.01		
Condition index *M. edulis*					
Fucus cover (present - absent)	0.19	1	0.19	17.28	**0.000**
Error	0.39	35	0.01		

3.3.3 Barnacle cover

Fouling barnacles had no effect on growth of juvenile and adult oysters (Fig. 10).



	df	MS	F	p
Oyster age group	1		12.56	**0.001**
Barnacles (present- absent)	1	26.30	0.23	0.636
Size x Barnacles	1	304.93	2.65	0.113
Error	31	114.94		

Fig. 10 Growth of juvenile and adult *C. gigas* with and without barnacle cover on the shells (mean + SE, n = 6-13) from 1 June 2003 to 8 October 2003. Inset: Results of ANOVA

4 Discussion

This study was conducted to detect differential performance in survival and growth of the invading oysters compared to the native mussels in order to predict to what extend the former might displace the latter. My data demonstrate that juvenile *Crassostrea gigas* have high survival and growth rates independent of substrate and tidal height. Growth was not affected by barnacle epigrowth but was enhanced underneath a cover of brown macroalgae *Fucus vesiculosus*. Performance of mussels was more variable. Growth was higher on a sand flat compared to mussels and oysters as substrate and higher in the subtidal than in the intertidal zone. *Fucus* cover enhanced length increment but reduced condition. The high survival of juvenile and adult oysters - the latter has been shown in a previous study (Diederich et al., in press) - may compensate for years with low recruitment and may facilitate a further increase in abundance and range. As the oysters grow faster and reach a larger size than the native mussels, they might have a competitive advantage over the mussels and might displace them to less favourable habitats. The survival and growth of both species is discussed in the corresponding order.

4.1 Survival

Approximately 70% of juvenile *C. gigas* survived the first three months on the mussel bed, and about 40% reached their first reproductive period in the summer one year after settlement. Survival was independent of tidal height, i.e. intertidal or shallow subtidal mussel bed area, and substrate, i.e. oyster or mussel bed. However, recruitment was much lower in the subtidal compared to the intertidal zone and on the mussel substrate compared to the oyster substrate (see also Diederich in press), which leads to the conclusion that recruitment patterns and not post-settlement mortality may determine the distribution of the population regarding tidal height and substrate. In comparison, the native mussels are known to be limited by predation pressure in the subtidal zone (Ebling et al. 1964, Seed 1993, Saier 2001).

The mortality rates found for *C. gigas* in this study (0.004 d^{-1} during the first three months post-settlement and 0.005 d^{-1} during the first winter) are very low compared to mortality rates of other juvenile bivalves in the Wadden Sea (e.g. Strasser 2002). For example, daily mortality rates for *Macoma balthica* of 0.034 d^{-1} to 0.093 d^{-1} and for *Cerastoderma edule* and *Mya arenaria* of 0.056 d^{-1} were described for the first three months after settlement (van der Veer et al. 1994 and references therein). From mussel populations in England annual mortality rates of 1st year mussels of 95 - 100% have been described and only few mussels survived beyond their second or third year (Dare 1976).

Over-winter survival of oysters varied widely between the two winters investigated. During the winter of 2001/2002 more than 90% of the 0-group juveniles survived until the following spring, but during the next winter of 2002/2003 only about 25% survived. It is notable that the first winter was very mild with only one day of freezing air temperatures accompanied by offshore winds that lead to prolonged emersion times. In the second winter, however, low air and water temperatures caused by a cold spell of 37 days with freezing air temperatures together with prolonged offshore winds (data from the local weather station of the German Weather Service), may have caused the high mortality of juvenile oysters. However, adult oysters seem not to be affected by cold winters. Data of length-frequency distributions revealed that oysters above one year of age experienced no detectable mortality during the next five years including the winter of 2002/2003 (Diederich et al. in press). This is in accordance with a study from Reise (1998) who found that about 66% of the oyster population in List tidal basin survived the anomalous severe winter of 1995/1996 with over 60 days of freezing air temperatures and formation of ice flows.

Also, the native mussels in the Wadden Sea seem to be very tolerant of freezing temperatures (Beukema 1990, Strasser et al. 2001). However, ice scouring as well as storm events can severely damage intertidal mussel beds (Nehls & Thiel 1993, Obert & Michaelis 1991, Strasser et al. 2001). The destruction of mussel beds by storms or ice scouring could be a reason for lower abundances of juvenile oysters after a severe winter. Young oysters together with mussels will be more easily scraped off the ground than larger oysters that are partly stuck in the sediment or that form solid reef structures. However, there is no evidence whether the oysters in this study died or were simply washed to other locations by storms or ice. Nevertheless, it can be assumed that the newly developed oyster reefs are more resistant to ice and storms than the native mussel beds, because the oysters form more solid structures by cementing their heavy and thick shells to each other (Fig. 11).

Survival of juvenile and adult *C. gigas* on intertidal and subtidal mussel beds in the Wadden Sea is very high compared to survival rates of other bivalves, including mussels. As high recruitment events that lead to a rejuvenation of the population occur only sporadic in oysters as well as in mussels (Strasser et al. 2001, Diederich et al. in press), high survival is important to ensure the persistence of the population and might permit population growth even if numbers of recruits are low.

4.2 Size and growth

Juvenile oysters reached a mean shell length of 35 - 53 mm after one year and of 68 - 82 mm after two years on intertidal mussel beds in the northern Wadden Sea. A mean growth rate of approximately 7 mm of shell length per month (maximum growth rate: 9.6 mm per month) was obtained during their first growing season that lasts from April to October. During the next growing season in the 2nd year, the growth rate was with 3 - 5 mm per month considerably lower. A comparison of the growth performance of *C. gigas* in different geographical regions reveals that in the Wadden Sea growth rates are somewhat lower compared to other areas (Table 5). However, growth is only slightly lower than in the native habitat (Japan and Korea). The oysters also do reach their maximum length of about 300 mm that has been described for other areas (Dinamani 1971, Quayle 1988, Dankers et al. 2004). Therefore it can be concluded that growth performance in the Wadden Sea is unlikely to hamper the spread of Pacific oysters in the Wadden Sea.

Table 5 Growth of *C. gigas* at different geographical locations as indicated in literature

Location	Tide level	Length at time after settlement		Reference
Japan	intertidal	60 mm 90 mm	(1 year) (1.5 years)	Kobayashi et al. 1997
Korea	subtidal	70 mm	(1 - 1.5 years)	Hyun et al. 2001
New Zealand	intertidal	80 - 100 mm	(1 year)	Dinamani 1971
	intertidal	60 mm	(1 year)	Dinamani 1991
British Columbia	subtidal	90 mm	(1 year)	Quayle 1988
	subtidal	60 - 100 mm 70 - 110 mm	(1 year) (2 years)	Brown and Hartwick 1988
California	intertidal	100 mm	(2 years)	Chew 1979
Mexico	intertidal	90 mm	(1 year)	García-Esquivel et al. 2000
Dutch Wadden Sea	intertidal	30 - 100 mm 130 mm	(1 year) (2 years)	Dankers et al. 2004
	intertidal	30 - 40 mm 60 mm 70 mm	(1 year) (2 years) (3 years)	Tydeman et al. 2002
North. Wadden Sea	intertidal	40 - 50 mm 70 - 80 mm	(1 year) (2 years)	this study

Growth of mussels on intertidal mussel beds in the Wadden Sea is well documented, including the sites of this study; juveniles reach about 10 - 30 mm shell length after one year, 30 - 40 mm after two years, and they approach their maximum size of 50 - 70 mm after three to four years (Buschbaum & Saier 2001, Nehls 2003). In the subtidal, mussels grow to about 20 mm in one year and they reach 55 - 60 mm after 2.5 years (Dankers & Zuidema 1995). The size differences in mussels and oysters are obvious, with oysters attaining about three times the length of mussels after one year. An advantage of the larger size could be a possible competitive advantage if food competition occurs on the densely packed mussel bed. Local food depletion may occur immediately above mussel beds when populations of suspension feeders occur at great densities or when currents are too low to replenish the food (Dame et al. 1984, Fréchette et al. 1989, Peterson & Black 1991). The filtration rate of large mussels (5 - 7 cm shell length) is with 70 l day^{-1} (Davenport & Woolmington 1982), much lower than of medium-sized oysters (9 - 10 cm shell length) which reach a filtration rate of 30 l h^{-1} (Quayle 1988). A comparison of filtration rates of similar-sized *C. gigas* and *M. edulis* revealed that filtration rates of *C. gigas* are two to three folds higher (Walne 1972). However, a different feeding behaviour and possibly also different food sources utilised by *C. gigas* and *M. edulis* lead to the assumption that mussels and oysters may not necessarily be strong competitors (Bougrier et al. 1997, Riera et al. 2002). Whether or not the oysters and mussels in the Wadden Sea are direct food competitors will need further study, as it is difficult to transfer physiological studies from laboratory experiments to the actual field situation. Nevertheless, the faster growth rate may enable the oysters to grow into a size refuge from predation much earlier than the native mussels. Most benthic predators are described as size-selective feeders that preferentially prey on food items that promise optimal energy gain (Elner & Hughes 1978, Hughes 1979). For example, mussels attain a size refuge from starfish predation when they reach a length of 35 mm (O’Neill et al. 1983, Reusch & Chapman 1997) and shore crabs seldom feed on mussels above 20 mm shell length (Ebling et al. 1964, Dare & Edwards 1976). The only predators that feed on larger mussels are shorebirds like oystercatchers and eider ducks (Goss-Custard et al. 1981, Zwarts & Drent 1981). However, it is unlikely that they will be able to feed on large oysters especially once the oysters are interconnected in solid reefs. Therefore, I conclude that *C. gigas* will have a competitive advantage over *M. edulis* because of faster growth and larger size.

4.3 Factors affecting growth

4.3.1 Substrate

Growth of juvenile *C. gigas* was not affected by substrate, i.e. sand flat, mussel bed, experimental mussel and oyster plot. Mussels on the other hand showed significantly higher growth rates on the sand flat compared to all other locations. This could be a hint towards density dependent growth in mussels but not in oysters. That mussel growth may be reduced due to intraspecific competition has been described before, one reason being that juveniles amongst the byssus of larger mussels are unable to compete successfully for food (Dare & Edwards 1976, Kautsky 1982, Bertness & Grosholz 1985, Okamura 1986). However, also for oysters reduced growth in the presence of intra- or interspecific competitors has been described (Zajac et al. 1989, Arakawa 1990, Rheault & Rice 1996). On the other hand, oyster reefs with a high profile have been described as bearing ideal conditions for oyster growth, because of high current velocities caused by the reef structure that counteract food depletion in boundary layers and smothering through sedimentation (Peterson & Black 1987, Fréchette et al. 1989, Lam & Wang 1990). Bearing in mind that the oysters show a higher filtration rate than mussels of similar size (Walne 1972), it is likely that the inferior mussels are more affected by competition than the oysters and are therefore growing faster on the sand flat compared to mussel or oyster beds.

4.3.2 Tide level

Mussel growth was strongly affected by emergence time with significantly higher growth rates in subtidal than in intertidal zones on both sand flat and mussel bed. Oyster growth, on the other hand, was only on the sand flat higher in the subtidal than in the intertidal zone. On the mussel bed, no significant effect of emergence time on oyster growth occurred. Lower growth rates in intertidal compared to subtidal zones is a well known phenomenon in mussels (Seed 1969, Bertness & Grosholz 1985, Buschbaum & Saier 2001), and is seen as a consequence of reduced feeding times (Peterson & Black 1987) or metabolic stress due to anaerobiosis (Widdows & Shick 1985, De Zwaan & Mathieu 1992). Growth of *C. gigas* seems to be less affected by emergence time. Roegner and Mann (1995) describe no effect of exposure on oyster growth as long as the aerial exposure stays below 25% as in the study at hand. Another study found reduced growth in the intertidal (20% exposure during a tidal cycle) only during the first month after settlement, but not thereafter (Crosby et al. 1991). Hydrodynamic factors that may enhance the food supply on the shore due to resuspension of orgainc matter are considered to compensate for reduced feeding times in the intertidal (Bayne et al. 1988). In conclusion it may be assumed that emergence time has a stronger effect on mussels than on oysters. This may hint towards oysters having a broader physiological niche.

4.3.3 *Fucus* cover

Fucus cover on intertidal mussel beds significantly enhanced shell growth of both, mussels and oysters. However, condition indices of both species were lower underneath *Fucus* cover, but this effect was significant only for mussels. This shows that the enhanced shell growth was not accompanied by a corresponding increase in meat content and that this effect was stronger in mussels than in oysters, indicating that oysters may benefit from *Fucus* cover, whereas mussels might be negatively influenced.

The enhanced shell growth underneath *Fucus* canopy compared to uncovered mussel bed patches is surprising, because the algal canopy leads to higher sedimentation due to reduced current velocities (Albrecht & Reise 1994), which is known to be disadvantageous for shellfish growth (Loosanoff & Tommers 1948, Widdows et al. 1979, Barillé et al. 1997). On the other hand, the modified flow regimes caused by the *Fucus* canopy may lead to accumulation of food (Leonard 1999) and thereby promote growth. However, the shape of *M. edulis* and *C. gigas* is known to vary with environmental factors such as density and type of substrate on which they are growing (Seed 1968, Quayle 1988). On very soft ground, like it occurs on mussel beds underneath *Fucus* canopy, oysters grow longer and narrower, possibly because they want to escape suffocation in mud. But as shell width also showed a higher increase underneath *Fucus* cover, the higher growth rate underneath *Fucus* canopy cannot be sufficiently explained by an elongated shape. Additionally, during the experiment on site KH III where growth of *C. gigas* and *M. edulis* in relation to *Fucus* cover were compared, oysters and mussels were kept in mesh cages above the surface and were therefore prevented from sinking into the mud. In conclusion, the lower condition index of *Fucus* covered mussels is a hint that *Fucus* interferes with mussel performance, while *C. gigas* is less affected or may even benefit from the algal cover.

4.3.4 Barnacle epigrowth

Whereas growth of *C. gigas* was not affected by barnacle cover (this study), mussel growth is significantly reduced by barnacle epigrowth (Buschbaum & Saier 2001). The reason for lower mussel growth is considered to be not food competition but changed hydrodynamic conditions and modified microcurrents due to the barnacle shells (Buschbaum & Saier 2001). As oyster shells are undulated and much rougher than mussel shells, it is likely that barnacle epigrowth on oyster shells will not change hydrodynamic conditions in the same way as on the smooth mussel shells. Another possible reason for reduced mussel growth is a drag-induced trade-off effect caused by epigrowth, because mussels with epibionts have a greater surface area and are more vulnerable to being washed away by currents. Therefore, the mussels need to invest more energy in byssus thread production (Price 1983, Okamura 1986). As the oysters do not produce byssus but attach themselves very firmly to hard substrates and to each other by releasing cement from a food gland, this would explain why mussels are affected by barnacles and oysters are not. Further, the much larger size of oysters relative to barnacles than the size ratio of mussels to barnacles may render epigrowth of barnacles as insignificant to the oyster. In conclusion, the very common and widespread barnacle fouling on mussels and oysters may interfere with mussel growth while oysters remain unaffected.

5 Conclusion

The persistence and further increase of the oyster population in the Wadden Sea will be facilitated by high survival rates in juveniles and adults, because this may compensate for years with low recruitment. The settlement preference of *C. gigas* for conspecifics in the intertidal zone (Diederich in press) leads at present to the formation of massive oyster reefs that are expected to be more resistant to environmental stress like storms and ice scouring than the native mussel beds, which they replace (Fig. 11). In addition, high growth rates independent of tide level, substrate, *Fucus* cover and barnacle epigrowth, contribute a wide niche. The faster growth of invading oysters compared to native mussels might give them a competitive advantage if food and/or space is limiting. Therefore it can be concluded that the recent massive increase of *C. gigas* in the northern Wadden Sea following high recruitment during three consecutive anomalously warm summers (Diederich et al. in press), and a positive feedback of adult oysters on settlement (Diederich in press) is likely to lead to a permanent transformation in the benthic community of this area.

Fig. 11 Resident mussel bed (*Mytilus edulis*) and non-native oyster reef (*Crassostrea gigas*) in the northern Wadden Sea in summer 2004. Inset: start of oyster reef formation. Photos: K. Reise, S. Diederich

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Chapter 5

Pacific oysters *Crassostrea gigas* in the Wadden Sea: invasion facilitated by weak predation?

Abstract

In the Wadden Sea (North Sea), bivalve populations are often limited by benthic predation, with shore crabs *Carcinus maenas* and starfish *Asterias rubens* being important predators. Introduced Pacific oysters *Crassostrea gigas* recently increased in abundance and range, overgrowing resident epibenthic mussel beds *Mytilus edulis*. Even though recruitment success of *C. gigas* is confined to years with particularly high summer water temperatures, high survival rates of juveniles and adults compensate for years with low recruitment. Using predator exclusion experiments and laboratory feeding preference trials, I tested the hypothesis that *C. gigas* is subjected to low predation pressure because the main benthic predators prefer mussels to oysters. Predation was only found to affect oyster recruitment in the subtidal, but not subsequent survival in either intertidal or subtidal locations. Juvenile and adult shore crabs and starfish strongly preferred mussels to oysters in feeding trials. It is concluded that the invasion success of *C. gigas* is supported by (1) selective feeding by the main mussel predators, (2) a possible mismatch between oyster recruitment and predator abundances and (3) a larger size and faster growth of oysters compared to native mussels that may facilitate an early size refuge from predation. The competitive advantage of *C. gigas* over *M. edulis* may lead to a permanent displacement of mussels and to a shift in the food web of the Wadden Sea.

Keywords

Introduced species, Predation, Size refuge, Competitive advantage, Mussel beds

1 Introduction

Predation may have a profound impact on structuring marine benthic communities (Reise 1985a, b, Seed 1993, Hunt & Scheibling 1997). By keeping their prey below carrying capacity, predators may allow coexistence of competing species and thus prevent monopolization by a dominant species (Paine 1974). This steady state may be threatened by invaders if these escape predation pressure by resident predators and become superabundant (Keane & Crawley 2002, Colautti et al. 2004).

Pacific oysters *Crassostrea gigas* have been introduced to the Wadden Sea by aquaculture in the 1980s (Reise 1998). They reproduced naturally and recently started to increase dramatically in abundance and range (Dankers et al. 2004, Smaal et al. 2004, Diederich et al. in press). As they need hard substrates for settlement, they are overgrowing shell beds as well as resident epibenthic mussel beds *Mytilus edulis*, thus posing a threat to this native species. Mussel beds are characterized by a high productivity (Asmus 1987, Dankers & Zuidema 1995) and biodiversity (Riesen & Reise 1982, Tsuchiya & Nishihira 1986, Dittmann 1990), which makes them important food resources for various crustaceans, fish, birds, and humans (Seed & Suchanek 1992). Their overgrowth and possible replacement by oyster reefs may therefore have a profound impact on the benthic community of the coastal North Sea.

As recruitment success of *C. gigas* in the northern Wadden Sea is confined to a few years with exceptionally high summer water temperatures, the high survival rates of juveniles and adults that have been found in a previous study are important prerequisites for the invasion success, because they compensate for recruitment failures (Diederich et al. in press, Diederich submitted). The question arose, whether a lack of predation may cause the high survival rates and may facilitate the invasion process by giving *C. gigas* a competitive advantage over its native congener.

Mussel populations in the Wadden Sea are often limited by predation and depend on high recruitment success in years when predator abundances are low, usually following severe winters (Beukema 1991, Strasser et al. 2001, Strasser 2002). Especially epibenthic predators like shore crabs *Carcinus maenas* and starfish *Asterias rubens* have profound impacts on the density and distribution of mussels (Scherer & Reise 1981, Jensen & Jensen 1985, Dankers & Zuidema 1995, Kristensen & Lassen 1997, Saier 2001). Even though shrimps *Crangon crangon* and various fish species like gobies *Pomatoschistus microps*, flounders *Platichthys flesus* and plaice *Pleuronectes platessa* are known to prey on juvenile bivalves, their impact is considered to be low (Reise 1977, Jensen & Jensen 1985). Birds like eiders *Somateria mollissima*, oystercatchers *Haematopus ostralegus* and herring gulls *Larus argentatus* may intensively prey on medium to large sized mussels (Zwarts & Drent 1981, Hilgerloh et al. 1997, Nehls et al. 1997). However, under the premise that population dynamics are largely determined by survival of juveniles, the impact of birds seems to be low compared to benthic predators (Reise 1985b). Thus, in this study the focus will be on predation by shore crabs and starfish, because they are abundant and voracious mussel consumers in the Wadden Sea and are known to feed on oysters on other shores (e. g. Parsons 1974, Walne & Davies 1977, Chew 1998).

Predator exclusion experiments were conducted on intertidal and subtidal mussel beds in order to assess the impact of benthic predation on recruitment and survival of juvenile *C. gigas*. Laboratory feeding preference experiments with different sized *C. maenas* and *A. rubens* were added to show whether species and size selective predation preferences may explain the high survival rate of juvenile *C. gigas*. In this respect the possible advantage of faster growth and larger size of an introduced species compared to a native congener is discussed in view of size refuge from predation and missing predators in the recipient ecosystem.

2 Material and methods

2.1 Study site

Field experiments on survival of juvenile *Crassostrea gigas* were carried out in the List tidal basin in the northern Wadden Sea (North Sea, Germany, 54°50’ - 55°10’N and 08°20’ - 08°40’E). This shallow basin (404 km² area) is surrounded by the mainland and two islands (Sylt and Rømø) that are connected with the mainland by dams. Intertidal sand flats, seagrass meadows, and natural epibenthic mussel beds characterize the area. Tides are semidiurnal and the mean tidal range is 2 m; the average salinity is close to 30 psu. Primary production is about 300 g C m^{-2} y^{-1}. Monthly mean water temperatures range from 18.2°C in August to 2.3°C in February. Detailed information on hydrography, geology, sediments and biota of the bay is given in Gätje and Reise (1998). A commercial oyster farm that produces about two million oysters per annum has been in operation in this basin since 1986.

2.2 Predator exclusion experiments

Three separate predator exclusion experiments were conducted in order to assess the impact of benthic predation on recruitment and survival of juvenile *C. gigas* on intertidal and subtidal mussel beds. The first experiment, designed to test whether predation may limit early recruitment of *C. gigas*, was carried out from 31 July to 15 September 2003, which is the settlement period of oysters in this area. Shell collectors made from eight clean (i.e. with no epigrowth) dead oyster shells (mean shell length ± SD: 87.7 ± 7.9 mm) that were strung on a plastic covered line were used as attachment surfaces for oyster larvae. The experimental design included full cages to exclude all possible predators, partial cages to control for potential cage artefacts and shell collectors without any protection (Fig. 1).

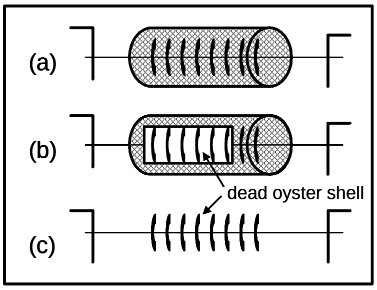

Fig. 1 Schematic diagram of the experimental set-up used in the predator exclusion experiments: (a) shell collector protected by a full cage, (b) shell collector with partial cage and (c) shell collector without cage

Although partial cages cannot control for all possible artefacts of caging, they were employed in consideration of known artefacts such as changes in light, hydrodynamics and attractiveness for predators that may influence settlement and survival (e.g. Connell 1997). To achieve full protection, shell collectors were placed separately in cylindrical cages (250 mm long, 125 mm diameter) made from plastic rings and gauze (1 mm mesh opening). Partial cages were constructed in the same way, but two holes (70 × 15 mm) were cut into the gauze at opposite sides. Shell collector lines without a cage around them were used as control treatments. All experimental units (six replicates for each treatment and two tidal levels) were pinned with iron bars horizontally on intertidal and subtidal parts of a natural mussel bed so that the shells touched the mussels beneath. The intertidal location had an exposure time of about 2 h per tide and the subtidal location was located 0.5 - 1 m below the surface level at low tide. At the end of the experimental period, all collectors were brought back to the laboratory and attached juvenile oysters were counted and shell length (largest diameter of the shell) was measured with electronic vernier callipers accurate to 0.1 mm. Analysis of variance (ANOVA) followed by Tukey’s HSD test was used to compare abundances of recruits on the shell collectors in relation to tidal level and cage protection. Data on shell length of recruits were compared using non-parametric tests (Kruskal-Wallis-ANOVA) because of a failure to satisfy the heterogeneity of variances assumption. Effects were considered to be statistically significant if p-value was < 0.05.

The survival of juvenile *C. gigas* was investigated on a subtidal mussel bed from 10 October 2003 (which is about 1 - 2 months after settlement) until 19 March 2004. The experimental setup consisted of full and partial cages and no protection controls as described above. The same cages and no cage setups were used (eight replicates), but only two dead oyster shells with two juvenile *C. gigas* attached to each shell were strung on the line. The oysters had an initial shell length of 2 - 12 mm (on each shell there was one juvenile oyster with 2 - 6 mm shell length and one with 6 - 12 mm). At the end of the experimental period all remaining oysters were counted and measured and the length increment of individual oysters was determined.

A third caging experiment was conducted in order to assess survival of juvenile *C. gigas* on an intertidal mussel bed during the first three to four months after settlement. This time frame was used because *Carcinus maenas*, which is one of the most common predators that may prey on juvenile *C. gigas* in the intertidal, is only present in this area from spring to fall (Reise 1977). Thus, it was not necessary to extend this experiment over the winter period. The experimental setup was similar to the one described above, consisting of full cages, partial cages and no cage replicates, but the cages differed somewhat. Dead oyster shells with 1 - 3 attached juvenile *C. gigas* were screwed on wooden boards (150 × 100 mm), which were fixed on an intertidal mussel bed with iron bars. On 20 of these boards, cylindrical mesh cages were mounted (80 mm height, 100 mm diameter, 5 mm mesh opening). On another 20 boards the same cages were mounted, but these had two openings (70 × 40 mm) cut into opposite sides of each cage. Altogether 60 experimental units were deployed on an intertidal mussel bed from 11 September to 12 December 2002 when the remaining juvenile *C. gigas* were counted and measured. Data for abundance, length and growth of juvenile *C. gigas* were analysed using ANOVA.

2.3 Length – meat weight relationship for *Crassostrea gigas* and *Mytilus edulis*

The relationship between shell length and meat dry weight was established for *C. gigas* and *M. edulis* in order to assess whether shell length would be an appropriate parameter to be used in feeding preference experiments. Shell length and dry meat weight of 83 oysters (shell length: 24 - 160 mm) and 109 mussels (shell length: 20 - 71 mm) was obtained from bivalves collected on two different mussel beds in May 2002. For dry weight determination, the oysters and mussels were stored in a deep freezer at –20°C for several days. The bivalves were then cooked in seawater for 4 minutes. Afterwards meat and shell of the individuals were separated and dried to constant weight at 80°C (6 - 7 days). After cooling in an exsiccator meat and shell were weighed separately on a torsion balance accurate to 0.01 g. An exponential relationship between meat dry weight and length was established (Fig. 2). For bivalves from 20 to 40 mm shell length there was no difference in meat content in relation to shell length. For larger bivalves, however, meat content was higher in *C. gigas* than in *M. edulis* of similar size.

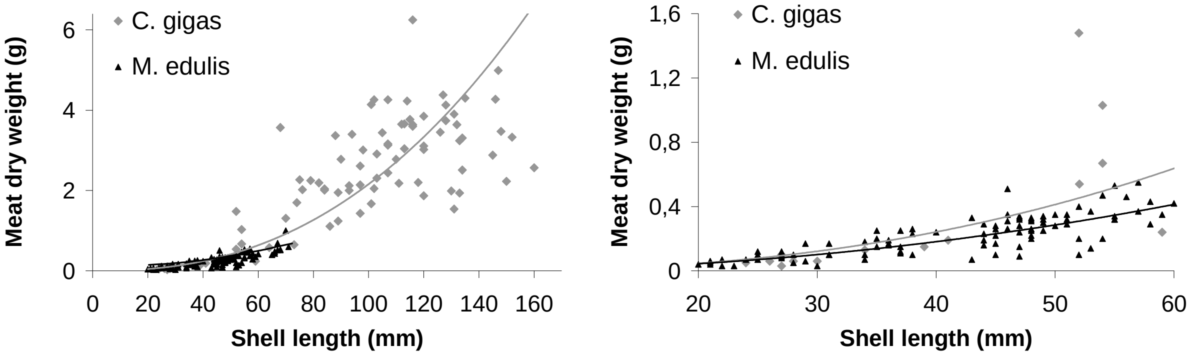

Fig. 2 Meat dry weight of *C. gigas* and *M. edulis* in relation to shell length (left) and enlargement of the 20 - 60 mm shell length section (right). Equations for regression lines are: *C. gigas* $y = 0.00004x^{2.387}$, $R^2 = 0.834$, $n = 83$; *M. edulis* $y = 0.0001x^{2.028}$, $R^2 = 0.750$, $n = 109$ with y = meat dry weight (g) and x = shell length (mm)

2.4 Feeding preference experiments

Laboratory feeding preference experiments with different sized *Carcinus maenas* (13 - 73 mm carapax width, the latter is about the maximum size of *C. maenas* in this area) were carried out in July 1999, June 2002 and September 2003. For each set of experiments, crabs were collected by hand on intertidal mussel beds in the List tidal basin and kept in an indoor aquarium tank (1000 l) with running seawater (ambient water temperature; in July and August approximately 18°C) prior to experiments. Only undamaged crabs free of parasite *Sacculina carcini* infestations were selected. Prey items, i.e. *Mytilus edulis* and *Crassostrea gigas* of different size classes, were collected on the same intertidal mussel beds. All bivalves were measured with vernier callipers to the nearest millimetre (shell length = largest diameter of the shell) and cleaned from epigrowth with an iron scraper to avoid confounding artefacts, because epibionts may alter predator preferences (see Enderlein et al. 2003). For the same reason, only oysters attached to dead shell material were used in the feeding trials.

Table 1 *Carcinus maenas*. Laboratory feeding preference experiments with different sized shore crabs which were offered different sizes of *Crassostrea gigas* and *Mytilus edulis* as prey. f = female, m = male, n = number of replicates (each *C. maenas* is one replicate), Cra = *Crassostrea*, Myt = *Mytilus*. Consumed bivalves = bivalves consumed crab^{-1} day^{-1} divided by bivalves offered crab^{-1} day^{-1}

Trial	Carapax width (mm)	Sex	n	Time (days)	No. and size of prey (mm length)	Consumed *C. gigas* (% ± SE)	Consumed *M. edulis* (% ± SE)
a	13 - 17	f	3	2	2 Cra (6-8)	0	
					2 Myt (6-8)		66.7 ± 0.0
b	23 - 25	m	4	2	2 Cra (6-8)	0	
					2 Myt (6-8)		100.0 ± 0.0
c	34 - 42	m	13	14	4 Cra (10-30)	5.8 ± 0.8	
					4 Myt (10-30)		57.6 ± 1.7
d	47 - 50	m	10	14	4 Cra (20-30)	1.6 ± 0.9	
					4 Myt (20-30)		56.4 ± 2.8
e	61 - 69	m	8	16	5 Cra (30-40)	2.7 ± 0.8	
					5 Myt (30-40)		15.0 ± 1.9
f	10 - 15	f	6	2	2 Cra (3-5)	8.3 ± 8.3	
					2 Cra (6-8)	0	
					2 Cra (9-11)	4.2 ± 4.2	
					2 Myt (3-5)		62.5 ± 4.2
					3 Myt (6-8)		69.4 ± 8.3
					3 Myt (9-11)		8.3 ± 2.8
g	20 - 25	m	6	2	2 Cra (3-5)	0	
					2 Cra (6-8)	0	
					2 Cra (9-11)	0	
					2 Myt (3-5)		100.0 ± 0.0
					3 Myt (6-8)		100.0 ± 0.0
					3 Myt (9-11)		91.7 ± 2.8
h	20 - 25	m	5	3	2 Cra (4-6)	26.7 ± 3.3	
					2 Cra (6-8)	20.0 ± 0.0	
					2 Myt (4-6)		100.0 ± 0.0
					2 Myt (6-8)		90.0 ± 5.8
					2 Myt (8-10)		73.3 ± 13.3
i	60 - 73	m	10	16	1 Cra (20-30)	18.8 ± 4.1	
					1 Cra (35-40)	6.3 ± 2.2	
					1 Myt (20-30)		98.8 ± 0.9
					1 Myt (35-40)		23.1 ± 3.4

At the start of each experiment, crabs were placed separately in 25 × 15 × 17 cm aquaria filled with aerated seawater (5 l, circa 18 - 20°C), a sand layer and a *Fucus* cluster to provide shelter from visual stress. Carapax width of *C. maenas* was measured with vernier callipers to the nearest millimetre. After starving the crabs for 4 days to standardize hunger levels, mussels and oysters of different sizes were added. Each day of the experimental periods, which lasted between 2 and 16 days, the water inside the aquaria was changed and the number and size of consumed mussels and oysters was noted (see Table 1 for experimental set-up).

Subsequently, all eaten bivalves were replaced by bivalves of the same species and size. Results are expressed as mean number of consumed bivalves per crab per day divided by the number of bivalves of the respective species offered per day:

% Consumed = No. of consumed bivalves crab^{-1} day^{-1} / No. of offered bivalves crab^{-1} day^{-1}.

This method of data presentation was chosen, because prey choice was the focus of this investigation and not absolute numbers of bivalves that are consumed by *C. maenas*.

Prey choice experiments with different sized *Asterias rubens* (14 - 151 mm arm length, the latter being the largest starfish size class present in this area) were conducted in August and September 1999, in June 2002 and in September and October 2003 in similar experimental set-ups as described above. All starfish used in the experiments were fished with a traditional oyster dredge from subtidal habitats in the List tidal basin and only undamaged individuals were selected. Mean arm length of each *A. rubens* was determined by measuring the distance from the tip of each arm to the mouth opening with vernier callipers to the nearest millimetre. Mussels and oysters used as prey items were collected on intertidal mussel beds, cleaned from all epigrowth and stored in an indoor tank (1000 l) with running aerated seawater. Each starfish was placed in a separate aquarium (size of aquaria depending on starfish size: 30, 60, and 110 l) with running aerated seawater (circa 18°C) and was offered a choice of sets of large and small *M. edulis* and *C. gigas* of similar size (see Table 2 for experimental set-up). Number and size of prey items consumed was recorded daily and every bivalve eaten was replaced with an individual of the same species and size. Experiments lasted from 1 to 37 days.

From September to October 1999 an additional feeding experiment was conducted with 17 large *A. rubens* (mean arm length 103 - 130 mm) that were placed together in a 1000 l indoor tank with running aerated seawater. 100 mussels and 100 oysters (shell length of both species 30 - 60 mm) were added and number of individuals eaten was recorded every day for 2 weeks. Consumed bivalves were replaced with individuals of the same size and species. After 2 weeks, the remaining mussels were removed and for the next 37 days only oysters remained as food items. Again, numbers of individuals eaten were recorded and replaced every day.

Table 2 *Asterias rubens*. Laboratory feeding preference experiments with different sized starfish which were offered different sizes of *Crassostrea gigas* and *Mytilus edulis* as prey. n = number of replicates (each *A. rubens* is one replicate), Cra = *Crassostrea*, Myt = *Mytilus*. Consumed bivalves = bivalves consumed starfish^{-1} day^{-1} divided by bivalves offered starfish^{-1} day^{-1}

Trial	Arm length (mm)	n	Time (days)	No. and size of prey (mm length)	Consumed *C. gigas* (% ± SE)	Consumed *M. edulis* (% ± SE)
a	19 - 22	5	1	2 Cra (6-8)	20.0 ± 12.2	
				2 Myt (6-8)		60.0 ± 24.5
b	26 - 31	5	1	2 Cra (6-8)	30.0 ± 20.0	
				2 Myt (6-8)		60.0 ± 24.5
c	14 - 17	6	5	2 Cra (6-8)	25.0 ± 10.9	
				2 Cra (9-11)	18.3 ± 3.1	
				2 Myt (6-8)		41.7 ± 5.9
				2 Myt (9-11)		31.7 ± 9.6
d	23 - 28	6	5	2 Cra (6-8)	28.3 ± 8.6	
				2 Cra (9-11)	31.7 ± 4.9	
				2 Myt (6-8)		71.7 ± 4.2
				2 Myt (9-11)		86.7 ± 4.2
e	31 - 35	6	5	2 Cra (6-8)	16.7 ± 3.7	
				2 Cra (9-11)	11.7 ± 5.0	
				2 Myt (6-8)		90.0 ± 3.1
				2 Myt (9-11)		86.7 ± 4.2
f	35 - 41	6	5	2 Cra (6-8)	30.0 ± 4.2	
				2 Cra (9-11)	16.7 ± 4.6	
				2 Myt (6-8)		88.3 ± 7.3
				2 Myt (9-11)		85.0 ± 3.1
g	84 - 102	9	11	2 Cra (10-25)	1.3 ± 0.8	
				2 Cra (26-40)	2.7 ± 1.2	
				3 Myt (10-25)		38.4 ± 5.4
				3 Myt (26-40)		44.4 ± 6.3
h	122 - 151	8	37	4 Cra (40-50)	0.3 ± 0.1	
				4 Cra (50-60)	0.2 ± 0.1	
				4 Myt (40-50)		9.7 ± 1.2
				4 Myt (50-60)		2.2 ± 0.5

Data analysis of feeding preference experiments is difficult because of a lack of independence of variables and inappropriate use of controls (Peterson & Renaud 1989, Roa 1992). Solutions proposed for this problem which suggests physically pairing experimental chambers containing a predator and randomly arranged multiple food items with a control chamber containing no predator but the same food items (Prince et al. 2004) were not applicable for the experiments presented here, because the prey items would not change without a predator present and therefore a control chamber would provide no additional information. As there is no unimpeachable solution for this problem, and the results obtained during the feeding experiments were clear-cut, I refrained from statistical analysis.

3 Results

3.1 Predator exclusion experiments

Recruitment of juvenile *C. gigas* was significantly affected by tide level, cage coverage and interaction between the two factors (Fig. 3, Table 3). For the intertidal location, Tukey's HSD Test revealed significant differences only between full and partial cages, suggesting cage artefacts confounded the results. On the subtidal location, however, abundances of recruits were about three times and significantly higher on fully protected oyster shells (2.29 ± 0.33 juveniles shell^{-1}) than on unprotected (0.77 ± 0.17 juveniles shell^{-1}) and on partly protected ones (0.71 ± 0.12 juveniles shell^{-1}), suggesting a predation effect on abundance of 0-group *C. gigas*. The length of juveniles in the subtidal locations did not differ between the three treatments (mean length ± SD = 5.5 ± 1.3 mm; Kruskal-Wallis ANOVA, H (2, N = 18) = 1.73, p = 0.421), but in the intertidal cage cover had a significant influence on shell length (Kruskal-Wallis ANOVA, H(2, N = 18) = 7.45, p = 0.024).

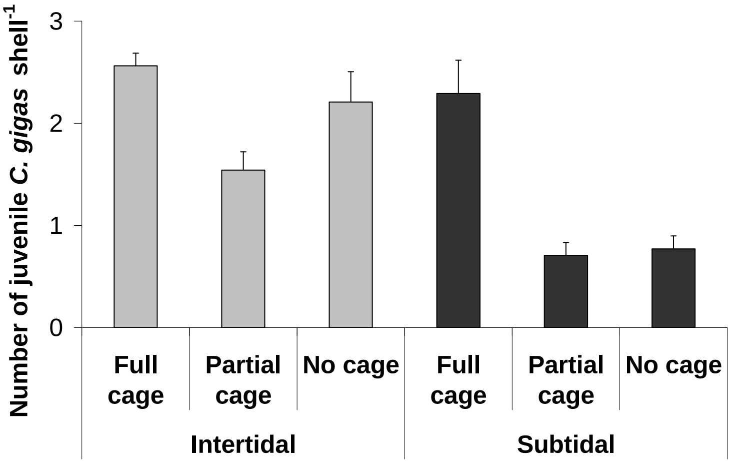

Fig. 3 *Crassostrea gigas*. Mean abundance (+ SE) of juveniles that settled on dead oyster shells with and without cage protection in intertidal and subtidal locations. Cages (n = 6) in the field from 31 July 2003 - 15 September 2003

Table 3 2-way analysis of variance (a) and Tukey's HSD Test (b) on effect of predation on abundance of juvenile *C. gigas* in intertidal and subtidal locations. Bold face values: $p < 0.05$

(a)	df	MS	*F*	p
Tide level	1	6.46	23.69	**< 0.001**
Cage	2	5.42	19.85	**< 0.001**
Tide level x Cage	2	1.02	3.74	**0.035**
Error	30	0.27		

(b)	Full cage	Partial cage	No cage
Intertidal			
Full cage		**0.022**	0.845
Partial cage	**0.022**		0.263
No cage	0.845	0.263	
Subtidal			
Full cage		**< 0.001**	**< 0.001**
Partial cage	**< 0.001**		1.000
No cage	**< 0.001**	1.000	

There was no significant difference in survival of juvenile *C. gigas* in relation to cage protection in either the intertidal or the subtidal location (Fig. 4, Table 4). In the intertidal, survival varied between 82% on shells in full cages and 61% and 59% on partly and unprotected shells, respectively. In the subtidal, 64 - 75% of juveniles survived. Length and growth of juveniles was independent of caging, in the intertidal as well as in the subtidal experiment (ANOVA).

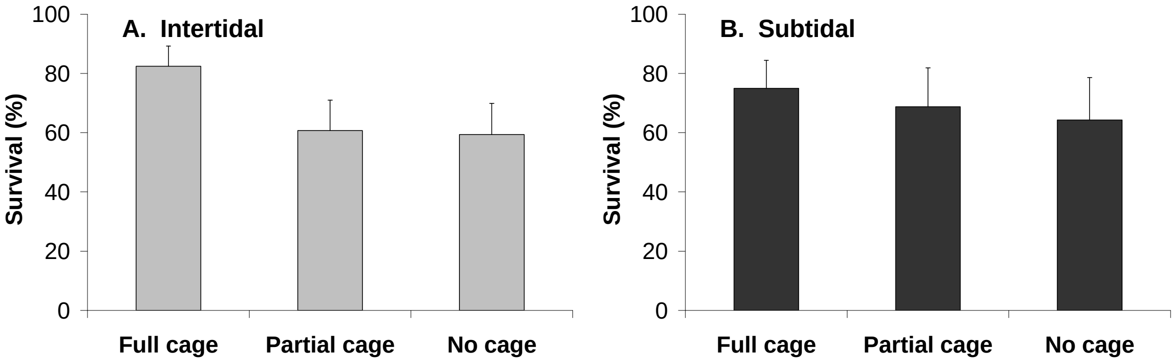

Fig. 4 *Crassostrea gigas*. Mean survival (% + SE) of 0-group juveniles on intertidal (A) and subtidal (B) mussel beds with and without cage protection. A: n = 14 -19 replicates with 1-3 juvenile oysters each; from 11 September to 12 December 2002. B: n = 8 replicates with 4 juvenile oysters each; from 10 October 2003 to 19 March 2004

Table 4 Analysis of variance (ANOVA) on effect of predation on survival of juvenile *C. gigas* in intertidal and subtidal locations

	df	MS	*F*	p
Intertidal				
Cage	2	2939.7	2.19	0.123
Error	46	1341.2		
Subtidal				
Cage	2	218.4	0.24	0.789
Error	20	912.9		

3.2 Feeding preference experiments

Prey choice experiments showed that juvenile and adult *Carcinus maenas* strongly preferred mussels to oysters (Table 1, Fig. 5). When offered different size classes of mussels and oysters, smaller individuals were preferred.

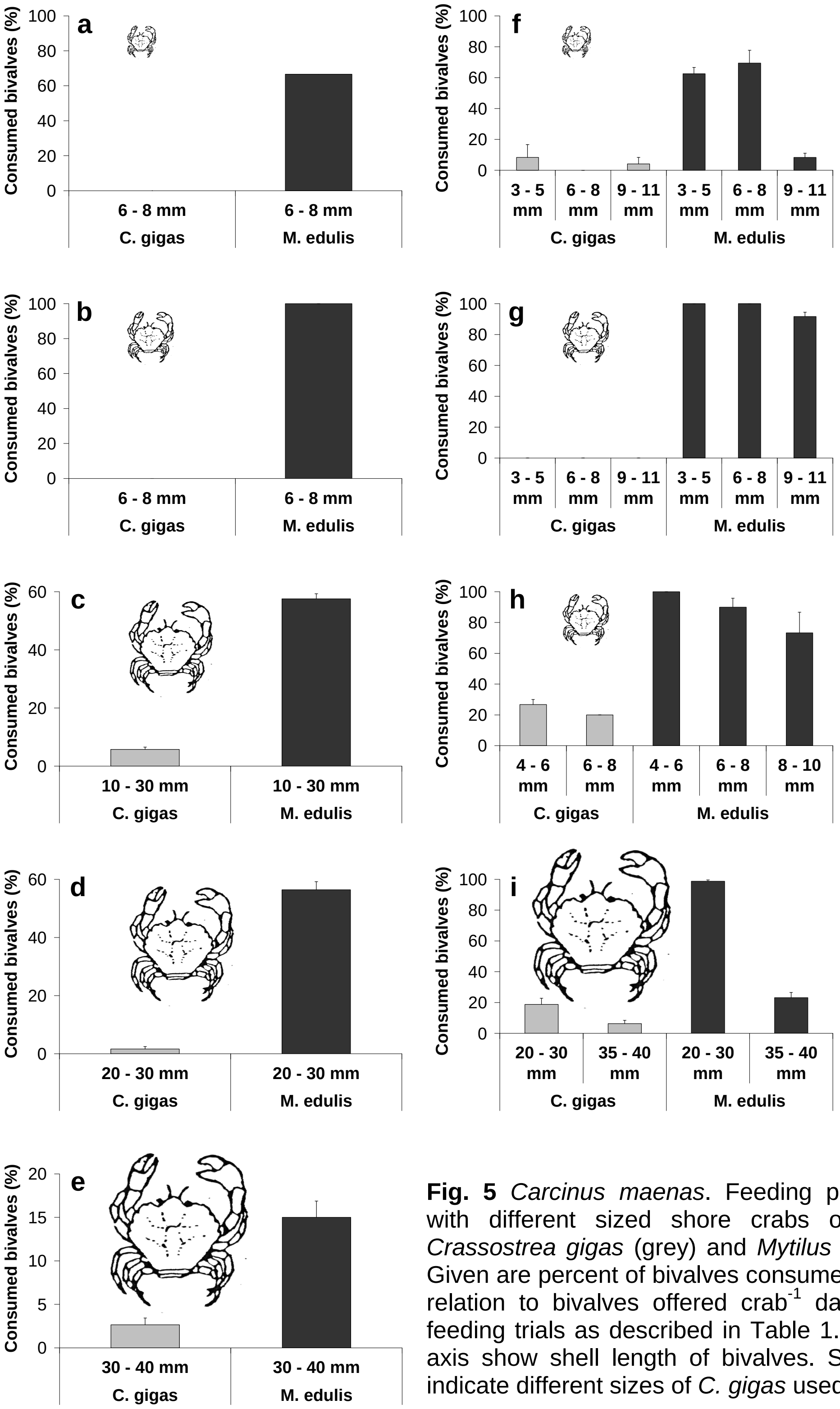

Fig. 5 *Carcinus maenas*. Feeding preference experiments with different sized shore crabs offered different sized *Crassostrea gigas* (grey) and *Mytilus edulis* (black) as prey. Given are percent of bivalves consumed crab^{-1} day^{-1} (+ SE) in relation to bivalves offered crab^{-1} day^{-1}. (a) – (i): different feeding trials as described in Table 1. Length data on the x-axis show shell length of bivalves. Sizes of crab drawings indicate different sizes of *C. gigas* used in experiments

Prey choice experiments with *Asterias rubens* showed that starfish with arm lengths greater than 20 mm strongly preferred mussels to oysters (Table 2, Fig. 6). Only one feeding trial (c) with the smallest size class of *A. rubens* (14 - 17 mm arm length) showed no clear preference for either of the prey species.

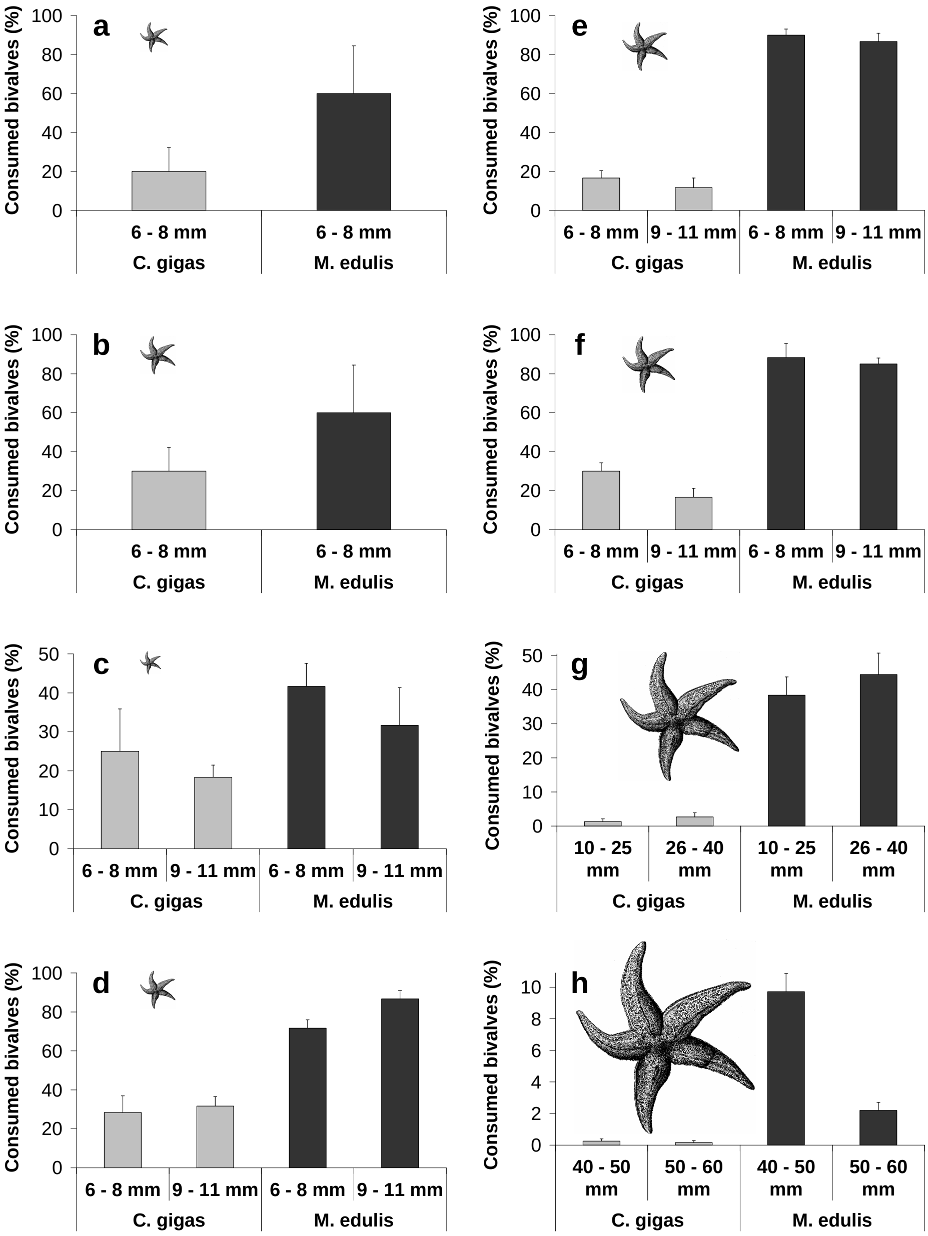

Fig. 6 *Asterias rubens*. Feeding preference experiments with different sized starfish offered different sized *Crassostrea gigas* (grey) and *Mytilus edulis* (black) as prey. Given are percent of bivalves consumed crab^{-1} day^{-1} (+ SE) in relation to bivalves offered crab^{-1} day^{-1}. (a) – (g): different feeding trials as described in Table 2. Length data on the x-axis show shell length of bivalves. Size of starfish drawings represent different sizes of *A. rubens* used in feeding trials

Large starfish with 102 - 130 mm arm length exclusively fed on *M. edulis* when given the choice between *M. edulis* and *C. gigas* for 14 days (Fig. 7). When *M. edulis* were removed and *C. gigas* remained as only prey items from day 14 on, they stopped feeding for about 2 weeks until they started to eat increasing amounts of *C. gigas* up until the end of the experiment at day 51.

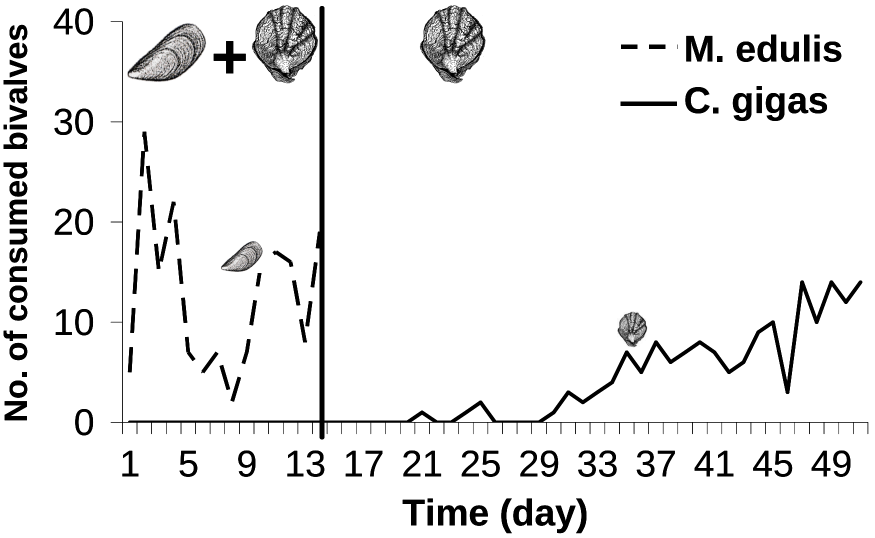

Fig. 7 *Asterias rubens*. Laboratory feeding preference experiment with 17 large starfish (102 -130 mm arm length) together in one aquarium tank. During the first 14 days 100 *Mytilus edulis* and 100 *Crassostrea gigas* (30 - 60 mm shell length) were offered as prey. Consumed bivalves were replaced every day. At day 14, mussels were removed and from then on 100 *C. gigas* were the only food items. Given is the number of consumed bivalves from day 1 to day 51

4 Discussion

This study was conducted in order to assess whether low predation pressure may explain high survival rates of introduced *Crassostrea gigas* and may facilitate a competitive advantage over resident mussels. Predator exclusion experiments revealed high survival rates of juvenile *C. gigas* and no significant mortality due to predation. Only recruitment in the subtidal might have been affected by predation pressure. In laboratory feeding preference experiments it was demonstrated that two of the main predators in this area, the shore crab *Carcinus maenas* and the starfish *Asterias rubens*, strongly preferred mussels to oysters.

4.1 Predator exclusion experiments

The experiment on predation effects on recruitment of *C. gigas* showed significant effects only subtidally, where about three times as many recruits survived in the exclusion cages than in partial and no cage treatments. In the intertidal, however, no clear results were obtained, because a significant difference occurred only between full cages and partial cages, but not between full cages and no cages. The experiments on survival of juvenile oysters during the first months after settlement revealed no differences in mortality between exclusion cages and partial and no cage treatments in the intertidal as well as in the subtidal location, suggesting predation to play a minor role for post-settlement mortality. However, caging experiments are susceptible to misinterpretation due to cage artefacts confounding the results (Connell 1985, Peterson & Black 1994, Hunt & Scheibling 1997, Anderson & Connel 1999, Strasser 2002). In most cases, it is not possible to separate effects of differential recruitment versus differential post-settlement mortality among treatments, because cages may enhance settlement that will be erroneously interpreted as lower post-settlement mortality (Keough & Downes 1982). The method of using partial cages to test for caging artefacts is not free of implications either, because the effects due to caging artefacts and due to the variable of interest could both occur to some extent within partial cages, but neither to the extent that they occur in the full cages or no cage treatments (Kennelly 1991). However, a profound knowledge of the characteristics of the species studied may help to evaluate possible artefacts. Caging, for example, often leads to changed hydrodynamic conditions that may have an influence on settlement and survival of sessile species because of sediment accumulation (Kennelly 1991, Ólafsson et al. 1994, but see also Strasser 2002). In the study at hand, no enhanced sedimentation on the oyster shells inside cages was observed that could potentially lead to lower recruitment because of smothering of settlement surfaces (Rothschild et al. 1994). Also, length and growth of juveniles was not affected by cage coverage, except for in the recruitment experiment in the intertidal location, where juveniles in the no cage treatments were significantly smaller than in the full and partial cages, supporting the assumption that this part of the experiment was confounded with cage artefacts. A possible attraction of larvae by the mesh cover seems to be unlikely, because oyster larvae settle preferentially on the shells of conspecifics (Diederich in press) and are not capable of byssus drifting (Quayle 1988). Another problem with partial cages is the fact that predators such as shore crabs seek shelter inside these cages which may lead to a higher predation effect in partial cages compared to uncaged plots rendering them useless as controls (Strasser 2002). However, in the study at hand no significant differences in oyster abundance or survival between partial cages and no cage controls occurred.

In summary, the results obtained by the predator exclusion experiments suggest that low post-settlement predation pressure might be one reason for the high survival rate of juvenile *C. gigas* in this area. This has also been observed in a previous study (Diederich submitted) where about 70% of juvenile *C. gigas* survived the first three months after settlement on an intertidal mussel bed and approximately 65% survived their first winter, independent of tide level. However, the generally lower abundances of juvenile oysters in subtidal compared to intertidal locations in this area (Diederich in press) may not only be caused by differential settlement but also by predation pressure acting directly after settlement.

4.2 Feeding preference experiments

To verify the low predation pressure acting on introduced *C. gigas*, laboratory feeding preference experiments with two of the main resident predators for juvenile bivalves were conducted. Both, *Carcinus maenas* and *Asterias rubens* strongly preferred mussels to oysters. Only juvenile starfish < 20 mm did not show a clear preference for mussels. However, it is important to note that species may behave differently in the field than under laboratory conditions. Additional food sources, predation, and competition stress may alter foraging behaviour (Lawton & Zimmer-Faust 1992). For example, juvenile starfish < 10 mm arm length strongly prefer the very abundant balanid epibionts (*Semibalanus balanoides, Balanus crenatus, Elminius modestus*) to mussels (Hancock 1955, Mertel 2002), suggesting predation pressure exerted by juvenile starfish to be low for oysters as well as for mussels in the field situation.

The feeding behaviour of *C. maenas* and *A. rubens* generally follows the optimal foraging or energy maximization premise, whereby a predator should choose its diet in order to maximize net energy intake per unit of handling or feeding time (Elner & Hughes 1978, Hughes 1979, O’Neill et al. 1983). Size-selective and species-selective feeding of shore crabs and starfish is well known. When feeding on mussels, a linear increase between crab and preferred prey size has been observed with crabs generally preferring mussels that are small enough to be easily crushed (Elner & Hughes 1978, Ameyaw-Akumfi & Hughes 1987). On the other hand, when feeding on oysters (*Ostrea edulis* and *Crassostrea gigas*), large *C. maenas* (55 - 70 mm carapax width) showed no preference for any particular size of oyster species within a range of 10 to 40 mm shell length, which might be explained by weak parts of the more irregular shell where crabs can insert their claws (Dare et al. 1983, Mascaró & Seed 2001). However, whether the crabs would invest this extra time in the field situation, when they themselves are in danger of predation, remains doubtful (see Ameyaw-Akumfi & Hughes 1987). Regarding species selective feeding, it has been shown that shore crabs seem to prefer mussels and clams to oysters, which has been attributed to the different shell morphology (Dare et al. 1983, Chew 1998, Mascaró & Seed 2001). However, crabs are able to learn handling skills that may enable them to feed more effectively on novel and larger prey (Hughes 1979, Cunningham & Hughes 1984, Kaiser et al. 1993, Hughes & O'Brian 2001). Especially if a suboptimal bivalve becomes more abundant, a switching of prey preferences may occur (Ameyaw-Akumfi & Hughes 1987).

For *A. rubens*, similar size and species-specific feeding patterns have been observed, with small starfish preferring barnacles and larger individuals showing the following preference order: mussels *Mytilus edulis* > slipper limpets *Crepidula fornicata* > oysters *Ostrea edulis* (Hancock 1955, Dolmer 1998, Saier 2001). One reason for this pattern might be explained by the more irregular, scaly and sharp-edged oyster shell compared to mussel shells that may hamper attachment of the starfish's tube feet to the shell. Studies on the impact of epigrowth on mussel shells on prey selection showed that starfish prefer clean mussels to mussels fouled with barnacles, possibly because the epigrowth interferes with the feeding mode and hampers attachment of the tube feet (Laudien & Wahl 1999, Saier 2001).

In summary, the results obtained in the feeding preference experiments stand in line with previous studies, which highlighted size- and species-selective feeding of *C. maenas* and A. *rubens*. Both predators prefer relatively small and easy to open prey, which leads to a higher predation pressure on juvenile mussels compared to juvenile oysters. However, as both predators are able to feed on *C. gigas* and may improve their opening techniques by learning, they may switch to *C. gigas* once these outnumber *M. edulis* in the Wadden Sea.

4.3 Implications for the invasion success of *Crassostrea gigas*

Pacific oysters recently started to increase dramatically in abundance and range and are locally overgrowing resident mussel beds in the Wadden Sea (Dankers et al. 2004, Diederich et al. in press). The question arose whether the oysters might outcompete the local mussels and which factors might be responsible for a possible competitive advantage of *C. gigas*. Previous studies have shown that the recent strong increase in abundance was caused by high recruitment success during three consecutive years with high summer water temperatures and a positive feedback of adult oysters on settlement (Diederich et al. in press, Diederich in press). A larger size and faster growth compared to mussels, together with high survival rates that may compensate for recruitment failures, suggest a competitive advantage of *C. gigas* over *M. edulis* (Diederich submitted). The question arose, whether low predation pressure might explain the high survival rates of *C. gigas* and might facilitate a possible displacement of mussels.

Predation may have a profound impact on structuring mussel populations (Seed 1969, Seed & Suchanek 1992, Strasser 2002). Whereas epibenthic predators like shore crabs and starfish are important sources of mortality for juvenile mussels in the Wadden Sea (Scherer & Reise 1981, Jensen & Jensen 1985, Dankers & Zuidema 1995, Kristensen & Lassen 1997), adult mussels are more often preyed upon by birds like eiders *Somateria mollissima*, oystercatchers *Haematopus ostralegus* and herring gulls *Larus argentatus* (Zwarts & Drent 1981, Hilgerloh et al. 1997, Nehls et al. 1997). Even though most of these resident predators are known to feed on oysters in other areas (Korringa 1976, Walne & Davies 1977, Quayle 1988), information about predation on *C. gigas* in the Wadden Sea is scarce.

Predation pressure on early juveniles is considered to have a stronger quantitative effect on population dynamics than predation that acts on later development stages (Reise 1985b, Gosselin & Qian 1997, Hunt & Scheibling 1997). Therefore, predation by birds is expected to play a minor role in determining the population dynamics of *C. gigas* and *M. edulis*. However, if predation intensity is very high, birds like herring gulls, oystercatchers and especially eiders may severely decrease adult mussel densities (Goss-Custard et al. 1981, Nehls et al. 1997). Only herring gulls are known to have already learned to prey on introduced *C. gigas* in the Wadden Sea, however, feeding on oysters was less effective than feeding on mussels because only about 30% of the oysters were broken by shell-dropping whereas almost 100% of mussels broke (Cadée 2001). Even though nothing is known about oystercatchers preying on *C. gigas* in this area, they might be able to switch to oysters if other food sources are scarce. The similar sized American oystercatcher *Haematopus palliates* feeds predominantly on oysters *Crassostrea virginica* in Virginia, because of shorter handling times compared to the mussel *Geukensia demissa* (Tuckwell & Nol 1997a, b, Crockett et al. 1998). However, the most important bird predator in the Wadden Sea, the eider, is not likely to switch to oyster prey because of their feeding mode which includes diving and swallowing mussels whole. This method would not work with sharp edged oysters that are cemented to each other in a solid reef structure. Therefore, predation pressure by birds seems to be unimportant for oysters while it could deplete adult mussels.

In the intertidal, 0-group *C. maenas* are the main predators that may limit mussel populations (Scherer & Reise 1981, Jensen & Jensen 1985, Dankers & Zuidema 1995). From July to mid October they are very abundant on intertidal mussel beds where they seek shelter from predation (Klein Breteler 1976, Thiel & Dernedde 1994). A temporal mismatch between the occurrence of 0-group *C. maenas* and 0-group bivalves caused by severe winters has been shown to greatly enhance bivalve survival, including mussels (Strasser & Günther 2001, Strasser 2002). Settlement of *M. edulis* in the northern Wadden Sea may take place during the whole year, but peak settlement occurs from May to September (Strasser & Günther 2001), which is the time when abundances of juvenile *C. maenas* are highest (Klein Breteler 1976). Higher survival rates, that ensure population persistence, mainly occur after severe winters, when the advent of predators is delayed and in lower densities on the tidal flats (Strasser 2002). The settlement period of *C. gigas* is confined to a short period in late summer (August to mid September). At this time, abundance of 0-group *C. maenas* has already declined (Klee 2001) and the remaining crabs might be too large to feed on small oysters (Fig. 8). This temporal mismatch between predator and prey may facilitate high survival rates of juvenile *C. gigas* even if crabs may learn to feed on this novel prey.

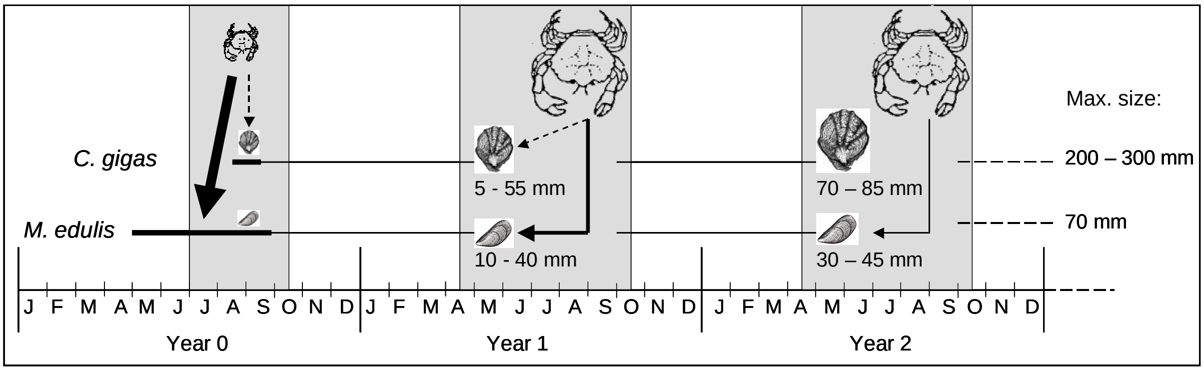

Fig. 8 Schematic diagram of predation pressure by *Carcinus maenas* on *Crassostrea gigas* and *Mytilus edulis* during different life stages. Bold horizontal lines indicate main settlement period of *C. gigas* and *M. edulis*. Shaded areas indicate time periods when 0-group *C. maenas* (small crab) and adult *C. maenas* (large crab) are present on tidal flats (after Reise 1977). Given are mean shell lengths of *C. gigas* and *M. edulis* during the time periods when *C. maenas* is present and maximum shell lengths (shell lengths of *M. edulis* after Nehls 2003, of *C. gigas* after Diederich submitted). Bold arrows indicate high predation, medium arrows medium predation and dotted arrows very low predation as inferred from feeding trials

During the winter months, shore crabs are absent from the intertidal zone, but adults reappear in mid April. Then, juvenile mussels will have attained a size of 10 - 20 mm and will grow to 20 - 40 mm by autumn (Nehls 2003). Juvenile oysters grow in the same period from 5 - 35 mm in spring to 35 - 55 mm in autumn (Diederich submitted). Concerning the size- and species selective feeding preference of shore crabs, the predation pressure on *M. edulis* is expected to be much higher than on *C. gigas* during this time. As large shore crabs are able to open mussels up to 50 mm shell length (Elner & Hughes 1978, Ameyaw-Akumfi & Hughes 1987), they will not find a size refuge from predation before their third or fourth year of life (Nehls 2003). Oysters will reach a size refuge much earlier; they may reach 50 mm shell length during their first year after settlement. However, studies from Britain have shown that *C. maenas* can open larger oysters than mussels because of weak parts of the oyster shell, which enable the crabs to open larger sized individuals (Dare et al. 1983). Large crabs of 75 mm carapax width were able to open oysters of 55 - 60 mm shell length, whereas they could not feed on mussels > 45 mm (Dare et al. 1983). Nevertheless, these size differences seem to be of minor importance compared to the much faster growth of *C. gigas*. In summary, the late settlement period and fast growth rate of juvenile *C. gigas* are likely to lead to a temporal mismatch between predator and prey and an early size refuge from predation. These factors may facilitate high survival rates even if crabs might switch their feeding preference from mussels to oysters.

Starfish are voracious predators that may control the distribution and abundance of mussels in low intertidal and subtidal zones (Seed 1969, Dare 1976, Seed & Suchanek 1992, Kristensen & Lassen 1997, Saier 2001). They are size-selective feeders and generally prefer mussel size classes below the maximum size that they are able to open (Reusch & Chapman 1997, Dolmer 1998). In the study at hand, the largest starfish that occur in the area (120 - 150 mm arm length) strongly preferred mussels with a shell length of 40 - 50 mm over larger mussels. However, Saier (2001) showed that large starfish in the Wadden Sea do feed on the largest mussels available (about 70 mm shell length), indicating that mussels do not reach a size refuge from starfish predation. However, abundance of *A. rubens* is highly variable and mass occurrences alternate with periods of relatively low densities, presumably triggered by food availability (Dare 1982, Saier 2001). In the Wadden Sea, the erratic distribution of *A. rubens* and the preference for barnacles as prey items by juvenile starfish reduces the direct impact of starfish predation on mussel populations (Saier 2001). However, as juvenile starfish prey severely on barnacles, they have an indirect negative effect on mussel recruitment, because barnacle epigrowth strongly enhances mussel recruitment (Navarette & Castilla 1990, Saier 2001, Diederich in press). As oyster recruitment does not depend on the presence of barnacles (Diederich in press), this indirect negative effect of starfish predation does not affect *C. gigas*.

Species-selective feeding of shore crabs and starfish may facilitate a competitive advantage of *C. gigas* over *M. edulis*. As predation pressure on juvenile oysters is low, they show high survival rates that may compensate for years with low recruitment success due to unfavourable environmental conditions such as cold summer water temperatures. Mussels, on the other hand, are strongly limited by predation pressure. High recruitment success is therefore erratic depending on low predator densities, normally in the wake of a cold winter. Under the premise that the invasion success of *C. gigas* will continue and mussels will become more and more displaced by oysters, they might experience an ever-increasing predation pressure because the remaining mussels are the preferred prey. However, as *C. maenas* and *A. rubens* are both able to feed on oysters, they might at some stage switch to oyster prey. It has been shown that *C. maenas* is able to adapt to larger sized prey by developing larger crusher claws (Smith 2004). Nevertheless, as oysters reach an early size refuge from predation and are a less profitable prey because of longer handling times, a possible regime shift from mussel beds to oyster reefs may impair predator performance.

Unfortunately, there is a lack of information about predation pressure on *C. gigas* in its native habitat of Japan and Korea. However, as these areas host very large predatory crabs like *Scylla serrata*, it is likely that *C. gigas* is subjected to higher predation pressure in its native habitat than at the temperate Atlantic and North Sea coasts (Vermeij 1977). For example, *Crassostrea virginica*, a native to the east coast of the United States with similar shell morphology as *C. gigas*, is subjected to heavy predation by the large crab *Callinectes sapidus* (carapax width up to 190 mm) and *Menippe mercenaria* (carapax width up to 128 mm; Menzel & Hopkins 1955, Vermeij 1977, Bisker & Castagna 1987, Egglestone 1990). At the North Sea coasts, *C. maenas* (maximum carapax width 75 mm) and *Cancer pagurus* (maximum carapax width 250 mm) are the largest crab species, however, the latter is rare and confined to subtidal parts of rocky shores (Hayward & Ryland 1995). Even if a local trend towards an increase of *C. pagurus* densities will continue (Buschbaum, pers. observation), they would most likely first decimate subtidal mussel populations before switching to oyster prey, because they also prefer mussels to oysters (Mascaró & Seed 2001).

5 Conclusion

It is concluded that low predation pressure by the main benthic predators, *Carcinus maenas* and *Asterias rubens*, will facilitate a competitive advantage of *C. gigas* over *M. edulis*. Whereas mussel populations are strongly limited by predation pressure and depend on high recruitment success during years when predator abundances are low, the high survival rates of juvenile and adult *C. gigas* may facilitate population persistence and growth even if cold summers lead to low oyster settlement. A possible regime shift with mussel beds being largely replaced by oyster reefs may have profound impacts on the Wadden Sea food web.

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6 General Discussion

Different aspects of spread and niche occupation of introduced Pacific oysters were highlighted in the previous chapters. It was shown that high recruitment success is facilitated by high summer water temperatures, a positive feedback of adults on settlement, and low predation pressure by resident predators. In addition, high growth and survival rates found in different locations suggest a broad ecological niche. Comparisons with resident blue mussels indicate that *C. gigas* might be a stronger competitor if space and/or food are limiting, mainly because of higher survival and growth rates, and less predation pressure. In the general discussion these results will be combined in order to generate an overall picture of possible impacts of *C. gigas* on the recipient community.

6.1 Factors facilitating the establishment of *C. gigas*

Pacific oysters are habitat generalists with a broad environmental range (Quayle 1988). They have been distributed to various parts of the world due to aquaculture activities, and in many locations wild oyster populations have established soon after oyster farming had commenced (e.g. Korringa 1976, Andrews 1980, Quayle 1988, Chew 1990). *C. gigas* is able to reproduce and grow in salinities of 14 - 32 psu, and to settle in intertidal as well as in subtidal locations of rocky coasts and sandy flats (Quayle 1988, Mann et al. 1991, de Kluijver & Leewis 1994, Leewis et al. 1994). They are able to grow in temperatures ranging from 5 to 35°C and to survive temperatures as low as -5°C; however, for reproduction they need more than 20°C (Korringa 1976, Buroker 1985, Mann et al. 1991). Together with an r-selected life history trait (high fecundity and dispersal capacity, fast growth), the broad environmental tolerances predispose *C. gigas* as a species likely to be a successful invader (Lodge 1993, Williamson & Fitter 1996, McMahon 2002).

In addition, aquaculture seems to be a very efficient vector that leads to a high probability of species becoming established in the recipient habitat (Reise et al. 1999, Naylor et al. 2001). The continuous input of larvae from the local oyster farm will surely have facilitated the invasion of *C. gigas*. Young oysters are imported regularly from hatcheries in England and Ireland, and placed on the culture plot where they grow to marketable size. When the oysters found suitable conditions for reproduction, natural spatfalls occurred and oysters settled in the wild. Due to the general aquaculture practice to crossbreed different strains in order to select for preferable characteristics, a high genetic variability within the newly established population can be assumed (Quayle 1988). This is important because it prevents that genetic drift caused by a population bottleneck due to a small number of initial colonists will lead to a low genetic variability within the new population (Sakai et al. 2001). A reduced genetic diversity would then limit population growth and the likelihood of persistence because it reduces the potential of the population to evolve (Sakai et al. 2001, Cox 2004).

Another factor that may have facilitated the establishment of *C. gigas* within the area is the location of the aquaculture plot in the List tidal basin, an almost enclosed bay. High larval retention will certainly facilitate the establishment of a species with a planktonic larval stage because it prevents the larvae to drift away from suitable habitats. Therefore, even low initial numbers of larvae may be sufficient to allow a population to increase.

The recipient habitat, namely the Wadden Sea, is a very dynamic and relatively young habitat that exists in its present state only since about 7,000 years. No endemic species have evolved and species richness is relatively low, suggesting the presence of empty habitats and free resources for invading species (Reise 1985, Armonies & Reise 2003). In addition, disturbances like storms and ice winters frequently lead to a change in species abundances and composition (Beukema 1992, Nehls & Thiel 1993, Strasser et al. 2001). These factors, low species richness, free resources, and frequent disturbances, are considered to enhance the invasibility of an ecosystem (Elton 1958, Crawley 1987, Lodge 1993, Stachowics et al. 1999). In fact, even though about 80 nonindigenous species are established in the North Sea, they have driven no native species to extinction; the exotics are rather considered as an addition to the resident community (Reise et al. 2002). Nevertheless, exotic species irreversibly changed the North Sea ecosystem, and as the rate of successful introductions is still increasing, there is a severe risk of new invaders becoming established that may have negative impacts on ecosystem functioning and/or human health (Reise et al. 2002). In addition, the increasing number of established exotics may facilitate the invasion by other species, a phenomenon that is called invasional meltdown (Simberloff & Von Holle 1999).

In summary, the successful establishment of *C. gigas* in the northern Wadden Sea may have been facilitated by species-specific characteristics of the invader, by an efficient vector, and by characteristics of the recipient habitat that renders it susceptible to invasion (see Box 1).

Box 1 Generalisations about biological invasions applied to the invasion of *C. gigas* in the northern Wadden Sea

(after Crawley 1987, Di Castri 1990, Lodge 1993, Williamson & Fitter 1996, Sakai et al. 2001, McMahon 2002, Shea & Chesson 2002).

Characteristics of a successful invader:	***C. gigas***
➢ r-selected trait (high fecundity, high dispersal and growth rate)	Yes
➢ habitat generalist	Yes
➢ high genetic variability	Yes
Efficient vector:	**Aquaculture**
➢ continuous input of larvae	Yes
➢ no population bottleneck	Yes
Recipient habitat with characteristics of high invasibility:	**Wadden Sea**
➢ free habitat and resources, low species richness	Yes
➢ high disturbance rate	Yes (ice, storms)

6.2 Spread of *C. gigas* in the northern Wadden Sea

In 1991, 5 years after the local oyster farm had started its business, the first wild oysters were found on intertidal mussel beds about 6.5 km north of the culture plot (Reise 1998). However, the expansion of the wild oyster population in the List tidal basin started off slowly. In 1995, 14 out of 17 investigated mussel beds contained living *C. gigas*, but mean abundances remained low (3.6 individuals m^{-2}; Reise 1998). By 1999, all mussel beds in the area were colonised by *C. gigas*, but densities were still on a low level (3.7 individuals m^{-2}). Only after three consecutive years with high recruitment success (2001, 2002, and 2003), a massive population increase occurred with mean densities of 126 individuals m^{-2} and maximum densities of over 300 oysters m^{-2} on single mussel beds in 2003 (chapter 2). In 2004, about 2000 - 3000 t oyster biomass were calculated for the List tidal basin; in comparison, mussel biomass was about 3000 t (G. Nehls and own unpubl. data).

The colonisation of the subtidal zone occurred much slower and up until 2004 only scattered oysters were found in subtidal locations. However, in 2004, spatfall was observed on former mussel culture plots, indicating that *C. gigas* is able to colonise subtidal habitats and might be able to generate subtidal oyster reefs as has happened in the Oosterschelde (The Netherlands, Kater & Baars 2003) and in the Dutch Wadden Sea near Texel (N. Dankers, pers. comm.).

Outside the List tidal basin, abundances of *C. gigas* are still low although the oyster population did spread north- and southwards along the coastline. Only on one intertidal mussel bed east of the island of Amrum (about 40 km south of the List tidal basin) abundances of over 150 oysters m^{-2} were recorded in summer 2004 (G. Nehls, unpubl. data).

In summary, the wild oyster population in the northern Wadden Sea increased slowly. It took about 17 years until a population of several million oysters became established, even though *C. gigas* is a species with an r-selected life history trait that includes high fecundity and dispersal capacities (Quayle 1988). The main reason for the relatively slow expansion is the fact that high recruitment events were erratic and occurred only in years with abnormally high summer water temperatures (1991, 1994, 1997, 2001, 2002, and 2003). Therefore, climatic conditions are considered to play a key role in determining the future population development of *C. gigas* in the northern Wadden Sea. That *C. gigas* is a reef building species that creates its own habitat might be another reason for a so called lag period, which is a common phenomenon in invasion processes and describes the time between the initial colonisation and the onset of rapid population increase (Sakai et al. 2001). As the oysters settle preferentially on conspecifics, a positive feedback of adults on recruitment is assumed with higher recruitment proportional to the amount of oysters already present (chapter 3).

6.3 Interaction with recipient community

In order to assess the future development of the oyster population and possible impacts on the recipient ecosystem, the study of biotic interactions with the native community is essential. Unfortunately, I have no information on the population ecology of *C. gigas* in its native habitat from Japan to Taiwan. Therefore, a comparison of species interactions in the native habitat versus the introduced habitat is not possible at this stage, even though the importance of home and away comparisons is unquestionable (Lohrer et al. 2000, Hierro et al. 2005).

In the Wadden Sea, *C. gigas* is not invading free habitat patches, but is settling on top of epibenthic mussel beds *Mytilus edulis* (Reise 1998). These are centres of high species richness, biomass, and production, and represent the only extensive habitat for sessile organisms (Seed & Suchanek 1992). In addition, mussels and their associated organisms are an important food resource for various benthic predators, fish, birds, and humans (Dankers & Zuidema 1995, Nehls et al. 1997, Saier 2001). Therefore, *C. gigas* is invading a complex community, and various interactions with resident species are likely to occur that determine the impact of *C. gigas* on the recipient ecosystem.

6.3.1 Spatial coexistence of *C. gigas* and *M. edulis*

Pacific oysters are large, suspension-feeding bivalves that need hard substrates for settlement. As mussel beds are the only extensive hard substrata available on the mud and sand flats of the Wadden Sea, the oysters are attaching themselves to the shells of living and dead mussels. Therefore, competition for space and food may occur, if these resources are limiting. Space is not considered a limiting factor in the Wadden Sea in general; however, habitat for sessile organisms is restricted to mussel beds and therefore scarce. Mussel beds are very stable and may persist for decades provided that no mussel fishery occurs (Obert & Michaelis 1991, Reise et al. 1994, Dankers et al. 1999). However, stochastic events such as ice scouring and storms may severely damage and dislodge mussel beds (Obert & Michaelis 1991, Nehls & Thiel 1993, Strasser et al. 2001). Therefore, mussel beds are generally confined to semi-exposed locations, where they are sheltered from wave action, but where currents are still high enough to guarantee adequate food supply (Brinkman et al. 2002). In addition, a tidal zonation is apparent, because locations too high up the shore are less favourable because of food limitation by short submersion periods and by desiccation stress, and the locations at or below the low water line are susceptible to heavy predation by crabs and starfish (Seed & Suchanek 1992, McGrorty et al. 1993, Saier 2001, Brinkman et al. 2002). That suitable habitat for stable mussel beds may be limited in the Wadden Sea is supported by the fact that mussel beds that were destroyed often reappear at the same location (Obert & Michaelis 1991).

High mussel recruitment, however, is rare and confined to years when predator densities happen to be low, usually following severe winters (Beukema 1992, Beukema et al. 2001, Strasser et al. 2001). High oyster recruitment, on the other hand, is facilitated by high summer water temperatures (chapter 2); post-settlement mortality due to predation seems to play only a minor role (chapter 5). Therefore, a succession of warm summers as has recently occurred (2001, 2002, and 2003) is expected to lead to an overgrowth of mussel beds by *C. gigas* and to a transition from mussel beds to mixed beds and finally to oyster reefs (Fig. 1). However, a dense cover of *Fucus vesiculosus* that frequently occurs on intertidal mussel beds reduces oyster settlement and may provide a spatial refuge for *M. edulis*, albeit under suboptimal conditions. The next cold winter may then lead to high mussel recruitment and to an overgrowth of oyster reefs by *M. edulis*. As mussels have a high reproductive capacity, they may reach a strong population increase even if numbers of adults are low (Seed 1975, Sprung 1983). However it may be possible that mussel recruitment will be reduced on oyster reefs, because of predation by oysters that filter mussel larvae from the water column (Troost 2004). Furthermore, biotic interactions like food competition and high predation pressure might repress the overgrowth of mussels on oyster reefs even if initial recruitment success is high.

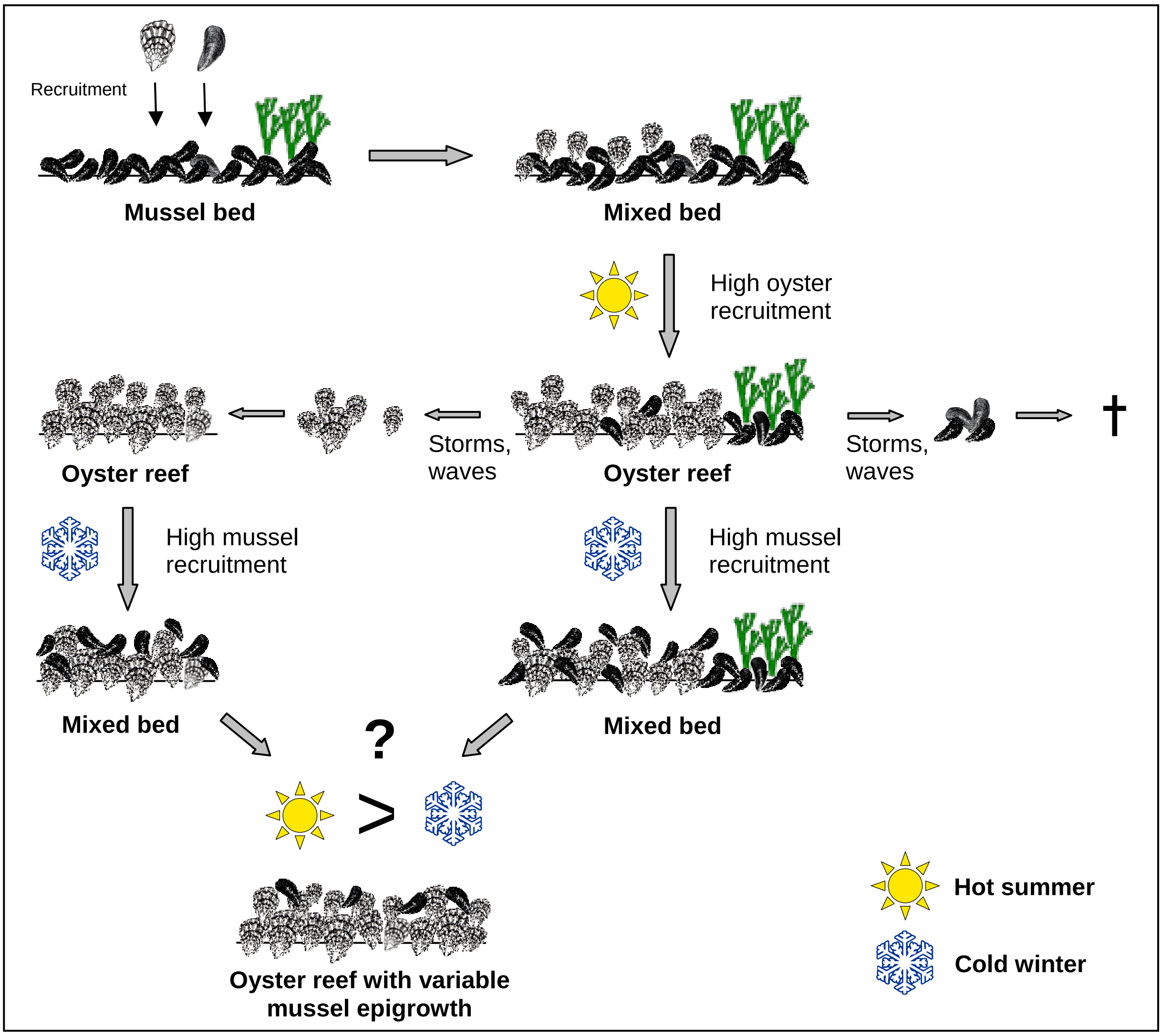

Fig. 1 Schematic diagram of the possible development of intertidal mussel beds and oyster reefs based on differential recruitment success of *Crassostrea. gigas* and *Mytilus edulis*. High oyster recruitment is facilitated by high summer water temperatures and the presence of conspecifics, whereas mussel recruitment is facilitated by low predator densities after sever winters and the presence of barnacles. The future development will primarily depend on climatic conditions. Climate change leading to a higher frequency of hot summers and a lower frequency of cold winters will favour the dominance of oyster reefs

As climatic conditions seem to be important for determining recruitment success of both, oysters and mussels, a possible climate change leading to warmer summers and milder winters in the wake of an increasing North Atlantic Oscillation index (Roeckner 2001, Meincke et al. 2003), will favour the development of oyster reefs that may contain a variable amount of mussel epigrowth depending on recruitment success in different years.

Whether or not mussels may find a spatial refuge higher in the intertidal zone will depend on different tolerances towards desiccation and freezing temperatures. Zonation as a consequence of predation or interspecific competition is a well known phenomenon on rocky shores (e.g. Connell 1961, Underwood 1992, Paine 1994). For example, *M. edulis* finds a spatial refuge from competition with *M. galloprovincialis* by settling higher on the shore at the coast of Washington (Suchanek 1981), and barnacles *Balanus balanoides* avoid competition with *M. edulis* by settling in the upper intertidal where only *Balanus* can exist (Peterson 1979). However, even though a zonation with mussels remaining higher up the shore and oyster reefs emerging in the lower intertidal zone is apparent in some locations in the northern Wadden Sea, further studies are needed to test for performance of both species under suboptimal conditions that prevail in the high intertidal zone.

Another interesting aspect is the fact that *C. gigas* might be able to create its own habitat on the sandy flats of the Wadden Sea. Especially in years with high barnacle abundances on oyster and mussel shells, juvenile oysters are often not attached to the bivalve, but to barnacle shells. Subsequently, the barnacles become overgrown, die, and get easily detached from their basibiont. Then, the young oysters are without substrate and are prone to drift with the currents away from the mussel bed. Oysters attached to dead barnacle shells are frequently found on the sand flats of the Wadden Sea (Fig. 2). There, they seem to survive and grow well because they do not sink even into muddy sediments and can free themselves from sediment cover (own unpubl. data). The species selective settlement of oyster larvae – they settle preferentially on conspecifics – may then lead to the generation of oyster reefs on formerly bare sand flats. Storms may act in the same way and may lead to dislodgement not only of mussel clumps (Nehls & Thiel 1993), but also of oysters,

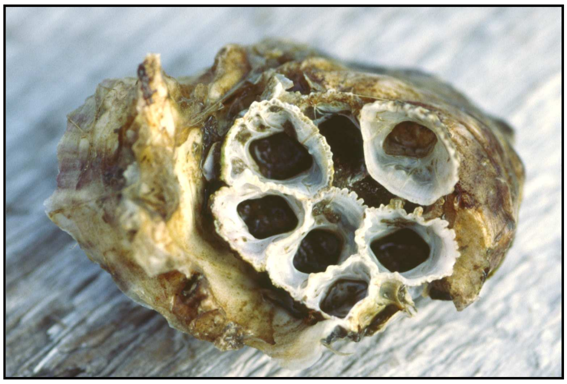

Fig. 2 Juvenile *C. gigas* attached to dead barnacles

thereby facilitating the creation of new reef structures. The generation of new oyster reefs on formerly bare sand is expected to be strongly facilitated by low predation pressure on juvenile oysters. The development of new mussel beds, on the other hand, is considered to be limited firstly by unfavourable conditions like currents being too strong or too low (Brinkman et al. 2002), and secondly by predation, because juvenile mussels are subjected to high predation pressure and the bare sand flats provide no spatial refuges from predation (Scherer & Reise 1981, Revelas 1982, Dankers & Zuidema 1995, Frandsen & Dolmer 2002). As oyster reefs might be more stable and resistant to high currents, storms and ice scouring, they may develop on areas that are not suitable for mussel beds, suggesting that oyster reefs may potentially become more abundant than mussel beds have ever been.

In the subtidal zone, the situation might be different, because of different factors influencing population dynamics. For example, higher predation pressure and stronger currents than in the intertidal are known to limit subtidal mussel populations (Kitching et al. 1959, Ebling et al. 1964, Seed 1993, Saier 2001, Brinkman et al. 2002). In the List tidal basin, recruitment of *C. gigas* was much lower in shallow subtidal compared to intertidal locations (chapter 3), which may partly be explained by higher predation pressure on early recruits (chapter 5). Another reason could be differential settlement of *C. gigas* that is widely considered as an intertidal species and might be limited by cold water or high currents in the subtidal zone (Buroker 1985, Quayle 1988, Arakawa 1990). However, as the oysters suffer much less predation pressure compared to mussels, they are likely to be able to survive and grow well in subtidal locations. This is supported by the fact that single adult oysters are frequently found in the subtidal zone and that in 2004 the first significant subtidal spatfall was recorded with juveniles being attached to dead shells and to scattered adult oysters. Therefore, the development of subtidal oyster reefs as has occurred in the Oosterschelde (western Netherlands; Kater & Baars 2003) is expected, albeit with a longer lag phase than in the intertidal zone.

In summary, oyster reefs are expected to develop in intertidal as well as in subtidal locations. Whether or not mussels will be able to recolonise oyster reefs in high recruitment years needs to be awaited because the last high recruitment event of *M. edulis* dates back to 1996 (Nehls 2003). However, the mussels may find a spatial refuge in the high intertidal zone provided that they are better adapted to the suboptimal conditions prevailing there.

6.3.2 Is *C. gigas* a stronger competitor than *M. edulis*?

High survival rates of juvenile and adult *C. gigas* and the ability to reach an old age on mussel beds as well as on sand flats are assumed to guarantee population persistence and growth even if ‘cool’ summers will lead to low oyster recruitment during most years. A competitive displacement of native mussels may occur if *C. gigas* is a stronger competitor for limiting resources. As mentioned above, space might be a limiting factor, however, as both species show high fecundity and dispersal capacities and are able to settle on top of each other, coexistence may be possible. Nevertheless, the stronger competitor might displace the weaker congener to less favourable habitats and may cause a severe population decline.

Comparisons of life-history characteristics of *C. gigas* and *M. edulis* may allow tracing possible competitive advantages (summarised in Table 1). Both species are habitat generalists with a broad global distribution (e.g. Quayle 1988, Gosling 1992). However, as mentioned above, *C. gigas* is at its northern distributional limit in the Wadden Sea, because the oysters need about 20°C water temperature for successful reproduction (Korringa 1976, Mann 1979, Buroker 1985).

Table 1 Summary of life history characteristics of *Crassostrea gigas* and *Mytilus edulis* as derived from literature

Life history trait	***C. gigas***	***M. edulis***
Tolerance to abiotic factors	Habitat generalist	Habitat generalist
Adapted to climatic conditions of the Wadden Sea	Yes, but northern limit of distribution	Yes
Size and life span	Max. size: 30 cm Max. age: ~ 30 years	Max. size: 7 cm Max. age: ~ 20 years
r-selected life history traits: high fecundity, high growth rate early maturity	 50 - 100 million eggs per female rapid (30 - 70 mm during 1st year) 1 year	 7 - 8 million eggs per female rapid (10 - 30 mm during 1st year) 1 year
Dispersal rate	High (planktonic larval period: 3 - 4 weeks)	High (planktonic larval period: 1 - 4 weeks, secondary byssus drifting possible)
Relative juvenile survivorship	High	Low (exception: low predator densities after cold winters)
Predation pressure	Low	High
Resistance to disturbances (ice scouring, storms)	High (solid reef structure)	Medium (mussel beds dislodged by ice and storm)

Oysters and mussels are both long-living, but *C. gigas* is much larger and reaches about 3 to 4 times the size of *M. edulis*. Both bivalves have a high dispersal capacity due to an extended larval period, but *C. gigas* has a higher fecundity with adult females releasing 50 - 100 million eggs whereas large mussels produce only 7 - 8 million eggs (Quayle 1988, Seed & Suchanek 1992).

One important difference between oyster and mussel recruitment is the fact, that oyster settlement is confined to a short period from late July to early September, whereas mussel settlement may occur year round with the main peak in spring and minor peaks in summer and/or autumn (Pulfrich 1995, Strasser & Günther 2001). This may in part explain the low predation pressure on juvenile oysters, because a temporal mismatch between predator abundances and oyster recruitment is assumed (chapter 5). Studies on biological factors affecting recruitment of *C. gigas* and *M. edulis* revealed that oyster recruitment is facilitated by the presence of conspecifics, while mussel recruitment is enhanced in the presence of barnacle cover (Fig. 4). A dense layer of the brown macroalga *Fucus vesiculosus* reduced recruitment of both, mussels and oysters (C. Buschbaum unpubl. data and chapter 3). However, as survival rates of newly settled oysters are very high (about 70% survived their first three months on the mussel bed), presumably due to low predation pressure, the oysters are expected to be stronger competitors compared to mussels and to be able to increase even if number of recruits are still low.

A regular plankton survey (10 l seawater sampled per day) revealed that abundances of *C. gigas* larvae are increasing in the List tidal basin since 2002, when the first oyster larvae were found (8 individuals in total). In 2003, 27 larvae were recorded and in 2004 the number of larvae increased even further (M. Strasser, pers. comm.), reflecting the increasing oyster recruitment that has been observed on spat collectors (Fig. 3).

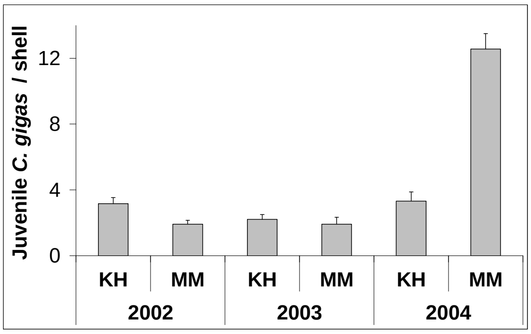

Fig. 3 Abundance of *Crassostrea gigas* recruits on spat collectors made from dead oyster shells (mean + SE, n = 6 collectors with 8 shells each) on two intertidal mussel beds (KH and MM) in August 2002, 2003, and 2004.

Growth experiments revealed a much higher growth rate of *C. gigas* compared to *M. edulis* (chapter 4). Whereas 1-year-old mussels reach about 10 - 30 mm shell length on intertidal mussel beds (Nehls 2003), oysters will grow to a length of about 30 - 70 mm. In addition, growth of *C. gigas* was neither affected by barnacle overgrowth nor by the presence of mussels and oysters (Fig. 4). Mussel growth, on the other hand, is reduced due to barnacle cover (Buschbaum & Saier 2001), and the presence of mussels and oysters, indicating competitive inferiority. A larger size paired with a filtration rate an order of magnitude higher – medium sized oysters of 90 - 100 mm shell length reach filtration rates of 30 l h^{-1} (Quayle 1988) whereas large mussels of 50 - 70 mm filter about 3 l h^{-1} (Davenport & Woolmington 1982) – will be of competitive advantage if food limitation is occurring in dense aggregations of suspension feeders. Especially in low current situations food depletion may occur directly above mussel beds (Dame et al. 1984, Fréchette et al. 1989, Peterson & Black 1991). In addition, if the trend towards decreasing eutrophication leading to reduced phytoplankton biomass is continuing (van Beusekom et al. 2005), food competition may become more important as carrying capacity for filter feeders declines. However, a different feeding behaviour and possibly also different food sources utilised by *C. gigas* and *M. edulis* lead to the assumption that mussels and oysters are not necessarily strong competitors (Bougrier et al. 1997, Riera et al. 2002). Whether or not *C. gigas* and *M. edulis* may compete for food in the Wadden Sea will need further study, because it is difficult to transfer results from physiological laboratory experiments to the actual field situation.

Another advantage of faster growth and larger size is an early size refuge from predation, because most benthic predators are size-selective feeders which prey preferentially on food items that promise optimal energy gain (Elner & Hughes 1978, Hughes 1979). Lack of predation pressure by resident mussel predators is considered to be a main reason for the observed high survival rate of juvenile and adult oysters (chapter 5). Species- and size-selective feeding of crabs (*Carcinus maenas*) and starfish (*Asterias rubens*) which both strongly prefer mussels to oysters, will certainly give *C. gigas* a competitive advantage, because mussel populations are known to be strongly limited by benthic predation (Seed 1969, Seed & Suchanek 1992, Dankers & Zuidema 1995, Saier 2001, Strasser 2002). In addition, birds like eiders *Somateria mollissima*, herring gulls *Larus argentatus*, and oystercatchers *Haematopus ostralegus* may severely decrease adult mussel densities (Goss-Custard et al. 1981, Nehls et al. 1997). However, even though herring gulls learned to feed on

C. gigas (Cadée 2001), their impact on oyster densities is considered to be low, especially if oysters are cemented to each other in massive reefs.

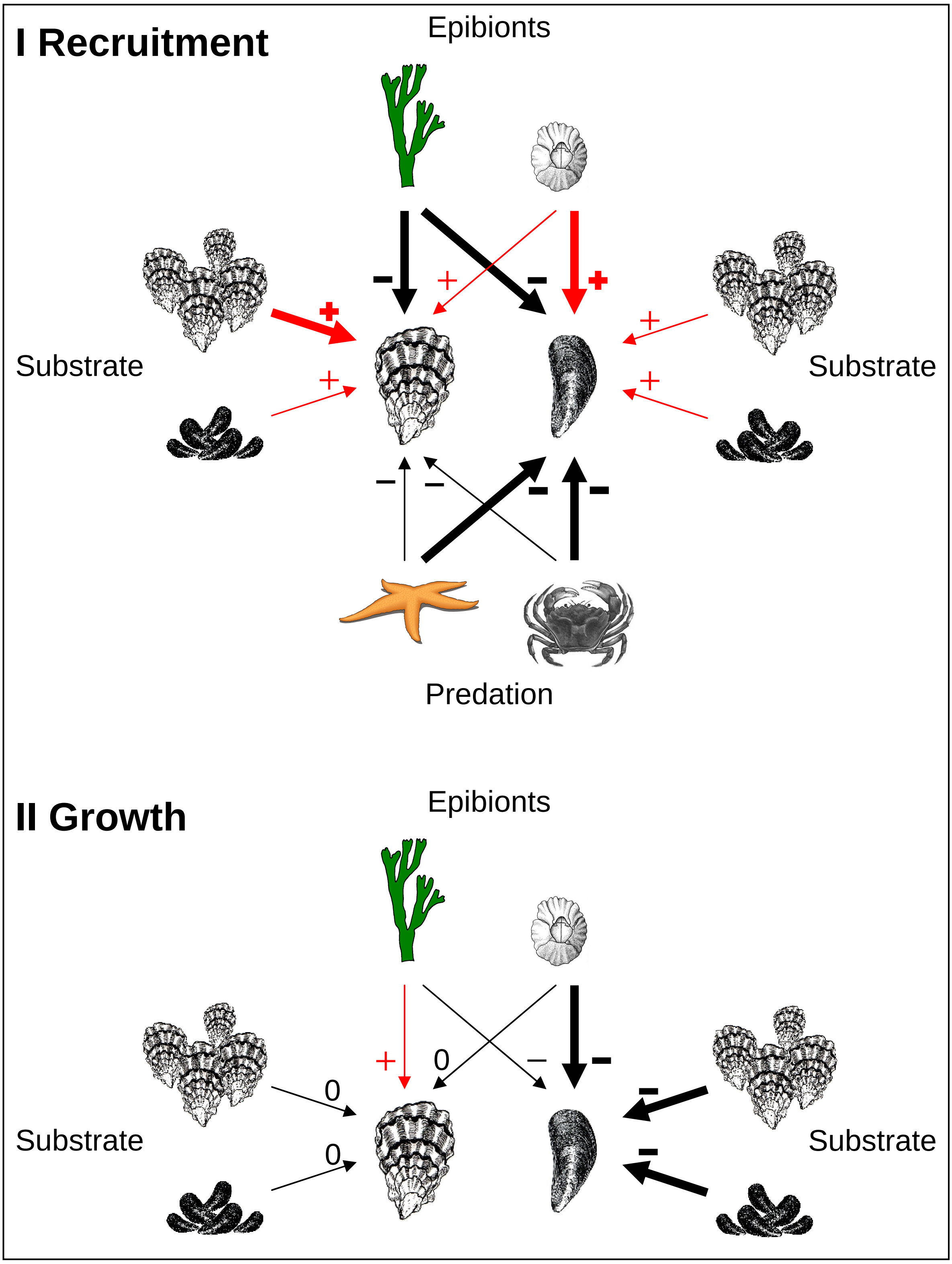

Fig. 4 Biotic factors affecting recruitment (I) and growth (II) of *Crassostrea gigas* and *Mytilus edulis*. Positive effects (+) are marked in red, negative (-) and neutral (0) effects are marked in black. Thick arrows indicate strong effects, thin arrows weaker effects

Nevertheless, whether or not birds will be able to use oysters as a food resource needs further study, especially in the face of impacts that a possible shift from mussel beds to oyster reefs might have on bird populations that use the Wadden Sea as an essential feeding ground.

In conclusion, *C. gigas* seems to be the stronger competitor compared to *M. eduli*s, especially because of high survival rates due to low predation pressure. However, as food and space is abound in the Wadden Sea ecosystem, not a displacement, but a shift in dominances is expected with oyster reefs becoming abundant in intertidal and possibly also in subtidal locations and mussels being mainly restricted to the existence as one of many epifauna species on oyster reefs. Their densities are expected to vary according to recruitment success in different years, a well known phenomenon known for many bivalves in the area (Strasser et al. 2001, Strasser 2002). A similar phenomenon occurs in the Sea of Japan, where *Crassostrea* reefs are subjected to a succession of epifauna communities dominated by barnacles (*Balanus improvisus*) and mussels (*Mytilus trossulus*) that settle on the oyster shells during summer and die off in winter (Zvyagintsev 1992). In late fall, the oyster reef may look like a mussel bed due to the heavy overgrowth and in spring the oyster reef comes back into view after the mussels have died off (Zvyagintsev 1992).

6.3.3 Impacts on the Wadden Sea ecosystem

A possible regime shift with mussel beds being largely replaced by oyster reefs may have profound impacts on ecosystem dynamics and functioning. First of all, a different associated community may develop on oyster reefs. Even though oyster reefs are known to harbour a diverse associated community by providing settlement surfaces for sessile species and shelter for mobile organisms (Arakawa 1990, Zvyagintsev 1992, Soniat et al. 2004), their structure differs from mussel beds, because the oysters are larger and they are forming more solid reef structures by cementing themselves to each other. Mussel beds, on the other hand, are more dynamic because mussels are able to move with their foot and byssal threads. This is expected to have impacts on organisms seeking shelter form predation in between and underneath the mussels and that may not find suitable hideouts in oyster reefs. For example juvenile shore crabs (< 10 mm carapax width) are more abundant on mussel plots compared to oyster plots, whereas larger shore crabs were more abundant on oyster plots (own unpubl. data). For sessile species like barnacles, however, no significant differences in abundances between oyster and mussel substrate were found (S. Görlitz and own unpubl. data). In general, the composition and diversity of epi- and endobenthic species did not differ between intertidal oyster reefs and mussel beds (S. Görlitz, unpubl. data). However, the brown macroalga *Fucus vesiculosus* that may cover mussel beds in dense layers and supports various herbivores and increases overall macrobenthic diversity (Albrecht & Reise 1994, Albrecht 1998) will be missing on oyster reefs because it lacks a holdfast and is attached to the mussel bed only by the mussels' byssal threads. Therefore, the occurrence of these algae depends on the presence of mussels. However, a recent invader in the Wadden Sea, the Japanese seaweed *Sargassum muticum* readily grows on oyster shells in the shallow subtidal and hosts a more diverse associated community than *F. vesiculosus* (Buschbaum in press).

To follow up a possible development of subtidal oyster reefs would certainly be very interesting, because it may facilitate the establishment of an associated community that may be similar to the one that existed on the former reefs of the native European oyster *Ostrea edulis*, which became extinct in the Wadden Sea at the start of the 20th century (Möbius 1877, 1893, Hagmeier & Kändler 1927, Hagmeier 1941, Reise 1982). However, it has to be taken into account that *O. edulis* was restricted to the subtidal habitat and possessed different life history characteristics than *C. gigas*, such as smaller size (maximum size about 12 cm), lower fecundity and dispersal capacity, and lower temperature and salinity tolerance (Möbius 1877, Korringa 1952, Mann 1979, Andrews 1980, Buroker 1985). Therefore, the establishment of *C. gigas* cannot be considered as a substitute for the loss of *O. edulis*. Especially as *C. gigas* is much larger, it may have different impacts on the food web because of higher filtration capacity and lower risk of predation (Walne & Mann 1975, Korringa 1976, Dean 1979, Mann 1979).

If oysters will become superabundant in the Wadden Sea, the higher filtration rate of oysters may have impacts on food availability for other suspension feeders, like mussels, cockles (*Cerastoderma edule*), and clams (*Macoma balthica*, *Mya arenaria*). In addition, oyster reefs may become more abundant than mussel beds have ever been, mainly because of a presumed wider ecological niche. Even though at present food is not considered to be a limiting factor for suspension-feeding bivalve populations, and only locally food depletion may occur directly above dense aggregations of filter feeders (Fréchette & Bourget 1985, Fréchette et al. 1989, Peterson & Black 1987, 1991), a massive increase in oyster abundances may lead to a depletion of phytoplankton in the water column (Dame & Prins 1998). In addition, decreasing phytoplankton biomass caused by reduced riverine nutrient inputs (van Beusekom et al. 2005) may contribute to food limitation. Therefore, food competition between *C. gigas* and other filter feeders may occur, as is assumed for cockles and oysters in the Oosterschelde (The

Netherlands; Geurts van Kessel et al. 2003) and for the oyster cultivation area of Marennes-Oléron bay in France (Sauriau et al. 1989). A possible top-down control of phytoplankton biomass may modify benthic-pelagic coupling by forcing a shift from pelagic to benthic consumers because of food depletion in the water column (Leguerrier et al. 2004). However, as the oysters release nutrients into the water column, phytoplankton productivity may increase (Righetti 1999, Mazouni et al. 2001). In addition, pseudofaeces production may increase food for meiofauna that in turn provides food for juvenile and adult nekton (Leguerrier et al. 2004). In oyster cultivation areas in France high oyster densities caused a severe decline in macrofauna and zooplankton but enhanced bacteria, microfauna and meiofauna which in turn promoted the more active trophic fluxes towards birds and nektonic fishes (Leguerrier et al. 2004).

As the oysters suffer very low predation pressure in the Wadden Sea, a possible regime shift with oysters dominating the benthic filter feeding population may have profound impacts on the food web, because oysters may constitute a more or less dead end in the food chain (Fig. 5). However, it has to be taken into account that benthic predators like shore crabs and starfish as well as herring gulls are known to feed on *C. gigas* in other countries and may learn to feed on novel prey (Korringa 1976, Walne & Davies 1977, Quayle 1988, Cadée 2001). In addition, as the associated community of oyster reefs and mussel beds is not expected to differ in great extent, their impact on the food web will not change. Nevertheless, large oysters are not expected to be preyed upon by any of the resident predators and if *C. gigas* will once constitute the majority of the benthic biomass, their large filtration capacity will transfer most of the primary production into oyster reefs. A possible decline of benthic predators may have impacts on higher levels of the food web such as migratory birds. For example, in the Dutch Wadden Sea the declining cockle populations have caused a severe decrease in oyster catcher abundances (Verhulst et al. 2004).

However, these predictions are drawn from studies on the present situation and may not be valid for processes that may occur once a regime shift has occurred, because then other interactions may appear whose outcome is impossible to predict. Many introduced species experience a boom phase with a massive population increase that is followed by a bust period when abundances decline and remain on a low level from then on (Simberloff & Gibbons 2004). The reasons for the population crash often remain unknown, however, predation or competition by subsequently introduced species is frequently considered as a likely cause. For example, in the Black Sea the arrival of a predatory ctenophore (*Beroe ovata*) may have caused a decline of the previously introduced comb jelly *Mnemiopsis leidyi* and therewith contributed to the recovery of the ecosystem (Kideys 2002, Bilio & Niermann 2004). However, the recipient ecosystem may also adapt to the invader (Cox 2004). For example, resident species may evolve new characteristics like growing larger or learning new prey handling skills (Townsend 1996, Trussel 2000, Hughes & O'brian 2001, Smith 2004).

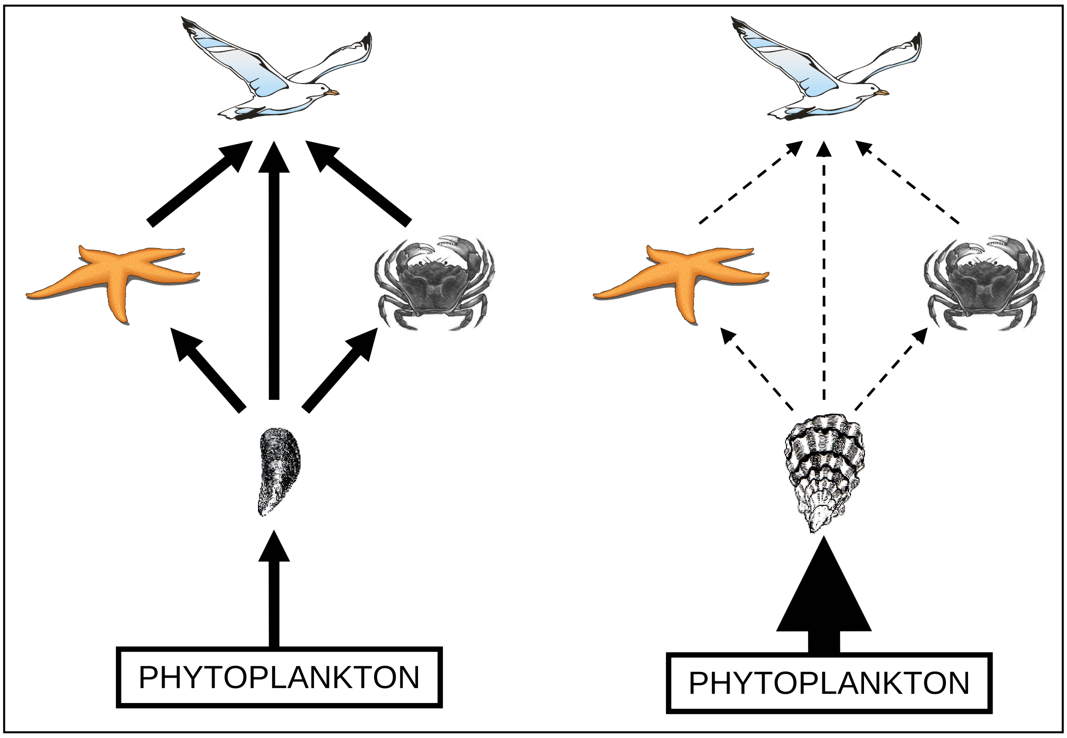

Fig. 5 Simplified food chain in the Wadden Sea. Before the introduction of *Crassostrea gigas* (left): mussels feeding on phytoplankton and being preyed upon by starfish, crabs and birds. After a possible regime shift (right): large oyster reefs replacing other filter feeders and taking up most of the phytoplankton biomass. Low predation pressure on *C. gigas* may lead to declining predator densities (including birds) and a transformation of the Wadden Sea ecosystem

In comparison, previously introduced filter feeders, the American slipper limpet *Crepidula fornicata* and the American razor clam *Ensis americanus*, did not cause major changes in the Wadden Sea ecosystem. *C. fornicata* was introduced with American oysters in the 1870s and now inhabits shallow subtidal zones. However, even though slipper limpets reduce survival and growth of mussels if attached to mussel shells, their abundances are limited by high mortality in cold winters (Thieltges et al. 2004, Thieltges 2005), which reduces their overall impact. *Ensis americanus*, on the other hand, became very abundant after its accidental introduction in the 1970s and is now a prominent member of the macrobenthos in shallow subtidal sands (Armonies & Reise 1999). However, as *E. americanus* invaded a sparsely faunated habitat, no significant interactions with resident species occurred.

6.4 Conclusion

The further increase of the oyster population in the Wadden Sea may lead to a regime shift with mussel beds being largely replaced by oyster reefs. Intertidal and possibly also subtidal oyster reefs with a varying amount of mussel overgrowth is considered to be a likely future scenario. Even though oyster recruitment depends on high summer water temperatures, high survival rates due to low predation pressure and a higher efficiency of using space and food resources compared to resident mussels are considered to facilitate a strong increase in oyster abundances. This may have profound impacts on the Wadden Sea food web, because oysters are not as well integrated in the food chain as resident bivalves. This may have consequences not only for benthic predators, but also for foraging birds, and may transform the Wadden Sea ecosystem. However, it has to be taken into account that the Wadden Sea is a very dynamic habitat and that another regime shift has occurred before when the native European oyster *Ostrea edulis* was driven to extinction due to overfishing. Then, mussels occupied the vacant niche thereby causing a shift in species composition (Reise et al. 1989). However, this species shift was restricted to the subtidal zone and therefore had fewer impacts on overall ecosystem dynamics.

Concerning impacts on human issues, different advantages and disadvantages are likely. For example, the traditional mussel fishery might be hampered because seed mussels become overgrown by oysters (N. Dankers, pers. comm.). Fishery on wild oyster stocks, on the other hand, seems to be unprofitable because of the low commercial value of unshaped oysters cemented to huge bulks. However, collection of wild oyster spat instead of importing seed oysters may reduce the possible introduction of new invaders, like epibionts or parasites and pathogens. Whether or not oyster reefs may facilitate coastal protection would be an interesting subject to study.

In general, the worldwide distribution and subsequent establishment of *C. gigas* is a striking example of a species that has not caused species extinctions, but changed ecosystem dynamics and has a share in an advancing similarity between coastal biota around the world.

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