



Causes and effects of a highly successful marine invasion: Case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries

Karin Troost

Marine Benthic Ecology and Evolution, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands
IMARES-Delta, P.O. Box 77, 4400AB Yerseke, The Netherlands

ARTICLE INFO

Article history:

Received 19 July 2009
Received in revised form 29 January 2010
Accepted 4 February 2010
Available online 12 February 2010

Keywords:

Crassostrea Gigas
Wadden Sea
Oosterschelde Estuary
Characteristics of Invasive Species
Consequences of Marine Invasions
Non-indigenous Species

ABSTRACT

Since the 1960's, the Pacific oyster *Crassostrea gigas* has been introduced for mariculture at several locations within NW Europe. The oyster established itself everywhere and expanded rapidly throughout the receiving ecosystems, forming extensive and dense reef structures. It became clear that the Pacific oyster induced major changes in NW European estuaries. This paper reviews the causes of the Pacific oyster's remarkably successful establishment and spread in The Netherlands and neighbouring countries, and includes a comprehensive review of consequences for the receiving communities.

Ecosystem engineering by *C. gigas* and a relative lack of natural enemies in receiving ecosystems are identified as the most important characteristics facilitating the invader's successful establishment and expansion. The Pacific oyster's large filtration capacity and eco-engineering characteristics induced many changes in receiving ecosystems. Different estuaries are affected differently; in the Dutch Oosterschelde estuary expanding stocks saturate the carrying capacity whereas in the Wadden Sea no such problems exist. In general, the Pacific oyster seems to fit well within continental NW European estuarine ecosystems and there is no evidence that the invader outcompetes native bivalves. *C. gigas* induces changes in plankton composition, habitat heterogeneity and biodiversity, carrying capacity, food webs and parasite life cycles. The case of the Pacific oyster in NW European estuaries is only one example in an increasing series of biological invasions mediated by human activities. This case-study will contribute to further elucidating general mechanisms in marine invasions; invasions that sometimes appear a threat, but can also contribute to ecological complexity.

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E-mail address: troost.karin@gmail.com.

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1. Introduction

The Pacific oyster *Crassostrea gigas* is one of the best known non-indigenous animals in coastal north-western Europe. Whether the species is an enrichment to estuarine and coastal ecosystems, or a nuisance, or both, is currently under debate. On one hand it adds habitat heterogeneity and hence promotes biodiversity, on the other hand it may eventually out-compete native bivalves and induce cascading effects on other trophic levels. In this paper the spatial spread of *C. gigas* throughout the NW European countries The Netherlands, Belgium, Germany, Denmark, Sweden and Norway is discussed, followed by reviews of causes of the species' successful establishment and natural spread, and consequences of induced changes in receiving ecosystems. Causes of success are mainly based on the situation in The Netherlands, where *C. gigas* was first introduced. Consequences of induced changes are reviewed for continental NW Europe in general, with a focus on The Netherlands and Germany, where the most studies were performed (specifically in the Oosterschelde estuary and Wadden Sea). Finally, a future perspective is given which includes expected effects of climate change. This case-study of the introduced Pacific oyster will

contribute to further elucidating general mechanisms in marine invasions.

In this paper, the term “invasions” refers to non-indigenous species that were moved outside their natural range both by human activities (deliberate and accidental introductions) and natural range expansions (after Carlton, 1989). The term “introduced species” is used specifically for species introduced by human activities, while “invasive species” refers to non-indigenous species that manage to establish successfully and have a certain impact on the receiving ecosystem.

2. Biology of *C. gigas*

Pacific oysters are lamellibranch suspension-feeding bivalves of the class Pelecypoda. They live attached to hard substrates along exposed shores and form reef structures on tidal flats (Fig. 1) (Arakawa, 1990a; Reise, 1998; Dupuy et al., 1999). Pacific oysters are oviparous; in the Northern Hemisphere they release their gametes into the water mainly in July and August, when water temperatures are highest. After a pelagic phase of about 3 weeks (Fig. 2), the veliger larvae settle onto hard substrate: oyster shells, rocks, or pieces of other hard substrate. After settlement, by excretion of cement their lower (left) cupped valve



Fig. 1. Left: Oyster reef in the Oosterschelde estuary (Neeltje Jans); Right: aggregation of oysters settled onto each other.

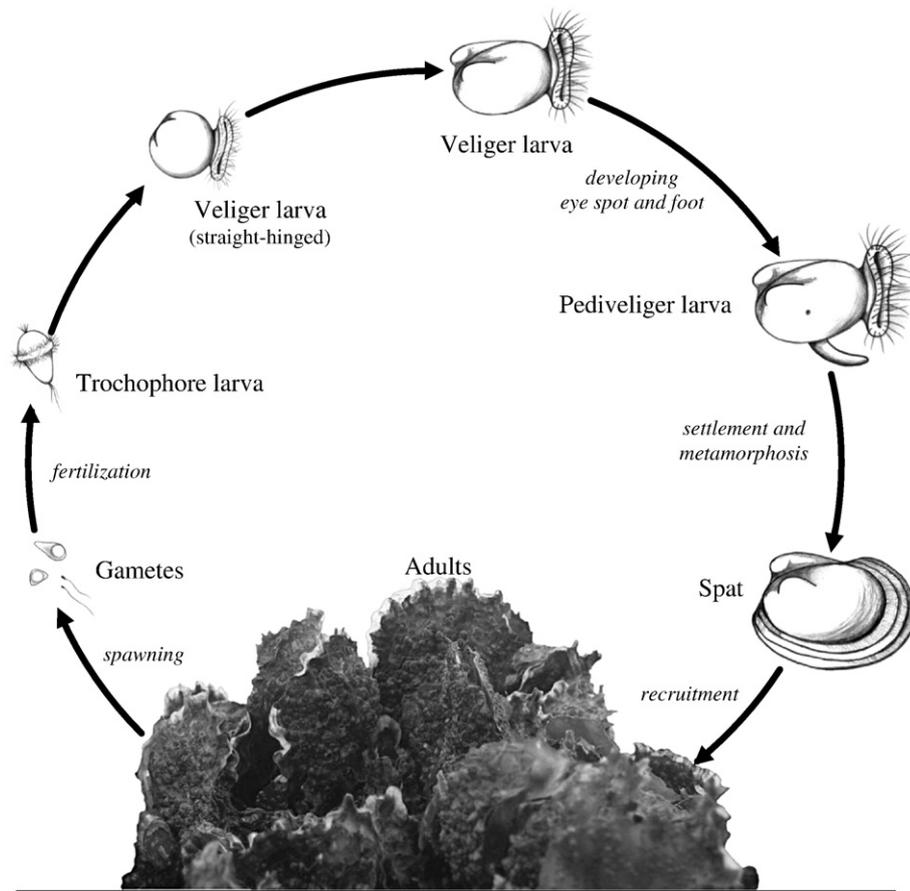


Fig. 2. Life cycle of oviparous bivalve filter-feeders (*C. gigas* as example; not drawn to scale). Adults release eggs and sperm into the water column where fertilisation takes place. Fertilised eggs usually develop via the trochophore stage into veliger larvae within approximately 2 days. The veliger larvae, about 70 to 300 μm in length, swim and forage with their velum. The first veliger stage is called the D-veliger or straight-hinged veliger. Veligers continue to develop through the veliconcha stage into the pediveliger stage, in which the larvae have developed a foot and eye spot. At this stage the velum begins to degenerate, resulting in reduced swimming abilities. The larvae are now competent to settle on a suitable substrate and to metamorphose into the benthic juvenile stage, approximately 3 weeks after fertilisation. The benthic juveniles grow and recruit into sexually mature adults (Seed, 1976; Butman, 1987; Arakawa, 1990b; Gosling, 2003).

becomes partially or almost completely attached to the substrate. As the oyster grows, generally the shell assumes the form of the substrate to which it attaches (Arakawa, 1990a; Reise, 1998; Gosling, 2003). Pacific oysters reach maturity at a shell length of about 50 mm (Kobayashi et al., 1997), which may already be reached in the first year after settlement. Pacific oysters feed by filtering planktonic organisms and detritus from the surrounding water. Relative to other bivalve species in Dutch estuaries individual *C. gigas* process larger volumes of water per time unit (Table 1).

Table 1

Filtration rates measured (as clearance rates) for mussels *M. edulis*, cockles *C. edule*, Pacific oysters *C. gigas* and European oysters *O. edulis*, given per individual and per standardized gram dry-tissue-weight.

Species	Dry tissue weight (g)	Temperature ($^{\circ}\text{C}$)	Individual filtration rate ($\text{l h}^{-1} \text{ind}^{-1}$)	Bodymass-specific filtration rate ($\text{l h}^{-1} \text{g}^{-1}$)	References
<i>M. edulis</i>	0.06–0.5	10–20	1.5–6.0	0.7–11.0	1–7
<i>M. edulis</i>	0.5–1.0	10–15		9.2	12
<i>C. edule</i>	0.3–0.5	10–15	1.3–5.0	0.7–7.4	1, 7–9
<i>C. gigas</i>	1.0–2.0	5–25	1.2–12.5	2.0–5.9	4, 10–11
<i>O. edulis</i>	0.5–2.0	20–22	5.7–10.3		4

References: 1) Møhlenberg and Riisgård, 1979, 2) Prins et al., 1996, 3) Petersen et al., 2004, 4) Walne, 1972, 5) Riisgård, 1977, 6) Famme et al., 1986, 7) Smaal et al., 1997, 8) Widdows and Navarro, 2007, 9) Foster-Smith, 1975, 10) Bougrier et al., 1995, 11) Gerdes, 1983.

3. Spatial spread of *C. gigas*

3.1. Initial introduction in The Netherlands

Nowadays, *C. gigas* is the main oyster species cultured in The Netherlands. Traditionally however, from the 1870's until the 1970's, Dutch oyster culture concentrated on European flat oysters *Ostrea edulis*. Between 1940 and 1950, flat oysters had already largely disappeared from the Dutch Wadden Sea due to habitat change and overfishing (Dijkema, 1997; Drinkwaard, 1999a). A combination of severe winters, mixing of native brood stocks with foreign strains and the accidental introduction of the parasite *Bonamia ostreae* led to the final downfall of the European oyster in Dutch waters (Drinkwaard, 1999b; Haenen, 2001). The decline of the European flat oyster instigated a search for alternative oyster species to culture. In 1964 a successful trial with Pacific oyster spat imported from British Columbia was carried out in the Oosterschelde estuary (Shatkin et al., 1997; Drinkwaard, 1999b). More introductions followed. In 1966, oyster farmers were told that the introduction of the Pacific oyster was acceptable since water temperatures in The Netherlands were assumed to be too low for this species to be able to reproduce, as had been the case with the closely related Portuguese oyster *C. angulata* (Dijkema, 1997; Drinkwaard, 1999b). Additionally, plans for closing off the Oosterschelde estuary from the North Sea had already been made. According to plan, this would have resulted in a fresh or brackish tide-free lake, unsuitable for oyster growth and reproduction. But plans were changed and the Oosterschelde estuary

remained a marine tidal system (Smies and Huiskes, 1981). The Pacific oyster soon proved to be able to reproduce in Dutch waters after all. In 1971, young *C. gigas* of approximately one year old were collected from the harbour of Zierikzee by F. Kerckhof (in prep.). In 1975, Pacific oyster spat were observed to have settled onto mussel shells and some intertidal mussel beds. In 1976 and 1982 extensive spatfalls were observed, which were attributed to prolonged periods of high water temperatures. From then on, most oyster farmers started to culture *C. gigas* (Drinkwaard, 1999b).

3.2. Area of origin

Pacific oysters occur from the Russian island of Sakhalin and Primorskiy Kray on the continent in the north (latitude $\sim 48^\circ$ N) to the Japanese island of Kyushu and the east coast of China in the south (latitude $\sim 30^\circ$ N; Fig. 3; Arakawa, 1990a). In Japan four regional strains of *C. gigas* were discerned by Imai and Sakai (1961), that originate from different geographical areas: Hokkaido, Miyagi, Hiroshima, and Kumamoto. However, the Kumamoto oyster was later shown to be a different species, *Crassostrea sikamea*, by Buroker et al. (1979) for Japanese populations and by Banks et al. (1994) for cultured oysters from the United States. The Miyagi and Hokkaido oysters come from a relatively cool climate with temperate conditions. They are relatively larger and grow faster than Hiroshima oysters that originate from a warmer region (Imai and Sakai, 1961). Oysters imported in British Columbia and The Netherlands were mainly (but not exclusively) of the Miyagi and Kumamoto strains, but experiments with Hiroshima oysters have also been conducted in The Netherlands (Shatkin et al., 1997; Drinkwaard, 1999b). It is not clear what happened with the Kumamoto *C. sikamea* oysters in The Netherlands. They may have hybridized with *C. gigas*, or they may have disappeared (see English et al., 2000). *C. sikamea* also seems to have disappeared from its native range in Japan and may now only be found in culture in North America (Banks et al., 1994). Mann et al. (1991) described *C. gigas* oysters in North American and European cultures as Miyagi-like and pointed out that there has been much intentional inter-breeding of introduced stocks, but that precise pedigrees are lacking.

The Portuguese oyster *Crassostrea angulata* was introduced in Portugal already somewhere between 1500 and 1800, probably on

ships' hulls (Wolff, 2005). These “Portuguese” oysters originated from a strain of *C. gigas* living at Taiwan (Ó Foighil et al., 1995; Boudry et al., 1998) and are therefore the same species as *C. gigas*. From Portugal these Portuguese oysters were introduced elsewhere in continental NW Europe but the species never established itself in Belgium, The Netherlands, and Germany and was completely wiped out by a disease in France around 1970 (Wolff and Reise, 2002).

3.3. Feral Pacific oysters in Dutch estuaries

Natural spatfall of *C. gigas* throughout the Oosterschelde estuary resulted in the formation of large and dense feral oyster reefs in the intertidal and subtidal areas. By means of stock assessments and reconstructions, the RIVO (Netherlands Institute for Fisheries Research, presently “IMARES”) estimated that on the 118 km² of intertidal flats in the Oosterschelde estuary the cover by oyster beds increased from 0.25 km² in 1980 to 8.1 km² in 2003 (Kater and Baars, 2004; Dankers et al., 2006). Oyster cover on hard substrates (160 km of dikes and sea walls, 2–4% of the total bottom surface area; Leewis et al., 1994) generally increased from 0–10% in 1985 to 50–60% in 2002, and even to 90% on some locations (AquaSense, 2003). Within this period, during the 1990's, stocks of the native blue mussel *M. edulis* and common cockle *C. edule* showed a decrease (Geurts van Kessel et al., 2003; Dankers et al., 2006).

The introduction of *C. gigas* into the Wadden Sea goes back to the late 1970's at the island of Texel, in the cooling water basin of a power and desalinization plant. In 1976, someone intentionally released a bucket-full of Pacific oyster spat here (Tydeman, 2008). In 1978, the RIVO released juvenile Pacific oysters that were mixed with *O. edulis* spat from a French hatchery in the relatively warm waters of the cooling water basin (Smaal et al., 2009). Today, the oysters are still steadily spreading throughout the Dutch Wadden Sea where they locally cover rubble-mound breakwaters and tidal flats (mostly on existing mussel beds and shell banks) in high densities (Cadée, 2001; Tydeman et al., 2002; Wolff, 2005; Fey et al., 2009). Total cover of the intertidal by oyster beds was estimated at 4 km² in 2004 (Smaal et al., 2005) and at 5.5 km² in 2005 (Dankers et al., 2006).

In Lake Grevelingenmeer a first natural spatfall of *C. gigas* was observed in 1987 (Drinkwaard, 1999b) and the Pacific oyster is now one of the dominant bivalve species (Sistmans et al., 2005). In the



Fig. 3. Native range of the Pacific oyster *C. gigas*.

Westerschelde estuary, Pacific oysters are only found in low numbers and almost exclusively on man-made hard substrates (Drinkwaard, 1999b; pers. obs.).

3.4. Introduction and spread of Pacific oysters in Belgium

Following the initial introduction in The Netherlands in 1964, Pacific oysters were also introduced in Belgium (1969), Germany (1971), Denmark (1972), Sweden (1973) and Norway (1979). In Belgium, oysters of different species and from different regions have been imported in the Sluice Dock of Ostend (Kerckhof et al., 2007). The Sluice Dock was used for cultivating and/or relaying oysters from the 1930's until World War II and again from 1957 to 1974. European flat oysters *O. edulis* were cultured here, but also *C. virginica* imported from the east coast of the United States and *C. angulata* imported from southern Europe (Kerckhof et al., 2007). Neither *C. virginica* nor *C. angulata* became established in Belgian coastal waters. In 1969 and the early 1970's, Pacific oysters *C. gigas* were imported. The first oysters originated from The Netherlands, but later imports were also made from Japan, Canada, France and the Mediterranean (Kerckhof et al., 2007; F. Kerckhof, pers. comm.). In 1974 oyster culture in the Sluice Dock stopped because of poor water quality. Although all imports and culture activities were stopped, *C. gigas* remained a

resident of the Sluice Dock. Apparently this species was able to reproduce in Belgian waters (Kerckhof et al., 2007). Since the 1970's the Pacific oyster has colonized the Belgian coast, and now forms extensive reefs in the harbours of Ostend, Nieuwpoort, Zeebrugge and Blankenberge (Kerckhof et al., 2007). The species is regularly found living on piers and jetties and washed ashore (Kerckhof, 1997; Jonckheere, 2006). Especially the 1990's saw a rapid proliferation of the species in Belgian waters (F. Kerckhof, pers. comm.). Since 1996, oyster culture in the Sluice Dock has resumed. Next to the limited use of local brood stock, again *C. gigas* are imported from European countries and Canada (Kerckhof et al., 2007).

3.5. Introduction and spread of Pacific oysters in Germany

Pacific oysters are also spreading throughout the German Wadden Sea (Fig. 4; Reise, 1998; Diederich et al., 2005; Nehls et al., 2006). The western part of the German Wadden Sea, the East Frisian Wadden Sea, has been systematically searched for wild *C. gigas* on mussel beds since 1996 (Wehrmann et al., 2000). Here, the first naturally dispersed oysters were detected in 1998. Although an experimental culture plot for *C. gigas* had existed for one farming season in 1987 near the island of Norderney, this was considered an unlikely source for the observed wild *C. gigas*. Instead, the East Frisian Wadden Sea

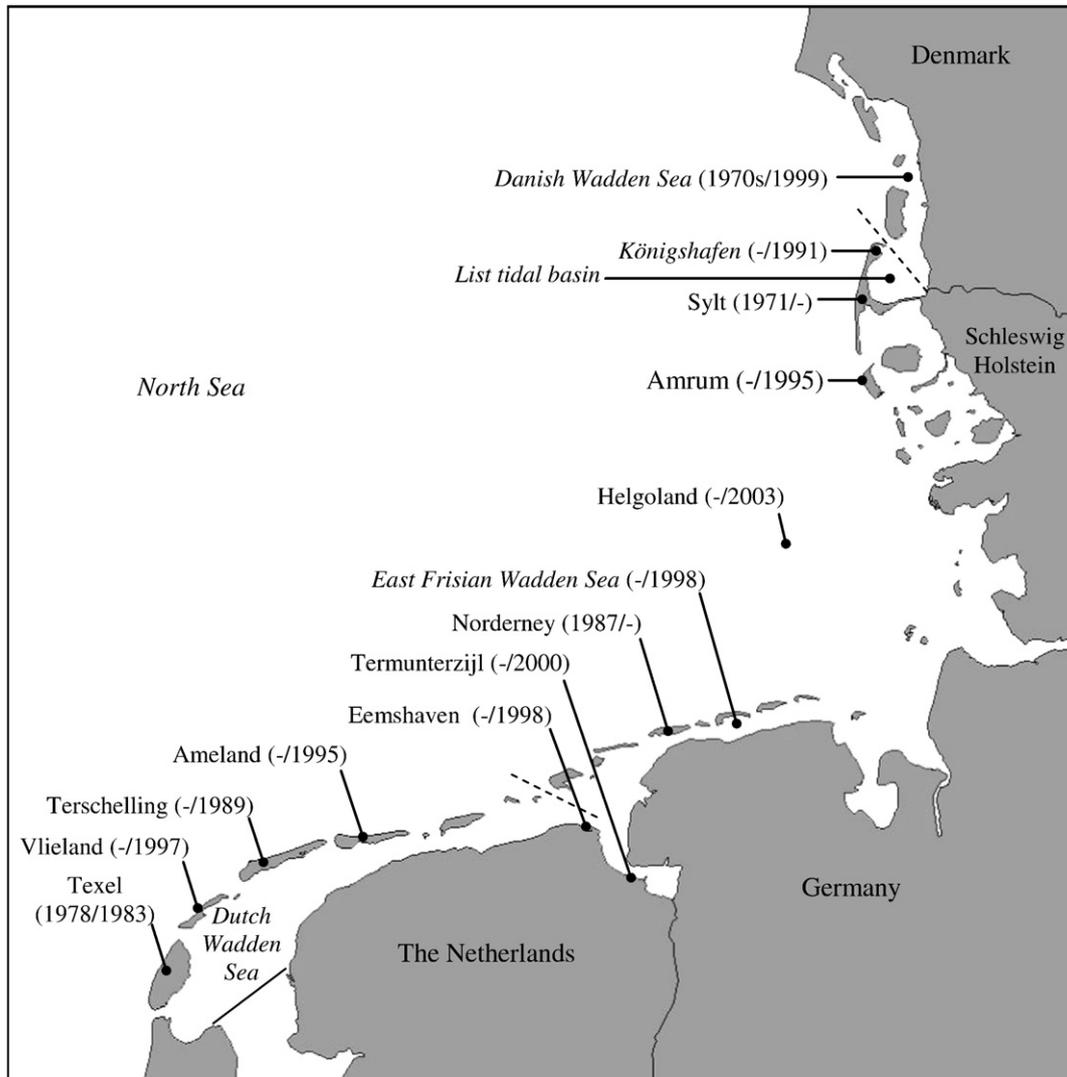


Fig. 4. Locations where *C. gigas* was first introduced/encountered (years between brackets) in the Wadden Sea area (Bruins, 1983; Reise, 1998; Drinkwaard, 1999b; Tydeman, 1999; Wehrmann et al., 2000; Tydeman et al., 2002; Diederich et al., 2005; Wolff, 2005; Nehls et al., 2006). Locations of islands and water bodies are given, not exact locations of introductions/encounters.

was probably invaded from the Dutch Wadden Sea (Wehrmann et al., 2000).

In the northern part of the German Wadden Sea, the List tidal basin in the Wadden Sea of Schleswig–Holstein was colonized from an oyster culture site at the northernmost German island of Sylt (Reise, 1998; Wehrmann et al., 2000). Here, *C. gigas* spat from a Scottish hatchery were imported for the first time in 1971 and again in 1972 for a raft culture experiment (Drinkwaard, 1999b). At the end of the 1970's, outdoor experiments on growth and fattening and indoor experiments on rearing of spat from larvae were continued (Drinkwaard, 1999b). At Sylt, regular oyster culture on trestles started in 1986 (Reise, 1998; Drinkwaard, 1999b). Juvenile and seed oysters were imported regularly from hatcheries and a nursery on the British Isles and Ireland (Drinkwaard, 1999a,b). The first *C. gigas* individual outside the culture plot at the island of Sylt was observed in 1991 in the Königshafen Bay (Reise, 1998; Drinkwaard, 1999b). Since 1995, *C. gigas* is also found on mussel beds near the island of Amrum, south of Sylt, which became the second centre of oyster distribution in the Wadden Sea of Schleswig–Holstein (Nehls et al., 2006). Since 2000, the abundance of *C. gigas* in this area increased markedly. In Schleswig–Holstein, as in the East Frisian Wadden Sea and the Dutch Wadden Sea, *C. gigas* settles preferentially on mussel beds (Reise, 1998), and by 2004 almost all mussel beds in the List tidal basin near Sylt had been colonized (Nehls et al., 2006). Densities of *C. gigas* on mussel beds in Schleswig–Holstein were on average 290 m^{-2} , up to a maximum of 600 m^{-2} (Nehls et al., 2006). Highest densities were found in the List tidal basin near Sylt (Diederich et al., 2005). The first wild oysters on the offshore German island of Helgoland were found in 2003 (Diederich et al., 2005).

3.6. Introduction and spread of Pacific oysters in Scandinavia

Also in Scandinavia, Pacific oysters were introduced for culture purposes (reviewed by Wrangle et al., 2009). In Denmark, the first introduction took place in Limfjorden in 1972. In the following years, seed oysters were introduced to establish cultures in the Limfjorden, the Wadden Sea and at several locations along the Danish Baltic coast (Little Belt, Isefjorden, Mariager Fjord, and Horsens Fjord). At some of these sites, farming continued during the 1980's and 1990's. In the 1990's the first naturally occurring oysters were found in the Danish Wadden Sea (Diederich et al., 2005). In the period 2005–2008, Wrangle et al. (2009) made an effort to map the distribution and abundance of Pacific oysters in Scandinavian waters. By then, the population in the Wadden Sea had increased rapidly. Densities of up to 55.8 kg m^{-2} were found in 2007. In Limfjorden, densities of several to $<20\text{ specimens m}^{-2}$ were found and a reef structure was observed in the western part of the fjord. Five size cohorts were discerned (unfortunately not supported by graphs, Wrangle et al., 2009). At the Baltic coast locations, densities of $<1\text{ m}^{-2}$ were found.

In Sweden, oyster spat were imported at the west coast, northern Bohuslän, between 1973 and 1976. Only few specimens were reported from the wild until 2007, when feral Pacific oysters were reported from many locations along the west coast. In the period 2007–2008, a mean density of $<1\text{ m}^{-1}$ was found, with a maximum density of $505 \pm 173\text{ m}^{-2}$ in the most northern region (mostly 60–70 mm shell length). Two size cohorts were discerned (Wrangle et al., 2009).

In Norway, Pacific oysters were imported in 1979 for the establishment of a brood stock population. Three hatcheries produced millions of spat from 1987 to 1990 (in Vallersund, Espevik and Øygarden, 64° – 60° North). From 1981 until 1986, farmers imported seed oysters from Scotland for cultivation along the Norwegian coast. This practise became largely restricted in 1986. During the last two decades, adult oysters have been imported and re-laid in Norwegian waters. In the period 2006–2008, Wrangle et al. (2009) only found single oysters at several locations, but discerned 4 size cohorts. The

largest oysters may have been remnants of live-stored imported oysters (Wrangle et al., 2009).

Although in Scandinavia water temperatures had been assumed to be too low for reproduction of *C. gigas*, as had been the case in The Netherlands, Pacific oysters are now naturally reproducing in Danish, Swedish and Norwegian waters. The recent success of *C. gigas* in Scandinavia and northern Germany appears to be related to the occurrence of exceptionally warm summers and mild winters during the last decade (Diederich et al., 2005; Wrangle et al., 2009).

4. Causes of successful establishment and natural spread

4.1. Characteristics of successful invaders and invisable ecosystems

In many cases an invader is not discovered until after the invasion event, at a point where the invader already is a part of the ecosystem (Williamson, 1996). Consequently, ecological responses to the invasion may go unnoticed for a long time, and the mechanism of invasion and the causes of its success may never be elucidated. A large body of scientific work is devoted to finding general rules in invasion ecology. What characteristics determine whether species are invasive? And what characteristics determine whether a community is invisable? Species that are introduced into new habitats encounter many abiotic and biotic barriers (Colautti et al., 2006). They have to be able to live in or adapt to the new habitats. Generally three determining stages are identified in invasion ecology: 1) colonization of the receiving habitat, 2) establishment in the receiving habitat, 3) natural range expansion after establishment (Sakai et al., 2001). Common causes of failure to establish are: an unsuitable climate, disturbance, predation, competition and disease. Species that do manage to establish themselves face many different interactions with native species in the new community (Lodge, 1993; Sakai et al., 2001). Many attempts have been made to identify characteristics of species that allow predictions about their invasiveness (Lodge, 1993; Williamson and Fitter, 1996; Morton, 1997; Kolar and Lodge, 2001; Sakai et al., 2001). For a successful invasion, different traits may be required for the different stages of the invasion (colonization, establishment and natural range expansion) (Sakai et al., 2001). The applicability of these traits to the introduced Pacific oyster will further be discussed for each of these three invasion stages (Table 2) except for the first stage: colonization. Traits contributing to successful

Table 2

A selection of characteristics generally attributed to successful invaders, especially relevant for bivalve invaders and for the three principal stages from first colonization to natural range expansion (from Lodge, 1993; Williamson and Fitter, 1996; Morton, 1997; Sakai et al., 2001; Marvier et al., 2004; Wallentinus and Nyberg, 2007; and references therein).

Stage	Trait
Colonization	<ul style="list-style-type: none"> <i>r</i>-selected life history strategy: <ul style="list-style-type: none"> Rapid growth Rapid sexual maturation High fecundity Generalists: <ul style="list-style-type: none"> Ability to colonize wide range habitat types Broad diet Tolerance to wide range environmental conditions Gregarious behaviour Genetic variability and phenotypic plasticity Ability to recolonize after population crash
Establishment (Section 4.2)	<ul style="list-style-type: none"> Lack of natural enemies Ecosystem engineering Association with humans Repeated introductions Genetic variability and phenotypic plasticity Competitiveness
Natural range expansion (Section 4.3)	<ul style="list-style-type: none"> Traits of successful colonists (see above) Dispersability

colonization are important for invaders that are accidentally and incidentally introduced somewhere, but are of minor importance for invaders that are imported multiple times for cultivation, such as *C. gigas*. Initial colonization by *C. gigas* was entirely facilitated by oyster farmers. Pacific oysters were introduced repeatedly, providing the species with a repeated chance at every reproduction season of becoming established.

4.2. Traits contributing to successful establishment

4.2.1. Lack of natural enemies

A lack of natural enemies in the receiving community is often suggested as a reason for fast proliferation of introduced non-indigenous species (Table 2; Williamson and Fitter, 1996; Keane and Crawley, 2002; Liu and Stiling, 2006). To find out whether this “enemy release hypothesis” is applicable to the successful establishment and rapid expansion of *C. gigas* in Dutch waters, an overview of predators, parasites and diseases affecting *C. gigas* in the North-West Pacific and in The Netherlands is given here.

In the Wadden Sea and Dutch estuaries native bivalves are generally heavily preyed upon by various bird species (Reise, 1978; Beukema et al., 1993; Nehls et al., 1997), but *C. gigas* is affected much less by bird predation. Herring gulls (*Larus argentatus*) and oystercatchers (*Haematopus ostralegus*) are the only bird species reported to feed on *C. gigas*. Herring gulls prey upon *C. gigas* locally. They take a loose individual up in the air, and break the shell by dropping the oyster several times on a hard surface, usually a stone-covered dike (Cadée, 2001; 2008b at Texel, Wadden Sea; own unpublished observations in the Oosterschelde estuary). Recent anecdotal information suggests that oystercatchers *H. ostralegus* are learning to feed on *C. gigas* in the Wadden Sea (Scheiffarth et al., 2007; Cadée, 2008a) and Oosterschelde estuary (Baptist, 2005) by prying gaping individuals open with their beak. However, predation by herring gulls and oystercatchers in Dutch estuaries still occurs locally at low rates and is not expected to cause significant losses (Cadée, 2008b).

Little information on the role of bird predation in the North-West Pacific could be found. The local species of oystercatcher (*H. ostralegus osculans*) is said to be an uncommon species (Del Hoyo et al., 1996). The black-tailed gull *Larus crassirostris* is a common omnivore in Japan, and reported to feed on molluscs (Del Hoyo et al., 1996). However, no information was found on whether Pacific oysters are also included in its diet. No indications were found that bird predation pressure in the Pacific differs very much from that in The Netherlands.

Fish species in The Netherlands reported to feed on bivalve spat are the gobies *Pomatoschistus microps* and *P. minutus*, and juvenile flatfish of the species *Pleuronectes platessa*, *Platichthys flesus* and *Solea solea* (Hiddink et al., 2002 and references therein). Whether these fish also predate on spat of *C. gigas* is not known. In Japan, Pacific oyster spat is reportedly preyed by the black sea bream *Acanthopagrus schlegelii* and the fine-patterned puffer *Takifugu poecilonotus* in Hiroshima Bay (Saito et al., 2008).

In The Netherlands especially juvenile stages of bivalves are preyed upon by a variety of epibenthic invertebrate predators (Beukema, 1991; Beukema et al., 1998; Van der Veer et al., 1998; Hiddink et al., 2002). The most common invertebrate shellfish predators in the Wadden Sea and Dutch estuaries are the brown shrimp *Crangon crangon*, the shore crab *Carcinus maenas* and the common starfish *Asterias rubens*. Of these the shore crab and the starfish have been shown in laboratory experiments to predate on *C. gigas* as well (Diederich, 2005a: oysters with shell lengths of up to 40 mm offered to and preyed by *C. maenas*, and oysters of up to 60 mm offered to and preyed by *A. rubens*). However, both predators have a preference for *Mytilus edulis* over *C. gigas* of similar shell length, and Diederich (2005b) found no significant effects of predation on post-settlement survival of *C. gigas* juveniles in the German Wadden Sea at Sylt. *C. crangon* causes high mortality rates

among native bivalve spat (Van der Veer et al., 1998), but no empirical studies on whether it also feeds on *C. gigas* spat were found. *C. crangon* may not be adapted to scrape oyster spat from shells or stones.

In its native range, the Pacific oyster is preyed by crabs (Fukui, 1988). It is also attacked by a variety of other epibenthic predators not occurring in Dutch waters. In Japan oysters are preyed by several species of predatory flatworms (Turbellaria, Polycladida; Kato, 1944; Galleni et al., 1980) among which *Pseudostylochus ostreophagus*, especially dangerous to oyster spat, and *Stylochus ijimai* that predate on adult oysters (Korringa, 1976). Gruet et al. (1976) describe how Pacific oysters imported from Japan into France were immersed in freshwater to kill these flatworms; apparently this treatment was successful. Fujiya (1970) describes the following natural enemies of *C. gigas* in hanging-culture in Japan, all oyster drills: *Thais tumulosa clavigera*, *Thais bronni*, *Tritonalia japonica*, *Rapana thomasiana* (presently referred to as *R. venosa*), and *Ceratostoma burnetti*. Among these species, *T. tumulosa clavigera* is the most serious enemy of oysters (Fujiya, 1970). Some of these predators were introduced with early oyster shipments to North America, before Canadian and American authorities developed and implemented control measures in cooperation with Japanese authorities and seed growers (Quayle, 1988). Lavoie (2005) mentions the flatworm *P. ostreophagus* and the Japanese oyster drill *Ocenebra japonica* (Dunker 1860) (also called *Tritonalia japonica* (Dunker 1850), *Ceratostoma inornatum* (Recluz 1851), and presently referred to as *Ocenebrellus inornatus* (Recluz 1851)). This oyster drill originates from the same geographical range as *C. gigas*, and was introduced in North America in 1924 and, from there, to France in 1995 (Martel et al., 2004). The veined whelk *Rapana venosa* was introduced to several areas over the world (Black Sea, Aegean Sea, Adriatic Sea, Uruguay, the eastern USA, and north-western France) and was found in the southern North Sea in 2005 (Kerckhof et al., 2006). So far no veined whelks or flatworms predate on *C. gigas* have been reported from Dutch estuaries. The oyster drills *Ocenebrellus inornatus* and *Urosalpinx cinerea* (native to the US east coast) have been found in the Oosterschelde estuary in 2007 and 2008 (Faasse and Ligthart, 2007; Goud et al., 2008). They were likely introduced only recently and still occur very locally and in low numbers. It may therefore be concluded that the predation pressure from epibenthic invertebrate predators in previous years was likely to be much higher in the North-West Pacific than in the Netherlands, thus giving support to the “enemy release hypothesis” as an explanation for the proliferation of *C. gigas* in Dutch estuaries. In addition, Schmidt et al. (2008) observed exceptionally low mortality rates among juvenile Pacific oysters and decreasing survival rates during the early years of invasion. Among other possible explanations they suggested that predators may gradually adapt to the new prey items available (Schmidt et al., 2009, a reply to Beukema and Dekker, 2009), but this needs further investigation. Pacific oysters are furthermore also preyed by humans. In the Oosterschelde estuary Pacific oysters are hand-picked for consumption mainly by Asian immigrants (unpublished observations). This suggests that collection of seafood by hand may be a more common practise in Asian countries (see Sechena et al., 1999) and that predation pressure on oysters by humans is higher in the NW Pacific than it is in NW Europe.

The “enemy release hypothesis” does not appear applicable to parasites and diseases. From Japan and British Columbia, live adult Pacific oysters were introduced directly into the Oosterschelde estuary. Therefore, most parasites and diseases that are present in the areas of origin and that have been able to survive and establish in the receiving ecosystem, are likely to be present in the Oosterschelde estuary. The copepod parasites of the Pacific oyster *Mytilicola orientalis* and *Myicola ostreae* were thus introduced with Pacific oyster imports from Japan or British Columbia (Stock, 1993; Wolff, 2005). It is not known whether the latter species is presently established in Dutch waters (Wolff, 2005). *M. orientalis* causes loss of gonadal mass in *M. edulis* (Mann 1956 and Williams 1969 in Steele

and Mulcahy, 2001), but it hardly affects *C. gigas* (Steele and Mulcahy, 2001). The bacterium *Nocardia crassostreae* also seems to have been introduced from Japan and/or the west coast of North America. In these regions, occurrence of this bacterium in Pacific oysters is associated with summer mortalities (references in Engelsma et al., 2008). *N. crassostreae* was recently found, together with the bacterium *Vibrio aestuarianus*, in *C. gigas* from Lake Grevelingenmeer (The Netherlands; Engelsma et al., 2008). The infected oysters were collected after an extensive mortality in the summer of 2006. However, Engelsma et al. (2008) concluded that the oysters had mainly died because of physiological stress due to adverse environmental conditions in Lake Grevelingenmeer, and the bacteria may only have contributed as a secondary cause to the observed mortality. Parasites of *C. gigas* that were already described from Dutch estuaries before the first introduction of *C. gigas* are the fungus *Ostracoblabe implexa* and spionid polychaetes of the genus *Polydora* (Korringa, 1952). The fungus *O. implexa* affects and weakens *C. gigas*' shell, but this does not seem to lead to significant mortalities (Engelsma and Haenen, 2004). *Polydora* spp. weaken the shell of *C. gigas* and the native oyster *O. edulis* by burrowing into it (Korringa, 1951; Almeida et al., 1996), but this does not appear to cause mortalities among the two species (Engelsma and Haenen, 2004). In Japan, *C. gigas* is also infected by polychaetes of the genus *Polydora*, but as in The Netherlands these do not cause serious damage (Fujiya, 1970). In the German Wadden Sea, *C. gigas* is furthermore infected by the native trematode *Renicola roscovita* and a single infection by the native turbellarian *Paravortex* sp. was reported near the island of Sylt (Krakau et al., 2006). Krakau et al. (2006) demonstrated that introduced bivalves (*C. gigas* and *Ensis americanus*) are infected by a fraction of the native parasites of bivalves present, and that trematode intensity was always lower in the introduced species. *C. gigas* was furthermore infected by the native trematode *Himasthla elongata* in the laboratory, but in *C. gigas* the cercariae did not develop into metacercariae, as they would normally do in their common second intermediate host *M. edulis* (Thieltges et al., 2009). No infections with *H. elongata* were found in the field (Krakau et al., 2006). Krakau et al. (2006) hypothesized that native parasites adapt to the new hosts, possibly leading to significant infestations in the future. The Pacific oyster is furthermore not affected by bonamiosis (Renault, 1996). After its introduction with oyster imports from Brittany in 1980, bonamiosis has caused very high mortality rates among *O. edulis* (Drinkwaard, 1999a). The protist *Bonamia ostreae* that causes bonamiosis possibly originates from the north-east Pacific (Wolff, 2005 and references therein). Tentatively, Pacific oysters do not seem to be released from their Pacific parasites and diseases in the receiving NW European estuaries, and are infected by native European parasites as well. In comparison to native bivalves, however, Pacific oysters do seem to be affected less by these natural enemies.

4.2.2. Ecosystem engineering by *Crassostrea gigas*

Habitat modification by introduced and invasive ecosystem engineers facilitates establishment and subsequent colonization of new areas (Table 2) by adapting the encountered habitat, that may have been suboptimal, to the demands of the invader (Cuddington and Hastings, 2004). The Pacific oyster is such an invasive ecosystem engineer since it modifies habitats by constructing large three-dimensional reef structures (Jones et al., 1994; Gutiérrez et al., 2003). Reef formation is enhanced by the gregarious settling behaviour of Pacific oyster larvae. The larvae preferentially settle onto shells of Pacific oysters (Diederich, 2005a) and settlement is triggered by presence of adult oysters (Tamburri et al., 2007) and apparently also by previously settled spat (Troost, 2009). By settling on top of each other, cementing their shells together during growth, Pacific oysters create a strong reef structure. The reef structure modifies the habitat to the demands of the invader in several ways. Besides through gregarious behaviour, larval settlement is also

enhanced by the baffling of water movements by the oysters in the bed (Commito and Rusignuolo, 2000). The three-dimensional structure provides shelter against extreme environmental conditions such as heat and desiccation (Bartol et al., 1999; Gutiérrez et al., 2003). It also offers a refuge from predation by e.g. birds that have difficulty reaching into the oyster bed, and from benthic predators such as crabs. The high degree of structural complexity in an oyster reef reduces the predator-prey encounter rate (Bartholomew et al., 2000; Grabowski, 2004) resulting in higher growth and survival of oyster spat (Nestlerode et al., 2007). Additionally, the firm attachment of oyster spat and juveniles to adult oysters may serve to reach a size refuge from the beginning with respect to predators that consume solitary individuals. Oyster beds may also affect particle and solute transports by altering near-bed flow (Gutiérrez et al., 2003). The roughness of oyster reefs enhances near-bed turbulence levels, thereby increasing the food flux towards the bivalves and reducing refiltration of already filtered seawater (Jonsson et al., 2005; Widdows and Navarro, 2007; Troost et al., 2009b). Furthermore, the reef structure offers a large area of suitable settlement substrate that, in general, seems very persistent. Pacific oyster reefs, consisting mainly of empty oyster shells cemented together after a mass mortality, were observed to largely remain in place (Fey et al., 2009; own unpublished observations). Following mass mortality, an extensive spatfall of larvae from another brood stock will then be sufficient to recolonize the entire reef. Pacific oysters therefore increase the area suitable for settlement by building reefs, and in this way ensure settlement possibilities on a longer time scale. This process will be enhanced by the oysters' gregarious settling behaviour and high dispersability.

4.2.3. Other traits contributing to successful establishment of *Crassostrea gigas*

Other traits generally thought to contribute to successful establishment (Table 2) all seem applicable to *C. gigas*. Because Pacific oysters are associated closely to humans in the sense that they are cultured world-wide for consumption, they have been introduced all over the world. In The Netherlands, Pacific oysters have been introduced repeatedly from 1964 to around 1980 (Drinkwaard, 1999b). Propagule pressure was therefore high, increasing the genetic variation of the introduced stock, widening the genetic bottleneck and increasing chances of establishment and adaptation to the new environment. Japanese populations show a high genetic variation, and most of this high variation appears to have been retained by populations of *C. gigas* introduced for mariculture world-wide (Hedgecock et al., 1996; English et al., 2000; references therein). In addition to the relatively large gene pool in the new area, the species also appears highly adaptable phenotypically, as are many species of sessile bivalves (Bayne, 2004). In terms of survival, growth and reproductive effort, *C. gigas* responds plastically to spatial variability in food abundance (Ernande et al., 2003). Pacific oysters are also flexible in the morphology of their feeding organs (relative sizes of gills and labial palps; Honkoop et al., 2003), and in their limits of thermal tolerance (Hamdoun et al., 2003). As in many other bivalves, also the larvae and spat of *C. gigas* exhibit high phenotypic variation, particularly in terms of growth and survival (Taris et al., 2006). High phenotypic flexibility enables an invader to adapt to a wide range of conditions, and increases chances of becoming established and of competing successfully with native species.

Pacific oysters apparently have all the right tools to adapt to new environments quickly. But did they really need to adapt to Dutch waters that much? Diederich et al. (2005) showed that the invasion of the northern German Wadden Sea was accelerated by an increasing frequency of warm summers. The more southern and relatively warmer Oosterschelde estuary, however, has sea surface temperatures that are comparable to those in the area of origin of the Miyagi and Kumamoto strains that were mainly imported in the Netherlands (Oceanographic atlas of the Bering Sea, Okhotsk Sea and Japan/East

Sea, www.pacificinfo.ru/en/, January 2009). Summer temperature was therefore likely not limiting for recruitment of the Pacific oyster in the Oosterschelde estuary, which will have contributed to its fast establishment. The natural occurrence at the Russian island of Sakhalin, between the Sea of Japan and the subpolar Okhotsk Sea, should have been a warning that Dutch waters were not at all too cold for *C. gigas* to reproduce.

Competitiveness is also a characteristic contributing to successful establishment of non-native species. Its applicability to *C. gigas* will be discussed in Section 5.

4.3. Traits contributing to successful natural spread after establishment

4.3.1. Colonization capabilities

Once an invader is established, subsequent spread is related to the dispersability and colonization capabilities of the invader (Table 2). Successful colonists are generally species with fast reproductive rates. They are characterized by fast growth rates, rapid sexual maturation and a high fecundity (Lodge, 1993; Williamson and Fitter, 1996; Morton, 1997; Sakai et al., 2001) (Table 2). These are traits of an *r*-selected life history strategy (Pianka, 1970) of which the Pacific oyster exhibits many features. Growth of Pacific oysters is rapid. Two-year old Pacific oysters have been reported to reach lengths of up to 80 mm at Sylt, Germany (Diederich, 2006), and lengths of 30 mm on average at Texel and Yerseke, The Netherlands (Cardoso et al., 2007). The oysters, that can live up to about 10 years (Cardoso et al., 2007), reach maximum lengths of up to 300 mm (Reise, 1998; Cardoso et al., 2007; own unpublished observations). Fast growth may enable the oysters to reach a size refuge from invertebrate and fish predation quickly. In addition, Diederich (2006) observed very high survival rates of *C. gigas* juveniles in comparison to native species. The combination of fast growth and high survival may account for a fast population increase, and may compensate for recruitment failures near the distribution limits (Diederich, 2006).

Another trait of successful colonists that may have contributed to successful natural spread after establishment is habitat generalism (Marvier et al., 2004). Characteristics of habitat generalists include: broad tolerances for wide ranges of environmental conditions, the ability to occupy a wide range of habitat types, and a broad diet (Table 2; Lodge, 1993; Morton, 1997; Sakai et al., 2001; Marvier et al., 2004). Although Pacific oysters in first instance settle onto hard substrates in the subtidal and intertidal, they also develop beds on soft bottoms by first settling onto small pieces of shell and stones (Quayle, 1988; Mann et al., 1991; Lewis et al., 1994; Wolff, 2005; Dankers et al., 2006). This is facilitated by their gregarious settling behaviour. The native geographical range of *C. gigas* is very wide (Fig. 3), comprising a large range of abiotic conditions. The regions where *C. gigas* was successfully introduced also cover a wide geographical range (including countries in North and South America, Europe, Asia, Africa and Oceania; Arakawa, 1990a; Dinamani, 1991; Grizel and Héral, 1991; Shatkin et al., 1997; FAO, 2004; Wolff, 2005). Hence, the Pacific oyster was already adapted to a wide range of environmental conditions, and appears able to quickly adapt to new habitats. This is confirmed by its ability to sustain a wide range of environmental conditions. The oysters can survive water temperatures up to 40 °C (Shamseldin et al., 1997) and at low tide air temperatures as low as −5 °C (Korringa, 1952) and even lower, depending on the salinity of the water enclosed in their shells (>75% survival at 30 psu, at −12 °C air temperature; exposure during 7 days, 6 h per day, mimicking tidal emersion; Wa Kang'eri, 2005). Growth occurs between 10–40 °C and 10–30 psu, and spawning between 16–30 °C and 10–30 psu. Larvae can sustain temperatures between 18 and 35 °C and salinities between 19 and 35 psu (Mann et al., 1991 and references therein; Rico-Villa et al., 2009).

Furthermore, gregarious settlement of the larvae, genetic variability and phenotypic plasticity, as well as an ability to recolonize areas rapidly following a population crash are considered to be general

traits of successful colonists (Table 2). The applicability of these traits to *C. gigas* was already established in the previous section (Section 4.2. Traits contributing to successful establishment). The ability of recolonizing areas results from the Pacific oyster's ecosystem engineering capacities and its high dispersability (discussed below).

4.3.2. Dispersability

Pacific oysters are broadcast spawners and are highly fecund. An oyster female may produce more than 50 million eggs per spawning, which is high compared to native bivalves (Helm et al., 2004). *A. M. edulis* female may produce 5–12 million eggs per spawning (Helm et al., 2004), a *C. edule* female 0.2–0.7 million eggs (Honkoop and Van der Meer, 1998) and a *Macoma balthica* female 0.02–0.07 million eggs (Honkoop and Van der Meer, 1998). Per square meter bed, however, total egg production of *C. gigas* and *M. edulis* is comparable because the latter generally occurs in higher densities (see Nehls et al., 2006). In The Netherlands, Pacific oysters produce more and relatively smaller eggs than their more southern kin in France (Cardoso et al., 2007). These smaller eggs have a lower energy content and therefore result in a longer duration of the pelagic larval phase (Van der Veer et al., 2006; Cardoso et al., 2007). This enables a wider dispersion range, although smaller eggs may also result in a lower fertilisation rate (Luttikhuis et al., 2004) and a prolonged pelagic phase may result in an increased pre-settlement mortality. Although the bulk of the larvae travel up to 5 to 15 km, a smaller part will be carried further with residual currents (Wehrmann et al., 2000; Brandt et al., 2008). The Pacific oyster shows a large capability of spreading rapidly after first introduction and establishment. From the moment the first spatfall was observed the rate of spread to new areas has been very fast in France, The Netherlands and Germany (Grizel and Héral, 1991; Kater and Baars, 2004; Diederich, 2005b; Cognie et al., 2006; Nehls et al., 2006; Fey et al., 2009). This illustrates the high potential for range expansion of *C. gigas*.

4.4. Invasiveness of receiving communities

Many attempts have been made to identify characteristics that determine the invasiveness of receiving communities. Despite conflicting evidence, disturbance is often considered such a characteristic (Lodge, 1993; Occhipinti-Ambrogi and Savini, 2003; Marvier et al., 2004). Although many coastal ecosystems in continental NW Europe are considered to be disturbed, the nature of these disturbances varies widely from one ecosystem to another (e.g. pollution, dredging, shipping, coastal engineering). Furthermore, anthropogenic disturbance is a factor which is hard to quantify. *C. gigas* has invaded so many ecosystems that it is difficult to believe that disturbance played an important role and it seems impossible to prove so, or otherwise.

A lack of predators in the receiving community is furthermore often suggested as a reason for fast proliferation of introduced non-indigenous species. This was already concluded to have played a role in the fast proliferation of *C. gigas* in Section 4.2.

Finally, species-poor estuarine communities seem more susceptible to invasions than species-rich, more saturated communities (Wolff, 1973; Lodge, 1993; Stachowicz et al., 1999; Wolff, 1999). This is thought to be a contributing factor to the relatively large number of non-indigenous species recorded in brackish (5–20 psu) estuaries (Wolff, 1973; Wolff, 1999; Nehring, 2006). Highest densities of *C. gigas* are, however, found at salinities higher than 20 psu. The Oosterschelde estuary itself is not at all poor in native species (Wolff, 1973; Hostens and Hamerlynck, 1994; Sistermans et al., 2005; Wolff, 2005), and moreover harbours many non-indigenous species that were imported through shellfish culture activities (Wolff, 2005). Hence, species richness did not play a part in the establishment of *C. gigas* in the Oosterschelde estuary. The Wadden Sea has lost many habitat building species and associated communities due to overexploitation (Reise, 1982; Wolff, 2000; Lotze, 2005; Airoidi and

Beck, 2007) although it also gained some non-indigenous species (Reise et al., 1999). Macro-benthic species richness of the tidal flats is rather low compared to other marine soft-bottom areas, which is likely related to the harsh and unstable environment (Beukema, 1976). Whether this has contributed to establishment success of *C. gigas* in the Wadden Sea cannot be excluded.

4.5. Causes of success

All traits of successful invaders investigated in this review and listed in Table 2 are applicable to *C. gigas*, without any exceptions. However, some traits will have contributed more strongly to the Pacific oyster's remarkably successful establishment and subsequent natural spread to other areas. Regarding many of the traits considered, *C. gigas* does not appear very different from native bivalves. An *r*-selected life history strategy, wide tolerances (generalism), genetic variability and phenotypic plasticity, competitiveness and dispersability all contributed to *C. gigas*' success but are rather common traits among sessile bivalves inhabiting the often unstable environment of the intertidal zone, where the bivalves have to be adapted to environmental extremes. A close association with humans, which was responsible for initial colonization by *C. gigas* and which contributed to its establishment success, is common for bivalve species that are of commercial interest, especially ones that are cultured intensively such as *M. edulis* and *C. gigas*. Both successful establishment and successful natural spread by *C. gigas* seem mainly attributable to two traits in which the species appears to differ the most from native bivalves: "ecosystem engineering" (associated with "gregarious behaviour" and "ability to recolonize after population crash", Table 2) and a "lack of natural enemies". In continental NW European estuaries, the lack of natural invertebrate predators applies specifically to *C. gigas* and not to native bivalves. A lack of invertebrate predators resulted in exceptionally high survival rates of spat and juveniles and offered *C. gigas* a competitive advantage over native bivalves. The only native bivalve reef-building ecosystem engineer is *M. edulis*. Ecosystem engineering facilitated successful establishment by *C. gigas* by modifying habitats to the oyster's demands in several ways: by facilitating settlement, by enhancing food intake and by offering shelter. Whether competition with native bivalves for resources also contributed to successful establishment will be discussed in the following chapter.

Additionally, life history theory predicts a trade-off between fast reproductive rates, that facilitate colonization, and competitive ability, that facilitates establishment (Pianka, 1970). In some invaders both strategies are represented (Keddy et al., 1994). Blossey and Notzold (1995) suggested that non-indigenous species that have been released from the pressure of diseases or predators in their native habitat, reallocate energy used for defence into reproduction and growth. Whether this is applicable to *C. gigas*, that also appears to be a successful competitor, needs further investigation.

5. Changes induced by *C. gigas* in NW European estuarine ecosystems

In this paragraph, a review is given of (potential) consequences of the expansion of Pacific oyster beds on the receiving ecosystems in The Netherlands and neighbouring countries. Changes induced by the ecosystem engineering *C. gigas* in receiving estuaries are mainly caused by the complexity of the added structure and by the suspension feeders' filtration activity. Potential ecological consequences as discussed below are therefore subdivided in effects of habitat modification and effects of the oysters' filtration activity.

5.1. Consequences of habitat modification by *C. gigas*

5.1.1. Habitat modification by Pacific oysters

Although Pacific oyster beds are expanding in both the Oosterschelde estuary and the Wadden Sea, the habitat that they are modifying differs

between both ecosystems. In the Oosterschelde estuary, oyster reefs mainly developed on hard substrates (e.g. dikes, jetties), former mussel culture plots, and former culture sites for the European flat oyster *O. edulis*. Former culture sites for *M. edulis* may still have contained some mussels or mussel shell debris, offering some hard substrate that stimulated colonization by *C. gigas*. On former culture sites for *O. edulis*, hard substrate was present in the form of low walls constructed of roof tiles. From these initial pieces of hard substrate the oyster beds have been mainly developing on former essentially bare flats. The speed of reef formation on soft substrates appears dependent on the amount of hard substrate (generally shell debris) present (Wijsman et al., 2008). In the Wadden Sea area, *C. gigas* is reported to mainly colonize areas with a high cover of hard substrate, such as mussel beds and (cockle-)shell ridges (Dankers et al., 2006; Nehls et al., 2006; Schmidt et al., 2008). Spatfall and an increasing biomass is mainly observed within existing oyster beds, mussel beds and shell banks (Dankers et al., 2006) and to a lesser extent outside these beds (pers. comm. G. Nehls).

Mussel beds are argued to raise and stabilize the sediment surface locally (Reise, 2002; Commito et al., 2008). Pacific oyster reefs have the same effect on the sediment surface, but mature oyster reefs appear more persistent and may therefore stabilize the sediments on a larger time scale. These mature reefs are anchored deep in the sediment thereby consolidating the substrate firmly (Reise and Van Beusekom, 2008; own unpublished observations). Because of this property Pacific oyster reefs have been suggested to be a valuable tool in preventing further erosion of intertidal flats in the Oosterschelde estuary. Here, as a consequence of the construction of a storm surge barrier and compartmentalisation dams (the "Delta" coastal engineering project) sediment deposition on tidal flats is reduced while erosion still continues, causing tidal flats to slowly submerge (Van Zanten and Adriaanse, 2008). Oyster reefs may thus locally protect the intertidal habitat of native bivalves and other invertebrate fauna, and the intertidal foraging grounds of species at higher trophic levels (such as shorebirds). Furthermore, by excreting vast amounts of faeces and pseudofaeces Pacific oysters, like mussels, enrich the sediment organically. This results in fine-grained sediments with high organic content, ammonia and hydrogen sulphide, and low oxygen levels (Hartstein and Rowden, 2004; Commito et al., 2008). How this impacts local macrofaunal communities will be discussed in the following paragraph.

5.1.2. Consequences for species richness and biodiversity

Overexploitation of living resources and habitat destruction are the main causes for biodiversity loss and species extinctions worldwide (Wolff, 2000). In the Wadden Sea and other estuaries in NW Europe, many habitat building species have been lost due to overexploitation in the 20th century (Reise, 1982; Wolff, 2000; Lotze, 2005; Airoldi and Beck, 2007). Associated communities consequently disappeared due to habitat loss. Seagrass meadows, oyster beds (*O. edulis*), mussel beds (*M. edulis*), *Sabellaria spinulosa* reefs, and sea moss stands provided hard substrate, shelter and food to associated species in NW European estuarine areas. Of these, only mussel beds remain today although old and mature mussel beds with a relatively higher complexity are not encountered anymore (Reise, 1982; Lotze, 2005). The Pacific oyster, although an alien species, reintroduces structural complexity and may be considered to restore habitat diversity and biodiversity. Pacific oyster reefs, especially the more mature ones, are furthermore avoided by most fishermen because they can cause damage to the netting. Hence, the associated benthic community may be given better opportunities to mature in the more stable environment of an oyster reef, compared to mussel beds and other, largely disappeared, biogenic structures. In the following text, a review is given of species richness and associated communities in Pacific oyster reefs, in comparison to mussel beds and bare tidal flats in the Wadden Sea and Oosterschelde estuary.

In the Wadden Sea Pacific oysters mainly settle onto intertidal mussels beds (Reise, 1998; Schmidt et al., 2008). Mussel beds are thereby transformed to mixed oyster/mussel beds with varying proportions of oysters and mussels. Soft bottom mytilid beds were already known to generally enhance habitat heterogeneity and species diversity at the ecosystem level (Günther, 1996; Buschbaum et al., 2009). Because *C. gigas* also enhances habitat heterogeneity by constructing complex reef structures, oyster reefs are expected to enhance local biodiversity as well. This was confirmed by two studies in the German Wadden Sea. Markert et al. (2009) and Kochmann et al. (2008) made a comparison between macrofaunal communities associated with mussel beds and oyster reefs. Markert et al. (2009) selected a mussel bed in the back barrier area of the island of Juist that had been colonized by *C. gigas*. They compared the macrofaunal communities between an area dominated by *M. edulis* and an area dominated by *C. gigas*. Kochmann et al. (2008) chose an experimental approach, and constructed artificial reefs of *C. gigas*, *M. edulis*, and a mix of both, in the outer Königshafen bay at the island of Sylt. They compared the number of invertebrate recruits of several species, and the abundance of vagile epifauna. Both studies showed that associated communities of *C. gigas* and *M. edulis* are largely similar, although they revealed some significant differences that were attributed mainly to differences in the structure of the beds. Markert et al. (2009) found a higher species richness in the oyster bed compared to the mussel bed, an exclusive occurrence of anthozoans and a higher abundance and diversity of sessile suspension feeders, epibionts, epibenthic predators (*Carcinus maenas*, *Asterias rubens*, and *Harmothoe imbricata*) and infauna. This was explained by a permanently sediment-free upper part of the reef (in contrast to mussels that are frequently buried) and a more turbulent current flow that enhances food flux towards suspension feeders. Markert et al. (2009) concluded that *Crassostrea*-reefs compensate for the conceivable loss of *Mytilus*-beds in the intertidal of the Wadden Sea by replacing the ecological function of *M. edulis*. The earlier study by Kochmann et al. (2008) confirmed that *C. gigas* beds harbour a higher abundance of sessile suspension feeders. In contrast to the results by Markert et al. (2009), they found higher abundances of *Carcinus maenas* in mussel plots compared to oyster plots. However, survival appeared higher in the oyster plots, possibly due to a higher level of shelter offered by the structurally more complex oyster beds (Kochmann et al., 2008). Furthermore, biodeposition enriches the sediments underneath both oyster and mussel beds, enhances local species abundance and structures the infaunal community (Kochmann et al., 2008; Markert et al., 2009). Both Kochmann et al. (2008) and Markert et al. (2009) found subtle differences in dominant associated infaunal species between Pacific oyster reefs and mussel beds.

A Pacific oyster bed offers a high level of habitat heterogeneity. The oyster shells themselves represent a large area of hard substrate settlement opportunities for species that previously only occurred on man-made structures (e.g. dikes and embankments), mussel beds and other (disappearing) biogenic structures. Furthermore, most oyster beds in Dutch and German coastal areas do not show a 100% cover of the substrate, and contain many bare patches (see Fig. 5) where soft-bottom communities are still present (Dittmann, 1990; Commito and Dankers, 2001). This resembles the topography of structurally complex older mussel beds (Bayne, 1976). In the shallow water retained in these patches during low tide, many species such as shrimps and gobies can be observed (own unpublished observation). Many species find refuge from physical stress and predation within the oyster bed, but may also serve as prey for shorebirds. Commito et al. (2008) demonstrated effects of small-scale variability within bivalve (*M. edulis*) beds on macrofaunal communities and stressed its importance for most macrofauna and biodiversity. This was also confirmed for Pacific oyster beds in the Oosterschelde estuary by Van Broekhoven (2005). He showed that species richness is higher in oyster beds compared to the surrounding bare flat, with the highest

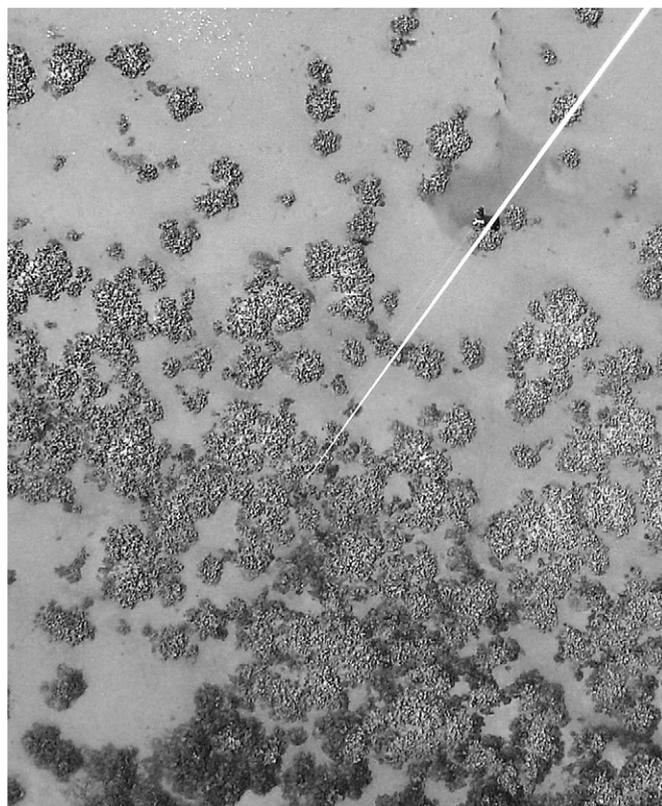


Fig. 5. Aerial photograph of part of the oyster bed at Neeltje Jans, the Oosterschelde estuary (courtesy Johan van de Koppel). The picture shows patches of oysters, and bare patches in between. In the lower part of the picture, the oyster patches are fringed by sea lettuce *Ulva* sp. The person in the upper right corner and her foot prints give an indication of scale. The picture was taken in July 2005, from a height of about 50 m (with a camera suspended from a blimp (balloon)); the white line in the picture is the line holding the blimp, see www.blimppics.com.

species richness occurring at the edge of oyster bed where oyster patches are alternated with bare patches. Concluding, increased habitat heterogeneity generally results in a higher biodiversity in an oyster bed as a whole, compared to the surrounding bare flats and also compared to mussel beds.

Pacific oyster reefs may furthermore facilitate establishment of other exotics from the same region of origin. For example, Pacific oyster beds in The Netherlands already offer substrate and shelter to the japweed *Sargassum muticum*, wakame weed *Undaria pinnatifida*, the red alga *Heterosiphonia japonica*, the crab *Hemigrapsus penicillatus*, the sea squirts *Botrylloides violaceus* and *Styela clava*, and many more species originating from north-east Asian Pacific coasts (Wolff, 2005; Haydar and Wolff in prep.). By increasing local biodiversity Pacific oysters may, alternatively, decrease the success of future invasions from regions other than the NW Pacific coasts (Stachowicz et al., 1999; Stachowicz et al., 2002).

5.1.3. Competition for space with native bivalves

Pacific oysters are strong competitors for space, since persistent oyster reefs can develop very fast once a sufficient amount of hard substrate is present (e.g. shell debris, a mussel bed or a pioneer-stage oyster bed). This is facilitated by their gregarious settling behaviour (Diederich, 2005a; Tamburri et al., 2007; Troost, 2009). Pacific oyster beds increase the area suitable for settlement of hard substrate species and locally turn former soft-substrate communities into hard substrate communities. Infaunal species would be expected to be affected negatively by expansion of oyster beds, since the area suitable

for settlement decreases, and oyster reefs are difficult if not impossible to recolonize for infaunal species. However, only a limited fraction of the total estuarine intertidal area available to bivalves can actually be occupied at a given time, due to limiting physical processes at local scale (e.g. current velocity, mixing) and limiting primary production on a system scale (Heip et al., 1995).

Furthermore, *C. gigas* does not occupy exactly the same habitat as most native bivalves. While *C. gigas* are generally found around MLW and below, cockles *C. edule* are generally found at higher elevations (Table 3). Significant competition for space between the two species primarily occurs at locations that are less suitable for cockles (Kater et al., 2006). In the Oosterschelde estuary, the area of locations suitable for cockles is decreasing because the tidal flats are slowly submerging. Competition for space among both species is therefore expected to become relatively more important in the coming decades. Another dominant native burrowing bivalve in NW European estuaries is the Baltic tellin *Macoma balthica*. This species is found from the high intertidal to the subtidal (Table 3). Therefore, it does not occupy the exact same locations as *C. gigas* that is mainly found in the low intertidal to subtidal. The soft-shelled clam *M. arenaria*, introduced centuries ago and therefore treated here as a native species, is found at roughly the same range in tidal elevations as *M. balthica* and therefore also does not have to compete for space with *C. gigas* in the higher intertidal areas. Additionally, in the Wadden Sea the distribution of endobenthic bivalves appears to shift towards the shore, towards higher intertidal levels (Beukema and Dekker, 2005) and therefore away from the oyster bed locations in the lower intertidal. This appears to result from increasing predation by benthic invertebrates (further discussed in Section 6.1). Pacific oysters do occupy the same habitat as *M. edulis*. In the Wadden Sea, Pacific oysters occupy areas with mussels or areas where sometime in the past mussels have been before. This suggests that either shell rubble was left behind that facilitated first settlement of *C. gigas*, or that these sites are particularly suitable for epibenthic suspension feeders. The latter explanation could mean that, although bivalve suspension feeders may not compete directly for the same space, they do interfere with each other by reducing the availability of potential high quality sites.

In the German and Danish Wadden Seas a long-term decline in mussel bed area is observed (Nehls et al., 2006; Nehls and Büttger, 2007). Roughly in the same period Pacific oyster bed area showed an increase. However, both trends do not appear to be causally related but rather an effect of global change (Nehls et al., 2006). Moreover, mussel beds showed a recovery in the eastern part of the Dutch Wadden Sea since 2002 (Nehls and Büttger, 2007). Any evidence for a large scale displacement of *M. edulis* by *C. gigas* is therefore lacking. Diederich (2005a) concluded that *C. gigas* and *M. edulis* may co-exist since *M. edulis* settle and grow in oyster beds. She also found that mussels may find a refuge from the invading oyster under a canopy of *Fucus vesiculosus* (forma *mytili* Nienburg). Kochmann et al. (2008) furthermore observed oyster settlement mainly on adult conspecifics while *M. edulis* showed no preference for either oyster or mussel

shells. They hypothesized that the lack of substrate specificity in *M. edulis* will secure a coexistence of *M. edulis* with a dominant *C. gigas* in the Wadden Sea. Mussels were also frequently found growing between oysters in the Oosterschelde estuary (Van Broekhoven, 2005; Troost, 2009). With an increasing oyster biomass in an oyster bed in the northern compartment, numbers of *M. edulis* increased but their condition decreased (Troost, 2009). The decrease in condition suggests food limitation, but the increasing numbers suggest good settlement opportunities and/or shelter from predation and environmental extremes. Similar results were also obtained by Markert et al. (2009), who found a lower abundance of juvenile *M. edulis* in an oyster patch compared to a mussel patch within the same bivalve bed. Mortality of juvenile and adult *M. edulis* appeared to be lower in the oyster patch than in the mussel patch. A lower abundance of juveniles may be explained by larviphagy by the adult suspension feeders (further addressed in Section 5.2.3). Reduced mortality of the mussels may be explained by reduced predator–prey encounter rates in the structurally more complex oyster reef (Bartholomew et al., 2000; Grabowski, 2004; Section 4.2), as well as a reduced accessibility for predatory birds such as the oystercatcher *H. ostralegus*. Cadée (2007) even suggested that Pacific oyster beds may facilitate a return of *M. edulis* to tidal flats of the western Dutch Wadden Sea. This is similarly hypothesized for the Oosterschelde estuary that has not seen natural intertidal mussel beds since several decades (pers. comm. A.C. Smaal). Here, mussels *M. edulis* are almost exclusively found hidden between the oysters, just above the bottom (Troost, 2009).

5.2. Consequences of the Pacific oysters' filtration activity

5.2.1. Competition for food with native bivalve filter-feeders

Bivalve filter-feeders feed on phytoplankton, but also on other particles in the water column that are large enough to be retained by the gills and that are not too large or evasive, such as dead particulate organic material or certain species of zooplankton (Fréchette et al., 1989; Navarro et al., 1992; Smaal, 1997; Dupuy et al., 1999; Davenport et al., 2000; Dupuy et al., 2000; Karlsson et al., 2003; Lehane and Davenport, 2004; Troost et al., 2008a). All particles above a species-specific retention threshold (2–12 µm, Møhlenberg and Riisgård, 1978; Barillé et al., 1993) are retained by the gills (Fig. 6). Selection of particles for ingestion takes place on the gills and labial palps (Shumway et al., 1985; Ward et al., 1998). Particles retained on the gills are transported towards the labial palps through ciliary movement. At the labial palps, rejected particles are covered in mucus and excreted as pseudofaeces. Particles selected for ingestion move into the stomach through the mouth (Gosling, 2003). Post-ingestive selection of particles for absorption occurs in the stomach and guts (Brillant and MacDonald, 2002). The species may differ in selection and absorption efficiencies, but also in how they optimize a food flux towards the bed, how they minimize refiltration inside the bed, and how efficiently they entrain zooplankton. A comparison of these aspects between *C. gigas* and native bivalves will be made in the

Table 3
Habitat occupation of native bivalves dominant in Dutch estuaries, and the introduced Pacific oyster *C. gigas* (From Korringa, 1952; Bayne, 1976; Hayward and Ryland, 1990; Mann et al., 1991; Gosling, 2003; De Bruyne, 2004).

	<i>Crassostrea gigas</i>	<i>Mytilus edulis</i>	<i>Cerastoderma edule</i>	<i>Mya arenaria</i> ^a	<i>Macoma balthica</i>
Tidal range	Low intertidal to subtidal	Mid intertidal to subtidal	High intertidal to shallow subtidal	High intertidal to shallow subtidal (to 200 m depth)	High intertidal to subtidal
Sediment	Attachment to hard surfaces, bed occurrence on any substrate	Attachment to hard and filamental surfaces, bed occurrence on any substrate	Sand, soft mud, gravel	Firm mud/sand	Mud to muddy sand
Salinity	Estuarine to fully marine	Estuarine to fully marine	Estuarine to fully marine	Estuarine	Estuarine to fully marine
Burrowing depth	–	–	<5 cm	~15 cm	5–10 cm
Exposure	Semi-exposed to sheltered	Exposed to sheltered	Semi-exposed to sheltered	Sheltered	Semi-exposed to sheltered

^a *Mya arenaria* is not native to Dutch waters, but is included here because its introduction dates centuries back.

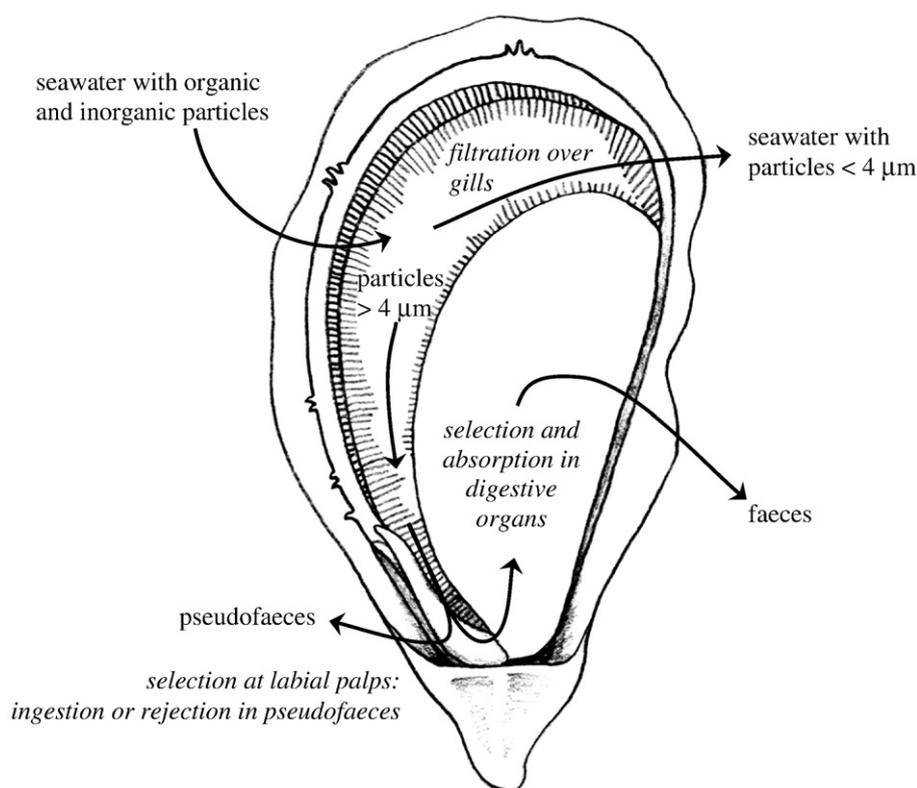


Fig. 6. Schematic drawing of filtration, selection, ingestion and digestion of food particles in bivalves (example: *C. gigas*). Bivalve filter-feeders collect their food by filtering and sorting particles from the water column. Their ciliated gills create a water current through the mantle cavity and over the gills. Particles above a certain threshold size, generally 2–7 μm (Møhlenberg and Riisgård, 1978), are retained efficiently. Selection of particles for ingestion takes place on the gills and labial palps (Shumway et al., 1985; Ward et al., 1998). Particles retained on the gills are transported towards the labial palps through ciliary movement. At the labial palps, rejected particles are covered in mucus and excreted as pseudofaeces. Particles selected for ingestion move into the stomach through the mouth (Gosling, 2003). Post-ingestive selection of particles for absorption occurs in the stomach and guts (Brilliant and MacDonald, 2002).

following sections, with the purpose of evaluating whether *C. gigas* competes for food with native bivalves, and whether *C. gigas* is a stronger competitor.

5.2.1.1. Food intake of bivalves in relation to hydrodynamics. Troost et al. (2009b) showed that differences in inhalant feeding currents of individual *C. gigas*, *M. edulis* and *C. edule* are small despite apparent differences in morphology. Differences in inhalant feeding currents are therefore not expected to result in differences in food intake between the introduced oyster and native bivalves. However, processes on a larger scale (a patch or bed of bivalves) may be more determining. Bivalve filter-feeders can optimize food flux towards the bed by enhancing near-bed turbulence levels with their filtration activity (mainly with their exhalant feeding currents) and/or physical roughness of the bed. Although exhalant feeding current speeds of *C. gigas* were found to be higher than in the two other species, differences were modest (Troost et al., 2009b). Moreover, exhalant feeding currents in *C. gigas* were oriented horizontally instead of vertically as in *M. edulis* and *C. edule*. How this affects differences between the species in their effect on the benthic boundary layer is not known yet. In conclusion, Troost et al. (2009a, b) predicted no important differences in food intake as a result of differences in exhalant jet speeds of individual animals.

The much larger differences in roughness height of oyster, mussel and cockle beds are expected to contribute more strongly to differences in food intake (Troost et al., 2009b and references therein). Oysters create larger roughness structures than mussels and cockles. Cockles do not produce any protruding roughness structures at all and seem entirely dependent on roughness created by their filtration activity. By creating larger roughness structures,

Pacific oysters probably affect near-bed turbulence levels more strongly than native bivalves (that are all infaunal except for *M. edulis* and the now rare *O. edulis*). In that way they may enhance food flux and intake rate that is also facilitated by their large filtration capacity. Additionally, since many zooplankton species use hydro-mechanical signals to detect and escape from predators (Singarajah, 1975; Kingsford et al., 2002; Titelman and Kjørboe, 2003), higher levels of turbulent mixing cause more “background noise” to these zooplankters, reducing (the effectivity of) escape reactions, potentially resulting in a higher zooplankton intake rate by oysters than by mussels and cockles (Troost et al., 2009b).

5.2.1.2. Diet of filter-feeding bivalves. That Pacific oysters and native bivalves may not utilize the exact same diet was shown in various studies. Bougrier et al. (1997) showed in the laboratory that from various algal species simultaneously available in the surrounding water, *C. gigas* and *M. edulis* selected different species for ingestion. Based on different stable isotope signatures of $\delta^{13}\text{C}$ (ratio of ^{13}C to ^{12}C) and $\delta^{15}\text{N}$ (ratio of ^{15}N to ^{14}N) of the bivalve tissue, *C. gigas* was found to utilize a diet different from that of *M. edulis* and the filter-feeding snail *Crepidula fornicata* in the French Bays of Veys (Dubois et al., 2007) and Mont Saint Michel (Riera, 2006) and the Dutch Oosterschelde estuary (Riera et al., 2002). Differences in these signatures can indicate different food sources, but also a utilization of the same food sources but in different proportions is possible. Riera et al. (2002) and Riera (2006) hypothesized that the differences found between *C. gigas* and *C. fornicata* in the Oosterschelde estuary and Bay of Mont Saint Michel may be due to utilization of different size classes of consumed particulate organic matter. They therefore concluded that both species may not necessarily be competitors for the same food sources. Results

from the Bay of Veys indicated that *C. gigas* is capable of a greater trophic plasticity than *M. edulis*. Pacific oysters showed a larger spatial variation in isotope signatures, indicating that they are better able to adapt to the local environmental availability of food items (Dubois et al., 2007).

Ostreids have reduced eulatero-frontal cirri and have a slightly higher retention threshold than species with long latero-frontal cirri (such as *C. edule*, *M. edulis* and *M. arenaria*). In the latter, all particles larger than 4 µm are 100% efficiently retained (Møhlenberg and Riisgård, 1978). Ostreids have a retention threshold of 4–6 µm (Møhlenberg and Riisgård, 1978; Riisgård, 1988; Barillé et al., 1993). In addition, at high seston load the retention threshold in *C. gigas* changes from about 4 µm to 12 µm (Barillé et al., 1993). This is thought to ensure a good functioning of the ciliary systems at the gills and labial palps, but it also renders *C. gigas* unable to utilize plankton <12 µm at high seston load (Barillé et al., 1993). In addition to this mechanism and in comparison to Dutch native species of bivalve filter-feeders, larger components of the seston, such as ciliates, larger phytoplankton cells, debris of macro-algae and zooplankton, may play a more important role in the diet of *C. gigas* (see Dupuy et al., 1999). Although lower thresholds have been determined experimentally, it is more difficult to determine the upper size limit of what bivalves can still filter. Davenport et al. (2000) found 260 planktonic animals in stomach contents of 100 mussels *M. edulis* from the field. The mussels appeared to routinely ingest particles of 100–1000 µm, and occasionally particles of 3–6 mm.

Furthermore, Pacific oysters may be more efficient in entrapping zooplankton because they probably create more background turbulence than native bivalves (although this yet needs to be studied, see previous section). Hence, they may utilize a broader diet. Zooplankton has been shown to be a useful additional food source. Bivalves grown on a mix of phytoplankton and zooplankton showed faster growth than bivalves fed with phytoplankton only (Wong and Levinton, 2004).

Concluding, although Pacific oysters and native bivalves appear not to utilize the exact same diet, they filter largely the same particles from the surrounding water (barring zooplankton species that may have different escape successes for different species of bivalves). This includes particles that they do not ingest, but instead reject in their pseudofaeces. Therefore, even if they do not compete directly for the same food sources, they do interfere with each other by reducing food levels available to other species (Green, 1971; Case and Gilpin, 1974).

5.2.1.3. Feeding physiology of filter-feeding bivalves. Bivalve filter-feeders adjust their feeding rate and feeding and absorption efficiencies to changes in total particulate matter (TPM) and organic content of the TPM (e.g. Navarro et al., 1992; Hawkins et al., 1998; Bayne, 2002). Species with a relatively high food intake, efficient particle selection and absorption, and low metabolic loss will have a relatively high net energy gain and will be stronger competitors for food (Hawkins et al., 1998; Bayne, 2002). In the Bay of Marennes-Oléron, at the French Atlantic coast, Hawkins et al. (1998) found differences in feeding physiology parameters between *C. gigas*, *M. edulis* and *C. edule* (after standardizing for 0.5 g dry soft tissue weight). The infaunal *C. edule*, feeding on natural seston, showed a lower efficiency in selecting organic particles for ingestion than the other two species at higher TPM levels, but this was probably compensated by a longer gut passage time for the extraction of available nutrients. This appears to be an adaptation to less turbid, more sandy habitats (Hawkins et al., 1998). Compared to *M. edulis* the Pacific oyster had a higher ingestion rate but handled filtered particles less efficiently. Because the absorption rate of ingested organic matter in the stomach and gut by *M. edulis* was twice as fast compared to *C. gigas*, ultimately *C. gigas* gained less energy from filtered matter than *M. edulis* (Hawkins et al., 1998). However, *C. gigas* may be metabolically more efficient than native bivalves. *C. gigas* has a

competitive advantage over the Sydney rock oyster *Saccostrea glomerata* in Australia, due to faster rates of feeding and greater metabolic efficiencies of both feeding and growth (Bayne, 2002).

5.2.1.4. Growth of bivalve filter-feeders. Food-limited growth is a common phenomenon among bivalves, demonstrated to occur on a local scale in the Wadden Sea (Kamermans, 1993; Beukema and Cadée, 1997) and on a larger scale in the Oosterschelde estuary (Hoek, 1902; Van Stralen and Dijkema, 1994; Smaal et al., 2001). The most efficient feeder, *M. edulis*, would be expected to show a lower dependence of growth on food availability. This could, however, not be confirmed by field observations in NW European estuaries. Using the Dynamic Energy Budget theory (Kooijman, 1986, 2000), Cardoso et al. (2006) reconstructed food conditions for different bivalve species in Dutch estuaries, based on growth curves determined from the field. The results suggested that growth of both *M. edulis* and *C. gigas* is suboptimal in Dutch coastal waters (in contrast to *M. balthica* and *C. edule*), probably due to food limitation during some months (Cardoso et al., 2006). Diederich (2006) studied growth of juvenile *C. gigas* and *M. edulis* in an oyster bed, a mussel bed and on a sandflat in the German Wadden Sea, and found density-dependent growth in *M. edulis* but not in *C. gigas*. This corresponds to the results of a graduate (MSc) study in the Oosterschelde estuary (in Troost, 2009). Here, growth of caged mussels in an intertidal bed of wild Pacific oysters was negatively related to local oyster biomass, whereas caged oysters at the same locations showed density-independent growth. The results of these studies suggest that Pacific oysters either ingest more food, or an additional different type of food (e.g. zooplankton), or utilize the ingested food more efficiently. The first option is supported by e.g. the oyster's large filtration rate and large roughness of oyster beds (Section 5.2.1.1). The second option is supported by results of Riera et al. (2002; 2006) and Dubois et al. (2007) (Section 5.2.1.2). The third option is refuted by the results of Hawkins et al. (1998) (Section 5.2.1.3).

5.2.2. Carrying capacity of estuarine ecosystems

Food competition between bivalve filter-feeders becomes more and more important as food levels drop and the carrying capacity of the ecosystem for bivalve filter-feeders is reached. Rapid expansion of *C. gigas* in the Oosterschelde estuary resulted in an increasing filtration capacity of the bivalve filter-feeder stock (Troost et al., 2009a). This apparently already has a large effect on the phytoplankton community, as indicated by the observed shift towards smaller phytoplankton species (Noren et al., 1999; Geurts van Kessel et al., 2003). Furthermore, after comparing the turn-over time of the phytoplankton in the Oosterschelde estuary with the estimated time needed for oysters, mussels and cockles to filter the volume of these compartments, Geurts van Kessel et al. (2003) concluded that the carrying capacity (total bivalve biomass supported by a given estuarine ecosystem) may already have been reached in some parts of the estuary. Although the approach of Geurts van Kessel et al. (2003) ignored the complex dynamics of carrying capacity, and did not take into account the various feedback mechanisms between bivalve grazing and ecosystem processes (Prins et al., 1998), field observations on growth and condition of cultured stocks of *M. edulis* and *C. gigas* seem to confirm a saturated carrying capacity (unpublished data IMARES, the Dutch Fish Product Board and A. Cornelisse). A simple model shows that the Dutch (and probably the entire international) Wadden Sea may have a relatively larger carrying capacity for bivalve filter-feeders than the Oosterschelde estuary. In the Dutch Wadden Sea, where *C. gigas* is presently not a dominant species, the carrying capacity does not appear to be reached yet. Carrying capacity may be defined as a function of the water residence time, primary production time and bivalve clearance time (Dame and Prins, 1998). The water residence time is the time it takes for the entire volume of the estuary to be refreshed by tidal exchange with

the coastal sea. Import of nutrients and organic matter from the coastal zone into estuaries through tidal exchange enhances the carrying capacities of these estuaries for bivalve filter-feeders (Bacher et al., 1998; Dame and Prins, 1998; Van Beusekom and De Jonge, 2002; Wetsteyn et al., 2003). Heip et al. (1995) demonstrated an inverse relationship between water residence time and biomass of bivalve filter-feeders in different estuaries (based on data collected by Smaal and Prins, 1993). Primary production time (PPT) is the ratio of yearly averages of phytoplankton biomass to phytoplankton primary production within the estuary. It describes the time it takes for primary production within the system to replace the standing crop biomass of phytoplankton within the system. Bivalve clearance time is defined as the time that is theoretically needed for the total bivalve filter-feeder biomass to filter particles from a volume of water equivalent to the total system volume (Smaal and Prins, 1993). In comparison to the Oosterschelde estuary the Wadden Sea is a more open and shallow system with higher rates of tidal exchanges with the coastal zone. The western Dutch Wadden Sea has a much shorter residence time (on average 10 days) than the Oosterschelde estuary (40 days). Around 1990 the phytoplankton turnover time was shorter than in the Oosterschelde estuary (a PPT of 0.97 days vs. 3.08 days for the Oosterschelde estuary, references in Dame and Prins, 1998), but this difference was apparently reduced during the 1990's due to a decrease in primary production in the Wadden Sea which resulted in an increase in PPT (twofold at most) (Philippart et al., 2007).

Determining the carrying capacity of an estuarine area is, however, very difficult because of the narrow and complex coupling between the filter-feeder community and food availability (Prins et al., 1998). Bivalve suspension feeders enrich their immediate environment by producing biodeposits. These biodeposits are mineralized rapidly, resulting in a release of nutrients that stimulate primary production (Prins and Smaal, 1994; Prins et al., 1998). The complexity of such processes, and difficulties in monitoring them, makes it difficult to accurately predict the carrying capacity of the system. Like mineralization, bivalve clearance time is also very difficult to estimate and capture in a model. It is a function of the biomass of the bivalves and the seasonal influences of particulate concentrations, seston quality, and temperature on the filtration rate of the bivalves (Smaal and Prins, 1993). Due to the increase in total bivalve filter-feeder stock as a result of the expansion of *C. gigas*, bivalve clearance time in the Oosterschelde estuary decreased from roughly 10 days in 1990 to 7 days in 2000 (Geurts van Kessel et al., 2003). In the Dutch Wadden Sea, the total filtration pressure does not appear to have increased significantly since the introduction of *C. gigas* (Brinkman and Jansen, 2007; Philippart et al., 2007). Here, the oyster still constitutes only a fraction of the total filter-feeder biomass in the Dutch Wadden Sea (Brinkman and Jansen, 2007) although it is now the most dominant bivalve in the Oosterschelde estuary (Troost et al., 2009a). Finally, the carrying capacities of the Oosterschelde estuary and (Dutch) Wadden Sea are difficult to compare, especially when carrying capacity is considered as the maximum achievable bivalve biomass given natural recruitment processes. The Oosterschelde estuary differs markedly from the Wadden Sea in that recruitment success of *M. edulis* is very low and the stock size is controlled for >95% through import and removal by mussel farmers (Van Stralen and Dijkema, 1994). Effects of feedback mechanisms between adult stock size and recruitment on the total *M. edulis* stock, through effects on primary production and phytoplankton composition, are therefore presently negligible in the Oosterschelde estuary but may still play a role in the Wadden Sea (Bos et al., 2006).

In conclusion, considering the more open and shallow character of the Wadden Sea and the consequently shorter water residence time and faster primary production time, the carrying capacity of the Wadden Sea will probably not be reached in the near future. On a smaller spatial scale however, food competition does occur in the Wadden Sea (Kamermans, 1993; Beukema and Cadée, 1997).

Competitive interactions between *C. gigas* and native bivalve filter-feeders (especially *M. edulis*) are therefore expected to structure the composition of epifaunal bivalve beds locally.

5.2.3. Larviphagy

Bivalve filter-feeders retain all particles above a certain threshold size (2–6 μm : Møhlenberg and Riisgård, 1978; Riisgård, 1988; Barillé et al., 1993), and selection of particles only occurs after retention, on the gills, labial palps and/or in the stomach and guts (e.g. Shumway et al., 1985; Brillant and MacDonald, 2002). Larviphagy, the feeding on (bivalve) larvae, therefore must be a common phenomenon among bivalve filter-feeders (Lehane and Davenport, 2004; Troost et al., 2008a). Increasing stocks of bivalve filter-feeders, as happened in the Oosterschelde estuary due to the expansion of *C. gigas*, may not only reduce food levels but also bivalve larval abundance.

Adult *C. gigas*, *M. edulis* and *C. edule* were shown to routinely filter and ingest larvae of both *C. gigas* and *M. edulis* in a laboratory study (Troost et al., 2008a). However, a difference in filtration risk was found between the larvae of both species. Larvae of *C. gigas* were filtered approximately 50% less than larvae of *M. edulis* in still water in a laboratory study (Troost et al., 2008a). The reduction in filtration rate was not caused by escape reactions of the larvae in response to hydro-mechanical stimuli in the inhalant flow field of the adult bivalves, since both *M. edulis* and *C. gigas* larvae did not respond to a suction current mimicking a bivalve inhalant current in another laboratory study (Troost et al., 2008b). Instead, the difference appeared to be caused by *C. gigas* larvae migrating upwards in the water column in response to the presence of an adult filter-feeder on the bottom (Troost, 2009). Larvae of *M. edulis* did not show this response but remained distributed homogeneously over the water column whether an adult filter-feeder was present or not.

The hypothesis that larviphagy reduces bivalve larval abundance was confirmed by a field study (Troost et al., 2009a). In the water column overlying a dense oyster bed in the northern compartment of the Oosterschelde estuary, abundance of *M. edulis* larvae was reduced but abundance of *C. gigas* larvae was not. Reduction of mussel larvae must have been due to larviphagy by the relatively high filter-feeder biomass in the oyster bed. The results of *C. gigas* larvae were thought to have been influenced by spawning activity of the adult oysters, since significantly more newly produced oyster veligers were caught at the oyster bed location than at the reference site (Troost et al., 2009a). Furthermore, Troost et al. (2009a) calculated the order of magnitude of the mortality rate of bivalve larvae through larviphagy in the Oosterschelde estuary. Assuming a homogeneous distribution of larvae throughout the Oosterschelde estuary, a homogeneous distribution of adult bivalves on the bottom of the estuary, a continuous complete mixing of the estuary and no washing out of larvae to the North Sea with tidal exchange, 95% of the larvae would have been filtered during an average pelagic stage of 20 days. In this calculation a CR of 398 million $\text{m}^3 \text{day}^{-1}$ for the year 2000 was used, as (roughly) estimated by Kater (2003). A larviphagy mortality rate f of 0.95 is in the same order of magnitude as total mortality rates generally estimated or determined for bivalve larvae and larvae of other benthic invertebrates (Thorson, 1950; Rumrill, 1990). Therefore, larviphagy appears to contribute significantly to mortality of bivalve larvae in the Oosterschelde estuary. Considering the magnitude of the effect, recruitment is expected to be affected as well. Although successful oyster spatfall appears mainly dependent on calm weather conditions (pers. comm. A. Cornelisse, oyster farmer) and high water temperatures during spatfall (Diederich et al., 2005), Brandt et al. (2008) show that recruitment of *C. gigas* in the German East Frisian Wadden Sea, during the early stage of invasion, was dominated by larval supply rather than environmental factors at the location of settlement. This supports the hypothesis that recruitment of *C. gigas* itself may also be affected by the estimated high mortality rate due to larviphagy in the Oosterschelde estuary.

Troost et al. (2008a) showed that *C. gigas* larvae were filtered 50% less than *M. edulis* larvae in a still-water set-up in the laboratory. Regardless of the reservations in translating this result directly to the field (see discussion in Troost et al., 2008a), for the situation in 2000 this would result in a reduction of f from 0.95 to 0.78 for *C. gigas* larvae whereas f would still remain 0.95 for *M. edulis* larvae. An increasing stock of *C. gigas* in the Oosterschelde estuary may therefore affect larval abundance and subsequent recruitment of *M. edulis* more strongly than its own larval abundance and recruitment. A contributing factor is the increased larval production of *C. gigas* with an increasing parent-stock. Potential effects on recruitment remain, however, hypothetical. A study into the effect of the increasing filter-feeder stock in the Oosterschelde estuary (mainly due to the increase in Pacific oyster stock) on larval abundance of *C. gigas* and *M. edulis* showed a decline in larval abundance of oysters but, unexpectedly, no effect on larval abundance of mussels (Troost et al., 2009a). The declining Pacific oyster larval abundance was suggested to be a result of increased larviphagy, possibly in combination with food limitation (reducing the reproductive output of adults and/or reducing the survival of larvae). A trend in larval abundance of mussel larvae may have been undetectable due to the relatively short sampling period of 6 years (vs. 13 years for oyster larvae).

Summarizing, the results for *M. edulis* larvae on bed scale and the results for *C. gigas* larvae on estuary scale do suggest that larviphagy may be an important mortality factor for bivalve veliger larvae. The increasing stock of filter-feeders in the Oosterschelde estuary is therefore expected to reduce abundance of bivalve larvae, but also of other slow-swimming zooplankton species with weak escape capabilities (see Singarajah, 1969, 1975; Kiørboe and Visser, 1999; Titelman and Kiørboe, 2003; Maar et al., 2007). Eventually, bivalve grazing may exert a top-down control on zooplankton communities through direct grazing on weak escapers and weak swimmers, and on benthic communities through filtration of pelagic larvae. In addition, larvae of *C. gigas* swim faster than larvae of *M. edulis*, and can migrate faster in vertical direction (Troost et al., 2008b). This may enable them to more successfully avoid benthic predators, find food-rich water layers (Raby et al., 1994) or transport themselves with the tides into favourable directions (Shanks and Brink, 2005).

5.3. Consequences of induced changes for other trophic levels

Hypothetically, *C. gigas* may change entire ecosystems through cascading effects on other trophic levels. The increased filtration pressure in the Oosterschelde estuary due to an increased oyster stock already appears to have affected the phytoplankton community. The oysters exert a top-down control on phytoplankton abundance and composition that may in turn affect higher trophic levels in the food web (e.g. zooplankton → fish → fish-eating birds and seals). Similarly, the oysters might induce cascading effects by exerting a top-down control on zooplankton abundance and composition.

Since Pacific oysters are hardly eaten by birds in the Netherlands, expansion of *C. gigas* may threaten the food supply of shorebirds if they (partially) replace native bivalves. With expanding oyster reefs, the foraging area available for birds that feed on infaunal invertebrates would be expected to decrease only slightly. Stronger effects may be expected for shorebirds that preferentially or obligatorily feed on *M. edulis*, if mussel biomass within the now mixed beds would be reduced below a critical level. Scheiffarth et al. (2007) consider the Eider duck *Somateria mollissima* and to a lesser extent the oystercatcher *H. ostralegus* and the herring gull *L. argentatus* as the most vulnerable birds in this respect. On the other hand, development of oyster beds may also have a positive influence on food availability for shorebirds. In the Oosterschelde estuary more intertidal mussels may now be available to foraging birds because of their natural occurrence in expanding oyster reefs on tidal flats. Since the replacement of all mussel culture plots to the subtidal in the 1990's,

this may constitute the only availability of mussels to shorebirds such as the oystercatcher *H. ostralegus*. This species was observed to feed on mussels in an intertidal oyster bed (own unpublished observation). Oyster beds furthermore harbour high abundances of epifaunal invertebrates that may constitute a suitable food source for shorebirds. However, hardly any studies have been conducted that could support or refute this hypothesis. In the Oosterschelde estuary, some observations on the occurrence of foraging birds in oyster reefs and nearby reference sites indicated no apparent differences (Wijsman et al., 2008). Furthermore, mussels may again disappear from the intertidal of the Oosterschelde estuary as a consequence of reduced food levels (see Section 5.2.2).

C. gigas may also interfere with native parasite–host interactions, thereby affecting the life cycle of parasites and reducing the parasite load in final hosts. Thieltges et al. (2009) demonstrated that both the introduced *C. gigas* and gastropod *Crepidula fornicata* reduce the parasite load of mussels in mixed beds by acting as a decoy, and argued that the invaders interfere with the life cycle of parasites. All cercariae of the trematode *Himasthla elongata* that had infected invaders in a laboratory set-up were blocked from developing into the following stage and hence from infecting their final host. Final hosts of trematodes are mostly birds. Krakau et al. (2006) argued that for the trematode *Renicola roscovita* infecting *C. gigas*, transmission of metacercariae into their final host may be reduced considerably if potential final hosts do not consume oysters.

6. Future scenarios and conclusions

6.1. Expected effects of climate change

Predicting effects of climate change on biomass and species composition of bivalve suspension feeders is difficult because of the variety of possible effects, complexity of food-web relationships and interactions between different aspects of climate and global change. Here, I will make an effort to predict effects of global warming on the development of *C. gigas* in NW European estuaries, relative to stocks of dominant native bivalves.

In the western Dutch Wadden Sea, global warming decreases the frequency of severe winters, thereby increases the abundance of benthic invertebrate predators of bivalve spat, causing a decline in abundance of the native bivalves *C. edule*, *M. arenaria* and *M. balthica* in the lower intertidal (Beukema and Dekker, 2005). Successful recruitment of these species (including *M. edulis*) is dependent on severe winters as these reduce benthic invertebrate predator abundance and retard their arrival in spring (Beukema, 1991, 1992; Beukema et al., 1998; Strasser and Günther, 2001; Strasser et al., 2001). *C. edule*, *M. arenaria* and *M. balthica* still find a refuge from predation at higher intertidal levels (Beukema and Dekker, 2005). Whether recruitment of the Pacific oyster is also dependent on severe winters has not been studied yet. Survival of Pacific oyster spat appears to be high, even in severe winters (Reise, 1998) although higher in mild winters (Diederich, 2006). Successful recruitment of Pacific oysters may be less dependent on severe winters if the spat of *C. gigas* is less vulnerable to predation by benthic invertebrate predators. Shrimps and crabs may prefer to feed on bivalve spat that do not have to be scraped off a hard substrate over spat of *C. gigas*. Recruitment success of *C. gigas* is rather dependent on warm summers that promote extensive spatfalls near its northern distribution limit (Diederich et al., 2005). Global warming may therefore increase spatfall success of *C. gigas* in summer and survival of spat in the following winter, leading to increased rates of population increase of the Pacific oyster while the abundance of native bivalves is expected to decline due to increased predation rates in the subtidal and lower intertidal.

Furthermore, Reise and Van Beusekom (2008) predict that a combination of global warming and reduced nutrient loads will lead

to a composition shift and a reduction in biomass of phytoplankton. This is expected to severely impact bivalve filter-feeders although it is at this stage impossible to predict the outcome. Reduced phytoplankton biomass will likely cause a reduced carrying capacity for bivalve filter-feeders and affect the condition of most species as is presently observed in the Oosterschelde estuary. This may eventually, in a worst-case scenario, lead to extirpations of species that are the weakest competitors for food. This may be *M. edulis* although the possibility that *C. gigas* is a weaker competitor for food cannot be excluded (Section 5.2.1). However, we are currently still unable to measure and model the complex coupling between bivalves and food availability accurately enough to predict the potential of the different estuaries for bivalve biomass.

Another consequence of global warming is sea level rise. The Oosterschelde estuary is already slowly turning into a lagoon as a result of the “Delta” coastal engineering project, which will be accelerated by sea level rise. The same is expected to happen in the Wadden Sea when sedimentation cannot keep pace with sea level rise anymore. This is expected to affect the Pacific oyster less than native bivalves that are more dependent on the higher intertidal. The rate of new species introductions is furthermore expected to increase in the coming years as a result of increasing facilitation by man (e.g. a proliferating global trade) in synergism with global warming (Reise and Van Beusekom, 2008). Introduction of species from the Pacific may be facilitated by the existence of Pacific oyster beds (see Section 5.1).

6.2. Conclusions and expected future developments

The Pacific oyster possesses all traits that are generally attributed to successful invaders. Especially the oyster's close association to humans, ecosystem engineering and (relative) lack of predators probably facilitated the species' successful establishment in continental NW European estuaries, in the most northern areas aided by relatively warm summers and mild winters. The advantage of *C. gigas* over native bivalve filter-feeders caused by its relative lack of predators may, however, disappear in the future since more and more non-native species, including invertebrate predators of *C. gigas*, are introduced in NW Europe. Competitive ability of *C. gigas* also contributed to its establishment success. Competition with native species in receiving communities is often a bottleneck for establishment, but may also lead to replacement of native species. Although *C. gigas* is a strong competitor, the species only appears to compete with native bivalves on a local scale. Habitat requirements overlap, but not completely. *C. gigas* appears to partially fill in an empty niche (possibly the one left behind by *O. edulis*; Reise, 1998; Cadée, 2007; Troost, 2009) and to only compete with native bivalves in the margins. Invasion by *C. gigas* may thus have caused a decrease in actual niche breadth of native bivalves (Colwell and Futuyma, 1971); they will only compete for resources where requirements overlap, and only if resources are limiting.

Although the Pacific oyster induced many changes in the receiving ecosystems, mainly related to its ecosystem engineering activities and high filtration rate and sediment bio-deposition, these effects appear relatively small and local considering the remarkably rapid expansion of the oyster. Instead of threatening the Wadden Sea ecosystem by inducing major changes, the Pacific oysters merely seem to benefit from on-going large scale changes. Furthermore, development of oyster reefs may compensate for habitat loss and biodiversity loss in estuarine environments that were caused by human activities in previous decades. Oyster reefs may in the future even play an important role in the capturing of sediment and the protection of tidal flats from erosion, thereby buffering the effects of sea level rise.

Compared to the Wadden Sea, however, effects induced by *C. gigas* have a higher impact on the Oosterschelde estuary. The rapid increase in stock size of *C. gigas*, combined with the presence of large stocks of

cultured bivalves, already led to a saturation of the carrying capacity of the Oosterschelde estuary for bivalve filter-feeders. This apparently resulted in a reduced condition of cultured bivalves and could, in a worst-case scenario, lead to a replacement of the native *M. edulis* locally although it is still not clear whether *C. gigas* is a better competitor for food than *M. edulis*.

Future developments of the Pacific oyster stock are difficult to predict because of interacting effects of climate change. In the Oosterschelde estuary, expansion of *C. gigas* appears to have come to a halt due to the saturated carrying capacity. In the Wadden Sea however, there is still ecological space left for expansion of the Pacific oyster stock. Considering the development until now, further expansion of Pacific oysters in the Wadden Sea is expected to occur more rapidly on hard substrates presented by existing mussel/oyster beds and shell banks than on soft bottoms. All mussel beds will probably turn into mixed mussel/oyster beds with different proportions of both species depending on local environmental parameters. Eventually an equilibrium situation would be expected to establish, with more or less stable stock sizes of native bivalves and the introduced oyster. However, different aspect of global change such as new biological invasions and climate change are expected to frequently upset these ecosystems in the coming decades and may constantly prevent the establishment of a new stable state.

Acknowledgements

Comments by Wim Wolff, Pauline Kamermans, Gerhard Cadée, Georg Nehls, Maria van Leeuwe, Aad Smaal, Peter Herman, Norbert Dankers, Eize Stamhuis and anonymous reviewers greatly improved earlier versions of the manuscript. The author was sponsored by the Netherlands Organization for Scientific Research — Earth and Life Sciences (NWO—ALW) (project number 812.03.003). This publication was partially financed by the Wadden Sea Society.

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