

NOBANIS – Invasive Alien Species Fact Sheet

Crassostrea gigas

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Species description

Scientific names: *Crassostrea gigas* (Thunberg 1793), Ostreidae, Bivalvia

Synonyms: *Gryphaea angulata* Lamarck 1819; *Ostrea gigas* Thunberg 1793; *Ostrea laperousii* Schrenk 1861; *Ostrea talienwhanensis* Crosse 1862.

Note: The Portuguese oyster *Crassostrea angulata* is a name often used for this species. According to genetic studies it was shown that *Crassostrea angulata* is likely a strain of *Crassostrea gigas* originating from Taiwan (Huvet *et al.* 2002). However, the identity of *C. gigas* and *C. angulata* remains unsettled. Molecular data indicate higher similarity than usual for distinct species, but still show distinct differences (Huvet *et al.* 2002, Boudry *et al.* 2003, Lam 2003, Cross *et al.* 2005).

Common names: giant oyster, Japanese oyster, Pacific oyster, Portuguese oyster (GB), ústřice obrovská (CZ), stillehavsøsters, japansk østers (DK), Felsenauster, Pazifische Auster, Pazifische Felsenauster, Portugiesische Auster (DE), Suur hiidauster (EE), risaostra (IS), Austre (LT), lielā austere (LV), ostryga pacyficzna (PL), Japanskt jätteostron (SE)



Fig. 1 and 2. *Crassostrea gigas*, right and left valve respectively of a more than 20 years old specimen, Dutch Oosterschelde estuary, undated; photos by Stefan Nehring.



Fig. 3. *Ostrea edulis* and *Crassostrea gigas*, left values, (Oe) Limfjord, Denmark, December 2003, (Cg) German Wadden Sea near the island of Sylt, January 2005, photo by Kathe R. Jensen.



Fig. 4. Farming of *Crassostrea gigas* near the German island of Sylt, April 2003. **Fig. 5.** Oyster bed *Crassostrea gigas* in the German Wadden Sea near the island of Sylt, January 2005. **Fig 6.** Oyster bed *Crassostrea gigas* in the Dutch Oosterschelde estuary, November 2005; photos by Stefan Nehring.

Species identification

The Pacific oyster shell is extremely variable and irregular in shape. Its shape depends on the type of bottom on which it is grown, as well as the degree of crowding. It will have a rounded shape with extensive fluting on hard substrates, an ovate and smooth shell on soft substrates, and a solid shape with irregular margins on mini-reefs. The two valves are solid, but unequal in size and shape. The left valve is slightly convex and the right valve is quite deep and moderately cup shaped. One valve is usually entirely cemented to the substrate. The shells are sculpted with large, irregular, rounded, radial folds with overlapping, concentric lamellae in mature specimens. Colour usually whitish with many purple streaks and spots radiating away from the umbo. The interior of the shell is white, with a single muscle scar that is sometimes dark, but never purple or black. Normally the length of shells is 80-200 mm, exceptional specimens can attain 400 mm. A Pacific oyster may live up to thirty years. Key references: NIMPIS 2002, ISSG 2005, Miossec *et al.* 2009.

Native range

The Pacific oyster occurs naturally in estuarine and coastal marine waters of Japan and south-east Asia. Specimens are found in the intertidal and shallow sub tidal zones (NIMPIS 2002).

Alien distribution

History of introduction and geographical spread

More than once during the 19th century, attempts have been made to revive exploited stocks of the European oyster (*Ostrea edulis*) with American oysters (*Crassostrea virginica*) and ‘Portuguese oysters *Crassostrea angulata*’ at several sites in coastal waters of Northern Europe. These attempts largely failed (Wolff and Reise 2002). In 1964 Dutch oyster farmers imported spat of the Pacific oyster (*Crassostrea gigas*) from British Columbia (Canada) for aquaculture activities in the Oosterschelde estuary. In the following years more imports of spat and adult specimens followed, starting in 1966 also from Japan. In 1975 and 1976 natural spatfalls occurred during very warm summers and resulted in millions of so-called weed oysters in the Oosterschelde estuary. Within several years the Pacific oyster has developed explosively and in the 1980’s other Dutch estuaries started to be colonized (Wolff and Reise 2002, Smaal *et al.* 2009). In 1983 first specimens were observed near the island of Texel in the Dutch Wadden Sea (Bruins 1983), probably originating from seed oysters imported from a French hatchery (Smaal *et al.* 2009), which were introduced in the cooling basin of the electricity plant in Texel in the late 1970s (Tydeman 2008). Spread from there was rather slow at first but since the late 1990s the invasion progressed rapidly throughout the Dutch Wadden Sea (Dankers *et al.* 2004, Fey *et al.* 2010).

In Germany ‘Portuguese oysters *C. angulata*’ were imported from Portugal and Spain and introduced into the Wadden Sea near Norddeich in 1913-14 and in the Jadebusen and near Sylt in 1954, 1961 and 1964. This did not lead to lasting cultures or establishment of the species (Meyer-Waarden 1964, Neudecker 1992, Wehrmann *et al.* 2000). Between 1971 and 1987 spat and larvae of the Pacific oyster were repeatedly imported by Federal institutes from Scottish hatcheries for scientific aquacultural experiments and studies at different sites in the German Wadden Sea and at the German Baltic Sea coast in the Flensburg Fjord (Meixner and Gerdener 1976, Seaman 1985, Wehrmann *et al.* 2000). All these attempts possessed only an experimental character and were successive stopped. However, as early as 1984, a first settlement of the Pacific oyster occurred in the western Wadden Sea area of Germany as well, which may have been dispersed from the Netherlands by natural means (Meixner 1984). Since 1986 commercial farming activities began in the northern area of the German Wadden Sea near the island of Sylt, primarily with spat taken from British and Irish hatcheries (Reise 1998, Nehring 1999). Pacific oysters are cultivated in plastic mesh bags on trestles in the intertidal zone. It takes about 2 years until the oysters reach marketable

size. Shortly after oyster farming had commenced, natural spatfalls occurred and in 1991 the first oysters were found outside the culture plot (Reise 1998). In the following years several, sometimes strong spatfalls were recorded at Sylt and subsequently, these oysters spread into the North Frisian Wadden Sea (Reise 1998, Nehring 2003a, Diederich *et al.* 2005). The development of the *C. gigas* population in the East Frisian Wadden Sea was apparently facilitated from an inflow of Pacific oysters from the southwest which was most probably enhanced by larvae drift with current from the Dutch Wadden Sea (Meixner 1984, Wehrmann *et al.* 2000). In 2003 the records imply that *C. gigas* has achieved a continuous distribution throughout the entire Wadden Sea (Reise *et al.* 2005, Nehring *et al.* 2009). On the German Baltic Sea coast first freeliving Pacific oysters were found in 2009 (S. Korpinen, pers. comm.), which may have been dispersed from the Kattegat by natural means (Wrange *et al.* 2010).

In Denmark, the first introduction of 'Portuguese oysters *C. angulata*' occurred in Limfjorden around 1972 (Jensen and Knudsen 2005). In 1979 Pacific oysters from German aquaculture experiments in the Flensburg Fjord were planted in the Little Belt of the Baltic Sea around the island Bogø. During the last thirty years of the last century large amount of *C. gigas* (> millions) seed oysters were imported from England, The Netherlands, and France to different Danish marine waters for culture in marine aquaculture experiments. The aquaculture took place in the Little Belt, in the waters south of the island Funen, in Horsens fjord, around the island Samsø in Kattegat and in Isefjorden (Kristensen 1986, Kristensen and Hoffmann 2006). Commercial production has taken place in Isefjorden from 1986, and 100,000 to 300,000 Pacific oysters were harvested annually until 1999. The cultivation was abandoned and the species was believed not to spread but to survive for several years. However, presently several patches of Pacific oysters have been located in Horsens Fjord and Isefjorden. None of the oysters were estimated to be more than 6 years old, suggesting that natural recruitment has occurred (Wang *et al.* 2007, Wrange *et al.* 2010). Pacific oysters imported by the Limfjord Oyster Company were kept in basins for depuration. They were not cultured - though there are anecdotal information of finding escapees years after the company ceased its activities (K. Jensen, pers. comm.). Presently established populations occur in the western Limfjord (Christensen and Elmedal 2007, Davids *et al.* 2007), and a few specimens have been observed along the Danish North Sea coast (Wrange *et al.* 2010). In summer 2009 several large live specimens were observed at the Northern entrance to Great Belt (WGITMO 2010). In the mid 1990s low numbers of freeliving Pacific oysters were found in the intertidal zone by Danish mussel fishermen in Lister Deep and on mussel beds in Ho Bight in the Wadden Sea, which may have been dispersed from the northern German Wadden Sea by natural means (Reise *et al.* 2005, Wrange *et al.* 2010). At the end of the last century commercial production have taken place in the Danish Wadden Sea (very limited scale with a few thousands oysters annually) (P. Dolmer and P.S. Kristensen, pers. comm.). In the following years a significant dispersal with increasing abundances took place in the Danish Wadden Sea (Wrange *et al.* 2010). The biomass of *C. gigas* was estimated to be 1,100 tons in 2005 and had increased to about 6,300 tons in 2007 (Kristensen and Pihl 2008, Wrange *et al.* 2010).

In the early 1970ties a few specimens of Pacific oysters were introduced and cultivated in Sweden, just south of the town Strömstad in the county of Bohuslän (J. Haamer, pers. comm.). In the summer of 2005 one live individual from this area was brought for examination to the Tjärnö Marine Biological Station (H.-G. Hansson, pers. comm.). A first survey of oysters was conducted during the autumn of 2007, along the approximately 400 km coastline from Strömstad to Öresund on the Swedish west coast. A total of 68 sites were investigated, Pacific oysters were found at 42 sites (Wrange *et al.* 2010). In 2008 and 2009 reproduction and newly settled larvae were seen (WGITMO 2009, Nyberg 2010). Most sites where oysters were not observed had either low salinity (<20 psu) or no hard substrate present (Wrange *et al.* 2010).

The first findings of Pacific oysters at the Norwegian coast occurred on shallow water in the Skagerrak, near Kragerø, in 2005 (Wrange *et al.* 2010). In 2006 and 2007, Pacific oysters were

reported from several sites, and during 2008 a high number of Pacific oysters were observed during a flat oyster sampling at Veierland (Wrangle *et al.* 2010). For the first time, wild Pacific oysters were also found as far north as 60°N in Norway (Wrangle *et al.* 2010). No large-scale survey has yet been conducted in Norway leaving uncertainty about the true distribution and population size in Norway.

In 1969 and the early 1970s, Pacific oysters were imported in Belgium into the Sluice Dock as an alternative to the failing farming of the European oyster, mainly as secondary introductions from the Netherlands (Kerckhof *et al.* 2007, Gofas 2010). Specimens survived even after oyster culture, and imports ceased in 1974 (Kerckhof *et al.* 2007). In the early 1990s, *C. gigas* became established outside areas of culture only, most probably as a result of an increase in water temperatures. Since then, Pacific oysters had colonized most parts of the Belgian coast with increasing abundances and are also found on buoys far offshore (Kerckhof *et al.* 2007).

Translocations of 'Portuguese oysters *C. angulata*' from southern Europe to Ireland were first made in the late 1800s and the early 1900s (Miosec *et al.* 2009). These failed because summer temperatures were not sustained at levels high enough to permit settlement (Miosec *et al.* 2009). However, occasional settlements of *C. gigas*, which has been cultured in Ireland since 1974, has been confirmed from a number of lined ponds and in the nearby shallows in Cork Harbour in Ireland since the 1980s (Miosec *et al.* 2009, WGITMO 2009). In 2008 varying levels of recruitment have been observed with multiple year classes being observed in Strangford Lough and in Loughs Swilly and Foyle (WGITMO 2009).

Pathways of introduction

Today the Pacific oyster is an important aquaculture species worldwide, only the equatorial and polar regions are less favourable for culture (CABI 2010). The majority of introductions of the Pacific oyster in Europe have been undertaken as a replacement/alternative for collapsed fisheries of native species, especially of the European oyster (*Ostrea edulis*) (Nehring 1999, Wolff and Reise 2002). To maintain viable hatchery broodstocks, different strains of the Pacific oyster have been used from various locations (Drinkwaard 1999). Depending on natural conditions, oysters are either placed directly on the bottom, on trestles or on longlines suspended off the bottom. In many regions, natural spatfalls occurred and wild oyster populations were established: e.g. Argentina, Australia, British Columbia, California, New Zealand, South Africa, and several European countries (CABI 2010). For a better understanding of the patterns and processes that lead to wild Pacific oyster populations in Europe, assumptions, statements and findings about naturally reproduction are of specific concern:

In 1965, a small consignment of *C. gigas* was imported in Great Britain from British Columbia. In a controlled breeding programme the oysters were successfully induced to spawn in 1965 and 1966 (Drinkwaard 1999). To investigate the growth, mortality and condition of Pacific oysters in British coastal waters, fixed trays were placed at two sites in Emsworth Harbour in 1970 (Askew 1972). The Pacific oyster showed a good growth rate through the summer and also grew appreciably during the winter. A decline in condition index during the summer was found, indicating spawning activity. Among the mussel spat found in the harbour during the spring of 1972 were two specimens of *C. gigas* (Askew 1972). This appears to be the first record of this species reproducing naturally in British waters.

In 1966 in France, a first introduction of Japanese spat of *C. gigas* was carried out by an oyster farmer to the Marennes area (Gouilletquer *et al.* 2002, Wolff and Reise 2002). Faced with the increase in unofficial introductions of *C. gigas* by French oyster farmers in the following years, government officials became involved and led to the official decision to introduce this alien species to the French coast to sustain the oyster industry (Grizel and Heral 1991). As a result Pacific oysters were massively introduced between 1971 and 1977 into all major oyster areas (Grizel and Heral 1991). As early as 1968, the Pacific oyster reproduced successfully in the Marennes area (Comps

1972) and since 1975 natural spatfall in French coastal waters was sufficient to sustain the oyster production (Goulletquer *et al.* 2002).

In the case of the Dutch and Belgian Pacific oysters' importations, it was not predicted that offspring were to be expected (Drinkwaard 1999, Gofas 2010). In 1966 the Dutch oyster farmers were informed that the introduction of the Pacific oyster as seed stock was acceptable since these oysters could not reproduce at the latitude of the Dutch coastal waters (Drinkwaard 1999). However, in 1976 spat settlement on jetties and rocky dike foos was obvious enough. At that time 20-30 million freeliving Pacific oysters was to estimate in Dutch waters (Drinkwaard 1999). Since 1971 Pacific oysters were repeatedly imported in Germany for aquaculture experiments from a Scottish hatchery. They were reared in German coastal waters of the North and Baltic Sea in perforated plastic boxes (Meixner 1973, Meixner and Gerdener 1976). It could be shown that Pacific oysters, while wintering in a container at the bottom of the Flensburg Fjord, had exceptionally low losses (Meixner 1974). In 1975 it was found that this species becomes mature in the Flensburg Fjord as well as in the German Wadden Sea which lead Meixner and Gerdener (1976) to the assumption that *C. gigas* is able to reproduce itself in German coastal waters. A first freeliving Pacific oyster was found in the East Frisian Wadden Sea near Juist in 1984, which may have been dispersed as larvae from the Netherlands by natural means (Meixner 1984). Because of the prevailing meteorological and hydrographic conditions an origin from the German experimental culture plot of *C. gigas* near the East Frisian Island Wangerooge, which was set up in 1982 (Wolff and Reise 2002), was possible but not very likely. However, after more than 10 years of German research activities on *C. gigas*, Neudecker (1985) concluded that the establishment of a natural stock of Pacific oysters as well as a commercially viable operation of an oyster hatchery seems to be unlikely at the German Baltic Sea coast while both might be possible under North Sea conditions. Only one year later a first permit was given by German authorities for the setting up of a commercial aquaculture plot at Sylt on the German North Sea coast. From a present day view but probably also from a historic perspective it was not surprisingly that in 1991 the first Pacific oyster outside the culture plot was found (Reise 1998). The Pacific oyster reproduced repeatedly successfully at Sylt and more freeliving oysters were encountered from summer 1993 onwards (Reise 1998).

This brief review demonstrates that in many situations where *C. gigas* was introduced to revive existing aquaculture, the species naturalized and expanded its range along the coastlines slowly at first but since the late 1990s the invasion progressed rapidly throughout European waters. It takes only four decades after first importation that European and adjacent coastal waters are more or less continuously colonized by this alien species.

Alien status in region

The Pacific oyster is found established in European coastal waters from Scandinavia to Portugal as well as in the Mediterranean Sea and Black Sea (see figure 7 and table 1). In general the Pacific oyster has not yet established permanent populations northerly than 60°N or in north-eastern areas because most of the coastal waters of Norway are probably too cold and especially most of the Baltic is probably too limnic for *C. gigas* to reproduce. However, a recent study of growth and reproduction suggested that this species has not yet reached its eco-physiological limits, and their reproductive performance may result in a further expansion (Cardoso *et al.* 2007). From a geographic point of view, the worldwide distribution of *C. gigas* demonstrates that only the equatorial and polar regions are less favourable for culture (CABI 2010).

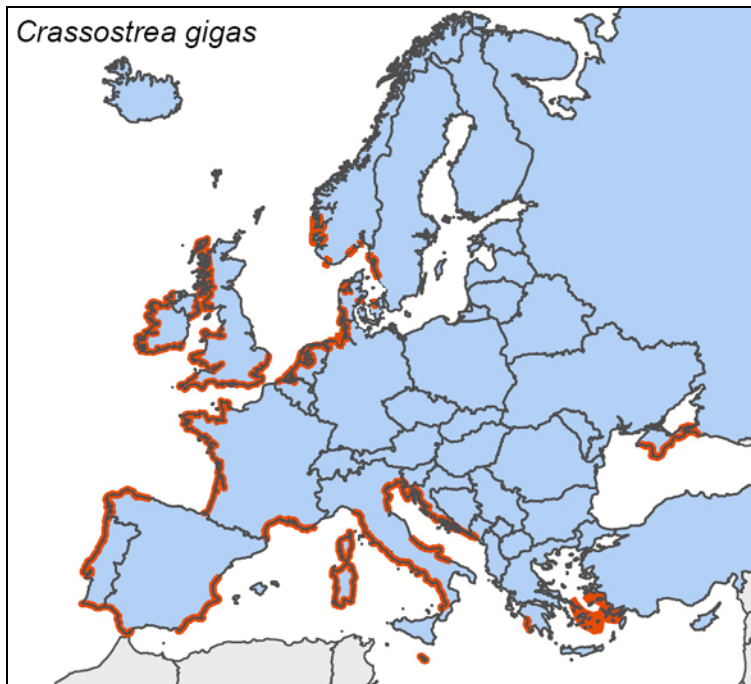


Fig 7. Occurrence of Pacific oyster (*Crassostrea gigas*) populations in European and adjacent coastal waters (updated and modified from Gollasch and Minchin 2009).

Country	Not found	Not established	Rare	Local	Common	Very common	Not known
Austria	X						
Belgium					X		
Czech Republic	X						
Denmark				X			
Estonia	X						
European part of Russia	X						
Finland	X						
Faroe Islands	X						
Germany						X	
Greenland	X						
Iceland	X						
Ireland				X			
Latvia	X						
Lithuania	X						
Netherlands						X	
Norway				X			
Poland	X						
Sweden				X			

Table 1. The frequency and establishment of *Crassostrea gigas*, please refer also to the information provided for this species at www.nobanis.org/search.asp. Legend for this table: **Not found** –The species is not found in the country; **Not established** - The species has not formed self-reproducing populations (but is found as a casual or incidental species); **Rare** - Few sites where it is found in the country; **Local** - Locally abundant, many individuals in some areas of the country; **Common** -

Many sites in the country; **Very common** - Many sites and many individuals; **Not known** – No information was available.

Ecology

Habitat description

Pacific oysters will attach to almost any hard surface in sheltered waters. Whilst they usually attach to rocks in their native range, the oysters can also be found in muddy or sandy areas. Oysters will also settle on adult specimens of the same or other mollusc species. In its native range they prefer sheltered waters in estuaries where they are found in the intertidal and shallow subtidal zones, to a depth of about 15 meters (NIMPIS 2002, CABI 2010).

In the European Wadden Sea, however, hard surfaces are scarce on the extensive mud and sand flats. Mainly rocky dike foots, stone walls, harbor facilities, and especially dead shell material and epibenthic Blue mussel beds (*Mytilus edulis*) provide a secondary hard substrate for sessile species. Therefore, Pacific oysters are mainly found in the Wadden Sea as epibionts on Blue mussel beds, attached to the shells of living and dead mussels. Other molluscs were of minor importance as substrates (Reise 1998, Nehring 1999, Markert *et al.* 2010).

The actual records imply that there are probably no more mussel beds without any Pacific oysters in the entire Wadden Sea (Nehring *et al.* 2009). Because of good spatfalls in the last years many oyster aggregations are now rapidly developing into oyster beds at several sites in the region (Reise *et al.* 2005, Nehring *et al.* 2009, Markert *et al.* 2010). Abundances generally attain densities up to 1,000 to 2,000 oysters m⁻² with a total weight of 30 to 50 kg m⁻², but on established beds they may go as high as 140 kg m⁻² (Fey *et al.* 2010). In 2007, the oyster mass including shells was estimated to be at least 190,000 t in the Wadden Sea (Nehls *et al.* 2009). Pacific oysters live primarily in the intertidal, the colonisation of the subtidal zone occurred much slower. Up to now only scattered oysters were found in subtidal locations of the German Wadden Sea. However, the Pacific oyster might be able to generate sub tidal oyster beds in the next years as has happened in Dutch waters (Smaal *et al.* 2009).

Reproduction and life cycle

The Pacific oyster is a filter feeder and will ingest bacteria, protozoa, a wide variety of diatoms, larval forms of other invertebrate animals, and detritus. Oysters are able to reproduce and grow in salinities of 10-42 psu (23-36 psu optimum range for fertilisation). The species can temporarily survive very low salinities of 5 psu. They are able to grow in temperatures ranging from 4 to 35°C and to resist freezing air temperatures as low as -17°C; however, for reproduction they need 4 to 8 weeks with more than 18°C. Some mortality is recorded at 30°C, 40°C for 1 hour results in 100% mortality. Pacific oysters have very high growth rates (in the Wadden Sea they can grow to 100 mm in their first 12 months). Pacific oysters which have not been harvested may live up to thirty years. Key references: NIMPIS 2002, Dankers *et al.* 2004, PWSRCAC 2004, Diederich 2005a, CABI 2010.

Like most oyster species, Pacific oysters change sex during their life, usually spawning first as a male and subsequently as a female. Environmental conditions may affect the sex. When food supplies are plentiful, males tend to change their sex to become females, and vice versa when food supplies are scarce. A few individuals are hermaphroditic. The Pacific oyster reached their first reproductive period in the summer one year after settlement. In northern waters, this happens in July and August. During the breeding season the reproductive organs may constitute 50% of the body's volume. Pacific oysters are extremely fertile and typically produce between 50-100 million eggs which are released over several spawning bursts. The male oyster also discharges its sperm. Fertilization must occur within 10-15 hours after spawning. The larvae are planktonic and free

swimming. The larval period ranges from 3 to 4 weeks, dependent of the water temperature. Given the right hydrographic conditions, larvae can travel distances of up to 1,300 km. When settling, the larvae group together and crawl around the sea floor, searching for a suitable hard substratum to which they can partially or almost completely cement their lower shell valves. Pollutants induce abnormal developments and mortality at the egg and larval stages, the most sensitive of them. In contrast, adult and juveniles *C. gigas* have a large capacity to bioaccumulate pollutants as a filter feeder species, therefore leading to products unsuitable for human consumption in polluted area without abnormal mortality rate. Key references: PSMFC 1996, Reise 1998, NIMPIS 2002, PWSRCAC 2004, ISSG 2005, CABI 2010.

Dispersal and spread

Its present distribution in areas where no aquaculture activities with Pacific oysters have taken place suggests that uncontrolled natural invasion and expansion has occurred. Juveniles and adults of the Pacific oyster are sedentary and normally cemented to hard substrates. However, fertilization occurs externally and larvae are planktonic, spending about 3 to 4 weeks in this free-swimming phase. The larvae develop organs that allow it to swim, although water currents remain the dominant means by which it is dispersed naturally. According to Reise (1998) residual currents along the Wadden Sea coast rarely exceed 0.1 m s^{-1} , a larva of the Pacific oyster could theoretically travel 240 km in maximum there before it attaches to a hard surface. However, the observed spread towards areas outside the surroundings of the culture plots occurred at a much slower rate (Drinkwaard 1999, Nehring 2003a, Reise *et al.* 2005, Brandt *et al.* 2008, Wrangé *et al.* 2010). This presumably does not result from a lack of dispersal but from limited larval supply or poor initial survival after settlement. High recruitment events were erratic in the Wadden Sea area and occurred only in years with abnormally high summer water temperatures above 20°C . Between 1986 and 2006, at Sylt significant recruitment success occurred only in 8 years (Diederich *et al.* 2005, Nehring *et al.* 2009). In addition, food required for developing larvae, and the presence of predators, especially shore crabs, can influence its spread (Eno *et al.* 1997).

The uncontrolled spreading of Pacific oyster larvae along the European coastlines is very likely. However, Dutch mussel farmers have reported that Pacific oysters have been found in current transports of seed mussels (*Mytilus edulis*) from the German to the Dutch Wadden Sea (Wolff and Reise 2002). It follows from this that increasing commercial activities with seed mussels will become important sources for the inter- and intraregional spreading of Pacific oysters. Larvae prefer to attach themselves to almost any type of hard surface, including ships' hulls. Local dispersal of Pacific oysters through this transport vector is also likely.

Impact

Affected habitats and indigenous organisms

The Pacific oyster has been introduced from Asia across the globe and become the leading shellfish culture species (CABI 2010). As a filter-feeder, *C. gigas* does not need additional food to sustain its growth; this species is therefore relatively inexpensive and easy to produce. It also has the capacity to adapt to various environmental conditions, has rapid growth and resistance to highly turbid areas and environmental stress. However, the invasiveness pattern of *C. gigas* has been demonstrated in several countries and it is therefore considered as an invasive alien species in such areas (CABI 2010). The potential environmental impacts related to *C. gigas* introduction are:

- Displacement of native species by competing for food and space
- Benthic-pelagic interactions and likely food web modifications
- Habitat change
- Hybridization with local oyster species

- Transfer of parasites, diseases and pest species

In North America and the Australasia-Pacific regions the oyster is known to settle into dense aggregations, resulting in the limitation of food and space available for other intertidal benthic species. It has been documented destroying habitat and causing eutrophication of the water bodies it invades (NIMPIS 2002). In Dutch waters, at the same time as Pacific oysters increased, the stocks of Blue mussels and cockles decreased. This decrease was accompanied by a decrease of the population of an important shellfish-feeding bird, the oystercatcher (*Haematopus ostralegus*). However, it is not yet clear if this is a causal relationship (Wolff and Reise 2002). In oyster cultivation areas in France high oyster densities caused a severe decline in macrofauna and zooplankton but enhanced bacteria, microfauna and meiofauna which in turn promoted the more active trophic fluxes towards birds and nektonic fishes (Leguerrier *et al.* 2004).

In the Wadden Sea *C. gigas* tends to settle in the same locations and on the same tidal level as the native Blue mussel (*Mytilus edulis*) resulting in an overgrowth of mussel beds (Nehls *et al.* 2006). Many Pacific oyster clusters are now rapidly developing into massive oyster beds at several sites in the region (Nehring *et al.* 2009). However, there are also several reports of Blue mussel spat settling on Pacific oysters. Thus, although Pacific oysters can overgrow mussel beds, they themselves again form substrates for mussels (Fey *et al.* 2010). However, *C. gigas* is a universal ecosystem transformer and the Pacific oyster is expected to take over in the mudflats, both as an ecosystem engineer generating extensive solid calcareous rocks and as a competitive suspension feeder (Reise *et al.* 2005, Nehring *et al.* 2009). First results from the East-Frisian Wadden Sea showed that total mean abundance and total mean biomass in *Crassostrea*-patches were twice as high as they were in *Mytilus*-patches (Markert *et al.* 2010). An increased abundance was detected for all functional groups in *Crassostrea*-patches whereas the increase in biomass was related to vagile epifauna (Markert *et al.* 2010). In the North-Frisian Wadden Sea a field experiment with blue mussels and Pacific oysters revealed that differences in the habitat matrix generated by these two bivalve aggregates entailed different abundances of associated infauna and epifauna (Kochmann *et al.* 2008). Further, a cover with native furoid algae common on sheltered mussel beds rarely develops where Pacific oysters prevail. In contrast patches of Pacific oyster form a suitable substrate for the invasive alien seaweed *Sargassum muticum* (Lang and Buschbaum 2010). It seems that *C. gigas* has also beneficial effects on other (invasive) alien species such as the American slipper limpet *Crepidula fornicata*, the Asian ascidian *Styela clava*, the Australasian barnacle *Austrominius modestus* and two Pacific shore crabs of the genus *Hemigrapsus* (a.o. Liebich 2007, Thieltges *et al.* 2009, Wolff *et al.* 2010). Thus, *C. gigas* seems to be a key species for enhancing the trend of global homogenization of flora and fauna.

The recent increase of Pacific oysters is responsible that also intertidal snails are now exposed to high epibiotic loads. Field surveys demonstrated that up to 10% of native periwinkles *Littorina littorea* occurring on epibenthic bivalve beds and up to 25% of snails living on sand flats may be fouled by *C. gigas* (Eschweiler and Buschbaum 2011). As shown by Eschweiler and Buschbaum (2011) body dry weight of snails without Pacific oyster overgrowth was twice as high compared to periwinkles covered with oysters. Also crawling speed of snails with oyster epigrowth was significantly slowed down and about ten times lower than in unfouled periwinkles. Additionally, Pacific oyster epibionts caused a strong decrease in reproductive output. However, no profound detrimental effect could be observed on periwinkle population so far, but Eschweiler and Buschbaum (2011) concluded that it seems to be a question of time until the compound of a numerousness of epibiotic alien species might turn the tide and strongly impair periwinkle population dynamics and consequently its ecological function, such as grazing effect, on benthic community structure in the Wadden Sea.

The Pacific oyster has a large filtration capacity and filters on average 5 l/g/h but values up to 25 l/g/h have been recorded (Ren *et al.* 2000). A possible top-down control of phytoplankton biomass may modify benthic-pelagic coupling by forcing a shift from pelagic to benthic consumers because

of food depletion in the water column (Diederich 2005a). However, as the oysters release nutrients and pseudofaeces into the environment, planktonic and benthic productivity in the Wadden Sea may increase (Diederich 2005a). As a coastal filter the oyster beds may be a functional analogue to the mussel beds but the structural effects differ. In particular, the Pacific oysters are still poorly integrated into the food web of the Wadden Sea. Birds like eider, oystercatcher and herring gull which particularly feed on mussels may run into a shortage of food because most oysters are too large for consumption or fused into clusters, and shells are too strong for the birds to break them open (Blew and Südbeck 2005, Wehrmann and Schmidt 2005; but see also Cadee 2008 a,b). This situation may deviate considerably from the actual nature conservation objectives that focus on the role of the Wadden Sea as one of Europe's most important wetlands for migratory bird populations (Smaal *et al.* 2005).

There were reports of mass Pacific oyster deaths in a restricted area along the Dutch coast in August 2004 and in several harbour areas on the German Wadden Sea coast in September 2005. Up to 80% of oysters were found dead. There were no clear indications of the causes and there have been no indications of any disease or parasite. Possible explanations are a.o. high water temperatures, low water exchange and low plankton concentration during these periods (Wehrmann and Schmidt 2005). Since 2008, events of mass mortalities of Pacific oysters were recorded in France, in Ireland, in Spain and in the United Kingdom yet again (WGITMO 2009, 2010, EFSA 2010). Mortalities are affecting diploid and triploid oyster spat and juvenile, irrespective of their origin (natural or hatcheries) in most French oyster production areas. Several infective agents were detected in moribund oysters including several species of *Vibrio* and the OsHV-1 virus, which origin is still unknown (WGITMO 2010). While the causes of the mortalities still remain uncertain, the epidemiological investigations undertaken in Ireland and the United Kingdom in 2009 suggest that OsHV-1 virus play a major role in the mortalities (EFSA 2010, European Commission 2010). Continued importation of Pacific oyster seed creates a potential risk for introduction of other alien species and diseases. In 1981 all importations of Pacific oysters from France to The Netherlands were stopped and all planting of such oysters in the Oosterschelde was prohibited, because a new disease, caused by a protozoan (*Bonamia ostreae*), had been introduced (Drinkwaard 1999). Reise *et al.* (2002) listed 32 alien species probably transferred with the Pacific oyster in the North Sea and the Channel. Several of these alien species are known to be invasive, can negatively affect the native environment (Leppäkoski *et al.* 2002).

In conclusion, the Pacific oyster has established firmly in European coastal waters and seems to particularly benefit from the current trend of warming. Together with several other alien invaders parallel to or interacting with *C. gigas*, the benthos around low tide level has already been overturned with cascading effects on foraging birds and the functioning of the ecosystem. In this context, *C. gigas* has been judged by the European experts of the DAISIE research project (<http://www.europe-aliens.org/speciesTheWorst.do>) to be one of the “100 of the Most invasive Alien Species in Europe”.

Genetic effects

Different strains of Pacific oysters are recognised. In 1970 ‘Portuguese oysters *Crassostrea angulata*’ became the victim of disease in The Netherlands. The complete stock disappeared in Dutch waters, whereas it was replaced by Pacific oysters imported from British Columbia and Japan in the same areas without any problem (Wolff and Reise 2002, Wolff 2005). The genetic variability in the introduced stocks and their offspring may be high. These genetic aspects need further study (Drinkwaard 1999). However, the multiple origins of imported seed oysters combined with the ability to hybridize makes it difficult to establish the actual origin of the established population (K. Jensen, pers. comm.).

The Pacific oyster has been found to be capable of interbreeding with several other *Crassostrea* species (Gaffney and Allen 1993). The coexistence of two oyster species, the native European

oyster (*Ostrea edulis*) and the Pacific oyster, raises the possibility of natural hybridization and possible introgression. However, no hybrid individuals were observed yet.

Human health effects

Pacific oysters pose a direct threat to human safety because of their propensity to cut feet and shoes with their sharp shells. In The Netherlands they nowadays interfere with the recreational use of the Oosterschelde estuary (Wolff and Reise 2002). As the Pacific oyster is well adapted to the Wadden Sea ecosystem and competitive superior to their native antagonists, a further increase of the oyster population in the Wadden Sea is expected, probably combined with an increase of cut injuries among walkers and swimmers.

Economic and societal effects (positive/negative)

In historic times, beds of the native European oyster (*Ostrea edulis*) were of wide-spread occurrence in the Wadden Sea and an important fisheries resource. However, overexploitation by oyster fishery since the 18th century exterminated these populations. Several attempts to revive the former oyster stock in the Wadden Sea have failed (Drinkwaard 1999, Nehring 1999). The cultivation of Pacific oysters in recent years in a culture plot near Sylt gave a new and rising production. Fishery on wild Pacific oyster stocks is at present not allowed due to nature conservation directives. However, in July 2005 a first licence was given by German authorities for collecting of wild oyster spat in a small area of the Wadden Sea near Sylt. Whether such exploitation will be profitable compared to the importations of seed oysters is not yet known. However, collection of wild oyster spat instead of importing seed oysters may reduce the possible introduction of new invaders, like epibionts or parasites and pathogens. It may be that in the near future harvesting of adult oysters will also be allowed. However, once the oysters have developed beds the product quality for the consumers decreases dramatically due to clumping, increase of shell size and decrease of meat content. Harvesting wild Pacific oysters is unlikely to be effective and profitable.

The actual records imply that the Pacific oyster has achieved a continuous distribution throughout the entire Wadden Sea (Reise *et al.* 2005, Nehring *et al.* 2009). Spat settle on any hard substrate, but preferentially upon conspecifics and wild beds of the native Blue mussel (*Mytilus edulis*) (Diederich 2005b, Nehls *et al.* 2006). However, there is evidence that the recently observed decline of mussel beds in the Wadden Sea is mainly caused by failing spatfall possibly due to mild winters, whereas the increase in oysters is facilitated by mild winters and warm summers, respectively (Nehls *et al.* 2006, 2009). But it is to be expected that in the near future the traditional Blue mussel fishery might be even more hampered because still existing seed mussels and mussel beds become overgrown by oysters. This is estimated to result in a maximum loss in the German Blue mussel fishery of about 25 Mio Euro per annum (Nehring unpubl.).

Solid calcareous rocks of Pacific oysters are a completely new biogenic structure for the intertidal area of the Wadden Sea. Whether or not oyster beds may facilitate coastal protection is not yet investigated and estimated. In this context, Pacific oysters in northern Europe may benefit from global warming and may become more abundant than mussel beds have ever been (Nehring 2003b). Due to a further increase of the oyster population Pacific oysters will interfere with the recreational use of the Wadden Sea because of their razor-sharp shells. Analyses about the potential economic effects are needed.

Management approaches

Prevention methods

The analysis on overall impact potential on environmental, economic and human interests suggests

that the Pacific oyster is a high risk alien species in temperate regions. In 1994 the ICES Code of Practice on the Introductions and Transfers of Marine Organisms was adopted. As a legal instrument, the European Council enacted in 2007 a council regulation concerning the use of alien and locally absent species in the European aquaculture industry (Council of Europe 2007). However, to prevent uncontrolled spreading of the Pacific oyster in Europe waters both instruments came too late to be of use. Besides translocations of *C. gigas* into new areas were made at a time when management practices were limited (Miossec *et al.* 2009). The consequences for the local environments were not estimated and, more generally, not condemned. Because of the high potential for natural dispersal in introduced aquatic species, and many human vectors for secondary dispersal along European coasts, adequate precautionary measures are needed beyond an international management plan. A decision not to introduce Pacific oysters for culturing would have merely postponed the invasion unless the same decision would have been for all suitable European coasts and adjacent waters (Reise *et al.* 2005, Nehring and Klingenstein 2005). Continued importation of Pacific oyster seed creates a potential risk for introduction of other alien species and diseases. To avoid the introduction of non-native species into Dutch coastal waters a new policy on the importation of shellfish and crustaceans was developed in 1996. Since the year 2001 the introduction of native species from populations outside the North Sea area (boreal) into Dutch coastal waters is no longer allowed. To prevent wild settlement of Pacific oysters in aquaculture plots sterile triploid seed oysters can be used. There are two methods to produce triploid animals. One is via chemical induction and the other is crossing of tetraploids with diploid broodstock. The dangers in the former technique are that less than 100% of the animals produced are triploid while the dangers of the latter technique would be the unintentional release of tetraploids into the marine environment, which could potentially interact with natural diploids producing sterile triploids. Since 1988 triploid *C. gigas* are commercially available. However, in 1999/2000 triploid Pacific oysters made only up 30% of all Pacific oysters farmed on the West Coast of North America (Mariculture Committee 2003). Currently, five French companies provide the majority of hatchery produced Pacific oyster spat for the European market (EFSA 2010). The proportion of triploid spat is estimated to be about 80% of the hatchery production in France (EFSA 2010). However, Pacific oyster culture in Europe is traditionally based on supply of spat collected from the wild. Precise figures are not available and, depending on authors it is estimated that between 40 to 70% of the cultured Pacific oyster in France is of wild origin (EFSA 2010). Evidence now suggests *C. gigas* can breed in Ireland and a change of policy on its use in aquaculture is occurring by using only triploid specimen in Ireland in future (J. Early, pers. comm.).

Eradication, control and monitoring efforts

Handpicking was used between 1976 and 1981 in The Netherlands to reduce the wild stock of Pacific oysters in the Oosterschelde estuary. These attempts failed and from that time on the new inhabitant was accepted as belonging to the Dutch fauna (Drinkwaard 1999). However, in March 2006, a large-scale oyster removal experiment was conducted in the Oosterschelde (Wijsmann *et al.* 2008). A total area of 50 ha Pacific oysters, with a total biomass of 12.5 million kg, are removed with mussel dredges from natural littoral and sub-littoral oyster beds in the Oosterschelde. The oysters were dumped at designated dumping locations in the Oosterschelde where they should die from suffocation and starvation. The results showed that a complete removal of the Pacific oysters from the Oosterschelde is impossible. However, control of oysters with mussel dredges at locations where abundant growth leads to problems seems feasible (Wijsmann *et al.* 2008).

In other European countries no eradication or control programmes were carried out up to now. There was unanimous agreement that after an extensive establishment of Pacific oysters no eradication or control methods are feasible which would not also harm other components of the native ecosystem, especially of the Wadden Sea ecosystem (Reise *et al.* 2005). In the Danish

Wadden Sea guided tours take tourists out to hand collect Pacific oysters for personal consumption. However, it is realized that this is not enough to control the population (K. Jensen, pers. comm.). The Pacific oyster is one of the most damaging species in the Wadden Sea. However, no coordinated international monitoring programme to document the spreading and impacts is designed and realized yet. Thus, it is still a challenge to act on the Pacific oyster. Therefore, an unlimited observance of existing management initiatives and instruments as well as the implementation of new and purposeful ones is absolutely essential (Nehring *et al.* 2009).

Information and awareness

Every time when the Pacific oyster occurred in new areas, reproduced naturally or settled in dense aggregations, it caught the public attention and was followed by a broad media interest. However, purposeful information platforms are not yet installed in Europe. Education and awareness raising is needed.

Knowledge and research

Together with an r-selected life history trait (high fecundity and dispersal capacity, fast growth), the broad environmental tolerances predispose the Pacific oyster as a species likely to be a successful invader. Thus, research is ongoing on the establishment success and impacts of the Pacific oyster in different areas of European coastal waters.

Recommendations or comments from experts and local communities

Until now the introduction, establishment and spreading of alien species in European coastal waters has been perceived only on a descriptive level in some ways. Especially a purposeful strategy in dealing with the phenomenon in regard to the protection and conservation of the Wadden Sea, which was inscribed on the World Heritage List in June 2009, is missing. The development of an alien species plan on the level of the Trilateral Cooperation on the Protection of the Wadden Sea is absolutely essential (Nehring and Klingenstein 2005, Nehring *et al.* 2009, Wolff *et al.* 2010). In 2009, the World Heritage Committee encourage the State Parties of the Wadden Sea Cooperation to implement a strict monitoring program to control invasive species associated with ballast water, marinas and aquaculture in the property. In this context, efforts to protect *Crassostrea* beds in the Natura 2000 programme as natural habitat type of community interest (Reefs, code 1170) should not to be pursuing further as long as no extensive conclusion about the significance of ecological effects of *C. gigas* on biodiversity is available (Nehring *et al.* 2009).

References and other resources

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Links

Global Invasive Species Data Base - [Crassostrea gigas](#), a world overview

ISSG - Invasive Species Specialist Group

Species Fact sheet - [Crassostrea gigas, a world overview](#)

FAO - Food and Agriculture Organization of the United Nations

Species Fact Sheet - [Crassostrea gigas in Europe](#)

DAISIE - Delivering Alien Invasive Species Inventories for Europe

Species Fact Sheet - [Crassostrea gigas in Great Britain](#)

JNCC - Joint Nature Conservation Committee

Species Fact Sheet - [Crassostrea gigas in the Mediterranean Sea](#)

CIESM - International Commission for the Scientific Exploration of the Mediterranean Sea

Species Fact Sheet - [Pacific \(Japanese\) Oyster Crassostrea gigas](#) (Alaska)

PWSRCAC - Prince William Sound Regional Citizens' Advisory Council

Species Fact Sheet - [Pacific oyster Crassostrea gigas in USA](#)

PSMFC - Pacific States Marine Fisheries Commission

Species summary - [Crassostrea gigas in Australia](#)

NIMPIS - National Introduced Marine Pest Information System

UK Non-Native Organism Risk Assessment - [Crassostrea gigas - Pacific oyster](#)

NNSS - Non-Native Species Secretariat

[Workshop on Crassostrea invasion in the Wadden Sea](#), March 2007

[Conference on Crassostrea invasion in the Wadden Sea](#), August 2010

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