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## 10 The Pacific Oyster (*Crassostrea gigas*) Invasion in Scandinavian Coastal Waters: Impact on Local Ecosystem Services

### 10.1 Introduction

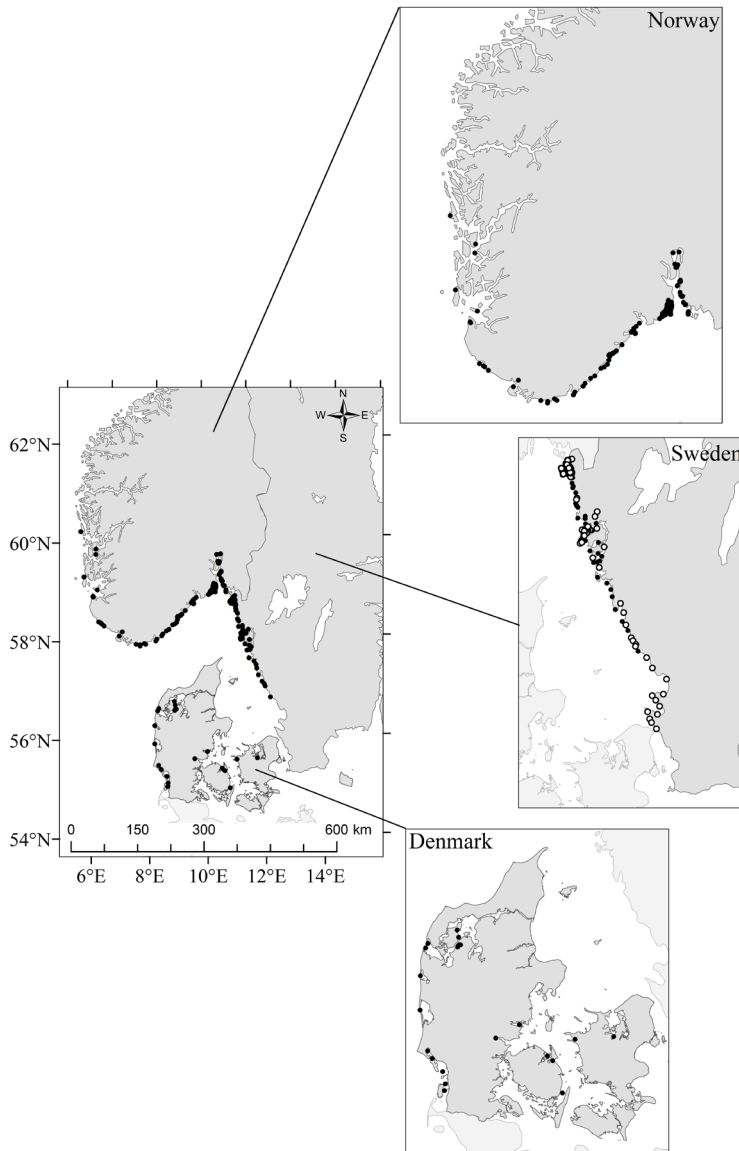
Shellfish have always played an important role in subsistence and income for coastal communities. Shallow-water bivalve beds are easily accessible and have been exploited and overexploited for centuries. Depletion of stocks has led to farming and aquaculture of many species. Few species, if any, have been as popular and successful as the Pacific oyster (*C. gigas*). Its highly efficient filter feeding, high growth rates, massive reproductive output, and tolerance of a large range of abiotic conditions, has not only made it one of the world's 20 most cultured species, but also one of the most invasive. This chapter tracks the Pacific oyster on its way towards the North-eastern corner of its European distribution, predicts its future distribution, and discusses the implications for local ecosystems.

### 10.2 Invasion History of Pacific Oysters: from Deliberate Introduction to Establishment of Feral Populations

*Crassostrea gigas* (hereafter *C. gigas* or oysters) originates from the coastlines of the Japanese Sea. Due to its suitability for aquaculture, it has been introduced to several geographical areas, and now has a world-wide distribution (Ruesink *et al.*, 2005). In the mid-1960s, European shellfish farmers started oyster production using *C. gigas*, and by the mid-90s, feral populations emerged from the French Atlantic coast to the German and Danish Wadden Sea (Héral, 1989; Drinkwaard, 1999; Reise *et al.*, 2005; Couzens, 2006; Kochmann *et al.*, 2008). In this section, we will briefly review the current status of the species in Scandinavia.

*Denmark.* From the early 1970s spat was introduced to several Danish fjords for aquaculture, and production continued until the late 1990s. Oysters were left in the sea when farming discontinued under the assumption that natural reproduction would not occur in the present environmental conditions, but feral populations appeared both around the trial areas and at new sites (for current known distribution, see Figure 10.1). Common habitats are blue mussel beds and mudflats in sheltered intertidal areas. Densities in three well-studied areas range from very high (500-2000

individuals  $\times$  m<sup>2</sup> in the Wadden Sea), to medium (50 individuals  $\times$  m<sup>2</sup> in the Limfjord), to low (max 0.11 individuals  $\times$  m<sup>2</sup> in the Isefjord) (Dolmer *et al.*, 2014).



**Fig. 10.1:** *C. gigas* distribution in Scandinavia (filled circles) and monitored stations (open circles).  
Figure credit: Mark Wejlemann Holm (Roskilde University).

*Sweden.* Aquacultural trials in the vicinity of Tjärnö between 1973 and 1976 introduced oysters to the Swedish west coast. When the trials ended, oysters were left in the sea. For the next three decades the oysters were absent, until the public reported several independent sightings of the species in 2007. Presently, we know of about 250 sites with a total live biomass of 100 000 – 500 000 tonnes (Strand & Lindergart, 2014), along the Swedish west coast, mostly concentrated north of Gothenburg (Figure 10.1). In contrast to Denmark, vast shallow areas are scarce and tidal variations are low. The oysters instead settle in small, shallow bays, narrow sounds, and short beaches – sites with high current velocities or high water exchange rates. Densities have increased dramatically since the initial colonization event and now range from 0.06 to 1170 individuals  $\times$  m<sup>2</sup> at colonized sites. Currently, at least eight different cohorts exist in Sweden (oysters settled 2006–2013). Recent reports about increasing densities of oysters in deeper sub-tidal areas indicate that the species may now be extending its depth range.

*Norway.* Oyster observations started in 2002, and by 2012 more than 100 oyster locations had been registered along the coast. The oysters grow mostly in habitats very similar to those in Sweden, along the southern coast from Østfold in the east to Rogaland in south-west Norway (Figure 10.1). Dolmer *et al.* (2014) reported population densities up to 91 individuals  $\times$  m<sup>2</sup>, and increasing densities in recent years. Additionally, Bodvin *et al.* (2013) described several new populations in Rogaland in 2012 and 2013.

The sources of the Danish oyster populations are probably a combination of larval drift from the German Wadden sea and abandoned aquaculture trials (Dolmer *et al.*, 2014). Meanwhile, the origins of the Swedish and Norwegian populations are still unknown. The prevailing hypothesis is that larvae of the species hitch-hiked with ocean currents from Denmark to the Swedish west coast and then onward to Norway. In Box 10.1 we present results from two research approaches that, together, aim to reveal the source and the pathways of the intra-Scandinavian dispersal.

### **Box 10.1. Origin and Dispersal of *Crassostrea gigas* Larvae in Scandinavia**

*Oceanographic modelling.* Based on the prevailing currents in the North Sea, Skagerrak and Kattegat, the distance between the Danish and Swedish west coasts, and required size of the source population, the most likely origin of the oysters in Sweden is the Limfjord population at the Danish north-western coast. To evaluate the likelihood of dispersal via the oceanographic coastal circulation, we used a biophysical model combining ocean current velocities with a particle-tracking routine to simulate dispersal of oyster larvae at three different depth intervals between four sampling sites (Figure 10.2); Wadden Sea (Wa; south-west Denmark), Limfjord (Li), Kristineberg (Kr), and Tjärnö (Tj; north-western Swedish coast).

We based the biophysical model on the 3D oceanographic circulation model BaltiX (Hordoir *et al.*, 2013), a NEMO ocean engine-based (Madec, 2010) regional model covering the Baltic Sea and the North Sea (see Hordoir *et al.*, 2013 for a detailed model description with preliminary validations). To simulate larval dispersal we used a particle-tracking model that calculates transport of particles using temporal and spatial interpolation of flow-field data from the BaltiX circulation model using a time step of 15 min. We released particles (70500 in total) from 4 sites (Fig. B1A) during August and September for 8 years (1995–2002). To account for development time from spawning to settling, we set the pelagic larval phase to 20–30 days, which is common in this area. Finally, we explored three depth intervals; 0–2, 10–12, and 24–26 m. To estimate dispersal probability between the sampling sites we calculated the proportion of particles released from the focal site that ended up at one of the other sites. In the figure, the colours indicate areas to which there is a certain probability that larvae will disperse if drifting at a depth of 10–12 m. Increasing probability is indicated by a transition from blue to red color. The calculation of connectivities was performed by Per Jonsson (BioEnv, GU).

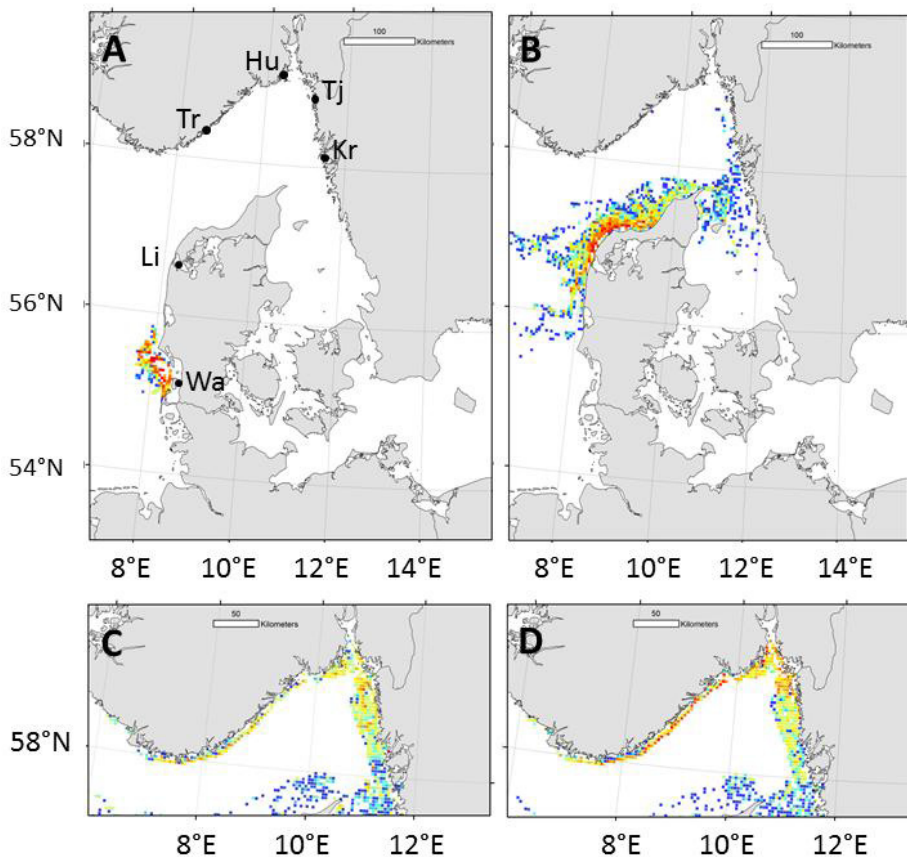
Our model results indicate that the Danish Wadden Sea is relatively isolated from the northern populations because northward larval dispersal was only possible in surface water (Figure 10.2A). The Limfjord appears to be better connected to the surrounding water masses; Limfjord larvae dispersed to Kristineberg and Tjärnö with surface water, and to Kristineberg at medium water depth (Figure 10.2B). It is therefore highly unlikely that the Pacific oysters in Sweden arrived from the Danish Wadden Sea, while dispersal from the Limfjord to Sweden is possible. Larvae may disperse both north and south along the Swedish west coast, although the northward dispersal is more likely (Figure 10.2B). Furthermore, dispersal from the Swedish west coast to Norway is also probable, indicating that the populations in Norway may be enriched by drifting larvae from Swedish populations (Figure 10.2C, D).

Adult oysters already existed in Norway in 2007 when the main invasion event in Sweden occurred (Dolmer *et al.*, 2014), thus the origin of the Norwegian oysters is still unclear and the relative importance of dispersal from Sweden versus other origins for the dynamics of Norwegian populations between the Pacific oysters in Sweden and Norway need to be studied further.

*Molecular genetics.* Source populations can also be found or validated by comparing molecular signatures of the target population and a range of possible source populations. A study using microsatellite genetic markers to compare the genetic make-up of six Scandinavian populations (Wadden Sea, Limfjord, Kristineberg, Tjärnö, Hui, and Tromlingene, Figure 10.2A) with French oysters found that the Scandinavian populations are different enough to exclude France as a direct source (Meurling, 2013; Strand & Lindgarth, 2014; Strand, unpublished data). The data also indicated that the majority of the investigated Scandinavian populations either have significant gene flow between them or that they were very recently separated.

Earlier studies of the genetic structure of the Pacific oysters in Europe (not including Scandinavia) have shown very little genetic differentiation between populations, with the exception of a population outside the island of Sylt in the northern Wadden Sea (North-Western Germany; Moehler *et al.*, 2011). The introduction history may explain the differentiation between the south European populations and the Sylt population. Most of the European populations descend from individuals directly imported from the aquaculture gene pool in British Columbia. The direct origin of the Sylt population, however, are farmed oysters from the British Isles.

The Scandinavian populations may have the same origin as the Sylt population (Meurling, 2013). However, one of the Norwegian populations, Hui, did not resemble any of the other populations in the study, indicating a different source (Strand & Lindegarh, 2014).



**Fig. 10.2:** Source populations for oceanographic modelling; Wadden Sea (Wa), Limfjord (Li), Kristineberg (Kr) and Tjörn (Tj), and genetic analyses; Wa, Li, Kr, Tj, Hui (Hu) and Tromlingene (Tr), as well as dispersal probabilities from the Danish Wadden Sea (A), larval dispersal probabilities from the Limfjord population (B), larval dispersal probabilities from the Kristineberg population (C), and larval dispersal probabilities from the Tjörn population (D). The colours indicate areas to which there is a certain probability that larvae will disperse if drifting at a depth of 10–12 m. Increasing probability is indicated by a transition from blue to red color.

### 10.3 Invasion Future of Pacific Oysters: from Present to Forthcoming Distribution

Spatiotemporal variation in distribution limits of a species depends on both biotic and abiotic environmental factors. Each species has its own unique optimal environmental range in which its fitness is optimized, and can survive only limited periods of time when the environmental conditions approach the species' critical tolerance limits. *C. gigas* is — like many invasive species — very tolerant to varying conditions. As an intertidal species, *C. gigas* has a very broad temperature range for survival, from sub-zero degrees to 30°C (Quayle, 1969; Walne, 1974; Le Gall & Raillard, 1988; Bougrier *et al.*, 1995; Diederich *et al.*, 2005; Diederich, 2006; Carrasco & Baron, 2010; Strand *et al.*, 2011). Normal temperature ranges in Scandinavia are  $-1 \pm 24^{\circ}\text{C}$  and  $-12 \pm 30^{\circ}\text{C}$  for surface seawater and air temperature, respectively (Strand *et al.*, 2012). This indicates that neither surface seawater nor air temperature in Scandinavia should cause any problems for survival and continued dispersal of the species under normal conditions. However, long periods of extremely cold conditions may push the oysters beyond their lower thermal limits. For instance, the extreme conditions during the winter of 2009–2010 killed large proportions of the oysters at many Scandinavian loactions (Strand *et al.*, 2012). In Box 10.2, we present results from the first effort to use an ecological niche modelling approach to find suitable habitats for *C. gigas* in Scandinavia.

The Intergovernmental Panel on Climate Change (IPCC) predicts that global mean temperature will increase over the next 100 years, with extreme meteorological conditions becoming more common (IPCC, 2007). As the geographical distribution of species is highly dependent upon abiotic factors, species distributions will shift in response to climatic change. A meta-analysis of the effects of climate change on marine ecosystems (Poloczanska *et al.*, 2013) found that widespread systemic shifts in processes such as distribution of species and phenology are comparable to or greater than those observed on land. Moreover, the front-line of marine species distributions is moving toward the poles 12 times faster than that of terrestrial species. In Box 10.2, we present forecasts for changes in suitable oyster habitats in Scandinavia from 2013 to 2050 and 2100.

The dynamics of the geographical range of a species not only depend on a suitable abiotic environment, but also on the mode of dispersal and capability of overcoming dispersal barriers. Due to the current trends in globalization, the range expansion of many species has increased dramatically through human-mediated vector transfer (for more details, please refer to Chapter 1). Indeed, global human-assisted distribution of *C. gigas* started almost a century ago and will likely continue in the future as global warming facilitates aquaculture in new areas (see also section 10.4). The topic of range limits have been reviewed repeatedly (see Brown *et al.*, 1996; Gaston, 1996; Gaston, 2003; Gaston, 2009; Parmesan *et al.*, 2005) and will not be discussed further in this chapter.

### Box 10.2. Current and Predicted Habitat Suitability for *Crassostrea gigas* in Scandinavia

Ecological niche modelling methods are widely used to describe the potential range shifts of species from current and future projections of suitable habitat. We developed species distribution models for the invasive oyster using openModeller webservices (Muñoz *et al.*, 2011) and following the methods described by Leidenberger *et al.* (2015). We obtained *C. gigas* occurrence data (Figure 10.3A) from collaborators and the Global Biodiversity Information Facility (<http://gbif.org>), and filtered these for environmentally unique points with the BioClim algorithm for the environmental layers specified in Table 10.1. The BioClim algorithm (Busby, 1986; Nix, 1986) also calculated the range for each environmental factor shown in Table 10.1. Environmental layers were obtained from Bio-Oracle at 5 arc-minutes (Tyberghein *et al.*, 2012), and AquaMaps (Kaschner *et al.*, 2010) at 30 arc-minutes. For the projections of 2050 and 2100 climate conditions, we used layers from the ECHAM5 A1B climate change scenario (Jungclaus *et al.*, 2006; IPCC, 2007).

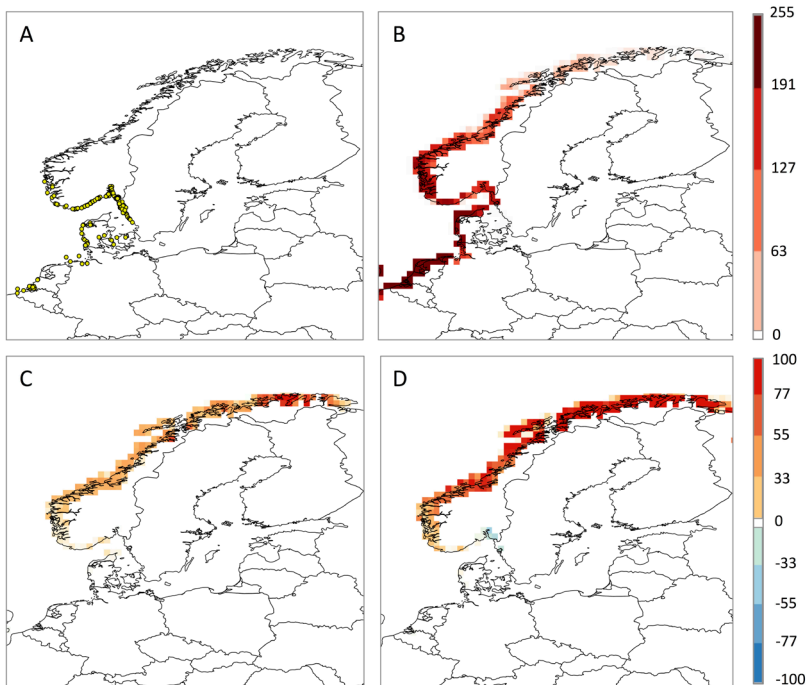
To calculate habitat suitability, we used all environmentally unique points available from the global *C. gigas* distribution and the environmental layers (Table 10.1) in the Ecological Niche Modelling workflow (ENM), applying the Mahalanobis distance method (Mahalanobis, 1936; Farber and Kadmon, 2003). Model performance was assessed using 10-fold cross-validation, measuring AUC (Area Under the Curve), which was calculated using the proportional area approach (Phillips *et al.*, 2006), and omission error, which was calculated using the lowest presence threshold (LPT). Model testing resulted in Mean AUC =  $0.92 \pm 0.02$  and omission error = 1.77%.

We projected three climatic scenarios (2013, 2050, and 2100) into 50 km coastal bands of Norway, Sweden, and Denmark. Extent of potential species distribution was calculated with the ENM Statistical Workflow (Leidenberger *et al.*, 2015). The workflow computes the coverage and overall intensity of suitable habitat, as well as the difference between these values for two climate scenarios in a given area, using the R statistical environment (R Core Team, 2013). Overall coverage was computed as the percentage of raster cells with values  $> 0$ , while overall intensity was computed as the sum of all cell values divided by the number of raster cells. Habitat suitability values are presented as a heat map (Figure 10.3B) ranging from white (not suitable) to red (suitable). The calculation of difference values represents the maximum possible change between two scenarios and are presented as eight positive and negative classes on a heat map (Figure 10.3C, D). Cells with colours from white–red indicate increasing habitat suitability, while cells with colours from white–blue indicate decreasing habitat suitability.

The suitable habitat as inferred by the model matches the known distribution of *C. gigas* in Scandinavia with one exception (Figure 10.3A, B). Along the western coast of Norway, suitable habitats exist as far as to the Lofoten Islands, while sustained populations are only reported to latitudes of around Bergen, approximately 800 km south of the Lofoten Islands. This indicates that the current range distribution of *C. gigas* in Scandinavia may increase northward along the Norwegian coastline, and that the invasion may still be in an initial stage in Norway.

The most affected Scandinavian coastlines are those of Norway and Denmark, where suitable habitat currently covers 90.41% and 34.08% of the coastal band, respectively (Table 10.1). We found no indications of suitable habitats in the Baltic (Figure 10.3A, B), while the transitional area between the North Sea and the Kattegat showed decreasing habitat suitability values from the Skagerrak towards the Kattegat and into the Belt region. Consequently, only minor parts of the Swedish coastline currently provide suitable habitat (6.72%) for *C. gigas* (Table 10.1).

Our model scenarios for 2050 and 2100 (Figure 10.3C, D) predict that *C. gigas* will shift its Scandinavian range towards the north-east along the coastline of the Scandinavian shield. We found no indications of suitable habitat in the Baltic in any of the climatic scenarios. The projected range shift has highest impact in Norway, where both coverage and intensity of suitable habitat increase in the coastal band facing the Atlantic until 2100 at 4.75% and 27.87%, respectively (Table 10.1). In Sweden and Denmark, the extension of the species declines slightly under the projected range shift because of less suitable habitat in the Kattegat region. It is worth noting, however, that the modelling approach relies solely on current distribution of the focal species and does not account for possible evolutionary adaptation or increased phenotypic plasticity in response to new environmental conditions.



**Fig. 10.3:** Distribution of confirmed occurrence points (A), present distribution of suitable habitat (B), changes in habitat suitability between 2013 and 2050 (C), and changes in habitat suitability between 2013 and 2100 (D). See text for description of colour coding.

**Tab. 10.1:** Summary of occurrence data and environmental parameters (including their range) used for modelling, as well as statistical output of 12 spatio-temporal projections for *Crassostrea gigas*; n = number of environmental unique points, MD = mean depth, DL = distance to land, SIC = sea ice cover, SSS = sea surface salinity, SST = sea surface temperature. Asterisks indicate environmental factors used for modelling.

	Global	Denmark	50 km coastline Sweden	Norway
<b>Data</b>				
Occurrence points	1249			
n	338			
DL [km]*	0 – 92			
MD [m]*	1 – 1738			
SIC*	0 – 0.2			
SST [°C]*	-1.34 – 30.17			
SSS [PSU]*	11.86 – 35.64			
pH	7.88 – 8.31			
<b>Projection</b>				
DIFF statistic [%]				
Coverage 2013	-	34.08	6.72	90.41
Coverage 2050	-	34.08	6.72	95.12
Coverage 2100	-	31.83	6.14	95.16
2100-2013	-	-2.24	-0.57	4.75
Intensity 2013	-	10.12	1.37	32.59
Intensity 2050	-	10.71	1.42	45.42
Intensity 2100	-	10.27	1.26	60.47
2100-2013	-	0.15	-0.10	27.87

## 10.4 Invasion Impacts of Pacific Oysters: from Ecosystem Engineering to Community Restructuring

A recent risk assessment report (Dolmer *et al.*, 2014) evaluated the potential impacts of the *C. gigas* invasion on four different habitat types common to Scandinavian waters: low energy rock, littoral sand and mud, littoral biogenic reefs, and sub-littoral sediments. The report concluded that the biogenic reefs and sub-littoral sediments are under moderate to high risk of an invasion in the future – especially on high-energy sites. This section outlines the possible impacts such an invasion would have on species and communities in these ecosystems.

#### 10.4.1 Ecosystem Engineers

*C. gigas* is what Jones *et al.* (1994) describe as an ecosystem engineer. Ecosystem engineers are species with the ability to directly or indirectly modify, create or destruct habitats. There are both negative and positive effects ecosystem engineers can have on species richness and species abundance at a small scale, but on a larger scale, Jones *et al.* (1997) argue that the net effect is probably mainly positive.

*C. gigas* reefs, often with shells tightly packed on top of each other, may occupy hundreds of meters of shallow bottoms where they trap sediment, restrict water movement, and contribute to sediment stability. Moreover, oyster reefs may increase the organic richness of sediments through biodeposition and influence nutrition levels through benthic-pelagic coupling (Ruesink *et al.*, 2005; Grabowski & Peterson, 2007). In Sweden, Norling *et al.* (2015) have observed sediment enrichment in live oyster beds. Moreover, in areas with dense populations of oysters, water movement has been restricted with increasing sedimentation as a result. The physical structures of the bivalves may also be of great importance as post-mortem ecosystem engineers. This has been demonstrated both by Guo and Pennings (2012) for salt march plant communities, and by Norling *et al.* (2015) for epifauna in Swedish shallow sublittoral habitats. In the following section, we will describe the effects of *C. gigas* on inter-species interactions and communities.

#### 10.4.2 Impacts on Species-level Interactions

*Mytilus edulis*. There is always a risk that new invading species will compete with indigenous fauna. Both in the Wadden Sea (Diederich, 2005) and in Scandinavia (Dolmer *et al.*, 2014), *C. gigas* prefers similar habitats to the native blue mussel *Mytilus edulis*. Negative effects include competition for space and food (Nehring, 2003; Nehls *et al.*, 2006). Competition for space is probably not a limiting factor for the blue mussels in the Wadden Sea for two reasons: large areas are still unoccupied, and blue mussels utilize oyster reefs for settlement and protection from predation (Troost, 2009). Similar results have been obtained in Sweden (Hollander *et al.*, 2015; Norling *et al.*, 2015). Competition or interference for food between blue mussels and oysters cannot, however, be excluded (Troost *et al.*, 2009). Furthermore, because the oyster filtering capacity is high (Ruesink *et al.*, 2005; Troost, 2009), there is a risk that species with planktonic larval stages will be reduced if oysters become abundant. Data from the Wadden Sea indicate that even though the recruitment of blue mussels may decline due to climate change (Diederich *et al.*, 2005; Nehls *et al.*, 2006), larviphagy, and food limitations for the adults and larvae (Troost *et al.*, 2008a, b; Troost *et al.*, 2009), local extinction of blue mussels is unlikely. To summarize, there are strong indications that the two species will be able to coexist (Diederich, 2005; Troost, 2009; 2010).

*Ostrea edulis*. The ecological distribution of the native flat oyster (*Ostrea edulis*), still occurring in Scandinavia, is somewhat different from *C. gigas*. Flat oysters prefer deeper habitats, mainly the subtidal zone, while *C. gigas* most often reside in the intertidal. Many therefore assume that the interference seen between *C. gigas* and the blue mussel would not occur between *C. gigas* and the flat oyster (Reise, 1998). However, the ecological distribution pattern among *C. gigas* populations varies geographically. For instance, as noted above, *C. gigas* occupy much deeper waters in Norway and Sweden than along the Danish Wadden Sea coast. In addition, new data indicate that *O. edulis* may have a more shallow distribution than previously thought (L. Thorngren, pers. comm.). Moreover, in addition to being attracted to adult conspecifics (Kochmann *et al.*, 2008; Wilkie *et al.*, 2013), *C. gigas* larvae also appear to approach flat oyster beds (L. Thorngren, pers. comm.). If this is a consistent pattern, there is an imminent risk that *C. gigas* may, when populations in Scandinavia grow larger and more sustainable, interfere with the native flat oyster.

### 10.4.3 Impacts on Community-level Interactions

The oyster reef accommodates various types of organisms, such as infauna, sessile and mobile epifauna, and necton. The formation of oyster reefs on soft and sandy substrates leads to much stronger changes in substrate modification and habitat complexity than reefs forming on hard bottoms and will therefore have more pronounced effects on local biodiversity. In addition, while epifauna species thrive on oyster beds (Gutierrez *et al.*, 2003), infauna species are usually not successful in colonizing sediments covered by oysters. Thus, emerging oyster reefs will eventually replace soft-bottom communities with hard-substrate communities (Troost, 2009).

Numerous studies have examined how bivalves affect the community structure. Bivalve beds tend to have higher species richness, and higher total abundance or biomass of both infauna, epifauna (mobile and sessile) and necton than bare sediment habitats (Van Broekhoven, 2005; Hosack *et al.*, 2006; Royer *et al.*, 2006; Kochmann *et al.*, 2008; Troost, 2010; Lejart & Hily, 2011). Oyster reefs provide a hard biogenic substrate that increases habitat complexity, provides living space for other species, and offers shelter, foraging grounds, and nesting sites (Crooks, 2002; Escapa *et al.*, 2004; Ruesink *et al.*, 2005; Green *et al.*, 2012; Kingsley-Smith *et al.*, 2012). In addition, the extended shell surface area contributes to increased attachment substrate for sessile species and larger access to microbial films for grazing species (Kochmann *et al.*, 2008; Markert *et al.*, 2010). The infauna community will be dominated by predators and deposit feeders, whereas in bare sediment suspension feeders dominate (Norling & Kautsky, 2007; Mendonça *et al.*, 2009; Markert *et al.*, 2010; Lejart & Hily, 2011). Similar effects are also found in post-mortem structures of oysters (Guo & Pennings, 2012; Norling *et al.*, 2015). Increased epifauna and infauna abundance in bivalve beds and in post mortem structures of the species has also been observed in Sweden (Hollander *et al.*, 2015; Norling *et al.*, 2015).

For instance, resident fish species prefer both oyster shells and live mussels, while small crustaceans prefer blue mussel shells (Norling *et al.*, 2015).

Bivalves also influence trophic structure (reviewed by Grabowski & Peterson, 2007). By removing plankton from the water column, they promote benthic flora and fauna, and prevent nutrients from entering and staying in lower trophic levels. Moreover, by enhancing the nutrient transfer to benthic invertebrates, the nutrient flux also increases to higher trophic levels such as crabs, demersal fish, and ultimately to predatory fish, many of which are fished commercially.

Bivalve beds also provide prey for other species. In European estuaries and coastlines there are two main predators of invertebrate shellfish: the shore crab (*Carcinus maenas*) and the common starfish (*Asterias rubens*, Dare *et al.*, 1983; O'Neill, 1983; Cohen *et al.*, 1995). Both species are abundant in shallow waters and estuaries along Scandinavian coastlines, and may cause severe damage to wild and commercial bivalve stocks (Hancock, 1955; Walne & Davies, 1977; Allen, 1983). Experimental evidence (Y. Fredriksson and Å. Strand, unpubl. data) suggests that both shore crabs (*Carcinus maenas*) and starfish (*Asterias rubens*) in Sweden identify and utilize *C. gigas* as prey, and have the ability to open live oysters. In addition, land-based predators such as herring gulls (*Larus argentatus*) or oystercatchers (*Haematopus ostralegus*) may also take advantage of oysters as a new food source (Cadée, 2008a, b; Scheiffarth *et al.*, 2007).

Increased presence of *C. gigas* will thus affect local species interactions, communities, and ecosystems. In the next section we will review how these potential changes will affect ecosystem services and future management decisions.

## 10.5 Invasion Consequences of Pacific Oysters: from Perceived Nuisance to Valuable Resource?

Since the arrival of *C. gigas* in Scandinavia, the only two factors believed to be able to stop the oysters from establishing permanently were harsh winter conditions and disease (Nyberg, 2010; Wrangé *et al.*, 2007). Both these factors have now been discarded as potential threats to the oysters in the region. First, the unusually severe winter conditions of 2009–2010 caused high mortalities (Strand *et al.*, 2012), but not enough to prevent subsequent reproduction. Second, in 2014 high summer mortalities affected populations in Sweden and Norway (see Box 10.3 for details), but many large populations remain. Thus, natural factors seem inadequate to eradicate the species from the region. On the contrary, they will likely disperse further (Box 10.2). Moreover, because larvae are attracted to already existing populations (Kochmann *et al.*, 2008; Wilkie *et al.*, 2013), the number of dense aggregations of oysters and reef formations may increase. Finally, the Norwegian populations may receive larvae from Swedish populations, which in turn may be enhanced by Danish larvae (Box 10.1, 10.2) This makes management of the invasion and its impact on local ecosystem services an urgent and international issue.

### Box 10.3. Summer Mortality 2014

Abnormal mortalities in *C. gigas* during the summer months have occurred for more than five decades in major oyster production areas across the world (reviewed in Samain and McCombie, 2008; EFSA 2010). The etiology underlying these recurrent episodes has not been clearly defined, but the events have been denoted "summer mortalities" due to the typical seasonal occurrence (Samain & McCombie, 2008; EFSA 2010). Suggested explanations include physiological stress during spawning (Cho & Jeong, 2005) in combination with environmental stressors such as reduced salinity (Luna-Gonzalez et al., 2008), eutrophic conditions (Malham et al., 2009), decrease in dissolved oxygen (Cheney et al., 2000), toxicity of sediments (Soletchnik et al., 2005) and contamination with anthropogenic pollution (Luna-Acosta et al., 2010). Biotic stressors often associated with summer mortalities in *C. gigas* are the bacteria *Vibrio splendidus* and *V. aestuarianus* (Lacoste et al., 2001; Garnier et al., 2007; Samain & McCombie, 2008), and the virus OsHV-1  $\mu$ var (Renault et al., 1995; Segarra et al., 2010; Renault et al., 2014).

Scandinavian populations of *C. gigas* have hitherto appeared healthy, but in mid-September 2014 mass-mortalities in oyster populations were observed along the coasts of Vestfold and Østfold in Norway and in Bohuslän in Sweden. The initial observations were followed by several independent sightings of mass mortalities in wild and cultivated oysters exceeding 90%. By the end of 2014, no mortalities had been reported from Denmark. Initial demographic examinations of four *C. gigas* populations in the Koster-Strömstad-Tjärnö archipelago indicated that 60–90% of the individuals were affected. The pattern was complex with only spat and juveniles being affected at some sites, while at other sites all individuals died. Provisional inspection of *O. edulis* and *M. edulis* in affected habitats suggests that these native bivalves were not affected.

Preliminary reports show that oyster herpes virus OsHV-1  $\mu$ var was present in affected populations in Scandinavia (Mortensen et al., 2014; Anders Alfjorden pers. com.). Although the virus has not yet (as of December 2014) been causally linked to the mortality, its presence in Scandinavian waters causes concern as it may also infect other bivalves (Farley et al., 1972; Hine & Thorne, 1997; Arzul et al., 2001), such as the native flat oyster, *O. edulis* (Comps & Cochenec, 1993).

The mortality pattern reported in Sweden (high mortalities of both juveniles and adults) is not consistent with herpes-related mortality in Europe (high mortalities among juveniles and low lethality among adults) (Segarra et al., 2010; Dégremont, 2011). Furthermore, preliminary observations indicate an extremely patchy occurrence of mortalities, approaching 100% in populations at some sites while neighboring stocks (approximately 1 km away) are unaffected. This may indicate that factors other than pathogens are involved in the observed mortalities, and ongoing research should aim at elucidating the importance of other factors, including pathogens and environmental conditions.

Despite high mortalities in affected populations, large unaffected oyster populations still remain in Scandinavia. Thus we expect only a similar temporary setback as observed after the winter mortality of 2009–2010 (Strand et al., 2012), followed by recovery.

Marine ecosystem services refer to benefits that people obtain from marine ecosystems, including the open ocean, coastal areas and estuaries. Supporting services (e.g. primary production and nutrient cycling) are the basis for the three following service categories: regulating services (e.g. climate regulation, natural hazards control, and water quality), provisioning services (e.g. food, job opportunities, building materials and pharmaceutical compounds), and cultural services (e.g. recreational, traditions, esthetic and spiritual benefits). Oysters in general (not just *C. gigas*) contribute to all four service categories (Ruesink *et al.*, 2005; Grabowski & Peterson, 2007; Grabowski *et al.*, 2012). At the same time, invasives such as *C. gigas* may also have some negative effects, which may cause substantial economic loss to the region where it establishes. In the following section we will discuss the impacts of *C. gigas* may have on local ecosystem services in Scandinavia, and the implications for coastal management.

Nehring (2011) outlines the main drawbacks of a *C. gigas* invasion. These include displacement of native species by competition for food and space, altered benthic-pelagic and food-web interactions, habitat modifications, hybridization with local oyster species, and transfer of parasites, diseases and pests. Currently, the main concern for managers and commercial stakeholders is competition with native blue mussels and flat oysters. The concern for the blue mussel may be less well founded than previously thought, as successful coexistence with oysters is now considered a reality. For flat oysters, the situation is different. International treaties (e.g. OSPAR) now regard the flat oyster as a species of particular importance, thus forcing governmental stakeholders to label the potential competition from *C. gigas* as a severe concern. If recent results from the Swedish west coast – that flat oysters grow in shallower waters than previously thought – also apply to similar habitats along the Norwegian coast, this might indeed be a real concern for flat oysters.

Large oyster reefs already exist in many places. Especially in shallow, narrow sounds and bays, the reefs alter currents and increase sedimentation. After the winter of 2009–2010 that killed a substantial part of the Swedish oysters, reefs became a sanitary problem when several thousand newly dead oysters decomposed. At public beaches, reefs hamper recreational activities. Moreover, fouling of boats, docks, drainage pipes, and other underwater constructs is an increasing problem.

Notwithstanding the previously discussed negative impacts, *C. gigas* provides a range of different ecosystem goods and services (Grabowski & Peterson, 2007). Some of the most obvious services are the contributions to rural development and economy through provisioning and cultural services. The species is one of the top 20 most cultured species in the world (FAO), and as such is an important food resource and source of income. In Denmark and Sweden, the interest in exploiting the species is growing. Hand picking oysters is popular in both countries, and there are ongoing discussions about possibilities for aquaculture. However, in Sweden exploitation is hampered by the old fishing law, attributing the rights to the oysters to the coastal land owners. Furthermore, aquaculture may not be allowed due to national and inter-

national regulations of invasive species. Nevertheless, the exploitation of wild oyster populations could become a valuable source of income for many coastal communities. *C. gigas* is being exploited not only for commercial food production, but also by tourist enterprises organising day trips to easily accessible sites for hand picking of oysters. Regular commercial and touristic harvesting of existing oyster populations could be a realistic way to reduce the risk of reef formation, but it is highly unlikely that such management actions will be socioeconomically possible unless commercial interests are involved.

In addition to contributing to provisioning and cultural services directly, increased presence of bivalves may indirectly boost local fisheries (Peterson *et al.*, 2003). If the community re-structuring discussed in section 10.4 increases the nutrient flux to higher trophic levels, which includes commercially important fish, then commercial, recreational, and tourist fishing may benefit from more *C. gigas*. This may be further enhanced by the suitability of bivalve beds as nursery areas for fish and decapods, which feed on the higher abundance of macrofauna and find refuge from predators in the complex structures (Jansson *et al.*, 1985; Tolley & Volety, 2005; Hosack *et al.*, 2006; Mendonça *et al.*, 2009). Juvenile transient fish species prey upon resident fish (Coen & Luckenbach 2000; Coen *et al.*, 2007), making bivalve beds important nursery areas for young stages of fish that support coastal communities and commercial and recreational fisheries (Ruesink *et al.*, 2005).

Eutrophication of shallow coastal areas is, like in many other regions, a major concern in Scandinavia (Diaz & Rosenberg, 2008). Bivalve filter feeders have the potential to alleviate this situation (Officer *et al.*, 1982; Coen & Luckenbach, 2000; Rice, 2001; Newell, 2004; Grabowski & Peterson, 2007). Accordingly, bivalve cultures are currently being presented and evaluated in Sweden as a possible management option for restoring eutrophicated coastal areas to healthy environments (Lindahl *et al.*, 2005; Bergström *et al.*, 2013; Bergström, 2014). In addition, being a very efficient filter feeder with high growth rates and dense populations in shallow areas (Ren *et al.*, 2000; Ruesink *et al.*, 2005), *C. gigas* has the potential to, without much human intervention, improve the status of eutrophicated ecosystems (Ruesink *et al.*, 2005).

Oysters provide additional important services. Due to their reef-building abilities, oysters have been proposed as a tool for reducing erosion of intertidal flats in the Wadden Sea (Troost, 2010), and reducing erosion from boat wakes (Beck *et al.*, 2009). Because reefs reintroduce structural complexity to areas where native communities such as seagrass meadows, blue mussel beds and *O. edulis* beds may have been lost, *C. gigas* beds may replace the function of the lost communities. Indeed, oysters may even increase the occurrence of such habitats. Seagrass meadows may benefit from reduced water turbidity and increased nutrient content of sediments (Beck *et al.*, 2009; Grabowski & Peterson, 2007), and blue mussels benefit from the shelter and a settlement substrate (Troost, 2009). Finally, blue mussel meal is considered a realistic, environmentally friendly and healthy alternative to the use of fish meal in the fish feed used in aquaculture and in chicken feed for egg production (Duinker *et al.*, 2005; Kollberg &

Lindahl, 2006). If technological solutions for the utilization of oyster meat as a similar product can be developed, the proportion of environmentally friendly components in fish feed could increase even further.

Despite the potential positive impacts on many direct and indirect ecosystem services (e.g. filtering capacity, benthic–pelagic coupling, nutrient dynamics, sediment stabilization, provision of habitat, etc.), the values of these services have been largely ignored or underestimated in management decisions (Coen & Luckenbach, 2000). This is also the case in Scandinavia. The general management discussion on *C. gigas* has focused on the oysters status as invasive, as well as the governmental responsibilities related to national and international regulations of invasive species.

Climate change presents an additional challenge for management. Because species distributions are continuously altered by the changing environmental framework, agencies are increasingly looking to modeled projections of species' distributions under future climate scenarios to be able to make informed management decisions. Species distribution models such as the one presented in Box 10.2 are numerical tools that combine observations of species occurrence or abundance with estimates of environmental parameters. In the case of *C. gigas* in Scandinavia, predictions from the ecological niche models highlight the urgent need for informed management actions along the Norwegian coast.

Established populations of *C. gigas* will undoubtedly affect the ecosystem in many different ways. How its presence will be valued will depend on the point of view and agenda of the observer. Regardless of stakeholder interests, *C. gigas* will likely be a substantial part of the Scandinavian ecosystem in the future. Thus, there is an urgent need to consolidate stakeholders, develop research and monitoring programmes, and create evidence-based management plans for how to handle the species.

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### In a nutshell

- The Pacific oyster originates from the Pacific Ocean, but has been the subject of widespread introductions all over the world. In addition to being deliberately transferred in large numbers for farming, Pacific oysters have also dispersed by hitch-hiking with long-distance vessels and local and regional ocean currents. Natural spatfall has established feral populations on almost all continents with sometimes-large ecological and socioeconomic consequences.
- Since the mid 2000s, *Crassostrea gigas* has been observed in Scandinavia and is now forming dense populations in both Denmark, Sweden and Norway. In this chapter we outline existing knowledge of the species origin and dispersal routes in Scandinavia, predicted future distribution in relation to climate change, and observed alterations to habitat structure and ecosystem function. We related this information to ecosystem services provided by the oysters, and to expected changes in community ecosystem services, with special emphasis on Scandinavian ecosystems.
- We anticipate that *C. gigas* will affect the Scandinavian ecosystem in both negative and positive ways, and the valuation of *C. gigas* will depend on the point of view and agenda of the observer. Despite the potential positive impact on many direct and indirect ecosystem services (e.g. source of food and income, filtering capacity, benthic-pelagic coupling, nutrient dynamics, sediment stabilization, provision of habitat), the values of these services have so far been largely ignored or underestimated by management.
- Regardless of stakeholder interests, *C. gigas* will likely be a substantial part of the Scandinavian ecosystem in the future. Thus, there is an urgent need to consolidate stakeholders, develop research and monitoring programmes, and create evidence-based management plans for how to handle the species.

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