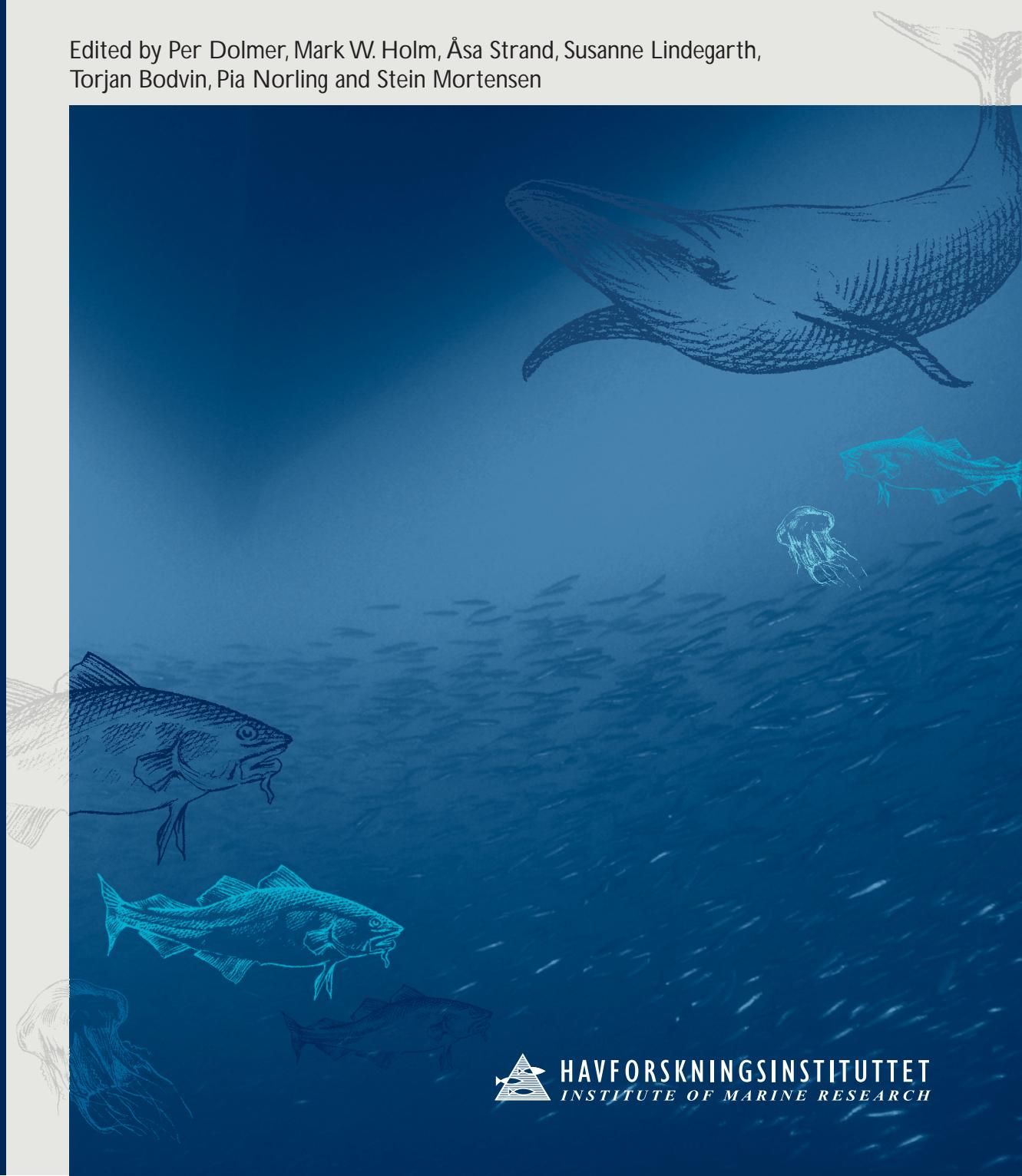


The invasive Pacific oyster, *Crassostrea gigas*, in Scandinavian coastal waters:

A risk assessment on the impact in different habitats
and climate conditions

Edited by Per Dolmer, Mark W. Holm, Åsa Strand, Susanne Lindegarth,
Torjan Bodvin, Pia Norling and Stein Mortensen



HAVFORSKNINGSINSTITUTTET
INSTITUTE OF MARINE RESEARCH

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Bergen, March 2014



GÖTEBORGS UNIVERSITET

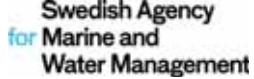


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Sammendrag (norsk): Stillehavssøstern blir gradvis registrert på flere og flere lokaliteter i Skandinavia. Forskere ved Havforskningsinstituttet, Göteborg Universitet, Danmarks tekniske Universitet og ORBICON har - med støtte fra Nordisk Ministerråd – arbeidet med å kartlegge denne artens utbredelse og spredning og utarbeidet en risikovurdering på effekter av spredningen, basert på ulike klimascenarier. Risikovurderingen som er presentert i denne rapporten er basert på en oversikt over vitenskapelig litteratur, ekspertvurderinger om stillehavssøsters og data samlet inn gjennom et felles-nordisk samarbeidsprosjekt i 2011 – 2013.					
Summary (English): A massive invasion of the Pacific oyster, <i>Crassostrea gigas</i> , has occurred in Scandinavia during the last decade. The introduction and dispersal was described through collaboration between scientists from Sweden, Denmark and Norway. This work has been followed up by national activities that clearly visualized the need for a continued collaboration between scientists in the Scandinavian countries, as the bio-invasion is a cross-border issue and management actions then have to be synchronized, and based on a “state of the art” knowledge of the Scandinavian bio-invasion of the species. The risk assessment presented in this report is based on available scientific literature, expert judgments and data collected during a Nordic collaboration project on Pacific oysters in 2011 – 2013.					
Emneord (norsk): Stillehavssøsters, <i>Crassostrea gigas</i> , Skandinavia, bioinvasjon, spredning, risikovurdering, klima, habitat	Subject heading (English): Pacific oysters, <i>Crassostrea gigas</i> , Scandinavia, bio-invasion, spreading, risk assessment, climate, habitats				

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Sammendrag

Denne risikovurderingen er basert på en oversikt over vitenskapelig litteratur og ekspertvurderinger om stillehavssøsters, *Crassostrea gigas*. Bakgrunnsdata og -informasjon ble gjennomgått og evaluert på et arbeidsmøte i april 2012, hvor det deltok 14 eksperter på stillehavssøsters i Skandinavia. Det ble under og etter dette møtet gjort en analyse av tilgjengelig kunnskap om utbredelse og spredning i Skandinavia, inklusiv en endring i tetthet over tid.

Riskovurderingen er bygget opp rundt langtids-klimascenarier tilpasset IPCC (Scenarie A1B og A2) og korttids-scenarier fra en nordisk analyse av klimaendringer. Det er videre definert fire ulike habitattyper som inkluderes i risikovurderingen, og som regnes som viktige for stillehavssøsters i Skandinavia. Disse er:

1. Sub-littoral hardbunn uten tidevann/strøm
2. Tidevannsone med sand og mudder
3. Tidevannsone med biogene rev
4. Sub-littorale sedimenter

I risikovurderingen konkluderes det med at det for habitattypen **sub-littoral hardbunn uten tidevann/strøm** på kort sikt (2050) er en lav risiko for en bioinvasjon av stillehavssøsters i Skandinavia som har en signifikant innvirkning på habitatet (se Summary, tabell S1). I et lengre tidsperspektiv (2100) vurderes risiko for en bioinvasjon som moderat.

For habitattypen **tidevannsone med sand og mudder** er det – i et kort tidsperspektiv og på lokaliteter med lite tidevann – en lav risiko for en bioinvasjon av stillehavssøsters som vil påvirke habitatet (se Summary, tabell S2). I et lengre tidsperspektiv (2100) konkluderes det med at det både på lokaliteter med lite tidevann/strøm og med mye tidevann er en moderat risiko for at stillehavssøsternes vil forårsake en bioinvasjon.

For habitattypen **tidevannsone med biogene rev** (tabell S3) konkluderes det med at det både i et kort- og langtidsperspektiv er en moderat risiko for at stillehavssøsternes på lokaliteter med lite tidevann vil utvikle seg til en bioinvasjon, på en slik måte at den har innvirkning på form og funksjoner på habitatet. På lokaliteter med mye tidevann regnes risikoen for en bioinvasjon som høy.

På habitattypen **sub-littorale sedimenter** (tabell S4) regnes risiko for en bioinvasjon både i et kort- og langtidsperspektiv som lav på lokaliteter med lite tidevann. På lokaliteter med mye tidevann regnes risikoen for en bioinvasjon som moderat på kort sikt og høy på lang sikt.

Informasjonen i denne risikovurderingen kan brukes for å utvikle en lokalitets-spesifikk strategi for forvaltning av områder hvor stillehavssøsternes er etablert – eller hvor arten kan etablere seg i de neste årtiene. En strategi kan være å akseptere stillehavssøsternes tilstedeværelse og den effekten den måtte ha på habitatene. En alternativ strategi er å forsøke å kontrollere tettheten på bestandene og spredning i definerte områder. For å moderere de effektene invaderende arter har på kystekosystemene vil det være mest hensiktmessig å

prioritere kontrolltiltak på de områdene hvor det er høyest risiko for en bioinvasjon som kan endre habitatet. På lokaliteter hvor det er stor tidevannsforskjell og/eller smale sund med høy strømhastighet regnes risiko for en bioinvasjon av stillehavsosters som høy på tidevannssone med biogene rev og på sub-littorale sedimenter. Tettheten av østers - særlig på tidevannsone med biogene rev - har de siste årene blitt redusert i løpet vinter med mye is. Lokaliteter med dagens lave tettheter kan representer et godt startpunkt for å iverksette kontrollstrategier. Lett tilkomst og muligheter for å inspirere tidevannsområder kan gjøre det mulig å fjerne østers fra mindre områderfor å hindre endringer i biodiversitet og habitatsstruktur. Steder hvor østersonen dekker større områder kan det være aktuelt å etablerte samarbeid med fiskere/skjellhøstere. Risiko for en bioinvasjon i habitater med lite tidevann/strøm med hardbunn, sand og mudder og sub-littorale sedimenter regnes som lav til moderat. I disse områdene kan det være hensiktsmessig å iverksette overvåkingsprogrammer som gjør det mulig å sette i gang kontroll- og bekjempelsesprogrammer på kort varsel hvis bestandene av stillehavsosters øker så mye at tiltak regnes som nødvendig.



Summary

This risk assessment evaluate the impact on the ecosystem of the invasive Pacific oyster, *Crassostrea gigas*, as function of climate change on four different Scandinavian habitats:

1. Low energy rock
2. Littoral sand and mud
3. Littoral biogenic reefs
4. Sub-littoral sediments

The risk assessment is based on a review of existing scientific literature and expert judgments, and the data was evaluated on a workshop in April 2012 with the participation of 14 experts on *C.gigas* in Scandinavia. Long-term climate scenarios are adapted from IPCC (Scenario A1B and A2) and a short term climate scenario is adapted from a Nordic analysis on climate change. Four different habitat types are included in the assessment. The habitat types represent important habitats for *C. gigas* in Scandinavia. The risk assessment is based on an analysis of the present scientific knowledge of the distribution patterns of *C. gigas* in Scandinavia, including the change in density over time. It is concluded that at the habitat types **Low energy rock**, **Littoral sand and mud** and **Sub-littoral sediment** in low energy areas there is a limited to moderate risk that a bio-invasion of *C. gigas* will develop. For **Biogenic reefs** and **Sub-littoral sediment** in high energy areas there is a moderate to high risk for a bio-invasion.

A risk assessment was performed for each of the four habitat types:

It is concluded that for the habitat type **Low energy rock** there is on a short term (Year 2050) a limited risk that *C. gigas* will develop a bio-invasion in Scandinavia impacting the form and function of the habitat type (Table S1). On a long term (Year 2100) the assessment concludes that there is a moderate risk that *C. gigas* will develop a bio-invasion.

In the risk assessment, it is concluded that for the habitat type **Littoral sand and mud** there is, on a short term, a limited risk at low energy sites, that *C. gigas* will develop a bio-invasion in Scandinavia impacting the form and function of the habitat type (Table S2). On a long term (Year 2100) the assessment concludes that on low energy sites there is a moderate risk that *C. gigas* will develop a bio-invasion. On high energy sites, there is a moderate risk that *C. gigas* develops a bio-invasion.

In the risk assessment, it is concluded that for the habitat type **Littoral biogenic reefs** there is on a short and long term a moderate risk at low energy sites, that *C. gigas* will develop a bio-invasion in Scandinavia impacting the form and function of the habitat type (Table S3). On high energy sites, there is on a short and long term a high risk that *C. gigas* develops a bio-invasion.

In the risk assessment, it is concluded that for the habitat type **sub-littoral sediment** there is on a short and long term a limited risk at low energy sites, that *C. gigas* will develop a bio-invasion in Scandinavia impacting the form and function of the habitat type (Table S4). On

high energy sites, there is on a short term a moderate risk that the species will develop a bio-invasion. On a long term, there is a high risk that *C. gigas* develops a bio-invasion.

The information in this risk assessment may be used to develop site-specific strategies for conservation in areas with a present or an expected presence of *C. gigas* in the next decades. Different strategies can be implemented. One strategy is to accept the presence of the species in the ecosystem and the impact on coastal habitats. An alternative strategy for conservation is a control of density and dispersal of *C. gigas* in smaller or larger areas.

A mitigation of invasive species should prioritize a control strategy in Scandinavian coastal waters targeting areas with the highest risk for a bio-invasion. In high energy areas with high tidal amplitude and/or narrow straits with high current speed, a high risk for an invasion of *C. gigas* is identified on Littoral biogenic reefs and on Sub-littoral sediments. The density of *C. gigas* on especially Littoral biogenic reefs have been reduced the last winters due to impact from drifting ice, and the current low density may be an excellent starting point for the implementation of a control strategy. The easy access and the ability to visually inspect littoral sites may allow an implementation of a strategy for removing oysters from smaller areas in order to protect the undisturbed biodiversity and habitat structure. Cooperation with commercial fisheries may allow a control strategy for a larger area, whereas cooperation with local groups of volunteers may allow a control strategy of a smaller area by handpicking of the species. The risk assessment finds a limited to moderate risk that a bio-invasion of *C. gigas* will develop in low energy habitats as Low energy rock, the Littoral sand and mud, and the Sub-littoral sediment. The optimal strategy in these areas may include a monitoring program, that allow an early implementation of a control program in order to detect if a local population of *C. gigas* change to an expansive phase of invasion and calls for an effort to reduce density.

Table S1. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type low energy rock. The green colour indicates a limited risk and the yellow colour indicates a moderate risk for a bio-invasion.

A1.3 Low energy Rock	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			

Table S2. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type littoral sand and mud. The green colour indicates a limited risk and the yellow colour indicates a moderate risk for a bio-invasion.

A2.2 Littoral sand and mud	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			
High energy			

Table S3. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type littoral biogenic reefs. The yellow colour indicates a moderate risk and the red colour indicates a high risk for a bio-invasion.

A2.7 Littoral biogenic reefs	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			
High energy			

Table S4. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type sub-littoral sediments. The green colour indicates a limited risk, the yellow colour indicates a moderate risk and the red colour indicates a high risk for a bio-invasion.

A5.1-6 sub-littoral sediment	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			
High energy			



1 Background and aim

A massive invasion of the Pacific oyster, *Crassostrea gigas*, has occurred in Scandinavia during the last decade. The introduction and dispersal was described through collaboration between scientists from Sweden, Denmark and Norway ([Wrange et al. 2010](#)). This work has been followed up by national activities that clearly visualized the need for a continued collaboration between scientists in the Scandinavian countries, as the bio-invasion is a cross-border issue and management actions then have to be synchronised, and based on a “state of the art” knowledge of the Scandinavian bio-invasion of the species.

Crassostrea gigas is considered invasive, and its establishment and dispersal may conflict with both commercial and recreational interests, conservation and goods and benefits from marine ecosystems from several areas outside the natural distribution of the species. As an example to visualize its impact, we may look at a study undertaken by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) for the Department of Environment and Heritage (Australia) in order to identify and rank introduced marine species found within Australian waters and those not found within Australian waters. All of the non-native potential target species identified in that report are ranked with high, medium and low priority, based on their invasion- and impact potential. *Crassostrea gigas* was identified as one of ten most damaging species, based on overall impact (economic and environmental). A hazard ranking of potential species based on invasion potential from infected to uninfected bioregions identifies *C. gigas* as a 'medium priority species'. These are species that have a reasonably high impact or invasion potential (For further details, see [Hayes et al. \(2005\)](#)). In the Wadden Sea, Oosterschelde and in Scandinavian waters, the *C. gigas* is reported to change the ecosystem, and key issues are; impact on blue mussel populations, cascade effects on mussel eating birds such as eider ducks and oystercatchers, impact on biodiversity and modifications on the form and function of the ecosystem. In order to target management of the *C. gigas*, in relation to conservation, fisheries and tourism, a forecast of the development of the bio-invasion is a prerequisite. Risk assessments or development of scenarios with a constant climate or a changing climate are tools, which can aid in forecasting the development of the bio-invasion in specific habitats.

The aim of the present study is to conduct an environmental risk assessment for the invasive process of *C. gigas* in Scandinavian waters. The study reviews knowledge regarding the invasion history including the present distribution. The impact of *C. gigas* on the ecosystem and the factors that determine the rate of invasion is thereafter reviewed. Based on a short-term climate scenario (NMR) and two long-term scenarios (IPCC), one including the impact of acidification, a risk-assessment on the effects of *C. gigas* invasion on coastal ecosystems is presented. The risk-assessment is conducted for four EUNIS habitats representing important habitats for the present distribution of *C. gigas* in Scandinavia.

2 The active and passive dispersal of *Crassostrea gigas*

The *Crassostrea gigas* originates from the Pacific Ocean (Japan) (Nehring 2006, Miossec *et al.* 2009), but has been the subject of widespread introductions elsewhere (Ruesink *et al.* 2005, Reise *et al* 2005) either to replace stocks of indigenous oysters severely depleted by over-fishing or disease (Nehring 1999, Wolff and Reise 2002), or to create an industry where none existed before. The most significant introductions have been to the western seaboard of the United States of America from the 1920s and to France beginning in 1965 - 1966, but the species has also been introduced to Africa, The Australasia-Pacific region and South America.

In addition to active movements, *C. gigas* have been dispersed by passive transport on vessels as vectors (Eno *et al.* 1997). After dispersal to new areas, self-sustaining populations have established. Through natural spatfall the species has dispersed and established feral populations in for example British Columbia, California, South Africa, Australia, New Zealand, France, and in the British Isles (Reise 1998, Diederich 2005).



Figure 1. Expansion of *Crassostrea gigas* in the Wadden Sea. Blue stars indicate sites with aquaculture, Years indicate first record of settlement and the red circles indicate distribution in 2003 (From Reise *et al.* 2005)

2.1 Distribution of the Pacific oyster, *Crassostrea gigas*, in Europe

In Europe today, the Pacific oyster can be found along the Atlantic coast, in the Mediterranean, around the British Isles and north to Scandinavia.

In France, Japanese *C. gigas* were introduced from 1965 - 1966 and onwards. After a period of heavy mortalities of Portuguese oysters, *Crassostrea angulata* in 1967 – 1971 due to gill disease – an infection caused by an iridovirus, the *C. gigas* totally replaced the Portuguese. In most oyster producing areas, self-sustaining population gradually established. Today the industry is based mostly on natural spatfall of *C. gigas* on collectors placed within the production areas.

In 1964, Dutch oyster farmers imported spat of the *C. gigas* from British Columbia to the Oosterschelde estuary for aquaculture activities, assuming the water temperature was too low for natural reproduction. In the following years more imports of spat and adult specimens followed, and from 1966 also from Japan. In 1975 and 1976, natural spatfalls occurred and resulted in the settlement of millions of oysters in the Oosterschelde estuary. In the 1980's other Dutch estuaries started to be colonized (Wolff and Reise 2002). Since the 1990's the species has been observed along the entire Dutch coast (Dankers *et al.* 2004). Due to the dominating meteorological and hydrographical conditions in the Netherlands, oyster larvae were dispersed in an eastwards direction along coastal sites and arrived at the western German Wadden Sea in 1996 (Reise *et al.* 2005, Wehrmann *et al.* 2000, Figure 1).

In the German Wadden Sea spat and larvae were repeatedly imported between 1971 and 1987 from Scottish hatcheries for scientific aquaculture experiments at different sites (Meixner and Gerdener 1976, Seaman 1985, Wehrmann *et al.* 2000). In 1986, commercial farming activities began in the northern area of the German Wadden Sea near the island of Sylt, primarily with spat imported from British and Irish hatcheries (Reise 1998, Nehring 1999). In 1991, the first oysters were found outside the culture plot (Reise 1998) and in the following years, the oyster population slowly expanded its range north- and southwards along the coastline (Nehring 2003, Diederich *et al.* 2005, Wehrmann and Schmidt 2005). The Danish Wadden Sea was reached in 1999 and since 2004 the distribution gap of the *C. gigas* between the western and northern Wadden Sea has been closed (Reise *et al.* 2005).

2.2 Distribution of *Crassostrea gigas* in Scandinavia

Since the beginning of the 2000's, the distribution of *C. gigas* has been monitored in all three Scandinavian countries (Figure 2). Different methodologies are has been applied, including reports from citizens and monitoring programs.

Denmark

In Denmark, the first introduction of *C. gigas* occurred around 1972 in the Limfjord (Jørgen Kamp, pers. comm. 2011). In the following years, large numbers of seed oysters were imported from England, Germany, the Netherlands and France (Kristensen 1986). They were used in production and aquaculture experiments, which beside the Limfjord was initiated in the Wadden Sea, Little Belt, Isefjord, Mariager Fjord, and Horsens Fjord (Kristensen 1989, Jensen and Knudsen, 2005). At some of these locations production continued up through the 1980s and 1990s (Troost 2010). The last site of production, situated in the Isefjord, closed down in 1998 (Nehring 2006, Wrangle *et al.* 2010). After termination of the productions and experiments, oysters were abandoned in the areas. Permission to farm *C. gigas* in Denmark was granted as it was assumed that the prerequisites for successful reproduction were not met in Danish waters, thus risk of dispersal and establishment in natural habitats were considered negligible (Wrangle *et al.* 2010). In the mid-1990s the first specimens of feral *C. gigas* was observed in the Wadden Sea, where Danish mussel fishermen caught them as a bycatch (Wrangle *et al.* 2010). By the end of the 1990s feral populations were found in the Danish Wadden Sea near Mandø and in 2003 near Esbjerg ($6.8 \text{ oysters m}^{-2}$) (Diederich *et al.* 2005). These oysters could originate from occasions of larval drift from other established population

in the German Wadden Sea or abandoned specimens from aquaculture. Another unidentified hypothetical source of oysters could be unreported small-scale relays of oysters, as leftovers from kitchens. At present, populations of *C. gigas* are found in most parts of Denmark (Figure 2). Of these, only the populations in the Danish Wadden Sea, Limfjord and Isefjord have hitherto been studied.

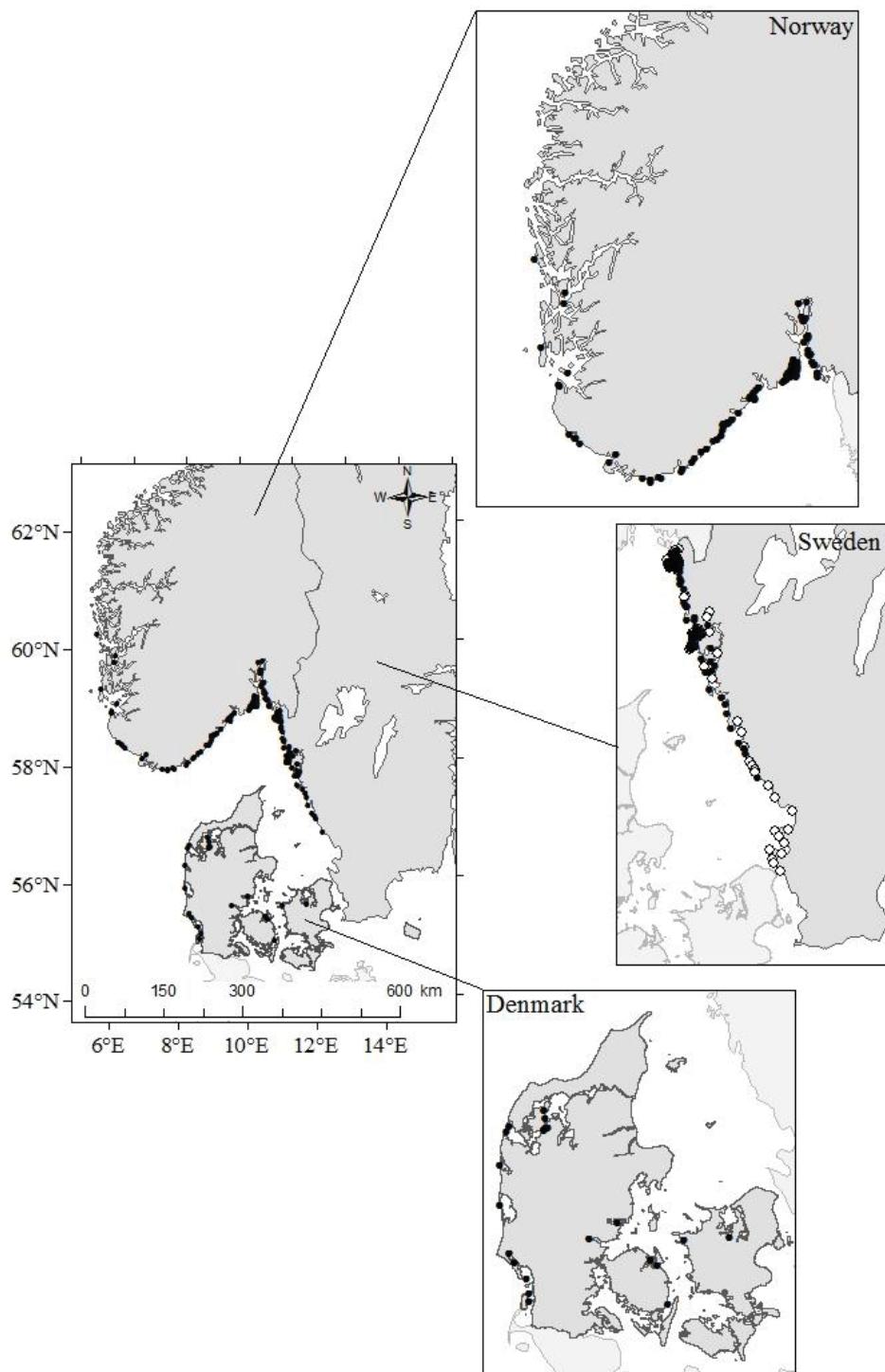


Figure 2. Distribution of *Crassostrea gigas* in Scandinavia. Distribution of *C. gigas* in Denmark is based on personal observations and literature (ICES 2010, ICES 2011). The maps shows the distribution of locations with *G. gigas* (●), monitored stations without *C. gigas* (○).

The Limfjord (N 56° 43', E 8° 15'):

In 2006, a study was conducted to examine whether *C. gigas* had established populations in the Limfjord. Seven sites with *C. gigas* were identified. Densities at these sites ranged from 0.03-3.12 oysters m⁻². Analysis of the shell lengths, using both the method of Bhattacharyas (1967) and by counting growth-rings in the shells (*sensu* Harding and Mann 2006), showed the presence of five different age cohorts (Wrange *et al.* 2010). The presence of several ages classes suggested that recruitment was occurring, and not necessarily an infrequent event. The seven sites, where *C. gigas* had established populations in 2006 were revisited in 2011 in order to examine how the populations had developed during the intervening five years. The study showed that *C. gigas* remain in the area, but that there has been a significant reduction in the population density at most sites (Table 5). Only two sites out of the seven, showed an increased density. It was examined whether this reduction could be attributed to the harsh winters of 2009/10 and 2010/11, where mean air temperatures were 1.5- 2.5°C and 0.5-2.0 °C below average, respectively (DMI 2010, DMI 2011). During the two winters, the average mortality ranged between 17% and 13% at Agger Tange in the Limfjord in the western part of Denmark, and no size dependent mortality was observed. The findings suggest that winter mortality, in this type of environment, is of minor importance as a regulating factor for population development (Groslier *et al.* in prep.). This results was supported by Strand *et al.* (2012) who showed that winter mortality during the ice winter 2009/2010 was only 3-29 % in the Limfjord.

Table 5. Overview of mean density (\pm SD) of *Crassostrea gigas* at each location. Statistical significance ($P<0.05$) between 2006 and 2011 is marked ‘s’, non-significance ($P>0.05$) is marked ‘ns’. Arrows mark an increase (up) or decrease (down) in density. Densities are stated for the long transects where those were applied in 2011. No density data were collected for Rønland in 2006 (Groslier *et al.* in prep.).

Location	2006		2011		Significance	
	Density m ⁻²	SD	Density m ⁻²	SD		
Klosterbugten	0.02	0.04	0.230	0.10	s	↑
DråbyVig	0.04	0.01	0.060	0.01	s	↑
Harrevig	0.18	0.04	0.030	0.01	s	↓
Lysen Bredning	0.02	0.02	0.004	0.01	ns	↓
Vile Vig	0.06	0.06	0.000	0.00	s	↓
Hjortholm	0.04	0.02	0.005	0.01	s	↓
Agger Tange	3.12	1.37	0.280	0.19	s	↓
Rønland	n/a	n/a	0.050	0.06	-	-

During 2009, 2010 and 2011 a study was conducted on the population of *C. gigas* at Agger Tange (not same area as the revisit study) in the western part of the Limfjord. The population has established on an existing mussel bed in this sheltered intertidal area. From 2010 to 2011, there was no significant change in the abundance of *C. gigas* on the mussel bed (2010: 41 ± 40 oysters m⁻², 2011: 47 ± 28 oysters m⁻²). However, using cohort analysis and growth rings, there could be identified three years with successful recruitment (2004, 2007 and 2008) out of the seven years that could be accounted for in the cohort analysis (Holm *et al.* In prep.).

The recruitment at Agger Tange seems to be of local origin, as preliminary particle tracking model based on the MIKE21 HD (DHI 2007), where passive particles were released at the

Agger Tange mussel bed and allowed a pelagic phase of 21 days, suggest that oyster larvae released at Agger Tange are retained within Nissum Bredning (unpublished data). Gonad development and spawning has been observed during the studies. Thus, *C. gigas* at Agger Tange seems able to reproduce relatively frequently.

The Isefjord (55° 41' N, 11° 49' E)

In 2007, it was examined whether *C. gigas* had established populations. The study showed that the *C. gigas* was present in the Isefjord, but at very low density. The mean density was 0.03 ± 0.03 oysters m^{-2} , with the highest occurrence of *C. gigas* near the Munkholm Bridge in the southern part of the area. Here the mean density was 0.11 oysters m^{-2} . Despite the low densities a cohort analysis, based on shell lengths, identified three different age classes (1 to 3 years old), indicating that the oysters left after the aquaculture facility was closed down had been able to reproduce (Wang *et al.* 2007).

The Wadden Sea (55° 20' N, 8° 33' E)

Three studies have been conducted in the Danish part of the Wadden Sea (from 2005 to 2007) (Kristensen and Pihl 2006, 2008). The total biomass of *C. gigas* was estimated to have increased from 1056 t in 2005 to 6264 t in 2007 (Figure 3). There are, however, not at longer time series from the Danish Wadden Sea, but in List Tidal Basin, just across the German border, the population development of *C. gigas* has been monitored since 1999 to 2011, and from 2003, the monitoring has been conducted annually. The data showed that from 2005 to 2007, there was a rapid population increase, after which there has been a decline (Figure 3). The decline seems to be further supported by the harsh winter of 2009/2010. Büttger *et al.* (2011) reported winter mortalities of 85-90 % for *C. gigas* in the intertidal areas of List Tidal Basin after this winter and Strand *et al.* (2012) reported a mortality of 66 % in the northern part of the Danish Wadden Sea.

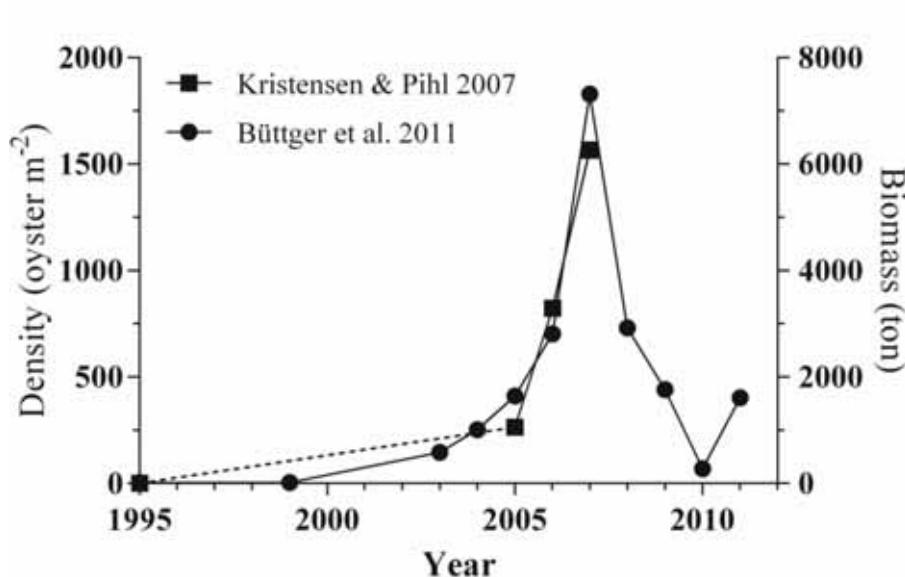


Figure 3. Population development of *C. gigas* in the Danish Wadden Sea. The dashed line displays years where the biomass is unknown. Data from Kristensen and Phil (2007) is for the total biomass of *C. gigas* in the Danish Wadden Sea. Data from Büttger *et al.* (2011) is the mean density from List Tidal Basin. Note the difference in the units between the two y-axes. Data from Büttger *et al.* (2011) is displayed at the 1st y-axis and Kristensen and Pihl (2007) on the 2nd y-axis.

Sweden

Between 1973 and 1976, a limited number of *C. gigas* were imported from Wales to Sweden for aquaculture trials. The activities took place just outside the town of Strömstad in the county of Bohuslän ([J. Haamer, pers. comm.](#)). The oysters demonstrated high growth rate and survival but no reproduction was observed. It was concluded that the low summer temperatures did not favour reproduction in Swedish waters. A few oysters were left in the sea after the experiment was finished. 30 years later, during the summer of 2007, many independent observations about a new, unknown oyster species were reported to staff at the marine research station at Tjärnö, near Strömstad. The species was identified as *C. gigas*.

A large-scale survey along the west coast of Sweden was initiated during autumn 2007, from the Norwegian border north of Strömstad to the Öresund region. A total of 68 sites were selected, based on the criteria of being accessible from land, having a depth of maximum 2 m and including some kind of hard bottom substrate ([Wrange et al. 2010](#)). Primarily one year old *C. gigas* were discovered in many of the locations north of Gothenburg (31 of 43) but less in the southern part of the coastline (6 of 25), and no oysters were discovered south of the city of Falkenberg ([Wrange et al. 2010](#)). Habitat preferences for the oysters were recorded and the habitat characteristics where the oysters mainly occurred were as follows:

- Shallow areas (0- 2 m)
- Variable seabed characteristics, but often on mud or sand
- Preference to settle on blue mussel beds or oyster shells
- Occurs from extremely protected to not fully exposed sites
- Channels, sandbanks and reefs with high current velocities

The same sites were revisited in 2013 and surveyed using the same method as in 2007. From the obtained data it could be concluded that the geographical distribution of the species had been shifted northward, the most southern site was in 2013 just north of the town Varberg. The number of sites with live oysters was also lower compared to 2007. Oysters were more frequently gone extinct in 2013 at sites where low oyster densities were recorded in 2007. Furthermore, in 2007, the highest density of oysters recorded was 4 individuals m⁻² while in 2013 the density had increased to 113 individuals m⁻². Based on length frequency data, cohort analysis were performed, revealing a strong connection between the number of adults at each site and the number of newly recruited oysters, thus sites with high densities of adult oysters also had high numbers of newly recruited oysters, and were also the sites which had increased most in oyster density ([Strand et al. In prep.](#)).

In 2009, a detailed survey of two areas around Strömstad and Lysekil in Bohuslän (see map Figure 4) was conducted. Oysters were found in 60 % of the 250 visited sites, confirming the previously noted habitat preferences of the species in this region. Currently, approximately 250 sites with live oysters present are recorded along the Swedish west coast (from research and public reports).

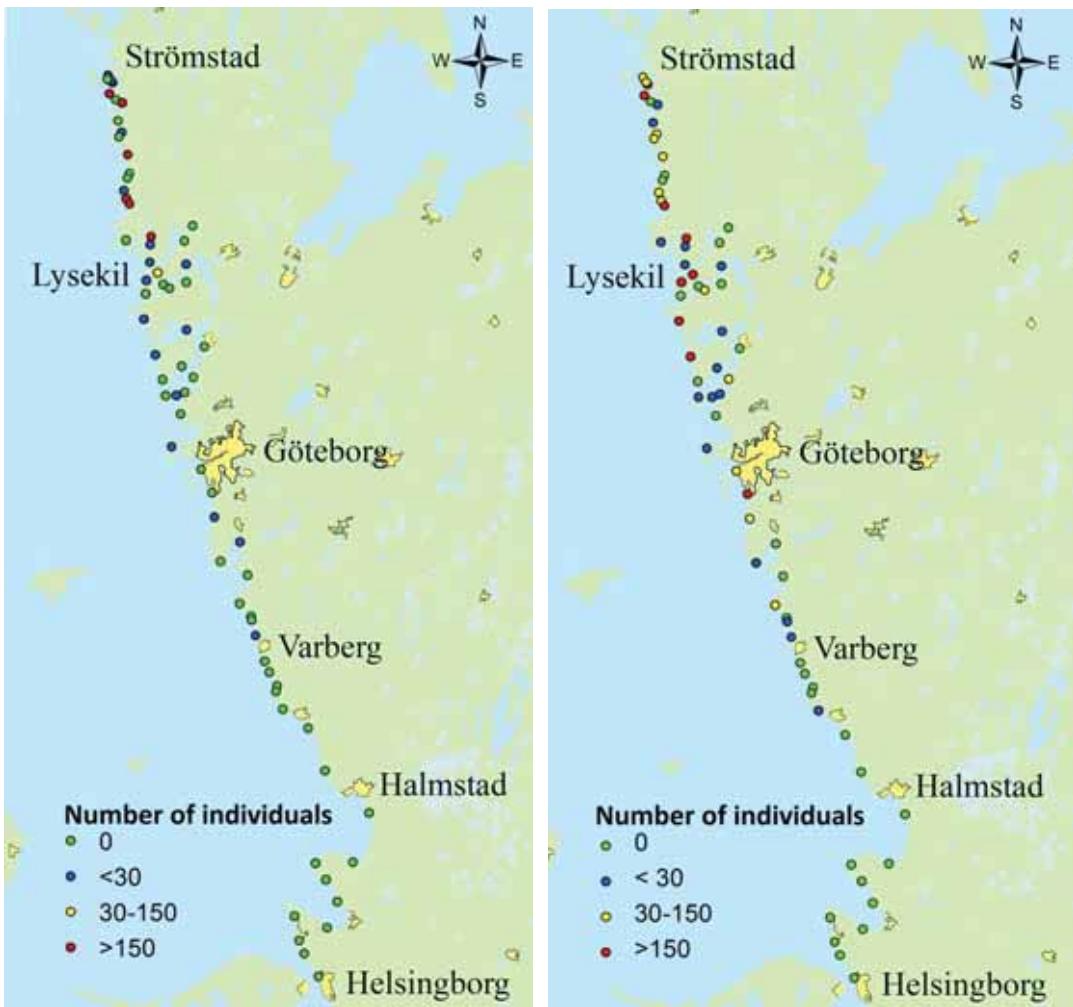


Figure 4. The 2007 (left) and 2013 (right) large-scale survey of *Crassostrea gigas* along the Swedish west coast. 68 locations were selected and screened for the presence of oysters.

Since 2007, an annual monitoring of the development of oyster populations has been performed by revisiting five bays in mid-north Bohuslän. In general, both the average and maximum densities increased between 2007 and 2009, and the mortality was generally low (Table 6). High mortality from 2009 to 2010 resulted in both reduced average and maximum densities in 2010. The reduction was explained by the harsh winter (Strand *et al.* 2012) with an elongated period of ice coverage in the shallow coastal areas along the Swedish west coast. Winter mortalities 2011 were low, probably due to the reduced number of oysters remaining in the shallowest areas. Recruitment 2010 and 2011 was high, resulting in an increase in average densities again, but also in winter mortalities as recruits were often found in very shallow areas. Recruitment 2012 was low, probably due to the low summer temperatures, but there are indications that the recruitment 2013 was successful (*own observation*, Å. Strand). Despite the high mortalities 2009/2010, large populations of adult oysters with maximum densities > 200 individuals m^{-2} still exist at some sites, and reef-like structures had started to form. At all five revisited sites, juvenile oysters have also been observed yearly, indicating a yearly reproduction. At this stage, at least eight different cohorts exist in Sweden (oysters settled 2006-2013). By following the average increase in shell length at each site, it is evident that despite recruitment of new oysters, the cohort settled in 2006 (and discovered in 2007)

was dominating the population structure until 2011, when a new strong cohort emerged. Furthermore, reports about increasing densities of oysters in deeper sub-tidal areas are emerging, indicating that the species may now also be extending its depth range.

Table 6. Observations of the average and maximum oyster densities, mortality and recruitment. The numbers are the mean from five bays re-visited between 2007 and 2013.

	Average density (N. ind. · m ⁻²)	Maximum density (N. ind. · m ⁻²)	Mortality (%)	Recruitment (%)
2007	79	748	1	96
2008	117	848	4	15
2009	135	1384	5	5
2010	4	212	87	16
2011	4	208	2	23
2013	8	148	16	10

Norway

In autumn 2005 two specimens of *C. gigas* were found on the Norwegian Skagerrak coast in the archipelago east of the town Kragerø. The oysters were 5 - 6 years old, and they seemed to have settled on local mussel shells. In 2008, *C. gigas* were found at several locations in Vestfold, and during the following years *C. gigas* have been registered at more than 100 locations along the coast from the Swedish border in east to Rogaland in the south-western part of Norway (Figure 5). The largest population found consisted of 10. 000 -15. 000 specimens with a maximum density of 40 oysters m⁻².

During the winters 2009/2010 and 2010/2011, low temperatures and a long period with ice coverage reduced the populations along the Norwegian coast with about 90% ([Bodvin et al. 2010, 2011](#), [Strand et al. 2012](#)). In 2012 and 2013, an increase was observed in several populations. In addition, several new observations in Rogaland were reported ([Bodvin et al. 2013](#)).

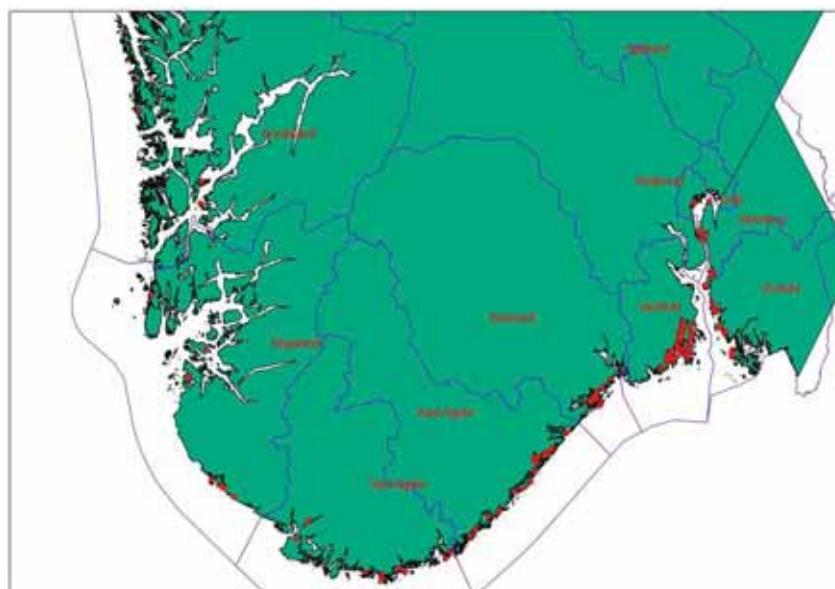


Figure 5. The distribution of *Crassostrea gigas* in Norway.

In 2013 a population at Hui (Tjøme municipality) that had been followed since 2010 showed an increase from a maximum density of 2 oysters/m² to 91 oysters m⁻² (Table 7). There were, however, no similar changes observed at the other sites. Observations from 2008 and 2009 at Hui indicate a similar situation in 2009 to a maximum density of about 40 *C.gigas* m⁻².

Table 7. Average density and mortality at Hui (Tjøme municipality) 2010-2013

Hui Year	Alive		Dead	
	Average number/m ²	Max density number/m ²	Average number/m ²	Max density number/m ²
2010	0,8	4	5,2	31
2011	0,4	3	2,9	8
2012	0,5	2	0,8	6
2013	7,5	91	0,9	5



In 2005, a few Pacific oysters were found on mussel beds near Kragerø, Southern Norway. The oysters were attached to mussel shells, and were suspected to have settled there. Photo: Stein Mortensen.

3 The impact of *Crassostrea gigas* on coastal ecosystems

The present chapter aim to review the impact of a bio-invasion of *Crassostrea gigas* on the ecosystem, including impact on the physical environment and the biological interactions. An understanding of the coexistence of *C. gigas* and the blue mussel, *Mytilus edulis*, is important, as this issue is important for the form and function of the ecosystem, and the conservations targets.

3.1 Physical changes of environment

Subtidal oysters can be characterized as ‘ecosystem engineers’ (Jones *et al.* 1994), in the sense that they create biogenic habitat with physical structure provides resources for other species. *C. gigas* establish reefs of hard structure above an estuarine seafloor, which is otherwise relatively flat and composed of unconsolidated, mobile sediments. *C. gigas* reefs raise and stabilize the sediment surface locally. The mature reefs are well-anchored, solid structures that may persistent for a long time (Reise and Van Beusekom 2008). Oysters themselves recruit onto and grow on the shells of other oysters, thereby extending the reef upward over time. The oyster reef is one of the temperate-zone analogue of the tropical coral reef, which likewise provides a complex, three-dimensional habitat of hard surface and vertical relief, which numerous other species can utilise (Peterson *et al.* 2000). The physical structure and location of the oyster habitats controls local physical variables (flow speed and hydrographics), which in turn influence recruitment, growth and survival of benthic species (Lenihan 1999). The *C. gigas* reefs may thus locally protect the intertidal habitat of native bivalves and other invertebrate fauna by preventing erosion of intertidal flats like in the Oosterschelde estuary (Troost 2010). Furthermore, by excreting vast amounts of faeces and pseudo-faeces *C. gigas*, like blue mussels, enrich the sediment organically (Norling *et al.* In prep.). This results in fine-grained sediments with high organic content, ammonia and hydrogen sulphide, and low oxygen levels (Castel *et al.* 1989, Commito *et al.* 2008, Norling *et al.* In prep.). How these sediment conditions influence macro-infauna and meiofauna is discussed in the following paragraph.

Crassostrea gigas is considered an ecosystem engineer , with the ability to modify its habitat by creating sold reef structures. In the Wadden Sea, *C. gigas* beds have rapidly developed into solid reefs at several sites in the region significantly impacting the form and function of the habitats. Due to this ability *C. gigas* is expected to dominate the mudflats on the German and Danish North Sea coast (Reise *et al.* 2005). Such reefs may significantly change the structure and complexity of the habitat. Investigations by Lejart and Hily (2011) demonstrated that the surface area of an oyster reef is increased four times, compared to a rocky or soft bottom habitat. On the Swedish west coast, extremely high densities of oysters have been found in narrow sounds in the Gullmar Fjord, which indicates that *C. gigas* has the potential to limit water circulation (Pers obs. Norling, 2007).

3.2 Interactions with other species

The effects of established non-native species on native populations vary with the ecology of the invader, phase of invasion, nature of the invaded community and with shifting ambient conditions (Reise *et al.* 2006) The impact of *C. gigas* is also depend on the trophic level and ecological role of the species affected, and whether similar ecological types are found within the system (Padilla 2010). There are several examples of native community modification as a result of *Crassostrea* spp. introductions by direct competition with native species (Shatkin *et al.* 1997, Reise 1998), by dispersal other invasive species (Carlton 1992, Wolff and Reise 2002), diseases (e.g., Grizel and Heral 1991, Mann *et al.* 1991, Shatkin *et al.* 1997, Wolff and Reise 2002) by decreasing benthic oxygen levels (Castel *et al.* 1989) and by replacing native habitat types (Norling *et al.* In prep.).

Being an ecosystem engineering species, *C. gigas* influence the presence of other species by modifying the environment directly and indirectly. The effects of *C. gigas* on associated communities are not very well studied, especially not in newly invaded areas (Escapa *et al.* 2004, Kochmann *et al.* 2008, Markert *et al.* 2010, Lejart and Hily 2011). A *C. gigas* bed offers a high level of habitat heterogeneity. The oyster shells themselves represent a large area of hard substrate settlement opportunities for other species and provide refuge from physical stress and predation. Van Broekhoven (2005) demonstrated that species richness is higher in oyster beds compared to the surrounding bare flat, with higher species richness occurring at the edge of oyster bed where oyster patches are alternated with bare patches. Similar results were obtained by Norling *et al.* (In prep) and Hollander *et al.* (In prep) for sites in Sweden. Moreover, not only species richness, but also abundance and species composition at bare sediment and blue mussel patches were altered in comparison to that of oyster patches. In conclusion, increased habitat heterogeneity generally results in a higher biodiversity in the oyster bed as a whole.

In the Bay of Brest, France, Lejart and Hily (2011) demonstrated that *C. gigas* reefs increase species richness and abundance of intertidal macrofauna on both, mud (4 and 20 fold respectively) and rock (5 fold for both) and the dominance of suspension feeders in mud changed to carnivores in reefs and their underlying sediment. This is in accordance with observations from Sweden, where increased macro-infauna species richness and abundance was observed at oyster patches compared to bare sediment both at sand, shell gravel and soft/mud sediment (Hollander *et al.* In prep.). In the Wadden Sea, different effects on biodiversity of associated species have been found between areas with *C. gigas* and *Mytilus edulis* in different study settings. No diversity effects on associated fauna where found by Kochmann *et al.* (2008) in a field experiment between these bivalves, while Markert *et al.* (2010) found higher species richness of macrofauna in a natural *C. gigas* dominated area (45 taxa) compared to *M. edulis* dominated area (28 taxa). This is also in accordance with observations from Sweden where higher infauna abundance was found in oyster patches compared to in blue mussel patches. The two habitat types also favoured different species composition of the infauna (Hollander *et al.* In prep.). Both Kochmann *et al.* (2008) and Markert *et al.* (2010) showed that *C. gigas* beds harbour a higher abundance of sessile

suspension feeders than *M. edulis* beds and concluded that the oysters alter habitat structures which entail differential abundances of associated organisms.

Very few studies on ecological effects of *C. gigas* have included fish assemblages (Posey *et al.* 1999, Breitburg 1999, Tolley and Volety 2005, Norling *et al.* In prep.). Breitburg (1999) classified the fishes found on oyster reefs as residents or transient species and argued that oyster reefs were essential fish habitat for the first group. Harding and Mann (2001) concluded that the term essential fish habitat was inappropriate, but suggested that organisms are drawn to oyster reefs because of greater availability and diversity of food, or higher quality of food on reefs compared to other habitats. There are several fish species that use empty oyster shell as spawning substrate, for example skilletfish, blennies and gobies. When *C. gigas* is introduced to soft and sandy sediment areas, there is a large increase in diversity and abundance of epifauna (Van Broekhoven 2005, Kochmann *et al.* 2008, Markert *et al.* 2010, Lejart and Hily 2011, Norling *et al.* In prep.). Moreover, the secondary production of oysters and the 3-dimensional reef structure also attract numerous invertebrates and fishes (Tolley and Volety 2005). On the Swedish west coast, manipulative field experiments have been conducted to study the effects of *C. gigas* on associated epifauna including fish (Norling *et al.* In prep.). *C. gigas* and *M. edulis* treatments had positive effects on native mobile epifauna by increasing species richness, total abundance and biomass compared to sand control. However, empty shells of the *C. gigas* had different structuring functions compared to *M. edulis*. The fish assemblage was positively influenced by the presence of *C. gigas* shells, especially species such as *Gobius niger*, *Pholis gunnellus*, *Pomatoschistus spp.*, *Myoxocephalus scorpius* and *Gobiusculus flavescens*, while small crustaceans were favoured by *M. edulis* shells (Norling *et al.* In prep.). In another field experiment, Norling and Kautsky (in prep.) showed that the rough surface structure of *C. gigas* shells also facilitates settlement of macroalgae, such as *Fucus vesiculosus*, which in turn increase the diversity of associated species even more.

In the comparative field study between *C. gigas* and *M. edulis* on the Swedish west coast, 12 fish species was found, ranging from relatively mobile fishes like *Syphodus melops* and *Ctenolabrus rupestris* to more stationary species like *Myoxocephalus scorpius* and *Pholis gunnellus* (Norling *et al.* In prep.). Thus, enhancing heterogeneity and topographical relief within mussel beds by adding oyster reef structures will attract more fish to this habitat.

In North America and the Australasia-Pacific regions the *C. gigas* is known to settle into dense aggregations, resulting in the limitation of food and space available for other intertidal benthic species (NIMPIS 2002). *C. gigas* has a large filtration capacity and filters on average 5 l/g/h but filtration rates 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 2005). In accordance, in oyster cultivation areas in France, high oyster densities caused a severe decline in macrofauna and zooplankton but enhanced bacteria, microfauna and meiofauna which in turn promoted the more active trophic fluxes towards birds and

nektonic fishes (Leguerrier *et al.* 2004). As the oysters release nutrients and pseudofaeces into the environment, planktonic and benthic productivity may increase (Diederich 2005).

3.3 Coexistence or competitive exclusion of *Mytilus edulis*?

Crassostrea gigas tends to settle in the same locations and on the same tidal level as the native Blue mussel (*M. edulis*) (Nehls *et al.* 2006). The overgrowth of *M. edulis* and pre-emption of space, and possibly also competition for phytoplankton and filtering of larvae (larviphagy), will probably limit the distribution and biomass of native species (Nehring 2003a). There is, however, evidence that the recently observed decline of mussel beds near Sylt 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, Diederich *et al.* 2005). A study by Eschweiler and Christensen (2011) demonstrated that *M. edulis* using a reef of *C. gigas* as habitat has an increased survival, due to reduced predation in the complex habitat at a cost of reduced growth due to a reduced transport of food particles to mussels located in refuges in the reef. The living on oyster reefs is then a trade-off between increased protection and reduced availability of food.

Holm *et al.* (In prep.) studied the effects of *C. gigas* on a bed of *M. edulis* in Agger Tange, a microtidal area in the Limfjord. The study showed that there was no vertical displacement of *M. edulis* due to the presence of *C. gigas* (Figure 6, left). Furthermore, the abundance of *M. edulis* was unaffected by the presence of *C. gigas* (Figure 6, right).

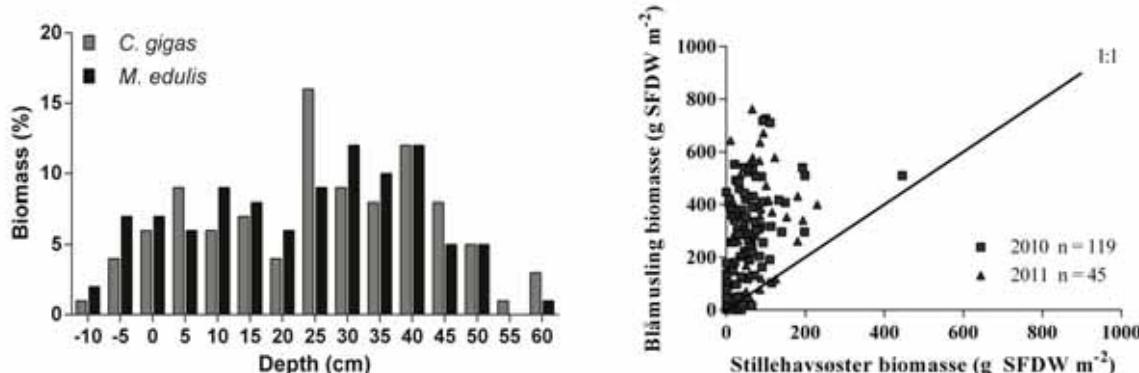


Figure 6. Left: The vertical distribution of *Crassostrea gigas* and *Mytilus edulis* on an intertidal mussel bed at Agger Tange. Negative values indicate that these areas of the mussel bed are exposed at low tide (From Holm *et al.* In prep. b). Right: The relationship between the biomass of *M. edulis* and *C. gigas*, y and x-axis respectively (From Holm *et al.* In prep. a)

Thus, in contrast to the Wadden Sea, *C. gigas* and *M. edulis* seems to coexist in this microtidal area. However, the study also showed that *M. edulis* governed the spatial development of the mussel bed. In the newly established areas of the mussel bed only one young cohort of *C. gigas* was present, whereas several age classes and in general older individuals were present in the old part of the bed, where *C. gigas* had the largest biomass.

Crassostrea gigas are competitively superior and may have a higher fitness compared to *M. edulis* in relation to reproductive output (Troost 2010), predation - including predation of

larvae -, growth, and filtration rates (Vismann *et al.* In prep.). An overlapping niche for the two species creates a potential risk for *M. edulis* to go locally extinct. Recruitment or winter mortality may cause the two species to co-exist despite an overlapping niche.

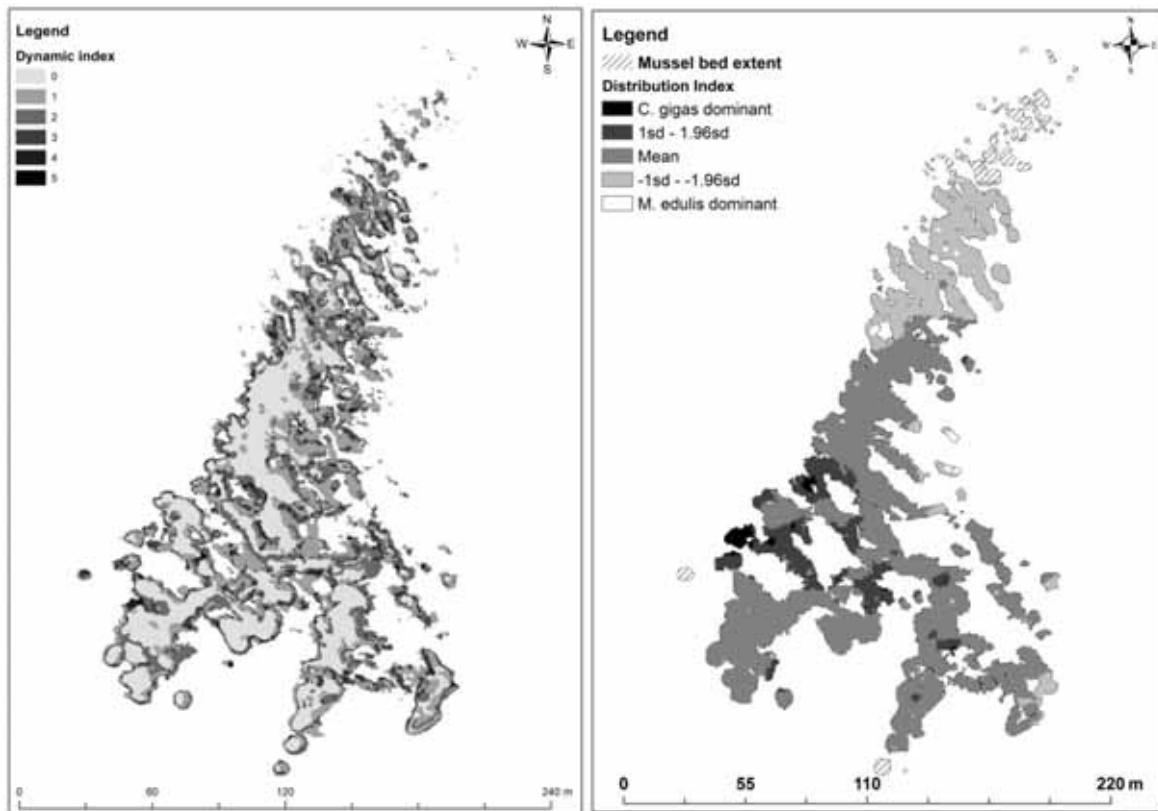


Figure 7. -The dynamic index and the distribution index of *Crassostrea gigas* at a mussel bed at Agger Tange in the western part of the Limfjord. Left: The dynamic index is an expression of the ages of the different parts of the mussel bed. The lightest colours are the oldest parts of the mussel bed, and the white the youngest. Right: The distribution index displays the relative distribution of the two species on the mussel bed. The dark areas are where *Crassostrea gigas* have the largest biomass, and the white areas where *Mytilus edulis* have the highest biomass. (From Holm *et al.* In prep.).

Changes in the factors enabling the present coexistence can alter this status, as it can favour the competitively superiority of *C. gigas*. Presently, the factor(s) responsible for the coexistence, and thus the different course in the bio-invasion between the Wadden Sea and Limfjord, has not yet been identified. However, one of the obvious differences between the Wadden Sea and Limfjord is the tidal amplitude. In the Wadden Sea, the difference between high and low tide of approximately 2 meters, while in the Limfjord, it is only 0.5 meter. This induces a large difference in the predicted diurnal renewal of the food source. Thus, differences in the ability of *C. gigas* and *M. edulis* to cope with low food situations, could explain the present situation. At Agger Tange, the food availability primarily depends on tidal fluctuations, as the water body is reduced substantially during low tide, due to the low mean water level of the mussel bed (0.16 ± 0.15 m). Modelling of the potential clearance of the two bivalves at the mussel bed at Agger Tange revealed that changes in water level (tidal amplitude 0.25 ± 0.03 m) lead to a reduction in the potential food uptake, as they, are able to clear the water column up to six times per hour at low tide (Holm *et al.* In prep. b). Thus both species rarely reaches their clearance potential, and they are periodically very food limited.

3.4 Impact on the native flat oyster, *Ostrea edulis*

The ecological niche of *C. gigas* is different from the native flat oysters (*Ostrea edulis*). *O. edulis* occurs sub-tidally, and has a more limited tolerance range for temperature and salinity compared to *C. gigas*, which lives primarily in the intertidal. Interference between the two oyster species in the Wadden Sea is not to be expected (Reise 1998). However, in Swedish waters, *C. gigas* has been observed in deeper waters from 1-9 m where flat oysters also occur. This has also been observed at some Norwegian sites. Here, observations of *O. edulis* in the intertidal have increased. It can be expected that *C. gigas* continue to establish populations and disperse deeper into areas that native flat oysters inhabit today, resulting in an increasing overlap of populations. *C. gigas* may then, because of its very rapid growth, dominate the localities over time.



Per Dolmer sceening a Danish mud flat.

Photo: S. Mortensen

4 Factors controlling population size

The impact of the *Crassostrea gigas* is dependent of the population size. As the species forms reef habitats when established at a certain density at a new location the factors that control population size are crucial for understanding the bio-invasion process.

4.1 Larval behaviour and dispersal

The establishment of a new population of *C. gigas* on a given site is dependent on a number of factors, such as successful production of larvae, transport mechanisms and settlement of larvae, and post settlement survival.

Crassostrea gigas are protandrous hermaphrodites, most commonly maturing first as males. In areas with good food supply the sex ratio in older oysters shows a predominance of females, whereas the reverse is true in areas of low food supply. Females can revert back to males when food supply is limiting. Gametogenesis begins at around 10°C, at salinities of between 15 and 32‰ and is rarely completed at higher salinities. Spawning generally occurs at salinities of 23-28‰ and at 16 °C (Ruiz *et al.* 1992), however, 18-20 °C is more commonly considered to be the lower limit (Mann 1979; Ruesink *et al.* 2005; Dutertre *et al.* 2010). The species is very fecund with 8–15 cm length females producing between 50–200 million eggs in a single spawning (Quayle 1988). The *C. gigas* 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. Fertilization must occur within 10-15 hours after spawning and occurs externally.

Larvae are planktonic and are distributed throughout the water column. They measure 70 µm shell length at the prodissoconch I stage and settle out of the water column for attachment when they are 300–340 µm. This may take two to four weeks, depending on water temperature, salinity and food supply. Over these weeks, larvae can disperse great distances by water currents. 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. However, a *C. gigas* larva could theoretically travel up to 240 km before it attaches to a hard surface. At higher water velocities longer distances can be achieved and larvae have been documented dispersing up to 1 300 km on ocean currents (AMCS Bulletin 1998). In the Wadden sea, the observed dispersal towards areas outside the surroundings of the culture plots occurred at a much slower rate than the theoretical maximum (Nehring 2003a, Reise *et al.* 2005). Brandt *et al.* (2008) created a dispersal model for *C. gigas* larvae in the German Wadden Sea. They found that the maximum dispersal distance was 50 km, but that the typical drift distance is 5 to 15 km. Similar to other oyster species, once the *C. gigas* larvae find a suitable habitat, they attach to it permanently using cement, secreted from a gland in their foot. After settlement, the larvae metamorphose into juvenile spat.

Due to the low temperature it was formerly unknown whether the *C. gigas* could reproduce in Scandinavia. Investigations of size distributions of *C. gigas* in the central part of the Limfjord

in 2006 (Christensen and Elmedal 2007) showed five cohorts, and indicated a successful reproduction during the previous five years. In 2008, gametes from *C. gigas* populations were observed in Bohuslän (Sweden) and summer 2011 high abundances of juvenile oysters recruited 2010 were found at several locations along the Swedish west coast. Whether the juveniles were a result of local reproduction or in drift from other regions is still to be determined. Sexually mature *C. gigas* at the stage of spawning have been observed at several sites in Norway, indicating local recruitment.

4.2 Habitat preferences

The distribution of available habitats can normally limit population growth. However, *C. gigas* can establish population in different habitat types. *C. gigas* will attach to almost any hard substrate. Whilst they usually attach to rocks, the oysters can also be found in sandy or muddy areas where they attach to small stones, shell fragments or other debris. Oysters will also settle on conspecific oyster shells or on other bivalve species. For example, in the European Wadden Sea, secondary hard substrates such as rocky dike foots, stone walls, harbour facilities, shell debris and blue mussel beds (*Mytilus edulis*) are used by the *C. gigas*, as hard substrate are scarce on the extensive mud and sand flats. Oysters and both living and dead *M. edulis* seem to be preferred as substrate while shells of other bivalves are of minor importance (Reise 1998, Nehring 1999, Diederich 2005, Nehls *et al.* 2006). At very dense oyster sites, reef-like structures are formed by oysters attaching to each others.

The *C. gigas* prefers sheltered waters in coastal marine and estuarine areas, yet with good water circulation. They are found in the intertidal and shallow sub-tidal zones to a depth of about three metres. In some cases the species can be found down to 40 m, but the majority of the oyster populations are located very shallow. Subtidal oyster reefs have been found in Dutch waters (Diederich 2005).

Investigations from Scandinavian show that *C. gigas* is limited to water down to 2-3 meters depth. In The Limfjord in Denmark the distribution was limited to 0 – 1 meter depth (Groslier *et al.* in prep.), and in experimental dredging at 3-6 meters depth, only a few individual have been found. In Sweden, the majority of the oysters are distributed from approximately 0.5 to 1.5 m depth, although the species has frequently been observed at greater depths, down to 9 meters.

In Norway, several registrations of *C. gigas* have been done down to 2-3 meters depth (Bodvin 2011, 2012, 2013). IMR has also received reports of findings down to 6 meters, but these are not verified. All registrations have been large specimens. During the cold winters no increased mortality has been registered in these deeper localities. These populations of oyster situated at deeper localities, can potentially reseed intertidal populations displaying high mortalities after severe winters.

4.3 Temperature

Distribution

As an intertidal species, the Pacific oyster is very tolerant to varying abiotic conditions. Ecological niche modeling based on surface seawater (SST) and atmospheric (AT) temperature records has been used to predict the potential range of distribution (Carrasco and Baron 2010). In its native range, the species maintains self-sustaining populations at thermal regimes with mean SST ranging from 14.0°C to 28.9°C for the warmest month and from -1.9°C to 19.8°C during the coldest month of the year (Figure 8). The distribution is also constrained to mean AT varying between 15°C and 31°C for the warmest month and between -23°C and 14°C for the coldest month of the year.

Investigations conducted by Strand *et al.* (2011) at the Swedish west coast tested the mortality of dry *C. gigas* dry exposed to winter temperatures (-22 °C) for 24-72 hours. The results showed that the species was extremely tolerant to freezing with approximately 50% survival after 24 hours of freezing. The freeze tolerance was also affected by pre-treatment conditions (simulated autumn conditions or summer conditions), with oysters exposed to simulated autumn conditions before the experiment demonstrating a significantly higher survival compared to the other oysters, i.e. 50% survival after 72 hours of freezing. This was attributed to acclimatization to winter conditions that increased the oysters freeze tolerance.

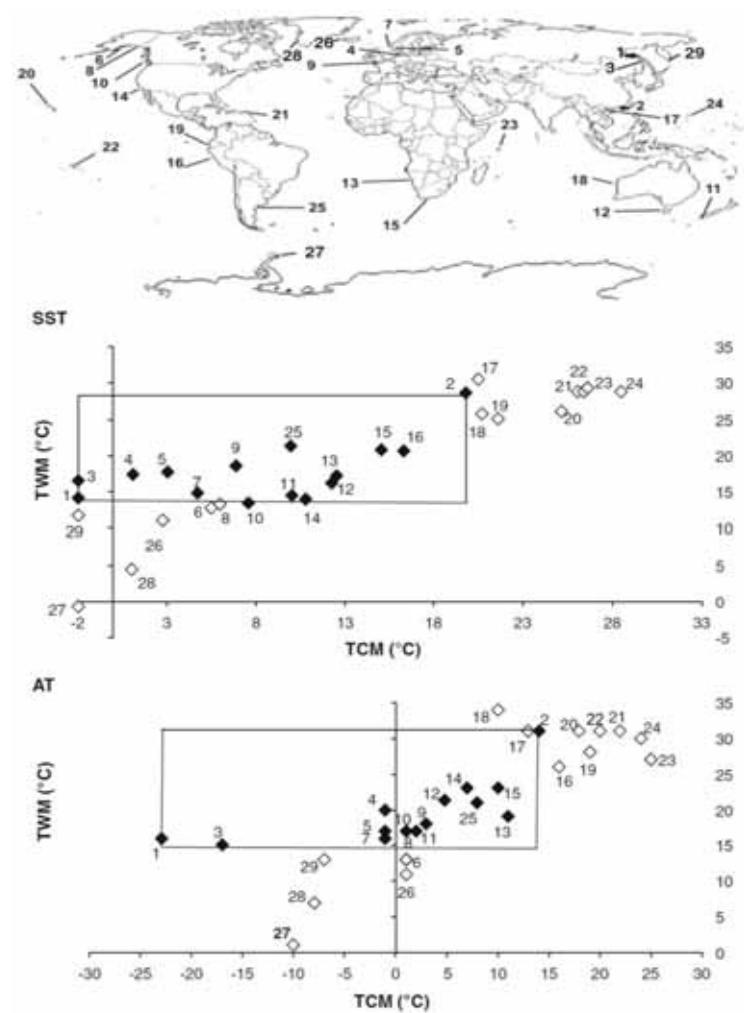


Figure 8. The distribution of *Crassostrea gigas* in a global perspective as a function of temperature in cold months (TCM) and temperature in warm months (TWM) (From Carrasco and Baron 2010).

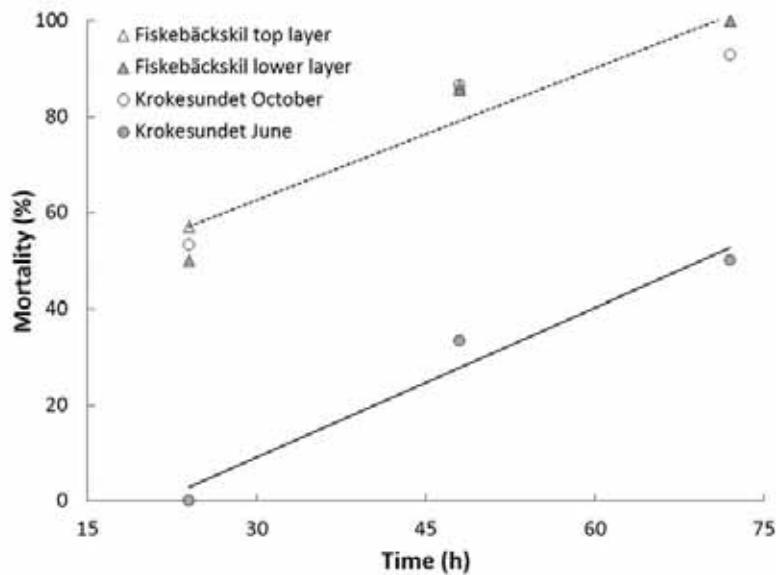


Figure 9. Mortality of *Crassostrea gigas* exposed to -22 °C in 24, 48 or 72 hours (From Strand *et al.* 2012).

Recruitment

One of the reasons for allowing import of *C. gigas* to Europe in the first place was that one thought that the water temperature was too low for the oyster to reproduce. History has shown that this was wrong. The temperature observations that were used as background for this conclusion had been collected at 1 meter depth. However, most *C. gigas* are found on 0-1 meters depth, where the water temperature potentially can reach high levels during the summer.

Significant diurnal warming (DW) events (of the order of several °C) may occur at mid latitudes and even in the Arctic during summer months. DW at mid-latitudes, such as the North Sea, is identified by e.g. Gentemann *et al.* (2008), and DW events in the Arctic are quantified and reported by Eastwood *et al.* (2011). If it is taken into account that the DW at the surface will be stronger than for the entire mean warm layer amplitude as modelled in Eastwood *et al.* (2011), the SST in the Arctic may increase substantially and introduce a strong vertical temperature gradient even for the upper meter. The estimated temperature change during one day is shown in Figure 10a (middle panel) for two different surface layer depths (Bodvin *et al.* 2012). The warm layer also depends on the surface wind speed and solar radiation, and a thin layer corresponds to our assumption on calm winds. In practice, these summer conditions imply a small temperature decrease during night and a warming during daytime, in the order of 2.5 °C for the 2 meter layer and twice as much for a 1 meter layer. In addition, a very shallow sea floor (~1m) may absorb solar radiation and amplifies the water temperature increase. Some of the oysters will also be directly exposed to sunlight at low tide, amplifying the temperature increase inside the oyster even more. These temperature differences may have a major effect on gonad development and reproduction.

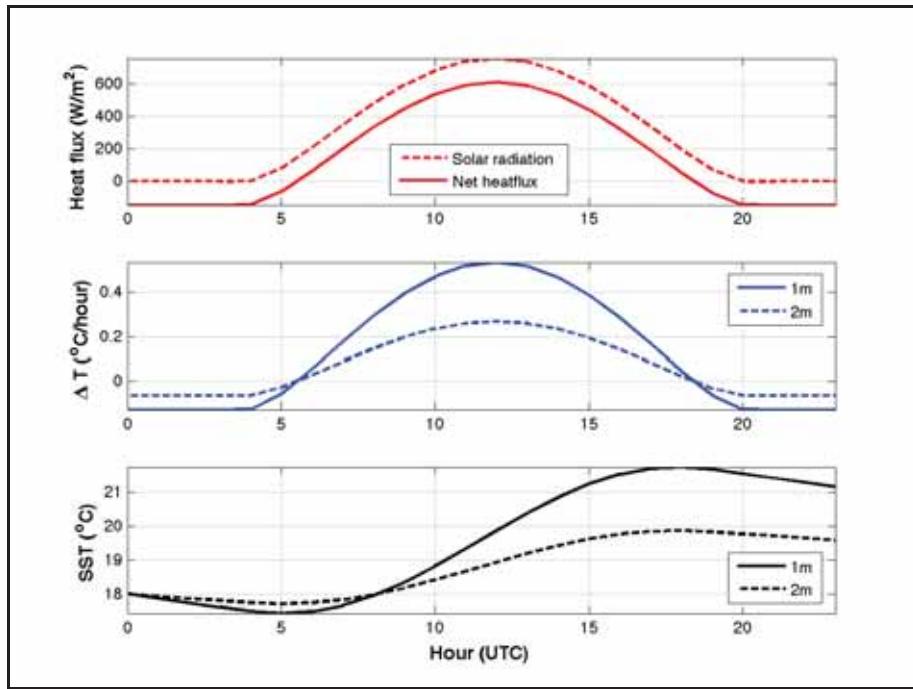


Figure 10a. A simple model evolution of heat fluxes (upper panel), temperature increase per hour (middle panel), and actual temperature for the surface layer (lower panel) during one typical day in Skagerrak (From Bodvin *et al.* 2012).

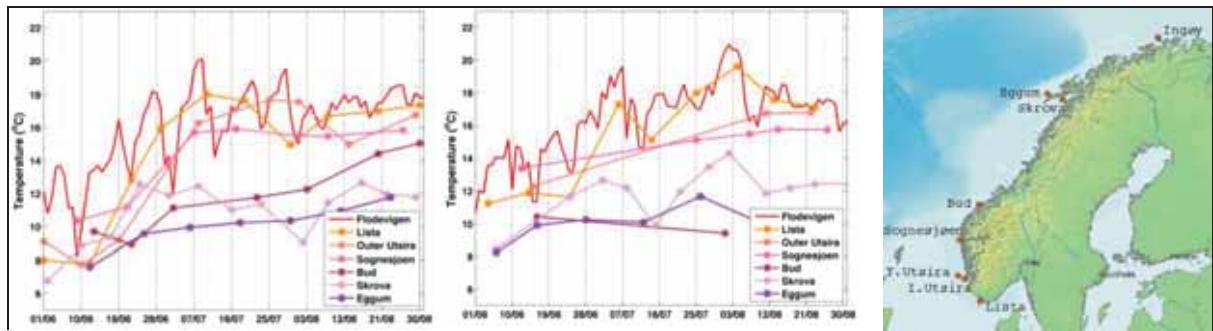


Figure 10b. Water temperature June-August (1 m depth) along the Norwegian coast in 2001 and 2011 at stations along the west- and north coast (From Bodvin *et al.* 2012).

Water temperature on the west and north coast of Norway seldom reach levels supporting recruitment (Figure 10b). However, temperature differences up to more than 5 $\text{ }^\circ\text{C}$ during the summer can be expected between the weather stations measurements at 1 meter depth and the water temperature at a shallow location protected from wind and waves. Low water temperature during the summer will therefore probably not be a sufficient barrier to avoid a further spreading along the Norwegian coast (Bodvin *et al.* 2012, 2013).

The increase of the populations of *C. gigas* in the Wadden Sea since 2003 coincides with water temperatures 1 to 3 $\text{ }^\circ\text{C}$ above average during summer. In the Lister Deep, recruitment occurred in years with a positive deviation of water temperatures to the long-term average (Figure 11).

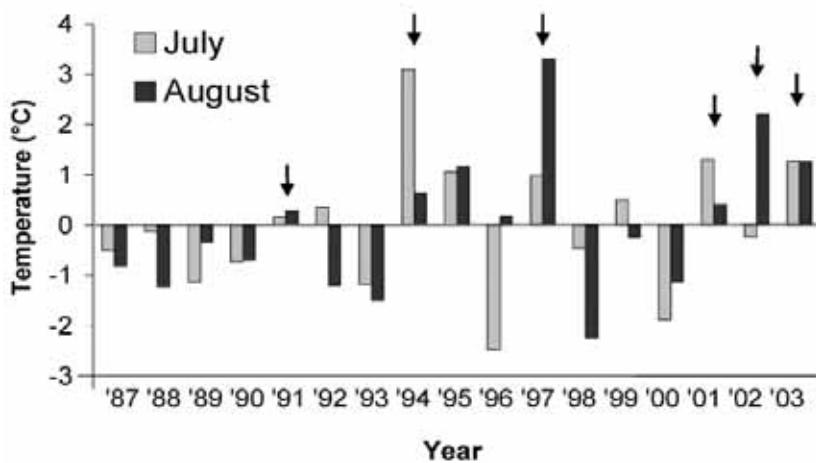


Figure 11. Deviation of mean monthly water temperature in July and August from the long-term mean (1987 - 2003). Arrows mark years with high *Crassostrea gigas* recruitment (1991, 1994, 1997, 2001, 2002, 2003) (From Diederich *et al.* 2005).

4.4 Salinity and temperature

Optimal salinity range is between 20 and 25‰ although the species can occur at salinities below 10‰ and will survive salinities in excess of 35‰. At this level, however, reproduction is unlikely to occur. It also has a broad temperature tolerance, with a range of +5 to 35°C.

4.5 Acidification

Approximately one third of anthropogenic CO₂ emissions have been absorbed by the oceans (Sabine *et al.* 2004). As the oceans absorb CO₂, the dissolved CO₂ reacts with water to produce bicarbonate ions (HCO³⁻), a chemical process that reduces pH. The pH of ocean surface water has declined by ~0.1 unit, equivalent to a 26% increase in acidity, since humans began emitting large quantities of CO₂ (IPCC 2007) and the forecast is that the pH of the oceans will decline by an additional 0.3 to 0.4 pH units by 2100. Coastal waters are more exposed to acidification due to a larger number of acid sources and due to a less buffered body of water when contrasted to open waters.

The reduced pH impacts a very wide range of marine organisms. ICES (WGMASC) have conducted a review of the impact of acidification on commercial shellfish (Table 7). In relation to oysters (*Crassostrea* spp.) the review show effects on metabolism, shell-calcification of juvenile and adults, increased mortality and reduced growth and some of the effects were additive to temperature stress.



Table 7. Review of the impact of acidification on commercial shellfish conducted by ICES –WGMASC (2012).

Species	pH	Response	Reference
<i>Mytilus edulis</i> Crassostrea gigas (juvenile & adult)	7.4 to 8.2	Mussel calcification declined linearly with decreasing pH and shells dissolve at pCO ₂ values - pH 7.5. Oyster CR also declined linearly but at a lower rate.	Gazeau <i>et al.</i> (2007)
<i>Crassostrea gigas</i>	7.7 & 8.07	Effects on energy metabolism detected.	Lannig <i>et al.</i> (2010)
<i>Crassostrea virginica</i> (juveniles)	7.5 & 8.3	Significant increase in juvenile mortality rates, inhibition of shell and body growth, altered physiology and shell properties. Reduced survival.	Beniash (2010)
<i>Mytilus edulis</i> (small adults)	6.7 to 8.1	No shell growth at pH 6.7 and reduced at 7.1. Higher mortalities for smallest mussels.	Berge <i>et al.</i> (2006)
<i>Mytilus edulis</i> (adults)	6.7 to 7.8	Inunune response (levels of phagocytosis) declined during 32 day exposure to acidified sea water.	Bibby <i>et al.</i> (2008)
<i>Saccostrea glomerata</i> (embryos)	- 7.5 to 8.3	Increasing temperature and pCO ₂ combined to significantly decrease fertilization success, leading to fewer veligers, increased abnormalities and smaller sizes.	Parker <i>et al.</i> (2009)
<i>Saccostrea glomerata</i>	7.6 to 8.1	With decreasing pH, survival of larvae decreased, and growth and development were retarded.	Watson <i>et al.</i> (2009)
<i>Mytilus edulis</i> (adults)	7.5 to 8.2	Calcification can be maintained at control rates at pH 7.5. Long term acclimation to elevated pCO ₂ .	Thomsen <i>et al.</i> (2010)
<i>Mercinaria mercinaria</i> (juvenile)	7.1 to 7.8	Maximum mortality of 11% at lowest pH and evidence of massive external shell dissolution in smallest size-classes.	Green <i>et al.</i> (2004)
<i>Mercinaria mercinaria</i> (juvenile)	pH not reported	Buffering of sediments with crushed shell reduces mortalities caused by aragonite undersaturated sediments.	Green <i>et al.</i> (2009)
<i>M. mercenaria</i> <i>Argopecten irradians</i> (larvae)	7.5 to 8.1	Thicker, more robust shells and faster growth at preindustrial CO ₂ levels. Malformed and eroded shells at reduced pH.	Talmage & Gobler (2010)
<i>M. mercenaria</i> <i>Argopecten irradians</i> <i>Crassostrea virginica</i> (larvae & juvenile)	7.8 to 8.2	Larvae were substantially more vulnerable to elevated CO ₂ than juvenile stages. The negative effects of CO ₂ and temperature were additive for 2 species of larvae.	Talmage & Gobler (2011)
<i>Mytilus edulis</i> (larvae)	7.6 to 8.1	Effects on both hatching rates and D-veliger shell growth that could lead to decreased settlement success.	Gazeau <i>et al.</i> (2010)
<i>Crassostrea virginica</i> (juvenile)	7.4 to 8.3	Biocalcification declined significantly with pH reduction.	Waldbusser <i>et al.</i> (2011a)
<i>Crassostrea virginica</i>	7.2 to 7.9	Dissolution rates were significantly different among all 4 pH treatments. Lowering pH increased dissolution rate.	Waldbusser <i>et al.</i> (2011b)
<i>Crassostrea virginica</i> <i>Crassostrea ariakensis</i> (larvae)	7.8 to 8.2	Only the Eastern oyster showed shell loss and growth reduction. Contrary to previous expectations, both species demonstrated net calcification and growth when aragonite was undersaturated.	Miller <i>et al.</i> (2009)
<i>Haliotis rufescens</i> (larvae)	7.9 & 8.1	Decreased thermal tolerance for some developmental stages.	Zippay <i>et al.</i> (2010)
<i>Chlamys farreri</i>	7.3 to 8.1	Calcification and respiration significantly declined as pH decreased.	Mingliang <i>et al.</i> (2011)
<i>Pinctada fucata</i>	7.6 to 8.1	Signs of malformation and/or dissolution in shells and decrease in shell strength	Welladsen <i>et al.</i> (2010)
<i>Pinctada fucata</i>	7.6 to 8.1	no significant difference in the number of byssal threads produced	Welladsen <i>et al.</i> (2011)

4.6 Growth

Crassostrea gigas display very high growth rates, when exposed to good conditions. They can live for up to 20 years or more (Reise 1998), and due to their relatively long lifespan and high growth rates they can attain shell lengths of more than 200 mm (Reise 1998, Cardoso *et al.* 2007, Troost 2010). *Crassostrea gigas* have the highest growth rates within the first growth season. They can grow to over 75 mm in shell length within the first 18 months (Kobayashi *et al.* 1997), and there are reports from the Wadden Sea, reporting that oysters may reach 100 mm in their first 12 months (Nehring 2011). At larger sizes, the oyster grow around 25 mm per year (Lejart *et al.* 2012, Diederich *et al.* 2006, Harding and Mann 2006, Holm *et al.* (In prep, a)) (Figure 12). In the Limfjord, Denmark, *C. gigas* reach a shell length of 20 mm the first spring after settlement. After the first growth season they reach 50 mm, and the following year 72 mm (Table 8). These growth rates are comparable to shell growth reported in the Wadden Sea and, in fact, with growth rates from their native habitat. Thus it seems unlikely that the growth performance in the Limfjord restrict the dispersal of *C. gigas* in this system, which has also been suggested to be the case in the Wadden Sea (Diederich 2006).

Table 8. Comparison between determining the age of different size classes using cohort analysis and growth rings estimates.

Age (yr)	Cohort analysis			Growth ring analysis		
	Shell length (mm)	SD	N	Shell length (mm)	SD	N
0	20	10	24	-	-	-
1	50	13	564	55	6	16
2	72	18	402	71	10	45

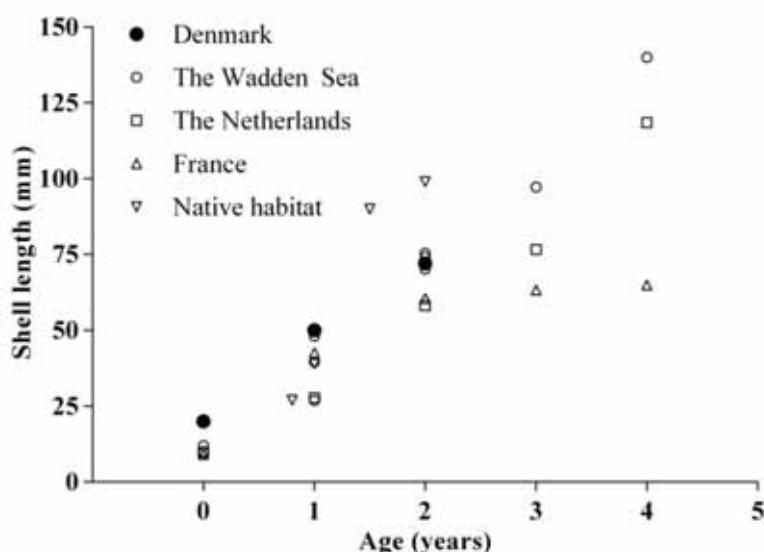


Figure 12. Shell growth of *Crassostrea gigas* worldwide. Note that the method for estimating growth differs between the studies. For further information, consult referred literature. Denmark; Holm *et al.* (in prep, a). Wadden Sea; Diederich 2006, Cardoso *et al.* 2007. The Netherlands; Cardoso *et al.* 2007. France; Cardoso *et al.* 2007. Native habitat; Kobayashi *et al.* 1997, Harding and Mann 2006.

4.7 Mortality due to predation

Impact on mussel-eating birds

The blue mussel, *M. edulis*, is important prey for a number of birds, including eider ducks (*Somateria mollissima*) and oystercatcher (*Haematopus ostralegus*). In Dutch waters, the stocks of *M. edulis* and cockles decreased at the same time as *C. gigas* increased. This decrease was accompanied by a decrease of the population of an important shellfish-feeding bird, the oystercatcher (Wolff and Reise 2002). Whether or not birds will be able to use oysters as a food resource needs further study, especially in the face of impacts that a possible shift from mussel beds to oyster reefs might have on bird populations that use the Wadden Sea as an essential feeding ground (Diederich 2005a, Wehrmann and Schmidt 2005). However, in one location on the Swedish west coast, seagulls have been observed to pick up oysters, fly up and drop the oysters on the cliffs to crack the shells and then consume the flesh (Figure 13). It is, however, unclear if the oysters were healthy and alive, or dead after the winter 2009/2010 and thus already half open, as this behaviour was observed in early spring when the ice had disappeared. This illustrates that bird populations may develop behavioural shifts towards changing food resources.



Figure 13. Empty shells on a rock on the Swedish west coast, where seagulls feed on *Crassostrea gigas* by dropping individuals on the rock to crack the shells and get access to the meat.
Photo: Carlo Nyberg

Other predators

In the coastal areas and estuaries of the European coastline there are two predators that prey vastly on invertebrate shellfish, the shore crab (*Carcinus maenas*) and the common starfish (*Asterias rubens*) (Dare et al. 1983, Troost 2010). Already in the mid fifties it was reported that the common starfish predated vigorously on different kinds of bivalves and may cause damage on wild and cultivated oyster beds (Hancock 1955, Alien 1983). Later has Walne and Davies (1977) reported that *C. maenas* preys on juvenile bivalves, such as *C. gigas*, to the

extent that it was considered a pest for fisheries. Both the shore crab and the common starfish are abundant in shallow waters and estuaries along the Danish coast, Swedish west coast and along the Norwegian coastline and thereby share the same habitat as the Pacific oyster.

In studies performed in Sweden ([Y. Fredriksson and Å. Strand, own observation](#)), both shore crabs (*Carcinus maenas*) and starfish (*Asterias rubens*) have been found to identify *C. gigas* as prey, and to have the ability to open live oysters. Blue mussels were, however, the preferred prey for at least starfish if given a choice. The vulnerable size of oysters will of course depend on the size of the predator. However, shore crabs as small as 36 mm (carapax width) have been seen to open 33 mm long oysters and crabs of approximately 60 mm have been observed to prey on 50 mm long oysters. The maximum prey size is, however, yet unknown.

Small starfish (<4 cm diameter from the tip of one arm to the tip of the opposite arm) did not seem to attack oyster juveniles (10-40 mm) although 6 cm starfish were observed preying on oysters up to 33 mm. Furthermore, large starfish, 16, 20 and 24 cm in diameter, have been observed to prey on oysters 7, 8.5 and 9.5 cm long, respectively.

4.8 Winter mortality

The two winters 2009/10 and 2010/11 were harsh, with mean air temperature in the Wadden Sea 1.5-2 °C and 1-2 °C below average, respectively ([DMI 2010, 2011](#)). [Büttger et al. \(2011\)](#) showed a mortality of 85-90% of *C. gigas* in the Wadden Sea (List Tidal Basin), due to the harsh winter of 2009/2010. The following winter, however, the population increased more than fivefold. In Scandinavia, the winter of 2009/2010 also had an influence on the winter mortality. [Strand et al. \(2012\)](#) showed that winter mortality in Scandinavia ranged from 3% to 100%. In general, mortality was related to latitude, with lowest mortality in Denmark (25%) and increasing mortality in Norway and Sweden (55 and 87%, respectively). The differences in mortality between Norway and Sweden could be explained by site-specific conditions, however, in general mortality declined with increasing depth. The correlation between reduced mortality and increasing depth could be explained by oysters located in deeper areas experience a reduced mechanical stress, otherwise induced by ice formation, and that they were not exposed to the extremely cold air temperatures experienced by the shallowest oysters as water level was very low during the winter ([Strand et al. 2012](#)). Thus, ice cover and low air temperatures seems to be two of the environmental factor that affects winter mortality in both Scandinavia and the Wadden Sea. The studies from Scandinavia indicate that winter mortality can temporarily reduce the population size of *C. gigas* ([Bodvin et al. 2010](#)). However, it does not seem to be able to eradicate them ([Strand et al. 2012](#)). It is therefore expected that *C. gigas* will persist in the Wadden Sea ([Büttger et al. 2011](#)), and continue invading Scandinavia ([Strand et al. 2012](#)).

4.9 Mortalities due to diseases

When diseases occur in oyster populations, they may become an important factor influencing the population dynamics. The Pacific oyster has generally been considered a robust species.

Several hatcheries in Europe, Asia and North America have established large scale production of this species, supplying oyster growers with spat. Still, the worldwide production of *C. gigas* is mainly based on the collection of spat from natural settlements. The production is known for not having been affected by major epizootics of infectious diseases until recently. However, a number of diseases are known, including viral, bacterial and protozoan pathogens (Elston 1993). Among these, infections with *Perkinsus marinus* and *Microcytos mackini* have been listed as exotic in Europe, and included as listed diseases in the EU Council Directives 91/67 and the more recent 2006/88/EC, annex IV (Anon. 2006).

Recently, summer mortalities have severely affected the production of *C. gigas* in France, Ireland and the UK. Some production areas have experienced high mortality of juvenile oysters and the annual production of oysters has dropped dramatically. There has been a large effort in order to clarify the cause of the mortalities. A variant of the Oyster herpesvirus named Oyster herpesvirus μvar (OsHv-1 μvar) is identified and appears to be associated with all disease outbreaks (Segarra *et al.* 2010). It is, however, still not clear whether the virus alone may cause the mortalities, or if mortalities occur if the virus appears in combination with opportunistic bacteria (like *Vibrio splendidus* and *V. aesturianus*) (summarized by EFSA, see Anonymous 2010 or <http://www.efsa.europa.eu/fr/efsajournal/pub/1894.htm>). So far, infections with OsHv-1 μvar is not listed as a notifiable disease, but a EC decision states that no trade with *C. gigas* should take place unless the production place of origin is declared free from OsHv-1 μvar (Commission Regulation No 350/2011, see <http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2011:097:0009:0019:EN:PDF>). A process is however started, in order to include infections with OsHv-1 μvar in the OIE list of notifiable diseases.

The health status of Scandinavian oysters

Based on historical data, no severe disease outbreaks have been recorded in Scandinavian bivalve molluscs. There is almost no data on *C. gigas*, as the surveillance has mainly been carried out on the indigenous flat oyster, *Ostrea edulis*.

In Norway, a basic investigation was carried out between 1989 and 1992. No diseases were uncovered (Mortensen 1993). The study was used as a fundament for a two year surveillance programme of flat oysters, carried out by the National Veterinary Institute in collaboration with the Institute of Marine Research. The surveillance programme (as well as its continuation) confirmed the absence of diseases (Hellberg *et al.* 2002). In 2009, there was however, a positive diagnose of the notifiable oyster parasite *Bonamia ostreae* in flat oysters from Aust-Agder, Southern Norway. A protection zone was established around the affected population and investigations were initiated by both the National Veterinary Institute and the Institute of Marine Research. *Bonamia* was not detected in histological and PCR samples collected in 2009 and 2010 (Mortensen *et al.* 2011). The status is thus unclear, and the site remains under investigation. Samples have been collected also in 2011 and 2012, still with negative results. The Swedish west coast is declared free from bonamiasis, limited south by the southern border of Hallands län, north by the Norwegian border. Both marteiliasis and bonamiasis have been controlled through a surveillance programme of wild flat oysters. In order to fulfil the EC requirements for surveillance of *Bonamia* sp. and *Marteilia* sp., extra

samples of *M. edulis* (that may be a vector of *Marteilia refringens*) were included in 2009. *M. refringens* type M, (blue mussel type) was detected in one area on the Swedish west coast. A protection zone was established around the site. Other areas are considered free from *Marteilia*. *Marteilia* has not been detected in mussels sampled in South-eastern Norway – north of the Swedish coast. In Denmark, Limfjorden is approved as a free zone after documentation of freedom from bonamiasis and marteiliosis.

Risk of introducing alien species and diseases

Introductions and dispersal of alien species and diseases may be a result of both active and passive movements of live animals. The dispersal of shellfish diseases is usually a result of active movement of live spat or broodstock carrying pathogens as so-called latent carriers. Once introduced, bivalve diseases may not be possible to eradicate.

Both oyster shells and mantle fluid may have numerous organisms, from microbes to algae and a variety of marine invertebrates. A continuous importation of broodstock thus represents a risk of introduction of other alien species and diseases. In 1981 all importations of *C. gigas* 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 *C. gigas* in the North Sea and the Channel. Several of these alien species are known to be invasive, and may negatively affect the native environment (Leppäkoski *et al.* 2002).

The three Scandinavian hatcheries have based their production on the native European flat oyster, *Ostrea edulis*. All on-growth of oysters has also been performed with flat oysters. Ostrea AB – the Swedish hatchery, based on Koster, has recently got a permission to farm Pacific oysters. This may change the present situation

However, *C. gigas* are imported live and placed on the market for direct human consumption. Re-laying or live storage in non-approved systems is illegal, and should not occur. It has however been observed at several occasions. Re-laying of oysters could result in the introduction of a high number of species – including alien species and potential pathogens.

If the spreading of *C. gigas* occurs as a consequence of larval drift, and / or local recruitment, the establishment of the oysters will in principle not lead to the establishment of other species. However, oysters may change the environment, and thus establish new niches for other organisms. They may also represent a host environment for microbes – potentially a reservoir of parasites.

Disease transmission between species

In general, most pathogens seem to be host specific. There are however agents that apparently are capable of infecting different species. One example is the Oyster herpes virus (OsHv-1), which is suspected to be involved in the present summer mortalities of *C. gigas* (see Anonymous 2010 or <http://www.efsa.europa.eu/fr/efsajournal/pub/1894.htm>). This virus may

infect other bivalve species, including larvae. The presence of herpes virus may thus represent a hazard – both in hatcheries and grow-out systems of different bivalve species.

Bivalves may contain a variety of bacteria – some of which may be pathogenic. Larvae and spat are particularly vulnerable, and infestations with pathogenic or opportunistic bacteria in larvae gut and mantle may lead to high mortalities and total collapses of entire batches.

Parasites are usually host specific on a genus or species level. Although host specificity in many cases has to be clarified, we must consider some parasites as capable of infecting several bivalve species. Examples are *Haplosporidium* spp and *Perkinsus* spp. The above mentioned *Bonamia* spp. posing a serious threat to the flat oyster populations is considered genus specific. However, some scientists have suggested that the *C. gigas* may act as a carrier or reservoir of the parasite (Lynch *et al.* 2010). Addressing this potential risk, movements of live *C. gigas* between areas with different status with regard to bonamiasis should thus never occur.

4.10 Genetics and local adaptation

Crassostrea gigas population structure is strongly affected by stock transfers and introductions related to aquaculture. Although most cultured populations are based on collection of wild spat or wild brood stock, Kochmann *et al.* (2012) demonstrated a strong differentiation between farmed and wild populations, even if located closely to each other. Significant reduction of genetic variability, due to a limited number of broodstock individuals and/or high variance in individual reproductive success, is known to cause strong bottlenecks in hatchery-propagated stocks.

Compared to fish species, little is known about interactions between farmed and wild *C. gigas* populations. This is mainly because most farmed populations are not yet domesticated or selected. A putative negative impact of farming triploid oysters is related to their partial fertility. Triploidy is not considered as a safe genetic confinement tool for oysters because some triploids can in fact breed. The potential impact of their incomplete sterility on wild populations is questionable as their progeny has been shown to be either diploid or aneuploid. Another risk is the potential impact of escaped tetraploid broodstock, because these are fully fertile. The fate of tetraploids in the wild (i.e. their fitness relative to diploids and the impact of their breeding with diploids) is of concern in Europe where tetraploid broodstock is presently confined to prevent their release into the wild.

5 Risk assessment of invasion of *Crassostrea gigas*

Based on the reviewed knowledge, presented in the first part of the present report, the impacts of a bio-invasion of *Crassostrea gigas* on the ecosystem and factors that control the development of the oyster population were evaluated. This analysis is formulated as an ecological risk assessment for four different coastal habitats (including soft and hard bottom and inter-and subtidal habitats) and for three climate scenarios- one short-term and two long-term, whereas one include effect of acidification.

The coupling of ecological knowledge and the climate scenarios is based on present knowledge, published in peer reviewed papers and scientific reports. Where no published evidence where available the assessment is based on expert judgements in a consensus roundtable process.

The bio-invasion can be described in four phases ([Reise et al. 2006](#), Figure 14). The species arrive to the new habitat (Phase 1) and start to establish a population, but occur at low density without changing the habitat (Phase 2). As the population starts to expand it starts to change the habitats and forms reefs (Phase 3). When established in the habitat other species as predators, competitors and diseases/parasites will reduce the density in an adjustment phase (Phase 4).

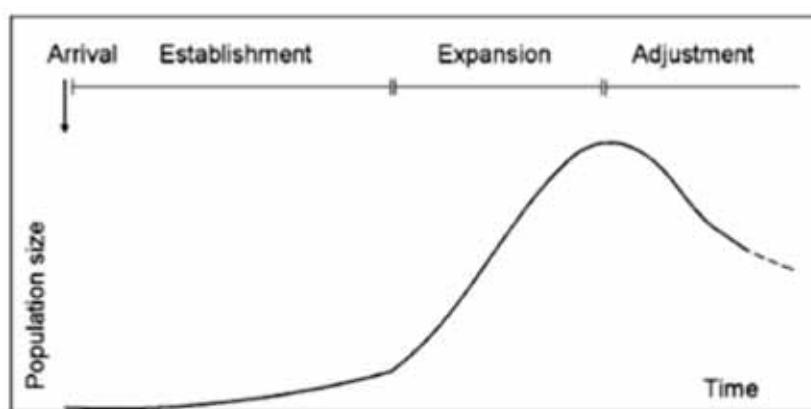


Figure 14. The four different phases in a bio-invasion.

In the risk assessment, the impact of *C. gigas* was assessed as a limited risk for the habitat if the bio-invasion was in phase 1-2, of moderate risk for the habitat if the bio-invasion was in phase 2-3 and a high risk if the bio-invasion was in phase 3-4 (Table 9).

Table 9. The categories of risk used in the risk assessment. The colour indicator refers to the colour indications in risk assessment tables, and the invasion phases refer to [Reise et al. \(2006\)](#).

Colour indicator	Risk category	Invasion phase
Green colour	limited risk	Invasion phase 1-2
Yellow colour	moderate risk	Invasion phase 2-3
Red colour	high risk	Invasion phase 3-4

The impact of the bio-invasion on four habitats, and three different climate scenarios was scored by a group of experts at a workshop in Arendal in April 2012, with the following participants:

Norway:

Stein Mortensen, IMR

Torjan Bodvin, IMR

Ellen S. Grefsrud, IMR

Pia Norling, NIVA

Sweden:

Åsa Strand, GU

Johan Hollander, Lund University

Jonathan Havenhand, GU

Sara Meurling, GU

Ane Laugen, SLU

Denmark:

Per Dolmer, Orbicon and DTU Aqua

Benni W. Hansen, RUC

Jens K. Davids, RUC

Mark W. Holm, RUC

Helle Torp Christensen, DTU Aqua



Pacific (left) and flat (right) oysters.
Photo T. Bodvin

5.1 Habitat classification

Four coastal habitats were identified as important habitats for *Crassostrea gigas* at present. The habitats are classified according to the EUNIS system ([Davies et al. 2004](#)):

EUNIS habitat code and names A1.3 Low energy littoral rock

Description

Sheltered to extremely sheltered rocky shores with very weak to weak tidal streams are typically characterised by a dense cover of fucoid seaweeds which form distinct zones (the wrack *Pelvetia canaliculata* on the upper shore through to the wrack *Fucus serratus* on the lower shore). Where salinity is reduced (such as at the head of a sea loch or where streams run across the shore) *Fucus ceranoides* may occur. Fucoids also occur on less stable, mixed substrata (cobbles and pebbles on sediment) although in lower abundance and with fewer associated epifaunal species; beds of mussels *Mytilus edulis* are also common. In summer months, dense blankets of ephemeral green and red seaweeds can dominate these mixed shores. Two biological subtypes have been described: Dense blankets of fucoid seaweeds dominating sheltered, fully marine littoral rocky shores (A1.31) and fucoids dominating variable salinity rocky shores (A1.32).

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Legal instruments

Legal instrument	Legally designated habitat	Code
EU Habitats Directive Annex I	Estuaries	1130
	Coastal lagoons	1150
	Large shallow inlets and bays	1160
	Reefs	1170

Descriptive or diagnostic parameters

Parameter	Value(s)
Altitude zones (terrestrial and marine):	Littoral (marine)
Depth zones (for marine habitats):	Upper shore; Mid-shore; Lower shore
Human activities and impacts:	Urbanised areas; human habitation, constructed artificial surfaces; Other industrial / commercial areas; Port areas
Exposure characteristics:	Sheltered from wind action; Very sheltered from wind action; Extremely sheltered from wind action; Tidal action; Weak tidal stream; Very weak or no tidal stream; Sheltered from wave action; Very sheltered from wave action; Extremely sheltered from wave action; Ultra sheltered from wave action
Geomorphology or landform:	Coastal flat; Lagoon; Reef
Characteristics of wetness or dryness:	Aquatic; Frequently submerged
Substrate types:	Bedrock; Clay; Hard; Artificial hard; Boulders (undefined); Very large non-mobile boulders; Large non-mobile boulders; Small non-mobile boulders; Non-mobile cobbles; Cobbles (undefined); Pebbles; Mixed
Salinity levels:	Fully saline; Reduced salinity; Low salinity; Variable salinity

EUNIS habitat code and names A2.2 Littoral sand and muddy sand

Description

Shores comprising clean sands (coarse, medium or fine-grained) and muddy sands with up to 25% silt and clay fraction. Shells and stones may occasionally be present on the surface. The sand may be duned or rippled as a result of wave action or tidal currents. Littoral sands exhibit varying degrees of drying at low tide depending on the steepness of the shore, the sediment grade and the height on the shore. The more mobile sand shores are relatively impoverished (A2.22), with more species-rich communities of amphipods, polychaetes and, on the lower shore, bivalves developing with increasing stability in finer sand habitats (A2.23). Muddy sands (A2.24), the most stable within this habitat complex, contain the highest proportion of bivalves.

Situation: A strandline of talitrid amphipods (A2.211) typically develops at the top of the shore where decaying seaweed accumulates. Fully marine sandy shores occur along stretches of open coast, whilst muddy sands are often present in more sheltered lower estuarine conditions and may be subject to some freshwater influence.

Temporal variation: Littoral sandy shore environments can change markedly over seasonal cycles, with sediment being eroded during winter storms and accreted during calmer summer months. The particle size structure of the sediment may change from finer to coarser during winter months, as finer sediment gets resuspended in seasonal exposed conditions. This may affect the sediment infauna, with some species only present in summer when sediments are more stable. More sheltered muddy sand shores are likely to be more stable throughout the year, but may have a seasonal cover of green seaweeds during the summer period, particularly in nutrient

enriched areas or where there is freshwater input.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Legal instruments

<u>Legal instrument</u>	<u>Legally designated habitat</u>	<u>Code</u>
EU Habitats Directive Annex I	Estuaries	1130
	Mudflats and sandflats not covered by seawater at low tide	1140
	Coastal lagoons	1150
	Large shallow inlets and bays	1160
Council of Europe Bern Convention Res. No. 4 1996	Soft sediment littoral communities	11.27
	MUD FLATS AND SAND FLATS	14

Descriptive or diagnostic parameters

Parameter	Value(s)
Altitude zones (terrestrial and marine):	Littoral (marine); Driftline
Depth zones (for marine habitats):	Upper shore; Mid-shore; Lower shore
Exposure characteristics:	Exposed to wind action; Moderately exposed to wind action; Sheltered from wind action; Very sheltered from wind action; Tidal action; Exposed to wave action; Moderately exposed to wave action; Sheltered from wave action; Very sheltered from wave action
Geomorphology or landform:	Beach; Coastal flat; Lagoon
Characteristics of wetness or dryness:	Aquatic; Frequently submerged
Substrate types:	Mobile; Mobile shingle; Sand; Muddy sand
Salinity levels:	Fully saline; Variable salinity

EUNIS habitat code and names A2.7 Littoral biogenic reefs

Description

The Littoral Biogenic Reefs habitat contains two biological subtypes, littoral *Sabellaria* reefs (A2.71) and mixed sediment shores with mussels (A2.72), encompassing the littoral biotope dominated by the honeycomb worm *Sabellaria alveolata*, and littoral *Mytilus edulis*- dominated communities. *S. alveolata* can form honeycomb reefs on mid to lower shore on exposed coasts, where there is a plentiful supply of sediment. The underlying substratum may consist primarily of rock or stable cobbles and boulders, or of cobbles and boulders on sand. Mixed sediment shores characterised by beds of adult mussels *Mytilus edulis* occur principally on mid and lower eulittoral mixed substrata (mainly cobbles and pebbles on muddy sediments) in a wide range of exposure conditions. In high densities the mussels bind the substratum and provide a habitat for many infaunal and epifaunal species.

Temporal variation: *S. alveolata* reefs may be susceptible to storm damage in the winter, although they can regenerate remarkably quickly in a season as long as some adults are left as they facilitate the larval settlement. *S. alveolata* is tolerant to burial under sand for several weeks. Changes in desiccation over a period of time can cause part of the population to die. One of the mussel-dominated subtypes, A2.7212, could change to A2.7213 over time as pseudofaeces build up forming a layer of mud. This cannot happen where wave action or tidal streams wash away pseudofaeces and prevent a build up. In areas where mussel spat ("mussel crumble") settles on the surface shell layer of cockle beds, the mussel cover may be ephemeral.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Legal instruments

<u>Legal instrument</u>	<u>Legally designated habitat</u>	<u>Code</u>
EU Habitats Directive Annex I	Estuaries	1130
	Large shallow inlets and bays	1160
	Reefs	1170

Descriptive or diagnostic parameters

Parameter	Value(s)
Altitude zones (terrestrial and marine):	Littoral (marine)
Depth zones (for marine habitats):	Mid-shore; Lower shore
Exposure characteristics:	Exposed to wind action; Moderately exposed to wind action; Sheltered from wind action; Very sheltered from wind action; Tidal action; Moderately strong current; Weak current; Exposed to wave action; Moderately exposed to wave action; Sheltered from wave action; Very sheltered from wave action
Geomorphology or landform:	Beach; Coastal flat; Lagoon
Characteristics of wetness or dryness:	Aquatic; Frequently submerged
Substrate types:	Biogenic; Peat; Shells; Mixed
Salinity levels:	Fully saline; Variable salinity

EUNIS habitat code and names A5 Sub-littoral sediment

Description

Sediment habitats in the sublittoral near shore zone (i.e. covering the infralittoral and circalittoral zones), typically extending from the extreme lower shore down to the edge of the bathyal zone (200 m). Sediment ranges from boulders and cobbles, through pebbles and shingle, coarse sands, sands, fine sands, muds, and mixed sediments. Those communities found in or on sediment are described within this broad habitat type.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Legal instruments

<u>Legal instrument</u>	<u>Legally designated habitat</u>	<u>Code</u>
Council of Europe Bern Convention Res. No. 4 1996	Sublittoral soft seabeds	11.22

Descriptive or diagnostic parameters

<u>Parameter</u>	<u>Value(s)</u>
Altitude zones (terrestrial and marine):	Offshore circalittoral; Circalittoral (marine); Infralittoral (marine)
Depth zones (for marine habitats):	0 - 5m; 5 - 10m; 10 - 20m; 20 - 30m; 30 - 50m; 50 - 100m
Exposure characteristics:	Very exposed to wind action; Exposed to wind action; Moderately exposed to wind action; Sheltered from wind action; Very sheltered from wind action; Extremely sheltered from wind action; Strong tidal stream; Moderately strong tidal stream; Weak tidal stream; Very weak or no tidal stream; Very exposed to wave action; Exposed to wave action; Moderately exposed to wave action; Sheltered from wave action; Very sheltered from wave action; Extremely sheltered from wave action
Geomorphology or landform:	Reef; Open sea
Characteristics of wetness or dryness:	Aquatic
Substrate types:	Mobile; Mobile rock; Cobbles (undefined); Mobile cobbles; Pebbles; Gravel; Sand; Muddy sand; Mud; Silt; Biogenic; Peat; Shells; Mixed; Rock, Sand, Gravel; Pebbles, Cobbles; Sand, Gravel; Mud, Sand, Gravel; Mud, Gravel; Mud, Sand; Sand, Organic
Salinity levels:	Fully saline; Reduced salinity; Low salinity; Variable salinity

Subgroup A5.1 Sub-littoral coarse sand

Coarse sediments including coarse sand, gravel, pebbles, shingle and cobbles which are often unstable due to tidal currents and/or wave action. These habitats are generally found on the open coast or in tide-swept channels of marine inlets. They typically have a low silt content and a lack of a significant seaweed component. They are characterised by a robust fauna including venerid bivalves.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Subgroup A5.2 Sub-littoral sand

Clean medium to fine sands or non-cohesive slightly muddy sands on open coasts, offshore or in estuaries and marine inlets. Such habitats are often subject to a degree of wave action or tidal currents which restrict the silt and clay content to less than 15%. This habitat is characterised by a range of taxa including polychaetes, bivalve molluscs and amphipod crustacea.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Subgroup A5.3 Sub-littoral mud

Sublittoral mud and cohesive sandy mud extending from the extreme lower shore to offshore, circalittoral habitats. This biotope is predominantly found in sheltered harbours, sealochs, bays, marine inlets and estuaries and stable deeper/offshore areas where the reduced influence of wave action and/or tidal streams allow fine sediments to settle. Such habitats are often dominated by polychaetes and echinoderms, in particular brittlestars such as *Amphiura* spp. Seapens such as *Virgularia mirabilis* and burrowing megafauna including *Nephrops norvegicus* are common in deeper muds. Estuarine muds tend to be characterised by infaunal polychaetes and oligochaetes.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Subgroup 5.4 Sub-littoral mixed sediments

Sublittoral mixed (heterogeneous) sediments found from the extreme low water mark to deep offshore circalittoral habitats. These habitats incorporate a range of sediments including heterogeneous muddy gravelly sands and also mosaics of cobbles and pebbles embedded in or lying upon sand, gravel or mud. There is a degree of confusion with regard nomenclature within this complex as many habitats could be defined as containing mixed sediments, in part depending on the scale of the survey and the sampling method employed. The BGS trigon can be used to define truly mixed or heterogeneous sites with surficial sediments which are a mixture of mud, gravel and sand. However, another 'form' of mixed sediment includes mosaic habitats such as superficial waves or ribbons of sand on a gravel bed or areas of lag deposits with cobbles/pebbles embedded in sand or mud and these are less well defined and may overlap into other habitat or biological subtypes. These habitats may support a wide range of infauna and epibiota including polychaetes, bivalves, echinoderms, anemones, hydroids and Bryozoa. Mixed sediments with biogenic reefs or macrophyte dominated communities are classified separately in A5.6 and A5.5 respectively.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Subgroup 5.5 macrophyte-dominated sediment

This habitat type includes maerl beds, seaweed dominated mixed sediments (including kelps such as *Laminaria saccharina* and filamentous/foliose red and green algae), seagrass beds, and lagoonal angiosperm communities. These communities develop in a range of habitats from exposed open coasts to lagoons and are found in a variety of sediment types and salinity regimes.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

Subgroup 5.6 Sub-littoral biogenic reefs

This habitat type includes polychaete reefs, bivalve reefs (e.g. mussel beds) and cold water coral reefs. These communities develop in a range of habitats from exposed open coasts to estuaries, marine inlets and deeper offshore habitats and may be found in a variety of sediment types and salinity regimes.

Source Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. (2004)

5.2 Climate scenarios

Assuming continued emission of greenhouse gas at or above the current rate [Philippart et al. \(2011\)](#) suggested that a temperature increase at 2 °C could be expected in NE Atlantic in 2090 and 2 to 4 °C in the Baltic (Table 10).

Table 10. Observed and projected changes in the surface temperature of European Seas (From [Philippart et al. 2011](#)).

European Sea	Observed Change	Predicted Change
Arctic Ocean	ca. +0.2 °C per decade (1965–'95)	+4 to 7 °C (1990s–2090s)
Barents Sea	+0.12 °C (1982–2006)	+1 to 2 °C (1990s–2080s)
Nordic Seas	+0.85 °C (1982–2006)	+1 to 2 °C (1990s–2080s)
NE Atlantic	+1 °C (1975–2005)	+2 °C (1990s–2090s)
North Sea	+1.31 °C (1982–2006)	+0.8 °C (1990s–2040s)
Baltic Sea	+1.35 °C (1982–2006)	+2 to 4 °C (1990s–2090s)
CB Shelf	+0.72 °C (1982–2006)	+1.5 to 5 °C (1990s–2090s)
Iberian upwelling	+0.68 °C (1982–2006)	+1.4 to 2.4 °C (1960/1990–2070/2100)
Mediterranean	+0.71 °C (1982–2006)	+2.6 °C (1961/1990–2070/2099)
Black Sea	+0.96 °C (1982–2006)	

Based on different assumption about the global development in relation to use of fossil energy sources, and development and implementation of new technology four different families of scenarios are developed (Table 11). Based on the scenarios, the development in the concentration of greenhouse gases (CO₂, CH₄, N₂O and F-gases) and the development of global surface temperature until 2100 are shown (Figure 15).

The climate change in the Nordic countries has been assessed in a report from Nordic council of Ministers ([Thorstensson and Björnsson 2011](#)). The results of 15 regional climate change scenarios are shown in Figure 16, contrasting the temperature in 1961-1990 and 2021-2050. In both summer and winter a temperature increase of 1-2° can be expected in 2050, in the area where *Crassostrea gigas* is distributed in Scandinavia.

Table 11. Different scenarios of global development in use of fossil-energy and development of new non-fossil technology. Developed by IPCC.

Scenario	Description from IPCC (2007)
A1	The A1 scenario family describes a future world of very rapid economic growth, global population that peaks in mid-century and declines thereafter, and the rapid introduction of new and more efficient technologies. Major underlying themes are convergence among regions, capacity building, and increased cultural and social interactions, with a substantial reduction in regional differences in per capita income. The A1 scenario family develops into three groups that describe alternative directions of technological change in the energy system. The three A1 groups are distinguished by their technological emphasis: fossil intensive (A1FI), non-fossil energy sources (A1T), or a balance across all sources (A1B).
A2	The A2 storyline and scenario family describes a very heterogeneous world. The underlying theme is self-reliance and preservation of local identities. Fertility patterns across regions converge very slowly, which results in continuously increasing global population. Economic development is primarily regionally oriented and per capita economic growth and technological change are more fragmented and slower than in other storylines.
B1	The B1 storyline and scenario family describes a convergent world with the same global population that peaks in midcentury and declines thereafter, as in the A1 storyline, but with rapid changes in economic structures toward a service and information economy, with reductions in material intensity, and the introduction of clean and resource-efficient technologies. The emphasis is on global solutions to economic, social, and environmental sustainability, including improved equity, but without additional climate initiatives.
B2	The B2 storyline and scenario family describes a world in which the emphasis is on local solutions to economic, social, and environmental sustainability. It is a world with continuously increasing global population at a rate lower than A2, intermediate levels of economic development, and less rapid and more diverse technological change than in the B1 and A1 storylines. While the scenario is also oriented toward environmental protection and social equity, it focuses on local and regional levels.

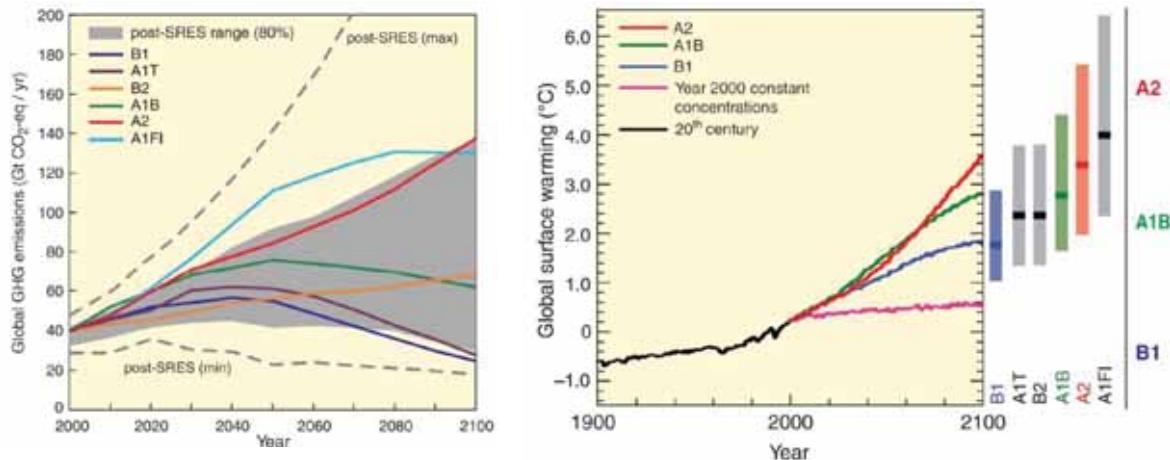


Figure 14. Left: development of greenhouse gases (GHG) in the different scenarios. Right: Development of global surface temperature in the different scenarios.

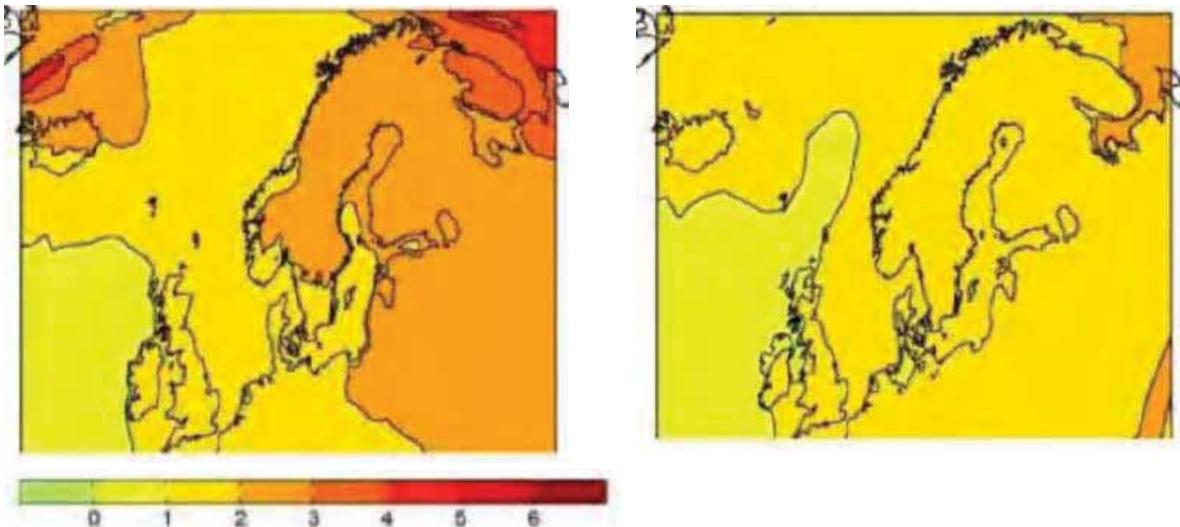
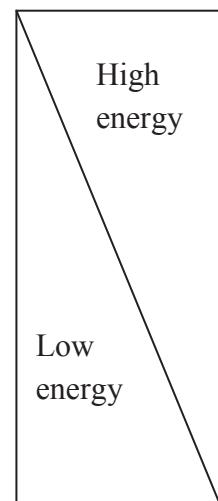


Figure 16. Change in air temperature in the Nordic countries from 1961-1990 to 2021-2050, based on means from 15 different scenarios. Left: Change in temperature in winter (December-Februar). Right: Change in temperature in summer (June-August).

5.3 Risk assessment

Based on the identified EUNIS habitats, the IPCC long term climate change scenarios and the short term climate change scenarios for the Nordic countries risk assessments were conducted. The results of the assessments are shown in Table 12. In order to include variation in wind and tidal forces, the habitat types is separated in high and low energy habitats. High energy habitats is defined as sites with high tide fluctuations, strong currents and high wave exposure, and low energy habitats as sites with little or no tide, little currents and low wave exposure. In the Risk assessment table (Table 12), the colour of the left part of the analysis of each climate indicates status for low energy habitats, and the right part indicates status for high energy habitats.



Based on the reviewed knowledge presented in section 5-8 in this document, some general conclusions can be made. The oysters are primarily found in the littoral zone but are also well represented in the shallow sub littoral environment. They seem to prefer the habitat types with available substrate, and thrive in high energy areas. Neither temperature, nor salinity, seem to be a limiting factor for the survival, reproduction and continued dispersal of the species, although in the littoral zone the species may experience high winter mortalities which temporarily may reduce the populations. Spawning most likely occurs locally in all three Scandinavian countries, but the success may vary depending on summer temperatures. To this point, predation has not been large enough to notably affect the dispersal of the species in Scandinavia. The species may have large effects both on the physical environment (especially in shallow, narrow sounds) and on associated fauna. Parasites, bacteria, virus can be expected to be introduced or to adapt to *C.gigas*, and may represent an important control mechanism in the future.

Table 12. Results of Risk assessment – see in text for explanation.

	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC AIB 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
A1.3 –Low energy Rock	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) Reduced winter mortality due to reduced ice cover.</p> <p>3) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>4) Invertebrate predation</p> <p>5) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>6) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>The pacific oyster will have a limited impact on the habitat</p>	<p>1) Yearly recruitment, due to temperature increase</p> <p>2) Reduced winter mortality due to reduced ice cover.</p> <p>3) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>4) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>5) Invertebrate predation</p> <p>6) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>7) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>8) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>9) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species</p> <p>The pacific oyster will have a moderate impact on the habitat</p>	<p>1) Yearly recruitment, due to temperature increase</p> <p>2) Increased larval mortality on bivalves due acidification.</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>6) Invertebrate predation</p> <p>7) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>8) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>9) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>10) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species</p> <p>The pacific oyster will have a moderate impact on the habitat</p>

	Low uncertainty: Short term climate scenario, Many studies on distribution and ecology on habitat type.	Moderate uncertainty: long term climate scenario, many studies on distribution and ecology on habitat type.	Moderate uncertainty: long term climate scenario, Many studies on distribution and ecology on habitat type.
A2.2 Littoral sand and mud	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) Substrate limitation may reduce recruitment</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>6) Invertebrate predation</p> <p>7) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>8) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>9) Sediment modification due to increased sedimentation of organic material.</p> <p>The pacific oyster will have a limited impact in low energy areas and a moderate impact in high energy areas</p>	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) Substrate limitation may reduce recruitment</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>6) Invertebrate predation</p> <p>7) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>8) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>9) Sediment modification due to increased sedimentation of organic material.</p> <p>10) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>The pacific oyster will have a moderate impact in low energy areas and a moderate impact in high energy</p>	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) Increased larval mortality on bivalves due acidification.</p> <p>3) Substrate limitation may reduce recruitment</p> <p>4) Reduced winter mortality due to reduced ice cover.</p> <p>5) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>6) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>7) Invertebrate predation</p> <p>8) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>9) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>10) Sediment modification due to increased sedimentation of organic material.</p> <p>11) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>The pacific oyster will have a moderate impact in low energy areas and a moderate impact in high energy</p>

A2.7 Littoral biogenic reefs	Low uncertainty: Short term climate scenario, Many studies on distribution and ecology on habitat type.	Moderate uncertainty: long term climate scenario, many studies on distribution and ecology on habitat type.	Moderate uncertainty: long term climate scenario, Many studies on distribution and ecology on habitat type.
<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>6) Invertebrate predation</p> <p>7) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>8) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>9) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>9) Sediment modification due to increased sedimentation of organic material.</p> <p>The pacific oyster will have a moderate impact in low energy areas and a high impact in high energy areas</p>	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>6) Invertebrate predation</p> <p>7) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>8) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>9) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>9) Sediment modification due to increased sedimentation of organic material.</p> <p>10) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>The pacific oyster will have a moderate impact in low energy areas and a high impact in high energy areas</p>	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) increased larval mortality on bivalves due acidification.</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Increased bird predation as birds can adapt to predate on pacific oysters.</p> <p>6) Invertebrate predation</p> <p>7) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>8) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>9) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>9) Sediment modification due to increased sedimentation of organic material.</p> <p>10) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>The pacific oyster will have a moderate impact in low energy areas and a high impact in high energy areas</p>	

A5.1-6 sublittoral sediment	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) Substrate limitation may reduce recruitment</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Invertebrate predation</p> <p>6) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>7) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>8) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>9) Sediment modification due to increased sedimentation of organic material.</p> <p>The pacific oyster will have a limited impact in low energy areas and a moderate impact in high energy areas</p>	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) Substrate limitation may reduce recruitment</p> <p>3) Reduced winter mortality due to reduced ice cover.</p> <p>4) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>5) Invertebrate predation</p> <p>6) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>7) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>8) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>9) Sediment modification due to increased sedimentation of organic material.</p> <p>10) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>The pacific oyster will have a limited impact in low energy areas and a high impact in high energy areas</p>	<p>1) Increased frequency of years with recruitment due to increase in temperature.</p> <p>2) increased larval mortality on bivalves due acidification</p> <p>3) Substrate limitation may reduce recruitment</p> <p>4) Reduced winter mortality due to reduced ice cover.</p> <p>5) Increased local distribution due to increased recruitment and reduced mortality.</p> <p>6) Invertebrate predation</p> <p>7) Increasing biomass of suspension feeding pacific oysters may increase predation of larvae and reduce recruitment of other species.</p> <p>8) Increasing biomass of suspension feeding pacific oysters may induce Local food limitation and food competition</p> <p>9) Increased biomass of pacific oysters change the habitat which will increase recruitment and survival of some species and induce competition for space with other species changing the trophic structure.</p> <p>10) Sediment modification due to increased sedimentation of organic material.</p> <p>11) Parasites, bacteria, virus can be expected to be introduced or to adapt.</p> <p>The pacific oyster will have a limited impact in low energy areas and a high impact in high energy areas</p>

6 Conclusion

The risk assessment is based on a review of existing scientific literature and expert judgments, and the data is evaluated on a workshop in April 2012 with the participation of 14 experts on *Crassostrea gigas* in Scandinavian. The long term climate scenarios are adapted from IPCC (Scenario A1B and A2) and the short term from a Nordic analysis on climate change. Four different habitat types are included in the assessment. These habitat types represent important habitats for *C. gigas* in Scandinavia. This chapter presents the conclusions from the risk assessment and a discussion of the risk assessment in relation to a strategy for the control of the species in relation to conservation of biodiversity and habitats.

The risk assessment is based on an analysis of the present scientific knowledge to the distribution patterns of *C. gigas* in Scandinavia, including the change in density during time. As the Blue mussel, *Mytilus edulis*, is a very important engineering species, forming important habitats with a high density, knowledge to interactions between *C. gigas* and *M. edulis* is important to evaluate the impact of the presence of *C. gigas* in coastal habitats. Several factors control the density of *C. gigas* including larval production and recruitment. Temperature is a key parameter controlling the distribution, recruitment is correlated to warm summers, and during icy winter a massive mortality of *C. gigas* is observed due to drifting ice. Other factors as acidification, predation and health status is included in the body of knowledge that forms the basis for this risk assessment.

In the risk assessment it is concluded that for the habitat type **Low energy rock** there is on a short term (Year 2050) a limited risk, that *C. gigas* will develop a bio-invasion in Scandinavia impacting the form and function of the habitat type, although the species is presented in the habitat (Table 13). On a long term (Year 2100) it is concluded that there is a moderate risk that *C. gigas* will develop a bio-invasion.

In the risk assessment it is concluded that for the habitat type **Littoral sand and mud** there is on a short term a limited risk at low energy sites, that *C. gigas* will develop a bio-invasion (Table 14). On a long term it is concluded that on low energy sites there is a moderate risk that *C. gigas* will develop a bio-invasion. On high energy sites, there is a moderate risk that *C. gigas* develops a bio-invasion.

In the risk assessment it is concluded that for the habitat type **sub-littoral sediment** there is on a short and long term a limited risk at low energy sites, that *C. gigas* will develop a bio-invasion (Table 15). On high energy sites, there is on a short term a moderate risk that the species will develop a bio-invasion. On a long term, there is a high risk that *C. gigas* develops a bio-invasion.

In the risk assessment it is concluded that for the habitat type **Littoral biogenic reefs** there is on a short and long term a moderate risk at low energy sites, that *C. gigas* will develop a bio-invasion (Table 16). On high energy sites, there is on a short and long term a high risk that *C. gigas* develops a bio-invasion.

Table 13. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type low energy rock. The green colour indicates a limited risk and the yellow colour indicates a moderate risk for a bio-invasion.

A1.3 Low energy Rock	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			

Table 14. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type littoral sand and mud. The green colour indicates a limited risk and the yellow colour indicates a moderate risk for a bio-invasion.

A2.2 Littoral sand and mud	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			
High energy			

Table 15. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type sub-littoral sediment. The green colour indicates a limited risk, the yellow colour indicates a moderate risk and the red colour indicates a high risk for a bio-invasion.

A5.1-6 sub-littoral sediment	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			
High energy			

Table 16. Overview of the risk assessment of bio-invasion of *C. gigas* on the habitat type littoral biogenic reefs. The yellow colour indicates a moderate risk and the red colour indicates a high risk for a bio-invasion.

A2.7 Littoral biogenic reefs	Short term NMR 1-2 °C (air) pH: -0.15	Long term IPCC A1B 2.5-3.0 (air) pH: -0.25	Long term IPCC A2 3.0-3.5 °C (air) pH: -0.35
	Moderate uncertainty: Short term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.	Large uncertainty: long term climate scenario, few studies on distribution and ecology on habitat type.
Low energy			
High energy			

6.1 Development of strategies for Conservation

At the habitat types **Low energy rock**, the **Littoral sand and mud** and the **Sub-littoral sediment** in low energy areas there is a limited to moderate risk that a bio-invasion of *C. gigas* will develop. For the **Biogenic reefs** and the **Sub-littoral sediment** in high energy areas there is a moderate to high risk for a bio-invasion.

In order to develop site-specific strategies for conservation in areas with a present or an expected presence of *C. gigas* in the next decades the information from the risk assessment can be used. Different strategies can be implemented. In the three Scandinavian countries, Norway, Sweden and Denmark, no specific strategies have been formulated for control of the invasive *C. gigas*. So, the *de facto* strategy is to accept *C. gigas*, including the formation of reef habitats as an integrated part of marine ecosystems. An alternative strategy for conservation is a control of density and dispersal of *C. gigas* in smaller or larger areas.

In the Wadden Sea in the Netherlands an experiment with removal of habitats of *C. gigas* was tested in 2006 ([Wijisman et al. 2008](#)). In a 500.000 m² tidal flat area with reefs of *C. gigas*, the reef structures were removed by fishing with a mussel dredge. The test indicated that it took approximately 20 hours to remove oyster reefs from 10.000 m², but that all oysters could not be removed. Due to new recruitment the dredging process should be repeated every 3-6 years. The test indicate that control of oysters reefs can only be implemented locally in smaller areas, that the control activity is a continuous process, and the control is an expensive strategy.

Manual destruction as a method for reducing the development and dispersal of Pacific oyster populations at very low densities (<1 m⁻²) has been tried successfully in Ireland ([Guy and Roberts 2010](#)). In Scandinavia, the oyster densities are in general much higher, thus this approach may not be suitable for limiting the oyster populations in most parts of this region. At a few sites, like Isefjord in Denmark, and after the winter 2009/2010 some locations in Sweden, the method may however be considered a possibility. Extreme winter conditions causing high mortalities thus offer a unique opportunity for management of Pacific oyster populations which before winter had already reached moderate densities. Furthermore, non-commercial handpicking of Pacific oyster may locally prevent the formation of dense populations. In Norway and Sweden, private handpicking is, however, regulated by the rights of the landowner adjacent to the coastline. In Sweden this law is currently under revision. In Denmark private handpicking is legal, and may be of local importance.

In the Netherlands, a commercial fishery and bottom culture production of *C. gigas* is developed and the production was MSC certificated in 2012. This indicate that *C. gigas* actually has a commercial value, and that a control strategy may be financed by a commercial fishery?

A mitigation of invasive species should prioritize a control strategy in Scandinavian coastal waters targeting areas with the highest risk for a bio-invasion, that change the natural habitats. In high energy areas with high tidal amplitude and/or narrow straits with high current speed, a

high risk for a invasion of *C. gigas* is identified on **Littoral biogenis reefs** and on **Sub-littoral sediments**. The density of *C. gigas* on especially **Littoral biogenis reefs** have been reduced the last winters due to impact from drifting ice (Strand *et al.* 2012), and the present low density may be an excellent starting point for the implementation of a control strategy. The easy access and the ability to visually inspect littoral sites may allow an implementation of a strategy for removing oysters from smaller areas in order to protect the undisturbed biodiversity and habitat structure. Cooperation with commercial fisheries may allow a control strategy for a larger area, whereas cooperation with local groups of volunteers may allow a control strategy of a smaller area by handpicking of oysters. The risk assessment finds a limited to moderate risk that a bio-invasion of *C. gigas* will develop in low energy habitats as **Low energy rock**, the **Littoral sand and mud** and the **Sub-littoral sediment**. The optimal strategy in these areas may include a monitoring program that allows an early implementation of a control program in order to detect if a local population of *C. gigas* change to an expansive phase of invasion and calls for an effort to reduce density.



Measuring the size of a Pacific oyster.
Photo: Åsa Strand

7 References

- Allen PL (1983). Feeding behavior of *Asterias rubens* (L.) on soft bottom bivalves: a study in selective predation. Journal of Experimental Marine Biology and Ecology 70: 79-90.
- AMCS Bulletin (Australian Marine Conservation Society) (1998) Marine and Coastal Updated. Bulletin Volume 20, No.2 Autumn 1998.
- Anonymous (2006) EU Council directive 2006/88/EC of 24 October 2006 on animal health requirements for aquaculture animals and products thereof, and on the prevention and control of certain diseases in aquatic animals.
- Bhattacharya CG (1967) A simple method of resolution of a distribution into Gaussian components. Biometrics 23: 115-135.
- Bodyvin T, Moy F, Norling P, Jelmert A (2010) Winter mortality of *Ostrea edulis* and *Crassostrea gigas* – some observations from the southern coast of Norway. Poster at “The 45th European Marine Biology Symposium” (Edinburgh, Scotland).
- Bodyvin T, Mortensen S, Moy F, Jelmert A (2011) Registrering av vekst og fortetning av stillehavssøsters (*Crassostrea gigas*) på utvalgte lokaliteter. Årsrapport DN 2011. (In Norwegian).
- Bodyvin T, Mortensen S, Moy F, Jelmert A (2012) Registrering av vekst og fortetning av stillehavssøsters (*Crassostrea gigas*) på utvalgte lokaliteter. Årsrapport DN 2012. 12 s. (In Norwegian).
- Bodyvin T, Albretsen J, Moy F, Mortensen S, Bysveen I, Jelmert A, Espeland S (2012) How important is water temperature for an innovation on the coast of Norway?. Poster at “The 47th European Marine Biology Symposium” (Arendal, Norway).
- Bodyvin T, Jelmert A, Moy F, Husa V, Bysveen I, Mortensen, S (2013) First reef of *Crassostrea Gigas* in the Oslo fjord – a warning for future developments? Poster Nordic Marine Science Conference 2013.
- Brandt G, Wehrmann A, Wirtz KW (2008) Rapid invasion of *Crassostrea gigas* into the German Wadden Sea dominated by larval supply. Journal of Sea Research 59:279-296.
- Breitburg DL (1999) Are three-dimensional structure and healthy oyster populations key to an ecologically interesting and important fish community? Pp. 239-250 in *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*, M.W. Luckenbach, R. Mann, and J.A. Wesson. Virginia Institute of Marine Science, Gloucester Point.
- Büttger H, Nehls G, Witte S (2011) High mortality of *C. gigas* in a cold winter in the North-Frisian Wadden Sea. Helgoland Marine Research 65: 525-532.
- Büttger H, Witte S, Nehls G (2010) Miesmuschelmonitoring 2010 im Nationalpark Schleswig-Holsteinisches Wattenmeer. Auftrag des Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein. Trilateral Monitoring and Assessment Program (TMAP). Bericht an das Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer. Husum, p 1–38. [In German]
- Cardoso JFMF, Langlet D, Loff JF, Martins AR, Witte JJ, Santos PT, van der Veer HW (2007) Spatial variability in growth and reproduction of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) along the west European coast. Journal of Sea Research 57: 303-315.
- Carlton JT (1992) Introduced marine and estuarine molluscs of North America: an end of the-20th-century perspective. Journal of Shellfish Research 11: 489-505.
- Carrasco MF, Barón PJ (2010) Analysis of the potential geographic range of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) based on surface seawater temperature satellite data and climate charts: the coast of South America as a study case. Biological Invasions 12: 2597-2607.

Castel J, Labourg PJ, Escaravage V, Auby I, Garcia ME (1989) Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. *Estuarine, coastal and shelf science*, 28: 75-85.

Christensen H, Elmedal I (2007) Den invasive stillehavssøsters, *Crassostrea gigas*, i Limfjorden - inddragelse af borgere og interesser i forslag til en forvaltningsplan. Master's thesis, Roskilde University, Denmark: 182pp

Commito JA, Como S, Grupe BM, Dowa WE (2008) Species diversity in the softbottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales. *Journal of Experimental Marine Biology and Ecology* 366: 70–81.

Dankers NMJA, Dijkman EM, Jong ML de, Kor G de, Meijboom A (2004) De verspreiding en uitbreiding vande Japanse Oester in de Nederlandse Waddenzee. Wageningen, Alterra, Alterra-rapport 909, pp. 51.

Davies CE, Moss D, Hill MO (2004) EUNIS habitat classification revised 2004. Report to European Environment Agency

Diederich S (2005) Invasion of Pacific oysters (*Crassostrea gigas*) in the Wadden Sea: competitive advantage over native mussels. PhD thesis, University of Kiel, Germany: 151pp

Diederich S, Nels G, van Beusekom JEE, Reise K (2005) Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers. *Helgol. Mar Res.* 59: 97-106.

Diederich S (2006) High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 328: 211-227.

Guy C, Roberts D (2010) Can the spread of non-native oysters (*Crassostrea gigas*) at the early stages of population expansion be managed? *Marine Pollution Bulletin* 60: 1059-1064, <http://dx.doi.org/10.1016/j.marpolbul.2010.01.020>

Drinkwaard A (1999) Introductions and developments of oysters in the North Sea area: a review. *Helgolander Meeresuntersuchungen* 52: 301-308.

DMI (2010) The Danish Meteorological Institute:
http://www.dmi.dk/dmi/vejret_i_danmark_-_vinteren_2009-2010 (In Danish)

Dutertre M, Beninger PG, Barille L, Papin M, Haure J (2010) Rising water temperatures, reproduction and recruitment of an invasive oyster, *Crassostrea gigas*, on the French Atlantic coast. *Marine Environmental Research* 69:1-9.

Eastwood S, Le Borgne P, Pére S, Poulter D (2011) Diurnal variability in sea surface temperature in the Arctic. *Remote Sensing of Environment*, Volume 115: 2594-2602.

Elston RA (1993) Infectious diseases of the Pacific Oyster, *Crassostrea gigas*. *Annual Review of Fish Diseases* 259 – 276.

Eno NC, Robin A, Sanderson CVG (1997) Non-native marine species in British waters: a review and directory. Joint Nature Conservation Committee Monkstone House, City Road Peterborough PE1 1JY UK.

Escapa M, Isacch JP, Daleo P, Alberti J, Iribarne O, Borges m, et al. (2004) The distribution and ecological effects of the introduce Pacific oyster, *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia. *Journal of Shellfish Research* 23:765–772.

Eschweiler N, Christensen HT (2011) Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. *Journal of Experimental Marine Biology and Ecology* 403: 90-95.

FAO 2005-2012. Cultured Aquatic Species Information Programme. *Crassostrea gigas*. Cultured Aquatic Species Information Programme. Text by Helm, M.M. In: FAO Fisheries and Aquaculture Department [online]. Rome.

Gentemann CL, Minnett PJ, Le Borgne P, Merchant CJ (2008) Multi-satellite measurements of large diurnal warming events. *Geophysical Research Letters*, 35, L22602.

Grizel H, Heral M (1991) Introduction into France of the Japanese Oyster (*Crassostrea gigas*). *J. Cons. Int. Explor. Mer* 47:399-403.

Groslier T, Christensen HT, Davids J, Dolmer P, Elmedal I, Holm MW, Hansen BW (in prep.) Status of the Pacific Oyster *Crassostrea gigas* (Thunberg, 1793) in the western Limfjord, Denmark – Five years of population development. *Aquatic Invasions*, in press.

Harding JM, Mann R (2006) Age and growth of wild Suminoe (*Crassostrea ariakensis*, Fugita 1913) and Pacific (*Crassostrea gigas*, Thunberg 1793) oysters from Laizhou Bay, China. *Journal of Shellfish Research* 25: 73-82.

Hayes K, Silwa C, Migus S, McEnnulty F, Dunstan P (2005) National priority pests: Part II-Ranking of Australian marine pests. *CSIRO Marine Research*.

Hellberg H, Mortensen S, Hernar I, Knutsen GH (2002) Resultater fra overvåknings- og kontrollprogrammet for parasittene *Bonamia ostreae* og *Marteilia refringens* i norske bestander av europeisk flatøsters (*Ostrea edulis* L.). *Norsk Veterinærtidsskrift* 114 (4): 395-399. (In Norwegian).

Hollander J, Blomfeldt J, Carlsson P, Strand Å (In prep.) The effects of the alien pacific oysters (*Crassostrea gigas*) on benthic infauna in Sweden.

Holm MW, Davids JK, Dolmer P, Holmes E, Nielsen TT, Vismann B, Hansen BW (In prep) Temporal and spatial development of a mussel bed inhabited by the invasive Pacific oyster, *Crassostrea gigas*, and the native Blue mussel, *Mytilus edulis*, in a sheltered intertidal area in the Limfjord.

Holm MW, Davids JK, Dolmer, P Holm-Hansen TH, Vismann B, Hansen BW (In prep.) Population development of the invasive Pacific oyster, *Crassostrea gigas*, and the native Blue mussel, *Mytilus edulis*, in a sheltered intertidal area in the Limfjord, Denmark.

IPCC Climate Change (2007) Synthesis Report An Assessment of the Intergovernmental Panel on Climate Change

Jensen RK, Knudsen J (2005) A summary of alien marine benthic invertebrates in Danish waters. *Oceanological and Hydrobiological Studies* 34 (Supl. 1): 137-162.

Kobayashi M, Hofmann EE, Powell EN, Klinck JM, Kusaka K (1997) A population dynamics model for the Japanese oyster, *Crassostrea gigas*. *Aquaculture* 149: 285-321.

Kockmann J, Buschbaum C, Volkenborn N, Reise K (2008) Shift from native mussels to alien oysters: Differential effects of ecosystem engineers. *JEMBE* 364 1-10.

Kristensen PS (1989) Mussel and oyster culture in Denmark. - In: N. De Pauw, E. Jaspers, H. Ackerfors, N. Wilkins (eds.) *Aquaculture - A biotechnology in progress*. European Aquaculture Society, Bredene, Belgium: 342-350.

ICES (2010) Report of the ICES Working Group on Introductions and Transfers of Marine Organisms (WGITMO), 10 - 12 March 2010, Hamburg, Germany. ICES CM 2010/ACOM:29. 130 pp.

ICES (2011) Report of the Working Group on Introduction and Transfers of Marine Organisms (WGITMO), 16 - 18 March 2011, Nantes, France. ICES CM 2011/ACOM:29. 180 pp.

Kristensen PS, Pihl NJ (2006) Blåmuslinge- og stillehavsostersbestandene i det danske Vadehav efteråret 2006. Book DFU-rapport nr. 167-06. Danmarks Fiskeriundersøgelser. [In Danish]

Kristensen SP, Pihl JN (2007) Blåmuslinge- og stillehavssøstersbestandene i det danske Vadehav efteråret 2007. DTU Aqua-rapport. 181-08: 33pp. [In Danish]

Kristensen PS, Pihl NJ (2008) Blåmuslinge- og stillehavssøtersbestandene i det danske Vadehav efteråret 2007. DTU Aqua-rapport nr. 181-08. Danmarks Tekniske Universitet, DTU Aqua. Institut for Akvatiske Ressourcer [In Danish]

Lasta M (2004) The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in Northern Patagonia. *The Free Library* (December, 1), [http://www.thefreelibrary.com/The distribution and ecological effects of the introduced Pacific...-a0130777663](http://www.thefreelibrary.com/The%20distribution%20and%20ecological%20effects%20of%20the%20introduced%20Pacific...-a0130777663) (accessed May 17 2013).

Leguerrier D, Niquil N, Petiau A, Bodoy A (2004) Modeling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France). *Marine Ecology Progress Series* 273: 147-162.

Lenihan HS (1999) Physical–biological coupling on oyster reefs: how habitat structure influences individual performance. *Ecological Monographs* 69:251–276.

Lejart M, Clavier J, Chauvaud L, Hily C (2012) Respiration and calcification of *Crassostrea gigas*: contribution of an intertidal invasive species to coastal ecosystem CO₂ fluxes. *Estuar Coast* 35:622-632.

Lejart M , Hily C (2011) Differential response of benthic macrofauna to the formation of novel oyster reefs (*Crassostrea gigas*, Thunberg) on soft and rocky substrate in the intertidal of the Bay of Brest, France. *J. Sea Res* 65: 84-93.

Lejart M, Clavier J, Chauvaud L, Hily C (2012) Respiration and Calcification of *Crassostrea gigas*: Contribution of an Intertidal Invasive Species to Coastal Ecosystem CO₂ Fluxes. *Estuaries and coasts*:1-11.

Leppäkoski E, Gollasch S, Olenin S (eds.) (2002) *Invasive Aquatic Species of Europe -Distribution, Impacts and Management.* - Kluwer, Dordrecht: 583 pp.

Lynch, SA, Abollo E, Ramilo A, Cao A, Culloty SC, Villalba A (2010) Observations raise the question if the *C. gigas*, *Crassostrea gigas*, can act as either a carrier or a reservoir of *Bonamia ostreae* or *Bonamia exitiosa*. *Parasitology* 137: 1515-1526.

Mann R, Burreson EM, Baker PK (1991) The decline of the Virginia oyster fishery in Chesapeake Bay: considerations for the introduction of a non-endemic species, *Crassostrea gigas*. *Journal of Shellfish Research* 10:379-388.

Markert A, Wehrmann A, Kroencke I (2010) Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions* 12: 15-32.

Meixner R, Gerdener Ch (1976) Untersuchungen über die Möglichkeiten einer Fortpflanzung der eingeführten Pazifischen Auster *Crassotrea gigas* in deutschen Küstengewässern. *Arch. FischWiss.* 26: 155-160.

Miossec L, Le Deuff RM, Goulletquer P (2009) Alien species alert: *Crassostrea gigas* (Pacific oyster). ICES Cooperative Research Report 299: 42 pp.

NIMPIS (2012) *Crassostrea gigas* general information, National Introduced Marine Pest Information System, viewed 14 August 2012 <<http://www.marinepests.gov.au/nimpis>>.

Mortensen SH (1993. A health survey of selected stocks of commercially exploited Norwegian bivalve molluscs. *Diseases of Aquatic Organisms* 16: 149-156.

Mortensen S, Skår CK, Harkestad LS, Einen ACB, Jelmert A (2011) Finnes det bonamiose i norske bestander av flatøsters, *Ostrea edulis*? *Norsk Veterinærtidsskrift* 123 (2): 67-73.(In Norwegian).

Nehls G, Diederich S, Thieltges DW, Strasser M (2006) Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? *Helgoland Marine Research* 60: 135-143.

Nehring S (1999) Oyster beds and Sabellaria reefs. In: De Jong, F., Bakker, J.F., van Berk, C.J.M., Dankers, N.M.J.A., Dahl, K., Gätje, C., Marencic, H. & Potel, P. (Eds.), Wadden Sea Quality Status Report. Common Wadden Sea Secretariat Wilhelmshaven, Wadden Sea Ecosystem No. 9: 146-147.

Nehring S (2003) Alien species in the North Sea: invasion success and climate warming. Ocean Challenge 13(3): 12-16.

Nehring S (2003) Pacific oysters in the European Wadden Sea - an irreversible impact in a highly protected ecosystem. Aliens 17: 20-21.

Nehring S (2006) NOBANIS – Invasive Alien Species Fact Sheet *Crassostrea gigas*, Online Database of the North European and Baltic Network on Invasive Alien Species - NOBANIS www.nobanis.org

Nehring S (2011): NOBANIS – Invasive Alien Species Fact Sheet – *Crassostrea gigas*. – From: Online Database of the European Network on Invasive Alien Species - NOBANIS www.nobanis.org, Date of access 31/01/2013.

Norling P, Lindegarth M, Lindegarth S, Strand Å (In prep) Ecological consequences of the establishment of the invasive Pacific oyster (*Crassostrea gigas*, Thunberg) on the Swedish west coast - effects on mobile epifauna and infauna.

Padilla DK (2010) Context-dependent Impacts of a Non-native Ecosystem Engineer, the *C. gigas Crassostrea gigas*. Integrative and Comparative Biology 50:213-225.

Peterson CH, Summerson HC, Thomson E, Lenihan HS, Grabowski JH, Manning L, Micheli F, Johnson G (2000) Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat. Bull. Mar. Sci. 66:759–774.

Philippart CJM, Anadón R, Danovaro R, Dippner JW, Drinkwater KF, Hawkins SJ, Oguz T, O'Sullivan G, Reid PC (2011) Impacts of climate change on European marine ecosystems: observations, expectations and indicators. Journal of Experimental Marine Biology and Ecology 400:52-69.

Posey MH, Alphin TD, Powell CM, Townsend E (1999) Use of oyster reefs as habitat for epibenthic fish and decapods. In: M. W. Luckenbach, R. Mann & J. A. Wesson (editors). *Oyster reef habitat restoration: a synopsis and synthesis of approaches*. Virginia Institute of Marine Science Press, Gloucester Point, USA, pp 229-237.

Quayle DB (1988) Pacific oyster culture in British Columbia. Canadian Bulletin of Fisheries & Aquatic Sciences 218:241.

Ren JS, Ross AH, Schiel DR (2000) Functional descriptions of feeding and energetics of the Pacific oyster *Crassostrea gigas* in New Zealand. - Marine Ecology Progress Series 208: 119-130.

Reise K (1998) Pacific oysters invade mussel beds in European Wadden Sea. Senckenbergiana Maritima 28: 167-175.

Reise K, Gollasch S, Wolff WJ (2002) Introduced marine species of the North Sea coasts. In: Leppäkoski, E., Gollasch, S., Olenin, S. (Eds), *Invasive aquatic species of Europe. Distribution, impacts and management*. Kluwer Academic Publ, Dordrecht, 260-266.

Reise K, Dankers N, Essink K (2005) Introduced species. In: Essink K, Dettmann C, Farke H, Laursen K, Lu'erßen G, Marencic H, Wiersinga W (eds) Wadden Sea quality status report 2004. Common Wadden Sea Secretariat, Wilhelmshaven, pp 155–161.

Reise K, Olenin S, Thieltges DW (2006) Are aliens threatening European aquatic coastal ecosystems? Helgol Mar Res 60: 77-83.

Reise K, van Beusekom J (2008) Interactive effects of global and regional change on a coastal ecosystem. Helgoland Marine Research, 62: 85-91.

- Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of Non-Native Oysters: Ecosystem Effects and Restoration Implications. Annual Review of Ecology, Evolution, and Systematics 36: 643-689.
- Sabine CL, Feely RA, Gruber N et al. (2004) The oceanic sink for anthropogenic CO₂. Science, 305, 367–371.
- Seaman MNL (1985) Ecophysiological investigations on the oyster, *Crassostrea gigas*, in Flensburg fjord. - Veröff. Inst. Küst. Binnenfisch., Hamburg Bd. 89: 71 pp.
- Segarra A, Pepin JF, Arzul I, Morga B, Faury N, Renault T (2010) Detection and description of a particular Ostreid herpesvirus 1 genotype associated with massive mortality outbreaks of Pacific oysters, *Crassostrea gigas*, in France in 2008. Virus Research 153: 92-99.
- Shatkin G, Shumway SE, Hawes R (1997) Considerations regarding the possible introduction of the Pacific oyster (*Crassostrea gigas*) to the gulf of Maine: A review of global experience. Journal of Shellfish Research 16: 463–477.
- Strand Å, Waenerlund A, Lindegarth S (2011) High Tolerance of the Pacific Oyster (*Crassostrea gigas*, Thunberg) to Low Temperatures. Journal of Shellfish Research 30:733-735.
- Strand Å, Blanda E, Bodvin T, Davids JK, Jensen LF, Holm-Hansen TH, Jelmert A, Lindegarth S, Mortensen S, Moy FE, Nielsen P, Norling P, Nyberg C, Christensen HT, Vismann B, Holm MW, Hansen BW, Dolmer P (2012) Impact of an icy winter on the *C. gigas* (*Crassostrea gigas* Thunberg, 1793) populations in Scandinavia. Short communication: Aquatic Invasions 7 (3): 433-440.
- Thorstensson T, Björnsson H (2011) Climate Change and Energy Systems - Impacts, Risks and Adaptation in the Nordic and Baltic countries. TemaNord report 502
- Tolley S G, Volety AK (2005) The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. Journal of Shellfish Research 24: 1007-1012.
- Troost K (2010) Causes and effects of a highly successful marine invasion: Case-study of the introduced *Crassostrea gigas* in continental NW European estuaries. Journal of Sea Research 64:145-165.
- Van Broekhoven W (2005) Macrofaunal diversity on beds of the Pacific oyster (*Crassostrea gigas*) in the Oosterschelde estuary. MSc thesis, 36 pp.
- Vismann B, Davids JK, Dolmer P, Holm MW, Blanda E, Christensen HT, Nielsen P, Hansen BW (Submitted) *In situ* clearance rate and carbon removal by co-occurring populations of Pacific oysters.
- Wang J, Christoffersen K, Buck S, Tao Y (2007) The Pacific oyster (*Crassostrea gigas*) in the Isefjord, Denmark. - Student report, Roskilde University, Department of Environmental, Social and Spatial Change, June 2007: 49 pp.
- Wehrmann A, Schmidt A (2005) Die Einwanderung der Pazifischen Auster in das Niedersächsische Wattenmeer. - Report WWF Frankfurt/M.: 26 pp.
- Wehrmann A, Herlyn M, Bungenstock F, Hertweck G, Millat G (2000) The distribution gap is closed—first record of naturally settled Pacific oysters *Crassostrea gigas* in the east Frisian Wadden Sea, North Sea. Senckenbergiana Marit. 30: 153–160.
- Wilsman JWM, Dubbeldam M, De Kluijver MJ, van Zanten E, van Stralen M, Smaal AC (2008) Wegvisproef Japanse oesters in de Oosterschelde. Eindrapportage. Wageningen IMARES.
- Wolff WJ, Reise K (2002) Oyster imports as a vector for the introduction of alien species into northern and western European waters. - In: Leppäkoski, E., Gollasch, S. and Olenin, S. (eds.), Invasive aquatic species of Europe. Distribution, impacts and management. Kluwer, Dordrecht: 193-205.

Wrangé AL, Valero J, Harkestad LS, Strand Ø, Lindegarth S, Christensen HT, Dolmer P, Kristensen PS, Mortensen S (2010) Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. Biological Invasions, 12 (5):1145- 1152 (DOI : 10.1007/s10530-009-9535-z).

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