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Research Article

Effects of a bio-invasion of the Pacific oyster, *Crassostrea gigas* (Thunberg, 1793) in five shallow water habitats in Scandinavia

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Abstract

Management of invasive species is addressed in both national and international regulations regarding the protection of marine habitats and biodiversity and in regulations of aquaculture. The geographical range of the invasive Pacific oyster, *Crassostrea gigas*, is expanding, both through human mediated vectors and by natural dispersal. The species is now spreading in Scandinavia. In order to optimize the management of the oyster, including targeted monitoring and mitigation activities, knowledge on the present and future distribution and impact on the ecosystem is important. The development of the population and the potential impacts on native ecosystems were analyzed, based on the present scientific knowledge on the distribution in Scandinavia, data on new settlements and existing literature. Data was first evaluated by 14 experts (including the authors) during a workshop, relating the current status of habitats where Pacific oysters are found in Scandinavia (Low energy rock, Littoral sand and mudflats, Littoral biogenic reefs, Sublittoral sand and Sublittoral biogenic reefs) to a predicted development, thereafter assessed in relation to impact on the habitats. The assessment was done as a function of climate change in a long-term IPCC climate scenario (A1B). We conclude that Littoral biogenic reefs are at risk to obtain the highest expected increase, while all other habitats are at risk of low to moderate development of the oyster populations. Accordingly, Littoral Biogenic reefs was assessed as the habitat type at risk of the largest ecosystem effects as high densities of oysters already exist in these areas, and the densities are expected to increase rapidly until reaching a threshold density. Low energy rock and Littoral sand and mud were assessed as being subjected to moderate to high ecosystem effects. Sub-littoral sand and Sub-littoral biogenic reefs were assessed as currently being at risk of moderate ecosystem effects as there are low densities of oysters in these habitats, although densities in sublittoral biogenic reefs has the potential to increase. We discuss management and mitigation strategies based on the forecasted development and effects of the Pacific oyster populations.

Key words: invasion, climate, habitats, ecosystem effects, management

Introduction

Invasive species may have serious impacts on ecosystems and may alter biodiversity or other goods and services from the ecosystems (Mooney and Cleland 2001; Mooney et al. 2005; Ruesink et al. 2005; Laugen et al. 2015). In order to protect native biodiversity and ecosystem services, and to minimize and mitigate the human health or economic impacts that these species can have, the EU-Commission decided on a new regulation of invasive species in 2014. The EU Regulation 1143/2014 on invasive alien species entered into force on 1 January 2015, and includes three types of interventions; 1) prevention, 2) early detection 3) rapid eradication and management. In order to implement these regulations in a management plan and achieving efficient and economic interventions, there is a need for detailed information on the risk of dispersal to different habitat types and expected impact on these habitats.

The Pacific oyster (*Crassostrea gigas*) is an invasive species which has been widely dispersed, both intentionally (for aquaculture) and unintentionally and now has an almost worldwide distribution (Ruesink et al. 2005). The species originates from Japan and southern China, where it inhabits shallow water habitats (Nehring 2011; Miossec et al. 2009). In Europe, the Pacific oyster was introduced for aquaculture to the Netherlands in 1964 (Smaal et al. 2009), and during the following years to France, Germany, The British Isles, Denmark, Sweden, and finally in 1979 to Norway (Eklund et al. 1977; Grizel and Héral 1991; Humphreys et al. 2014; Strand and Vølstad 1997; Troost 2010). Several assessments and reviews concluded that water temperatures in Northern Europe were too low for reproduction (Drinkwaard 1998; Miossec et al. 2009). These assumptions proved to be wrong. The Pacific oyster has a high phenotypical plasticity, and self-sustaining populations gradually established in new areas. In Sweden and Norway, the colonization occurred late, with populations developing rapidly around 2006 (Wrange et al. 2010; Strand and Lindegarth 2014; Laugen et al. 2015). It has been observed that the Pacific oyster can establish populations in a wide variety of habitat types, e.g. hard substrates, sandy or muddy areas where they attach to small stones, shell fragments or other debris (Dolmer et al. 2014; Strand and Lindegarth 2014), on conspecifics, forming reef-like structures at high densities, or on other bivalve species.

The coastal environment in Denmark, Sweden and Norway where the oysters have established differ significantly. In Denmark, the oysters are often found at variable densities over vast soft bottom tidal areas. In Sweden and Norway, such environments are rare. The oyster populations therefore display a patchier distribution and can be found at varying densities in small bays, narrow sounds and similar environments with good water circulation (Strand et al. 2012), and often in areas with soft bottom. Exposed or sandy areas do not seem to be favored habitats (Strand and Lindegarth 2014), as oysters are commonly found in intertidal and shallow sub-tidal zones down to a depth of about 3 meters, in some areas overlapping native, flat oyster (*Ostrea edulis*) beds (Bodvin et al. 2014; Strand and Lindegarth 2014). In sheltered micro-tidal areas with reduced water circulation a reduced population growth has been observed (Groslier et al. 2014; Holm et al. 2015) which may be due to food limitations (Holm et al. 2016; Vismann et al. unpublished data).

A hazard ranking of different species from invaded to pristine bioregions identified the Pacific oyster as a "medium priority species", having a high invasion potential or impact when established in a new area (see Hayes et al. 2005). In the Wadden Sea, Oosterschelde and in Scandinavian waters, the Pacific oyster changes the ecosystem. In the Wadden Sea the Pacific oysters primarily settle on established blue mussel beds (Reise 1998; Nehring 1999; Diederich et al. 2005; Nehls et al. 2009). The settlements have influence on native bivalve populations (Nehring 2003; Diederich et al. 2005; Nehls et al. 2009; Kochmann et al. 2008; Troost 2010) with cascade effects on mussel-eating birds such as eider ducks and oystercatchers (Wolff and Reise 2002; Diederich et al. 2005; Wehrmann and Schmidt 2005; Markert et al. 2013; Waser et al. 2016) and modifications of the original form and function of the ecosystem (see e.g. Ruesink et al. 2005; Troost 2010; Hollander et al. 2015; Norling et al. 2015).

Reise et al. (2006) described four invasion phases. In the first phase, 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 increases in density and may change the habitat (Phase 3). Once established in the habitat, other species such as predators, competitors and/or diseases/parasites may reduce the density of the invasive species in an adjustment phase (Phase 4), potentially reducing, or altering, the effects of the non-native species on the ecosystem. The effects on the ecosystem may thus differ as the invasion progresses.

The time oysters need to establish in new areas, and the dynamics of the invasion phases, are rather unpredictable (Holm et al. 2015). The process is presumably related to the dynamics of climate change, leading to optimal summer periods where both temperature, photoperiod (in the northern distribution area) and availability of suitable phytoplankton are key factors (Fabioux et al. 2005; Thomas et al. 2015). Additionally, a genetic adaptation to north European conditions has recently been proposed (Sussarellu et al. 2015).

Different habitats are to variable degrees susceptible to establishment and population expansion, and establishment in different habitats will affect the native community in different ways. The northwards expansion in Scandinavia is recent (Wrange et al. 2010). Knowledge on local habitat preferences and predictions of what environments may be colonized, as well as knowledge on the effects of the establishment in different coastal habitats, is crucial for the development of suitable management strategies.

By using existing scientific literature and experts' judgments we have analyzed the further establishment of populations of Pacific oysters in Scandinavia, and the potential impact on the ecosystems, with the objectives to:

1. Identify the habitats at risk for an expansion of Pacific oyster populations, and which habitat types that are expected to support the largest oyster densities. This information supports the development of efficient management of these habitats.
2. Identify the factors that are most important for predicting future establishment in Scandinavia. This knowledge may support the development of efficient programs for monitoring and estimating the risk of invasions.
3. Discuss mitigation as important elements in the management strategies.

Methods

During a workshop in April 2012 with the participation of 14 experts linked in a Scandinavian network project on Pacific oysters in Scandinavia (including the authors), different aspects of both invasion biology and ecology were combined, in order to identify habitats at risk for future expansion of the oyster population and factors that are most important for predicting future expansion. We used expert judgments in a consensus roundtable process (Dolmer et al. 2014). The use of expert judgement is in a context of management an accepted methodology that allow filling out gaps of missing knowledge in a systematic process (Wittmann et al. 2015). A knowledge platform was discussed and agreed upon, and the impacts on different habitats were thereafter evaluated based on different climate scenarios developed by the United Nations' Intergovernmental Panel on Climate Change (IPCC), in order to forecast the future development and effects of a bio-invasion.

Identification of invaded habitat types and habitats at risk of invasion

The assessment of which types of habitats that have already been colonized, or might be colonized during a future expansion, was performed based on the European Nature Information System for habitat classification (EUNIS); Habitats class A: Marine habitats (Davies et al. 2004). Five subgroups of habitats (A3 Infralittoral rock and other hard substrata, A4 Circalittoral rock and other hard substrata, A6 Deep-sea bed, A7 Pelagic water column and A8 Ice-associated marine habitats) were identified as unsuitable for oysters due to habitat depth (A4 and A6) or lack of substrate (A7 and A8). Based on the EUNIS habitat descriptions for A3 (Atlantic and Mediterranean habitats), the habitats were assessed as unsuitable for oysters due to exposure (too high or too low), and habitat characteristics (presence of kelp). Three subgroups (A1 Littoral rock and other hard substrata, A2 Littoral sediment and A5 Sublittoral sediments) were evaluated further. Of these, based on exposure levels, substrate characteristics and description in the EUNIS classification, the following classes were considered the most important present or potential habitats for Pacific oysters in Scandinavia; A1.3 Low energy rock, A2.2 Littoral sand and muddy sand, A2.7 Littoral biogenic reefs, A5.2 Sublittoral sand, and A5.6 Sublittoral biogenic reefs. National surveys in Denmark, Sweden and Norway show that Pacific oysters in Scandinavia thrive in high energy areas (i.e. sheltered from wave action but with high tidal fluctuations and/or strong currents) (Wrange et al. 2010; Strand et al. 2012; Dolmer et al. 2014; Strand and Lindegarth 2014). Therefore, habitat types were separated in high and low energy habitats. Only high energy areas in the selected habitats were included in the further analysis.

Selection of climate scenario

Different scenarios of global development in use of fossil-energy and development of new non-fossil technology have been developed by IPCC (Philippart et al. 2011), and the development in the concentration of greenhouse gases (CO_2, CH_4, N_2O and F-gases) and global surface temperature until 2100 have been estimated. In the present study, the assessments were performed using a long-term climate scenario (IPCC Scenario A1B, IPCC 2007). In the A1B scenario a global surface warming of 2.8 °C is expected, ranging from 1.7 to 4.4 °C. It assumes a future world of strong economic growth, global population that peaks in mid-century (2050) and declines after 2100. A significant introduction of new and more efficient technologies will take place in a balance between fossil and non-fossil energy-sources. In a scenario with strong economic growth based on non-fossil growth, the global surface warming can be reduced to 2.4 °C (Scenario A1T). The scenario is exceeding the temperature maximum increase decided at the COP 21 meeting in Paris 2015. Here the target was to hold the increase in the global average temperature to below 2 °C above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5 °C above pre-industrial levels (FCCC/CP/2015/L.9/Rev.1).

Table 1. Effects on population development and on native ecosystems of the establishment of the Pacific oyster, *Crassostrea gigas*, in 5 habitats, classified according to the EUNIS system (Davies et al. 2004): Low energy rock, Littoral sand and mud, Littoral biogenic reefs, Sublittoral sand and Sublittoral biogenic reefs. The effect was evaluated in a long-term climate scenario (IPCC, Scenario A1B (2.5-3.0° increase in air temperature and decrease in pH at -0.25) (IPCC 2007). The impacts on the population development (production, survival and larval stages) are graded, where + and ++ indicate a positive or strong response in relation to bio-invasibility, 0 indicates no response, and – and – – indicate a negative response. The sum of the ratings indicates the risk of a bio-invasion of the evaluated habitat. The lower row refers to the estimated impact on the habitat, adapted from the risk assessment report by Dolmer et al. (2014). M=moderate, H=high.

	Habitats		**A1.3 Low energy rock**	**A2.2 Littoral sand and mud**	**A2.7 Littoral biogenic reefs**	**A5.2 Sublittoral sand**	**A5.6 Sublittoral biogenic reefs**
	Phase	**Factor**					
Population development	a) Densities and growth	Growth	++	++	++	+	+
		Access to food	0	0	-	0	-
		Population density	+	+	++	+	++
	b) Survival of spat and adults	Diseases	--	--	--	-	-
		Winter survival	+	+	+	0	0
		Predation: birds	-	-	0	0	0
		Predation: invertebrates	-	-	0	-	0
	c) Larvae production and survival	Larval production	++	++	++	+	+
		Larval survival - pH	-	-	-	-	-
		Larval survival- predation	0	0	0	0	0
		Substrate availability	+	+	++	+	++
	Risk of bioinvasion		2	2	6	1	4
	Potential impact on the habitat		M/H	M/H	H	M	M

Definition of factors influencing the establishment of Pacific oysters

Definition of factors having the largest influence on the continued development of the establishment in Scandinavia, were based on existing scientific literature and expert judgments during the workshop (Dolmer et al. 2014). Factors having a major influence on the future population development in Scandinavia were identified as:

A. Habitat type (substrate, exposure, current conditions, depth and nutrient availability)

B. Population development, which was further subdivided into;

   i. Oyster densities and growth (density, growth and access to food)

   ii. Survival of spat and adults (diseases, winter mortality, bird and invertebrate predation)

   iii. Larvae production and survival (larval production/fecundity, larval survival-pH and predation, and substrate availability)

Each aspect within B:i to B:iii was assessed as having a moderate or strong positive effect (+ or ++, respectively), no effect (0) or moderately or strong negative effect (- or --, respectively) on the oyster population development (Table 1). The resulting net effect was calculated for each habitat and indicates the risk of a bio-invasion of the evaluated habitat.

Results and discussion

Factors influencing the establishment of Pacific oysters

Densities and growth (B:i)

Temperature is likely to be a key parameter, based on its importance for recruitment, growth and survival of Pacific oysters. The IPCC scenarios were investigated in relation to the global socio-economic development from 1992 to 2010 by comparing observed and projected levels of global emission intensity of CO_2 and fossil fuel CO_2 (Pretis and Roser 2016). Their analysis shows that IPCC scenario A1B may under-estimate the emission of CO_2 in 2100. The analysis of risk of bio-invasion of Pacific oysters then represents a conservative evaluation. In the process of assessing the expansion and effects of oyster establishment on the identified habitats, there are various degrees of uncertainty linked to each parameter or effect. Assuming a continued emission of greenhouse gas at or above the current rate, it is suggested that a temperature increase of 2 °C could be expected in the NE Atlantic in 2090, 1–3 in the North Sea and 2 to 4 °C in the Baltic (Philippart et al. 2011; Schrum et al. 2016). In general, an increased growth rate can be expected based on increased temperatures, but as temperature will vary with depth and exposure (van Aken 2008; Dutertre et al. 2010), growth rates in the two sublittoral habitats can be expected to be less affected by climate change than in the three shallow habitats.

In general, an increase of Pacific oysters can be expected in Scandinavia in the coming years. As Pacific oyster larvae are attracted to bivalves and conspecifics (Kochmann et al. 2008; Wilkie et al. 2013; Laugen et al. 2015), areas with biogenic reefs may be more attractive for settling larvae than bare substrates, favoring the oyster population development in areas dominated by biogenic reefs.

Survival of spat and adults (B:ii)

High temperatures may also favor the propagation of pathogens, and lead to negative effects on the development of the oyster populations, as in the case with the summer mortalities experienced after the warm summer of 2014 (Petton et al. 2013; Mortensen et al. 2016). Although temperature is expected to increase in both intertidal and subtidal areas, the negative effects of pathogen attacks on the oyster population development in shallow areas may be more pronounced, both as a result of a greater magnitude of temperature change, additional stress caused by more unstable abiotic conditions, and a potentially higher prevalence of pathogens in surface waters.

In addition, extreme low temperatures may influence the population dynamics by exposing bivalves in the littoral zone to high winter mortalities, which could temporarily reduce the populations (Büttger et al. 2011; Strand et al. 2012). Higher winter temperatures may reduce winter mortality, thereby causing a positive effect on the population development, but mainly in the shallow, protected areas. In sublittoral habitats, the winter mortality has never been very high due to little ice formation, which is believed to be the primary reason for winter mortalities, as the Pacific oyster tolerate sub-zero temperatures (Strand et al. 2011).

Predation might also act as a regulating factor on the population development (Markert et al. 2013). In the Wadden Sea, large number of waterfowls such as eider ducks (*Somateria molissima*) and oystercatchers (*Haematopus ostralegus*) depend on blue mussels, *Mytilus* spp. as a food resource (Scheiffarth et al. 2007; Laursen et al. 2010). There are indications that birds already have developed techniques for exploiting the new food resource (Cadée 2008a, 2008b), herring gulls (*Larus argentatus*) by dropping oysters onto the rocks to crack the shells, and oystercatchers (*H. ostralegus*) mainly by feeding on weakened and dead, gaping, individuals. The negative effects on the oyster population development of bird predation can be expected to be most pronounced in littoral habitats, although the success of predators in biogenic reefs may be restricted due to reduced predation efficiency in aggregations of bivalves (Bertness and Grosholz 1985; Okamura 1986; Lin 1991; Cadée 2008b; Casey and Chattopadhyay 2008). The extent to which birds will use Pacific oysters as an alternative food source needs further study (Diederich et al. 2005; Wehrmann and Schmidt 2005), but based on the recent development, the predation can be expected to increase.

In European coastal areas there are two main invertebrate predators on shellfish, the shore crab (*Carcinus maenas*) and the common starfish (*Asterias rubens*) (Dare et al. 1983; Troost 2010). It is known that the common starfish predates on different kinds of bivalves and may cause damage on wild and cultivated oyster beds (Hancock 1955; Allen 1983). Shore crabs prey on juvenile bivalves, including Pacific oysters, to the extent that it has been considered a pest for fisheries (Walne and Davies 1977). Both the shore crab and the common starfish are abundant in Scandinavia, and share the same habitats as the Pacific oyster. In prey choice experiments, both crabs and starfish in Scandinavia have been observed to feed equally intense on oysters as on blue mussels if oysters were the sole prey item offered, but to prefer blue mussels if given a choice (Strand Å. own observation.). The effects of predation on the development of the oyster population needs further quantification, but may at this stage be considered to have a low, negative impact on population development. As crabs can feed also on clutched spat (spat attached to larger shells or other structures, (Krantz and Chamberlin 1978), no differences in predation is expected between hard and soft substrates. However, as in the case with bird predation, the oysters may find refuge in dense aggregations of oysters, thus a lower predation pressure per prey item can be expected on bivalve beds.

Larvae production and survival (B:iii)

Pacific oysters have early maturation and large reproduction output potential (Troost 2010) and are long lived (Nehring 2011). Sexual maturation and spawning of oysters are temperature dependent and will vary depending on local summer temperatures, with high summer water temperatures supporting high recruitment (Diederich et al. 2005). Due to effects of solar heating, the temperature will rise higher at a littoral habitat than at a sublittoral habitat (van Aken 2008; Mortensen et al. 2016), and the positive effects on the oyster population development of future increases in temperature may therefore be more pronounced in shallow areas.

Newly settled spat show high survival in Scandinavia (Fomsgaard and Petersen 2015), and the bottleneck for a further establishment in northern areas may therefore be in the larval phase. A direct impact of increased concentrations of carbon dioxide in the atmosphere is ocean acidification, where the pH of the ocean lowers as the carbon dioxide is absorbed by the ocean. This might to be a threat to bivalves, changing the population dynamics and physiological responses of bivalves (Gazeau et al. 2007; Lannig et al. 2010). A general decrease in larval survival in all habitats is therefore expected, affecting population development negatively.

Larvae survival is also affected by predation, for example larviphagy by conspecifics (Troost 2009). Although higher densities of oysters may cause a reduced survival of oyster larvae through larviphagy, this reduction is likely to be well compensated by the increased number of larvae available. No major changes in larval mortality is therefore expected.

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. Formation of biogenic reefs may thus have strong positive effects on the oyster population development. In addition, an increased settlement on bare rock observed on the Norwegian coast in 2015 (Bodvin and Jelmert 2016), shows that there will probably be no substrate limitation on low energy rock. Due to the expected increase in oyster populations and the broad variety of substrates used by the species, substrate availability is predicted to increase.

Overall risk of bio-invasion and potential impact on the habitat structure

The potential effects of changing climatic conditions on the factors controlling population development identified by the expert panel were used to evaluate the likelihood of a bio-invasion in Scandinavia occurring in the selected marine habitats (Table 1). We hypothesize that the further expansion of the Pacific oyster in Scandinavia will be influenced by climate, habitat availability, a number of ecological factors in the recipient ecosystems, as well as the adaptation of the oyster to new environments. In areas where the oysters build up biogenic reefs, available substrates will gradually increase.

Based on the present knowledge, we have identified five different habitats as suitable for Pacific oysters in Scandinavia. Littoral biogenic reefs were found to be at risk of the highest expected increase in Pacific oysters, and the habitats Low energy rock, Littoral and sublittoral sand and mud and sublittoral biogenic reefs at risk of low to moderate development of the oyster populations. Accordingly, Littoral Biogenic reefs was assessed as the habitat type at risk of the largest ecosystem effects caused by the oyster population development, followed by Low energy rock and Littoral sand and mud. For Sub-littoral sand and Sub-littoral biogenic reefs, moderate ecosystem effects of an establishment can be expected, although oyster densities in sub-littoral biogenic reefs has the potential to increase rapidly.

The coastal currents, as well as local hydrodynamic conditions in fjord areas, will determine the dispersal of larvae. The dispersal of Pacific oysters observed in Scandinavia since 2006 is considered a consequence of local spawning events and of a northward drift of larvae (Wrange et al. 2010; Laugen et al. 2015). Settling of larvae in suitable habitats has led to the establishment of small populations that may again become source populations and contribute to the dispersal of the species through a stepping stone pattern. The dynamic of the northwards expansion is to some degree unpredictable, influenced by climate change and food availability (as proposed by Thomas et al. 2015 and Holm et al. 2015), and dependent on the adaptation of the newly established populations to reproduce under new, and local, conditions (Sussarellu et al. 2015).

The long-lived individuals, high reproductive potential and high survival of spat and adults enables favorable years to be stored in the form of strong year classes. Therefore, local population development is expected to occur in steps, as years with favorable conditions for survival in the larval phase will produce these strong year classes. It may also enable establishment of populations in areas where average conditions are unfavorable for larval survival, as long as events with favorable conditions for recruitment occur at an interval that is shorter than the generation time of the populations. Evidence of this is provided by Cardoso et al. (2007), who showed that northern populations of Pacific oysters have a larger reproductive output than southern populations, and by Sussarellu et al. (2015) who demonstrated that the population of Pacific oysters in the Limfjord (Denmark) have a females-biased sex-ratio.

Recent niche modelling of the Pacific oyster in Scandinavia highlights the continued, and increasing, habitat suitability for the species in the region (Laugen et al. 2015). Although the analyses were performed at different resolution, Laugen et al. (2015) using general habitat suitability, and our study as a response of specific habitat suitability to predicted climate change, our results are in accordance. Complementary to the results presented by Laugen et al. (2015), we have identified both an increased habitat suitability for oysters in the future and also which specific habitats will be most affected, and why. Biogenic reefs were for example identified as "hot spots" for Pacific oyster populations, mainly as a consequence of the increased availability of substrate and larvae in high density areas. Such information is valuable, as this habitat type is clearly more urgently in need of management compared to for example sublittoral sand habitats.

Ecosystem effects

The Pacific oyster is considered an ecosystem engineer (Jones et al. 1994), with the ability to modify its habitat by creating solid reef structures. In the Wadden Sea, Pacific oyster beds have rapidly developed into solid reefs at several sites, significantly impacting the form and function of the habitats (Kochmann et al. 2008; Markert et al. 2010). Development of reefs may significantly change the structure and complexity of the habitat. The formation of oyster reefs on soft and sandy substrates lead to much stronger changes in substrate modification and habitat complexity than reefs forming on hard bottoms, and will therefore have more pronounced effects on local biodiversity. Emerging oyster reefs will eventually replace soft-bottom communities with hard-substrate communities (Troost 2010). The effects of oysters on the ecosystem may also be density dependent (Green and Crowe 2013), with increasing effect with increasing oyster densities.

Of the habitat types identified as suitable oyster habitats in Scandinavia in this study, the greatest ecological effects can thus be expected to arise in biogenic reefs, especially in intertidal areas, while Low energy rock and subtidal sandy substrates may be less affected, mainly due to habitat characteristics (hard bottom) or oyster expansion potential (subtidal sandy sediments). Identification of where the largest effects on the ecosystem form and function will occur, are important in order to support the development of efficient management strategies.

Management

A high population density of Pacific oysters call for a management regime that balance protection of biodiversity and exploitation of the resource and the socio-economics of coastal aquaculture and fishing communities (Herbert et al. 2016). Based on the recent years' development Scandinavia, it is evident that the species will not disappear due to natural mortality events (Strand et al. 2012; Mortensen et al. 2016). Eradication of established invasive species has been proven notoriously difficult (Cardigos et al. 2015; Shine 2015), and focus should therefore be directed towards management and mitigation in specific areas, and targeting specific species of interest. Adequate and research-based mitigation strategies are therefore important elements in management strategies of the Pacific oyster in Scandinavia. Predictions of the effects of the establishment and up-dated information on the dynamics of the affected ecosystems may be used to develop site-specific strategies for conservation.

Today, the *de facto* strategy in Scandinavia is to accept the establishment of the Pacific oyster, including the formation of reef habitats as an integrated part of the marine ecosystems. An alternative strategy for conservation that is being tested is the control of oyster density in defined areas, like marine protected areas and public beaches. In the Dutch Wadden Sea, an experiment with removal of substrates for Pacific oysters was carried out in 2006 (Wijsman et al. 2008): In a 500.000 m^2 tidal flat area, the reef structures were removed with a mussel dredge. It took approximately 20 hours to remove oyster reefs from 10.000 m^2, but not all oysters were removed. Due to new recruitment, the dredging process should be repeated every 3–6 years. The results suggest that control of oyster reefs can only be implemented in limited areas, is a continuous process, and is an expensive strategy.

Manual destruction as a method for reducing the development and dispersal of 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 cold winter 2009/2010 at some locations in Sweden, the method may however be considered a possibility. Extreme winter conditions or summer mortality events causing high mortalities therefore offer a unique opportunity for management of Pacific oyster populations which before had reached moderate densities.

Presently, a recent initiative to control the occurrence of Pacific oysters in Norwegian marine national parks has been launched. In this campaign, initiated by the County governor, non-profit associations are invited to apply for voluntary work in specific areas, which they will then rid of Pacific oysters, which will be placed in waste containers and transported to a waste facility. The selected associations will receive economic compensation for the performed service. Such non-commercial handpicking may locally limit the formation of dense populations, however only a part of the local populations is removed, as small specimens are often overlooked. Thus such attempts may reduce the environmental impact of the establishment, but must be performed repeatedly with regular intervals.

In Norway and Sweden, the rights of the landowner of the coastline regulate private handpicking, causing legal constraints on governmental mitigation initiatives. In Denmark, handpicking is legal, and may be of local importance, and commercial fishing and picking is allowed in the Limfjord.

In 2014, the possibility to start up a commercial dredge-fishery was examined in the Wadden Sea; however, it proved unsuccessful due to low density and quality of the oysters in the northern part of the Danish Wadden Sea. Investigations in other parts of the Wadden Sea may however demonstrate a potential for a commercial fishery. In the Netherlands, a commercial fishery and bottom culture production of Pacific oysters has developed and the production was MSC certificated in 2012. This exploitation of wild Pacific oyster populations in combination with culture demonstrates the possibility of combining a control strategy with commercial fisheries, thereby increasing the economic incentives for the industry to engage in nature restoration and preservation.

Conclusions

Due to its potentially significant effect on the environment, it is useful to predict the susceptibility of different habitat types to a bio-invasion and identify potential effects of Pacific oysters on the ecosystem. At the present stage, it is important to follow the dynamics of the Scandinavian populations. A mitigation of invasive species should prioritize a control strategy in Scandinavian coastal waters targeting areas with the highest risk for a bioinvasion that change the natural habitats, for example biogenic reefs as identified in this study. In low energy habitats, as Low energy rock, the Littoral sand and mud and the Sub-littoral sand, a strategy should include a monitoring program that allows an early implementation of a control program in order to detect if a local population change to an expansive phase of invasion and calls for an effort to reduce density.

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