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INVASION NOTE

Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia

Anna-Lisa Wrange · Johanna Valero · Lisbeth S. Harkestad · Øivind Strand · Susanne Lindegarth · Helle Torp Christensen · Per Dolmer · Per Sand Kristensen · Stein Mortensen

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Abstract The Pacific oyster (*Crassostrea gigas*) is an important aquaculture species world-wide. Due to its wide environmental tolerance and high growth rate, it has also become a successful invader in many areas, leading to major ecosystem changes. Low water temperatures were previously believed to restrict the establishment of Pacific oysters in Scandinavia. However, recent surveys reveal that the Pacific oyster is now established in many areas in Scandinavia. The biomass of oysters in the Danish Wadden Sea has increased dramatically between 2005 and 2007, large numbers were observed along the Swedish west coast from settlement in 2006, and in Norway, populations are established along the southwest coast to 60°N.

Keywords *Crassostrea gigas* · Invasive species · Spreading · Recruitment · Scandinavia · Water temperature

A.-L. Wrange · J. Valero · S. Lindegarth
Department of Marine Ecology, Göteborg University, Sven Lovén Centre for Marine Sciences Tjärnö, 45296 Strömstad, Sweden

L. S. Harkestad · Ø. Strand · S. Mortensen (✉)
Institute of Marine Research, P.O. Box 1870, 5817 Nordnes, Bergen, Norway
e-mail: stein.mortensen@imr.no

H. T. Christensen · P. Dolmer · P. S. Kristensen
Technical University of Denmark, National Institute of Aquatic Resources, 2920 Charlottenlund, Denmark

Introduction

The Pacific oyster, *Crassostrea gigas*, (Thunberg 1793) originates from East Asia. It has been imported to shellfish producing areas all over the world and has become one of the world's main aquaculture species (FAO 2007). Many introduced stocks have established permanent and self-sustaining populations in the wild (Ruesink et al. 2005). The Pacific oyster is considered adaptable and even invasive, and may compete with local bivalve species for space and food (Diederich 2005, 2006; Krassoi et al. 2008). It can also build aggregates or reefs, which trap sediment and restrict water movement in shallow areas (Ruesink et al. 2005). This may have consequences for local biodiversity, leading to changes of the entire littoral ecosystem (Cognie et al. 2006; Markert et al. 2009).

The Pacific oyster is already locally abundant in the Dutch, German and Danish Wadden Sea (Diederich et al. 2005; Cardoso et al. 2007). A recent study suggested that this species has not yet reached its ecophysiological limits, and thus may expand further (Cardoso et al. 2007). In this paper, we document its expansion northwards into Scandinavia, by compiling results of surveys in the region carried out between 2005 and 2008. The investigated area, from the southwest part of Denmark to the west coast of Norway was divided into eight geographical regions for a better overview (I–VIII), presented in Table 1 and Fig. 1.

Table 1 Summary of surveys and observations of the Pacific oyster, *Crassostrea gigas*, in Scandinavia, from 1996 to 2008. The geographical regions are shown in Fig. 1

Region	Sites	First observation	Year of survey	No. of size classes	No. of sampling sites	Mean density (oysters/m^2) ($\pm$ SD)
I. Danish Wadden Sea	Danish Wadden Sea	1996	2005; 2006; 2007		18; 57; 39	Biomass: 33.5 ± 57.2; 0.14 ± 0.11; 0.56 ± 0.21[a]
II. Danish West coast	Hvidesande; Thorsminde	2007				>100 oysters
III. Limfjorden	Limfjorden; Agger Tange	2002–2003	2006; 2007	5	7; 1	0.97 ± 0.85; 1.43 ± 0.86
IV. Eastern Denmark	Isefjorden	Introd. 1990s	2007	4	12	0.03 ± 0.03
V. Swedish southwest coast	Helsingborg–Gothenburg	2007	2007		25	0.64 ± 0.67
VI. Swedish northwest coast	Gothenburg–Stromstad	2007	2007; 2008	2	43	0.86 ± 1.10
VII. Southern Norway	Veierland–Tjøme	2007				
	Kragerø–Farsund	2005				
VIII. Western Norway	Espevik	2006	2006; 2008	4	1	
	Halsnøy; Kvitsøy; Telavåg	2007				

[a] Only biomass estimates (kg m^{-2}) available. Note also that the survey in 2005 only included a single site with high densities of oysters in the Danish Wadden Sea

History

The history of the Pacific oyster in Scandinavia dates back to the 1970s, when it was introduced for aquaculture. It was previously assumed that the risk of spreading to natural habitats was low, since water temperatures in these areas were lower than required for reproduction. Temperatures above 20°C and salinities above 20 psu are believed to be important factors for successful establishment of the Pacific oyster in new areas (Muranaka and Lann 1984; Fabioux et al. 2005).

In Denmark, the first introduction occurred in Limfjorden around 1972 (Fig. 1, Region III; Jensen and Knudsen 2005). During the following years, several oyster seed imports took place in an attempt to establish cultures in the Wadden Sea, Limfjorden, Little Belt, Isefjorden, Mariager fjord and Horsens Fjord (Fig. 1, Regions I, III and IV; Kristensen 1989; Jensen and Knudsen 2005). There have been few records of Pacific oyster in Horsens Fjord and Isefjorden since the farming stopped in 1998. In the mid 1990s, low numbers of Pacific oysters were found in the intertidal zone by Danish mussel fishermen in Lister Deep and on mussel beds in Ho Bight in the Wadden Sea (Fig. 1, region I; Diederich, Personal communication).

In Sweden, oyster spat were imported from Wales to the northern part of Bohuslän for cultivation trials between 1973 and 1976 (Fig. 1, region VI; Eklund et al. 1977). The general conclusion from these trials was that the environmental conditions were suitable for cultivation, but did not promote spawning. Since then, no further cultivation has been performed in Sweden. There have only been a few reports of large specimens, until the summer of 2007, when many independent observations were reported along the Swedish west coast.

In Norway, Pacific oysters were introduced in 1979 (Strand and Vøllstad 1997). The terms for this introduction included a plan for the establishment of a brood stock population, which could supply the Norwegian oyster producers with spat through hatchery production. From 1981 until 1986, farmers imported Pacific oyster seed from Scotland, but in 1986 strong restrictions were placed on the importation of molluscs for cultivation purposes. From 1987 to 1990, three hatcheries (Vallersund 64°N, Espevik and Øygarden 60°N; Fig. 1, region VIII) produced several

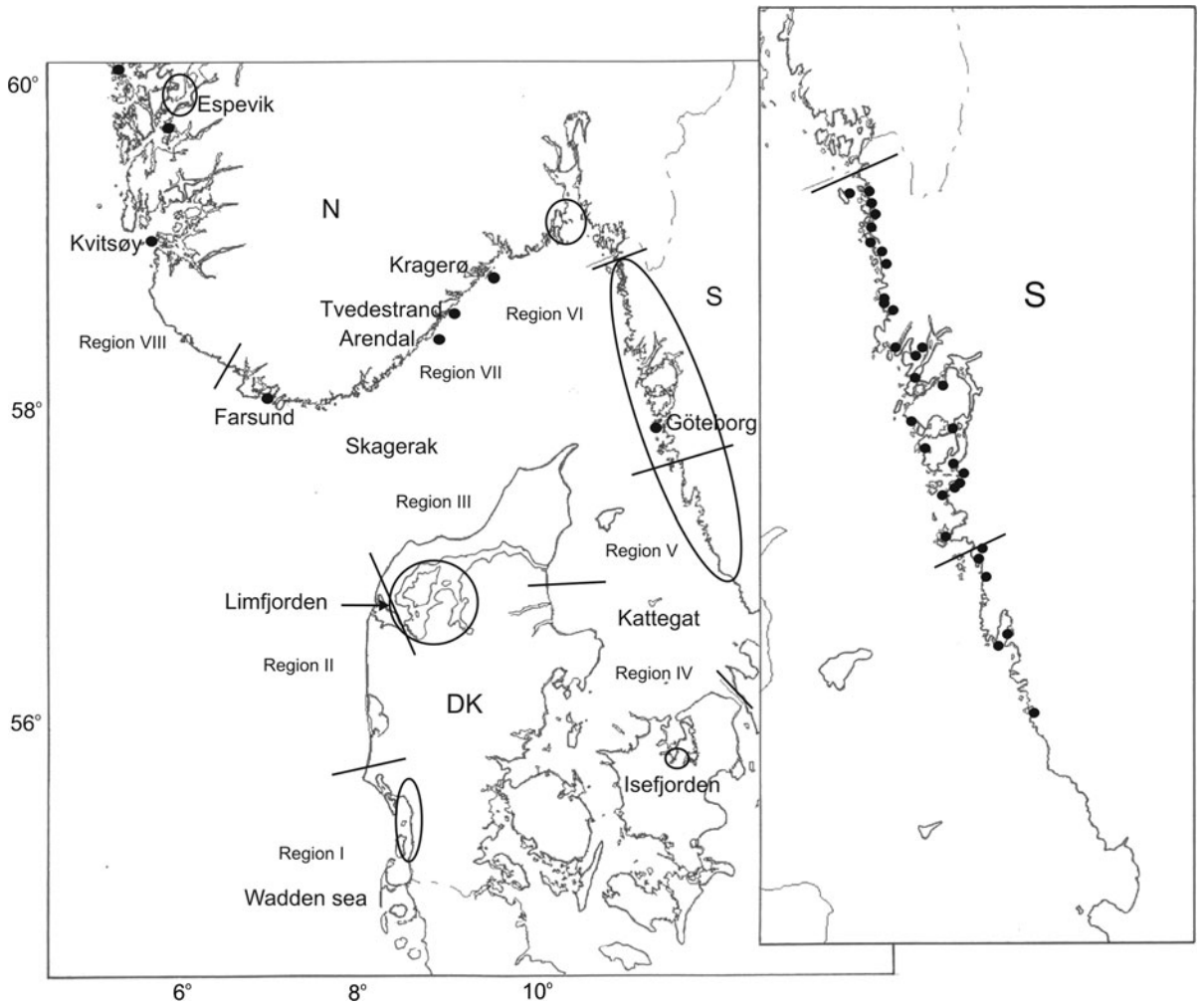

Fig. 1 The distribution of Pacific oyster, *Crassostrea gigas*, in Scandinavia based on data from Denmark (DK), Sweden (S) and Norway (N) during 2005–2008. Surveys have been performed in the *encircled* areas. Observations are marked with (●). The enlargement shows a more detailed map of the sampling sites along the Swedish west coast. Data from each geographical region are presented in Table 1

million spat (Strand and Vøllstad 1997). After this time, the market has been supplied with imported oysters, which have been re-laid in Norwegian waters. The origin of these oysters has been obscured, and they have erroneously been marketed as "Norwegian".

Current status

Denmark

Surveys of the distribution and biomass of Pacific oysters in the Danish Wadden Sea (region I) were conducted in 2005, 2006 and 2007. Samples were collected from tidal and intertidal flats using dredges or frames. Dredged areas were estimated by multiplying the dredged distance with the width of the dredge. On flats not accessible by boat, samples were collected applying frames (0.04 m^2) and estimating the degree of coverage of oysters in each frame. The biomass in the Danish Wadden Sea was estimated at 1,056 tonnes in 2005 increasing to 3,289 tonnes in 2006 and 6,264 tonnes in 2007. Local biomasses were up to 55.8 kg m^{-2}. The biomass varied considerably, as shown by the standard deviations in Table 1. True total biomasses were probably 50–200% larger than

recorded since there were areas not included in the survey. Most oysters were found on mussel beds. Along the west coast of Denmark (region II), oysters were reported from two sites (Table 1), however no survey was conducted in this area. Surveys in Limfjorden (region III) were performed in 2006 and 2007. In 2006, seven sites were investigated using the line transect method described in Krebs (1999). Five transects of varying length were placed perpendicular to the shore at each site. The mean oyster density varied between 0.03 and 6.05 oysters m^{-2}. Shell length distribution was analysed using the method of Bhattacharyas (1967) (FISAT II version 1.2.1). Age of individual oysters was analysed by cutting the oyster in two from the hinge to the outer edge and counting the year rings (Harding and Mann 2006). Five cohorts were identified. The survey in 2007 was performed at Agger Tange in the western part of Limfjorden, with two transects at two different locations. Here, the density of oysters varied considerably (1.43–15.30 oysters m^{-2}). Five cohorts were identified and oyster reef structures were also observed. Surveys in Isefjorden (region IV) were performed at 12 sites grouped in three areas in the inner parts of the fjord in 2007 (Munkholm Bridge, Ejby Harbour and Sømine Station) using transects. Oysters were found at five sites, with local densities of 0.00–0.11 oysters m^{-2}, and four cohorts were identified (Table 1).

Sweden

On the Swedish west coast (regions V and VI), a survey was conducted in 2007. Altogether, 68 sites were selected for accessibility from land, maximum depth of 2 m, and hard substrate. At each site, approximately 100 m^2 was examined using an aquascope. In the southern part (region V), Pacific oysters were found at 6 out of 25 sites, with the most southerly location close to Falkenberg (56°N). The mean density at sites with oysters present was 0.39 ± 0.42 oysters m^{-2} with a maximum density of 0.81 oysters m^{-2}. In the northern part (region VI) oysters were found at 36 of 43 sites, with a mean density of 1.07 ± 1.30 oysters m^{-2}. The highest density during the Swedish survey (505 oysters m^{-2}) was also found in region VI. At five sites, frames of 0.25 m^2 were used to estimate density and size distribution in November 2007 and June 2008. Large variation was observed both among and within sites, indicating patchy recruitment. The highest densities were always associated with shallow mussel beds, but oysters were also attached to other hard substrates. Two size-classes were identified, with most oysters at 60–70 mm and smaller (30–50 mm). A few larger specimens were found. Reef formations were observed at three sites. Most sites where oysters were not observed had either low salinity (<20 psu) or little hard substrate present.

Norway

Records of Pacific oysters along the southern coast (region VII) were based on reports from the public, and data from a survey monitoring health status of European flat oyster, performed by the National Veterinary Institute. The first findings were on a mussel bed off Burøy, near Kragerø, in 2005 (Fig. 1). Three large (100–120 mm shell length) oysters were found, attached to mussel shells. In 2007, Pacific oysters of the same size were reported from Veierland in Vestfold, and during 2008, many Pacific oysters were observed during flat oyster sampling in this area. Oysters were also reported from Tvedestrand, Arendal and Farsund (Fig. 1). In western Norway (region VIII), surveys were performed at Espevik, on the island of Tysnes in 2006 and 2008. This site consists of a sheltered marine basin, connected with the outside fjord through a narrow, shallow channel with a tidal current. During sampling in 2006, 94 Pacific oysters were collected in the channel. Another 16 were collected in 2008. Oysters ranged from 48 to 123 mm shell height, and four cohorts were identified. The youngest specimens were attached to local substrates. Most large specimens were not attached to any substrate. For histological examination of gonads, tissue sections were collected from 10 specimens in July 2006, fixed in Davidson's fixative (Shaw and Battle 1957), embedded in paraffin, sectioned at 3 μm, stained with hematoxylin-eosin and observed in a Leica DMRBE microscope at 100 to 400× magnification. Histological examination revealed acini filled with ripe eggs and sperm. In western Norway (region VIII), single Pacific oysters were reported from Kvitsøy, Halsnøy and Telavåg (Fig. 1) in 2007.

Discussion

Pacific oysters are now established in Denmark, Sweden and Norway, including areas where they were not previously introduced. Along the Swedish west coast, large populations of Pacific oysters are found in many areas, displaying similar densities as previously observed in the Wadden Sea (Diederich et al. 2005). For the first time, wild Pacific oysters were also found as far north as 60°N in Norway. No large-scale survey has yet been conducted in Norway, leaving an uncertainty about the true distribution and population size. In all countries, most oysters were attached to local substrates, suggesting that natural recruitment has occurred. The five and four cohorts from Limfjorden and Isefjorden also indicate re-occurring reproduction. The largest oysters found during the sampling at Tysnes, western Norway, were probably remaining specimens from previous live storage of oysters at the site, and possibly the genitors of the younger generations found. Both observations of gross morphology and the histological examination verified that new generations of oysters were sexually mature.

The timing of the widespread appearance of oysters in Scandinavia coincides with warming water temperatures, particularly contributing to successful larval recruitment in 2006. The massive occurrence in Sweden in 2007 correlated with unusually warm summer water temperatures in 2006. A general increase in mean water temperatures, as well as an increase in frequency of high summer temperatures and mild winters has occurred in Scandinavian waters during recent decades (Asplin et al. 2008). Over-winter survival of spat is also sensitive to water temperature, while adult oysters are less affected and may even survive cold winters when ice covers the tidal flats (Diederich 2006).

The location of Pacific oyster recruitment in Scandinavia indicates two separate origins: a northward expansion via the Jutland Current from the Wadden Sea, and an establishment from oysters previously introduced as hatchery broodstock to Norway. The Jutland coastal current, which runs northwards along the west coast of Denmark, has likely spread Pacific oysters from the Wadden Sea into Danish waters and further to the Swedish west coast. The highest abundances of Pacific oyster in Sweden were found in the area where the Jutland coastal current reaches the coast. The distribution along the Swedish west coast is so far restricted to areas with salinity above 20 psu. The freshwater input from the Baltic current may be a limiting factor for further expansion into the Baltic Sea (Muranaka and Lann 1984; Fabioux et al. 2005). The circulation pattern in the Skagerrak area (Sætre et al. 1988; Skjoldal and Dundas 1991) potentially supports larval drift from the western coast of Denmark and from Kattegat to the Norwegian coast, since time scales of several weeks for the water transport is within the range of the planktonic larval period of the Pacific oyster (Brandt et al. 2008). However, the oysters found in Espevik (western Norway) are most likely a result of abandoned farmed oysters in the mid 1990s. Our surveys will be continued in order to study the future spread and potential ecological effects of the Pacific oyster in Scandinavian waters.

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