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The Japanese oyster drill *Ocinebrellus inornatus* (Récluz, 1851) (Mollusca, Gastropoda, Muricidae), introduced to the Limfjord, Denmark

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Abstract

The predatory neogastropod *Ocinebrellus inornatus* was first reported from Europe in W France in 1995 and has since been detected at other sites in NW and N France and The Netherlands. It is native to the North Pacific where it preys on the Pacific oyster *Crassostrea gigas*. Here we report on the occurrence of the species in beds of European oysters (*Ostrea edulis*) in the Limfjord, NW Jutland, Denmark. The morphology-based identification has been confirmed by genetic analysis. The species was probably introduced with oysters imported from France in the 1970s and 1980s. The invasion is still relatively localized but as the species has established a reproductive population, it may eventually spread to other parts of the fjord and in time pose a problem to the oyster fishery. The species' invasion history is reviewed.

Key words: *Ocinebrellus inornatus*, Japanese oyster drill, *Crassostrea gigas*, *Ostrea edulis*, *Ocenebra erinacea,* The Limfjord

Introduction

The Japanese oyster drill, *Ocinebrellus inornatus* (Récluz, 1851), is a predatory muricid prosobranch gastropod, the natural distribution of which ranges from Northern China through Korea and all seas around Japan to Sakhalin and the Kurile Islands (Choe and Park 1997; Garcia-Meunier et al. 2003) and from 33º to 51ºN (Radwin and D'Attilio 1976). Its distribution partially overlaps that of the Pacific oyster, *Crassostrea gigas* (Thunberg, 1793), which forms the snails' principal diet and substrate for deposition of its egg capsules. During the spawning season, the snails congregate in large numbers to copulate before egg-laying. The females produce a cluster of 20–40 bright yellow egg capsules each of which contains several hundred nurse eggs resulting in the final production of 10–15 embryos. The hatched larvae have no planktonic phase (Pigeot et al. 2000) and the juveniles settle directly upon the bottom. In NW America they require 1–2 years to become sexually mature and the adult survival rate is 10–30% annually (White 2007). Because of the low fecundity and the lack of a free-swimming larval stage, the species' capacity of recruitment and dispersal is consequently rather limited.

Outside its native area of distribution, *Ocinebrellus inornatus* was first recorded in Puget Sound, Washington State in 1924 (Galtsoff 1929). From there it later spread north to British Columbia (1931), and south to Netarts Bay, Oregon (1930–1934). Subsequently, it was recorded from Morro Bay and Tomales Bay, California in 1941 and from Willapa Bay, Washington State in 1965 (Harbo 1999; Garcia-Meunier et al. 2003; Carlton 2007). The first discovery of *O. inornatus* in Europe was made in 1995 on the Atlantic coast of France in the Marennes-Oléron Bay [de Montaudouin and Sauriau 2000, erroneously identified as

Ocenebra erinacea (L., 1758)], from where it spread northwards to Morbihan Gulf (2000) and Bay of Bourgneuf (2001), both in Brittany (Goulletquer et al. 2002). Finally it was reported from the St. Malo Gulf, Normandy in 2003 (Martel et al. 2004b). During a survey of selected localities in The Netherlands, *O. inornatus* was detected in the Oosterschelde in 2007. Initially it was identified as *O. erinacea* (Faasse and Ligthart 2007), but later on correctly as *O. inornatus* (Goud et al. 2008).

While performing regular surveys of the bottom fauna of the Limfjord, NW Jutland, Denmark, during 2006–2010, a number of a non-indigenous gastropod were collected from dredge hauls made in the westernmost part of the fjord, Nissum Broad (Figure 1) and identified as the W European *Ocenebra erinacea* (see Jensen and Hoffmann 2007). In this paper we report data that shows that the Danish snails actually belong to *Ocinebrellus inornatus*, and review its distribution as an alien species and its invasive history in Europe. The species was originally described by Récluz (1851) as *Murex inornatus* but has often been named as *Ocenebra inornata* or *Ceratostoma inornata*. *Ocinebra japonica* (Dunker, 1860) is a junior synonym.

Materials and methods

Field and laboratory

Dredge hauls were performed in June and August/September each of the years 2006–2010. The area surveyed comprises Nissum Broad, the waters around the island of Venø, and Kaas Broad (Figure 1), with most dredging being performed on a sandy bottom at depths of 5–6 m. The native oyster, *Ostrea edulis* L., 1758, occurs scattered all over the area, but is by far most abundant in Nissum Broad. Since oysters and oyster drills live sublittorally in the Limfjord, they can be sampled only by dredging. This is contrary to the other European sites where *O. inornatus* lives in the middle part of the littoral zone and on rocky shores (Pigeot et al. 2000) and can be picked up by hand. For each dredge haul, the presence of snails and their egg capsules (mostly attached to the oysters), not their number, were noted. More than thirty adult *O. inornatus* and many egg capsules were collected throughout the years. Nearly all snails and egg capsules were collected from within a radius of one nautical mile from 56º37′30″N, 08º25′30″E. Whenever dredge hauls were performed outside the area with oysters, neither the snails nor their egg capsules were found. The gear used is a large-meshed dredge which is first and foremost designed to retain oysters of marketable size. In general, the snails were caught only in the few cases when the contents of each dredge was landed and sorted on board the ship. The normal sorting procedure is to drag the dredge behind the fast sailing ship, a procedure which retains most of the oysters, while the comparatively smaller snails are obviously lost together with sediment and unwanted objects. This may also explain why egg capsules, usually attached to the larger oyster shells, were recorded much more often than the snails.

In addition to the dredged specimens, two adult live snails were hand-picked 5 August 2009 in Nørskovvig, an inlet of the island Venø, located in Venø Bay. The shell of one of them is illustrated in Figure 2A and B and compared with a shell of *Ocenebra erinacea* from Ireland (Figure 2C and D).

To study the salinity tolerance of *O. inornatus*, five adult specimens were offered adult Pacific oysters and 6 cm long mussels, *Mytilus edulis* L., 1758, and kept at 25 psu (18ºC) in the laboratory for four weeks, and at 23 psu for five more weeks.

SEM of radulas

Radulas of specimens of *Ocenebra erinacea* from W. France and a specimen of *Ocinebrellus inornatus* from the Limfjord were freed from the radular sac and cleaned with commercial bleach. Then they were washed in distilled water, preserved in 96% alcohol, mounted on aluministubs with double-sided tape, coated with gold and examined in a JEOL JSM 840 scanning electron microscope.

Molecular identification

Genomic DNA was extracted using the Qiagen DNeasy Blood and Tissue Kit following standard protocols. DNA from four individuals of *Ocenebra erinacea* and one *Ocinebrellus inornatus* was extracted using ca 1 mm^3 of muscle tissue. Specimens were sequenced for mitochondrial COI to confirm species identity. PCR amplification of partial COI was performed with the Folmer et al. (1994) primers LCO1490 and HCO2198 in 25 µl reactions. Each reaction

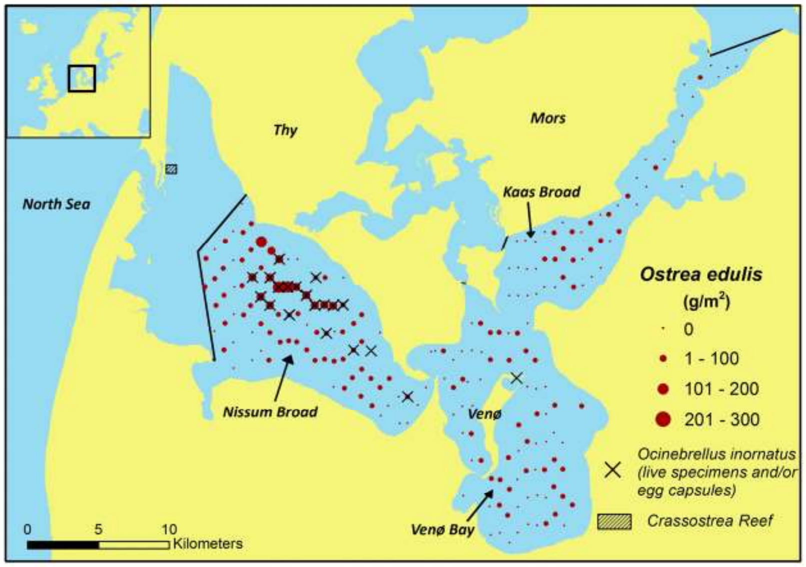

Figure 1. Comparison between 2010-finds of *Ocinebrellus inornatus* (snails and egg capsules) and distribution and quantity of oyster, *Ostrea edulis*, in the western part of the Limfjord. Size of the red dots show the weight (g/m²) of oysters caught in 2009. Lines demarcate the area surveyed. Square indicates position of a reef made up of Pacific oyster, *Crassostrea gigas*.

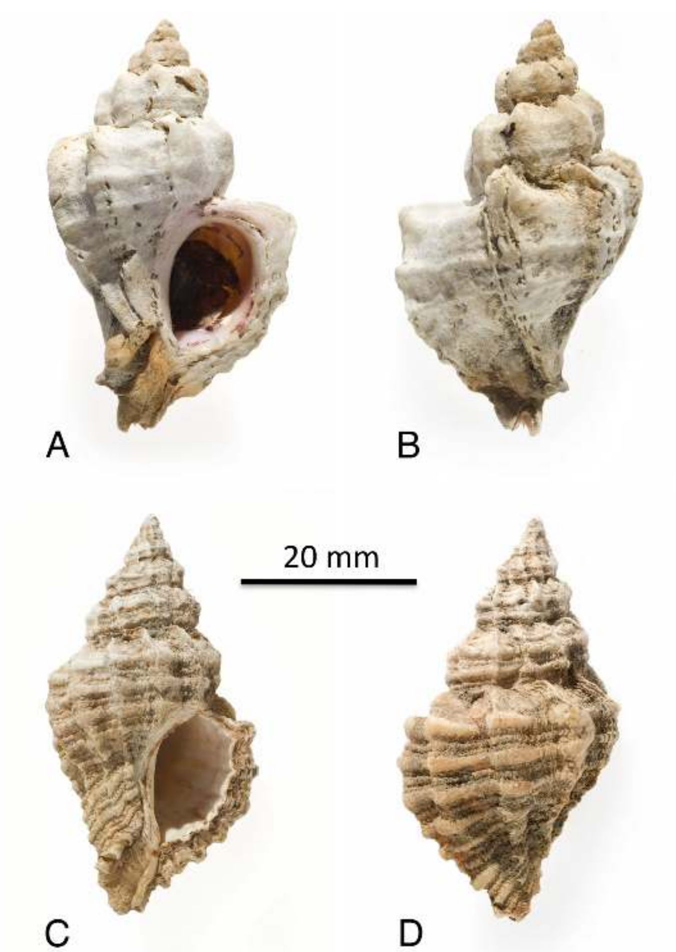

Figure 2. A-B, *Ocinebrellus inornatus*, specimen from Venø Bay, the Limfjord, August 2009. **C-D**, *Ocenebra erinacea*, specimen from W.Ireland (Zoological Museum, Copenhagen). Photo by Jørgen Lützen.

contained 13.6 µl ddH2O, 1X PCR buffer, 2.5 µl 25 mM $MgCl_2$, 2 µl 2.5 µM of each dNTP, 1.2 µl of each 10 µM primer, 1U of AmpliTaq polymerase and 2 µl of DNA template: PCR reactions were run on an Eppendorf thermal cycler and visualised on 1% agarose gels prior to purification and sequencing.

The resulting sequences were aligned and compared against *Ocenebra erinacea* and *Ocinebrellus inornatus* sequences from GenBank. GenBank accession numbers are AY995796, AY995797, AY995798 and AY995799 (*Ocenebra erinacea*) and FN677403 (*Ocinebrellus inornatus*).

Results

When first recorded from Europe, the shells of *Ocinebrellus inornatus* were misidentified with those of its autochthonous relative *Ocenebra erinacea* (de Montaudouin and Sauriau 2000; Faasse and Ligthart 2007; Jensen and Hoffmann 2007). The shells of both species exhibit considerable variation and especially when worn, may be difficult to tell apart. However, we found that the Limfjord shells were indistinguishable from shells of *O. inornatus* collected in the Oosterschelde, The Netherlands.

The radulas which we studied for both species are rachiglossate consisting in each transverse row of a central (rachidian) tooth and a pair of laterals. The radular dentition of *Ocenebra erinacea* illustrated by Radwin and D'Attilio (1976, Figure 73) is not only similar in all details to that of our specimens of the same species, but also matches that of *Ocinebrellus inornatus* (Figure 4A, B). Thus, radular structure does not offer a mean to distinguish between the two species. However, sequencing the mitochondrial CO1 gene unambiguously separated *O. inornatus* from *O. erinacea* indicating that molecular analysis might be the only reliable identification tool at this point for non-specialists. The DNA analyses which we have performed on adult specimens (present paper) as well as egg capsules (Gittenberger et al. 2010a) have confirmed that the Danish specimens belong to *O. inornatus*.

Two species of oysters occur in the Limfjord, the European oyster, *Ostrea edulis* and the Pacific oyster, *Crassostrea gigas*. Wild populations of *O. edulis* occur in most parts of Nissum Broad (salinity 30–31 psu) at 5–6 m depth and, more scattered and at similar depths, in the neighbouring Venø Bay and Kaas Broad (salinity 29 psu). The Japanese oyster drill seems to be exclusively associated with *O. edulis* and snails as well as their egg capsules occurred only where the oysters were most abundant (40–50 kg per square meter), namely in Nissum Broad (Figure 1). In the past year (2010), the oyster fishermen have noticed that several Nissum Broad oysters show bore holes made by the drill. *O. inornatus* has not yet been reported outside this part of the fjord, except for a couple of specimens taken at Venø, which probably had been transferred to this place together with oysters relayed there by fishermen for later use.

The Pacific oyster was introduced to the Limfjord around 1972 (Jensen and Knudsen 2005), but has only recently become more abundant (Wrange et al. 2010). It is mostly confined to more shallow water and often to areas with lower salinities. The scattered populations of *C. gigas* were not surveyed, but *Ocinebrellus inornatus* were not found to occur at a few reef-like intertidal aggregations of *C. gigas*, that are located ca 10 km from the nearest record of *O. edulis*-associated snails and visited twice, in 2010 and 2011 (pers. comm. by B.W. Hansen) (Figure 1).

The bore holes made by adult *Ocinebrellus inornatus* are funnel-shaped, widest on the shell's outside. The outer diameter in a full-grown oyster, whether *O. edulis* or *C. gigas*, is ca. 2.5 mm, in blue mussels consumed in the laboratory ca. 2.0 mm, with an interior diameter in all shells of 1.3 mm (Figure 3).

Nearly all the egg capsules from the Limfjord were attached to empty shells or live individuals of the European oyster, the only exceptions being three cases where they were fastened to an empty shell of *Mytilus edulis*, the test of the ascidian *Ascidiella aspersa* (O. F. Müller, 1776), and a live shell of its own kin. Egg capsules were found in all three months (June, August, and September) in the five surveyed years (2006–2010). However, egg-laying probably starts earlier, since a few capsules collected on 25 March 2010 (Figure 5) already contained live embryos (Gittenberger et al. 2010a).

The aquaria-kept *Ocinebrellus inornatus* survived at salinities of 23–25 psu for more than two months, and during that time fed solely on a diet of mussels, although they were also offered Pacific oysters. They required ca. two days to drill a hole through a mussel shell.

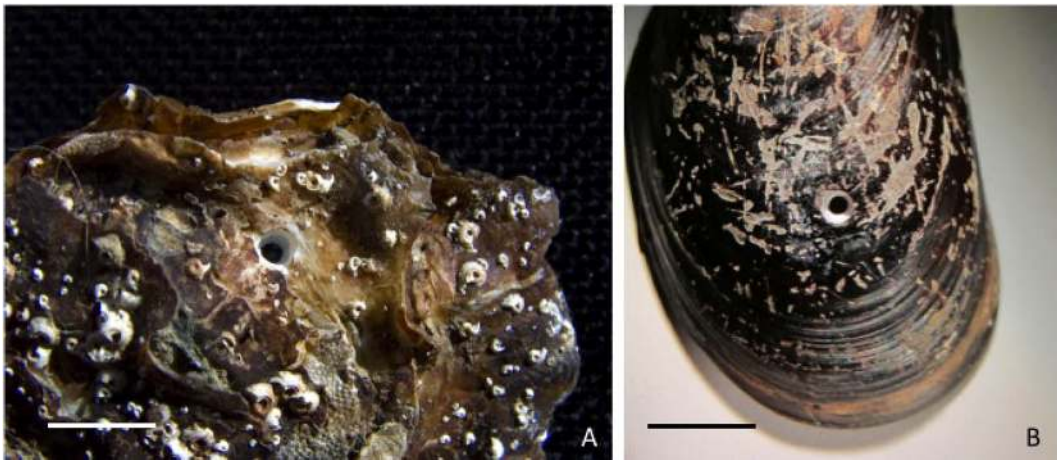

Figure 3. Holes drilled by *Ocinebrellus inornatus* in shells of an adult Pacific oyster, *Crassostrea gigas* (**A**) and a mussel, *Mytilus edulis* (**B**). Outer diameter of holes 2.5 and 2.1 mm, respectively. Scale bars indicate 10 mm. Photographs by Marco Faasse and Henrik Glenner.

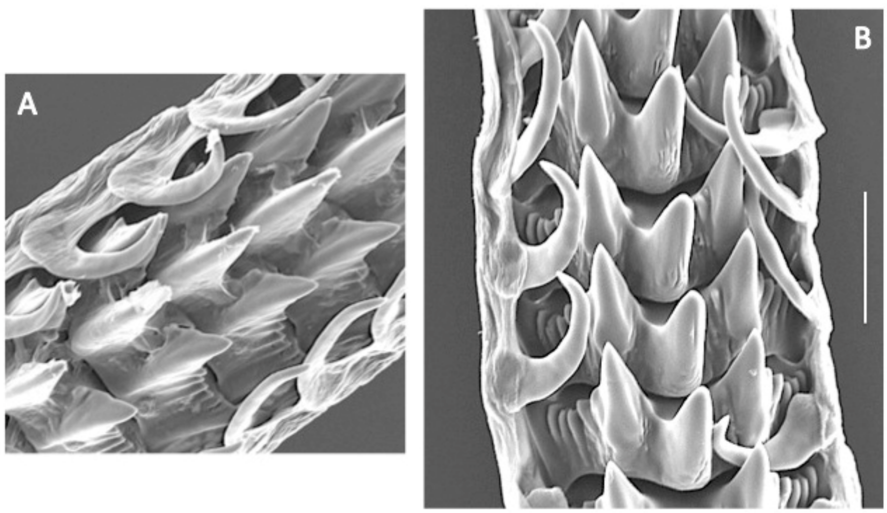

Figure 4. SEM of radulas of *Ocinebrellus inornatus* from the Limfjord (**A**) and *Ocenebra erinacea* from W. France (**B**). Scale bar indicates 40 µm.

Discussion

Feeding and reproduction

To get access to the soft parts of the oysters, *Ocinebrellus inornatus* drills a perfectly circular hole through one of its prey's valves by means of acid secretions and its radula; it subsequently introduces its proboscis through the hole to suck out the soft interior.

The species shows a spatial variability in its prey preference. The co-occurrence of *O. inornatus* and *O. edulis* in the Limfjord strongly suggests that this oyster species forms the drill's principal food. Drilled oyster shells were occasionally found. However, when offered mussels, these were consumed as well. In France and The Netherlands *O. inornatus* seems to prey mostly on the introduced *C. gigas*, and alternatively

Figure 5. Egg capsules of *Ocinebrellus inornatus* attached to *Ostrea edulis*, March 25, 2010, Nissum Broad, the Limfjord. Most egg capsules measure 15 to 20 mm in length. Photo by Arjan Gittenberger.

Mytilus edulis. Diseases among the indigenous *O. edulis* and *C. angulata* (Lamarck, 1819) have almost eliminated the local stocks in both countries (Comps et al. 1976).

In NW America the choice of food varies considerably. In Willapa Bay, Washington State, just as in W France, it prefers Pacific oysters to the native species (Pigeot 2000; Buhle and Ruesink 2009). Chapman and Banner (1949) reported that in NW America *O. inornatus* attacks Olympia oysters (*Ostrea lurida* Carpenter, 1864) even in the presence of *C. gigas* and that it may also eat mussels and barnacles, if these are offered. Chew and Eisler (1958) offered a choice of clams [*Venerupis japonica* (Deshayes, 1853)], mussels (*Mytilus edulis*), Olympia oysters, and Pacific oysters to snails that were collected from oyster beds. Over a period of 65 days, the food that the animals consumed in greatest numbers were mussels, which constituted 42.6% of all specimens eaten compared to clams (36.5%) and the two species of oysters (20.9%). It required from 5–7 days to consume a clam or mussel, but much longer, two weeks, to eat an adult Pacific oyster.

When given the choice to fasten the egg capsules onto the shells of mussels, clams, Olympia oysters and Pacific oysters, *O. inornatus* always attached them to the latter, and in no case to any other test animal (Chew and Eisler 1958), while in the Limfjord it has switched to *O. edulis*. The spawning season in the Limfjord extends from at least late March to September, similarly to in The Netherlands, where Faasse and Ligthart (2009) found egg-laying to occur during spring and summer. In W France, spawning preferentially takes place at the end of autumn and in winter (Pigeot et al. 2000).

The invasion history of Ocinebrellus inornatus in Europe

The initial spread of *Ocinebrellus inornatus* outside its native area of distribution is in all probability connected with the introduction of *Crassostrea gigas* to many parts of the world. During the early part of the 20th century (1902), large amounts of *C. gigas* were imported from Japan and relaid on the West coast of North America both as spat and adults (Wolff and Reise 2002). Since no subsequent imports of oysters took place, the *O. inornatus* that were first observed in Puget Sound in 1924 must have been unintentionally introduced at the same time, and through transfers of oysters secondarily spread to other parts of the West coast.

How *Ocinebrellus inornatus* arrived and spread in France has been investigated by Martel et al. (2004a, b). Based on mitochondrial DNA and allozyme polymorphisms, they found that the populations from the primary introduction sites in France and NW America were closely related and substantially different from the native populations in Asia (Korea). From this, they concluded that the source population of the Marennes-Oléron Bay *O. inornatus* is located in NW America (Martel et al. 2004a). This tallies with the fact that 256 tons of broodstock *C. gigas* were imported from British Columbia to exactly this region during 1971–1975 and further 20 tons to Baie Bourgneuf during 1972–1973 (Grizel and Héral 1991), both places where

O. inornatus was found later on. It took about twenty years before the species was discovered in France, probably because recruitment is slow and since the snails were initially misidentified as a variety of the local *Ocenebra erinacea* (see de Montaudouin and Sauriau 2000). In view of the species' limited dispersal power and because of the genetic homogeneity between several populations from the Marennes-Oléron Bay and the Brittany populations separated by 300 km, Martel et al. (2004b) explained the species' arrival to the latter destination as the result of unregulated shellfish transfers along the French West coast. It was discovered that cultured oysters kept in bags often also contained juvenile and adult *O. inornatus*. These bags are not only moved from farm to farm within the area, but some are even transported long distances, e.g. to Brittany, which is how the snails must have been introduced to that area.

It is most likely that *Ocinebrellus inornatus* were introduced to the Oosterschelde, The Netherlands, an important centre of shellfish trade, together with imported aquaculture products, most probably Pacific oysters. Two imports, in 1964 (of spat) and 1971 (of adult oysters) came from British Columbia (Drinkwaard 1999; Wolff and Reise 2002), where *O. inornatus* was well established. Another possibility is an introduction together with mussels imported since the 1980s from two regions (Morbihan and Marennes-Oléron Bay) in France, where the snail must have occurred at that time (Faasse and Ligthart 2009). Two of us (Marco Faasse and Arjan Gittenberger) have studied the invertebrate fauna in the Oosterschelde for more than 15 years without finding the oyster drill before 2007. In that year rather few were found, but they increased considerably in numbers since then, which suggests a rather recent introduction. In 2010 a small number of egg capsules resembling those of *O. inornatus* were found in a sample of European oysters from Nissum Broad, the Limfjord, that was specifically taken with the purpose to check whether invasive species were present in the area (Figure 5). To confirm the identification as *O. inornatus*, DNA was extracted and sequenced from the egg capsules. When the identification was confirmed (Genbank accession nr. HM439429), the Dutch shellfish industry decided to quarantine all European oyster imports from the Limfjord upon arrival in The Netherlands. Since 2006, to minimize the chance that invasive species are imported with shellfish transports, such samples are continuously taken and checked for invasive species in all areas from where shellfish are transported to the Oosterschelde (Gittenberger et al. 2010a).

Unintentional transfer of *Ocinebrellus inornatus* with shellfish seems to be the only explanation of how the species first appeared in the Limfjord. During the 1970s and also later on in the 1980s, smaller amounts of *O. edulis* (possibly together with a few *C. gigas*) were imported from oyster beds near Brest, W Brittany, and planted in Nissum Broad (Stæhr et al. 2000; Jensen and Knudsen 2005). However, *O. inornatus* was first observed in 2006 during regular surveys commenced in 2002 (Kristensen and Hoffmann 2006). Apparently the species survived in the years between, but not until the increase in the biomass of *O. edulis* around 2000 (Kristensen and Hoffmann 2006) has it become more numerous. As indicated above, human-mediated transport of oysters is in all probability responsible for the long-range dispersal of the oyster drill along the French coasts, which very well may have been introduced also to the Brest oyster beds, where its occurrence remained unnoticed (and unpublished), and from there exported to Denmark.

In the European Wadden Sea, the Pacific oyster has established itself permanently after two primary introductions off the island of Texel, The Netherlands, in 1983 and the island of Sylt, N Germany, in 1986 (Reise 1998). By natural dispersal of larvae, the Sylt population spread during the 1990s to the south into the North Frisian Wadden Sea and north to the Danish Wadden Sea and further to several South Scandinavian localities (Wrange et al. 2010). According to two authorities on the Wadden Sea fauna, Karsten Reise (Wadden Sea Station, Sylt, Germany) and Klaus Melbye (Vadehavscentret, Ribe, Denmark), no snails resembling *O. inornatus* have ever been observed in areas populated by descendents of the Sylt Pacific oysters. This is also not to be expected since these oysters originated primarily from hatcheries in England and Ireland (Reise 1998; Drinkwaard 1999; and see below) and *O. inornatus* has never been reported from any of these two countries. The Texel population, was probably brought deliberately from the Dutch Delta region (Dankers et al. 2004), expanded towards the east to the Dutch Wadden Sea, but *O. inornatus* was not found during a 2009 survey of the fauna of hard substrate in this region (Gittenberger et al. 2010b).

A small consignment of broodstock *C. gigas* from British Columbia were imported to Conwy, Wales, in 1965 (Wolff and Reise 2002). These oysters were all used for a breeding program, and if they had included *O. inornatus*, these most likely would have been discovered and removed. Until now, the oyster drill has never been reported from either Britain or Ireland.

Perspectives of further expansion

When evaluating the prospects of future spread of *Ocinebrellus inornatus* in NW Europe one should consider that although the Pacific oyster constitutes its principal food, the snail is perfectly capable of switching to other species of oysters in its absence, or even presence, and may also survive on a diet of common mussels.

The species' demand with respect to temperature has not been studied but its presence in the Sea of Japan and along the coasts of Sakhalin indicates that it can easily tolerate the sea temperatures of the North Sea and southern Scandinavia. A cold spell in the winter 2009 with inshore temperatures in the Oosterschelde of 0ºC to -1º C obviously posed no problem to the survival of the species (Faasse and Ligthart 2009) and it has also easily survived the low winter temperatures in 2010/2011. The mean of the five lowest bottom temperatures recorded in each of eleven consecutive winters (1999/2000 to 2009/2010) in Nissum Broad is 2.7ºC with a range from1.4 to 4.6ºC and subzero temperatures (down to -0.5ºC) recorded only twice. The species is likely to tolerate the average minimum salinity of the Limfjord (23 psu) since all five specimens subjected to salinities between 23 and 25 psu salinities survived until the experiment was interrupted.

Because of its size and thick shell, *O. inornatus* is likely to be confronted with few predators. One likely candidate in NW Europe is the edible crab, *Cancer pagurus* L., 1758, a relative of which, the equally large red rock crab, *C. productus* Randall, 1840, is known to feed on *O. inornatus* in Willapa Bay, Washington State (White 2007). As with many introduced species it will probably suffer from relatively few parasites (Torchin et al. 2003). Within the coastal regions of NW Europe it has only one competitor, i.e. the European sting winkle *O. erinacea* (Figure 2C and D) but experience from W France, where the two species co-exist, shows that *O. inornatus* tends to outnumber this local species (Pigeot et al. 2000). As *O. inornatus* is now well established in W France, Brittany and along the Normandy coast, one would expect it to slowly spread to all suitable shellfish habitats along the entire French Atlantic and Channel coasts either unaided or by human-mediated relaying of shellfish. At the Marennes-Oléron Bay, the species has been observed regularly since its first discovery in 1995 and expanded to such an extent that it has turned into an invasive species (Pigeot et al. 2000). During 2008 and 2009, in The Netherlands the Oosterschelde population increased in numbers at the original site and the species spread to a neighbouring locality (Faasse and Ligthart 2009). In time it will probably invade all suitable parts of the Oosterschelde, and perhaps other parts of the Delta Region (Zeeland) although at present they are partly separated from the Oosterschelde. Until now the species has not been reported from any other Dutch locality (Gittenberger et al. 2010b).

In Denmark *O. inornatus* is chiefly confined to Nissum Broad. At present (2011) it has not managed to invade two *C. gigas* "reefs" located only about 10 km away from the nearest *O. edulis*-associated record. Since it may feed on mussels which are extremely abundant in all central parts of the fjord it has the potential to spread further east. Because of its limited dispersal capability this will happen slowly unless it is being spread by transfer of mussels between the various mussel beds. Everywhere in the Limfjord the salinity and temperature are above what is probably the species' threshold values, although it is not known whether they also satisfy the requirements for successful breeding. During the last twenty years, the average yearly sea temperature in the Limfjord has increased ca.1.5ºC (Limfjordsovervågningen 2006) and is likely to rise further in the future. A spread to Southern Norway, Kattegat and the Swedish West coast is possible, as wild Pacific oyster populations have now been established there (Wrange et al. 2010), but introduction to these areas will depend entirely on human-mediated dispersal by uncontrolled shellfish transfers.

Management

Along the west coast of N America, the Japanese oyster drill is considered to be potentially the most serious predator of the native Olympic oyster and the imported *Crasosstrea gigas* (see Chew and Eisler 1958). The species is known to cause up to 25% mortality in stocked populations of *C. gigas* (see Elston 1997) and predation reduces the survival of the Pacific and Olympia oysters in field enclosures. In spite of this, the effect on the oyster populations was considered modest (Buhle and Ruesink 2009). In W France, *Ocinebrellus inornatus* competes successfully with *Ocenebra erinacea*, which in 2000 – 25–30 years after its first introduction – it had clearly outnumbered. This is expected to happen also in other areas where the two species co-exist. *O. inornatus* is considered a serious threat to French oyster farming. Significant damage has already been reported where it occurs as an invasive species (Pigeot et al. 2000). Thus, predation on Pacific oysters by *O. inornatus* is heavier than by *O. erinacea*, and in smaller areas may cause mortalities of up to 50%. In Japan oyster growers ward off attacks by *O. inornatus* by using strings of oysters hung on trellises that do not touch the bottom (Shaw 1974), which forces the drills to feed exclusively on the economically unimportant wild oysters.

Buhle et al. (2004) have studied the dynamics and impact of the Japanese oyster drill on oyster populations in Willapa Bay, Washington State, and used population statistics and biological data to determine the most cost-effective way of decimating the population of the predator. Because of the low survival rates of the adults, it was shown that manually collecting and destroying the drill's egg capsules is much more effective than removing the snails. It is recommended to do this in the reproductive peak season, which in NW America occurs from April to July. This is only possible – and actually implemented each year – because most oyster drills live in the intertidal zone and the spawn attached to the oyster shells can easily be discovered and removed by hand. However, even local eradication has proven elusive and growers have had to abandon some oyster beds because of intense predation (Buhle and Ruesink 2009). Removing shells and spawn would be possible to practice also along the French tidal coasts.

In the last half of the 19^{th} century, the European oyster has suffered a dramatic decline owing to overexploitation and diseases, in particular caused by the two protistans *Marteilia refringens* and *Bonamia ostreae* (see Grizel 1983). Even if both parasites occur in the Limfjord oysters**,** they are one of the few European populations which are resistant to them. In the likely event that the Japanese oyster drill will disperse further in the future, this may pose a problem to the preservation of this otherwise healthy oyster population. Because the snails live sublittorally in the Limfjord, combating them by removing the spawn is difficult and can be done only when the oysters are harvested by dredges. However, present regulations of the fishery demands that this takes place only in wintertime, which is out of the drills' spawning season.

Comparison with Ocenebra erinacea

The fact that *Ocinebrellus inornatus* has been repeatedly confused with the W European *Ocenebra erinacea*, warrants a brief comparison between the two species.

O. inornatus and *O. erinacea* differ in shell ornamentation (Figure 2), but the sculpture varies to such an extent that it often makes identification difficult. Shell height may reach 48 mm in *O. erinacea*, and 50–60 mm in *O. inornatus*. The shell of *O. inornatus* is more solid and has a coarser ornamentation. Both species have a sculpture of costae and spiral ridges, the ridges being fewer (4–7) in *O. inornatus* than in *O. erinacea* (8–9), with a few minor ridges intercalated. The best distinctive character is that the costae in *O. inornatus* are more prominent and angulated at the periphery or shoulder. The inner side of the outer lip in the shell of *O. inornatus* usually has five small denticles (Goud et al. 2008). The flesh in both species is cream with white flecks and the siphon only projects a little outside the siphonal canal which is short and usually closes with age. Radular dentition is similar in the two species and molecular identification seems to be the only reliable way of differentiating between them.

Ocenebra erinacea is distributed around the British Isles, along the Atlantic coasts of continental W Europe and N Africa and western basin of the Mediterranean Sea. In the North Sea it occurs only along the British coasts. As a mainly sublittoral species, it has a wide range of prey organisms, including mussels, cockles, clams and barnacles. When such food becomes less abundant, the snails change to eating oysters (Orton 1929; Hancock 1960). Although more generalistic in its choice of food and habitat than *O. inornatus*, the risks that *O. erinacea* will establish viable populations in N Europe outside its original area of distribution are small because its susceptibility to cold. Thus, during the exceptionally severe winters 1928–1929 and

1962–1963, the population along the British North Sea coasts almost suffered annihilation (Orton and Lewis 1931; Mistakidis and Hancock 1955; Crisp 1964). A few vacant shells of *O. erinacea* that were discovered in The Netherlands in 2007 probably originated from individuals, alive or dead, transferred with mussels from S England (Faasse and Ligthart. 2009). Since then, live specimens have not been found and most likely the low winter temperatures occurring in the Netherlands will prevent the species from becoming permanently established there (Faasse and Ligthart 2009). In 1982, a few specimens were spotted among a cargo of *O. edulis* imported from W Ireland to the Limfjord, but they were eliminated before release of the oysters to the sea (Jensen and Knudsen 2005; Jensen and Hoffmann 2007). The spawn is similar to that of *O. inornatus* but the larvae pass through a short planktonic phase of 2–3 days duration (Gibbs 1996). This affords the species a considerably greater dispersal power than *O. inornatus*.

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