Oceanological and Hydrobiological Studies
Vol. XXXIV, Supplement 1

Institute of Oceanography (137-162) University of Gdańsk
2005

Research Article

A SUMMARY OF ALIEN MARINE BENTHIC INVERTEBRATES IN DANISH WATERS

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Key words: alien invertebrates, distribution, Danish waters, dispersal

Abstract

There are 18 established alien marine benthic invertebrates in Danish waters. In addition, there are nine species that have been recorded one or more times in these waters, but which do not form reproducing populations in this area. The most important recipient localities in Danish waters are the Limfjord (n=4) and the Wadden Sea (n=3). The species found in these areas are mostly marine species that have spread through secondary dispersal from their original location of introduction. Data on distribution, dispersal, vectors, and donor regions are presented, and the adequacy of Danish monitoring programs is discussed.

INTRODUCTION

Alien species have been listed as one of the three most serious threats to the marine environment. The number of introduced species has increased particularly since transoceanic shipping times became shorter than the larval life of most marine invertebrates. On a global scale, ballast water is the most important vector for unintentional introductions whereas aquaculture continues

to be important for the intended transfer of organisms from one region to another.

Denmark is situated between the North Sea and the Baltic Sea. Hence, Danish waters may function as a gateway or a barrier to the dispersal of alien species, either from the North Sea or the Baltic Sea. Danish waters between Skagen and Bornholm are characterized by vertical stratification and latitudinal gradients in salinity, and are thus usually referred to as the Transition Area (TA). It might be expected that planktonic larvae of alien species established in the Baltic would disperse into the TA, and also that larvae of species established in the North Sea should be able to disperse into this area. Furthermore, shipping traffic through the TA is very high (>50,000 ships per year), which should increase the likelihood of alien species introductions.

The present paper presents an overview of the alien benthic invertebrates recorded in Danish waters and provides a description of the dispersal of permanently established species through Danish waters. Most of the information has been extracted from existing literature, including unpublished reports from monitoring authorities. In addition, the authors studied the collections of the Zoological Museum, Copenhagen and found additional records. Descriptions are provided of some of the localities that have been especially susceptible as receptor areas for alien species. Distributions of alien species in Danish waters are compared to those of neighboring countries. Finally, the adequacy of existing monitoring programs to deal with the detection and prevention of establishment of alien species is discussed.

STUDY AREA

The Danish North Sea coast is comprised of highly dynamic, sandy shores. There is a considerable amount of sediment transport. The coastline in some places is eroding up to several meters every year. In other places sediment is deposited. The North Sea coast is interrupted at three places by inlets to shallow lagoons or fjords - Ringkøbing Fjord, Nissum Fjord, and the Limfjord. Coastal surface currents generally run along the shore from south to north, which means that planktonic larvae are also transported towards the north. Atlantic water enters the North Sea from the north through a deep channel between the Shetland Islands and the coast of Norway or through the narrow strait between the Shetland Islands and the coast of Scotland, but also from the south through the English Channel.

The Danish part of the Wadden Sea comprises about 800 km². It is bordered by three barrier islands - Fanø, Mandø, and Rømø. These islands and the Skallingen peninsula protect the shallow mudflat behind them. There is a deep

navigation channel, regularly dredged to maintain depth, which leads to the harbor of Esbjerg, the largest fishing port in Denmark and also an international ferry terminal. The tidal range in this area is much higher than in other Danish waters, *i.e.*, about 2 m, and the mainland coast is protected from flooding by dikes. Only one of the streams entering the Danish Wadden Sea has a tidal brackish estuary; the others are regulated by sluice gates.

Ringkøbing Fjord is the largest coastal lagoon in Denmark (about 300 km²). It receives an average of 30 $m^3 s^{-1}$ of fresh water from one of the largest streams in Denmark, Skjern Å. The depth is generally between 1 and 2 m, but there are a few deeper holes (4-6 m). The natural inlet was highly unstable, and in 1910 a channel was dug at Hvide Sande located centrally on the sand bar separating the lagoon from the North Sea. This was closed again in 1915. During the 1910-1915 period, salinity was 15-20 PSU. Sluice gates were added in 1931 to control the flooding of agricultural land on the east coast of the lagoon. The flow of the Skjern Å has also been regulated and deregulated at various times. Thus, salinity, nutrient input, and water height have changed several times. This has also influenced the bottom fauna in the fjord (Mortensen 1900, Johansen 1913, Johansen and Blegvad 1933-1936). Since 1995, salinity has been regulated to about 12-15 PSU through sluice gates at Hvide Sande.

Nissum Fjord is a smaller (about 70 km²) coastal lagoon or fjord to the north of Ringkøbing Fjord. It is actually composed of three lagoons connected by narrow channels. The inlet is presently regulated by sluice gates to control the flooding but not the salinity of the lagoon. Salinity can vary from 1 to 33 PSU, but it is generally between 2 and 15 PSU (Laursen *et al*. 2004). The narrow dune barrier separating the lagoon from the North Sea has had to be reinforced with concrete to prevent coastal erosion.

The Limfjord is currently a long, convoluted sound separating the northern part of Jylland (Jutland) from the peninsula. Before 1825 the fjord was only open towards the east, into Kattegat, and salinity decreased eastwardly to almost fresh water in the west. In 1825, the sea broke through the narrow Agger Tange during a storm. This gap later closed and another gap formed during a storm in 1862 near the small town of Thyborøn. This gap has been maintained for navigation by dredging the sand deposited by currents. The Limfjord covers about 1700 km². Towards the west the fjord is composed of rather wide, mostly shallow "bredninger" ("broads") interconnected by narrow sounds. The westernmost broad is Nissum Bredning, where oyster and mussel fishery is an important industry, but this has also been an important source for intentionally and unintentionally introduced species. Between Løgstør and the eastern opening into Kattegat, the Limfjord is rather narrow (1-2 km). Salinity currently varies from about 32 PSU towards the western end to about 20 PSU at the

eastern end. However, lower salinities are found in the broads where streams enter the fjord. Temperatures are generally a few degrees higher than in the North Sea, which makes the culture of oysters possible, but this is also conducive to the establishment of alien species.

Surface salinity in Danish waters decreases from full strength seawater (about 35 PSU) in the North Sea and the Skagerrack, to distinctly brackish (<10 PSU) around the easternmost island of Bornholm. Surface currents in the Transition Area are mostly northbound, *i.e.*, they carry the surplus of freshwater runoff from rivers and melting snow in the countries surrounding the Baltic through the Belt Sea and Kattegat to the Skagerrack. The surface outflow is compensated by a southbound undercurrent of saline water from the Skagerrack to the Baltic. These two water masses mix in shallow, narrow passages, primarily in the Sound (Øresund), where the shallow threshold at Drogden (7-8 m) causes a decrease in salinity of bottom water from about 30 PSU to about 17 PSU. Similar mixing takes place at the second shallow threshold between Gedser and Darsser Ort (16-17 m) in the western Baltic. On the other hand, stable haloclines as well as thermoclines are usually formed during most of the summer months, and oxygen depletion is also common at this time. Summer temperatures are about 12-16°C, and are slightly higher in protected fjords. The physical and hydrographic conditions in the Transition Area mean that there is a natural decline in the number of marine benthic invertebrates from more than 1000 in Skagerrack and the North Sea to about 150 in the Baltic around Bornholm.

The Danish Kattegat coast is characterized by a series of fjords along the east coast of Jylland, *e.g.*, Limfjord, Mariager Fjord, and Randers Fjord; Odense Fjord on the north coast of Fyn (Fuhnen); Isefjord and Roskilde Fjord on the north coast of Sjælland (Zealand). There are also a number of islands in Kattegat, *e.g.*, Hirsholmene off Frederikshavn, Læsø in the center of Kattegat, Anholt further south, Samsø, Sejrø, Nexelø and Hesselø in the southern part. Some of these areas have received more attention than others. Randers Fjord, which receives fresh water from the longest Danish stream - Gudenå; was studied in detail by A.C. Johansen and others (Johansen 1918). It received national attention in 1997 when all the benthic fauna died due to anoxia. Isefjord and Roskilde Fjord were described in the monograph by Rasmussen (1973) and in Rasmussen (1989). The salinity of Isefjord is generally higher than in southern Kattegat, and there is very little difference between the entrance of the fjord and the southern part (Rasmussen 1973). The area off of Frederikshavn, including Hirsholmene, has been used for summer biology courses for students from the University of Copenhagen for more than one

hundred years, which explains why many single records have been made in this area.

At the southern end of the Kattegat there are three rather narrow sounds: the Lillebælt (Little Belt) towards the west, the Storebælt (Great Belt) in the middle, and Øresund (the Sound) towards the east. Combined, these three sounds are referred to as the Belt Sea. Sometimes the southernmost part of Kattegat is included in the Belt Sea, and in a few cases, even the westernmost part of the Baltic Sea has been included (Esping and Grönquist 1995). The sounds are characterized by high currents and great depth (>40 m) in the Storebælt and Øresund. International shipping traffic is high in the Belt Sea, which increases the probability of alien species transfer.

The Baltic Sea west of the threshold at the Gedser-Darsser Ort is characterized by recurring oxygen depletion and stagnant water. Several rivers enter this area from the south (Germany), and the islands south of Fyn create narrow, shallow passages. There is a man-made connection from the North Sea, the Kiel Canal, and it has been speculated that this has been a corridor for the introduction of some alien species in both directions.

The island of Bornholm in the central Baltic Sea separates the Arkona Basin from the Bornholm Basin. This is part of the Baltic proper, which has not received many alien species, probably because of greater depth, recurring and long-lasting oxygen depletion, and the distance from international ports and river mouths. The only rocky shores in Denmark are found on Bornholm.

ACCOUNT OF SPECIES

Cnidaria

Bougainvillea rugosa Clarke, 1882
Origin: NW Atlantic (Chesapeake Bay to South Carolina).
Status in Danish waters: Not established. There are a few unpublished records from off of Frederikshavn (NW Kattegat) in the 1960s.

Cordylophora caspia (Pallas, 1771)
Origin: Brackish water (<10 PSU) in the Black Sea and Sea of Azov.
First record: Uncertain, but spread in Europe during the 1800s.
Vector: Probably shipping.
First recorded in 1895 in Ringkøbing Fjord; also recorded in Holbæk Fjord (in Isefjord) and around Bornholm in the Baltic Sea at about the same time. There are also individual records from the Limfjord, Randers Fjord, and Kattegat.
Present status: Established? Found in Von Å (connecting Stadil Fjord and Ringkøbing Fjord) in 1960-1961 (Muus 1967). Not found in Holbæk Fjord in

1960-1961 (Rasmussen 1973). As epifauna is not part of the regular monitoring programs of the Danish counties, there are no recent records.

Gonionemus vertens Agassiz, 1862
Origin: NW Pacific?
Vector: May have been introduced to Europe with oysters, either directly from Japan or from the NW Atlantic.
First record: Possibly Portugal with oysters from Japan. It was noted in 1867 in France and in 1913 in the UK.
Secondary dispersal: The species was originally described from the west coast of North America, but it had probably been introduced there from Japan. It also occurs in the NW Atlantic, and it is unclear whether the introduction to Europe was directly from Japan or by way of oysters from the NW Atlantic.
Present status: Not established. There is one record from off of Frederikshavn, 1960 (Kramp 1961). There are also single records from Sweden and the Netherlands. It may be established in the German Wadden Sea, just south of the Danish border. It is usually attached to seagrass in the daytime and free swimming during the night.

Platyhelminthes
Pseudodactylogyrus anguillae (Yin & Sproston 1948)
Origin: East Asia, parasitizing Japanese eel.
First record: 1977 in an eel farm in the Soviet Union.
Vector: Probably introduced with imported Japanese eels.
First Danish record: A survey in 1985 showed that this parasite was common in Danish eels both in fresh and brackish water.
Present status: Established and common (Køie 1988, 1991).

Pseudodactylogyrus bini (Kikuchi 1929)
Origin: East Asia, parasitizing Japanese eel.
Vector: In Denmark, the eels were probably released into Esrom Sø when the farm closed down.
First Danish record: 1985 in Esrom Sø
Present status: Established in eels in Esrom Sø, although not found in all years (Køie 1988, 1991)

Nematoda
Anguillicola crassa Kuwahara, Niimi & Itagaki, 1974
Origin: Parasitizing the swim bladder of eels in Japan and Taiwan.
First record: 1980 in Germany.

Vector: Probably with eels imported from Taiwan.
Secondary dispersal: In 1985 it was found in the Netherlands, and it has rapidly spread throughout western Europe and in the Mediterranean.
First Danish record: 1985 during a survey of eels. It had probably arrived some years earlier (Boetius 1989, Køie 1988, 1991).
Present status: Established, widespread, nuisance. This nematode can completely fill the swim bladders of eels. Whereas it does not cause damage in its native host, the Japanese eel, it is harmful to the European eel. It may prevent normal migration to breeding grounds in the Sargasso Sea. Infection can be up to 90% of the population (Pedersen 2004).

Annelida
Neanthes succinea (Frey and Leuckart 1847)
Origin: Cryptogenic. It was originally described from Heligoland and was later found along the European west coast and in the Mediterranean. It is also known from both coasts of North America, the east coast of South America and from West Africa (Smith 1963).
Vector: unknown.
First Danish record: It was first recorded in Kattegat in 1940, in 1945 in the Belt Sea and in the western Baltic in 1953.
Present status: Established. Stable populations found in Isefjord (Rasmussen 1973) and Limfjord (Hedeselskabet 2004).

Marenzelleria viridis (Verrill 1873)
Recent taxonomic revision by Sikorski and Bick (2004)
Origin: NW Atlantic (Nova Scotia to Delaware).
First record: 1979 in the Firth of Forth, UK.
Vector: Ballast water?
Secondary dispersal: 1983 in the estuary of the Ems, Netherlands.
First Danish record: A dense population was found in Ringkøbing Fjord in 1990 (Kierkegaard 1990).
Present status: Established. Presently found in Ringkøbing Fjord and Nissum Fjord (Laursen *et al*. 2004).
Remarks: Sikorsky and Bick (2004) state that the species occurring in the North Sea is *M. viridis*, and the species occurring in the Baltic is described as a new one - *M. neglecta* Sikorsky and Bick, 2004. *M. viridis* apparently does not occur below 16‰. However, the salinity in Ringkøbing Fjord is mostly below this level (Laursen *et al*. 2004). Specimens from this locality should be examined to confirm their identity.

Ficopomatus enigmaticus (Fauvel 1923)
Origin: Cryptogenic. It was originally described from the northwestern coast of France, but Fauvel thought it originated in India. Others have speculated that it came from Australia with warships during World War I (1914-18).
First record: 1922? near Caen, France and shortly after in the docks of London, UK.
Vector: Hull fouling?
First Danish record: 1939 on a ship in the docks of Marstal (Ærø, a small island in the western Baltic) (Wesenberg-Lund 1941). The next record is from 1953 when it was found in the southern harbor of Copenhagen along with the crab *Rhithropanopeus harrisii* near the outlet for cooling water from a power plant; both adult worms and free-swimming larvae were found (Rasmussen 1958).
Present status: Established. The southern harbor of Copenhagen near power plant H. C. Ørstedsværket is the only locality where this species is found permanently (G. H. Petersen, pers. comm). Dense growths were observed in 1997 and 1998, and it probably depends on the slightly elevated temperature near the power plant.

Mollusca
Potamopyrgus antipodarum (Gray, 1853)
(=*Potamopyrgus jenkinsi* (Smith, 1889); =*Hydrobia jenkinsi*).
Origin: New Zealand
First record: When Smith described *Hydrobia jenkinsi* from the Thames estuary, he assumed that it had been present there since 1859. Several hypotheses were put forward to explain the sudden appearance of this species in a well-studied area. However, in 1988 it was finally determined that this species was identical to the New Zealand species now known as *Potamopyrgus antipodarum* (Ponder 1988).
Vector: Probably shipping.
Secondary dispersal: 1899 Kiel Canal (Germany); 1913 Netherlands; 1926-30 central Baltic; 1936 Gulf of Finland; 1945 northern Gulf of Bothnia.
First Danish record: For many years, 1915 was cited as the first record in Danish waters, namely in Randers Fjord. A re-examination of the collections in the Zoological Museum in Copenhagen (ZMUC) indicated that several specimens had been collected in 1914 from that same locality and by the same collector. Additionally, the collection includes two vials labeled *Potamopyrgus jenkinsi* that are even older. One specimen was collected at Kalvebod beach near the harbor of Copenhagen in 1897. This specimen appears to have been separated after preservation from a larger lot of specimens labeled *Hydrobia ventrosa*. It is unclear who separated, identified, and labeled the single

individual and when this was done. The second vial contained three small specimens colleted at Raadvad at the stream Mølleåen north of Copenhagen in 1906. These were identified by the malacologist Prof. C. M. Steenberg. Since *P. antipodarum* cannot be identified unequivocally on the basis of shell morphology, it cannot be confirmed with certainty that these specimens represent an introduction 10-20 years before that in Randers Fjord.
Present status: Established. The distribution in Danish waters was described by Bondesen and Kaiser (1949). More recently it has been collected in several brackish fjords and estuaries (Muus 1967), in Selsø, a brackish lake close to Roskilde Fjord (Rasmussen 1973) and three brackish water inlets - Kysing Fjord, Odense Fjord, and Roskilde Fjord as well as in freshwater localities (Jacobsen and Forbes 1997).

Potamopyrgus antipodarum is an apomictic parthenogenetic species with genetically distinct populations in freshwater and brackish water localities (Jacobsen and Forbes 1997).

Crepidula fornicata (Linnaeus 1758)
Origin: NW Atlantic (Gulf of St. Lawrence to Texas).
First record in Europe: 1887-1890 on the south coast of England.
Vector: Probably introduced with American oyster spat (*Crassostrea virginica*).
First Danish record: 1934 Wadden Sea and Nissum Bredning (W Limfjord). Probably introduced with juvenile oysters from the Netherlands (Spärck 1935).
Secondary dispersal: 1940 Livø Bredning (Limfjord), 1948 off Frederikshavn (N Kattegat) (Spärck 1950).
Present status: Established. There is a stable population in the Danish Wadden Sea. There are dense, reproducing populations in the Limfjord (Hedeselskabet 2004) and N Kattegat (own collections). Not found south of the eastern opening of the Limfjord.

Ocinebra erinacea (Linnaeus 1758)
Origin: This is a warm-water species of the East Atlantic, and presumably it could invade Danish waters if conditions were favorable.
First Danish record: There is only one record of this species. It was found in a shipment of oysters, *Ostrea edulis* from western Ireland, which was intended for culture in the western Limfjord (Haumann, pers comm.). There were two adult specimens, so if they had not been spotted and removed, the consequence could have been at least a temporary infestation of the natural oyster beds. The preserved specimens are now located in the ZMUC.
Present status: Not established.

Crassostrea gigas (Thunberg 1793)
?=*C. angulata* (Lamarck 1819)
Origin: The identity or difference between the Portuguese oyster (*C. angulata*) and the Pacific oyster (*C. gigas*) has been discussed for many years. Initial molecular data indicated that the Portuguese oyster was identical to *C. gigas* (Menzel 1974), but more recent work on several DNA sequences has shown that there is a whole complex of different *Crassostrea* species, and that *C. angulata* and *C. gigas* are separate species (Boudry *et al*. 1998, O'Foighil *et al*. 1998, Lam and Morton 2004). However, hybridization produces fertile offspring, so the two species are still claimed to be identical (Huvet *et al*. 2002).
First record: The Portuguese oyster was probably introduced from Taiwan for culture several hundred years ago. The species currently called *Crassostrea gigas* in Europe was introduced to Belgium from Japan.
Secondary dispersal: It has been transplanted from Belgium to France and Portugal. It has formed reproducing populations in several places since 1995, and it has now established a reproducing population in the German Wadden Sea (Wehrmann *et al*. 2000).
First Danish record: The Portuguese oyster was imported for culture in the Limfjord around 1972. Japanese oysters were imported from the UK for culture in the Isefjord around 1987. In both cases culture was abandoned after a few years. Culture has also been attempted in the Danish Wadden Sea at Rømø.
Present status: Not established? There may be a small population in the Limfjord (Nissum Bredning) and at Rømø in the Wadden Sea. Live specimens have been collected many years after culture was abandoned, but it is not known whether specimens living in Danish waters are actually reproducing there.

Crassostrea virginica (Gmelin 1791)
Origin: NW Atlantic (Gulf of St. Lawrence to Gulf of Mexico and Caribbean)
First record: Around 1850 (south coast of UK)
Vector: Imported for aquaculture.
First Danish record: 1880 in Lillebælt where culture was unsuccessfully attempted.
Present status: Not established.

Dreissena polymorpha (Pallas 1771).
Origin: Ponto-Caspian.
The first records from central Europe date to 1780 when it was found in the River Rhine near Karlsruhe.
First Danish record: 1843 in Ladegårdsåen in Copenhagen, but it had probably arrived a few years before (Mandahl-Barth 1949). It spread to other lakes

around Copenhagen, *e.g.*, Furesø in 1914 and Esrom Sø in 1926, and further out to lakes on Sjælland (Zealand). Apparently, it did not spread any further than this for many years. There is only one lot of specimens in the ZMUC collected from a lake in Jylland, Jels Nedersø, in 1983.
Present status: Established in fresh water. At the present time *D. polymorpha* is still abundant in many lakes on Sjælland, *e.g.*, Esrom Sø and Furesø. *D. polymorpha* does not occur in coastal waters in Denmark. There is one lot of specimens in the ZMUC from the mouth of Suså, a stream in western Sjælland.
Remarks: Adverse effects have only been recorded once, when the power plant at Sortedamssøen in Copenhagen had to be shut down in 1909 to clean out mussels.

Ensis americanus Gould, 1870
(=*Ensis directus* auctt. - non (Conrad 1843): based on fossil shells)
Origin: NW Atlantic
First record: 1979 in the German Bight, North Sea. The shells indicated that the species had been living there for several years.
Vector: Presumably larvae were transported in ballast water.
First Danish record: 1981 in the Wadden Sea near Rømø.
Secondary dispersal: In 1982, shells were found washed up at Hirtshals on the Danish Skagerrack coast. In the same year, it was also recorded in the Netherlands. In 1984, it was found near Hals in northwestern Kattegat. In 1987, it was recorded in Belgium. In 1988, it was recorded in the western Limfjord. In 1989, it was first recorded in the UK. In 1994, it was first recorded in the western Baltic (Knudsen 1989b, 1997).
Present status: Established. It is now one of the most common bivalves in the Limfjord and northern Kattegat. There also must be dense populations along the Danish North Sea and Skagerrack coasts. It now also occurs on the west coast of Sweden. Planktonic larvae occur in Øresund all year round (Ockelmann, pers. comm.).

Petricola pholadiformis Lamarck, 1818
Origin: NW Atlantic (Gulf of St. Lawrence to Uruguay).
First record: 1890 southeastern coast of England.
Vector: Associated with import of American oysters?
First Danish record: 1905 in the Wadden Sea.
Secondary dispersal: 1912 Esbjerg harbor (Wadden Sea), 1915 Lønstrup (Skagerrack coast). The first record from the Limfjord is from 1926. In northern Kattegat it was found in 1931 and was found in Storebælt in 1943. There is a

record from the western Baltic in 1927. It might have migrated through the Kiel Canal.
Present status: Established. It has been collected many times in the Wadden Sea, along the Skagerrack coast, the Limfjord, and in northern Kattegat (Knudsen 1989a).
Remarks: This specimen requires a hard substrate such as calcareous cliffs or hardened marine peat. This is only found in a few places in Danish waters. The only specimen in the ZMUC from Ringkøbing Fjord was collected in 1911, *i.e.*, one year after the canal at Hvide Sande had been dredged. This canal was closed in 1915, and the salinity has probably been too low since then. The shell is also very small, and it is likely that there is no suitable substrate for larger specimens to bore into.

Mya arenaria Linnaeus, 1758
Origin: This species has a long geological history. It probably originated in Japan where fossils are known from the Tertiary. It spread to the coasts of North America during the Miocene and to Europe during the Pleistocene. It went extinct in Europe but remained on the east coast of North America, where it is presently found from Labrador to Georgia (Strasser 1999).
First record: unknown
Vector: Shipping (intentional or unintentional)
First Danish record: unknown.
Present status: Established and very common in all Danish waters.
Remarks: Shells of *Mya arenaria* are unknown in archeological sites from the Stone Age and up till about 800 A.D. Shells from a geological study at Skagen turned out to be from the thirteenth century (Petersen *et al*. 1992). This indicates that this species was probably (re)introduced to Europe by Vikings returning from North America. Present distribution in Europe is from the White Sea to Spain and in the Baltic to the Bothnian Bay and the Gulf of Finland. *M. arenaria* is present and absent in Ringkøbing Fjord according to changes in salinity. It re-established soon after the change in salinity in 1995 (Laursen *et al.* 2004). It should be noted that *M. arenaria* only reached Iceland in 1958 and that it does not occur in the Faroe Islands.

Teredo navalis Linnaeus, 1758
Origin: Cryptogenic. It is possible that this species is a native of the North Atlantic. It is also uncertain whether anthropogenic activities have been responsible for its introduction; it could have arrived on driftwood. Hence it has usually been omitted in Danish lists of alien species. As it is now included in

most lists of alien species from the Baltic Sea, we have decided to include it in the present paper.
Vector: Shipping? Driftwood?
First Danish record: Unknown
Present status: Established in most Danish waters, *e.g.*, Kattegat, Lillebælt, Isefjord, Øresund to Copenhagen, W Baltic Sea (Kristensen 1969, 1979, Miljøstyrelsen 2003).
Remarks: Until recently, it was accepted that *Teredo navalis* does not form stable, reproducing populations in the Baltic proper. However, successful settling has been observed at Bornholm in the central Baltic Sea, so planktonic larvae must be present (Miljøstyrelsen 2003).

Crustacea
Mytilicola intestinalis Steuer, 1902
Origin: Mediterranean. Parasitizes *Mytilus galloprovincialis* Lamarck, 1818.
First record: 1937 in Portsmouth, UK; 1939 German Wadden Sea.
First record in Danish waters: 1964 in Nissum Bredning, Limfjord (Theisen 1964, 1966).
Vector: As this species can also parasitize oysters, it is possible that it was introduced into Danish waters with imported oyster spat from the Netherlands. However, it could also have dispersed through free-swimming larvae or from mussels attached to ships' hulls.
Present status: Established in *Mytilus edulis* Linnaeus, 1758 in the Limfjord, where it has a negative impact on the condition of the mussels. Not known elsewhere in Danish waters (Theisen 1987).

Balanus improvisus Darwin, 1854
Origin: Cryptogenic
First record: Possibly 1844 in Königsberg (= Kaliningrad) (Münter and Buchholz, 1870). Darwin's specimens were from Peru, La Plata, southern Patagonia, Nova Scotia and some localities in the British Isles. He also had specimens from the hull of the "Beagle".
First Danish record: 1880 in the harbor of Copenhagen.
Vector: Probably fouling the hulls of ships.
Present status: Established, common in most parts of Danish waters.

Elminius modestus Darwin, 1854
Origin: Australia and New Zealand.
First record: 1939-40 in Southampton, UK
Vector: Warships from WWII?

Secondary dispersal: Remaining part of British Isles shortly after first record. 1946 - first Dutch record; 1953 - recorded in German North Sea. A survey in 1960 did not reveal specimens from the Danish North Sea coast.
First Danish record: 1978, Rømø, Wadden Sea, attached to blue mussels and stones (Theisen 1980).
Present status: Established? This species probably dies out during cold winters and recolonizes after mild winters. It is not known whether it reproduces in the Danish Wadden Sea, and it has not been found anywhere else in Danish waters.

Eriocheir sinensis Milne-Edwards, 1854
Origin: China (Fukien Province to Korea).
First record: 1912 in a tributary to the River Weser (Germany).
Vector: Ballast water?
Secondary dispersal: 1920s - spread to other rivers in Germany. 1930s - found in rivers of the Netherlands, Belgium and France. Single individuals found in the UK, but apparently not established in this country. In 1965, it was first recorded in the Great Lakes, USA.
First Danish record: 1927 off the coast of Thy, northern Jylland (Rasmussen 1987).
Present status: Not established, but there are numerous records over the years from several localities, both freshwater and marine. Mass occurrence has been recorded in 1933 in Højer in the Danish Wadden Sea. In 1997 a population was observed in Holbæk Fjord. Many records are from localities near harbors, indicating transport in ships. Only three ovigerous females have been recorded in Danish waters, in three different localities (Rasmussen 1987, 1993, Tendal 2003).

Rhithropanopeus harrisii (Gould 1841)
Origin: NW Atlantic (Nova Scotia to Mexico)
First record: 1874 in the Zuidersee, Netherlands (as *Heteropanopa tridentata* Maitland, 1874).
Vector: Hull fouling or ballast water.
Dispersal: 1936 near Kiel, Germany; 1951 - first recorded in Poland, where it became common during the 1960s. Now also found in the Black Sea and on the west coast of the USA.
First Danish record: There is only one record of this species from Danish waters. In 1953 numerous specimens were found in the southern harbor of Copenhagen together with the polychaete *Ficopomatus enigmaticus*, close to the cooling water outlet of a power plant (Wolff 1954).

Present status: Not established. Although *F. enigmaticus* has established a population in this locality, *R. harrisii* has not been found since the original record.

Callinectes sapidus Rathbun, 1896
Origin: NW Atlantic
Vector: ?Shipping
First Danish record: 1951 in Øresund (Wolff 1954). This is the only record of a live animal.
Present status: Not established.

Chelicerata
Limulus polyphemus (Linnaeus 1758)
Origin: NW Atlantic (Maine to Yucatan).
First record: Introduced for aquaculture at Heligoland in the German Wadden Sea around 1860. This introduction was unsuccessful and the species did not establish itself.
First Danish record: 1968 at Læsø (N Kattegat).
Present status: Not established. There are several records of specimens from the Transition Area during the 1968-1976 period. These were probably specimens brought from the coast of the USA by seamen who then threw them overboard when they passed through Danish waters (Wolff 1977).

Ascidiacea
Styela clava Herdman, 1882
Origin: NW Pacific (Sea of Okhotsk and Korea)
First record: 1953 at Plymouth, UK. It has also been found on both coasts of the USA and in Australia.
Vector: Warships returning from the Korea War (Minchin and Duggan 1988) or associated with oysters (Lützen 1999).
Dispersal: 1970 it was found in France (Channel coast), 1972 in Ireland, 1974 in the Netherlands.
First Danish record: 1978? in the western Limfjord (Christiansen and Thomsen 1981).
Present status: Established throughout the Limfjord from west to east. It has recently been found in the Danish Wadden Sea (Lützen 1999). It attaches to oysters, blue mussels and horse mussels, and also to stationary fishing gear.

Table 1

Established alien benthic invertebrates in Danish coastal waters.

Species	First Danish record (year)	Present distribution
Cordylophora caspia	Ringkøbing Fjord (1895)	?Ringkøbing Fjord (Von Å)
Pseudodactylogyrus anguillae	Parasitic in eels from several localities (1985)	Common in eels in marine, brackish, and fresh water
Pseudodactylogyrus bini	Parasitic in eels in Esrom Sø (1985)	In eels in Esrom Sø, though not found in all years
Anguilicola crassa	Parasitic in eels from several localities (1985)	Widespread in eels in Danish waters; up to 90% infected
Neanthes succinea	Kattegat (1940)	Isefjord, Limfjord, possibly other localities
Marenzelleria viridis	Ringkøbing Fjord (1990)	Ringkøbing Fjord, Nissum Fjord
Ficopomatus enigmaticus	(on ship in dock in Marstal, W. Baltic (1939)), southern harbor of Copenhagen (1953)	Southern harbor of Copenhagen
Potamopyrgus antipodarum	(?Kalvebod Strand, Copenhagen (1897); ?Mølleå at Raadvad (1906)); Randers Fjord (1914)	Several brackish and estuarine fjords and freshwater localities
Crepidula fornicata	Wadden Sea and W Limfjord (1934)	Dense reproducing populations in the Limfjord and N Kattegat; also in Wadden Sea
Dreissena polymorpha	Ladegårdsåen, Copenhagen (1843)	Common in fresh water on Sjælland; one or two localities in Jylland
Ensis americanus	Rømø, Wadden Sea (1981)	Abundant in Wadden Sea, North Sea, Skagerrack, Limfjord, Kattegat; few records from the Belt Sea and W Baltic
Petricola pholadiformis	Wadden Sea (1905)	Wadden Sea, Skagerrack coast, N Kattegat, Limfjord
Mya arenaria	?Skagen (?1250-1300)	Common in all Danish waters at shallow depths.
Teredo navalis	? (before 1800)	Common in all Danish waters on suitable substrata.
Mytilicola intestinalis	Parasitic in *Mytilus edulis* in W Limfjord (1964)	Nuisance species in mussels in the Limfjord; not established elsewhere.
Balanus improvisus	Harbor of Copenhagen (1880)	Common in most parts of Danish waters
Elminius modestus	Rømø, Wadden Sea (1978)	?Rømø, Wadden Sea (disappears in cold winters)
Styela clava	W Limfjord (1980?)	throughout the Limfjord

Table 2

Incidental alien marine invertebrates in Danish waters.

Species	Records (year)
Bougainvillea rugosa	Frederishavn, NW Kattegat (1960s, few records)
Gonionemus vertens	Frederikshavn, NW Kattegat (1960)
Eriocheir sinensis	Thy, Skagerrack (1927); many records from numerous localities (Rasmussen, 1987; Tendal, 2003)
Rhithropanopeus harrisii	Southern harbour, Copenhagen (1953)
Limulus polyphemus	Several records between 1968-1976 (Wolff, 1977)
Callinectes sapidus	Øresund (1951)
Ocinebra erinacea	Limfjord, oyster culture area (1982)
Crassostrea gigas	Limfjord (1972); Isefjord (1987); Wadden Sea (2004 - established?)
Crassostrea virginica	Lillebælt (1880)

Table 3

Donor regions and vectors for established alien species introduced in Danish waters. Species marked with an * have invaded Danish waters through secondary dispersal.

Donor region	Species	Year	Vector
NW Atlantic	*Marenzelleria*	1990	Ballast water*
	Crepidula	1934	Oysters
	Petricola	1905	Oysters?
	Ensis	1981	Ballast water*
	Mya	ca. 1280	Shipping(*?)
NW Pacific	*Pseudodactylogyrus bini*	1985?	Aquaculture
	P. anguillae	1985?	Aquaculture
	Anguillicola	1985?	Aquaculture
	Styela	1978?	Shipping?/ oysters?
Ponto-Caspian	*Cordylophora*	1895	Shipping(*?)
	Dreissena	1843	Unknown
S Pacific	*Potamopyrgus*	1914	Shipping
	Elminius	1978	Shipping(*?)
Mediterranean	*Mytilicola*	1964	Shipping?/ oysters?
Cryptogenic	*Balanus*	1880	Shipping(*?)
	Neanthes	1940?	Unknown
	Ficopomatus	1953	Shipping
	Teredo	? <1800	Shipping?

Table 4

Vectors for the introduction of established alien marine species in Danish waters.

Vector	Number of species
Fouling	7(9)
Ballast water	2
Aquaculture (unintentional)	7(5)
Unknown	2

Table 5

Period of alien marine invertebrate introduction in Danish waters.

	Before 1800	1801-1900	1901-1950	After 1950
Established species	2	3	4	9
Not established	0	1	1	7

Table 6

Summary of donor regions for established alien marine invertebrates in Danish waters.

Region	Number of species
NW Atlantic	5
NW Pacific	4
Ponto-Caspian	2
S Pacific	2
Mediterranean	1
Cryptogenic	4

Table 7

Recipient areas for alien species in Danish waters. The numbers in the columns cannot be added as one species may be established in more than one locality, and species that are widespread may also be recorded in fresh water.

Locality	First record	Established	Single records/not established
Wadden Sea	3	3(4)	
Ringkøbing Fjord	2	2	1
Nissum Fjord		1	
North Sea			1
W Limfjord	4	4	
Skagerrack	1	1	
N Kattegat	1	2	2
E Limfjord		3	
Randers Fjord	1		
S Kattegat	1		
Isefjord	1	1	
Øresund	2(3)	1	1
Bornholm			1
Fresh water	4	5	
Widespread		5	2
Unknown	1	2	

DISCUSSION

About 27 alien marine species have been recorded in Danish waters (Tables 1 and 2). Four of them are parasitic - three in eels and one in mussels. The majority of species have been introduced through shipping activities, first and foremost as hull fouling (Tables 3 and 4). Aquaculture is the second most important vector. It should be noted that, thus far, species that have been intentionally introduced into Danish waters have not been able to establish reproducing populations in the wild. Half of the established species were introduced after 1950, and the majority of non-established species were also introduced after 1950 (Table 5). The majority of the alien species originate from

the Northwest Atlantic (Table 6) and only two are of Ponto-Caspian origin. The species that originate from the Northwest Pacific region have all been introduced in association with aquaculture (Table 3). The Wadden Sea and the Limfjord are the most important recipient areas in Danish waters (Table 7). However, many species are widespread and many also occur in fresh water. In fact, two species, *Pseudodactylogyrus bini* and *Dresissena polymorpha*, occur exclusively in fresh waters in Denmark and should not be included on lists of alien marine species.

Recent studies on alien species list about 50 alien marine benthic species as permanently established in the North Sea (Reise *et al.* 2002), but only 14 have established in the Danish part of the North Sea, including the Wadden Sea, Limfjord, Ringkøbing Fjord, and Nissum Fjord (present study). Several of the species established in the southern and western parts of the North Sea are occasionally found in Danish waters, but they have not established permanent reproducing populations. In some cases, *e.g.*, *Crassostrea gigas* and *Elminius modestus*, this is simply due to borderline low temperatures. For most species, however, no clear explanation can be given. None of the large European rivers extend into Denmark, and Danish rivers and streams are generally not navigable for larger vessels. Thus, rivers cannot function as dispersal corridors. Furthermore, water flow and the influx of salt waters to most streams in western Denmark have been regulated for many years and therefore larval influx is impeded. The majority of established alien species (14 of 18) in Danish waters are found in the Wadden Sea, the Limfjord, and the two coastal lagoons on the west coast (Table 1). In most cases they have arrived through secondary dispersal from the south. The North Sea coast of Germany has 26 permanently established alien benthic species (Nehring 2002), and many of these species that have not been recorded in Danish waters are very small and difficult to identify, *e.g.*, hydroids and amphipods.

It is difficult to determine the number of established alien marine benthic species in the Baltic Sea because most papers include Kattegat and the Belt Sea in their lists (Leppäkoski 1984, Leppäkoski *et al.* 2002). However, Nehring (2002) listed 14 species from the Baltic coast of Germany. Very few of the species that have become established in the Baltic Sea, but not in the North Sea, are found in Danish waters, and only eight alien species are established in the Danish part of the Baltic Sea, excluding Kattegat and the Belt Sea. Secondary dispersal patterns for species introduced to the Baltic are generally towards the north and east along the Swedish and Finnish coasts rather than through the Belt Sea and into Kattegat. The present study has shown that the alien species found in Kattegat and the Belt Sea have dispersed from the North Sea, and their present distribution is determined by their tolerance of low salinities. The alien

species found in the Danish part of the Baltic Sea are the ones that also occur in the North Sea, Kattegat, and the Belt Sea.

Other countries in northern Europe have extensive research programs on the current impacts of alien species in marine waters. The ecology of *Crepidula fornicata* has been studied in France (de Montaudouin *et al*. 1999), Ireland (Minchin *et al*. 1995), and Germany (Thieltges *et al*. 2003, 2004). There have also been extensive studies on the invasive species of *Marenzelleria viridis* and *M. negelcta* in the Baltic as well as in the Wadden Sea (Norkko *et al*. 1993, Bastrop *et al*. 1998, Essink 1999); however, no research on them has been conducted in Danish waters, except to record their presence in Ringkøbing Fjord and Nissum Fjord (Kierkegaard 1990, Laursen *et al*. 2004). Current distributions for other species, such as *Cordylophora caspia* and *Potamopyrgus antipodarum*, are unknown. It is to be suspected that some of the species that have been recorded in the western Baltic could be present, but unnoticed, in Danish waters. Most Danish counties do not identify polychaetes to the species level. There are at least four native species of *Polydora* found in Danish waters, and it is possible that *P. redeki* (=*Boccardia redeki*) could also be present. However, it is also possible that it cannot compete with the congeners.

Danish marine waters are not only a transition zone in the ecological sense, but also with regard to management. The North Sea, Skagerrack, and the northern part of Kattegat are managed through the OSPAR convention, whereas the Baltic Sea, Belt Sea, and Kattegat are managed through the HELCOM convention. ICES fisheries regions also divide Danish waters, and administrative borders are different for all these management bodies. Thus, there is considerable overlap among management bodies, especially in the Kattegat area. In addition, environmental monitoring in Danish waters is split between two authorities: coastal waters and fjords are the responsibility of the counties, and open water is the responsibility of the Ministry of Environment. Habitats included in Natura2000, *e.g.*, the Wadden Sea, Ringkøbing Fjord, Nissum Fjord, and parts of the Limfjord, require special attention, but so far few reports are available. Presently, there is no special program to monitor the introduction of alien species to Danish waters.

The present study indicates that despite heavy international shipping traffic through Danish waters apparently no alien species have been released with ballast water into Danish waters. However, several species that have been introduced with ballast water in the coastal waters of other North Sea countries, especially the Netherlands, have invaded Danish waters through secondary dispersal, but very few have dispersed all the way to the Baltic. This is also the case for species that have been introduced in association with oysters for culture. Denmark is located at the northern limit for oyster culture, and

apparently the associated species cannot tolerate the low salinity in the Baltic. The decrease in the number of native species seen through the Transition Area is reflected in the distribution of established marine alien species. Thus, Danish waters in general act as a barrier to the dispersal of alien species. As most of the alien species have arrived by secondary dispersal along the North Sea coast, it is obvious that the Wadden Sea, the Limfjord, and the coastal lagoons on the west coast should be carefully monitored for the settlement of alien species in these sheltered habitats. It is also recommended that a careful survey be performed along the Baltic coast of southern Denmark as alien species may have been overlooked by the regular monitoring programs.

ACKNOWLEDGEMENTS

The first author wishes to acknowledge a travel grant from the Institute of Oceanography, University of Gdansk, which allowed her to participate in the conference *Baltic – The Sea of Aliens*, which was held in Gdynia, 24-27 August 2004. The organizers and participants are thanked for valuable discussions during the conference.

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