

Non-native species and rates of spread: lessons from the brackish Baltic Sea

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Abstract

The Baltic Sea, a semi-enclosed brackish water region, has been inoculated by non-indigenous species for centuries. Today, much of its biological diversity is of foreign origin (i.e. xenodiversity), intentionally or unintentionally moved by humans over ecological and geographical barriers. As many as 98 introduced species have been recorded in the Baltic Sea and Kattegat. The role and abundance of much of the unique native brackish water fauna of the Baltic Sea are threatened by these non-indigenous species. The rate of primary introductions into the Baltic has increased since the 1950s; the secondary rate of spread of non-indigenous species within the basin varies from 30-480 km/year. We review here the invasion histories of the brown alga *Sargassum muticum* (introduced in the early 1990s), the mud snail *Potamopyrgus antipodarum* (1887), the barnacle *Balanus improvisus* (1844), the polychaetes *Marenzelleria viridis* (1985) and *Polydora redeki* (1963), the cladoceran *Cercopagis pengoi* (1992) and the mysid shrimp *Hemimysis anomala* (1962).

Introduction

The global exchange of aquatic species is accelerating. The geographic isolation of continents as a creator and conservator of global biodiversity has been breached for several centuries. For example, an air-flight of a few hours delivers species for aquaculture along with their parasites and other associated biota from one continent to another. In recent years, especially since Carlton's (1985) review on ships' ballast water as a vector of transoceanic introductions, both scientific and public interest have turned to the non-indigenous estuarine and marine organisms and their impact on aquatic ecosystems. Many natural barriers to dispersal have been weakened and, consequently, both the number of potential invaders and the number of remote donor areas have increased through human-mediated dispersal (Ruiz et al. 1997).

The Baltic Sea is an enclosed brackish region, isolated from both fully marine and fully freshwater milieus. Much of its present biological diversity is of foreign origin, i.e., composed of species intentionally or unintentionally moved by humans over intrinsic environmental barriers. We define the current situation as illustrating *xenodiversity* (Gr. *xenos* - strange) to indicate structural and functional diversity caused by non-indigenous species (Leppakoski and Olenin, in press). The biogeographical peculiarities (e.g., the characteristic mixture of marine, brackish water and freshwater species, and relicts from previous periods), developed since the last glacial period in the Baltic, Black and Caspian Seas are threatened by the introduction of non-indigenous species (Leppakoski and Mihnea 1996). These seas are, to an increasing extent, subject to the world-wide biological homogenisation of the brackish-water fauna.

The Baltic Sea ecosystem is characterised by physical, chemical and biological gradients. Traditionally, most marine biological research has dealt with the distribution of species, structures of populations and communities, as well as links among organisms and subsystems in relation to these gradients. In the Baltic Sea the hydrographical gradients are three-dimensional (north-south, east-west, surface-bottom), and further vary diurnally, seasonally, interannually as well as across longer time spans (cf. Leppäkoski and Bonsdorff 1989).

Within the Baltic, salinities vary from 20 to 25 psu in the Kattegat to about 3 psu in the inner parts of the Gulfs of Bothnia and Finland. Annual phytoplankton primary production falls approximately 90% along the same gradient. However, the salinity gradients are broad even over short distances, e.g., from fresh water at the mouths of rivers to 20 psu in the southwestern Baltic. This habitat variability offers hospitable conditions for non-indigenous species of different ecological tolerance and origin: marine, brackish and fresh water (cf. Gollasch and Leppäkoski 1999).

Nevertheless, most of the Baltic Sea has a stable surface salinity of 5-8 psu. The sea has a primary halocline eastward and northward to the Aland Sea (northern Baltic proper) at about 50-70 m depth, below which depth the salinity is several psu higher and oxygen content is lower. During summer a distinct thermocline forms in the Baltic proper at 10-30 m. This situation separates the cold intermediate water formed during winter from the warmer surface layer. The intensity of this discontinuity layer is lower towards the Gulf of Finland and the Gulf of Bothnia.

These vertical and horizontal gradients influence not only the structure and function of the native biotic communities (see Leppäkoski and Bonsdorff 1989; Wallentinus 1991; Olenin 1997 for a discussion of the Baltic gradients), but also their vulnerability to biotic invasions. The probability of a biotic invasion is fundamentally different along these gradients. For example, freshwater species are unlikely to establish self-sustaining populations in the waters with the higher salinity in the southern part or deeper areas of the Baltic (Olenin 1997; Gollasch and Leppäkoski 1999).

We deal here with recent human-mediated changes in species composition in the Baltic Sea. The region's long history of marine biology and national and international (HELCOM 1988) environmental monitoring provide a good opportunity to derive ecological lessons from well-documented introductions.

Barriers, vectors and rate of primary spread into the Baltic Sea

Introduction of non-indigenous species into the Baltic and other European brackish seas occurs in three main ways: (1) intentional introductions of species for fisheries, aquaculture, animals introduced for their fur, hunting and the aquarium trade, (2) transportation of aquatic habitat itself with the potentially invasive organisms, e.g., plankton assemblages in ballast water, fouling communities on ship hulls, or organisms associated with intentionally transferred species, and (3) active or passive intracontinental dispersal via canals (opened from 1775 to 1952) between the rivers that belong to the catchment areas of the Baltic, Black and Caspian Seas.

Invasion rates for the Baltic Sea appear to have increased in the past 50 years (Figure 1), due to changes in factors (e.g., duration of the voyages, anthropogenic disturbance, such as pollution, in donor and receiving areas) that once prevented the species' introductions. More ships now arrive with larger volumes of ballast water from more regions in less time than 50 years ago (Ruiz et al. 1997). In addition, the outflow of introduced crustaceans (Mysidacea and Amphipoda) has increased into the Baltic's coastal inlets and lagoons from the adjacent freshwater sources.

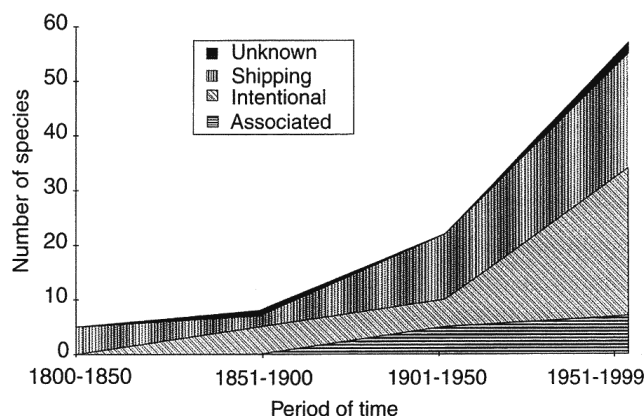


Figure 1. The rate of introductions into the Baltic Sea during the 19th and 20th centuries.

These introductions stem from numerous acclimatisation experiments performed, especially in the northwestern parts of the former USSR, in the 1960s and 1970s to improve the food base for commercial fish.

Ship traffic is currently the most important vector for spreading aquatic organisms into northwestern Europe, including the Baltic Sea (Gollasch and Leppakoski 1999). A representative volume of the donor area's pelagic ecosystem will be enclosed in any ship's ballast tanks. In addition, many mobile species can hitchhike over long distances on the ship's hull. The number of species transported at any moment by ships (so-called floating islands, Vermej 1996) has been estimated, on a global scale, at 3000-4000 (Carlton 1985; Gollasch 1996). The number of species brought into the Baltic Sea on ship hulls or in ballast water tanks within any time interval remains unknown.

We summarise here the dispersal mechanisms, timing and origins of biological invasions for non-indigenous species in the Baltic Sea (Table 1). At least 97 species are considered non-native in the Baltic Sea (incl. Kattegat inside the northernmost tip of Denmark); the exact routes of their introduction are often unknown. Of the 56 unintentional species introductions into the Baltic for which some dispersal history is known, 37 are trans-oceanic and 14 are trans-Atlantic with American origin. The Atlantic coast of North America has been the source for more species to the European brackish water seas than any other donor area (Figure 2); in both the Baltic and Black Seas, 35 species or 30% of all known introductions are native to North America (Leppakoski and Olenin, in press). This number may be related more to the successive opening of routes of commerce across the North Atlantic in the post-Columbian era than to the adaptability or competitive vigor of the potential invaders from North America.

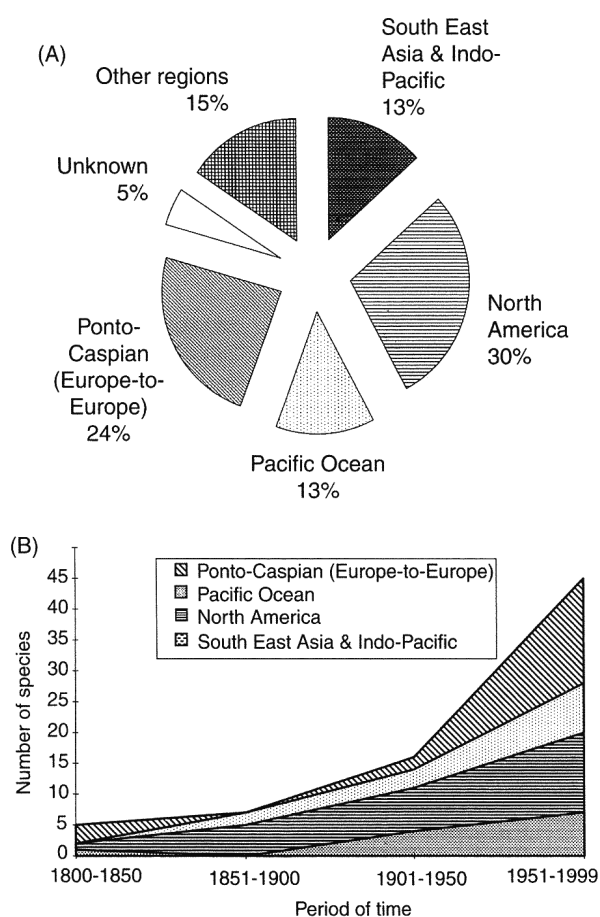


Figure 2. Origin of the Baltic Sea xenodiversity: (A) percentage of total number of non-indigenous species recorded; (B) the rate of introductions from the major donor areas.

Table 1. Current status of knowledge on the non-indigenous marine, brackish and fresh water species recorded in the Baltic Sea (incl. Kattegat).^a

Species	Date	Est.	Origin	Vector
Phytoplankton				
<i>Alexandrium tamarense</i>	No data	+?	Unknown	Shipping
<i>Coscinodiscus wailesii</i>	1983	+	N America, Indo-Pacific	Associated
<i>Gymnodinium catenatum</i>	1993	+	Unknown	Shipping
<i>Gyrodinium mikimotoi</i>	1981	+	Unknown	Shipping
<i>Odontella sinensis</i>	1903	+	SE Asia, Indo-Pacific	Shipping
<i>Pleurosigma simonsenii</i>	1987	?	Indian Ocean?	Shipping
<i>Pleurosira leavis f. polymorpha</i>	1900s	+	Unknown	Associated
<i>Thalassiosira punctigera</i>	1979	+	Unknown	Associated?
Phytobenthos				
<i>Bonnemaisonia hamifera</i>	1902	+	SE Asia, Japan	Shipping
<i>Chara connivens</i>	1858	+	W Europe	Shipping
<i>Codium fragile</i>	1932	+	SE Asia, Japan	Associated
<i>Colpomenia peregrina</i>	1930s	+	NE Pacific	Associated
<i>Dasya baillouviana</i>	1940s	+	S Atlantic, Mediterran.	Shipping
<i>Fucus evanescens</i>	1924	+	N Atlantic	Shipping
<i>Polysiphonia harveyi</i>	No data	+	SE Asia, Japan	Unknown
<i>Sargassum muticum</i>	1980s	+	SE Asia, Japan	Associated
<i>Elodea canadensis</i>	1870s	+	N America	Ornamental
Cnidaria				
<i>Bougainvillia rugosa</i>	No data	+	N America	Shipping
<i>Clavopsella navis</i>	1960	?	S Africa?	Shipping
<i>Cordylophora caspia</i>	1800s	+	Ponto-Caspian	Shipping
<i>Garveia franciscana</i>	1950	?	N America?	Shipping
<i>Gonionemus vertens</i>	1921	?	N America, N Pacific	Shipping
<i>Maeotias inexpectata</i>	1999	?	Ponto-Caspian	Shipping
Platyhelminthes				
<i>Pseudodactylogyrus anguillae</i>	1980s	+	Pacific	Associated
<i>P. bini</i>	1980s	+	Pacific	Associated
Nematoda				
<i>Anguillicola crassus</i>	1980	+	SE Asia, Indo-Pacific	Associated
Annelida				
<i>Branchiura sowerbyi</i>	1990s	+	SE Asia	Shipping
<i>Ficopomatus enigmaticus</i>	1953	+	SE Asia, Indo-Pacific	Shipping
<i>Marenzelleria viridis</i>	1985	+	N America	Shipping
<i>Paranais frici</i>	1995	+	Ponto-Caspian	Shipping
<i>Polydora redeki</i>	1960	+	North Sea	Shipping
<i>Potamothrix heuscheri</i>	1990s	+	Ponto-Caspian	Shipping
<i>P. vejvodskyi</i>	1990s	+	Ponto-Caspian	Shipping
Crustacea				
<i>Acartia tonsa</i>	1925	+	N America, Indo-Pacific	Shipping
<i>Ameira divagans</i>	1974	+	N America	Shipping
<i>Balanus improvisus</i>	1844	+	N America	Shipping
<i>Callinectes sapidus</i>	1951	–	N America	Shipping
<i>Cercopagis pengoi</i>	1992	+	Ponto-Caspian	Shipping
<i>Chaetogammarus ischnus</i>	1962	+	Ponto-Caspian	Stocking
<i>C. warpachowskyi</i>	1962	+	Ponto-Caspian	Stocking
<i>Corophium curvispinum</i>	1920s	+	Ponto-Caspian	Shipping
<i>Eriocheir sinensis</i>	1926	+	SE Asia	Shipping
<i>Gammarus tigrinus</i>	1975	+	N America	Shipping
<i>Gmelinoides fasciatus</i>	1996	+	Baikal Lake	Stocking
<i>Hemimysis anomala</i>	1962	+	Ponto-Caspian	Stocking

Table 1. Continued.

Species	Date	Est.	Origin	Vector
<i>Limnomysis benedeni</i>	1962	+	Ponto-Caspian	Stocking
<i>Obessogammarus crassus</i>	1962	+	Ponto-Caspian	Stocking
<i>Orconectes limosus</i>	1890	+	N America	Stocking
<i>O. virilis</i>	1960	+	N America	Stocking
<i>Pacifastacus leniusculus</i>	1960s	+	N America	Stocking
<i>Paramysis lacustris</i>	1962	+	Ponto-Caspian	Stocking
<i>Pomatocypis humilis</i>	1948	?	Africa NW Coast	Shipping?
<i>Pontogammarus robustoides</i>	1962	+	Ponto-Caspian	Stocking
<i>Rhithropanopeus harrisi</i>	1951	+	N America	Shipping
Mollusca				
<i>Crassostrea gigas</i>	1980s	–	SE Asia, Japan	Stocking
<i>C. virginica</i>	1880	–	N America	Stocking
<i>Crepidula fornicata</i>	1940s	+	N America	Associated
<i>Dreissena polymorpha</i>	1800s	+	Ponto-Caspian	Shipping
<i>Ensis americanus</i>	1981	+	N America	Shipping
<i>Lithoglyphus naticoides</i>	1800s	+	Ponto-Caspian	Shipping
<i>Mya arenaria</i>	12 century?	+	N America	Shipping
<i>Mytilopsis leucophaeata</i>	1930s	+	NW Africa, America?	Shipping
<i>Tapes philippinarum</i>	1983	?	SE Asia, Japan	Associated
<i>Petricola pholadiformis</i>	1931	+	NW Atlantic	Associated
<i>Potamopyrgus antipodarum</i>	1887	+	New Zealand	Shipping
<i>Teredo navalis</i>	18 century	+	SE Asia	Shipping
Bryozoa				
<i>Victorella pavida</i>	1960s	+	Indian Ocean?	Shipping
Tunicata				
<i>Styela clava</i>	1994	+	Pacific	Shipping
Pisces				
<i>Acipenser baeri</i>	1962	–	Siberia	Stocking
<i>A. gueldenstaedti</i>	1962	–	Ponto-Caspian	Stocking
<i>A. ruthenus</i>	1982	–	Ponto-Caspian	Stocking
<i>A. stellatus</i>	1999	?	Ponto-Caspian	Stocking?
<i>Ameirus nebulosus</i>	1982	–	N America	Stocking
<i>Aristichthys nobilis</i>	1970s?	?	E Asia	Stocking
<i>Catostomus catostomus</i>	1984	?	Siberia	Stocking
<i>Coregonus peled</i>	1965	?	Siberia	Stocking
<i>Ctenopharyngodon idella</i>	1970	–	Asia Amur	Stocking
<i>Cyprinus carpio</i>	14 century?	–	Ponto-Caspian, E Asia	Stocking
<i>Huso huso</i>	1960s	?	Ponto-Caspian	Stocking
<i>Hypophthalmichthys molitrix</i>	1970s?	?	E Asia	Stocking
<i>Ictalurus melas</i>	1984	+	N America	Stocking
<i>Lepomis gibbosus</i>	1998	+	N America	Ornamental
<i>Micropterus dolomieu</i>	1890	?	N America	Unknown
<i>Mugil labrosus</i>	1998	+?	SE Asia, Indo-Pacific?	Unknown
<i>Neogobius melanostomus</i>	1990	+	Ponto-Caspian	Shipping
<i>Oncorhynchus clarki</i>	1960s	–	N Pacific	Stocking
<i>O. gorbusha</i>	1973	–	N Pacific	Stocking
<i>O. keta</i>	1971	–	N Pacific	Stocking
<i>O. kisutch</i>	1975	–	N Pacific	Stocking
<i>O. mykiss</i>	1890	+	NE Pacific	Stocking
<i>O. nerka</i>	1959	–	N Pacific	Stocking
<i>O. tshawytsa</i>	1933	–	N Pacific	Stocking
<i>Percottus glehni</i>	1916	+	Amur River	Ornamental

Table 1. Continued.

Species	Date	Est.	Origin	Vector
<i>Salvelinus fontinalis</i>	1872	–	N America	Stocking
<i>S. namaycush</i>	1959	–	N America	Stocking
Aves				
<i>Branta canadensis</i>	1930	+	N America	Stocking
Mammalia				
<i>Mustela vison</i>	1925	+	N America	Stocking
<i>Ondatra zibethica</i>	1920s	+	N America	Stocking

^aFor references see database kept by Klaipeda University, Lithuania, available at <http://www.ku.lt/nemo/mainmemo.htm>. The database is an activity of the Baltic Marine Biologists' Working Group on Non-indigenous Estuarine and Marine Organisms.

Date – year of the first record in the area (if known) or probable time of introduction; Est. – established in the Baltic or adjacent freshwater bodies (+), not established (–) or status unknown (?); Origin – known or probable area of origin; Vector – known or probable vector of introduction.

The number of immigrant species is increasing throughout the world and is an important element of global change (Ruiz et al. 1997; Dukes and Mooney 1999). This apparent increase may, in part, also reflect increasing awareness. Studies of the bottom fauna in the Baltic began in the 1870s. As a result, the species composition of the Baltic Sea biota is probably one of the most thoroughly monitored in the world, and thus any newcomer will be readily detected.

The speed of trans-oceanic transport is of crucial importance in predicting invasions. The Baltic Sea can be reached today by ships within 4-6 weeks even from the most remote regions. By contrast, about 80% of the pelagic larval stages of shallow water invertebrates cannot survive an ocean passage longer than 8 weeks (Thorson 1961); more than 80% of bivalve spp. must settle within 5 weeks (Hedgpeth 1994). For example, the soft-shell clam *Mya arenaria* from the east coast of North America, may have been the earliest human-mediated introduction into the Baltic Sea; it was apparently carried by the Vikings (Petersen et al. 1992; Strasser 1999) or early post-Columbian seafarers (Hessland 1946).

Rate of secondary spread within the Baltic Sea

The hulls of vessels, ballast water and bilge water facilitate spread from the sites of initial introduction. In addition, most of the non-indigenous species initially assisted by humans in crossing geographical and ecological barriers appear to have spread from their bridgeheads without further assistance (Leppakoski 1984; Jansson 1994; Gollasch and Dammer 1996; Gollasch and Mecke 1996). On the other hand, in most situations it is not possible to separate natural and human dispersal vectors within a single water body.

Approximately two-thirds of the 46 species of benthic invertebrates introduced into the Baltic Sea have a pelagic larval stage enabling their within-basin spread by currents or by ship traffic. Due to the predominating anti-clockwise current patterns, marine species often appear confined to the eastern part of the Baltic proper, which has a slightly higher salinity than the western part of the sea (Leppakoski and Bonsdorff 1989).

Luther (1950) and Nikolaev (1951) were among the first to recognise human-mediated introductions of aquatic species into the Baltic Sea. Even in this well-investigated sea, the history of within-sea spread of introduced species has seldom been satisfactorily documented. We illustrate here the direction and rate of spread in seven case histories.

Sargassum muticum (Phaeophyceae)

The Japanese brown alga *Sargassum muticum* (Yendo) Fensholt was first discovered on the coasts of England and France in the early 1970s; it spread to the German and southern Scandinavian coasts within 15 years. In 1987, the first attached algae were observed on the Swedish west coast; today *S. muticum* is a permanent member of the algal flora to approx. 57° N on the Swedish coast (Jansson 1994). Since

1993, *S. muticum* has expanded southward along the Swedish coast 100 km and has expanded from the outer archipelago to the mainland's coastline. It now competes with native algae for light and hinders local fisheries and boating (Wallentinus 1992; Swedish Environmental Protection Agency 1997; Godhe and Wallentinus 1999).

Balanus improvisus (Crustacea; Cirripedia)

The acorn barnacle *Balanus improvisus* Darwin became established in Western Europe in the 19th century (Walford and Wicklund 1973); it was probably introduced by hull fouling of ships from North America. In the mid-1800s, it was known only in a few European localities (the British Isles, possibly one locality in Belgium; Gislén 1950). It was first recorded in the Baltic Sea in 1844 at Königsberg (presently Kaliningrad) (Gislén 1950; Luther 1950, and references therein), 10 years before the species was described by Darwin (1854) from North and South America. From this likely dispersal centre it spread rapidly and became common, especially in ports. It may have invaded most of its present new range in the 1870s or, at the latest, before 1900. However, its spread continues in the inner parts of the Baltic. There are few records of it from the Swedish east coast before the 1920s (Gislén 1950). It was not found north of the Åland Islands before 1950 (Luther 1950), while in the 1990s, *B. improvisus* was recorded as far north as the Northern Quark (64° N; Leppakoski 1994; Figure 3A). Today, it occurs from the Gulf of Bothnia and Gulf of Finland to the west coast of Sweden (Jansson 1994).

B. improvisus is one of the most common species in ship hull fouling in North Sea and Baltic ports (Gollasch 1996). Its successful establishment and rapid range expansion in the central and northern Baltic has most likely been due to the dispersal of planktonic larvae, assisted by the sea-wide anti-clockwise current pattern. Adults are also transported as fouling organisms on boats and ships or attached to drifting debris.

B. improvisus is the most important fouling organism in the Baltic and the only barnacle species living in the coastal waters of the Baltic proper. It can even survive in fresh water. It was found in the late 1860s in southwestern Finland (in the lower Aura River, in the middle of Turku) associated with obligate freshwater organisms (Luther 1950). The approximate (minimum) rate of spread for *B. improvisus* from Königsberg (1844) to Turku (1868) was 30 km/year.

In addition to most of the Baltic, the southeastern seas of Europe have also been colonised by *B. improvisus*. It was first detected in the Black Sea in 1899 (Gomoiu and Skolka 1996). When the Volga-Don Canal opened in 1952, it penetrated into the Caspian Sea and became dominant locally, before 1976 (Kasymov 1982).

B. improvisus can cause marked habitat alteration through the construction of dense crusts on hard surfaces and secondary hard substrates (e.g. Olenin and Leppakoski 1999). One of the main effects of the barnacle is its facilitation of other organisms. Amongst dense populations of *B. improvisus*, associated species, such as chironomid larvae, ostracods, copepods and juvenile bivalves, increase in numbers compared to their performance in adjacent sites without crusts (A. Åvåil, personal communication).

Potamopyrgus antipodarum (Gastropoda, Hydrobiidae)

The small New Zealand mud snail, *Potamopyrgus antipodarum* (J.E. Gray), probably brought to Europe via ships' ballast, was first observed in the western Baltic Sea in 1887 (Wismar Bight; Lassen 1978) and in the North Baltic archipelago (Åland Islands) in 1926 (Hubendick 1950; Figure 3B). The gastropod's approximate (minimum) rate of spread from Wismar Bight to Gotland (1920) was 20 km/year, from there to the Åland Islands (1926) 50 km/year, and further to the Bothnian Bay (1945) 30 km/year. *P. antipodarum* has also invaded North America. It was first collected in Lake Ontario in 1991 and is expected to spread rapidly throughout the remaining Great Lakes (Zaranko et al. 1997). Today it is found frequently all along the coasts of the Baltic proper as well as in oligohaline parts of coastal lagoons and recently isolated freshwater coastal lakes in Finland (Leppakoski 1984; Olenin 1987; Jansson 1994). Most of the invasive invertebrates in the Baltic Sea have a pelagic larval stage, which increases their dispersal ability over long distances by currents. In contrast, *P. antipodarum* lacks a plankton larval stage; it is viviparous and parthenogenetic. Given its hard-shell, it has been hypothesized that *P. antipodarum* is largely disper-

sed by birds (Lassen 1978). The snail can survive gut passage and can be transported long distances by both fish and birds (Aarnio and Bonsdorff 1997).

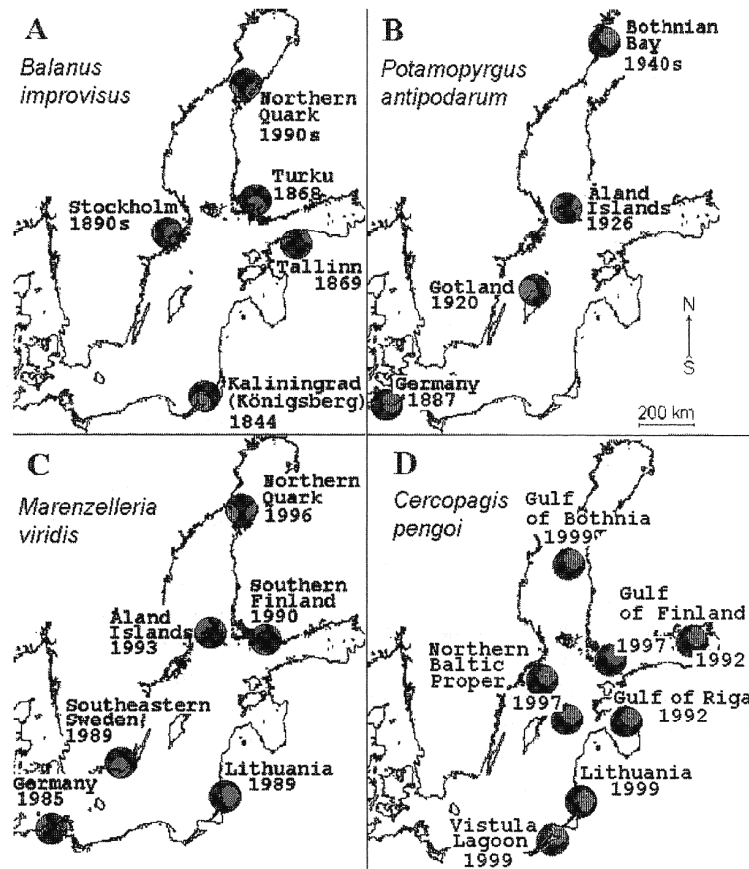


Figure 3. Spread of (A) *Balanus improvisus*, (B) *Potamopyrgus antipodarum*, (C) *Marenzelleria viridis* and (D) *Cercopagis pengoi* in the Baltic Sea.

Polydora redeki (Polychaeta; Spionidae)

So far, there have been no reported human-mediated primary introductions directly into the Baltic Sea north of 60° N; non-indigenous species in this region are the products of spread from elsewhere in the Baltic. Exceptions may be the cladoceran *Cercopagis pengoi* and the polychaete *Polydora redeki* (Horst). *P. redeki* is not known at sites between Kiel (southwestern Baltic) and the Turku area where it was first recorded in the mid-1960s (Eliason and Haahtela 1969; Östman and Leppakoski 1999).

The polychaete fauna of the northern Baltic Sea is very small. For example, on the south coast of Finland only 9 species have been discovered (Bonsdorff 1981; Norkko et al. 1993). Consequently, the introductions of two spionid polychaetes, *P. redeki* and *Marenzelleria viridis*, represent a substantial increase in polychaete diversity. *P. redeki*, first found in southwestern Finland in 1963, probably arrived in ballast water or hull fouling. The Kiel Canal (northwestern Germany) is the nearest known occurrence and is nearly 1000 km from the Finnish coast (Eliason and Haahtela 1969). Since 1963, the polychaete's range has coincided mainly with shipping channels and harbors. *P. redeki* was found in the Åland archipelago (120 km from the Finnish coast) in 1979 (Bonsdorff 1981) and off Porvoo in the inner part of the Gulf of Finland in 1972 in water with salinities of 3.5-6.5 psu (Halsinaho 1984).

Marenzelleria viridis (Polychaeta; Spionidae)

The North American spionid polychaete *Marenzelleria viridis* (Verrill) is one of the most rapidly dispersing non-indigenous species in the Baltic Sea. It was first recorded in the South Baltic in 1985 (Bick and Burckhardt 1989). It had successfully colonised most of the Baltic Sea by 1996 and has become a major faunal member locally. Its populations have grown to remarkably large numbers predominantly in the coastal waters, which provide some of the more variable and unstable abiotic conditions (e.g., Zettler 1996; Schiedek 1997; Bastrop et al. 1998; Olenin and Leppakoski 1999). It first appeared in Polish coastal waters in 1988 and on the southern coast of Finland in 1990 (Gruszka 1991; Norkko et al. 1993). *M. viridis* has spread widely along the Finnish coast. From 1990 to 1995, it expanded its distribution into the eastern Gulf of Finland and into southern Bothnian Bay (Stigzelius et al. 1997; Figure 3C). First records in the Baltic Sea were often made near ports, suggesting introduction via ballast water. It was already present at most sampling stations in the ports of southwestern Finland by 1995, as well as in the intermediate archipelago zone (Östman and Leppakoski 1999).

Although the abundance and biomass of *M. viridis* in open coastal waters is low, the species seems to have become a permanent member of the macrozoobenthos in the North Baltic (Stigzelius et al. 1997). In some Polish and German estuaries it developed high densities (up to 5000-30,000 ind. m⁻²) and large biomass (up to 400-800 g wwt m⁻²) (Bochert et al. 1996; Zettler 1996, 1997; Zmudzinski et al. 1997). For example, in the Vistula Lagoon (southeast Baltic) 95% of the total biomass of bottom fauna consists of *M. viridis* (Zmudzinski 1996). The deepest known open sea occurrence (78 m) is in the South Bothnian Bay (Laine 1995). The depth distribution of *M. viridis* provides an excellent example of brackish water submergence (Remane 1958; Zmudzinski et al. 1997).

The recent invasion history of *M. viridis* has been studied more thoroughly than any other non-indigenous species in the Baltic Sea. This polychaete possesses several attributes of a highly successful coloniser. It has high fecundity; each female produces 10,000-46,000 eggs per spawning period, and the pelagic phase lasts 4-12 weeks (Bochert, 1997). *M. viridis* has an unusually long life span for a polychaete (2-3 years). As many as three coexisting generations have been observed in a single year (Zettler 1997). Successful larval development is not possible if salinity is < 5 psu, but colonisation of oligohaline regions takes place by larvae or by swimming juveniles (Bochert 1997; Bochert et al. 1996). Furthermore, both larvae and benthic juveniles are being transported in the Baltic.

Adult *M. viridis* live in deeper sediment layers than the sediments in which native polychaetes and amphipods occur. In highly diluted coastal inlets the adults dig much deeper than chironomid larvae and oligochaetes (Daunys 1997). Consequently, competition for space may play a minor role in its distribution (Olenin and Leppakoski 1999). Although the larvae and young adults of *M. viridis* may be an additional food source for benthic fishes, adults are well protected and not readily available to predators (Bochert 1997; Schiedek 1997; Zettler 1997). Its burrowing into deep sediments may enhance denitrification and the exchange of material and energy in the sediment-water interface. The approximate (minimum) rate of spread from German Boddens (1985) to Lithuania (1989) was 170 km/year, from there to southern Finland (1990) 480 km/year, and further to northern Quark (1996) 90 km/year.

Hemimysis anomala (Crustacea; Mysidacea)

The reddish mysid shrimp *Hemimysis anomala* G.O. Sars, a Ponto-Caspian endemic, was introduced into artificial water reservoirs in Latvia and Lithuania in the 1950s and 1960s (Gasiunas 1963; Salemaa and Hietalahti 1993). After initial detection of *H. anomala* in the western part of the Gulf of Finland in 1992, it remained undetected in the Archipelago Sea (Salemaa and Hietalahti 1993). However, it has recently been found in large numbers along the southwest and southern coast of Finland from Rauma (eastern part of the Bothnian Sea) to Kotka (inner Gulf of Finland), 150-200 km from its putative introduction site in Finland (Salemaa 1998).

Cercopagis pengoi (Crustacea; Cladocera)

The most recent introduction of a non-indigenous species into the Baltic Sea is *Cercopagis pengoi* (Ostroumov), a predacious cladoceran of Ponto-Caspian origin. As with other non-indigenous species, this water flea was probably carried into the Baltic in ballast water. *C. pengoi* spread from its native habitats to freshwater reservoirs in the Volga and Don basins (Panov et al. 1999). In 1992, the species was

found in the Baltic Sea (Gulf of Riga, Estonia) (Ojaveer and Lumberg 1995) and in the pelagic part of the Gulf of Finland (A. Laine, personal communication). In 1995, *C. pengoi* was detected as a fouler of fishing nets in coastal Finnish waters and the Neva estuary (Panov et al. 1999). Since then it has become established in the northern Baltic and is also reported from the Stockholm archipelago and the Gotland Basin (Central Baltic) (Gorokhova et al. submitted; Figure 3D). It comprised 25% of the total zooplankton biomass at some stations in the Gulf of Riga in September 1995. *C. pengoi* is an important component of the diet of Baltic herring, sticklebacks, bleak and smelt (Ojaveer and Lumberg 1995; Ojaveer et al. 1998). It has become abundant during late summer, and during its mass occurrences it may clog fishing nets. The recent invasion by *C. pengoi* into the eastern Gulf of Finland has important economic consequences. Losses in the Primorsky Ribak fishery farm, at the northern shore of the lower Neva estuary, averaged a minimum of USD 50,000 in 1996-1998 and were caused by the fouling of fishing equipment by this cladoceran (Panov et al. 1999).

C. pengoi was not among species of the Ponto-Caspian fauna predicted to invade the Great Lakes of North America (Ricciardi and Rasmussen 1998). However, it was found in Lake Ontario in 1998 (MacIsaac et al. 1999). This occurrence is most likely a secondary introduction from the eastern Baltic via an existing invasion corridor (Panov et al. 1999).

Vertical spread

Several species that live only on shallow bottoms or in the intertidal zone in their native range occur at deeper depths upon introduction in the brackish Baltic Sea. This brackish water submergence (Remane 1958) has been explained as a function of salinity stratification, or the absence of predators and competitors in the Baltic, or both. Brackish water submergence among introduced species (Figure 4) illustrates their flexibility (acclimation or phenotypic plasticity) in a novel environment (cf. Vermeij 1996). Non-indigenous species that colonise deeper bottoms in the Baltic than in their native range include the barnacle *Balanus improvisus*, found at 44-53 m and the bivalve *Mya arenaria* at 45 m depth (Finnish Institute of Marine Research, unpublished; Olenin 1997), as well as the spionid polychaetes *Polydora redeki* at 29 m (Halsinaho 1984) and *Marenzelleria viridis* at 78 m depth; in Finnish waters the maximum abundance of *M. viridis* is 6-40 m (Stigzelius et al. 1997). In fact, *M. viridis* (normally mentioned as an intertidal or estuarine species in its area of origin; Hines and Comtois 1985) is the first non-indigenous species detected in the Baltic to colonise soft bottoms below the halocline.

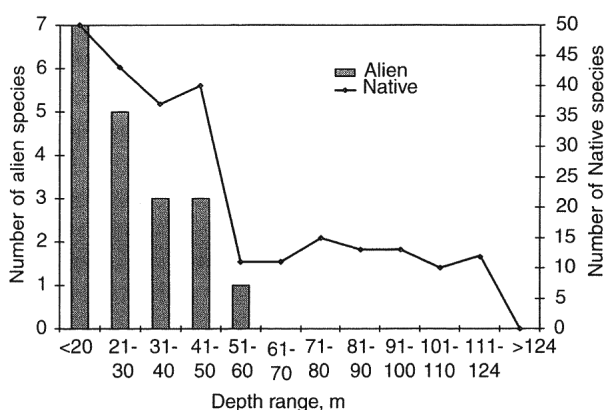


Figure 4. Vertical distribution of native and non-indigenous macrozoobenthic species in the Eastern Baltic (derived from Olenin 1997).

Mechanical and chemical properties of the invaded habitat may be extensively modified by introduced organisms as they burrow within the sediment, produce pellets, construct sandy and muddy tubes within or on the sediment, and transport fluid when burrowing (Olenin and Leppakoski 1999 and references therein). Consequently, non-indigenous species increase the three-dimensional complexity of the invaded

ecosystem. In the coastal lagoons of the Baltic Sea, *M. viridis* penetrates sediment to a 40 cm depth (Daunys 1997). Oligochaetes originally inhabited the uppermost 5 cm layer, but due to the porosity caused by *M. viridis*, they now extend to 15 cm (Zmudzinski 1996). *M. viridis* is much larger than the native burrowing organisms (chironomid larvae and oligochaetes). It dwells in muddy bottoms of the Baltic coastal lagoons and increases the thickness of the populated sediment layer and the maximum depth of bioturbation. In addition, *M. viridis* is reported to migrate by active swimming (cf. Dauer et al. 1982; Bochert et al. 1996). This movement may serve as an important link in energy transfer between pelagic and benthic subsystems. As a result, *M. viridis* mobilizes organic matter deposited in deeper sediment strata, links benthic and pelagic subsystems, and creates new microhabitats for associated fauna.

Discussion and conclusions

Examining the geographic spread and population growth of the most prominent invasive species in semi-enclosed seas will increase our understanding of the pathways, rate and dynamics of marine biotic invasions. For studies in invasion biology, enclosed seas offer several parallels and analogies to oceanic islands. These seas become more biologically uniform as more invasive species arrive. In the 1990s, brackish seas offered excellent opportunities for following natural experiments at a basin-wide scale with newly established populations of non-indigenous species (Gollasch and Mecke 1996; Anonymous 1997; Zaitsev and Mamaev 1997; Zettler 1997; Ojaveer et al. 1998; Olenin and Leppakoski 1999). Interestingly, the mean rates of spread of invaders within the Baltic Sea (approximately 50 km/year; excluding the extreme value of 480 km/year for *Marenzelleria viridis*) compare well with those calculated for marine invaders in other regions (Grosholz 1996).

Until establishment of permanent populations of *M. viridis* and *Cercopagis pengoi*, scientific interest in non-indigenous species was directed towards assessment of their abundance and invasion history. These two species' invasions provide the opportunity to study the fundamental role of non-indigenous species as consumers in, and regulators of brackish water ecosystems. The appearance of *C. pengoi* in the Baltic heightened public and scientific awareness of aquatic biotic invasions. Its further spread will be monitored carefully (Gorokhova et al. 2000), *C. pengoi* is one of the few recent introductions (and obviously the most important one in both ecological and economic terms) into the pelagic subsystem of the Baltic Sea.

Intracontinental seas, such as the Baltic and Black Seas, are faced with unique environmental threats, regardless of events outside their drainage basins, and they are also sensitive to global changes. Global warming could result in chain reactions in these ecosystems (e.g., increased nutrient flux from surrounding land, elevated production, decomposition and mineralisation rate) and thereby accelerate eutrophication. For example, *B. improvisus* is abundant in eutrophicated harbours where its abundance can be one or two orders of magnitude greater than the values in natural environments (Vuorinen et al. 1986).

Even small changes in inflow and outflow through the Danish Straits or in freshwater run-off may have long-term ecological consequences all through the Baltic Basin (Vuorinen et al. 1998; Hanninen et al. 2000). Most of the euryhaline, brackish water non-indigenous species now persistent in the Baltic originate from areas with warmer and more saline hydroclimate (Table 1). If global warming continues, more warm water species could become established in the Baltic Sea (cf. Duker and Mooney 1999; Reise et al. 1999).

Estuaries have been especially common sites of invasions; approximately 400 non-indigenous species are known in estuaries along the Pacific, Atlantic and Gulf coasts of the United States (Ruiz et al. 1997). Similarly, Baltic Sea estuaries have most likely functioned as stepping stones that have aided in the establishment of non-indigenous species. Centres of xenodiversity, i.e., areas that host many well established non-indigenous species, occur along the Baltic coasts: the Curonian (Lithuania/Russia) and Vistula (Poland/Russia) Lagoons, German Boddens, and the Neva estuary (Russia). These sites serve to introduce species to non-estuarine coastal and offshore areas.

Species-poor communities in the Baltic Sea appear more vulnerable to introductions than are species-rich communities, as predicted by the Eltonian invasion model (Elton 1958). Up to now, 97 non-native species have been reported from the Baltic Sea; approximately three fourths of these species have established self-reproducing populations (Table 1; see <http://www.ku.lt/nemo/mainnemo.htm> for an updated list of species). This number is high relative to the low number of native species in the Baltic. The

number of marine faunal species changes rapidly from the Kattegat (some 850 macroscopic animal species) to the Baltic proper (about 80), the Bothnian Sea (about 50) and the innermost Bothnian Bay (< 10) (Leppakoski and Bonsdorff 1989; Snoeijs 1999).

Most of the recently-arrived non-indigenous species appear benign and increase both species and functional diversity (Olenin and Leppakoski 1999). Of the non-indigenous species occurring in the coastal waters of southwest Finland today, only two fouling species, the barnacle *B. improvisus* and the hydrozoan *C. caspia*, impose costs to shipping, boating and fish farming, as well as to industries for which cooling water from the sea is used (Östman and Leppakoski 1999). *B. improvisus* occurs commonly as a fouling organism in power plants between Vaasa (Gulf of Bothnia; 63° N) and Kotka (Gulf of Finland; 27° E) whereas *C. caspia*, which is a genuine brackish water species, occurs along the entire Finnish coast (Vuorinen et al. 1986). The ecosystem and economic impacts of recently introduced species such as the polychaete *Marenzelleria viridis* and the cladoceran *Cercopagis pengoi* are not yet fully understood.

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References

- Aarnio K and Bonsdorff E (1997) Passing the gut of juvenile flounder, *Platichthys flesus* (L.) - differential survival of zoobenthic prey species. *Marine Biology* 129: 11-14
- Anonymous (1997) Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. *GESAMP Reports and Studies* 58: 1-84
- Bastrop R, Jurss K and Sturbauer C (1998) Cryptic species in a marine polychaete and their independent introduction from North America to Europe. *Molecular Biology and Evolution* 15: 97-103
- Bick A and Burckhardt R (1989) Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee. *Mitteilungen des Zoologischen Museums Berlin* 65: 237-247
- Bochert R (1997) *Marenzelleria viridis* (Polychaeta: Spionidae): a review of its reproduction. *Aquatic Ecology* 31: 163-175
- Bochert R, Bick A, Zettler M and Arndt EA (1996) *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae), an invader in the benthic community in Baltic coastal inlets - investigation of reproduction. In: Andrushaitis A (ed) *Proceedings of the 13th Baltic Marine Biologists Symposium*, pp 131-139. Institute of Aquatic Ecology, University of Latvia, Riga
- Bonsdorff E (1981) Notes on the occurrence of Polychaeta (Annelida) in the archipelago of Åland, SW Finland. *Memoranda Societatis pro Fauna et Flora Fennica* 57: 141-146
- Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanography and Marine Biology Annual Review* 23: 313-371
- Darwin C (1854) *A Monograph on the Subclass Cirripedia, with Figures of All the Species*. Royal Society, London, 684 pp
- Dauer DM, Ewing RM, Sourbeer JW, Harlan WT and Stokes TL (1982) Nocturnal swimming of *Scolecoplepides viridis* (Polychaeta: Spionidae). *Estuaries* 3: 148-149
- Daunys D (1997) Ecology of polychaete *Marenzelleria viridis* Ver-ril 1873 (Spionidae, Annelida) in the shallow habitats of the Lithuanian coastal zone, the Baltic Sea. MSc Thesis. Ecology Department, Klaipeda University, 39 pp
- Dukes JS and Mooney HA (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14:135-139
- Eliason A and Haahtela I (1969) *Polydora* (Boccardia) *redeki* Horst (Polychaeta, Spionidae) from Finland. *Annales Zoologici Fennici* 6: 215-218
- Elton CS (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London, 181 pp

- Gasiunas I (1963) The acclimatisation of forage crustaceans into the Kaunas Waterpower Plant Reservoir and the possibility of their migration into another waters of Lithuania. Proceedings of the Academy of Sciences of the Lithuanian SSR, B, 1(30): 79-85 [in Russian]
- Gislén T (1950) On the invasion and distribution of *Balanus improvisus* along the Swedish coasts. Fauna och Flora 45: 32-37 [in Swedish, with English summary]
- Godhe A and Wallentinus I (1999) The ports in the Stenungsund area, west coast of Sweden. In: Gollasch S and Leppäkoski E (eds) Initial Risk Assessment of Alien Species in Nordic Coastal Waters. Nord 1999: 8, pp 140-184. Nordic Council of Ministers, Copenhagen
- Gollasch S (1996) Untersuchungen des Arteintrages durch den inter-nationalen Schiffsverkehr unter besonderer Berücksichtigung nichtheimischer Arten. PhD Thesis, University of Hamburg, 314 pp
- Gollasch S and Dammer M (1996) Nicht-heimische Organismen in Nord- und Ostsee. In: Gebhardt H, Kinzelbach R, and Schmidt-Fischer S (eds) Gebietsfremde Tierarten. Auswirkungen auf ein-heimische Arten, Lebensgemeinschaften und Biotope, 97-104. Ecomed, Landsberg
- Gollasch S and Leppäkoski E (1999) Initial Risk Assessment of Alien Species in Nordic Coastal Waters. Nord 1999: 8. Nordic Council of Ministers, Copenhagen, 244 pp
- Gollasch S and Mecke R (1996) Eingeschleppte Organismen. In: Lozan JL, Lampe R, Matthäus W, Rachor E, Rumohr H and v. Westernhagen H (eds) Warnsignale aus der Ostsee, pp 146-150. Parey Buchverlag, Berlin
- Gomoiu M-T and Skolka M (1996) Changements récents dans la bio-diversité de la Mer Noire d'is aux immigrants. Geo-Eco-Marina, Romanian Centre of Marine Geology and Geoecology, 1/1996: 34-47
- Gorokhova E, Aladin N and Dumont H (2000) Further expansion of the genus *Cercopagis* (Crustacea, Branchiopoda, Onychopoda) in the Baltic Sea, with notes on the taxa present and their ecology. Hydrobiologia 429: 207-218
- Grosholz ED (1996) Contrasting rates of spread for introduced species in terrestrial and marine systems. Ecology 77: 1680-1686
- Gruszka P (1991) *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae) - a new component of shallow water benthic community in the southern Baltic. Acta Ichthyologica et Piscatoria 21: 57-65
- Halsinaho E (1984) The distribution of *Polydora redeki* (Polychaeta, Annelida) on the Baltic coast of Finland. Memoranda Societatis pro Fauna et Flora Fennica 60: 55-59
- Hänninen J, Vuorinen I and Hjelt P (2000) Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnology and Oceanography 45: 703-710
- Hedgpeth JW (1994) Nonanthropogenic dispersals and colonization in the sea. In: Proceedings of the Conference and Workshop Nonindigenous Estuarine and Marine Organisms (NEMO), Seattle, Washington, April 1993, pp 45-62. US Department of Commerce
- HELCOM (1988) Guidelines for the Baltic Monitoring Programme for the Third Stage. Baltic Marine Environment Protection Commission - Helsinki Commission
- Hessland I (1946) On the Quaternary Mya period in Europe. Arkiv för Zoologi 37A(8): 1-51
- Hines AH and Comtois KL (1985) Vertical distribution of estuarine infauna in sediment of a subestuary of central Chesapeake Bay. Estuaries 8: 296-304
- Hubendick B (1950) The effectiveness of passive dispersal in *Potamopyrgus jenkinsi*. Zoologiska Bidrag Uppsala 28: 493-504
- Jansson K (1994) Alien species in the marine environment. Swedish Environmental Protection Agency. Report 4357, 67 pp
- Kasymov AG (1982) The role of Azov-Black Sea invaders in the productivity of the Caspian Sea benthos. Internationale Revue der gesamten Hydrobiologie 67: 533-541
- Laine A (1995) New benthic macrofauna species in the Gulf of Finland. Finnish Institute of Marine Research (<http://www2.fimr.fi/algaline/arc95/newspec.htm>)
- Lassen HH (1978) *Potamopyrgus jenkinsi* in Jutland. Distribution, dispersal, and colonization. Fauna og Flora 84: 73-79 [in Danish, with English summary]
- Leppäkoski E (1984) Introduced species in the Baltic Sea and its coastal ecosystems. Ophelia 3: 123-135
- Leppäkoski E (1994) The Baltic and the Black Sea - seriously threatened by non-indigenous species? In: Proceedings of the Conference and Workshop Nonindigenous Estuarine and Marine Organisms (NEMO), Seattle, Washington, April 1993, pp 37-44. US Department of Commerce
- Leppäkoski E and Bonsdorff E (1989) Ecosystem variability and gradients. Examples from the Baltic Sea as a background for hazard assessment. In: Landner L (ed) Chemicals in the Aquatic Environment, pp 6-58. Springer-Verlag, Berlin/Heidelberg
- Leppäkoski E and Mihnea PE (1996) Enclosed seas under man-induced change: a comparison between the Baltic and Black Seas. Ambio 25: 380-389
- Leppäkoski E and Olenin S (in press) Xenodiversity of the European brackish water seas: the North American contribution. In: Proceedings of the First National Conference of Marine Bioinvasions. Massachusetts Institute of Technology, Cambridge, Massachusetts, 25-27 January 1999
- Luther A (1950) On *Balanus improvisus* in the Baltic Sea. Fauna och Flora 45: 155-160 [in Swedish]

- Maclsaac HJ, Grigorovich IA, Hoyle JA, Yan ND and Panov VE (1999) Invasion of Lake Ontario by the Ponto-Caspian cladoceran predator *Cercopagis pengoi*. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1-5.
- Nikolaev II (1951) On new introductions from distant areas in fauna and flora of the North and the Baltic Seas. *Zoologicheskij Zhurnal* 30:556-561 [in Russian]
- Norkko A, Bonsdorff E and Boström C (1993) Observations of the polychaete *Marenzelleria viridis* (Verrill) on a shallow sandy bottom on the South coast of Finland. *Memoranda Societatis pro Fauna et Flora Fennica* 69: 112-113
- Ojaveer E, Lumberg A and Ojaveer H (1998) Highlights of zoo-plankton dynamics in Estonian waters (Baltic Sea). *ICES Journal of Marine Science* 55: 748-755
- Ojaveer H and Lumberg A (1995) On the role of *Cercopagis pengoi* (Ostroumov) in Parnu Bay and the NE part of the Gulf of Riga ecosystem. *Proceedings of the Estonian Academy of Sciences, Ecology* 5: 20-25
- Olenin S (1987) Zoobenthos of the Curonian Lagoon: results of biological monitoring, 1980-1984. In: *Chemistry and Biology of the Seas. Proceedings of the State Oceanographic Institute*, pp 175-191. Hydrometizdat, Moscow [in Russian]
- Olenin S (1997) Benthic zonation of the Eastern Gotland Basin, Baltic Sea. *Netherlands Journal of Aquatic Ecology* 30: 265-282
- Olenin S and Leppakoski E (1999) Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. *Hydrobiologia* 393: 233-243
- Östman M and Leppakoski E (1999) The ports of Southwest Finland - Turku, Naantali and Pargas. In: Gollasch S and Leppakoski E (eds) *Initial Risk Assessment of Alien Species in Nordic Coastal Waters*. Nord 1999: 8, pp 203-224. Nordic Council of Ministers, Copenhagen
- Panov VE, Krylov PI and Telesh IV (1999) The St. Petersburg harbour profile. In: Gollasch S and Leppakoski E (eds) *Initial Risk Assessment of Alien Species in Nordic Coastal Waters*. Nord 1999: 8, pp 225-244. Nordic Council of Ministers, Copenhagen
- Petersen KS, Rasmussen KL, Heinemeier J and Rud N (1992) Clams before Columbus? *Nature* 359: 679
- Reise K, Gollasch S and Wolff WJ (1999) Introduced marine species of the North Sea coasts. *Helgolander Meeresuntersuchungen* 52: 219-234
- Remane A (1958) Ökologie des Brackwassers. In: Remane A and Schlieper C, *Die Biologie des Brackwassers*, pp 1-216. Die Binnengewässer 12. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart
- Ricciardi A and Rasmussen JB (1998) Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1759-1765
- Ruiz GM, Carlton JT, Grosholz ED and Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* 37:621-632
- Salemaa H (1998) Mysid shrimps. In: Heliövaara K (ed) *Nature of Finland - Invertebrate Animals*, pp 46-47. Weilin & Goos, Helsinki [in Finnish]
- Salemaa H and Hietalahti V (1993) *Hemimysis anomala* G.O. Sars (Crustacea: Mysidacea) - immigration of a Pontocaspian mysid into the Baltic Sea. *Annales Zoologici Fennici* 30: 271-276
- Schiedek D (1997) *Marenzelleria cf. viridis* (Polychaeta: Spionidae) - ecophysiological adaptations to a life in the coastal waters of the Baltic Sea. *Aquatic Ecology* 31: 199-210
- Snoeijs P (1999) Marine and brackish waters. In: Rydin H, Snoeijs P and Diekmann M (eds) *Swedish Plant Geography. Acta Phyto-geographica Suecica* 94: 187-212
- Stigzelius J, Laine A, Rissanen J, Andersin A-B and Ilus E (1997) The introduction of *Marenzelleria viridis* (Polychaeta, Spionidae) into the Gulf of Finland and the Gulf of Bothnia (northern Baltic Sea). *Annales Zoologici Fennici* 34: 205-212
- Strasser M (1999) *Mya arenaria* — an ancient invader of the North Sea coast. *Helgolander Meeresuntersuchungen* 52: 309-324
- Swedish Environmental Protection Agency (1997) *Alien species in the marine environment. Status and National Activities in the OSPAR Convention Area (based on information from Contracting)* prepared for IMPACT 97/7/1
- Thorson G (1961) Length of pelagic life in marine bottom invertebrates as related to larval transport by ocean currents. *Science* 67: 455-474
- Vermeij GJ (1996) An agenda for invasion biology. *Biological Conservation* 78: 3-9
- Vuorinen I, Hänninen J, Viitasalo M, Helminen U and Kuosa H (1998) Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. *ICES Journal of Marine Science* 55: 767-774
- Vuorinen I, Laihonon P and Lietzén E (1986) Distribution and abundance of invertebrates causing fouling in power plants on the Finnish coast. *Memoranda Societatis pro Fauna et Flora Fennica* 62: 123-125
- Walford L and Wicklund R (1973) Contribution to a worldwide inventory of exotic marine and anadromous organisms. *FAO Fisheries Technical Paper* 121: 1-49
- Wallentinus I (1991) The Baltic Sea gradient. In: Mathieson AC and Nienhuis PH (eds) *Intertidal and Littoral Ecosystems*, pp 83-108. Elsevier, Amsterdam
- Wallentinus I (1992) The dispersal of *Sargassum muticum* in the ICES countries. *ICES Working Group on Introductions and Transfers of Marine Organisms meeting at Lisbon, Portugal, April 14-17, 6 pp*

- Zaitsev Y and Mamaev V (1997) *Marine Biological Diversity in the Black Sea. A Study of Change and Decline.* United Nations Publications, New York, 208 pp
- Zaranko DT, Farara DG and Thompson FG (1997) Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). *Canadian Journal of Fisheries and Aquatic Sciences* 54: 809-814
- Zettler ML (1996) Successful establishment of the spionid poly-chaete, *Marenzelleria viridis* (Verrill, 1873), in the Darss-Zingst estuary (southern Baltic) and its influence on the indigenous macrozoobenthos. *Archive of Fishery and Marine Research* 43: 273-284
- Zettler ML (1997) The newcomer *Marenzelleria viridis* (Verrill, 1873), its development and influence on the indigenous macrozoobenthos in a coastal water of the Southern Baltic. In: Ojaveer E (ed) *Proceedings of the 14th Baltic Marine Biologists Symposium, 5-8 August 1995, Parnu, Estonia*, pp 280-296. Estonian Academy Publishers, Tallinn
- Zmudzinski L (1996) The effect of the introduction of the American species *Marenzelleria viridis* (Polychaeta: Spionidae) on the benthic ecosystem of Vistula Lagoon. *Marine Ecology* 17: 221-226
- Zmudzinski L, Chubarova-Solovjeva S, Dobrowolski Z, Gruszka P, Olenin S and Wolnomiejski N (1997) Expansion of the spionid polychaete *Marenzelleria viridis* in the southern part of the Baltic Sea. In: Andrushaitis A (ed) *Proceedings of the 13th Baltic Marine Biologists Symposium, 1-4 September 1993*, pp 127-129. Institute of Aquatic Ecology, University of Latvia, Riga