THE BALTIC SEA - A FIELD LABORATORY FOR INVASION BIOLOGY

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Abstract
Since the early 1800s, about 101 NIS have been recorded in the Baltic Sea. In this brackish sea (salinity range from less than 2 to approximately 20 PSU) horizontal and vertical gradients provide the nonindigenous species of different origin an extended repertoire of hospitable conditions. Several ecological functions of the non-native animals are new (and hence unique) for the species-poor Baltic Sea ecosystem. A review of the research into invasion biology in the Baltic Sea countries reveals a timeline from first records of single new species toward more sophisticated studies in invasion biology.

1 Introduction

The Baltic Sea is a young, and in a historical perspective, environmentally unstable sea. After the latest deglaciation, freshwater periods alternated with conditions, slightly more marine than what is prevailing today. Around 7,000 BP, the Baltic became brackish. Consequently, most animal and plant species living in the Baltic Sea are postglacial immigrants, many of them living close to their salinity tolerance limits.

The Baltic is the world's largest brackish-water sea area (382,000 km^2 or 415,000 km^2 with the Kattegat included), and this semi-enclosed water body is isolated from the North Sea by both geographical and ecological barriers: sill depth is 18 m; the salinity drops from 20-24 PSU in the Kattegat to 6-8 PSU in the Baltic Proper and further to 1-2 PSU in the inner parts of the large gulfs (Gulf of Bothnia and Gulf of Finland). The water is strongly stratified, especially in the Baltic Proper. Temperature conditions vary from boreal Atlantic in the southwestern areas of the sea to sub-Arctic in its northernmost part. The Baltic Sea area (i.e. Kattegat and Belt Sea, Arkona Basin, Baltic Proper, major gulfs, adjacent brackish-to-fresh water lagoons and inlets) represents a chain of sub-regions, well defined by their geomorphological configuration, hydrological regime and biogeographical composition of their biota. These horizontal and vertical gradients influence not only the native biota, but provide also the nonindigenous species (NIS) of different origin an extended repertoire of hospitable conditions. There is scientific proof of inoculation events that have taken place at particular sites, along the whole salinity gradient of the Baltic Sea, from Kattegat in the west to the diluted, innermost parts of the Baltic. Thus, the present Baltic Sea represents an ecological continuum, being a result of significant natural alterations during the past 10,000 years of its postglacial history. During the last two centuries, human-mediated introductions have added a new dimension to this continuum (Leppäkoski & Olenin 2001). In the Baltic Sea countries

NIS were added to the environmental policy agenda in the mid-1990s only, although both intentional and unintentional introductions had existed long before their environmental and/or economic impact was recognized and formulated.

There are several recent reviews available on the NIS, their origin, spread and impacts in the Baltic Sea (Jansson 1994; Gollasch & Mecke 1996; Gollasch & Leppäkoski 1999; Olenin & Leppäkoski 1999; Jansson 2000; Leppäkoski & Olenin 2000a). This paper briefly describes the history of human-mediated biological invasions and their consequences in the Baltic Sea area and outlines the history of invasion biology in the region.

2 Invasion history of the Baltic Sea

As with communities on islands, the structure of species assemblages in semi-enclosed seas is the product of immigration and extinction. No species are yet known to have become extinct in the Baltic Sea in historical times, whereas immigration continues through both natural dispersal and human-mediated introduction of species. The invasion rate for the Baltic Sea region was approximately one NIS every year over the period 1960-2000 (Baltic Sea Alien Species Database 2002).

Several invasion corridors, other than ship traffic, open into the Baltic Sea. The sea and its drainage area are connected to the Ponto-Caspian brackish seas (Black, Azov and Caspian Seas) by rivers and canals. Some 250 rivers discharge fresh water into the Baltic from a drainage area that is 4 times greater than its sea surface itself. Consequently, every single NIS, released into the wild somewhere in the drainage basin, can be transported to the sea or its most diluted coastal areas. Today the Baltic is exposed to other brackish- and fresh-water biota of the world, due to reduced geographical barriers (i.e. ships' traffic and the century-long history of intentional introductions). In brackish-water conditions, the ability of organisms to live and reproduce at the low salinity is a key factor, also in the Baltic. Highly euryhaline species of both marine and fresh-water origin are potential invaders. Consequently, there is a substantial pool of both intra- and intercontinental NIS already established in adjacent water bodies. In the peripheral parts of the drainage area of the Baltic, they consist mainly of the Ponto-Caspian element whereas the northwest European river mouths harbor a number of marine and brackish-water NIS native to other seas. Because of the brackish conditions and low winter temperatures, the Baltic Sea is often thought to be relatively well protected against species invasions. It is however important to keep in mind that this protected status is only hypothetical. Many major harbors, even along fully oceanic coasts, are situated in brackish waters (e.g. river mouths and estuaries). Ballast water may be loaded in the brackish part of a harbor, to be discharged later somewhere in the brackish Baltic Sea; thus, the risk of successful species introductions appears to be relatively high.

The Baltic has a long history of human mediated invasions (see Baltic Sea Alien Species Database 2002 for references). The bivalve *Mya arenaria* probably appeared already in the 12-13th centuries in Danish waters. First benthic species recognized as non-native was the barnacle *Balanus improvisus* found in 1844 in former Königsberg (now Kaliningrad) area of the Vistula lagoon. Introduction for stocking purposes of lobster, crabs, oysters and blue mussels from Denmark to the Finnish and Estonian coasts was planned by Russian authorities as early as in the mid-1700s (Hamel 1852). Delivery of settlings failed, however, and further efforts were questioned by scientists because of the low salinity. Ponto-Caspian species (the bivalve *Dreissena polymorpha*, and probably the gastropod *Lithoglyphus naticoides* and the hydrozoan *Cordylophora caspia*) first appeared in the southeastern lagoons of the Baltic Sea in the early 1800s after opening of the canals (e.g., Neman - Dniepr and Vistula - Bug in the end of the 1700s). In the early 1960s, a number of Ponto-Caspian mysids and gammarids (*Paramysis lacustris*, *Limnomysis benedeni*, *Hemimysis anomala*, *Corophium curvispinum*, *Pontogammarus robustoides*, *Obesogammarus crassus*, *Chaetogammarus ischnus*, *C. warpachowskyi*) were successfully intentionally introduced into the Lithuanian waters, including the Curonian Lagoon (Gasiunas 1963).

Since the early 1800s, about 101 NIS have been recorded in the Baltic Sea (the Kattegat included) most of them being introduced by shipping (ballast water or hull fouling), or spread from their primary sites of introduction in adjacent freshwater bodies (Leppäkoski & Olenin 2000a; see also Baltic Sea Alien Species Database 2002 for full list of species). It is assumed that some 70 species have been able to establish and maintain self-sustaining populations (Table 1). NIS are abundant and even dominant throughout the shallow benthic and fouling communities of the Baltic Sea - at present, no shallow-water habitat is entirely free of human-mediated invaders. Their number is lowest in the northern part of the Gulf of Bothnia and highest in the coastal lagoons of the southern and southeastern Baltic as well as in the Belt Sea and Kattegat area (Leppäkoski & Olenin 2001). The most important source areas for these species have been western European waters, the Atlantic coast of North America and the Ponto-Caspian realm. In addition, at least 5 species are listed as cryptogenic to the area (e.g., the dinoflagellate *Prorocentrum minimum* and the ship worm *Teredo navalis*).

Table 1. Number of nonindigenous species recorded in the Baltic Sea (Kattegat included) 1800-2001. W = in the most parts or in the whole Baltic; R = within one of the Baltic sub-regions (see Gollasch & Mecke 1996; Leppäkoski & Olenin 2000a and Baltic Sea Alien Species Database 2002 for further data).

Ecological or taxonomic group	Number of species recorded	Established species W(R)*	Ecological or taxonomic group	Number of species recorded	Established species W(R)*
Phytoplankton	8	0? (8)	Mollusca	12	2 (7)
Phytobenthos	9	0 (9)	Bryozoa	1	0 (1)
Invertebrates			Tunicata	1	0 (1)
Cnidaria	6	2? (1)	**Vertebrates**		
Platyhelminthes	2	0 (2?)	Pisces	30	0 (8?)
Nematoda	1	0 (1)	Aves	1	1 (0)
Annelida	7	1 (6)	Mammalia	2	2 (0)
Crustacea	21	4 (13)			
			TOTAL	101	12? (57?)

There are very few primary introductions known from the Baltic Sea (e.g., the fish hook water flea *Cercopagis pengoi* and some Pacific salmonids *Oncorhynchus* spp.); the Baltic has been and still is subject to secondary introductions from both the North Sea area and adjacent inland waters. Based on published first findings, the minimum rates of secondary spread within the Baltic basin were estimated (Leppäkoski & Olenin 2000a) for the barnacle *Balanus improvisus* from Königsberg (1844) to Turku (1868) 30 km a^{-1}, for the North American polychaete *Marenzelleria viridis* (German Boddens 1985 to Lithuania 1989) 170 km a^{-1}, further to the south coast of Finland (1990) 480 km a^{-1}, and to the Northern Quark (1996) 90 km a^{-1}, and for the mud snail *Potamopyrgus antipodarum*, native to New Zealand (from Wismar Bight, Germany to Gotland, Sweden 1920) 20 km a^{-1}, to the Åland Islands (1926) 50 km a^{-1}, and to Bothnian Bay (1945) 30 km a^{-1}.

Until very recently (up to mid-1980s), most of the abundantly occurring invaders in the Baltic Sea were benthic organisms. Since then, several planktonic (e.g., *Cercopagis pengoi*) and benthic species having pelagic life-stages (*Marenzelleria* cf. *viridis*), appeared in the Baltic Sea. Receiving areas in the Baltic Sea, which are at high risk from NIS introductions, are the Gulf of Finland, the Gulf of Riga, the coastal lagoons and the German boddens. All these areas are known as centres for xenodiversity (Gr. *xenos* = strange; Leppäkoski & Olenin 2000b), i.e. areas that host many well-established NIS (Gruszka 1999; Panov et al. 1999; Olenin et al. 1999; Leppäkoski & Olenin 2000a, 2001). These "hot spots" serve not only as entrance gates for many invasions into the Baltic but they also function as bridgeheads for secondary introductions that are carried towards the inner parts of the Baltic either naturally, by currents, or by regional ship traffic and recreational craft.

Few estimates are available for the proportion of NIS in relation to the total number of species in different parts of the Baltic. In the brackish waters of the German Baltic Sea coast, about 450 bottom-living species have been recorded**;** of these 15 species or 3% are non-native (Nehring 1999). In a benthos study in the eastern Bothnian Sea, 22 species were recorded, among them four NIS (18%). In the Curonian Lagoon (Lithuania), 16 (17%) of the about 95 benthic animal species recorded are nonindigenous; in the oligohaline part of the lagoon, the ratio would be 16 to 55 (29%) (Olenin & Leppäkoski 1999). An updated list of species found in the Baltic and its sub-regions is available as an interactive database (Baltic Sea Alien Species Database 2002; see Jazdzewski (1980), Kinzelbach (1995), Tittizer (1996) and Jazdzewski & Konopacka (2000) for detailed information of NIS in the rivers and lakes of the drainage area of the Baltic).

3 Impacts and consequences

Functional (ecological) and economic aspects of biological invasions are yet insufficiently studied in the Baltic Sea, therefore it may seem that many of nonindigenous species found in the region have had no obvious effect on the native environment and, consequently, there has been no known impact on human uses of the sea. However, it is clear that at least some functions of the non-native animals are new (and hence unique) for the species-poor Baltic Sea ecosystem. As examples of novelty in functions serve: (i) the mud snail *Potamopyrgus antipodarum* (surface deposit feeding on extremely soft bottoms where native gastropods *Hydrobia* spp. do not occur); (ii) the zebra mussel *Dreissena polymorpha* (filter feeding in oligohaline and freshwater parts of the coastal lagoons where the blue mussel *Mytilus edulis* is absent); (iii) the barnacle *Balanus improvisus* (suspension filter feeding in the uppermost hydrolittoral zone); (iv) the polychaete *Marenzelleria* cf. *viridis* (deep bioturbation of the sediment); (v) the hydroid *Cordylophora caspia* (sessile raptorial suspension feeding); (vi) the crabs *Rhithropanopeus harrisi* and *Eriocheir sinensis* (epibenthic invertebrate predators and scavengers in the diluted parts of the inlets where native marine decapod shrimps do not occur); (vii) the mysidacean *Paramysis lacustris* (nektobenthic crustacean in the inner parts of some lagoons where native marine mysids are absent); (viii) B. *improvisus* and *D. polymorpha* play a role as microhabitat engineers - their empty shells create patches of hard substrate for sessile species on uniform soft bottoms (Olenin & Leppäkoski 1999).

Studies on selected species, especially in recent years, proved that NIS in the Baltic Sea area compete with native species for food and/or space (e.g. case studies on *Cercopagis pengoi*, *C. caspia*, *D. polymorpha*, *Gammarus tigrinus*, *M.* cf. *viridis*, *Pontogammarus robustoides*), they became numerically dominant in native communities (*Acartia tonsa*, *B. improvisus*, *C. pengoi*, *M.* cf. *viridis*, *Mya arenaria*), they change energy/matter flows between pelagic and benthic compartments and modify trophic structure of invaded ecosystems (*A. tonsa, C. caspia*, *Coregonus nasus*, *D. polymorpha*, *M. arenaria*, *Neogobius melanostomus*), transfer parasites and diseases to local species (*Coregonus nasus*, *Pacifastacus leniusculus*).

NIS have no direct value of food resources in the Baltic as none of them support commercial fisheries and invertebrates are not harvested for food because of their small size. Some planktonic invaders (e.g., the fishhook water flea *C. pengoi*) and planktonic larvae of several benthic NIS have a high value as food source for commercially harvested fish such as the Baltic herring (e.g. Antsulevich & Välipakka 2000). However, on the basis of existing knowledge approximately 20 NIS (i.e., less than 30% of all introduced species) can be classified as nuisance organisms in the Baltic; only 7 of them have caused significant damage (Leppäkoski 2002). These are three Ponto-Caspian species (*C. caspia*, *C. pengoi*, and *D. polymorpha*), two North-American species (*B. improvisus* and the American mink *Mustela vison*), the Japanese swim-bladder nematode *Anquillicola crassus* and the ”ship worm” mollusc *Teredo navalis*, believed to be of Indo-Pacific origin. The economic impacts of NIS have rarely been quantified. The clogging of reels and fouling of nets makes *C. pengoi* a potential nuisance species. This may cause substantial economic loss in fisheries. The estimated loss in one fishery enterprise in the eastern Gulf of Finland, in average during 1996–1998, was at minimum USD 50,000, caused by the drastic decline in fish catches in the coastal zone due to fouling of fishing equipment by *C. pengoi* (Panov et al. 1999). During the exceptionally warm summer in 1999, clogging of fishing equipment by *C. pengoi* became a serious problem in the eastern Gulf of Finland, the inner parts of the Archipelago Sea, Finland, the northern Bothnian Sea and Lithuania (Gasiunaite & Didziulis 2000; Leppäkoski 2002). The cryptogenic ship worm *T. navalis* is now fully established in the southwestern Baltic region. It caused approximately USD 15 to 25 million damage to submerged wooden installations along the German Baltic coast, since 1995 (K. Hoppe pers. comm.). The ship worm also causes damage to marine archaeological objects.

Introduction of alien species interferes with research and monitoring. Establishment of any single NIS in a novel region and ecosystem opens opportunities to ecological research. These ”transplantation experiments” can be used for studies of concepts such as adaptive strategies, niche dimensions, interspecific relationships, dispersal mechanisms etc. The Baltic Sea with its low number of indigenous species and relatively simple food webs offers excellent opportunities for detailed studies in invasion biology. However, species introductions may also result in reduced research possibilities in causal biogeography (it is difficult to explain causalities behind present distribution of species) and population genetics. Benthic communities of the Baltic Sea have been monitored by quantitative methods since the 1910s. The results of this effort, based on international sampling programmes, may be invalidated by the establishment of any successful NIS, which becomes dominating, utilizes the space and energy resources in different manner and rate, and re-structures the food webs. For example, the soft-bottom community was totally changed by the polychaete *M. viridis* in the Vistula Lagoon, where it became a dominant species in sandy and muddy habitats in mid-1990s, reaching 216 g m^{-2} and making up to 95% of total benthic community biomass (Zmudzinski et al. 1997). Positive economic impacts include the recreational resources provided for sport fishing by some nonindigenous fish, such as the rainbow trout (escapees from fish farms along the Finnish coast), the round goby (in the Gulf of Gdansk) and hunting (the muskrat, trapped for their fur, and the Canada goose).

4 The Baltic Sea as a donor area of nonindigenous species

The Baltic Sea acts as donor of alien species for e.g., the North American Great Lakes. The predatory cladoceran *Bythotrephes longimanus*, native to Lake Ladoga and the Neva Estuary, invaded the Great Lakes in ballast water of a ship from the port of Leningrad (St. Petersburg) in the early 1980s (Berg et al. 1998). Likewise, *Cercopagis pengoi* was introduced into the Great Lakes in 1998 (MacIsaac et al. 1999), almost certainly carried in ballast tanks the eastern Baltic (Cristescu et al. 2001). *C. pengoi* was among the species of Ponto-Caspian origin, which were predicted to invade the Great Lakes based on ships' traffic from key European to Great Lakes' ports (MacIsaac 1999). The diatom *Thalassiosira baltica* (first found in Lake Ontario in 1988) likely originated from the Baltic Sea, though other sources were also possible (Edlund et al. 2000).

5 The formative years of the biology of invasions in the Baltic Sea

This brief review demonstrates that the biota of the Baltic Sea, in spite of its isolated state, is closely linked with the oceans of the world. The present knowledge of introduction of non-native species into the Baltic Sea has developed through a stepwise process from first records of single new species (e.g. Luther 1927; Schlesch 1937; Gislén 1950) toward more sophisticated studies in invasion biology (Fig. 1). Nikolaev (1951) and Segerstråle (1957) were the first to draw attention to the changes in the Baltic Sea fauna, related to human-mediated introduction of NIS. The first inventories (Leppäkoski 1984; Jansson 1994) revealed 35-40 established NIS. The first PhD worldwide based on ballast water sampling of ships was published in Germany (Gollasch 1996). Further, in 1999 the German group Neobiota was formed dealing with exotic species in Germany, including the Baltic shores.

International cooperation in the field of invasion biology started in 1994, when a working group on estuarine and marine nonindigenous organisms was established by the Baltic Marine Biologists (BMB), a non-governmental scientific organisation. Its systematic work on comprehensive inventories resulted in the first Internet-based inventory, issued in 1997, where 78 nonindigenous species (both established and occasional) were listed.

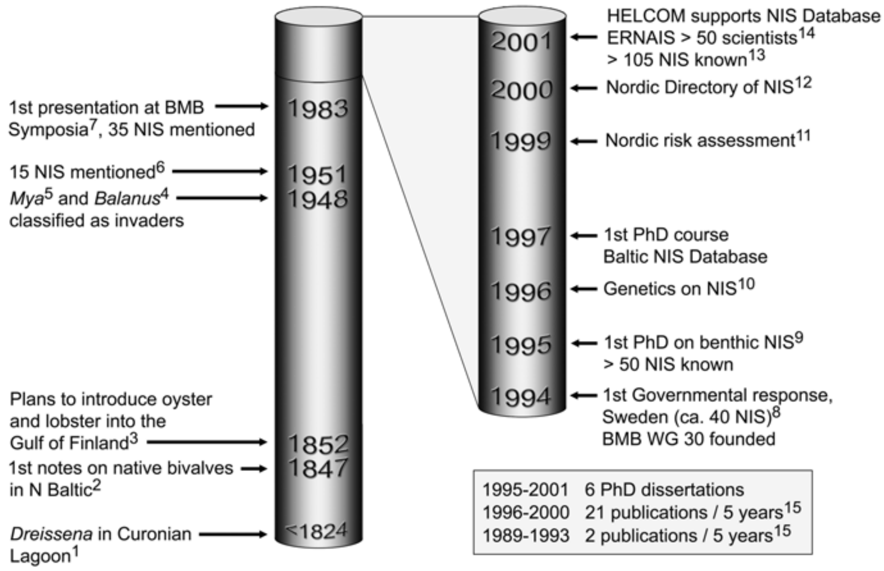

Figure 1. Timeline of research into invasion biology in the Baltic Sea countries. 1) Nikolaev (1963), 2) von Siemaschko (1847), 3) Hamel (1852), 4) Hägg (1948), 5) Hessland (1946), 6) Nikolaev (1951), 7) BMB - The Baltic Marine Biologists; Leppäkoski (1984), 8) Jansson (1994), 9) Fritzsche (1995), 10) Röhner et al. (1996), 11) Gollasch & Leppäkoski (1999), 12) Weidema (2000), 13) Baltic Sea Alien Species Database (2002), 14) ERNAIS (2001; European Research Network on Aquatic Invasive Species), 15) Baltic Marine Environment Bibliography 2002.

Traditionally a major part of marine biological research in this area has been focused on studies of distribution of species, structures of populations and communities, as well as links within and between different sub-systems in relation to natural environmental gradients. A major task for invasion biology is to investigate how these gradients modify the effects of invaders on the indigenous biological systems. The invasion of the North American polychaete *Marenzelleria* cf. *viridis* in the mid-1980s and the Ponto-Caspian predatory fishhook water flea *Cercopagis pengoi* in the early 1990s, in addition to tens of historical and recent invaders already present in the Baltic, have had a major impact on the structure and function of both the benthic and pelagic subsystems. These recent invaders have also increased both the common and scientific awareness of bioinvasions. Increased understanding of the ecological and economic impacts of NIS and effective monitoring of their spread are essential elements in the study of xenodiversity. Interpretation of functional changes related to NIS at a regional or basin-wide scale is a difficult, but essential task for the near future to assess the total impact of NIS. Due to its low number of native species and simplified food webs, the Baltic Sea offers unique opportunities for detailed studies on the autecology of NIS and, in particular, their interspecific relations with indigenous fauna and flora. Even if the modes of impacts are understood for a number of these species, quantitative data on impacts are rare and very little is known about their economic consequences and impact on human activities.