PERSPECTIVE

The Baltic—a sea of invaders[1]

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Abstract: There are about 100 nonindigenous species recorded in the Baltic Sea. Invasive species have resulted in major changes in nearshore ecosystems, especially in coastal lagoons and inlets that can be identified as "centres of xenodiversity". Fewer than 70 of these species have established reproducing populations. Dominant invasion vectors include unintentional introductions via ballast water, tank sediments, and hull fouling, aquaculture, and the construction of canals that have facilitated active or passive natural dispersal. Of the approximately 60 unintentionally introduced species with a known invasion history, 38 are transoceanic (including 19 Atlantic species of American origin) and 18 of Ponto-Caspian origin. Species that have caused economic damage to fisheries, shipping, and industry include the hydrozoan *Cordylophora caspia*, the barnacle *Balanus improvisus*, the cladoceran *Cercopagis pengoi*, and the bivalve *Dreissena polymorpha*. The Baltic Sea has served as a secondary source of nonindigenous species to the North American Great Lakes. Further study is warranted to quantify large-scale ecosystem changes in the Baltic associated with establishment and population growth of nonindigenous species and to prevent future invasions.

Résumé : On a recensé une centaine d'espèces non indigènes dans la Baltique. Les espèces envahissantes ont causé des changements majeurs dans les écosystèmes côtiers, particulièrement dans les lagunes et les anses qui peuvent être qualifiées de centres de « xénodiversité ». Moins de 70 de ces espèces ont réussi à établir des populations qui se reproduisent. Les principaux vecteurs d'introduction sont les apports involontaires par les eaux de ballastage, les sédiments des réservoirs et l'encroûtement des coques, ainsi que la construction de canaux qui ont facilité la dispersion naturelle active ou passive. De la soixantaine d'espèces introduites involontairement dont l'histoire est connue, 38 sont d'origine transocéanique (dont 19 espèces atlantiques d'origine américaine) et 18 proviennent de la région pontocaspienne. Parmi les espèces qui ont nui aux pêches commerciales, au transport maritime et à l'industrie, on trouve l'hydrozoaire *Cordylophora caspia*, la balane *Balanus improvisus*, le cladocère *Cercopagis pengoi* et le bivalve *Dreissena polymorpha*. La Baltique sert de source secondaire d'espèces non indigènes qui envahissent les Grands-Lacs d'Amérique du nord. Des études supplémentaires sont nécessaires pour arriver à quantifier dans l'écosystème de la Baltique les changements à grande échelle qui sont dus à l'établissement et à la croissance démographique des espèces non indigènes et ainsi prévenir les invasions futures.

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Introduction

All ecosystems are susceptible to invasion by non-indigenous species. During the last two centuries, about 100 alien species have been recorded in the Baltic Sea, most of which were introduced unintentionally by ship ballast water or hull fouling or by spreading from their primary sites of introduction into adjacent freshwater bodies (Leppäkoski and Olenin 2000*a*). Future species introductions may be caused by increasing volumes of ship traffic, which is the main global vector of introduction of alien marine organisms (Gollasch and Mecke 1996; Gollasch and Leppäkoski 1999). As an example, shipping activity in the Kiel Canal, connecting the North and Baltic seas, has increased in terms of

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transported cargo during the last few decades, whereas the number of ships has decreased since the 1960s from 40 000 to 15 000 ships in the late 1990s (Mr. Glau, Kiel Canal Administration, 24106 Kiel, Germany, personal communication). The volume of cargo transported by sea has increased four- to five-fold since World War II (Breitzmann 1999).

Being both a recipient and donor area, the Baltic Sea has become an important node in a global network of non-indigenous species transfers during recent decades, thereby facilitating the process of homogenization of the world's aquatic fauna and flora (Leppäkoski and Olenin 2000*b*). The aim of this paper is to provide an overview on the invasion status of the Baltic Sea and its main subbasins along the gradients from the entrance area in southwest up to the semi-arctic Bothnian Bay in the north.

The Baltic Sea

Physicochemical characteristics

The Baltic Sea covers less than 0.1% of the total area of the world's oceans. It is a large, irregularly shaped basin that supports a large variety of distinctive underwater biotopes for both native and introduced organisms. This characteristic results from its complicated bottom relief and coastal topography (e.g., length of the Finnish coastline is 39 000 km), accompanied by a complex systems of currents. It is also a young sea, geologically and hydrographically unstable. After the last glaciation period, a freshwater lake was formed. It was followed by a short marine period and then a second freshwater period lasting until about 7500 years before present, at which time it became brackish. Consequently, most animal and plant species living in the Baltic Sea are postglacial immigrants (e.g., Segerstråle 1957). In this respect, the Baltic Sea closely resembles the geological and biological history of the North American Great Lakes.

The semi-enclosed Baltic Sea represents the world's largest brackish-water sea area, with a total surface of 382 000 km^2. It is isolated from the North Sea and northeastern Atlantic Ocean by both geographical (sill depth 18 m, total opening less than 20 km) and ecological barriers (e.g., coldness and low salinity).

The nontidal Baltic is shallow (maximum depth 459 m, mean depth 55 m; 17% of bottom areas < 10 m deep; Voipio 1981) and long (1400 km), with notably colder climatic conditions prevailing in the northern parts (particularly Bothnian Bay) than in the southern parts (Table 1), which has a mean surface water temperature in summer of 14–16°C. In autumn, the temperature difference between southwestern and northern parts of the sea is approximately 8°C. The ice cover in the northern parts of Bothnian Bay usually lasts between 170 and 190 days, whereas in the entrance area of the Gulf of Finland, it can persist for 70 days. Furthermore, ice may also form in the inner parts of bays and fjords on the Swedish west coast and in the entrance area.

The salinity varies from 2–3‰ in the inner parts of the large gulfs, through 6–8‰ in the Baltic Proper, to 20–24‰ in the Kattegat (Fig. 1). The inward flow of saline waters via the Kattegat, the shallow Belt Sea, and the Sound constitutes one of the main factors affecting the salinity regime in the whole region. There is a primary halocline from the entrance up to the Åland Sea (northern Baltic Proper) at depths of 50–70 m, below which the water has higher salinity and is irregularly subjected to hypoxia or anoxia and presence of H_2S. A distinct summer thermocline is formed in the Baltic Proper at 10–30 m. This separates the cold intermediate winter water from the warmer surface layer. The intensity of this discontinuity layer declines towards the gulfs of Finland and Bothnia (Voipio 1981).

Native biota

Horizontal and vertical gradients occur regularly and not only strongly influence the native biotic communities, but also provide nonindigenous species of different origins (from cold stenothermal to eurythermal species) with an extended repertoire of hospitable abiotic conditions within a salinity range of 0 to >20‰. There are few and perhaps no truly endemic species in the Baltic (Voipio 1981). The flora and fauna consist mainly of euryhaline species that have extended their natural range from the North Atlantic, relicts from previous periods of sea history, brackish and freshwater species, as well as species recently introduced by humans (see Segerstråle (1957) for a comprehensive review).

Most euryhaline species assemblages of the North Sea occur in the Kattegat area, but many fully marine groups are more or less absent inside the Danish Sounds (e.g., sea anemones, starfish, sea urchins, brittle stars, crabs, lobsters, squids, and sharks). In this transient area, the number of macroscopic species drops by approximately one order of magnitude. Several major groups of marine animals are absent in the Baltic Sea. The decrease in marine species from the southwestern Baltic towards the Gulf of Bothnia is partly, but not fully, compensated for by an increase in species of freshwater origin.

Along the gradients, the number of animal species of marine origin decreases from the Kattegat (>850 species) to the Baltic Proper (about 80), the Bothnian Sea (50), and the innermost Bothnian Bay (<10). Less than 3% of the marine macroinvertebrates in the waters of the Skagerrak are able to survive conditions in the Bothnian Sea. Phytoplankton diversity declines from some 420 taxa in the southern Baltic Sea to about 160 taxa in Bothnian Bay. There are only about a dozen species of marine macroalgae in Bothnian Bay out of the about 180 species found in the Kattegat (Table 1). The number of marine fish species falls from about 70 in the southwestern Baltic to about 20 in the Bothnian Sea and 6–10 in Bothnian Bay (for reviews, see Voipio (1981), Leppäkoski and Bonsdorff (1989), and Elmgren and Hill (1997)). Freshwater species dominate in all groups of organisms in the most freshened parts of the gulfs of Bothnia and Finland.

The coastal lagoons along the southern coast of the Baltic are strongly influenced by river water outflows. In the Curonian and Vistula lagoons, approximately 80 native species of zoobenthos, excluding insects and oligochaetes, and about 100 species of zooplankton occur (Kube et al. 1996; Zmudzinski 1996).

Three major groups of organisms have adapted to the conditions of the gulfs of Riga and Finland. The first group includes euryhaline, eurythermal species of marine boreal origin (e.g., the copepods *Acartia* spp. and *Eurytemora hirundoides*, the bivalve *Macoma balthica*, the amphipod *Corophium volutator*, the polychaete *Nereis diversicolor*,

Table 1. Some abiotic and biotic gradients in the Baltic Sea.

	Southern Baltic	Northern Baltic Proper	Bothnian Bay
Insolation, annual sum (kWh·m^{-2})	1010	990	880
Air temperature, annual mean (°C)	8	5–7	2–3
Average duration of the growing season (≥ +5°C), days	220	185	145
Beginning of the growing season	April 19	May 5	May 25
Effective temperature sum (degree-day units for daily means ≥ +5°C)	1600	<1300	<920
Water temperature (°C)			
Mean in July, surface	16	15	12
Sum of days >10°C, surface	140	120	90
Annual maximum, 20 m depth	>14	13	>10
Ice-cover duration (days)	Occasional	~20	110–190
Salinity (‰)			
Surface water	7–8	6–7	2–3
Bottom water	14–17	10–13	3–4
Primary production (phytoplankton) (g C ·m^{-2}·year^{-1})	150–190	140–160	15–30
Approximate date of vernal phytoplankton bloom	April 20	May 15	June 15
Macrozoobenthos (soft bottom) above the halocline			
Taxa·0.1 m^{-2} sampling unit	10–11	<8	<2
Wet biomass (>10 m depth), g·m^{-2}	100–500	50–150	<1
Marine macroalgae, number of species	>110	50–90	10–12

Note: Data from Voipio (1981) and Leppäkoski and Bonsdorff (1989) and references therein.

Baltic herring (*Clupea harengus membras*), and three-spined stickleback (*Gasterosteus aculeatus*)). The marine species that require higher salinities (e.g., copepods *Temora longicornis* and *Pseudocalanus elongatus* and Atlantic cod (*Gadus morhua*)) do occur but are not abundant. The second group consists of freshwater species, which dominate in coastal areas (e.g., the rotifers *Keratella* spp., the copepods *Mesocyclops* spp., the gastropod *Theodoxus fluviatilis*, European perch (*Perca fluviatilis*), and pikeperch (*Stizostedion lucioperca*)). The third group consists of glacial relict species, including the copepod *Limnocalanus grimaldii*, the mysid *Mysis relicta*, the isopod *Saduria entomon*, the amphipod *Monoporeia affinis*, fourhorned sculpin (*Triglopsis quadricornis*), and European smelt (*Osmerus eperlanus*)) in the deep water with the Pan-Arctic biocoenoses colonizing almost the whole lower part of the eulittoral (Ojaveer 1995).

In the easternmost part of the Gulf of Finland, organisms of freshwater origin are abundant. In Neva Bay, 51 native species of macrozoobenthos, excluding insects and oligochaetes, have been recorded. In the eastern Gulf of Finland, this value is reduced to 15 species. The number of native fish species increases westward with increasing salinity from 38 in Neva Bay to 53 in the eastern Gulf of Finland. Towards the west, population abundances of several marine euryhaline species (e.g., *Acartia bifilosa*, *E. hirundoides*, *M. balthica*, *Mytilus edulis*, and European flounder (*Platichthys flesus*)) increase. In the western part and the entrance area, marine species with a higher salinity requirement (e.g., the copepods *T. longicornis* and *P. elongatus*, European sprat (*Sprattus sprattus*), and periodically *G. morhua*) gradually increase in importance. Among the

fish, herring is probably the best adapted to prevailing environmental heterogeneity, forming separate populations in the eastern and western parts of the basin. In deeper waters in the central part of the basin, cold-water species such as the copepod *Limnocalanus macrurus*, amphipods *Pontoporeia femorata* and *M. affinis*, and the isopod *S. entomon* are present. Conversely, *M. balthica*, *M. edulis*, and *N. diversicolor* are more abundant in shallower areas.

Marine faunal and floral diversities are low in the northern Baltic Sea, for example, only seven native polychaete species have been recorded on the south coast of Finland. Therefore, the introduction of two nonnative and invasive spionid polychaetes (see below) is noticeable. The total macrobenthic biomass remains around 60 g·m^{-2} in the Bothnian Sea and below 1 g·m^{-2} wet weight in Bothnian Bay. In the deep sections of the Gulf of Bothnia, only two or three species (*M. balthica*, *M. affinis*, and *S. entomon*) dominated the community before the introduction of the polychaete *Marenzelleria viridis* (Leppäkoski and Bonsdorff 1989; Table 1).

Invasion status of the Baltic Sea

The first nonnative fish stocks were most probably transplanted by Stone-Age fishermen into the lakes of northwestern Europe after the end of the last glaciation period. These introductions and their spread into coastal waters of the Baltic remain cryptic. The first known human-mediated introduction of North American species to northwestern Europe is of the soft-shelled clam (*Mya arenaria*), which is believed to have been carried across the Atlantic by the

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Fig. 1. Map of the Baltic Sea showing subregions discussed and isohalines. Bar graphs represent number of nonindigenous species (NIS) according to their area of origin: I, Ponto-Caspian; II, North America; III, South East Asia and Indo-Pacific; IV, other areas of the World or origin unknown. Only NIS known to be established were taken into account. BBs, Bornholm Basin; BB, Bothnian Bay; BS, Bothnian Sea; GB, German Boddens; GBs, Gotland Basin; GD, Gulf of Gdansk; KB, Kiel Bight; NQ, Northern Quark; Sk, Skagerrak.
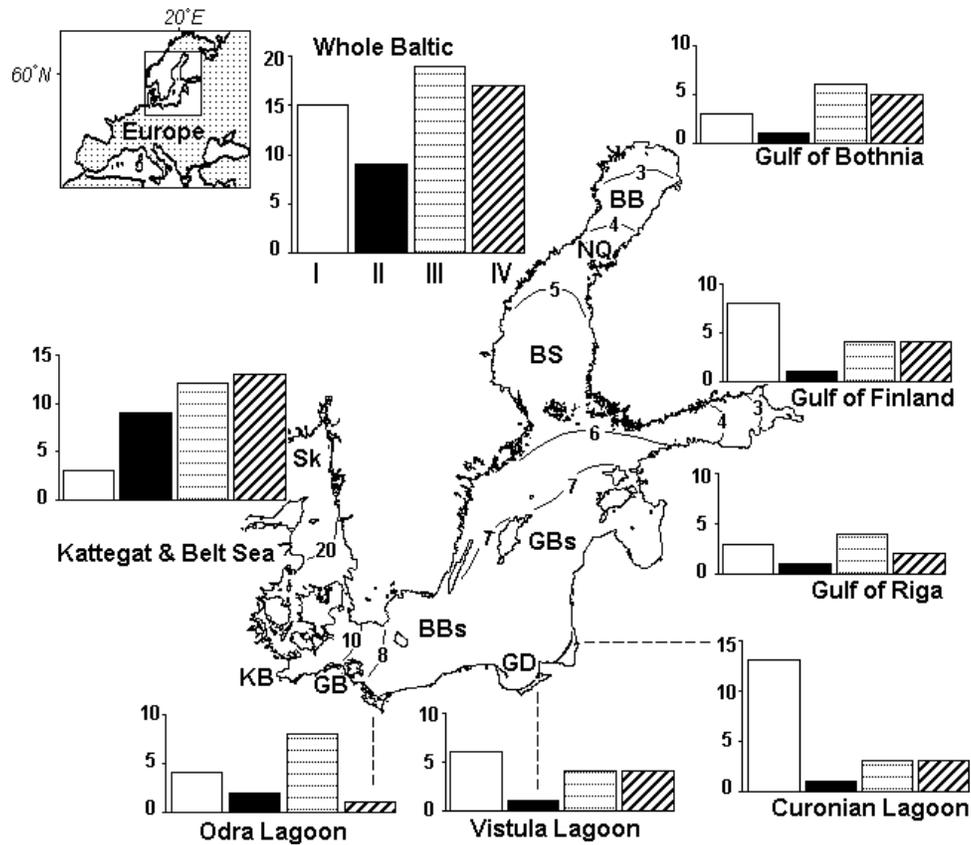
Vikings. Among the earliest introductions to the Baltic Sea is the Ponto-Caspian zebra mussel (*Dreissena polymorpha*), which spread into southeastern coastal lagoons in the early 1800s, and the likely North American barnacle (*Balanus improvisus*), which was first recorded in the Baltic in 1844. The charophyte *Chara connivens* is believed to be an early, dry ballast release species introduced in the 1850s (for references, see Baltic Sea Alien Species Database 2001).

The brackish nature of the Baltic Sea does not protect its waters from new introductions. Today, the fauna and flora of the Baltic are exposed to other brackish-water biota of the world because of the breakdown of large-scale geographical barriers by ship traffic, which is also leading to an exchange of species. In addition to its contact with the Atlantic through the Danish Straits, the Baltic and its drainage area are connected to the Ponto-Caspian brackish seas by rivers and canals, which were opened during the period from 1775 to 1952. Species endemic to Ponto-Caspian basins (Black, Caspian, and Azov seas and the adjacent rivers emptying into these seas) have become established in inland Europe, the Baltic Sea, and most recently, the North American Great Lakes. The Caspian and Ponto-Azovian fauna have spread, in different manners and at different geological periods, to Turkey, the Aral Basin, the Euphrates River, European river systems, and the Adriatic Sea (Bacescu 1966; Jazdzewski and Konopacka 1999). In the Baltic Sea, 22 species of

Ponto-Caspian origin have been recorded; of them, 16 have been able to establish permanent populations, mainly in coastal lagoons and inlets. Their proportion diminishes westward: *D. polymorpha* is the only species belonging to this group in Danish coastal waters, and the same can be said of the hydroid *Cordylophora caspia* on the North Sea coast of Germany (for references, see Baltic Sea Alien Species Database 2001).

Ponto-Caspian crustaceans were transplanted as food to stimulate fish production in European lakes and reservoirs during the 20th century; within an immense former U.S.S.R. program of transplantations of Peracarida that begun about 1950, more than 30 amphipod species from the "Caspian complex" were used for acclimatization purposes (Gasiunas 1964). Consequently, a biased selection of over 40 Ponto-Caspian species has expanded their ranges from the southeastern European source pool into central and western Europe (Gasiunas 1964; Jazdzewski and Konopacka 1999; Olenin and Leppäkoski 1999; Fig. 2). The colonization of European ports by these species led to their introduction to North America through transoceanic shipping. Most nonindigenous species discovered in the Great Lakes since the mid-1980s are Ponto-Caspian endemics and more are expected to arrive in the future (Ricciardi and MacIsaac 2000).

Nonnative species in the Baltic Sea have been documented by Nikolaev (1951), Leppäkoski (1984), Gollasch

Fig. 2. Number of new nonindigenous species recorded in the Baltic Sea during quarter-century intervals since 1800 according to their area of origin: Ponto-Caspian (black); North America (shaded); South East Asia and Indo-Pacific (hatched); other regions or unknown (stippled).

and Mecke (1996), and others. The Baltic Sea and especially its coastal inlets and lagoons are heavily infested with non-indigenous species (Gruszka 1999; Leppäkoski and Olenin 2000a, 2000b; Figs. 1, 2). By the beginning of 2001, 100 nonindigenous species had been recorded in the basin, although fewer than 70 have established reproducing populations. Of the approximately 60 unintentional introductions (including nonestablished species) with more or less known dispersal histories, 38 are transoceanic (among them, 19 are of trans-Atlantic, i.e., North American, origin), and a further 18 are native to the Ponto-Caspian region (Baltic Sea Alien Species Database 2001).

The dominant vectors for species introductions are shipping, including introductions via ballast water, tank sediments, and hull fouling, aquaculture (including unintentionally introduced nontarget species), and the opening of canals that have facilitated active or passive dispersal from adjacent fresh- and brackish-water systems. River systems and canals connect the Baltic with the Black, Caspian, and White seas. Thus, several geographical invasion corridors, other than ship traffic, open into the Baltic Sea and its different subregions.

Based on published first findings, the minimum rates of secondary, within-basin spread were estimated as follows: the barnacle *B. improvisus* from Königsberg (now Kaliningrad) (1844) to Turku, Finland (1868), 30 km·year^{-1}; the polychaete *M. viridis* from German Boddens (1985) to Lithuania (1989), 170 km·year^{-1}, to South Finland (1990), 480 km·year^{-1}, and to Northern Quark (1996), 90 km·year^{-1}; the gastropod *Potamopyrgus antipodarum* from Wismar Bight, Germany, to the Swedish island Gotland (1920), 20 km·year^{-1}, to the Åland Islands, Finland (1926), 50 km·year^{-1}, and further to the Bothnian Bay (1945), 30 km·year^{-1} (Leppäkoski and Olenin 2000a).

Several species known to live on shallow bottoms only, for example in the North Sea, extend their depth range in the brackish Baltic Sea. This phenomenon, known as brackish-water submergence, may depend on salinity stratification or the absence of predators and competitors in the Baltic. Nonindigenous species that colonize deeper bottom waters in the Baltic include *B. improvisus*, found at 44–53 m, the bivalve *M. arenaria* at 45 m, the spionid polychaetes *Boccardia redeki* at 29 m, and *M. viridis* at 78 m. *Marenzelleria viridis* was the first nonindigenous species in the Baltic to colonize the deeper soft bottoms below the halocline (Leppäkoski and Olenin (2000a) and references therein).

The entrance area

The entrance area connects the brackish Baltic Sea with the marine North Sea and is distinguished by a series of basins of varying depths separated by shallow areas and sills: the Belt Sea, the Sound, and the Kattegat Strait. The western Baltic Sea is characterized by several sills followed by deep regions. The sills (e.g., the Darss Sill, 18 m) limit the influx of water from the North Sea and pose a limitation to commercial shipping in some areas.

The habitat surfaces in the Baltic region range from soft to hard bottoms, the latter being of minor importance in the western part of the sea except on the west coast of Sweden. Small tidal amplitudes reduce the dimension of the habitat in supra- and meso-littoral zones and have only a minor importance for the induction of water currents. Wind-induced currents in the western Baltic region result in a surface current of less saline water into the North Sea and a countercurrent of higher salinity in deeper water layers. As a result, salinity declines from west to east and increases from

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surface to bottom layers. In the North Sea, salinity is typically higher than 30‰. Between Skagerrak and Kattegat, the surface water salinity decreases to 20‰ and further down to 8–9‰ in the area between southern Sweden and the German island Rügen. The northwards-directed current on the Swedish west coast and in the Belt Sea counteracts further spread of marine nonindigenous species from the Skagerrak coast towards the inner Baltic.

The surface water temperature in the western Baltic fluctuates highly between seasons, ranging from a minimum of –1–0°C in January to a maximum of 14–16°C in July. The temperature drops to 12–13°C during September, though higher values are recorded from the Belt Sea and Sound areas (Voipio 1981). Ice cover may form in the inner parts of bays and fjords on the Swedish west coast and the Danish and German east coasts for 20–30 days.

Nonindigenous species

The main vectors of species invasions into the western Baltic are secondary introductions from neighbouring regions, species migrations through waterways, aquaculture activities, and shipping (Reise et al. 1999). Besides the Suez and Panama canals, the Kiel Canal is the third-most important manmade seaway in the world, connecting the mouth of the River Elbe (North Sea) to the Baltic Sea. A second direct connection with the North Sea is the Danish Limfjord, which cuts across the Jutland peninsula. Both waterways are used for commercial and recreational shipping.

Aquaculture in the Baltic Sea area is based on imported fish species, such as the North American rainbow trout (*Oncorhynchus mykiss*), and native fish, including salmon (*Salmo salar*) and eel (*Anguilla anguilla*). Some experiments have been conducted in the Kiel Bight with the Pacific oyster (*Crassostrea gigas*), without success, however. Compared with many other European regions, aquaculture is of minor importance in the Baltic and plays only a minor role as a potential vector for species invasions.

In 1990, more than 8200 ships larger than 100 deadweight tons called on German ports. In total, ships from approximately 50 countries visit Baltic ports. Predominant traffic routes outside the Baltic Sea include the Black Sea and North Sea (United Kingdom, Ireland, Germany, and the Netherlands). Few ships visit from trade routes to northwestern Africa, the North American east coast, the Mediterranean Sea, and Asia (Gollasch and Leppäkoski 1999). The annual import and export of goods in Baltic ports total 300 million tonnes, including 120 million tonnes of inner Baltic shipping (Anonymous 1995). It has been estimated that 2000 ships travel across the Baltic Sea each day, excluding pleasure boats (HELCOM 1996). Even with low numbers of specimens, when recalculated for the total volume of ballast tanks, millions of organisms may be released into new environments.

Several nonindigenous phytoplankton species have been recorded from the western Baltic region. The Indo-Pacific species *Odontella sinensis* (Diatomophyceae) was first reported from the North Sea in 1903 and was probably introduced via ballast water. The potential paralytic shellfish toxin (PST) inducing species *Alexandrium tamarense* and *Alexandrium minutum* (Dinophyceae) have been found along the Swedish west coast.

Gyrodinium cf. *aureolum* (Dinophyceae) was first observed in Kattegat in 1981 and has caused massive fish mortalities during mass occurrences by clogging the gills of fish in Danish, Norwegian, and Swedish waters. *Prorocentrum minimum* (Dinophyceae), a species known to produce PST, was first recorded in Kattegat in 1981 and in the Baltic Proper in 1983, and today it is also present in the Skagerrak. The diatoms *Coscinodiscus wailesii* and *Thalassiosira punctigera* were first reported in Norway in 1979 and are believed to have arrived in Europe with imported oysters. Today, *C. wailesii* is present in Skagerrak and in the Oslo Fjord, and *T. punctigera* is reported in the Kattegat (Jansson 1994).

The first findings of the Japanese seaweed *Sargassum muticum* were from Limfjord, Denmark, in 1984, and drifting specimens were subsequently recorded in the mid-1980s in the adjacent Skagerrak. This species was first observed on the Swedish west coast in 1987 and is now an established and permanent member of the algal flora. The fast expansion of this macroalga along the Swedish west coast has caused a severe change in the sublittoral vegetation belt in affected areas (Wallentinus 1992). *Fucus evanescens* was first recorded in the Belt Sea in 1989 and had spread to the western Baltic by 1991 (Jansson 1994).

Teredo navalis (Bivalvia), the shipworm, was probably brought to Europe from East Asia several centuries ago and is now widespread in the southwestern Baltic region. This species has had major direct negative economic impacts in the Baltic. For example, it caused approximately US$ 25 million damage to wooden installations since 1995 along the German Baltic coast (K. Hoppe, Coastal Research and Management, Kiel, Germany, personal communication).

The first records of *M. viridis* (Polychaeta) were made in 1985, and it now occurs in various brackish waters of the southern Baltic Sea (e.g., the German Boddens) in great numbers (Zettler et al. 1995). *Gonionemus vertens* (Hydrozoa) was first recorded in Scandinavian waters in 1921, where it was introduced via the ballast water of ships, hull fouling, or with oysters. *Crepidula fornicata* (Gastropoda) was brought to Europe unintentionally with imported oysters from North America and is currently established in the Kattegat and Skagerrak where it competes with oysters for space and food. The American razor clam (*Ensis americanus*) was also introduced to Europe from North America with ballast water and was first observed in German North Sea waters in 1978. It established itself on the Swedish west coast in the early 1980s and is reported today as far south as the Sound region. *Mya arenaria* (Bivalvia) and *B. improvisus* (Cirripedia) are common species along the shores of the western Baltic (Leppäkoski 1984; Jansson 1994).

Specimens of the Chinese mitten crab (*Eriocheir sinensis*), introduced to Germany in 1912, are found several times each year in the Baltic Sea. To complete its life cycle, this species needs to migrate into marine waters. It is assumed that specimens found in the Baltic Sea belong to established populations in German rivers that flow into the North Sea and probably migrate through the Kiel Canal. *Acartia tonsa* (Calanoida) was first recorded in European waters in 1927 off the French coast and was subsequently recorded from the western Baltic Sea in 1934, probably as a result of ballast water discharge (Jansson 1994).

Coastal lagoons (southern Baltic)

The southern Baltic consists of three large basins (the Arkona Sea, the Bornholm Basin, and the southern part of the Eastern Gotland Basin) as well as adjacent large gulfs (the Gulf of Gdansk and Pomeranian Bay). The three largest Baltic coastal lagoons, the Szczecin, the Vistula, and the Curonian, are all situated in the southern and southeastern parts of the Baltic Sea. They were formed off the estuaries of the major rivers Odra–Oder, Vistula, and Nemunas–Neman, respectively, during early postglacial periods about 6000–8000 years ago.

All three lagoons are enclosed, large, shallow (mean depth 3–4 m), brackish-to-freshwater bodies, connected to the Baltic Sea by narrow straits. In the Szczecin and Vistula lagoons, the salinity fluctuates from 7–8‰ in the vicinity of the sea strait to less than 1‰ in their inner parts. The Curonian Lagoon contains freshwater in its southern and central parts owing to discharge from the Nemunas River, and in its narrow northern part, the salinity fluctuates irregularly from 7‰ to <0.5‰ within days or even hours. Water temperature displays a typical boreal pattern with the highest values occurring in July (absolute maximum 29°C), and the surface water temperature exceeds 10°C from late April until early October, which is 170–180 days. Because of shallow depths and extensive mixing, no stable thermocline or permanent hypoxic zones are formed in these lagoons. The lagoons are usually covered by ice from December to February (WWF Baltic Bulletin 1994).

Nonindigenous species

Several large seaports are situated on or near the inner parts of the lagoons or are connected to the sea by artificially deepened waterways (e.g., Szczecin, Kaliningrad, and Klaipeda). Thus, shipping may be one of the important sources of primary and secondary introductions. Moreover, several artificial inland waterways connect the estuaries and coastal lagoons with the Black Sea basin (Gruszka 1999; Jazdzewski and Konopacka 1999). Ponto-Caspian species (*D. polymorpha* and probably the gastropod *Lithoglyphus naticoides* and the hydrozoan *C. caspia*) first appeared in the Baltic Sea within the lagoons during the late 1700s to early 1800s, after the opening of Neman–Dniepr and Vistula–Bug canal connections. The first benthic species recognized as nonnative were the barnacle (*B. improvisus*) and the estuarine mud crab (*Rhithropanopeus harrisii*), found in the Vistula Lagoon in 1844 and 1948, respectively (Leppäkoski and Olenin 2000*a*).

In the early 1960s, Ponto-Caspian mysids (*Paramysis lacustris*, *Limnomysis benedeni*, and *Hemimysis anomala*) and amphipods (*Corophium curvispinum*, *Pontogammarus robustoides*, *Obesogammarus crassus*, *Chaetogammarus ischnus*, and *Chaetogammarus warpachowskyi*) were intentionally introduced into Lithuanian waters, including the Curonian Lagoon (Gasiunas 1964). Recently, in 1999, the Ponto-Caspian round goby (*Neogobius melanostomus*) appeared in the Vistula Lagoon from the adjacent Gulf of Gdansk (Borowski 2000).

In total, at least 19 species of macrozoobenthos in the three lagoons are identified as nonnative (Gruszka 1999; Olenin and Leppäkoski 1999). These species include *C. caspia* (Cnidaria); *M. viridis* (Polychaeta), *B. improvisus*, *P. lacus-*

tris, *L. benedeni*, *H. anomala*, *C. curvispinum*, *Gammarus tigrinus*, *P. robustoides*, *O. crassus*, *C. ischnus*, *C. warpachowskyi*, *Orconectes limosus*, *R. harrisii*, and *E. sinensis* (Crustacea), and *P. antipodarum*, *D. polymorpha*, *L. naticoides*, and *M. arenaria* (Mollusca). The functional roles of most of these species were discussed by Olenin and Leppäkoski (1999). In the Curonian Lagoon, *D. polymorpha* is the dominant species (mean wet weight biomass 880 g·m^{-2}, 86% of total), forming mussel beds over approximately 23% of the Lagoon's bottom area, mainly in the freshwater central and southern regions. Within the northern oligohaline region, abundance of *Dreissena* declines towards the sea; a similar situation occurs in the Szczecin Lagoon (Wiktor 1969). There is no evidence that *Dreissena* has displaced the marine bivalve *M. edulis* in the Lagoon, as the species are spatially separated.

The colonial hydroid *C. caspia*, the polychaete *M. viridis*, the barnacle *B. improvisus*, and Ponto-Caspian gammarids predominate in different benthic habitats of the northern part of the Curonian Lagoon, and some species are dominant only on sites within specific microhabitats. For instance, *C. caspia* and *B. improvisus* densely foul firm substrates on soft bottom. Ponto-Caspian gammarids inhabit floating mats of filamentous green algae in the Curonian Lagoon, reaching a wet biomass of 120 g·m^{-2}, compared with 10 g·m^{-2} for native species (D. Daunys, Coastal Research and Planning Institute, Klaipeda University, Klaipeda, Lithuania, personal communication).

The soft-bottom community structure was totally changed by the polychaete *M. viridis* in the Vistula Lagoon when it became a dominant species on sandy and muddy habitats in the middle of the 1990s. It reached high biomasses (216 g·m^{-2}) and comprised up to 95% of the total community biomass (Zmudzinski 1996). *Marenzelleria viridis* managed to dominate the benthos and even the plankton seasonally in the northern Szczecin Lagoon, where the maximum density recorded was 28 000 individuals·m^{-2} (Kube et al. 1996; Gruszka 1999). The successful colonization of the lagoons by this polychaete was facilitated by low precipitation and lower water flow in the rivers in the late 1980s and early 1990s. Drought allowed greater intrusion of Baltic water, laden with *M. viridis* eggs and larvae in autumn, into the lagoons. Increased salinity also provided more favourable conditions for reproduction and development of *M. viridis* and for its range extension in the estuaries (Gruszka 1999).

Another recent newcomer in the Szczecin Lagoon, the North American amphipod *G. tigrinus*, inhabits a wide range of habitats from hard bottom covered by algal vegetation to muddy and sandy sediments at very shallow depths, where it co-occurs with the Ponto-Caspian gammarid *P. robustoides* (Gruszka 1999). In 1998, both species were also found in the shallow littoral of the Vistula Lagoon (Jazdzewski and Konopacka 1999). Moreover, another two Ponto-Caspian species, *Dikerogammarus villosus* and *Dikerogammarus haemobaphes*, have recently reached the lower sections of rivers Odra–Oder (P. Gruszka, unpublished data) and Vistula (Jazdzewski and Konopacka 1999), respectively.

As many as ~90 zooplankton species (taxa) can be found in the three lagoons (Wiktor 1963; Gollasch and Leppäkoski 1999; Gasiunaite 2000). *Marenzelleria viridis* and *D. polymorpha* are nonindigenous species that can season-

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ally dominate plankton communities in the southern Baltic estuaries (Wiktor 1969; Gruszka 1999), and the copepod *A. tonsa* is a widely spread holoplanktonic animal in the southern Baltic (Jansson 1994). In 1999, the cladoceran *Cercopagis pengoi* appeared in both Curonian and Vistula lagoons as well as in adjacent seawaters (Gasiunaite 2000). No quantitative data on its distribution and seasonal dynamics is available, although biofouling of fishing equipment by *Cercopagis* was a serious problem for local fishermen on the Lithuanian coast in September 1999 (Gasiunaite 2000).

The Gulf of Riga

The Gulf of Riga is shallow, with a maximum depth of 60 m. The basin is connected to the Baltic Sea via two narrow sounds, the Muhu Sound in the north (sill depth 5 m) and the Irbe Sound in the northwest (sill depth ca. 20 m). The drainage area of the basin is about 10 times larger than the surface area of the Gulf. Five relatively large rivers discharge 31 km^3 of freshwater into the Gulf annually, of which 86% flows into the southern part. Water exchange between the Gulf of Riga and the open Baltic averages about 360 $km^3 \cdot year^{-1}$, nearly the volume of the basin (Ojaveer 1995).

The salinity regime of the Gulf of Riga is characterized by a lack of a halocline and high spatiotemporal variability from 0.5–2.0‰ in spring in the surface layers up to 7.7‰ at the bottom of the Irbe Strait in spring and summer. The average annual salinity of the basin varied considerably during the 1920s–1990s from 5.2‰ in the late 1920s to 6.4‰ in 1977 (Ojaveer 1995). The relatively low salinity of the Gulf of Riga is the result of isolation of the basin from the Baltic Proper and high freshwater inflow.

An important characteristic of the temperature regime of the Gulf of Riga is a vertical convective mixing in spring and autumn that penetrates almost to the bottom. During the warm season, a strong thermocline separates the upper (>15°C) and deeper (<6°C) water layers. Surface water (0–10 m) temperature exceeds 10°C from the third week of May until the end of September. Long-term mean ice cover duration in the northeastern Gulf of Riga is 132 days (Ojaveer 1995).

Nonindigenous species

There are no documented invasion corridors for primary introductions into the Gulf of Riga. Secondary invasions within the Baltic Sea include ballast water exchange and fish stocking as the primary mechanisms for invasions.

There are 54 fish species recorded in the Gulf of which eight are nonindigenous. These species have been introduced intentionally during the last few decades with the exception of the carp (*Cyprinus carpio*), which was introduced to Estonia in the 18th century. During the 1940s–1960s, various sturgeon stocks were released into the Gulf of Riga for the enhancement of commercial fish stocks: sterlet (*Acipenser ruthenus*), beluga (*Huso huso*), Siberian sturgeon (*Acipenser baeri*), and Russian sturgeon (*Acipenser gueldenstaedti*). In addition, chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbusha*) were released in the 1970s (Ojaveer (1995) and references therein).

A total of 58 macrozoobenthic species have been recorded in the Gulf of Riga (Kotta et al. 1998*a*), including seven nonindigenous species. The status of the *C. caspia* population in the Gulf of Riga is largely unknown. *Marenzelleria viridis* was first recorded in the Gulf of Riga in 1988 where it occupies the entire area and all possible substrates in the Gulf. The highest abundance and largest biomass (566 individuals·m^{-2} and 10.1 g·m^{-2}, respectively) were recorded in the southern and southeastern parts of the basin. Arrival of *M. viridis* has caused substantial changes to the soft-bottom macrofauna. The abundance contribution of annelids has increased from 25% to 42% in the 1970s and 1980s, and they now constitute 12% of biomass, up from their previous value of 1% before the *M. viridis* invasion into the Gulf of Riga (Ojaveer et al. (1999) and references therein).

Mya arenaria is one of the most frequent zoobenthic species at the 0- to 10-m depth, found in 22% of samples. Mean abundance and biomass of the species are 20 individuals·m^{-2} and 12 g·m^{-2}, respectively (Kotta et al. 1998*a*). Distribution of *P. antipodarum* is patchy and does not coincide with anthropogenic activities (i.e., the species does not occur more abundantly in harbour areas). It is presently confined to the northern basin – southern coast of Saaremaa Island, where it can reach 10 000 individuals·m^{-2} (J. Kotta, Estonian Marine Institute, 10617 Tallinn, Estonia, personal communication). *Dreissena polymorpha* was first recorded in 1855 and is relatively common in the basin. Permanent populations occur in the northeastern, eastern, and southern regions. Recent studies confirm the distribution of the species in the coastal areas, although it does not occur in the middle of the basin or off the southern coast of Saaremaa. Maximum abundance (8400 individuals·m^{-2}) and biomass (1463 g·m^{-2}) were recorded in the southern basin, where its filtering activities are an important factor limiting phytoplankton growth (Kotta et al. (1998*b*) and references therein).

Balanus improvisus is common in the Gulf of Riga and co-dominates at the 0- to 10-m depth in several areas by frequency of occurrence (46%; Kotta et al. 1998*a*). There has been an increase in the number of *E. sinensis* reported in commercial fishing nets during the late 1990s. However, estimates of population size are not available.

The first record of the copepod *A. tonsa* dates back to 1926 (Nikolaev 1951). Despite its relatively long history in the Gulf of Riga, its status is still unclear. Introduction of the most recent nonindigenous species, the cladoceran *C. pengoi*, into the Gulf of Riga may have resulted from secondary spread from Muuga Bay, Gulf of Finland, where the species was found in 1992. *Cercopagis* is more abundant in sheltered locations than in open areas or in regions characterized by currents. Maximum abundance recorded is 800 individuals·m^{-3} (Ojaveer et al. 1999). After the invasion of *C. pengoi*, the abundance of its potential prey, the cladoceran *Bosmina coregoni maritima*, decreased significantly. The most abundant pelagic fish (herring, sticklebacks, and smelt) can prey on *C. pengoi*, potentially reducing its abundance. However, *Cercopagis* remains a rare prey item in fish diet, accounting for an average of 7% of recovered prey items (Ojaveer et al. 2000). The Ponto-Caspian coelenterate *Maeotias marginata* was recorded in

the northwestern part of the area in 1999; its vector of introduction is unknown (Väinölä and Oulasvirta 2001).

The Gulf of Finland

The Gulf of Finland (mean depth 37 m) is an east–west elongated basin, freely connected to the Baltic Proper. A sill situated in the central basin separates the Gulf into western and eastern parts. The Neva River, the largest river on the Baltic Sea, discharges ca. 95 km^3 of freshwater into the eastern Gulf annually, or more than 80% of the total freshwater inflow.

A halocline in the western part of the basin at about 60–70 m weakens towards the east but sharpens and rises up to a depth of 10–30 m in the easternmost part. The water salinity increases from almost 0‰ at the surface in the easternmost basin to over 11‰ at the bottom of the entrance area. In addition, steep horizontal and vertical salinity gradients, with mean values of 1–2‰ at the surface, 4–5‰ at 20 m, and >7‰ at depths greater than 50 m, occur in the Gulf of Finland.

During the warm season, strong thermal vertical stratification with a warm upper water layer of about 10–20 m with cold water beneath is typical. Another important characteristic of the temperature regime is convective mixing of the water column down to 50–60 m during the spring and autumn. Higher summer temperatures (18–20°C) occur in the eastern basin with an absolute maximum of 24–26°C occurring, in warm summers, during late July – early August. The period with water temperatures above 10°C lasts from May to late September – early October (Voipio (1981) and references therein).

Nonindigenous species

There are at least two invasion corridors to the Gulf of Finland: (*i*) Lake Ladoga – Baltic Sea (confirmed by genetic studies of the cladoceran *Bythotrephes cederstroemi* (Berg et al. 2002), and (*ii*) a river system from the Ponto-Caspian region. This corridor consists of the Volga–Don river system, which opened in the early 1950s, and the Volga–Baltic system, which opened in 1965. Since then, this system has allowed ship transit from the Caspian Sea to the Baltic (Gollasch and Leppäkoski (1999) and references therein). The latest primary introduction into the Gulf of Finland is probably the cladoceran *C. pengoi*, which was most likely introduced from the Ponto-Caspain basin (Asov Sea or Don and lower Volga reservoirs) to the Baltic via this corridor (first *Cercopagis* was found in eastern Baltic). Significance of this corridor will increase in the future. Secondary spread from the Baltic Proper and intentional introductions of fish are also important sources of nonindigenous species.

Nonindigenous fish (*A. ruthenus*, *A. baeri*, *A. gueldenstaedti*, *O. mykiss*, *Coregonus autumnalis migratorius*, *Coregonus nasus*, *Coregonus muksun*, *Coregonus peled*, *Catostomus catostomus*, *Perccottus glenii*, and *C. carpio*) have been recorded as rare findings only in the Gulf of Finland. Therefore, their impact at the ecosystem level is probably insignificant.

Cordylophora caspia was first found in water intakes of the Leningrad Nuclear Power Station in 1979. At present, the species is common in littoral habitats in the eastern basin

only (Orlova et al. 1999). The polychaete *M. viridis* was first reported in the Gulf of Finland on the northern coast in 1990, and the species occurred at all sampling depths down to ca. 60 m, where its maximum abundance was 4000 individuals·m^{-2}. The polychaete spread to the southern coast in 1994 and to easternmost parts of the basin in 1996, where it became a common component of the benthic community (Leppäkoski and Olenin 2000*a*).

The crustacean *H. anomala* was first found in the western Gulf of Finland in 1992 (Salemaa 1998). Some amphipods have been successfully introduced into the Neva Estuary. For example, *P. robustoides* was found in Neva Bay, the freshwater part of the Neva Estuary, in 1999 (Orlova et al. 1999). Its vector of invasion is unknown, although southern lagoons from the Baltic or invasion via the Volga–Baltic waterway are possibilities. The Baikalian amphipod *Gmelinoides fasciatus* was first found in Neva Bay in 1996. By 1999, its occurrence had extended to adjacent littoral habitats in the eastern Gulf of Finland, probably as a result of secondary introduction from Lake Ladoga (Orlova et al. 1999), and it is currently replacing the native amphipod *Gammarus lacustris* (Panov et al. 2000).

The fouling bivalve *D. polymorpha* (zebra mussel) was first found in the Gulf of Finland in the late 1980s. By 1998, it was well established in littoral communities in the coastal zone of the easternmost Gulf of Finland, reaching densities up to 150 individuals·m^{-2} and a biomass of 350 g·m^{-2}. The first record from the northern coast originates from 1995, where population abundances were 1 to 3 orders of magnitude lower than in the easternmost region (Orlova et al. 1999). At the southern coast, the zebra mussel is found only in Narva Bay in the eastern Gulf of Finland (Kotta et al. 1998*b*). *Potamopyrgus antipodarum* is common in the littoral zone in the eastern Gulf of Finland. At sites influenced by warm water effluent from a power station, it reaches abundances up to 10 000 individuals·m^{-2} (Orlova et al. 1999).

The copepod *A. tonsa* was first found in the Gulf of Finland in 1934; here it occasionally accounts for up to 40–50% of total copepod abundance. By 1995, the cladoceran *C. pengoi* had achieved a wide spatial distribution, including the northern coast, easternmost basin, and the whole southern coast (Krylov et al. 1999; Ojaveer et al. 2000). The species has formed permanent populations in the basin and can reach abundances up to 1800 individuals·m^{-3}. Appearance of *C. pengoi* in the eastern Gulf of Finland coincided with recent declines in total cladoceran density. The species has significant adverse, economic impacts in the region. For example, economic losses reached a minimum of US$ 50 000 in one fishery farm in the eastern basin between 1996 and 1998 owing to loss of catch associated with biofouling of fishing equipment (Panov et al. 1999).

The Gulf of Bothnia

The Gulf of Bothnia consists of two separate basins, the Bothnian Sea and Bothnian Bay (separated by a 25-m sill at the Northern Quark) and the Åland Sea and the Archipelago Sea (southwestern Finland). In the Gulf of Bothnia, salinity of surface water diminishes from 5–7‰ in the south to 2–4‰ in its northernmost part. Many Finnish and Swedish rivers discharge about 200 km^3 of freshwater into the Gulf

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of Bothnia annually. Salinity gradients are weak in this sub-area; even in the southernmost part of the Bothnian Sea, the difference between the surface water and the 150-m-deep layer does not exceed 1‰. Because of wind-driven transport and the Coriolis force, salinity is somewhat higher (0.5–1.0‰) along the eastern coast of the Gulf of Bothnia. Seasonal temperature variability is extensive, ranging from <0°C to >20°C at northern latitudes (60–66°N) in the Bothnian Bay, and the number of ice-days is 110–190. The number of days with surface temperature >10°C is about 90. The mean temperature for July does not exceed 12°C in offshore areas (Leppäkoski and Bonsdorff 1989; Table 1).

Nonindigenous species

No invasion corridors open directly into the Gulf of Bothnia. Rather, most introductions occur as a result of secondary spread within the basin as the result of ship traffic and intentional introductions. The only known primary introduction to the Finnish coast is the spionid polychaete *B. redeki* (see below).

Cordylophora caspia is very common up the northern Bothnian Bay and causes problems by clogging water intakes for cooling water (Jansson 1994). The North American spionid polychaete *M. viridis* has been one of the fastest dispersing nonindigenous species in the Baltic Sea. It was first recorded in the southern Baltic in 1985, had colonized most of the Baltic Sea by 1996, and appeared on the southern coast of Finland by 1990. At present, *M. viridis* has spread widely along the Finnish coast and from 1990 to 1995 expanded its distribution up the southern part of Bothnian Bay (Leppäkoski and Olenin 2000*a*). In a benthos study in the eastern Bothnian Sea, it was found in 82% of the samples (mean density 290 individuals·m^{-2}) at a <15-m depth in 1994 (Olenin and Leppäkoski 1999).

Boccardia redeki is believed to be the only primary introduction directly into the northern Baltic Sea north of 60°N. This polychaete has obviously not been reported from studied sites between Kiel (southwestern Baltic) and the inner Archipelago Sea (southwestern Finland) area where it was first recorded in the mid-1960s. It has developed self-sustaining populations from the archipelago of Åland, 120 km off the Finnish coast, to the inner part of the Gulf of Finland in salinities ranging from 3.5 to 6.5‰ (Leppäkoski and Olenin 2000*a*).

Balanus improvisus was found in the late 1860s in southwestern Finland, in the lower Aura River, adjacent to the City of Turku and among entirely freshwater organisms. Until the second half of the 20th century, it was not found north of the Åland Islands, although by the 1990s, *Balanus* was recorded up to the Northern Quark (64°N; Leppäkoski 1984). The mysid shrimp *H. anomala* was first found in the western part of the Gulf of Finland in 1992. Today, it has been found in remarkably high numbers from the eastern part of the Bothnian Sea to Kotka (inner Gulf of Finland), 150–200 km from the site where its first introduction in Finland is believed to have taken place (Salemaa 1998). *Mya arenaria* occurs up to the Northern Quark, but only in low numbers. *Potamopyrgus antipodarum* was first observed in the North Baltic archipelago (Åland Islands) in 1926. Today it occurs primarily in sheltered bays with muddy bottoms all along the coasts of the Baltic Proper up to Bothnian Bay (Leppäkoski 1984; Jansson 1994).

The first record of the Chinese mitten crab (*E. sinensis*) in Finland is from 1933. It has since been found almost yearly along the entire coast of the Gulf of Bothnia. This species was recently reported from inland Finnish lakes in 1999 (Valovirta and Eronen 2000).

In the zooplankton community, the North American copepod *A. tonsa* and meroplanktic larvae of nonindigenous species (*B. improvisus*, *M. arenaria*, and *M. viridis*) occur in low numbers in the Bothnian Sea. Their frequency of occurrence and importance to total community abundance decline towards the Northern Quark (Voipio 1981).

Cercopagis pengoi, the most recent invader in this area, developed mass occurrences during the exceptionally warm summer of 1999 in the inner Archipelago Sea and in the northern part of the Bothnian Sea. As with other regions of the Baltic Sea, fouling of fishing gear by *Cercopagis* caused problems especially to whitefish fisheries (K-E. Storberg, West Finland Regional Environment Centre, 65101 Vaasa, Finland, personal communication).

Occasionally caught nonindigenous fish species include rainbow trout (*O. mykiss*; escapees from net cages), the whitefish *C. peled*, sturgeons (*Acipenser* spp.), and North American salmonids (*Salvelinus* spp. and *Oncorhynchus* spp.) (Leppäkoski 1984).

Ecological impacts

Nonindigenous species have affected both abiotic environment and biotic components in the Baltic Sea. In many cases the invasive species represent a new function (e.g., feeding strategy, Olenin and Leppäkoski 1999) or an entirely new trophic level and will thus restructure the community into which they were introduced. However, ecological impacts caused by alien species have been documented for a few species only in recent publications. As an example, *D. polymorpha* is known to have caused increases in local density and diversity of other benthic invertebrates in lakes and rivers and coastal lagoons. The mussels also offer refuge from large predators for associated species. Shell deposits of *D. polymorpha* have changed former soft bottoms (sand or silt) into shell gravel and have created patches of hard substrate for sessile species on sites in the coastal lagoons of the Baltic Sea. Introduced nektobenthic species (e.g., mysids and amphipods) swim actively and spend part of their time in the water column and may also dwell within or on the bottom. They form dense populations in the Curonian Lagoon and serve as an important link in energy transfer between pelagic and benthic subsystems. *Cordylophora caspia* forms dense colonies on submerged trees, hydrotechnical constructions, piers, etc., and traps particulate material on its stolons; it also creates microhabitats for several associated species in the Curonian Lagoon, for example (Olenin and Leppäkoski 1999). The round goby *N. melanostomus*, an unintentionally introduced fish species of Ponto-Caspian origin, is numerous in the Gulf of Gdansk, Poland. It has been suggested that competition for food and displacement of several native demersal fishes (e.g., flatfishes, the eelpout (*Zoarces viviparus*), and the black goby (*Gobius niger*)) by invading *N. melanostomus* takes place here (Skóra and

Stolarski 1993; K.E. Skóra and J. Rzeznik, Hel Marine Station, University of Gdansk, 84-150 Hel, Poland, unpublished data). In addition, the same authors claimed that high abundances of the round goby may cause weakening of predation pressure on several native fish in the Baltic Sea (small sandeel (*Ammodytes tobianus*) and European sprat (*S. sprattus*)) by being more favourable food for most abundant piscivores.

Invasions by nonindigenous species have not resulted in native species loss to date, and so they have generally increased local species richness in the Baltic. However, several native species have declined locally following invasion (see below). A more subtle long-term consequence of invasions is the increasing homogenization of aquatic ecosystems (Leppäkoski and Olenin 2001). Nonindigenous species have become dominant members of several food webs in inland Europe (Kinzelbach 1995), the Baltic Sea (Olenin and Leppäkoski 1999), and the Great Lakes (Stewart et al. 1998; MacIsaac et al. 1999). Thus, variation in species composition between regions has been reduced.

Significantly lower population abundances of a small-bodied cladoceran *Bosmina* sp., a probable prey of *C. pengoi*, were recorded after invasion of this predatory cladoceran to the Gulf of Riga. By consuming *C. pengoi*, the diet composition of Baltic herring (*Clupea harengus membras*), European smelt (*O. eperlanus*), and three-spined stickleback (*Gasterosteus aculeatus*) has changed after invasion of the cladoceran (Ojaveer et al. 1999). The introduction of *C. pengoi* to the Baltic Sea may prove beneficial to fisheries production if it enhances utilization of mesozooplankton (e.g., *Bosmina*) and transfers zooplankton biomass to planktivorous fishes. In contrast to several other sea areas, documented direct evidence is lacking to date on the decrease or loss of exploited fish populations owing to the presence of nonnative species in the Baltic Sea.

It becomes clear from these examples that invasive species are able to modify abiotic and biotic conditions for other species, alter composition of both pelagic and benthic communities, and affect organic matter and energy transfer pathways in a variety of food webs, thus acting as habitat and ecosystem engineers in the Baltic Sea (Olenin and Leppäkoski 1999; Table 2).

The Baltic Sea as a donor area of non-indigenous species

The Baltic Sea can be a source of alien species, especially for the North American Great Lakes. For example, the predatory cladoceran *Bythotrephes longimanus*, a native species 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. 2002). Likewise, *C. pengoi* invaded the Great Lakes in 1998 (MacIsaac et al. 1999), after invading the Baltic Sea before 1992. The population in the Baltic Sea produces a large number of resting eggs during summer months (Krylov et al. 1999). It has been suggested that this large pool of resting eggs has enabled *C. pengoi* to be carried abroad in ships' ballast and achieve rapid population growth in new environments. *Cercopagis pengoi* was among the species of Ponto-Caspian fauna predicted to invade the Great Lakes – St. Lawrence

River system based on shipping traffic from key European ports and on the occurrence of invading species in European waterways (MacIsaac 1999). As in the Baltic Sea, *Cercopagis* in Lake Ontario snag on sportfishing lines (MacIsaac et al. 1999). Genetic studies have revealed that the invasion of the Great Lakes almost certainly occurred as a secondary introduction from the eastern Baltic via an existing invasion corridor (Cristescu et al. 2001). The invasion of the Great Lakes by *C. pengoi* suggests that ballast water exchange programs may have limited effectiveness in preventing introductions of aquatic invertebrates producing resting eggs that may accumulate in sediments of ballast tanks. The same is true for phytoplankton, as the diatom *Thalassiosira baltica* was discovered in Lake Ontario in 1988 and is now dominant there. Edlund et al. (2000) suggest that it likely came from the Baltic Sea, though other sources were also possible.

Discussion

The introduction of nonindigenous species into the Baltic Sea and their further spread within the basin has resulted in major changes in nearshore ecosystems, especially in coastal lagoons and inlets. By contrast, hypolimnetic and pelagic regions of the Baltic Sea have been practically free of nonindigenous species until the 1980s (Segerstråle 1957; Olenin and Leppäkoski 1999; Leppäkoski and Olenin 2000*a*).

Three recent introductions into the Baltic Sea serve as examples of the dispersal capacity of aquatic nonindigenous species. *Marenzelleria viridis* spread from the southern Baltic coastal inlets up to Bothnian Bay within 10 years. *Hemimysis anomala*, first found at the entrance to the Gulf of Finland in 1992, was detected in both the Stockholm archipelago and the inner part of the Gulf of Finland some years later (Salemaa 1998; H. Kautsky, Department of Systems Ecology, Stockholm University, Stockholm, Sweden, personal communication). A new cladoceran species for the Baltic, *C. pengoi*, an introduction from the Black Sea area, spread from its bridgeheads in the gulfs of Finland and Riga up to the Northern Quark and down to the Gulf of Gdansk in 7 years.

The Baltic Sea should be well protected against introductions owing to low salinity and temperature variations. However, most of the important harbours in the world are located at river mouths. The salinity range of these estuarine habitats covers the oligo- and meso-haline conditions prevailing in the Baltic Sea. The Baltic is characterized by a complicated, three-dimensional (i.e., physical, chemical, and biological) network of environmental gradients. This complexity can be expected to facilitate invasions by offering a wide range of hospitable conditions for a great variety of life forms.

Until the establishment of permanent populations of *M. viridis* and *C. pengoi*, scientific interest in nonindigenous species was mostly descriptive in the Baltic Sea area (e.g., documentation of invasion history, studies on distribution pattern, and abundance assessment; Gollasch and Mecke 1996; Leppäkoski and Olenin 2000*a*). The functional role of these species in brackish-water ecosystems and their realized niches in the invaded communities remains to be quantified.

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Table 2. Examples of habitat engineering and ecosystem changes caused by Ponto-Caspian invasive species in the Baltic Sea.

Species	Function[a]										
	1	2	3	4	5	6	7	8	9	10	11
Cordylophora caspia	×	×	×								
Cercopagis pengoi							×				
Pontogammarus robustoides						×	×				
Echinogammarus ischnus	×					×	×		×		×?
Corophium curvispinum	×	×	×	×	×	×	×		×		×?
Hemimysis anomala						×	×				
Dreissena polymorpha	×	×	×	×	×	×	×	×	×	×	×
Neogobius melanostomus						×	×	×	×		×

[a]Criteria largely adopted from Stewart et al. (1998) and Olenin and Leppäkoski (1999): 1, modifies rocky bottom or sediment substrate; 2, provides refuges from predators and currents; 3, traps and accumulates particulate organic matter in interstitial microhabitats; 4, increases water clarity; 5, affects macrophyte canopy; 6, redirects energy from pelagic to benthic subsystems or vice versa; 7, provides additional prey to planktivorous and (or) benthivorous fish; 8, provides food for waterfowl; 9, excludes competing species; 10, increases soluble (bioavailable) nutrients (N, P); 11, influences cycling of contaminants.

The appearance of *M. viridis* and *C. pengoi* contributed widely to the scientific awareness of aquatic bioinvasions. The first risk assessment study for the Baltic Sea area was only recently completed. It included risk profiles for five northwest European harbours along the salinity gradient from St. Petersburg, Russia, to Bergen, Norway (Gollasch and Leppäkoski 1999). The first shipping study in the Baltic Sea was undertaken as a part of a recently completed (July–August 1998) European research initiative to quantify the survival of organisms in ballast tanks during ship voyages. With one exception, phytoplankton and zooplankton species were found in lower numbers at the end than at the beginning of the voyage (Olenin et al. 2000).

Most of the nonindigenous species of brackish-water or freshwater origin in the Baltic, with the exception of several Ponto-Caspian invaders, originate from warmer areas. Therefore, even slight changes in the temperature and salinity conditions may influence the invasion pattern and population dynamics of nonnative species. If the process of global warming continues, the risk that warm-water species become established in large areas of the Baltic Sea will increase. This hypothesis is supported by documented invasion history of *C. pengoi*: this warm-water species remarkably expanded its distribution area in warm years.

Baltic Sea estuaries have functioned as bridgeheads aiding in the establishment of several nonnative species. The Curonian, Vistula, and Szczecin lagoons, German Boddens, and the Neva Estuary are known to host a high number of well-established nonindigenous species and can be identified as "centres of xenodiversity" along the Baltic coasts (Leppäkoski and Olenin 2000a).

There have been few quantified ecological or economic problems with nonindigenous species established in the Baltic Sea. Most effects are relatively benign, and the invaders appear to have served to increase both species and functional diversity (Olenin and Leppäkoski 1999). Of the nonindigenous species occurring in the coastal waters, four fouling species (*C. caspia*, *B. improvisus*, *C. pengoi*, and *D. polymorpha*) cause economical damage to fisheries, shipping, and boating or fish farming and industry.

In conclusion, several ecosystem processes (e.g., nutrient and contaminant cycling, energy flow), involving multiple trophic levels, are affected in the Baltic Sea owing to recent successful introductions of nonindigenous species. In general, the largest community changes are recorded for zooplankton and zoobenthos. However, effects on diversity have not been well studied for most of these invasions; although most invasions appear to add to local diversity, in some cases diversity declines have occurred at this scale. With this human-mediated change of the Baltic ecosystem, we can expect regional diversity to decline (Leppäkoski and Olenin 2001).

With the recent invasions of *M. viridis* and *C. pengoi* in the 1990s, the Baltic Sea entered into a new era in its history of invasion biology. However, ecological impacts of these species are not well understood and require further investigation. An essential component of this new era of invasion research in the Baltic ought to incorporate a process-oriented approach consisting in parallel of field observations and experimental studies. As well, further information is required to fully document economic consequences of biological invasions, including direct loss of fisheries production or tourism. Until very recently, most abundant invaders were benthic organisms. Since then, several species of holo- or mero-plankton have appeared in the Baltic Sea. When considering potential indirect effects through the food web, in addition, it is apparent that recent invasions have increased the risk for larger impacts also in the pelagic subsystem. As it was shown above, several species still expand their distribution area. Thus, we suggest that impacts of nonindigenous species to the Baltic Sea ecosystem will certainly widen in spatial scale and these will became more complex by encompassing both pelagic and benthic systems as the number of nonindigenous species increases.

Conclusions

The high number of nonindigenous species in the western Baltic region compared with the inner Baltic is probably due to its higher salinity. Moreover, the number of ship arrivals, and hence vector activity, from overseas is considerably higher in the western Baltic.

In terms of species number, xenobiota constitute a small portion of the macrozoobenthos and zooplankton even in the

Baltic coastal lagoons. However, their functional role in recipient ecosystems is much more important, as most of these species became dominant in the communities and significantly change the native environment. The Curonian Lagoon has the highest number of introduced Ponto-Caspian species resulting from intentional introductions in the 1960s.

The polychaete *M. viridis* and the cladoceran *C. pengoi* have caused measurable and documented changes in the Gulf of Riga ecosystem. While the impact of the polychaete could be characterized as basin-wide, that of the cladoceran is apparently confined mostly to sheltered, coastal areas. However, lack of study precludes quantitative estimation of ecosystem changes caused by earlier invaders, including *D. polymorpha*, *M. arenaria*, and *B. improvisus*. These species collectively dominate various benthic communities, and thus their impacts may be appreciable. By contrast, intentionally introduced fish probably play only minor role in the Baltic Sea ecosystem.

Generally, nonindigenous species are most abundant in littoral habitats of the Gulf of Finland, and most of these species originated from the Ponto-Caspian region. As a result, new communities developed dominated by *C. caspia*, *D. polymorpha*, *P. antipodarum*, and *B. improvisus* in more saline areas and by *G. fasciatus* and *P. robustoides* in freshwater locations. Pelagic communities of the Gulf of Finland are now inhabited by the predatory cladoceran *C. pengoi*, a species that has already had substantial ecological and economic consequences. Extension of the distribution area and increase in abundance of nonindigenous species such as *D. polymorpha*, *C. pengoi*, and *M. viridis* is an ongoing process. Therefore, further changes in the ecosystem of the Gulf of Finland can be expected.

The number of nonindigenous species is low and their role is much less important in the Gulf of Bothnia than in the Gulf of Finland and in coastal waters of the southeastern Baltic Sea. Before the invasion of *M. viridis* and *C. pengoi*, *B. improvisus* and *C. caspia* were the only nonindigenous species with some ability to alter their shallow water habitats. On the other hand, it is not possible to predict the impact on the benthic and pelagic systems of the two new invasive species that only recently entered the Gulf of Bothnia.

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References

Anonymous. 1995. 4. Hamburger Logistik-Kolloqium. Tagungsunterlage Transport und Hafenlogistik, Technische Universität Hamburg-Harburg, Hamburg, Germany.

Bacescu, M. 1966. Die kaspische Reliktfauna im ponto-asowschen Becken und in anderen Gewässern. Kiel. Meeresforsch. **22**: 176–188.

Baltic Sea Alien Species Database. 2001. Alien species directory. *Edited by* S. Olenin and E. Leppäkoski. Coastal Research and Planning Institute, Klaipeda University, Lithuaina (http://www.ku.lt/nemo/mainnemo.htm).

Berg, D.J., Garton, D.W., MacIsaac, H.J., Panov, V.E., and Telesh, I.V. 2002. Changes in genetic structure of North American *Bythotrephes* populations following invasion from Lake Ladoga, Russia. Freshwater Biol. **47**: 275–282.

Borowski, W. 2000. Round goby in the Vistula Lagoon. Magazyn Przemyslu Rybnego, **4**(12): 39. [In Polish.]

Breitzmann, K.-H. 1999. Baltic Sea transport—structure, development and future challenges. *In* International Conference Integrating the Baltic Region and the European Union, 7–8 October 1999. Rœnne, Bornholm.

Cristescu, M.E.A., Hebert, P.D.N., Witt, J.D.S., MacIsaac, H.J., and Grigorovich, I.A. 2001. An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. Limnol. Oceanogr. **46**: 224–229.

Edlund, M.B., Taylor, C.M., Schelske, C.L., and Stoermer, E.F. 2000. *Thalassiosira baltica* (Grunow) Ostenfeld (Bacillariophyta), a new exotic species in the Great Lakes. Can. J. Fish. Aquat. Sci. **57**: 610–615.

Elmgren, R., and Hill, C. 1997. Ecosystem function at low biodiversity—the Baltic example. *In* Marine biodiversity: patterns and processes. *Edited by* R.F.G. Ormond, J.D. Gage, and M.V. Angel. Cambridge University Press, Cambridge. pp. 319–336.

Gasiunaite, Z. 2000. Seasonal dynamic and spatial heterogeneity of the plankton crustaceans in the eutrophic coastal lagoon. Ph.D. thesis, Klaipeda University, Klaipeda, Lithuania.

Gasiunas, I. 1964. Acclimatisation of forage crustaceans into the Kaunas Waterpower Plant reservoir and possibility of their migration into other waters of Lithuania. Trudy Akad. Nauk Lit. SSR, Ser. B, **1**(30). [In Russian.]

Gollasch, S., and Leppäkoski, E. (*Editors*). 1999. Initial risk assessment of alien species in Nordic coastal waters. Nordic Council of Ministers, Copenhagen. Nord 1999:8.

Gollasch, S., and Mecke, R. 1996. Eingeschleppte Organismen. *In* Warnsignale aus der Ostsee. *Edited by* J.L. Lozan, R. Lampe, W. Matthäus, E. Rachor, H. Rumohr, and H.v. Westernhagen. Parey Buchverlag, Berlin. pp. 146–150.

Gruszka, P. 1999. The River Odra estuary as a gateway for alien species immigration to the Baltic Sea basin. Acta Hydrochim. Hydrobiol. **27**: 374–382.

HELCOM (The Baltic Marine Environment Protection Commission – Helsinki Commission). 1996. Third periodic assessment of the state of the marine environment of the Baltic Sea, 1989–1993. Baltic Sea Environ. Proc. 64B.

Jansson, K. 1994. Alien species in the marine environment. Swedish Environment Protection Agency, Stockholm, Sweden, Rep. 4357.

Jazdzewski, K., and Konopacka, A. 1999. Immigration history and present distribution of alien crustaceans in Polish waters. *In* The biodiversity crisis and Crustacea. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998. *Edited by* J.C. von Vaupel Klein and F.R. Schram. A.A. Balkema, Rotterdam, Brookfield. pp. 55–64.

Kinzelbach, R. 1995. Neozoans in European waters—exemplifying the worldwide process of invasion and species mixing. Experientia, **51**: 526–538.

Kotta, J., Kotta, I., Martin, G., and Kukk, H. 1998*a*. A survey of data published on the littoral zoobenthos of the Gulf of Riga. Proc. Estonian Acad. Sci. Biol. Ecol. **47**: 83–97.

Kotta, J., Orav, H., and Kotta, I. 1998*b*. Distribution and filtration activity of the zebra mussel, *Dreissena polymorpha*, in the Gulf

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of Riga and the Gulf of Finland. Proc. Estonian Acad. Sci. Biol. Ecol. **47**: 32–41.

Krylov, P.I., Bychenkov, D.E., Panov, V.E., Rodionova, N.V., and Telesh, I.V. 1999. Distribution and seasonal dynamics of the Ponto-Caspian invader *Cercopagis pengoi* (Crustacea, Cladocera) in the Neva Estuary (Gulf of Finland). Hydrobiologia, **393**: 227–232.

Kube, J., Powilleit, M., and Warzocha, J. 1996. The importance of hydrodynamic processes and food availability for the structure of macrofauna assemblages in the Pomeranian Bay (Southern Baltic Sea). Arch. Hydrobiol. **138**: 213–228.

Leppäkoski, E. 1984. Introduced species in the Baltic Sea and its coastal ecosystems. Ophelia, Suppl. **3**: 123–135.

Leppäkoski, E., and Bonsdorff, E. 1989. Ecosystem variability and gradients. Examples from the the Baltic Sea as a background for hazard assessment. *In* Chemicals in the aquatic environment. *Edited by* L. Landner. Springer-Verlag, Berlin, Heidelberg. pp. 6–58.

Leppäkoski, E., and Olenin, S. 2000*a*. Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biol. Inv. **2**: 151–163.

Leppäkoski, E., and Olenin, S. 2000*b*. Xenodiversity of the European brackish water seas: the North American contribution. *In* Marine bioinvasions: Proceedings of the First National Conference, January 24–27, 1999. *Edited by* J. Pederson. Massachusetts Institute of Technology, MIT Sea Grant College Program, Cambridge, Mass. pp. 107–119.

Leppäkoski, E., and Olenin, S. 2001. The meltdown of biogeographical peculiarities of the Baltic Sea: the interaction of natural and manmade processes. Ambio, **30**: 202–209.

MacIsaac, H. 1999. Biological invasion in Lake Erie: past, present and future. *In* State of Lake Erie—past, present and future. *Edited by* M. Munawar and T. Edsall. Backhuys Publishers, Leiden, The Netherlands. pp. 305–322.

MacIsaac, H.J., Grigorovich, I.A., Hoyle, J.A., Yan, N.D., and Panov, V.E. 1999. Invasion of Lake Ontario by the Ponto-Caspian cladoceran predator *Cercopagis pengoi*. Can. J. Fish. Aquat. Sci. **56**: 1–5.

Nikolaev, I.I. 1951. On new introductions in fauna and flora of the North and the Baltic Seas from distant areas. Zool. Zh. **30**: 556–561. [In Russian.]

Ojaveer, E. 1995. Large-scale processes in the ecosystem of the Gulf of Riga. *In* Ecosystem of the Gulf of Riga between 1920 and 1990. *Edited by* E. Ojaveer. Estonian Academy Publishers, Tallinn. pp. 268–277.

Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I., and Lumberg, A. 1999. Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. ICES J. Mar. Sci. **56**(Suppl.): 33–40.

Ojaveer, H., Simm, M., and Lankov, A. 2000. Consequences of invasion of a predatory cladoceran. ICES CM2000/U:16.

Olenin, S., and Leppäkoski, E. 1999. Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. Hydrobiologia, **393**: 233–243.

Olenin, S., Gollasch, S., Jonusas, S., and Rimkute, I. 2000. Enroute investigations of plankton in ballast water on a ships' voyage from the Baltic sea to the open Atlantic coast of Europe. Int. Rev. Hydrobiol. **85**: 573–592.

Orlova, M.I., Panov, V.E., Krylov, P.I., Telesh, I.V., and Khlebovich, V.V. 1999. Changes in planktonic and benthic communities of the eastern part of the Gulf of Finland (Baltic Sea) due to biological invasions. Russian Academy of Sciences. Proc. Zool. Inst. St. Petersburg, **279**: 305- 325. [In Russian.]

Panov, V.E., Krylov, P.I., and Telesh, I.V. 1999. The St. Petersburg harbour profile. *In* Initial risk assessment of alien species in Nordic coastal waters. *Edited by* S. Gollasch and E. Leppäkoski. Nord 1999:8. Nordic Council of Ministers, Copenhagen. pp. 225–244.

Panov, V.E., Timm, T., and Timm, H. 2000. Current status of an introduced Baikalian amphipod *Gmelinoides fasciatus* Stebbing, in the littoral communities of Lake Peipsi. Proc. Estonian Acad. Sci. Biol. Ecol. **49**: 71–80.

Reise, K., Gollasch, S., and Wolff, W.J. 1999. Introduced marine species of the North Sea coasts. Helgol. Meeresunters. **52**: 219–234.

Ricciardi, A., and MacIsaac, H.J. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol. Evol. **15**: 62–65.

Salemaa, H. 1998. Mysid shrimps. *In* Nature of Finland—Invertebrate Animals. *Edited by* K. Heliövaara. Weilin & Göös, Helsinki. pp 46–47. [In Finnish.]

Segerstråle, S.G. 1957. Baltic Sea. *In* Treatise on marine ecology and paleoecology. I. Ecology. *Edited by* J.W. Hedgpeth. Geol. Soc. Am. Mem. **67**: 751–800.

Skóra, K.E., and Stolarski, J. 1993. New fish species in the Gulf of Gdansk: *Neogobius* sp. (cf. *Neogobius melanostomus* (Pallas 1811)). Bull. Sea Fish. Inst. **1**(128): 83.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998. Quantifying mechanisms for zebra mussel effects on benthic macro-invertebrates: organic matter production and shell-generated habitat. J. North Am. Benthol. Soc. **17**: 81–94.

Väinölä, R., and Oulasvirta, P. 2001. The first record of *Maeotias marginata* (Cnidaria, Hydrozoa) from the Baltic Sea: a Pontocaspian invader. Sarsia, **86**: 401–404.

Valovirta, I., and Eronen, R. 2000. First record of *Eriocheir sinensis* from Finnish inland. Memo. Soc. Fauna Flora Fenn. **76**: 23–25. [In Finnish, with English summary.]

Voipio, A. (*Editor*). 1981. The Baltic Sea. Elsevier Oceanography Series 30.

Wallentinus, I. 1992. The dispersal of *Sargassum muticum* in the ICES countries. ICES Working Group on Introductions and Transfers of Marine Organisms, Lisbon, Portugal, April 14–17.

Wiktor, J. 1969. The biology of *Dreissena polymorpha* (Pall.) and its ecological importance in the Firth of Szczecin. Stud. Mat. MIR Gdyni, **5**/A: 1–88. [In Polish.]

Wiktor, K. 1963. Zooplankton of the Pomeranian Bay. Prace Morskiego Instytutu Rybackiego w Gdynia, **12**/A: 51–78. [In Polish.]

WWF (World Wide Fund For Nature). 1994. Coastal lagoons and wetlands in the Baltic. WWF Baltic Bulletin 1/1994.

Zettler, M.L., Bick, A., and Bochert, R. 1995. Distribution and population dynamics of *Marenzelleria viridis* (Polychaeta, Spionidae) in a coastal water of the southern Baltic. Arch. Fish. Mar. Res. **42**: 209–224.

Zmudzinski, L. 1996. The effect of the introduction of the American species *Marenzelleria viridis* (Polychaeta: Spionidae) on the benthic ecosystem of Vistula Lagoon. Mar. Ecol. **17**: 221–226.