The Meltdown of Biogeographical Peculiarities of the Baltic Sea: The Interaction of Natural and Man-made Processes

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The biogeographical peculiarities of the Baltic Sea have developed since the last glacial period. The characteristic mixture of marine, brackish water, and freshwater species, and relicts from previous periods in the Baltic, is threatened by ongoing environmental changes. This review focuses on the recent impacts of non-indigenous species, eutrophication, and a temporary oxygen deficit in the deep basins, on the biogeographical integrity of the Baltic on different spatial and time scales. Today the biota of brackish waterbodies are exposed to each other because of the breakdown in geographical barriers due to shipping traffic, leading to an exchange of species and further homogenization of aquatic animal and plant life worldwide.

INTRODUCTION

Biogeography traditionally operates at species and higher levels of biological organization. A major issue is time. Living nature is never in a state of equilibrium; biotic assemblages are constantly changing. All ecosystems are dynamic and characterized by a continual succession of species both in time and space.

The present Baltic Sea exists as an ecological continuum, being a result of significant natural environmental alterations during the past 10 000 years of its post-glacial history. The present, naturally formed continuum, was described and discussed as a specific biogeographical feature of the Baltic in the 1950s and 1960s, when Ekman (1), Segerstråle (2) and Zenkevich (3) published their classic reviews. They distinguished the following main components of the Baltic fauna: i) North Atlantic boreal marine fauna; ii) Arctic relicts; iii) brackish water species of North Sea origin; iv) brackish water species of Sarmatian origin; and v) freshwater species. Shurin (4) discriminated 7 zoogeographical groupings (complexes), among them the Yoldian and boreal Atlantic complexes and the complex of newly introduced species (see 5). Since the 1960s, the biogeography of the Baltic Sea has not been a key research item. An Internet search on the Baltic Marine Environment Bibliography (6) for 1970—1998 yielded 14 hits on "biogeogr*", 13 on "phytogeogr*" and only 2 on "zoogeogr*".

The Baltic Sea is exposed to both gradual and stepwise (many times fully stochastic) changes related to human influences. In this review, we discuss the biogeographical aspects of the recent environmental changes induced by both anthropogenic and natural processes, or by synergistic effects of both these driving forces. As a starting point we use the concept of biological integrity, defined as "the capability of supporting and maintaining a balanced, integrated, adaptive biological system having a full range of elements (genes, species, assemblages) and processes (mutations, biotic interactions, nutrient and energy dynamics, and metapopulation processes) expected in a natural habitat of a region" (7). We will consider changes at species level and their effects on the biogeographical integrity of the Baltic Sea at different scales, from global through inter- and intracontinental to regional ones.

BIological INvAsions: A GLOBAL CHANGE

The global scale of biological invasions associated with human activities, resulting in large-scale mixing of previously isolated biotas, became more and more evident at the end of the 20th century. This process is recognized as an important element of global change (8-13). Many natural barriers to dispersal for both terrestrial and aquatic species have been weakened and, consequently, both the number of potential invaders and the number of remote donor areas have increased through human-mediated dispersal (12, 13). Thereby, geographic isolation of seas and continents as a creator and conservator of global biodiversity was breached several centuries ago and has continued to decrease at an increasing rate in recent decades.
Results of this global exchange of species are evident in all European brackish-water seas, including the Baltic (Fig. 1). Much of their present biological diversity is foreign origin, i.e. composed of species intentionally or unintentionally transported by humans over intrinsic environmental barriers (14—17). We have defined this human-mediated addition of nonindigenous species and even higher taxa as xeno-diversity (Gr. xenos = strange) to indicate structural and functional diversity caused by nonindigenous (nonnative, alien, exotic, introduced) species (18).

Dozens of nonindigenous species have been introduced, intentionally or unintentionally, into the Baltic Sea during historic time. Invasion rates appear to have increased in the past 50 years, due to changes in factors that once prevented the introduction of aquatic species. Without doubt this apparent increase also reflects increasing awareness and research efforts. By the year 2000, 99 species of animals and plants that are known or believed to be nonnative have been recorded in the Baltic Sea (19). These include 41 zoobenthos, 29 fish, 9 phytoplankton, 9 phytobenthos, 4 zooplankton, 3 nektobenthos, 3 parasitic invertebrates, 2 mammals and 1 bird species (1). Of these species, less than 70 have been able to establish reproducing populations (18, 19). However, we have to look at the invaders over at least several decades to determine which species failed or were successful, i.e. whether or not they became naturalized. The failures are not usually documented and even our knowledge of winners in this "ecological roulette" (20) is still in its cradle.

Generally, estuaries and embayments have been affected by alien invaders more frequently than the outer coast (11). In Europe, this appears to be true for whole brackish-water seas, such as the Baltic, Black, and Caspian Seas (14, 16, 21). Characteristically, the recent stage (since ca 500 BP) of the Baltic has been described as the "Mya Sea" (22) decades before the status of the nominator species (Mya arenaria, the soft shell clam) was recognized as a globally successful marine invader from North America, probably transported by the Vikings (23, 24).

![Shipping and particularly ballast water are increasingly important as vectors for intercontinental exchange of nonnative species. Photo: C Boström.](image)

The enrichment of the Baltic Sea fauna and flora by nonindigenous species can, from a biogeographer’s point of view, be interpreted as a successive recovery from the last glaciation, anthropogenic dispersal being a spreading mechanism complementary to natural ways of dispersal (25, 26). However, human activities have opened invasion corridors, e.g. via ship traffic and intentional introductions, which were not possible at all by spontaneous range expansion across the oceans (27) or could be expected to take hundreds of thousands or even millions of years. In addition, global communications have increased the speed of human-mediated species transfers from one coast or sea to another. Today, rapid transportation increases the survival probability of the sea stowaways and, thus, there are ecological and economic risks associated with these invasions. A trip with a modern cargo ship across the Atlantic Ocean takes...
less than 10 days, therefore, the survival rate of ballast or hull fouling travellers is much higher than in the sailing vessel or steamship era (28).

At present, ship traffic is the most important vector for the spread of aquatic organisms into the coastal waters of northwestern Europe, including the Baltic Sea (29, 30). More ships now arrive with larger volumes of ballast water from more regions in less time than was the case 50 years ago (11). The largest deep-sea vessels have a ballast capability of 250,000 tonnes (t) (31). The first European study of species transported by shipping, undertaken in 1992–1996, collected more than 400 species in the ballast tanks or on the hulls of 211 ships visiting German ports. More than 60% of these species (ranging from microalgae to crustaceans, mollusks and fish 15-cm long) were nonindigenous to German waters (32). The number of species transported by ships has, on a global scale, been estimated at 3000 to 7000 (or even 10,000) at any time (27, 28, 32). A global homogenization of aquatic biota is underway due to the establishment of nonnative species, and the environmental effects of these species continue to accrue (11, 28, 33, 34).

**INTERCONTINENTAL EXCHANGE OF SPECIES**

Species introduced into the Baltic Sea originate from all continents except Antarctica. North America, predominantly its east coast, is the most important donor area, contributing approximately 30% of all known introductions (Table 1). One third of nonnative free-living invertebrates, one fourth of fish species, the only bird species and both species of mammals are of American origin. These species originated from unintentional (58%) rather than intentional (42%) introductions (29). This might be related more to the successive opening of routes of commerce in the post-Columbian era than to the adaptability of the potential invaders from America. Ongoing Americanization, reviewed here from a biogeographical point of view is thus one of the most important processes contributing to the xenodiversity of all semienclosed European seas, including the Baltic (29, 30).

**From Europe to America and Vice Versa**

The Eastern and Western hemispheres are not remote. Bidirectional exchange of species has, in many cases, formed the basis for their agriculture-based economies. The success of emigrating Europeans largely depended on their ability to Europeanize the fauna and flora of the New World (35, 36).

The intercontinental exchange of animal species between the Old and New Worlds has been anything but even. Terrestrial species introduced from Europe into North America are 10 times as numerous as those transported in the opposite direction (37). In olden times, sailing vessels went on their way west almost exclusively with solid ballast, transporting soil fauna and propagules of terrestrial plants. Ships have used water as ballast since the 1880s (31, 38); with this global conveyer, more aquatic species have been and continue to be transported.

Analogically, a successive Europeanization of the aquatic life of North America has occurred both intentionally and unintentionally. Of all aquatic species introduced to the United States, 29% are native to Europe or Eurasia (39). For some US estuaries, the number of known normative species ranges from 60 to 212, with Asia and Europe being the most common areas of origin (11). Approximately 55% of 139 nonindigenous aquatic or semiaquatic species established in the Great Lakes since the 1800s are native to Eurasia (40). Some 90 of these species can be regarded as true aquatic organisms, i.e. wetland species

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<th>Table 1. Origin of xenodiversity in the Baltic Sea. Not all species are known to reproduce in their new area. Compiled from different sources. Species list is available at <a href="http://www.ku.lth/nemo/mainnemo.htm">http://www.ku.lth/nemo/mainnemo.htm</a>.</th>
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excluded; more than 40% of them are native to Europe (29, 41). These include the Eurasian watermilfoil (Myriophyllum spicatum), faucet snail (Bithynia tentacularata), common carp (Cyprinus carpio) and rudd (Scardinius erythrophthalmus; 41). The most recent Neo-Americans of European origin in the lakes, the predatory water fleas Bythotrephes cederstroemi and Cercopagis pengoi, zebra mussel (Dreissena polymorpha), ruffe (Gymnocephalus cernuus) and round goby (Neogobius melanostomus), have appeared to be highly aggressive invaders that have had a heavy impact on the ecology of the lakes (42, 43). All of these species occur in the coastal waters of the brackish Baltic Sea also.

Undeclared "Biological War" and Other Unwanted Consequences

The 20th century was characterized by several accidental introductions that had tremendous ecological and economic impacts on both continents. The first episode in an undeclared (and unintentional) "biological war" between the Old and New Worlds was the invasion of the Colorado beetle (Leptinotarsa decemlineata) into Europe. From the early 1920s, this species infested all countries of Western and Eastern Europe and caused great damage to their potato-based agricultural production. Currently its distribution covers about 6 million km$^2$ in Europe and Asia (44).

The European "response" took place 6 decades later, but it was equally important. The zebra mussel invaded the North American Great Lakes in the mid-1980s with the epizootic dimension of ecological impact costing the US and Canadian economies USD 3.1 to USD 5 billion by the year 2000 (12).

An assessment of the importance of introductions from an ecosystem or economic point of view cannot be based merely on the number of nonnative species present nor on their abundance in the invaded ecosystems. Some of them can, on a rather subjective basis, be regarded as nuisance species. Of the Neo-Europeans of American origin living in or along the brackish waters of Europe, the comb jelly Mnemiopsis leidyi, the polychaete Marenzelleria viridis, the barnacle Balanus improvisus, the muskrat Ondatra zibethicus and the American mink Mustela vison have had a significant ecological or economic impact on the invaded areas (29). The recent deterioration of the Black Sea ecosystem and the collapse of its commercial fisheries offers a dramatic example of an ecological catastrophe caused by nonindigenous species. Within 10 years (since 1982), a decrease in the anchovy catch took place simultaneously with
the expansion of *Mnemiopsis* (21). In its donor area (the Atlantic coast of the US) the comb jelly does not pose a major problem whereas in the recipient area, the Black Sea, traditional fisheries and fish industries were severely affected (21).

Introduced species are known to take roles that the native species do not have. Several new life forms, and thus an “American style” of aquatic animal life, have been introduced into European brackish water seas. In many cases an invader represents a new functional group in the invaded community and differs substantially from natives in life form and efficiency of resource utilization (17). The only barnacle species living in the Baltic Sea, *B. improvisus*, is native to the Americas, as is the dwarf crab *Rhitropanopeus harrisi*, one of only two crabs found in Polish coastal lagoons. The muskrat is the only herbivorous mammal seen in coastal bays and inlets.

Successful animals in stressed ecosystems have been argued to be small and exotic (45). However, some of the Neo-Europeans of American origin in European enclosed seas have appeared to be large and aggressive habitat conquerors in comparison with previously dominant native organisms in the same habitats. There were no polychaetes in the inner parts of the Baltic coastal lagoons until the appearance of *M. viridis* in the mid-1980s. This North American polychaete has significantly altered the community structure of the bottom fauna in the Baltic coastal lagoons. The biomass of benthos has increased up to 10 times due to this species, which became dominant within less than 5 years after its invasion (17, 46, 47). *Marenzelleria*, which digs down to 40 cm into the sediment, is a giant compared to native burrowing organisms (chironomid larvae and oligochaetes) dwelling in muddy bottoms of the Baltic coastal lagoons (17). On rocky shores, *Balanus* exceeds by hundreds of times the size of other sessile animals, such as the bryozoan *Electra crustulenta*. The soft-shell clam *Mya arenaria* grows bigger and digs more deeply into the bottom sediment than other (native) bivalves (*Macoma balthica* and *Cerastoderma* spp.).

Thus, the nonnative species, native to transoceanic biogeographical realms, contribute not only to the species diversity both within and between habitats but also to the functional diversity, i.e. the range of functions performed by organisms in a system (8, 17). The most successful invaders in enclosed European seas have, without doubt, been capable of altering fundamental ecosystem level processes and thus control the functioning of whole ecosystems (14, 28). The newcomers also affect the ecosystem services available for man, such as primary production, fish production, degradation capacity, recreational services, and amenities (48).

**Ongoing Americanization**

It has been generally thought that the isolation between the Eastern and Western Hemispheres was broken and the 2 worlds reunited on 12 October, 1492. With increasing maritime connections between the Old and New Worlds, a vector was established for bilateral exchange of aquatic fauna and flora. Along this vector, 2 previously isolated biotas have been exposed to each other for 500 years. Ongoing Americanization of European brackish-water seas gives continued evidence of post-Columbian exchange between North America and northwestern Europe. However, the history of marine introductions from North America to Europe is believed to go back to the pre-Columbian era, at least to the 13th century (23).

Many of the prehistoric, and since long fully acclimatized, introductions will remain unknown forever, due to the difficulty in distinguishing which species were or were not transferred into the coastal seas by early man. These species will remain as cryptogenic, neither clearly native or exotic (49). Their contribution to the early succession and long-term dynamics of the young (less than 10 000 years) ecosystem of the Baltic Sea remains undocumented as well.

Ecologically and biogeographically, the uncontrolled intercontinental transportation of nonindigenous species is resulting in large-scale mixing of and greater uniformity among both terrestrial and aquatic faunas and floras - a "McDonaldization" of the biosphere (10). The post-Columbian exchange continues; today there is a built-in piece of America in the European enclosed seas, and a piece of Europe on the other side of the Atlantic, in the Great Lakes.
PONTO-CASPIAN SPECIES: INTRACONTINENTAL INVADERS

One-way Invasion Corridors?

Species endemic to Ponto-Caspian basins (the Black and Caspian Seas, the Sea of Azov and their catchment areas) have spread and become established in inland Europe, the Baltic Sea and the North American Great Lakes. More than 40 Ponto-Caspian species have expanded their ranges into central and western Europe (17, 50, 51). This active or passive intracontinental dispersal was facilitated by the construction of numerous canals (opened between 1775 to 1952) and reservoirs on Ponto-Caspian rivers that allowed species to disperse to Central and West European river systems through previously disconnected waterways by active migration, attachment to barge hulls or transport in ballast tanks (50). In addition, several Ponto-Caspian crustaceans were transplanted between the 1950s and 1980s to stimulate fish production in western lakes and reservoirs of the USSR; more than 30 species of amphipods and opossum shrimps from the "Caspian complex" were used for these acclimatization experiments (52).

Migration of Ponto-Caspian species upstream is an ongoing process in all great European rivers. Astonishingly, there are no known introductions in the opposite direction (14, 53). The polychaete *Hypania invalida* spread from the lower reaches to the middle Volga in the 1980s and 1990s (54); in 1990s it was also found in the River Rhine, where it came through the canal connection with Danube (55).

For a long time Caspian elements in fauna of the Volga River were considered to be relicts of former sea transgressions of the Ponto-Caspian Basin (56); probably that is why the Ponto-Caspian invaders, with their genetically "build-in euryhalinity", so easily conquered northwestern European rivers and brackish-water estuaries. The process is considered to be a natural range expansion if it takes place within the limits of the maximal transgressions (57). However, the major European inland waterway systems constructed during the last 2 centuries have bridged intracontinental barriers between formerly isolated water basins and their biotas.

Centers of Xenodiversity

In the Baltic Sea, species of Ponto-Caspian origin constitute the second largest part of xenodiversity: 22 have been recorded; of them a dozen have been able to establish self-reproducing populations (19). Their proportion is greatest in the sheltered, low-salinity coastal lagoons along the southern and southeastern coast of the Baltic and in the eastern Gulf of Finland, but diminishes westward (Fig. 1). Estuaries and coastal lagoons have functioned as stepping stones that may have aided in the establishment of numerous nonindigenous species in nonestuarine coastal areas. Sheltered coastal waterbodies are subject to a broad variety of anthropogenic stressors that interact with invasion processes (11). However, the presence of nonindigenous species cannot be taken as a cause, but only as a consequence of environmental deterioration.

There are fewer introduced species on the open coast of the Baltic than in the sheltered bays and estuaries. Baltic centers of xenodiversity, known to host a high number of established non-native species, are the Curonian, Vistula, and Szczecin Lagoons, German Boddens and the Neva Estuary (17, 58, 59). The vectors that have served to introduce most of the nonnative species to the Baltic bring species from and deliver them to estuaries. Most of the major harbors of the world are located at river mouths. Somewhere along their estuarine gradient these harbors exhibit salinity conditions matching those of the Baltic; environmental matching plays a major role in invasion success (38). Fewer or no vectors are available to transport species between beaches or rocky shores of the world (11). In the Baltic Sea, eutrophicated inlets, coastal lagoons and artificial hard substrate habitats (e.g. harbor constructions), especially in the southern part of the area, serve as examples of subsystems that have been highly modified by introduced species, whereas the open coast and pelagic systems were relatively free from them until the mid-1980s (17). For example, the Ponto-Caspian complex is represented by only 5 species in the Baltic outside lagoons and river mouths (*Cercopagis pengoi*, the hydrozoan *Cordylophora caspia*, *Dreissena polymorpha*, the opossum shrimp *Hemimysis anomala* and the round goby *Neogobius melanostomus*).

Ecosystems have assimilated nonindigenous Ponto-Caspian species to a certain extent. Even if most of them appear to be rather benign in their new Baltic areas of occurrence, there is evidence of large-scale effects on structural and functional diversity with marked food-web impacts in the most heavily invaded
waterbodies (17, 25, 60). Ponto-Caspian species have had the highest impact on benthic communities; the impact of recently invaded C. pengoi on the pelagic subsystem remains to be assessed in more detail (60-62). The zebra mussel invaded freshwater parts of the southeastern Baltic coastal lagoons nearly 2 centuries ago. In the 1990s, it spread further in the oligohaline parts of the Gulf of Finland and the Gulf of Riga, where it co-occurs with the native bivalve Mytilus edulis (63, 64).

The Ponto-Caspian predacious water flea Cercopagis pengoi was first found in 1992 in the Gulfs of Riga and Finland (62; A. Laine, pers. comm. Finnish Institute of Marine Research). By 1999 it had invaded nearly the whole Baltic proper (61, 65, 66), the Gulf of Bothnia up to the Vaasa area (K.-E. Storberg, pers. comm. West Finland Regional Environment Centre), the Curonian and Vistula Lagoons (67, 68) and the Gulf of Gdansk (65).

The Ponto-Caspian round goby Neogobius melanostomus was first recorded in the Gulf of Gdansk, Poland, in 1990 (69). By 1999, the round goby had spread to the mouth of the Vistula River, adjacent canals, the Vistula Lagoon (70) and the Riigen area (71). The most recent representatives for Ponto-Caspian invasion into the Baltic are the sevruga sturgeon Acipenser stellatus and the hydromedusa Maeotias marginata, both of which were recorded in the northern Baltic in 1999 (72, 73).

CHANGES AT THE REGIONAL LEVEL

Ongoing Eutrophication and Shifts towards "Limnification" in Coastal Areas

Overall consequences of eutrophication reflected in the changes in the biogeographical composition of brackish-water biota are becoming evident at the regional and local levels. Generally, there seems to be an increasing predominance of freshwater species with increasing eutrophication (74) - a successive "limnification" of the pristine brackish ecosystems.

In bottom fauna, the North American barnacle Balanus improvisus is abundant in eutrophicated harbor areas; its abundance is generally one or two orders of magnitude greater than the numbers in more natural environments (18, 75). Green algae of freshwater origin (e.g. Cladophora glomerata and Enteromorpha spp.) benefit from increasing nutrient levels and replace marine algae in eutrophicated coastal waters (76). In the straits off the city of Turku, southwestern Finland, the structure of both benthic and fish fauna was largely determined by eutrophication in the early 1970s when nutrient loading from municipal sources was a major environmental issue in this area (sewage treatment plants were started between 1967 and 1972). In the most eutrophicated inner parts of the inlets, the dominance of freshwater species among bottom fauna (expressed in terms of density, the marine/freshwater species ratio being 0.04:1) was very apparent (77). In fish fauna, freshwater cyprinids such as roach Rutilus rutilus and white bream Blicca björkna, comprised 40 to 65% of the biomass (78).

From the 1950s on, the populations of Arctic tern Sterna paradisaea increased and spread towards the inshore archipelago of southwestern Finland, obviously benefiting from the increase in emerging midges (Chironomus plumosus) as food objects, the bottom-living larvae of which became very numerous with increasing eutrophication (79). Other species of water fowl that benefit from eutrophication in the archipelago waters are typical inhabitants of eutrophic lakes, among them the pochard Aythya ferina, coot Fulica atra, great crested grebe Podiceps cristatus (80) and the mute swan Cygnus olor (81).

Hypoxia Excludes Arctic Relicts

Another process with consequences at the regional level has taken place in the deep basins of the Baltic, frequently exposed to hypoxia and anoxia due to water stagnation below the primary halocline (82). This process has resulted in the extinction of several Arctic relicts in the subhalocline bottom fauna. In the 1950s and 1960s, the bivalve Astarte borealis was a dominant species comprising up to 100% of community biomass in the Bornholm Basin (southern Baltic), and reaching the southern slope of the Gotland Basin in the east (83, 84). The boundary between this Arctic relict community and the zoogeographically more heterogeneous Macoma balthica community, typical of most of the Baltic Sea, was situated at approximately 85 m depth. Since the early 1970s, cosmopolitan and Atlantic-boreal species, probably being more resistant to hypoxia and/or having a higher recolonization capacity, took over in the subhalocline areas of the southern Baltic. The previously bivalve-dominated benthic communities progressively
become polychaete-dominated; in the early 1970s, cosmopolitan and Atlantic-boreal species comprised more than 90% of the total density (84).

From this example it becomes clear that some of the postglacial Arctic relict species are threatened by worsened oxygen conditions in the deepest parts of the Baltic Sea. Their occurrence is restricted to a transition zone between the oxygen-poor deep waters and the low-saline waters above the halocline (16, 26, 84-86). With this, the deeper parts of the southern Baltic have lost their most fascinating biogeographical peculiarity, namely that of offering hospitable conditions for the marine glacial relicts, and thereby also their close zoogeographical connection with Arctic shallow-water biomes. At present, the Bornholm Basin (if not lifeless due to oxygen deficiency) is linked with boreal areas by the most euryhaline cosmopolitan and Atlantic-boreal soft-bottom fauna (82, 85).

DISCUSSION

Impact of Global and Regional Factors

Biogeography aims at understanding the history of formation of flora and fauna, dealing with both qualitative and quantitative aspects of this process. The scale of the factors that presently affect the biogeographical integrity of the Baltic Sea ranges from global to regional ones. More than 20-years ago Leppäkoski (87) listed the most important anthropogenic impacts on the Baltic Sea ecosystem, among them the introduction of nonindigenous species. Since then more than 20 new species have been brought into the Baltic Sea (19), among them *Neogobius, Marenzelleria,* and *Cercopagis,* which have had a much more noticeable impact on the Baltic ecosystem than any earlier newcomers. Today, nonindigenous species act on the all-Baltic (whole region) basis, affecting the biogeographical integrity of the sea from the Bothnian Bay in the north to the Kattegat in the southwest, and from shallow coastal lagoons to the sub-halocline depths. Their secondary dispersal within the waterbody is largely a natural process (18), which, however, may be accelerated by intensive exchange of ballast water between the Baltic sub-regions (88). From the biogeographical point of view, eutrophication seems to cause changes mainly at the local level, giving benefits to freshwater species.

Loss of Biogeographical Integrity

Nonindigenous species are increasingly affecting the biological and even biogeographical integrity of coastal waters all over the world. In Europe, all the brackish seas (the Baltic, Black, Caspian, and Aral Seas) are highly pervaded by nonindigenous species (14, 29, 30). Today, the biota of brackish-waterbodies are exposed to each other because of the breakdown of geographical barriers by shipping traffic, leading to an exchange of species.

The losses of biogeographical integrity described above seem to be more pronounced in the southeastern Baltic lagoons compared with the Baltic proper and the northern Baltic archipelago waters (17). Their susceptibility to invasions may be due to *i*) their topography; *ii*) their repeatedly early successional status subsequent to stochastic changes of abiotic environmental factors (fluctuations and especially sudden salinity fluctuations in the outer parts of the lagoons; unstable ecosystems have been postulated to be more open for nonnative species than stable ones); *iii*) their relative poverty in species numbers and, consequently, the high number of imaginary “vacant” niches (89); *iv*) environmental changes such as increasing eutrophication or other disturbance; and *v*) stochastic inoculation events (e.g. intentional introductions of forage species to nearby freshwater reservoirs in the Baltic republics of the former USSR) (17, 49, 90, 91).
Different subsystems of the stratified Baltic Sea are not equally exposed to species invasions either. Most of the newcomers belong to the littoral or shallow sublittoral subsystems. The hydrozoan *Cordylophora caspia*, the barnacle *Balanus improvisus* and the zebra mussel *Dreissena polymorpha* are, in places, common members of the biofouling community in shallow waters. Deeper water layers below the primary halocline at 30-70 m depth have maintained much of their biogeographical integrity. The soft shell clam *Mya arenaria* can occasionally be found down to 45 m depth; on sheltered sedimentation bottoms, *Polydora redeki* has been recorded at 29 m depth. *Marenzelleria*, the North American newcomer, has been recorded at 50-78 m depth (18).

Because of its ecological and evolutionary history, the Baltic Sea seems to be predominantly a receiver area of introduced species, donor areas of which are to be found both in the adjacent inland waters and oceanic coasts but also in remote seas (38). Recently, the appearance of 2 zooplanktonic species in the North American Great Lakes has been attributed to the existing invasion corridor between the eastern Baltic and the lakes: *Bythotrephes longimanus* in the early 1980s and *Cercopagis pengoi* in 1998 (92, 93).

Until the 1980s, the nonindigenous element occupied only marginal areas and, in most cases, only marginal niches (25, 89). Biogeographically, however, this element signifies a great addition to the Baltic fauna and, in Kattegat, even flora, with respect to the naturally low number of species present. Nonindigenous species have contributed to species diversity and community structure, introduced novel functions and created new interspecific relationships (17, 53). For a conservationist, however, this addition indicates contamination of the biota by nonindigenous elements, reflecting the history of man's economic interests and activities. Unlike chemical pollutants, established nonindigenous species can become a permanent and exponentially growing problem: they reproduce and spread with unpredictable and irreversible consequences, prey on native species, compete for food and space, degrade habitats, food webs and water quality, and often transport and spread diseases and parasites (93, 94).
Nonindigenous species are a major threat to indigenous biodiversity leading to restructuring of communities. Until now, not one species has become extinct in the Baltic Sea due to the introduction of non-indigenous species, but there is no guarantee that this will be the case in the future. This international concern has been included in the Convention on Biological Diversity (Article 8, h): “Contracting Parties shall, as far as possible and appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species.”

All trophic levels are represented among the nonindigenous organisms in the Baltic Sea but not equally subjected to a biogeographical change by them. In certain coastal waters, food chains and whole macrobenthic communities can be based upon introduced species. In the early 1960s, the zebra mussel made up 88% of the total benthic biomass in the Szczecin Firth, Poland. Here the North American freshwater crayfish *Orconectes limosus* fed mainly upon the Ponto-Caspian coelenterate *Cordylophora caspia*, which used planktonic larvae of *Dreissena* as food (25). In Dead Vistula (a cut-off arm of the Vistula River in Poland), the adult dwarf crab *Rhithropanopeus harrisii*, native to North America, fed mainly upon *Dreissena*, whereas young individuals consumed *Balanus* larvae and *Cordylophora* (25, 95).

Most of the recent invaders originate from warmer climates and hydroclimates. If global warming continues, not only spontaneously spreading European invaders but also more nonindigenous species from warmer regions of the world can be expected to establish in the Baltic. Two target species are potentially able to spread with climatic warming. The zebra mussel has not been recorded in the Gulf of Bothnia yet. In North America, its northward distribution is expected to be assisted by warming, provided that other requirements (calcium, pH) are favorable (96). Due to several striking similarities between the Baltic and Black Seas such as brackish water and the annual temperature range (16), the Baltic is to be regarded as an area of special concern related to a *Mnemiopsis* outbreak (21, 38, 97).

**LONG-TERM SOLUTIONS**

Not all windows of introduction can be closed. More than 90% of the transported ballast water originates from marine areas (32). Therefore, on the global and intercontinental scales, management practices for ballast water are the first step to be taken to minimize the risks associated with species introductions (38).

Mid-ocean exchange of ballast water is currently the most reliable (but not fully effective) method to reduce the number of tank travellers (98). Several shipboard treatment options considered and tested to date include both physical and chemical measures (31): filtration, ozonization, treatment by ultraviolet radiation, ultrasound, electric pulses, heat, etc. The preventive methods to be developed must be effective and applicable but also environmentally safe and sound. There is a need to develop effective and environmentally safe methods to prevent hull fouling as well. In research and aquaculture, quarantine procedures and import restrictions (99) should be followed. Advanced methods for risk assessment, monitoring programs and warning systems are needed (97), as well as guidelines for identifying potential high-risk invaders, donor regions and dispersal pathways of future invaders (38, 100).

Xenodiversity tends to reach and even exceed native biodiversity in terms of number of species and life forms, as well as number and rate of ecosystem functions. Much of what was created over millions of years of evolutionary separation and specialization of animal and plant life on both sides of the Atlantic Ocean has been lost forever over the last 500 years because of the activities of agricultural, industrialized and maritime man. This trend towards homogeneity is one of the most important aspects of the geography of life since the retreat of the continental glaciers (35). This issue must be placed on all relevant agendas worldwide, not only in the fields of environmental and marine biology and water-dependent technology but also in sectors of human activities such as trade, transportation and tourism, food, and human health security.


88. Atlantic factors and interspecific relationships will determine the resident niche of an introduced species in its novel environment. niche dimensions will vary in different ecosystems. Any introduced species will have an impact on the recipient community (11) and adequate a reason that are not fully explored or "opportunity hypothesis". This does not necessarily mean that the niche was "vacant". Leach, J.H. 1995. Nondiskin


97. A project called "Risk Assessment for Marine Alien Species in the Nordic Area" was founded in 1997–1999 by the Nordic Council of Ministers. In the first report from the project (4), individual, physical, chemical and biological profiles for five harbours are provided (Bergen area, Norway; Stemmengrund area, Sweden; Klagenfurt, Lithuania; Turku, Åbo, Finland; St. Petersburg, Russia). A list of target species with high invasion potential to be considered as probable future immigrants to the Baltic Sea is presented.

98. The International Maritime Organization’s (IMO) Marine Environment Protection Commission has concluded that voluntary guidelines were the appropriate first step in addressing the ballast water problem. In 1997 the IMO Assembly adopted Resolution A.859(20) “Guidelines for the Control and Management of Ship’s Ballast Water to Minimize the Transfer of Harmful Aquatic Organisms and Pathogens”.


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