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Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem

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Abstract

The Baltic Sea, formed after the latest glaciation, is an enclosed, low-saline, non-tidal ecosystem and has steep latitudinal and vertical gradients from sub-arctic conditions in the north to temperate in the south. The sea has undergone rapid changes since the glaciation, and the "ecological age" of the present ecosystem is only about 8000 years. Primary successional processes are still ongoing, and numerous ecological niches (e.g. large-bodied sediment bioturbators) remain available for immigration. The system is species-poor and vulnerable to the threat of exotic invasive species, and to date about 50 zoobenthic species have established populations in the Baltic Sea. The present biota is a mixture of species of different ecological and zoogeographical origin (marine to limnic; northern Arctic marine and limnic, to North Sea and Atlantic marine). The current distribution patterns of zoobenthos are illustrated, using marine, limnic and non-indigenous examples of structure and ecosystem functions. The species richness decreases from over 1600 marine benthic species in the open Skagerrak to about 500 in the western parts of the Baltic Sea, approximately 80 in the southern regions, to less than 20 in the northern regions. On the other hand, limnic species increase diversity in the inner reaches of the Gulf of Finland and the Gulf of Bothnia. Polychaetes, molluscs and echinoderms are dramatically reduced in numbers from the south to the north.

Keywords: Baltic Sea; Biodiversity; Environmental gradients; Zoobenthos

1. The Baltic Sea ecosystem

The Baltic Sea is a young ecosystem, continuously undergoing post-glacial successional changes, driven both by the still available niches for succession, and the steepness of the physical and chemical environmental gradients (Elmgren, 1984; Kautsky and Kautsky, 2000; Jansson and Jansson, 2002). The "ecological age" of the entire basin as a marine–brackish–limnic continuum is about 8000 years, and the current regime in terms of salinity and basic climatological conditions (covering six climatological zones, from the temperate to the sub-arctic zone) is about 3000 years old (Voipio, 1981; Kullenberg, 1992; Sjörs, 1999), being the result of the large-scale glaciation covering most of the Arctic 10,000–20,000 years ago (Siegert et al., 2002).

The Baltic Sea is some 1300 km in length from south to north, 1200 km from west to east, has a surface of 415,000 km^2, and a total volume of 21,700 km^3 (with a water renewal time of 30 to 40 years). The mean depth is about 60 m (max depth 459 m), with a threshold of only 17 m in the Danish Sound. Salinity ranges from limnic waters (<1 psu) in the innermost reaches in the north and north-east (Gulf of Bothnia and Gulf of Finland) to

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almost fully marine (25 psu) in the southwest (Kattegat), with strong horizontal and vertical gradients, including a permanent halocline at 50–70 m depth in the central Baltic Sea (Voipio, 1981; Kautsky and Kautsky, 2000; Karlson et al., 2002). The main freshwater inflow comes via rivers (Oder, Vistula, Nemunas, Daugava, and Neva accounting for approximately half the nutrient inflow to the sea) and direct runoff from land, showing only small changes over the last 50 years. Mean salinity in the central Baltic Sea has remained relatively stabile during the 20th century (7.2–8.2 psu), with periods of both increasing and decreasing overall salinity, primarily driven by climatic factors. These factors, often presented as the NAO-index, also affect the biota, including the zoobenthos, as shown by Hagberg and Tunberg (2000) for the Swedish west coast, where the ecosystem is driven by these large-scale mechanisms (climate-driven changes in the water exchange between the Baltic Sea and the North Sea), and further stressed by eutrophication (Rosenberg, 2001). The long-term (milennia) salinity trends has settled at its current levels about 3000–4000 years ago, after slightly higher levels for 2000–3000 years after the initial fresh-water phase (Gustafsson and Westman, 2002). In the north, the post-glacial land-uplift after the last glaciation still ranges between 0.5 and 0.9 m per century (Jerling, 1999), and new littoral areas are continuously formed, emphasising the instability of near-shore production. The sea is non-tidal; however there are water-level fluctuations of up to over 1.5 m annually driven by internal waves and air pressure changes (Jerling, 1999). The drainage area is about 4 times larger than the surface of the sea (some 1,641,650 km^2), and is populated by over 85 million people in 14 countries (9 coastal nations), executing strong anthropogenic impact both on land and on the marine ecosystem (HELCOM, 2002).

The aim of this paper is to illustrate current trends in zoobenthic biodiversity-gradients in the Baltic Sea in relation to the principal environmental gradients and their importance for the current trends and patterns in the zoobenthic assemblages. A naturalistic approach was chosen in order to illustrate the gross patterns of the current limitations in the distribution of species of various ecological origin (see e.g. Dayton and Sala´, 2001 for a discussion on this approach).

2. Biotic successional processes

The biota in the open Baltic sedimentary habitats largely follows the physical settings (salinity, topography, temperature, food supply; Bonsdorff and Pearson, 1999), modified by periods of oxygen deficiency (see Karlson et al., 2002 for a review). In the long-term perspective (since the glaciation) marine algae, invertebrates and fish (Wallentinus, 1991; Rumohr et al., 1996; Snoeijs, 1999) have all displayed a slow migration-history, indicative of the embayment effects (Rapoport, 1994). The Baltic primary benthic successional patterns resemble those described in marine environments over short distances and periods of time (Rumohr et al., 1996; Rosenberg, 2001), with laminated sediments as one endpoint (Persson and Jonsson, 2000) and diverse benthic assemblages the other, often as a result of secondary succession after periods of hypoxia or anoxia (Laine, 2003; Rosenberg et al., 2004). The slow natural colonisation rates and the harsh environmental conditions, including highly complex coastal habitat-diversity and typology (Schernewski and Wielgat, 2004), have opened the ecosystem for alien or non-native species, currently invading large regions of the Baltic Sea, and the question remains as to whether they are ecologically damaging or perhaps positive for the ecosystem (Leppäkoski and Olenin, 2000), or whether they just take advantage of the naturally reduced species numbers in the inner reaches of the sea (Paavola et al., 2005). One of the key-questions discussed for the Baltic gradient is whether or not the relative functional poverty, i.e. the lack of large-bodied sediment burrowers and active bioturbators, and the relative poverty of suspension feeders and surface deposit feeders (sensu Bonsdorff and Pearson, 1999) is reflected in the stability of the ecosystem (Snelgrove et al., 1997), or – reversibly – in its potential inertia instability (Jansson and Jansson, 2002). For the shallow coastal ecosystems of the Baltic Sea similar issues have been analysed also for marine algae and phanerogams, illustrating both gradual species-reductions and morphological adaptations along the Baltic salinity gradient (Snoeijs, 1999; Boström et al., 2003). Recently possibly the first evidence of regional speciation was found within the brown alga *Fucus*, when a new species (*F. radicans* sp. nov.) was described for the low-saline regions of the inner Bothnian Bay (Bergström et al., 2005). Until now genetic speciation in the inner Baltic Sea has been a largely unknown phenomenon, although genetic differentiation is well-known, with profound implications for the invasion-history of several key species (e.g. the bivalves *Macoma balthica* and *Mytilus edulis*/*trossulus*) in the ecosystem (Väinölä and Hvilsom, 1991; Väinölä, 2003).

3. Environmental stress

The Baltic Sea ecosystem is also under heavy anthropogenic stresses (over-fishing, eutrophication,