ELSEVIER

Journal of Experimental Marine Biology and Ecology 330 (2006) 383 – 391

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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

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Received 12 October 2005; received in revised form 5 December 2005; accepted 15 December 2005

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.
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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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doi:10.1016/j.jembe.2005.12.041

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,

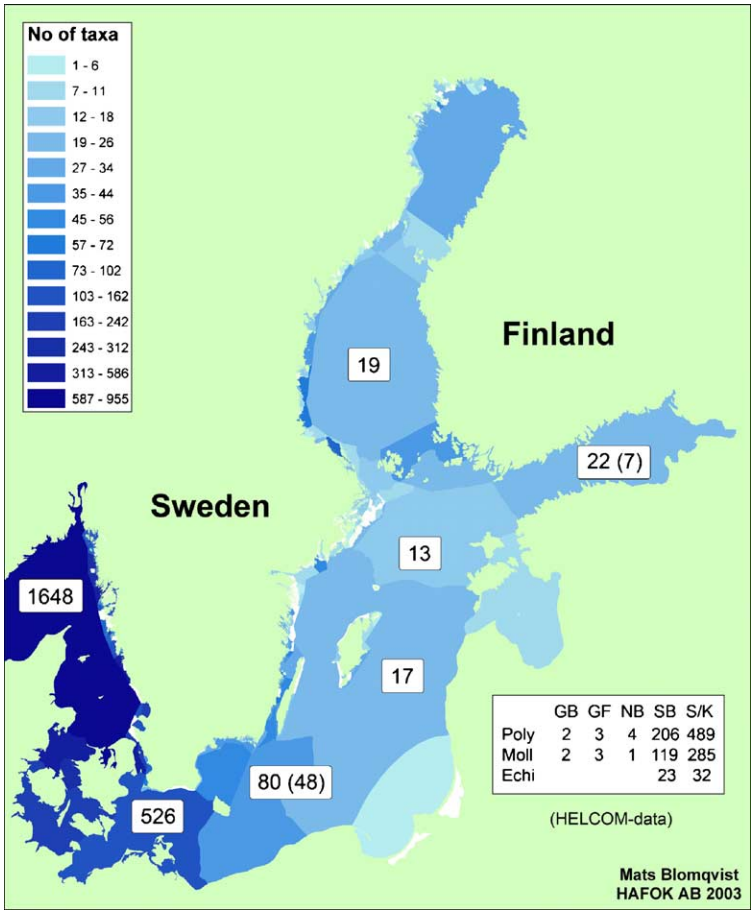

Fig. 1. A gross-distribution of sub-littoral soft-sediment species richness across the Baltic Sea environmental gradient. Numbers in brackets refer to data from below the halocline in areas with annual to semi-annual hypoxia. The inserted box indicates the number of selected higher taxa along the gradient (from north to south): GB = Gulf of Bothnia, GF = Gulf of Finland, NB = Northern Baltic, SB = Southern Baltic, S/K = Skagerrak/Kattegat. Poly = polychaetes, Moll = molluscs, Echi = echinoderms. Data from the HELCOM-data base; map compiled by Mats Blomqvist (HAFOK AB, 2003).

hazardous chemicals etc.), and the biota are vulnerable. Due to stagnation periods in combination with eutrophication-induced hypoxia/anoxia benthic 'ecological deserts' annually covers over 30% of the seafloor (over 100,000 km^2), inducing secondary successional patterns seldom leading to 'mature' benthic communities (Karlson et al., 2002). The current anoxic conditions in the deep waters seem to be persistent, independent of seasonality, whereas coastal hypoxia is largely seasonal (Karlson et al., 2002). In that context the Baltic Sea is one of many coastal or marginal seas around the world affected by organic enrichment and subsequent hypoxia (Cloern, 2001; Gray et al., 2002; Levin, 2003). In the Baltic Sea nutrient concentrations have increased 4–8 times during the 20th century with profound ecological consequences, such as increased pelagic productivity and turbidity of the surface layers (Sandén and Håkansson, 1996; Kautsky and Kautsky, 2000) and shifts in biomass distribution (ratio meiofauna/macrofauna and role of bivalves as examples) above/below the halocline and altered trophic dynamics of the entire ecosystem and food webs in it (Cederwall and Elmgren, 1980; Elmgren, 1984; Elmgren and Larsson, 2001). These significant changes are largely driven by anthropogenic input of nutrients, but development from an oligotrophic towards a slightly more eutrophic state may also reflect the long-term successional status of the ecosystem.

4. Principal patterns in benthic biodiversity of the Baltic Sea

The Baltic Sea was colonised many times, before and after the latest glaciation, and the immigration routes have only recently begun to materialise in their full

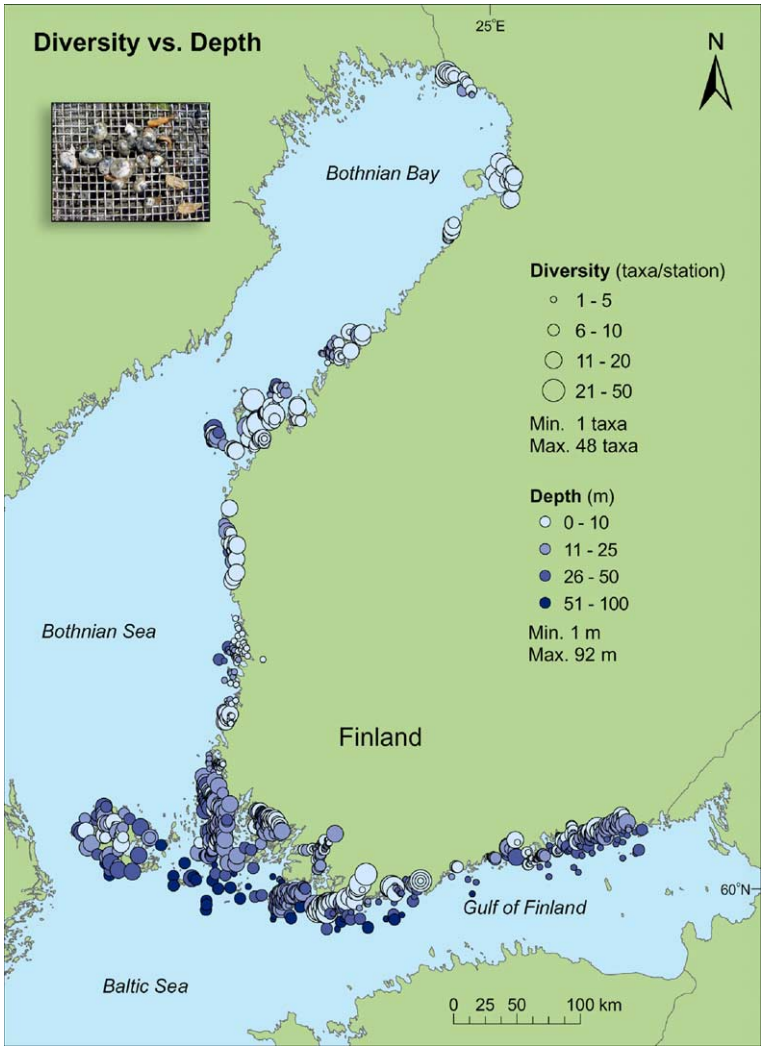

Fig. 2. Overall zoobenthic species diversity in the Finnish coastal waters (1–92 m; 1–48 spp) 1267 stations (1990–2000; mean depth 18 m; range: 1–92 m) vs. depth, showing rather uniform diversity-patterns along the entire coast, reflecting the topography with shallow slopes in the north, and wider amplitudes in depth in the south, where diversity clearly decreases with increasing depth (unpublished data; Perus and Bonsdorff).

extent in that genetic markers show the relationships between populations of common species over long time periods (millions of years) and distances (such as the links between North America and Europe, and the Pacific and the North Atlantic). The most common bivalve in the Baltic soft sediments, *Macoma balthica*, and similarly the *Mytilus*-complex on hard substrates are eminent examples of this (Väinölä and Hvilsom, 1991; Väinölä, 2003). Currently the only natural invasion corridor for zoobenthos is through the Danish Sound, where the drop in salinity is steep, and the number of species occurring declines rapidly (Fig. 1). This phenomenon can also be viewed as a bottle-neck for species invasions at large, as the system along the steep environmental gradient may be saturated with species occupying the potential niches and/or functions in a benthic flow-system (Bonsdorff and Pearson, 1999; Stachowicz et al., 1999; Jumars et al., 2001; Bremner et al., 2003). The rapid decline in the overall number of species along the Baltic Sea gradient illustrated in Fig. 1 (open waters, deeper than 20 m) is largely true for the open Baltic Sea, but closer to the coasts and in shallow waters the patterns are blurred as organisms of different origin mix, and freshwater species and insect larvae make up large parts of the species richness (Haahtela, 1996). Thus, for instance, the low diversity along the Finnish coasts in Fig. 1 (13–22 species) is not representative for shallow waters of above 15 m (80–140 species recorded ranging from the SW inwards along the Gulf of Bothnia and the Gulf of Finland), and below

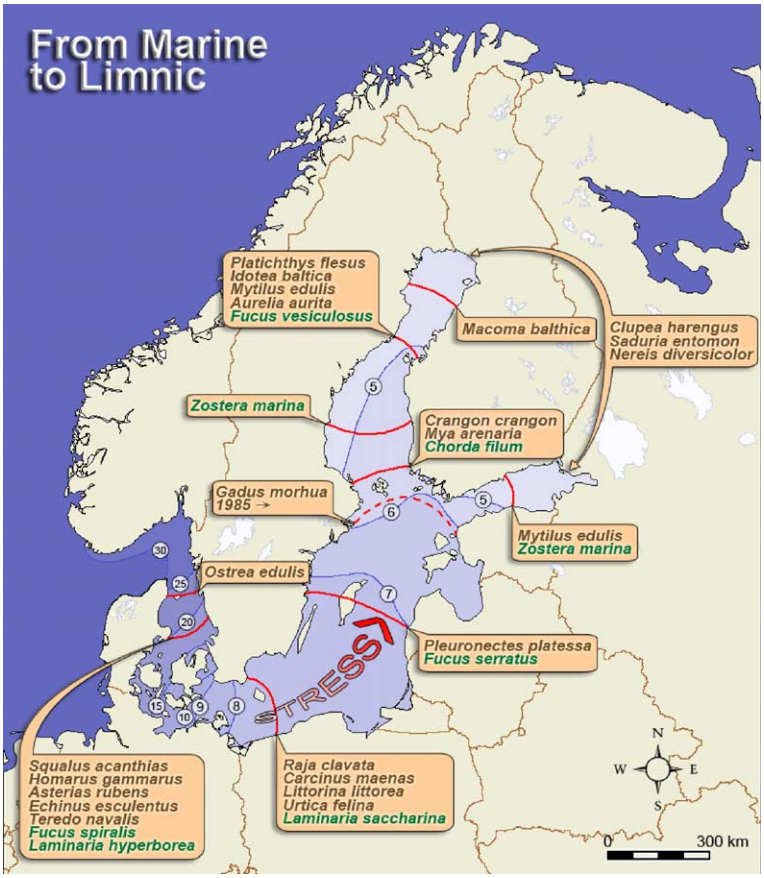

Fig. 3. The distributional ranges of selected marine species in the Baltic Sea (fish, benthic invertebrates, macrovegetation). The environmental stress increases with distance from the North Sea as salinity drops (salinity indicated as psu). The red arrows indicate the limit of distribution within the Baltic Sea. Data from the HELCOM-data base and various sources (basic background map from http://www.grida.no/baltic).

15 m (25–70 species recorded along the same gradient). In a more detailed analysis, however, depth is not the main driving force for coastal zoobenthos along the Finnish coasts above the halocline, but the deeper more exposed off-shore stations generally also display lower species richness, just as shown for the open Baltic Sea (Fig. 2). The coastal and archipelago areas differ not only due to limnic species and insect larvae, but also because of a higher habitat complexity and variable substrates (Bonsdorff, 1988; Bonsdorff and Blomqvist, 1993; Bonsdorff et al., 1996, 2003; O'Brien et al., 2003; Perus and Bonsdorff, 2004). In the deep waters of the major basins, the distribution-patterns of the most common species were analysed in detail by Laine et al. (1997) and Laine (2003), who found clear patterns of distribution coupled with salinity, temperature and oxygen. Hence, the closely related amphipods *Monoporeia affinis* (a glacial relict of freshwater origin) and *Pontoporeia femorata* (a post-glacial marine immigrant), in spite of overlaps in distribution in the Gulf of Finland, largely differ in distribution, with *M. affinis* having highest abundances in the cold, low-saline north, and *P. femorata* favouring the central Baltic waters of higher salinity. Further southern populations of *P. femorata* are seemingly outcompeted by other species occupying the same habitats and niches (Rumohr et al., 1996). Other species, such as the bivalve *Macoma balthica*, cover almost the entire range of depths and habitats, but displays surprisingly clear differences in genetic traits within the Baltic environmental gradient (Väinölä and Hvilsom, 1991). In the Baltic Sea, further, the role of meiofauna is enhanced both in terms of biomass (Elmgren, 1984) and function (Olafsson, 2003) as compared to fully marine systems.

5. The importance of the environmental gradient

The steep environmental gradients are not only manifested as rapidly reduced species numbers from the North Sea into the Baltic Sea, but also as a mixture of floral and faunal components (Figs. 3 and 4). As salinity

Fig. 4. The distributional ranges of selected limnic species (fish, benthic invertebrates, macrovegetation). The environmental stress increases towards the Danish Sounds and Kattegat/Skagerrak as salinity increases (salinity indicated as psu). Data from the HELCOM-data base and various sources (basic background map from http://www.grida.no/baltic).

drops from about 20 psu in the Kattegat to 8–10 psu in the German coastal waters, many species reach their physiological limits of tolerance. Such conspicuous species as *Ostrea edulis*, *Homarus gammarus*, *Asterias rubens*, and *Echinus esculentus* never make it into the Baltic proper, while others (*Carcinus maenas* and *Littorina littorea* as examples) manage to the level of the island of Bornholm (Fig. 3). Others, on the other hand, manage both the reduced salinity and the harsh environmental conditions even in the embayments of the northern Baltic Sea, namely *Nereis diversicolor*, *Aurelia aurita*, and *Macoma balthica* for example. For another suite of species, the problem is reversed. Species of limnic origin (Fig. 4) do not manage well in the open Baltic Sea, but show local distributions even into fully marine waters in some rare instances. The majority of these species are melandrous and migrating fish, being able to flee unfavourable conditions, but some genuinely limnic invertebrates manage occasionally, too (e.g. *Monoporeia affinis* can be found even in the southernmost parts of the Baltic Sea, as shown in Fig. 4). In light of the harshness of the environment, the overall benthic diversity may, in fact, be considered rather high. The present-day distribution patterns are the result of the ongoing successional pattern ever since the end of the glaciation, however, currently blurred by the impact of Man (both on the environment and through the intentional or unintentional transport of species across ecological barriers). The entire ecosystem of the Baltic Sea may thus have undergone not just one, but perhaps several catastrophic changes (Scheffer et al., 2001; Jansson and Jansson, 2002) that may be hard or even impossible to repair (MacKenzie et al., 2002), but in trying to reconstruct the structure benthic assemblages of the past, historic data (at least 100 years of information) are of prime value (Zettler and Röhner, 2004).

6. Invasive non-indigenous species

Currently, one of the main factors (positively) affecting the number of species in the Baltic Sea is the

Fig. 5. The distributional ranges of selected "alien" species in the Baltic Sea (fish, benthic invertebrates, macrovegetation) of both marine (*Balanus improvisus*, *Mya arenaria*, *Teredo navalis*, *Marenzelleria viridis* and *Fucus evanescens*) and limnic (*Coregonus peled*, *Dreissena polymorpha*) origin. Data compiled from the Baltic Sea database on alien species (http://www.ku.lit/nemo/alien_species_directory.htm), and Leppäkoski et al. (2002) (basic background map from http://www.grida.no/baltic).

invasion of non-native ('alien') species, either aided by Man, or naturally expanding their distributional ranges (Fig. 5). It is evident that many of the benthic species that are successful in occupying both habitats (environmental settings) and niches (ecological functions) are more plastic in their tolerance to environmental stress than the native ones, utilising wide ranges in salinity (0.5 to 7 psu) and habitat-wide characteristics (Paavola et al., 2005). Hence, some invasive species have become very successful, with the polychaete *Marenzelleria viridis* as arguably the most striking example in the soft-sediment system (Leppäkoski et al., 2002; Leppäkoski, 2005), and for example in the coastal waters off the Åland Islands in the Northern Baltic Sea, this species within 10 years from its first recordings ranked among the top-five species accounting for about 90% of the variability of the entire local benthic assemblages (Perus and Bonsdorff, 2004). Currently focus is on the functional importance of such successful invaders (e.g. Kotta and Olafsson, 2003). For the Baltic Sea zoobenthos it seems evident that the 50 or so established marine invasive species (about 35 benthic invertebrates, such as the polychaete *M. viridis* and the bivalves *Dreissena polymorpha* and *Mya arenaria*) have become forceful drivers of the entire ecosystem, as predicted to be the outcome for a variety of habitats by Didham et al. (2005). Put in a larger perspective, the spreading of non-indigenous species poses a major threat to both structure and functioning of the natural biodiversity along the entire coasts of Europe, with zoobenthos being the dominant group affected in all regions, rapidly increasing in numbers since the 1940s (Strefaris et al., 2005).

7. Concluding remarks

When analysing the coupling of the environment and environmental gradients (variability, amplitude etc.) with biodiversity, it is important to also link structure

and functioning of the biological assemblages (Bonsdorff and Pearson, 1999). The Baltic Sea of today is a result of both its entire post-glacial history, and the present stress added by human activity in the forms of large scale eutrophication, hypoxia, toxic chemicals, over-fishing and introduction of invasive species. The current debate to a large extent focuses on the stability or instability (vulnerability) of the entire ecosystem (Jansson and Jansson, 2002), and the terms 'catastrophy' or 'catastrophic shift' are being applied (Scheffer et al., 2001). On the other hand, it is vital to both acknowledge and understand that the Baltic Sea, just as any other (marine) ecosystem is not a unified static entity, but a highly dynamic complex of processes. To strive to preserve a balanced and multi-facetted ecosystem, we must understand and accept change in the system, and realise the value of biodiversity as such.

Acknowledgements

I am thankful to Bob Whitlatch for inviting me to the special Warwick-session on soft-sediment ecology at the 34th Annual Benthic Ecology Meeting in Williamsburg, Virginia (USA) in April 2005: Without that push, this brief overview might never have materialised. I am also grateful to several friends for fruitful debates and discussions on the topic. I thank Mats Blomqvist and Johan Lindholm for graphic design of the distribution maps, and Jens Perus for data-support for the Finnish coastal benthos. This paper is part of EU-MARBEF, and funded by the Academy of Finland (project IMAGINE under the Baltic Sea research programme BIREME). **[SS]**

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