



Ichnological trends along an open-water transect across a large marginal-marine epicontinental basin, the modern Baltic Sea

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ABSTRACT

Late Holocene sediments in the Baltic Sea provide an opportunity to study lateral changes in the assemblages of identifiable biogenic sedimentary structures (ichnofossils) in a large, high-latitude semi-enclosed sea with instrumentally determined gradients in biodiversity and environmental factors such as salinity and oxygen availability. Integrated sedimentological and ichnological analysis is carried out on 6 long cores collected along an open-sea, declining salinity transect across the basin. Muddy sediments in euhaline (Kattegat) and polyhaline (Mecklenburg Bight) sites are characterized by the archetypal *Cruziana* Ichnofacies, portrayed by subsurface deposit-feeding structures (*Scolicia* and *Planolites*), surface deposit-feeding structures (*Skololithos*), and structures that reflect both these feeding strategies (*Palaeophycus*, *Arenicolites*/*Polykladichnus* and unnamed biodeformational structures produced by bivalves). The ichnofossils are tiered to 3 levels. The *Cruziana* Ichnofacies is impoverished in the higher mesohaline Arkona Basin and even more so with declining salinity farther inland. The deepest, oxygen-restricted study sites (Gotland Deep and the western Gulf of Finland) below a permanent halocline are characterized by very small and shallow deposit-feeding structures (*Planolites* and rare flat *Arenicolites*/*Polykladichnus*), and poorly developed tiering. The nearly freshwater eastern Gulf of Finland is characterized by the Cenozoic archetypal *Mermia* Ichnofacies, dominated by narrow and shallow subsurface and surface deposit-feeding structures (*Planolites* and flat *Arenicolites*/*Polykladichnus*). Large *Planolites* (3–7 mm in diameter) at this site are untypical of *Mermia* Ichnofacies assemblages. These results confirm the earlier observations that marine forms dominate brackish-water ichnoassemblages, with the ichnofossil size and diversity decreasing with declining salinity. The results also confirm the predicted decreases in the ichnofossil size and vertical extent at low-oxygen levels. Poorly developed tiering is a particularly useful indicator of oxygen stress in the salinity-restricted system.

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1. Introduction

Identifiable biogenic sedimentary structures (ichnofossils or trace fossils) are useful for characterizing past zoobenthic communities and their living environments (Seilacher, 1964; Ekdale, 1985; Wetzel, 1991; Löwemark et al., 2004; Rodríguez-Tovar et al., 2011). Ichnofossils record behavior in endobenthic communities that more readily responds to changing environmental condition than the animal species composition. Consequently, trace fossils are more sensitive

indicators of change in the benthic environment than body fossils (Savrdá and Bottjer, 1986; Wetzel, 1991; Baas et al., 1997). Ichnofossils are particularly valuable in semi-enclosed epicontinental seas such as the Baltic Sea that typically are dominated by soft-bodied fauna with an extremely poor preservation potential (Tyson and Pearson, 1991). Holocene brackish-water organic-rich muds in the Baltic Sea Basin are well-suited for ichnological studies because of their high vertical (temporal) resolution warranted by the relatively high sedimentation rates (typically 0.5–2 mm a^{−1}), and the small sizes and shallow penetration depths of the traces (Virtasalo et al., 2006, 2011).

Marginal-marine settings are harsh living environments that are typically characterized by fluctuations in a number of environmental factors. Accordingly, ichnological characteristics of sediments in marginal-marine settings are controlled by several factors, primarily salinity, but also oxygen availability, sediment grain-size, consistency

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and food content, and near-bottom current velocities (e.g. Pemberton et al., 2001; MacEachern and Gingras, 2007). The two most significant, recurring ichnological responses to increasingly diluted salinities since the Carboniferous are: (1) size reduction and (2) ichnodiversity reduction (e.g. Pemberton et al., 2001; Buatois et al., 2005; MacEachern and Gingras, 2007). Both trends are broadly ascribed to macrofaunal adaptations to increasing osmotic stress with decreasing salinity (Remane, 1934; Remane and Schlieper, 1971). Also restricted oxygen availability results in the reduction of size and diversity of trace fossils, as well as in decreased burrow-penetration depths (Savrda and Bottjer, 1986, 1991). Crosscutting relationships (tiering) of ichnofossils are particularly sensitive to seafloor oxygenation (Wetzel, 1991; Baas et al., 1997; Rodríguez-Tovar et al., 2011). Various endobenthic fauna occupy different depth levels within the seafloor at the same time, and produce different depth zones (tiers) with different ichnological characteristics (Werner and Wetzel, 1982; Bromley and Ekdale, 1986; Wetzel, 1991). Under fully oxygenated conditions, several tiers containing co-occurring traces that crosscut pre-existing traces may develop in the subsurface, while decreasing oxygenation forces the reduction in the number and vertical extent of tiers.

The quantification and characterization of the ichnofossil size, diversity, penetration-depth and tiering trends in modern seafloor sediments have the potential to aid in the palaeoenvironmental, palaeoecological and palaeogeographical studies of ancient basins. However, previous studies in modern settings, aimed at understanding marginal-marine ichnological trends have concentrated on tidally modulated environments (Frey et al., 1987; Hertweck, 1994; Gingras et al., 1999; Dashtgard and Gingras, 2005; Hertweck et al., 2005; Dashtgard et al., 2006, 2008) or shallow microtidal coastal areas (Hertweck, 1972; Dörjes and Howard, 1975; Howard and Frey, 1975; Frey and Howard, 1986; Hauck et al., 2009), while the basin-scale studies of large semi-enclosed seas have not been carried out.

The current understanding of the effects of reduced salinity on the function, composition and distribution of macrobenthic animal communities is, in large part, based on early studies carried out in the North Sea and Baltic Sea (Remane, 1934; Ekman, 1953; Segerstråle, 1957a; Remane and Schlieper, 1971; Schäfer, 1972). During the past decades, benthic ecological studies in the Baltic Sea have largely been targeted at elucidating the effects of anthropogenic changes in the marine environment (e.g., eutrophication and associated oxygen deficiency) on the composition of macrobenthic communities and species' abundance (e.g., Pearson et al., 1985; Rumohr et al., 1996; Laine et al., 1997, 2007; Olenin, 1997; Bonsdorff and Pearson, 1999; Karlson et al., 2002). Some workers have used sediment surface-profile imaging (e.g., Bonsdorff et al., 1996; Rosenberg et al., 2000, 2001) or computer-aided tomography (Rosenberg et al., 2007, 2008) for studying open biogenic structures in the surface sediments. Only a few workers have investigated the behavior of burrowing macrofauna in these sediments (Dold, 1980; Powilleit et al., 1994), or studied the biogenic sedimentary structures and fabrics that are preserved after burial and compaction (Werner et al., 1987; Werner, 2002; Virtasalo et al., 2006, 2010, 2011; Winn, 2006). This oversight is notable because, due to the poor preservation of the trace producers in these muds, biogenic sedimentary structures and fabrics provide virtually the only means of studying changes in the Baltic Sea benthic environment and animal communities preceding the systematic oceanographic and zoobenthic studies that were initiated in the 1920s.

This is the first study to investigate ichnofossil assemblages in (sub) recent organic-rich muds along an open-water transect across the Baltic Sea, one of the largest and best studied modern brackish-water basins with strong gradients in salinity, oxygen and biodiversity. The purpose is to explore the sensitivity of trace fossils as indicators of environmental factors such as salinity, oxygen availability and sediment consistency in order to improve the ability of ichnologists to characterize past benthic environments and their animal communities. This approach is timely

because the Baltic Sea ecosystem is increasingly impacted by anthropogenic nutrient loading, eutrophication and amplified oxygen deficiency (HELCOM, 2009), which urgently calls for a tool for characterizing past zoobenthic communities in order to place the present state of the benthos into the context of natural variability. Elucidating the long-term development of the benthic communities is crucial for the adequate understanding of their varying function and significance in biogeochemical cycles during the Holocene and today (Karlson et al., 2007).

2. Study area

The Baltic Sea basin was covered by the Fennoscandian continental ice-sheet during the Late Weichselian (Late Pleistocene). The final ice-retreat from the basin started at ~15,000 years before present (BP), when an ice-dammed lake was formed in its southern parts (Mangerud et al., 2004). The ice retreat was followed by the successive deposition of ice-proximal tills and outwash deposits, glaciolacustrine rhythmites, scattered debris-flow deposits, postglacial lacustrine clays, and brackish-water mud drifts (Virtasalo et al., 2007). Brackish-water conditions were established at 8000–7000 BP, when the glacioeustatic ocean-level rise resulted in the incursion of the Atlantic into the basin through the shallow and narrow Danish Straits (Bennike et al., 2004; Jensen et al., 2005; Röbller et al., 2011). Substantially increased organic carbon contents from 2% up to 6% weight (Moros et al., 2002; Röbller et al., 2011) in muddy sediments denote the amplification of primary production at the onset of brackish-water conditions. The increased organic content and consequently lowered substrate consistency resulted in the dominance of shallow deposit-feeding in the macrobenthic communities (Virtasalo et al., 2006). The lithic component of these muds is dominated by clay minerals, mainly illite, with some chlorite and smectite and less kaolinite (Virtasalo et al., 2011). Feldspars are also common, dominated by K-feldspar and albite, with traces of plagioclase. Quartz is another major constituent. Minor authigenic components include Fe-sulfides and Mn-carbonates. Carbonate shells are increasingly rare north from the Bornholm Basin.

The modern Baltic Sea is located between maritime temperate and continental sub-Arctic climate zones. It has a surface area of 392,978 km², while its volume equals 21,205 km³ (Leppäranta and Myberg, 2009). The mean depth is 54 m, with the maximum depth of 459 m. Winter mean air temperature ranges in a north-south direction from –12 to 0 °C. Summer mean air temperature has a smaller range, 14–17 °C over the whole basin. On average, 45% of the sea area is covered by ice during winter (Leppäranta and Myberg, 2009). Tidal amplitude in the Danish Straits is 10 cm, and 2–5 cm in the rest of the sea (Witting, 1911). Variations in wind and air pressure result in the water-level variability of up to 2 m.

A permanent halocline located at the 70–90 m depth and a seasonal thermocline in summer substantially hamper the vertical mixing of the water mass. Combined with the high organic deposition from primary production, the restricted mixing results in seafloor oxygen deficiency in the deep areas of the central Baltic Sea and Gulf of Finland. Bottom water salinity ranges from fully marine (34 PSU) in Kattegat to almost freshwater (2–4 PSU) in the inner reaches in the north and north-east (Bothnian Bay and eastern Gulf of Finland). The salinity regime is determined by the amount and frequencies of saline water inflows (annual mean = 470 km³ a^{–1}) from the North Sea through the Danish Straits, and freshwater surplus (annual mean = 481 km³ a^{–1}) from river runoff and precipitation minus evaporation (HELCOM, 1986). The saline inflows enter the basin as dense near-bottom currents that annually renew deep waters up to the Bornholm Basin. The so-called major saline inflows occur every 1–10 years and penetrate all the way to the Gotland Deep, supplying oxygen to the oxygen-deficient basin (Matthäus et al., 2008). The oxygen is rapidly used up, however, and the net effect of the major inflows is decreasing oxygen levels due to strengthened stratification

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