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Critical Review

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Hypoxia, a growing worldwide problem, has been intermittently present in the modern Baltic Sea since its formation ca. 8000 cal. yr BP. However, both the spatial extent and intensity of hypoxia have increased with anthropogenic eutrophication due to nutrient inputs. Physical processes, which control stratification and the renewal of oxygen in bottom waters, are important constraints on the formation and maintenance of hypoxia. Climate controlled inflows of saline water from the North Sea through the Danish Straits is a critical controlling factor governing the spatial extent and duration of hypoxia. Hypoxia regulates the biogeochemical cycles of both phosphorus (P) and nitrogen (N) in the water column and sediments. Significant amounts of P are currently released from sediments, an order of magnitude larger than anthropogenic inputs. The Baltic Sea is unique for coastal marine ecosystems experiencing N losses in hypoxic waters below the halocline. Although benthic communities in the Baltic Sea are naturally constrained by salinity gradients, hypoxia has resulted in habitat loss over vast areas and the elimination of benthic fauna, and has severely disrupted benthic food webs. Nutrient load reductions are needed to reduce the extent, severity, and effects of hypoxia.

Introduction

Hypoxia, the lack of oxygen in bottom waters often defined as $O_2 < 2$ mL L^{-1} is a growing problem worldwide and dead zones have spread exponentially since the 1960s in coastal marine waters (*1*). Hypoxia not only kills the bottom-living

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organisms (*2*), thereby destroying benthic communities and fish habitat (*3*), but also alters the biogeochemical cycles of nutrients (*4, 5*). Oxygen concentrations decrease when oxygen supply does not meet the demand, so that an imbalance occurs between the physical processes that supply oxygen and the biological processes that consume it. Consequently, the bottom water eventually becomes hypoxic.

Hypoxia first occurred in the Baltic Sea after its transition from fresh water to brackish water ca. 8,000 cal. yr BP and has been present intermittently throughout the Holocene (*6*). Low water column dissolved oxygen concentrations have been observed locally since ca. 1900 (*7*) with increases observed in laminated sediments since the 1950s (*8*). The supply of oxygen is dominated by water exchange and vertical mixing processes, which are both closely coupled to climate, large-scale atmospheric circulation, and oceanographic conditions. The Baltic Proper is permanently stratified, consisting of an upper layer of brackish water with salinities around 7−8 and a lower layer of saline waters with salinities around 11−13. A strong permanent halocline is formed at the transition zone at depths varying between ca. 60−80 m, and prevents vertical mixing of the water column and transport of more oxygenated waters to the bottom.

The occurrence of hypoxia in the Baltic Sea is receiving increased attention and exploratory projects are in progress for remediation options to alleviate eutrophication (*9*). Although there have been significant advances over the last decades in our understanding of the causes, effects, and remedies needed to alleviate the detrimental effects of eutrophication and hypoxia in the Baltic Sea (*10*), the relative importance of individual processes of transport and consumption are incompletely understood. Before any remediation effort is implemented it is important that we have a better quantitative understanding of the causes, consequences, and risks (*11*). Here, we assemble the current knowledge regarding hypoxia in the Baltic Sea and identify some of the important gaps in our knowledge regarding the development of hypoxia and therefore its mitigation.

Occurrence of Hypoxia during the Holocene

The fact that hypoxia was present in the Baltic during different periods of the Holocene (*12*) has led to a discussion regarding the role of climate and eutrophication in its present day formation (*10*). Zillén et al. (*6*) compiled the available data on the occurrence of hypoxia using the presence of laminated sediments. One of the environmental prerequisites for the formation and preservation of laminated sediments is the absence of benthic fauna that bioturbate, or vertically mix, the uppermost sediments. Hypoxic conditions prevent the establishment of benthic fauna resulting in laminated sediments in deeper areas below the halocline. While hypoxic conditions may exist at the sediment−water interface, due to steep gradients through the benthic boundary layer, oxygen can still be present in the water column.

Hypoxia during the Holocene was strongly influenced by the postglacial history characterized by a complex interaction between changing sea levels, irregular land-uplift, and variable climate. Traditionally, the development of the Baltic Sea is separated into four stages, i.e., the Baltic Ice Lake (15000−11700 cal. yr BP), Yoldia Sea (11700−10700 cal. yr BP), Ancylus Lake (10700−10200 cal. yr BP), and the Littorina Sea, which can be further divided into three sub stages, i.e., the Early (or Initial) Littorina Sea (10200−8500 cal. yr BP), the Littorina Sea sensu stricto (s. str., 8500−3000 cal. yr BP), and Late Littorina Sea (3000 cal. yr BP to present). These changes represent intervals of brackish and freshwater conditions due to changes in water exchange with the North Atlantic/Kattegat (*13*). A circulation that supported a fully brackish system began around ca. 8000 cal. yr BP at the start of the Littorina Sea s. str. stage when the Öresund Strait began to function as an important inlet of salt water and initiated the establishment of a permanent halocline in the Baltic Sea (*12*). However, due to the lack of a robust geochronology, the timing of the first brackish/marine Littorina conditions is much debated (*13*), and it is hypothesized that a transitional phase, i.e. the Early (or Initial) Littorina Sea, existed with episodic marine influxes. Regardless of age differences, there is a general agreement that a permanent halocline was formed during the Littorina Sea s. str. transition.

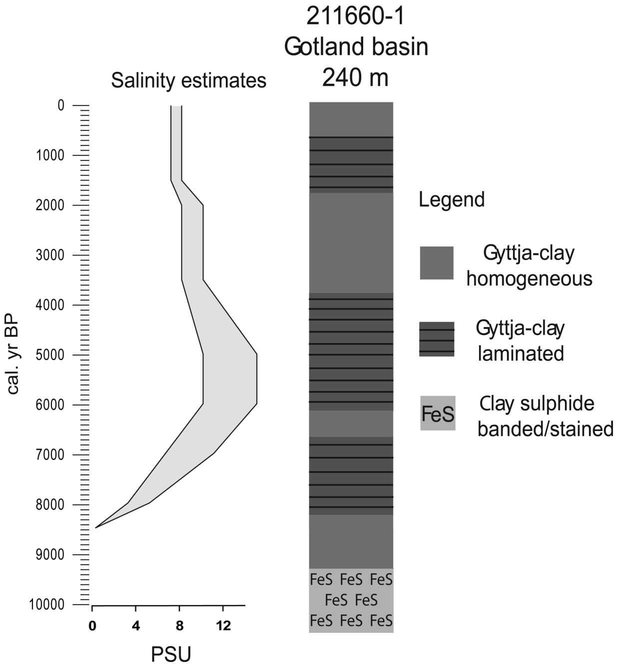

FIGURE 1. Modeled salinity estimates in the Baltic Proper (*69*) and the occurrence of laminated sediments at a station in the Baltic Proper (redrawn from ref (*6*)).

Laminae formation occurred basin-wide at depths between 73 and 250 m during three major periods in the Baltic Proper between ca. 8000−4000, 2000−800 cal. yr BP, and after AD 1900 (*6*), although the deepest areas of the Landsort Deep (>250 m) were probably continuously hypoxic during most of the Holocene (*14*). Laminae between 8000−4000 cal. yr BP coincide with increases in salinity and presumably with stratification restricting the ventilation of bottom waters (Figure 1). The shallower southern Baltic including the Bornholm and Arkona basins were frequently oxygenated during the Holocene with bioturbated sediments throughout, although geochemical records imply more reduced conditions after the Littorina Sea s. str. transition (*12*). Hypoxia was reported in the Bothnian Sea early in the history of the Baltic Sea (*15*); however, the decrease in the depth of sills with land uplift and weakening of salinity stratification has limited the formation of hypoxia in the Bothnian Sea during recent times. Improved spatial coverage of sediment records across depth gradients in depositional basins is required to improve our understanding of the historic spatial distribution of hypoxia.

Hypoxia again appeared in the Baltic Sea ca. 2000−800 cal. yr BP associated with the Medieval Warm Period (MWP), and the entire Eastern Gotland Basin in the Baltic Proper has accumulated laminated sediments since ca. AD 1900 (*16*). The area that is hypoxic has increased more than 10-fold during the last century (*17*). Large-scale changes in land use with development and expansion of agriculture were responsible for increases in nutrient concentrations in lakes during the MWP (*18, 19*). In addition, population increases

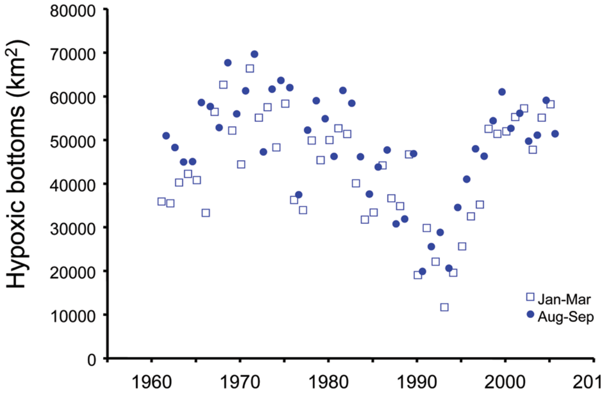

FIGURE 2. Seasonal and interannual variations of the bottom area covered by hypoxic waters containing less than 2 mL L^{-1} dissolved oxygen. Oxygen fields were averaged over August−September (filled circles) and January−March (open squares) for each year (updated from ref (*30*)).

during the industrial revolution, development of the water closet, tiling of fields for enhanced drainage, cutting of drainage ditches, and expansion of the forest industry in the watershed at the turn of the last century, and more recently the large-scale increases in nutrient inputs with agriculture, have been important drivers for the formation of hypoxia (*6*). During the last century nutrient loads have increased by ca. 2.5 for nitrogen and 3.7 times for phosphorus (*17*). Unraveling the importance of climate change on hypoxia relative to anthropogenic forcing with nutrients would be an important scientific step forward.

The occurrence of hypoxia in time and space in the coastal zone is less well-known than our knowledge in the open waters of the Baltic (*6*), although increases in laminated sediments over the last 50 years have been observed in the Stockholm Archipelago (*20*). Knowledge regarding whether the timing of the occurrence of hypoxia in the coastal zone is similar to open waters and information on the spatial extent of hypoxia in the coastal zone are scarce. Sediment records in the depositional bottoms of the coastal zone may record land-use changes and the increases in nutrient inputs better than the low accumulation rate sediments in open sea sediments, although studies to test this hypothesis do not exist.

Water Quality Records of Recent Hypoxia

Water column measurements of dissolved oxygen concentrations began at the turn of the last century (ca. 1900) with more regularly spaced measurements commencing in the 1960s (*21*). Assessments of oxygen trends were dominated by linear regression analysis to determine the rate of the long-term declines in oxygen. More recently, the volume and bottom area affected by hypoxia have been the metrics used to examine long-term variations. The quality of these metrics is dependent on the number and spatial coverage of observations, which has improved since the 1960s. Extensive anoxia in the Baltic Sea is reported as "negative oxygen," which is computed from the amount of oxygen equivalent to oxidize the hydrogen sulfide present in the water (*7*).

The area of bottom covered by hypoxic water in the autumn and at the maximum seasonal extent averaged ca. 49,000 km^2 over the time period 1961−2000 (Figure 2). The smallest hypoxic area of 12,000 km^2 occurred in 1993 during the peak of the "stagnation period" when saltwater inflows were at their minimum, and the peak hypoxic area occurred in 1971 with 70,000 km^2 (Figure 2) following large saltwater inflows in preceding years (*22*). While major saltwater inflows are well-known to displace and renew the deep water oxygen supplies (*23*), less well appreciated is the fact that they also strengthen stratification and inhibit subsequent ventilation, and thereby increase the areas where oxygen can become depleted (*22, 24*). In modern times most of the deep basins are continuously hypoxic including the Gotland Deep, Landsort Deep, northwest Baltic Proper, and Gdansk Deep (Figure 3). During years with large areas of hypoxia, low oxygen zones migrate higher up into the water column, and the individual basins become connected to form one large hypoxic area.

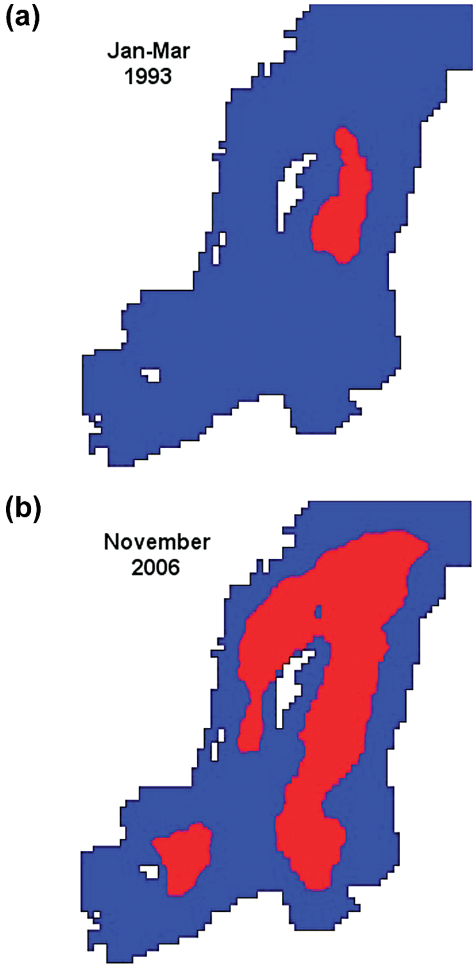

FIGURE 3. Location covered by hypoxic waters containing less than 2 mL L^{-1} dissolved oxygen. (A) During its minimum area in 1993 covering 11,050 km^2 of bottom and (B) in 2006 covering 67,700 km^2 of bottom.

The deep water in the Gulf of Finland originates near the halocline in the Baltic Proper. Thus, a strong and shallow halocline in the Baltic proper induces a stronger stratification in the Gulf of Finland. Because the volume of water under the halocline in the Gulf of Finland is small and primary production is high, oxygen is rapidly depleted below the halocline (*25*). The opposite applies when a weak and deep halocline in the Baltic Proper induces weak stratification and the extent of hypoxia is reduced. Observed trends in hypoxia in modern times in the Gulf of Finland demonstrate that hypoxia is related to variations in large salt water inflows to the Baltic, with less stratification and less hypoxia occurring during "stagnation periods" when major saltwater inflows are reduced.

Much anecdotal and qualitative evidence exists about hypoxia in various reaches of the Baltic Sea. A more thorough quantification that would summarize such information annually for specific areas would facilitate the comparison in space and time of the spread of hypoxia and would make it possible to more rigorously evaluate its controlling

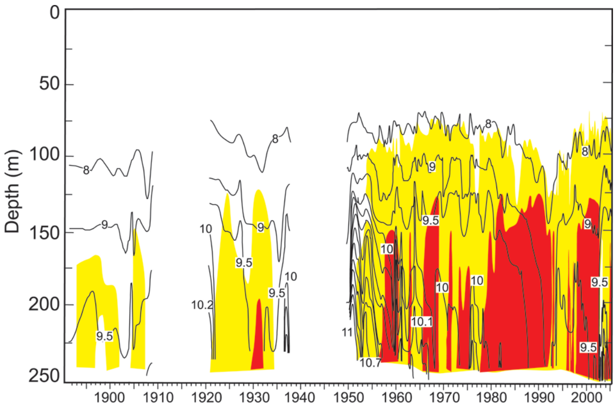

FIGURE 4. Isolines of density (subtracted by 1000, in kg m^{-3}) from hydrographic station BY15 in the Eastern Gotland basin. Yellow areas indicate hypoxic waters (<2 mL L^{-1}) and red areas indicate anoxic waters (<0 mL L^{-1}).

variables. Metrics that could be applied are those previously developed for lakes and reservoirs, such as the anoxic and hypoxic factors (*26*).

Physical Constraints

Physical processes, which control stratification and the renewal of oxygen in bottom waters, are important constraints on the formation and maintenance of hypoxia. In the enclosed basin of the Baltic Sea, oxygen supply is dominated by intermittently occurring water renewal and through vertical turbulent mixing (*27*). The flux of oxygen mediated by mixing is dependent on the vertical gradients of oxygen and density, and the mechanical energy supply. The oxygen supply by vertical mixing tends to increase with time after renewal of bottom waters with saltwater inflow as both density and oxygen concentrations decrease. More importantly, the probability for ventilation by advective water renewal increases as density decreases (*28*). Thus, there is a coupling between deep water mixing intensity and renewal frequency (*29*), where increased mixing due to stronger winds or weakened stratification promote more frequent lateral exchanges and is particularly evident for the upper deep waters (80−125 m).

The inflows of saline water across the sills in the Danish Straits are in part forced by regional winds and are, therefore, quite variable (*27*). However, the inflowing saline water is buffered in the Arkona Basin from which there is a near continuous flow of saline water into the deep waters of the Baltic Proper (*29, 30*). On average the flow from the Arkona Basin into the Baltic Proper has a salinity of about 14, ranging between 12 and 16 (*29*). Assuming a 3-fold mixing with surface water of a salinity of 7.5 during descent, we find that ventilation of Baltic Proper deep water predominantly occurs at salinities between 9 and 10.5, corresponding approximately to a density of 7.2−8.4 kg m^{-3}. Variations are expected from this order of magnitude estimate, but its general validity is evident in Figure 4. The upper bound of hypoxia coincides reasonably well with the 8 kg m^{-3} isopycnal suggesting good ventilation down to this depth. In periods with a larger than normal freshwater supply, the salinity decreases first in the inflowing water and later in the Baltic, which causes some deviations between the depths of the hypoxia isopleth and the 8 kg m^{-3} isopycnal. Thus, the upper limit of hypoxia is primarily determined by the stratification in the Baltic Proper. If the stratification is weak the dominating denser water inflows will reach relatively deep keeping the upper deep water well ventilated and oxic, as occurred in the early 1990s (Figure 4). However, if stratification is strong the inflows generally are not dense enough to penetrate through the halocline and hypoxia reaches its maximum extent, for example, as seen after 2000.

Strong stratification follows from a series of deep reaching high salinity water inflows, after which weak stratification follows. Paradoxically, the lack of complete deep water renewal will eventually lead to better oxygen conditions higher in the water column (*22, 24*). It is important to recognize that the volume and area of the deep basins below 150 m depth is comparably small. Increasing the vertical extension of hypoxia from 150 to 125 m approximately triples the volume of hypoxic water. If the hypoxic water mass extends up to 70 m, as happened during the mid-2000s, the hypoxic volume increases thirteen times and hypoxic bottom area increases ten times. Variations between strong and weak stratification occur due to the time-scale of vertical mixing that reduces density and creates variations in the salinity and the magnitude of the inflows. Strong stratification was present not only in the 2000s, but also in the 1960s, and a weak stratification period occurred in the late 1920s to early 1930s (Figure 4).

Although the principles of the physical control of hypoxia are known, there are still many unresolved physical processes related to the ventilation of the halocline and of the deep water (*28*). The dynamics of saltwater plumes (pathways, mixing, and the climatologically mean saltwater flows) after small- and medium-strength inflows are not well understood because such events are difficult to observe. In addition to large-scale gravity-driven dense bottom flows that renew the deepest layers in the Baltic proper, meso-scale cyclonic eddies appear to contribute significantly to the ventilation of the halocline. These eddies are eroded laterally by intrusions. As with other mixing processes the driving mechanisms of that erosion are not well understood.

Autotrophic Carbon Production and Sedimentation Dynamics

The amount of carbon delivered to the bottom waters of the Baltic Sea is another important control mechanism of oxygen consumption. The main periods of new primary production are the spring bloom and late summer bloom. The former consists of cold-water diatoms and dinoflagellates and the latter consists of nitrogen-fixing cyanobacteria (*31*). As nutrient inputs and concentrations change, the ratios between nitrogen and phosphorus change. The phytoplankton spring bloom is considered to be nitrogen limited (*32*); however, previously phosphorus was also exhausted to very low levels during spring. Some of the first observations on excess phosphorus remaining after the spring bloom were made in the mid-1980s (*33*), and has been a recurring phenomenon. The growth of diazotrophic cyanobacteria is considered to be phosphorus limited, and a considerable share of their phosphorus requirement arrives from the phosphorus remaining after the spring bloom (*34*).

The problem in estimating the effect of changing phytoplankton succession on benthic oxygen dynamics through sedimentation of organic material arises from our limited knowledge of the factors affecting settling. Sedimentation of organic matter in the Gulf of Finland during the spring bloom varied considerably between 65 and 31% of annual production in 1988 and 1992, respectively (*35*). The variability may be caused by differences in phytoplankton composition, specifically the proportion of dissolved silicate limited cyst-forming diatoms (*36*) or the ratio of dinoflagellates to diatoms (*35*). Knowledge of the phytoplankton community composition of the spring bloom remains limited.

The sedimentation of organic carbon during summer and autumn is also variable. The highest settling rates observed in late summer in the Gotland Deep were due to a large percentage of the annual proportion of N_2-fixing cyanobacteria (up to 50% of total settled nitrogen) reaching the bottom (*37*). High settling rates have also been observed in late summer from the Gulf of Finland with 65% of net primary productivity settling through the water column (*35*). The proportion of settling organic material from new production, the characteristics of the phytoplankton composition in the water column versus what settles, and the effects of nutrients on phytoplankton production, and thus sedimentation are important avenues for further research. Lastly, the importance of other sources of organic matter input remains unquantified. For example, chemoautotrophic production in deep waters fueled by reduced sulfur bacteria can support an active microbial food web in anoxic bottom waters (*38*). This possibility for deep-water heterotrophic carbon fixation needs to be evaluated for the Baltic Sea. In addition, increases in dissolved organic matter inputs (*39*), the so-called brownification of waters, and their impact on carbon inputs are unknown.

Biogeochemical Effects of Hypoxia on P

Phosphorus (P) availability for primary producers is determined by variations in terrestrial and marine P inputs, the recycling efficiency within the system, the sinks via outflow to the North Sea, and permanent burial in the sediments. Bottom water hypoxia typically leads to enhanced regeneration of P from aquatic sediments (*4, 40*) and thus an enhanced recycling of P in the system.

The biogeochemical cycling of P in the Baltic Sea has been quantified on many spatial scales. For example, Conley et al. (*22*) showed that interannual changes in dissolved inorganic phosphate (DIP) pools in the Baltic proper were positively correlated to changes in sediment area covered by hypoxic water. The changes in DIP, which ranged up to 112 kt P y^{-1}, were attributed to the release of P bound to Fe-oxyhydroxides upon the transition from oxic to hypoxic conditions, with P returning to the sediments during oxic conditions. Little is known, however, concerning the role of sediments as a permanent sink for P in the Baltic Sea, the processes that control this burial, and their modulation due to hypoxia. In a recent budget calculation for 1991–1999, Savchuk (*41*) estimated the net sediment P burial to be ca. 20 kt P y^{-1}, with all the basins, except the Baltic Proper and the Gulf of Riga, retaining more P than they received from external sources. This rate of P burial is comparable in magnitude to the net outflow through the Danish Straits, which is estimated at ca. 17 kt P y^{-1} (*41*). Thus, changes in net burial of P with hypoxia could significantly alter the P availability in the water column on decadal time scales.

On the basis of studies in other brackish and marine basins, permanent P burial is expected to occur largely in the form of organic P and calcium–phosphate (Ca–P) minerals. The Ca–P minerals can form in situ ("authigenic Ca–P") dispersed in the sediment (*42*), but may also consist of the remains of fish hard parts ("biogenic Ca–P"). The burial of both Ca–P forms and organic P is affected by bottom water redox conditions, with increased hypoxia typically leading to decreased formation of authigenic Ca–P, decreased burial of organic P, and increased preservation of biogenic Ca–P (*43*). The redox control of authigenic Ca–P formation is linked to macrofaunal activity, because sediment mixing typically drives the build-up of sufficiently high pore water phosphate levels to allow authigenic P formation (*44*). The mechanisms responsible for redox-dependent biogenic Ca–P and organic P burial remain incompletely understood.

Both organic P and Ca–P are important components of surface sediments (0–2 cm) in the Baltic proper (*44*) and Fe-oxide bound P is abundant in the surface sediment at sites overlain by oxic bottom waters. Because organic P and authigenic Ca–P are probably the major current sinks for P, increased expansion of the hypoxic area in the Baltic may significantly reduce the current P burial sink and enhance the pool of easily mobilized P.

Biogeochemical Effects of Hypoxia on N

Nitrogen (N) transforming processes are strongly influenced by oxygen concentration. As nitrogen removal (denitrification and anammox) is dependent on NO_2^- and NO_3^- produced in oxic conditions by nitrification, this process is of key importance in enabling nitrogen removal from the basins. No data exist on nitrification in the sediments of the Baltic Sea, but denitrification in depositional sediments has been calculated to remove about 23% and 31% of the annual nitrogen input to the Bothnian Bay and Bothnian Sea, respectively (*46*), and about 30% of the annual load in the Gulf of Finland (*47*). During seasonal hypoxia, coupled nitrification–denitrification rates can be restored to their previous levels when oxygen returns (*48*). By contrast, denitrification rates in highly reducing sediments remain low for long periods following reoxygenation (*49*).

Mass-balance calculations show that 751 kt of N is removed annually from the Baltic Proper by the combined action of N_2 production and sediment burial (*41*), and isotopic data suggest that 855 kt of N is denitrified in just the southern Baltic Sea (*50*). Direct rate measurements in relatively coarse grain size sediments are needed to verify the mass-balance estimates. Results from other studies suggest that these sediments can be extremely active through intense wave-induced ventilation (*51*). Anammox, which also removes nitrogen, has been found in the sediments of the Gulf of Finland, where it contributed ca. 10–15% to the total N_2 production (*48*). It has been suggested that a considerable amount of nitrogen in the Baltic Sea enters neither the denitrification nor anammox pathway, but rather is transformed through dissimilatory nitrate reduction to ammonium (DNRA) (*49*). Unlike denitrification and anammox, DNRA does not remove reactive N from the ecosystem, but stores it as elevated ammonium concentrations in hypoxic waters.

A significant negative correlation has been found between the amount of dissolved inorganic nitrogen (DIN = nitrite, nitrate, ammonium) and the volume of hypoxic water in the Baltic Proper, the Gulf of Finland, and the Gulf of Riga (*31*), suggesting enhanced nitrogen removal during expanded hypoxia. This result challenges the conventional belief that denitrification is reduced when oxygen concentrations are low (*5*). In addition, there is a recent observation that large losses of N resulting from denitrification and annamox occur in the water column of hypoxic zones in the open ocean (*52*). Nitrification in the water column has so far only been studied at three deep stations in the Baltic Proper (*53*). Nitrification was found to be highest at or below the halocline, indicating combined control by oxygen and ammonium availability. Since the volume of the water layer in which nitrification is possible fluctuates along these two variables, it justifies quantification. At the highest observed nitrification rates about the same amount of ammonium is oxidized in 1 m^3 of water as in 1 m^2 of oxic seafloor. The produced NO_2^- and NO_3^- are probably quickly consumed in denitrification and anammox in the hypoxic and anoxic water layers below.

Water column denitrification occurs at the interface between anoxic, stagnant deep water and overlying oxic water in the central Baltic Proper (*54*), however, denitrification was measured using the acetylene blockage method, which is now known to have serious flaws. A recent study using state-of-the-art stable isotope techniques failed to detect any heterotrophic denitrification in the Gotland Deep suboxic ($<10\ \mu M\ O_2$), sulfide-free water (*55*). The potential for N_2 production was found in the sulfide-containing deeper layer, making it very likely a chemolithotrophic rather than heterotrophic process (*55*). In the same study the potential for anammox, as well as the presence of bacteria capable of anammox, was observed in the water column of the Baltic Sea. Which process prevails seems to depend on the dynamic between nutrient and O_2 concentrations at and below the redoxcline that constitutes an efficient wall for vertical diffusive exchange of DIN. Below the redoxcline there is an upward flux of ammonium, and above there is a downward flux of nitrate; the sum of these fluxes is the formation of N_2 through denitrification and anammox. Advective processes, such as deep-water renewal, complicate this simple picture, but we presume that a large part of the nitrogen remineralized below the redoxcline is lost to N_2 formation at the redoxcline. This implies that all DIN available to production needs to be remineralized above the redoxcline (or externally supplied) and that a redoxcline high in the water column implies low DIN concentrations. Unfortunately, the scarce data do not allow extrapolation to larger water masses, but they clearly show a plausible mechanism for generating the observed dependency between hypoxic water volume and enhanced nitrogen removal.

Denitrification and anammox form major sinks for N (*41, 50, 56*) and these losses occur both in the sediments and the water column. However, the relative importance of fluctuating hypoxia and corresponding changes in denitrification and anammox, and the key process of nitrification remain open. Multiple site-specific measurements are lacking, which hampers both the empirical quantification of N removal processes spatially and temporally, and the development and validation of biogeochemical models.

Biological Effects of Hypoxia in the Baltic Sea

Benthic communities in the Baltic Sea are naturally constrained by strong salinity gradients that limit their distribution and diversity. In addition, benthic communities have been subjected to increasing anthropogenic nutrient inputs, which have transformed the Baltic Sea from an oligotrophic, clearwater sea into a eutrophic water body (*57*). Perhaps the strongest factor influencing the biodiversity of benthic communities is the increased prevalence of oxygen-depleted bottom water, which has resulted in habitat loss followed by the elimination of benthic macrofauna over vast areas and severely disrupted benthic food webs (*58*).

The formation of near-bottom hypoxia results in increasingly impoverished communities with macrobenthic responses often resembling the broad-scale successional pathways described in models of benthic disturbance and recovery (*59*). In the Baltic Sea the separation between normoxic and moderately hypoxic water masses and hypoxic or anoxic waters creates a temporal and spatial mosaic of hypoxic stress to benthic fauna (*60*). Macrobenthic communities in deeper water are never fully developed due to low oxygen concentrations and are characterized by small shallow-dwelling species due to transient hypoxia. Macrobenthic communities in deeper waters are severely degraded and below a 40-year average for the entire Baltic Sea (*61*). Hypoxia often eliminates large deep-burrowing, actively bioturbating species because their long generation times preclude development of viable populations (*62*). Moreover, even when species are not entirely lost, they may become functionally extinct due to their low abundances and subsequent recovery may never reach fully mature successional stages.

Healthy benthic communities provide important ecosystem services, including food for higher trophic levels, and they facilitate the mineralization of settling organic matter. These functions are compromised when hypoxia results in reduced abundance and diversity. Repeated hypoxic stress results in short-lived and small-sized benthic animals becoming more common in the diet of benthivorous fish, such as cod, plaice, and dab in the southeastern Kattegat, and could ultimately affect fish assemblages (*63*). Deep-burrowing organisms have a higher capacity for deeper vertical transport of organic matter into the sediment, resulting in a delayed remineralization of organic matter and oxygen consumption (*64*). In contrast, small surface-dwelling taxa with high population turnover rates facilitate a rapid remineralization with immediate oxygen consumption as a result.

Benthic fauna also play an important role in ecosystem resistance to the formation of hypoxia. Bioturbation enhances the vertical penetration of oxygen, which alters the rates and pathways of benthic mineralization and nutrient cycling, and is strongly influenced by species composition and abundance (*65, 66*). The increased surface area of oxic−anoxic interfaces and the ammonia excretion by bioturbators facilitates coupled nitrification−denitrification processes. The sediment P-retention capacity depends on ventilation and redox conditions, which are modified by bioturbation. In hypoxic conditions benthic uptake and processing of organic matter may shift from macrofauna to meiofauna or bacteria, which are not as efficient at processing organic matter (*67*). Thus, a reduction of bioturbation may decrease the natural purification capacity and increase the internal nutrient loading of Baltic sediments (*66*).

Hypoxia results in the loss of habitats, changes in biodiversity, associated with the removal of functionally important species. In a Baltic-wide perspective, these disturbances reduce the connectivity of populations and communities, which impairs recovery potential and threatens ecosystem resilience (*60*). Recovery depends on an available pool of mobile colonists. However, we lack an understanding of potential colonist sources, quantitative estimates on mobility and the connectivity of populations, and the effects on recruitment from the increasing volume and area of hypoxia in the Baltic.

Climate and Nutrient Inputs As Drivers

Climate is an important driver of hypoxia in the Baltic Sea, and its variability influences many of the physical processes that create conditions conducive to the occurrence of hypoxia (*68*). During warm periods such as the Holocene Thermal Optimum (HTO) or the Medieval Warm Period (MWP), the Baltic experienced long periods of hypoxia (*6*). However, during the HTO salinity was also at its Holocene maximum due to a larger opening through the Danish Straits (*69*), which also strongly influenced stratification and mixing. On shorter time scales, for example during the last three decades of the 20th century, the North Atlantic Oscillation (NAO) was in a positive phase with mild winters, humid and strong westerly winds creating conditions conducive to the formation of hypoxia in fjords along the Swedish west coast with significant shifts in benthic communities (*70, 71*). The influence of these short-term changes in the NAO on hypoxia is not clear, although NAO may influence biological communities in the Baltic (*72*). However, the impact of humans on the environment have occurred on the same time-scales as climate change, making it difficult to clearly separate between anthropogenic forcing and natural changes.

That nutrients are a major driver of hypoxia is well established (*3*). In addition, it is known from lake records in Europe that cultural eutrophication has a long history dating back to the development and expansion of agriculture with increases in phosphorus concentrations and associated eutrophication of lakes (*18, 19*). Hypoxia postdating ca. 2000 cal. yr BP correlates with population growth and large-scale changes in land use that occurred in much of the Baltic Sea watershed (*6*). The deposition of laminated sediments in the

Baltic during the last ca. 100 years coincides with the start of the industrial revolution in northwestern Europe when human impact dramatically increased in the drainage area. Investigations have revealed significant changes in diatom assemblages in the Baltic Sea ca. AD 1850−1900 attributed to eutrophication (*73*). Most recently, the widespread expansion of laminated sediments in the Baltic coincides with the industrialization of agriculture and widespread use of fertilizers (*8*).

A major scientific question is when did anthropogenic influence start to significantly affect the Baltic Sea environment? Österblom et al. (*57*) suggested that a large salt water inflow and subsequent stagnation period that occurred in the early 1950s triggered the positive feedback between hypoxia and release of sediment phosphorus that had previously accumulated in the deep basins, and enhanced eutrophication (*31*). It is, however, difficult to unravel the changes in climate and the influence of human activities that occurred simultaneously. It is also difficult to differentiate between the relative importance of the drivers for the conditions during the early Littorina Sea with changes in the morphology (decreasing depths of the Baltic basin from uplift, yet increases in the depth of the sills governing saltwater input) from the variations in climate. More research is needed to explore the driving mechanisms for hypoxia in the Baltic Sea.

It is likely that the interaction between nutrients and climate has enhanced the conditions for hypoxia to occur. The changes in biogeochemical cycling and loss of benthic communities during hypoxia may stimulate further eutrophication in a self-sustaining way and support the persistence of hypoxia in the Baltic Sea (*31, 64*). This change in functioning of the system can be considered as a regime shift (*64*), with perhaps several regime shifts occurring due to eutrophication, overfishing, and climate interactions (*57*).

Future Perspectives

Reductions in hypoxia will not occur until nutrient loads are reduced (*74*). Historically, the countries within the Baltic Sea watershed have made pledges to reduce nutrient loads according to recommendations and targets set through the Helsinki Commission (*75*). Although some point source reductions have occurred creating better local conditions (*10*), there have been neither appreciable reductions in nutrient loads nor improvements in eutrophication at the scale of the Baltic Sea. A new Baltic Sea Action Plan with country specific reductions has renewed the efforts to make nutrient reductions (*76*).

The current eutrophication models demonstrate that significant reductions must occur in both N and P loading for conditions to improve (*74, 77*). Phosphorus loads could be reduced through better wastewater treatment, a phosphorus ban on detergents in the watershed, and better manure management. Nitrogen reductions must include changes in agriculture practices and atmospheric deposition. While these reductions are similar to those that have been recommended in other coastal marine ecosystems suffering from nutrient-driven eutrophication (*3*), they are difficult to achieve due to the economic investment required and the difficulty to implement solutions through legislation.

It is not enough to just understand the response of the ecosystem to nutrient and climate forcing. We also need to quantify the effects of nutrient load reductions for different scenarios (*78, 79*). Even if nutrient source discharges on land are stabilized at present levels, nutrient loading will continue to increase (*80*) due to the slow transport and reversible mass transfer processes in the inland subsurface water system (soil, groundwater, stream and lake sediments), where much of the anthropogenic nutrient source inputs still reside (*78*). To decrease future overall nutrient loading to the Baltic Sea a much larger effort than anticipated may be necessary to achieve reductions in diffuse source loading (*78*). Projected population changes and increased meat production are expected to increase nutrient loading even with concurrent nutrient reduction strategies (*81*). To improve future prospects, it is therefore important to eliminate the gaps in our understanding so that the uncertainties in determining future nutrient loading to the Baltic Sea are diminished.

If and when large-scale remediation measures are implemented, we need to be able to quantify their potential effects. Experience from remediation in freshwaters demonstrates that no significant improvements in oxygen conditions will occur without concurrent nutrient reductions. Additional measures for nutrient load abatement should be considered such as constructed wetlands, reactive barriers, and other innovative measures for achieving a decrease in future nutrient loading. In light of global warming and increased anthropogenic pressures in the Baltic Sea region, it is essential to obtain a comprehensive view of the timing, extent, and mechanisms of hypoxia and to include this knowledge in the discussion of the present state and the future of the Baltic Sea.

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