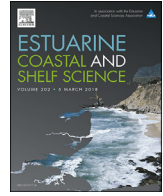




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# Nitrification and the ammonia-oxidizing communities in the central Baltic Sea water column

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## ABSTRACT

The redoxclines that form between the oxic and anoxic water layers in the central Baltic Sea are sites of intensive nitrogen cycling. To gain better understanding of nitrification, we measured the biogeochemical properties along with potential nitrification rates and analyzed the assemblages of ammonia-oxidizing bacteria and archaea using functional gene microarrays. To estimate nitrification in the entire water column, we constructed a regression model for the nitrification rates and applied it to the conditions prevailing in the area in 2008–2012. The highest ammonia oxidation rates were found in a thin layer at the top of the redoxcline and the rates quickly decreased below detection limit when oxygen was exhausted. This is probably because extensive suboxic layers, which are known to harbor pelagic nitrification, are formed only for short periods after inflows in the Baltic Sea. The nitrification rates were some of the highest measured in the water columns, but the thickness of the layer where conditions were favorable for nitrification, was very small and it remained fairly stable between years. However, the depth of the nitrification layer varied substantially between years, particularly in the eastern Gotland Basin (EGB) due to turbulence in the water column. The ammonia oxidizer communities clustered differently between the eastern and western Gotland Basin (WGB) and the composition of ammonia-oxidizing assemblages correlated with the environmental variables. The ammonia oxidizer community composition was more even in the EGB, which may be related to physical instability of the redoxcline that does not allow predominance of a single archetype, whereas in the WGB, where the position of the redoxcline is more constant, the ammonia-oxidizing community was less even. Overall the ammonia-oxidizing communities in the Baltic Sea redoxclines were very evenly distributed compared to other marine environments where microarrays have been applied previously.

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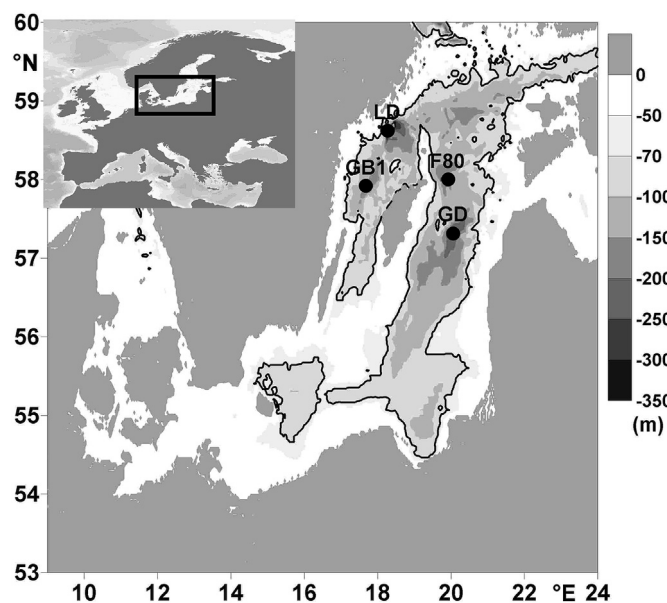
## 1. Introduction

The Baltic Sea is one of the largest brackish water basins (415 200 km<sup>2</sup>) in the world and subject to severe eutrophication (HELCOM, 2009). The high nutrient load from the drainage basin and salinity stratification caused by positive freshwater balance have led to formation of widespread anoxic areas in the deep

basins, which are separated by sills that prevent an even flow of water to the bottom areas. The widest anoxic basin in the central Baltic Sea is the Gotland Deep and the deepest the Landsort Deep (Fig. 1). These basins are characterized by suboxic transition zones, redoxclines, which form in the area between the oxygenated surface and the euxinic bottom water. Unlike in many other oxygen deficient zones (ODZ), the redoxcline intermittently disappears in the central Baltic Sea due to inflow of saline ( $\geq 17$ ) and oxygen rich water from the North Sea through the Danish Straits. During such events, termed as Major Baltic Inflows (MBI), the sulfidic water in the bottom of the deepest basins is replenished with oxygen (O<sub>2</sub>) and the redoxcline disappears. MBIs occur mainly during winter and since the mid-1970s the frequency of MBIs has decreased to almost decadal, which has led to a long-term stagnation and made

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**Fig. 1.** Topography of the Baltic Proper and the position of the sampling stations (LD, GB1, GD, and F80). GD is located in the Eastern Gotland Basin, LD and GB1 in the Western Gotland Basin and F80 in the Farö deep. The full line marks the 70 m depth contour, which encloses the area of hypoxic water.

anoxia a nearly permanent feature of the central Baltic Sea (Schinke and Matthäus, 1998). In addition to MBLs, there is also smaller scale mixing in the water column which occurs during stagnation. The drivers for the small scale mixing are not well understood, but they are in general a result of complex hydrodynamic processes such as upwelling, boundary mixing, Kelvin-Helmholtz and other shear instabilities and internal wave breakings (Zhurbas and Paka, 1999; Kuzmina et al., 2005; Reissmann et al., 2009; van der Lee and Umlauf, 2011).

ODZs have received a lot of interest because they are nitrogen cycling hotspots. In the Baltic Sea, a substantial portion of the nitrogen (N) entering the area is converted from reactive forms to dinitrogen gas ( $N_2$ ) via pelagic denitrification (Rönnner, 1983; Rönnner and Sörensson, 1985; Brettar and Rheinheimer, 1991; Hannig et al., 2007; Hietanen et al., 2012; Dalsgaard et al., 2013; Bonaglia et al., 2016). Globally, 30–50% of the total nitrogen (N) loss in the oceans occurs in the ODZs (Codispoti et al., 2001). Nitrification, which supplies the electron acceptor for denitrification, has also been measured at high rates in the ODZs. In the Baltic Sea Enoksson (1986) found potential nitrification up to  $280 \text{ nmol N L}^{-1} \text{ d}^{-1}$  in a station south-west from the island of Gotland, with the highest rates occurring below the halocline. However, the rate estimate may be hindered by bottle effects (i.e. senescence of cell material, which may increase the availability of ammonium,  $(\text{NH}_4^+)$ ) because the incubations lasted considerably longer than measurements done with modern, more sensitive isotopic ratio mass spectrometers (IRMS). Bauer (2003) measured potential nitrification rates of  $202 \text{ nmol N L}^{-1} \text{ d}^{-1}$  in the Gotland Deep and in more recent measurements, Hietanen et al. (2012) found potential nitrification rates of up to  $160 \text{ nmol N L}^{-1} \text{ d}^{-1}$  in the Landsort Deep and Berg et al. (2015)  $130 \text{ nmol N L}^{-1} \text{ d}^{-1}$  in the Gotland Deep. Rates this high in marine water columns have been detected previously only in the periodically hypoxic Bornholm Deep in the southern Baltic Sea ( $883.8 \text{ nmol N L}^{-1} \text{ d}^{-1}$ ; Berg et al., 2015), in the Peruvian oxygen minimum zone ( $144 \text{ nmol N L}^{-1} \text{ d}^{-1}$ ; Lam et al., 2009), and in the Saanich Inlet ( $319 \text{ nmol N L}^{-1} \text{ d}^{-1}$ ; Grundle and Juniper, 2011).

Both archaeal and bacterial ammonia oxidizers can be active in

ODZs. In the early 2000s, when the existence of ammonia-oxidizing archaea (AOA) was unknown, the ammonia-oxidizing community in the central Baltic Sea water column was suggested to be composed of  $\beta$ -proteobacteria (Bauer, 2003). Later on when AOA were discovered, the ammonia-oxidizing community in the central Baltic Sea was suggested to consist mainly of one thaumarchaeotal subcluster closely related to *Candidatus Nitrosopumilus maritimus* (Labrenz et al., 2010; Berg et al., 2015). In the northern Baltic Sea sediments, the ammonia oxidizer communities had surprisingly low diversity and were dominated by organisms with gene signatures unique to the sampling area (Vetterli et al., 2016). Hence, the ammonia-oxidizing communities in the Baltic Sea appear to have a low diversity and harbor unique species, but the overall community composition and its controlling factors are still largely unknown.

The diversity and community composition of ammonia oxidizers can be investigated using functional gene microarrays that are designed to specifically target the ammonia-oxidizing bacteria (AOB) and AOA, using sequences of their *amoA* genes, which encode ammonia monooxygenase subunit A. Since ammonia oxidizers are metabolically restrained, there is very little divergence of essential genes and consequently the diversity of ammonia oxidizers is relatively limited. All AOB and AOA sequences known at the time of these experiments (2010–2011), both cultivated and environmental, could be targeted with this method. Each microarray contains a set of archetype probes that are selected from the entire database of homologous sequences, using an algorithm (Bulow et al., 2008) that is similar to that used to select operational taxonomic units (OTUs) (e.g. program for Defining Operational Taxonomic Units and Estimating Species Richness (DOTUR); Schloss and Handelsman, 2005). Thus, each archetype represents all sequences within 85% identity with the probe sequence, and the comparisons between the samples are made on the basis of relative rather than absolute sequence identity because the intensity of the hybridization signal cannot be interpreted quantitatively (Ward et al., 2007).

We determined the spatial variation in the ammonia-oxidizing communities at three sites in the central Baltic Sea redoxclines, using functional microarrays, to investigate how ammonia oxidizer communities are composed in dynamic redoxcline where salinity and  $O_2$  concentration in the nitrification layer change frequently. We also measured the nitrification rates at four sites, created a regression model for nitrification and applied it to the high resolution monitoring data that was in the IOW molecular database to estimate the spatial and temporal variation of the pelagic nitrification. Thereafter, we tested whether composition of the ammonia-oxidizing community correlates with the potential nitrification rates, environmental conditions prevailing in the sampled areas and depths, and the differences in the hydrodynamic patterns between the sampling sites. Finally, since there is interest on the pelagic denitrification and anammox due to their capability to mitigate the effects of the excess N loading, we estimated how efficiently nitrification supplies electron acceptors for the  $N_2$  producing processes in this system.

## 2. Materials and methods

### 2.1. Sample collection

The samples for the nitrification rate measurements were collected from four stations during three cruises 2010–2011 (Table 1). Station LD is located at the western Gotland Basin (WGB), station GD at the Landsort Deep, station GD at them Eastern Gotland Basin (EGB), and station F80 at the Fårö Deep (Fig. 1). The microarray samples were collected in 2010 from GB1, GD, and LD (Table 1). At each of the sampling stations, the salinity, temperature, and  $O_2$  profiles were first determined, using a CTD

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