



Ideas and perspectives: The Baltic Sea nitrogen cycle in the 21st century – new findings, uncertainties, and future changes

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Abstract. The Baltic Sea, which is surrounded by countries with intensive industrial and agricultural activities, is
 25 affected by an excess of nitrogen causing large-scale eutrophication. Thus, the nitrogen cycle of the Baltic Sea has
 received considerable attention over the past five decades mainly due to the ongoing expansion of oxygen-free
 zones (anoxia), which was identified as a major threat already in the 1970s. Measures to reduce eutrophication
 have resulted in a decrease of nitrogen inputs since the 1980s, but the environmental status of the Baltic Sea is still
 far from good. The nitrogen cycle of the Baltic Sea is driven by various microbial processes, which occur to
 30 varying extent in both the water column and sediments under oxic and anoxic conditions. However, the overall
 nitrogen budget of the Baltic Sea is mainly controlled by microbial nitrogen fixation and denitrification in
 combination with riverine input, aerosol deposition, burial in sediments, and exchange with the North Sea. Other
 contributors to the nitrogen budget are minor, such as nitrous oxide emissions, or still uncertain, such as submarine
 groundwater discharge. In general, nitrogen flux estimates are associated with a high degree of uncertainties
 35 largely due to inadequate seasonal and spatial coverage of most measurements. To address the existing knowledge
 gaps and to decipher the processes and fluxes of the Baltic Sea's nitrogen cycle in the 21st century, we suggest
 establishing time-series measurements and joint process studies at representative sites in the open and coastal
 Baltic Sea, including the sea-ice covered areas. These studies should combine microbial, molecular, ecological
 and biogeochemical methods across nano- to kilometre scales to obtain a better understanding of the process rates,
 40 their controlling factors and the microbial communities involved. Such results will help to improve physical,
 biogeochemical and ecosystem models and allow us to reduce the uncertainties in projections of the future nitrogen
 cycle of the Baltic Sea which can advance/help management measures for ecosystem restoration.

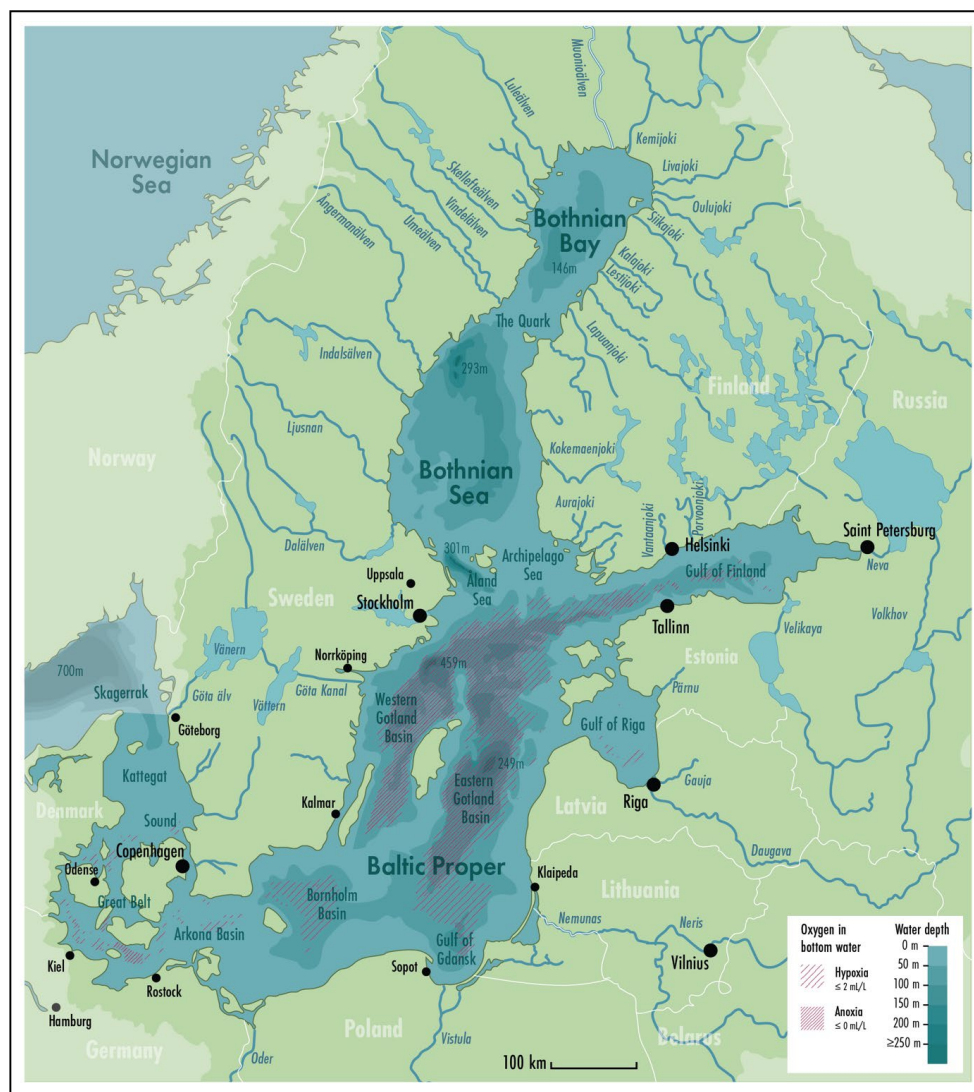


1 Introduction

Nitrogen (N) is an essential element for life. However, at the same time it is a limiting element of biological productivity due to the high energy demand to fix N (= to make it biologically available) from the huge pool of atmospheric N (N_2). In 1913, the first production facility using the Haber-Bosch process (fixation of N_2 to ammonia, NH_3) was commissioned (see e.g., Galloway et al., 2013), which was an important event as it allowed the fixation of N_2 on an industrial scale and resulted in a tremendously enhanced availability of nitrogenous compounds such as fertilizers, explosives, and others (e.g., Erismann et al., 2008). Since the 1950s, the anthropogenic production and release of so-called reactive N (N_r = all species except N_2 and nitrous oxide, N_2O) has strongly increased and led to unprecedented changes of the global N cycle in soils and the atmosphere as well as in freshwater and oceanic environments (e.g., Erismann et al., 2013). In 2011, about a century after the commissioning of the first Haber-Bosch plant, the European Nitrogen Assessment pointed out that the continuous production and excess release of N had resulted in five societal threats: for water quality, air quality, greenhouse balance, terrestrial ecosystems and biodiversity, and soil quality (Sutton et al., 2011).

The Baltic Sea is a shallow marginal sea with a surface area of 412,500 km² and an average water depth of 52 m (Leppäranta and Myrberg, 2009) (Fig. 1). Due to the limited exchange of water with the North Sea and high river discharge, pronounced salinity gradients exist: (i) a horizontal gradient ranging from about 20 in the Kattegat region to 2 in the Bothnian Bay, and (ii) a vertical gradient which causes a strong stratification of the water column separating the well-mixed surface layer from the more saline subsurface and bottom layers (e.g., Lehmann et al., 2022). The strong stratification in combination with seasonal high phytoplankton productivity and subsequent high remineralization is the main reason for quasi permanent anoxic and sulfidic subsurface waters in the deep basins of the Baltic Proper (Fig. 1), which are only ventilated with oxygen-rich North Sea waters during major Baltic Sea inflow events (MBI) (e.g., Mohrholz, 2018). Additionally, during the last decades the Baltic Sea has experienced a multi-stressor situation due to warming, eutrophication, deoxygenation, and other processes (Reckermann et al., 2022; HELCOM/Baltic Earth, 2024), and it has therefore been suggested that the Baltic Sea might serve as a ‘large-scale, real-world analogue for future conditions in other coastal regions’ (Reusch et al., 2018). The Baltic Sea is surrounded by highly-industrialized countries with intensive agricultural activities. Combined with a large catchment area (Fig. 1), the system has been exposed to excessive N_r inputs since around 1950, resulting in severe eutrophication (HELCOM, 2023). Even though nutrient inputs to the Baltic Sea have been declining for decades (e.g., Ehrnsten et al., 2025), 94% of the open Baltic Sea and 83% of the coastal waters were still classified as below good environmental status for eutrophication, threatening societal wellbeing and welfare for the period from 2016 to 2021 (HELCOM, 2023).

In 1974, the Baltic Sea States signed the Convention on the Protection of the Marine Environment of the Baltic Sea Area (i.e. the Helsinki Convention). This was the birth of the Helsinki Commission (HELCOM), which since 1992 has been the spearhead of the advancement of regional actions to improve the environmental status of the Baltic Sea, namely the Baltic Sea Action Plan (BSAP) (HELCOM, 2007; 2021). It is HELCOM’s strategic programme of measures and actions for achieving good environmental status of the Baltic Sea. Indicators are a critical component of the BSAP because they provide a mechanism to address the effectiveness of the measures put in place to reach the goals and objectives of the BSAP. Key indicators related to N can be classified as directly (nutrient inputs), partially (eutrophication effects) or indirectly (biological responses) related to N cycling in the Baltic Sea.



- 85 **Figure 1: Map of the Baltic Sea showing the sub-basins, catchment areas, major rivers, cities and countries. Water depths are indicated in blue (bathymetry from Giese et al., 2020). Hypoxia and anoxia are indicated by light and dark red-shaded areas, respectively (Hansson and Viktorsson, 2025). The locations of the Gotland Deep in the Eastern Gotland Basin and the Landsort Deep in the Western Gotland Basin are indicated by their water depths of 249 m and 459 m, respectively. Please note that the Bothnian Sea and the Bothnian Bay form the Gulf of Bothnia. The Western and Eastern Gotland Basins and the Bornholm Basin form the Baltic Proper.**
- 90 The major N cycle processes in the water column and underlying sediments of the Baltic Sea are shown in Fig. 2 (see also Voss et al., 2024; Kuliński et al., 2022). N sources to the Baltic Sea include microbial N_2 fixation (N_2 to ammonium, NH_4^+), input of N-containing inorganic (e.g., nitrate, NO_3^- and NH_4^+) and organic compounds (dissolved and particulate organic N, DON and PON) via rivers, atmospheric dry and wet deposition of aerosols and submarine groundwater discharge. Sinks of N include microbial denitrification (stepwise reduction of NO_3^- to N_2O and N_2) and anammox (anaerobic ammonium oxidation with nitrite, NO_2^- , to N_2), as well as the burial of organic N in sediments and the net export to the North Sea. Microbial nitrification (stepwise oxidation of NH_3 to
- 95



NO_2^- and NO_3^-), dissimilatory nitrate reduction to ammonium (DNRA), and N transfer through the pelagic and benthic food webs are neither sink nor source, but rather retention processes for N.

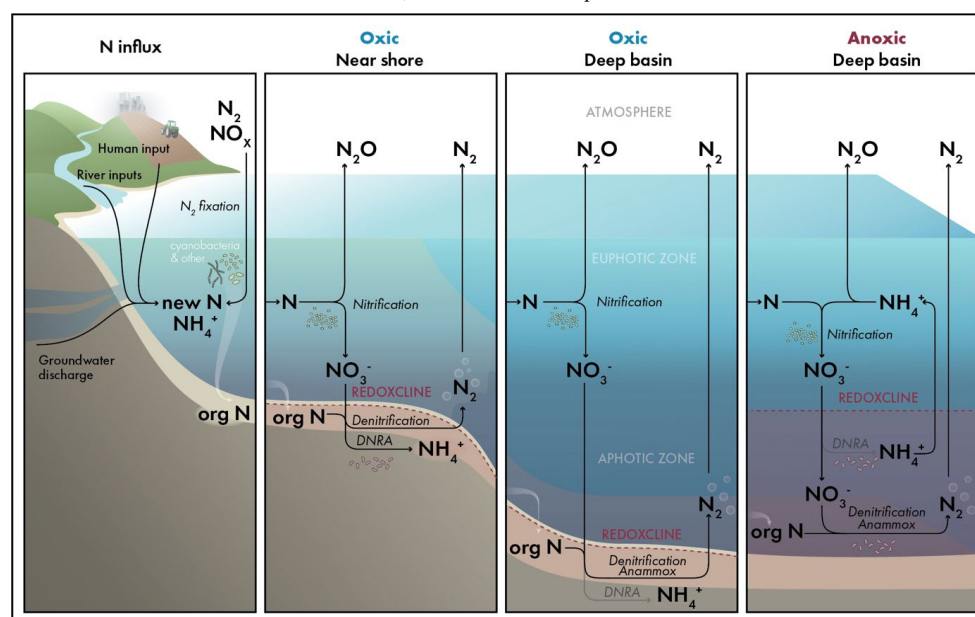


Figure 2: Overview of N inputs (rivers, N_2 fixation, and submarine groundwater discharge) and N cycle processes (anammox, denitrification, DNRA, nitrification) in the Baltic Sea sediments and water column, including (left to right) the N influx from land, the near shore habitats with oxic bottom water conditions, the deep basins with oxic bottom water conditions, and the deep basins with anoxic bottom water conditions. For the sake of simplicity, atmospheric N deposition via aerosols, the recirculation of seawater in the sediments as part of the submarine groundwater discharge, N_2 fixation in both the oxic and the anoxic basin, sedimentary denitrification and sedimentary DNRA in the near shore habitats, org N in the water column, and the N transfer into the food web are not shown.

To assess the N cycle of the Baltic Sea in the 21st century and its potential impacts by rapid changes in environmental conditions, we need to (i) decipher the major N cycle processes and their drivers, and (ii) quantify the N fluxes. To this end, significant advances have been made over the last decades in understanding and quantifying both the N cycle processes and the N budget of the Baltic Sea. An overview of the N trends and budget of the Baltic Sea can be found in Lønborg and Markager (2021) and Savchuk (2018). Kuliński et al. (2022) briefly summarized N processes and budgets in the context of the overall marine biogeochemistry of the Baltic Sea. In this article, we therefore focus on reviewing the advances in understanding the N cycle processes and fluxes in the Baltic Sea since the early 2000s. Based on this, we give an outlook on developments that could open the door for new scientific and methodological approaches, which can help to mitigate the effects of a changing N cycle on Baltic Sea ecosystems and society.

2 Nitrogen sources

2.1 River input

The Baltic Sea catchment ranges from highly agricultural, densely populated and temperate landscapes in the south, to boreal, sparsely populated and alpine landscapes in the north. This leads to large differences in magnitude and composition of riverine N loads to the Baltic Sea. Contrasting examples are the rivers originating in the



mountains of northern Scandinavia versus the rivers in the agricultural landscapes draining into the southern and western Baltic Sea: Only 20-30% of the N load from Sweden to the Gulf of Bothnia is anthropogenic compared to 80% of the N load to the western Baltic (HELCOM, 2022). Interannual variation is substantial primarily due to variations in discharge. Since the N load is much larger in the rivers with a high anthropogenic influence, about 75% of the total riverine N load to the Baltic Sea is estimated to be of anthropogenic origin (HELCOM, 2022). The dominant source for this is agriculture, although point sources such as wastewater treatment plants cannot totally be neglected (HELCOM, 2022). Declines of riverine N loads have been documented in catchments with a high density of agricultural activities in response to measures to reduce the N sources on land, for example in Denmark (e.g., Dessirier et al., 2023; Riemann et al., 2016). While riverine N loads to the Baltic Sea generally decreased over the past decades, trends have weakened or even reversed for several regions with intense agriculture (HELCOM, 2022).

2.2 Atmospheric deposition

The main sources of N compounds that are emitted into the atmosphere are combustion processes and agricultural activities (e.g., Sutton et al., 2011). Combustion processes lead to nitrogen oxide (NO_x = sum of nitric oxide, NO, and nitrogen dioxide, NO_2) emissions and the main sources are transportation, industry, power plants, and residential heating. NH_3 is released by fertilizer use and animal husbandry and to a lower extent by industrial processes and transportation (e.g., Sutton et al., 2011). Both, NO_x and NH_3 are also the most important precursors of nitrogenous aerosols. Atmospheric N chemistry affects the tropospheric ozone cycle and differs strongly between day and night. In addition, NH_3 is the main reaction partner for atmospheric acids like sulfuric acid and nitric acid to form aerosol particles. While aerosol particles mainly undergo wet deposition (e.g., by rain events), dry deposition is the main sink for gaseous species.

The deposition of reduced N (mainly as NH_4^+) shows a seasonal cycle with lowest emissions in winter and highest in summer; while deposition of oxidized N (mainly as NO_3^-) is higher in winter and early spring, and lower in summer (Murray et al., 2022). Agriculture and transport are the main sources of N deposition to the Baltic Sea with agriculture causing 92% of the deposition of reduced N and transport causing 62% of the deposition of oxidised N in 2017 (Gauss et al., 2021). Shipping also contributes large amounts of NO_x accounting for almost 25% to the deposition of oxidized N to the Baltic Sea with the highest contributions in the Baltic Proper (Gauss et al., 2021). Direct atmospheric N deposition of NH_3 to the Baltic Sea may be 5-10 times lower than over land (e.g., Sutton et al., 2011). This is mainly due to high NH_3 emissions from agriculture and enhanced deposition near the source, but also because vegetation increases dry deposition. N deposition over land contributes to the riverine input of N compounds to the Baltic Sea (see section 2.1).

The Baltic Sea experiences atmospheric deposition of oxidized and reduced N compounds with a strong gradient from low deposition in the northeastern Baltic Sea to high deposition in the southwestern Baltic Sea and highest deposition found close to the German and Danish coasts (EMEP, 2023). Germany was the main contributor to atmospheric N deposition to the Baltic Sea in 2017, followed by Poland, Denmark, and Baltic Sea shipping (Gauss et al., 2021). The reason for these different contributions is population size and whether they are located close and/or upwind of the Baltic Sea (Gauss et al., 2021).



2.3 Nitrogen fixation

160 N_2 fixation, in which dissolved N_2 is turned into NH_4^+ by N_2 -fixing (diazotrophic) organisms, increases the overall pool of N_r and thus enhances productivity, which is especially beneficial at low inorganic N to phosphorus (P) ratios. This is commonly the situation in the Baltic Proper during summer (Walve and Larsson, 2007), where diazotrophic filamentous cyanobacteria are well known for forming extensive blooms. The major taxa in surface waters are *Nodularia spumigena*, *Aphanizomenon* spp., and *Dolichospermum* spp. (Fig. 3); ongoing monitoring of

165 their distributions shows basin-specific trends in the Baltic Sea, such as an increase in the Gulf of Bothnia from 1979 to 2017 (Olofsson et al., 2020). This is in agreement with observations of N to P ratios in the Bothnian Sea declining over the recent decades (Andersson et al., 2015; Rolff and Elfving, 2015), thus imposing a source of uncertainty for estimating N_2 fixation in the future Baltic Sea.

For quantification of N_2 fixation rates, there has been a methodological switch in recent decades from using the indirect acetylene reduction method to the $^{15}N_2$ stable isotope incubation approach (Montoya et al., 1996). In the last 10 years, several studies have been conducted in the Baltic Proper, using variations of the $^{15}N_2$ -stable isotope incubation approach including the dissolution and direct gas injection methods (Bentzon-Tilia et al., 2015b; Svedén et al., 2015; Klawonn et al., 2016; Reeder et al., 2022; Adam et al., 2016; Zilius et al., 2021). The main uncertainties in the estimates of N_2 fixation are due to the uneven distribution of cyanobacterial filaments in surface

175 waters, which are shown to vary across spatial and temporal scales by up to a factor of eight (Klawonn et al., 2016), causing different amounts of N_2 fixers in the incubation experiments used to measure rates (Rolff et al., 2007). Moreover, quantification of the distribution of N_2 fixers using remote sensing techniques by satellites is difficult because most of the biomass of N_2 fixers is not always located directly on the surface (Karlson et al., 2022). The composition of diazotrophs in the Baltic Sea varies by season, salinity, and depth, and is also known

180 to differ between coastal and offshore locations (Farnelid et al., 2009; 2013; Klawonn et al., 2016; Reeder et al., 2022; Salamon Slater et al., 2023).

In the past decades, there have been several studies of the diversity, composition and distribution of diazotrophs with novel groups, in addition to filamentous cyanobacteria emerging as possible contributors to N_2 fixation (e.g., Farnelid et al., 2009; 2013; Salamon Slater et al., 2023). A common method for detecting diazotrophs and their activity is by amplification and/or quantification of the *nifH* gene and transcripts, encoding the Fe subunit of the nitrogenase enzyme used for N_2 fixation (Fig. 3). The *nifH* genes of the diazotrophic filamentous cyanobacteria *Pseudoanabaena* have been identified at high relative abundances in the northern parts of the Baltic Sea (Salamon Slater et al., 2023; Fig. 3). Further, in *nifH* gene amplicon libraries, non-cyanobacterial diazotrophs (NCDs) belonging to gammaproteobacteria and deltaproteobacteria frequently dominate (Salamon Slater et al., 2023;

185 Reeder et al., 2026). Although not thought to be widely distributed in the Baltic Sea, *nifH* gene amplicons and transcripts of UCYN-A, the nitrosome of a cosmopolitan unicellular algae, have been detected in the western parts of the Baltic Sea in waters with salinity >10 (Bentzon-Tilia et al., 2015a; Reeder et al., 2022; Salamon Slater et al., 2023). Despite the increasing evidence of additional diazotrophs, filamentous cyanobacteria appear to be the main contributors to *nifH* transcripts and are thus considered the main diazotrophs in the pelagic Baltic Sea (Fig.

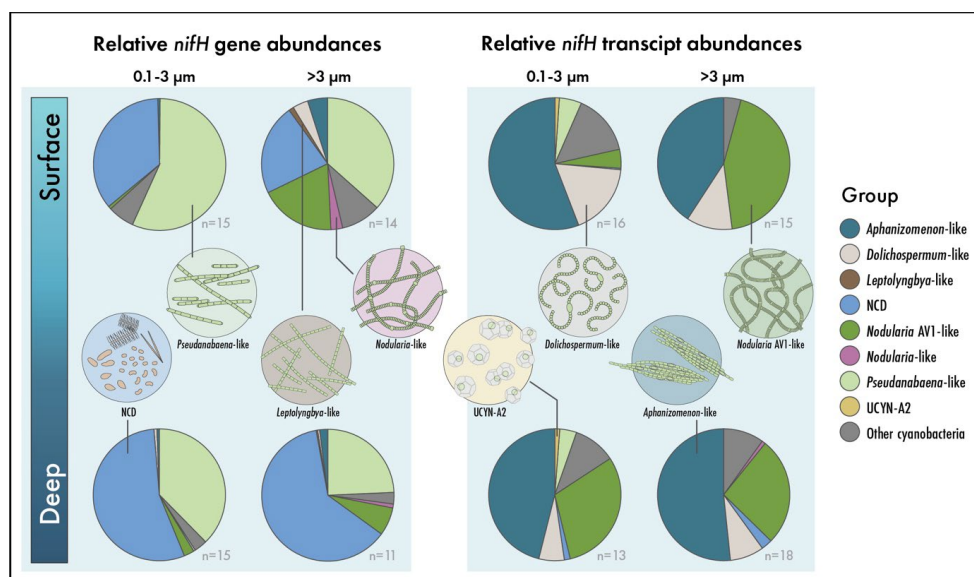
195 3).

In addition to sun-lit pelagic waters, N_2 fixation also occurs in suboxic zones and among benthic communities in sediments. Such environments may be particularly important for NCDs as low oxygen conditions are required for the function of the nitrogenase enzyme. Several Baltic Sea NCDs have been identified, isolated, and characterized (Bentzon-Tilia et al., 2015a; Boström et al., 2007; Farnelid et al., 2014). These isolates grow in N-depleted medium



200 under suboxic and anoxic conditions (Bentzon-Tilia et al., 2015a). Rates of N_2 fixation and *nifH* gene transcripts
 of NCDs have been detected in anoxic Baltic Sea waters (Farnelid et al., 2013). However, the importance of N_2
 fixation in suboxic and anoxic waters of the Baltic Sea and the potential coupling to denitrification (see section
 4.1) have yet to be determined.

Sediments exposed to seasonal hypoxia may also be a source of N through N_2 fixation. In a study in Eckernförde
 205 Bay (SW Baltic Sea), nitrogenase activity was coupled to sulphate reduction rates with the highest rates occurring
 in late summer and *nifH* genes of the sulphate reducers *Desulfovibrio vulgaris* and *Desulfonema limicola* were
 identified (Bertics et al., 2013). *NifH* genes were also reported from metagenomes from sediments of the Bothnian
 Sea with a shift in community composition from the oxic/anoxic interface to the methanogenic zone (Rasigraf et
 al., 2017). In shallow coastal waters, there may be a close coupling between sediments and pelagic N_2 fixation
 210 (e.g., Hallström et al., 2022), and resuspension of detritus and particles from sediments may enhance N_2 fixation
 by NCDs (Pedersen et al., 2018). Notably, Liesirova et al. (2023) demonstrated detectable rates of sediment N_2
 fixation by heterotrophic N_2 fixers under simulated resuspension, but studies reporting the composition of
 diazotrophs and N_2 fixation rates in Baltic Sea sediments are limited. Hence, the quantitative importance of benthic
 N_2 fixation remains unclear, but might add to the N budget in sediments and the flux across the benthic-pelagic
 215 boundary layer (see section 5).



220 **Figure 3:** Composition of present and active diazotrophs in the Baltic Sea represented by the average relative abundance
 of the *nifH* gene presence as copies (left) and the *nifH* gene expression (right), at the surface (average 1.8 m) and deep
 (average 24 m) layers, for the free-living (0.2 – 3 µm) and the particle-associated size fraction (>3 µm). n = number of
 samples, NCD = non-cyanobacterial diazotrophs, UCYN-A2 = *Candidatus Atelocyanobacterium thalassa*. Adapted from
 225 Salamon Slater et al. (2023).

2.4 Submarine groundwater discharge

Submarine groundwater discharge (SGD) is the flow of water from the seabed to the water column, regardless of
 the composition of the water or its driving force. Accordingly, SGD encompasses not only freshwater
 225 (groundwater) but also saline waters (recirculated seawater). Seawater can penetrate the seabed and be released
 again into the water column with a subsequently different salinity and chemical composition. Saline SGD is an



omnipresent diffuse pathway that discharges mainly recycled nutrients, whereas fresh SGD is a rather local source that releases new nutrients (e.g. dissolved inorganic nitrogen, DIN) to marine systems (Santos et al., 2021). SGD has been reported locally across the entire Baltic Sea within pockmarks (e.g., Eckernförde Bay, Gulf of Gdańsk, Hanko Peninsula) and along the coasts (e.g., Puck Bay, Mecklenburg-Western Pomerania, Forsmark) (Szymczycha et al., 2012, 2020, 2023; Virtasalo et al., 2019; Racasa et al., 2021; Purkamo et al., 2022; Kreuzburg et al., 2023; Ehlert von Ahn et al., 2024; Hinsby et al., 2025). In Eckernförde Bay, DIN fluxes through SGD were only six times lower than river discharge (Kreuzburg et al., 2023), while DIN fluxes in the Puck Bay are among the highest sediment-water DIN flux rates reported for the Baltic Sea (Szymczycha et al., 2012, 2020). Szymczycha et al. (2020) found that SGD is the most important source of DIN to Puck Bay and that NH_4^+ accounted for up to 94% of the total SGD-derived DIN flux. In this context, it is important to emphasize that the SGD-seawater mixing zones are reactive areas influencing diagenetic processes such as denitrification (Szymczycha et al., 2023) (see section 4.1) and consequently N availability (Purkamo et al., 2022). Recent large-scale hydrogeochemical observations across the Baltic Sea revealed substantial spatial variability in SGD (Tomer et al., 2025, 2026).

3 Internal nitrogen cycling

3.1 Nitrification

Nitrification, the stepwise oxidation of NH_3 (or NH_4^+) via NO_2^- to NO_3^- , is typically carried out by two different types of microbes (i.e., ammonia-oxidizing bacteria, AOB, or archaea, AOA, and nitrite-oxidising bacteria) for either step. It takes place in the water column and oxic surface sediments of the Baltic Sea, including the Gotland and Bornholm Basins, the Landsort Deep, and coastal waters in the Vistula and Öre estuaries (Bartl et al., 2019; Berg et al., 2015; Happel et al., 2018; Jäntti et al., 2018). Nitrification rates range from below detection limit to comparably high rates, with highest rates observed in the Bornholm Basin (Berg et al., 2015). The high rates in the basins of the central Baltic Sea are associated with low oxygen concentrations of $1\text{--}4\ \mu\text{mol L}^{-1}$ and availability of NH_4^+ at the redoxcline (Jäntti et al., 2018). Communities of nitrifiers are dominated by AOA in the Baltic Proper (Berg et al., 2015; Jäntti et al., 2018), whereas AOB are more important at coastal locations (Happel et al., 2018; Kache et al., 2021), where waters are characterized by higher organic matter (OM) and river loading. While rate measurements and descriptions of nitrifier communities, especially AOA and AOB, are available, seasonal observations as well as a representative coverage of coastal waters are missing. The latter is especially problematic considering the high land-derived riverine N loads from intensive fertilizer application, such as in the southern Baltic Sea region (Lønborg and Markager, 2021). These nutrient loads might facilitate nitrification and thus also the production of N_2O (see section 4.3) a by-product of nitrification at low oxygen concentrations (Codispoti, 2007; 2010).

3.2 Dissimilatory nitrate reduction to ammonium (DNRA)

Microbial DNRA is a long-known process (Tiedje, 1988) that reduces NO_3^- to NH_4^+ and therefore retains N_i in the system, in contrast to other NO_3^- reducing processes such as denitrification and anammox, see sections below. Knowing the share of NO_3^- removed versus retained is particularly important in eutrophic systems in view of eutrophication mitigation efforts (Jäntti and Hietanen, 2012). Being a strictly anaerobic process, DNRA commonly occurs in sediments, but has also been detected in the anoxic water column of the Baltic Sea (Fig. 3) (Hannig et al., 2007; Bonaglia et al., 2016), where both chemolitho- and heterotrophic DNRA have been found with varying



265 contributions to total NO_3^- reduction ($\leq 3\text{--}21\%$). In both coastal and open sea sediments, DNRA shows an even
 stronger variation regarding its contribution to total NO_3^- reduction ($0\text{--}60\%$; Jäntti et al., 2011; Jäntti and Hietanen,
 2012; Bonaglia et al., 2017; Benelli et al., 2024; Hellemann et al., 2020; Aalto et al., 2021; Zilius et al., 2022),
 including seasonal variation (Jäntti et al., 2011; Bonaglia et al., 2014a; Hellemann et al., 2020). While these shares
 clearly demonstrate the importance of benthic DNRA, the large observed variability suggests that we do not fully
 270 understand the underlying controlling mechanisms. Factors impacting DNRA rates in the Baltic Sea include: (i) a
 high electron (e^-) donor (organic carbon, OC, hydrogen sulfide, H_2S) to NO_3^- ratio (Jäntti and Hietanen 2012;
 Bonaglia et al., 2014a; Hellemann et al., 2020; Hylén et al., 2022; Aalto et al., 2021), (ii) substrate competition
 with denitrification if both processes are heterotrophic (Hellemann et al., 2020), and (iii) bioturbation by bivalves
 (Bonaglia et al., 2014b) and invasive polychaetes (Bonaglia et al., 2013). Aalto et al. (2021) also found a higher
 275 share of DNRA when system-internal (autochthonous) OM loading dominated over system-external
 (allochthonous) OM loading. However, as the internal OM loading coincided with lower NO_3^- concentrations, the
 larger contribution of DNRA could also have been due to a high e^- -donor to e^- -acceptor ratio rather than OM alone.
 While DNRA has been suggested to be of minor importance in cold environments (Giblin et al., 2013) and
 generally disfavoured in sediments with a high sand content due to commonly low availability of the e^- donors OC
 280 and H_2S , DNRA in the Baltic Sea was shown to be important in both cold habitats (Bonaglia et al., 2017) and
 sandy sediments (Hellemann et al., 2020; Benelli et al., 2024). DNRA is also particularly dominant in re-oxidized,
 previously anoxic sediments, where it contributes 44–65% to total NO_3^- reduction (De Brabandere et al., 2015;
 Hylén et al., 2022), mainly due to the maintained reduced nature of these sediments, i.e., strong negative redox
 potential. DNRA bacteria were also suggested to be able to adapt to organic and metal pollution in Baltic Sea
 285 sediments (Broman et al., 2023).

3.3 Nitrogen transfer in the food web

One major driver of species loss (loss of biodiversity) in oceanic ecosystems is a change in the N source at the
 base of the food web, but we do not yet fully understand its impact on higher trophic levels (Glibert et al., 2016;
 Mitra et al., 2014). In the Baltic Sea, loss of biodiversity has become apparent as biological regime shifts (Tomczak
 290 et al., 2022; Alheit et al., 2005) when changes in dominant phytoplankton functional groups take place (Wasmund
 et al., 2017), and when mesozooplankton (Möllmann et al., 2009) and pelagic fish populations collapse (Svedäng
 et al., 2024; Eero et al., 2023; Dippner, 2020). The significant replacement of NO_3^- utilizing diatoms by N_2 fixing
 filamentous cyanobacteria fundamentally have altered food web dynamics in the Baltic Sea (Loick-Wilde et al.,
 2019) with massive impact on higher trophic levels such as cod (Steinkopf et al., 2024). The eastern Baltic Sea
 295 cod stock has been in crisis for years and despite historically low fishing pressure, it is not recovering. Steinkopf
 et al. (2024) showed that the food web for cod has lengthened in the Baltic Sea due to a more dominant microbial
 food web associated with large-scale blooms of filamentous cyanobacteria (see section 2.3). Specifically, the food
 web position (or trophic position) of mesozooplankton and cod are higher in the central than in the western and
 coastal Baltic Sea. This means an energy loss from 60% up to 99% for the eastern cod compared to the western
 300 cod which makes a recovery of the eastern cod population unlikely without improving the nutrient regime
 (Steinkopf et al., 2024).

From a population point of view, species loss occurs when total mortality exceeds the harvestable secondary
 production. Recent developments in isotope ecology allow now to empirically quantify harvestable secondary
 production at the community and population levels using the trophodynamic approach (Libralato et al., 2008; Lalli



and Parsons, 1997). Here harvestable secondary production is estimated as a function of new production and the empirically determined trophic position and N-specific net growth efficiency, see Appendix A for details. The net growth efficiency is related to the habitat-specific trophic enrichment of a population or community (Fig. 4). In summary, results from recent empirical studies in the Baltic Sea show that two key terms (N-specific net growth rate and trophic enrichment), which are usually treated as constants in trophodynamic models, are in fact variables and systematically change with the N source supporting the food web.

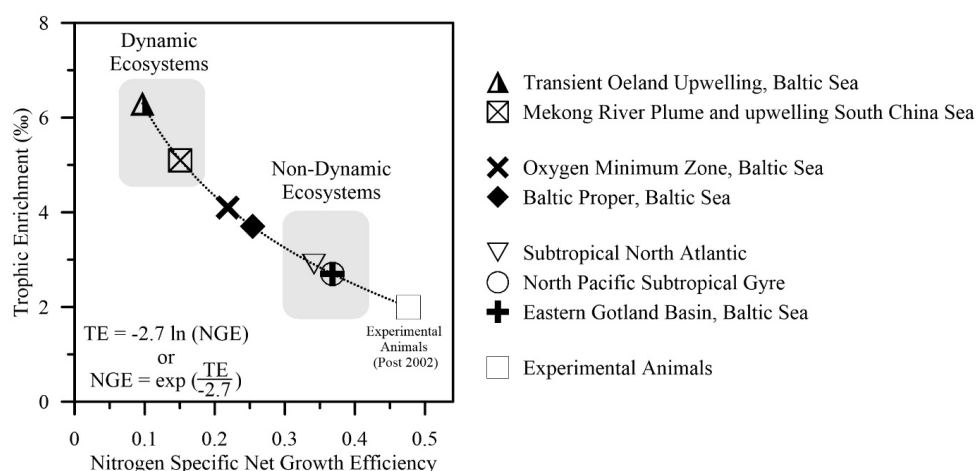


Figure 4: N-specific net growth efficiency (NGE) as expression of trophic enrichment (TE) in mesozooplankton from the Baltic Sea and other oceanic regions (Weber et al., 2021; Post, 2002).

In perspective, a revised census of N biomass across compartments of both benthic and pelagic food webs (Tomeczak et al., 2012; Gogina et al., 2016) in combination with systematic first estimates of the harvestable secondary production of key communities and populations would help to elucidate environmental and physiological factors regulating harvestable secondary production. This would help to validate model estimations of sustainable yields of key species in fisheries, and to support the management and conservation of biological diversity in the Baltic Sea.

3.4 Dissolved organic nitrogen (DON)

DON constitutes approximately 59% of the total N pool in the Baltic Sea (Lønborg et al., 2024), yet its role in ecosystem functioning remains poorly understood compared with other N pools (Jørgensen et al., 2013). This discrepancy is striking given that DON may represent an important pathway for N retention and recycling. One explanation is the complexity of the DON pool, which contains chemically diverse compounds spanning a wide range of origins and reactivities, with concentrations and distributions affected by physical, chemical and biological processes including mixing, advection, photochemical and microbial degradation (Lønborg et al., 2020). In the Baltic Sea, DON is largely of terrestrial origin (43-83%; Deutsch et al., 2012), particularly in regions influenced by intense agriculture, such as in the southern Baltic Sea (see section 2.1) (Voss et al., 2021). However, autochthonous DON, produced by phytoplankton and microbial communities, may be especially important as it is often more bioavailable and can sustain biological production over timescales of days to months when DIN becomes depleted (Lønborg and Álvarez-Salgado, 2012; Knudsen-Leerbeck et al., 2017). On average, the bioavailable fraction makes up 35% of the total DON pool (Lønborg and Álvarez-Salgado, 2012). The more



recalcitrant DON fractions can be transported over large distances, thus possibly fuelling production far away from their origins. This raises a key question: to what extent does DON act as a delayed-release N reservoir that buffers the ecosystem against reductions in external nutrient loading? Such a mechanism could help explain why ecological responses to nutrient management are sometimes slower or more variable than expected. The significance of DON cycling may be amplified in shallow coastal areas, where strong benthic-pelagic coupling involves a highly dynamic pattern of sedimentation, reworking of sediments by benthic communities, microbial degradation, resuspension and potential burial of OM (see section 4.4). While benthic cycling of DIN and PON has been studied extensively, DON fluxes in the benthic environment remain poorly quantified, despite often-high concentrations and dynamic nature (Cai et al., 2019), especially during sediment resuspension events (Harfmann et al., 2021).

Ongoing environmental changes of the Baltic Sea, including warming, stratification and runoff will affect the residence time and transformation of DON (Lønborg et al., 2020). Potential effects on DON cycling include increased microbial degradation at elevated temperatures and a reduction of the C:N ratio in DOM due to selective increase in phytoplankton excretion of dissolved organic C (DOC) (Engel et al., 2011). Further, changes in stratification can affect the vertical exchange of compounds, including DON, PON, and DIN, which in turn affects primary production, and thus new DON production. Understanding how these nonlinear interactions with several drivers shape DON dynamics requires approaches that extend beyond process studies and short-term experiments. Hydrodynamic-biogeochemical models can offer a different and whole system perspective. However, many global and coastal models either omit DON entirely (e.g., Yool et al., 2013; Schourup-Kristensen et al., 2023) or include only one semi-labile class (e.g., Aumont et al., 2015; Neumann et al., 2022). For the Baltic Sea, the ERGOM model has advanced the representation of OM by introducing variable DOC:DON stoichiometry, enabling more realistic simulation of the elevated DOM C:N ratios observed in the system (Neumann et al., 2022). Nevertheless, a single DON pool is unlikely to capture the broad spectrum of DON reactivities found in nature. To assess the role of DON in fuelling productivity through delayed recycling, future models may need to explicitly represent multiple DON fractions with contrasting degradation rates. Such an approach would improve our ability to quantify N retention and recycling, and to predict how the Baltic Sea ecosystem will respond to environmental change and nutrient management measures.

4 Nitrogen sinks

4.1 Denitrification

Denitrification is the dominant NO_3^- reduction pathway in the water column and sediments, and substantial efforts have been made to understand its distribution and mechanistic functioning in the Baltic Sea. Only recently, Sivasamy et al. (2025) measured excess N_2 (ΔN_2), which indicates the loss of N_r by denitrification and anammox (see below), at several stations in the Baltic Proper between 2017 and 2021. They found significant spatial difference in ΔN_2 with the highest values in the Gotland Deep. Complementary metagenomic observations from the Baltic Proper revealed substantial seasonal variability in denitrification-related genes across Bornholm Deep, Gdańsk Deep, and Gotland Deep, highlighting the importance of temporal changes in oxygen and nutrient conditions for pelagic N cycling (Grabski et al., 2025). Current research demonstrates that the quality of OM is more important than its bulk quantity for the functioning and efficiency of heterotrophic denitrification (Aalto et al., 2021; Albert et al., 2021; Helleman et al., 2020; Bartoli et al., 2021). As OM serves as a source of OC (e-



donor) and N (e⁻-acceptor) in heterotrophic denitrification, its rates commonly increase with the availability of high-quality labile, N-rich OM. However, at excessively high availability of high-quality OM, lab experiments indicate that denitrification efficiency, i.e., the amount of N permanently removed compared to N_i available in the system, can also decrease, potentially as the denitrification rates cannot keep up with the amount of N_i (Albert et al., 2021). These laboratory results are in line with field data, indicating comparatively low denitrification efficiency at coastal sites rich in high-quality OM (Benelli et al., 2024; Hellemann et al., 2020; Zilius et al., 2016) or during seasons of high benthic OM degradation (Bartoli et al., 2021). Similarly, denitrification efficiency has been shown to be low in previously anoxic, re-oxidized sediments, due to the high N degradation of accumulated OM and dominance of DNRA (see section 3.2) over denitrification at the early stage of re-oxidation (De Brabandere et al., 2015; Hylén et al., 2022).

Also, the quality of OC itself can affect denitrification. In aphotic coastal sediments of both the northern and southern Baltic Sea, low concentrations of high-quality OC were shown to reduce or even limit benthic denitrification in the period before sedimentation of spring bloom material, which serves as the main source of fresh, high-quality OC to these sediments (Bartl et al., 2019; Benelli et al., 2024; Hellemann et al., 2017; 2020; 2020; Hietanen and Kuparinen 2008). This is in line with Bartoli et al. (2021) who found that seasonal changes in the composition of OC compounds affect denitrification in muddy sediments of the Curonian Lagoon.

In stratified estuaries, PON was established as an integral link connecting pelagic riverine NO₃⁻ loads with benthic denitrification, for which PON becomes a N source after transformation of the organic N to NH₃/NH₄⁺ and subsequent nitrification (see section 3.1) (Bartl et al., 2019). Under those conditions, the highest seasonal benthic denitrification rates occur in late summer to early autumn (Hietanen and Kuparinen, 2008; Bonaglia et al., 2014a; Hellemann et al., 2020), whereas riverine NO₃⁻ inputs commonly peak in spring. The resulting time delay between NO₃⁻ loading and its eventual removal by denitrification, which is furthermore a function of estuarine water residence time (Bartl et al., 2019; Hellemann et al., 2017; Silvennoinen et al., 2007), needs to be accounted for when aiming to estimate how much of the riverine NO₃⁻ input gets denitrified (Bartl et al., 2019).

Benthic macrofauna has been found to both enhance and attenuate denitrification rates, as well as influence its NO₃⁻ source (water or sediment), with the response depending on faunal species, species' abundance, and species-specific interactions (Karlson et al., 2007; Bonaglia et al., 2014b; Zilius et al., 2022; Benelli et al., 2024; Moraes et al., 2017). Meiofauna has been shown to double denitrification rates (Bonaglia et al., 2014b), which increases the complexity of the benthic interactions. Denitrifying bacteria were suggested to adapt to organic and metal pollution in Baltic Sea sediments (Broman et al., 2023), comparable to DNRA bacteria (see section 3.2). Further, benthic denitrification was shown to result in significant isotopic fractionation, overturning the common understanding that there would be no significant fractionation (Dähnke and Thamdrup, 2013).

In the open Baltic Sea, denitrification at the pelagic oxic-anoxic interface is carried out by both chemolithoautotrophic (Brettar et al., 2006; Bruckner et al., 2013; Hietanen et al., 2012; Dalsgaard et al., 2013) and heterotrophic bacteria (Dalsgaard et al., 2013; Bonaglia et al., 2016), each with a different isotopic fractionation of NO₃⁻ (Frey et al., 2014) and use H₂S and OC, respectively, as e⁻ donor. In contrast, the involvement of manganese (Mn²⁺) and methane (CH₄) as alternative e⁻ donors still needs further investigation (Bonaglia et al., 2016; Jakobs et al., 2016). The significance of pelagic denitrification compared to benthic denitrification is still a topic of discussion. As pelagic denitrification requires the mixing of NO₃⁻-rich waters into the H₂S-rich anoxic water layers holding the denitrifier community, which can lead to very high N removal rates (Hietanen et al., 2012; Dalsgaard et al., 2013), it is also dependent on those mixing events. While small-scale internal mixing is assumed



to happen on a regular basis (Dalsgaard et al., 2013), large-scale mixing events are rare, and further, mixing might be patchy (Hietanen et al., 2012) and differing between seasons (Hietanen et al., 2012; Dalsgaard et al., 2013). In contrast, benthic denitrification rates are usually lower than pelagic rates and less variable as long as NO_3^- is available (i.e., no anoxia develops), which in turn results in a more constant rate of benthic N removal throughout the year (Hietanen et al., 2012). Hence, sediments have often been proposed as major N sinks, especially in coastal areas (Deutsch et al., 2010; Voss et al., 2005). Interestingly, the bacterial communities of pelagic and benthic denitrification were shown to be distinctly different and thus habitat-specific (Falk et al., 2007; Kim et al., 2011). Furthermore, no denitrification activity was found in pelagic cyanobacteria aggregates, despite containing the functional genes for it (Hietanen et al., 2002; Tuomainen et al., 2003).

4.2 Anammox

While anammox accounts on average for ~28% of N_2 production in global marine sediments, the process is generally less important in eutrophic than oligotrophic environments (Thamdrup, 2012). This is because anammox is a chemolithoautotrophic process that utilizes NH_4^+ and NO_2^- as e^- -donor and -acceptor, respectively, and inorganic carbon as carbon source. Since most Baltic Sea sediments are rich in OC from long-term eutrophication, they seem to favour denitrification over anammox. Only a few studies measured significant anammox activity in sediments of the coastal Gulf of Finland (Tvärminne archipelago: Hietanen and Kuparinen, 2008; Jäntti et al., 2011), and the coastal Baltic Proper (Himmerfjärden estuary: Bonaglia et al., 2014a), with anammox contributing 10-27% to total N_2 production. Interestingly, at the same sampling site in the Tvärminne archipelago and while using the same methodology, anammox activity was detected in spring and summer 2003 (Hietanen and Kuparinen, 2008) and winter 2008 and 2009, but not in spring and summer 2008 or 2009 (Jäntti et al., 2011). A potential anammox activity in the sediments of the open Gulf of Finland was reported by Hietanen (2007), but years later, Jäntti and Hietanen (2012) could not confirm their previous finding. Both examples suggest that some underlying control factors remain unknown. The majority of studies in coastal sediments of the Gulf of Finland (Hietanen, 2007; Bartl et al., 2019; Hellemann et al., 2020), Bay of Gdańsk (Benelli et al., 2024), and the major Baltic lagoons (Broman et al., 2021) do not report significant anammox activity. These field measurements are in line with a metagenomic study in Baltic Sea sediments suggesting anammox to be only of minor importance (Rasigraf et al., 2017).

In the Bothnian Bay, conditions have long been considered less eutrophied compared to the rest of the Baltic Sea (HELCOM, 2023), and thus the occurrence of anammox in its sediments could be expected there. Anammox activity was important in the deepest sediments of the open Bothnian Bay and open Bothnian Sea and contributed up to 26% of total benthic N_2 production (Bonaglia et al., 2017). The presence of anammox bacteria was additionally confirmed through the quantification of ladderane lipids and distinctive biomarkers (Bonaglia et al., 2017). Hence, the role of anammox in sediments of the northern Baltic Sea may be substantial, which might be explained by a higher $\text{NO}_3^-/\text{NO}_2^-$ to OC ratio (Bonaglia et al., 2017), affecting the competition with heterotrophic denitrification (see section 4.1). Yet, anammox was not detected in the oligotrophic Öre Estuary (Hellemann et al., 2017). As both Bothnian Bay and Bothnian Sea are becoming more eutrophic (HELCOM, 2023), anammox activity could be expected to decrease in the future.

Anammox was also detected at the permanent oxic-anoxic interface in the Baltic Proper (Hannig et al., 2007; Bonaglia et al., 2016; Hietanen et al., 2012), while other studies did not detect it (Dalsgaard et al., 2013; Grabski et al., 2025). Measured anammox rates were lower than the concomitant denitrification rates (Bonaglia et al., 2016)



and even assumed to be negligible (Hietanen et al., 2012), except when large-scale inflow events created an anoxic but H_2S -free zone favourable for anammox, resulting in anammox replacing denitrification as the main N_2 production pathway (Hannig et al., 2007). Potential anammox activity has also been reported in association with cyanobacterial aggregates in laboratory studies (Klawonn et al., 2015), which however still awaits confirmation by in-situ studies. So far, there are no manipulative studies on how anammox activity in the Baltic Sea might be influenced by potential stressors, such as fauna, pollution, or changes in environmental conditions.

4.3 Nitrous oxide (N_2O)

Open ocean and coastal areas are a major source of atmospheric N_2O (Yang et al., 2020; Tian et al., 2024). N_2O is produced as a by-product during nitrification (see section 3.1) and as an intermediate during denitrification (see section 4.1) under oxic and anoxic conditions, respectively. The major production process of N_2O in the open Baltic Sea is nitrification in the water column (Bardhan et al., 2026; Walter et al., 2006), whereas in shallow estuarine systems, benthic denitrification could also be an important source (Aalto et al., 2021; Cheung et al., 2025). Only recently, it was suggested that photochemodenitrification (a hitherto overlooked abiotic N_2O production process) may dominate N_2O production in the surface waters of the Eckernförde Bay (SW Baltic Sea) (Léon-Palmero et al., 2025). The increase in N_2O concentrations at oxic–anoxic interfaces in the water column of the Eckernförde Bay (SW Baltic Sea) was attributed to its production via nitrification, potentially in combination with the onset of N_2O production via denitrification when approaching anoxic conditions (Ma et al., 2019; Ji and Grundle, 2019). In deep waters of the Baltic Proper, N_2O is mainly produced via incomplete denitrification, which is driven by the presence of H_2S (Bonaglia et al., 2016; Dalsgaard et al., 2013). A significant N_2O depletion is usually observed in the anoxic waters in the coastal Baltic Sea (Ma et al., 2019) and the permanent anoxic deep basins of the Baltic Proper (Bardhan et al., 2026; Walter et al., 2006). N_2O concentrations in the coastal Baltic Sea can also be affected by N_2O -enriched river runoff (Silvennoinen et al., 2008). Only recently, Cheung et al. (2025) showed that N_2O production in the sediments of the three largest coastal lagoons in the Baltic Sea (i.e., the Curonian, Oder and Vistula lagoons) was driven by denitrification, which in turn was fuelled by NO_3^- . Thus, ongoing coastal eutrophication may enhance sedimentary N_2O production (and its subsequent emissions) in the coastal lagoons of the Baltic Sea. The accumulation of N_2O in groundwater is mainly due to denitrification and can result in very high concentrations (Jurado et al., 2017). However, the effect of SGD (see section 2.4) on the N_2O distribution in the water column of Baltic Sea has yet to be determined.

Time-series measurements of N_2O concentrations in the coastal Baltic Sea show a strong seasonality (Ma et al., 2019). Moreover, a strong increase of the water column N_2O inventory has been recorded as a result of nitrification after major inflows of water from the North Sea, ventilating the anoxic deep basins of the Baltic Proper (Walter et al., 2006; Myllykangas et al., 2017). A similar effect has been observed for N_2O production from denitrification in sediments of the Baltic Proper (Hylén et al., 2022). There is increasing evidence that plastic-associated biofilms can enhance local anoxic conditions, potentially favouring denitrifiers and stimulating N_2O production (Su et al., 2022). In view of the high concentrations of microplastics found in the Baltic Sea (Narloch et al., 2022), N_2O production associated with plastics might be a currently overlooked source. N_2O concentrations in Baltic Sea surface waters are usually close to equilibrium concentrations (i.e., N_2O saturation = 100%) or supersaturated (>100%). However, surface waters can also show temporal undersaturation (< 100%) (Ma et al., 2019; Silvennoinen et al., 2008). N_2O emissions from the northern basins of the Baltic Sea are affected by ice coverage during wintertime. Landfast sea ice in the Bothnian Bay has been identified as a temporary storage compartment



for N₂O and, therefore, reduces emissions from surface waters during wintertime (Geilfus et al., 2021). Nevertheless, the Baltic Sea seems to be an overall source of N₂O to the atmosphere throughout the year (Ma et al., 2019).

4.4 Nitrogen export and burial in sediments

DIN inputs from river input or atmospheric deposition fuel biological productivity and lead to the build-up of N-containing OM, which subsequently can settle near river mouths and within coastal regions, or can be exported to the open Baltic Sea (Zilius et al., 2018; Bartl et al., 2019). Over time, N accumulated in the settled OM (e.g., phytoplankton, zooplankton, or detritus) either is mineralized or becomes sequestered in the sediments of both the coastal and deep Baltic Sea basin. Substantial quantities of OM are also transported from shallow to deeper areas through the repeated cycles of resuspension-deposition (Nilsson et al., 2021). The OM flux to the seabed and burial largely depends on regional and seasonal patterns related to phytoplankton, food web structure, and hydrodynamics (Winogradow and Pempkowiak, 2014; Gustafsson et al., 2017; Beltran-Perez et al., 2023). The main deposition areas of OM - and thus PON- are the Gulf of Finland, Gulf of Bothnia, Gotland Deep, Bornholm Deep, and Gdansk Deep which account for >20% of the Baltic Sea surface and exhibit the highest N accumulation in the Baltic Sea (Emeis et al., 2000; Winogradow and Pempkowiak, 2014). While PON fluxes to the seabed can vary annually, they remain surprisingly similar in magnitude between coastal and deep deposition areas (Beltran-Perez et al., 2023; Zilius et al., 2024). Seasonally, the highest PON flux occurs after phytoplankton blooms (Beltran-Perez et al., 2023), but ongoing shifts in bloom timing and species composition may affect future PON fluxes (Spilling et al., 2018; Griffiths et al., 2020). In shallow coastal areas, macroalgae biomass represents an important source of PON that can be buried and ultimately stored in these systems.

The burial and recycling of PON in the sediments have rarely been considered in the quantification of N cycle processes (Asmala et al., 2017; van Helmond et al., 2020 and references therein). Due to specific geological and physicochemical conditions, the rates of N burial in sediments of the Baltic Sea can vary. Modelling studies suggest that approximately 13% of total N accumulated in sediments eventually becomes permanently buried, while the majority is removed through sedimentary denitrification (Almroth-Rosell et al., 2016; Gustafsson et al., 2017; Lønborg and Markager, 2021). The expansion of anoxic bottom conditions reduces sedimentary denitrification (Deutsch et al., 2010; Carstensen et al., 2014), resulting in reduced OM degradation that, in turn, leads to enhanced OM preservation and burial.

5 Nitrogen fluxes

Estimates of the N fluxes (including sources, sinks and internal cycling) of the Baltic Sea are listed in Table 1. The individual flux estimates are in reasonable agreement across the four budgets although the time periods do not match. In view of the large uncertainties of the individual flux estimates, the presented budgets seem to be balanced. Riverine input is the major source of N and microbial denitrification is the major N sink in the Baltic Sea.

N inputs by SGD are an additional N source to the Baltic Sea (see section 2.4). Indeed, SGD-derived DIN loads might exceed riverine DIN inputs on a local scale (Tomer et al., 2026). A rough Baltic Sea-wide estimate of the annual SGD-derived DIN input -based on the Baltic Sea-wide daily DIN input given in Tomer et al. (2026)- yields $11 \pm 22 \text{ kt N yr}^{-1}$. This implies that the N input by SGD is most probably of minor importance for the N budget of



the Baltic Sea. This estimate is associated with a high uncertainty because of a poor spatial and temporal data coverage.

N₂O emissions to the atmosphere represent an additional minor N sink of 130 ± 200 kt N yr⁻¹ (see Appendix B for details of the estimate) which equates to 3% of the global oceanic N₂O emissions (4200 ± 100 kt N yr⁻¹; Yang et al., 2020). Hence, the Baltic Sea share of the global N₂O emission budget is disproportionally large in view of its surface area of only approx. 0.1 % of the global ocean surface area. This estimate is, however, highly uncertain mostly due to lack of data availability and spatial coverage, with a strong bias towards observations carried out in the central and south-western Baltic Sea.

Table 1. Nitrogen flux estimates (mean $\pm$ standard deviation, when available) for the Baltic Sea in kilotons (kt) N yr⁻¹. Periods for the estimates are given in parenthesis. In- and outflows are from/to the northern Kattegat area. Sar19, LM21, Sav18 and E25 stand for Saraiva et al. (2019a), Lønborg and Markager (2021), Savchuk (2018) and Ehrsten et al. (2025), respectively.

	Sar19 ¹ (1980-2005)	LM21 (2011-2018)	Sav18 (2005-2014)	E25 (2012-2021)
Sources				
Atmosphere	331 $\pm$ 63	239 $\pm$ 20		254
Rivers	589 $\pm$ 112	630 $\pm$ 95	950 ²	588
N ₂ fixation	231 $\pm$ 118	473	400	743
Inflow to Baltic Sea	-	96	658	386
Sum of sources	1151	1438	2008	1971
Internal cycling				
Biological N uptake	2856 $\pm$ 500	-	-	8354
Remineralization	1886 $\pm$ 453	-	-	7228 ³ /778 ⁴
Sinks				
Denitrification	761 $\pm$ 73 ³ / 660 $\pm$ 60 ⁵	674 ⁵	1180	250 ³ /1089 ⁵
Permanent burial	325 $\pm$ 23	592	-	145
Outflow to North Sea	-	220	793	550
Sum sinks	1746	1486	1973	2034

¹Hindcast run; ²sum of atmosphere and rivers; ³pelagic; ⁴sediment release; ⁵benthic

5.1 Future projections

On-going environmental changes such as warming, deoxygenation, and eutrophication affect the present-day biogeochemical cycles and the ecosystems of the Baltic Sea (see e.g. Bogalecka and Dobrzycka-Kraheil, 2026; Kristensen and Flindt, 2026; Kuss et al., 2026; Voss et al., 2025). Projections of key variables such as water temperatures, salinity, dissolved oxygen concentrations, nutrient inputs and winds in a future climate depend largely on the scenario which in turn depend on the chosen model, the setup of the chosen models and on the



550 necessary forcing assumptions. Here we present the model results of climate change projections for the Baltic Sea, Kattegat, and Skagerrak by Saraiva et al. (2019a). Their projections for the periods 1978-2007 and 2069-2098, suggest that water temperatures will increase by +1.8 and +3.1°C in medium (representative concentration pathway, RCP, 4.5) and high-end (RCP 8.5) scenarios, respectively (Saraiva et al., 2019a). Salinity, in turn, is projected to decrease in the surface and bottom layers by about 0.6 g kg⁻¹ in both medium and high-end scenarios, due to the increasing total annual river discharge (Saraiva et al., 2019a). The projected changes in physical variables have strong impacts on the N cycle. Higher water temperatures will speed up N uptake (phytoplankton growth) and remineralization (OM degradation remineralization) causing an intensified nutrient cycling in the water column (e.g., Meier et al., 2011). However, the dominant impact is expected from changes in N (and P) inputs from the atmosphere and from the catchment via rivers (Saraiva et al., 2019a; 2019b; Meier et al., 2018; 560 2019).

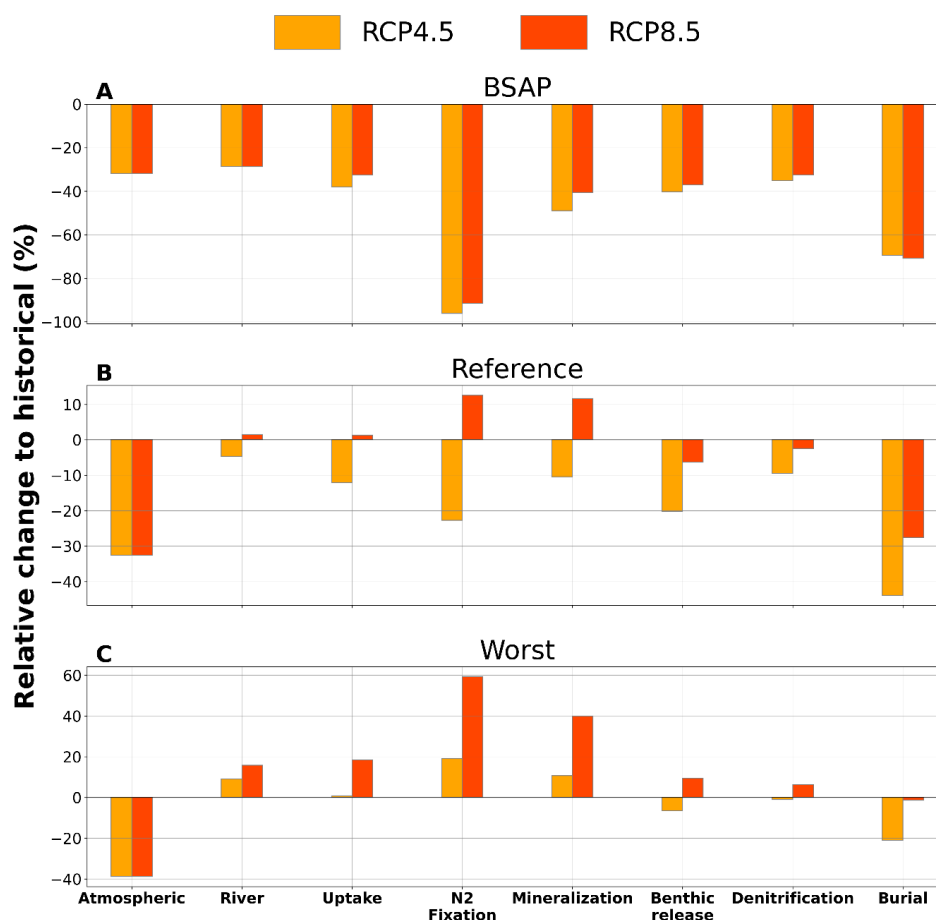


Figure 5: Changes in the annual nitrogen amount involved in the main processes: relative difference between the future climate scenarios representative concentration pathway (RCP) 4.5 and 8.5 (2069-2098) and the historical simulation (1976-2005) for the different nutrient load scenarios: A) Baltic Sea Action Plan (BSAP), B) reference, and C) worst-case scenarios (Saraiva et al., 2019a).



The projected change in the major N fluxes between the periods 1976-2005 and 2069-2098 is shown in Fig. 5 for three different nutrient input scenarios as well as two climate scenarios (RCP 4.5 and 8.5). The nutrient input scenarios constitute one scenario representing nutrient input in accordance with the Baltic Sea Action Plan (BSAP), one reference scenario, and one scenario that represents a fossil fuel driven future development (= worst-case scenario). Only the reduced nutrient loads of the BSAP scenario would lead to a decrease of all N fluxes for both climate scenarios (Fig. 5a) which, in turn, would lead to an improvement of the future environmental (eutrophication) status of the Baltic Sea. In addition, N₂ fixation is also reduced over the projected period as a result of decreased occurrences of cyanobacterial blooms (Saraiva et al., 2019a). The reduction in N₂ fixation adds to the decrease in N input in the BSAP scenario. Furthermore, the temperature dependence of biological N fluxes is apparent in the increase in degradation, uptake, benthic/pelagic denitrification, and burial in the high-end (RCP 8.5) climate scenario in both the reference and the worst cases scenario (Fig. 5b and 5c). The worst-case scenario (Fig. 6c) shows increasing N fluxes (except for atmospheric input, burial, and benthic denitrification). This in contrast to the BSAP scenario (Fig. 6a), and implies a degradation of the future environmental status of the Baltic Sea.

The projected basin-averaged NO₃⁻ and NH₄⁺ concentrations over time are shown in Fig. 6 for all nutrient (Baltic Sea Action Plan, reference and worst-case scenarios) and climate scenarios (RCP 4.5 and 8.5). The results show an overall increase in the Baltic Sea NO₃⁻ concentrations and a decrease in NH₄⁺ concentrations for the BSAP and reference scenarios and an increase in the worst-case scenario. The redistribution of N from NH₄⁺ to NO₃⁻ in the BSAP simulation could also be a result of decreased denitrification and increased nitrification resulting from increased oxygen concentrations (Saraiva et al., 2019b). These results confirm that the main driver of eutrophication are the external nutrient loads. In line with this conclusion, Ehrnsten et al. (2025) only recently demonstrated that due to the long residence time of the nutrients in the Baltic Sea, the environmental status of the Baltic Sea has improved only slightly, but it would be considerably worse today without the successful implementation of measures to reduce the nutrient loads.

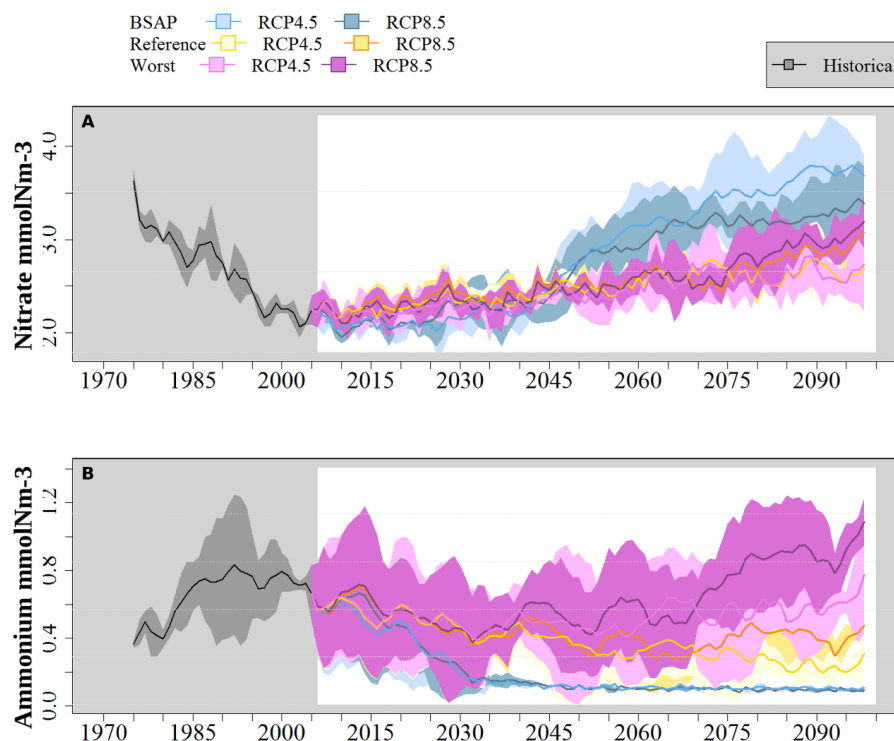


Figure 6: Temporal evolution of A) ensemble averaged nitrate (NO_3^-) and B) ammonium (NH_4^+) concentration in the entire Baltic Sea in the period from 1975 to 2098 and their standard deviations (ensemble spread) among ensemble members. For all combinations of the two greenhouse gas concentration scenarios (RCP 4.5 and 8.5) and the three nutrient load scenarios (Baltic Sea Action Plan, reference and worst-case scenarios) the ensemble average and spread were calculated from four regionalized global climate simulations (Saraiva et al., 2019a).

6 Future changes in nitrogen fluxes across interfaces and boundaries

6.1 Land-coast-open ocean continuum

Because the Baltic Sea has a very large catchment area in relation to its surface area, the river inputs strongly influence its biogeochemical conditions. The high river input of nutrients over decades are responsible for the eutrophication of the Baltic Sea (Andersen et al., 2017) and reduction measures only became effective in the early 1990s, particularly visible as a decline in TN concentrations in the coastal zone (Lønborg and Markager, 2021) (see also section 5). Land use still largely determines the export of inorganic and organic N, with fertilizer practices playing an important role. Precipitation determines the time and quantities of discharge and shifts to the winter months as climate change progresses, which means that inputs reach coastal waters at a largely biologically inactive time (Øygarden et al., 2014). This leads to less biological uptake and more efficient transport of N from the coastal zone to the open Baltic Sea. Societal drivers like dietary choices may also play a role and outweigh climate change effects on nutrient inputs to coastal waters (Pihlainen et al., 2020). Unfortunately, the current nutrient reduction efforts are not sufficient enough to reach good environmental status conditions in a period of



610 less than a few decades which is also due to the fact that N (and P) compounds are stored in the sediments (Ehrnsten et al, 2025) and NH_4^+ (and PO_4^{3-}) accumulates in the anoxic deep waters of the Baltic Proper.

Since the main source for riverine N loads are diffuse losses, the loads will be directly impacted by climate change through e.g., changed precipitation-evapotranspiration balance and impacts of increasing temperatures on N processes in soils and groundwater. Most scenario simulations indicate that climate change will lead to increasing
615 future N loads (Kuliński et al., 2022; and references therein). So far, these scenario simulations did not account for changes in land use, crop selection and similar effects that will be a consequence of a changing climate. However, it has been shown that the socio-economic development determining food demand and prices, environmental policy and other agriculture management aspects will have at least as large an impact on N loads as climate change itself (Kuliński et al., 2022; and references therein).

620 In addition, there are numerous catchments that are responsible for additional nutrient inputs besides the rivers and streams (Hannerz and Destouni, 2006). For instance, storm events can increase the height of extreme sea levels (Soomere and Pindsoo, 2016), which inevitably leads to an intensification of the exchange of substances between land and sea. Satellite altimetry data suggest an annual absolute mean sea level rise of 3.3 mm yr^{-1} that varies considerably across the basins and is strongly modulated by waves (Weisse et al., 2021). The resulting flooding
625 can increase nutrient discharge locally and for a limited time, but the effect of this input pathway across the Baltic Sea is unclear. Isostatic sinking southern coastlines likely experience increased flooding more often and thus an unknown nutrient input from land.

Warming of the entire Baltic Sea, which is already higher than that of the open oceans, will undoubtedly have the most lasting and severe consequences for nutrient cycling (Carstensen et al., 2014; Kniebusch et al., 2019).
630 Warming not only reduces the oxygen content, but, for example, also changes the benthic colonization, microbial processes and the fluxes between sediment and water (Seidel et al., 2022). The important function of the sediments as a filter for nutrients such as NO_3^- could be disrupted in the long term due to hypoxia and thus increase the N concentrations in the Baltic Sea.

6.2 Exchange between the North Sea and the Baltic Sea and MBI events

635 The net N output to the North Sea seemed to have decreased by about 13% between 1981-1990 and 2001-2010 (Gustafsson et al., 2017) probably due to decreasing N concentrations in the Kattegat and Danish Straits. Estimates of future N outputs to the North Sea are, however, associated with a high degree of uncertainty because the bottom inflow of North Sea water and surface outflow of Baltic Sea water is driven by various parameters, such as wind patterns, river discharge and the precipitation-evaporation balance (Lønborg and Markager, 2021).

640 The exchange between the North Sea and the Baltic Sea indirectly affects the N cycle via injection of oxygen-rich North Sea water into the (anoxic) deep basins of the Baltic Proper. Therefore, oxygen-sensitive N turnover processes such as N_2 fixation below the oxycline, denitrification, anammox, and nitrification are affected by such switches from anoxic to oxic conditions. For the period 1887–2017, major Baltic inflow events do not show a systematic trend, but a pronounced multi-decadal variability of about 25–20 years (Mohrholz, 2018). Hence, the
645 future trend of deep-water anoxia of the Baltic Sea is indeed not driven by decreases or increases in the Major Baltic Inflow Events but by future nutrient inputs as suggested by Meier et al. (2022).



6.3 Sediment-water (solute) interface

The solute exchange across the sediment-water interface in the Baltic Sea varies spatially and temporally (e.g., Carstensen et al., 2020; Hylén et al., 2021; 2022). Sediments are in continuous interaction with the overlying water column, receiving OM and experiencing wave effects while accumulating or releasing N compounds. In coastal areas, increasing storm frequency will impact sedimentary environments by redistributing settled OM and oxidizing surface sediment (Nilsson et al., 2021), potentially increasing the cycling of regenerated N (Niemistö et al., 2018). However, the impact of flushed porewater on N fluxes is unknown. Additionally, the response of N exchange to heat waves is uncertain. As the magnitude and frequency of heatwaves increase, benthic metabolism may lead to higher inorganic N fluxes due to enhanced mineralization of OM (Göbeler et al., 2025). In deeper sites, increasing temperatures will strengthen stratification (Meier et al., 2022; Safonova et al., 2024), facilitating oxygen depletion at the bottom and regenerating N primarily as NH_4^+ , which is available to the overlying water column.

In addition to physical processes, benthic micro- and macroorganisms play a crucial role in transforming N-containing compounds, affecting their availability for biological production and influencing ecosystem functioning (Carstensen et al., 2020). While studies have shown the effects of micro- and macroorganisms on benthic solute exchange (e.g., Karlson et al., 2007; Zilius et al., 2022), it remains unclear how warming of the benthic ecosystem will impact the N exchange. Recent studies have shown increased macrofaunal and microbial activity in response to heat waves (Kauppi et al., 2023; Kauppi and Villnäs, 2022), with macrofauna directly amplifying benthic N fluxes through excretion in response to temperature increases (Kauppi and Villnäs, 2022). However, prolonged and intense marine heat waves will change the macrofaunal community, with consequences for sediment reworking and solute exchange (Rousi et al., 2013; Kauppi et al., 2023).

Shifts in the community composition of primary producers in the water column are expected to alter benthic N fluxes in the Baltic Sea. Phytoplankton community composition, which is an important OM source, is changing (Viitasalo and Bonsdorff, 2022). These changes are likely to alter seasonal OM deposition to seafloor sediments (Spilling et al., 2018) and, consequently, the release of N to bottom waters. Sedimentation of heavier diatoms facilitates an important OM flux that sustains benthic microbial communities and macrofauna communities. However, the expansion of buoyant cyanobacteria will likely accelerate processes within the water column (Zilius et al., 2018), where N will be recycled, even in shallow coastal areas. Additionally, the buoyant cyanobacteria will cause light scattering and shadowing of previously euphotic sediments, specifically in shallow coastal areas. This will suppress N uptake (N assimilation) at the surface sediment and enhance the accumulation of reduced forms of N in the water column. Macrophyte deposition may also decrease in the future, as, for example, rising salinity is linked to declines in *Fucus vesiculosus* macroalgae (Kotta et al., 2022), and increasing water temperatures may negatively impact seagrass populations (Krause-Jensen et al., 2021), potentially impacting OM burial and nutrient uptake.

6.4 Sea-air interface

It can be expected that NO_x emissions from transportation, industry and households will continue to reduce in the coming two to three decades. This is mainly caused by the shift from fossil fuels and combustion-based energy production to renewable energy production. For example, Matthias et al. (2020) estimated a reduction of NO_x emissions from German traffic by 77% to 86% until 2040 compared to 2010. The numbers depend on the scenario, but it can be expected that road traffic will be mainly electrified. Also, for shipping, NO_x emission reductions are



expected until 2040 due to the introduction of an N emission control area in the North and Baltic Seas at the beginning of 2021. Based on new policies and predictions, a reduction of about 45-60% for the annual N deposition from shipping in the Baltic Proper is estimated by 2040 (Karl et al., 2019; Jutterström et al., 2021).

690 Atmospheric NH_3 emissions are also expected to decrease in the future, but at a much lower rate than NO_x emissions. While NO_x emissions in the European Union decreased by 63% from 1990 to 2021, NH_3 emissions dropped by approx. 25% between 1990 and 1995 and are more or less constant since then (EEA, 2023). Until 2030, the European Union aims at a reduction of NH_3 emissions by 19% on average compared to 2005 (UNECE, 2021). The largest reductions are expected from Germany (-29%) and Denmark (-24%). Although almost all
 695 scenarios point to a large reduction of atmospheric NO_x emissions from various sources as well as at least moderate reductions of NH_3 emissions, there are also risks for increased emissions connected to the energy transition towards renewable fuels. Biofuel production may require an intensified agriculture with the risk of new NH_3 emissions. In addition, hydrogen produced from renewable energy may be converted to NH_3 which is then transported on ships. It may even be used as ship fuel, which could result in NH_3 as well as NO_x emissions from shipping (Schwarzkopf
 700 et al., 2023). Intensified NH_3 production in Europe could also establish a new source of NH_3 emissions that counteracts emission reductions in agriculture.

Future N_2O emissions from the Baltic Sea are difficult to project since we do not know how its production and consumption pathways (i.e., nitrification and denitrification) are affected by warming, eutrophication, deoxygenation, and acidification. On the one hand, deoxygenation may result in an increased N_2O production by
 705 nitrification (see section 3.1) and denitrification (see section 4.1); while on the other hand, expanding anoxic zones of the Baltic Sea may lead to an increase in the consumption of N_2O during denitrification. Production and accumulation of N_2O within sea ice and under-ice waters is feasible (Geilfus et al., 2021), such that emissions from the northern Baltic Sea could potentially be affected under warming-driven decline in sea ice thickness, coverage and phenology. However, given the scarcity of sources of information on N_2O distribution, fluxes and
 710 seasonal variability the extent of such effects is highly uncertain.

7 Conclusions and outlook

It is clear from the overview presented here that the fundamental role of N in the biogeochemical cycles and ecosystems of the Baltic Sea requires a critical reassessment. The combination of economically strong countries surrounding the Baltic Sea which can afford the costs for marine research and the comparably small dimensions
 715 of the Baltic Sea have led to a large number of studies on the functioning and status of the Baltic Sea, also supported by HELCOM. However, the majority of studies on the N cycle have been performed in the western, southern and central basins of the Baltic Sea, with only relatively few studies performed in the northern basins of the Gulf of Bothnia, partly because access is challenging by its seasonal sea ice cover. There is also a discrepancy between the higher number of studies in coastal areas and the number of studies in the open waters of the Baltic Sea.
 720 Moreover, a seasonal coverage of the N cycle processes is missing in most cases, particularly regarding the winter months. This obviously inadequate temporal and spatial coverage of measurements result in large uncertainties in both the rate measurements and flux estimates for all the N cycle processes discussed (see sections 2-5). These uncertainties need to be reduced significantly to gain a complete picture of the N cycle. Additionally, there are some aspects of the N cycle which have received no or only limited attention:



- 725 (i) Microplastics is ubiquitous in the water column of the coastal and open Baltic Sea (see e.g. Narloch et al., 2022; Murawski et al., 2022; Mishra et al., 2025). Artificial surfaces such as those found on (micro)plastic seem to provide favourable conditions for the growth of biofilms. These biofilms can include N₂-fixing or denitrifying bacteria, which convert atmospheric N₂ into biologically available forms or produce N₂O and N₂, respectively. However, the contribution of N fluxes from biofilms on microplastics to the N budget of the Baltic Sea is unknown.
- 730 (ii) Both nitrification and denitrification have been detected in Baltic Sea ice (Kaartokallio, 2001) and experiments showed that ice maturity and melting, presumably through changes in bacterial community structure, impact N processes (Kuparinen et al., 2011). Given the fact that up to 40 % of the Baltic Sea area (i.e., Gulf of Bothnia, Gulf of Finland, and Gulf of Riga) can be covered with sea ice during winter (BACC II Author Team, 2015), sea-ice could play a significant role in the N fluxes, both the ice itself and the barrier it resembles for water-atmosphere exchange (e.g. regarding N₂O emissions).
- 735 (iii) The role of shallow waters (depths <15 m) – which account for about 20% of the Baltic Sea surface area (Hell and Öiås, 2014) – for the N cycling remains to be assessed.
- 740 (iv) We still lack an in-depth understanding of DNRA and anammox, as well as their major environmental drivers and contributions to N fluxes.
- (v) A revised census of N biomass across compartments of both benthic and pelagic food webs in combination with systematic first estimates of the harvestable secondary production of key communities and populations is missing.
- 745 (vi) Despite representing the predominant fraction of the TN pool, the role of DON for N cycling and productivity of the Baltic Sea is largely unknown.
- (vii) N cycling in sediments and the coupling of these processes with the overlying water column are still associated with large uncertainties. Accurate estimates of sedimentation rates, accumulation, and burial of N are missing.
- 750 If we are to successfully address existing knowledge gaps and fully decipher the processes and fluxes of the N cycle in a changing Baltic Sea, complementary suggestions to HELCOM's Baltic Sea monitoring network should be implemented (for details about the HELCOM monitoring network see <https://helcom.fi/action-areas/monitoring-and-assessment>). N cycle-focussed time-series measurements and joint process studies should be established at representative sites in both coastal and open Baltic Sea areas (including the sea-ice covered areas)
- 755 with high biological productivity and/or anthropogenic influence, conducted across multiple seasons and years. This approach should be designed holistically, combining microbial, molecular biological, and biogeochemical methods. Only through such a comprehensive, coordinated, and interdisciplinary approach will we (i) generate the data necessary to identify the relevant microbial communities, (ii) quantify the temporal and spatial variability of the rates, (iii) comprehend their major drivers, (iv) reduce the uncertainties in the N flux estimates, (v) improve the representation of N processes in physical/biogeochemical models, and (vi) improve the measures to reduce eutrophication in order to achieve a good environmental status of the Baltic Sea. There remains much to be learned about the (micro)biological and biogeochemical processes, the sea ice/water/atmosphere interactions, the sediment/water column coupling and the atmospheric chemistry of the Baltic Sea. Without this knowledge, the picture of the Baltic Sea's N cycle will remain incomplete.
- 760



765 To project future alterations of the N cycle, ongoing environmental changes such as warming, eutrophication, deoxygenation, and atmospheric pollution, and their effects on the N processes and fluxes need to be considered. Even though the reliability of model projections has been increasing, the inherent uncertainties in scenario simulations of the Baltic Sea still remain. Projections of the marine biogeochemical cycles (e.g., the N cycle) still suffer from uncertainties due to global and regional climate model biases, natural variability, and unknown
 770 greenhouse gas emissions and nutrient load scenarios (Meier et al., 2018, 2022). Although uncertainties of available scenario simulations are large, the implementation of nutrient load abatement scenarios such as the BSAP might result in improved environmental conditions in the Baltic Sea despite the counteracting impact of a changing climate (Meier et al., 2018, 2022). Therefore, the continuous development and implementation of regional ecosystem-based nutrient management strategies, such as HELCOM's BSAP are crucial for maintaining marine
 775 biodiversity and ecosystem integrity of the Baltic Sea (Saraiva et al., 2019a).
 Developing a deeper understanding and quantification of nutrient sources leading to N (and P) inputs to the Baltic Sea is critical. This includes assessing the efficiency of measures designed to curb these sources. By estimating the reduction potential from different areas and sectors within the various Baltic Sea catchments, countries can implement more effective and region-specific strategies. Furthermore, the development of novel, efficient, and
 780 environmentally sustainable techniques and practices is necessary to improve nutrient recycling and minimize nutrient loads from diffuse sources. This is illustrated by a recently published modelling study which showed that N removal via wetland conservation and restoration can be a cost-effective, policy-relevant solution that, if spatially targeted, can lead to significant reduction in the N loads of major European rivers including the Vistula river which drains into the southern Baltic Sea (Bertassello et al., 2025).

785 **Appendix A**

The harvestable secondary production (HSP in mg N m⁻² d⁻¹) can be computed as (Libralato et al. 2008; Lalli and Parsons, 1997):

$$HSP = NP \times NGE^{TP-1} \quad \text{Eq. 1}$$

790 or

$$HSP = NP \times \exp \left(\frac{TE}{\varepsilon} \left(\frac{(\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - \beta)}{TDF} + \lambda \right) \right) - 1 \quad \text{Eq. 2}$$

where NP is the new production (in mg N m⁻² d⁻¹), e.g., after Bronk et al. (1994) and Montoya et al. (1996). Net growth efficiency (NGE) is the empirically determined N-specific net growth efficiency (or k₂ in trophodynamic models), an expression of the habitat-specific trophic enrichment (TE) of a population or community. In
 795 mesozooplankton, TE ranges between 2.7 to 6.3 ‰ in different areas of the Baltic Sea (Weber et al., 2021). NGE is quantified from TE using a simple Rayleigh fractionation model (Montoya, 2007; Loick-Wilde et al., 2016) and ranged from 0.1 to 0.37 in mesozooplankton in those ecosystems. TP-1 is the number of trophic transfers that separate an organism from the primary producers. For mesozooplankton, TP can be empirically measured after Chikaraishi et al. (2009) and McClelland and Montoya (2002) with δ¹⁵N_{Glu} and δ¹⁵N_{Phe} as the N isotope values of
 800 the trophic amino acid glutamic acid (Glu) and the source amino acid phenylalanine (Phe) from a single sample, and β is the δ¹⁵N difference between Glu and Phe in the primary producers (-3.4 ± 0.9‰ for aquatic cyanobacteria and algae). TDF represents the trophic discrimination factor between Glu and Phe (7.6 ± 1.2‰) associated with



each trophic transfer between a consumer and its diet, and λ represents the first trophic level (1.0) of the food web. For mussels, fish, seabirds and marine mammals the TP term has to be adjusted accordingly (Choi et al., 2018; Steinkopf et al., 2024 and references therein; McMahon et al., 2015). N units can be translated into C units using the respective C/N ratio of a community or population (e.g., Walve and Larsson, 1999) to express HSP in $\text{mg C m}^{-2} \text{ d}^{-1}$.

Appendix B

According to current estimates, the mean N_2O flux densities from shelf and open waters of the Baltic Sea amount to $0.3 \pm 0.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Yang et al., 2020), while estuaries and areas with coastal vegetation emit $0.2 \pm 0.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Rosentreter et al., 2023). A first estimate of the overall contribution from major coastal lagoons in the Baltic Sea revealed N_2O fluxes densities of $0.013 \pm 0.003 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Cheung et al., 2025). The annual mean N_2O flux densities for the Baltic Sea were obtained by adding the reported mean values for coastal lagoons (Cheung et al., 2025), combined estuarine areas (Rosentreter et al., 2023) and various open ocean sites from the climatology by Yang et al. (2020). The total, annual N_2O emissions were then calculated by multiplying the overall mean flux density estimate by a surface area of $415,886 \text{ km}^2$. The surface area used here is larger as the area of $412,500 \text{ km}^2$ from Leppäranta and Myrberg (2009) because it includes the surface area of coastal lagoons in the Baltic Sea (3386 km^2) (Cheung et al., 2025).

Code and Data availability

No unpublished data are presented. Data mentioned in the article are available from the corresponding authors of the cited publications.

Author contributions

HWB and CRL drafted the concept of the article and coordinated writing of the article. All authors contributed to the writing and editing of the article.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Two (co-)authors are members of the editorial board of Biogeosciences.

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