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Drivers of ΔN_2 variability in the Baltic Sea: Insights from observations and ERGOM-MOM modeling

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Abstract

Excess dinitrogen (ΔN_2) is the net accumulation of N_2 produced by nitrate-reducing processes in the water column and sediments of oxygen-deficient marine systems. Therefore, biological production and physical processes shape its spatial distribution. This study investigates ΔN_2 distribution below the halocline in the Baltic Sea using a coupled biogeochemical model evaluated against observations from the Bornholm, Gdańsk, and Gotland Deeps during 2020–2021. Vertical distributions of temperature, salinity, oxygen (O_2), nutrients, N_2/Ar ratios, and ΔN_2 were compared to assess model performance and identify controls on N_2 production.

A persistent spatial gradient in ΔN_2 was observed, with highest concentrations in the Gotland Basin, intermediate levels in the Gdańsk Basin, and lowest values in the Bornholm Basin. These differences correspond to variations in stratification, ventilation, and organic matter (OM) accumulation. Seasonal variability was strongest in the Gdańsk Basin, where elevated winter ΔN_2 suggests enhanced nitrogen-loss processes supported by OM export and mixing-driven nutrient redistribution. In contrast, the Gotland Basin exhibited relatively stable, persistently reducing conditions, while the Bornholm Basin showed strong interannual variability related to episodic North Sea inflows.

The weak relationship between ΔN_2 and modeled denitrification rates (ranging from 0.0010 to 0.0200 μmol kg^{-1} day^{-1}) indicates that ΔN_2 should not be interpreted as a direct proxy for pelagic denitrification. Rather, it reflects the cumulative effects of both pelagic and benthic denitrification, together with physical transport processes. By comparison, denitrification rates were more strongly associated with particulate organic carbon (POC) availability. The reported ΔN_2 patterns are representative of the investigated post-inflow period rather than a long-term Baltic Sea baseline.

Keywords

Denitrification; Nutrients; Oxygen; Seasonality; Spatial variability; N_2/Ar

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1. Introduction

The Baltic Sea is the world's largest brackish water basin, characterized by low salinity and strong vertical stratification due to limited water exchange with the North Sea and high river runoff (Kullenberg, 1981, 1982; Voipio, 1981; Matthäus et al., 1992; Kohonen, 2019; Szymczycha et al., 2019). These conditions, together with long water residence time (over 30 years), make the ecosystem highly vulnerable to eutrophication and oxygen deficiency in bottom waters, disrupting marine biodiversity and ecosystem functioning (Kuliński et al., 2022). In response, international initiatives like the Baltic Sea Action Plan (BSAP) coordinated by the Helsinki Commission (HELCOM) have aimed to decrease nutrient inputs by implementing agricultural changes, upgrading wastewater management, and strengthening monitoring and research initiatives (HELCOM, 2021). Despite these efforts, the biodiversity and ecosystems of the Baltic Sea are still not healthy and resilient (HELCOM, 2021). The ongoing environmental stress highlights the importance of internal processes that help regulate nutrient levels.

Denitrification and anaerobic ammonium oxidation (anammox) are the two key microbial pathways that remove reactive nitrogen in the forms of nitrate (NO_3^-) and nitrite (NO_2^-) from aquatic systems by converting them to dinitrogen gas (N_2). Ammonium (NH_4^+) is not directly used in denitrification; instead, it contributes indirectly via nitrification, during which NH_4^+ is oxidized to NO_2^- and

subsequently to NO_3^-, thereby supplying substrates for denitrifiers. In contrast, NH_4^+ serves as a direct substrate for anammox, where it reacts with NO_2^- under anoxic conditions to produce N_2, providing an additional pathway for reactive nitrogen (N) removal.

In the Baltic Sea, denitrification and anammox in sediments represent the dominant N removal processes and play a crucial role in mitigating eutrophication (Seitzinger et al., 2006). However, denitrification rates generally exceed those of anammox (Bonaglia et al., 2014, 2016), indicating that heterotrophic denitrification is typically the primary N-loss pathway in these environments. Reported sediment denitrification rates can reach up to 5246 μmol N m^{-2} d^{-1} in the Szczecin Lagoon (Pastuszak et al., 2005) and up to 530 μmol N m^{-2} d^{-1} in open Baltic Sea areas (Stockenberg and Johnstone, 1997). In comparison, denitrification in the water column appears lower (and more variable), with reported rates ranging from 60 to 2110 μmol N m^{-2} d^{-1} and strongly influenced by sulphide concentrations and the availability of organic matter (Dalsgaard et al., 2013; Bonaglia et al., 2014). Nevertheless, water-column denitrification in the Baltic Sea remains poorly constrained. Direct rate measurements are sparse, and spatial coverage remains limited. Additional methodological challenges, including separation of water-column processes from sedimentary N_2 fluxes and microscale redox heterogeneity, introduce substantial uncertainty. As a result, the overall contribution of pelagic denitrification to total nitrogen removal in the Baltic Sea is still not well quantified. Anammox in the water column appears to be of minor importance in the Baltic Proper, as anammox-related genes were not detected in the deep Baltic Sea (Mazur-Marzec et al., 2024; Grabski et al., 2025), suggesting limited pelagic anammox potential in these basins. Uncertainty in estimating total nitrogen removal is further amplified by the complex interactions among stratification, redox dynamics, climate-driven variability, and benthic–pelagic coupling (Dalsgaard et al., 2013; Bonaglia et al., 2014). Recent observations of N_2 accumulated in the deep waters of the Baltic Proper show pronounced spatial and seasonal variability of N_2-releasing processes, yet the relative contributions of denitrification and anammox were not directly measured (Sivasamy et al., 2025). This underscores the need for improved large-scale process-based studies to resolve the spatial and temporal variability of nitrogen removal pathways, particularly in the water column, where knowledge gaps still remain substantial. This challenge can be met by harnessing biogeochemical modelling in research.

Among the state-of-the-art models, one of the most advanced is the three-dimensional coupled hydrodynamic-biogeochemical ERGOM-MOM. The model simulates key biogeochemical processes, including the complete nitrogen cycle. Its reliability has been demonstrated through previous validations against extensive observational datasets (Lessin et al., 2012; Wan et al., 2012). Moreover, the ERGOM-MOM model enables the isolation of denitrification rates and N_2 and argon (Ar) concentrations. This further allows the use of the N_2/Ar method to quantify the excess of N_2 in relation to its equilibrium with the atmosphere (ΔN_2), providing insights into the N_2 production, which corresponds to bioavailable nitrogen removal (Schmale et al., 2019; Sivasamy et al., 2025).

The goal of this study was to integrate a coupled physical–biogeochemical model (ERGOM-MOM 5.1) with observational data (Sivasamy et al., 2025) to gain deeper insights into ΔN_2 dynamics in the Baltic Sea, particularly its spatial and temporal variability. The observational dataset (2020–2021) was collected several years after the major inflow event of late 2014, when the temporary deep-water oxygenation had already diminished, and oxygen (O_2) depletion below the halocline had re-established conditions favorable for excess N_2 (ΔN_2) accumulation (Mohrholz et al., 2015; Myllykangas et al., 2017). We examined spatial and temporal patterns of ΔN_2 in the waters below the halocline and analyzed its correlations with O_2, and nutrient concentrations. In addition, we investigated whether the observed N_2 enrichments primarily resulted from microbial processes such as denitrification. The potential influence of physical transport, represented by meridional and zonal currents, was also evaluated. We focused on regions affected by hypoxia and anoxia, which provide favorable conditions for nitrogen removal processes: the Bornholm Deep, the Gdańsk Deep, and the Gotland Deep.

2. Material and methods

2.1 Study area

Baltic Sea

The Baltic Sea is the largest brackish water basin in the world, with a total surface area of 415,240 km^2 and a water volume of 21,706 km^3 (Kullenberg, 1981, 1982; Voipio, 1981; Matthäus et al., 1992). Limited water exchange with the open ocean through shallow and narrow straits connected to the North Sea, along with substantial riverine runoff, are the main causes of low salinity and the formation of strong vertical stratification (Neumann, 2007; Lehmann et al., 2022). Major Baltic Inflows (MBIs) episodically transport oxygen-rich saline water into the deep Baltic Sea, temporarily improving oxygen conditions. However, during subsequent stagnation periods, oxygen is gradually consumed by organic matter degradation, which can lead to the re-establishment of hypoxic and anoxic conditions, including the formation of hydrogen sulfide (Fonselius, 1981; Matthäus and Franck, 1992). While MBIs temporarily oxygenate the deep Baltic Sea, they also strengthen stratification, limiting vertical mixing and ultimately contributing to the persistence of anoxic conditions below the halocline once the supplied oxygen is consumed. Furthermore, the Baltic Sea exhibits a long residence time

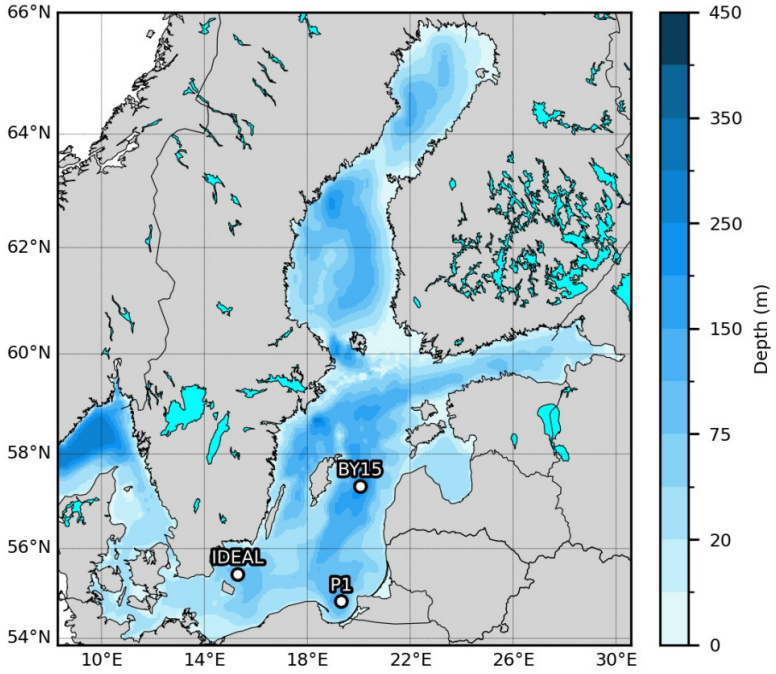

Figure 1. Map showing the sampling locations in the Baltic Sea: Bornholm Deep (IDEAL), Gdańsk Deep (P1), and Gotland Deep (BY15).

(over 30 years) for excessive inputs of biogenic substances (Neumann, 2007). For the purpose of this study, waters below the halocline were defined separately for each basin according to the characteristic vertical salinity structure and permanent stratification depth. Due to regional differences in bathymetry and hydrographic conditions, a fixed halocline depth was not applied. Halocline depths were defined based on published studies and regional hydrographic characteristics and were set to 60 m in the Bornholm Deep (Väli et al., 2012), 80 m in the Gdańsk Deep (Pempkowiak et al., 2000; Witak et al., 2025; Zglinicki et al., 2025), and 90 m in the Gotland Deep (Wieczorek, 2012). These thresholds were used consistently for the extraction and analysis of model and observational data below the halocline. Although the instantaneous halocline depth varied during the study period (e.g., from approximately 40 to 80 m in the Gdańsk Deep), the adopted thresholds represent basin-specific reference depths rather than the exact position of the halocline at the time of sampling.

Bornholm Deep

The Bornholm Deep (IDEAL; 55°20'N, 15°37'E, Figure 1) is situated in the south-western part of the Baltic Sea, near the Danish Straits, with depths of approximately 90–100 m. Due to its relatively close connection to the North Sea, it is characterized by more variable O_2 conditions (ranging from oxic to hypoxic) compared to the Gdańsk or the Gotland deeps. However, except during inflow events, this area typically has hypoxic bottom waters, with a long-term mean O_2 concentration of 38 µmol L^{-1} (Kuliński et al., 2022).

Gdańsk Deep

The Gdańsk Deep (P1; 54°30'N, 19°00'E, Figure 1) is located in the southern Baltic Sea to the east of the Bornholm Deep, with depths ranging from 80 to 120 m. The Gdańsk Deep is also influenced by the inflow of saline waters from the North Sea, though this impact is less evident. Compared to the Gotland Deep, the Gdańsk Deep is characterized by more dynamic hydrographic conditions and more active water exchange, influenced by its shallower depth and riverine input. Additionally, this region experiences significant dynamic changes due to the influence of local river inflows, particularly from the Vistula River, which delivers substantial amounts of OM and nutrients (Ostrowski et al., 2010), contributing to strong short-term variability in nutrient concentrations (Burska et al., 2005; Sikorowicz et al., 2005).

Gotland Deep

The Gotland Deep (BY15; 57°19'N, 20°03'E, Figure 1) is the deepest of the three basins, located in the central part of the Baltic Sea, reaching depths of up to 250 m. The Gotland Deep is characterized by a stable vertical stratification, with a well-defined halocline (Leipe et al., 2008). It is characterized by strong and persistent stratification, with limited deep-water ventilation (Leipe et al., 2008).

As a result, bottom waters are frequently anoxic and may contain hydrogen sulfide (Hannig et al., 2006; Hietanen et al., 2012; Dalsgaard et al., 2013). The stable redox structure promotes active nitrogen transformation processes at the oxic-anoxic interface (Hietanen et al., 2012; Dalsgaard et al., 2013). Compared to the other basins, the Gotland Deep represents a more permanently reducing environment, favoring sustained accumulation of excess N_2 below the halocline.

2.2 Observational data

Historical data on salinity (S), temperature (T), and oxygen concentration (O_2) (1962–2021) were retrieved from the International Council for the Exploration of the Sea (ICES) Datasets.

Environmental samples were collected from 3 stations (the Bornholm Deep, the Gdańsk Deep and the Gotland Deep) in the Baltic Sea (Figure 1) during research cruises with r/v *Oceania* conducted in September 2020, January 2021, April 2021, and September/October 2021. For seasonal analysis, winter was defined as December–February, spring as March–May, summer as June–August, and autumn as September–November. Observational data such as T, S, O_2, nitrate concentration (NO_3^-), ammonium (NH_4^+), measured (N_2/Ar) and calculated ΔN_2 were extracted from the dataset by Sivasamy et al. (2025). The Sea-Bird Scientific SBE 911 Plus profiler was employed for in situ measurements of T, S, and O_2 concentration. Samples for N_2/Ar analysis were collected in triplicate instantly from the Niskin bottles via Viton™ tubing in Exetainers® vials (12 mL gastight borosilicate glass vials; Labco, UK) and, after flushing with a volume of at least three times the volume of the vial, they were capped to prevent contamination. The biological activity was terminated through the injection of 50 μL of a saturated solution of $HgCl_2$. Vials were stored in a refrigerator at 4°C and analyzed within three months following collection.

2.3 Model setup

The ERGOM-MOM model combines the Ecological Regional Ocean Model (ERGOM) with the Modular Ocean Model (MOM) and was used by several applications (e.g., Schernewski et al., 2015; Naumov et al., 2023). The ERGOM ecosystem model was originally developed by Neumann (2000) and further improved (Neumann, 2000; Neumann et al., 2002), while MOM is based upon the work by Kirk Bryan, Michael Cox, Albert Semtner, and collaborators (Griffies et al., 2015). The three-dimensional coupled hydrodynamic–biogeochemical framework of the latest version and its state variables are described in detail by Neumann et al. (2022).

The comparison between model simulations and observational data was based on average values from five nearby model grid points, close to the sampling stations. This approach ensures the representativeness of the observed data by focusing on nearby model grid points.

The seasonal and spatial variability of ΔN_2 in the bottom water layer was investigated in three major basins of the Baltic Sea (Bornholm, Gdańsk, and Gotland basins), focusing on waters below the basin-specific halocline depths defined in Section 2.1 (Figure 2).

Pelagic denitrification rates in the model were calculated as the sum of organic matter remineralization processes under nitrate-reducing conditions, including the recycling of POC (particulate organic carbon), DON (dissolved organic nitrogen), POCN (nitrogen in particulate matter), DOC (dissolved organic carbon), and DOP (dissolved organic phosphorus) (Neumann et al., 2022). In these reactions, organic carbon is oxidized while nitrate is reduced to N_2, and phosphorus is released as phosphate during remineralization. All simulated denitrification rates, including values below 1 nmol L^{-1}, were retained for the subsequent statistical analyses. Although rates below this threshold are generally considered biogeochemically negligible, they were included to preserve the complete model output and may have influenced the strength of the observed statistical relationships. Detailed descriptions of the equations, variables, and chemical reactions used in the model are provided by Neumann et al. (2022). While most of the model variables were directly compared with observational data, additional parameters such as POC concentrations, denitrification rates, and hydrodynamic conditions (e.g., zonal and meridional currents) were available only from the model and served as the basis for further analysis.

2.4 Calculation of excess dinitrogen (ΔN_2)

For the model analysis, dissolved N_2 simulated by ERGOM-MOM was used to calculate excess N_2 relative to atmospheric equilibrium conditions. Therefore, modeled ΔN_2 was calculated as:

$$\Delta N_2 = N_{2\text{model}} - N_{2\text{sat}}$$

where $N_{2\text{model}}$ represents dissolved N_2 concentrations simulated by ERGOM-MOM, and $N_{2\text{sat}}$ represents the equilibrium concentration calculated from in situ temperature, salinity, and pressure using the solubility equations of Hamme and Emerson (2004). For observational data, ΔN_2 was derived from measured dissolved gas ratios following Schmale et al. (2019):

$$\Delta N_2 = \left(\left(\frac{N_2}{Ar} \right)_{\text{mes}} - \left(\frac{N_2}{Ar} \right)_{\text{sat}} \right) \times Ar_{\text{mes}}$$

where $(N_2/Ar)_{\text{mes}}$ is the measured dissolved gas ratio and $(N_2/Ar)_{\text{sat}}$ represents the equilibrium ratio expected from physical solubility. Because dissolved Ar was not available as a model variable, Ar concentrations were assumed to approximate equilibrium conditions ($Ar_{\text{mes}} \approx Ar_{\text{sat}}$). Under this assumption, the N_2/Ar approach for model output

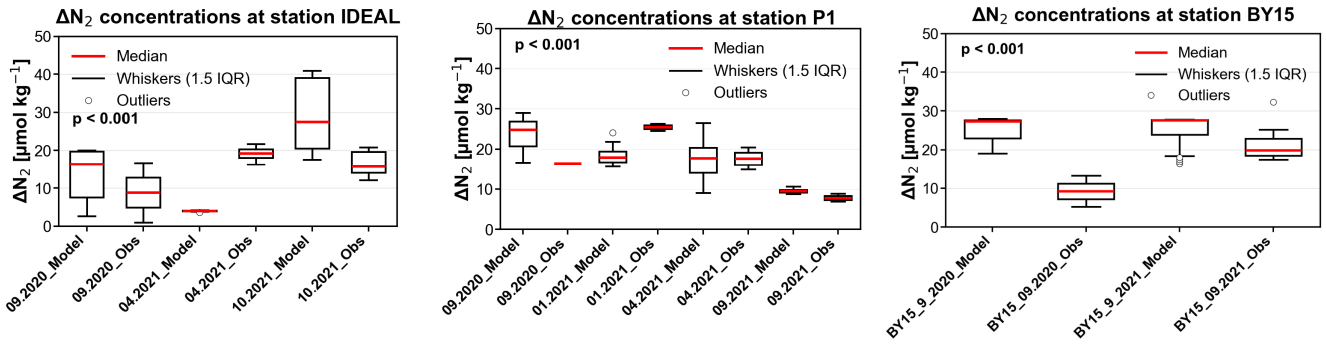

Figure 2. Box plots of ΔN_2 concentration from modeled and observational data measured below the halocline at the following stations: the Bornholm Deep (IDEAL), the Gdańsk Deep (P1), the Gotland Deep (BY15). ΔN_2 is defined as the excess dissolved N_2 derived from deviations of the measured N_2/Ar ratio from its equilibrium value and serves as an integrative tracer of nitrogen removal in stratified, oxygen-depleted waters. "Obs" indicates observational measurements, and "Model" represents corresponding model simulations.

simplifies to the difference between modeled dissolved N_2 and equilibrium N_2 concentration. The uncertainty associated with this approximation was estimated to be approximately 5%.

2.5 Statistical analysis

Statistical analyses were performed using Python and R statistical software. Spearman's rank correlation analysis was first applied to evaluate individual relationships between excess dissolved nitrogen gas (ΔN_2) and selected environmental variables. Correlation analyses were conducted separately for modeled and observational datasets; no mixed correlations between model output and measurements were calculated. It should be noted that correlations derived from modeled variables may partly reflect structural model behaviour and associated biases.

Because ΔN_2 represents an integrated signal influenced by both biogeochemical processes and physical transport, generalized additive models (GAMs) were additionally applied to evaluate the combined effects of multiple environmental drivers. GAMs are widely used for analysing potentially nonlinear relationships between environmental variables (Murase et al., 2009; Hastie, 2017; Wood, 2017; Pedersen et al., 2019). ΔN_2 was used as the response variable, whereas pelagic denitrification rate, dissolved oxygen concentration (O_2), nitrate concentration (NO_3^-), particulate organic carbon (POC), and zonal velocity were included as explanatory variables. Smooth functions were fitted for each predictor to account for potential nonlinear responses of ΔN_2 to environmental gradients.

Only model output corresponding to low-oxygen conditions ($O_2 \leq 10\ \mu$mol kg^{-1}) was included in the statistical analyses. GAMs were fitted using restricted maximum likelihood estimation (REML) with shrinkage smoothers to reduce overfitting and allow weak predictors to be penalized during model fitting. The significance and complexity of each smooth term were evaluated using approximate significance tests and estimated degrees of freedom (edf). Model performance was assessed using adjusted R_2 (coefficient of determination), Akaike Information Criterion (AIC), and the percentage of deviance explained. Model diagnostics, including basis-dimension checks and concurvity assessment, were performed to evaluate model reliability.

3. Results

3.1 Salinity, temperature, and oxygen distribution below the halocline in model results and observations

The simulated and observed vertical distributions of salinity (S), temperature (T), and oxygen (O_2) at the Bornholm Deep (IDEAL), Gdańsk Deep (P1), and Gotland Deep (BY15) are shown in Figures 3–5. All reported discrepancies represent mean model-observation differences calculated for waters below the halocline during the respective sampling periods.

At the Bornholm Deep, below the halocline (depths $>$ 60 m), modeled temperature deviated consistently from observations during all study periods (September 2020, April 2021, October 2021). The model overestimated temperature in autumn (up to +5.18°C in September 2020) and underestimated it in spring (down to −5.97°C in April 2021). Comparison with the long-term simulation (1962–2021), however, indicates a smaller overall mean bias, and the observed profiles generally fall within the modeled variability range. The vertical salinity profile below the halocline was generally overestimated in the upper layers and underestimated in deeper waters (Figure 3). The average bias ranged from −0.42 (April, October) to +0.38 (September). Comparison with the longer period (1962–2021) revealed a mean underestimation of −0.92 across all three months, with a tendency for salinity to increase gradually with depth. The model-observation comparison for O_2 in the Bornholm Deep showed a generally

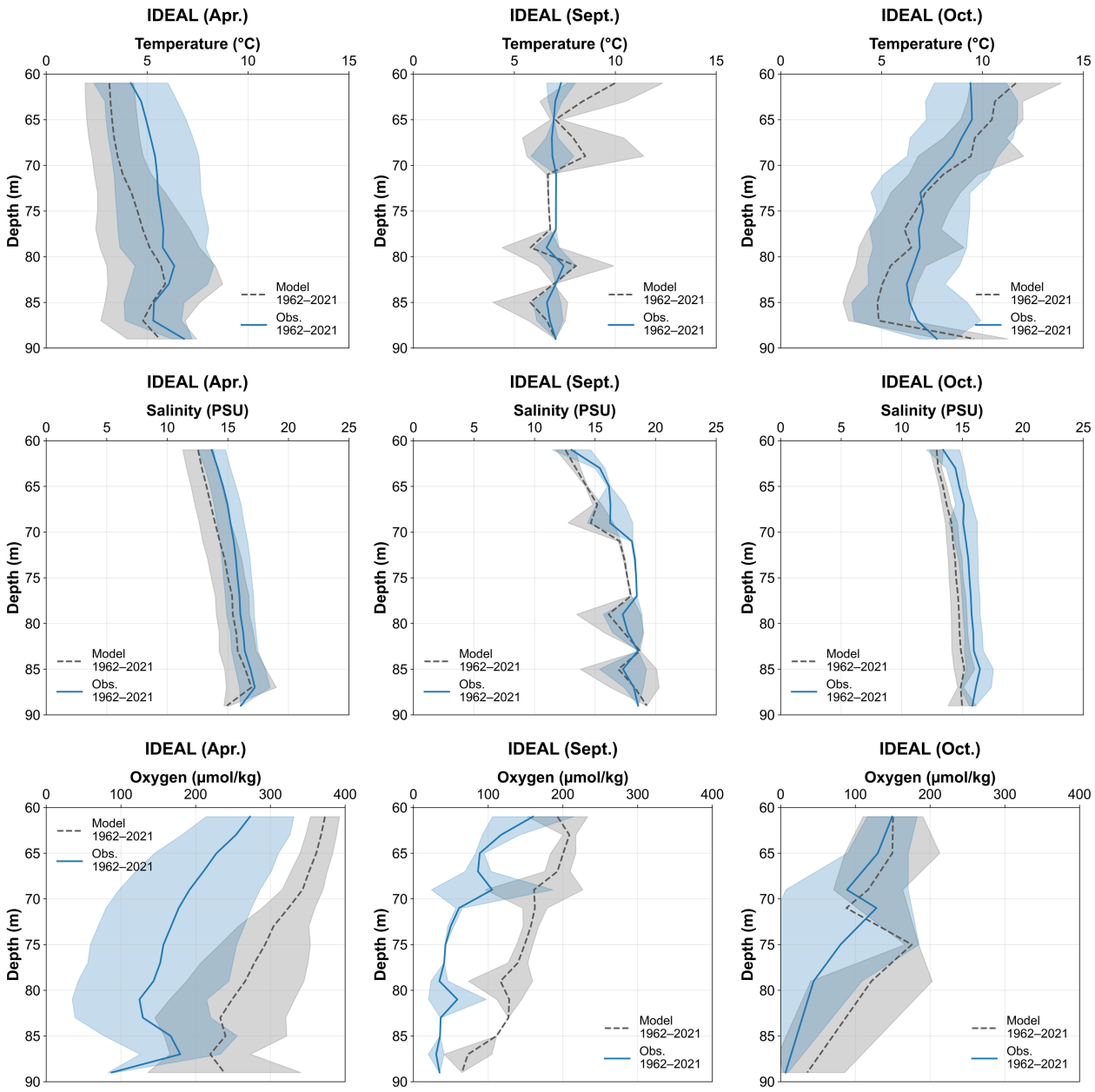

Figure 3. Vertical distribution of temperature, salinity and oxygen concentrations in the water column of the Bornholm Deep. The solid gray line represents model data, while the dots indicate observational data.

overestimated results, with moderate biases in autumn (+28.20 μmol kg^{-1} O_2) and more substantial overestimation in spring (+151.79 μmol kg^{-1} O_2) (Figure 3). This seasonal pattern was consistent with the long-term performance.

At the Gdańsk Deep, for waters below the halocline (> 80 m), agreement between modeled and observed temperature was generally good (Fig. S2). Slight overestimation occurred in September 2020 and January 2021 (mean +0.18°C), with a larger bias in April 2021 (+0.45°C). Long-term statistics confirm this strong performance (mean bias ≈ +0.05°C). Salinity was consistently but slightly overestimated (+0.18 to +0.47). Oxygen was also overestimated, with discrepancies ranging from +11.75 μmol kg^{-1} (April) to +104.47 μmol kg^{-1} (September). Smaller long-term biases suggest that short-term variability contributed to the larger deviations observed during the campaign period.

At the Gotland Deep, considering depths below the halocline (> 90 m), model–data agreement for temperature was strong (Fig. S3). September temperatures were

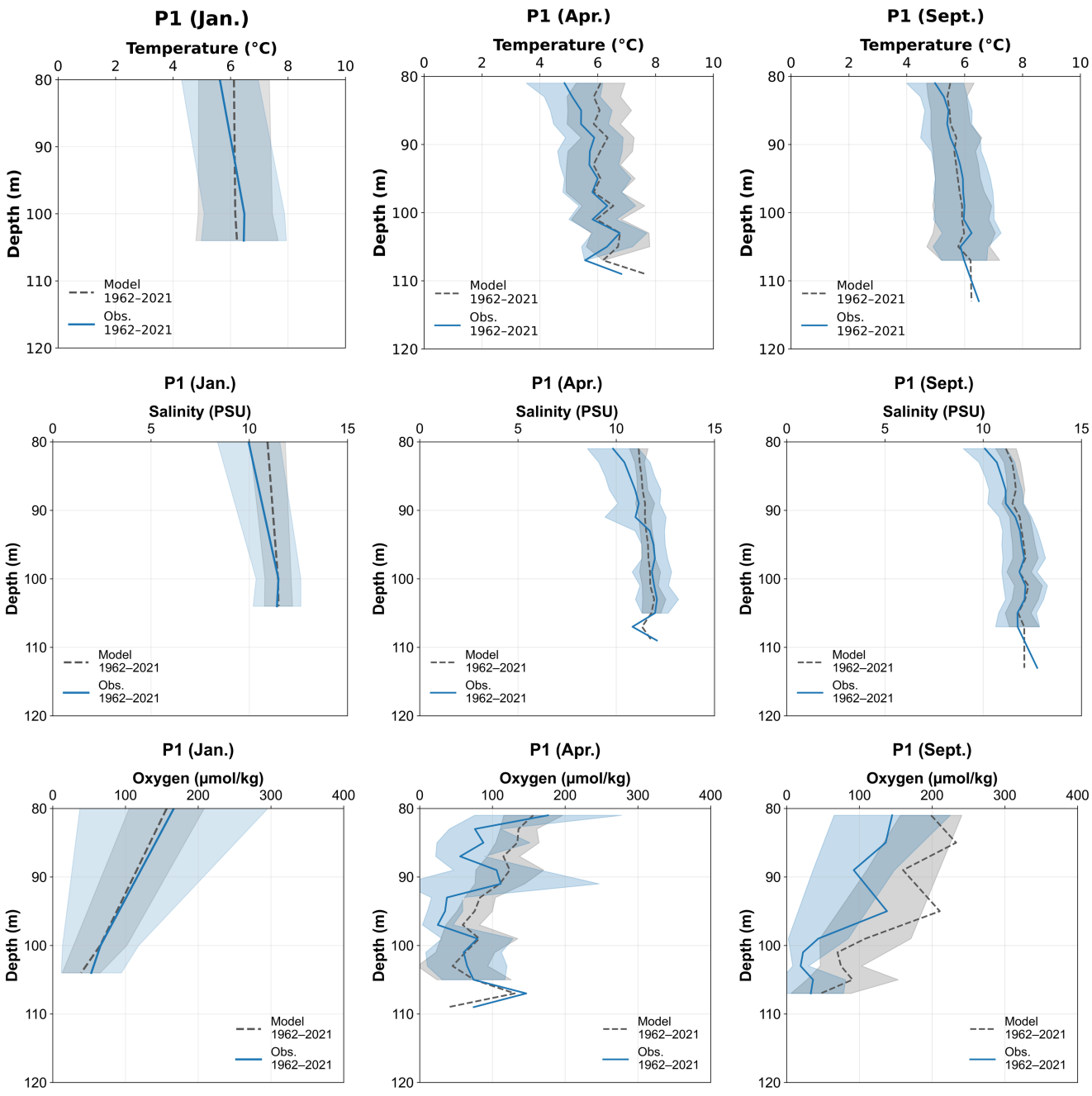

Figure 4. Vertical distribution of temperature, salinity and oxygen concentrations in the water column of the Gdańsk Deep. The solid gray line represents model data, while the dots indicate observational data.

only slightly overestimated (mean +0.20°C), with differences decreasing with depth. The long-term mean bias was even smaller (+0.08°C). Salinity biases were depth-dependent, with overestimation in the upper portion of the deep layer (+0.43 above 165 m) and underestimation below (−0.20). The long-term record indicates a mild overall overestimation (+0.28) and an increasing salinity trend with depth. Oxygen concentrations were moderately overestimated (+15.71 μmol kg^{-1}; $\sim$+39 μmol kg^{-1} in the long-term record), with near-perfect agreement in deeper layers (Fig. S3).

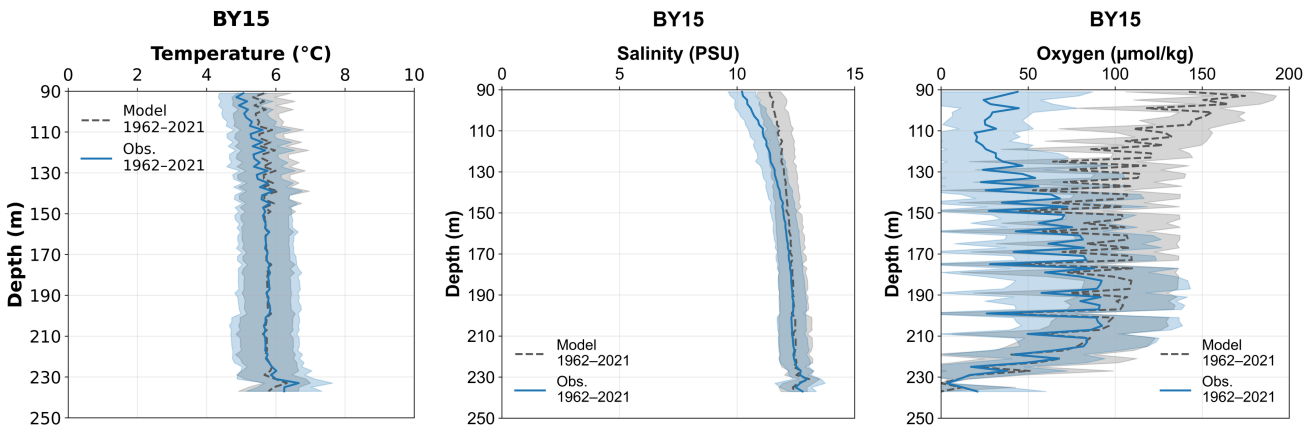

Figure 5. Vertical distribution of temperature, salinity and oxygen concentrations in the water column of the Gotland Deep. The solid gray line represents model data, while the dots indicate observational data.

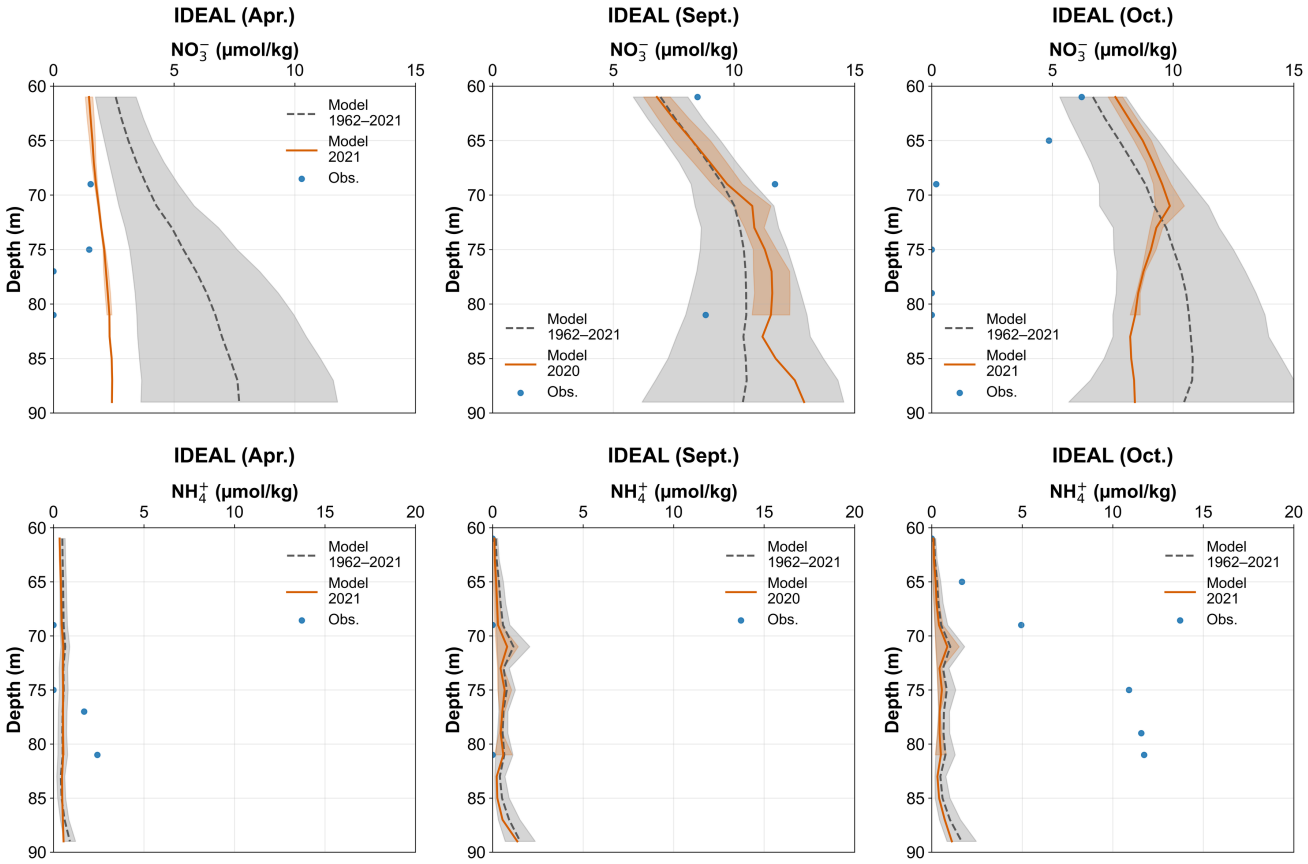

Figure 6. Vertical distribution of nutrient (NO_3^- and NH_4^+) distribution in the water column of the Bornholm Deep. The solid gray line represents model data, while the dots indicate observational data.

3.2 Nutrient (NO_3^- and NH_4^+) distribution below halocline

At the Bornholm Deep, nutrient distribution below the halocline (> 60 m) showed strong seasonality (Figure 6). NO_3^- was slightly underestimated in September 2020 (-0.25 μmol kg^{-1}), overestimated in April 2021 ($+1.03$), and strongly overestimated in October 2021 ($+7.53$). NH_4^+

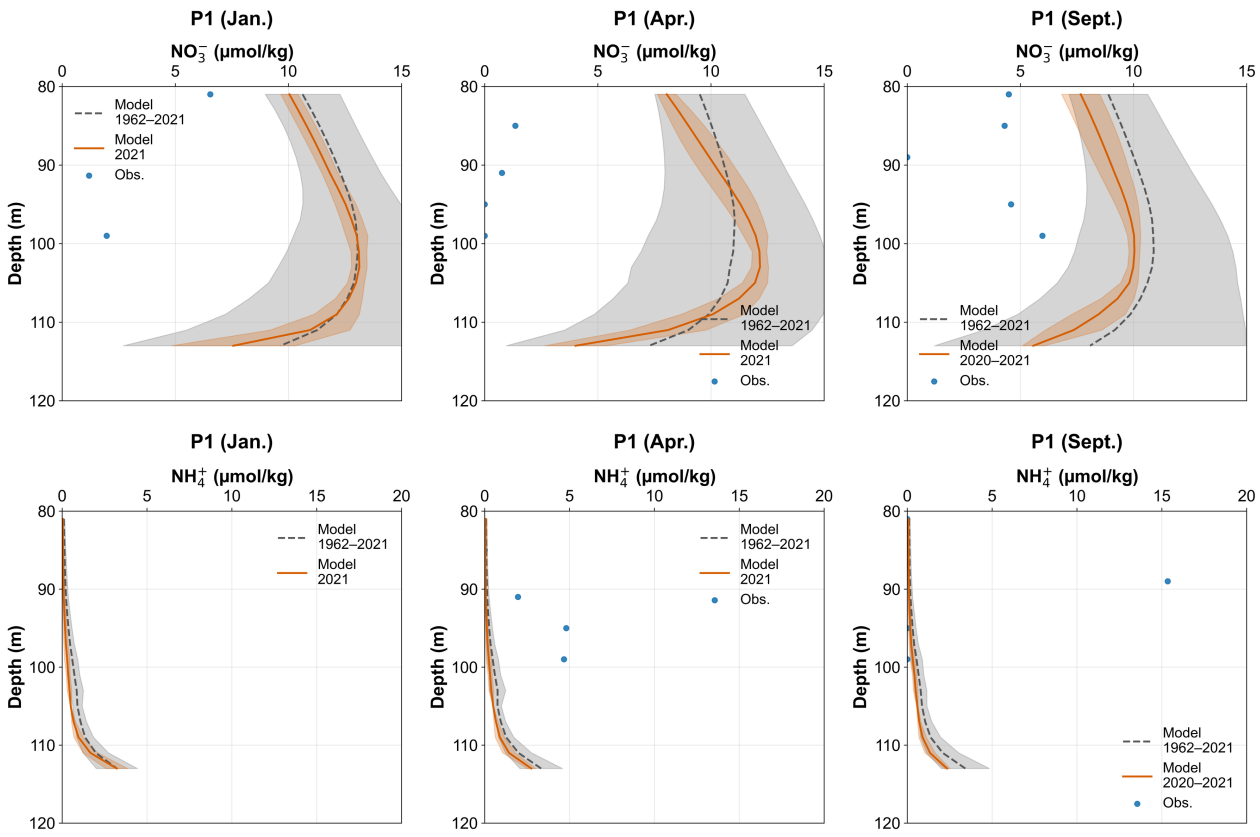

Figure 7. Vertical distribution of nutrient (NO_3^- and NH_4^+) distribution in the water column of the Gdańsk Deep. The solid gray line represents model data, while the dots indicate observational data.

followed a similar seasonal pattern, with small deviations in September (+0.56) and April (−0.17), but pronounced underestimation in October (−6.15). Long-term simulations suggest that October conditions were outside the typical range, and the single-event sampling limits strict model validation.

At the Gdańsk Deep (> 80 m), NO_3^- showed a general overestimation (mean +10.64 μmol kg^{-1}), whereas NH_4^+ was notably underestimated in September (−15.26 μmol kg^{-1}) (Figure 7).

At the Gotland Deep (> 90 m), comparisons were available for September in two different years. NO_3^- was overestimated in the upper part of the deep layer, while NH_4^+ was underestimated throughout the profile below the halocline (Figure 8).

3.3 N_2/Ar ratios distribution below the halocline

Model–observation differences in $(N_2/Ar)_{sat}$ and $(N_2/Ar)_{mes}$ below the halocline reflect discrepancies in N_2 concentrations and thus potential mismatches in biological N_2 production (Figs. S1–S3).

At the Bornholm Deep (> 60 m), the largest $(N_2/Ar)_{sat}$ deviations occurred in September 2020 and October 2021 (+0.57 and +0.34), while April 2021 showed good agreement (−0.08). In contrast, $(N_2/Ar)_{mes}$ was strongly underestimated in April (−0.99) and overestimated in autumn (+1.41).

At the Gdańsk Deep (> 80 m), $(N_2/Ar)_{sat}$ differences were small and consistent (+0.27). $(N_2/Ar)_{mes}$ exhibited larger seasonal variability but generally remained within the long-term variability range.

At the Gotland Deep (> 90 m), moderate discrepancies were observed for $(N_2/Ar)_{sat}$ (+0.29), while $(N_2/Ar)_{mes}$ showed a larger overestimation (+0.80).

3.4 Spatial variability and environmental controls of ΔN_2 accumulation below the halocline

At the Bornholm Deep (> 60 m), ΔN_2 exhibited pronounced variability (Figures 9–10). The model overestimated ΔN_2 in September 2020 (+10.71 μmol kg^{-1}) and October 2021 (+16.24 μmol kg^{-1}), but underestimated it in April 2021 (−14.23 μmol kg^{-1}). Notably, except for September 2020, modeled ΔN_2 decreased with depth, whereas observations showed the opposite trend.

At the Gdańsk Deep (> 80 m), agreement was generally strong. Moderate underestimation occurred in Septem-

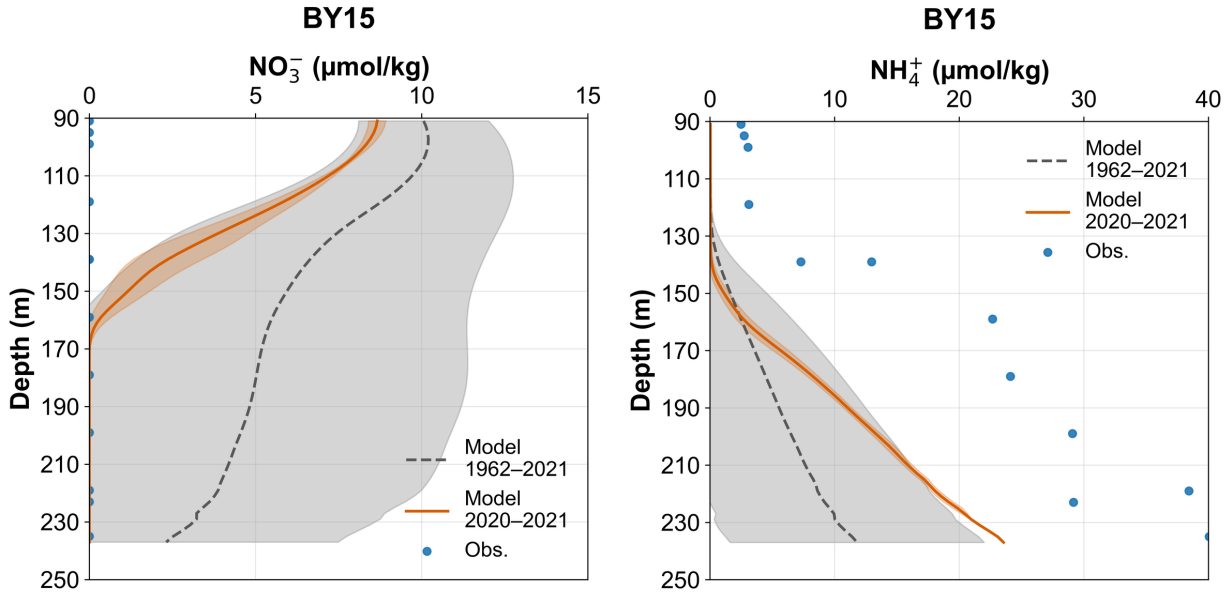

Figure 8. Vertical distribution of nutrient (NO_3^- and NH_4^+) distribution in the water column of the Gotland Deep. The solid gray line represents model data, while the dots indicate observational data.

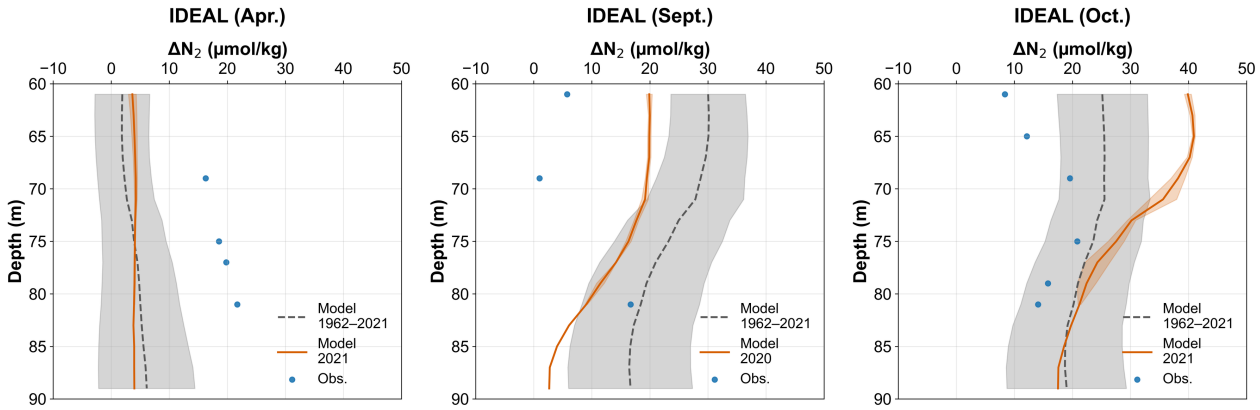

Figure 9. Vertical distribution of ΔN_2 in the water column of the Bornholm Deep. The solid gray line represents model data, while the dots indicate observational data. ΔN_2 is defined as the excess dissolved N_2 derived from deviations of the measured N_2/Ar ratio from its equilibrium value and serves as an integrative tracer of nitrogen removal in stratified, oxygen-depleted waters.

ber 2020 (−2.18 μmol kg^{-1}) and January 2021 (−7.91 μmol kg^{-1}), likely related to small differences in argon concentrations that propagate into ΔN_2 calculations. April and September 2021 showed very good agreement, with no statistically significant differences and a consistent increase of ΔN_2 with depth.

At the Gotland Deep (>90 m), significant model–data differences were found in September 2020 (+15.29 μmol kg^{-1}), whereas September 2021 showed much better agreement (+2.76 μmol kg^{-1}; no statistically significant differences). The earlier mismatch may reflect interannual environmental variability or limited observational coverage.

To further examine the large-scale spatial and seasonal variability in bottom-water ΔN_2, model simulations were analysed for the three Baltic Sea basins (Figures 12–13). The highest ΔN_2 concentrations occurred in the Gotland Basin, intermediate values were observed in the Gdańsk

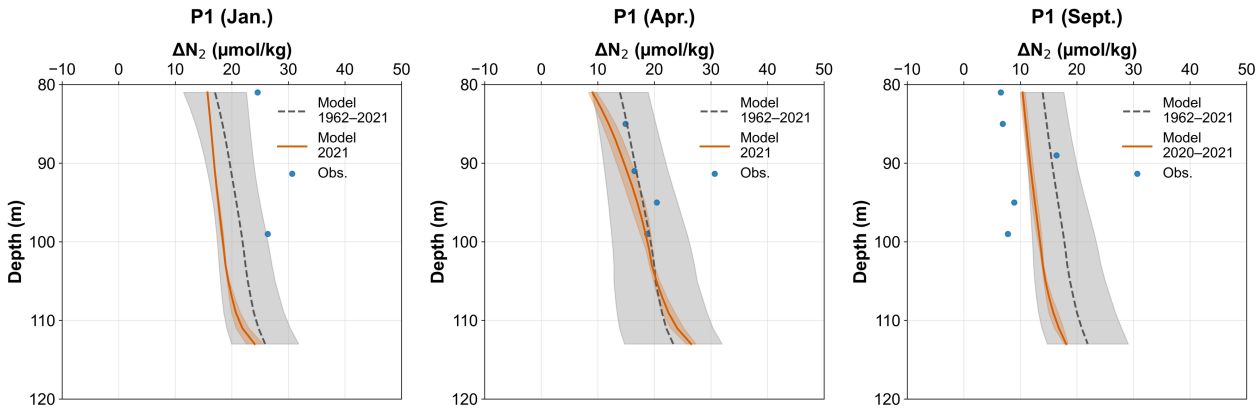

Figure 10. Vertical distribution of ΔN_2 in the water column of the Gdańsk Deep. The solid gray line represents model data, while the dots indicate observational data.

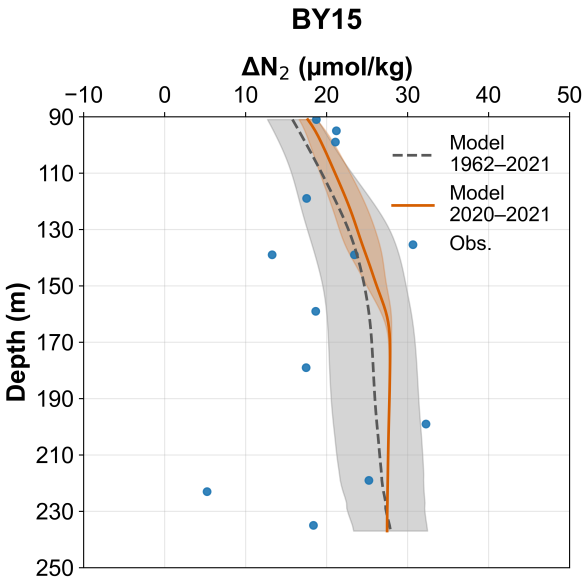

Figure 11. Vertical distribution of ΔN_2 in the water column of the Gotland Deep. The solid gray line represents model data, while the dots indicate observational data.

Basin, whereas the lowest values characterized the Bornholm Basin. Seasonal variability was most evident in the Gdańsk Basin, with generally higher ΔN_2 accumulation during winter than in summer. The Gotland Basin showed relatively stable ΔN_2 concentrations throughout the investigated period, while stronger variability was observed in the Bornholm Basin.

To identify the environmental factors underlying these spatial and seasonal patterns, relationships between ΔN_2 and selected environmental variables were further examined. In the model data, Spearman analysis showed no significant direct relationship between ΔN_2 and pelagic denitrification rates ($\rho = -0.05$, $p = 0.60$). However, significant negative correlations were observed between ΔN_2 and O_2 ($\rho = -0.41$, $p < 0.001$), NO_3^- ($\rho = -0.51$, $p < 0.001$), and POC ($\rho = -0.82$, $p < 0.001$). A weaker but significant negative relationship was also observed between ΔN_2 and zonal velocity ($\rho = -0.210$, $p = 0.049$).

The multivariate GAM including pelagic denitrification rate, O_2, NO_3^-, POC, and zonal velocity explained 91.7% of ΔN_2 variability (adjusted $R_2 = 0.91$, AIC = 79.13, $n = 88$). Despite the absence of a significant Spearman correlation, denitrification rate was identified as a significant predictor of ΔN_2 variability in the GAM analysis (edf = 0.96, $p < 0.001$). This indicates that the relationship between denitrification and excess N_2 accumulation becomes evident when other environmental controls are considered. Oxygen remained a significant predictor in the GAM (edf = 1.36, $p < 0.001$), supporting the importance of redox conditions in regulating ΔN_2 accumulation below the halocline. Similarly, POC showed a significant and nonlinear effect on ΔN_2 variability (edf = 3.83, $p < 0.001$), suggesting that organic matter availability and associated remineralization processes represent important controls on excess N_2 dynamics. Although NO_3^- showed a significant negative correlation with ΔN_2 in the Spearman analysis, it was not retained as an independent predictor in the multivariate GAM (edf ≈ 0, $p = 0.546$). This suggests that nitrate variability was largely associated with other controlling factors, such as oxygen conditions, organic matter availability, and denitrification activity. The relationship between ΔN_2 and NH_4^+ was weak and not statistically significant ($\rho = 0.138$, $p = 0.200$), suggesting that NH_4^+ variability was not a major factor explaining ΔN_2 patterns. Additional analysis of hydrographic variables showed that modeled ΔN_2 was moderately negatively correlated with temperature ($\rho = -0.504$, $p < 0.001$), while salinity showed a weak positive correlation with ΔN_2 ($\rho = 0.260$, $p = 0.009$). In

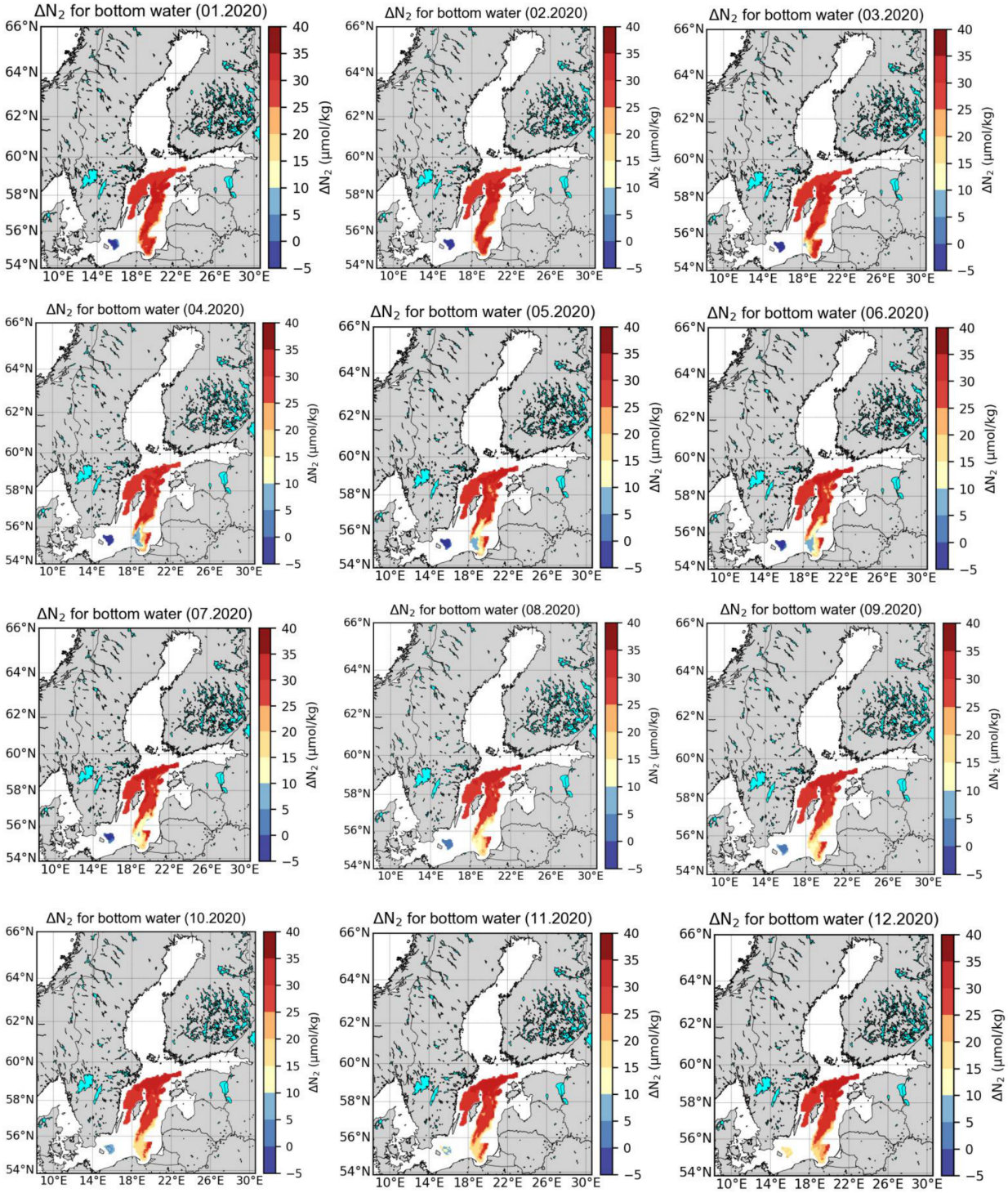

Figure 12. Modeled ΔN_2 distribution in bottom waters from January to December 2020. ΔN_2 is defined as the excess dissolved N_2 derived from deviations of the measured N_2/Ar ratio from its equilibrium value and serves as an integrative tracer of nitrogen removal in stratified, oxygen-depleted waters.

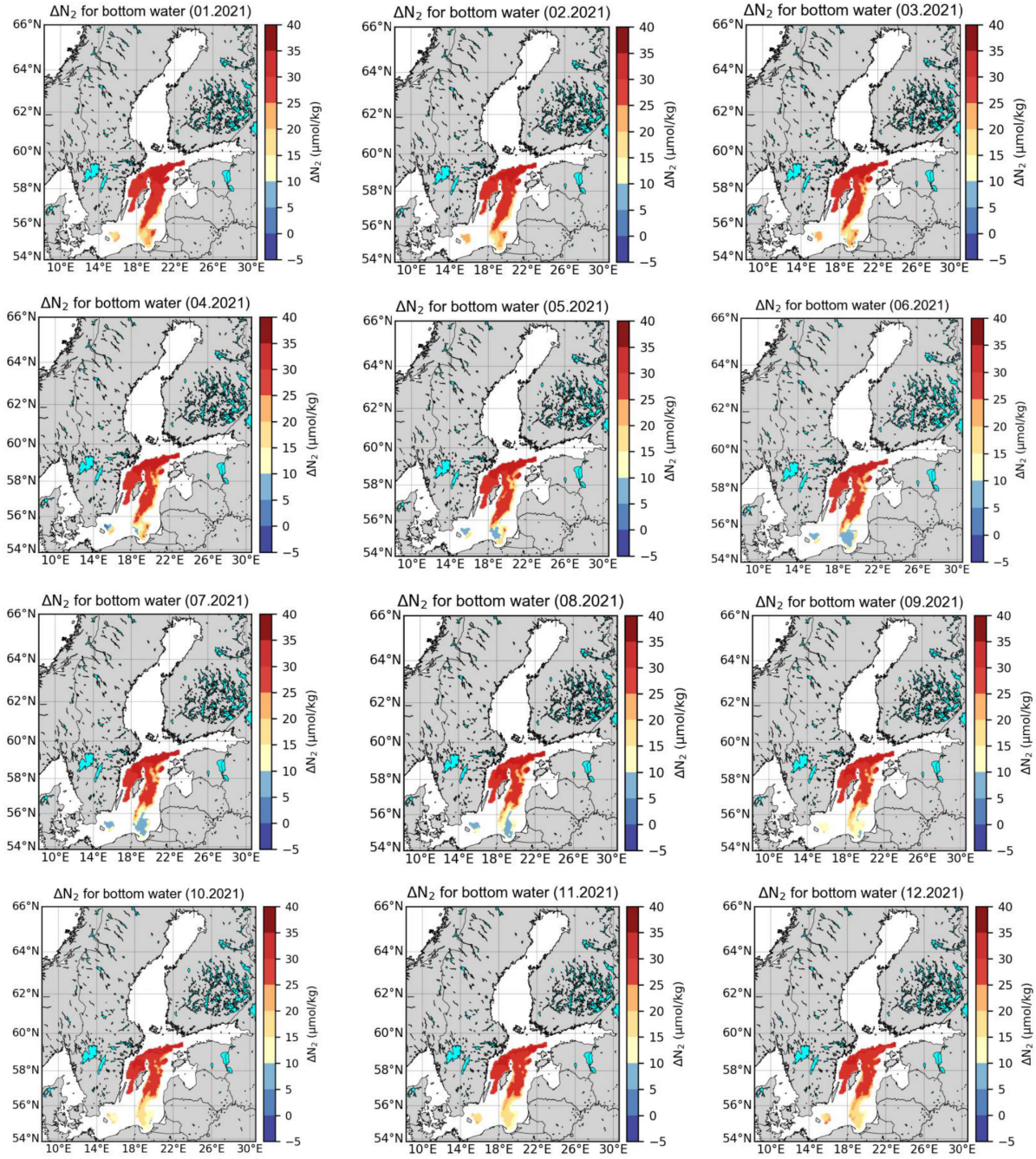

Figure 13. Modeled ΔN_2 distribution in bottom waters from January to December 2021. ΔN_2 is defined as the excess dissolved N_2 derived from deviations of the measured N_2/Ar ratio from its equilibrium value and serves as an integrative tracer of nitrogen removal in stratified, oxygen-depleted waters.

contrast, observational data did not show statistically significant relationships between ΔN_2 and temperature ($\rho = -0.443$, $p = 0.075$) or salinity ($\rho = -0.177$, $p = 0.498$). Our analysis revealed that hydrodynamic conditions appeared to influence ΔN_2 distribution, as indicated by a moderate negative correlation with zonal currents, while no

significant relationship was found with meridional currents.

Further identification of environmental factors controlling pelagic denitrification below the halocline was conducted. Modeled denitrification rates ranged from approximately 0.0010 to 0.0200 μmol kg^{-1} day^{-1}. Spearman analysis showed a significant negative relationship between denitrification rates and O_2 concentration ($\rho = -0.554$, $p < 0.001$), supporting enhanced nitrogen removal under oxygen-depleted conditions. A weaker but significant negative relationship was also observed with NO_3^- ($\rho = -0.262$, $p = 0.009$), whereas no significant direct correlation was detected between denitrification rates and POC concentration ($\rho = 0.130$, $p = 0.198$). Zonal velocity showed a weak but significant positive correlation with denitrification rates ($\rho = 0.285$, $p = 0.007$). The multivariate GAM including O_2, NO_3^-, POC, and zonal velocity explained 98.1% of the variability in modeled denitrification rates (adjusted $R_2 = 0.98$, AIC $= -1131.3$, $n = 88$). All tested predictors were identified as significant contributors to denitrification variability, including O_2 (edf $= 2.60$, $p < 0.001$), NO_3^- (edf $= 4.93$, $p < 0.001$), POC (edf $= 3.24$, $p < 0.001$), and zonal velocity (edf $= 4.79$, $p < 0.001$).

3.5 Sources of uncertainty in modeled ΔN_2

Differences in T, ranging from -5.97°C to $+5.18$°C, have the potential to alter ΔN_2 by up to ~ 8 μmol kg^{-1}. However, such large temperature mismatches occurred only in the Bornholm Deep, where they likely contributed to the pronounced deviations in modeled ΔN_2. At the other stations, T differences were much smaller ($\approx$0.5°C) and would result in ΔN_2 variations of only ~ 0.3 μmol kg^{-1}, which is negligible relative to the observed variability. Similarly, S differences of ~ 0.85 lead to minor ΔN_2 changes (~ 0.4 μmol kg^{-1}), suggesting that hydrographic biases in T and S play a secondary role outside the Bornholm region.

In contrast, discrepancies in O_2 were more substantial, particularly in the Bornholm and Gdańsk Deeps (from -17 to $+104$ μmol kg^{-1}). Because denitrification is highly sensitive to O_2, model overestimation of O_2 may suppress simulated denitrification rates, leading to indirect underestimation of biologically produced N_2. Thus, O_2 biases likely exert a stronger control on ΔN_2 errors than T or S mismatches.

Model-data differences in NO_3^- and NH_4^+ (often ~ 10 μmol kg^{-1}) are also important. NO_3^- directly fuels denitrification, while NH_4^+ contributes via nitrification and anammox pathways; therefore, biases in these substrates can propagate into nitrogen removal estimates. The strong seasonal variability in nutrient biases at the Bornholm Deep indicates that local biogeochemical conditions are particularly difficult to reproduce there, further contributing to ΔN_2 uncertainty.

Hydrographic discrepancies in T and S also influence calculations of (N_2/Ar)sat, leading to slight model overestimation at the Bornholm and Gdańsk Deeps (up to +0.57 and +0.31, respectively), whereas mismatches at the Gotland Deep were minimal. Additionally, model overestimation of O_2, especially during winter and spring, can reduce simulated (N_2/Ar)mes. ΔN_2 is derived from the difference between measured and equilibrium N_2/Ar ratios. Therefore, combined biases in (N_2/Ar)sat and (N_2/Ar)mes may lead to underestimation of excess N_2 in model outputs. This complicates the detection of biologically produced N_2 and partly explains the large ΔN_2 deviations observed in the Bornholm Deep, where errors ranged from strong underestimation (-14 μmol kg^{-1}) to overestimation ($+16$ μmol kg^{-1}).

The Bornholm Deep is particularly challenging to simulate due to its dynamic hydrography and frequent North Sea inflows through the Danish Straits (Fu et al., 2012; Stanev et al., 2015; Stockmayer et al., 2023). These events introduce saline, O_2-rich waters that rapidly alter stratification and redox conditions, making accurate representation of local biogeochemistry difficult. As a result, ΔN_2 variability in this basin likely reflects both real environmental fluctuations and model limitations.

Despite these regional discrepancies, especially in the Bornholm Deep, overall model observation agreement was good in the Gdańsk and Gotland Deeps. Differences below ~ 2 μmol kg^{-1} at Gdańsk and within ~ 5 μmol kg^{-1} elsewhere fall within the expected uncertainty range for combined hydrographic and biogeochemical simulations. Such deviations may arise from seasonal variability, internal system dynamics, or structural model limitations, and should therefore be interpreted cautiously. Nevertheless, the model performance is sufficient to support analysis of basin-scale spatial and seasonal patterns in N_2 distribution and denitrification.

4. Discussion

4.1 Seasonal and spatial variability of excess dinitrogen (ΔN_2) in the bottom layer

In this subsection, we focus on modeled bottom-layer conditions to examine the spatial distribution of ΔN_2 across the Baltic Sea below the halocline (Figures 12–13). Here, "bottom water" refers to the deepest available model layer at each station, representing the last depth above the sediment. Emphasizing bottom waters is particularly relevant, as these layers represent key zones for nitrogen removal. Coastal regions and bottom boundary layers are widely recognized as hotspots of nitrogen cycling due to elevated nutrient availability and intense microbial activity (Bartl et al., 2018; Wang et al., 2019). Denitrification rates are especially high in organic-rich muddy sediments compared with sandy substrates, highlighting strong spatial variability and the potential for substantial nitrogen loss in depositional areas (Lai et al., 2023). Therefore, identifying bottom-layer ΔN_2 hotspots provides important insight into the basin-scale functioning of the Baltic nitrogen cycle

(Schulz et al., 2021; Li et al., 2021). In the model formulation, ΔN_2 integrates multiple nitrogen transformation pathways and transport processes. As such, it represents a cumulative signal of nitrogen removal rather than a direct proxy for ongoing denitrification.

The observed spatial gradient in ΔN_2 accumulation likely reflects differences in hydrographic isolation, OM supply, and redox conditions. The persistently high ΔN_2 levels in the Gotland Basin support its established role as a potential nitrogen transformation and retention site in the Baltic Sea, where long-term stratification, limited ventilation, and sustained OM accumulation promote sediment anoxia and active microbial nitrogen transformation (Hannig et al., 2006; Thureborn et al., 2013, 2016; Frey et al., 2014). However, in the Gotland Deep, the deepest waters are often characterized by strongly reducing, sulfidic conditions, where nitrate concentrations are typically very low or absent. Under such conditions, pelagic denitrification may become substrate-limited due to nitrate depletion. Therefore, the high ΔN_2 concentrations observed in the bottom layer should not be interpreted as evidence of ongoing local denitrification at that depth. Instead, they likely reflect the cumulative signal of nitrogen loss occurring within the redoxcline, from ongoing benthic denitrification with subsequent diffusion of N_2 from the sediments, or via lateral transport from adjacent water masses. Moreover, model overestimation of nitrate in the Gotland Deep may artificially enhance simulated denitrification potential, and this limitation should be considered when interpreting basin-scale patterns.

In contrast, the comparatively low ΔN_2 concentrations in the Bornholm Basin suggest either weaker benthic nitrogen removal or a stronger influence of ventilation and water mass exchange, which may reduce the accumulation of excess N_2.

Seasonal changes in ΔN_2 accumulation in the Gdańsk Basin likely reflect variations in organic matter availability and redox conditions, which can enhance nitrogen removal processes during colder months. Increased availability of POC following phytoplankton production and subsequent export can fuel benthic respiration and promote conditions favorable for denitrification (Carstensen et al., 2014; Tamelander et al., 2017). Winter mixing may further support this process by redistributing OM and nutrients toward the bottom layer, intensifying O_2 consumption and promoting suboxic conditions favorable for denitrification. The resulting seasonal enhancement of N_2 production aligns with observational evidence of elevated wintertime ΔN_2 in hypoxic bottom waters. In contrast, the Gotland Basin displayed comparatively weak seasonal variability; ΔN_2 here should be interpreted as a basin-scale accumulation signal shaped by past nitrogen loss and redistribution processes.

The Bornholm Basin exhibited only minor seasonal changes, indicating a more variable or less efficient coupling between OM supply and nitrogen removal processes.

Interannual differences, particularly in the Bornholm Basin, point to the sensitivity of ΔN_2 accumulation to episodic hydrographic and biogeochemical conditions. Variability between 2020 and 2021 may reflect changes in stratification strength, inflow events, or differences in OM deposition, all of which can modulate O_2 dynamics and microbial activity at the sediment-water interface. Such variability underscores the importance of considering both physical forcing and biogeochemical feedbacks when interpreting basin-scale nitrogen removal.

Overall, the modeled ΔN_2 distribution highlights a stable spatial gradient across the Baltic basins, overlaid by seasonally and interannually varying intensity. These patterns emphasize the dominant role of deep, poorly ventilated basins in shaping the long-term accumulation and retention of excess N_2, and suggest that future changes in stratification, OM export, or O_2 conditions may substantially modify bottom-layer nitrogen dynamics.

4.2 Relationship between (ΔN_2) and oxygen, nutrients, POC, temperature and salinity below the halocline

This subsection examines the dynamics of ΔN_2 across the Bornholm, Gdańsk, and Gotland Deeps using primarily model-based results, with observational data used in parallel to evaluate relationships between ΔN_2 and selected variables (temperature, salinity, O_2, NO_3^-, NH_4^+; Table 1, Fig. S4). ΔN_2 is interpreted here as an integrative indicator of pelagic and benthic nitrogen loss potential together with transport processes (Neumann et al., 2022; Rolff et al., 2022; Sivasamy et al., 2025).

Denitrification preferentially occurs under low-O_2 conditions, typically below 10 μmol kg^{-1} (Bulow et al., 2010; Fuchsman et al., 2019), whereas concentrations above $\sim$ 60 μmol kg^{-1} can inhibit the process (Skiba, 2008; Eglīte et al., 2014; Devol et al., 2015). Even trace O_2 levels may suppress activity, with reductions in denitrification reported at concentrations as low as 205 kg^{-1} (Dalsgaard et al., 2014). Accordingly, our analysis focused on waters below the halocline, where O_2 concentrations decline into ranges potentially conducive to efficient denitrification.

Differences between modeled and observed ΔN_2-O_2 relationships may reflect that oxygen availability affects multiple nitrogen transformation processes, not only denitrification. The process also depends on the simultaneous availability of electron donors and acceptors. Thus, the absence of a simple ΔN_2-O_2 relationship in observations does not exclude active nitrogen loss but rather highlights the complex and integrated nature of ΔN_2 as a signal shaped by redox conditions, substrate availability, and physical transport processes.

NO_3^- availability is particularly critical, as it serves as the terminal electron acceptor in denitrification (Kritee et al., 2012). Although higher NO_3^- concentrations can support greater N_2 production when other conditions are

Table 1. The relationship between oxygen (O_2), nitrate (NO_3^-), ammonium (NH_4^+), particulate organic carbon (POC) (dissolved oxygen), denitrification rate, excess dinitrogen gas (ΔN_2), temperature and salinity; and the relationship between O_2, NO_3^-, POC, meridional current, zonal current, and denitrification rate. Correlations were calculated using model output from 2020–2021 for layers below the halocline, where O_2 concentration was equal to or below 10 μmol kg^{-1}.

Correlations	p-value (*model data; **observational data)	r_s (*model data; **observational data)
ΔN_2 vs. O_2	*< 0.05; **0.40	*-0.41 **0.22
ΔN_2 vs. NO_3^-	*< 0.05; **0.52	*-0.51; **-0.17
ΔN_2 vs. NH_4^+	*0.20; **0.70	*0.14; **0.1
ΔN_2 vs. POC	*<0.05; **no data	*0.82; **no data
ΔN_2 vs. denitrification rate	*0.60; **no data	*-0.05; **no data
Denitrification rate vs. O_2	*< 0.05; **no data	*-0.64; **no data
Denitrification rate vs. NO_{3-}	*< 0.05; **no data	*-0.54; **no data
Denitrification rate vs. POC	*0.21; **no data	*-0.14; **no data
ΔN_2 vs. zonal velocity	*< 0.05; **no data	*-0.21; **no data
ΔN_2 vs. meridional velocity	*0.93; **no data	*0.01; **no data
Temperature	*< 0.05; **0.08	*-0.50; **-0.44
Salinity	*< 0.05; **0.50	*0.30; **-0.18

favorable (Pina-Ochoa et al., 2006; Lin et al., 2017; Aalto et al., 2021), inverse relationships between denitrification and NO_3^- have also been reported (Shao et al., 2011; De La Fuente et al., 2021; Benelli et al., 2024). The GAM analysis showed that NO_3^- did not remain an independent predictor of ΔN_2 variability after accounting for denitrification activity, oxygen availability, organic matter supply, and hydrodynamic transport. However, it should be noted that the model tends to overestimate nitrate concentrations in the Gotland Deep (Chapter 3), which may influence the strength of this relationship. In reality, nitrate in the deepest waters is often strongly depleted, potentially limiting ongoing water-column denitrification. Moreover, in the highly stratified waters of the Gotland Deep, prolonged periods of stagnation and limited deep-water ventilation contribute to the accumulation of excess N_2 over time, as products of past nitrogen removal are retained in the deep layer. Therefore, the observed and modeled patterns likely reflect cumulative nitrate reduction and retention during stagnation periods rather than ongoing local pelagic denitrification in nitrate-depleted deep waters (Kritee et al., 2012).

Beyond electron acceptors, the supply of particularly labile POC is a fundamental control on denitrification, as it provides the energy source for heterotrophic respiration (Li et al., 2010; Ward et al., 2008; Burgin et al., 2007). When NO_3^- is scarce, it becomes the limiting factor; when NO_3^- is abundant, denitrification may instead be constrained by OM quantity or quality (Warneke et al., 2011). The negative relationship indicates that excess N_2 accumulation is primarily associated with regions where organic matter has already been utilized during previous respiration and denitrification processes. It also suggests that, beyond a certain threshold, pelagic denitrification rates may become less sensitive to further increases in substrate supply (Magri et al., 2022).

The weak relationship between ΔN_2 and NH_4^+ suggests a limited contribution of anammox to basin-scale ΔN_2 variability. Although anammox may contribute locally, its signal is likely minor compared to denitrification and transport-related processes, which is consistent with Grabski et al. (2025), who reported no anammox genes in Baltic Sea deep waters.

In addition to biogeochemical controls, hydrographic conditions may also contribute to ΔN_2 variability below the halocline. The negative relationship with temperature and positive relationship with salinity observed in the model suggests that ΔN_2 accumulation is partly associated with the characteristics and residence time of deep-water masses. This likely reflects enhanced retention of excess N_2 in colder, more saline waters characterized by restricted ventilation rather than a direct influence of temperature or salinity on nitrogen removal processes. The absence of statistically significant relationships in observational data may be related to the limited temporal coverage of the dataset.

The results emphasize that denitrification efficiency depends on the availability of both electron donors (POC) and acceptors (NO_3^-) under sufficiently low O_2 conditions. Biological factors further complicate interpretation: even under favorable geochemical conditions, nitrogen loss will remain limited without an active denitrifying microbial community. Recent metagenomic studies from the

Baltic Sea show that denitrification potential is strongly shaped by microbial community composition, varies seasonally, and is linked to taxa such as Nitrosopumilaceae and Thioglobaceae (Grabski et al., 2025). Consequently, weak or negative correlations between ΔN_2 and individual environmental variables are expected. This is because ΔN_2 represents a time-integrated signal shaped by multiple redox pathways and transport processes rather than a direct measure of local pelagic denitrification intensity. It should be noted that the observational dataset used in this analysis covers only a two-year period (2020–2021) and includes a limited number of sampling events. The restricted temporal coverage may not fully capture longer-term variability or the full range of environmental conditions in the studied basins. Analyses based on longer time series and broader spatial coverage could potentially reveal additional patterns or different relationships between ΔN_2 and environmental drivers. Nevertheless, the aim of this study was to synthesize the currently available observational data together with model results in order to improve understanding of ΔN_2 variability below the halocline.

4.3 Relationship of pelagic denitrification rates with excess dinitrogen gas (ΔN_2)

Modeled denitrification rates were up to 20 times lower than the upper range of in situ estimates reported for the Baltic Sea (e.g., Dalsgaard et al., 2013). Although no significant direct relationship was observed between ΔN_2 and instantaneous pelagic denitrification rates, the GAM analysis demonstrated that denitrification significantly contributed to ΔN_2 variability when oxygen availability, organic matter supply, nitrate dynamics and physical transport were considered simultaneously. This indicates that the relationship between ΔN_2 and pelagic denitrification is complex, suggesting that other factors, such as physical transport processes like diffusion from sediments, may play a significant role in shaping its distribution (Deutsch et al., 2010; Bonaglia et al., 2017).

Moreover, pelagic denitrification rates observed in the model data were relatively low (up to 0.020 μmol kg^{-1} day^{-1}), but were within the range reported by Dalsgaard et al. (2013), ranging from 0.006 to 0.382 μmol kg^{-1} day^{-1}. The relatively low denitrification rates in the model may be partly explained by occasional overestimations of O_2 concentrations in certain areas and times, e.g. the Bornholm Deep, which can inhibit denitrification. However, the model also tends to overestimate nitrate concentrations at P1 and BY15 (Chapter 3), potentially enhancing denitrification potential. The simulated rates therefore likely reflect the combined influence of opposing biases in oxygen and nitrate fields. Although the nitrogen removal process has low efficiency in the water column, it can still significantly contribute to the overall denitrification process in the Baltic Sea. According to the literature, it has been claimed that water column denitrification can be as significant as sedimentary denitrification (Carstensen et al., 2014). It was reported that in some cases, water column denitrification can exceed sedimentary denitrification (Dalsgaard et al., 2013). Though denitrification in the water column can exhibit high rates, it is more variable and less constant over time than sedimentary denitrification (Hietanen et al., 2012; Dalsgaard et al., 2013).

Since the efficiency of water column denitrification depends on multiple interacting factors, such as nutrient availability, OM content, microbial community composition, and physical transport processes, additional analyses were performed to identify the main controls on nitrogen removal. In some cases, the highest denitrification rates were observed at very low NO_3^- concentrations, while higher NO_3^- concentrations did not result in a significant increase in reaction rates. This suggests that denitrification is regulated by the combined availability of electron acceptors, electron donors, and suitable redox conditions. Similar negative or weak correlations have been reported in estuarine systems, where factors such as OM lability, sulfide, and iron availability had a greater contribution to the denitrification process (Deng et al., 2015; Yang et al., 2015).

Regarding O_2, it appears that concentrations below 10 μmol kg^{-1} are rather optimal for denitrifying bacteria (Walter et al., 2006). The results imply that once a low O_2 concentration is reached, a further decrease does not significantly enhance the denitrification rate. These findings suggest that while substrate availability and O_2 conditions do influence denitrification, they are not the sole drivers of its variability in the Baltic Sea below the halocline. The observed results emphasize the complexity of denitrification dynamics in this region and demonstrate how important a holistic approach is to fully understand and predict changes in N dissipative processes.

Further analysis showed that the relationship between denitrification rates and POC availability was more complex than a direct response to organic matter concentration alone. This indicates that organic matter availability contributes to controlling nitrogen transformation processes, but its effect depends on the interaction with other environmental factors. POC is crucial for denitrifying bacteria, and low availability of labile organic carbon can limit denitrification even when high NO_3^- concentrations are available (Le Moigne et al., 2017; Schneider et al., 2017). However, even here, we noticed that a POC concentration as high as 3 μmol kg^{-1} can lead to both the highest and the lowest denitrification rates observed in our study. This apparent inconsistency likely reflects that POC concentration alone does not determine pelagic denitrification intensity. Even at similar POC levels, denitrification depends on simultaneous nitrate availability, oxygen conditions, and the reactivity of organic matter. Therefore, comparable bulk POC concentrations may occur under different redox regimes and substrate conditions, resulting in contrasting pelagic

denitrification rates.

Despite limited water exchange with the upper layers in the Baltic Sea, other vertical and horizontal mixing processes remain important, even below the halocline. These mixing processes, including turbulent mixing induced by internal waves, significantly influence denitrification rates and nitrogen gas accumulation in the water column (Reissmann et al., 2009; Dalsgaard et al., 2013). Thus, we aimed to further investigate the impact of hydrodynamic conditions, specifically meridional (north-south) and zonal (east-west) currents, on the distribution of excess N_2 in the water column (Table 1; Fig. S13). Although the zonal component showed a stronger relationship with ΔN_2 variability in the present analysis, both velocity components represent horizontal circulation processes that may influence the redistribution and retention of excess N_2 below the halocline. Previous studies have demonstrated that deep-water circulation in the Baltic Sea is highly variable and controlled by density-driven flows, wind forcing, and episodic inflow events, which strongly affect the ventilation and residence time of deep-water masses (Hagen and Feistel, 2004; Wieczorek et al., 2008; Liblik et al., 2024).

In our model simulations, monthly averaged current velocities below the halocline during 2020–2021 ranged from approximately 0.005 to 0.015 m s^{-1} for the meridional component and from −0.006 to 0.002 m s^{-1} for the zonal component. These factors, together with overall circulation, vertical mixing, and transport processes, contribute to the complex and variable distribution of N_2 in oceanic regions. Observational studies have reported substantially higher instantaneous velocities in the Baltic Sea deep layers, particularly during periods of intensified deep-water transport and inflow-related circulation (Hagen and Feistel, 2004; Wieczorek et al., 2008; Liblik et al., 2024). Based on the data from Liblik et al. (2022), it was shown that the data obtained from three models (excluding ERGOM-MOM) estimated the average meridional northward current velocity in the range of 0–0.01 m s^{-1}, with most models indicating a value of around 0.001 m s^{-1}. These results were significantly underestimated compared to observational data, which showed a 30-fold higher value of 0.03 m s^{-1} (Hagen et al., 2004). Similarly, Liblik et al. (2022) reported higher observed zonal current velocities, with values ranging from approximately 0.019 to 0.040 m s^{-1}. These differences indicate that uncertainties in the representation of horizontal circulation, including both meridional and zonal components, may influence modeled transport processes and consequently contribute to discrepancies in the simulated distribution of excess N_2.

Data analysis revealed that although denitrification contributes to the production of excess N_2, its impact on the observed distribution of N_2 concentrations in waters below the halocline cannot be clearly determined. Overall, the results demonstrate that pelagic denitrification below the Baltic Sea halocline is controlled by the combined influence of redox conditions, nitrate availability, organic matter supply and physical transport processes. The GAM indicates that variability in denitrification rates cannot be attributed to a single environmental factor, but rather reflects the interaction between multiple biogeochemical and hydrodynamic controls.

In the model framework, ΔN_2 represents the net balance of multiple nitrate-reducing pathways, including pelagic and benthic denitrification, coupled nitrification-denitrification, nitrate-driven oxidation of reduced sulfur compounds, sediment-water exchange fluxes, and advective transport and N_2 fixation. Consequently, ΔN_2 should not be interpreted as a direct proxy for pelagic denitrification alone. Instead, it represents an integrated indicator of nitrogen loss processes and physical redistribution within the system.

Thus, while biological processes control N_2 production, the spatial distribution of excess N_2 below the Baltic Sea halocline appears to be strongly modulated by physical transport and sediment-water exchange processes. Recent studies indicated that although genes encoding the first step of denitrification (e.g., nar, nap) were abundant and primarily associated with Proteobacteria and Actinobacteria, metagenomic data indicated that these organisms lacked the genes necessary to carry out the subsequent steps of denitrification, leading to the final production of N_2 (Grabski et al., 2025).

4.4 Impact of model uncertainties on the data interpretation

Despite the overall ability of the ERGOM-MOM model to reproduce basin-scale ΔN_2 patterns, uncertainties related to oxygen and nutrient simulations should be considered when interpreting local denitrification dynamics. Previous MOM–ERGOM applications demonstrated that the model is able to capture spatial oxygen gradients, seasonal variability, and vertical oxygen dynamics, supporting its application for Baltic Sea oxygen assessments (Naumov et al., 2023; Piehl et al., 2023). Moreover, ERGOM simulations have shown good performance in reproducing nutrient distributions in surface waters, although regional deviations, including slight nutrient overestimations, may occur especially in the northern Baltic Sea and the Gulf of Bothnia (Neumann et al., 2022).

Nevertheless, model–observation discrepancies can vary between sub-basins and are particularly important in dynamically changing regions. Naumov et al. (2023) identified uncertainties in deep-water oxygen simulations in the Bornholm Basin, where modeled oxygen concentrations showed positive deviations below approximately 50 m. Such oxygen overestimation may maintain artificially more oxic conditions and consequently suppress simulated denitrification rates, which should be considered when interpreting local nitrogen removal processes.

In the Gotland Deep, our model validation indicated an

overestimation of nitrate concentrations. Since nitrate acts as the terminal electron acceptor during denitrification, this bias may increase the apparent availability of electron acceptors and therefore influence modeled denitrification potential (Neumann et al., 2022). This may lead to an overestimation of local denitrification potential. However, under stagnant and strongly reducing conditions, nitrate can become depleted, and accumulated ΔN_2 may instead reflect previous nitrogen removal processes.

Consequently, these biases in oxygen and nitrate fields may introduce uncertainty into the relationship between ΔN_2 accumulation and instantaneous pelagic denitrification rates. Considering these model uncertainties and to reduce overinterpretation of local denitrification patterns, analyses directly linking ΔN_2 with denitrification rates were restricted to low-oxygen conditions ($O_2 < 10$ μmol kg^{-1}). Furthermore, the interpretation of spatial ΔN_2 patterns focused primarily on bottom waters, where limited ventilation allows the accumulation of signals related to nitrogen removal processes over longer timescales.

Interpretation of ΔN_2 variability in the remaining water layers below the halocline remains more challenging, as uncertainties associated with simulated oxygen and nutrient fields may complicate the assessment of the contribution of specific local biogeochemical processes and seasonal dynamics to observed ΔN_2 changes.

This limitation is further enhanced by the restricted temporal coverage of observational data available for model evaluation compared with previous long-term validation studies (e.g., Neumann et al., 2022), which may not capture the full range of Baltic Sea variability associated with different phases of inflow-driven ventilation and stagnation. Therefore, the presented results should be considered as an approximation of the dominant mechanisms controlling ΔN_2 variability during the investigated period rather than an exact representation of all spatial and temporal variations in the Baltic Sea.

5. Conclusions

The aim of this study was to improve understanding of excess dinitrogen (ΔN_2) dynamics below the Baltic Sea halocline, with emphasis on spatial and temporal variability and its role in nitrogen removal. Using the coupled physical–biogeochemical model ERGOM-MOM 5.1 together with observations, we investigated three deep basins (Bornholm, Gdańsk, and Gotland deeps) which are affected by hypoxic and anoxic conditions.

Model–observation comparisons showed overall good performance, particularly at Gotland Deep and Gdańsk Deep. Larger discrepancies occurred in the Bornholm Deep, where dynamic hydrographic conditions and episodic North Sea inflows complicate simulation of O_2 and nutrient distributions. Among environmental variables, O_2 biases had the strongest influence on ΔN_2 uncertainty, while temperature and salinity mismatches contributed only marginally outside the Bornholm region.

A persistent spatial gradient in ΔN_2 was identified, with the Gotland Basin maintaining the highest mean concentrations (~ 28 μmol kg^{-1}) throughout the year, the Gdańsk Basin showing intermediate values, and the Bornholm Basin the lowest. This pattern reflects differences in stratification, ventilation, OM accumulation, and redox state, confirming the role of deep, poorly ventilated basins as nitrogen removal and N_2 accumulation hotspots. Seasonal variability was most pronounced in the Gdańsk Basin, where higher winter ΔN_2 suggests enhanced nitrogen removal supported by OM supply and mixing-driven nutrient redistribution.

Relationships between ΔN_2 and O_2, nutrients, POC, and modeled denitrification rates were weak, indicating that ΔN_2 does not solely reflect ongoing in situ water-column denitrification.

Instead, ΔN_2 reflects the net outcome of multiple interacting pathways, including pelagic and benthic denitrification, coupled nitrification-denitrification, nitrate-driven sulfur oxidation, sediment-water exchange fluxes, and physical redistribution processes. Given the limited temporal coverage of both modeled and observational datasets, these results should be regarded as indicative rather than definitive. The observational dataset used for model validation covered 2020–2021 and therefore captured one specific phase of the Baltic Proper hydrographic variability following the 2014 Major Baltic Inflow. Although the strongest ventilation signal associated with this event was no longer present, deep-water conditions during the investigated period reflected the subsequent transition toward stagnation, oxygen depletion, and the redevelopment of reducing conditions (Mohrholz et al., 2015; Myllykangas et al., 2017). Consequently, ΔN_2 patterns observed during this period should be interpreted in the context of this hydrographic stage and may not represent the complete variability occurring over different inflow and stagnation phases. However, the stronger association with zonal currents underscores the important role of hydrodynamic transport in redistributing excess N_2. In this framework, biological processes primarily regulate N_2 production, whereas physical circulation governs its spatial distribution. Future observational studies incorporating direct measurements of pelagic denitrification are needed to better constrain these coupled mechanisms and improve predictions of nitrogen cycling under changing Baltic Sea conditions.

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Conflict of interest

None declared.

Supplementary material

Supplementary material associated with this article can be found here.

References

Aalto, S.L., Asmala, E., Jilbert, T., Hietanen, S., 2021. *Autochthonous organic matter promotes DNRA and suppresses N_2O production in sediments of the coastal Baltic Sea*. Estuar, Coast. Shelf Sci. 255, 107369.

Artamonova, K.V., Demidov, A.N., Zuev, O.A., 2019. *Suboxic and Anoxic Conditions of Deep Waters in the Gdansk Basin of the Baltic Sea*. Oceanology 59, 639–647.

Bartl, I., Liskow, I., Schulz, K., Umlauf, L., Voss, M., 2018. *River plume and bottom boundary layer–Hotspots for nitrification in a coastal bay?* Estuar. Coast. Shelf Sci. 208, 70–82.

Benelli, S., Bartoli, M., Magri, M., Brzana, R., Kendzierska, H., Styrcz-Olesiak, K., Janas, U., 2024. *Spatial and seasonal pattern of microbial nitrate reduction in coastal sediments in the Vistula River plume area, Gulf of Gdańsk*. Front. Marine Sci. 11, 1333707.

Bonaglia, S., Deutsch, B., Bartoli, M., Marchant, H.K., Brüchert, V., 2014. *Seasonal oxygen, nitrogen and phosphorus benthic cycling along an impacted Baltic Sea estuary: regulation and spatial patterns*. Biogeochemistry 119, 139–160.

Bonaglia, S., Hylén, A., Rattray, J.E., Kononets, M.Y., Ekeroth, N., Roos, P., Thamdrup, B., Brüchert, V., Hall, P.O., 2017. *The fate of fixed nitrogen in marine sediments with low organic loading: an in situ study*. Biogeosciences, 14(2), 285–300.

Bulow, S.E., Rich, J.J., Naik, H.S., Pratihary, A.K., Ward, B.B., 2010. *Denitrification exceeds anammox as a nitrogen loss pathway in the Arabian Sea oxygen minimum zone*. Deep Sea Res. Pt. I 57(3), 384–393.

Burgin, A.J., Hamilton, S.K., 2007. *Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways*. Front. Ecol. Environ. 5(2), 89–96.

Burska, D., Pryputniewicz, D., Falkowska, L., 2005. *Stratification of particulate organic carbon and nitrogen in the Gdańsk Deep (southern Baltic Sea)*. Oceanologia 47(2), 201–217. https://www.iopan.gda.pl/oceanologia/472bursk.pdf

Carstensen, J., Conley, D.J., Bonsdorff, E., Gustafsson, B.G., Hietanen, S., Janas, U., Jilbert, T., Maximov, A., Norkko, A., Norkko, J., Reed, D.C., 2014. *Hypoxia in the Baltic Sea: biogeochemical cycles, benthic fauna, and management*. Ambio 43, 26–36.

Dalsgaard, T., De Brabandere, L., Hall, P.O., 2013. *Denitrification in the water column of the central Baltic Sea*. Geochim. Cosmochim. Acta 106, 247–260.

Dalsgaard, T., Stewart, F.J., Thamdrup, B., De Brabandere, L., Revsbech, N.P., Ulloa, O., Canfield, D.E., DeLong, E.F., 2014. *Oxygen at nanomolar levels reversibly suppresses process rates and gene expression in anammox and denitrification in the oxygen minimum zone off Northern Chile*. mBio 5 (6), e01966-14. https://doi.org/10.1128/mBio.01966-14

De La Fuente, M.J., De la Iglesia, R., Farias, L., Daims, H., Lukumbuzya, M., Vargas, I.T., 2021. *Electrochemical enrichment of marine denitrifying bacteria to enhance nitrate metabolization in seawater*. J. Environ. Chem. Eng. 9(4), 105604.

Deng, F., Hou, L., Liu, M., Zheng, Y., Yin, G., Li, X., Lin, X., Chen, F., Gao, J., Jiang, X., 2015. *Dissimilatory nitrate reduction processes and associated contribution to nitrogen removal in sediments of the Yangtze Estuary*. J. Geophys. Res. Biogeos. 120(8), 1521–1531.

Deutsch, B., Forster, S., Wilhelm, M., Dippner, J.W., Voss, M., 2010. *Denitrification in sediments as a major nitrogen sink in the Baltic Sea: an extrapolation using sediment characteristics*. Biogeosciences 7(10), 3259–3271.

Devol, A.H., 2015. *Denitrification, anammox, and N_2 production in marine sediments*. Annu. Rev. Marine Sci. 7(1), 403–423.

Eglīte, E., Lavrinovičs, A., Müller-Karulis, B., Aigars, J., Poikāne, R., 2014. *Nutrient turnover at the hypoxic boundary: flux measurements and model representation for the bottom water environment of the Gulf of Riga, Baltic Sea*. Oceanologia 56(4), 711–735. http://dx.doi.org/10.5697/oc.56-4.711

Emerson, D., et al., 2015 *Factors controlling denitrification in the marine environment*, Marine Chem. 176, 29–40.

Fonselius, S.H., 1969. *Hydrography of the Baltic Deep Basins III*, CB Boktryckeri A.-B., 97 pp.

Frey, C., Dippner, J.W., Voss, M., 2014. *Close coupling of N-cycling processes expressed in stable isotope data at the redoxcline of the Baltic Sea*. Global Biogeochem. Cy. 28(9), 974–991.

Fu, W., She, J., Dobrynin, M., 2012. *A 20-year reanalysis experiment in the Baltic Sea using three-dimensional variational (3DVAR) method*. Ocean Sci. 8(5), 827–844.

Fuchsman, C.A., Paul, B., Staley, J.T., Yakushev, E.V., Murray, J.W., 2019. *Detection of transient denitrification during a high organic matter event in the Black Sea*. Global Biogeochem. Cy. 33(2), 143–162.

Gaye, B., Nagel, B., Dähnke, K., Rixen, T., Emeis, K.C., 2013. *Evidence of parallel denitrification and nitrite oxidation in the ODZ of the Arabian Sea from paired stable isotopes of nitrate and nitrite*. Global Biogeochem. Cy. 27(4), 1059–1071.

Grabski, M., Kotlarska, E., Łuczkiewicz, A., Hryniewicz, K., Węgrzyn, G., Szymczycha, B., 2025 *Spatial and seasonal*

distribution of selected nitrogen cycle genes in deep waters of the Baltic Proper. Front. Marine Sci. 12. https://doi.org/10.3389/fmars.2025.1456825

Griffies, S., Stouffer, R., Adcroft, A., Bryan, K., Dixon, K.W., Hallberg, R., Harrison, M.J., Pacanowski, R.C. Rosati, A., 2015. *A historical introduction to MOM*. https://www.gfdl.noaa.gov/wp-content/uploads/2019/04/mom_history_2017

Hagen, E., Feistel, R., 2004. *Observations of low-frequency current fluctuations in deep water of the Eastern Gotland Basin/Baltic Sea*. J. Geophys. Res.-Oceans 109(C3), C03044. https://doi.org/10.1029/2003JC002017

Hamme, R.C., Emerson, S.R., 2004. *The solubility of neon, nitrogen and argon in distilled water and seawater*. Deep-Sea Res. 51, 1517–1528. https://doi.org/10.1016/j.dsr.2004.06.009

Hannig, M., Braker, G., Dippner, J., Jürgens, K., 2006. *Linking denitrifier community structure and prevalent biogeochemical parameters in the pelagial of the central Baltic Proper (Baltic Sea)*. FEMS Microbiol. Ecol. 57(2), 260–271.

Hastie, T.J., 2017. *Generalized additive models*, Chapter 7, [in:] *Statistical models in S*, e-book, (1st published in 1992, Taylor and Francis, New York, 624 pp.) 249–307. https://www.taylorfrancis.com/chapters/edit/10.1201/9780203738535-7/generalized-additive-models-trevor-hastie?context=ubx&refId=ac4fc112-c07a-4b6d-b24b-92ffd3116b9e

HELCOM. 2021. *Baltic Sea Action Plan*, 2021 Update, Adopted in Lübeck.

Hietanen, S., Jäntti, H., Buizert, C., Jürgens, K., Labrenz, M., Voss, M., Kuparinen, J., 2012. *Hypoxia and nitrogen processing in the Baltic Sea water column*. Limnol. Oceanogr. 57(1), 325–337.

Hietanen, S., Kuparinen, J., 2008. *Seasonal and short-term variation in denitrification and anammox at a coastal station on the Gulf of Finland, Baltic Sea*. Hydrobiologia 596, 67–77.

Kohonen, T., 2019. *Regional environmental policies in Europe: Baltic/Nordic cooperation*. [in:] *Environmental cooperation in Europe*, Routledge, 209–222. https://doi.org/10.4324/9780429041617-16

Kritee, K., Sigman, D.M., Granger, J., Ward, B.B., Jayakumar, A., Deutsch, C., 2012. *Reduced isotope fractionation by denitrification under conditions relevant to the ocean*. Geochim. Cosmochim. Acta 92, 243–259.

Kullenberg, G., 1981. *Physical oceanography*. Elsevier Oceanogr. Ser. Vol. 30, 135–181.

Kullenberg, G., 1982. *Mixing in the Baltic Sea and implications for the environmental conditions*. Elsevier Oceanogr. Ser. Vol. 34, 399–418.

Kuliński, K., Rehder, G., Asmala, E., Bartosova, A., Carstensen, J., Gustafsson, B., Hall, P.O., Humborg, C., Jilbert, T., Jürgens, K. Meier, H.M., 2022. *Biogeochemical functioning of the Baltic Sea*. Earth Sys. Dynam. 13(1), 633–685.

Lai, X., Li, X., Song, J., Yuan, H., Duan, L., Li, N., Wang, Y., 2023. *Nitrogen loss from the coastal shelf of the East China Sea: Implications of the organic matter*. Sci. Total Environ. 854, 158805.

Le Moigne, F.A., Cisternas-Novoa, C., Piontek, J., Maßmig, M., Engel, A., 2017. *On the effect of low oxygen concentrations on bacterial degradation of sinking particles*. Sci. Rep. 7(1), 16722.

Lehmann, A., Myrberg, K., Post, P., Chubarenko, I., Dailidiene, I., Hinrichsen, H.H., Hüssy, K., Liblik, T., Meier, H.M., Lips, U., Bukanova, T., 2022. *Salinity dynamics of the Baltic Sea*. Earth Syst. Dynam. 13(1), 373–392.

Leipe, T., Dippner, J.W., Hille, S., Voss, M., Christiansen, C. Bartholdy, J., 2008. *Environmental changes in the central Baltic Sea during the past 1000 years: inferences from sedimentary records, hydrography and climate*. Oceanologia 50(1), 23–41. https://www.iopan.gda.pl/oceanologia/501leipe.pdf

Lessin, G., Stips, A., 2012. *Modeling of eutrophication processes in the Gulf of Finland during 1991–2010*. IEEE/OES Baltic International Symposium (BALTIC), IEEE, 1–7.

Li, X., Li, L., Zhang, G., Mu, C., Mu, G., 2010. *Denitrification of wastewater with external carbon source of solid wastes in recirculating marine culture system*. Transact. Chinese Soc. Agricult. Eng. 26(4), 275–279.

Li, Y., Jin, H., Chen, J., Wang, D., Yang, Z., Wang, B., Zhuang, Y. Wang, R., 2021. *Nitrogen removal through sediment denitrification in the Yangtze Estuary and its adjacent East China Sea: a nitrate limited process during summertime*. Sci. Total Environ. 795, 148616.

Liblik, T., Väli, G., Salm, K., Laanemets, J., Lilover, M.J. Lips, U., 2022. *Quasi-steady circulation regimes in the Baltic Sea*. Ocean Sci. 18(3), 857–879.

Liblik, T., Rak, D., Siht, E., Väli, G., Karstensen, J., Tuomi, L., Biddle, L.C., Lilover, M.J., Skudra, M., Naumann, M. Lips, U., 2024. *Current structure, circulation and transport in the Central Baltic Sea observed by array of moorings and gliders*. EGUsphere, 1–37. https://doi.org/10.5194/egusphere-2024-2272

Lin, X., Liu, M., Hou, L., Gao, D., Li, X., Lu, K., Gao, J., 2017. *Nitrogen losses in sediments of the East China Sea: spatiotemporal variations, controlling factors, and environmental implications*. J. Geophys. Res. 122(10), 2699–2715. https://doi.org/10.1002/2017JG004036

Magri, M., Benelli, S., Castaldelli, G., Bartoli, M., 2022. *The seasonal response of in situ denitrification and DNRA rates to increasing nitrate availability*. Estuar. Coast. Shelf Sci. 271, 107856.

Matthäus, W., Franck, H., 1992. *Characteristics of major Baltic inflows – a statistical analysis*. Cont. Shelf Res. 12(12), 1375–1400.

Mazur-Marzec, H., Andersson, A.F., Błaszczyk, A., Dąbek, P., Górecka, E., Grabski, M., Jankowska, K., Jurczak-Kurek, A., Kaczorowska, A.K., Kaczorowski, T., Karlson, B., 2024. *Biodiversity of microorganisms in the Baltic Sea: the power of novel methods in the identification of marine microbes*. FEMS Microbiol. Rev. 48(5), fuae024. https://doi.org/10.1093/femsre/fuae024

Mills, M.M., Brown, Z.W., Laney, S.R., Ortega-Retuerta, E., Lowry, K.E., van Dijken, G.L., Arrigo, K.R., 2018. *Nitrogen limitation of the summer phytoplankton and heterotrophic prokaryote communities in the Chukchi Sea*. Front. Mar. Sci. 5, p. 362. https://doi.org/10.3389/fmars.2018.00362

Mohrholz, V., Naumann, M., Nausch, G., Krüger, S., Gräwe, U., 2015. *Fresh oxygen for the Baltic Sea – an exceptional saline inflow after a decade of stagnation*. J. Marine Syst. 148, 152–166.

Murase, H., Nagashima, H., Yonezaki, S., Matsukura, R., Kitakado, T., 2009. *Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill: a case study in Sendai Bay, Japan*. ICES J. Mar. Sci. 66, 1417–1424.

Myllykangas, J.P., Jilbert, T., Jakobs, G., Rehder, G., Werner, J., Hietanen, S., 2017. *Effects of the 2014 major Baltic inflow on methane and nitrous oxide dynamics in the water column of the central Baltic Sea*. Earth Syst. Dynam. 8, 817–826.

Naumov, L., Neumann, T., Radtke, H., Meier, H.M., 2023. *Limited ventilation of the central Baltic Sea due to elevated oxygen consumption*. Front. Mar. Sci. 10, 1175643. https://doi.org/10.3389/fmars.2023.1175643

Neumann, T., 2007. *The fate of river-borne nitrogen in the Baltic Sea – an example for the River Oder*. Estuar. Coast. Shelf Sci. 73(1–2), 1–7.

Neumann, T., Radtke, H., Cahill, B., Schmidt, M., 2022. *Non-Redfield carbon model for the Baltic Sea – implementation and udget estimates*. Geosci. Model Dev. 15(22), 8473–8540. https://doi.org/10.5194/gmd-15-8473-2022

Neumann, T., 2000. *Towards a 3-D ecosystem model of the Baltic Sea*, J. Mar. Syst. 25, 405–419.

Neumann, T., Fennel, W., Kremp, C., 2002. *Experimental simulations with an ecosystem model of the Baltic Sea: a nutrient load reduction experiment*. Global Biogeochem. Cy. 16. https://doi.org//10.1029/2001GB001,450

Ostrowski, R., Pruszak, Z., Skaja, M., Szmytkiewicz, M., 2010. *Variability of hydrodynamic and lithodynamic coastal processes in the east part of the Gulf of Gdańsk*. Arch. Hydro-Eng. Environ. Mech. 57(2), 139–153.

Pastuszak, M., Witek, Z., Nagel, K., Wielgat, M., Grelowski, A., 2005. *Role of the Oder estuary (southern Baltic) in transformation of the riverine nutrient loads*. J. Marine Syst. 57(1–2), 30–54.

Pedersen, E.J., Miller, D.L., Simpson, G.L., Ross, N., 2019. *Hierarchical generalized additive models in ecology: an introduction with mgcv*. PeerJ, 7:e6876.

Pempkowiak, J., Chiffoleau, J.F. Staniszewski, A., 2000. *The vertical and horizontal distribution of selected trace metals in the Baltic Sea off Poland*. Estuar. Coast. Shelf Sci. 51(1), 115–125.

Piehl, S., Friedland, R., Neumann, T. Schernewski, G., 2023. *Ocean models as shallow sea oxygen deficiency assessment tools: from research to practical application*. Biogeosciences Discuss. 2023, 1–33. https://doi.org/10.5194/bg-2023-152

Pina-Ochoa, E. Álvarez-Cobelas, M., 2006. *Denitrification in aquatic environments: a cross-system analysis*. Biogeochemistry 81, 111–130.

Reissmann, J.H., Burchard, H., Feistel, R., Hagen, E., Lass, H.U., Mohrholz, V., Nausch, G., Umlauf, L. Wieczorek, G., 2009. *Vertical mixing in the Baltic Sea and consequences for eutrophication – a review*. Progr. Oceanogr. 82(1), 47–80.

Rolff, C., Walve, J., Larsson, U., Elmgren, R. 2022. *How oxygen deficiency in the Baltic Sea proper has spread and worsened: The role of ammonium and hydrogen sulphide*. Ambio 51(11), 2308–2324.

Schernewski, G., Friedland, R., Carstens, M., Hirt, U., Leujak, W., Nausch, G., Neumann, T., Petenati, T., Sagert, S., Wasmund, N., von Weber, M., 2015. *Implementation of European marine policy: New water quality targets for German Baltic waters*. Mar. Policy 51, 305–321. https://doi.org/10.1016/j.marpol.2014.09.002

Schmale, O., Karle, M., Glockzin, M., Schneider, B., 2019. *Potential of nitrogen/argon analysis in surface waters in the examination of areal nitrogen deficits caused by nitrogen fixation*. Environ. Sci. Technol. 53, 6869–6876. https://doi.org/10.1021/acs.est.8b06665

Schneider, B., Dellwig, O., Kuliński, K., Omstedt, A., Pollehne, F., Rehder, G., Savchuk, O., 2017. *Biogeochemical cycles*. [in:] Snoeijs, P., Schubert, H., Radziejewska, T. (eds.), *Biological oceanography of the Baltic Sea*, Springer, 87–122.

Schulz, K.G., Achterberg, E.P., Arístegui, J., Bach, L.T., Baños, I., Boxhammer, T., Erler, D., Igarza, M., Kalter, V., Ludwig, A., Löscher, C., Meyer, J., Minutolo, F., von der Esch, E., Ward, B.B, Riebesell, U., 2021. *Nitrogen loss processes in response to upwelling in a Peruvian coastal setting dominated by denitrification – a mesocosm approach*. Biogeosci. 18(3), 4305–4320. https://doi.org/10.5194/bg-18-4305-2021

Seitzinger, S.P., Harrison, J.A., Böhlke, J.K., Bouwman, A.F., Lowrance, R., Peterson, B., Tobias, C., Van Drecht, G., 2006. *Denitrification across landscapes and waterscapes: a synthesis*. Ecol. Appl. 16(6), 2064–2095. https://doi.org/10.1890/1051-0761(2006)016[2064:dalawa]2.0.co;2

Shao, M.F., Zhang, T., Fang, H.H.P. Li, X., 2011. *The effect of nitrate concentration on sulfide-driven autotrophic denitrification in marine sediment*. Chemosphere 83(1), 1–6.

Sikorowicz, G., Falkowska, L., Burska, D., Dunajska, D., Pryputniewicz, D., Magulski, R., Lewandowska, A., 2005. *Diurnal variations in nitrogen, phosphorus and iron compounds in the southern Baltic Sea*. Oceanologia 47(2), 243–263. https://www.iopan.gda.pl/oceanologia/472sikor.pdf

Sivasamy, P., Diak, M., Winogradow, A., Bange, H.W., Borecka, M., Makuch, P., Koziorowska-Makuch, K., Kuliński, K., Mackiewicz, A., Szymczycha, B., 2025. *Spatial and seasonal variability of excess dinitrogen gas in the Baltic Sea*. Front. Marine Sci. 12, 1455803. https://doi.org/10.3389/fmars.2025.1455803

Skiba, U., 2008. *Denitrification*, [in:] Jorgensen, S.E., Fath, B.D., (eds.), *Encyclopedia of ecology*, Elsevier, Oxford, 866–871.

Stanev, E.V., Lu, X., Grashorn, S., 2015. *Physical processes in the transition zone between North Sea and Baltic Sea. Numerical simulations and observations*. Ocean Model. 93, 56–74.

Stockmayer, V., Lehmann, A., 2023. *Variations of temperature, salinity and oxygen of the Baltic Sea for the period 1950 to 2020*. Oceanologia 65(3), 466–483. https://doi.org/10.1016/j.oceano.2023.02.002

Szymczycha, B., Zaborska, A., Bełdowski, J., Kuliński, K., Beszczyńska-Möller, A., Kędra, M., Pempkowiak, J., 2019. *The Baltic Sea*. [in:] *World seas: An environmental evaluation*, Acad. Press., 85–111. https://doi.org/10.1016/B978-0-12-805068-2.00005-X

Tamelander, T., Spilling, K., Winder, M., 2017. *Organic matter export to the seafloor in the Baltic Sea: Drivers of change and future projections*. Ambio 46(8), 842–851. https://doi.org/10.1007/s13280-017-0930-x

Thureborn, P., Franzetti, A., Lundin, D., Sjöling, S., 2016. *Reconstructing ecosystem functions of the active microbial community of the Baltic Sea oxygen depleted sediments*. PeerJ 4, e1593. https://doi.org/10.7717/peerj.1593

Thureborn, P., Lundin, D., Plathan, J., Poole, A.M., Sjöberg, B.M., Sjöling, S., 2013. *A metagenomics transect into the deepest point of the Baltic Sea reveals clear stratification of microbial functional capacities*. PloS one, 8(9), e74983.

Väli, G., Meier, H.M., Elken, J., 2013. *Simulated halocline variability in the Baltic Sea and its impact on hypoxia during 1961–2007*. J. Geophys. Res.-Oceans 118(12), 6982–7000.

Voipio, A. (ed.), 1981. *The Baltic Sea*, Elsevier Oceanogr. Ser. Vol. 30, 418 pp. https://www.sciencedirect.com/bookseries/elsevier-oceanography-series/vol/30/suppl/C

Walter, S., Breitenbach, U., Bange, H.W., Nausch, G., Wallace, D.W., 2006. *Distribution of N_2O in the Baltic Sea during transition from anoxic to oxic conditions*. Biogeosciences 3(4), 557–570. https://doi.org/10.5194/bg-3-557-2006

Wan, Z., She, J., Maar, M., Jonasson, L., Baasch-Larsen, J., 2012. *Assessment of a physical-biogeochemical coupled model system for operational service in the Baltic Sea*. Ocean Sci. 8(4), 683–701.

Wang, J., Kan, J., Qian, G., Chen, J., Xia, Z., Zhang, X., Liu, H., Sun, J., 2019. *Denitrification and anammox: Understanding nitrogen loss from Yangtze Estuary to the east China sea (ECS)*. Environ. Pollut. 252, 1659–1670.

Ward, B.B., Tuit, C.B., Jayakumar, A., Rich, J.J., Moffett, J., Naqvi, S.W.A., 2008. *Organic carbon, and not copper, controls denitrification in oxygen minimum zones of the ocean*. Deep Sea Res. Pt. I 55(12), 1672–1683. https://doi.org/10.1016/j.dsr.2008.07.005

Warneke, S., Schipper, L.A., Matiasek, M.G., Scow, K.M., Cameron, S., Bruesewitz, D.A. McDonald, I.R., 2011. *Nitrate removal, communities of denitrifiers and adverse effects in different carbon substrates for use in denitrification beds*. Water Res. 45(17), 5463–5475. https://doi.org/10.1016/j.watres.2011.08.007

Wieczorek, G., 2011. *Spatiotemporal Scales of the Deep Circulation in the Eastern Gotland Basin/Baltic Sea*. Ph.D. Thes., Univ. Rostock, Rostock. https://doi.org/10.18453/rosdok_id00001068

Wieczorek, G., Hagen, E., Umlauf, L., 2008. *Eastern Gotland Basin case study of thermal variability in the wake of deep water intrusions*. J. Marine Syst. 74, S65–S79. https://doi.org/10.1016/j.jmarsys.2008.07.008

Witak, M., Cieślikiewicz, W., Granoszewski, W., Hetko, D., Pączek, U., Piotrowska, N., Uścinowicz, S., 2025. *Tracing storminess variability through seabed sediments in Puck Bay, southern Baltic Sea*. The Holocene 35(8), 677–700. https://doi.org/10.1177/09596836251332805

Wood, S.N., 2017. *Generalized additive models: an introduction with R*, 2nd edn., Chapman and Hall, New York. 496 pp. https://doi.org/10.1201/9781315370279

Yang, L.B., Lei, K., Meng, W., 2015. *Denitrification in water of Daliao River estuary in summer and the effect of environmental factors*. Huan Jing ke Xue (Huanjing Kexue – J. Environ. Sci.) 36(3), 905–913.

Zglinicki, K., Pilaszkiewicz, M., Wrzosek, A., Szamałek, K., Uścinowicz, S., Szefler, K., Nowak, J., Bylina, P., 2025. *Fenodules from the southern Baltic Sea: Morphology, mineralogy and geochemistry*. Marine Geol. 490, 107655. https://doi.org/10.1016/j.margeo.2025.107655