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Saltwater inflows and circulation dominantly influence Baltic Sea eutrophication (2010–2021)

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The Baltic Sea's chronic eutrophication is conventionally attributed to anthropogenic nutrient inputs, but physical processes-such as stratification, saltwater inflows, circulation, and ice cover-play a critical yet understudied role in modulating ecosystem responses. While nutrient load reductions remain a cornerstone of management, the extent to which physical factors influence eutrophication dynamics remains unclear. To address this, we applied a coupled physical-biogeochemical model (2010-2021) to assess the relative impacts of physical conditions versus nutrient reductions. We implemented extreme and partly hypothetical hydrographic scenarios-not as forecasts, but as conceptual experiments—to examine how changes in physical drivers affect ecosystem functioning. Ecosystem responses were evaluated using chlorophylla concentrations and the Trophic Transfer Index (TTI), with separate Good Environmental Status (GES) assessments calculated for each indicator. Results show that physical factors had disproportionately large effects, altering GEScompliant areas by up to +4% (chlorophyll-a) and +7% (TTI), while nutrient load reductions had minimal impact (<1.5%). Blocking North Sea inflows caused the most dramatic changes, increasing chlorophyll-a by up to +45% and reducing TTI by -29%, underscoring eutrophication's sensitivity to ventilation dynamics. Over short periods, physical factors could outweigh even extreme nutrient reductions (-50% loads), potentially amplifying or counteracting intended management outcomes. These findings underscore the crucial role of physical drivers in Baltic Sea eutrophication and emphasize the importance of incorporating them into assessments of ecosystem recovery and management effectiveness.

KEYWORDS

eutrophication indicators, effects of anthropogenic pressure, physical drivers of eutrophication, trophic transfer index, major Baltic inflows

1 Introduction

The Baltic Sea is a semi-enclosed, brackish basin characterized by limited water exchange, strong vertical stratification, and complex bathymetry (Leppäranta and Myrberg, 2009). These hydrographic features lead to prolonged nutrient residence times—particularly for phosphorus, which can remain sequestered in sediments for decades—while nitrogen exhibits greater mobility through biogeochemical cycling (Radtke et al., 2012; Kuliński et al., 2022). Despite significant reductions in external nutrient inputs—approaching 1970s levels (Tomczak et al., 2021; Pärn et al., 2024)—ecological recovery has been limited (HELCOM, 2018). Persistent deep-water

hypoxia, recurrent cyanobacterial blooms, and altered trophic dynamics point to strong system inertia (Reckermann et al., 2022).

The long-term eutrophication trajectory of the Baltic Sea reflects a coupled influence of anthropogenic pressures and climate-driven variability. Palaeoecological records suggest that nutrient enrichment began in the early 19th century, with increasing sedimentary nitrogen concentrations and $\delta^{15}N$ values indicating human-induced nutrient inputs (Andrén et al., 2015). Industrialization and intensified agriculture in the mid-20th century accelerated eutrophication, resulting in ecosystem restructuring, including changes in diatom assemblages and widespread hypoxia (Warnock et al., 2020). While modern hypoxia is mainly driven by nutrient over-enrichment (Reckermann et al., 2022), historical oxygen depletion events during the Holocene and the Medieval Climate Anomaly were linked to natural variations in basin morphology, salinity, and temperature (Zillén et al., 2008; Zillén and Conley, 2010; Börgel et al., 2023). However, contemporary deoxygenation represents an unprecedented state, leading to substantial decline in macrobenthic communities through the combined effects of basin shoaling, climate warming, and nutrient over enrichment (Jokinen et al., 2018; Papadomanolaki et al., 2018).

Today, the Baltic Sea hosts one of the world's largest anthropogenically driven hypoxic zones (Diaz and Rosenberg, 2008). Although episodic Major Baltic Inflows (MBIs) introduce oxygenated saline water from the North Sea, these events have become less frequent and offer only temporary relief (Mohrholz et al., 2015; Neumann et al., 2017). Circulation patterns and N:P stoichiometry further shape spatial eutrophication dynamics, with coastal regions exhibiting elevated N:P ratios due to riverine inputs, while central basins tend to be nitrogenlimited and phosphorus-rich, favoring cyanobacteria dominance during summer stratification (Vahtera et al., 2007; Savchuk, 2018). Cyanobacteria are often poorly grazed due to their low nutritional value, which diminishes energy transfer efficiency and contributes to detrital buildup and oxygen consumption (Chislock et al., 2013; Eddy et al., 2021).

A critical but understudied aspect is how hydrographic factors (Myrberg et al., 2019)—such as saltwater inflows, circulation dynamics, and warming—interact with nutrient availability to shape eutrophication outcomes. Recent Lagrangian transport modelling shows that cyclonic circulation (Palmén, 1930) redistributes riverine inputs (Pärn et al., 2023a), while declining N:P ratios may play a more central role than absolute nutrient levels in triggering cyanobacterial dominance (Löptien and Dietze, 2022). However, the relative contributions of physical forcing versus nutrient management remain poorly constrained.

Here, we investigate the extent to which hydrographic variability modulates eutrophication and food web dynamics across the Baltic Sea during 2010–2021. Using a suite of model scenarios—including closed boundary conditions, wind reversal, circulation barrier, atmospheric warming, and nutrient load reductions—we identify key processes shaping primary production and ecosystem response. These findings aim to support adaptive management strategies under the Baltic Sea Action Plan (HELCOM, 2021) by clarifying the role of physical drivers in ecosystem recovery.

2 Materials and methods

2.1 The marine modeling framework

The Blue2 Modelling Framework (Blue2MF), developed by the Joint Research Centre (JRC) of the European Commission, is an integrated tool designed to assess the impacts of policy options on the environmental status of EU marine regions, particularly within the framework of the Marine Strategy Framework Directive (MSFD) (Macias et al., 2022; Macias et al., 2018). It provides high-resolution numerical simulations of key environmental variables across the five EU marine regions. Blue2MF incorporates multiple model components, including atmospheric forcing from reanalysis or Global Circulation Models, land-use and hydrological models for freshwater dynamics, and region-specific hydrodynamic-biogeochemical coupled models. Additionally, it integrates high trophic level marine and Lagrangian models, enabling a comprehensive assessment of ecosystem dynamics (Macias et al., 2022).

Its configuration, based on Lessin et al. (2014a; b) and validated by Pärn et al. (2020), Pärn et al. (2021), has demonstrated strong predictive skill in simulating surface currents and reproducing Lagrangian drift patterns, closely matching observed surface drifter data (Pärn et al., 2023a; b). The model domain encompasses the entire Baltic Sea, with an open boundary in the northern Kattegat. Within the Blue2MF framework, MSI-ERGOM effectively simulates seasonal phytoplankton succession (Pärn et al., 2022), accurately capturing the transition from diatom to flagellate dominance in the western Baltic Sea (Pärn et al., 2021; 2024).

A key advancement in JRC-ERGOM is the implementation of the Line of Frugality (LoF) approach (Macias et al., 2019), which enables phytoplankton to dynamically adjust phosphate uptake based on its availability in seawater.

2.2 Modeled scenarios

All scenarios were implemented using the same model configuration, initial conditions, and input data. The specific characteristics of each scenario are described below. Details of the model configuration and input data are provided in Supplementary Information S1.

2.2.1 Impact of major Baltic inflows on eutrophication

Major Baltic Inflows (MBIs) are critical ventilation events that transport oxygenated, saline water from the North Sea into the deeper basins of the Baltic Sea (Mohrholz, 2018). Their formation depends on multiple factors, with wind direction and saltwater transport playing a particularly significant role. To evaluate the influence of MBIs on the Baltic Sea ecosystem, two numerical model scenarios were implemented.

 Closed boundary scenario: From May 2014 to January 2015, saline inflows from the North Sea were restricted by closing the model's western boundary conditions. This modification prevented high-salinity water intrusion, allowing an isolated analysis of the effects of reduced saltwater exchange on Baltic Sea hydrography and ecosystem dynamics.

• Reversed wind scenario: To examine the role of wind in MBI formation, wind components (U and V) in the 2014 meteorological forcing data were inverted (U = -U, V = -V) over the Baltic Sea. This modification altered wind-driven circulation patterns crucial for saltwater transport through the Danish Straits (Lass and Matthaus, 1996; Stips et al., 2008), enabling an assessment of wind-driven variability in ecosystem dynamics.

Model outputs were evaluated for changes in chl concentrations and TTI across Baltic Sea HELCOM basins to assess impacts on eutrophication status. The mean relative effect (Equation 1) was calculated as the percentage difference between the scenario and the reference simulation in 2014–2021.

2.2.2 Barrier scenario: circulation impact on eutrophication

To investigate the role of large-scale circulation patterns in eutrophication, a modified hydrodynamic scenario was implemented in the Baltic Sea model. In this scenario, a barrier structure was introduced to disrupt natural current into the Gotland basin. The artificial structure was positioned between longitude 19.85°–20.88° and latitude 55.92°, approximately 8 km offshore, extended 70 km in length and 4 km in width (Figure 1), thereby preventing the direct inflow of salt intrusions into the Gotland basin. This experimental setup enables for the assessment of circulation alterations on nutrient transport, retention, and eutrophication dynamics within affected regions.

2.2.3 Increased air temperature (warming)

To assess the effect of warming on TTI and Chl in a scenario, the air temperature in the atmospheric forcing data was increased by 1.7°C for the year 2014. All other initial and boundary conditions remained consistent with the reference simulation.

2.2.4 Nutrient reductions scenario

This scenario assesses the impact of a 50% reduction in nutrient loads from all rivers shown in Figure 2 that discharge into the Baltic Sea. Riverine nutrient loads were estimated using the GREEN model (Grizzetti et al., 2012; 2019) combined with the LISFLOOD hydrological model (De Roo et al., 2020), focusing on the 2010–2021 period. Total Nitrogen (TN) and Total Phosphorus (TP) fluxes, derived from an updated hydrological model (Vigiak et al., 2023), were integrated into a marine biogeochemical model to simulate eutrophication responses. Nutrient loads for the reference scenario, aggregated by major basins (Gulf of Finland, Baltic Proper, Gulf of Riga, Kattegat), are provided in Supplementary Material S6.

Hindcast simulations were conducted under a 50% reduction scenario, maintaining constant riverine discharge. The relative impact was quantified in 2014–2021:

$$Impact = \frac{Scenario - ReferenceScenario}{ReferenceScenario} 100$$
(1)

This approach enables a comparative evaluation of nutrient reduction effectiveness.

2.3 Eutrophication indicators

2.3.1 Chlorophyll-a

HELCOM's core indicators assess the average chlorophyll-a (chl) concentration in surface waters (0-10 m) during summer (June–September). The evaluation of good environmental status (GES) is based on scientifically established, sub-basin-specific threshold values that define acceptable concentration limits. These threshold values, detailed in the HOLAS II assessment, serve as the benchmark for chl evaluation.

In our study, model results were analyzed for each basin using these threshold values. If a model grid point exhibited a value below the threshold, that area was classified as meeting GES for the corresponding indicator. The percentages in the figures represent the proportion of the total possible area that achieves good status based on the indicator's value. To ensure comparability between TTI and chl scales, a 3-year rolling average was applied to the spatial chl data.

2.3.2 Trophic transfer index

The Trophic Transfer Index (TTI) is based on the assumption that eutrophication impacts a marine area when an increase in primary production (PP) is not accompanied by a corresponding increase in zooplankton grazing activity (Polimene et al., 2023; Tubay et al., 2013). This concept is supported by evidence showing that eutrophication is triggered by extended periods during which primary production remains ungrazed (Chislock et al., 2013; EEA, 2019; Eddy et al., 2021).

The central assumption of the TTI is that, in a healthy marine environment and over appropriate temporal scales, grazing activity should correlate with primary production (Kemp et al., 2001; Schmoker et al., 2013), regardless of the system's trophic status. The strength of this correlation (Equation 2) is assessed by combining both the linear (Pearson) and rank (Spearman) correlation coefficients as follows:

$$TTI = max(RL, RR)$$
(2)

where RL is the linear correlation coefficient between monthly depth-integrated primary production (*PP*) and grazing (*Grazing*) both expressed in mmol N m⁻² month⁻¹:

$$RL = corrcoe f[PP(t), Grazing(t, t+1)]$$
(3)

and *RR* is the rank correlation coefficient between *PP* and the *Grazing* to *PP* ratio:

$$RR = Spearman[PP(t), Grazing(t, t+1):PP(t)]$$
(4)

The rank correlation coefficient allows the TTI to capture monotonic relationships that may be non-linear or steeper than linear. In both Equations 3, 4, t represents the months over which the fluxes are averaged.

Following the approach of Polimene et al. (2023), the TTI was calculated at each model grid point over a 3-year period to identify "problem areas" (TTI-Eutrophic Zones). A problem area is defined as a region where primary production is not sufficiently balanced by grazing activity, leading to potential ecological dysfunctions such as organic matter accumulation and anoxia. The threshold value of 0.7 was chosen based on the findings of Polimene et al. (2023), where



areas with TTI values below this limit exhibited significant signs of eutrophication.

Conversely, regions where the TTI is equal to or greater than 0.7 are classified as unaffected areas by eutrophication, referred to in this study as areas in Good Environmental Status (GES_TTI), indicating a healthy balance between primary production and grazing.

Since the TTI calculation spans 3 years, the intermediate year is represented in the graphical outputs. For example, the year 2011 includes data from 2010 to 2012, and so on.

3 Results

3.1 Effects of physical and biogeochemical drivers on chlorophyll-a and trophic transfer index

GES_chl (Section 2.3.1) represents the percentage of the Baltic Sea area where chl concentrations remain below the HELCOM threshold, depending on the scenario (Figure 3). The general trend indicates that the GES_chl area has declined over time, whereas the GES_TTI area has improved, highlighting the differing sensitivities of these indicators to ecosystem changes. In the reference scenario,

interannual variability of GES_chl ranged between 12% and 21% (Δ 9%) during 2011–2020, while GES_TTI fluctuated between 55% and 78% (Δ 23%) (Figure 3).

Despite substantial variability, the impact of the studied scenarios on chl-based GES remained relatively minor compared to interannual fluctuations, with maximum deviations of up to 4% from the reference scenario. This indicates that the spatial extent of areas meeting GES_chl criteria either expanded or contracted depending on the scenario (Figure 3).

The most pronounced effect was observed in the barrier scenario (~4%), followed by the closed boundary scenario (-3.5%), the reversed wind scenario (-3%), and the nutrient reduction scenario (+1.5%). For the TTI indicator, the largest changes were recorded in the closed boundary scenario (-7%), followed by the reversed wind and warming scenario (-3.5%), the barrier scenario (-3%), and the nutrient reduction scenario (+2.7%).

These findings suggest that hydrographic factors exert a stronger influence on GES variations than nutrient reduction measures. It is important to note that the barrier, closed boundary, and reversed wind scenarios represent idealized and non-realistic sensitivity tests, designed to explore system responses under extreme conditions. Furthermore, the fact that interannual variability exceeds the magnitude of changes induced by individual drivers (e.g., Major Baltic Inflow, circulation, warming, nutrient reductions) indicates



that eutrophication is primarily governed by the synergistic or antagonistic interactions of multiple environmental components.

The closed boundary scenario, in particular, demonstrates that saltwater inflows—as expected—have a strong impact on ecosystem dynamics. In the reference scenario, deep-layer salinity peaked in 2014 (Figure 4), coinciding with GES_TTI expansion in 2013–2014 (Figure 3). In contrast, the closed boundary scenario, which restricted saltwater inflow, did not show this strong GES_TTI increase. Reopening the North Sea boundary in January 2015, after salinity remained low in 2014, created a strong salinity gradient, triggering a rapid inflow of saltwater. This inflow event expanded GES_TTI areas again (Figure 3). These results highlight the key role of saltwater inflows in shaping ecosystem responses and the sensitivity of GES_TTI to salinity changes.

3.2 Regional variability in response to hydrographic drivers and nutrient reduction

3.2.1 Chlorophyll-a

A decrease in chl concentration is considered a positive impact, while an increase indicates a negative impact. All percentage changes reported here refer to average values over the respective subbasins, not to spatial GES areas. The closed boundary scenario had the strongest effect on chl concentrations, leading to an average decrease of 80% between 2014 and 2021 across the affected sub-basins (Figure 5). A negative impact exceeding 20% was observed in sub-basins from Kattegat to Kiel, whereas in the Bay of Mecklenburg (BoM), average concentrations decreased by 14%. The most pronounced improvement occurred under the barrier scenario in the Gulf of Finland (GoF), where average chl concentrations declined by 40%. The impact of the reversed wind scenario exceeded 7% in sub-basins from Kattegat to Bornholm. In contrast, the nutrient reduction scenario had a stronger influence than hydrographic factors only in the Gdansk Basin and Gulf of Riga (GoR). In all other sub-basins, physical drivers had a greater effect on chl concentrations than nutrient reductions.

3.2.2 Trophic transfer index (TTI) and the role of hydrographic processes

TTI was most affected by the closed boundary scenario during 2014–2021 (Figure 6), with reduced salt inflow decreasing TTI values by more than 15% in the Kattegat to BoM region. Both the reversed wind and closed boundary scenarios had a greater impact on TTI than nutrient reduction in most basins. However, nutrient reductions were more effective in basins Gdansk, GoR, and GoF. Notably, the barrier scenario had the strongest effect in the Gulf of Finland, counteracting eutrophication mitigation efforts.

The average DIN:DIP ratio in the closed boundary scenario was more than 15% lower than in the reference scenario in basins Kattekat to BoM during 2014–2021. This decrease was reflected in both TTI and chl indicators. The DIN:DIP ratio increased in all basins under the barrier scenario except for the Gulf of Riga, though



the change remained below 4%. In contrast, under the reversed wind scenario, the DIN:DIP ratio increased by 11% in basin 6. However, while TTI remained unchanged in this basin, chl concentrations showed a 6% decline.

In the closed boundary scenario, cyanobacteria concentrations increased by more than 50% in basins Kattekat to Kiel Bay and by 34% in Bay of Mecklenburg between 2014 and 2021. This increase was linked to an ~8% reduction in bottom-layer oxygen concentrations. In other scenarios, bottom oxygen concentrations showed little change, while under the reversed wind scenario, oxygen levels improved by 5%–8% in basins 4–10. A minor oxygen increase (1%–2.5%) was also observed in the barrier scenario.

3.2.2.1 Bottom oxygen concentration under closed boundary scenarios

As shown in Figure 4, the closed boundary scenario leads to an overall decline in average salinity, which is consistent with expectations given the elimination of saline inflows from the North Sea. However, salinity changes in bottom layers across deep basins are spatially heterogeneous, with some areas exhibiting increases in salinity. This pattern can be attributed to the specific hydrographic conditions under the closed boundary configuration, where the inflowing water in Kattegat has lower salinity, and the water entering the Arkona Basin is relatively colder compared to the open boundary scenario.

According to Supplementary Figure S5, bottom oxygen concentrations generally decrease under the closed boundary scenario from Kattegat to EGB. Nevertheless, in certain deep areas where oxygen levels are already near zero, slight increases in oxygen are observed. These localized improvements are insufficient to reverse hypoxic conditions, indicating that despite minor enhancements, the overall oxygen deficit persists. Although slight increases in bottom water oxygen were observed, they remain insufficient to prevent the reductive dissolution of iron-bound phosphorus, thus failing to interrupt the internal loading feedback from sediments, and keep din:dip ratio low Supplementary Figure S3.1.



Time series of spatially averaged bottom layer salinity in different scenario simulations. Closed boundary scenario (green), North Sea inflows closed from May 2014 to January 2015.



4 Discussion

4.1 Physical factors dominate short-term eutrophication trends

Despite decades of nutrient reduction efforts, the Baltic Sea's limited recovery from eutrophication (HELCOM, 2018)

underscores that anthropogenic nutrient loads are not the sole drivers of ecosystem dynamics. Rather, eutrophication reflects a complex interplay between nutrient inputs and physical factors such as stratification, inflows, circulation, and warming. Our simulations revealed that physical factors—particularly Major Baltic Inflows (MBIs), circulation shifts, and boundary conditions—had stronger short-term impacts



on eutrophication indicators during 2010–2021 than nutrient reductions alone.

For example, blocking North Sea inflows resulted in extreme ecosystem responses: a 28% reduction in the Trophic Transfer Index (TTI) and a 45% increase in chlorophyll-a in western sub-basins (Kattegat, Great Belt, The Sound, Kiel Bay, and the Bay of Mecklenburg; Figures 5, 6). In contrast, simulated nutrient reductions led to relatively minor changes (maximum 6% in chlorophyll-a and 2% in TTI in the same regions during 2014–2021).

Other physical scenarios yielded comparably strong effects on eutrophication indicators. A barrier in the Eastern Gotland Basin led to a 4% TTI decline and a 40% chlorophyll improvement in the Gulf of Finland, demonstrating basin-scale connectivity. Reversed wind scenarios reduced chlorophyll-a by 8%–17% in the Kattegat to Arkona Basin region, while equivalent nutrient reductions yielded only 2%–6% improvement. These results are consistent with Schimanke et al. (2012), who noted that natural variability can introduce greater uncertainty than previously recognized.

These findings align with recent results by Barghorn et al. (2025), who showed that a shift in the seasonality of warm saltwater inflows from the North Sea has exacerbated oxygen depletion in the western Baltic Sea, further underscoring the importance of physical circulation dynamics as key modulators of biogeochemical responses (Löptien et al., 2025).

The divergent trends in GES_chlorophyll (declining) and GES_ TTI (improving) over 2011–2020 highlight their distinct sensitivities to ecosystem processes. The significant interannual variability observed in both indicators further highlights that eutrophication is primarily driven by the synergistic or antagonistic interactions of multiple environmental components, rather than single drivers. Interannual variability was significantly higher for TTI (σ = 7.6, max range $\Delta 23\%$ [55%–78%]) than for chlorophyll (σ = 2.9, max range $\Delta 9\%$ [12%–21%]), demonstrating TTI's stronger responsiveness to short-term trophic fluctuations. This contrast arises because chlorophyll metrics primarily reflect standing biomass, whereas TTI captures functional dynamics—including energy transfer efficiency and stoichiometric imbalances—that provide earlier and more nuanced signals of eutrophication shifts. Thus, while conventional chlorophyll assessments may lag, TTI's sensitivity to trophic reorganization makes it a valuable tool for detecting incipient ecosystem changes.

4.2 Functional metrics reveal hidden dynamics

Traditional state indicators, such as chlorophyll-a concentration, often obscure key ecological changes. Our findings support the integration of functional indicators—such as the Trophic Transfer Index (TTI) and stoichiometric ratios—that reflect energy transfer efficiency and nutrient cycling processes.

TTI successfully captured trophic regime shifts that remained invisible to chlorophyll-based assessments, including the late-1980s transition from diatom to flagellate dominance (Pärn et al., 2024). Under closed-boundary scenarios, cyanobacteria blooms surged by 50% and DIN:DIP ratios declined by 22%, highlighting that nutrient imbalance, rather than absolute load levels, is a primary driver of eutrophication. These findings suggest that functional metrics provide earlier and more ecologically meaningful signals of eutrophication shifts than conventional indicators.

4.2.1 Limitations

Several limitations should be acknowledged. First, annual aggregation of TTI may obscure seasonal trophic linkages and overrepresent winter-period correlations. Finer temporal resolution could help better resolve cause-effect relationships in energy transfer and nutrient cycling.

Second, the use of broad plankton functional groups may mask species-specific interactions that are critical for capturing shifts in food web structure and nutrient processing.

Third, our 11-year simulation window limits the ability to detect long-term processes such as ecological adaptation, regime shifts, and cumulative feedbacks. Consequently, while our findings highlight the short-term dominance of physical factors, the long-term effectiveness of nutrient load reductions—as underscored by Saraiva et al. (2019)—is likely underestimated.

4.2.2 Toward holistic management

Natural variability introduces more uncertainty into observed ecosystem indicators than previously recognized (Schimanke et al., 2012). Nevertheless, both Schimanke et al. (2012) and Saraiva et al. (2019) concluded that substantial improvements in Baltic Sea oxygen conditions can be achieved through continued nutrient load reductions—even under future climate change scenarios. Our results support this view but emphasize that ignoring the influence of physical factors may lead to misinterpretation of ecosystem responses.

For example, a lack of improvement in chlorophyll-a after nutrient reduction does not necessarily indicate management failure if improvements are observable in functional indicators such as TTI. Current eutrophication assessments under the Marine Strategy Framework Directive (MSFD, Descriptor 5) may be too narrow to fully capture the Baltic Sea's dynamic complexity.

Accurate assessment of eutrophication trends therefore requires accounting for physical variability, especially ventilation, stratification, and temperature shifts. We advocate for an integrated assessment framework that combines state indicators (e.g., chlorophyll-a) with process-oriented metrics (e.g., TTI, stoichiometry).

Functional indicators enhance early-warning capacity, improve interpretation of ecosystem trajectories, and reduce the risk of misjudging recovery progress. Future modeling efforts should aim to resolve plankton at the species level and extend simulations to better capture the long-term effects of climate-driven hydrographic change.

Ultimately, effective eutrophication management must address not only nutrient inputs but also the stoichiometric and functional shifts shaped by physical factors.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

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Author contributions

OP: Conceptualization, Investigation, Visualization, Writing – original draft, Data curation, Formal Analysis. DM: Funding acquisition, Methodology, Project administration, Supervision, Writing – review and editing. LP: Conceptualization, Methodology, Supervision, Writing – review and editing. AS: Conceptualization, Methodology, Supervision, Writing – review and editing.

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Author Ove Parn was employed by EstMare OU.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2025. 1608154/full#supplementary-material

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