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Long-Term Effects of Nutrient Shifts and Warming on Chlorophyll-*a* in a Temperate Coastal Environment

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Abstract

Anthropogenically driven nutrient shifts and warming are key stressors affecting phytoplankton in marine coastal environments. The German Bight, a coastal region in the North Sea, has undergone substantial nutrient reductions and rising sea surface temperature (SST) over recent decades. Despite extensive research, the combined long-term effects of nutrient shifts and warming, particularly in the river-influenced coastal area, remain unclear. Here, we aimed to evaluate trends and explore the partial and interactive effects of winter nutrient alterations and seasonal warming on spring chlorophyll-*a* (Chl-*a*) levels. For this purpose, we compiled a comprehensive spatiotemporal dataset (1980–2019) and applied generalized linear mixed models. Results showed that spring Chl-*a* concentrations peaked in the 1980s and 1990s, with values surpassing 30 $\mu g\ L^{-1}$ in the Elbe estuary. Concentrations declined to $< 15\ \mu g\ L^{-1}$ in the following decades, although values $> 15\ \mu g\ L^{-1}$ persisted in the southern inner coastal waters. Decreasing winter dissolved inorganic nitrogen (DIN) emerged as the primary driver of declining spring Chl-*a* in coastal waters (estimate $= 0.40$, $p < 0.01$), while winter phosphorus and nitrogen-to-phosphorus ratios were not significant predictors. Spring SST had a weak positive effect on Chl-*a* (estimate $= 0.09$, $p = 0.03$), suggesting that warming during spring may enhance phytoplankton growth. Together, winter DIN and spring SST explained 30% of the variance in spring Chl-*a*. Additional factors, such as light availability and grazing, likely contribute to unexplained variability. This study provides evidence that nutrient reductions have successfully lowered chlorophyll levels, but persistent hotspots in the inner coastal waters highlight the need for targeted management under continued warming.

Keywords Nutrient concentrations · Nutrient ratios · Ocean warming · Chlorophyll-*a* · North Sea · German Bight

Introduction

Phytoplankton growth in marine environments strongly depends on light availability, nutrient availability, and temperature (Field et al., 1998). Nutrient dynamics and sea surface temperature (SST) have been significantly impacted on a global scale by anthropogenic activities over the past decades (Bulgin et al., 2020; Paerl et al., 2014; Peñuelas & Sardans, 2022). Given that phytoplankton form the foundation of aquatic food webs, anthropogenic-driven shifts in phytoplankton biomass will potentially influence higher trophic levels, with implications for fisheries and overall ecosystem stability (Glibert et al., 2011; Sarker & Wiltshire, 2017; Yang et al., 2023).

The German Bight, a shallow coastal area in the southeastern North Sea, is a prime example of an environment which has experienced alterations in anthropogenic nutrient supply due to management (van Beusekom et al., 2019; Wiltshire et al., 2010) as well as significant SST increase over the past 60 years (Amorim et al., 2023). Since the 1960s, population growth, industrialization, and extensive fertilizer applications have led to a sharp increase in nitrogen (N) and phosphorus (P) run-offs from major European rivers causing coastal eutrophication (Pätsch & Radach, 1997; Westernhagen & Dethlefsen, 1983). Subsequent de-eutrophication efforts since the mid-1980s disproportionately reduced P relative to N, resulting in elevated nitrogen-to-phosphorus (N:P) ratios in riverine and coastal waters, far exceeding the Redfield ratio of 16:1 (Burson et al., 2016; Radach & Pätsch,

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2007). This imbalance has caused severe P limitation in the coastal southeastern North Sea during spring (Burson et al., 2016; Loebl et al., 2009), which could constrain the overall phytoplankton biomass (Glibert et al., 2011; Howarth, 1988; Sarker, 2018).

Concomitantly, SST in the German Bight has been rising by approximately 0.3 °C per decade (Amorim et al., 2023; Holliday et al., 2009; Hughes et al., 2011), affecting primary producers both directly and indirectly (Wiltshire et al., 2015). For example, elevated temperatures near/below species-specific optimal conditions directly enhance growth rates, but exceeding these thresholds can hinder growth and reduce primary production (Edwards et al., 2016; Eppley, 1972). Indirect effects in this region include the intensification of water column stratification in seasonally stratified and transitional areas between estuarine and offshore zones (Amorim et al., 2024; Capuzzo et al., 2018; van Leeuwen et al., 2015). This stratification may limit vertical phytoplankton movement, affecting the onset of the spring bloom and thereby reducing primary productivity (Capuzzo et al., 2018). Additionally, changes in the spatial extent of stratification can affect nutrient and light availability in the water column, controlling the conditions necessary for phytoplankton growth (Capuzzo et al., 2018).

Many studies have investigated the variability of phytoplankton biomass in the German Bight and its relationship with riverine nutrient loads and warming, highlighting the complexity of the system. In this region, phytoplankton biomass is often assessed using indicators such as chlorophyll-*a* (Chl-*a*), derived from satellite observations or in situ measurements, and the phytoplankton colour index (PCI), obtained from the Continuous Plankton Recorder. Xu et al. (2020), for instance, demonstrated an increase in phytoplankton biomass since the 1980 s using a physical-biogeochemical model, satellite Chl-*a* and PCI data, despite the documented reductions in nutrients during this period. Kerimoglu et al. (2018) reconstructed the pre-industrial nutrient and Chl-*a* levels in the region and found either non-significant differences or even increases in current Chl-*a* levels compared to pre-industrial times, particularly near the mouth of the Elbe River. These changes could not be explained by reduced nutrient inputs. More recently, Amorim et al. (2024) confirmed through satellite-derived Chl-*a* data that concentrations have been increasing in the coastal areas near the Elbe River since the 1990s. This increase could not be solely explained by rising SST or changes in mixed layer depths. On the other hand, in situ Chl-*a* measurements at several monitoring stations in the surrounding areas have shown a declining trend in Chl-*a* levels since the 1980 s (Brockmann et al., 2018; Desmit et al., 2020; van Beusekom et al., 2019). van Beusekom et al. (2019) showed that the decrease in summer Chl-*a* was associated with a concurrent decrease in the previous autumn's N and P concentrations of Elbe, Weser, Rhine, and Meuse at several stations in the Wadden Sea. However, Desmit et al. (2020) found no linear relationship between annual Chl-*a* levels and either SST or winter nutrients in the Dutch and Belgian coastal waters and concluded that the precise mechanisms behind their observed decrease in Chl-*a* in the region remained unclear.

Despite such previous research on chlorophyll variability in the German Bight, few studies have examined the combined effects of nutrients and temperature on chlorophyll levels using long-term, in situ data spanning the entire region. Contradictory findings on chlorophyll trends between satellite-derived Chl-*a*/PCI data and in situ Chl-*a* data in the southeastern North Sea (Xu et al., 2020) underscore the need for further investigations. This is especially true for the inshore area near the Elbe River, where stability is strongly influenced by riverine run-off. In this area, PCI data are limited (McQuatters-Gollop et al., 2007), and satellite-derived Chl-*a* measurements may be biased due to the influence of non-algal optical properties, such as suspended matter (Upadhyay Staehr et al., 2022; Wilson et al., 2024). Therefore, studies based on in situ measurements are essential for evaluating the effectiveness of nutrient reduction strategies and informing decision-making on nutrient management.

In this study, we compiled a comprehensive spatiotemporal dataset of in situ nutrient, SST, and Chl-*a* measurements in the German Bight, spanning from 1980 to 2019, sourced from several open-access databases and upon request. The primary aim was to evaluate trends using a consolidated dataset of all available in situ data and to explore the partial and interactive effects of winter nutrient alterations, as well as both winter and spring warming, on spring Chl-*a* levels. We focused on winter nutrients to examine the influence of anthropogenic activities and the overall nutrient availability in the system. Winter nutrients are primarily affected by river discharges and atmospheric deposition, which are heavily influenced by anthropogenic factors, while biological processes, such as nutrient uptake by primary producers (Brockmann et al., 1999; Heyden & Leujak, 2022), play a lesser role. Our analyses considered both winter and spring SST, acknowledging the various indirect and direct ways SST can affect phytoplankton biomass (Amorim et al., 2024; Sarker & Wiltshire, 2017; Wiltshire et al., 2010).

We hypothesize that both nutrient reduction and changes in SST influence variation in spring phytoplankton biomass in the German Bight. Specifically, we anticipate that reductions in N and P concentrations, along with elevated N/P ratios, will constrain phytoplankton growth due to phosphorus limitation (Burson et al., 2016; Sarker, 2018). Regarding temperature, we hypothesize that SST exerts two potential types of influence on phytoplankton biomass:

- (i) during winter, higher SST is expected to delay the onset of phytoplankton growth and reduce spring biomass due to increased grazing pressure (van Beusekom et al., 2009; Wiltshire & Manly, 2004; Wiltshire et al., 2008); and
- (ii) conversely, during spring, higher SST may positively affect phytoplankton biomass by enhancing metabolic rates and promoting growth under favorable light and nutrient conditions (Anderson et al., 2022; Edwards et al., 2016; Kremer et al., 2017).

As long-term observations indicate that persistent stratification is rare in the German Bight and unlikely to be a primary driver of phytoplankton blooms in this region (Wiltshire et al., 2015), we do not expect warming to significantly alter vertical mixing (Amorim et al., 2024). Thus, we expect that the effect of SST on Chl-*a* concentrations will depend on the seasonal context: a negative relationship with winter SST (due to enhanced grazing) and a positive relationship with spring SST (due to metabolic stimulation of phytoplankton growth).

To test these hypotheses, we will address the following questions:

1. How have changes in riverine nutrient runoffs affected nitrogen and phosphorus concentrations and their ratios in the coastal German Bight over the long term?
2. Is the increase in SST homogeneous across the entire region during both the winter and spring seasons?
3. What is the spatiotemporal variability of spring Chl-*a* levels over the past four decades?
4. How do changes in nutrients and SST relate to spring Chl-*a* levels in the German Bight, and which factors have the most significant effects?

Methods

Study Area

The German Bight is a coastal area (about 24,400 km^2) of the southeastern North Sea and bounded by the Netherlands (NL) and Germany (DE) to the south, and Denmark (DK) and Germany to the east (Fig. 1). The area is characterized by complex topography and hydrography, with depths ranging from less than 5 m nearshore to over 40 m offshore. The largest freshwater inputs to the Bight are from the Elbe, Weser, and Ems. The area has a semidiurnal tidal cycle, with tidal amplitudes ranging from 1.5 to 4 m (e.g., Speidel et al., 2024). Water masses in the areas where depth is less than 20 m are continuously mixed due to the large tidal amplitudes, whereas at depths greater than 20 m, stratification events can take place, mediated by tidal and wind forcing. The largest (in terms of vertical density gradient and area of presence) stratification events take place in spring, driven by the large discharge from the Elbe and Weser rivers—resulting from snowmelt and seasonal rainfall—together with favorable wind conditions (Chegini et al., 2020; Nied et al., 2013; Rubinetti et al., 2023). Salinity in the area is highly variable and exhibits clear seasonality. Generally, salinity ranges from 0 to 35 psu with variability exceeding 30% closer to the mainland (Brockmann et al., 2021). Based on salinity, four different types of waters are defined: estuarine (salinity 0–18), inner coastal (salinity 18–30 psu), outer coastal (salinity 30–34.5 psu), and offshore (salinity > 34.5 psu) (Fig. 1) (OSPAR, 2017).

Data Sources

We compiled a comprehensive dataset of the whole study area from 1980 to 2019, which included in situ measurements of dissolved inorganic nutrient concentrations, sea surface temperature (SST), and chlorophyll-*a* (Chl-*a*). The nutrients encompassed nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), and phosphate ($[PO_4]^{3-}$). Each data entry in the dataset was characterized by its respective depth, geographical coordinates, and the date of measurement. All nutrients were expressed in µmol L^{-1}, SST in °C, and Chl-*a* in µg L^{-1}.

The data were provided by several institutions upon request or obtained from open-access sources. Specifically, the data was gathered from the following:

1. Biologische Anstalt Helgoland (BAH) (Dummermuth et al., 2023; Wiltshire et al., 2024) (https://doi.org/10.1594/PANGAEA.960375);
2. Alfred-Wegener-Institut, Wattenmeerstation Sylt (AWI-Sylt) (Rick et al., 2020; Dummermuth et al., 2023) (https://doi.org/10.1594/PANGAEA.918023);
3. Bundesamt für Seeschifffahrt und Hydrographie (BSH);
4. Küstennahe Stoff- und Energieflüsse – Der Übergang Land-Meer in der südöstlichen Nordsee – Projekt (KUSTOS);
5. Landesamt für Landwirtschaft, Umwelt und ländliche Räume Schleswig–Holstein (LLUR);
6. Niedersächsisches Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLKWN);
7. The Department of Coastal Systems, Netherlands Institute for Sea Research (NIOZ) (Lenhart et al., 2010; van Leeuwen et al., 2021; 2023);
8. CORIOLIS (https://www.coriolis.eu.org/);
9. International Council for Exploration the Sea (ICES) (https://www.ices.dk/data/Pages/);
10. Meeresumweltdatenbank (MUDAB) (https://www.umweltbundesamt.de/daten); and

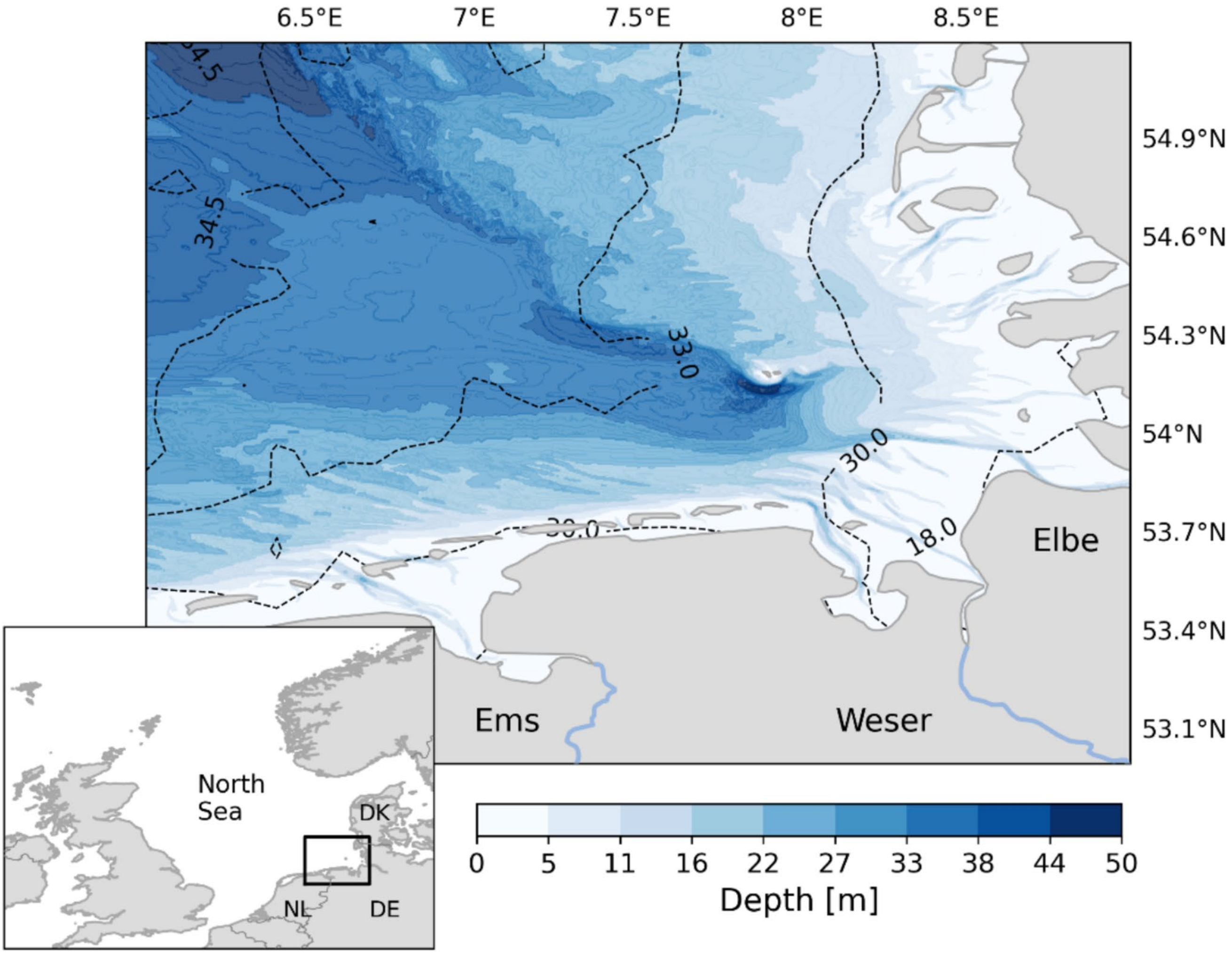

Fig. 1 Bathymetry of the German Bight in the southeastern North Sea, bordered by the Netherlands (NL), Germany (DE), and Denmark (DK). Light- and dark-blue colors indicate shallow and deep depths, respectively. Black dashed lines show winter median surface salinity (< 7 m; 1980–2019)

(11) World Ocean Database (WOD) (https://www.ncei.noaa.gov/products/world-ocean-database.

Bathymetry data were extracted from the General Bathymetric Chart of the Oceans (GEBCO) (https://www.gebco.net/). Information related to data sources for each variable separately is provided in Supplementary Material, Table S1.

Data Preprocessing

After gathering and concatenating the data, we eliminated duplicated values and extracted surface (< 7 m) winter (December to February, e.g., "winter 2019" represents December 2018 to February 2019) nutrient concentrations and SST, and spring (March–May) SST and Chl-*a*. Surface waters were considered for two main reasons:

(i) they are associated with nutrient loads from rivers (Brockmann et al., 2021), and
(ii) shallow regions (< 20 m) are permanently mixed due to large tidal amplitudes (Brockmann et al., 2021).

To identify and minimize the influence of anomalous values, we applied a site-specific outlier screening based on the Median Absolute Deviation (MAD), a robust approach suitable for skewed environmental data (Leys et al., 2013). Outliers were flagged when their modified *z*-score exceeded the MAD threshold. Several thresholds were tested (3.5–6.5 MAD; Fig. S1), and a final cutoff of 6.5 MAD units was selected as a compromise between sensitivity to extreme values and avoidance of over-filtering (see for example, Fig. S2). MAD screening was only applied at sites with at least eight observations. In total, < 2.5% of observations for any variable were flagged as outliers (Fig. S3) and excluded from subsequent analyses. Non-detects were rare (< 1.5% of the dataset) and were retained without substitution, ensuring that their negligible contribution did not bias subsequent aggregation. After data cleaning, dissolved inorganic nitrogen (DIN) was computed as sums of NO_3^-, NO_2, and NH_4^+, and nutrient ratios were estimated as dissolved inorganic nitrogen-to-phosphorus ratios (DIN:DIP) for each sampling point. Medians of winter nutrient concentrations and ratios, winter and spring SST, and spring Chl-*a* were computed per year for each sampling point. Medians were selected for data aggregation because they are robust to outliers and skewed data (Balkoni et al., 2023). To verify that the aggregated values were consistent with plausible spatial variability, we inspected annual boxplots of per-site median values across all sites (Fig. S4). These plots show that although statistical outliers (in the boxplot sense) are frequent, especially for nutrients, they fall within plausible environmental ranges and largely reflect estuarine dynamics rather than data errors. Data compilation and preprocessing were done in Python (v3.11.6) using Pandas (v2.2.0) and NumPy (v1.26.0) packages.

Data Coverage

Winter and spring SST had the highest spatial and temporal coverage, followed by, in decreasing order, winter DIP, winter DIN, and spring Chl-*a* (Figs. S5 and S6). Sampling frequency was higher near the mainland (Fig. S5) due to the presence of numerous long-term monitoring stations and transects. The temporal distribution of data was uneven, with particularly low coverage from 1980 to 1985, especially for Chl-*a* (Fig. S6f). The total number of data points was over 2000 for each variable (Fig. S7). Among these, 731 data points included measurements of nutrients, temperature, and chlorophyll at the same sampling site and year. This subset became available from 1985, with a significant increase in the amount of data after 1991 (Fig. S8). The subset primarily represents estuarine and coastal waters (both inner and outer) with salinities ranging from 0 to 33 psu, including the region near the mouth of the Elbe River (Fig. S5f).

Data Analysis

Spatiotemporal Variation of Nutrients, SST, and Chl-*a*

We examined the spatiotemporal variation of winter nutrient concentrations and ratios, winter and spring SST, and spring Chl-*a* on a decadal basis, emphasizing major shifts in the North Sea ecosystem (Wiltshire et al., 2015). The maps were produced using all available data from 1980 to 2019 (Fig. S7) in three steps:

(i) computation of the medians per decade at each sampling site,
(ii) construction of longitude-latitude grids with a resolution of 0.1° × 0.1°, and
(iii) application of radial basis functions (RBFs) using a multi-quadratic spline function with a smoothing factor of 0.05 (Hardy, 1971; Rusu & Rusu, 2006).

The smoothing factor was chosen by iterating through all possible values ranging from 0.01 to 1, selecting the one that mitigated small-scale variability between neighboring data points and minimized errors (Rusu & Rusu, 2006). Errors resulting from smoothing in the interpolation process were estimated comparing the interpolated values to the actual values and presented using histograms and Kernel density distributions. Spatial interpolation and mapping were implemented using SciPy (v1.12.0) and Cartopy (v0.23.0) packages in Python.

Long-Term Temporal Trends of Nutrients, SST, and Chl-*a*

In addition to the decadal maps, we analyzed long-term temporal trends of winter nutrients, winter and spring SST, and spring Chl-*a*. Annual time series for each variable were constructed from a consistent subset of the dataset comprising simultaneous measurements of nutrients, temperature, and chlorophyll at the same sampling sites and years, representing the estuarine and coastal waters of the German Bight (see Data Coverage subsection). Focusing on this subset ensured temporal consistency across variables and reduced potential biases caused by the uneven offshore sampling. Annual medians were used for aggregation. Temporal trends were assessed using the non-parametric Mann–Kendall test (Kendall, 1975; Mann, 1945), with statistical significance evaluated at $\alpha = 0.05$, and the magnitude of significant trends was estimated with Sen's slope (Sen, 1968). Both tests were conducted in Python (v3.11.6) using the package pymannkendall (v1.4.3).

Effects of Nutrients and SST on Chl-*a*

Generalized Linear Mixed Models (GLMMs) were used to investigate the partial and interactive effects of environmental variables on spring Chl-*a* levels. The analyses focused on a subset of data that included simultaneous measurements of nutrients, temperature, and chlorophyll taken from the same sampling site and year (see Data Coverage subsection). Although this approach reduces the dataset, the use of measurements from the same time and place is crucial for avoiding biases caused by incomplete datasets (e.g., Zhao et al., 2019).

GLMMs extend classical linear models by incorporating random effects to account for correlated data structures, such as spatial and temporal autocorrelation (Zuur et al., 2009). By including random effects for sampling locations and years, this method accommodates the uneven sampling design in both space and time, allowing for the appropriate modeling of spatial and temporal clustering (Gillies et al., 2006). Random effects also improve model fit by handling unbalanced sampling and enable the interpretation of both marginal (*p*opulation-level) and conditional (group-level) responses (Gillies et al., 2006). This makes GLMMs particularly useful for addressing data complexities where uneven sampling and autocorrelation are present, which are often challenging for conventional analysis methods (e.g., Bisanzio et al., 2011; Gillies et al., 2006; Zhong et al., 2020).

Two global models were fitted to examine the relationships between environmental variables and Chl-*a* concentrations. The first model (global model 1, Table 1) included winter DIN (DIN_winter_log), winter DIP (DIP_winter_log), winter DIN/DIP (DIN_DIP_winter_log), and winter (SST_winter) and spring SST (SST_spring) as fixed effects. The second model (global model 2, Table 1) incorporated interaction terms between pairs of all environmental factors, denoted in the formula by the ":" symbol. Both models treated sampling locations (spatial_group) and years (year) as random effects, modeled as individual entities to account for spatial and temporal variation. To address deviations from normality, nutrient and Chl-*a* data were log-transformed (base 10) prior to analysis, and all continuous variables were standardized using the scale function in R (V4.3.2). Both models employed a Gaussian distribution with an identity link function. GLMMs were executed in R (v4.3.2) using the glmmTMB (v1.1.11) (Brooks et al., 2017) package.

A multimodel inference approach was employed to reduce subjectivity in model selection (Burnham & Anderson, 2002; Defeo et al., 2017). Initially, a set of candidate models was tested by exploring all additive combinations of the fixed effects, as well as those incorporating interaction terms. Collinearity among the fixed variables was assessed using the variance inflation factor (VIF), with values above 1.5 indicating collinearity (Zuur et al., 2009). Models involving both nutrient concentrations and ratios as fixed effects exhibited high collinearity (VIF > 4) and were excluded from further analysis.

During model fitting, we calculated the corrected Akaike Information Criterion (AICc), log-likelihood scores, and AICc weights (AICcw) to guide model selection (Burnham & Anderson, 2002; Defeo et al., 2017). Model weights were used to assess the relative probability of each model outperforming the others, and models with a ΔAICc greater than 4 were excluded from further analysis (Defeo et al., 2017). The remaining models were used to compute model-averaged parameter estimates and their associated standard errors. The variance explained by fixed effects alone (marginal R^2_m) and by both fixed and random effects (conditional R^2_c) of the fitted GLMM were calculated using the R package performance (v0.15.0) (Lüdecke et al., 2023).

Model validation included checking the homogeneity and normality of residuals using diagnostic plots, following the protocol outlined by Zuur et al. (2009). Spatial autocorrelation was assessed using Moran's I (Bivand & Wong, 2018; Tiefelsdorf & Boots, 1995), where values closer to 1 indicate clustering and values closer to −1 indicate dispersion. A *p*-value above 0.05 was considered weak evidence against the null hypothesis of no spatial autocorrelation. Moran's I test was implemented in R using the spdep package (v1.3.13) (Bivand & Wong, 2018; Pebesma & Bivand, 2023). To enhance confidence in the results of the selected model, the analysis was repeated using two additional subsets of data: one included sites with at least 10 consecutive years of observations and another included sites with at least 15 consecutive years of observations. This approach allowed us to assess whether unevenness in the dataset influenced the results by comparing the outcomes derived from different subsets.

Results

Spatiotemporal Variation of Nutrients, SST, and Chl-*a*

The spatiotemporal variation of winter nutrient concentrations, ratios, SST, and spring SST and Chl-*a* on a decadal basis from 1980 to 2019 is presented in Fig. 2. Winter nutrient concentrations were highest in the estuarine and inner coastal waters, gradually decreasing toward the offshore areas over the four decades. Winter dissolved inorganic nitrogen (DIN) exceeded 200 µmol L^{-1} at the mouths of the rivers Elbe, Weser, and Ems. DIN concentrations between 50 and 200 µmol L^{-1} were observed in the inner

Table 1 Full formula for the two global GLMMs (Gaussian distribution and identity link)

<table>
<tr><td>Global model 1 (additive)</td><td>Chla_spring_log ~ DIN_winter_log + DIP_winter_log + DIN_DIP_winter_log + SST_winter + SST_spring + (1 | year) + (1|spatial_group), data = df, family = gaussian(link = "identity")</td></tr>
<tr><td>Global model 2 (interactive)</td><td>Chla_spring_log ~ DIN_winter_log: SST_winter + DIN_winter_log: SST_spring + DIP_winter_log: SST_winter + DIP_winter_log: SST_spring + DIN_DIP_winter_log: SST_winter + DIN_DIP_winter_log: SST_spring + (1 | year) + (1 | spatial_group), data = df, family = gaussian(link = "identity")</td></tr>
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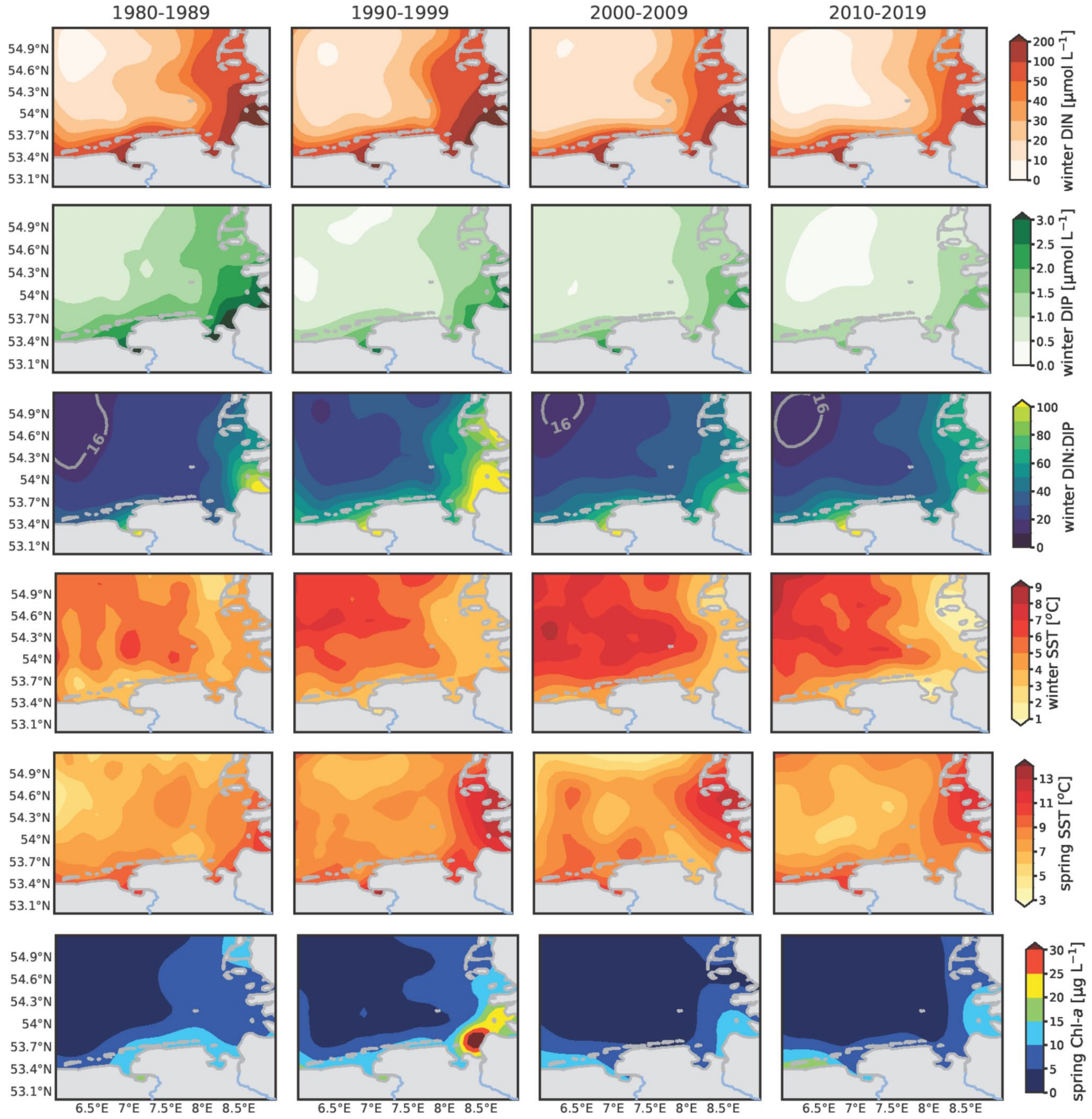

Fig. 2 Median concentrations of winter dissolved inorganic nitrogen (DIN, µmol L^{-1}), winter dissolved inorganic phosphorus (DIP, µmol L^{-1}), winter dissolved inorganic nitrogen-to-phosphorus (DIN:DIP) ratios, winter sea surface temperature (SST, °C), spring SST, and spring chlorophyll-*a* (Chl-*a*, µg L^{-1}) in the German Bight per decade from 1980 to 2019. The gray lines in DIN:DIP plots represent the Redfield ratio (16:1)

coastal waters (18–30 psu, Fig. 1), while in the outer coastal waters (30–34.5 psu, Fig. 1), DIN concentrations varied between 10 and 50 µmol L^{-1}. In the offshore waters (salinity > 34.5 psu, Fig. 1), DIN concentrations did not exceed 10 µmol L^{-1}. During the 1980s and 1990s, winter DIN levels remained high, whereas since 2000, there has been a clear decline in DIN levels across the entire region.

Winter dissolved inorganic phosphorus (DIP) concentrations were highest during the 1980s. During this decade, DIP concentrations exceeded 3 µmol L^{-1} in the Elbe, Weser, and Ems estuaries, varied between 1.5 and 3 µmol L^{-1} in the inner coastal waters, and ranged from 0.5 to 1.5 µmol L^{-1} in the outer coastal and offshore areas. Since 1990, DIP concentrations have gradually decreased, with the lowest concentrations recorded in the most recent decade. During this period, both estuarine and inner coastal waters remained below 1.5 µmol L^{-1}, while outer coastal and offshore waters did not exceed 1 µmol L^{-1}.

The different decreases of winter DIN and DIP were reflected in the seawater ratios. The highest DIN:DIP ratios were recorded in the 1990 s, exceeding 100 in estuarine and inner coastal waters. During this decade, DIN/DIP ratios were above the Redfield ratio (16:1) throughout the region. In contrast, DIN:DIP ratios were relatively stable in the 1980 s, 2000 s, and 2010 s, displaying a clear gradient from approximately 60 to 100 in riverine and inner coastal waters to below 16 in the offshore areas.

Winter sea surface temperature (SST) exhibited significant spatial and temporal variability. A marked increase in SST was observed in the outer coastal and offshore waters. In the 1980 s, for instance, SSTs in these areas ranged from 5 to 6 °C, while the inner coastal and estuarine waters recorded temperatures between 2 and 5 °C. Throughout the 1990 s and 2000 s, SST in the outer coastal areas rose above 6 °C and 7 °C, respectively. However, SST in the inner coastal and estuarine waters remained stable, fluctuating between 3 and 6 °C during these decades. In the 2010 s, winter SST remained high in offshore and outer coastal waters, with some regions reaching up to 9 °C. Conversely, a decrease in SST was observed in the inner coastal waters, particularly in the northeastern part of the region, where temperatures dropped to about 1 to 2 °C.

Spring SST, which tended to exhibit less variability than winter SST, displayed higher temperatures ranging between 9 and 13 °C in the shallower parts of the Bight. In contrast, SST variations in the offshore, outer, and southeastern inner coastal regions ranged from approximately 6 to 9 °C. Notably, since the 1990 s, higher SSTs have been observed, particularly in the northeastern inner coastal areas and estuaries, where temperatures exceeded 11 °C.

From the 1980 s to the 2010 s, there was a general decline in spring Chl-*a* concentrations, albeit with some regional deviations. Higher concentrations were recorded in the inner coastal and estuarine waters, decreasing toward the offshore areas in all decades. In the 1980 s, Chl-*a* concentrations exceeded 5 µg L^{-1} in the outer coastal waters, reached 10 µg L^{-1} in the inner coastal waters, and peaked at 20 µg L^{-1} in the Ems estuary. During the 1990 s, Chl-*a* concentrations decreased in the outer coastal waters but increased significantly in the inner coastal waters, particularly near the Elbe and Weser estuaries, with concentrations surpassing 30 µg L^{-1}. Over the past two decades, Chl-*a* concentrations further declined in the outer coastal waters and estuaries. However, in the inner coastal waters, especially in the southeastern Bight, Chl-*a* concentrations remained high. Overall, interpolation reliability analyses confirmed that these mapped patterns are robust. While Chl-*a* in the 1980 s showed slightly higher uncertainties due to the scarcity of data, errors for all other decades and for nutrients and SST were generally small and clustered near zero (Fig. S9).

Long-Term Temporal Trends of Nutrients, SST, and Chl-*a*

Figure 3 illustrates the long-term trends of winter nutrient concentrations, nutrient ratios, SST, and spring Chl-*a* in the estuarine and coastal waters of the German Bight (salinities ranging from 0 to 33 psu; Fig. 1) from 1985 to 2019. Significant trends were detected for all variables except the winter DIN/DIP ratio. Winter DIN concentrations declined steadily, with Sen's slope estimates indicating a reduction of approximately –0.96 µmol L^{-1} per year ($p < 0.01$; Fig. 3a), while winter DIP showed a pronounced drop in the 1990 s with an overall decline of –0.04 µmol L^{-1} per year ($p < 0.01$; Fig. 3b). The differing magnitudes of DIN and DIP declines caused DIN/DIP ratios to rise sharply during the 1990 s, after which the ratios fluctuated but generally remained above the levels observed in the 1980 s, although no significant long-term trend was detected (Fig. 3c). Winter and spring SST increased significantly at rates of + 0.05 °C per year ($p < 0.05$) and + 0.06 °C per year ($p < 0.05$), respectively (Fig. 3d and e). Spring Chl-*a* exhibited a marked long-term decrease of –0.23 µg L^{-1} per year ($p < 0.01$; Fig. 3f).

Effects of Nutrients and SST on Chl-*a*

Using sampling locations and years as random effects, the best GLMM, identified based on the lowest AICc value (1243.82) and highest Akaike weight (AICcw = 0.44), retained only the effects of winter DIN, spring SST, and winter SST, with no interaction terms (Table 2). This model explained 30% of the marginal variance (R^2_m = 0.30) and 64% of the conditional variance (R^2_c = 0.64). Adding winter DIP to this model slightly improved the log-likelihood but increased the AICc (1245.56), resulting in a ΔAICc of 1.73 and an AICcw of 0.18. Simpler models with fewer predictors, such as the model with winter DIN and spring SST or the model with winter DIN and winter SST, had higher ΔAICc values (2.56 and 2.91, respectively) and lower AICc weights (0.12 and 0.10), suggesting these models were less competitive. Models including the DIN/DIP ratio were not competitive, as they had ΔAICc values exceeding 4 (Defeo et al., 2017). This indicates that the DIN:DIP ratio did not substantially improve model performance or contribute meaningfully to explaining the observed variability.

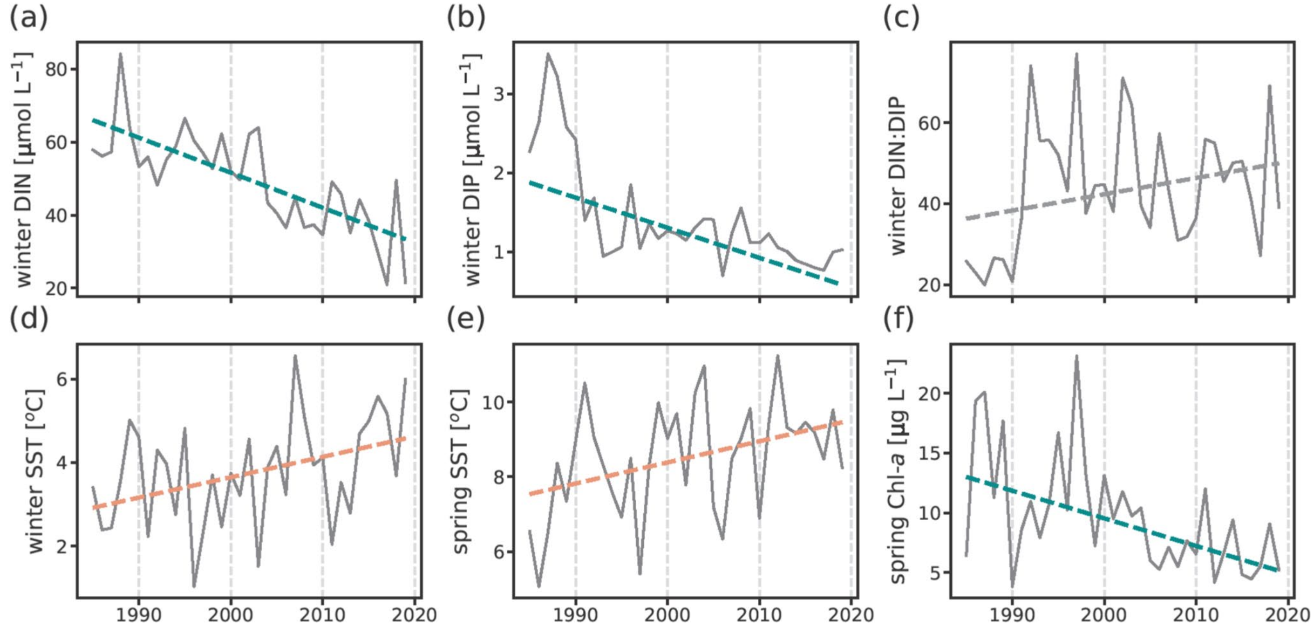

Fig. 3 Annual median concentrations of winter dissolved inorganic nitrogen (DIN, µmol L^{-1}), winter dissolved inorganic phosphorus (DIP, µmol L^{-1}), winter dissolved inorganic nitrogen-to-phosphorus (DIN:DIP) ratios, winter sea surface temperature (SST, °C), spring SST, and spring chlorophyll-*a* (Chl-*a*, µg $L.^{-1}$) in the estuarine and coastal waters of the German Bight (salinities ranging from 0 to 33 psu) from 1985 to 2019. Dashed lines represent Sen's slope estimates of long-term monotonic trends. Line colors denote both direction and significance based on the Mann–Kendall test: gray, no significant trend ($p \geq 0.05$); green, significantly decreasing trend ($p < 0.05$); orange, significantly increasing trend ($p < 0.05$)

Table 2 Generalized linear mixed models (GLMMs) relating spring Chlorophyll-*a* to winter nutrient concentrations and winter and spring sea surface temperature (SST, °C) across 66 sampling sites in the German Bight

Candidate models		d.f	logLik	AICc	ΔAICc	AICcw	R_m^2	R_c^2
Additive	**winter DIN + spring SST + winter SST**	**7**	**− 614.82**	**1243.82**	**0**	**0.44**	**0.30**	**0.64**
	winter DIN + winter DIP + spring SST + winter SST	8	− 614.66	1245.56	1.73	0.18	0.30	0.64
	winter DIN + spring SST	6	− 617.12	1246.39	2.56	0.12	0.28	0.64
	winter DIN + winter SST	6	− 617.30	1246.74	2.91	0.10	0.25	0.64
Interactive	winter DIN:spring SST + winter DIN:winter SST	6	− 644.68	1301.49	0	0.12	0.02	0.69
	winter DIN:spring SST + winter DIN:winter SST + winter DIP:winter SST	7	− 644.26	1302.71	1.21	0.06	0.02	0.69
	winter DIN:spring SST + winter DIN:winter SST + winter DIP:spring SST	7	− 644.67	1303.51	2.02	0.04	0.02	0.69
	winter DIN:winter SST + winter DIP:spring SST	6	− 646.12	1304.38	2.89	0.02	0.02	0.69
	winter DIN:winter SST	5	− 647.68	1305.47	3.97	0.01	0.01	0.68

The best model is highlighted in bold. Models are ranked by AICc values, and only the best models, with a difference in AICc below the threshold for exclusion (ΔAICc < 4), are shown

d.f. Degrees of freedom, *logLik* log-likelihood, *AICc* corrected Akaike information criterion, *AICcw* AICc weights, R_m^2 marginal R^2, R_c^2 conditional R^2

For interactive effects, the model incorporating interactions between winter DIN and both spring SST and winter SST had the lowest AICc (1301.49), though its AICcw was only 0.12, indicating weaker support compared to the additive models. Additional interaction terms, such as winter DIP:winter SST or winter DIP:spring SST, increased the complexity but did not substantially improve the fit, with ΔAICc values exceeding 1.21. These models explained only 2% of the marginal variance ($R_m^2 = 0.02$) but retained high conditional variance explained ($R_c^2 = 0.69$), suggesting that random effects contributed significantly to the overall variance. Overall, the additive model with winter

DIN, spring SST, and winter SST provided the best balance of explanatory power and parsimony, as indicated by its strong support in the model selection criteria.

Model-averaged coefficients revealed that among the predictors, winter DIN had the strongest and most significant positive effect on spring Chl-*a* concentrations (estimate = 0.40, $p < 0.01$) (Table 3 and Fig. 4). Spring SST also showed a significant positive effect (estimate = 0.09, $p = 0.03$), albeit weaker than winter DIN. Winter SST had a negative but non-significant effect (estimate = − 0.07, $p = 0.12$), while winter DIP had a negligible and non-significant effect (estimate = − 0.004, $p = 0.81$). None of the interactive effects—including winter DIN:spring SST, winter DIN:winter SST, winter DIP:winter SST, and winter DIP:spring SST—were significant (all $p > 0.2$). These results suggest that partial effects, particularly winter DIN and spring SST, play a more critical role in explaining the variability in spring Chl-*a* than interactive effects.

Model results, expressed on the original response variable scale, showed that spring Chl-*a* levels increased with both winter DIN and spring SST (Fig. 4). This indicates that higher spring Chl-*a* levels occurred following winters with elevated DIN concentrations in the water column and under warmer spring sea surface temperatures. The variance inflation factor (VIF) values ranged from 1.01 to 1.22, confirming the absence of collinearity among variables. Moran's I test showed no significant spatial autocorrelation in the data (Moran's $I = -0.0008$, $p = 0.37$). The observed Moran's I was close to the null expectation (− 0.0015), with a standard deviate of 0.30, suggesting that the spatial distribution of the variable is consistent with a random pattern, and no clustering or dispersion was detected in the model's residuals. The relationship between predicted and observed spring

Table 3 Model-averaged coefficients for the relationship between spring chlorophyll-*a* and predictor variables

Model averaged estimates		Estimate	SE	SE adj	*z*-value	*p*-value
Partial	**winter DIN**	**0.40**	**0.05**	**0.05**	**7.23**	**< 0.01**
	spring SST	**0.09**	**0.04**	**0.04**	**2.17**	**0.03**
	winter SST	− 0.07	0.05	0.05	1.53	0.12
	winter DIP	− 0.004	0.02	0.02	0.23	0.81
Interactive	winter DIN:spring SST	− 0.06	0.04	0.04	1.25	0.20
	winter DIN:winter SST	0.08	0.07	0.07	1.12	0.25
	winter DIP:winter SST	0.01	0.04	0.04	0.45	0.64
	winter DIP:spring SST	− 0.009	0.02	0.02	0.35	0.72

Model averaging was performed using the models with ΔAICc < 4. *SE* Standard errors and *SE adj* adjusted standard errors, account for model uncertainty; *z*-values and *p*-values indicate the significance of each parameter estimate. Significant results are highlighted in bold

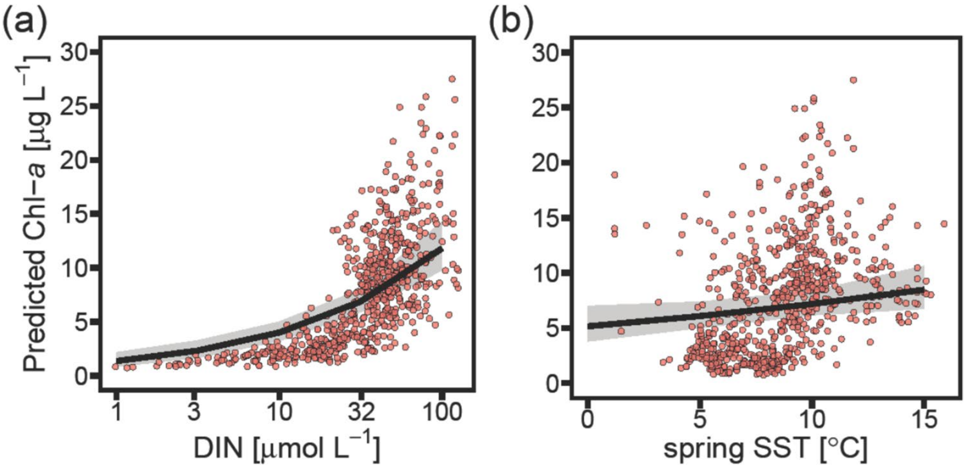

Fig. 4 Generalized linear mixed model showing the relationship between spring Chlorophyll-*a* (Chl-*a*) levels, winter dissolved inorganic nitrogen (DIN) (**a**), and spring sea surface temperature (SST) (**b**) for sampling sites in the coastal German Bight that involve simultaneous measurements of Chl-*a*, nutrients, and SST. Solid lines represent the mean partial effects of winter DIN and spring SST, with shaded envelopes indicating the 95% confidence intervals. The points represent actual data points from the subset that includes measurements of nutrients, temperature, and chlorophyll taken at the same sampling site and year

Chl-*a* values (Fig. S10a), along with the diagnostic plots of homogeneity (Fig. S10b) and normality of the residuals (Fig. S6c), validated the robustness of the selected model.

Further analyses using model-averaged coefficients, restricted to sampling sites with a minimum of:

(i) ten consecutive years of observations (Table S2), and
(ii) fifteen consecutive years of observations, reinforced the critical role of nitrogen (Table S3 and Fig. S11).

Spring SST was identified as a significant predictor in the subset of sampling sites with at least 10 years of observations but not in the subset with at least 15 years. This discrepancy likely reflects differences in sample size and spatial–temporal coverage between the subsets. The larger 10-year subset may better capture the variability and episodic significance of spring SST, whereas the smaller 15-year subset could underrepresent such variability or lack the statistical power to detect weaker effects.

Discussion

Since the mid-1980s, nitrogen and phosphorus loadings from major European rivers surrounding the North Sea have substantially decreased due to de-eutrophication strategies (Grizzetti et al., 2012; van Beusekom et al., 2019). Despite these efforts, several studies have reported increases in phytoplankton biomass (Llope et al., 2009; McQuatters-Gollop et al., 2007), even in regions directly influenced by river runoffs, such as the Elbe River mouth in the German Bight (Amorim et al., 2024; Kerimoglu et al., 2018; Xu et al., 2020). This unexpected result has raised questions about the effectiveness of nutrient reduction measures, with some studies suggesting that rising SST and improved water clarity may have offset the impact of nutrient reductions (Llope et al., 2009; McQuatters-Gollop et al., 2007; Xu et al., 2020). Given this context, we aimed to evaluate trends and explore the partial and interactive effects of winter nutrient alterations and seasonal (winter and spring) warming on spring Chl-*a* levels. To address this, we analyzed spatiotemporal trends in spring in situ Chl-*a* measurements from the German Bight (1980s–2019) to evaluate whether observed trends support earlier findings and to assess the roles of nutrients and SST. Our results revealed that spring Chl-*a* concentrations peaked in the 1980s and 1990s but have since declined, although they remain relatively high in southern inner coastal waters. Winter DIN and spring SST emerged as the most significant predictors of spring Chl-*a* levels, indicating that rising levels of these factors enhance phytoplankton biomass, partially supporting our initial hypothesis.

Nutrient Concentrations and Ratios

Our data show that winter DIN and DIP concentrations in the German Bight decreased between the 1980s and 2010s, reflecting reductions in riverine nutrient loads. Winter DIP concentrations declined as early as the 1990s due to improved wastewater treatment and restrictions on phosphorus-containing detergents (Bouraoui et al., 2014). In contrast, winter DIN reductions became more apparent after 2000, likely due to early challenges in controlling agricultural runoff and delayed nitrogen storage responses in soils and aquifers (Bouraoui & Grizzetti, 2011).

This imbalance in nutrient reductions increased winter DIN/DIP ratios in the estuarine and inner coastal waters, significantly surpassing the Redfield Ratio (16:1), while offshore waters continued to have levels near or below the Redfield Ratio across all decades. Burson et al. (2016) found similar trends in DIN:DIP ratios in Dutch coastal and offshore waters during spring in 2012 and 2013. They concluded that elevated N:P ratios from river inputs led to severe P-limitation in the coastal waters of the North Sea. Here, we showed that winter DIN:DIP ratios were very high—above 70—in inner coastal and estuarine waters of the German Bight over four decades, which could potentially exacerbate P-limitation of phytoplankton growth during spring. Our data indicate that the 1990s exhibited the highest winter DIN:DIP ratios across the entire region, whereas levels in the last two decades have been closer to those observed in the 1980s. Sarker (2018) suggested that the P-limitation is increasing over time across the region based on winter total nitrogen-to-phosphorus ratios (TN/:TP). This contradicts our findings, potentially due to differences in the chemical species analyzed. DIN:DIP ratios, unlike TN:TP, better reflect autotrophic nutrient status, as TN:TP includes biologically unavailable nutrient fractions (Ptacnik et al., 2010). Supporting our findings, OSPAR (2017) also used winter DIN:DIP data and showed a statistically significant decline in ratios in waters with salinities of 32–34.5 psu during 1990–2014, higher ratios during the 1990 s in waters with salinities between 30 and 32 psu, but no significant trends in waters with salinities below 30 psu.

Although N:P ratios related to the Redfield ratio are commonly used for determining whether phytoplankton productivity is (or will become) N- or P-limited (Redfield, 1963; Burson et al., 2016; Sarker, 2018; Siems et al., 2024), this approach is only a rough indicator. The N:P ratio of phytoplankton is highly variable, and the Redfield ratio is not an absolute threshold (Geider & La Roche., 2002; Sarthou et al., 2005; Ptacnik et al., 2010). Therefore, additional methods, such as bioassays, are recommended for more accurate assessments (Beardall et al., 2001; Burson et al., 2016). However, applying such alternative methods in long-term studies can be challenging, making it necessary to also examine actual nutrient concentrations. In the past decade, winter DIN and DIP concentrations in the estuarine and coastal waters of the German Bight have remained high, exceeding 40 μmol L^{-1} for DIN and ranging between 1 and 1.5 μmol L^{-1} for DIP. Heyden and Leujak (2022) suggested that, to achieve good ecological status, winter DIN and DIP concentrations should not exceed 30 μmol L^{-1} and 1.1 μmol L^{-1}, respectively. These levels are derived from a historic pre-eutrophic reference situation, applicable to winter nutrient concentrations, and are not indicative of limiting conditions for phytoplankton during the spring bloom. However, further reductions from these levels are suggested for the mitigation of overall eutrophication in the region (Heyden & Leujak, 2022).

Sea Surface Temperature

Since the 1960s, there has been a marked increase in the SST in the German Bight. Long-term data from coastal monitoring stations revealed a significant upward shift in the late 80 s, with an average increase of approximately 0.3 °C per decade (Amorim et al., 2023; Wiltshire & Manly, 2004). Our observations also indicated a positive trend in SST throughout the region during both winter and spring seasons. However, it is important to note that the increasing trend in SST was not uniform across the entire region or time period. For instance, the northeastern tidal basin recorded the lowest SST during the 2010 s, at around 1 °C. The negative trend of winter SST in this part of the region is corroborated by long-term observations from the Sylt Roads monitoring stations, with winter SST being near or below zero from 2010 to 2019 (Rick et al., 2023). This negative trend might be related to a persistent negative North Atlantic Oscillation (NAO) phase (Amorim et al., 2023). However, this anomaly might not be extreme relative to winters of the past six decades (Cattiaux et al., 2010). Spatial variability was also observed in spring SST. For example, the highest values were recorded in the eastern part of the Bight during the 1990 s, at approximately 12 °C. This is consistent with observations from the Sylt Roads monitoring stations, where the highest SST from 1985 to 2019 was recorded during the 1990 s (Rick et al., 2023). Therefore, despite the global increase in average temperatures, it is important to note that spatial differences can be significant. This is critical because

(i) single-point measurements may not represent global processes, and
(ii) warming is not occurring at the same rate everywhere.

Phytoplankton Biomass

In situ Chl-*a* data suggest a general decline in spring phytoplankton biomass in coastal waters during spring from 1980 to 2019, with some regional variations. Specifically, spring Chl-*a* levels have decreased in coastal waters, except for the southeastern part of the Bight, where a consistent increase was observed throughout the entire period. Similar trends have been reported by the European Environment Agency (2022) for summer Chl-*a* concentrations in this region. Decreasing phytoplankton biomass has also been documented using in situ Chl-*a* measurements in the surrounding coastal North Sea. van Beusekom et al. (2019) demonstrated a decrease in summer Chl-*a* at several monitoring stations in the Wadden Sea, except for Dantziggat in the southeastern part of the region, where a positive trend was observed from 1985 to 2017. Annual Chl-*a* levels also decreased in the Dutch and Belgian coastal waters (Desmit et al., 2020) as well as in the coastal waters in Denmark (European Environment Agency, 2022) and in the inner Oslofjord (Lundsør et al., 2020).

Satellite-derived and in situ Chl-*a* observations reveal differing trend patterns in the estuarine and inner coastal German Bight (salinity $<$ 30 psu). Xu et al. (2020) reported a long-term increase in satellite-derived Chl-*a* (1961–2012), suggesting persistently high levels despite nutrient reductions, while Amorim et al. (2024) found a significant upward trend, particularly near the Elbe River, during 1998–2020. However, Amorim et al. (2024) also observed no trend or even a decline in spring satellite-derived Chl-*a*, consistent with our results and with other studies reporting summer decreases in in situ Chl-*a* concentrations in coastal waters (van Beusekom et al., 2019; European Environment Agency, 2022). This indicates that the positive trends in satellite records may instead reflect changes in other seasons.

An important factor to consider in interpreting satellite-derived Chl-*a* trends is the potential influence of suspended particulate matter (SPM) on satellite retrievals. High SPM concentrations can interfere with remote sensing algorithms, leading to overestimation of Chl-*a* (Alvera-Azcárate et al., 2021; Schiller & Doerffer, 2005). The German Bight is an optically complex coastal system where dynamic riverine inputs and frequent sediment resuspension further complicate retrieval accuracy (Alvera-Azcárate et al., 2021; Doerffer et al., 2003; Hommersom et al., 2010). Comparisons of satellite-derived Chl-*a* with in situ High-Performance Liquid Chromatography (HPLC) measurements from Helgoland Roads (2004–2020) show that satellite products reproduce overall variability but tend to overestimate low concentrations (Amorim et al., 2024). This bias is likely stronger near the Elbe mouth than at Helgoland Roads, where validation was conducted, since SPM concentrations are generally higher near the river outlet across all seasons

(Desmit et al., 2024). Consequently, it remains uncertain whether the reported increase in satellite-derived Chl-*a* near the Elbe reflects a genuine seasonal rise or is largely an artifact of retrieval biases associated with high SPM.

Relationships Between Nutrients, SST, and Chl-*a*

Based on the variation of winter nutrient concentrations, nutrient ratios, and SST, our analyses indicate that winter DIN was the strongest explanatory factor of spring Chl-*a* levels in the German Bight over the past four decades. Previous studies, based on both riverine and seawater TN and DIN and covering different seasonal periods (e.g., summer Chl-*a*), have also identified positive relationships between nitrogen availability and chlorophyll in the region (Brockmann et al., 2018; van Beusekom et al., 2009, 2019). In contrast, winter DIP concentrations and DIN:DIP ratios were not significant predictors in our analyses, although many studies have highlighted phosphorus as the main nutrient limiting phytoplankton growth in the coastal waters of the German Bight and surrounding regions during spring (Burson et al., 2016; Loebl et al., 2009; Ly et al., 2014). Based on this, a significant positive relationship between phosphorus concentrations and chlorophyll would have been expected. The ongoing debate about nitrogen versus phosphorus limitation in North Sea coastal waters complicates this simplified view. For instance, Loebl et al. (2009), using a diagnostic method developed by Cloern (1999), found that coastal phytoplankton growth was frequently limited by phosphate availability over the long term in European coastal waters. However, they also noted that spatial variations in annual chlorophyll levels across sites were best explained by mean annual DIN levels, suggesting their model may underestimate the role of nitrogen limitation in the system. Consistent with this, our statistical analyses indicate that nitrogen is likely the primary driver influencing spring Chl-*a* levels in the German Bight over the long term. One possible explanation for this pattern could lie in the adaptive strategies of phytoplankton to cope with phosphorus shortages. For example, phytoplankton can produce alkaline phosphatase, an enzyme that hydrolyzes organic phosphorus into bioavailable phosphate, enabling growth under low DIP conditions (Lin et al., 2015). Additionally, sedimentary remineralization may provide extra phosphorus, particularly in shallow areas (<20 m) (Leote et al., 2016). Lastly, while phosphorus limitation may affect phytoplankton growth during spring, it does not necessarily dictate total spring Chl-*a* levels. Species-specific nutrient demands could play a role, with certain phytoplankton species thriving under conditions of high nitrogen availability and maintaining elevated Chl-*a* concentrations despite potential phosphorus limitation (Burson et al., 2018).

The impact of decreasing winter DIN on spring Chl-*a* levels can be mitigated by rising SST in spring. We identified a weak positive relationship between spring SST and spring Chl-*a* levels, supporting our initial hypothesis claiming that rising SST in spring can enhance phytoplankton growth. We observed that the highest levels of spring Chl-*a* were recorded during the 1990s in the coastal waters between the Elbe and Weser rivers. During the same decade, this region also experienced the highest spring SST, while winter DIN levels remained high. The elevated spring Chl-*a* levels during the 1990s could be due to the interplay between high nitrogen levels and high spring temperature. This hypothesis aligns with the study of Anderson et al. (2022), who showed that spring phytoplankton growth can be significantly increased by rising spring temperatures under nutrient-replete conditions. Moreover, Edwards et al. (2022) demonstrated a positive correlation between annual SST and diatom abundances in the North Sea, proposing that phytoplankton growth in well-mixed areas, where nutrient limitation is not a cut off, could be enhanced by rising temperatures.

In contrast, increasing winter SST could contribute to reduced phytoplankton biomass during spring. Previous studies suggest that rising winter SST favors increased grazing pressure during the autumn–winter seasons, leading to a delayed onset of vernal phytoplankton blooms (Wiltshire et al., 2008, 2015) or decreasing phytoplankton peak biomass (Sommer & Lengfellner, 2008). This heightened grazing pressure may negatively impact phytoplankton biomass (Beusekom et al., 2009; Keller et al., 1999). Since the late 1980s, warm-water copepods have increased in the North Sea (Alvarez-Fernandez et al., 2012), and the German Bight harbors large overwintering stocks of these in the area, which could influence grazing pressure on spring phytoplankton production (Neven et al., 2024). However, our results do not support this hypothesis, as we identified a negative but nonsignificant relationship between winter SST and spring Chl-*a* levels.

In reality, the dynamics of phytoplankton depend on the interplay of multiple factors, including changes in stratification and light availability (Capuzzo et al., 2018; Wiltshire et al., 2008, 2015). Changes in stratification or mixed layer depths are not significant drivers of variation in phytoplankton biomass in the shallow well-mixed coastal German Bight (Wiltshire, et al., 2015); Amorim et al., 2024). However, light has great potential to become a limiting factor in phytoplankton growth. Colijn and Cadee (2003) compared nutrient and light limitation at various sites of the Wadden Sea and found that in many instances light limitation far exceeded the effects of nutrient limitation. Using Secchi measurements, an index of water turbidity, McQuatters-Gollop et al. (2007) and Wiltshire et al. (2015) underscored that light availability was the primary driver of variation in phytoplankton biomass in the North Sea. Several studies have indicated that water transparency has not changed or has been improved in the coastal regions of the North Sea over the time period of our study (Gebühr et al., 2009; McQuatters-Gollop et al., 2007; van Beusekom et al., 2019; Wiltshire et al., 2008, 2015). Such improvements in water transparency would be expected to promote phytoplankton biomass over the past decades, yet this is not observed in the spring Chl-*a* trends. We therefore suggest that nitrogen is the most important driving factor for spring Chl-*a* variability in this system at the current stage and over the past 40 years, with spring warming mitigating its effects.

Overall, we have shown how the long-term spatiotemporal dataset from the German Bight can be used to understand how anthropogenic pressures contribute to eutrophication and changes in phytoplankton biomass. We found that nutrient concentrations and ratios in the German Bight have substantially changed over the past four decades, in line with reductions in riverine inputs reported in previous studies, and that Chl-*a* has generally decreased following de-eutrophication strategies. We identified that winter DIN was the best explanatory factor of spring Chl-*a* spatiotemporal variation, with decreasing DIN reducing spring phytoplankton biomass. Spring SST also had a positive effect but was weaker and less significant. Together, winter DIN and spring SST explained only 30% of the total spring Chl-*a* variance, suggesting that other factors such as light availability and grazing pressure likely contribute significantly to the unexplained variability.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-025-01620-2.

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Author Contributions AB, MB, SS, and KHW conceived the idea. Data compilation and analysis were performed by AB. The first draft of the manuscript was written by AB. All authors contributed to editing the manuscript, read, and approved the final manuscript.

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Data Availability Data will be available upon reasonable request.

Declarations

Competing Interests The authors declare no competing interests.

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