



# Long-term changes in phytoplankton phenology, biomass, and community structure in the northern Baltic Sea

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**Abstract.** Phytoplankton seasonality integrates signals of climate forcing, anthropogenic pressure, and natural physical variability, making it a sensitive indicator of ecosystem change in coastal seas. We analysed a 52-year phytoplankton monitoring time series (1966–2018) from twenty-six stations in the Helsinki Archipelago, Gulf of Finland, to examine long-term changes in phytoplankton phenology, biomass, and community composition.

15 Generalized additive mixed models revealed a pronounced seasonal cycle dominated by a short spring bloom, whose timing advanced steadily at an average rate of approximately 2.7 days per decade. In contrast, total phytoplankton biomass exhibited stepwise changes rather than gradual trends, with a marked decline in both spring and summer biomass in the late 1980s and early 1990s. This shift coincided temporally with a period of major restructuring of municipal wastewater treatment in the Helsinki metropolitan area.

20 Community composition responded differently from biomass. Distance-based ordination showed that long-term temporal trends and seasonal variation acted largely independently on community structure, with compositional change more strongly associated with decadal-scale trends than with seasonality. Time-series decomposition identified change points in community seasonality around 1972 and 2000. Following the latter, summer biomass increased while spring bloom intensity remained comparatively unchanged, consistent with a reorganisation of seasonal community structure rather than a reversal of long-term recovery.

25 Together, these results demonstrate that phytoplankton phenology, biomass, and community composition capture complementary aspects of ecosystem change. Long-term observations allow disentangling gradual climate-driven shifts, targeted management effects, and episodic physical disturbances, highlighting the value of phytoplankton seasonality as an integrative indicator in the northern Baltic Sea.

## 30 1 Introduction

The Baltic Sea is one of the world's largest brackish inland seas, characterized by a strong salinity gradient, long water residence times, and a large catchment area shared by multiple countries. Since the mid-20th century, it has been affected by

chronic eutrophication driven by excessive inputs of nitrogen and phosphorus from riverine discharge, atmospheric deposition, and point sources such as urban wastewater (Andersen et al., 2017; Murray et al., 2019). These nutrient inputs  
35 have resulted in elevated phytoplankton biomass, recurrent harmful algal blooms, and deteriorating oxygen conditions in deeper waters (e.g. Richardson and Heilmann, 1995; Wasmund et al., 2008).

Since the late twentieth century, substantial investments have been made to reduce external nutrient loading, particularly through the upgrading of wastewater treatment plants and improved nutrient management practices (Carstensen et al., 2020).  
40 Consequently, nutrient inputs to the Baltic Sea have declined in several regions. However, ecological recovery has been slower and more complex than initially anticipated, reflecting the combined influence of internal nutrient cycling, physical forcing, and long-term ecosystem responses (Heiskanen et al., 2019; Jansson et al., 2019; Murray et al., 2019).

Phytoplankton dynamics in the northern Baltic Sea are characterised by a pronounced seasonal cycle, dominated by a short but intense spring bloom that typically lasts only a few weeks. During this period, a substantial fraction of the annual  
45 primary production is generated, following winter mixing that replenishes nutrients in surface waters and increasing light availability (e.g., long-term monitoring studies compiled by Wasmund et al., 2019). The fate of the spring bloom is critical for ecosystem functioning: a large proportion of bloom biomass sinks rapidly to the seafloor, where its decomposition leads to oxygen consumption in bottom waters (Spilling et al., 2018; Tamelander et al., 2017).

50 Under stratified conditions, this oxygen consumption can result in hypoxia or anoxia. Anoxic sediments subsequently release substantial amounts of phosphorus back into the water column, thereby enhancing internal nutrient loading (Lehtoranta et al., 2008). This internal feedback favours summer blooms of nitrogen-fixing cyanobacteria, which benefit from elevated phosphorus availability and introduce new reactive nitrogen into the system. Together, these processes create a self-reinforcing eutrophication cycle that complicates management efforts, despite extensive reductions in external nutrient inputs  
55 under HELCOM agreements (Carstensen and Conley, 2019; Vahtera et al., 2007).

While nutrient dynamics and phytoplankton biomass have been studied intensively in the Baltic Sea, increasing attention has recently focused on phenology, defined as the timing of recurring biological events (Cloern and Jassby, 2010; Sommer et al., 2012; Zhang et al., 2018). Across both terrestrial and aquatic ecosystems, phenological shifts have emerged as sensitive  
60 indicators of climate change (Edwards and Richardson, 2004; Parmesan and Yohe, 2003). Earlier onset of spring events has been documented widely, including advances in flowering on land (Fitter and Fitter, 2002) as well as shifts in plankton blooms, fish spawning, and zooplankton development in marine systems (Edwards and Richardson, 2004). Such changes can have profound ecological consequences by altering trophic interactions, biogeochemical cycling, and the coupling between physical and biological processes (Winder and Schindler, 2004).

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Across the approximately 1200 km length of the Baltic Sea, phytoplankton phenology exhibits a strong latitudinal gradient driven primarily by light availability, temperature, and ice cover. In the southern Baltic Sea, the spring bloom may begin as early as March, whereas in the northern Baltic Proper it typically occurs in April, and in the Bothnian Bay even later, sometimes not until early summer (Klais et al., 2013; Spilling et al., 2018; Wasmund et al., 2019). Superimposed on this spatial pattern are temporal changes associated with climate warming, reduced ice cover, and altered nutrient regimes (Groetsch et al., 2016; Sommer et al., 2012). Long-term time series therefore provide a valuable opportunity to disentangle the relative roles of global climate change, local anthropogenic pressures, and natural physical forcing in shaping phytoplankton seasonality.

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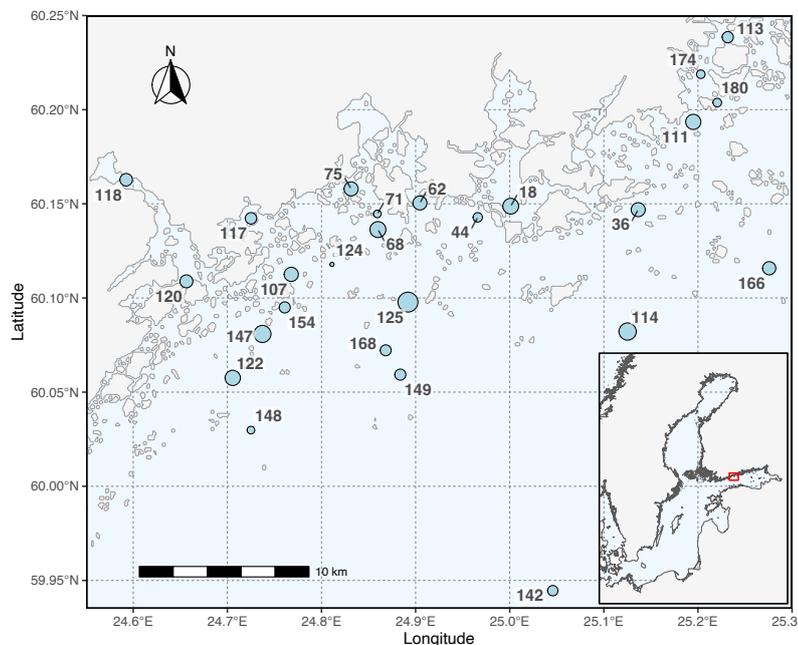
Here, we analyse a 52-year phytoplankton monitoring time series from twenty-six sampling stations in the Helsinki Archipelago, Gulf of Finland. Using these long-term observations, we examine changes in phytoplankton phenology as a sensitive indicator of ecosystem change. Specifically, we test the hypotheses that (i) phytoplankton seasonality has shifted in response to global climate warming, with an earlier onset of the spring bloom; (ii) anthropogenic nutrient management actions, such as the commissioning of advanced wastewater treatment plants in the Helsinki region, have altered seasonal phytoplankton dynamics; and (iii) major natural regime shifts, including the Major Baltic Inflows of North Sea water in the early 1990s, have left detectable signatures in phytoplankton phenology. By integrating long-term biological observations with environmental context, this study aims to clarify how multiple drivers interact to shape phytoplankton seasonality in the northern Baltic Sea.

## 85 **2 Methods**

### **2.1 Origin of data**

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The 52-year phytoplankton time series, covering the period 1966–2018, was compiled from monitoring data provided by the City of Helsinki Urban Environment Division. The dataset is geographically constrained, spanning a maximum latitudinal and longitudinal range of approximately 20 and 30 km, respectively (Fig. 1). Annual sampling frequency varied between 22 and 286 observations (interquartile range: 43–129) and was seasonally well distributed within individual years.



95 **Figure 1: Sampling stations in the Helsinki Archipelago, denoted by numeric station codes. The location of the study region within the Baltic Sea is indicated by a rectangle in the inset map (bottom right). Symbol size in the main panel is proportional to the square root of the number of quantitative phytoplankton samples collected at each station (total  $n = 5537$ ).**

The study region comprises a coastal archipelago, with station depths ranging from 2.5 to 71 m and distances to the nearest mainland shoreline ranging from 80 m to 23.6 km. Salinity and temperature conditions were characteristic of the Gulf of Finland, with the 5th–95th percentile range of salinity between 4.4 and 6.1 and temperature between 2.1 and 18.6. Only samples collected from the upper 5 m of the water column were included (where station depth permitted). In rare cases, pooled samples extending down to 10 m were used, but these remained within the surface mixed layer.

105 The majority of phytoplankton samples were analysed by a small number of personnel using consistent sampling, analytical, and taxonomic protocols. Potential observer effects were evaluated statistically, and after accounting for the dominant sources of community variation (time and seasonality), personnel-related variation explained less than 4% of total community variability.

110 During data processing, taxonomic nomenclature was harmonised and updated according to the World Register of Marine Species (WoRMS Editorial Board, 2026). All phytoplankton data were species-specific and fully quantitative. Species-specific biovolumes were converted to wet-weight biomass ( $\mu\text{g L}^{-1}$ ), assuming a density of  $1 \text{ g mL}^{-1}$ .



## 2.1 Data analysis

### 2.1.1 GAMM

115 Long-term trends in phytoplankton biomass were analysed using generalized additive mixed models (GAMMs) fitted with thin-plate regression splines, as implemented in the *mgcv* package in R. To quantify and compare the relative contributions of long-term temporal change and seasonality, phytoplankton biomass (log-transformed) was modelled as a smooth function of calendar time and day of year:

$$y_i = \beta_0 + f_1(\text{time}_i) + f_2(\text{doy}_i) + \varepsilon_i$$

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where  $y_i$  denotes phytoplankton biomass,  $\beta_0$  is the intercept,  $f_1$  represents the smooth long-term trend (calendar year),  $f_2$  represents seasonal variation (day of year), and  $\varepsilon_i$  is the Gaussian error term.

125 Because the response variable constitutes an irregularly sampled time series, residual autocorrelation was explicitly accounted for by specifying a continuous-time first-order autoregressive [CAR(1)] correlation structure. This approach allows the strength of temporal dependence between residuals to decline exponentially with increasing time lag and is well suited for time series with uneven sampling intervals (Elorrieta et al., 2019). All models were fitted assuming Gaussian error distributions.

### 130 2.1.2 GAMMs with seasonal–long-term interactions

In addition to models with additive effects of seasonality and long-term trend, we fitted generalized additive mixed models incorporating interactions between these components using tensor-product smoothers. In these models, phytoplankton biomass (log-transformed) was modelled as:

$$135 \quad y_i = \beta_0 + te_1(\text{time}_i, \text{doy}_i) + \varepsilon_i$$

where  $te_1$  denotes a tensor-product smooth that captures the joint effects of calendar time and seasonal position (day of year), including their interaction, and  $\varepsilon_i$  is a Gaussian error term with the same autocorrelation structure as described above. This formulation allows seasonal patterns to vary smoothly over long-term time.

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### 2.1.3 Bloom peak and duration

Daily phytoplankton biomass was predicted from the fitted GAMM using calendar year and day of year as interacting predictors. The day of maximum predicted biomass during the spring period (defined as day of year  $\leq 200$ ) was identified as the spring bloom peak. The timing of bloom initiation was estimated as the day of the steepest increase in predicted biomass  
145 prior to the peak, corresponding to the maximum of the first derivative of the seasonal biomass curve. Similarly, the day of the steepest decline in biomass following the peak was used as a proxy for bloom termination.

### 2.1.4 Trends and changepoints in seasonality

Temporal changes in long-term trends and seasonal structure were analysed using the *Bayesian Estimator of Abrupt change, Seasonal change, and Trend* (BEAST), implemented in the R package Rbeast. BEAST is a Bayesian nonparametric time-series decomposition method that represents an input series as the sum of a harmonic seasonal component, a piecewise linear background trend, potential changepoints in both components, and random noise, allowing simultaneous estimation of trends, seasonality, and abrupt shifts. Changepoints in both trend and seasonal components are detected automatically using a reversible-jump Markov chain Monte Carlo (RJMCMC) algorithm, without requiring prior specification of their number or  
155 timing. The Bayesian framework provides posterior distributions for all estimated components, enabling uncertainty in trends, seasonality, and changepoints to be quantified through credible intervals. In this study, monthly aggregated time-series data were used for all BEAST analyses to ensure that model assumptions were met.

### 2.1.5 Community analysis

160 Phytoplankton community structure was analysed using a community matrix constructed from species-specific biomass values, with samples in rows and taxa in columns ( $5537 \times 581$ ). Biomass data were square-root transformed and Wisconsin double-standardised (species standardised by maxima, samples by totals), and analysed using distance-based redundancy analysis (dbRDA) with two axes (function *dbrda*, vegan package in R). dbRDA was applied as a metric ordination method to represent differences in community composition among samples.

165 Temporal and seasonal gradients were subsequently fitted onto the unconstrained dbRDA ordination using environmental fitting (*envfit*, vegan), with calendar year and day of year treated as continuous variables. This procedure identified the direction and strength of association between community composition and temporal descriptors, with statistical significance assessed using permutation tests (9999 permutations).

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To facilitate interpretation of temporal dynamics, Procrustes rotation (*procrustes*, *vegan*) was applied to align the ordination such that the fitted time and seasonal vectors were parallel to the first ordination axis. This rotation preserves relative distances among samples while reorienting the ordination space to correspond more directly with temporal gradients.

175 The seasonality scores extracted from the rotated ordination space, with the time gradient aligned to the first axis, were subsequently used as input for BEAST analysis to identify changepoints in phytoplankton community seasonality.

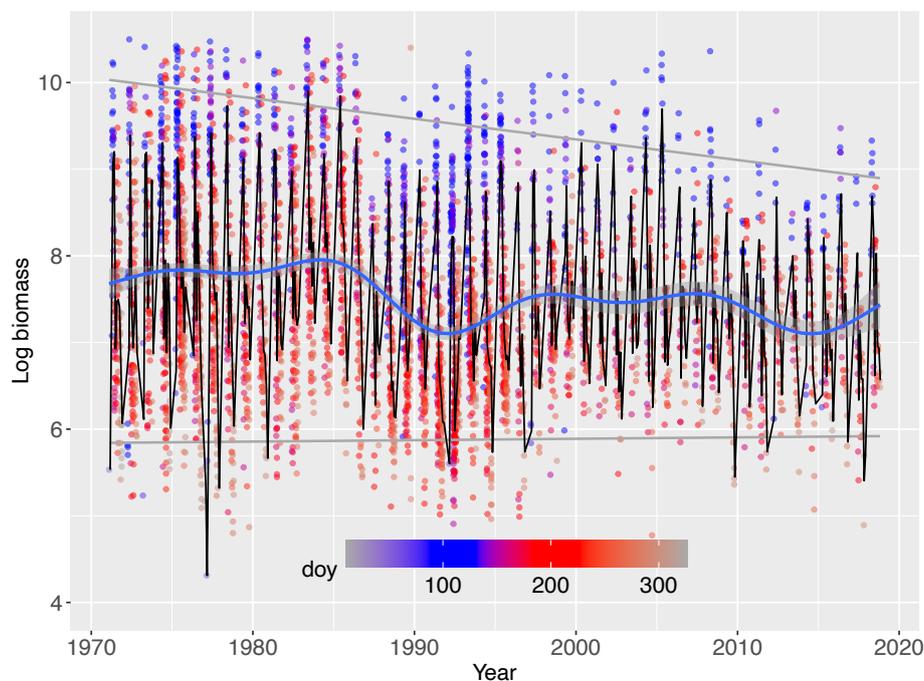
### 2.1.6 Seasonality changepoint detection via rotated ordination

180 The dbRDA ordination was rotated using Procrustes transformation such that the long-term temporal gradient (calendar year) was aligned with the first ordination axis. Ordination scores orthogonal to this axis were interpreted as representing seasonal variation in phytoplankton community composition independent of long-term trends. These seasonality scores were subsequently used as the response variable in a BEAST analysis to identify changepoints in the seasonal structure of phytoplankton communities, without confounding effects of gradual directional change captured by the ordination's first axis.

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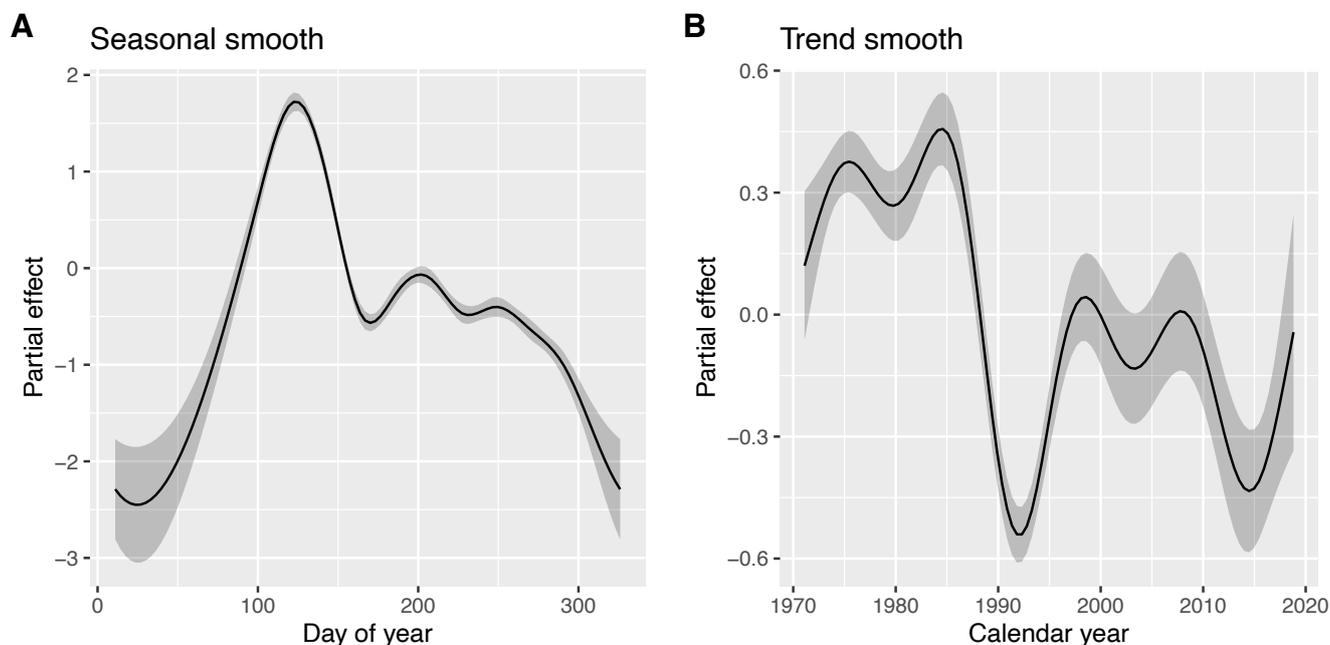
## 3 Results

Total phytoplankton biomass exhibited pronounced seasonal variability together with long-term changes over the observation period (Fig. 2). Linear quantile regression (0.05 and 0.95 quantiles) indicated that lower biomass values remained relatively stable on a decadal scale, whereas the upper biomass values declined over time. The highest biomass values occurred primarily during the spring bloom, while exceptionally high summer biomass values—comparable to spring bloom levels—were observed mainly in the 1970s and 1980s and became increasingly rare thereafter.



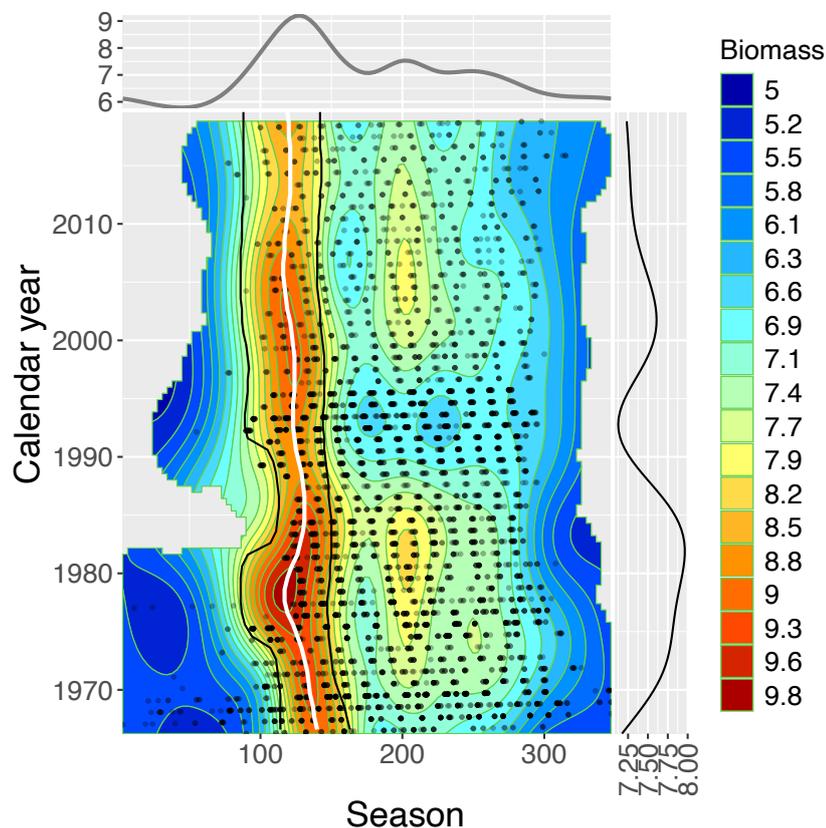
195 **Figure 2: Decadal time series of total phytoplankton biomass.** Symbols represent individual samples (samples prior to 1970 are omitted;  $n = 4565$ ) and are colour-coded by season (day of year): blue indicates the spring bloom period, red the summer period, and grey winter. The thin black line shows monthly mean biomass. Linear quantile regression lines (0.05 and 0.95 quantiles) delineate the lower and upper biomass envelopes. The thick blue line represents the fitted GAMM smooth of the long-term biomass trend, with the shaded grey band indicating the standard error.

200 Seasonal dynamics were characterised by a strong spring bloom peaking in early May, followed by lower summer biomass and a winter minimum (Fig. 3). On a decadal scale, the highest overall biomass levels occurred during the 1970s and 1980s, followed by a marked reduction in the mid-1990s and a lower, relatively stable baseline from the 2000s onwards. Variance partitioning using a GAMM indicated that seasonal variation accounted for the largest proportion of total variance in phytoplankton biomass (0.60), followed by the long-term trend component (0.11). The interaction between seasonality and  
205 long-term trend explained 0.025 of the variance, while the remaining 0.27 was attributed to residual variability (Fig. 3).



210 **Figure 3: Partial effects from the GAMM fitted to total phytoplankton biomass ( $n = 4565$ ).** (A) Seasonal smooth as a function of day of year ( $F = 196$ ,  $\text{edf} = 9.6$ ) and (B) long-term smooth as a function of calendar year ( $F = 41$ ,  $\text{edf} = 8.7$ ). Both smooth terms are statistically significant ( $p < 0.001$ ), and the model explains an adjusted  $R^2$  of 0.54. Note that the y-axis scales differ between panels, reflecting differences in effect size between seasonal and long-term components.

The two-dimensional visualisation of the tensor-product GAMM smooth revealed a distinct band of elevated phytoplankton biomass associated with the spring bloom (Fig. 4). Over the observation period, both the timing of the spring bloom peak and the end of the bloom shifted towards earlier dates. The estimated rate of advancement was approximately one day per 215 3.5–3.7 years (or 2.7 days per decade), corresponding to a shift of the bloom peak from mid-May in the early part of the time series to late April–early May in recent decades. Estimated spring bloom duration ranged between one and two months, although uncertainty was high due to limited sampling resolution prior to bloom onset.



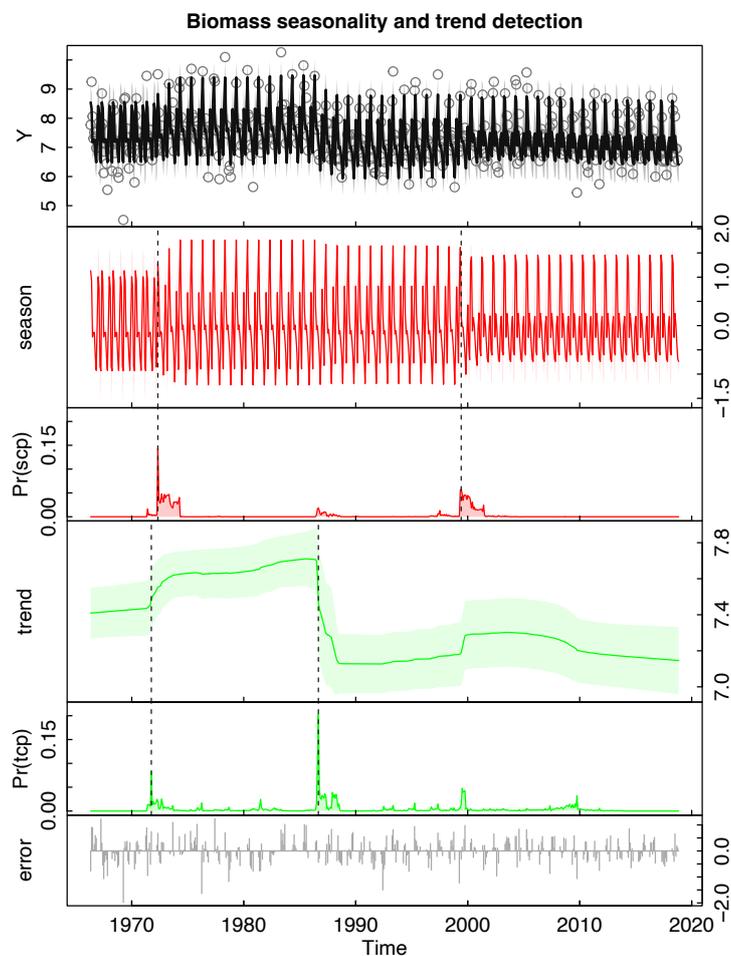
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**Figure 4: Two-dimensional tensor-product GAMM smooth of phytoplankton biomass, illustrating the interaction between seasonality (x-axis; day of year) and long-term trend (y-axis; calendar year) ( $F = 40$ ,  $edf = 77$ ,  $adjusted\ R^2 = 0.54$ ,  $n = 5537$ ). Warm colours indicate higher biomass values. The white curve denotes the estimated timing of the spring bloom peak, while thin black curves indicate bloom onset and termination. Black symbols represent observed samples. Marginal mean distributions of the smooth surface are shown along the x- and y-axes. Regions of the smooth surface with insufficient data density are not displayed and were excluded from marginal estimates.**

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BEAST analysis indicated uncertainty in the number of changepoints in the long-term trend of total phytoplankton biomass, with posterior support for between one and four trend changepoints. The highest posterior probability was associated with a changepoint in 1987 (posterior probability = 0.99), followed by changepoint in 1972 (0.50) and 2000 (0.37) (Fig. 5). In contrast, the seasonality component showed stronger support for two changepoints, occurring in 1973 (posterior probability = 1.00) and in 2000 (0.97) (Fig. 5).



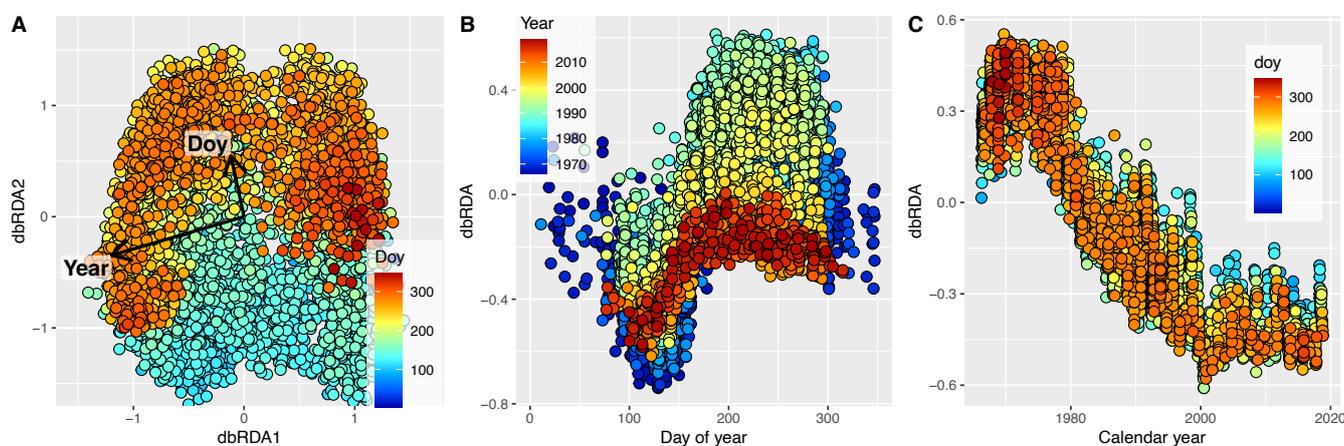
235 **Figure 5: BEAST decomposition of the total phytoplankton biomass time series. Y shows the observed time series, excluding data-poor winter months (November–March). Season represents the estimated recurring seasonal component independent of the long-term trend. Pr(scp) indicates the posterior probability of changepoints in the seasonal structure. Trend shows the long-term component after removal of seasonal variation, and Pr(tcp) denotes the posterior probability of changepoints in the trend. Error represents residual variation not explained by trend or seasonality. Vertical dashed lines indicate the timing of detected**  
240 **changepoints.**

### 3.1 Seasonality and trends in community composition

Phytoplankton community composition was primarily associated with the long-term temporal trend, represented by the first dbRDA axis, and secondarily with seasonal variation, represented by the second dbRDA axis (Fig. 6A). The effects of the  
245 decadal-scale trend and seasonal cycle on community composition were approximately orthogonal in ordination space. In contrast to total phytoplankton biomass, community composition showed a stronger association with the long-term trend than with seasonality (Fig. 6A).



250 Plotting ordination scores against time (calendar year) and season (day of year) further illustrated how community composition varied along these temporal gradients (Fig. 6B–C). Ordination scores displayed systematic variation both across years and within the annual cycle, indicating distinct long-term and seasonal structuring of phytoplankton community composition.



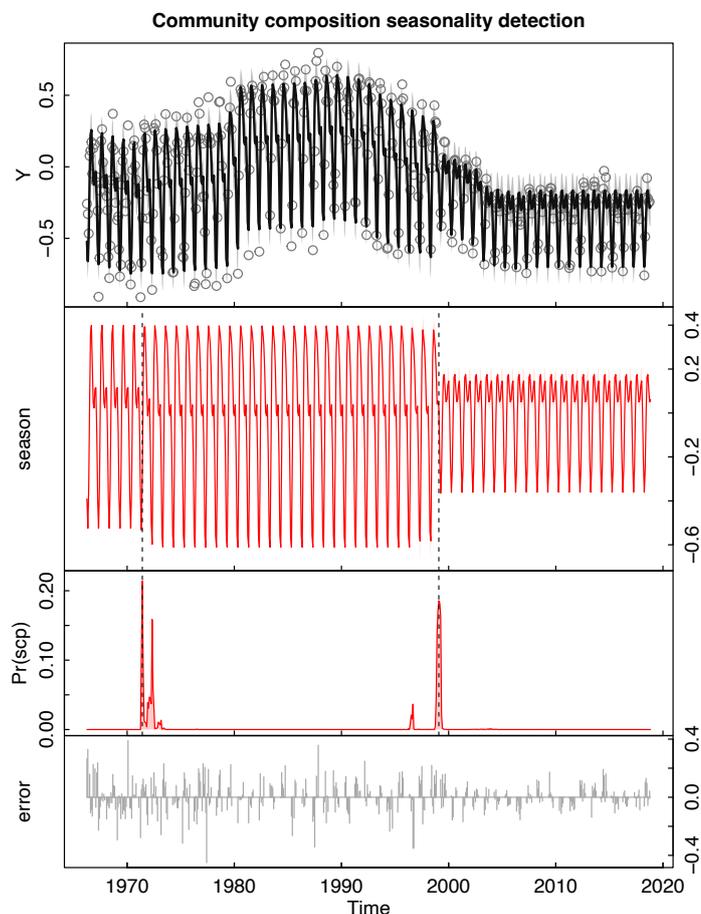
255 **Figure 6: Distance-based redundancy analysis (dbRDA) ordination of phytoplankton community composition (5537 samples × 581 taxa).** (A) Ordination plane with fitted vectors representing seasonal (day of year;  $r = 0.37$ ) and long-term temporal gradients (calendar year;  $r = 0.83$ ). Arrow length is proportional to the strength of the association. (B) Seasonal variation in ordination scores after Procrustes rotation aligning the seasonal vector with the x-axis. (C) Long-term temporal variation in ordination scores after rotation aligning the year vector with the x-axis.

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The seasonal trajectory of phytoplankton community composition showed reduced seasonal amplitude in the period after 2000 (Fig. 6B). In contrast, the long-term trajectory indicated a persistent unidirectional shift in community composition, with the strongest displacement occurring between the 1970s and the early 2000s, followed by a period of comparatively limited change during the last two decades (Fig. 6C).

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BEAST decomposition of community composition identified strong posterior support for two changepoints (joint posterior probability = 0.95), occurring in 1972 (posterior probability = 0.95) and in 2000 (posterior probability = 1.00). These changepoints were associated with shifts in the seasonal component of community composition (Fig. 7).



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**Figure 7: BEAST decomposition of the phytoplankton community composition time series derived from rotated ordination scores. Panels Y, Season, Pr(scip), and Error are interpreted as in Fig. 5. The long-term trend component was not analysed, as the ordination was rotated to maximise the seasonal signal, leaving the orthogonal long-term component strongly reduced.**

275 Overall, phytoplankton dynamics in the Helsinki Archipelago exhibited strong seasonality superimposed on long-term  
temporal change. Total phytoplankton biomass was dominated by seasonal variation, with a pronounced spring bloom whose  
timing advanced steadily over the observation period. In contrast, long-term trends were characterised by stepwise changes  
rather than gradual shifts. Phytoplankton community composition responded differently from biomass, showing a stronger  
association with long-term temporal trends than with seasonality, and exhibiting clear shifts in both seasonal structure and  
280 long-term trajectories. Together, these results demonstrate that phytoplankton biomass, phenology, and community  
composition capture complementary aspects of ecosystem change across multiple temporal scales.



#### 4 Discussion

285 Phytoplankton dynamics in the northern Baltic Sea are structured by strong seasonal cycles superimposed on long-term  
temporal change, both in total biomass and in community composition. Our results indicate that long-term trends and within-  
year seasonal dynamics represent largely independent dimensions of phytoplankton community variation, allowing their  
effects to be examined simultaneously. Across the five-decade time series, three distinct patterns emerged that can be linked  
to (i) gradual climate-driven change, (ii) targeted anthropogenic interventions, and (iii) natural physical disturbances.

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Phenology—the timing of recurring biological events—has emerged as one of the most sensitive indicators of ecological  
responses to climate change. In this study, the spring phytoplankton bloom advanced at an estimated rate of approximately  
2.7 days per decade, corresponding to an advance of roughly two weeks over the observation period. This magnitude of  
change is consistent with reported phenological shifts across a wide range of terrestrial and marine ecosystems in response to  
295 global warming (Edwards and Richardson, 2004; Walther et al., 2002). A global meta-analysis of more than 1,700 species  
documented mean advancement of spring events by 2.3 days per decade (Parmesan and Yohe, 2003). Comparable trends  
have also been documented in the northern Baltic Sea, where earlier onset of phytoplankton blooms by one to two weeks has  
been reported over recent decades (Hjärne et al., 2019). Together, these observations place the phenological shift observed in  
the Helsinki Archipelago within a broader, climate-driven context.

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The Baltic Sea, and the Gulf of Finland in particular, has been subjected to severe eutrophication pressure throughout much  
of the twentieth century (Andersen et al., 2017; Vahtera et al., 2007). Eutrophication in the northern Baltic Sea intensified  
during the 1970s and 1980s and reached its peak in the mid-1980s, followed by a gradual and uneven recovery in response to  
increasingly stringent nutrient management measures implemented by the surrounding countries, including the Helsinki  
305 metropolitan area (Finni et al., 2001; Heiskanen et al., 2019). This period was characterised by elevated phytoplankton  
biomass during both the spring bloom and the summer period (Fig. 4). By the early 1990s, phytoplankton biomass declined  
in both seasons. Because reductions occurred in spring and summer simultaneously, no changepoint was detected in seasonal  
biomass structure, whereas the long-term biomass trend exhibited a clear changepoint (Fig. 5).

310 The biomass decline observed in the late 1980s and early 1990s coincides temporally with a major restructuring of municipal  
wastewater treatment in Helsinki. Prior to 1987, wastewater from the Helsinki metropolitan area was treated at several  
smaller facilities, with effluents discharged directly into coastal waters. From late 1987 to 1994, the city progressively  
transitioned to a centralized and more efficient wastewater treatment system (Vaalgamaa, 2004). Although causality cannot  
be established unequivocally, the timing of this management intervention is consistent with the observed changepoint in  
315 phytoplankton biomass trends around 1987 (Fig. 5). Similar long-term responses have also been documented in



phytoplankton biodiversity in the Helsinki Archipelago, suggesting a broader ecosystem response to reduced nutrient inputs (Olli et al., 2023).

320 Following the period of reduced phytoplankton biomass in the early 1990s, the time series shows a renewed increase in summer biomass during the late 1990s and early 2000s, while spring bloom intensity remained comparatively unchanged (Fig. 4). This divergence between spring and summer dynamics indicates a redistribution of biomass within the annual cycle rather than a return to uniformly elevated biomass levels. Consistent with this pattern, time-series decomposition identified a shift in seasonal structure together with a modest changepoint in long-term biomass trends around the year 2000 (Fig. 5).

325 The timing of this change coincides with the period when the ecological effects of the 1993 Major Baltic Inflow (MBI) propagated into the surface waters of the central Gulf of Finland (Kahru et al., 2000). The Baltic Sea is a permanently stratified eutrophic system, where salinity-driven stratification results from freshwater input at the surface and episodic inflows of saline North Sea water through the Danish Straits. These inflow events, which depend on specific combinations of atmospheric and oceanographic conditions, play a central role in regulating vertical stratification and deep-water ventilation (Lehmann et al., 2022). In the Baltic Proper, prolonged periods between major inflows are typically associated with stagnation and bottom-water anoxia due to sustained oxygen consumption. In contrast, in the Gulf of Finland, reduced salinity gradients during stagnation periods can enhance vertical mixing, leading to temporarily increased oxygen availability in deeper waters (Kahru et al., 2000). Such changes in physical forcing provide a plausible context for the observed reorganization of phytoplankton seasonality after major inflow event impact reached the Gulf of Finland.

335 The 1993 Major Baltic Inflow, which introduced approximately 3.5 Gt of salt into the Baltic Sea, terminated a prolonged stagnation period lasting nearly a decade, during which anoxia intensified in the bottom waters of the Baltic Proper. Following the inflow, dense North Sea water filled the deep basins of the Baltic Proper and displaced less dense, stagnant water northwards into the Gulf of Finland, a basin lacking pronounced topographic sills. When saline and oxygen-depleted waters reached the Gulf of Finland in the late 1990s, bottom-water stratification strengthened, oxygen concentrations declined, and phosphate release from sediments increased. Phosphorus stored in oxic sediments is known to be mobilised rapidly once sediments become anoxic (Lehtoranta et al., 2008). Consistent with this mechanism, bottom-water phosphate concentrations in the Gulf of Finland approximately doubled in the late 1990s compared with the early 1990s (Kahru et al., 2000). Together with enhanced denitrification under low-oxygen conditions, this led to a reduction in the N:P ratio in the water column, creating conditions favourable for nitrogen-fixing cyanobacteria once mixed into surface waters. Satellite observations indicate that diazotrophic cyanobacterial blooms expanded eastwards into the central and eastern Gulf of Finland during this period, a pattern temporally associated with the aftermath of the 1993 inflow event (Kahru et al., 2000).



350 The intensification of cyanobacterial blooms in the Gulf of Finland coincided with elevated summer phytoplankton biomass  
(Fig. 4), altered seasonal biomass distribution (Fig. 5), and resulted in a pronounced changepoint in the seasonal structure of  
community composition (Fig. 7). At the same time, the reduced seasonal amplitude of total biomass (Figs. 2, 5) indicates that  
spring bloom biomass did not increase proportionally in response to enhanced phosphorus availability. This observation is  
consistent with the longer-term decline in spring bloom intensity reported across the Baltic Sea, which has been linked to  
sustained reductions in external nutrient loading (Groetsch et al., 2016). It also aligns with the view that spring blooms in the  
355 eutrophied northern Baltic Sea are primarily limited by nitrogen availability (Tamminen and Andersen, 2007). During  
summer, nitrogen-fixing cyanobacteria release a substantial fraction of newly fixed nitrogen into the surrounding water,  
facilitating the development of specific summer phytoplankton assemblages beyond the diazotrophs themselves (Olli et al.,  
2015). The emergence of these distinct summer communities is consistent with the detected shift in community composition  
seasonality during this period.

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In conclusion, long-term phytoplankton observations from the Helsinki Archipelago reveal that phenology, biomass, and  
community composition respond to environmental change in distinct and complementary ways. Gradual climate warming  
was reflected in a steady advance of spring bloom timing, while targeted nutrient management led to stepwise reductions in  
phytoplankton biomass across seasons. Superimposed on these trends, natural physical disturbances such as the 1993 Major  
365 Baltic Inflow reorganised seasonal biomass distribution and community structure without reversing long-term recovery  
trajectories. Together, these results demonstrate the value of phytoplankton seasonality and community composition as  
sensitive indicators for disentangling climatic, anthropogenic, and physical drivers of ecosystem change in the northern  
Baltic Sea.

#### 370 **Code, data, or code and data availability**

All datasets and analysis code used in this study are publicly available at [https://github.com/kalleolli/hel\\_seasonality](https://github.com/kalleolli/hel_seasonality).

#### **Competing interests**

375 The author declares that they have no conflict of interest.



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