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Long-term phytoplankton community dynamics in Lake Stechlin (north-east Germany) under sudden and heavily accelerating eutrophication

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Abstract

1. Climate warming and legacy phosphorus (P) in sediments are two main factors counteracting current efforts to prevent eutrophication of temperate freshwater lakes and reservoirs. Climate warming impacts lacustrine thermal regimes, accelerates harmful cyanobacterial growth, and increases the probability of periodic anoxic bottom conditions. Legacy P in sediments becomes influential over eutrophication because of its reactivation under anoxic conditions.

2. Lake Stechlin is a deep glacial lake of the Baltic Lake area, Germany in which artificial external P loading has been effectively blocked for more than 3 decades. The lakes trophic status was oligotrophic, until roughly 2 decades ago when it accelerated toward higher trophic levels. Here we analyse the temporal dynamics of Lake Stechlin phytoplankton biomass and composition in relation to chemical and hydrological covariates, based on monitoring data from 1994 to 2019 at sampling frequency of *c*. 27 samples per year.

3. Our results show an assemblage change toward cyanobacterial dominance that took place at several temporal scales. Intra-annual compositional change became more pronounced over the study period, mainly because of changes during the autumn and winter seasons.

4. Results from a structural break point analysis of the phytoplankton time series with covariates, and from a hierarchical cluster analysis show that major changes occurred in 2007–2011. An analysis of early warning indicators did not unambiguously support this period as a critical transition. The change rather occurred as a rapid succession of major events during these years.

5. Results from convergent cross-mapping causality tests are consistent with the hypothesis that increasing relative water column stability may drive eutrophication, and additionally, that the intra-annual timing of the biomass change plays an important role in the lakes P loading.

6. Although quantitative data on internal P loading are unavailable, internal P mobilisation from sediments appears to be the most plausible mechanism behind the increased phytoplankton biomass. Lake Stechlin, therefore, is an example of the challenges that legacy P poses to the management of freshwater ecosystems

in the context of climate warming, even when external P sources are effectively blocked, and local protective measures are in place.

KEYWORDS
convergent cross mapping, legacy phosphorus, structural change, temporal β diversity, temporal distance decay

1 | INTRODUCTION

Anthropogenic pressure drives freshwater lakes and reservoirs increasingly toward eutrophication (e.g., Ho et al., 2019; Steffen et al., 2015). The trend toward eutrophication continues despite decade long efforts to limit anthropogenic nutrient loading (e.g., Carvalho et al., 2019; Musacchio et al., 2020; Schindler et al., 2016). The reasons for the limited success in these efforts are multifaceted. However, two of the main factors, which counteract efforts of reducing external anthropogenic nutrient loads are climate warming (Shimoda et al., 2011; Winder & Sommer, 2012) and reactivation of legacy phosphorus (P) from the sediments (Jarvie et al., 2013; Sharpley et al., 2013).

Climate warming has a massive impact on lake thermal regimes resulting in prolonged and intensified stratification (e.g., Jankowski et al., 2006; Kirillin et al., 2013; North et al., 2014; Stainsby et al., 2011). The reduced turbulence promotes cyanobacterial growth because it gives advantage to buoyant taxa (Huisman et al., 2004; Winder & Sommer, 2012). Cyanobacterial blooms also represent a direct effect of climate warming via increased growth rates and their impact on food webs (Huisman et al., 2004; Paerl & Huisman, 2009; Sommer & Lewandowska, 2011). The combined effects of phytoplankton (mostly cyanobacterial) mass growth and increased stratification, in turn, promote hypolimnic anoxia (Salmaso, 2005, 2011; Wilhelm & Adrian, 2008) and shifts in nitrogen (N)/P ratios toward elevated P levels (Jansson et al., 2010; Posch et al., 2012).

These dynamics, which include drastic changes in phytoplankton composition can unleash vicious feedback cycles of P release from sediments counteracting efforts to reduce external nutrient loads (Gebremariam et al., 2021; Jensen & Andersen, 1992; Kangro et al., 2007; Orihel et al., 2015; Schindler, 2012; Søndergaard et al., 2003). Legacy P in lake sediments here can play a crucial role.

Previous work on effects of climate change on recycling of sedimentary P back to the water column is mainly based on shallow polymictic lakes, on mesocosm experiments, and/or on relatively short monitoring intervals. A notable exception is the study of North et al. (2014), which reports long-term (39 years) change in the large, deep, stratifying, temperate Lake Zürich (Switzerland). In Lake Zürich, which in the past decades underwent long-term oligotrophication due to improved wastewater management, change in the mixing regime, probably initiated by climate, change led to increasing deep-water hypoxia, which in turn are correlated with increasing concentrations of soluble reactive P (SRP) via internal loading (North et al., 2014).

Here we report results from an analysis of long-term (1994–2019), high frequency (*c.* 27 samples per year) phytoplankton monitoring data from Lake Stechlin, a deep, dimictic lake in the Baltic-lake area, Germany. The lake was originally oligotrophic but changed its trophic status toward mesotrophy during the past 2 decades without known changes in external nutrient loading (Selmeczy et al., 2019; Szabó et al., 2017). The catchment area of the lake is situated in a natural reserve with very low external nutrient load. The lake carries a P pool in its sediments originating from anthropogenic pollution during the 1960s–1980s, which, however, did not affect its oligotrophic status for quite a long time.

In the absence of known external nutrient loading, legacy P, released from sediments, could explain Lake Stechlin eutrophication. Processes induced by climate change, similar as described from Lake Zürich (North et al., 2014), hypothetically could be a plausible mechanism behind Lake Stechlin eutrophication.

Here we provide a comprehensive analysis of the timing and temporal scale of the change in phytoplankton composition, its biomass, and its relation to nutrient load and other covariates. To test this hypothesis, we use the temporal development of these variables, but lack quantitative data on internal or external P loading. Our report should be seen as a starting point and motivation for more detailed analyses, which are a precondition for targeted protection of potentially similarly endangered lakes and an effective treatment of the human impacts.

2 | MATERIALS AND METHODS

2.1 | Study site

Lake Stechlin is a deep (mean depth: 23.3 m, max depth: 69.5 m) glacial lake with a volume of $98.7 \times 10^6 \, m^3$, positioned at 53°N latitude in Brandenburg, Germany (Koschel & Adams, 2003) (Figure 1). The lake is basically dimictic with intermittent years when it does not freeze at all. The lake is in the center of a natural reserve since 1938, with a 95% wood covered catchment area, and without effective natural surface inflows (Pöschke et al., 2018); its geographic position theoretically protects the lake from direct anthropogenic nutrient inputs such as agriculture.

From 1966–1990 the lake was part of a cooling water circuit for a nuclear power plant (NPP). The heat waste led to an average of 0.8°C in the surface-water temperature increase during the time of the NPP operation (Kirillin et al., 2013). The cooling system included

FIGURE 1 Bathymetric map and basic morphological parameters of Lake Stechlin with the sampling location: the mark in the north-east basin indicates the sampling point (after Casper, 1985). Total volume is given as 98.7×10^6 m³ in Koschel and Adams (2003).

Surface area (km²)	4.25
Mean depth (m)	23.3
Maximum depth (m)	69.5
Euphotic depth (m)	20–25
Catchment area (km²)	12.4
Volume (m³)	$96.9{*}10^6$
Effective fetch (m)	2000
Water retention time (year)	>40
Secchi transparency[1] (m)	6.4 ± 1.7
NO_3- nitrogen[2] (µgL⁻¹)	16 ± 24
TP[2] (µgL⁻¹)	11 ± 3
SRP[2] (µgL⁻¹)	2 ± 1
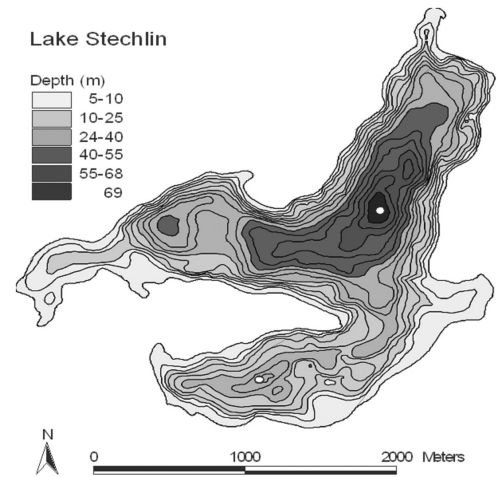
a canal system that connected Lake Stechlin into a circuit of canals with the neighbouring, much smaller, mesotrophic Lake Nehmitz. Its construction reduced the water level of the Lake Stechlin by 0.5 m and allowed for pumping of 300,000 m³ of water per day during NPP operation. The mixing and heating of the surface water caused, among others, a significant rise in the total phosphate content of the lake water, a drastic change in the phytoplankton community, a drop of the average summer Secchi disc transparency from 10 m to 6 m, and a severe damage and reduction of the formerly widespread characean meadows (e.g., Casper, 1985; Koschel & Casper, 1986; Périllon et al., 2018). Additionally, an increasing population, tourism, improper sewage treatment, and an intensive fish management led to temporarily increased nutrient load until it was drastically reduced during the early 1990s (Koschel, 1995; see also Oldorff & Päzolt, 2010 for an historical account).

The NPP operation and heat contamination was terminated in 1990, but the canal-water circulation continued at low levels (c. 15,000 m³) until 1995. Therefore, there may potentially have been a rebound of the lake's state to pre-NPP conditions.

In the years immediately after the termination the oxygen saturation in the hypolimnion at the end of the summer stratification remained constant, and the P concentration in the euphotic zone was steady at moderate to low levels (1990–2000 means: total P [TP] = 32.8 µg/L, SRP = 24.3 µg/L, Gonsiorczyk et al., 2003; Koschel et al., 2002). By the mid 1990s, in concert with the primary production, the P concentration began to rise slowly, and, as an alarming sign, the oxygen saturation at the lake bottom began increasingly to drop (Gonsiorczyk et al., 2003; Kasprzak et al., 2010; Koschel et al., 2002). An ongoing proliferation of heterocytic cyanobacteria and concomitant change among the functional groups of the phytoplankton indicated a continuing trend toward eutrophication until 2008 (Padisák, Hajnal, Krienitz, et al., 2010; Üveges et al., 2012). Moreover, a comparison of Lake Stechlin phytoplankton with that of communities of other European lakes indicated that it is highly sensitive to climate-induced physical drivers (Padisák, Hajnal, Naselli-Flores, et al., 2010). Eventually, an analysis of long-term monitoring data supported earlier suggestions of Kasprzak et al. (2010) that climate change drives eutrophication in Lake Stechlin via an increased

and prolonged lake stratification (Selmeczy et al., 2019). An extreme summer storm in 2011, which led to a temporal disturbance of the lake stratification in the euphotic zone and a massive short-term cyanobacterial bloom, raised further concerns on the growing impact of climate warming on the status of the lake (Kasprzak et al., 2017).

2.2 | Sampling

Integrated phytoplankton samples during most of the years were taken biweekly during the stratified period and monthly during the rest of the year from the euphotic zone (0–25 m). On average c. 27 samples were taken per year. However, the sampling frequency was not even. Between 1994 and 2001, samples were taken almost every week (c. 41 pear year) and, in 2003 and 2004, only 14 and 16 samples, respectively (Figure 2).

Water samples were taken, and temperature and Secchi transparency was measured at the deepest point of the lake. Concentration of TP, SRP, NO_2^-, NO_3^-, and NH_4^+ were measured at 0 m, 5 m, and 10 m depths, and analysed according to OECD standards and German Standard Methods.

Phytoplankton biomass was estimated based on water samples collected at 5-m increments between 0 and 25 m depth, and pooled before microscopic analysis. Samples were preserved in Lugol's solution and at least 400 settling units (cells, filaments, and colonies) were counted in each sample using a Zeiss Axiovert 100 (Oberkochen, Germany) inverted microscope (Lund et al., 1958; Utermöhl, 1958). Phytoplankton biomass was calculated based on cell volumes from the most similar geometric forms according to Hillebrand et al. (1999) aided by the Opticount cell counting software (Opticount, 2008). Phytoplankton taxa were determined according to the most up-to-date references. The coccoid green picoalgae *Neocystis* sp., *Pseudodictyosphaerium jurisii* (Hindák) Hindák, and *Choricystis minor* Skuja were grouped together, and cyanobacterial picoalgae were also treated as one taxon. Centric diatoms were determined at species level until 2001, then they were sorted into size classes in 5-µm increments, the details are given in Padisák, Barbosa, et al. (2003) and Padisák, Hajnal, Krienitz, et al. (2010).
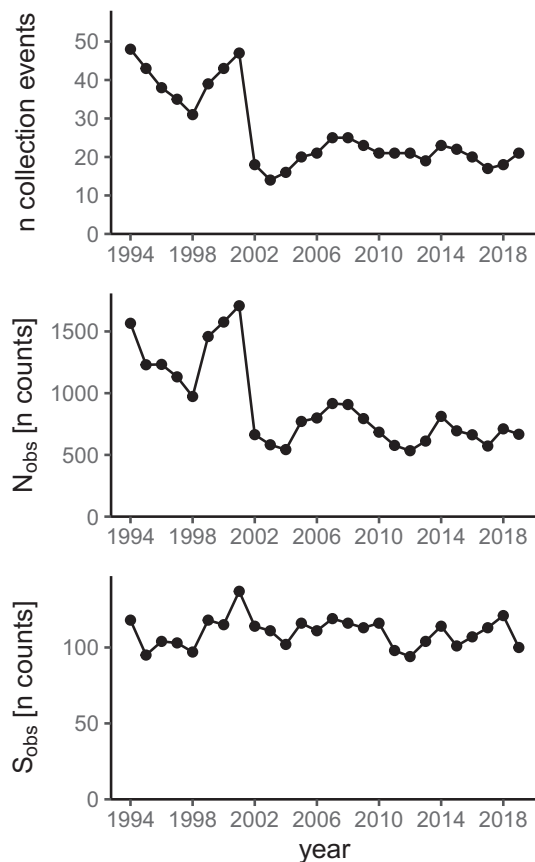
FIGURE 2 Annual sampling effort for the Lake Stechlin phytoplankton monitoring during 1994–2019. Collection events are sampling occasions per year; N_{obs}: number of taxon incidents per year; S_{obs}: number of observed taxa per year. Note the change in sampling effort after 2002. Sampling effort and number of observed taxa are not related. See text for discussion.

Phytoplankton taxa were sorted into functional groups according to the classification of Reynolds et al. (2002), and Padisák et al. (2009) using the codon abbreviations of Padisák et al. (2009). The functional groups represent taxa with common morphological features, which share common ecological attributes, and which co-occur in specific lake-types. The classification is based on expert judgement and experience (see also Salmaso & Padisák, 2007). The complete phytoplankton, and covariate data are published at the Freshwater Research and Environmental Database of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (Kiel et al., 2023; Lentz et al., 2023; Padisák et al., 2023).

2.3 | Data analyses

2.3.1 | Time series

Because phytoplankton samples and covariate samples were not taken at regular dates and because sampling intervals varied, we constructed regularised time series with monthly pooled samples.

In the time series containing total biomass and covariates, the 310 monthly samples represent the monthly means of the original datasets. The seven missing total biomass values (=2.3% of the total number of samples) and the eight missing covariate values (=2.5%) in the combined monthly time series with pooled samples, were added by linear interpolation.

Additionally, we constructed time series from the annually pooled samples for (1) the observed number of incidences of a taxon (N_{obs}), which gives the number of samples with the taxon's presence per year; and (2) the per taxon mean annual biomass (μP_{ta} = mean biomass of taxon), which is the mean annual biomass of a taxon in the samples of the respective year.

2.3.2 | Compositional change

The compositional change through time (i.e., the temporal turnover) was measured as temporal β-diversity. We used the Sørensen pairwise dissimilarity as basic measure for β-diversity; it ranges from 0 to 1, where a value of 0 indicates that the assemblages are identical, while a value of 1 indicates that the assemblages contain no shared taxa. We chose the Sørensen dissimilarity index and its complementary Bray–Curtis index for abundance data because they are widely used in studies of β-diversity and therefore allow for comparison with other relevant studies (see e.g., Chao et al., 2006; Koleff et al., 2003).

Presence–absence diversity indices may be excessively influenced by the presence of rare taxa. Therefore, we also calculated the relative-abundance corrected (RAC) Bray–Curtis dissimilarity (Brocklehurst et al., 2018; Koleff et al., 2003) for assemblages of the annually pooled samples; this is our β_{RAC}. Abundance here is incidence abundance per year (N_{obs}).

The Sørensen index (among other indices) does not directly allow for a distinction between replacement or loss and gain or replacement and nestedness (Baselga, 2010). A methodological framework to distinguish between replacement and nestedness has been developed by Baselga (2010) and Cardoso et al. (2014), where β-diversity is measured as edge-length difference in trees resulting from hierarchical cluster analysis, and edge length is a measure of the similarity between the clusters. Although in our study distinction between nestedness and species richness differences are not relevant, we used the method of Cardoso et al. (2014) to allow for a better comparability with other studies. We termed this measure β_{ts} where it is based on N_{obs}, and β_{tb} (using taxa) and β_{fg} (using functional groups) where it is based on μP_{ta}. Before calculating similarities and edge-length differences from distance matrices, we standardised the data with logarithmic transformation as suggested by Anderson et al. (2006) using the decostand() function in R version 4.0.4 (R Project for Statistical Computing, https://www.r-project.org/). The Ward.D2 method as implemented in the R function hclust() is used consistently throughout.

We calculated β_{ts}, β_{tb}, and β_{fg} between all pairs of samples and analysed them based on the temporal distance Δ_t. Additionally we

grouped pairs of samples into sets with similar ranges of temporal distance (i.e., bandwidth). We distinguished between three groups with increasing temporal distance from shorter than 1 month to up to 1 year. This allows to detect time intervals with exceptional change at a certain temporal scale. We performed this analysis for β_{tb} and β_{fg}.

2.3.3 | Structural breakpoint and early warning indicator analysis

A structural breakpoint analysis was performed based on the *F* statistics (see Zeileis et al., 2002) with the function Fstats() of the strucchange-Package Version 1.5–2 (Zeileis et al., 2002). The *F* test is a generalised fluctuation test for linear regression models. When its statistics is larger than a critical value (in this case the mean of the sequence of the *F* statistic) the null hypothesis of no structural change can be rejected. When the process has a clear statistically significant break it is marked by a single maximum with *F* statistic larger than the critical value.

For the *F* test we used the standard linear regression model suggested by Zeileis et al. (2002). The model is implemented via residuals from principal component (PC) axes PC1 and PC2 resulting from single value decomposition PC analysis (PCA) of different multivariate datasets of the Stechlin phytoplankton. The datasets include combinations of the monthly time series of total biomass, covariates (temperature, Secchi transparency, TP, SRP, NO_2^-, NO_3^-, and NH_4^+), and β_{ts}, β_{tb}, and β_{fg}. Prior to the analysis each dataset was standardised to zero mean and unit. *F* statistics were calculated for all datasets with phytoplankton data where the two main principal axes of the PCA explain more than 50%.

To support the structural breakpoint analysis, we calculated 12 early warning indicators (EWIs) using the coefficient of variation (CV) and the autocorrelation coefficient of lag one (AR-1). The EWIs were calculated from the regularised interpolated time series of the monthly means of TP, SRP, total phytoplankton biomass, and from the monthly means of β_{ts}, β_{tb}, and β_{fg} with $\Delta_t \leq 1$ month. We selected the covariates TP and SRP because they are among the most important predictors for the functional phytoplankton composition (Selmeczy et al., 2019). *SD* and AR-1 are often interpreted as EWIs for critical transitions in nonlinear chaotic systems (e.g., Gsell et al., 2016; Scheffer et al., 2009). We used CV instead of *SD*, because it shows the variation in relation to the mean of the population. The two metrics were calculated from a rolling window of 60 months (5 years), because this results in smooth curves,m which show the general trend of the time series.

2.3.4 | Causal inference

We used convergent cross-mapping (CCM, Sugihara et al., 2012) to test the biomass time series for causal relationships with selected covariates. We selected TP and SRP a priori as relevant covariates for the analysis because a causal relationship between TP and plankton biomass had previously been identified at Lake Stechlin (Selmeczy et al., 2019).

Before the analysis we detrended the monthly time series with the Beveridge–Nelson decomposition method (Beveridge & Nelson, 1981) where the trend is modelled as a random walk with a drift and the cycle as a stationary process with zero mean, using the function bnd() of the R-package tsm Version 0.1.0 (https://rdrr.io/github/KevinKotze/tsm/).

Convergent cross-mapping is based on state space reconstruction in potentially high-dimensional, deterministic nonlinear dynamical systems from time delay-embedding (Takens, 1981). Delay embeddings reveal if unidirectional or bidirectional forcing is likely between two time series (e.g., X and Y): if X drives Y information about X is embedded in Y or vice versa (Ye et al., 2015).

In CCM the *library* of points in the attractor manifold built from Y is mapped against points in the X manifold (Sugihara et al., 2012). The skill of the cross-map is represented by the correlation coefficient (ρ). To infer unidirectional or bidirectional forcing we computed cross-map skill (ρ) for different time lags of the original time-series using the R-package rEDM Version 1.9.3 (https://cran.r-project.org/web/packages/rEDM/).

We performed CCM with two subsets of the monthly time series: Time series 1 (ts_e) ranges from March 1994 to December/2009 and has a length of 190 observations. Time series 2 (ts_l) ranges from January 2010 to December /2019 and has a length of 120 observations. In both time series, the full interval was used as both prediction and library set, respectively. The two intervals were empirically selected based on the following criteria: (1) the time series should be as long as possible and should cover roughly one of the two intervals distinguished by breakpoint analysis; and (2) CCM must show evidence of convergence with ρ at maximum library size significantly exceeding forecast of linear correlation (Sugihara et al., 2020) (necessary criterion for detecting causality). CCM was performed with embedding dimensions m = 10 for the early, and m = 9 for the late dataset, and with delay time step $\tau = 1$ throughout. We detected the optimal embedding dimensions with the function EmbedDimension() from the R-package rEDM Version 1.9.3 by selecting the dimension with the maximum forecast skill.

The results of the lagged CCM analyses for biomass and SRP are reported as median CCM skill at each lag (12-month negative to 12-month positive). When there is true causality between two time series the cross-map skill is expected to peak at negative lag, because causation only acts backward in time (Ye et al., 2015). Because biomass and SRP vary seasonally, a seasonal surrogate test was performed using the function SurrogateData () from the rEDM-package using the seasonal method. CCM skill results are calculated with 95% confidence intervals and are considered significant when they exceed the 95th percentile of the surrogate null distribution (Sugihara et al., 2020, see also: Cobey & Baskerville, 2016).

3 | RESULTS

3.1 | Changes in covariates

The concentrations of TP, SRP, and of the phytoplankton biomass increased significantly during the entire sampling interval and within the top 10 m of Lake Stechlin. The SRP concentration rose by a factor of eight (from *c.* 0.0025 to 0.0143 mg/L), the TP concentrations doubled (from 0.0173 to 0.0318 mg/L), and the mean annual phytoplankton biomass increased by a factor of 5–6 (Figures 3 and 4). Additionally, the annual variance of the phytoplankton biomass, calculated from the monthly time series, increased strongly from 1994 to 2019 by a factor of 91 and with a significant positive trend ($\tau = 0.483$, $p < 0.005$).

The most prominent common feature of these time series is their rapid increase from *c.* 2010 onward. Although the trends are similar, there is no correlation between first differences of phytoplankton biomass and SRP, and TP, respectively (Kendall rank tests with *p*-values >0.05) in the monthly datasets.

The trend of the Secchi transparency is unique, it increased during the 1990s, plateaued during the first half of the 2000s at around 9 m and decreased since then toward values that are roughly half of the maximum values, which were reached during the early 2000s.

Although the mean temperature of the upper 10 m of the water column did not increase significantly, we estimated mean values of 10.13°C for 1994 and 10.72°C for 2019 (difference = 0.59°C). No trends occur in concentrations of NO_2^-, NO_3^-, and NH_4^+, although a conspicuous short time peak occurred for NH_4^+ in 2004–2007.

3.2 | Changes in assemblage composition

In the total set of samples, 257 taxa could be identified, which belong to 27 functional groups. The assemblage composition changed profoundly during the observational period with respect to the per taxon frequency of incidences (N_{obs}) and the per taxon mean biomass (μP_{ta}; Figure S1). The compositional change included seasonal variations, distinctive short-term fluctuations with strong shifts toward a massive dominance of single taxa, and a succession of gradual shifts in abundances of groups of taxa.

Prominent events were a 1998 and 2018 *Planktothrix rubescens* (De Candolle ex. Gomont) Anagnostidis & Komárek mass growth, an *Aphanizomenon flos-aquae* Ralfs ex. Bornet & Flahault mass growth in 2010, and massive spring blooms of *Aulacoseira islandica* (O. Müller) Simonsen in the period 2000–2004.

The abundance of cyanobacteria notably increased gradually in the annually pooled dataset ($\tau = 0.311$, $p < 0.05$; Figure 4b). The cyanobacterial biomass in Lake Stechlin was not associated with changing NO_3^-/SRP ratios (Kendall rank test with $p > 0.05$), which herein serves as a rough proxy for N/P ratios.

Two groups containing predominantly taxa with gradual temporal shifts in μP_{ta} can be identified based on hierarchical cluster
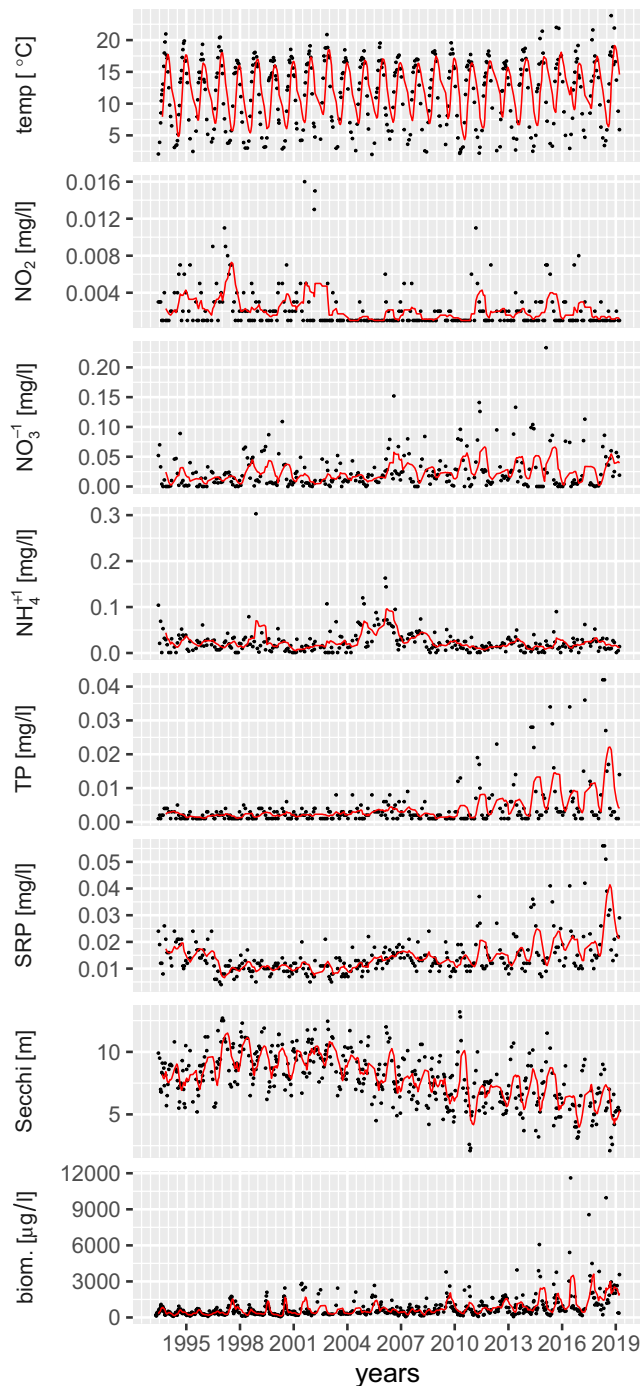

FIGURE 3 Selected epilimnetic characteristics of Lake Stechlin in the year 1994–2019. Points for Temperature (temp), NO_2, NO_3^-, NH_4^+, total phosphorus (TP), and solulable reactive phosphorus (SRP) mean values of measurements at 0 m, 5 m, and 10 m water depth of each sample occasion. Secchi: Secchi transparency; biom: phytoplankton biomass. Red line: moving average over seven sample occasions, representing approximately 14 weeks or 1/3 year.

analysis (Figure S1): (1) taxa with decreasing biomass (Table S1); and (2) taxa with increasing biomass (Table S2). *Planktothrix rubescens* is unique in its frequency and abundance pattern and forms a single high-level cluster (Figure S1).
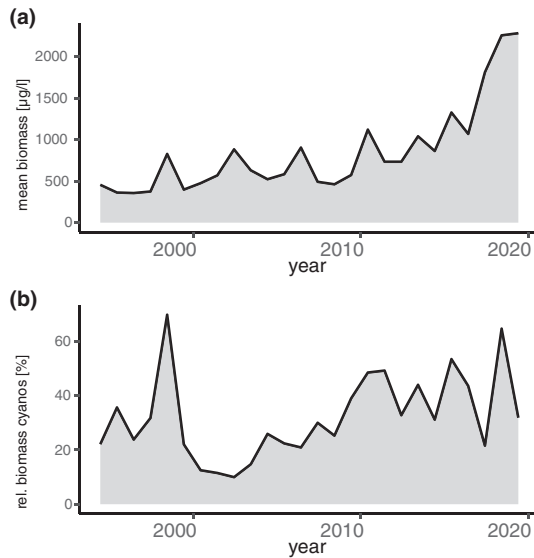
FIGURE 4 Development of the mean annual phytoplankton biomass of the Lake Stechlin during the 1994–2019 monitoring interval (a) and percentage of cyanobacteria among total phytoplankton biomass (b).
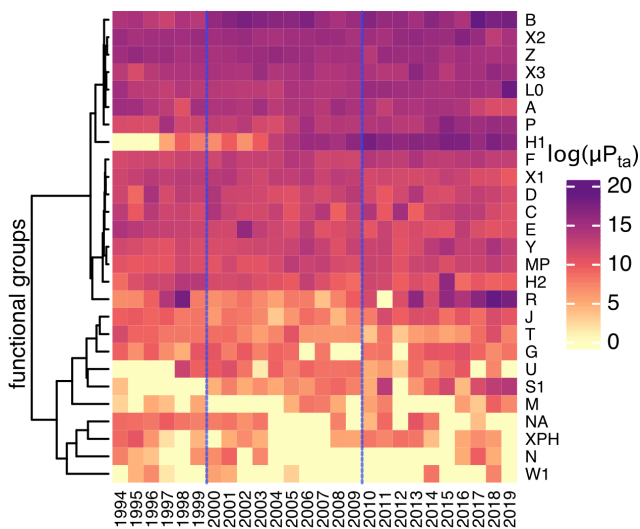

FIGURE 5 Heatmap of annual per taxon mean biomass (μP_{ta}) of functional groups of Lake Stechlin phytoplankton from 1994–2019 monitoring interval. Functional groups and acronyms as suggested by Padisák et al. (2009). Values are natural log transformed as suggested by Anderson et al. (2006) for better visibility. Clustering based on Bray–Curtis dissimilarity and calculated with "ward.D2" method as suggested by Murtagh and Legendre (2014).

When comparing the assemblage change among functional groups, a number of coda stands out because of their consistent temporal μP_{ta} trends (Figure 5): All taxa of functional group coda **B**, **H1**, **P**, **R**, **S1**, and **Y** have positive trends (Kendall rank tests with *p*-values <0.05). Specifically, **H1** and **P** became rapidly dominant during the mid-2000s. The opposite trend can be observed for coda **C**, **N**, and **N**$_A$. The taxa of these latter groups became less abundant (μP_{ta} decreased) during the observational interval.
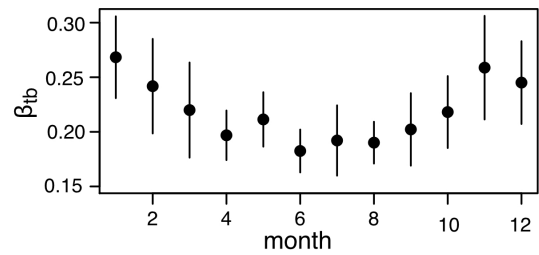

FIGURE 6 Mean annual turnover of Lake Stechlin phytoplankton in the years 1994–2019, calculated from per taxon biomass (β_{tb}) and sorted per month. Vertical bars are 95% confidence intervals. Note the seasonal variability in mean turnover levels.

3.3 | Changes of temporal turnover

The annual turnover of β_{RAC}, β_{ts}, and β_{tb} is relatively low (*c.* 0.05–0.15), with high dispersion (CV: 0.22–0.24), without trend (Kendall rank tests with $p > 0.1$), and the different estimates are not correlated (Kendall rank tests with $p > 0.1$; Figure S2). Annual turnover compared by month (i.e., annual turnover of pooled January samples, pooled February samples, etc.) resulted in a distinctive seasonal pattern with largest mean β-diversity during autumn and winter and lowest values during spring and summer (Figure 6). The only 2 months with a trend (Kendall rank test with $p < 0.05$) are October and December, where annual turnover increased from 1994 to 2019 ($\tau = 0.333$, $p < 0.05$; $\tau = 0.300$, $p < 0.05$, respectively).

Directional turnover, directly estimated from pairs of samples, reveals that the decay of the similarity (or what is the same: the increase of β) is highest within the first year and slows down with temporal distance (Figure 7). The slope of the decay distinctively increases at a temporal distance between pairs of samples larger than *c.* 18 years. This corresponds to pairs of samples with youngest samples not older than *c.* 2012 and hence reflects enhanced change in the interval 2012–2019. The change from 1994 to 2019 is larger than the average annual change, which illustrates well the magnitude of the long-term shift of the Lake Stechlin phytoplankton composition (Figure 7).

Directional turnover depends not only on temporal distance, but also changed over time (Figure 8). An increasing trend occurs in β_{tb} at monthly ($\tau = 0.415$, $p < 0.005$), and in β_{ts} at bi-monthly ($\tau = 0.305$, $p < 0.05$) time scale, but not at 3-monthly and annual time scale. An early β-peak occurs in 1998 (reflecting a massive *P. rubescens* bloom, codon **R**, see also, Figure 5).

3.4 | Structural change and causal inference

The total phytoplankton biomass in Lake Stechlin varied in the observational interval between an annual mean of 357 μg/L in 1995 and 2,280 μg/L in 2019. In the 1990s the annual means were generally well below 500 μg/L (except 1998, a year with a *P. rubescens* mass growth with 827 μg/L). During the last 5 years the mean annual
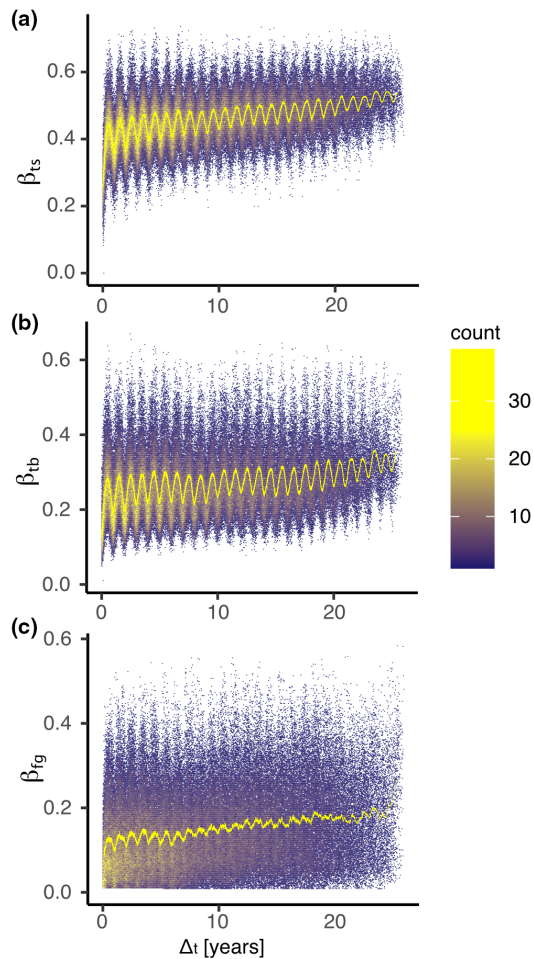
FIGURE 7 Distance decay plot of Lake Stechlin phytoplankton samples from monitoring during 1994–2019, i.e., β of pairs of samples plotted against their temporal distance, (a) calculated from taxon incidences (β_{ts}), (b) from per taxon biomass (β_{tb}), (c) from per functional group biomass (β_{fg}). Heat-colour scheme illustrates plot density (counts per area pixel). Yellow line marks moving average over 360 sample pairs. Note that in all three plots the average annual β is smaller than that of the total study interval.

FIGURE 8 Means of distance decay of pairs of samples with different temporal distance (Δ_t) against time from Lake Stechlin phytoplankton monitoring during 1994–2019. Means are estimated (a) from per taxon incidence β_{ts}, (b) from per taxon biomass β_{tb}, (c) per functional group biomass β_{fg}.

biomass was always above 1,000 μg/L and since 2010 an unprecedented rapid, and accelerating increase in phytoplankton biomass occurred (Figures 3 and 4a). This rapid increase is associated with higher percentages of cyanobacteria (Figure 4b), with higher intraseasonal turnover, and is also visible in the temporal distance decay diagrams as a period with elevated distance decay (Figure 7).

Several single structural breakpoints can be identified through PCA and *F* statistics of the total dataset and its subsets (Table S3). The breakpoints are concentrated in the years 2008, 2011, and 2016, with datasets containing β-diversity and P time series resulting in break points in 2007 and 2008, datasets containing total phytoplankton biomass and P mostly resulting in break points in 2011, and datasets containing additional covariates (e.g., T, NO_2, NO_3^-) resulting mostly in breakpoints in 2016.

Hierarchical cluster analyses, based on the taxonomic composition and per taxon biomass, consistently result in two main clusters
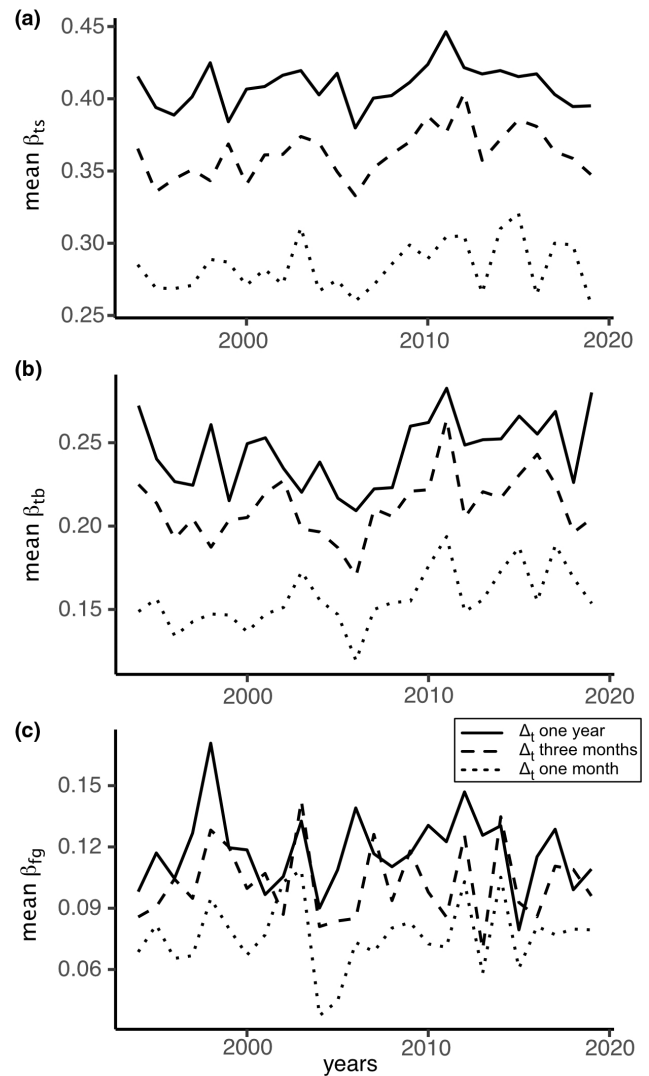
of the annually pooled samples: a pre-2010 cluster and a post-2009 cluster (Figure S3). The temporal proximity of the 2009/2010 divide between the two main clusters resulting from hierarchical cluster analysis of the phytoplankton assemblage and the 2011 structural break points detected in the multivariate datasets indicate a major change in nutrient (P), total phytoplankton biomass and phytoplankton composition during this time interval.

However, the results from EWI analysis are ambiguous (Table 1). Only in four of the 12 EWIs did a rising trend and/or peak values occur in the 5 years prior to 2010. The best indicator is β_{ts}, which reached maximum AR-1 value in 2010 and its CV was consistently very high in the 5 years prior to 2010.

The two intervals, the early interval 1994–2009 and the late interval 2010–2019, which were chosen based on the results of the hierarchical cluster analysis of the phytoplankton composition, for

CCM show differences in the position of the peaks of the CCM skill (Figure 9). The early interval shows a peak at 12 months negative lag in the SRP to phytoplankton biomass cross map and at positive lag in the reverse biomass to phytoplankton cross map. The late interval has a peak at 10 months negative lag in the SRP to phytoplankton biomass cross map and at positive lag in the reverse biomass to phytoplankton cross map. This is consistent with a unidirectional forcing of the phytoplankton biomass by SRP with a *c.* one year lag in both time intervals.

TABLE 1 Summarised results from early warning indicator analysis of the time series of the monthly means of total phosphorus (TP), soluable reactive phosphorus (SRP), total biomass, β_{ts}, β_{tb}, and β_{fg}.

Variable	CV	AR-1
TP	2019, $\tau = -0.288$, $p < 0.005$	2019, $\tau = -0.499$, $p < 0.005$
SRP	2013, $\tau = 0.655$, $p < 0.005$	2015, $\tau = 0.275$, $p < 0.005$
biomass	2019, $\tau = -0.835$, $p < 0.005$	2000, $\tau = -0.819$, $p < 0.005$
β_{ts}	2007, $\tau = -0.534$, $p < 0.005$	2010, $\tau = 0.750$, $p < 0.005$
β_{tb}	2015, $\tau = -0.084$, $p = 0.298$	2018, $\tau = -0.049$, $p = 0.466$
β_{fg}	2018, $\tau = -0.062$, $p = 0.437$	2000, $\tau = -0.678$, $p < 0.005$

Note: Indicators: coefficient of variation (CV) and the autocorrelation coefficient of lag 1 (AR-1). Year gives year of maximum value, and Kendall rank tests τ and p for the 2005–2010 interval. Red: maximum value and increasing trend within the 5 years prior to or in 2010; yellow: increasing trend or maximum within the 5 years prior to or in 2010.

4 | DISCUSSION

4.1 | The temporal scale of the phytoplankton change

Our analyses demonstrate that temporal resolution matters for detection of change in phytoplankton biomass and composition. Some major patterns are visible from the annually pooled samples, such as the accelerating rise of the total phytoplankton biomass from 2010 onward, and a clustering of phytoplankton samples into two main groups divided by 2009/2010.

However, β-diversity estimates appear to be non-sensitive to these changes when pooled annually. Temporal trends here are visible only when β-diversity is estimated directly from pairs of samples with intra-annual temporal distance or when compared per month: throughout the year the phytoplankton composition (β_{tb}, β_{ts}, see above) changed increasingly at monthly and bi-monthly scale. The months October and December stand out with increasing long-term (1994–2019) turnover trends (β_{tb}), when the phytoplankton composition of a month is compared with the composition of the same month 1 year later. Additionally, and consistent with these trends, the monthly variability of the phytoplankton biomass, expressed as annual variance of the monthly time series, increased significantly from 1994–2019. These results suggest that important changes in the phytoplankton biomass, its composition, and its covariates occurred at intra-annual scale, specifically during autumn and early winter.

Such a pattern is consistent with previously published analyses from Lake Stechlin, which predicted an increase in the annual temporal dissimilarity of the phytoplankton composition under rising physical and chemical stressors, such as nutrient limitation and
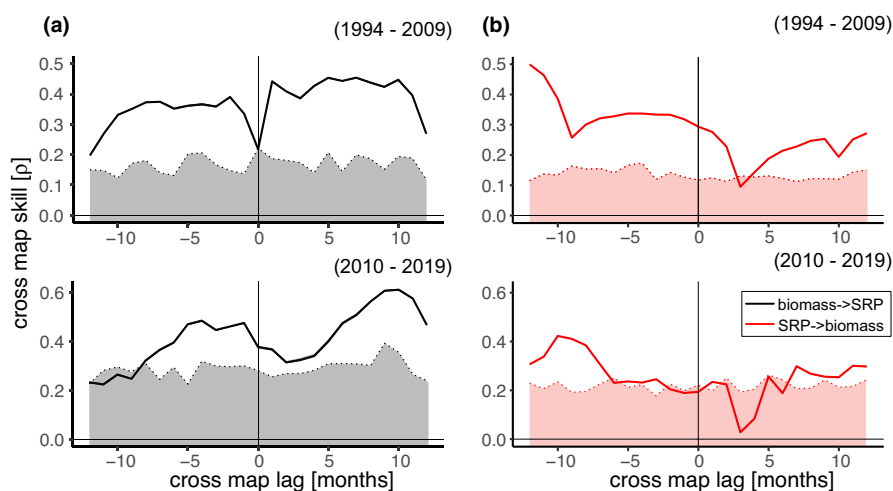

FIGURE 9 Causality analysis between Lake Stechlin phytoplankton biomass and soluble reactive phosphorous (SRP). Cross map skill (solid lines) as function of time lag. Causality is inferred if the highest cross-map skill for negative time lag is positive, significantly greater than the highest value for nonnegative lag, and larger than the 95% percentiles of surrogates (dotted lines). (a) total phytoplankton biomass causes SRP, (b) SRP causes total phytoplankton biomass. Time series range from 03/1994 to 12/2009, and from 01/2010 to 12/2019 respectively. 95% confidence of the cross map skill is too narrow to be visible in the diagrams. Space below 95% percentiles of surrogates is colour-filled—grey in (a) and red in (b)—to enhance visibility.

intensified stratification (Padisák, Hajnal, Naselli-Flores, et al., 2010). Indeed, in Lake Stechlin, climate warming led to increased surface water temperatures (Kirillin et al., 2013), which are associated with increasing relative water column stability, strikingly with most consistent long-term trends detected during autumn seasons (Selmeczy et al., 2019). Surface water warming and a prolonged stratification period have been evaluated in Lake Stechlin to be the critical mechanisms driving the increase in the intra-annual phytoplankton change (Selmeczy et al., 2019). Earlier warming of the surface waters forces a rapid growth of the zooplankton earlier during the year, which initiates a highly contingent seasonal chain of events of rise and fall of different phytoplankton taxa (Padisák, Hajnal, Krienitz, et al., 2010; Padisák, Hajnal, Naselli-Flores, et al., 2010; Salmaso, 2005).

Filamentous cyanobacteria generally are favoured under these changing conditions because their buoyant cells float better in stagnant water and because many cyanobacteria are an inaccessible food source for zooplankton (Carey et al., 2012; Huisman et al., 2004; Lewandowska & Sommer, 2010; Naselli-Flores et al., 2021; Winder & Sommer, 2012). Conversely, taxa without buoyancy regulation are negatively affected, such as heavy or skeletal phytoplankton. The long-term trend of increasing numbers of filamentous cyanobacteria and the associated decline of taxa of the coda **MP** and **N_A** are probably an effect of these changing conditions.

Filamentous cyanobacteria probably also contributed to the outstanding changes in βt_b during the late autumn–early winter season. Commonly, *A. flos-aquae* is known from lakes in the temperate zone as a species causing late summer blooms. However, a mass growth of *A. flos-aquae* during winter, and under ice and snow cover, was observed in Lake Stechlin in 2009/2010, and it was proved by photosynthesis measurements that the species exhibited net photosynthesis under low-light–cold-temperature conditions (Üveges et al., 2012). This was, to our knowledge, the first time such growth has been documented in the scientific literature. Later, the species became the second known nostocalean cyanobacterium to be a contributor to a deep chlorophyll maximum, which is also a low-light–cold-temperature environment (Selmeczy et al., 2016, 2018). Before, only *Raphidiopsis raciborskii* was known (Padisák, Scheffler, et al., 2003) from a tropical lake to be a contributor to a deep chlorophyll maximum. The latter studies suggest that changes in the thermocline and associated changes in niche separation among cyanobacteria (Selmeczy et al., 2016, 2018) are an important factor for the substantial changes observed during autumn in Lake Stechlin.

4.2 | The timing of the phytoplankton change

The complex long-term dynamics of the Lake Stechlin phytoplankton composition and biomass must be seen in the context of the 1990 shutdown of the NPP with a sudden drop of the heat contamination in the same year and the counteracting climate warming (see e.g., Kirillin et al., 2013; Koschel et al., 2002). Both factors set baseline conditions for a very specific gradual long-term change at Lake Stechlin, which includes a rapid offset of heat pollution in 1990, a

long-term climate warming with increasing surface temperatures and increasing relative water column stability (Kirillin et al., 2013). The discontinuation of the NPP led to a stop of external P-load and with nearly unchanged conditions in the catchment it caused a temporally decreasing TP during the early 1990s (Koschel, 1995).

Evidently, changes in relative water column stability forced zooplankton biomass to decrease and indirectly seem to have promoted phytoplankton biomass to increase at annual scales (Selmeczy et al., 2019). Thus, our results support the relative water column stability hypothesis of Selmeczy et al. (2019) in stressing the importance of the autumn season as the time with the most significant change in phytoplankton composition and relative water column stability.

Generally, the compositional change of the phytoplankton assemblage was relatively slow within the first two decades since the shutdown of the NPP, punctuated only by an exceptional mass growth of *P. rubescens* in 1998. The trend has gained momentum since then, resulting (in retrospect) in two distinct periods, which differ in their phytoplankton dynamics, and which are divided by a transitional period with major shifts in *c*. 2007–2011.

A massive winter bloom of *A. flos-aquae* with peak biomass values during December 2009 and January 2010 (Üveges et al., 2012) is especially noteworthy in this context. The mass growth was immediately followed by a rapid breakdown during an ice- and snow-covered period in February 2010 which fuelled an extraordinarily high heterotrophic bacterial abundance and an increased deep water de-oxygenation (Bižić-Ionescu et al., 2014).

Aphanizomenon flos-aquae was not present in Lake Stechlin before 2001. It occurred sporadically until 2006, and after that the species increasingly provided late summer biomass peaks (Üveges et al., 2012). Hence, the winter 2009/2010 records the first massive winter bloom of this species, a second comparable bloom occurred during November–December 2013. These winter blooms indicate that, from 2009 onward, nutrient conditions were reached that allowed, under certain instances, cyanobacterial mass growth during and after the autumn mixing period. On top of the prolonged (summer) stagnation period these mass growth events entail additional oxygen stress for the deeper strata of the lake. The onset of a continuous varve formation in the sediments of the deepest part of Lake Stechlin by 2010 (Scholtysik et al., 2020) may be directly related to this major transition.

4.3 | The question of internal P release

Our results from CCM confirm that SRP is a major cause of the change phytoplankton biomass and its dynamic. This is not surprising as P is long known as a major driver of phytoplankton growth (e.g., Schindler, 1977, but see Lewis Jr. & Wurtsbaugh, 2008).

The total phytoplankton biomass increased moderately in 1994–2006 ($\tau = 0.564$, $p < 0.05$), but no trend occurred in relative content of cyanobacteria during this time. Since at least *c*. 2009–2010, this dynamic has changed, with an accelerating increase in total phytoplankton biomass, massively increased relative content

of cyanobacteria, and with massively increased and accelerating TP and SRP concentrations in the epilimnion. What happened?

Since the early 1990s external P loading abruptly dropped and remained low, mainly because of the discontinuation of the NPP and improved local sewage treatment (Koschel, 1995). Other significant external nutrient sources are unknown, but at this stage cannot be not fully excluded (see e.g., discussion in Oldorff & Päzolt, 2010; Pöschke et al., 2018).

In the lack of any known external P loading the most plausible mechanism for the increase is release of heritage P from sediments. The possible existence of a P release mechanism at Lake Stechlin was already discussed in Mothes (1974) and Babenzien and Babenzien (1985) but under the premise of continuously aerobic bottom conditions, which existed during this time. It can be assumed that in Lake Stechlin sediments, phosphate exists predominantly in its redox sensitive Fe- and Mn-bound form (Gonsiorczyk et al., 1998, 2001) and in a pH sensitive calcite-bound form (Koschel et al., 1987), both as a consequence of intensive decomposition of sedimented organic matter. Therefore, P remobilization from the sediments, although not quantitatively budgeted, is likely to be directly related to the reductive dissolution of manganese and iron under anoxic conditions (Gonsiorczyk et al., 1998, 2001). A massive intensification of these processes is probably because prolonged periods of summer stagnation, intensified hypoxia, and a generally declining oxygen saturation of the hypolimnion are reported from Lake Stechlin (Kasprzak et al., 2010; Scholtysik et al., 2020; Selmeczy et al., 2019). These mechanisms of internal P loading are well known from eutrophic lakes elsewhere with temporal anoxic conditions driving internal P release, shifting N/P ratios toward more P, and eventually prompting cyanobacterial mass growth (e.g., Istvánovics et al., 2022; Jensen & Andersen, 1992; Orihel et al., 2015). Similarly, in oligotrophic Lake Zürich increases in deep-water hypoxia due to climate warming are reportedly correlated with increasing concentrations of SRP via internal loading (North et al., 2014).

4.4 | A self-reinforcing cycle of phytoplankton growth

A shortened lag interval in the causation pattern, evident from CCM from c. 2010 onward, points toward a potential critical role of the complex timing of the intra-annual phytoplankton change as suggested by Selmeczy et al. (2019). The period 2009–2010 also marks the onset of accelerating TP and SRP concentrations in the epilimnion and a rise in total phytoplankton biomass. Notably, these increases are not associated with accelerated change in other covariates monitored, and an external source for the P increase is currently unknown.

Currently, the best explanation of the mysterious rise is that during the transition period, which probably (approximately) ranged through the years 2007 to 2009, the phytoplankton biomass reached levels at which its decomposition could cause additional hypolimnic CO_2 pressure and lowered pH values. This additional contribution to

deep hypoxia could in turn have led to an increased release of calcite bound phosphate in Lake Stechlin (Selmeczy et al., 2019).

It seems as if a self-reinforcing cycle of phytoplankton growth and P mobilisation became fully active at the end of the first decade of the new millennium. Mass growth of filamentous cyanobacteria and elevated biomass of desmids belonging to coda **H1** and **P**, respectively, probably played a key role in this process and prolonged and intensified stratification could be its ultimate cause.

The end of the transition period at c. 2009–2010, then, represents the timepoint of no return, a time when enough biomass was produced in the euphotic zone to cause regularly recurring deep water oxygen depletion during the productive season, which mobilised even more P to feed even more cyanobacteria. Therefore, cyanobacteria became part of a self-proliferating process (see e.g., Kangro et al., 2007; Søndergaard et al., 2003). This self-enforcing eutrophication process can be described as a case of ecosystem engineering (i.e., an environmental modification by a group of species that affects the resource availability of other species, Jones et al., 1994; Hastings et al., 2007). Further research is needed to identify specific spatio-temporal networks of interacting phyto- and zooplankton groups, and macrophytes and fish, which maintain this process of ecosystem engineering. Additionally, a quantification of potential internal P loading could further support the hypothesis presented herein.

4.5 | Conclusions

The phytoplankton assemblage of Lake Stechlin changed drastically during the 26-year study interval since 1994. The most striking aspect of this change is the increase in filamentous cyanobacteria in absolute and relative numbers. The increase was not constant but gained momentum at around 2010; it was punctuated by short-lasting events of massive blooms, such as in 1998, and 2018 for *P. rubescens*, and in 2010 for *A. flos-aquae*.

Temporal change in the phytoplankton assemblage can be quantified as temporal β-diversity for which several methodological and computational options exist. We calculated β as Sørensen and Bray–Curtis dissimilarities between samples based on per taxon incidence abundance, taxon biomass, and based on the biomass of their functional groups. We used the original samples (with a resolution of up to 1-week temporal distance), and additionally constructed time series with monthly and annually pooled samples. From them, we calculated β as a function of temporal distance. The results of these analyses show that the changes in the phytoplankton community took place at different time scales, and that the rate of change differs among seasons. The annual changes were smaller than the total change over the 26-year study interval. The intra-annual change became more pronounced over time with the biggest changes during autumn and winter seasons.

A structural break point analysis based on monthly time series of total phytoplankton biomass, β-diversity, and covariates, and a hierarchical cluster analysis of the phytoplankton composition revealed

that the years 2007–2011 marked a profound change in the lake's planktonic ecosystem with an ongoing accelerating dynamic toward eutrophication. The results of an analysis of EWIs could not unambiguously support this change as a period with a critical transition. Instead, the change occurred as a rapid succession of major events taking place during this time interval.

Results from CCM causality analyses indirectly support previous interpretations, in which increasing relative water column stability has been identified as a main driver of eutrophication. Since *c.* 2009–2010 a self-enforcing process is in place in which phytoplankton biomass drives P loading. Internal P release from sediments probably plays a critical role in this process.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors assert that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available under https://doi.org/10.5281/zenodo.7727571 (code); https://doi.org/10.18728/igb-fred-824.1 (phytoplankton data); https://doi.org/10.18728/igb-fred-823.1 (multiparameter probe data); https://doi.org/10.18728/igb-fred-825.1 (photometry data).

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