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Phytoplankton biomass in northern lakes reveals a complex response to global change

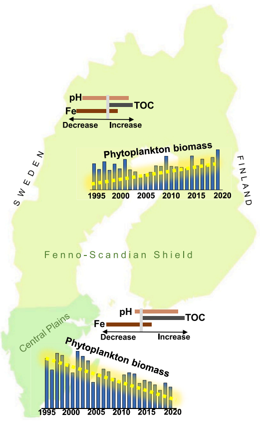
Aleksey Paltsev [a,*], Ann-Kristin Bergström [a], Kristiina Vuorio [b], Irena F. Creed [c], Dag Olav Hessen [d], Pirkko Kortelainen [b], Jussi Vuorenmaa [b], Heleen A. de Wit [d,e], Danny C.P. Lau [f], Tobias Vrede [f], Peter D.F. Isles [g], Anders Jonsson [a], Erik Geibrink [a], Kimmo K. Kahilainen [h], Stina Drakare [f]

[a] Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
[b] Finnish Environment Institute (SYKE), Helsinki, Finland
[c] Department of Physical and Environmental Sciences, University of Toronto, Toronto, Ontario, Canada
[d] Centre of Biogeochemistry in the Anthropocene and Department of Bioscience, University of Oslo, Oslo, Norway
[e] Norwegian Institute for Water Research, Oslo, Norway
[f] Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
[g] Watershed Management Division, Vermont Department of Environmental Conservation, Montpelier, VT, USA
[h] Lammi Biological Station, University of Helsinki, Helsinki, Finland

HIGHLIGHTS

- Spatial and temporal drivers of phytoplankton biomass in Fennoscandia
- Long-term effects of global change on phytoplankton
- Phytoplankton biomass is changing differently across Fennoscandia lakes.
- *Gonyostomum semen* biomass is decreasing, while cyanobacterial biomass is increasing.
- Spatial and temporal changes in phytoplankton have different underlying factors.

GRAPHICAL ABSTRACT



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ABSTRACT

Global change may introduce fundamental alterations in phytoplankton biomass and community structure that can alter the productivity of northern lakes. In this study, we utilized Swedish and Finnish monitoring data from lakes that are spatially (135 lakes) and temporally (1995-2019, 110 lakes) extensive to assess how phytoplankton biomass (PB) of dominant phytoplankton groups related to changes in water temperature, pH and key nutrients [total phosphorus (TP), total nitrogen (TN), total organic carbon (TOC), iron (Fe)] along spatial (Fennoscandia)

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* Corresponding author.
E-mail address: aleksey.paltsev@umu.se (A. Paltsev).

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and temporal (25 years) gradients. Using a machine learning approach, we found that TP was the most important determinant of total PB and biomass of a specific species of Raphidophyceae - *Gonyostomum semen* - and Cyanobacteria (both typically with adverse impacts on food-webs and water quality) in spatial analyses, while Fe and pH were second in importance for *G. semen* and TN and pH were second and third in importance for Cyanobacteria. However, in temporal analyses, decreasing Fe and increasing pH and TOC were associated with a decrease in *G. semen* and an increase in Cyanobacteria. In addition, in many lakes increasing TOC seemed to have generated browning to an extent that significantly reduced PB. The identified discrepancy between the spatial and temporal results suggests that substitutions of data for space-for-time may not be adequate to characterize long-term effects of global change on phytoplankton. Further, we found that total PB exhibited contrasting temporal trends (increasing in northern- and decreasing in southern Fennoscandia), with the decline in total PB being more pronounced than the increase. Among phytoplankton, *G. semen* biomass showed the strongest decline, while cyanobacterial biomass showed the strongest increase over 25 years. Our findings suggest that progressing browning and changes in Fe and pH promote significant temporal changes in PB and shifts in phytoplankton community structures in northern lakes.

1. Introduction

Northern lakes are under pressure from global change (Bergström et al., 2024; Creed et al., 2018; Richardson et al., 2018). Global change includes changing climate especially warming (Steffen et al., 2004), changes in precipitation patterns and the duration of growing season and ice cover (Hebert et al., 2021; Kraemer et al., 2022; Sharma et al., 2019; Wollrab et al., 2021), intensified land use and land cover activities (Björnerås et al., 2017; De Wit et al., 2016; Finstad et al., 2016), changing concentrations of essential nutrients such as nitrogen (N) (Bergström et al., 2022; Isles et al., 2018; Meunier et al., 2016) and phosphorus (P) (Isles et al., 2023), increasing pH levels (Futter et al., 2014; Skjelkvåle et al., 2001), and increasing terrestrially derived dissolved organic carbon (DOC) and associated iron (Fe) concentrations (Björnerås et al., 2017; Leach et al., 2019; Senar et al., 2018). The later phenomenon is called lake browning, due to the distinct light attenuation caused by DOC and Fe (Blanchet et al., 2022; Härkönen et al., 2023; Meyer-Jacob et al., 2019; Monteith et al., 2007; Weyhenmeyer et al., 2014). Northern Fennoscandian lakes are especially sensitive to environmental changes driven by global change as they typically are nutrient-poor with substantial risks of having structural alterations in phytoplankton biomass (hereafter: PB) and community composition (Bergström and Karlsson, 2019; Hansson et al., 2013; Keva et al., 2021) impacting phytoplankton productivity and diversity (Blanchet et al., 2022; Calderini et al., 2023; Puts et al., 2023; Urrutia-Cordero et al., 2017).

Since phytoplankton are a diverse group of organisms with differing physiology, environmental preferences, and competition strategies, they exhibit various responses to global change in terms of changes in PB and composition (Freeman et al., 2020). This is one of the main reasons why studies examining temperature impacts on PB often yield conflicting results (e.g., see Kosten et al., 2012; Kraemer et al., 2017; Paltsev and Creed, 2022; Rasconi et al., 2017). Furthermore, there is consensus that the main limiting nutrients for phytoplankton growth are P and N (Bergström, 2010; Downing et al., 2001; Guildford and Hecky, 2000), although colimitation of N and P is common in aquatic ecosystems (Harpole et al., 2011). Also, certain phytoplankton genera may find other nutrients equally crucial. For example, some Cyanobacteria such as the filamentous *Dolichospermum* have an ability for N_2 fixation (Bothe et al., 2010), which is an energetically expensive process that requires, besides availability of light, elevated concentration of Fe (Paerl et al., 2001; Sorichetti et al., 2016) as well as P for ATP production (Cottingham et al., 2015; Ward et al., 2013). Generally, Fe is associated with DOC, and thus abundant in boreal lakes; however, in Swedish sub-alpine ultraoligotrophic clearwater lakes with low DOC and Fe, iron has also found to be at least as important as P and N in constraining primary production (Vrede and Tranvik, 2006).

Two groups of phytoplankton - Raphidophyceae and Cyanobacteria - have received much attention over the last 40 years because of their expanding distribution and increasing abundances in Fennoscandian lakes. Although Raphidophyceae include several species, *Gonyostomum semen* is the most dominant and problematic species in Fennoscandian lakes (typically constituting >98 % of the biomass of the group) (also see Münzner et al., 2021), which has widely expanded its distribution over the past years (Hagman et al., 2015; Lepistö et al., 1994). Both *G. semen* and Cyanobacteria are noxious phytoplankton that can develop thick mats and nuisance blooms, and therefore have negative effects on the ecosystem function of lakes (Johansson et al., 2013a; Lau et al., 2017; Reinl et al., 2021; Rohrlack, 2020; Trigal et al., 2011; Vuorio et al., 2020). *G. semen* is not accessible to many zooplankton groups (e.g., small cladocerans) due to its large size (Johanssonet al., 2013b; Strandberg et al., 2020) while Cyanobacteria are poor food sources for zooplankton because of the low nutritional quality (Senar et al., 2021; Taipale et al., 2016) and toxicity (Erratt et al., 2023), and due to their size when filamentous and/or large colonies are formed (Bednarska et al., 2014; Gliwicz and Lampert, 1990; Lebret et al., 2012; Strandberg et al., 2023).

G. semen appears to prefer low-light and DOC-rich acidic environments - common conditions for many small boreal lakes (Hagman et al., 2015; Strandberg et al., 2020; Trigal et al., 2013). Since many Fennoscandian lakes are becoming browner (Kritzberg et al., 2020) due to rising DOC (Hagman et al., 2019; Weyhenmeyer and Bloch, 2012) and Fe (Münzner et al., 2021) concentrations, these factors have been suggested as important contributors to the increases of *G. semen* in these ecosystems. Fe also attenuates light over much of the same parts of the spectrum as DOC, and thus per se contribute to the browning trend (Maloney et al., 2005). In contrast, Cyanobacteria have received relatively less attention over the last years in oligotrophic Fennoscandian lakes compared to *G. semen*, since this group is mostly - but not always - associated with eutrophication, which is more common in populated southern areas. Nevertheless, some studies report increasing cyanobacterial abundance in Sweden (Freeman et al., 2020; Li et al., 2021) and Finland (Vuorio et al., 2020), and cyanobacterial blooms do occur in nutrient-poor oligotrophic lakes of the temperate and boreal zones in North America (Reinl et al., 2021; Senar et al., 2021; Winter et al., 2011). Further, since higher temperatures (Paerl and Huisman, 2008), elevated DOC and Fe concentrations, and higher pH levels (Senar et al., 2021; Sorichetti et al., 2014a, 2014b) seem to favour Cyanobacteria, it is possible that these factors are already causing a substantial increase in the biomass of this group in certain lakes, at least in lakes with sufficiently high total phosphorus (TP) concentrations. In nutrient-poor boreal lakes, a major fraction of total nitrogen (TN) and TP can also be associated with DOC, and thus browning will also imply increased inputs of TN and TP (Karlsson et al., 2009; Thrane et al., 2014). Browning and recovery from acidification (a decline in atmospheric sulfur deposition) will also impact pH levels as well as the acid neutralization capacity or the alkalinity in lakes (Futter et al., 2014).

The cumulative effects of global change on phytoplankton productivity and composition are not well understood. While increasing temperatures and browning (and associated increases in DOC and Fe, but also TP and TN) are shown to contribute to an increase in PB due to an enhanced input of nutrients to lakes (Isles et al., 2020; Keva et al., 2021), browning also inherently leads to reduced light penetration in the water column (Seekell et al., 2015; Thrane et al., 2014) and declines in PB (Bergström and Karlsson, 2019; Brothers et al., 2014; Kelly et al., 2018; Seekell et al., 2015); hence there is a trade-off unimodal response to browning. It is also unclear whether these changes in PB result in shifts in the composition of phytoplankton (but see Deininger et al., 2017; Senar et al., 2021) and to what extent pH may play a role in this context. It can be reasoned that elevated temperatures and browning (more nutrients, less light penetration) would especially promote phytoplankton that prefer warmer and darker waters with elevated concentration of nutrients, i.e., *G. semen* (darker waters) and Cyanobacteria (warmer waters) (Hagman et al., 2020; Moss et al., 2003; Paerl and Huisman, 2008). These phytoplankton also benefit from low zooplankton grazing pressure. Although most phytoplankton groups are generally stimulated by nutrient supply, only a few studies (e.g., Freeman et al., 2020; Verspagen et al., 2022) examined broad spatial and temporal patterns of dominant phytoplankton groups in northern landscapes caused by global change (e.g., warming, browning, eutrophication, acidification). These studies found large variability in the responses of phytoplankton to global change depending on various factors including latitude, lake type and size, and phytoplankton group (see also Stomp et al., 2011). Furthermore, despite recent technological and modelling advances (e.g., in remote sensing; Kraemer et al., 2022; Paltsev and Creed, 2021), the lack of large-scale (countries or regions) and long-term (decades) high-quality in-situ data from different types of lakes is still often constraining the possibilities for finding relevant links between environmental changes and patterns in phytoplankton.

In this study, we compiled Swedish and Finnish lake monitoring data that are spatially (135 lakes, from 55°N to 68°N) and temporally (1995-present) extensive, covering substantial gradients in water temperature, water chemistry, and PB and composition as well as lake size. With this dataset, we were able to (1) analyse the relationship between total PB and the biomass of six of the most dominant phytoplankton groups and hypothesised environmental controls (i.e., variables), with a particular focus on the biomass of *G. semen* and Cyanobacteria; and (2) quantify annual trends of total PB and the biomass of these six phytoplankton groups over a period of 25 consecutive years (1995-2019), and then relate the trends in total PB and the biomass of *G. semen* and Cyanobacteria to associated trends in selected environmental variables. We chose environmental variables that represent global change and that were previously found to be particularly important for primary producers in boreal lakes, i.e., water temperature (hereafter: temperature), TP, TN, total organic carbon (TOC), and Fe concentrations, as well as pH. *G. semen* and Cyanobacteria were a focus of this study because they are of significant concern in Fennoscandia due to their capacity to develop blooms and the expanding distribution of *G. semen* (see details above). Our aim was to address the following three questions:

Question 1. Is total PB and the biomass of the dominant phytoplankton groups – especially *G. semen* and Cyanobacteria - related to temperature and water chemistry? Here we predict that TP and TN are the most important variables regulating PB (Schindler, 1974), while temperature and parameters associated with lake browning (i.e., TOC, Fe) and acidification recovery (i.e., pH) are less important and more *group-dependent* because of specific requirements of certain phytoplankton groups. We also predict that temperature and water chemistry are considerably different in lakes with *G. semen* and without *G. semen*.

Question 2. Is total PB of individual lakes showing long-term temporal trends, and if so, what phytoplankton group(s) is (are) driving these trends? We predict that total PB is increasing in most study lakes and that the composition of phytoplankton is changing towards an increase in the biomass of *G. semen* and Cyanobacteria due to increasing temperature and browning. We also predict that *G. semen* is spreading to new lakes.

Question 3. Are the temporal changes in total PB and the biomass of *G. semen* and Cyanobacteria related to changes in temperature and water chemistry? We predict that these changes are mainly associated with global change, namely increasing temperature and lake browning (i.e., increasing TOC and Fe concentrations).

2. Materials and methods

2.1. Data on temperature, water chemistry, and phytoplankton

Data for temperature, water chemistry parameters (TP, TN, TOC, pH and Fe) and phytoplankton were obtained from ongoing Swedish and Finnish lake monitoring programs. Lakes in the Swedish lake monitoring program have been continuously sampled on an annual basis since 1995 (with some gaps/missing data for some years – see below for details), while lakes in the Finnish lake monitoring program have been continuously sampled on an annual basis since 2006. This resulted in annual phytoplankton dataset for 150 lakes (Sweden = 137 lakes, and Finland = 13 lakes) for a maximum period from 1995 to 2019. Lakes were located within three Fennoscandian ecozones - the Borealic uplands, Fenno-scandian Shield and Central plains (Trigal et al., 2013). For simplicity, we divided our study region into the northern (or *the north*; Borealic uplands and Fennoscandian shield) and the southern (or *the south*; Central plains) subregions. The division line is approximately at 60°N (Figs. 1-2).

All data used in this study are from national monitoring programs funded by the Swedish Agency for Marine and Water Management in Sweden and by the Ministry of the Environment in Finland. In Sweden, monitoring data are available from the national data host at Swedish University of Agricultural Science (Miljodata-MVM, 2021).

Temperature measurements for this study were taken at 0.5 m depth in Sweden and at 0.2-1 m depth in Finland. Water for analysis of lake water chemistry was collected at the same depth yearly between three and four times over the open water season (June to early October).

Phytoplankton data from June to late September were used in this study. Samples were collected on up to three occasions during this period from epilimnion with a 2-m long tube sampler. In Sweden, in lakes with a large surface area (>1 km^2) a single mid-lake site was used for sampling, while in lakes with a smaller surface area (<1 km^2) five randomly located epilimnetic water samples from the center of the lakes were collected to account for the potential for larger spatial heterogeneity in these smaller lakes. In Finland, phytoplankton samples were collected at the site of maximum lake depth. In both countries, several water samples from epilimnion were mixed to form a composite sample and a subsample was taken for analysis. Samples for phytoplankton analyses were preserved with acid Lugol's iodine solution (2 g potassium iodide and 1 g iodide in 100 mL distilled water supplemented with acetic acid) and kept dark at 4-5 °C prior to analysis. Phytoplankton was counted using an inverted light microscope and a modified Utermöhl (1958) technique according to Olrik et al. (1998). Phytoplankton was identified to the finest taxonomic unit possible (usually species level). Biovolume (μg L^{-1}) was estimated using geometric forms and biomass from counts of individuals of each taxon (Olrik et al., 1998). Biomass was estimated assuming a density of 1 g cm^{-3}.

All analyses and assessments were performed at accredited laboratories: at the Department of Aquatic Sciences and Assessment of Swedish University of Agricultural Sciences in Sweden, and Finnish Environmental Administration and consultant Eurofins Environment Finland. Field and laboratory analyses were done in accordance with international (ISO) or European (EN) standards (Fölster et al., 2014).

For this study, we aggregated phytoplankton to a class, division, or phylum. Temperature, water chemistry, total PB, and the biomass for each phytoplankton group were averaged for each year. Total PB was calculated as the sum of all phytoplankton groups in each sample before estimating annual means. pH values were transformed to H^+ concentrations before estimating means, which were than transformed back to pH for visualization. TOC concentration was used as a proxy for DOC

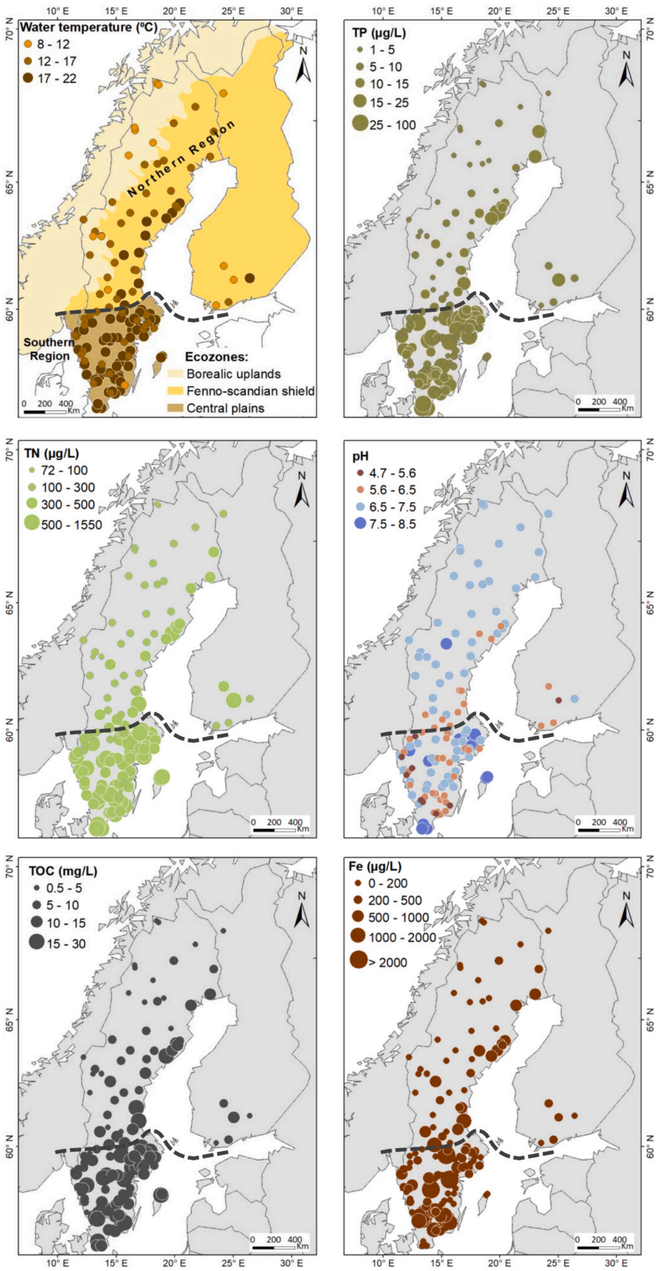

Fig. 1. Spatial distribution of water temperature and water chemistry parameters (mean values over the 2006-2019 period) in 135 study lakes in Fennoscandia. Dashed lines indicate a boundary between the northern and the southern regions (i.e., *the north* and *the south*).

concentration based on previous studies on Finnish and Swedish lakes showing that >90 % of TOC is DOC in these lakes (Köhler et al., 2002; Kortelainen et al., 2006). The shapefiles for Fennoscandian ecoregions (ecozones) were downloaded from the European Environmental Agency's website: https://www.eea.europa.eu/data-and-maps/figures/ecoregions-for-rivers-and-lakes.

Since not all of 150 lakes were sampled in all years (i.e., there were missing data for some chemical parameters and/or phytoplankton) and to maximize the number of years with complete datasets with water chemistry and phytoplankton, we selected two periods with data for as many lakes as possible. The first dataset included lakes with data from 2006 to 2019 (14 years), which were used for spatial analysis ("spatial dataset"). The second dataset included lakes from the spatial dataset with the longest overlapping time series (25 years; from 1995 [Sweden] or 2006 [Finland] to 2019), which were used for temporal analysis ("temporal dataset"). We screened these two datasets again and considered the trade-off between the proportion of missing data and equal distribution of lakes throughout the study region. In each dataset, we selected those lakes that had up to maximum 15 % of missing data. This screening process resulted in 135 lakes in the spatial dataset (129 lakes for Sweden and 6 for Finland) and 110 lakes in the temporal dataset (104 lakes for Sweden and 6 for Finland) with a median lake surface area of 56.7 ha (lower quartile I = 23.7 ha and upper quartile III = 167 ha; Tables S1-S2; Figs. 1-2). Raphidophyceae was the only phytoplankton group that was not present in all lakes (i.e., the biomass was 0 µg L^{-1} in some lakes; Fig. 2, Table S1). Therefore, this group was analyzed with a special caution (see details below).

We used six dominant phytoplankton groups (see *Results*) for the general description of the spatial (the Spearman's correlation) and temporal (the Mann–Kendall test) trends. However, we were particularly interested in the patterns of two groups of noxious phytoplankton - Raphidophytes and Cyanobacteria. Therefore, the biomass of these groups as well as total PB were examined in more detail. We used Raphidophytes as proxy for *G. semen*, as this species accounted for ~ 98 % of the biomass of this group in the study lakes (there was also a small biomass (<2 %) of *Merotricha capitata, Gonyostomum depressum* and *Vacuolaria virescens*).

Seven lakes from the Swedish lake monitoring program were also part of the Integrated Studies of the Effects of Liming Acidified Waters (IKEU) project (Table S2) (for details, see https://www.slu.se/centrumbildningar-och-projekt/ikeu/). Since spatial and especially temporal patterns in pH and Fe (e.g., Fe can precipitate with Ca to lake sediments; Riise et al., 2023; Wersin et al., 1991) might be different in *limed* lakes, we performed an additional analysis on these seven lakes and the rest of the lakes independently to check possible influences of liming. In particular, we: (1) performed the Spearman's correlation test (Bonett and Wright, 2000) on the spatial dataset to determine if associations among environmental variables and phytoplankton were similar in *limed* and *non-limed* lakes, and (2) calculated linear slopes (rates of changes) of pH and Fe in the temporal dataset to assess if the rates of change are similar between *limed* and *non-limed* lakes. We found that the magnitude and direction of associations among environmental variables and phytoplankton groups were similar in *limed* and *non-limed* lakes (Fig. S1). In addition, the rates of change in pH and Fe in *limed* lakes were also small (between -0.01 and 0.01 for pH and between -4 and 4 µg Fe L^{-1} yr^{-1}) and within the distribution of *non-limed* lakes (Fig. S2). Based on this outcome, we concluded that liming does not substantially affect patterns in water chemistry and PB in the study lakes; therefore our analysis was performed on the whole lake dataset (i.e., by including both *limed* and *non-limed* lakes).

2.2. Spatial analysis

The Spearman's correlation test (*rho* statistic) was used to determine associations among environmental variables (temperature, water chemistry parameters) and phytoplankton. The test was performed on mean data (i.e., mean values over the 2006-2019 period) from each lake for the dataset with spatial focus (Table S1).

Random forest analyses (Auret and Aldrich, 2012; Breiman, 2001) were performed for three separate models (for total PB, *G. semen* biomass, and cyanobacterial biomass) to investigate the *relative* importance of environmental variables (temperature, TP, TN, TOC, pH, and Fe) on PB in the spatial dataset. Random forest is a machine-learning technique that is based on a combination of multiple regression trees created using bootstrap samples from data. These data were randomly split into training set (80 %) and test set (20 %), where the latter was used to evaluate the performance of the models using *the percent of variation explained term* ("pseudo-R-squared"; hereafter: *%Var*) (see Liaw and Wiener, 2002). Environmental variables were used as explanatory variables, while total PB (*model 1*) and the biomass of *G. semen* (*model 2*)

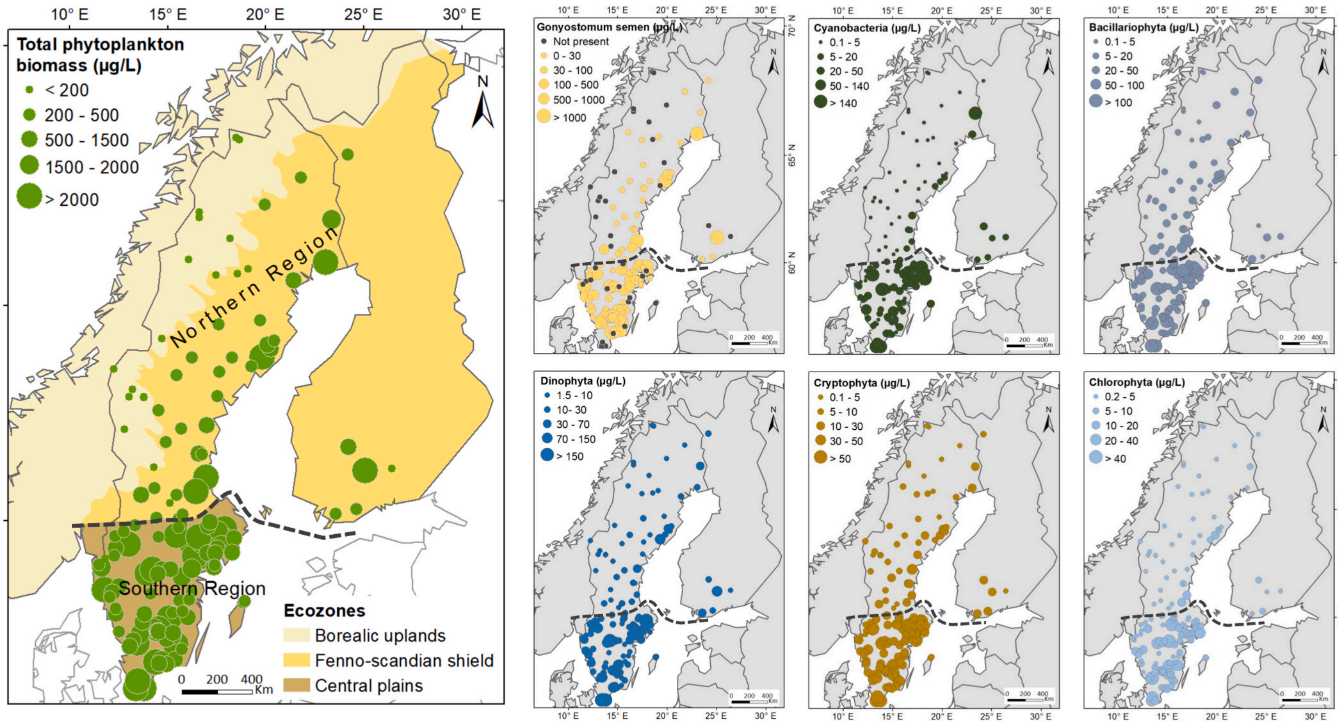

Fig. 2. Spatial distribution of total phytoplankton biomass (PB) and the biomass of six most dominate phytoplankton groups (mean values over the 2006-2019 period) in 135 study lakes in Fennoscandia. Dashed lines indicate a boundary between *the north* and *the south*.

and Cyanobacteria (*model 3*) were used as response variables. Each random forest analysis was performed with 5000 trees. The percent increase in mean squared error (*%IncMSE*) was calculated to determine the *relative* importance of explanatory variables ("variable importance"; De'ath and Fabricius, 2000); the further the *%IncMSE* score was from 0, the more important it was (Strobl et al., 2009).

Since TP, TN, and TOC were highly correlated with each other, and therefore potentially contributing to a bias in variable importance (Strobl et al., 2009), we performed a sensitivity analysis where we used only one of the three variables at a time per model (i.e., TP *or* TN *or* TOC). We then compared *%IncMSE* scores of these models with the model containing all three variables. A similar order of variables on a variable importance plot and similar *%IncMSE* scores for these variables would mean that collinearity had a little (if any) effect on the *relative* importance of explanatory variables.

We used Partial Dependence (PD) plots to demonstrate the relationship between a response variable (i.e., phytoplankton) and an individual environmental variable while all other variables were held constant (Friedman, 2001; Goldstein et al., 2015). Random forests were performed in R (R Core Team, 2022) using *randomForest*, *caret*, and *pdp* packages.

To determine the difference in temperature and water chemistry between lakes with and without *G. semen*, we classified all lakes used for the spatial analysis (i.e., 135 lakes) into three groups. *Group I* included lakes with *G. semen* present in ≥12 years over the 1995-2019 period (i.e., *constantly* present, $n = 38$), *Group II* included lakes with *G. semen* data present in <12 years (i.e., *sporadically* present, $n = 45$), and *Group III* included lakes where *G. semen* was not detected at all ($n = 52$). For each group, we calculated mean values of each environmental variable and made box plots showing their medians and the interquartile ranges. Measurements of all variables between groups were compared with either a one-way ANOVA or a Kruskal–Wallis test (the non-parametric equivalent of the one-way ANOVA). For post hoc tests, we used a Holm-Sidak test for ANOVAs and Dunn's test for Kruskal–Wallis tests. We also compared environmental variables in each group with known (published) thresholds found to promote *G. semen* growth (i.e., Fe >200 µg L^{-1} [Lebret et al., 2018; Münzner et al., 2021]; pH <7 [Trigal et al., 2013]; TP >15 µg L^{-1} [Lebret et al., 2018] and TOC >10 mg L^{-1} [Rengefors et al., 2008]).

2.3. Temporal analysis

The nonparametric Mann–Kendall test (Kendall, 1975) was performed on environmental variables and total PB as well as the six major phytoplankton groups in individual lakes (with total number of lakes = 110), and Kendall rank correlation statistics (*tau* and *p* values) was analyzed to determine temporal changes and trends (for a 25-year period for Sweden and 14-year period for Finland). Significance level was set to $p \leq 0.1$ following Wasserstein et al. (2019) and Wasserstein and Lazar (2016) (but also some recent ecological studies e.g., Bergström et al., 2024; Oliver et al., 2017; Paltsev and Creed, 2021), where $p \leq 0.1$ is considered reasonable probability of the error to accept due to the source (two different monitoring programs), nature of data (ecological time series), and the approach the data are used for (time series analysis). Further, we did not use *p* value as a threshold to eliminate or promote data and results (Wasserstein et al., 2019), and we showed all the results (i.e., with both $p \leq 0.1$ and $p > 0.1$).

We defined a temporal change when Kendall's *tau* (a positive change for a positive *tau* or a negative change for a negative *tau*) for a variable was at $p > 0.1$, and we defined a temporal trend when Kendall's *tau* (positive or negative) for a variable was significant (i.e., $p \leq 0.1$; Dakos et al., 2019; Paltsev and Creed, 2021). We calculated Sen's slopes (Sen, 1968) to estimate the rates of change (µg L^{-1} yr^{-1}) in the phytoplankton groups in each lake. For visualization purpose, we also interpolated the calculated Sen's slopes for Sweden and Finland using the local polynomial interpolation function of *the Geostatistical Analyst Tool* in ArcGIS (Esri ArcMap v.10.8.1).

Since *G. semen* (and Raphidophytes) was not present in all lakes and all years (i.e., the biomass was 0 µg L^{-1}; Fig. 2), performing the Mann–Kendall test on such data from *individual* lakes could lead to biased results with artificially high or low Kendall *tau* values (Hamed, 2011). Therefore, for the temporal analysis, we used only lakes from *Group I* (lakes where *G. semen* was detected in ≥12 years). This resulted in a fewer number of lakes for *G. semen* than for total PB and other phytoplankton groups (38 lakes with *G. semen constantly* present *versus* 110 lakes in total). Only one Finnish lake had *G. semen* present in ≥12 years (see Table S1). In these 38 lakes, *G. semen* constituted at least 96 % of total PB.

To examine if *G. semen* was spreading to new lakes, we calculated the total number of lakes (for a given year) with *G. semen* for lake *Groups I* and *II* for the 1995-2019 period for *the north* and *the south* separately (see Section 2.1 for definition for *the north* and *the south*). To investigate changes in *G. semen* expanding distribution *versus* changes in mean *G. semen* biomass across the study region, we constructed time series of mean *G. semen* biomass (mean biomass across all lakes in a given year) for the same lakes (i.e., from *Groups I* and *II*) and for the same 1995-2019 period. The Mann–Kendall test was then performed on the time series of mean *G. semen* biomass to extract Kendall statistics.

2.4. Analysis of temporal drivers of phytoplankton

The Pearson correlation was used to determine synchrony, direction (positive or negative) and the significance of the trends between time series of environmental variables and time series of total PB and the biomass of *G. semen* and Cyanobacteria. For this, we calculated means of biomass of these three groups across lakes for a given year. We calculated these means *independently* in lakes that were found to have positive changes in total PB, the biomass of *G. semen* and Cyanobacteria, and in lakes that were found to have negative changes in the biomass of these groups (see Section 2.3 for details). This categorization was based on the premise that the response of PB to global change is shaped by the direction of global change factors (e.g., warming is likely to result in an increase in PB, browning may lead to both an increase and a decline in PB, etc.; see *Introduction*). The number of lakes was 110 for total PB and cyanobacterial biomass, and it was 38 for *G. semen* biomass. We then calculated mean concentrations of Fe, TOC, TP and TN as well as mean pH and temperature for the same lakes (i.e., for lakes with positive and negative changes). This resulted in six time series (two time series [positive and negative] per phytoplankton group) of mean total PB, mean biomass of *G. semen* and mean biomass of Cyanobacteria *versus* corresponding time series of environmental variables for the 1995-2019 period. The Shapiro-Wilk test was used to check whether data from the time series were normally distributed. PB and environmental variables (except for pH) were log-transformed to fulfil the assumption of normality.

Random forests analysis was performed for six separate models (two models per phytoplankton group) to investigate the *relative* importance of environmental variables over time. In each of the six models, we determined *%Var* for the whole model and for the model containing only environmental variables found to be important - i.e., variables that had *%IncMSE* score higher than the threshold identified (see Results).

3. Results

3.1. Impact of temperature and water chemistry on phytoplankton

The Fennoscandian lakes displayed substantial spatial gradients in temperature and water chemistry (see descriptive statistics in Table 1, Table S2), with an increase in mean concentrations of TP, TN, TOC, and Fe from the north-west to the south-east but with a notable exception of pH that showed more complex spatial patterns (Fig. 1). Phytoplankton were dominated by six taxonomic groups: Raphidophyceae (with *G. semen* constituting 98 % of the biomass of the group), Bacillariophyta, Cyanobacteria, Dinophyta, Cryptophyta, and Chlorophyta. Similar to the environmental variables, total PB and the biomass of the six groups displayed substantial gradients across the study region (Fig. 2; Table 1). In general, lakes in *the north* had lower total PB than lakes in *the south*. *G. semen* was more common in *the south* and in lakes along the coast of the Gulf of Bothnia than in lakes in *the north* (especially in the Borealic uplands) where it was not present at all in many (22) lakes. Cyanobacteria were identified in all study lakes; however, their biomass varied across the study region with generally lower biomass in *the north* (Fig. 2).

The total PB and the biomass of the six groups had weak to strong positive associations to temperature and nutrients, with the strongest association to TP and TN (Fig. 3; Table S3), but weak and variable relationships to pH, with *G. semen* having the strongest negative association (i.e., a decline in *G. semen* was associated with an increase in pH; *rho* = -0.28, $p = 0.0009$) and Bacillariophyta having the strongest positive association (*rho* = 0.33, $p = 0.0001$). *G. semen* was also strongly positively related to Fe (*rho* = 0.59, $p < 0.0001$). Cryptophyta and Chlorophyta were strongly positively related to TOC (*rho* = 0.61 and 0.60 for Cryptophyta and Chlorophyta, respectively [*p* for both <0.0001]), while this relationship was moderate for Cyanobacteria (*rho* = 0.47, $p < 0.0001$).

Random forest and the associated partial dependence (PD) plots identified complex non-linear relationships between environmental variables and phytoplankton (Fig. 4). These models explained 62 % of the variation in total PB, 28 % of the variation in the biomass of *G. semen* and 40 % of the variation in the biomass of Cyanobacteria. Sensitivity analysis performed on TP, TN, and TOC separately (i.e., variables that had strong collinearity with each other; see Fig. 3) revealed that the three most important variables remained the same in the combined model (Fig. 4) and in separate models (Fig. S3). Further, the order of the variables in the separate models mainly followed the order in the combined model, except for temperature, which became the least important variable in each of the separate models.

Random forests revealed that TP was the most important environmental variable for total PB and the biomass of *G. semen* and Cyanobacteria (Fig. 4). This was clearly shown in the PD plots where TP spanned the largest range in biomass of these three groups. Yet, the increases in the biomass of *G. semen* and Cyanobacteria with increasing TP occurred only until TP concentration reached 25 µg L^{-1} and 55 µg L^{-1},

Table 1
Descriptive statistics of environmental variables, total PB and the biomass of six phytoplankton groups used in the study (number of lakes: 135).

	Minimum	Quartile I	Median	Mean	Quartile III	Maximum
Temperature (°C)	8.0	13.1	16.9	16.2	19.2	21.3
TP (µg L^{-1})	1.6	5.1	9.6	15.9	18.9	141.6
TN (µg L^{-1})	71.8	258.9	374.0	430.9	531.3	1545.5
pH	4.9	6.2	6.7	6.7	7.2	8.4
TOC (mg L^{-1})	0.7	5.8	8.9	9.7	13.0	29.7
Fe (µg L^{-1})	8.5	49.4	179.6	454.9	477.0	4266.4
Total phytoplankton (µg L^{-1})	41.2	314.9	571.5	1292.3	1463.5	13,143.5
Raphidophyceae (*G. semen*; µg L^{-1})	0	0	5.0	279.6	170.5	2744.0
Cyanobacteria (µg L^{-1})	0.02	2.1	5.8	29.0	17.1	593.06
Bacillariophyta (µg L^{-1})	0	6.7	15.7	36.9	33.2	686.3
Dinophyta (µg L^{-1})	1.7	7.9	14.5	44.6	27.5	1698.5
Cryptophyta (µg L^{-1})	0.1	7.8	12.8	25.2	24.6	391.9
Chlorophyta (µg L^{-1})	0.2	2.4	4.0	12.4	8.5	479.3

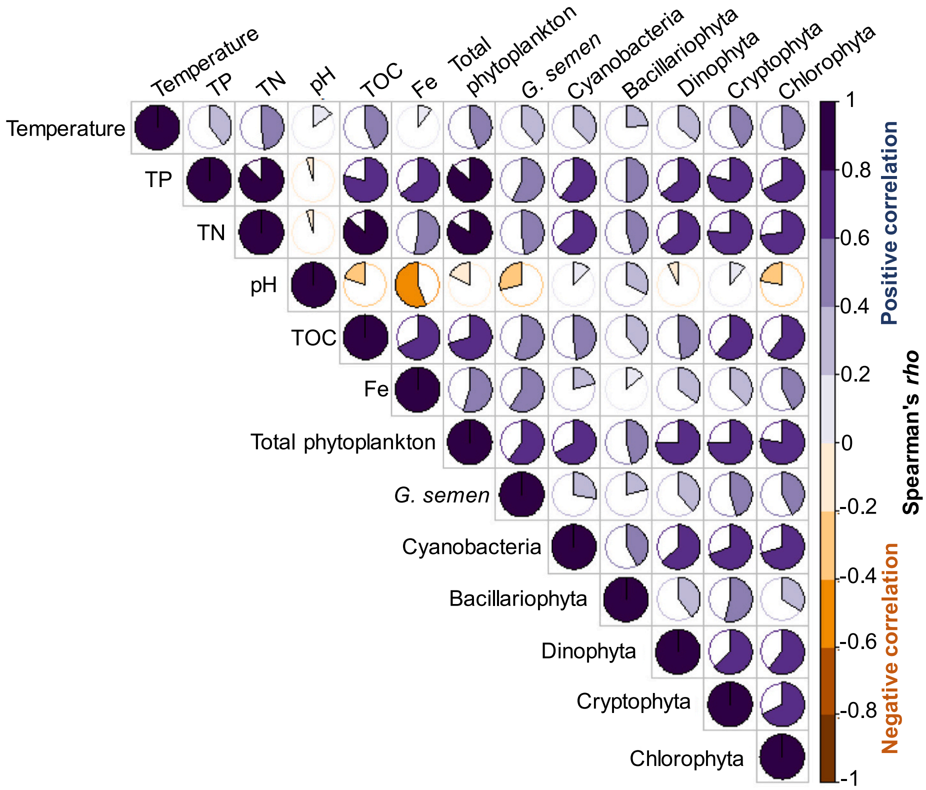

Fig. 3. Results of the Spearman correlation test performed on water temperature, water chemistry parameters (mean concentrations for the 2006-2019 period), total PB and the biomass of six phytoplankton groups (mean biomass for the 2006-2019 period) (number of lakes: 135). Pie-like pictograms reflect magnitude (measured as Spearman's *rho*) and direction of correlations. The size of “the piece” of the pie is a rounded *rho* value from -1 to 1 (e.g., “the piece” equal to the half of the pie has *rho* = 0.5). Blue colours indicate positive correlations, orange colours indicate negative correlations, while white colours indicate no relationship. See exact Spearman's *rho* and *p* values in Table S3.

respectively. TN was the second most important variable for total PB and cyanobacterial biomass, while it was the least important for *G. semen* biomass (also see Fig. S1). Fe was the second and pH was the third most important variable for *G. semen* biomass, but of moderate importance for cyanobacterial biomass and total PB. The biomass increased with increasing Fe concentration, with the largest change found between 230 and 530 μg L^{-1} for *G. semen* biomass, with Fe concentrations ranging from <5 to 1800 μg L^{-1}. For Cyanobacteria, Fe was important when their biomass was low (between ~28 and 35 μg L^{-1}). Total PB and cyanobacterial biomass increased with increasing pH, while the biomass of *G. semen* decreased with increasing pH. TOC was the third most important variable for total PB, but of moderate to low importance for cyanobacterial and *G. semen* biomass (Fig. 4).

Our separate analyses on *G. semen* revealed that all water chemistry parameters in *Group I* (*G. semen* was present *constantly*) were significantly different from these parameters in *Group II* (*G. semen* was *sporadically* present) and *Group III* (lakes with no *G. semen*) (Fig. 5; also see Table S4 for the details of the test). Lakes from *Group I* had higher TOC, TP, TN and Fe concentrations and lower pH compared to *Groups II* and *III*. Temperature was higher in *Groups I and II* than in *Group III*. Further, the majority (> 80 %) of lakes in *Group I* had Fe concentrations above 200 μg L^{-1} and pH below 7 – the thresholds known to promote conditions for *G. semen* growth (Münzner et al., 2021; Trigal et al., 2013).

3.2. Temporal trends in phytoplankton of individual lakes

Temporal changes and trends were assessed for the environmental variables and total PB and the biomass of the six dominant phytoplankton groups over the 1995-2019 period for Swedish lakes and the 2006-2019 period for lakes in Finland (Fig. 6). Lake summer (June-September) temperature was increasing in 75 % of lakes in *the north,* while this proportion was almost equal (~50 %) for lakes with positive and negative changes in temperature with time in *the south*. TP was mostly decreasing (in 75 % of lakes) in *the north* but had mixed changes (negative and positive) in *the south.* TN and Fe showed mostly negative changes in both regions. Even though TOC had positive changes in both regions, this increase was more widespread in *the south* where TOC was increasing in 96 % of lakes; however, significant changes (trends) in TOC were exclusively positive in both regions. pH had mixed (negative and positive) changes in *the north*, and mostly positive changes (in 65 % of lakes) in *the south* (Fig. 6a).

Total PB was mostly increasing in *the north* (in 70 % of lakes) with positive trends identified in 32 % of lakes*,* and it was decreasing in 55 % of lakes in *the south* with 27 % of lakes having negative trends and 23 % having positive trends (Fig. 6a). In *the north,* only seven lakes (out of 38) had *G. semen* detected for ≥12 years over the 1995-2019 period (Fig. 6a, Table S1). Even though *G. semen* biomass was increasing in more than half of these lakes (*n* = 4 or 57 %), only one lake had a positive trend in its biomass. All lakes with decreasing *G. semen* biomass (*n* = 3) had negative trends in their biomass. In *the south*, more lakes had *G. semen* (31 out of 38 lakes), and *G. semen* biomass was decreasing in 61 % of lakes, while trends in their biomass were mixed with both negative (35 %) and positive (19 %) trends. The total number of lakes with *G. semen* increased in *the north* (from 5 to 17 lakes) and in *the south* (from 19 to 33 lakes) from the first 5 years (1995-1999) to the last 5 years (2015-2019) (Fig. 6b). Yet, mean *G. semen* biomass significantly decreased both in lakes in *the north* (from 178 μg L^{-1} to 30 μg L^{-1}; Kendall's *tau* = -0.53, *p* = 0.0002) and in *the south* (from 804 μg L^{-1} to 180 μg L^{-1}; Kendall's *tau* = -0.57, $p < 0.0001$) between the first 5 years and the last 5 years (Fig. 6b).

The rate of change in total PB was higher in lakes with negative changes (median rate = -15.3 μg L^{-1} yr^{-1}) than in lakes with positive

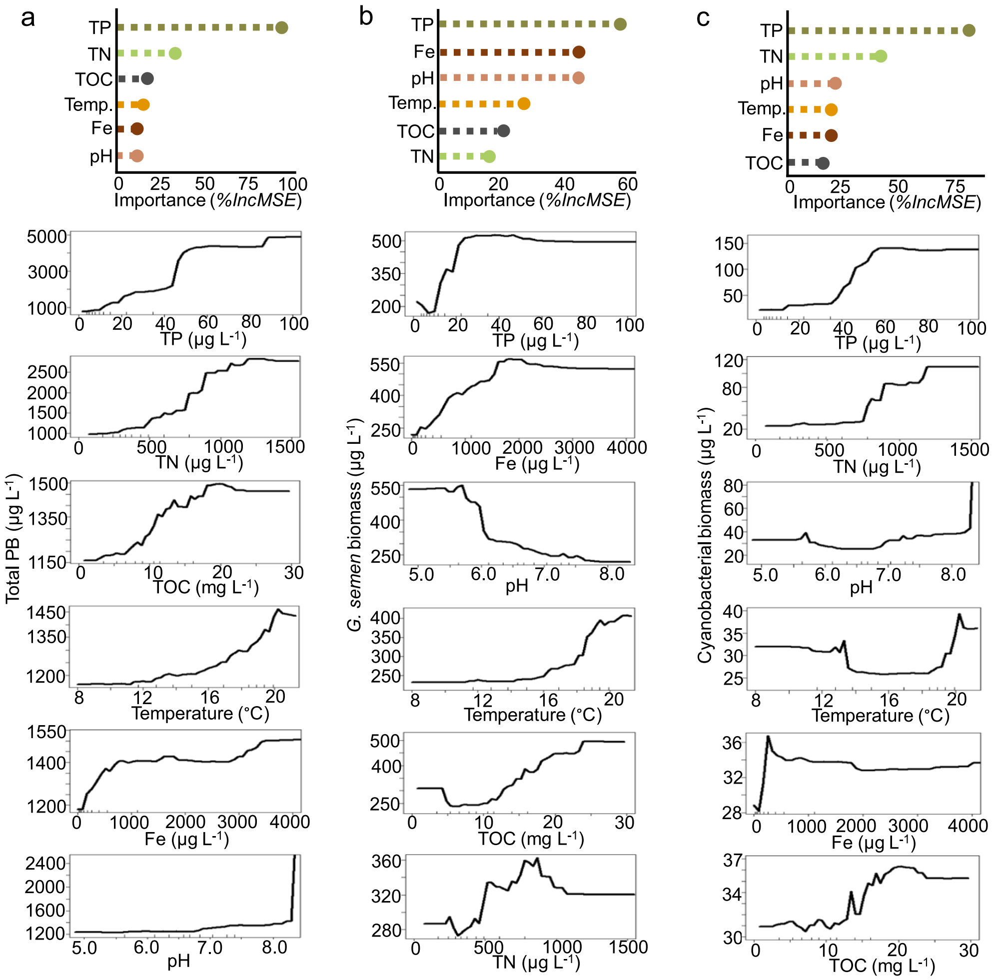

Fig. 4. Results of the random forest analysis (importance plots [top panel] and partial dependency plots) between environmental variables (i.e., temperature and water chemistry parameters) and **(a)** total PB, **(b)** *G. semen* biomass, and **(c)** cyanobacterial biomass performed on spatial data from 135 study lakes. "Importance" was measured by the percent increase in mean squared error (*%IncMSE*); the higher the *%IncMSE* score, the higher the importance of the variable in the model. Analysis was performed on annual mean concentrations and biomass for the 2006-2019 period.

changes (median rate = 5.5 µg L^{-1} yr^{-1}; Fig. 6c). In lakes with positive changes in total PB (Fig. 6d), temperature and TOC were also increasing, TP and TN were mostly decreasing, while pH and Fe showed mixed changes. In these lakes, Cyanobacteria showed the strongest positive trend (i.e., a temporal change with $p \leq 0.1$) among phytoplankton groups, followed by *G. semen* and Chlorophyta; however, *G. semen* was detected in only 16 lakes, and with a positive change found in only 11 lakes. In lakes with negative changes in total PB (Fig. 6d), pH and TOC were increasing, while TP, TN and Fe were decreasing, with Fe mostly showing decreasing changes and negative trends. In these lakes, *G. semen* showed the strongest temporal decrease among phytoplankton groups, followed by Dinophyta.

3.3. Temporal changes in phytoplankton related to changes in temperature and water chemistry

The complex interactions between time series of environmental variables and time series of total PB and the biomass of *G. semen* and Cyanobacteria were identified (Fig. 7). In most of the random forest models, environmental variables that had the *%IncMSE* score ≥ 10 also had *significant* relationships with PB in the Pearson correlation analysis. Therefore, we used the *%IncMSE* score ≥ 10 as the threshold to distinguish the most important variables from those less important. In each random forest model, we then determined *%Var* for these most important variables and for the *whole model* (with all variables).

The Pearson correlation revealed that temporal incline of PB was significantly related to increasing pH ($r = 0.63$, $p = 0.0007$) and TOC ($r = 0.46$, $p = 0.0221$; Fig. 7a). In the random forest model, pH was the most important variable for increasing total PB followed by TOC (Fig. 7b). These two variables explained 43.4 % of variation in total PB, while the *whole model* (with temperature, TN, TP, and Fe also included in the model) explained 31.7 % of the variation. The PD plots showed that total PB was relatively stable at ~620 µg L^{-1} below pH ~6.1, above which total PB started to rise to ~800 µg L^{-1} (Fig. 7c).

Temporal decline of total PB was significantly related to decreasing Fe ($r = 0.63, p = 0.0008$) and increasing TOC ($r = -0.41, p = 0.0392$) and pH ($r = -0.39, p = 0.0459$). The most important variables contributing to decreasing total PB were Fe, TOC, and pH, which explained 39.5 % of variation in total PB (Fig. 7b). The *whole model* explained 37 % of the variation. Decreasing Fe concentration accounted for the largest range of the decline in total PB (from ~3050 to ~2150 µg L^{-1}; Fig. 7c). Further, lakes with negative changes in total PB had overall higher concentrations of nutrients, higher temperatures, and slightly lower pH than lakes with positive changes in total PB (Tables S5-S6).

Temporal incline of *G. semen* biomass was significantly related to only one variable – increasing Fe ($r = 0.46$, $p = 0.021$; Fig. 7d). The random forests also showed that Fe was indeed the most important factor contributing to the positive changes in *G. semen* biomass, and it also revealed that temperature was the second important variable. These variables explained 16 % of variation in *G. semen* biomass, while the

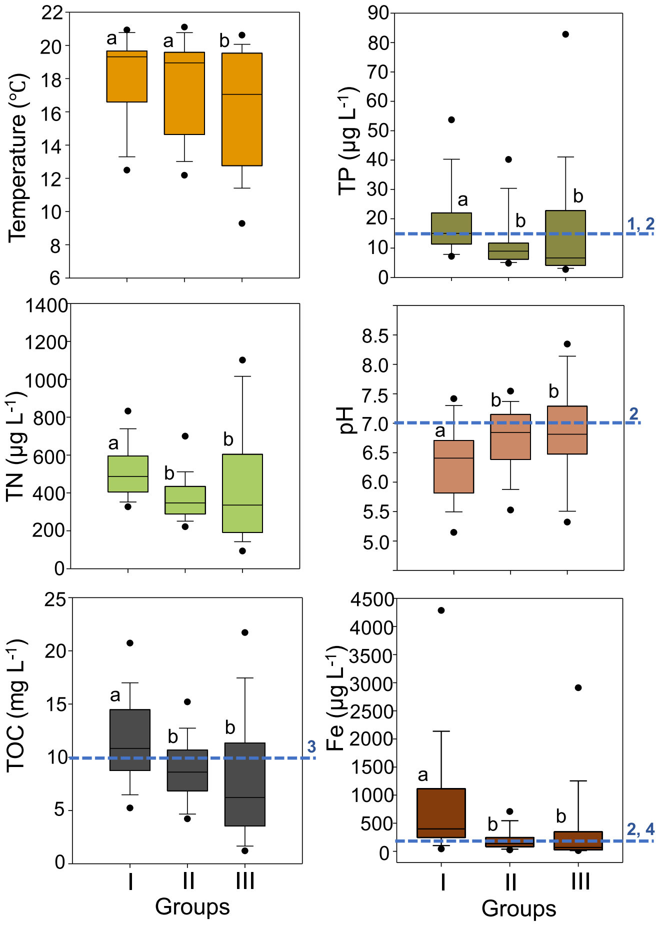

Fig. 5. Boxplots of environmental variables in each group of lakes according to the presence/absence of *G. semen*. *Group I*: *G. semen* was present in ≥12 years (i.e., lakes used in the trend analysis: Figs. 6 and 7), *Group II: G. semen* was present in <12 years (i.e., *sporadically* present), and *Group III*: *G. semen* was not detected at all during 1995-2019. Boxes show interquartile range and median, and whiskers show 10 % and 90 % percentiles. Letters above the boxes indicate significant differences in temperature (in °C) and water chemistry parameters (concentrations) among the groups (i.e., *I*, *II* and *III*) calculated with the two-way ANOVA and the Kruskal–Wallis test. Blue dashed lines represent thresholds identified in the literature for each environmental parameter, and numbers above the lines are references to a literature source: [1] Weyhenmeyer and Bloch (2012); [2] Lebret et al. (2018); [3] Rengefors et al. (2008); [4] Münzner et al. (2021). For Temperature and TN, no thresholds were found.

whole model explained only 5.7 % of the variation. The PD plots showed a non-linear relationship between increasing temperature and *G. semen* biomass with a large spike in *G. semen* biomass (reaching 600 µg L^{-1}) at 17.5 °C followed by a drop to its "below-spike" biomass level (300 µg L^{-1}).

Temporal decline of *G. semen* biomass was significantly related to decreasing Fe ($r = 0.48$, $p = 0.0151$) and increasing pH ($r = -0.44$, $p = 0.028$), TOC ($r = -0.44$, $p = 0.0294$) and TN ($r = -0.39$, $p = 0.0482$). In random forests, pH was the most important variable contributing to the decline in *G. semen* biomass followed by TOC, Fe, and TN. These four factors explained 21.3 % of variation in *G. semen* biomass, while the *whole model* explained 19.6 % of the variation. The PD plots identified a sharp decrease in *G. semen* biomass with increasing TOC concentrations above 10.5 mg L^{-1} and with pH increasing above 5.7, and with decreasing Fe concentrations below 1400 µg L^{-1}.

Temporal incline of cyanobacterial biomass was significantly related to increasing pH ($r = 0.53$, $p = 0.0062$) and Fe concentration ($r = 0.46$, $p = 0.0202$; Fig. 7g-i). Random forests showed similar results with Fe and pH as the most important variables contributing to the increase in the biomass of this group, explaining 12.7 % of the variation. The *whole model* explained 9 % of the variation in the biomass.

Temporal decline of cyanobacterial biomass was significantly related to decreasing TP ($r = 0.40$, $p = 0.0455$), TN ($r = 0.51$, $p = 0.0078$), and Fe ($r = 0.41$, $p = 0.0427$) concentrations (Fig. 7g-i). TP, TN, Fe, and TOC were the most important variables for the decline in cyanobacterial biomass as identified by random forests. These parameters explained 20.7 % of the variation in the biomass, while the *whole model* explained 16.3 % of the variation. Although, the random forests revealed that increasing TOC concentration was an important contributor to the group of lakes with decreasing cyanobacterial biomass (Fig. 7h), the linear correlation between these two parameters was not significant ($r = -0.12$, $p = 0.58$; Fig. 7g).

4. Discussion

Our analyses revealed high spatial and temporal variability in total PB and the biomass of *G. semen* and Cyanobacteria, where the spatial distributions were primarily related to lake nutrient TP and TN concentrations, and the temporal trends in biomass were primarily linked to long-term changes in lake environment attributed to browning (i.e., changes in TOC and Fe concentrations) and acidification recovery (changes in pH). This discrepancy between our *spatial* and *temporal* results indicates that substitutions of data for space-for-time may not be adequate to describe (and predict) long-term impacts of global change (especially browning) on phytoplankton.

4.1. Environmental variables associated with phytoplankton

In line with our first prediction, the spatially most important determinant of total PB, the biomass of *G. semen* and Cyanobacteria was lake TP concentration, followed by TN concentration, with concentrations of TOC and Fe, and pH the least important determinants. Phosphorus (P) has long been recognized as the primary limiting nutrient for phytoplankton growth in freshwater systems (Schindler, 1977; Sterner, 2008). TP was highly correlated not only with total PB but also with all six dominant phytoplankton groups, which increased towards *the south* (Figs. 1-3). Total PB also increased monotonically over the entire range of increasing TP (Fig. 4a), suggesting that total PB was firstly limited by P, and secondly by N, in line with the observation that lakes are commonly co-limited by N and P (Harpole et al., 2011). Furthermore, previous studies have demonstrated that systems may shift from N to P-limitation in response to elevated N-deposition (Elser et al., 2009). Contrary to our first prediction, temperature did not play an important role in regulating total PB in space (Fig. 4). In fact, when performing random forest models on TP, TN and TOC independently, temperature came up as the least important variable in every model (Fig. S3). Southern more nutrient rich lakes were, however, warmer compared to the northern more nutrient poor lakes (Figs. 1, 2), which to some extent might mask the response of total PB to temperature (see Bergström et al., 2013). The finding that TOC was the third most important variable for total PB (Figs. 4a and S1), and that total PB increased with increasing TOC supports previous findings that overall nutrient enrichment related to lake browning promotes increases in total PB in Fennoscandian lakes (Bergström and Karlsson, 2019; Isles et al., 2021; Keva et al., 2021).

The finding that *G. semen* experienced a sharp increase in biomass at TP = 12-15 µg L^{-1} (Fig. 4b) is consistent with previous studies (Lebret et al., 2018; Weyhenmeyer and Bloch, 2012). Fe and pH were more important for spatial patterns of *G. semen* biomass than the indicator of browning (i.e., TOC), although TOC has been recognized to enhance growth of *G. semen* in experimental studies (Hagman et al., 2020). In line with our prediction, lakes where *G. semen* was constantly present had higher concentration of nutrients and lower pH than the rest of the lakes (Fig. 5). *G. semen* biomass also appeared to be influenced by the specific thresholds identified for water chemistry parameters. Fe concentration of ~200 µg L^{-1} (Münzner et al., 2021), pH ~7 (Trigal et al., 2013) and

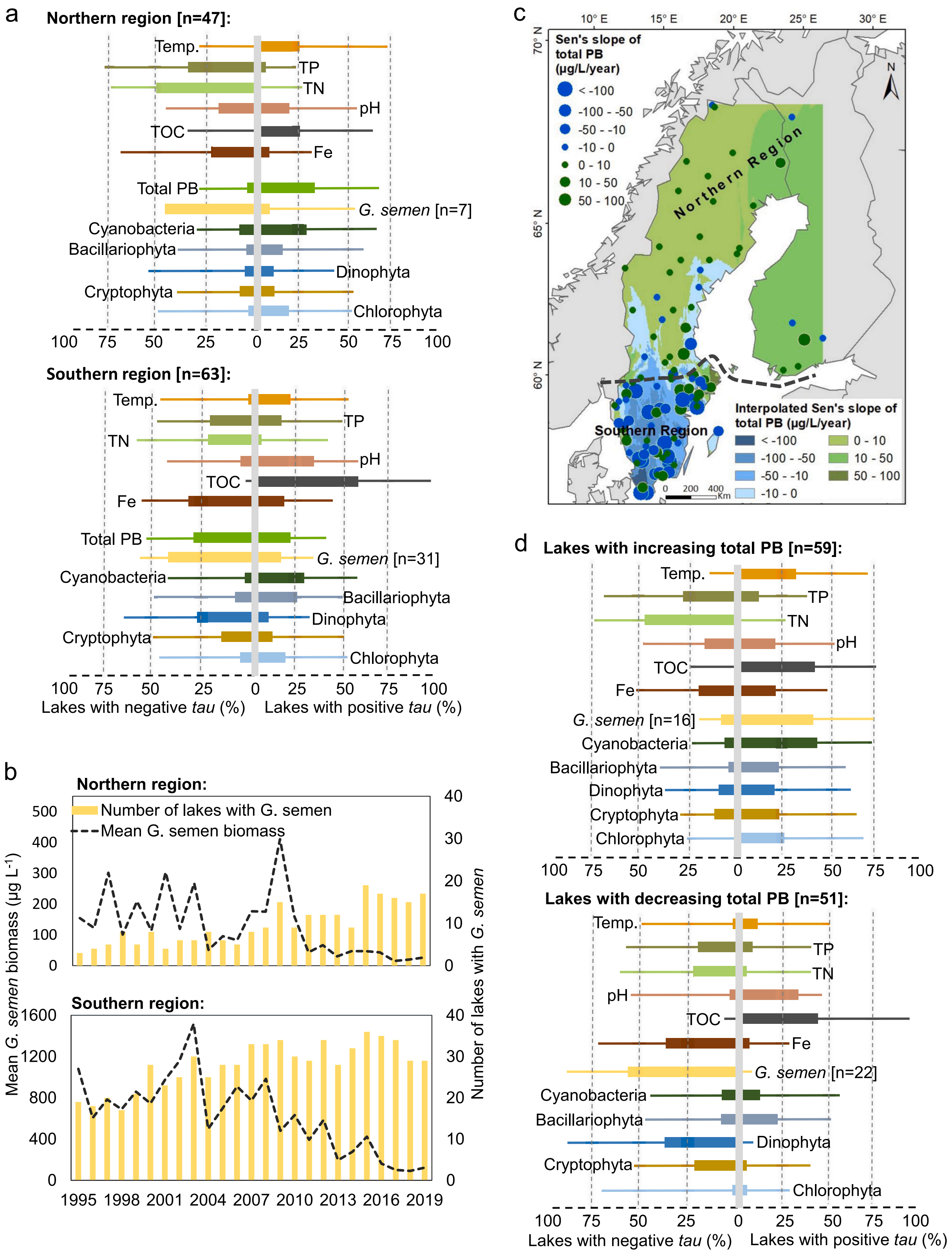

Fig. 6. **(a)** Monotonic trends in environmental variables (i.e., temperature and water chemistry), total PB, and the biomass of six phytoplankton groups in study lakes for the 1995-2019 period for *the north* and *the south* shown as Kendall *tau*; **(b)** Changes in the number of lakes with *G. semen* and mean biomass of *G. semen* in *Groups I* and *II*; **(c)** Rates of change (calculated as *Sen's* slopes) of total PB (µg L^{-1} yr^{-1}); **(d)** Monotonic trends in environmental variables, total PB, and the biomass of six phytoplankton groups in study lakes for lakes with increasing total PB and lakes with decreasing total PB (shown as Kendall *tau*). In inserts **(a)** and **(d)**, the lengths of thin lines represent the proportion of lakes with positive or negative *tau*, and the length of thick lines represents the proportion of lakes with trends ($p < 0.1$). Note, the total number of lakes with *G. semen* is different and shown in square brackets.

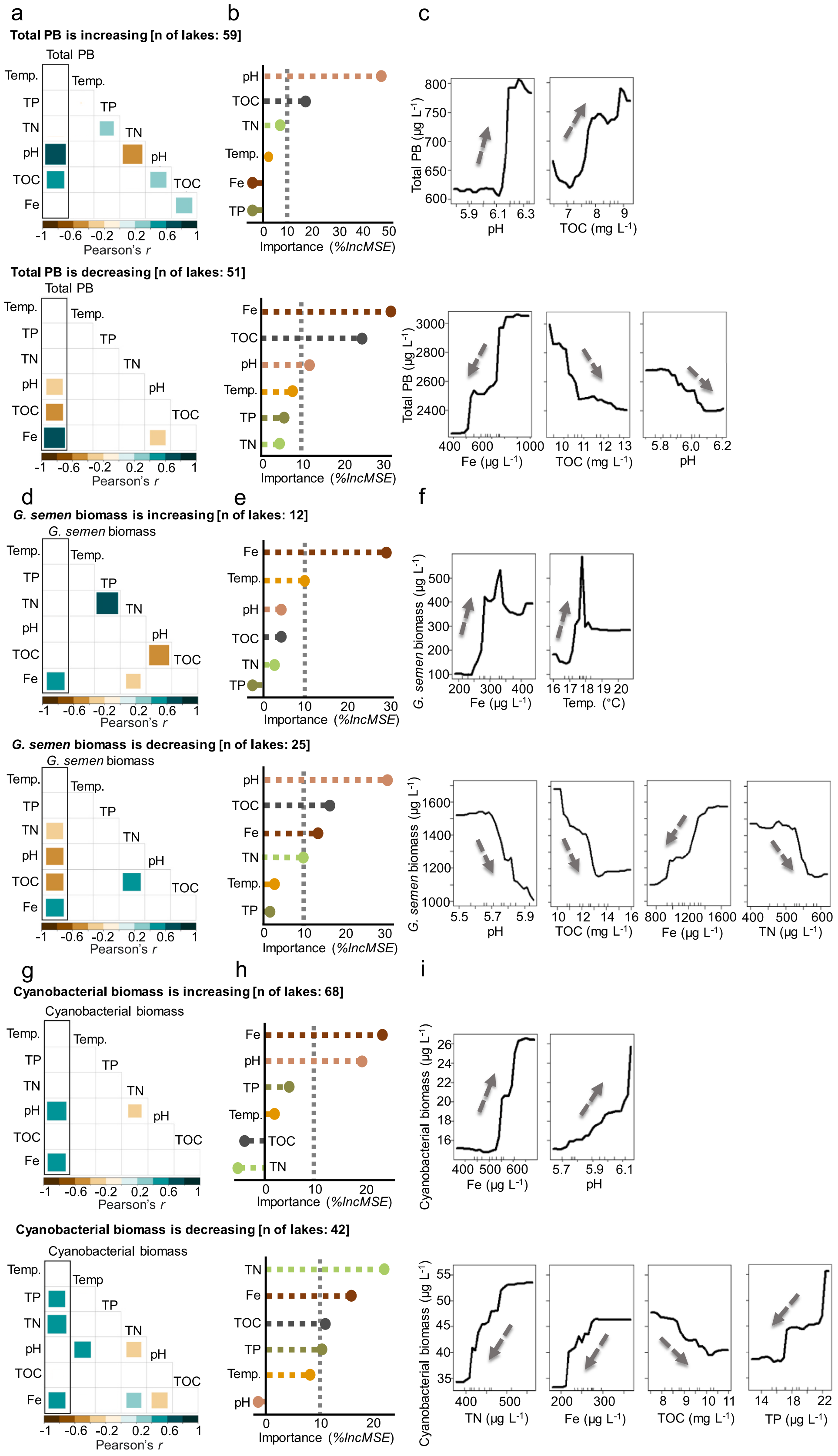

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Fig. 7. Results of the Pearson correlation tests between time series of **(a)** total PB, **(d)** *G. semen* biomass and **(g)** cyanobacterial biomass (mean values over lakes in each year, number of lakes: 110) and time series of environmental variables (mean values over lakes in each year) for the 1995-2019 period. Only significant correlations are shown. Size of square pictograms reflects magnitude and direction of correlations (*r*). Blue square pictograms indicate positive correlations, while orange square pictograms indicate negative correlations, e.g.: *G. semen* biomass is *decreasing* over time with *decreasing* Fe (significant positive correlation) but simultaneously with *increasing* TOC, pH and TN (significant negative correlation). Results of the random forest analyses: Importance plots between time series of environmental variables and time series of **(b)** total PB, **(e)** *G. semen* biomass, and **(h)** cyanobacterial biomass. "Importance" on importance plots was measured by the percent increase in mean squared error (*%IncMSE*). A vertical dashed line is a threshold that distinguishes important variables from those less important. Partial dependency plots between time series of environmental variables and time series of **(c)** total PB, **(f)** *G. semen* biomass, and **(i)** cyanobacterial biomass. Only important variables (above the threshold – i.e., dashed lines on importance plots) are shown on partial dependency plots. Arrows represent directions of a change of PB and environmental variables, i.e.: an arrow on the partial dependency plot with cyanobacterial biomass *versus* pH shows that cyanobacterial biomass is *increasing* with *increasing* pH.

TOC ~10 mg L^{-1} (but to a lesser extent; Rengefors et al., 2008) were clearly separating many lakes where *G. semen* was constantly present from other lakes. Our results agree with other studies showing high demand for Fe in *G. semen* (Münzner et al., 2021) and its preference for acidic waters (Trigal et al., 2013). The reasons for *G. semen* having high Fe requirements might be its high need for Fe for chloroplasts production (Lebret et al., 2018) combined with its low Fe uptake ability (Münzner et al., 2021). The preference of *G. semen* for low pH conditions might be a physiological adaptation for regulating the internal pH close to neutral levels (Trigal et al., 2013). This preference can also be related to Fe bioavailability at different TOC concentrations (brown lakes *versus* less brown/clear water lakes) and pH (acidic *versus* neutral conditions). Fe is generally not in a bioavailable (ferric) form in circumneutral waters (Maranger and Pullin, 2003; Shaked and Lis, 2012). However, elevated TOC concentrations can modify this pattern by bringing more dissolved Fe attached to the dissolved organic matter (DOM) and thereby preventing Fe precipitation and settling (Maranger and Pullin, 2003; Taillefert et al., 2000). Similar to Cyanobacteria, which can modify the bioavailability of ferric Fe by utilizing Fe-binding siderophores (Sorichetti et al., 2014a, 2016), there is evidence suggesting that *G. semen* may also benefit from an association with specific bacteria that produce siderophores (Münzner et al., 2021; Seymour et al., 2017). Hence besides the traditional focus on TN and TP, the interplay between DOC, Fe and pH appears an important determinant of "nuisance" phytoplankton like *G. semen* and Cyanobacteria.

Cyanobacterial biomass also increased with increasing TP with the slope varying across the TP gradient (Fig. 4). Notably, there was no change in cyanobacterial biomass until TP concentration reached ~16 μg L^{-1}. Above this threshold, cyanobacterial biomass increased up to TP concentrations 50 μg L^{-1}, beyond which the biomass leveled off, indicating a saturation point in TP. Other studies have found similar (Dolman et al., 2012; Li et al., 2021; Vuorio et al., 2020) or higher (100 μg L^{-1}; Carvalho et al., 2013) TP thresholds and subsequent plateaus for lakes across Europe. Although TN was the second most important variable regulating spatial patterns in cyanobacterial biomass, it did not cover the entire range in the biomass again stressing the importance of P for the development of cyanobacterial biomass in lakes. Temperature was of lower importance for the spatial distribution of cyanobacterial biomass compared to TP and TN, even though many species of Cyanobacteria are known to be favored in warm lakes (Carey et al., 2012; Paerl and Huisman, 2008). The finding that pH and Fe were important for cyanobacterial biomass is aligned with the ability of Cyanobacteria to live in various pH conditions but with preference of more neutral/alkaline environments (Vinebrooke et al., 2002). High pH favors growth of many cyanobacterial species due to their carbon concentrating mechanisms, providing them with a competitive advantage over other phytoplankton groups under low CO_2 conditions (Shapiro, 1990; Wilson et al., 2010). Elevated concentrations of Fe are also advantageous to nitrogen fixing species of Cyanobacteria due to their requirement for Fe in N_2 fixation and inorganic N assimilation (Kerry et al., 1988; Lin and Stewart, 1997), and Fe can also be a limiting nutrient for Cyanobacteria in boreal lakes (Sorichetti et al., 2014a).

To the best of our knowledge, no previous study has simultaneously examined the relationship between pH and Fe and the biomass of *G. semen* alongside the relationship between these parameters and cyanobacterial biomass. Lake pH seems crucial in distinguishing spatial patterns between the biomass of *G. semen* and Cyanobacteria in the study lakes. Furthermore, pH and Fe were more important for *G. semen* biomass than for cyanobacterial biomass (Fig. 4). Fe and pH accounted for almost the entire range of *G. semen* biomass showing a relationship close to linear, while these parameters accounted for just short intervals in the model describing variance in cyanobacterial biomass. Since we examined the potential impacts of temperature and water chemistry on PB with a special focus on the biomass of *G. semen* and Cyanobacteria, we cannot rule out that top down food-web (zooplankton grazing, the presence of fish; Findlay et al., 2005; Johansson et al., 2013b; Roozen et al., 2007; Trigal et al., 2011) and/or physical (lake bathymetry, stratification patterns; Paltsev and Creed, 2022; Stomp et al., 2011; Trigal et al., 2013; Weithoff et al., 2000) factors to some extent might have influenced their spatial distribution in the study lakes. We also acknowledge that our consideration of Cyanobacteria as an aggregated group limits our ability to discern species-specific preferences in Cyanobacteria for nutrients and pH. Thus, the observed spatial patterns in cyanobacterial biomass do not necessarily reflect preferences of individual species for these parameters.

4.2. *Diverging temporal changes in phytoplankton*

In line with our second prediction, we found that total PB was mostly increasing with time in *the north* (attributed mainly to increasing cyanobacterial biomass as expected) but had mixed trends in *the south* (attributed mainly to the declining biomass of *G. semen* and Dinophyta, that was not expected, and increasing cyanobacterial biomass, as expected) (Fig. 6). Total PB exhibited not only contrasting temporal changes and trends (positive *versus* negative) but also varying rates of change, where total PB was experiencing a gradual increase in *the north*, while it was declining at an accelerated rate (reaching below -100 μg L^{-1} yr^{-1} for some lakes) in *the south*. The large decline in total PB was mainly associated with declining *G. semen* biomass, which contradicts our second prediction and the finding by Weyhenmeyer and Bloch (2012) who described a strong increase in *G. semen* biomass in Swedish lakes for the period of 1988-2007, although Trigal et al. (2013) did not find a significant increase in the biomass for the 1992-2010 period. Declining temporal trends of *G. semen* biomass also corresponded with an expansion of *G. semen* – i.e., this species was spreading to new lakes, particularly in the northeast (upland lakes; Fig. 6b, also Fig. 2), thus in line with our second prediction and findings of other authors (Weyhenmeyer and Bloch, 2012; Trigal et al., 2013). Even though Cyanobacteria had the largest contribution to increasing total PB, the increase in cyanobacterial biomass was not overwhelming with only 37 % of lakes experiencing positive trends in the biomass.

4.3. *Temporal changes in phytoplankton are related to global change*

We found no relationship between temporal increases in temperature and total PB (Fig. 7). However, changes in total PB were associated with lake browning. Both positive and negative changes in total PB were related to increasing TOC concentration, which is in line with our third prediction. Since lakes with decreasing total PB had high concentrations of TOC and Fe, as well as TP and TN (Tables S5-S6), nutrients were not limiting in these lakes. Median concentration of TOC for lakes with decreasing total PB was 10.9 mg L^{-1}, while it was 7.8 mg L^{-1} for lakes with increasing total PB. These levels correspond to the DOC threshold found by Bergström and Karlsson (2019) in Swedish lakes; i.e., that in lakes with DOC concentration higher than ~10-11 mg L^{-1}, light becomes increasingly limited and phytoplankton cease to respond to increases in nutrients leading to a decrease in PB, whereas below this threshold TOC promotes total PB by increasing nutrient availability (Isles et al., 2021; Kelly et al., 2018). Further, we observed that the temporal patterns in total PB were also associated with recovery from acidification (increasing pH). Notably, the impact of pH was more pronounced in lakes with increasing total PB (Fig. 7c), particularly when pH exceeded 6.1.

A temporal incline of *G. semen* biomass was, however, associated with increasing Fe concentration and increasing temperature as revealed by random forests (Fig. 7) partly supporting our third prediction. Although lakes with increasing *G. semen* biomass had lower Fe concentration (median = 290.9 μg L^{-1} and minimum = 225.6 μg L^{-1}) compared to lakes with decreasing *G. semen* biomass (median Fe concentration = 1277.9 μg L^{-1}; Tables S7-S8), this concentration was still above the Fe threshold (200 μg L^{-1}) known for promoting *G. semen* growth (Münzner et al., 2021). This suggests that Fe plays an important role in regulating not only spatial patterns in *G. semen* but also its temporal dynamics. With the gradual increase in temperature over time, there was a corresponding increase in *G. semen* biomass. Yet, this increase was only observed up to 17.5 °C, after which there was a marked decline in *G. semen* biomass, which may indicate an upper limit (17.5 °C) of the optimum temperature range for the growth of *G. semen*. Experimental studies (e.g., Weyhenmeyer and Bloch, 2012) showed that although optimal temperature for the growth of *G. semen* was between 9 and 12 °C, this species continued to grow at temperatures >12 °C. However, the response to temperature can also vary in mixed phytoplankton communities, where competition occurs between species with different temperature optima compared to those in single-species cultures (Åkesson et al., 2021).

A temporal decline of *G. semen* biomass was associated with decreasing Fe and increasing pH, TOC, and TN (Fig. 7d-f). Lakes with declining *G. semen* biomass had very high Fe concentration (median = 1277.91 μg L^{-1}; Table S8), which corresponded to Fe level of ~1500 μg L^{-1} beyond which *G. semen* biomass did not change with Fe (see Fig. 7f). Therefore, the temporal decline in *G. semen* biomass was likely linked to the saturation level of *G. semen* for Fe. Further, the inverse correlation observed between increasing pH and decreasing *G. semen* biomass indicates that recovery from acidification may have contributed to the decline in *G. semen* due to its preference for acidic waters (pH < 7) (cf., Lau et al., 2017; Trigal et al., 2013). The inverse correlation between declining *G. semen* biomass and increasing TOC at TOC concentration above 10 mg L^{-1} suggests that excessive browning levels can contribute to a decline in *G. semen* biomass. This contradicts with previous studies that described positive correlations between TOC and *G. semen* biomass (Findlay et al., 2005; Hagman et al., 2015, 2019). However, these previous studies were primarily performed on spatial data of mean *G. semen* biomass (and for a fewer lakes), thus employing a similar approach to the one we used in Question 1.

While previous studies reported lake browning (TOC, Fe) and acidification recovery (pH) as important but yet complex drivers of cyanobacterial biomass (e.g., Freeman et al., 2020; Senar et al., 2021), we found that increasing Fe and pH (but not TOC) were the main variables associated with an increase in the biomass of this group (Fig. 7g-i). The increase in cyanobacterial biomass at pH 6.1 supports our observation from the analysis of temporal changes of phytoplankton (Question 2) that Cyanobacteria contributed the most to the increasing total PB – i.e., both Cyanobacteria and total PB had a sharp increase around this pH level. The increase in pH could potentially be biogenically-induced, attributed to high biomass of Cyanobacteria and/or other phytoplankton groups (Ibelings and Maberly, 1998; Talling, 1976). However, we found that pH was mainly increasing even in lakes with negative trends in cyanobacterial biomass and total PB. Further, the species constituting the most to total PB in the study lakes - *G. semen* - was also decreasing in lakes with positive trends in pH, which suggests that biogenic-driven increases in lake pH do not seem be occurring in the study lakes, although this scenario cannot be entirely ruled out.

Temporal decreases in Fe, TP, and TN were the primary contributors to temporal declines in cyanobacterial biomass, implying a combined negative impact on the biomass by gradually declining concentrations of major growth-limiting elements (TP, TN, and Fe). The finding that TN was decreasing concurrently with Fe may provide insight to the decline in cyanobacterial biomass, despite the presence of nitrogen-fixing Cyanobacteria genera, such as *Dolichospermum* and *Aphanizomenon*, in the study lakes. The process of N_2 fixation requires high Fe concentration and availability of light (Bothe et al., 2010; Grossman et al., 1994; Sorichetti et al., 2016). These conditions likely were not met in lakes with declining cyanobacterial biomass, which were also experiencing declining Fe concentrations and increasing TOC concentrations (and therefore reduced light attenuation; Fig. 7i).

5. Conclusions

Phytoplankton biomass (PB) and the taxonomic composition of phytoplankton in northern lakes are changing along spatial (southern *versus* northern Fennoscandia) and temporal (from 1995 to 2019) gradients. Spatial patterns of total PB and Cyanobacteria were influenced by the main growth-limiting nutrients (TP, TN) and spatial patterns of *G. semen* were influenced by TP, Fe and pH. In contrast, temporal changes in the biomass of these groups were influenced by changes in water chemistry related to global change – i.e., browning (increasing TOC, changes in Fe concentration) and recovery from acidification (increasing pH). The temporal changes of phytoplankton were not unidirectional across Fennoscandia. Nutrient-poor lakes with low PB in *the north* were predominantly experiencing an increase in PB, while nutrient-richer lakes with higher PB in *the south* were predominantly experiencing a decrease in PB. The rise in total PB was driven primarily by Cyanobacteria, while the decline was driven primarily by *G. semen*. Even though *G. semen* was found to be spreading to new lakes, the decline in its biomass was ubiquitous in Fennoscandian lakes, which was mostly related to a declining Fe concentration, increasing pH and TOC concentration. These findings imply that trophic transfer efficiency in pelagic food webs in northern lakes is likely to be modified by these divergent trends of *G. semen* (negative) and Cyanobacteria (positive). Our findings suggest that global change driving Fennoscandian lakes towards warmer and browner conditions will continue to promote an increase in PB in some lakes (especially in *the north*), but not in others (especially *in the south,* due to the combined effects of excessive browning, increasing pH, and alterations in Fe concentration and its bioavailability). Finally, we clearly illustrate the importance of using long-term (decadal) monitoring data to reveal the complex, region-specific, and constantly changing effects of global change on PB and composition in lakes, which cannot be discerned using short-term spatial data.

CRediT authorship contribution statement

Aleksey Paltsev: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Ann-Kristin Bergström:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing. **Kristiina Vuorio:** Data curation, Investigation, Resources, Validation, Writing – review & editing. **Irena F. Creed:** Conceptualization, Funding acquisition, Methodology, Resources, Visualization, Writing – review & editing. **Dag

Olav Hessen: Conceptualization, Investigation, Methodology, Resources, Writing – review & editing. **Pirkko Kortelainen:** Conceptualization, Data curation, Resources, Writing – review & editing. **Jussi Vuorenmaa:** Data curation, Writing – review & editing. **Heleen A. de Wit:** Data curation, Writing – review & editing. **Danny C.P. Lau:** Conceptualization, Data curation, Investigation, Writing – review & editing. **Tobias Vrede:** Conceptualization, Data curation, Investigation, Methodology, Resources, Writing – review & editing. **Peter D.F. Isles:** Investigation, Resources, Writing – review & editing. **Anders Jonsson:** Data curation, Resources, Validation, Writing – review & editing. **Erik Geibrink:** Data curation, Investigation, Writing – review & editing. **Kimmo K. Kahilainen:** Investigation, Methodology, Visualization, Writing – review & editing. **Stina Drakare:** Conceptualization, Data curation, Investigation, Methodology, Resources, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.173570.

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