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RESEARCH ARTICLE

Environmental conditions for phytoplankton influenced carbon dynamics in boreal lakes

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Abstract

The partial pressure of CO_2 (pCO_2) in lake water, and thus CO_2 emissions from lakes are controlled by hydrologic inorganic carbon inputs into lakes, and in-lake carbon transformation (mainly organic carbon mineralization and CO_2 uptake by primary producers). In boreal lakes, CO_2 uptake by phytoplankton is often considered to be of minor importance. At present, however, it is not known in which and how many boreal lakes phytoplankton CO_2 uptake has a sizeable influence on the lake water pCO_2. Using water physico-chemical and phytoplankton data from 126 widely spread Swedish lakes from 1992 to 2012, we found that pCO_2 was negatively related to phytoplankton carbon in lakes in which the phytoplankton share in TOC (C_{phyto}:TOC ratio) exceeded 5%. Total phosphorus concentration (TP) was the strongest predictor of spatial variation in the C_{phyto}:TOC ratio, where C_{phyto}:TOC ratios > 5% occurred in lakes with TP > 30 µg l^{-1}. These lakes were located in the hemi-boreal zone of central and southern Sweden. We conclude that during summer, phytoplankton CO_2 uptake can reduce the pCO_2 not only in warm eutrophic lakes, but also in relatively nutrient poor hemi-boreal lakes.

Keywords Phytoplankton · CO_2 emission · Authochthonous organic carbon · TOC · Global carbon cycle · Lake carbon cycling

Introduction

Aquatic ecosystems are regarded as predominantly net heterotrophic systems that emit CO_2 into the atmosphere (Cole et al. 1994; Duarte and Prairie 2005). Global inland water carbon budgets commonly consider lakes as active carbon transformers, in which CO_2 is produced by in-lake mineralization of allochthonous organic carbon (Cole et al. 2007; Del Giorgio et al. 1999). In contrast, CO_2 uptake by phytoplankton is very poorly constrained in global inland water carbon budgets (Tranvik et al. 2009). This is because gross primary production (GPP) in global lakes has been estimated to amount to merely ~ 1% of the global terrestrial GPP, and thus GPP in lakes has been deemed to be irrelevant for the global carbon budget (Anav et al. 2015; Lewis Jr 2011; Tranvik et al. 2009). Phytoplankton driven primary production in the ocean, has been found to influence the partial pressure of CO_2 (pCO_2) in the water (Fay and McKinley 2017). However, this influence was highly variable on both spatial and temporal scales, suggesting that the influence of phytoplankton on CO_2 dynamics in lakes may vary on different scales as well. Comparing the global annual CO_2 outgassing from lakes and reservoirs of 0.32 Pg C $year^{-1}$ (Raymond et al. 2013), to the global lake phytoplankton GPP of 1.3 Pg C $year^{-1}$ (Lewis Jr 2011) reveals that phytoplankton CO_2 uptake in lakes is a very important carbon flux in the carbon budget of global inland waters (Engel et al. 2018).

In boreal lakes, commonly ~ 97% of the total organic carbon (TOC) is in dissolved form (Kortelainen et al. 2006; von Wachenfeldt and Tranvik 2008), and mineralization of allochthonous dissolved organic carbon (DOC) is an important regulator of CO_2 emissions from boreal lakes (Algesten et al. 2004; Rantakari and Kortelainen 2005; Sobek et al. 2003). CO_2 uptake by phytoplankton is often considered to be of minor importance in boreal lakes. However,

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lake characteristics vary across the boreal zone. In humic lake ecosystems, allochthonous organic carbon is the major carbon source to the system (Jansson et al. 2000; Jonsson et al. 2003, 2001). In contrast, in clearwater lakes the main organic carbon flux to the lake can be through in-lake primary production (Andersson and Kumblad 2006; Jansson et al. 2000), suggesting a reduced $p\mathrm{CO}_2$ in these lakes due to increased phytoplankton CO_2 uptake. However, $p\mathrm{CO}_2$ in lakes is not necessarily low when net ecosystem production (NEP) is high. In numerous net autotrophic boreal lakes, CO_2 emissions were found to exceed GPP, as CO_2 outgassing was controlled by hydrologic inorganic carbon inputs and internal carbon mineralization (Bogard and Giorgio 2016). This suggests that even in lakes with positive NEP, the control of phytoplankton on $p\mathrm{CO}_2$ can be overwhelmed by the influence of hydrologic inorganic carbon inputs (i.e. allochthonous inorganic carbon inputs via ground and surface water inflows). Nevertheless, in lakes with substantial GPP, CO_2 emissions can be reduced as a consequence of high phytoplankton CO_2 uptake, even in cases of considerable hydrologic inorganic carbon inputs and mineralization of allochthonous organic carbon (Wilkinson et al. 2016).

Analyzing regional-scale patterns in the conterminous United States, lake water $p\mathrm{CO}_2$ has been found to be negatively related to chlorophyll *a* concentration, a proxy for phytoplankton biomass (Lapierre et al. 2017). This suggests that phytoplankton CO_2 uptake plays an important role in lake CO_2 dynamics in the temperate ecoregion, and might influence the $p\mathrm{CO}_2$ in boreal lakes as well. Boreal lakes in which phytoplankton CO_2 uptake can have a detectable influence on lake water $p\mathrm{CO}_2$ are likely to be characterized by little influence from inflowing dissolved inorganic carbon (Maberly et al. 2013; Vogt et al. 2017; Weyhenmeyer et al. 2015), moderate to high nutrient concentrations that result in increased primary production (Schindler 1977), and a CO_2 production by mineralization of organic carbon which does not overwhelm the signal from phytoplankton CO_2 uptake. Thus, to detect an effect of phytoplankton CO_2 uptake on lake water $p\mathrm{CO}_2$, the CO_2 uptake by phytoplankton and the CO_2 production by mineralization need to be related. Phytoplankton CO_2 uptake and CO_2 production by mineralization can be related using mass balances that directly compare CO_2 uptake and CO_2 production rates; however, such mass balances are rarely available. Therefore, we used here the amount of phytoplankton carbon as a proxy for the CO_2 uptake by phytoplankton, and the amount of TOC as proxy for the CO_2 production by mineralization of organic carbon. The ratio of phytoplankton carbon to TOC ($\mathrm{C}_{\mathrm{phyto}}$:TOC ratio) indicates then how important the CO_2 uptake by phytoplankton is in relation to the CO_2 production by mineralization, i.e. in lakes in which the $\mathrm{C}_{\mathrm{phyto}}$:TOC ratio is high, an increased phytoplankton influence on $p\mathrm{CO}_2$, and reduced $p\mathrm{CO}_2$ values can be expected.

In this study we analyzed under which environmental conditions phytoplankton CO_2 uptake may influence the $p\mathrm{CO}_2$ in boreal lakes. We considered the phytoplankton influence on $p\mathrm{CO}_2$ as sizeable when we were able to show a significant relation between phytoplankton carbon and the $p\mathrm{CO}_2$. We hypothesized that lake water $p\mathrm{CO}_2$ is increasingly negatively related to phytoplankton carbon with increasing $\mathrm{C}_{\mathrm{phyto}}$:TOC ratio. Further, we predicted the lake specific $\mathrm{C}_{\mathrm{phyto}}$:TOC ratio by easily available lake water physico-chemical variables, and analyzed and predicted the spatial distribution of the $\mathrm{C}_{\mathrm{phyto}}$:TOC ratio in Swedish lakes along a latitudinal gradient from 55 to 68°N. Finally, we examined temporal variation in the $\mathrm{C}_{\mathrm{phyto}}$:TOC ratio in 126 lakes.

Materials and methods

Data source

We analyzed a dataset of water physico-chemical and phytoplankton data from 126 Swedish lake sites over a time period of 21 years, i.e. from 1992 to 2012, taken from the Swedish national lake inventory program that can be freely accessed at http://www.slu.se/vatten-miljo. The data was chosen due to its completeness and homogeneity. The dataset comprised a large range of lakes concerning their size, trophic state, and hydrology, although most lakes were small, oligotrophic lakes with a water residence time exceeding one year (Table 1). The study lakes were distributed along a latitudinal gradient from 55 to 68°N, allowing us to compare differences between the biogeographical region of northern and southern Sweden.

In addition to the dataset of 126 lake sites, we used a larger dataset, also taken from the Swedish national lake inventory program, to evaluate how common lakes with a $\mathrm{C}_{\mathrm{phyto}}$:TOC ratio might be in Sweden. It comprised lake water total phosphorus concentrations (TP) for the months June, July, August, and September from 3177 lake sites for the period 1992–2018 and can be freely accessed at http://www.slu.se/vatten-miljo.

Sampling and laboratory analyses

Sampling and analysis of water chemistry and phytoplankton samples was performed at the SWEDAC (Swedish Board for Accreditation and Conformity) accredited laboratory at the Department of Aquatic Sciences and Assessment at the Swedish University of Agricultural Sciences (SLU) following standard procedures (Fölster et al. 2014). Water physico-chemical data were obtained from surface water samples taken at 0.5 m depth representing conditions in the epilimnion. The sampling was carried out with a Plexiglas sampler at a mid-lake site in each lake, and

Table 1 Physical, chemical, biological, and geographical variables used in this study. Shown are range and median value based on long-term August measurements from the 126 lake sites

Variable (unit)	Abbreviation	Median	Minimum	Maximum
Lake area (km^2)		0.80	0.030	5550
Latitude (°N)		59	55	68
Mean water depth (m)		5.0	0.80	39
Water residence time (days)		487	2.0	29,000
Altitude (m a.s.l.)		130	1.0	974
Phytoplankton biovolume (mm^3 l^{-1})		0.477	0.030	12
Chlorophyll *a* concentration (µg l^{-1})		4.0	0.50	68
Surface water temperature (°C)	WT	19	11	21
Total organic carbon concentration (mg l^{-1})	TOC	8.8	1.2	23
pH		6.9	4.7	8.5
Alkalinity (meq l^{-1})		0.12	−0.039	2.2
Dissolved oxygen concentration (mg l^{-1})		8.9	7.6	14
Absorbance (420 nm/5 cm)		0.11	0.012	1.0
Conductivity (mS m^{-1})		4.5	0.50	56
Total phosphorus concentration (µg l^{-1})	TP	9.0	2.0	86
Total nitrogen concentration (mg l^{-1})	TN	0.40	0.16	1.5
Ammonium-N (µg l^{-1})		9.5	4.0	39
Nitrate-nitrite-N (µg l^{-1})		4.0	1.5	710
Calcium concentration (meq l^{-1})		0.18	0.010	3.1
Magnesium concentration (meq l^{-1})		0.073	0.004	1.0
Sodium concentration (meq l^{-1})		0.14	0.007	1.2
Potassium concentration (meq l^{-1})		0.014	0.003	0.16
Iron concentration (µg l^{-1})		139	7.8	5000
Sulfate concentration (meq l^{-1})		0.090	0.013	2.2
Silicon concentration (mg l^{-1})		0.88	0.12	3.9
Annual precipitation (mm year^{-1})		750	550	1250
Annual surface water runoff (mm year^{-1})		350	150	950
Size of the catchment area (km^2)		8.4	0.38	22,649

samples were kept cool during transport to the laboratory. The water samples were analyzed following international (ISO) or European (EN) standards when available (Fölster et al. 2014).

Phytoplankton data were obtained through epilimnion samples (upper 0–8 m depending on the lake and its prevailing stratification pattern), and sampling was carried out in the middle of each lake using a 2-m-long Plexiglas tube sampler. Five random epilimnetic waters samples were pooled to form a composite sample. A subsample was taken and preserved with Lugol`s iodine solution (2 g potassium iodide and 1 g iodide in 100 ml water) supplemented with acetic acid (Olrik et al. 1989). Phytoplankton counts and taxon identification (usually at the species level) were made using an inverted microscope and the modified Utermöhl technique. Biovolumes were obtained with geometric formulas (Olrik et al. 1989).

Calculation of C_{phyto} and pCO_2

We calculated the amount of carbon contained in phytoplankton (C_{phyto}) by multiplying phytoplankton biovolumes by 0.15. A conversion factor of 0.15 was chosen since the phytoplankton community in the studied lakes was dominated by eukaryotes, which commonly are associated with a conversion factor of about 0.15 (Blomqvist et al. 1995; Rocha and Duncan 1985).

Further, we estimated lake water CO_2 concentrations based on WT, alkalinity, and pH measurements according to Weyhenmeyer et al. (2012b). Values for pCO_2 were calculated from CO_2 concentration values using the Henry's constant and the atmospheric pressure at the sample site elevation (Weyhenmeyer et al. 2012b).

The calculation of the lake water pCO_2 using carbonate equilibria has been criticized to produce high random errors (Golub et al. 2017), and to overestimate pCO_2, especially in acidic and organic-rich waters (Abril et al. 2015). As many lakes in the boreal region are acidic and organic-rich, our estimates might overestimate pCO_2. Further, at high phytoplankton production a phytoplankton induced change in lake water pH might have caused a bias in the calculated pCO_2. In this study, we tried to minimize this bias in pCO_2 by using median values. To verify that the random errors arising from the calculation of pCO_2 did not influence our results, we re-ran our analysis after adding a random error to each of the calculated median pCO_2 values according to Golub et al. (2017). Adding random errors with a mean of 0 and a standard deviation of 7.7% of the original pCO_2 value (±7.7% is the maximum relative standard error for calculated median pCO_2 values using the pCO_2-pH-alkalinity equilibrium according to Golub et al. (2017)), did not change the results of our analysis. We only used pCO_2 for one initial prediction that was not influenced by the uncertainty arising from random errors. All further results and conclusions are based on the C_{phyto}:TOC ratio.

Data selection and structure

In this study, we used August measurements for our analyses. The choice of August values was driven by data availability, since most phytoplankton measurements within the Swedish freshwater inventory program are conducted in August. Further, August is considered being most suitable for the comparison of phytoplankton data from Swedish lakes that are distributed over different climatic regions (Weyhenmeyer et al. 2013). For other months, phytoplankton data were only available for a subset of lakes that did not allow an analysis of spatial variability at the regional scale.

To examine spatial differences between northern and southern Sweden, we analyzed lakes north and south of a distinct biogeographical borderline, known as *limes norrlandicus*, separately, since phytoplankton biomass in Swedish lakes was found to shift at this borderline which corresponds to the mean growing season length of 220 days (Weyhenmeyer et al. 2013; the borderline is here abbreviated as GSB_{220}). Mean growing season length was defined as the duration of the open-water season in days. When we divided the 126 lake sites from our dataset into lakes located north and south of this borderline, 47 lake sites were located in northern and 79 sites in southern Sweden.

For analyses at the spatial scale (dataset of 126 lake sites), we used site-specific long-term median values based on measurements in August calculated from a total of 2118 samples. Since some time series had missing data, we verified that the number of missing values did not influence the overall results, by re-running our statistical tests with randomly sampled subsets of the entire dataset (sampling rate of 0.975, i.e. 2.5% of observations were randomly removed). The statistical analyses on the data subsets revealed the same results as the analyses on the original dataset.

For analyses at the temporal scale, we used the dataset of 126 lake sites as well as a subset of those lakes. All 126 lake sites were used to examine year-to-year variation in the overall median C_{phyto}:TOC ratio based on August measurements across all 126 sites. Since for the years 1992–1994 data from a substantial proportion of lakes were missing, we restricted the temporal analysis over all lake sites to the period 1995–2012. The subset of lakes used for temporal analyses comprised 35 out of 126 lake sites. For these lakes data from the entire time period 1992 to 2012 were available. We used the data subset to analyze temporal trends for single lakes separately, as temporal trends in physico-chemical lake water conditions can be highly lake specific.

To evaluate how common lakes with a high C_{phyto}:TOC ratio might be in Sweden (dataset of 3177 lake sites), we calculated the median TP per lake site over all available years using data from the months June, July, August, and September from a total number of 27,122 samples, and used the median TP to predict in which lakes conditions for a high C_{phyto}:TOC ratio prevail.

Statistical analyses

To test for correlation between phytoplankton carbon and pCO_2 as well as for correlation between TP, TN (for abbreviations see Table 1), ammonium-N, latitude, and the C_{phyto}:TOC ratio, respectively, in all 126 lakes, we used Kendall`s tau coefficient, since the data did not follow the normal distribution, tested using a Shapiro–Wilk test for normality. The data from lakes with high C_{phyto}:TOC ratio (11 lakes in our dataset) were normally distributed. For these data, we applied linear regression analyses.

To identify the most important drivers of spatial variation in the C_{phyto}:TOC ratio, we applied a partial least squares analysis (PLS). We used a PLS because it is relatively insensitive for interdependencies between *X*-variables, and deviations from normality. The PLS allowed to predict the C_{phyto}:TOC ratio (*Y*-variable) by lake water physico-chemical and geographical characteristics (*X*-variables; for the *X*-variables used in the PLS consult Tab. S1). The PLS result provides a ranking of *X*-variables according to their relevance in explaining the *Y*-variable, expressed as VIP-values (Wold et al. 2001). The higher the VIP-value of an *X*-variable, the higher is its contribution in explaining the *Y*-variable. Commonly, *X*-variables with VIP-values > 1 are considered important *X*-variables.

To test for a temporal trend in the median C_{phyto}:TOC ratio from all 126 lake sites between 1995 and 2012, and to analyze long-term trends in lake water physico-chemical variables for 35 single lakes between 1992 and 2012, we used a non-parametric Mann–Kendall trend test. A non-parametric test was used, as most variables for single lakes were not normally distributed.

As we analyzed geographical data, we tested if spatial autocorrelation occurred in the dataset. Spatial autocorrelation is a measure to describe the degree of correlation between observations that occurs due to their spatial location. To test for spatial autocorrelation, we calculated a distance matrix based on the coordinates of the lake sites. Using the distance matrix and the observations for the environmental variables included in our study, we calculated Moran's I autocorrelation index using the R software package 'ape' (Paradis et al. 2018).

In the dataset of 126 lake sites, the data were spatially autocorrelated (Moran's I: $P < 0.05$). This has to be considered in the interpretation of the P values of our analysis, since the existence of spatial autocorrelation in the data increases the probability of detecting significant relationships and trends. As the correlations based on spatial data were highly significant ($P < 0.0001$), spatial autocorrelation has most likely not resulted in a misinterpretation of the described relations. In the subset of 11 lakes for which we applied linear regression analysis, the data were not spatially autocorrelated (Moran's I: $P > 0.05$).

Most of the data analyses were performed using JMP, version 12.0.1 (SAS Institute Inc., Cary, NC, U.S.A.). The analysis of spatial autocorrelation was carried out with the software R, version 3.4.2 (R Core Team, Vienna, Austria). For the spatial analysis both ArcMap 10.4 (Esri Inc., Redlands, CA, U.S.A), and JMP, version 12.0.1 were used.

Results

Influence of phytoplankton CO_2 uptake on lake CO_2 dynamics

Considering all 126 lake sites, the long-term median August lake water pCO_2 was not correlated with the long-term median August phytoplankton carbon concentration (Fig. 1a). To test our hypothesis that lake water pCO_2 is increasingly negatively related to phytoplankton carbon with increasing C_{phyto}:TOC ratio, we stepwise excluded lakes with lower ratios (1%-steps), and analyzed the relationship of phytoplankton carbon and pCO_2 for lakes showing a C_{phyto}:TOC ratio of > 1–7%, respectively. Most of the 126 lakes sites showed a rather low C_{phyto}:TOC ratio with long-term medians per lake site ranging from 0.1 to 16.6% in August, and an overall median of 0.9%. Considering single years and lakes, the C_{phyto}:TOC ratio ranged between 0.02 and 88% in August.

In lakes with a long-term median August C_{phyto}:TOC ratio > 5%, we found a significant negative relation between phytoplankton carbon and the lake water pCO_2 (Fig. 1b). A linear regression model explained a significant amount of the variation in lake water pCO_2 by variation in phytoplankton carbon ($R^2 = 0.39$, $n = 11$, $P = 0.039$; Fig. 1b). When we considered only lake sites with C_{phyto}:TOC ratios > 6%, and > 7% for the regression analysis, an even larger share of the variation in lake water pCO_2 was explained by variation in phytoplankton carbon ($R^2 = 0.50$, $n = 10$, $P = 0.022$, and $R^2 = 0.78$, $n = 6$, $P = 0.020$, respectively, Fig. 1b), and phytoplankton carbon and the lake water pCO_2 were increasingly negatively related (increasing negative slope of the regression line; Fig. 1b).

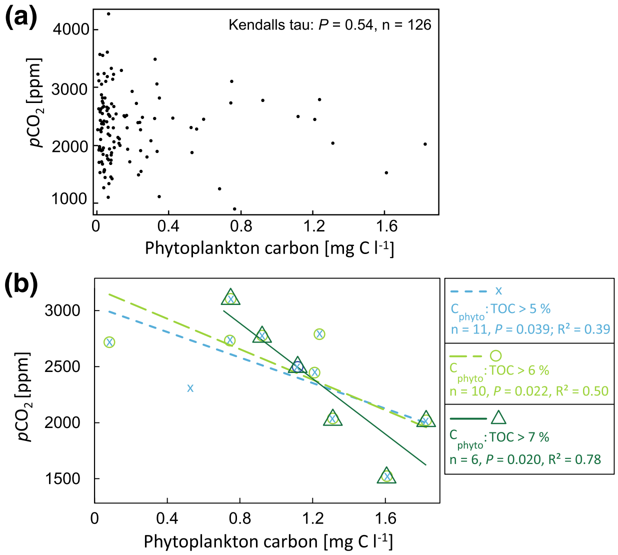

Fig. 1 **a** Relation of the long-term median August phytoplankton carbon concentration to the long-term median August partial pressure of CO_2 (pCO_2) in lake water where each data point represents one lake site. **b** Regression lines for the relation of the long-term median August phytoplankton carbon concentration to the long-term median August pCO_2 for a subset of lakes with C_{phyto}:TOC ratios > 5%. The higher the long-term median C_{phyto}:TOC ratio, the stronger was the relation between the phytoplankton carbon concentration and the lake water pCO_2

The C_{phyto}:TOC ratio and lake characteristics

To identify important drivers of spatial variation in the lake-specific C_{phyto}:TOC ratio, we applied a PLS analysis and found TP, ammonium-N, and TN to be most influential in explaining variation in the C_{phyto}:TOC ratio (VIP value of 1.96, 1.31, and 1.12, respectively, in the PLS; all other explanatory variables showed VIP < 1; Tab. S1). When we related TP, ammonium-N, and TN to the C_{phyto}:TOC ratio, respectively, we found TP and TN to be significantly correlated with the C_{phyto}:TOC ratio (Fig. 2). However, there was no significant correlation between ammonium-N and the C_{phyto}:TOC ratio (Kendall's tau: $P = 0.07$). C_{phyto}:TOC ratios high enough so that a phytoplankton signal on lake

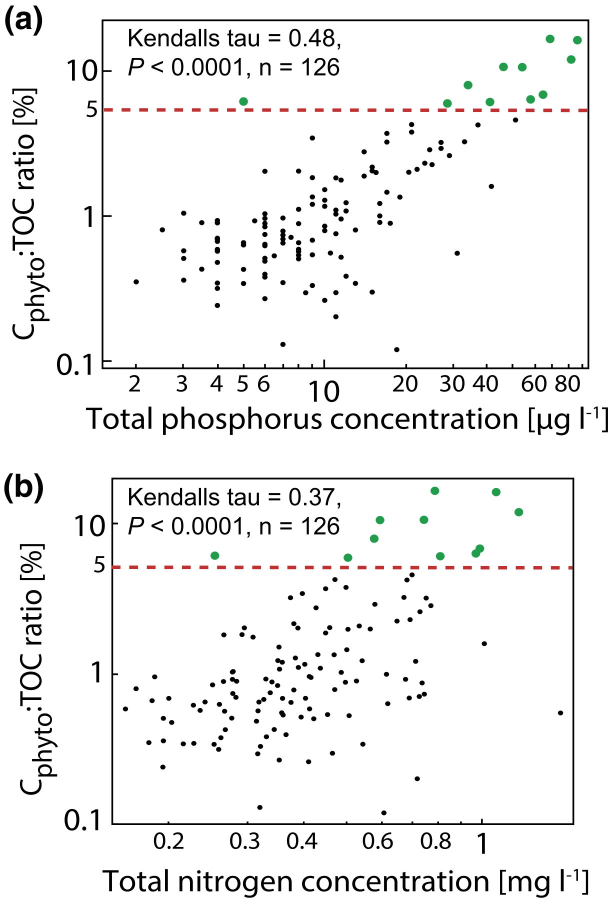

Fig. 2 Relationships between **a** total phosphorus concentration (TP), **b** total nitrogen concentration (TN), and the lake-specific C_{phyto}:TOC ratio, respectively, based on long-term median August values for each of the 126 lake sites. Dashed lines: C_{phyto}:TOC ratio of 5% at which phytoplankton carbon was negatively related to the lake water pCO_2 according to Fig. 1b. C_{phyto}:TOC ratios > 5% mostly occurred in lakes with TP > 30 µg l^{-1}, and TN > 0.45 mg l^{-1} (green dots)

water pCO_2 was detectable (i.e. lakes with C_{phyto}:TOC ratios > 5% according to Fig. 1b), occurred mostly in lakes with TP > 30 µg l^{-1}. TP was strongly influenced by the geographical position of lakes, with high TP at lower latitudes. Lakes with TP > 30 µg l^{-1} were mostly located south of GSB_{220} (Fig. 3c).

Spatial variability in the C_{phyto}:TOC ratio and related environmental variables

North of GSB_{220}, the long-term median August C_{phyto}:TOC ratio per lake site ranged between 0.1 and 8.0% with an overall median of 0.6%. South of GSB_{220}, the long-term median August C_{phyto}:TOC ratio ranged between 0.1% and 16.6% with an overall median of 1.2%. Very low C_{phyto}:TOC ratios of < 0.02% in single years were not restricted to northern Sweden, but occurred at all latitudes. All lakes with a C_{phyto}:TOC ratio high enough so that phytoplankton CO_2 uptake might reduce lake water pCO_2 (i.e. lakes with C_{phyto}:TOC ratio > 5% according to Fig. 1b) were located south of GSB_{220}, except for one lake located in the northern biogeographical region, but in close proximity to GSB_{220}. Almost all of the lakes, i.e. 45 out of 47, located north of GSB_{220} showed long-term median August C_{phyto}:TOC ratios < 2.5% (i.e. ratios lower than half the C_{phyto}:TOC ratio needed for a sizeable influence of phytoplankton on the lake water pCO_2 according to Fig. 1b).

There was no obvious spatial pattern in pCO_2 (Fig. 3b), and pCO_2 showed no relation to most lake water physico-chemical and geographical characteristics, except for a weak positive correlation with latitude, and a weak negative correlation with WT (Tab. S2). TP and TN ranged from 2 to 86 µg l^{-1}, and 0.16 to 1.5 mg l^{-1}, with an overall median of 9 µg l^{-1}, and 0.4 mg l^{-1}, respectively (Table 1). The spatial distribution of TP and TN coincided with the spatial distribution of the C_{phyto}:TOC ratio (Fig. 3a, c, d). TP, TN, and C_{phyto}:TOC ratio were all negatively correlated with latitude (Kendall`s tau: $P < 0.0001$, respectively), but there was no correlation between the $C_{phyto}$:TOC ratio and lake size (Kendall`s tau: $P = 0.44$).

To estimate the percentage of Swedish lakes in which pCO_2 might be influenced by phytoplankton CO_2 uptake, we used a dataset of easily available lake water physico-chemical variables from 3177 lake sites. Since TP had the strongest influence on the C_{phyto}:TOC ratio (see PLS analysis), we used TP for this estimate. We found that TP > 30 µg l^{-1} (i.e. lake conditions at which the C_{phyto}:TOC ratio is likely to exceed 5% according to Fig. 2a, and thus phytoplankton carbon might be negatively related to pCO_2 according to Fig. 1b), occur in 16% of Swedish lakes.

Temporal trends in the C_{phyto}:TOC ratio

The percentage of lakes with a C_{phyto}:TOC ratio > 5% in August did not significantly increase or decrease between 1995 and 2012 (Mann–Kendall trend test, $P = 0.08$). However, we found a significant decline in the median August C_{phyto}:TOC ratio over all lakes between 1995 and 2012 (Kendall's tau = − 0.54, $P = 0.0017$, n = 18; Fig. 4). The change in the median C_{phyto}:TOC ratio over all lakes between 1995 and 2012 was significant but small, with a total decline of 0.44% during the 18 years period (Fig. 4).

As temporal trends in lake water physico-chemical variables and phytoplankton are often very lake specific, we analyzed temporal trends in 35 lakes for which we had data from 1992 to 2012, and found large differences between lakes. The C_{phyto}:TOC ratio in August increased in three, and decreased in two out of 35 lakes ($P < 0.05$; Tab. S3). Over the same time phytoplankton biovolume and TOC increased at seven, and 16 lake sites, respectively

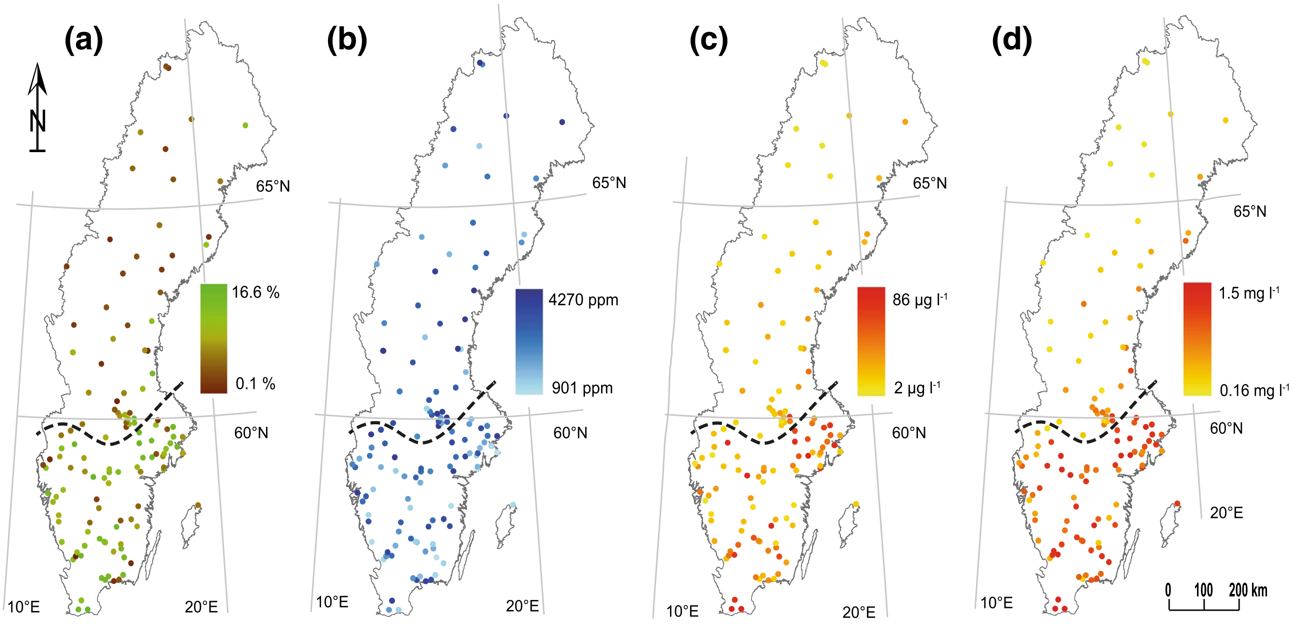

Fig. 3 Spatial distribution of the long-term median August lake water **a** C_{phyto}:TOC ratio, **b** partial pressure of CO_2, **c** total phosphorus concentration, and **d** total nitrogen concentration across 126 Swedish lake sites. Dashed line: mean growing season length borderline of 220 days (GSB_{220})

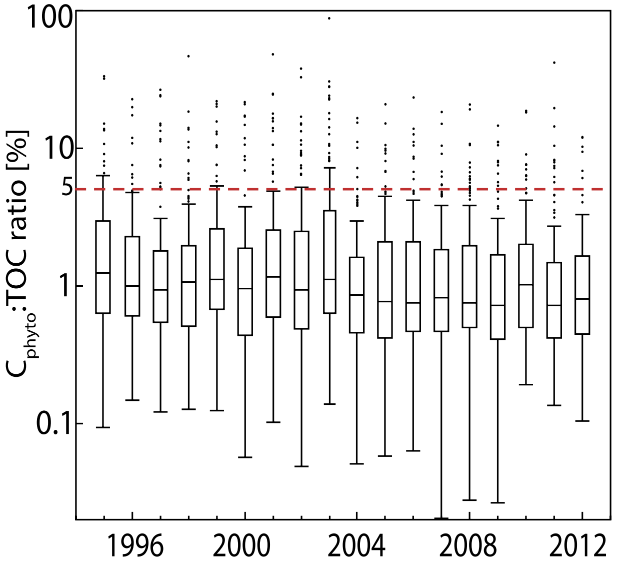

Fig. 4 Temporal development of the C_{phyto}:TOC ratio in August from 126 lake sites (lake sites per year ranged between 96 and 125) for the period 1995–2012. Dashed line: C_{phyto}:TOC ratio at which phytoplankton CO_2 uptake influenced lake water pCO_2 according to Fig. 1b. The median C_{phyto}:TOC ratio over all sites decreased significantly during the period from 1995 to 2012 (Kendall's tau = −0.54, $P = 0.0017$, n = 18)

($P < 0.05$; Tab. S3), while TP decreased at seven, and increased at one lake site ($P < 0.05$; Tab. S3). The pCO_2 increased in two lakes ($P < 0.05$; Tab. S3).

Discussion

The C_{phyto}:TOC ratio as a proxy for lake functioning

We showed that in lakes with a C_{phyto}:TOC ratio > 5%, phytoplankton carbon was negatively related to lake water pCO_2 (Fig. 1b). This relationship indicates that in lakes containing more phytoplankton carbon, a lower pCO_2 is found, suggesting that although all lakes were supersaturated with CO_2, the pCO_2 in lakes with a C_{phyto}:TOC ratio > 5% might, during summer, partly be controlled by phytoplankton. As hydrologic dissolved inorganic carbon inputs to lakes are common in the boreal zone (Weyhenmeyer et al. 2015), but were not quantified in this study, we suggest that at a C_{phyto}:TOC ratio > 5% the phytoplankton influence on pCO_2 was high enough to not be overcome by the influence of hydrologic dissolved inorganic carbon inputs. The relationship between phytoplankton carbon and the pCO_2 was not influenced by random errors arising from the calculation of pCO_2 using the pCO_2-pH-alkalinity equilibrium (Golub et al. 2017; see Methods).

The negative relation of lake water pCO_2 and phytoplankton carbon over a large pCO_2 gradient in our study is in contrast with a recent study by Vogt et al. (2017) showing that the chlorophyll *a* concentration in boreal lakes was only negatively related to lake water pCO_2 at lake water $pCO_2 \leq 400$ ppm. This difference might originate from the differing data material used in the two studies. While our study focuses on long-term median August values, Vogt et al. (2017) base their analysis on measurements over several months during the ice-free season of 3 years. Phytoplankton biovolumes in boreal lakes usually show maximum values in summer (Weyhenmeyer et al. 2013), which makes a sizeable influence of phytoplankton on lake water pCO_2 during August likely, while an influence across a wider time span (ice-free season) is less likely.

The C_{phyto}:TOC ratio of 5%, at which phytoplankton carbon was negatively related to pCO_2 (Fig. 1b), is surprisingly low, since a ratio of 5% indicates that the largest share of TOC is still dead organic matter that might be mineralized. Although mineralization is the most important organic carbon loss process in boreal lakes, the share of the incoming allochthonous organic carbon that is mineralized in lakes can vary widely depending on lake and catchment characteristics (Algesten et al. 2004). Thus, even at a relatively high dead organic carbon share in TOC compared to the phytoplankton share, phytoplankton might sizably influence the pCO_2, when mineralization rates are sufficiently low.

The pCO_2 in boreal lakes is not necessarily negatively related to primary production in the most productive lakes, but in lakes in which hydrologic CO_2 inputs are sufficiently low (Vogt et al. 2017). As hydrologic CO_2 inputs to boreal lakes are usually high (Weyhenmeyer et al. 2015), the number of lakes in which phytoplankton sizably influences CO_2 dynamics should be relatively low in the boreal zone. Comparing our C_{phyto}:TOC ratios to the phytoplankton biovolume and DOC values reported by Vogt et al. (2017) reveals that lakes in boreal Canada probably have C_{phyto}:TOC ratios at the same order of magnitude as the lakes analyzed in this study. C_{phyto}:TOC values in boreal lakes are by far smaller than the ratios found in warm eutrophic lakes in which the lake water pCO_2 can regularly be driven below the atmospheric equilibrium by primary production. In such lakes the average share of phytoplankton carbon in TOC can amount to around 30% (Balmer and Downing 2011).

Using a PLS, we were able to show that nutrient conditions were the main driver of spatial variation in the C_{phyto}:TOC ratio. Applying the TP conditions at which we found a sizeable phytoplankton influence on pCO_2 (i.e. $TP > 30\ \mu g\ l^{-1}$ according to Figs. 1b, 2a) to a much larger dataset of 3177 Swedish lakes distributed all across Sweden, we estimated that during summer as many as 16% of Swedish lakes presently show conditions that can sustain in-lake CO_2 dynamics that are sizably influenced by phytoplankton. This suggests that the influence of phytoplankton on pCO_2 in boreal lakes should be considered in regional and continental carbon budgets, especially in budgets calculated for the hemi-boreal region.

We suggest that the C_{phyto}:TOC ratio can be used as an indicator to locate lakes in which the pCO_2 during summer might be sizably influenced by phytoplankton CO_2 uptake (Fig. 5). Our approach contributes to elucidate the functioning of lakes in the global carbon cycle, as it reveals in which regions and lakes phytoplankton CO_2 uptake might sizably influence in-lake carbon transformation, and lake CO_2 emissions.

The lake water pCO_2 in our dataset showed no relation to lake water physico-chemical and catchment characteristics, except for a correlation with latitude and WT, respectively (Tab. S2). Lower lake water pCO_2 at lower latitudes and in warm lakes support our results on the spatial distribution of lakes with a sizeable phytoplankton influence on CO_2

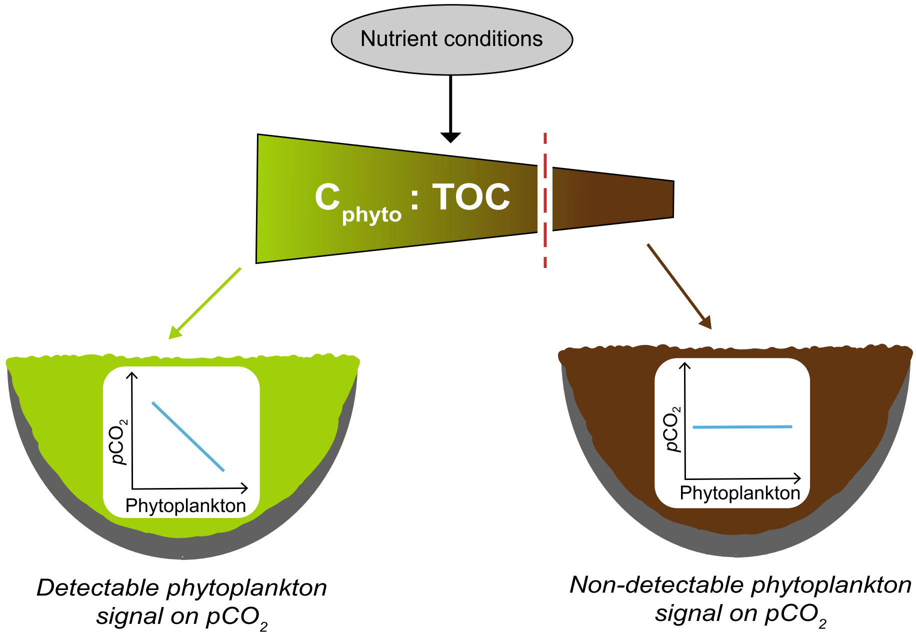

Fig. 5 Conceptual figure showing the effect of the magnitude of the phytoplankton share in TOC (C_{phyto}:TOC ratio) in lake water, on the relation of phytoplankton and the lake water partial pressure of CO_2 (pCO_2). The figure is based on the results from this study. In lakes with a high C_{phyto}:TOC ratio (in our study lake sites with a C_{phyto}:TOC > 5%), we found a phytoplankton signal on the pCO_2. In contrast, low C_{phyto}:TOC ratios indicate lakes in which no phytoplankton signal on the lake pCO_2 was detectable. CO_2 dynamics in such lakes might be driven by mineralization of allochthonous organic carbon and/or by hydrologic dissolved inorganic carbon inputs

dynamics (Figs. 1b, 3a), i.e. that such lakes are located in the hemi-boreal region of central and southern Sweden.

Quantifying the importance of lake primary production for lakes at the regional scale, like previously done for single lakes (e.g. Chmiel et al. 2016), exceeds the potential of the dataset used in this study. The availability of data restricted our analysis to lake conditions in August. C_{phyto}:TOC ratios during spring, autumn, and winter differ distinctly from August values. Consequently, an estimation of the influence of phytoplankton CO_2 uptake on the annual carbon budget of our study lakes is not possible. As phytoplankton biovolume in lakes in northern Sweden sometimes is highest in spring (Willén 2003), our analysis might have slightly overestimated the difference between the C_{phyto}:TOC ratio in lakes in northern and southern Sweden. It has also to be acknowledged that littoral primary production (by e.g. macrophytes) can significantly influence CO_2 assimilation into biomass in boreal lakes (Vesterinen et al. 2016), which cannot be accounted for by our approach, since data on macrophytes were not part of our dataset.

C_{phyto}:TOC ratio and environmental change

The median C_{phyto}:TOC ratio across all lakes decreased significantly during the period from 1995 to 2012 (Fig. 4). The negative trend reflects the fact that currently TOC increases occur more frequently in boreal lakes than increases in phytoplankton biovolume (Tab. S3). At the same time, the number of lakes showing C_{phyto}:TOC ratios > 5% did not decrease (Fig. 4), suggesting that the number of lakes in which phytoplankton might influence lake pCO_2 remained stable between 1995 and 2012. Temporal pCO_2 trends in boreal inland waters were recently found to be disconnected from the widespread TOC increases (Nydahl et al. 2017), which coincides with the trend analysis made in our study (Tab. S3). Further, temporal trends in physico-chemical variables in boreal lakes usually do not result in coherent phytoplankton biomass and community composition responses at the temporal scale, since the phytoplankton response to temporal changes in lake water physico-chemical conditions is highly lake specific (Bloch and Weyhenmeyer 2012). Consequently, we propose that the C_{phyto}:TOC ratio might probably not be an appropriate indicator of temporal changes in the phytoplankton influence on lake CO_2 dynamics, but can be used for the comparison of lake CO_2 dynamics between lakes.

The predicted increases in precipitation and discharge in the boreal region (Bergström et al. 2001) would exert a strong effect on freshwater ecosystems, and thus will probably influence C_{phyto}:TOC ratios in the future. Increased discharge rates may lead to higher dispersal rates of lake phytoplankton (Bergström et al. 2008; Jones and Elliott 2007), as well as to decreased underwater light conditions due to increased browning (Larsen et al. 2011; Weyhenmeyer et al. 2016), and thus lower phytoplankton abundances in lakes. As light can be the limiting factor for biomass production in unproductive, nutrient-poor lakes (Karlsson et al. 2009), increased browning might increase the importance of light as controlling factor for phytoplankton growth and community composition. However, increased runoff is also linked to increased nutrient loading (George et al. 2004), which exerts a stimulating effect on phytoplankton growth. Additionally, in oligotrophic lakes increases in allochthonous DOC input to lakes can stimulate primary production, if nutrients bound to humic substances are released (Drakare et al. 2002; Kissman et al. 2013; Klug 2002; Seekell et al. 2015). Consequently, analyzing past and predicted trends of a limited set of factors controlling phytoplankton biovolume, and TOC in boreal lakes does not allow prediction of whether the influence of phytoplankton on lake pCO_2 is in the long term going to increase or decrease, since temporal trends in phytoplankton biovolume in lakes depend on a wide range of controlling factors, and phytoplankton responses on changes in lake physico-chemical conditions are highly lake specific (Bloch and Weyhenmeyer 2012).

Regional and global perspective

Most Swedish lakes are small forest lakes, and sampling a subset of those showed that in most Swedish lakes TP remains below the TP condition for a sizeable phytoplankton influence on pCO_2 of 30 $\mu g\ l^{-1}$ (according to Figs. 1b, 2a) (Huser and Fölster 2013), suggesting a low influence of phytoplankton on pCO_2 in most Swedish lakes. However, focusing on eutrophic lakes in the productive lowlands of Sweden gives a different picture with TP > 25 $\mu g\ l^{-1}$ occurring in 790 out of 3500 lakes (Johansson and Persson 2001), indicating that although most Swedish lakes are nutrient-poor, thousands of these lakes might have the potential for phytoplankton influenced CO_2 dynamics. These lakes are mostly located in the hemi-boreal zone, south of the biogeographical borderline *limes norrlandicus* (for a definition of the borderline see methods). At this borderline the organic carbon content of the topsoil changes distinctly, as topsoils in southern Sweden show lower organic carbon contents than in northern Sweden (de Brogniez et al. 2015). As the hydrological TOC input to lakes depends on the soil organic carbon content in the catchment (Weyhenmeyer et al. 2012a), the C_{phyto}:TOC ratio might be greater in areas with lower soil organic carbon content.

Our results revealed that about 16% of Swedish lakes show conditions needed for a sizeable influence of phytoplankton on lake CO_2 dynamics (i.e. TP exceeding 30 $\mu g\ l^{-1}$). Like in boreal lakes, TP in most European lakes lie below 30 $\mu g\ l^{-1}$ (Cardoso et al. 2007). Thus, the percentage of European lakes with phytoplankton influenced CO_2 dynamics might also be rather low. At the global scale, however, the importance of phytoplankton for lake CO_2 dynamics might be higher, since TP in the warm temperate and tropical zone often exceeds 30 µg l^{-1}. Median TP in temperate and subtropical lakes in the east plain ecoregion of China currently exceed the TP condition for phytoplankton influenced CO_2 dynamics of > 30 µg l^{-1} by threefold and even baseline TP (reference conditions) for these lakes range around 30 µg l^{-1} (Huo et al. 2013). This suggests that phytoplankton CO_2 uptake may influence lake CO_2 dynamics in a large number of lakes on Earth. However, it has to be kept in mind that the TP condition of > 30 µg l^{-1} found in our study remains to be shown applicable for other ecoregions than the boreal zone. Compared to lakes at the global scale (Chen et al. 2015), TOC in boreal lakes is high (Table 1), suggesting that in other ecoregions a similar primary production rate could have a greater influence on the lake water pCO_2, since the CO_2 production by mineralization of organic matter might be comparably lower.

A substantial share of the pCO_2 variation between lakes at the global scale is still unexplained. Besides in-lake mineralization of allochthonous organic carbon (Sobek et al. 2005), and hydrologic inorganic carbon inflows to lakes (Weyhenmeyer et al. 2015), phytoplankton CO_2 uptake may account for a certain percentage of this unexplained variability (Lapierre et al. 2017). Up to now, no global estimate of the number of lakes with phytoplankton influenced CO_2 dynamics exists. As shown here for boreal lakes, environmental conditions for lakes in which phytoplankton exerts a sizeable influence on lake water pCO_2 can be used to identify those systems. Until now, CO_2 uptake by phytoplankton has rarely been quantified in inland water carbon budgets at large geographical scale (Tranvik et al. 2009). Our results suggest that CO_2 uptake by phytoplankton should be considered when refining inland water carbon budgets. This will require quantification of the contribution of phytoplankton CO_2 uptake to inland water carbon budgets at regional, continental and global scale.

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Compliance with ethical standards

Conflict of interest The authors declare no competing financial interests.

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