

Warmer climates boost cyanobacterial dominance in shallow lakes

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Abstract

Dominance by cyanobacteria hampers human use of lakes and reservoirs worldwide. Previous studies indicate that excessive nutrient loading and warmer conditions promote dominance by cyanobacteria, but evidence from global scale field data has so far been scarce. Our analysis, based on a study of 143 lakes along a latitudinal transect ranging from subarctic Europe to southern South America, shows that although warmer climates do not result in higher overall phytoplankton biomass, the percentage of the total phytoplankton biovolume attributable to cyanobacteria increases steeply with temperature. Our results also reveal that the percent cyanobacteria is greater in lakes with high rates of light absorption. This points to a positive feedback because restriction of light availability is often a consequence of high phytoplankton biovolume, which in turn may be driven by nutrient loading. Our results indicate a synergistic effect of nutrients and climate. The implications are that in a future warmer climate, nutrient concentrations may have to be reduced substantially from present values in many lakes if cyanobacterial dominance is to be controlled.

Keywords: climate change, cyanobacteria, Europe, light, nutrients, phytoplankton, shade, South America, temperature, trophic state

Received 31 August 2010 and accepted 4 June 2011

Introduction

Cyanobacteria rank prominently among causes of problems with water quality of lakes and reservoirs (e.g. WHO, 1999). This is, in part, caused by the toxins that many of them produce (Carmichael, 1997; WHO, 1999;

Cox *et al.*, 2005). Some of the toxins poison aquatic animals (Gustafsson *et al.*, 2005) and may make freshwaters unusable by humans (Huisman *et al.*, 2005). Cyanobacterial problems tend to increase with cyanobacterial abundance, and although cyanobacterial blooms predate human settlement (McGowan *et al.*, 1999), the frequency and extent of such blooms are increasing (Paerl & Huisman, 2008).

Cyanobacteria and their competitiveness relative to other phytoplankters are known to depend on

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particular traits. Many cyanobacteria, for example, spend part of their life-cycle at the sediment surface, from which there may be occasional mass-recruitment to the water column (Hansson, 2000). Although this capability is not limited to cyanobacteria, it is likely to be important for their strong competitive ability. Other variables known to influence their competitiveness are nutrient concentrations (e.g. Blomqvist *et al.*, 1994), TN : TP ratios (Smith, 1986), pH and CO₂ concentration (Shapiro, 1984; Caraco & Miller, 1998), stratification (Ganf, 1983; Steinberg & Hartmann, 1988; Wagner & Adrian, 2009), salinity (Sellner *et al.*, 1988), and light (Smith, 1986; Scheffer *et al.*, 1997).

Knowledge of the ecology of cyanobacteria has allowed successful management of them. For instance, species that can regulate their buoyancy to optimize their position in the water column need stable water columns to do so. Such species can sometimes be combated by forced mixing of the water column (Visser *et al.*, 1996). Also, slow-growing species may, in some situations, be eliminated from lakes by flushing (e.g. Reynolds *et al.*, 2002; Verspagen *et al.*, 2006; Elliott, 2010).

Despite the measures taken to reduce cyanobacterial blooms, their frequency and duration are increasing. This has been attributed in part to a warming climate (Romo *et al.*, 2004; Paerl & Huisman, 2008, 2009). Evidence for the relationship between temperature and cyanobacterial dominance comes from laboratory and field observations for individual lakes or lakes in a confined region, often in temperate climates. Laboratory experiments are available for only a few species (e.g. Reynolds, 2006), but comparison among these species suggests that cyanobacteria may have a higher optimum temperature for growth than eukaryotes. Although such laboratory data on isolated species are indispensable to help reveal mechanisms, they cannot easily predict what drives dynamics in more complex natural communities. However, laboratory observations of natural communities (De Senerpont Domis *et al.*, 2007), field observations of seasonal succession (Lin, 1972; Zhang & Prepas, 1996), studies of the impact of heat waves (Jöhnk *et al.*, 2008), and systematic comparisons among years (Weyhenmeyer, 2001; Huisman *et al.*, 2005; Reynolds, 2006; Jeppesen *et al.*, 2009; Wagner & Adrian, 2009), also indicate a positive temperature effect on cyanobacteria. In particular, buoyant cyanobacteria have been shown to be more common in warm summers (Jöhnk *et al.*, 2008; Shatwell *et al.*, 2008).

Recent work indicates that temperature and nutrients may have interactive effects on primary producers. Submerged macrophytes, for example, tend to disappear at lower nutrient concentrations in warmer than in cold lakes (Kosten *et al.*, 2009b), and the timing of the

phytoplankton spring bloom is influenced by both nutrient loading and winter temperatures (Huber *et al.*, 2008). Systematic studies to evaluate these interactions on primary producers at large scales are, however, scarce and restricted to narrow geographic ranges (Moss *et al.*, 2004; Jeppesen *et al.*, 2009, 2011). In this article, we use a long latitudinal gradient, from northern Scandinavia (Europe) to Tierra del Fuego (South America), to explore the potential interactive effects of temperature and nutrients on phytoplankton biovolume and on the percentage of the total phytoplankton biovolume attributable to cyanobacteria. We show that although the phytoplankton biovolume is only weakly related to climatic conditions, the percentage of cyanobacteria in the phytoplankton community rises steeply with temperature.

Methods

Study sites and sampling

Eighty-three lakes were sampled in South America (2004–2006) and 60 in Europe (2000–2001), between 5–55°S and 38–68°N (Fig. 1). Most lakes were sampled once, although 45 lakes were sampled twice within the same year, between June and October. To avoid temporal autocorrelation, only one sample per lake (mostly the July sample) was used in the statistical analyses, resulting in a total of 143 data points. Most were freshwater coastal lakes (Fig. 1) and situated at altitudes <200 m, but 26 lakes came from 200 to 800 m and 6 from

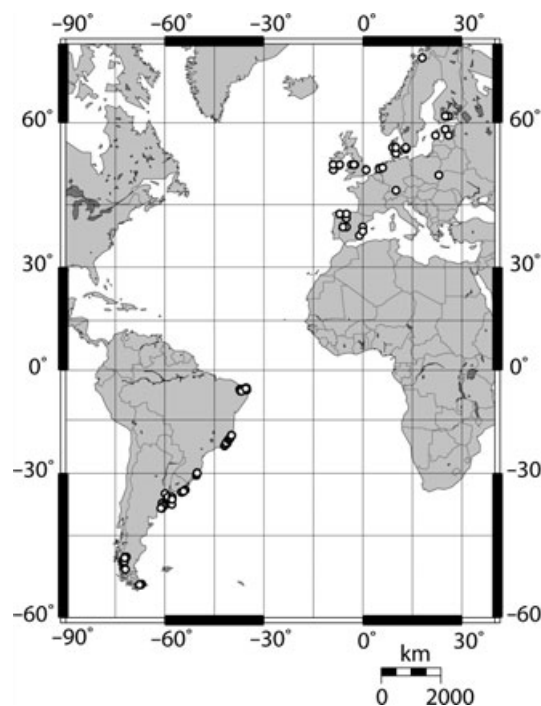


Fig. 1 Location of the studied lakes.

Table 1 General characteristics of the lakes used in the analysis ($n = 143$, except for chlorophyll *a* where $n = 141$)

	Min.	Max.	Mean	Median
Area (ha)	0.6	27 000	354	40
Mean depth (m)	0.5	5.6	1.8	1.6
Conductivity ($\mu\text{S cm}^{-1}$)	11	6400	473	195
Temperature ($^{\circ}\text{C}$)	6.7	29.1	21.1	21.1
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	0.5	2889	60.3	7.7
Total nitrogen ($\mu\text{g L}^{-1}$)	35	25 769	1667	800
Total phosphorus ($\mu\text{g L}^{-1}$)	5	9141	200	90
Total phytoplankton biovolume ($\text{mm}^3 \text{L}^{-1}$)	0.02	916.82	27.44	3.82
Cyanobacteria biovolume ($\text{mm}^3 \text{L}^{-1}$)	0	511.17	15.96	0.82
Cyanobacterial proportion of total phytoplankton biovolume (%)	0	100	39	33
Shade index (m/m)	0.31	19.99	3.02	1.88
Secchi depth (m)	0.04	6.8	1.3	0.9

>800 m. The lakes covered a wide climatic range. They were chosen so that the nutrient concentrations varied within each climate region (Table 1) (Moss *et al.*, 2003; Kosten *et al.*, 2009a). All lakes were shallow (mean depth = 1.9 m) and sampled during the dry season for tropical lakes in South America and during summer in all other lakes in South America and Europe. In South America, we collected depth-integrated water samples at 20 random points in each lake. Two liters of each integrated sample were combined in a bulk sample. In Europe, depth-integrated water samples were taken from the central part of the lake. Water for nutrient analyses was frozen until analysis or analyzed immediately after sampling. The water temperature in South America was measured from the surface to the bottom at intervals of 10 cm and subsequently averaged, whereas in Europe, temperature was measured on the depth-integrated water samples.

Sample analysis

Phytoplankton populations (individuals mL^{-1}) were fixed in Lugol's solution and settled for counting, using appropriate magnifications up to $\times 1000$, in chambers on inverted microscopes (Utermöhl (1958)). They were identified to species, or in some cases to genus. Biovolume ($\text{mm}^3 \text{L}^{-1}$) was estimated from standard geometric formulae (Hillebrand *et al.*, 1999). Total phosphorus (TP) and total nitrogen (TN) in the South American lakes were analyzed using a continuous flow analyzer (Skalar Analytical BV, Breda, the Netherlands) following Netherlands Normalization Institute protocols (NNI, 1986, 1990). TP in the European lakes was measured by the molybdenum blue reaction method after potassium persulphate digestion (Murphy & Riley, 1962). TN was analyzed using the Kjeldahl method or digestion with potassium persulphate in a Microwave digester and subsequent analysis of the derivative nitrate by cadmium reduction and diazotization to a colored dye (Stephen *et al.*, 2004). Chlorophyll *a* (chl-*a*) was extracted from filters (GF/C S&S; Whatman, GE Healthcare Bio-Sciences Corp., Piscataway, NJ, USA) with 96% ethanol and absorbance was measured at 665 and 750 nm (Nusch, 1980; Arvola, 1981).

pH and conductivity were measured *in situ*. Further details on the methodology are reported elsewhere (Moss *et al.*, 2003; Nöges *et al.*, 2003; Kosten *et al.*, 2009a; Peeters *et al.*, 2009).

Data analysis

To explore the relationships among total phytoplankton (chl-*a* and biovolume), cyanobacterial biovolume, temperature and nutrients (TN and TP), stepwise multiple linear regressions with forward selection were used. We used logistic regression using a quasi-likelihood function (McCullagh & Nelder, 1990) to explore the relationship between the percentage of the total phytoplankton biovolume attributable to cyanobacteria (hereafter percent cyanobacteria), with several potentially explanatory variables. Logistic regression allows analyses of data varying from 0 to 1 (or 0% and 100%) without transforming the data, which would be needed for linear regression of such data. Common logistic regression uses a dichotomous classification of the dataset, such as 'cyanobacteria dominated' vs. 'not cyanobacteria dominated', requiring an *a priori* cut-off level defining dominance. With the SAS events/trial technique, percentages can be used (SAS Institute Inc., Cary, NC, USA, 2004). The Nagelkerke r^2 value (Nagelkerke, 1991) and the Akaike Information Criterion (Akaike, 1974) were used as coefficients of determination to identify the best model. A large over-dispersion is inherent to the type of data obtained. It occurs when the observed variance is higher than the variance of the theoretic model. This over-dispersion is likely caused by variables not included in the models and possibly also by chaotic dynamics or other nonlinear effects on phytoplankton community composition and the percentage cyanobacteria. To account for part of the over-dispersion we multiplied the covariance matrix by the heterogeneity factor (deviance/degrees of freedom).

In a first round of forward stepwise logistic regression, we explored the relationship between percent cyanobacteria, nutrients (TN and TP), and temperature. In a second round, we added latitude as a variable to detect potential spatial autocorrelation. In a third round, the stepwise procedure

included other limnological variables known to influence the competitive advantage of cyanobacteria: TN : TP, pH, conductivity, and two proxies for the underwater light availability. These proxies were Secchi depth and the shade index. This index is defined as the ratio of average lake depth to Secchi depth transparency (Scheffer, 1998). The shade index may be a more informative measure of the underwater light climate for phytoplankton than Secchi depth because plankton cells may be dispersed throughout the mixed layer, which in most shallow lakes is the entire water column. All variables except for temperature and pH were log transformed. To avoid zeros in lakes where cyanobacteria were not detected, $0.001 \text{ mm}^3 \text{ L}^{-1}$ was added to the cyanobacterial biovolume in the linear regressions.

Collinearity among the independent variables might have influenced the stepwise selection procedure that we used and could complicate the interpretation of the models. Pearson correlations were thus first calculated between pairs of variables. There was no systematic change in the morphological lake characteristics (mean depth and area) along the temperature gradient (Table S1, Supporting Information). TP, however, was significantly correlated with temperature. This was mainly a result of the bias that the three coldest (Swedish) lakes were also the most oligotrophic. When these oligotrophic lakes were removed from the dataset, the correlation between

temperature and TP became insignificant ($P = 0.171$). The removal of the three lakes did not affect the general outcome of the logistic analysis. We were interested specifically in the interactive effect of temperature and nutrients on phytoplankton, and so we calculated multi-collinearity statistics for temperature, TN and TP. Both TN and TP varied considerably along the temperature gradient (Fig. 2). The variance inflation factor confirmed that although TN and TP were strongly correlated, this was not so for the combination of temperature and any of the nutrients, or both nutrients combined (Table S2).

All statistical analyses were performed using SPSS for Windows version 15.0 (SPSS, Chicago, IL, USA) and SAS version 9.1 (SAS Institute Inc.). The response surface shown in panel B of Fig. 3 was produced by interpolating the raw data using inverse distance weighting in SIGMAPLOT 10.0.

Results

Despite the extensive climatic gradient, temperature did not add to the variance in chl-a concentrations explained by nutrient concentrations (Table 2, multiple linear regression models 1 and 2). However, temperature added to the nutrient-explained variance in the

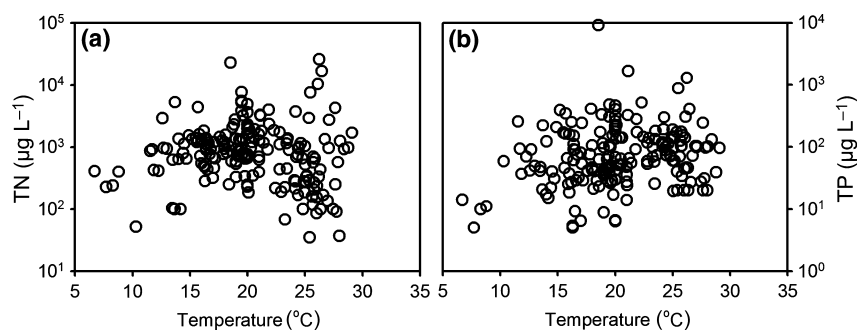


Fig. 2 Correlations between temperature and total nitrogen (TN) and total phosphorus (TP) concentrations.

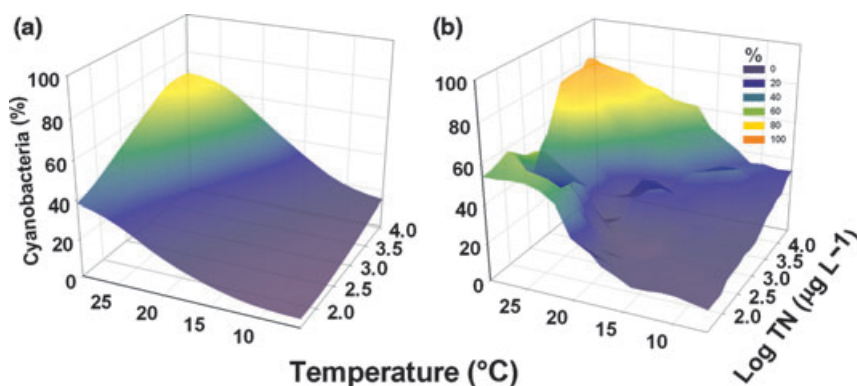


Fig. 3 Percentage of cyanobacterial biovolume in phytoplankton communities as a function of water temperature and nutrients in 143 lakes along a climatic gradient in Europe and South America. (a) Combined effects of temperature and nutrients as captured by a logistic regression model (corresponding to Table 3 model 2). (b) Response surface obtained from interpolation of the raw data using inverse distance weighting.

Table 2 Linear regression models explaining the quantity of phytoplankton. The models result from a forward stepwise selection procedure and explain chlorophyll *a* (log chl-*a* in $\mu\text{g L}^{-1}$), total phytoplankton biovolume (log TotBV in $\text{mm}^3 \text{L}^{-1}$), and cyanobacterial biovolume (log CyaBV + 0.001 in $\text{mm}^3 \text{L}^{-1}$) by the independent variables: water temperature (Temp in $^{\circ}\text{C}$), total nitrogen (log TN in $\mu\text{g L}^{-1}$), and total phosphorus (log TP in $\mu\text{g L}^{-1}$). All regression models were significant ($P < 0.0001$)

No.	Dependent variable	Linear model	r^2_{adj}	F
1	Log chl- <i>a</i>	$-2.05^{***} + 1.07^{***}\log \text{TN}$	0.63	236
2		$-2.21^{***} + 0.86^{***}\log \text{TN} + 0.41^{***}\log \text{TP}$	0.67	143
3	Log TotBV	$-2.14^{***} + 0.96^{***}\log \text{TN}$	0.37	84
4		$-2.31^{***} + 0.73^{***}\log \text{TN} + 0.44^{**}\log \text{TP}$	0.41	50
5		$-2.90^{***} + 0.79^{***}\log \text{TN} + 0.35^{*}\log \text{TP} + 0.03^{*}\text{Temp}$	0.42	36
6	Log CyaBV	$-2.34^{***} + 1.13^{***}\log \text{TP}$	0.15	26
7		$-3.81^{***} + 0.98^{***}\log \text{TP} + 0.08^{***}\text{Temp}$	0.22	21
8		$-5.35^{***} + 0.42 \log \text{TP} + 0.10^{***}\text{Temp} + 0.79^{**}\log \text{TN}$	0.28	19

$n = 143$, except for chlorophyll *a* where $n = 141$. The significance of the regression coefficients is indicated by

*** $P < 0.001$;

** $0.001 < P < 0.01$; and

* $0.01 < P < 0.05$.

biovolume of cyanobacteria (Table 2, models 6–8). Regression models for total phytoplankton biovolume explained slightly more variance if temperature was included as an independent variable (Table 2, models 3–5).

We found a highly significant increase in the percent cyanobacterial biovolume with temperature (model 1 in Tables 3 and 4). Temperature was the single most explanatory variable of the percent cyanobacteria (Tables 3 and 4). The percent of cyanobacteria also increased with TN (Table 3, model 2 and Fig. 3) and tended to increase with TP, although the contribution of TP was not significant. The residuals of the model, including temperature and TN (Table 3, model 2), correlated with latitude (Fig. S1) indicating spatial autocorrelation. Indeed, adding latitude to the model further

increased the r^2 values (Table 3, model 3). Limnological variables other than temperature and nutrients explained part of the variance in percent cyanobacteria. pH was the next most important explanatory variable after temperature (Table 4, model 2). The light conditions experienced by the phytoplankton, indicated by the shade index, also played a role (Table 4, model 3).

Discussion

In the shallow lakes studied, the proportion of cyanobacteria in phytoplankton communities increased with temperature. Warmer lakes did not differ in chl-*a* concentrations from cooler lakes, but had a substantially higher cyanobacterial volume, at a given nutrient concentration.

Table 3 Logistic regression models explaining the percentage of the total phytoplankton biovolume attributable to cyanobacteria by the independent variables water temperature (Temp in $^{\circ}\text{C}$), total nitrogen (log TN in $\mu\text{g L}^{-1}$), and total phosphorus (log TP in $\mu\text{g L}^{-1}$) (models 1 and 2). The models result from a forward stepwise selection procedure. Model 3 is the outcome of the forward stepwise logistic regression when adding latitude to the before mentioned independent variables. For comparison models with only total nitrogen or total phosphorus are also presented (models 4–6) [Correction added after online publication 24 August 2011: legend of Table 3 has been revised]

	Logistic model	r^2 (Nagelkerke)	AIC
1	$-3.45^{***} + 0.14^{***}\text{Temp}$	0.11	17 901
2	$-5.69^{***} + 0.16^{***}\text{Temp} + 0.66^{**}\log \text{TN}$	0.15	17 533
3	$-5.15^{***} + 0.12^{***}\text{Temp} + 0.75^{**}\log \text{TN} - 0.01^{**}\text{Latitude}$	0.18	17 168
4	$-1.78^{*} + 0.47^{*}\log \text{TN}$	0.02	18 965
5	$-1.61^{**} + 0.61^{*}\log \text{TP}$	0.03	18 882
6	$-0.38^{**} - 0.01^{***}\text{Latitude}$	0.07	18 358

$n = 143$. AIC, Akaike Information Criterion.

The significance of the regression coefficients is indicated by

*** $P < 0.001$;

** $0.001 < P < 0.01$; and

* $0.01 < P < 0.05$.

Table 4 Logistic regression models explaining the percentage of the total phytoplankton biovolume attributable to cyanobacteria. The models result from a forward stepwise selection procedure using the independent variables: water temperature (Temp in °C), total nitrogen (log TN in $\mu\text{g L}^{-1}$), total phosphorus (log TP in $\mu\text{g L}^{-1}$), TN : TP, pH, conductivity (log Con in $\mu\text{S cm}^{-1}$), Secchi depth (log Secchi in m), and shade index (log shade dimensionless)

	Logistic model	r^2 (Nagelkerke)	AIC
1	$-3.45^{***} + 0.14^{***}\text{Temp}$	0.11	17 901
2	$-7.97^{***} + 0.18^{***}\text{Temp} + 0.49^{***}\text{pH}$	0.18	17 169
3	$-7.49^{***} + 0.16^{***}\text{Temp} + 0.43^{**}\text{pH}$ $+ 0.61^{\dagger}\text{log Shade}$	0.19	17 032
4	$-8.03^{***} + 0.18^{***}\text{Temp} + 0.72^{***}\text{pH}$ $+ 0.96^{**}\text{log Shade} - 0.95^{\dagger}\text{log Con}$	0.21	16 760

$n = 143$. AIC, Akaike Information Criterion.

The significance of the regression coefficients is indicated by

*** $P < 0.001$;

** $0.001 < P < 0.01$;

* $0.01 < P < 0.05$; and

$^{\dagger}P > 0.05$.

The dataset covered many lakes and a considerable climatic variation, but obviously had some limitations. For instance, there was only one snapshot sample for most lakes, taken in the middle of the growing season. Analysis of data from a subset of the lakes, sampled twice within the same year, suggests that the proportion of cyanobacteria remained relatively steady during summer (Fig. S2). However, the data did not allow analysis of climate effects from variation among years or differences in phytoplankton phenology and bloom duration (e.g. Huber *et al.*, 2008). The variables included were also restricted, largely by time available and the practical considerations of extensive surveys. Watershed characteristics, catchment geology, and species composition may all influence the relation between climate and cyanobacterial abundance, but could not be taken into account. This may explain the modest r^2 values of our models. These may also be explained by the inherent chaotic behavior of phytoplankton communities, complicating the predictability of phytoplankton community composition (Beninca *et al.*, 2008) and hence the proportion of cyanobacteria within the community. Unpredictability arising from such nonlinearity may be of lesser influence at higher aggregation levels (Dakos *et al.*, 2009). For example, the r^2 values of the models explaining total phytoplankton biovolume were higher than for those explaining the cyanobacterial biovolume (Table 2).

The greatest challenge of correlational field data is the difficulty of inferring causality. The interpretation of a relationship between total nutrient concentrations and phytoplankton biomass (expressed either as chl-*a* or as biovolume) is, for example, notoriously problematic. Most of the nutrients are typically locked up in phytoplankton cells, and so the relationships may

in part be consequential rather than causative. Also, in shallow lakes, where the sediment-water exchange is intense, nutrient release to the water column may be affected by phytoplankton biomass and subsequent sedimentation. Settled phytoplankton stimulates mineralization at the sediment surface, thereby increasing the probability of anoxia and phosphorus release (Scheffer, 1998; Søndergaard *et al.*, 2003). To reduce the risk of circularity in interpreting the relationship between phytoplankton biovolume and nutrients, we focused on the percentage (rather than absolute biovolume) of cyanobacteria (Tables 3 and 4, Fig. 3). However, the percentage of cyanobacteria was still related to a cluster of mutually correlated factors, including pH, nutrient concentrations and underwater light conditions that merit further discussion.

The relationships of the percentage of cyanobacteria with temperature and TN suggest that the proportion of cyanobacteria increased with warming as well as with eutrophication. This is consistent with local scale findings in Danish lakes (Jeppesen *et al.*, 2009, 2011). In addition, the percentage of cyanobacteria was particularly well correlated with pH (Table 4). Cyanobacteria are efficient users of molecular carbon dioxide (Shapiro, 1984; Caraco & Miller, 1998), whose availability falls with increasing pH. Although this could explain the positive relation found between pH and the proportion of cyanobacteria, the high proportion of cyanobacteria at high pH may also arise from an indirect nutrient effect. pH increases as photosynthesis intensifies due to inorganic carbon uptake from the water. The high pH therefore often reflects high photosynthetic rates, which are linked with high nutrient concentrations (Table S1). The positive relationship between nutrient concentrations and cyanobacterial dominance coincides with

results of studies in temperate (Downing *et al.*, 2001; Jeppesen *et al.*, 2009) and Mediterranean lakes (Romo *et al.*, 2004), although extreme nutrient enrichment in temperate shallow lakes is associated with dominance by chlorophytes rather than by cyanobacteria (Jensen *et al.*, 1994).

That nitrogen-fixing cyanobacteria that might be favored by nitrogen-limiting conditions has been subject to considerable debate (e.g. Jensen *et al.*, 1994; Bulgakov & Levich, 1999; Reynolds, 1999; Diaz *et al.*, 2007; Schindler *et al.*, 2008). As in studies on temperate lakes (Jensen *et al.*, 1994; Downing *et al.*, 2001), our results suggest that TN or TP concentrations are better predictors of cyanobacterial dominance than the TN : TP ratio. An analysis of the relationship between cyanobacteria and nutrient concentrations in the South American lakes in the dataset showed that the TN : TP ratio was not related to cyanobacterial dominance, even when nitrogen-fixing bacteria were analyzed separately (see fig. 8 in Kosten *et al.*, 2009a). A lack of relationship between the TN : TP ratio and cyanobacterial dominance may show that this ratio is not a good indicator of nitrogen limitation, especially when both nutrients are in sufficient supply or when TN or TP largely comprise unavailable compounds. However, cyanobacterial dominance in the South American lakes occurred mostly in lakes with low dissolved inorganic nitrogen potentially indicating nitrogen limitation (Kosten *et al.*, 2009a).

Lastly, there is the possible role of light limitation in explaining the field patterns. A higher shade index in our lakes was correlated with a higher proportion of cyanobacteria (Table 4, model 3). Although it is difficult to distinguish between cause and effect from our data, controlled experiments and field data suggest that light availability might affect the competitive balance among a large group of shade-tolerant species of cyanobacteria, mainly Oscillatoriales, and other phytoplankton species (Smith, 1986; Scheffer *et al.*, 1997). Overall, our results suggest that higher temperatures interact with nutrient loading and underwater light conditions in determining the proportion of cyanobacteria in the phytoplankton community in shallow lakes. Nutrient concentrations and loading are important not only in determining the proportion of cyanobacteria in the phytoplankton community but also strongly influence the overall phytoplankton biovolume. Nutrient loading may therefore be considered a key driver determining the cyanobacterial biovolume and the impact that these organisms may have on ecosystem functioning and human uses.

The present data alone do not allow the reconstruction of causal relationships. Nonetheless, in combination with an increasing body of laboratory and field

studies (Weyhenmeyer, 2001; Huisman *et al.*, 2005; Reynolds, 2006; De Senerpont Domis *et al.*, 2007; Jeppesen *et al.*, 2009; Wagner & Adrian, 2009) they suggest that warming may promote cyanobacterial dominance (Fig. 4). Cyanobacteria may benefit more than other phytoplankton groups from warming owing to their higher optimum growth temperatures, but they may also be promoted by an increase in water column stability at higher temperatures (e.g. Wagner & Adrian, 2009). Indirectly, warming may also increase nutrient concentrations by enhancing mineralization (Gudas *et al.*, 2010; Kosten *et al.*, 2010) and by temperature or anoxia-mediated sediment phosphorus release (Jensen & Andersen, 1992; Søndergaard *et al.*, 2003). This implies that even though our analyses suggest that at a given nutrient concentration algal biomass is not related to temperature, temperature may indirectly increase algal biomass through its effect on nutrient concentrations. In addition, increased rainfall in some areas may increase nutrient concentrations with similar implications (Jeppesen *et al.*, 2009). Finally, warmer conditions may raise total phytoplankton biomass through an alteration of top-down regulation by grazers (Fig. 4) (Jeppesen *et al.*, 2009, 2010; Teixeira-de Mello *et al.*, 2009). Thus, the marked relationship between temperature and cyanobacterial dominance that we found may be explained not only from temperature effects on the competitive advantage for cyanobacteria but also from a set of temperature-induced mechanisms that cause lower underwater light levels favouring cyanobacteria.

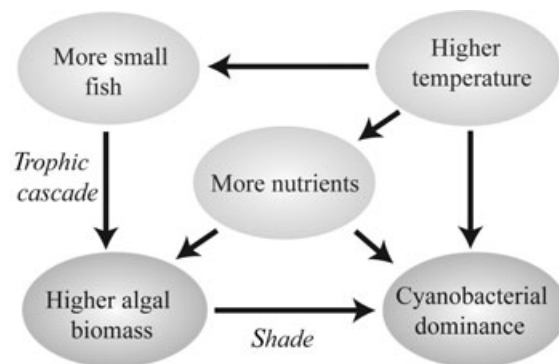


Fig. 4 Inferred relationships between climatic warming and the probability that a phytoplankton community will be dominated by cyanobacteria. Although warming appears to promote the competitive strength of cyanobacteria through either higher optimum growth temperatures or enhanced stratification, it also tends to lead to less effective top-down control of algal biomass and to promote nutrient levels in the water column through enhanced recycling as well as greater loading from the catchment.

Nutrient control has long been identified as an effective way of reducing cyanobacterial blooms (WHO, 1999; Paerl & Huisman, 2009). Our findings suggest that when temperatures rise, substantially lower nutrient loadings might be needed to reduce the risk of cyanobacterial dominance. Although inferring causality from correlational studies remains problematic and the unexplained variance in our data is large, our results (Table 3, model 3) could be interpreted as suggesting that to compensate for the effects of a 1 °C increase in temperature, TN should be reduced by as much as one-third.

Acknowledgements

We are grateful for the constructive comments by Chris Todd and two anonymous referees on previous versions of the manuscript. The study in Europe was partially financed by the European Community (ECOFRAME EVK1-CT-1999-00039), and in South America (SALGA) by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) grants 311427, 480122, 490487, Brazil; The Netherlands Organization for Scientific Research (NWO) grants W84-549 and WB84-586, The National Geographic Society grant 7864-5; PEDECIBA, Maestría en Ciencias Ambientales, Donación de Aguas de la Costa S.A. and Banco de Seguros del Estado, Uruguay. We thank all people involved in the sampling and all lake owners who gave us access to the lakes. In addition, we thank Elisabeth Gross as member of the ECOFRAME group. S. K. was supported by the Dutch 'Knowledge for Climate Programme'. E. J. was supported by the Danish Research Council for Nature and Universe, EU REFRESH, and by CRES. G. L. and N. M. were supported by SNI (ANII).

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