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The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa

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Abstract

Cyanobacteria are predicted to increase due to climate and land use change. However, the relative importance and interaction of warming temperatures and increased nutrient availability in determining cyanobacterial blooms are unknown. We investigated the contribution of these two factors in promoting phytoplankton and cyanobacterial biovolume in freshwater lakes. Specifically, we asked: (1) Which of these two drivers, temperature or nutrients, is a better predictor of cyanobacterial biovolume? (2) Do nutrients and temperature significantly interact to affect phytoplankton and cyanobacteria, and if so, is the interaction synergistic? and (3) Does the interaction between these factors explain more of the variance in cyanobacterial biovolume than each factor alone? We analyzed data from > 1000 U.S. lakes and demonstrate that in most cases, the interaction of temperature and nutrients was not synergistic; rather, nutrients predominantly controlled cyanobacterial biovolume. Interestingly, the relative importance of these two factors and their interaction was dependent on lake trophic state and cyanobacterial taxon. Nutrients played a larger role in oligotrophic lakes, while temperature was more important in mesotrophic lakes: Only eutrophic and hyper-eutrophic lakes exhibited a significant interaction between nutrients and temperature. Likewise, some taxa, such as *Anabaena*, were more sensitive to nutrients, while others, such as *Microcystis*, were more sensitive to temperature. We compared our results with an extensive literature review and found that they were generally supported by previous studies. As lakes become more eutrophic, cyanobacteria will be more sensitive to the interaction of nutrients and temperature, but ultimately nutrients are the more important predictor of cyanobacterial biovolume.

There is a growing concern that interactions between climate warming and eutrophication are enhancing the frequency and magnitude of cyanobacterial blooms globally (Hallegraeff 1993; Jöhnk et al. 2008; Huber et al. 2012) and expanding the geographic range of some cyanobacterial taxa (Ryan et al. 2003; Briand et al. 2004; Sinha et al. 2012). The toxins produced by a number of the dominant bloom-forming cyanobacteria present a considerable risk to drinking water (Codd et al. 2005) and pose a substantial economic cost (Ho et al. 2002; Steffensen 2008; Dodds et al. 2009). In addition, cyanobacterial blooms have considerable negative effects on aquatic food webs and ecosystem functioning (Bartram and Chorus 1999; Havens 2007; Paerl et al. 2011). As a result of these public health, ecological, and economic effects, there has been a considerable effort to understand the underlying processes leading to bloom formation (Falconer 2005; Huisman et al. 2005; Hudnell 2008).

Increased nutrients and temperature are believed to be two of the most important factors driving the increase in cyanobacteria (Paerl and Huisman 2008; Conley et al. 2009). Cyanobacteria have several ecophysiological adaptations that may allow them to dominate aquatic systems under warmer and more nutrient-rich conditions (Carey et al. 2012). For example, some cyanobacteria produce gas vesicles that allow them to regulate their buoyancy (Ganf and Oliver 1982; Huisman et al. 2005; Hudnell 2008). Cyanobacteria may take advantage of warming both directly, from temperature increases, and indirectly, from enhanced stratification of the water column (Carey et al. 2012). Under increased thermally stratified conditions, which are anticipated with global warming, these cyanobacterial taxa might be able to migrate between well-illuminated surface layers and nutrient-rich hypolimnetic waters (Ganf and Oliver 1982; Walsby 1994; Bouterfas et al. 2002), escaping the increasingly nutrient-depleted epilimnion of lakes during extended stratification periods (Livingstone 2003). Cyanobacteria may also take direct advantage of warming because their growth rate will increase with temperature, while the growth rates of many other phytoplankton taxa decline over 20°C (Reynolds 2006; Litchman et al. 2010); however, *see* Lürling et al. (2013). The ability to fix nitrogen (Oliver and Ganf 2000; Reynolds 2006) and the ability to produce dormant cells to survive unfavorable conditions (Bartram and Chorus 1999; Kaplan-Levy et al. 2010) are other physiological adaptations that may provide cyanobacteria a competitive advantage over other phytoplankton (Litchman et al. 2010; Carey et al. 2012), especially under increasingly unpredictable future climate conditions (IPCC 2007).

Although cyanobacteria as a group have many traits that make them highly adaptable to environmental changes, they are comprised of taxa with very different physiological characteristics. For example, the size range of a cyanobacterial phycosphere spans nearly eight orders of magnitude, from the smallest single-celled cyanobacterial picoplankton

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to the multicellular filaments and colonies; the photosynthetic rates and growth rates of different taxa vary by > 25%; some, but not all, taxa are able to fix nitrogen (e.g., *Aphanizomenon* and *Lyngbya* spp.), and only some taxa have gas vesicles to regulate buoyancy (e.g., *Microcystis* and *Anabaena* sp.) (Reynolds 2006). The different combinations of these traits, which characterize individual cyanobacterial taxa, might result in varied responses to changes in temperature and nutrients.

Traditionally, increasing nutrient concentrations have been considered the key factor responsible for promoting cyanobacterial blooms (Paerl et al. 2001; Schindler 2001). More recent studies using long-term monitoring data and modeling simulations have suggested that warmer temperatures, in addition to nutrients, are also an important driver of blooms (Anneville et al. 2005; Elliott et al. 2005; Wagner and Adrian 2009). Anneville et al. (2005) analyzed phytoplankton community changes among European peri-alpine lakes over 25 yr and observed that phosphorus concentrations were the main driver of changes in phytoplankton composition, which was also affected by warmer winters. Similarly, studies by Kosten et al. (2012), Posch et al. (2012), and Paerl and Huisman (2008) point to warmer temperatures as being more important than nutrient loading for cyanobacterial bloom formation. However, Jeppesen et al. (2005), using long-term data from 35 lakes located from the subtropics to the temperate zone in North America and Europe, argued that phytoplankton composition is primarily driven by nutrient loading, and climate change effects are less detectable.

Based on these studies and others, there is currently no consensus within the limnological community about the relative importance of nutrients and temperature in driving cyanobacterial blooms, as well as to the factors that might mediate their relative importance (e.g., trophic state, cyanobacterial taxa identity). In addition, little is known about how these two factors may interact to control cyanobacterial growth. Modeling studies indicate that temperature and nutrients may interact synergistically to promote blooms (Elliott and May 2008; Elliott 2012), but it remains unknown as to how these two factors would interact in systems of different trophic state. Brookes and Carey (2011) proposed that nutrients ultimately control cyanobacterial biomass and composition, but at high nutrient concentrations, nutrients and temperature may synergistically interact to control blooms. This hypothesis remains untested, however.

In this paper, we addressed the following questions: (1) Which factor, nutrients or temperature, is most important for controlling phytoplankton biomass (as chlorophyll *a*), cyanobacterial biovolume, and cyanobacterial dominance (i.e., the cyanobacterial proportion of total phytoplankton biovolume)? (2) Do nutrients and temperature interact to promote cyanobacterial blooms, and if so, is there a synergistic interaction? and (3) Does the interaction between nutrients and temperature vary with trophic state and cyanobacterial taxa composition? We conducted a meta-analysis of the U.S. Environmental Protection Agency National Lake Assessment (hereafter, EPA NLA) dataset of ~ 1000 U.S. lakes, which provided an in-depth opportunity to examine highly resolved snapshot data across a large geographic area. We contextualized the results of the meta-analysis with a literature review on studies that analyzed the effects and interaction between nutrients and temperature on cyanobacterial biovolume (making a distinction between studies that used modeling simulations, field observations, experimental data, and paleolimnology). We hypothesized that nutrients have a stronger positive effect than temperature on cyanobacterial dominance, but that the two drivers generally act synergistically. Moreover, we hypothesized that different cyanobacterial taxa would exhibit varying sensitivities to the two drivers and that the relative importance of temperature and nutrients (and their interaction) would vary depending on the trophic status of the system considered.

Methods

EPA NLA dataset analysis

Sampling and laboratory methods: We used data from the 2007 National Lakes Assessment, conducted by the U.S. Environmental Protection Agency (EPA 841-R-09-001). In total, 1076 natural freshwater lakes, ponds, and reservoirs (hereafter, lakes) with a minimum depth of 1 m and a minimum size of 1×10^{-2} km^2 across the lower 48 U.S. states were sampled once during summer 2007. Lakes were sampled at the ''Index Point'' i.e., the deepest point in a lake ($\leq$ 50 m), as determined using sonar. Temperature, conductivity, dissolved oxygen (DO), and pH were determined with a multiparameter probe at depth intervals appropriate to the particular lake depth (*see* EPA documentation on Field Procedures, http://www.epa.gov/lakessurvey/). Sensors were checked and calibrated before each sampling event. Water clarity was measured using a Secchi disk. Water samples were collected using an integrated sampler, a polyvinyl chloride (PVC) tube of 2 m length. A 4 liter sample was mixed thoroughly and subsequently divided into a 2 liter sample for chlorophyll *a*, a 1 liter sample for phytoplankton, and 250 mL for nutrients. Total nitrogen (TN) and total phosphorus (TP) were analyzed according to analytical methods of choice in participating laboratories, provided that the methods met a set of performance requirements with respect to precision objective, bias objective, and detection limit. Interlaboratory performance evaluation studies were performed. Laboratory reporting limits (equal to two times the detection limit) were 4 μg L^{-1} for TP and 20 μg L^{-1} for TN.

The analytical procedure for chlorophyll *a* samples was the following: samples were immediately placed in a cooler with ice and kept away from light. Onshore, the sample was filtered on a Whatman GF/F filter (equivalent 0.7 μm glass fiber filter) under subdued light. The filter was stored in a centrifuge tube on ice for transport to the laboratory. Here, the tubes were stored in the freezer at -20°C until analysis. The analytical procedure was similar to that described for nutrients, i.e., the participating laboratories used different methods to meet a reporting limit of 3 μg L^{-1}.

The sample for phytoplankton counting was fixed with Lugol's iodine and concentrated via sedimentation. Phytoplankton was counted in Palmer–Maloney or Utermöhl

Table 1. Regression models testing the effects of nutrient and temperature on chlorophyll *a*, cyanobacterial biovolume, and proportional cyanobacterial biovolume. For each regression model, the predictor (either temperature or nutrients) explaining the most variation in the response variable (determined by the amount of R^2 decomposed to each predictor) is in bold. If the differences between the two predictors' 95% confidence intervals (CI) did not include zero, the two predictors contributed a significantly different proportion of the overall R^2, which is noted. The nutrient (either TN or TP) explaining the most variation in the response variable (as determined by overall model R^2, and if identical, the F value of the overall regression model) is in bold. Significant interactions between nutrients and temperature are italicized.

Response variable	Nutrient being tested	Overall model R^2	Nutrient			Temperature			Significant difference between the contribution of nutrients and temperature?	Interaction		
			R^2	95% CI	p	R^2	95% CI	p		R^2	95% CI	p
Chlorophyll *a*	TN	0.60	**0.83**	**0.79–0.88**	**<0.0001**	0.15	0.11–0.20	<0.0001	Yes	*0.01*	*0.004–0.02*	*<0.0001*
	TP	0.61	**0.84**	**0.79–0.89**	**<0.0001**	0.15	0.11–0.20	<0.0001	Yes	*0.01*	*0.001–0.03*	*<0.0001*
Cyanobacterial biovolume	**TN**	0.15	**0.68**	**0.49–0.82**	**<0.0001**	0.32	0.18–0.48	<0.0001	Yes	0.01	0–0.08	0.25
	TP	0.15	**0.66**	**0.48–0.80**	**<0.0001**	0.34	0.19–0.50	<0.0001	No	0.0005	0–0.05	0.75
Proportional cyanobacterial biovolume	TN	0.04	**0.79**	**0.49–0.96**	**<0.0001**	0.16	0.01–0.41	0.02	Yes	0.0	0.0001–0.32	0.12
	TP	0.05	**0.85**	**0.59–0.97**	**<0.0001**	0.14	0.01–0.38	0.02	Yes	0.003	0–0.16	0.71

counting chambers to the lowest possible taxonomic level (usually genus). A target number of 300 organisms within a random systematic selection of field or transect was counted. Ten percent of all samples were reanalyzed in each laboratory to test for reproducibility of the processing and analysis methods. In addition, independent phycologists reanalyzed 10% of all taxonomic samples to ensure taxonomic accuracy.

A detailed description of the EPA NLA 2007 sampling campaign can be found in the following documents: (1) Quality Assurance Project Plan (EPA 841-B-07-003); (2) Lake Evaluation Guidelines (EPA 841-B-06-003); (3) Field Operations Manual (EPA 841-B-07-004); and (4) Laboratory Methods Manual (EPA841-B-07-005) (EPA 2009).

Lakes were chosen for sampling from the U.S. National Hydrographic dataset using a Generalized Random Tessellation Stratified survey design (Stevens and Olsen 2004). In total, 1076 lakes with a minimum depth of 1 m and a minimum size of 1×10^{-2} km^2 across the lower 48 U.S. states were selected, which were sampled once during the summer of 2007. For each lake, we used measurements of surface water temperature, TN, and TP concentrations, chlorophyll *a*, and phytoplankton taxa composition and biovolume (samples were identified to genus only). The water temperature measurements were made at the surface, while nutrient and phytoplankton samples were collected from 0 to 2 m depth as integrated samples. Much emphasis was placed on consistency in sampling and analytical procedures across all lakes so that the data could be compared across the United States.

Statistical analysis: Using the EPA NLA dataset, we first assessed whether water temperature or nutrient concentrations were a more important driver of variation in the cyanobacterial and phytoplankton response variables, and then we assessed whether the two predictors significantly interacted. Our focal response variables were chlorophyll *a* concentration, as a proxy for total phytoplankton biomass; cyanobacterial biovolume (μm^3 mL^{-1}); and proportional cyanobacterial biovolume (the proportion of total phytoplankton biovolume composed of cyanobacteria). Cyanobacterial biovolume and proportional cyanobacterial biovolume were chosen because biovolume reflects a true metric of biomass more closely than cell counts, considering the wide range of individual cell or colony sizes (Hillebrand et al. 1999). Large-sized species, for example, even if less abundant in number, might dominate the overall biomass, so cell counts may give a biased impression of the dominant taxon (Hillebrand et al. 1999). We used TN and TP as our proxy for eutrophication and nutrients, since we were unable to access soluble fractions of N and P for the EPA NLA dataset lakes, and water temperature as a proxy for climate warming. In most freshwater lakes, nitrogen and phosphorus are the dominant limiting nutrients for phytoplankton (Conley et al. 2009; Paerl et al. 2011; Dolman et al. 2012), so for the analyses described below, we conducted each analysis with both TN and TP separately, and then chose the nutrient most strongly correlated to the response variable. In our dataset, ln-transformed TN and TP were highly correlated (Pearson product-moment correlation $r = 0.81$, $p < 0.0001$).

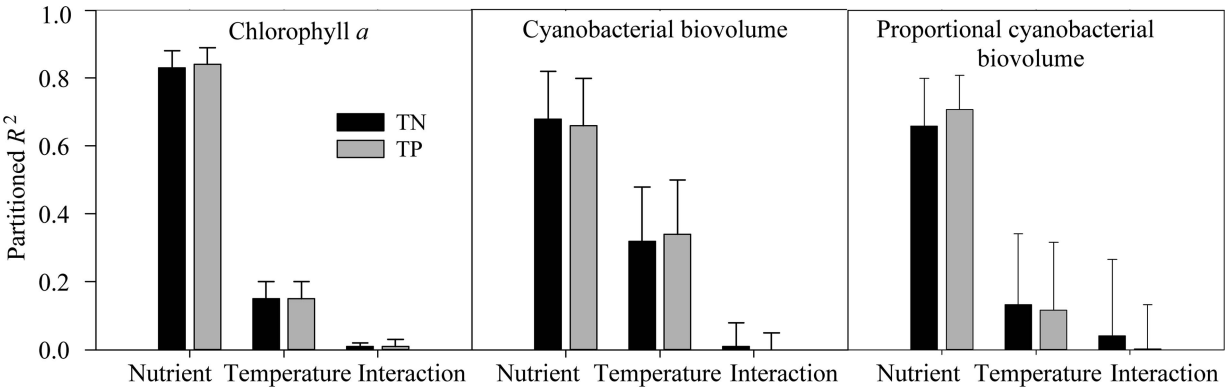

Fig. 1. The relative effects of nutrients (both TN and TP), temperature, and their interaction on chlorophyll *a*, cyanobacterial biovolume, and proportional cyanobacterial biovolume.

Consequently, in most cases, TN and TP were interchangeable and yielded very similar results.

We ln-transformed TN, TP, and all of our response variables, except for proportional cyanobacterial biovolume, to improve normality and equalize variance. For proportional cyanobacterial biovolume, we logit-transformed the proportions + x_{min}, following Warton and Hui (2011). The x_{min} altered parameter estimates but did not affect the overall significance or direction of the relationships investigated.

The primary multiple linear regression model we used for each analysis was

$$Y = B_0 + B_1 X_{\text{nutrient}} + B_2 X_{\text{temperature}} + B_3 X_{\text{nutrient} \times \text{temperature}} + \varepsilon \quad (1)$$

where Y represents the phytoplankton or cyanobacterial response variable of interest; B_0 is the intercept term; B_1, B_2, and B_3 are model parameters for the nutrient term, temperature term, and their interaction, respectively; and ε is a stochastic error term. We used backward elimination to arrive at a final model: if the interaction term was significant at $p = 0.05$, the lower order terms remained in the equation.

To determine the relative importance of nutrients vs. temperature, we used the definition of dispersion importance of Achen (1982), i.e., we assessed the amount of explained variation for each predictor. We also examined the proportional contribution of each predictor to the overall model R^2, including both its direct effect, or correlation with the criterion, and its indirect effect when combined with other variables in the regression model (Johnson and Lebreton 2004). We first constructed linear models as described above for each response variable and then used the metric "lmg" in the R package relaimpo (R Core Team 2008) to decompose the overall model R^2 into nonnegative contributions for each predictor term (Grömping 2006). The contributions of each predictor were then normalized and summed to the total R^2 (Grömping 2006). This approach is based on sequential R^2but removes the dependence on orderings that bias stepwise regression (Bring 1996) by averaging over orderings, using simple unweighted averages (Grömping 2006). This approach is recommended over other methods of decomposing the R^2 among predictors, since it uses both indirect and direct effects and adjusts for other regressors in the overall model (Johnson and Lebreton 2004; Grömping 2006).

To assess whether the effects of nutrient concentration and temperature varied across the range of their values, variability estimates of their R^2 contribution were also determined for each response variable. We created 95% confidence intervals around the R^2 contribution of each predictor term (nutrient, temperature, and their interaction) by using a bootstrapping approach and resampled the observed data 1000 times. We used the booteval.relimp function in R package relaimpo to determine whether the differences among the 95% confidence intervals of each of the predictors did not include zero, which indicated whether the predictors were significantly different from each other. We assessed whether temperature and nutrients interacted by the significance of the interaction term, at $\alpha = 0.05$. If the significant interaction term was positive, we interpreted the interaction to be synergistic.

We repeated this analysis to determine whether trophic state influenced the relative importance of temperature, nutrients, and their interaction. We subdivided the lakes in the EPA NLA dataset into four groups based on the trophic state conventions of Nürnberg (Nürnberg 1996), which delineated oligotrophic as TP < 10 μg L^{-1} ($n = 273$ lakes), mesotrophic as $10 \geq$ TP ≥ 30 μg L^{-1} ($n = 310$), eutrophic as $30 >$ TP ≥ 100 μg L^{-1} ($n = 253$), and hypereutrophic as TP > 100 μg L^{-1} ($n = 240$). Within each trophic state, we estimated the proportional contribution of the nutrient, temperature, and interaction terms for proportional cyanobacterial biovolume as described above. We focused on proportional cyanobacterial biovolume, or cyanobacterial dominance, following several other studies that have used this metric (Moss et al. 2003; Wagner and Adrian 2009; Kosten et al. 2012).

Finally, we repeated this analysis for the proportional biovolume of individual cyanobacterial taxa grouped across all trophic states, focusing on the 11 taxa that represented the 10 most common species ranked by abundance and biovolume that we were able to access data for. Again, we logit-transformed + x_{min} the proportional biovolume of each species, following Warton and Hui (2011).

Table 2. Regression models testing the effects of nutrients and temperature on proportional cyanobacterial biovolume. Both TN and TP were analyzed; the nutrient explaining the greatest proportion of variation is given here in parentheses (*see* Table 5 for data on both nutrients). The most important predictor term (nutrients, temperature, or their interaction) is in bold. If the differences between the two predictors' 95% confidence intervals (CI) did not include zero, the two predictors contributed a significantly different proportion of the overall R^2, which is noted. Significant interactions between nutrients and temperature are in italic.

Response variable	Trophic state	Overall model R^2	Nutrient			Temperature			Significant difference between the contribution of nutrients and temperature?	Interaction		
			R^2	95% CI	p	R^2	95% CI	p		R^2	95% CI	p
Proportional cyanobacterial biovolume (TN)	Oligotrophic	0.01	**0.58**	**0.02–0.93**	0.24	0.33	0.01–0.91	0.55	No	0.09	0.001–0.89	0.68
	Mesotrophic	0.04	0.11	0.004–0.66	0.17	**0.88**	**0.18–0.98**	0.001	No	0.01	0.0002–0.39	0.70
	Eutrophic	0.04	0.04	0.0001–0.52	0.54	0.09	0.0002–0.67	0.36	No	**0.87**	**0.17–0.99**	*0.005*
	Hyper-eutrophic	0.04	0.17	0.003–0.88	0.24	0.03	0.002–0.42	0.46	No	**0.79**	**0.03–0.99**	*0.007*

Literature review

Selection: We conducted a literature review with the Institute for Scientific Information Web of Science database (Web of Science®, Thomson Reuters) using the keywords "nutrients," "temperature," and "cyanobacteria," or "phytoplankton" (and their variants), and only included studies that were conducted on freshwater lakes and reservoirs. From an initial list of 49 peer-reviewed articles meeting those criteria, we selected publications that analyzed multiple environmental factors affecting phytoplankton and/or cyanobacteria. Only studies that considered both temperature and nutrients (N or P individually or both N and P together) as possible drivers of phytoplankton were included. Both short term ($\leq$ 1 yr) and long-term studies ($>$ 1 yr) were included. The studies selected spanned from 1998 to 2012.

Analysis: We grouped the studies into different categories depending on the methods used, i.e., (1) experiments, (2) modeling, (3) observations, (4) combination of experiments and modeling, (5) combination of observations and modeling, and (6) analysis of paleolimnological data. For each study, we identified the environmental variables considered as possible drivers of phytoplankton (e.g., temperature, nutrients, light) and then we identified the measured phytoplankton response variable (e.g., cyanobacterial abundance, phytoplankton biovolume, chlorophyll *a*) and the observed effects of the drivers. The main drivers identified by each study explaining phytoplankton biomass variation were listed. (1) We assessed whether temperature and nutrients were both selected as main drivers, or whether just one of them was selected. (2) If nutrients were selected, we analyzed whether N or P was more important or if both were considered as explanatory variables. (3) We analyzed whether each study quantified the combined effect of nutrients and temperature and, if so, what the effect was; i.e., no effect, negative, additive, or synergistic.

Results

EPA NLA dataset analysis—For all response variables, temperature and nutrients individually had positive, significant effects; however, nutrients were consistently significantly more important than temperature (Table 1). We also found that there were no significant interaction effects, either positive or negative, of nutrient concentration (either TN or TP) and temperature on cyanobacterial biovolume and proportional cyanobacterial biovolume (Fig. 1; Table 1). However, chlorophyll *a* concentration showed significant ($p < 0.0001$) positive effects of a nutrient and temperature interaction, indicating synergism, irrespective of whether TN or TP was used in the analysis (Table 1).

In general, the effects of TN and TP were interchangeable in the analyses for each of the three response variables; i.e., regardless of which nutrient was used, the same general result as to the relative importance of nutrient vs. temperature was observed. Taken together, the overall regression model with three predictor terms (nutrient concentration, temperature, and their interaction), explained a substantial amount of the total variation in

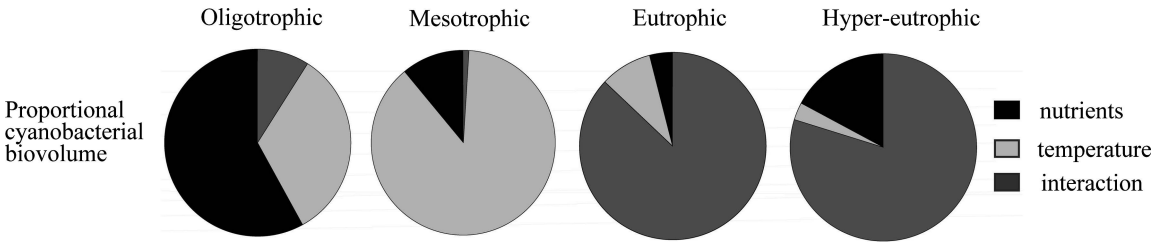

Fig. 2. The relative effects of nutrients, temperature, and their interaction on the proportional cyanobacterial biovolume in oligotrophic, mesotrophic, eutrophic, and hyper-eutrophic lakes.

chlorophyll *a* (60–61%), but only explained 4–15% of the variation in cyanobacterial biovolume or proportional cyanobacterial biovolume (Table 1).

The relative importance of nutrients and temperature for driving cyanobacterial dominance (proportional cyanobacterial biovolume) varied with trophic state (Table 2; Fig. 2). In oligotrophic lakes, nutrients were more important than temperature, whereas in mesotrophic lakes, temperature was more important, and in eutrophic and hyper-eutrophic lakes, the positive interaction between temperature and nutrients explained most of the variation in proportional cyanobacterial biovolume, despite the fact that the interaction between the two drivers was not significant when examined across all lake trophic states. Only eutrophic and hyper-eutrophic lakes exhibited significant interactions between the two drivers; both of these interactions were synergistic.

Moreover, we found that the sensitivity to nutrients and temperature was taxon-specific among cyanobacteria (Table 3). Nutrients contributed a significantly larger proportion of overall model R^2 than temperature for the proportional biovolume of *Aphanizomenon*, *Anabaena*, *Chroococcus*, *Coelosphaerium*, *Phormidium*, and *Synechococcus*, while temperature was significantly more important for *Lyngbya*, *Merismopedia, Microcystis*, and *Oscillatoria*. Of the 11 taxa, only one of them (*Aphanocapsa*) exhibited a significant interaction effect that was more important than the individual effects of nutrients or temperature (Fig. 3). For all taxa, regardless of the nutrient used (TN or TP), the relative sensitivity of nutrients vs. temperature did not change.

The parameters and their standard errors for the multiple linear regression models describing the three response variables, trophic states, and cyanobacterial taxa are listed respectively in Tables 4, 5, and 6.

Literature review—In total, we analyzed 35 published studies that measured the effects of nutrients, temperature, and other environmental factors on phytoplankton and cyanobacteria (Fig. 4; Web Appendix www.aslo.org/lo/toc/vol_59/issue_1/0099a.html). The number of published papers on this subject has increased considerably in the past few years, indicating a growing scientific interest in the effects of eutrophication and climate on cyanobacteria. The scope of the more recent papers tended to include not only the identification of the main drivers controlling phytoplankton and cyanobacterial biomass, but also how those multiple factors interacted. In addition, the more recent studies extended from a local to a regional scale, as shown by the larger number of studies that included multiple lakes and compared drivers among several systems (*see* Web Appendix).

Most of the studies (21 out of 35, 60%) (Anneville et al. 2002; Hamilton et al. 2002; De Senerpont Domis et al. 2007) found that both the individual effects of temperature and nutrients were important drivers of variation in cyanobacterial abundance or biomass. Most (19) of the 21 studies that found significant main effects of temperature and nutrients were conducted in eutrophic and hyper-eutrophic systems (Elliott and May 2008; Wagner and Adrian 2009; Kosten et al. 2012). Only a few studies (4 out of 35; 11%) (Blenckner et al. 2007; Thies et al. 2012) found that the direct or indirect effects of temperature in isolation were the main controlling driver of cyanobacterial biomass. Of these four studies, one was conducted in an oligotrophic lake (Bloch and Weyhenmeyer 2012), one in a eutrophic lake undergoing restoration (Thies et al. 2012), and two included multiple ecosystems with different trophic states ranging from oligotrophic to eutrophic (Blenckner et al. 2007; Shimoda et al. 2011). Nutrients (i.e., either TN or TP, or both) in isolation were found to be solely responsible for changes in cyanobacteria in 8 of the 35 studies (23%) (Battarbee and Bennion 2012; Feuchtmayr et al. 2012). Of those eight studies, four were conducted in microcosms or mesocosms with eutrophic conditions (Moss et al. 2003; Christoffersen et al. 2006; Feuchtmayr et al. 2010), three were conducted in eutrophic and mesotrophic lakes (Elliott 2010; Battarbee and Bennion 2012; Feuchtmayr et al. 2012), and one in a hyper-eutrophic system (Eilers et al. 2004). Only three studies found that other factors (e.g., zooplankton, macrophytes) were most responsible for driving variation in cyanobacterial biomass (Ruggiu et al. 1998; Genkai-Kato and Carpenter 2005; Loverde-Oliveira et al. 2009).

Finally, the study type (e.g., modeling, observations) played a role in whether nutrients or temperature was primarily responsible for cyanobacterial biomass (Web Appendix). Most of the experimental and paleolimnological studies identified nutrients as the most important driver. In contrast, the majority of the modeling articles found the interaction of temperature and nutrients to be most important. No clear trend was observed for the articles based on monitoring observations. It is unclear why the study type would have this effect on the importance of nutrients and temperature in driving cyanobacterial biovolume.

Table 3. Regression models testing the effects of nutrient and temperature on the proportional biovolume of 11 cyanobacterial species (p, R^2, 95% confidence intervals (CI) are shown). Only the nutrient (TN or TP) explaining the most variation in the response variable (determined by R^2 fit) was used in the analysis (in bold, *see* Table 6 for both nutrients' regression models). The most important predictor term (either nutrients, temperature, or their interaction) is in bold. If the differences between the two predictors' 95% confidence intervals (CI) did not include zero, the two predictors contributed a significantly different proportion of the overall R^2, which is noted. Significant interactions between nutrients and temperature are italicized.

Species	Model R^2 with TN	Model R^2 with TP	Nutrient			Temperature			Significant difference between the contribution of nutrients and temperature?	Interaction		
			R^2	95% CI	p	R^2	95% CI	p		R^2	95% CI	p
Anabaena	0.019	**0.022**	**0.54**	**0.15–0.86**	0.0002	0.46	0.09–0.80	0.002	No	0.002	0–0.22	0.81
Aphanizomenon	0.03	**0.04**	**0.94**	**0.73–0.99**	<0.0001	0.05	0.003–0.23	0.32	Yes	0.01	0–0.15	0.50
Aphanocapsa	**0.014**	0.012	0.15	0.002–0.57	0.17	0.23	0.003–0.86	0.049	No	**0.62**	**0.04–0.94**	*0.002*
Chroococcus	**0.018**	0.012	0.44	0.04–0.81	0.002	**0.56**	**0.13–0.92**	0.002	No	0.006	0.0001–0.25	0.72
Coelosphaerium	**0.03**	0.02	**0.86**	**0.51–0.98**	<0.0001	0.12	0.009–0.42	0.09	Yes	0.02	0–0.14	0.38
Lyngbya	**0.054**	0.048	0.08	0.01–0.26	0.0003	**0.84**	**0.63–0.96**	<0.0001	Yes	*0.08*	*0.004–0.20*	*0.02*
Merismopedia	**0.014**	0.012	0.02	0.003–0.41	0.46	**0.81**	**0.30–0.98**	0.0004	No	0.17	0.0007–0.59	0.10
Microcystis	0.092	**0.093**	0.05	0.006–0.16	0.23	**0.95**	**0.83–0.99**	<0.0001	Yes	0	0–0.03	0.33
Oscillatoria	**0.087**	0.085	0.02	0.004–0.10	0.45	**0.97**	**0.88–0.99**	<0.0001	Yes	0.007	0–0.07	0.41
Phormidium	**0.04**	0.03	**0.76**	**0.52–0.95**	<0.0001	0.15	0.02–0.35	0.002	Yes	0.09	0.001–0.28	*0.03*
Synechococcus	**0.06**	0.05	**0.97**	**0.82–1.00**	<0.0001	0.02	0.002–0.12	0.60	Yes	0.01	0–0.09	0.41

Discussion

Overall, nutrients and temperature were both important for explaining variation in cyanobacteria and phytoplankton, but generally nutrients were significantly more important than temperature for chlorophyll *a*, cyanobacterial biovolume, and proportional cyanobacterial biovolume. However, their relative importance varied depending on the trophic state of the system and the cyanobacterial taxon.

Contrary to our hypotheses, we found that across the entire EPA NLA dataset, nutrients and temperature did not synergistically interact to promote cyanobacterial biovolume or dominance. Rather, we observed that the effects of nutrients and temperature were predominantly additive, i.e., individually important in the absence of significant interactions. In the EPA NLA analyses, we focused specifically on the possibility of synergistic interactions, since this would amount to a "worst case scenario" in terms of bloom development. For subsets of the data, especially the eutrophic and hyper-eutrophic lakes, all of the significant interactions were positive, indicative of synergistic interactions. However, the interaction between nutrients and temperature could become antagonistic if lake water temperatures exceed the optimal temperature for cyanobacterial growth (present day mean optimal temperature for cyanobacteria is 29°C; Lurling et al. 2013). It is possible that antagonism between the two drivers may become increasingly likely, given the predicted increased incidence of heat wave temperatures (IPCC 2007).

The overall EPA NLA dataset results were generally in agreement with the findings in the literature review. Both analyses identified nutrients and temperature as being critical factors for phytoplankton growth and, when examining only one driver in isolation, nutrients were more important than temperature in the majority of cases. In the literature review, nine of the studies selected nutrients separately as most important, while only three selected temperature. Likewise, for the three response variables examined in the EPA NLA analysis, nutrients were generally the best explanatory variable.

There are a few caveats that affect the comparison between the literature review and the EPA NLA analysis, however. (1) In most of the published studies, only the effects of phosphorus (not the combination of nitrogen and phosphorus) on cyanobacteria were analyzed. (2) Only a few studies (6 out of 35) quantitatively examined the interaction between nutrients and temperature on phytoplankton. Of those six papers, four of them (e.g., Elliott and May 2008; Shimoda et al. 2011; Elliott 2012) were modeling studies that found synergistic interactions between the two drivers. (3) In the majority of the studies, the effects of nutrients and temperature were not analyzed for individual cyanobacterial taxa; instead, they considered cyanobacteria as an aggregate group (Jeppensen et al. 2005; Blenckner et al. 2007; Bloch and Weyhenmeyer 2012), with two exceptions: Posch et al. (2012) identified both nutrients and temperature individually as directly supporting the growth of *Planktothrix rubescens*, and Jöhnk et al. (2008)

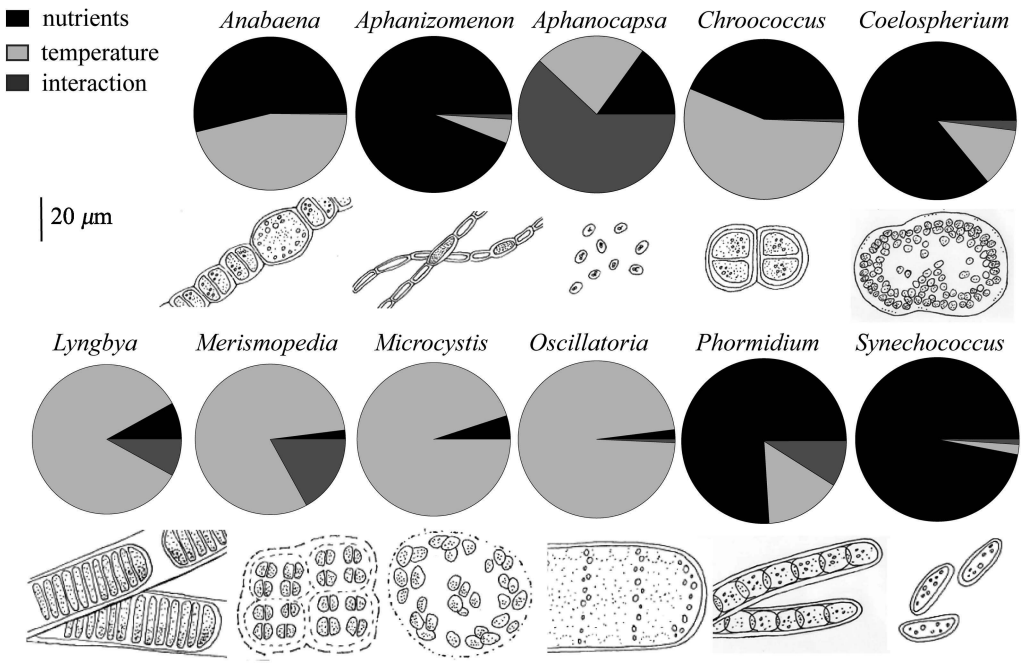

Fig. 3. The relative effects of nutrients, temperature, and their interaction on the proportional biovolume of 11 cyanobacterial taxa. Drawings by A. Rigosi show the typical morphology of each taxon, scaled to 20 μm.

identified temperature as the most important driver of *Microcystis aeruginosa*.

Importance of nutrients and trophic state—We found that the importance of nitrogen and phosphorus for the EPA NLA lakes was generally interchangeable in comparison with temperature. This result suggests that for the lakes in the NLA dataset, the importance of nitrogen vs. phosphorus in driving eutrophication (Schindler 2001; Schindler et al. 2008; Conley et al. 2009) may be less important than previously thought for explaining variation in cyanobacterial biovolume. It also emphasizes that efforts to control both nutrients will be beneficial for managing cyanobacteria.

Our results show an intriguing pattern with respect to how trophic state controls the relative importance of nutrients, temperature, and their interaction across the EPA NLA lakes (Fig. 2). In oligotrophic lakes, nutrients were much more important than temperature. Conversely, in eutrophic and hyper-eutrophic lakes, nutrients were still important, but overwhelmingly through their interaction with temperature and not individually. Interestingly, at the intermediate nutrient status of mesotrophic lakes, nutrients played a minor role in comparison with temperature. Brookes and Carey (2011) hypothesized that low-nutrient lakes are more sensitive to nutrient increases than temperature increases and consequently will not respond to increased water temperatures in isolation, which is supported by our findings. Brookes and Carey (2011) also hypothesized that cyanobacteria will only respond to increased temperature at higher nutrient levels. As such, the higher nutrient status of mesotrophic lakes, and their sensitivity to increased temperature, is still in line with Brookes and Carey (2011).

Surprisingly, however, the role of temperature as an individual driver decreased when nutrient status increased from mesotrophic to eutrophic and hyper-eutrophic, and the positive interaction of the two factors became more important. While we do not have the data to definitively determine the mechanisms driving this result, we hypothesize that this may be because at high nutrient levels another key phytoplankton resource, light, becomes limiting for cyanobacterial development (Ganf and Oliver 1982; Bouterfas et al. 2002; Huisman et al. 2004). The availability of light in high-nutrient systems is ultimately driven by both nutrient loading and temperature; thus, although light was not part of our original analysis, it is indirectly implicated through its interaction with high nutrients and temperatures. Specifically, it is well established that at high nutrient loading levels, increased productivity will result in greater light limitation for bloom development (Scheffer et al. 1997). Furthermore, the duration and strength of thermal stratification is affected both by temperature increases (Livingstone 2003) and by nutrient increases, promoting phytoplankton growth and thereby heat absorption at the surface layer (Kumagai et al. 2000). Thermal stratification and turbulent mixing determine the residence time of phytoplankton in the euphotic layer, thereby further affecting light availability (MacIntyre and Romero 2000; MacIntyre and Jellison 2001; Zohary et al. 2010). In eutrophic and hyper-eutrophic lakes, high nutrient levels may accentuate both resource (light) limitation as well as the (indirect) effects of warming on stratification, resulting in enhanced interactions between nutrients and temperature. Consequently, we suggest that an interaction between nutrient availability and temperature may alter the sensitivity of cyanobacteria to warming

Table 4. The overall regression models testing the effects of nutrients (ln-transformed total nitrogen (TN) or total phosphorus (TP)), temperature, and their interaction on phytoplankton response variables. SE refers to standard error.

Response variable	Nutrient tested	Intercept parameter ± SE	Nutrient parameter		Temperature parameter		Interaction parameter	
			Value ± SE	*p*	Value ± SE	*p*	Value ± SE	*p*
Chlorophyll *a*	TN	−0.09±0.21	0.37±0.14	<0.0001	0.11±0.01	<0.0001	0.03±0.01	<0.0001
Chlorophyll *a*	TP	0.76±0.43	0.28±0.10	<0.0001	0.16±0.02	<0.0001	0.02±0.004	<0.0001
Cyanobacterial biovolume	TN	8.12±0.62	0.43±0.42	<0.0001	0.17±0.03	<0.0001	0.02±0.02	0.25
Cyanobacterial biovolume	TP	9.71±1.29	0.50±0.31	<0.0001	0.17±0.05	<0.0001	0.004±0.01	0.75
Proportional cyanobacterial biovolume	TN	−3.49±0.65	−0.16±0.45	<0.0001	0.08±0.03	0.02	0.03±0.02	0.12
Proportional cyanobacterial biovolume	TP	−2.27±1.36	0.27±0.33	<0.0001	0.07±0.06	0.02	0.005±0.01	0.71

temperatures in nutrient-rich lakes via their combined effects on the light environment.

Thus, low nutrient availability controlled variation in cyanobacterial biomass in nutrient-poor (oligotrophic) lakes, and high nutrient availability with thermal stratification (as together both factors determine the light environment) controlled variation in nutrient-rich (eutrophic and hyper-eutrophic) lakes. In mesotrophic systems, the combined resources of nutrients and light were at levels that decreased the likelihood that they were limiting for phytoplankton growth (i.e., they were at sufficient levels to prevent nutrient limitation of growth, but not so high as to cause light limitation), allowing temperature to be the most likely resource that was controlling cyanobacterial development.

Our literature review generally provided complementary results to the EPA NLA analysis as to how trophic state may influence the drivers controlling cyanobacterial development. In agreement with our statistical findings, the studies that identified both temperature and nutrients as significant drivers were from lakes of eutrophic or hyper-eutrophic status, regardless of the type of study conducted (e.g., modeling, observations). For example, Wagner and Adrian (2009) identified both phosphorus and thermal stratification (i.e., the interaction between nutrient availability, temperature, and light) as key driving factors of cyanobacteria in hyper-eutrophic Lake Müggel (Müggelsee). This was also observed for 143 eutrophic and hyper-eutrophic lakes in South America, indicating that in systems characterized by high biovolume, the interaction of light availability with temperature and nutrients was the main driver of phytoplankton (Kosten et al. 2012). This was confirmed by other studies conducted in eutrophic systems either using modeling (Elliott et al. 2006; Elliott and May 2008) or monitoring data (Jöhnk et al. 2008; Blank et al. 2009).

Within the literature review, only a few studies on oligotrophic systems were available (Blenckner et al. 2007; Shimoda et al. 2011; Bloch and Weyhenmeyer 2012). In those studies, the phytoplankton community composition was primarily driven by changes in water temperature, and not nutrients, in contrast with the results of the EPA NLA dataset analysis. It is difficult to make conclusions about these studies due to their limited sample size of lakes and the difficulty in extracting data on oligotrophic lakes included within larger meta-analyses (Blenckner et al. 2007), especially without knowing the cyanobacterial taxa being considered.

Comparison of phytoplankton vs. cyanobacterial response variables—In our analysis, we examined the effects of nutrients and temperature on three different response variables: chlorophyll *a*, a proxy of total phytoplankton biomass; cyanobacterial biovolume, to quantify the biomass of cyanobacteria; and proportional cyanobacteria biovolume, to describe the dominance of cyanobacterial biovolume in respect to total phytoplankton biovolume. For all response variables, we found that the most important explanatory driver was nutrient availability, but a slightly different response was found when examining chlorophyll *a*, which exhibited a synergistic interaction

Table 5. The overall regression models testing the effects of nutrients (ln-transformed total nitrogen (TN) or total phosphorus (TP)), temperature, and their interaction on phytoplankton response variables for four trophic states. SE refers to standard error.

State	Nutrient tested	Intercept parameter ± SE	Nutrient parameter		Temperature parameter		Interaction parameter	
			Value ± SE	*p*	Value ± SE	*p*	Value ± SE	*p*
Oligotrophic	TN	−2.12±2.68	0.78±1.36	0.24	−0.01±0.11	0.55	−0.02±0.06	0.68
Oligotrophic	TP	−0.87±7.74	0.50±1.39	0.33	−0.04±0.34	0.45	−0.01±0.06	0.84
Mesotrophic	TN	−4.58±0.02	0.86±0.59	0.17	0.10±0.08	0.001	−0.03±0.07	0.7
Mesotrophic	TP	3.03±14.27	2.04±3.40	0.18	−0.13±0.57	0.001	−0.06±0.14	0.66
Eutrophic	TN	−1.27±1.16	−3.95±1.36	0.54	−0.002±0.05	0.36	0.16±0.06	0.005
Eutrophic	TP	−2.25±10.0	−0.66±3.40	0.42	0.08±0.38	0.36	0.04±0.13	0.75
Hyper-eutrophic	TN	0.80±2.09	−3.61±1.50	0.24	−0.09±0.08	0.46	0.17±0.06	0.007
Hyper-eutrophic	TP	−6.26±2.45	−3.91±1.64	0.96	0.23±0.11	0.76	0.17±0.07	0.02

between nutrients and temperature. This indicates that studies that only examine chlorophyll *a* as a response variable and find significant interaction effects may not be representative of the cyanobacterial population composing the total phytoplankton biomass signal. Genkai-Kato and Carpenter (2005) and Elliott et al. (2006) also found that total chlorophyll *a* and cyanobacterial biomass responded differently to changes in the nutrients and temperature. Consequently, studies on the synergistic effects of these two drivers on the phytoplankton community will be sensitive to the choice of response variable.

Taxon-specific effects on the importance of nutrients vs. temperature—In Figs. 1, 2, the cyanobacterial community was examined as one homogeneous group, highlighting how the community as a whole will respond to changes in their environment. However, as illustrated in Fig. 3, cyanobacteria are a heterogeneous group, spanning a large range in size and morphology. For some genera, nutrients explained almost all of the variation in proportional biovolume across the lakes (e.g., *Aphanizomenon, Synechococcus*), while for others temperature was much more important (e.g., *Microcystis, Oscillatoria*). Thus, studies on climate and eutrophication effects on cyanobacteria as a whole should be interpreted as the contribution of a community of diverse genera. These considerations also support the conclusions of Carey et al. (2012), who suggested that differences in the ecophysiology among cyanobacterial taxa will result in different responses to climate change.

In Table 7, we identify several traits that may be important for explaining the sensitivity of each genus to either nutrients or temperature. Trait-based approaches have a long history in phytoplankton ecology (Margalef 1983; Margalef 1997; Reynolds 2006) and have recently gained even more attention (Litchman et al. 2010; Pomati et al. 2012; Edwards et al. 2013). In contrast to taxonomic

Table 6. The overall regression models testing the effects of nutrients (ln-transformed total nitrogen (TN) or total phosphorus (TP)), temperature, and their interaction on phytoplankton response variables for each of cyanobacterial taxa. SE refers to standard error.

Cyanobacterial taxa	Nutrient tested	Intercept parameter ± SE	Nutrient parameter		Temperature parameter		Interaction parameter	
			Value ± SE	*p*	Value ± SE	*p*	Value ± SE	*p*
Anabaena	TN	−6.53±0.82	0.32±0.56	0.0006	0.09±0.03	0.002	0.0006±0.02	0.98
Anabaena	TP	−6.13±1.70	0.16±0.41	0.0002	0.10±0.07	0.002	0.004±0.02	0.81
Aphanizomenon	TN	−13.41±0.81	0.72±0.56	<0.0001	0.03±0.03	0.30	−0.006±0.02	0.80
Aphanizomenon	TP	−11.16±1.68	0.72±0.41	<0.0001	−0.02±0.07	0.32	−0.01±0.02	0.50
Aphanocapsa	TN	−5.23±0.87	1.99±0.60	0.17	−0.12±0.04	0.049	−0.08±0.03	0.002
Aphanocapsa	TP	−2.39±1.82	1.20±0.44	0.26	−0.26±0.08	0.10	−0.06±0.02	0.003
Chroococcus	TN	−8.43±0.83	0.50±0.57	0.002	0.08±0.03	0.002	−0.009±0.02	0.72
Chroococcus	TP	−8.57±1.73	0.12±0.42	0.73	0.07±0.07	0.0004	−0.008±0.02	0.66
Coelosphaerium	TN	−6.88±0.27	0.04±0.18	<0.0001	0.02±0.01	0.09	0.007±0.008	0.38
Coelosphaerium	TP	−6.17±0.56	0.20±0.13	0.0003	−0.001±0.02	0.049	−0.005±0.006	0.36
Lyngbya	TN	−9.99±0.52	−0.66±0.36	0.0003	0.14±0.02	<0.0001	0.04±0.02	0.02
Lyngbya	TP	−11.20±1.09	−0.45±0.26	0.01	0.21±0.05	<0.0001	0.02±0.01	0.04
Merismopedia	TN	−9.45±0.63	0.71±0.43	0.45	0.06±0.03	0.0004	−0.03±0.02	0.10
Merismopedia	TP	−0.10±1.30	−0.04±0.32	0.84	0.08±0.05	0.0003	0.0003±0.01	0.98
Microcystis	TN	−12.64±0.75	0.23±0.51	0.23	0.25±0.03	<0.0001	−0.02±0.02	0.33
Microcystis	TP	−0.14±1.56	−0.21±0.38	0.10	0.27±0.07	<0.0001	0.0005±0.02	0.98
Oscillatoria	TN	−11.07±0.71	−0.58±0.48	0.45	0.26±0.03	<0.0001	0.02±0.02	0.41
Oscillatoria	TP	−12.74±1.47	−0.59±0.36	0.23	0.34±0.06	<0.0001	0.03±0.02	0.09
Phormidium	TN	−4.59±0.43	0.98±0.30	<0.0001	−0.07±0.02	0.002	−0.03±0.01	0.03
Phormidium	TP	−2.47±0.90	0.77±0.22	<0.0001	−0.13±0.04	0.004	−0.02±0.009	0.009
Synechococcus	TN	−3.80±0.65	−1.08±0.44	<0.0001	−0.0006±0.03	0.60	0.02±0.02	0.41
Synechococcus	TP	−5.85±1.36	−0.76±0.33	<0.0001	0.03±0.06	0.51	0.01±0.01	0.35

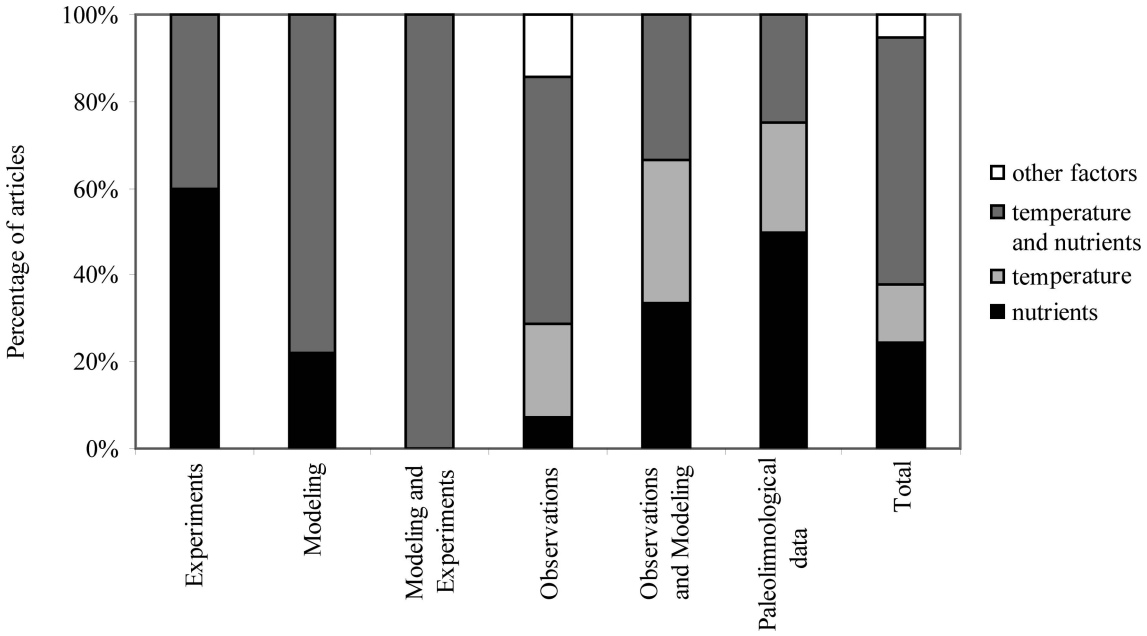

Fig. 4. Percentage of articles, depending on the method used, that identified nutrients, temperature, both nutrients and temperature (independently of the type of interaction), or other factors (e.g., zooplankton, macrophytes, or light) as the major driver of cyanobacterial biomass.

classifications, functional approaches allow the organization of phytoplankton taxa by key functional traits. In the functional classifications developed by Reynolds et al. (2002) and Kruk et al. (2010), cyanobacteria are categorized into several different groups, emphasizing the large differences among cyanobacterial taxa. All in all, we conclude that there is no support for the notion that cyanobacteria—as a group—will respond in a coherent manner to changes in their environment. More specifically, there is little to support the common perception that all cyanobacterial taxa will equally benefit from eutrophication and climate change.

A more important question is which taxa will respond favorably to nutrient enrichment and which will respond favorably to lake warming (or both and perhaps even synergistically)? The functional classification by Reynolds et al. (2002) is based upon general morphometric traits such as cell size and surface area to volume ratio (SA : V), as well as specific phytoplankton traits such as motility and the ability to fix nitrogen. Using the Reynolds classification (Table 7), small cyanobacteria such as *Synechococcus* belong to Group Z, which consists of prokaryotic picoplankton adapted to clear, low-nutrient waters. These small cells are strong competitors for limiting nutrients on the basis of their high SA : V. According to the Reynolds classification, their distinct preference for clear water and low nutrients may explain why nutrients are a better predictor than temperature for this taxon.

On the other end of the spectrum—with respect to tolerance to light deficiency—we find filamentous cyanobacteria such as *Planktothrix agardhii*, which is grouped into the Reynolds S1 classification (Reynolds et al. 2002). These slender cyanobacteria are strong competitors for light and tolerant to turbid environments because of their very low energy maintenance requirements (Mur et al. 1977). Given what we know about the key traits of *P. agardhii* and their preferred habitat—highly eutrophic conditions that enable the species to create sufficient shade—we would expect this group to be more sensitive to nutrients than temperature. We found the opposite, however; temperature explained almost all of the variation in *Oscillatoria* or *Planktothrix* abundance in the EPA NLA dataset. This may be because the EPA NLA dataset only classifies cells to genus, not species, and other *Oscillatoria* or *Planktothrix* species, such as *P. rubescens* (Reynolds group R), are highly tolerant to light deficient and mixed conditions (Dokulil and Teubner 2000; Walsby et al. 2001). *P. rubescens* produces gas vesicles resistant to high external pressure and allows them to maintain buoyancy even when carried to deeper layers by convective mixing (D'Alelio et al. 2011). Consequently, temperature, and in particular the indirect effects of temperature, are expected to play a major role in determining the abundance of *P. rubescens* (Reynolds 2006), as was observed in this study. A genus such as *Oscillatoria* or *Planktothrix* contains species with very different preferred habitats and has more than 60 taxonomically accepted species (Guiry and Guiry 2013). Posch et al. (2012) studied *P. rubescens* and identified both temperature and nutrients as directly supporting its growth. For many of these species, we have insufficient ecophysiological understanding to interpret their responses to drivers such as nutrients or temperature.

Likewise, Fig. 3 shows that temperature explains most of the variation in the occurrence of *Microcystis*, one of the most noxious cyanobacterial taxa. In Reynolds' functional classification, *Microcystis* species falls into Group L_M. *Microcystis* has often been pointed to as a species with an exceptionally high Q_{10} (Reynolds 2006), yet Lürling et al. (2013) found no evidence that *Microcystis* does better at

Table 7. Major characteristics of the cyanobacterial taxa analyzed in this study, with classification in morphological-based functional groups (MBFG) (Kruk et al. 2010) and Reynolds groups (Reynolds et al. 2002); tolerance and sensitivities to environmental factors are also included (Pollinger 1991; Komarek and Komarkova-Legnerova 1992; Padisak et al. 2009).

Genus	Morphology	MBFG	Vacuoles	Reynolds group	Habitat	Tolerances	Sensitivities
Anabaena	Filamentous, N fixer	III	Yes	H1, H2	N fixing	Low nitrogen	Mixing, poor light
Aphanizomenon	Filamentous, N fixer	III (filaments up to 2 cm)	Yes	H1	N fixing	Low nitrogen	Mixing, poor light
Aphanocapsa	Colonial, irregular, many celled	VII	No (depending on species)	K	Short nutrient rich columns		Deep mixing
Chroococcus	Colonial—few cells	II	No	L	Summer epilimnia, oligotrophic to mesotrophic lakes	Low carbon	Prolonged and deep mixing
Coelosphaerium	Colonial, aggregated in mucilaginous irregular sphere	IV (cells ~1 μm, colony 25–100 μm)	No	L_0	Summer epilimnia, mesotrophic lakes	Nutrients	Mixing
Lyngbya	Filamentous, non-heterocystous	III	No	S1	Turbid mixed layers (mat forming)	Light deficiency	Flushing
Merismopedia	Colonial 4–16 cells per colony	VII	Depending on species	L_0	Summer epilimnia, mesotrophic lakes	Nutrients	Mixing
Microcystis	Colonial	VII	Yes	L_M	Summer epilimnia, eutrophic lakes	Very low C	Mixing, poor stratification light
Oscillatoria	Filamentous, non-heterocystous	III	Yes	S1	Turbid mixed layer	Highly light deficient conditions	Flushing
Phormidium	Filamentous, non-heterocystous	III (microscopic to colony of several cm diameter)	No	S1, T_C	Well mixed epilimnia	Light deficiency	Nutrient deficiency
Synechococcus	Unicellular, solitary or aggregated	I	No	Z	Clear mixed layers	Low nutrient	Light deficiency

elevated temperature than other phytoplankton. Carey et al. (2012) concluded that the indirect consequences of climate warming—in particular, the enhanced stability of the water column—may be more important than the direct effects of temperature on metabolism and growth for promoting this species. *Microcystis* benefits greatly from water column stability, since its efficient buoyancy regulation allows it to concentrate its population in the illuminated near-surface layer of stable lakes (Ibelings and Maberly 1998; Brookes and Ganf 2001). The dominant role of temperature in explaining *Microcystis* biomass observed in our data (Fig. 3) seems in concert with what we know about key traits and preferred habitat of this genus. This was also supported by our literature results: the study by Jöhnk et al. (2008) on *M. aeruginosa* identified temperature as its most important driver.

Other well-studied taxa generally exhibit temperature or nutrient dependency that is partly in line with what is known about their ecophysiology and traits. *Merismopedia* is classified by Reynolds et al. (2002) as tolerant to changes in nutrients (Group L_0), which is in accordance with our finding that its variation is primarily explained by temperature. The taxa *Aphanizomenon* and *Anabaena* are clustered in Reynolds Groups H1 and H2 and are tolerant to low N because of their ability to fix N from the atmosphere. On the basis of this specific trait, one would expect nutrient levels to explain much of the variation in the biovolume of N fixers in lakes (as low N availability favors N fixers and high N may preclude them), as we observed. Moreover, since N fixation is an energetically costly process (Stal et al. 2010), it is also understandable why these taxa tend to be sensitive to low irradiance so that even under low N availability they may be excluded from very nutrient-rich and hence turbid lakes (Zevenboom and Mur 1980). All in all, it makes sense that nutrients explain most of the variation in the occurrence of these two taxa.

Perfect matches between species distributions and what we understand of the ecophysiology of individual taxa clearly cannot always be expected, especially across $>$ 1000 lakes that span a wide gradient of environmental conditions. This limits the possibilities for a full interpretation of the patterns shown in Fig. 3. On the other hand, the patterns we observed may be able to stimulate further research on key ecophysiological traits of cyanobacteria.

The EPA NLA analysis demonstrated that both nutrients and temperature were important factors controlling cyanobacteria, although nutrients generally explained more variation in cyanobacterial biovolume and dominance. We find support for this result in many papers published on this topic. In the future, the relative importance of these two factors may change, especially in countries that are able to successfully reduce eutrophication with legislation. Interestingly, we found that the sensitivity of cyanobacteria to these two drivers was dependent on the trophic state and taxon being considered, which may increase the challenge of comparing results from different systems and comparing outcomes between the literature review and the statistical analysis. Moreover, contrary to our hypotheses, our analyses showed that in the majority of the cases the interaction between nutrients and temperature was not synergistic. As such, it may be possible that the hypothesized interaction of both temperature and nutrients in driving cyanobacterial biovolume is overrepresented in the literature because the studies examining these relationships have primarily been conducted in lakes with high nutrient concentrations. Finally, our work supports the suggestion of Brookes and Carey (2011) and Kosten et al. (2012) that nutrient remediation could offset, to some degree, the stimulatory effect that increasing temperature is likely to have on most cyanobacteria.

Acknowledgments

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