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Comparison of cyanobacterial and green algal growth rates at different temperatures

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SUMMARY

1. The hypothesis that cyanobacteria have higher optimum growth temperatures and higher growth rates at the optimum as compared to chlorophytes was tested by running a controlled experiment with eight cyanobacteria species and eight chlorophyte species at six different temperatures (20–35 °C) and by performing a literature survey.
2. In the experiment, all organisms except the chlorophyte *Monoraphidium minutum* grew well up to 35 °C. The chlorophyte *Chlamydomonas reinhardtii* was the fastest-growing organism over the entire temperature range (20–35 °C).
3. Mean optimum growth temperatures were similar for cyanobacteria (29.2 °C) and chlorophytes (29.2 °C). These results are concordant with published data, yielding slightly higher mean optimum growth temperatures for cyanobacteria (27.2 °C) than for chlorophytes (26.3 °C).
4. Mean growth rates of cyanobacteria at 20 °C (0.42 day^{-1}) were significantly lower than those of chlorophytes at 20 °C (0.62 day^{-1}). However, at all other temperatures, there were no differences between mean growth rates of cyanobacteria and chlorophytes.
5. Mean growth rates at the optimum temperature were similar for cyanobacteria (0.92 day^{-1}) and chlorophytes (0.96 day^{-1}). However, analysis of published data revealed that growth rates of cyanobacteria (0.65 day^{-1}) were significantly lower than those of chlorophytes (0.93 day^{-1}) at their optimum temperatures.
6. Although climate warming will probably lead to an intensification of cyanobacterial blooms, our results indicate that this might not be as a result of higher growth rates of cyanobacteria compared with their chlorophyte competitors. The competitive advantage of cyanobacteria can more likely be attributed to their ability to migrate vertically and prevent sedimentation in warmer and more strongly stratified waters and to their resistance to grazing, especially when warming reduces zooplankton body size.

Keywords: blooms, climate change, competition, global warming, optimum growth

Introduction

Cyanobacteria dominate the phytoplankton community during the warmer periods of the year in temperate regions when sufficient resources are available to build heavy blooms (Watson, McCauley & Downing, 1997). Cyanobacterial blooms and surface scums are a threat to environmental health and public safety as many cyanobacteria produce a variety of potent toxins and nasty odours. Blooms may, furthermore, cause high turbidity, anoxia, fish kills and food-web alterations (Codd, Morrison & Metcalf, 2005; Dittmann & Wiegand,

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2006; Paerl, 2008; Paerl & Huisman, 2008, 2009). The incidence and intensity of cyanobacterial blooms are on the rise worldwide (Figueiredo de *et al.*, 2004). Climate change is expected to further aggravate these nuisance blooms. Altered precipitation patterns augmenting external nutrient loadings and increasing residence time, elevated atmospheric carbon dioxide concentration, higher salinity and direct and indirect temperature effects are all expected to act in concert in promoting cyanobacteria (de Senerpont Domis *et al.*, 2013; Ibelings & Maberly, 1998; Schippers, Lurling & Scheffer, 2004; Paerl & Huisman, 2009).

The indirect temperature effects favourable to cyanobacterial proliferations include enhanced water column stability and lower water density, increasing sinking loss of eukaryotic competitors, changes in zooplankton community structure which lower grazing pressure and enhanced nutrient efflux from the sediment (Jöhnk *et al.*, 2008; Jeppesen *et al.*, 2009; Paerl & Huisman, 2009). One of the most important temperature effects promoting cyanobacteria is the direct effect on phytoplankton growth rate. This notion is based on the assumption that cyanobacteria reach their maximum growth rate at temperatures at which the growth rates of competing eukaryotic phytoplankton are already declining (Jöhnk *et al.*, 2008; Paerl & Huisman, 2008, 2009).

Indeed, a whole range of studies indicate that cyanobacteria have higher optimal growth temperature than diatoms, which are generally better adapted to lower water temperatures than other phytoplankton species. Laboratory studies as well as studies comparing cold and warm field conditions, for example, indicate that the optimal growth temperatures of diatoms rarely exceeds 25 °C (Suzuki & Takahashi, 1995; Coles & Jones, 2000; Butterwick, Heaney & Talling, 2005; Jöhnk *et al.*, 2008; Shatwell, Köhler & Nicklish, 2008; Mitrovicz *et al.*, 2010). Comparisons between tropical and temperate lakes also indicate that diatoms are less abundant in tropical lakes than in temperate lakes, making up 14% and 37% of the overall phytoplankton biomass, respectively (Kalff & Watson, 1986). Controlled experiments with plankton communities as well revealed higher growth rates for cyanobacteria than for diatoms, where warming scenarios further stimulated cyanobacteria growth (de Senerpont Domis, Mooij & Huisman, 2007).

It is, however, not well substantiated that cyanobacteria have higher growth rates than chlorophytes. In laboratory experiments, chlorophyte growth rates were higher than cyanobacterial growth rates at all tested scenarios (de Senerpont Domis *et al.*, 2007). Additionally, in tropical lakes, on average 33% of the phytoplankton biomass was composed of chlorophytes, while this was only 7% in temperate lakes (Kalff & Watson, 1986). In that study, the share of cyanobacteria hardly differed between the climate regions: 30% in temperate lakes and 36% in tropical lakes (Kalff & Watson, 1986). In an overview of phytoplankton characteristics, Seip & Reynolds (1995) furthermore noted that both the optimum temperature for growth and maximum growth rates were slightly higher for chlorophytes than for cyanobacteria. Hence, the validity of the hypothesis that at higher temperatures growth rates of eukaryotic taxa decline when cyanobacterial growth rates reach their optima (Paerl & Huisman, 2009) is less evident for chlorophytes.

Therefore, we tested the hypothesis that cyanobacteria have higher optimum growth temperatures and higher growth rates at the optimum as compared to chlorophytes. We performed a literature survey on optimum growth temperatures and growth rates at the optimum temperature for both cyanobacteria and chlorophytes. Since different culturing techniques, experimental designs and endpoints might introduce variability among the compared studies, we also ran a controlled experiment with eight different cyanobacteria and eight different chlorophytes at six different temperatures in the same growth medium, light conditions and incubators.

Methods

Literature survey

A total of 62 optimum growth temperatures for cyanobacteria and 67 for chlorophytes were drawn from literature sources (Table S1), covering 16 cyanobacteria genera and 25 chlorophyte genera. In case exact numbers for growth rates were not given in text or tables, they were estimated from figures in the papers presented in Table S1.

Growth experiment

We estimated the optimum temperature for growth and corresponding growth rate of eight cyanobacteria and eight chlorophytes, all common inhabitants of freshwater systems. The cyanobacteria were *Anabaena* sp. Lemmermann 1896 strain PCC7122, *Aphanizomenon gracile* (Lemmermann) Lemmermann 1907 (isolate from pond Heikant, The Netherlands), *Cylindrospermopsis raciborskii* (Woloszýnska), Seenayya et Subba Raju 1972 strain LETC CIRF-01, *Microcystis aeruginosa* (Kützing) Kützing 1846 strains NIVA-CYA140 and PCC7941, *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek 1988 strains NIVA-CYA116 and NIVA-CYA126 and *Synechococcus*

elongatus (Nägeli) Nägeli 1849 strain PCC6301. The chlorophytes were *Ankistrodesmus falcatus* (Corda) Ralfs 1848 strain NIVA-CHL8, *Chlamydomonas reinhardtii* Dangeard 1888 strain NIVA-CHL13, *Desmodesmus bicellularis* (Chodat) An, Friedl & Hegewald strain CCAP276/14, *D. quadricauda* (Turpin) Hegewald strain UTEX614, *Monoraphidium minutum* (Nägeli) Komárková-Legnerová 1969 (originated from University of Konstanz, Germany), *Scenedesmus acuminatus* (Lagerheim) Chodat 1902 strain UTEX415, *S. maximus* (West & West) Chodat 1913 strain SAG39.81 and *S. obliquus* (Turpin) Kützing 1833 strain SAG276/3a.

Cyanobacterial and chlorophyte stock cultures were maintained in 250-mL Erlenmeyer flasks containing 100 mL modified WC (Woods Hole modified CHU10)-medium (Lürling & Beekman, 2006) closed with a cellulose stopper. The flasks were placed at 22 °C in 80 μmol quanta m^{-2} s^{-1} provided in a 16:8 h light–dark cycle. Stock cultures were transferred to fresh medium every 3 weeks. Prior to the experiment, the organisms were acclimatised to the experimental conditions. Each culture was transferred to clean 250-mL Erlenmeyer flasks that contained 100 mL medium. The initial phytoplankton concentration in each flask was 50 μg chlorophyll-*a* L^{-1}, which was determined using a PHYTO-PAM phytoplankton analyser (Heinz Walz GmbH Effeltrich, Germany). These flasks were placed in incubators (Sanyo, MLR-351H) for 6 days at the same light and temperature regimes that would be used during the experiment (see next paragraph). Flasks were shaken manually twice every day.

The experiment was based on a randomised design with three replications (n = 3), six experimental temperatures (20, 25, 27.5, 30, 32.5 and 35 °C) and 16 species of freshwater phytoplankton yielding $3 \times 6 \times 16 = 288$ experimental units. The experimental units consisted of 100-mL Erlenmeyer flasks containing 50 mL WC medium and inocula (at 50 μg chlorophyll-*a* L^{-1}) from the acclimatised cultures. Each flask was shaken manually twice every day. Chlorophyll-*a* concentration in each flask was determined daily over a 4- or 6-day experimental period (allowing exponential growth) using the PHYTO-PAM phytoplankton analyser.

Data analysis

The slope of the regression line between natural log-transformed chlorophyll-*a* concentrations and time (experimental period) was used to estimate the population growth rate (Lürling, 2006). Optimum temperature was defined as the incubation temperature that yielded the highest growth rate. Optimum temperatures and corresponding growth rates were statistically compared by *t*-tests. Growth rates between cyanobacteria and chlorophytes were statistically compared with nonparametric Kruskal–Wallis tests, because Levene's test indicated that equal variances could not be assumed. Differences in growth rate between individual species were compared using Mann–Whitney U tests. Mean growth rates and optimum growth temperatures for cyanobacteria and chlorophytes derived from the literature survey were statistically compared using a *t*-test. Optimum growth temperatures and growth rates of a selection from the literature data to only representatives of the species that were also used in the experiment were compared with data from the experiment by running a one-way ANOVA. All analyses were performed with the statistical tool pack PASW Statistics (version 17.0.3, IBM Corporation, Armonk, NY, U.S.A.).

Results

All eight cyanobacteria used in this study were able to grow at the six different incubation temperatures (Table 1). One strain, *P. agardhii* NIVA-CYA126, formed large aggregates in all replicates at 27.5, 32.5 and 35 °C making it impossible to obtain a reliable growth rate estimate. Data for a few strains at 30 °C were omitted because of a malfunctioning temperature control unit. Optimum temperatures for growth varied between 25 and 35 °C for cyanobacteria and between 27.5 and 35 °C for chlorophytes. The chlorophyte *M. minutum* was the only species that had a negative growth rate at 35 °C (Table 1). The optimum growth temperatures of cyanobacteria and chlorophytes found in this study (Table 1) were identical and for each on average 29.2 °C. Also the growth rates at optimum temperatures were similar (t = 0.36; P = 0.730) and on average 0.96 day^{-1} for chlorophytes and 0.92 day^{-1} for cyanobacteria.

Growth rates differed significantly among species at each of the incubation temperatures ($\chi^2 \geq 19.9$; $P \leq 0.014$). For example, at 20 °C, growth rates of the cyanobacteria *M. aeruginosa* CYA140 and *S. elongatus* were significantly lower than those of the chlorophytes *C. reinhardtii*, *M. minutum* and *S. obliquus* (Table 1). At 20 °C, five of the eight chlorophytes had growth rates that exceeded the highest growth rate of the cyanobacteria at the same temperature (Table 1). The chlorophyte *C. reinhardtii* showed the highest growth rate of all tested species at each of the temperatures (Table 1). At 20 °C, overall growth rates for cyanobacteria (0.42 day^{-1}) were significantly lower ($Z = -2.97$; P = 0.003) than those for chlorophytes (0.62 day^{-1}) (Fig. 1). However, at all other temperatures, overall

Table 1 Mean growth rates (day^{-1}, ±one standard error, n = 3) for eight cyanobacteria and eight chlorophytes cultured at six different temperatures (20–35 °C)

	Temperature (°C)					
	20.0	25.0	27.5	30	32.5	35.0
Cyanobacteria						
Anabaena sp. PCC7122	0.46 ± 0.10	**0.93** ± 0.12	0.75 ± 0.01	ND	0.53 ± 0.03	0.58 ± 0.03
Aphanizomenon gracile	0.42 ± 0.02	0.58 ± 0.03	0.81 ± 0.01	0.75 ± 0.01	**0.87** ± 0.02	0.85 ± 0.01
Cylindrospermopsis raciborskii CIRF-01	0.40 ± 0.03	0.74 ± 0.04	**0.81** ± 0.02	ND	0.79 ± 0.02	0.72 ± 0.03
Microcystis aeruginosa PCC7941	0.58 ± 0.01	0.67 ± 0.05	1.05 ± 0.01	ND	**1.16** ± 0.00	1.01 ± 0.01
Microcystis aeruginosa CYA140	0.26 ± 0.03	0.77 ± 0.02	0.82 ± 0.01	**0.94** ± 0.01	0.93 ± 0.02	0.70 ± 0.01
Planktothrix agardhii CYA116	0.50 ± 0.03	0.71 ± 0.04	**0.82** ± 0.02	ND	0.70 ± 0.01	0.40 ± 0.03
Planktothrix agardhii CYA126	0.43 ± 0.00	0.60 ± 0.03	∼∼	0.58 ± 0.01	∼∼	∼∼
Synechococcus elongatus PCC6301	0.30 ± 0.01	0.67 ± 0.01	0.64 ± 0.02	0.72 ± 0.02	0.82 ± 0.01	**0.91** ± 0.01
Chlorophytes						
Ankistrodesmus falcatus CHL8	0.60 ± 0.02	0.65 ± 0.02	0.75 ± 0.02	0.69 ± 0.05	**0.76** ± 0.01	0.19 ± 0.04
Chlamydomonas reinhardtii CHL13	1.16 ± 0.03	0.95 ± 0.01	**1.38** ± 0.03	ND	1.20 ± 0.02	1.20 ± 0.06
Desmodesmus bicellularis CCAP276/14	0.60 ± 0.02	0.72 ± 0.01	0.98 ± 0.01	ND	1.06 ± 0.02	**1.09** ± 0.02
Desmodesmus quadricauda UTEX614	0.33 ± 0.02	0.62 ± 0.02	0.75 ± 0.01	0.82 ± 0.03	**0.85** ± 0.01	0.36 ± 0.02
Monoraphidium minutum	0.75 ± 0.02	0.69 ± 0.06	**1.18** ± 0.01	ND	0.63 ± 0.08	−0.41 ± 0.01
Scenedesmus acuminatus UTEX415	0.58 ± 0.01	0.65 ± 0.04	**0.86** ± 0.01	0.62 ± 0.00	0.74 ± 0.01	0.67 ± 0.00
Scenedesmus maximus SAG39.81	0.24 ± 0.01	0.40 ± 0.01	0.69 ± 0.03	ND	0.78 ± 0.05	**0.86** ± 0.03
Scenedesmus obliquus SAG276/3a	0.70 ± 0.01	0.66 ± 0.01	**0.75** ± 0.01	0.68 ± 0.01	0.70 ± 0.01	0.65 ± 0.01

ND, not determined; ∼∼, filaments clogged into a large aggregate.
Optimum temperature for the growth rate of specified species indicated in bold.

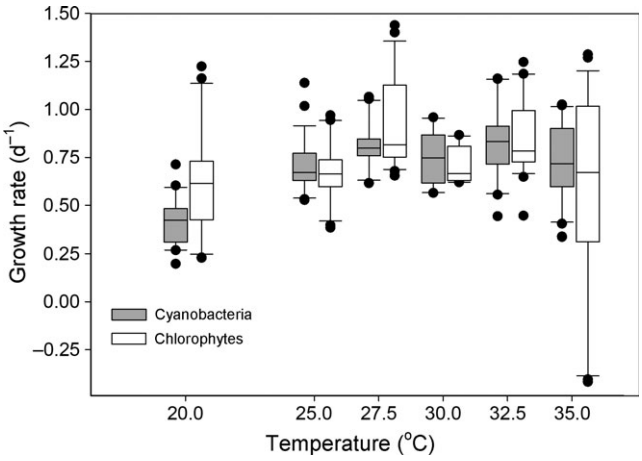

Fig. 1 Growth rates (day^{-1}) for cyanobacteria and chlorophytes (each composed of eight species) grown at six different temperatures (20–35 °C). Boxes indicate the 25th to 75th percentiles, the line within the boxes marks the median, whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, while symbols (•) indicate outliers.

growth rates of cyanobacteria and chlorophytes were equal ($Z \leq -0.85$; $P \geq 0.394$; Fig. 1).

The literature survey (Table S1) revealed that optimum growth temperatures for cyanobacteria (27.2 °C, n = 62) and chlorophytes (26.3 °C, n = 67) were similar (Fig. 2). However, chlorophyte growth rates at their optimum temperature (0.93 day^{-1}) were significantly higher than cyanobacteria growth rates (0.65 day^{-1}; Fig. 2). Restricting the literature data to only representatives of the species that were also used in our experiment yielded optimum growth temperatures for cyanobacteria of 28.6 °C (n = 28) and chlorophytes of 29.6 °C (n = 11). A one-way ANOVA indicated no differences in optimum growth temperatures of the organisms used in our experiment and published data ($F_{3,47}$ = 0.29; P = 0.835). The same was true for growth rates at the optimum temperature ($F_{3,47}$ = 1.87; P = 0.148; data transformed to the power two prior to analysis to fulfil homogeneity of variance requirements).

Discussion

The results of our experiment do not support the hypothesis that cyanobacteria have higher optimum temperatures for growth and higher growth rates at the optimum than chlorophytes. In fact, the optimum temperatures for both groups were similar and also growth rates were not different in the temperature range of 25–35 °C.

The optimum temperatures for cyanobacterial and chlorophyte growth found in our experiment were higher than those retrieved from published data indicating that we selected cyanobacterial and chlorophyte species that thrive under warm circumstances. When restricting the literature data to our experimental species only, no

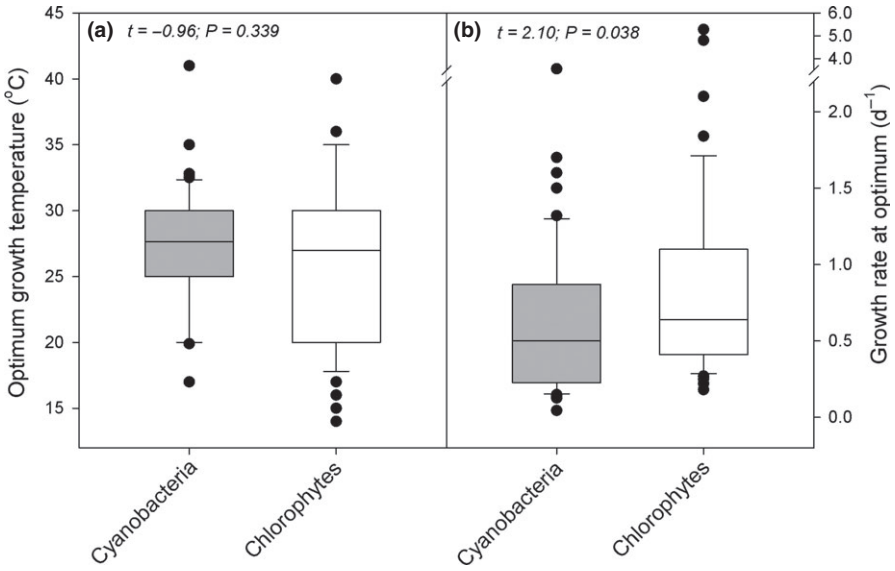

Fig. 2 Box plots of literature-derived optimum growth temperatures (°C, a) and growth rates at the optimum temperature (day^{-1}, b) of cyanobacteria (grey boxes, n = 62) and chlorophytes (white boxes, n = 67). Boxes indicate the 25th to 75th percentiles, the line within the boxes marks the median, whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, while symbols (•) indicate outliers.

differences between cyanobacteria and chlorophytes in the optimum temperatures for growth and growth rates at the optimum were found, which further validates our experimental results. The literature survey indicates that chlorophytes at their optimum temperature might even express higher growth rates than cyanobacteria. These findings contradict the suggestion that cyanobacteria dominate the phytoplankton community under warm circumstances owing to their relatively high growth rates compared with eukaryotic phytoplankton such as chlorophytes (Jöhnk *et al.*, 2008; Paerl & Huisman, 2008, 2009).

Although the stronger temperature dependence and the higher optimum growth temperature for cyanobacteria compared with other phytoplankton have been widely accepted and used in numerous modelling exercises focussing on climate change effects (e.g. Elliott *et al.*, 2005; Mooij *et al.*, 2007), its scientific support is rather weak. Paerl & Huisman (2008), for instance, base their statement 'Cyanobacteria generally grow better at higher temperatures (often above 25 °C) than do other phytoplankton species such as diatoms and green algae' on findings by Reynolds (2006) and Jöhnk *et al.* (2008). Reynolds (2006), however, only describes the temperature-dependent growth of one chlorophyte (*Ankyra judayi*) just up to a temperature of about 16 °C (Fig. 5.3a in Reynolds, 2006, p. 187). Jöhnk *et al.* (2008), furthermore, derived the temperature dependence of chlorophyte growth from a model assuming an optimal temperature of 17 °C and a maximum growth rate of 0.63 day^{-1}. Although cyanobacteria indeed tend to profit from warm – and eutrophic – conditions (Jeppesen *et al.*, 2009; Ndebele-Murisa, Musil & Raitt, 2010; Kosten *et al.*, 2012), our results indicate that the difference in growth rate among chlorophyte and cyanobacterial species is likely not its dominant driver. Several alternative explanatory mechanisms exist.

First, blooms can only develop when the grazing pressure on the bloom-forming organisms is low (Smayda, 2008). In general, the strongest grazing pressure on cyanobacteria could be expected from large-bodied cladoceran filter feeders. In warm climates, large herbivorous species such as *Daphnia* are less abundant, or are even absent, and are generally much smaller than in colder regions (Dumont & Segers, 1994; Gillooly & Dodson, 2000). Higher predation by fish under warmer conditions most probably plays an important role (Meerhoff *et al.*, 2007; Jeppesen *et al.*, 2010). Also in temperate systems, climate change is likely to lead to higher winter survival of fish, fewer large-bodied zooplankton and consequently lower zooplankton grazing of phytoplankton (Balayla *et al.*, 2010). In addition, in warmer climates, copepods typically dominate the crustacean zooplankton year-round and may indirectly facilitate cyanobacteria by grazing on competing phytoplankton (Ger, Panosso & Lürling, 2011).

Cyanobacteria themselves have different mechanisms to reduce the grazing pressure by large-bodied cladocerans. They can form colonies with sizes beyond the ingestion capacity; cyanobacterial filaments may cause mechanical interference in the filtering apparatus;

cyanobacteria may produce grazing deterrents and potent endotoxins that are released upon digestion, while cells that are embedded in mucus could be resistant to digestion (Lampert, 1987; Rohrlack *et al.*, 1999; Lürling, 2003). High temperatures may increase the sensitivity of large-bodied cladocerans (*Daphnia*) to these grazing defence mechanisms of cyanobacteria (Claska & Gilbert, 1998). The selective suppression of large-bodied generalist filter feeders by cyanobacteria may shift the zooplankton community towards a dominance by specialist grazers, such as rotifers and ciliates (e.g. Gilbert, 1988; Wickham & Gilbert, 1991; Jack & Gilbert, 1993). This shift may facilitate cyanobacteria by selective grazing on competing phytoplankton and through the subsequent regeneration of nutrients (DeMott, 1986; Bogdan & Gilbert, 1987; Fulton, 1988; Sterner, 1989; DeMott & Moxter, 1991). The important role of grazing and nutrients in steering the phytoplankton community composition at high temperatures (mean water temperatures of about 36 °C in the afternoon) was demonstrated recently when nutrient additions alone led to chlorophyte dominance, but nutrients and zooplankton to cyanobacteria dominance (Wang *et al.*, 2010).

Second, cyanobacteria seem to be among the most potent producers of allelochemicals interfering with the growth of competitors (Gross, 2003; Leão *et al.*, 2009). Allelopathic compounds could play a role in the proliferation of cyanobacteria in eutrophic lakes constraining phytoplankton succession (Keating, 1977, 1978; Schagerl, Unterrieder & Angeler, 2002). However, not much is known about how changes in temperature will affect allelopathy in phytoplankton (Granéli & Salomon, 2010).

Third, it is expected that a warmer climate will give an earlier onset, increased intensity and longer duration of thermal stratification (De Stasio *et al.*, 1996; Peeters *et al.*, 2002). Combined with lower water density and viscosity, warming of surface waters will favour buoyancy-controlled cyanobacteria (Jöhnk *et al.*, 2008; Wagner & Adrian, 2009). Intensified vertical thermal stratification is also expected to aggravate hypolimnion oxygen depletion resulting in an earlier and longer phosphorus release from anoxic sediments (Søndergaard, Jensen & Jeppesen, 2003; Jankowski *et al.*, 2006; Jeppesen *et al.*, 2009). Finally, at higher temperatures, enhanced mineralisation (Gudasz *et al.*, 2010) and increased rainfall and run-off (Jeppesen *et al.*, 2009) may increase nutrient concentrations, thereby fuelling the blooms (Watson *et al.*, 1997).

Cyanobacterial blooms are notorious examples of disrupted energy transfer from phytoplankton to zooplankton. These blooms and surface scums pose a threat to environmental health and public safety. From our study, we conclude that the expected intensification of such blooms under climate warming will most likely not result from higher growth rates of cyanobacteria compared with their chlorophyte competitors. We suggest that the increase in cyanobacterial dominance with warming will rather be caused by resistance to grazing, resistance to sedimentation and the ability to perform vertical migration (Sommer *et al.*, 1986).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Overview of literature data on the optimum growth temperature (°C) and growth rate (day^{-1}) of chlorophytes and cyanobacteria, including the range of temperature tested.

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