

Green algal over cyanobacterial dominance promoted with nitrogen and phosphorus additions in a mesocosm study at Lake Taihu, China

Jianrong Ma · Boqiang Qin · Hans W. Paerl · Justin D. Brookes · Pan Wu · Jian Zhou · Jianming Deng · Jinsong Guo · Zhe Li

Received: 16 February 2014 / Accepted: 1 December 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Enrichment of waterways with nitrogen (N) and phosphorus (P) has accelerated eutrophication and promoted cyanobacterial blooms worldwide. An understanding of whether cyanobacteria maintain their dominance under accelerated eutrophication will help predict trends and provide rational control measures. A mesocosm experiment was conducted under natural light and temperature conditions in Lake Taihu, China. It revealed that only N added to lake water promoted growth of colonial and filamentous cyanobacteria (*Microcystis*, *Pseudoanabaena* and *Planktothrix*) and single-cell green algae (*Cosmarium*, *Chlorella*, and *Scenedesmus*). Adding P alone promoted neither cyanobacteria nor green algae significantly. N plus P additions promoted cyanobacteria and green algae growth greatly. The higher growth rates of green algae vs. cyanobacteria in N plus P additions resulted in the biomass of green algae exceeding that of cyanobacteria. This indicates that further enrichment with N plus P in eutrophic water will enhance green algae over cyanobacterial

dominance. However, it does not mean that eutrophication problems will cease. On the contrary, the risk will increase due to increasing total phytoplankton biomass.

Keywords Eutrophication · Cyanobacteria · Green algae · Nitrogen · Phosphorus · Dominance

Introduction

Nitrogen (N) and phosphorus (P) are essential nutrients to support the synthesis of nucleic acids, ATP, or proteins, which are necessary for cell division and growth (Conley et al. 2009). The cycles of the key macronutrients N and P have been massively altered by anthropogenic activities (Canfield et al. 2010; Elser et al. 2007). Over-enrichment with N and P promotes eutrophication of water bodies and stimulates algal blooms (Brookes and Carey 2011; Conley et al. 2009; Paerl et al. 2011a). Increasing nutrient loading (especially P) in aquatic ecosystems can enhance cyanobacterial dominance in phytoplankton communities (Steinberg and Hartmann 1988). Downing (Downing et al. 2001) suggested that the risk of dominance by cyanobacteria is only 0–10 % when total phosphorus (TP) concentration ranged from 0 to 30 $\mu\text{g L}^{-1}$, rising abruptly to about 40 % between 30 and 70 $\mu\text{g L}^{-1}$, reaching an asymptote at around 80 % near 100 $\mu\text{g L}^{-1}$ in temperate lakes. When P concentration exceeded 0.2 mg L^{-1} and N concentration was greater than 0.8 mg L^{-1} , growth of the bloom-forming cyanobacteria *Microcystis* spp. was not nutrient-limited in Lake Taihu, China (Xu et al. 2010). Colonial or filamentous cyanobacterial dominance in eutrophic lakes may be attributed to their lower loss rate relative to other phytoplankton groups (Agusti et al. 1990; Knoechel and Kalff 1975). Large colonial cyanobacteria with sheaths and mucilage can prevent cells being grazed by zooplankton grazing, viral or bacterial attack, desiccation, and other potential

Responsible editor: Philippe Garrigues

J. Ma · J. Guo · Z. Li
Key Laboratory of Reservoir Aquatic Environment, Chongqing
Institute of Green and Intelligent Technology, Chinese Academy of
Sciences, Chongqing 400714, People's Republic of China

J. Ma · B. Qin (✉) · P. Wu · J. Zhou · J. Deng
State Key Laboratory of Lake Science and Environment, Nanjing
Institute of Geography and Limnology, Chinese Academy of
Sciences, Nanjing 210008, People's Republic of China
e-mail: Qinbq@niglas.ac.cn

H. W. Paerl
Institute of Marine Sciences, The University of North Carolina at
Chapel Hill, Morehead City, NC 28557, USA

J. D. Brookes
School of Earth and Environmental Science, University of Adelaide,
5005 Adelaide, Australia

negative environmental factors, which play an important role in the competitive advantage over other phytoplankton taxa (Cyr and Curtis 1999; Kearns and Hunter 2001; Wu and Kong 2009; Yamamoto et al. 2011).

However, there have also been reports of phytoplankton community shifts to greater dominance by chlorophyta (green algae) under hypertrophic conditions (Jensen et al. 1994). A number of field observations have also shown that phytoplankton species got smaller (miniaturization) in community succession as eutrophication proceeds (Chen et al. 2003, 2010; Jensen et al. 1994). Hence, an understanding of whether cyanobacteria maintain their dominance under accelerated eutrophication will help predict trends and provide rational control measures.

Here, a mesocosm experiment was executed to evaluate the responses of phytoplankton community groups to continuing increases of N and P availability in Lake Taihu, China.

Experimental procedures

Experimental design

A series of bioassays was set up with treatments of lake water containing various N and P concentrations to assess impacts of these nutrients on phytoplankton community composition. Thirty liters (30 L) of lake water was pumped into white plastic buckets (48 buckets, each bucket had a maximum volume of 35 L) on 10 September 2012. They were incubated under natural light and temperature conditions in a pond located at the lake shore of the Taihu Laboratory of Lake Ecosystem Research (TLLER), located near Wuxi, China. N and P were added as NaNO_3 and KH_2PO_4 , respectively, as three treatments: N only, P only, and N plus P. The concentrations of nutrient after additions were 2, 4, 8, 16, and 32 times of the controls (lake water placed in mesocosms without nutrient additions, Table 1). Each treatment had three replicates. Physicochemical parameters were measured between 0800 and 0900 hours on days 0, 3, 6, 9, 12, 15, and 18.

Coinciding with the sampling of physicochemical variables, 0.5 L of water was sampled from each bucket in order to determine phytoplankton cell concentrations, community composition, and concentration of chlorophyll α (Chl α). Meteorological conditions were recorded everyday. Each bucket was stirred daily at 0700 and 1900 hours. Plastic buckets were left open and exposed to natural light, but capped during rainy days to prevent rain water from entering.

Sampling and analyzing method

Physico-chemical parameters, including water temperature (WT), dissolved oxygen (DO), DO percent saturation (DO%), pH, and electrical conductivity (EC) were measured with a Yellow Springs Instruments (YSI) 6600 multi-sensor sonde.

Phytoplankton samples were preserved with Lugol's iodine solution (2 % final concentration) and sedimented in a plastic bottle for 48 h. Cell density was measured with a Sedgwick Rafter counting chamber under magnification of $\times 200$ – $\times 400$. Phytoplankton species were identified according to *Freshwater Algae in China* (Hu et al. 1980). Algal biovolumes were calculated from cell numbers and cell size measurements. Conversion to biomass was calculated by assuming that 1 mm^3 of volume was equivalent to 1 mg of fresh weight biomass (Chen et al. 2003). The concentrations of Chl α were determined spectrophotometrically after extraction in 90 % hot ethanol (Párista et al. 2002).

Statistical analysis

Data are presented as means \pm SD. Significant differences between controls and treated samples were determined by ANOVA with Tukey's post hoc test. Statistical analyses were conducted with SPSS17.0.

The growth rate (μ) of cyanobacteria and chlorophytes under each set of treatment was calculated according to the modified exponential growth equation,

Table 1 Overview of the experimental treatments and different forms of N and P in lake water (mg L^{-1})

	TP	TN	TDP	$\text{PO}_4^{3-}\text{-P}$	TDN	$\text{NH}_4^+\text{-N}$	$\text{NO}_3^-\text{-N}$
Lake water	0.082	1.55	0.053	0.008	0.95	0.87	0.063
2 times added	0.164	3.1		0.164			3.1
4 times added	0.328	6.2		0.328			6.2
8 times added	0.656	12.4		0.656			12.4
16 times added	1.312	24.8		1.312			24.8
32 times added	2.624	49.6		2.614			49.6

Nitrogen and phosphorus were added as NaNO_3 and KH_2PO_4 , respectively, corresponding to concentrations 2, 4, 8, 16, and 32 times the ambient concentration. NaNO_3 and KH_2PO_4 were dissolved in pure water before they were added to buckets to increase concentrations of N, P, and N plus P to the set level. In water from lake, TN: TP=18.9:1, TDN: TDP=17.9:1. Both N and P added treatment buckets were TN: TP=18.9:1

$$\mu = \ln\left(\frac{X_2}{X_1}\right) / (T_2 - T_1)$$

where X_1 is the concentration of biovolume of green algae or cyanobacteria at the initial incubation stage (T_1), and X_2 is the concentration of biovolume at day 18 (T_2).

Results

Environmental factors

The weather conditions during the experiment period were cloudy (days 0–2, 4, 11, 17–18), rainy (days 3 and 12), and sunny (days 5–10 and 13–16). Air temperature ranged from 16 to 28 °C. Water temperature ranged from 18.8 to 22.5 °C. The range of pH values, DO, DO%, and EC in N plus P additions was clearly greater than those observed in N additions, P additions, or controls (Table 2).

Biovolume of total phytoplankton varied after N, P, and N plus P additions

Initial total phytoplankton biovolume was $36.56 \pm 1.07 \text{ mg L}^{-1}$ in lake water (Fig. 1). The addition of N (2–32× initial concentration) resulted in growth that was significantly greater than controls which received no nutrients, especially after 15 days of incubation ($p < 0.05$; Fig. 1a). Total algal biovolume in the P addition (2–32× initial concentration) treatments appeared slightly higher than controls, but this was not significant ($p > 0.05$; Fig. 1b). Total biomass in buckets with N plus P added was much higher than the control and N only additions especially from day 6 ($p < 0.01$; Fig. 1c). The highest recorded chlorophyll was $481.43 \pm 29.71 \text{ mg L}^{-1}$ in 8× N plus P added treatment on day 18. There were no significant differences between 8 and 32× ($p > 0.05$) which were more than 4× ($p < 0.01$; Fig. 1c) and 2× was less than 4× ($p < 0.01$; Fig. 1c).

The initial Chl- α in lake water was $20.46 \pm 0.82 \text{ } \mu\text{g L}^{-1}$. The linear relationship between total biovolume and Chl- α in all buckets was significant (Fig. 2).

Growth of cyanobacteria and chlorophytes varied after adding N, P, and N plus P

The main phytoplankton phyla were cyanobacteria (Cyanophyta) and chlorophytes.

The main cyanobacterial genera were *Microcystis*, *Pseudoanabaena*, and *Planktothrix*. These species were present as large colonies or filaments (Table 3). The initial cyanobacterial biomass was $16.38 \pm 1.50 \text{ mg L}^{-1}$ (Fig. 3). Biovolumes of cyanobacteria in all N addition treatments were significantly higher than the controls ($p < 0.05$; Fig. 3a1). There were no significant changes in cyanobacterial biovolumes between the P addition treatments and controls ($p > 0.05$; Fig. 3b1). Cyanobacterial biomass in buckets with added N plus P was much higher than the control and N only additions especially from day 9 ($p < 0.01$; Fig. 3a1 and c1). The peak value was $179.11 \pm 11.19 \text{ mg L}^{-1}$ in 8× N plus P treatments on day 18.

The main Chlorophyta genera were *Cosmarium*, *Chlorella*, and *Scenedesmus*. These species grew as relatively small colonies and single cells and their cell and colony sizes were much smaller than cyanobacteria on average (Table 3). Initial Chlorophyta biomass in lake water was 13.44 ± 1.25 (Fig. 3). Biovolume of Chlorophyta in all N added treatments were higher than controls especially 8–32× addition from day 6 were significantly ($p < 0.05$; Fig. 3a2). Chlorophyte biomass in P addition treatments was higher than controls but not significantly ($p > 0.05$; Fig. 3b2). In buckets with both N and P added, Chlorophyta biovolume was much higher than control and N only additions especially after day 6 ($p < 0.01$; Fig. 3a2, c2.). The highest value was $301.75 \pm 23.12 \text{ mg L}^{-1}$ in 8× N plus P added treatment on day 15. In controls, cyanobacterial biovolumes showed no significant change, but Chlorophyta biovolume increased significantly ($p < 0.01$; Fig. 3).

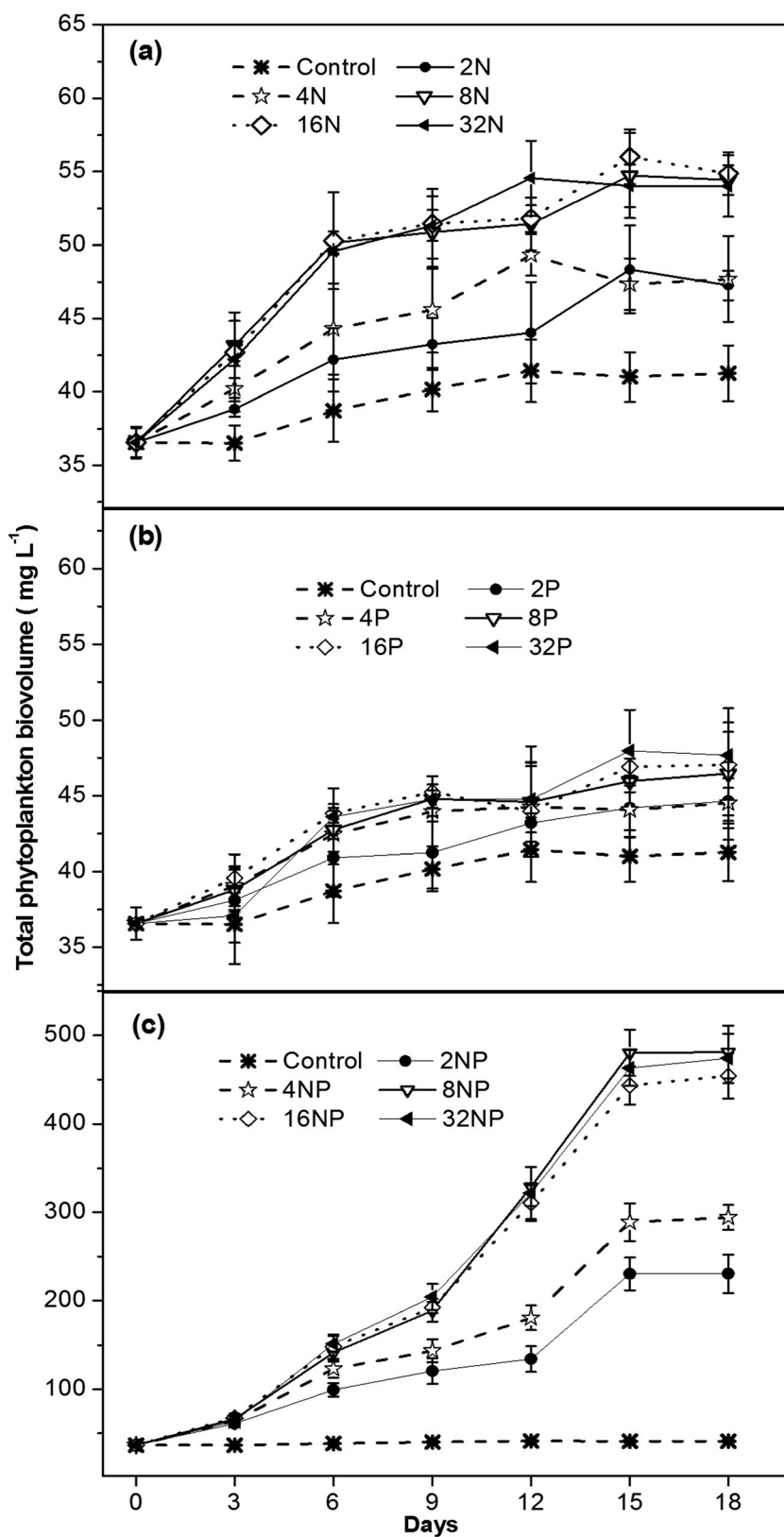
The initial proportion of cyanobacteria as part of total phytoplankton biomass was $44.84 \pm 3.45 \%$. There were no significant impacts on the proportions of cyanobacteria

Table 2 Range of pH values, DO, DO%, and EC in various treatment

Parameters	Controls	N additions	P additions	N plus P additions
pH	8.91–9.41	8.79–9.46	8.97–9.54	9.45–11.28
DO (mg L^{-1})	8.95–12.24	9.27–14.66	9.08–11.13	9.1–19.64
DO% (%)	102.9–113.4	105.3–120.9	101.1–124.7	101.4–232.3
EC ($\mu\text{S cm}^{-1}$)	495–638	439–1211	428–698	488–1346

Dissolved oxygen (DO), dissolved oxygen percentage (DO%), pH, and electrical conductivity (EC) were measured between 0800 and 0900 hours on days 0, 3, 6, 9, 12, 15, and 18 by a Yellow Springs Instruments (YSI) 6600 multi-sensor sonde

Fig. 1 Variations of total phytoplankton biovolume in buckets added N (a), P (b), and N plus P (c). Controls were the same in a, b, and c



in only N or P treatments ($p > 0.05$; Fig. 4a1, b1). However, N plus P additions promoted proportions of cyanobacteria declined at day 3 and continued to decrease

at day 6 ($p < 0.01$). However, at day 9 and from then on, they increased ($p < 0.05$; Fig. 4c1) but are still lower than controls.

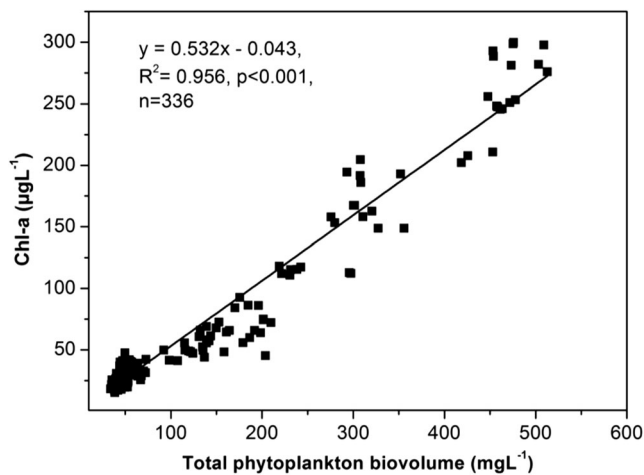


Fig. 2 The relationship between total phytoplankton biovolume and Chl- α in all buckets from days 0 to 18

The initial proportion of green algae to total phytoplankton biomass in lake water was $36.77 \pm 3.32\%$. The relative proportion of green algae changed very little compared with controls when N or P were added individually ($p > 0.05$; Fig. 4a2, b2). However, simultaneous additions of N and P increased the proportion of chlorophytes significantly when compared to the controls ($p < 0.01$; Fig. 4c2). The proportion of cyanobacteria declined, while chlorophytes increased significantly relative to the controls ($p < 0.05$; Fig. 4).

Growth rates of cyanobacteria ranged between 0.004 ± 0.009 and $0.133 \pm 0.005 \text{ day}^{-1}$ and that of chlorophytes ranged between 0.027 ± 0.006 and $0.173 \pm 0.003 \text{ day}^{-1}$ (Fig. 5). Growth rates of cyanobacteria in buckets receiving N additions were higher than controls ($p < 0.05$), and there was no significant change between P added alone and controls ($p > 0.05$). Chlorophyta growth in buckets to which N was added was higher than controls ($p < 0.05$). There were no significant differences between treatments with added P alone and the controls ($p > 0.05$). However, N plus P additions promoted a much higher growth rate of both cyanobacteria and chlorophytes than the controls ($p < 0.01$). In addition, growth rates of chlorophytes were much higher than those for cyanobacteria ($p < 0.01$).

Heterocystous nitrogen-fixing cyanobacteria were not observed in the initial samples, controls, N addition, and N plus P addition treatments. However, they were observed in P addition treatments by day 6. The biomass magnitude of nitrogen-fixing cyanobacteria ranged from 0.11 to 0.62 mg L^{-1} on day 18.

Discussion

Relative to controls, the treatments receiving only N promoted the growth of colonial and filamentous cyanobacteria and single cell chlorophytes (much smaller than cyanobacterial species, Table 3). The addition of P alone promoted neither cyanobacteria nor chlorophytes significantly. Interestingly, N plus P additions greatly stimulated cyanobacteria and chlorophytes growth. In all treatments, including the controls, chlorophyte growth rates were higher than those for cyanobacteria (Fig. 5), which resulted in the biomass of chlorophytes increasing more rapidly than cyanobacteria in N plus P treatments.

Results from this study appear to contradict previous studies which indicated that cyanobacteria became increasingly dominant as eutrophic conditions increased (Downing et al. 2001; Pick and Lean 1987; Smith 1986; Trimbee and Prepas 1987).

One of the reasons why chlorophytes outcompete cyanobacteria at high nutrient levels may be the balance between the rates of cellular growth and losses (Jensen et al. 1994). Chlorophytes have a high demand for nutrients as reflected in their high growth rates. In contrast, cyanobacteria have a lower demand for nutrients because of their relatively low growth rates (Reynolds 1988). Hence, chlorophytes dominated in hypertrophic shallow lakes as the fast-growing chlorophytes were a superior competitor compared with the relatively slow-growing cyanobacteria (Jensen et al. 1994).

Algal particle (single cell or colony) sizes play an important role in green algae dominance over cyanobacteria. It is one of

Table 3 Main genera of cyanobacteria and green algae in the experiment

	Genus	Morphology	Size (μm)
Cyanobacteria	<i>Microcystis</i>	Colonial, near spherical	Diameter 205 ± 21
	<i>Pseudoanabaena</i>	Filamentous	380 ± 121 long, 2 ± 0.5 wide
	<i>Planktothrix</i>	Filamentous	421 ± 129 long, 5 ± 2 wide
Chlorophyta	<i>Cosmarium</i>	Near spherical	Diameter 25 ± 2.2
	<i>Chlorella</i>	Spherical	Diameter 11 ± 2.5
	<i>Scenedesmus</i>	Meniscus	20 ± 10 long, 7 ± 2 wide

Algal particle sizes measured 50 individuals in all samples, include initial lake water. Except for colony sizes of *Microcystis*, which have declined (Ma et al. 2014), all other genera have no significant change in experimental period

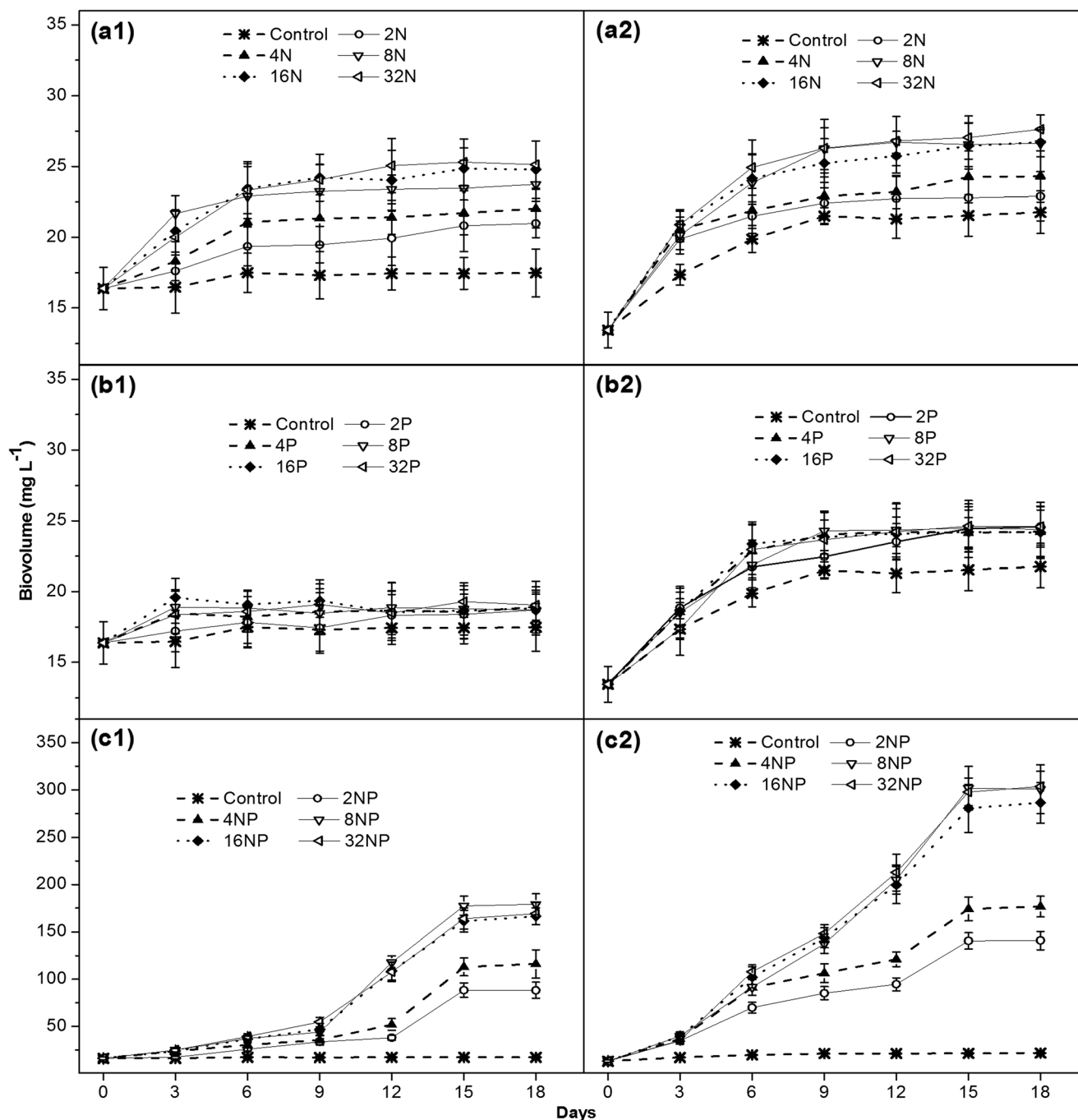


Fig. 3 Variations of cyanobacteria (a1, b1, c1) and chlorophyta (a2, b2, c2) biovolume in buckets added N (a), P (b), and N plus P (c). Controls were the same in all treatments

the most pervasive patterns in biology that maximum intrinsic population growth rate of organisms decrease when their body size increasing (Fenchel 1974). This has major implications for the ecology and evolution of all organisms (Brown et al. 2004). Phytoplankton competitive ability decreases for N and P uptake as cell size increases (Edwards et al. 2011). At high ambient concentrations, algal species having large particle sizes possess high ability to take up N (relative to their requirements) and large storage capacity, but their growth is

limited by the conversion of nutrients into biomass (Marañón et al. 2013). This makes large cells especially well adapted for taking advantage of intermittent nutrient supply (Litchman et al. 2007). Therefore, chlorophytes with small particle sizes are capable of higher growth rates than large colonial and filamentous cyanobacteria, especially under the influence of adequate N and P supplies.

In addition, predation may play an important role in whether chlorophytes or cyanobacteria dominate under in different

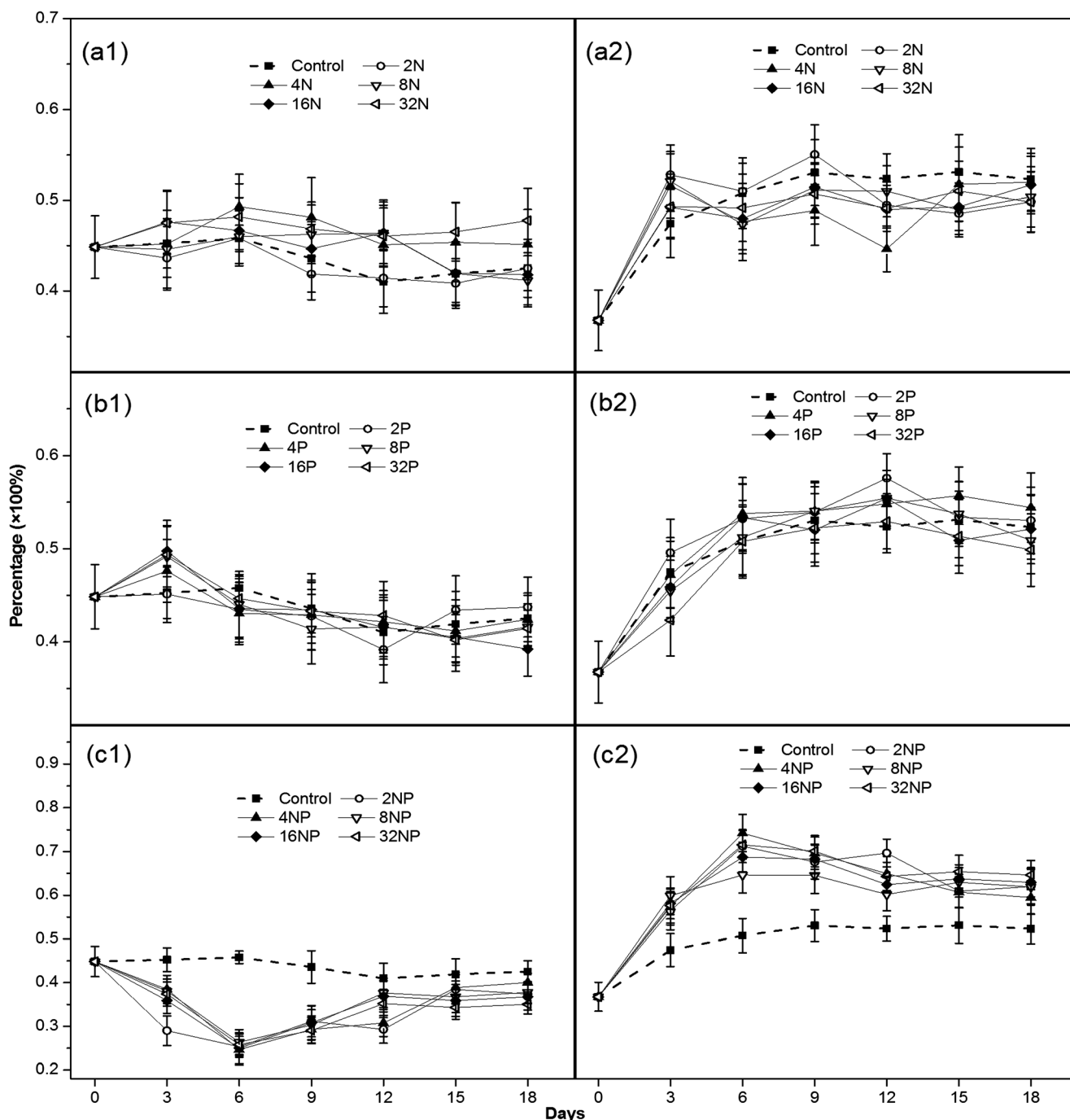


Fig. 4 Variations of cyanobacteria (a1, b1, c1) and green algae (a2, b2, c2) proportion (bio volume) in buckets added N (a), P (b), and N plus P (c). Controls were the same in all treatments

nutrient regimes (Bergquist and Carpenter 1986; Kiørboe 1993). Watson (Watson et al. 1992) suggested that total biomass is dominated by edible algae (<35–50 μm) if TP concentration is below 8–10 $\mu\text{g L}^{-1}$; above this TP concentration range, there is a transition zone in which both edible and inedible (>35–50 μm) biomass take similar proportion of relative abundance in total phytoplankton; when concentrations of TP increase to about 30 $\mu\text{g L}^{-1}$, the inedible algae rapidly dominate the phytoplankton community; if TP >

50 $\mu\text{g L}^{-1}$, the phytoplankton biomass consists almost entirely of large, inedible algae. The smaller size algae have higher maximum growth rate but also possibly a greater loss rate because of predation or death by viral or bacterial attack (Chisholm 1992). Large colonial or filamentous cyanobacteria having sheaths and mucilage can prevent cells from being grazed by zooplankton, and protects cells against viral and bacterial attack, desiccation, and other potential negative environmental factors (Cyr and Curtis 1999; Kearns and Hunter

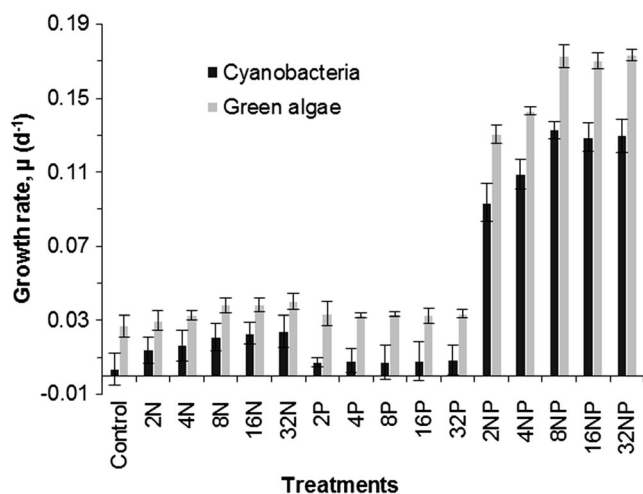


Fig. 5 The growth rates of treatment added N, P, N plus P, and controls

2001; Scheffer et al. 1997; Wu and Kong 2009; Yamamoto et al. 2011). Large colonial algae also favor buoyancy and stimulate the development of beneficial bacterial associations (Munoz and Guieysse 2006; Reynolds et al. 1987). Hence, they dominate in the succession of phytoplankton community in eutrophic lakes and form blooms under favorable weather and hydrodynamic conditions. However, when nutrients continue to increase, the growth rate of small-size algae will be much higher than the loss rate (although predation pressure may increase) due to greater nutrient availability (Li et al. 2013; Wilson et al. 2010). Microbial miniaturization has been shown to occur during periods of stress to increase the surface to volume ratio of cells (Morita 1975). Therefore, dominant phytoplankton species shifted from large colonial or filamentous cyanobacteria to smaller size algae. Field observations also support these results (Chen et al. 2003, 2010; Jensen et al. 1994).

According to observations in 178 Danish shallow lakes, heterocystous cyanobacteria were dominant at low total P (TP) ($<0.25 \text{ mg L}^{-1}$) and non-heterocystous cyanobacteria at intermediate TP ($0.25\text{--}0.8 \text{ mg L}^{-1}$), while chlorophytes often were dominant at high TP ($>1 \text{ mg L}^{-1}$) (Jensen et al. 1994). In our study, N plus P addition ($4.65 \text{ mg L}^{-1} \leq \text{TN} \leq 51.15 \text{ mg L}^{-1}$; $0.246 \text{ mg L}^{-1} \leq \text{TP} \leq 2.706 \text{ mg L}^{-1}$) promoted increased the biomass of small particle size (small colony or single cell) chlorophyte than large colonial or filamentous cyanobacteria (Fig. 3c1, c2; Fig. 4c1, c2).

The bioassays also revealed N limitation (Fig. 1a, b), which has been observed in Lake Taihu during summer and autumn (Xu et al. 2010; Paerl et al. 2011b). N additions promoted cyanobacterial and chlorophyte growth simultaneously, and the growth rates of chlorophytes than cyanobacteria were low resulted in there was no obvious difference in phytoplankton community with controls (Fig. 5). When P was added, neither cyanobacterial nor chlorophyte growth were promoted relative to controls

(Fig. 3). P addition promoted the occurrence of nitrogen-fixing cyanobacterial species with heterocyst. However, they only contributed a small fraction of total cyanobacterial biomass. This is also shown by Paerl et al. (2014).

It appears that cyanobacterial dominance may only respond to specific nutrient concentrations. This is also shown in Lake Taihu by Chen et al. (2003). Blooms initially dominated by large colonial or filamentous cyanobacteria shifted to smaller particle (rather than cell) algae when N and P loads continued to increase during the hyper-eutrophication process. However, it does not mean that eutrophication problems will disappear. On the contrary, the risk will increase. Total phytoplankton biomass will increase greatly (Fig. 1c). There are additional factors that contribute to species selection and phytoplankton community succession. These include hydrodynamics and the degree of mixing relative to light attenuation. The degree of mixing and stratification plays a major role in determining which species dominate in lakes and reservoirs (Reynolds 2006). The rate of nutrient uptake varies between species and can explain some of the competition between species (Tilman 1976). Aquatic ecosystems are complex and the physiological characteristics of their resident algal species vary substantially. It is often difficult to predict which algae will dominate and/or form blooms because models are based on historically generated empirical relationships between light, nutrient, and algal responses (Oliver et al. 2012). Our study provides evidence that chlorophyta can increase in dominance in eutrophic water when N and P continue input greatly.

Mesocosm experiments alter the prevailing hydrodynamic conditions that the phytoplankton community experiences in the lake. However, the controls (no nutrient addition) allow comparison for nutrient addition treatments and the results are interpreted cognizant of the additional role hydrodynamics play in shaping the phytoplankton community assemblage. It is worth noting that even with bigger containers, there are still many differences from the environment of mesocosms with the natural lakes. For example, such bioassays alter hydrodynamics, the degree of mixing relative to light attenuation and contain no sediments. Regardless, there is experimental evidence from the mesocosm experiments presented here that there is potential for increases in dominance of green algae over cyanobacteria in natural lakes as nutrients increase.

Acknowledgments We are grateful to all the staff in Taihu Laboratory for Lake Ecosystem Research (TLLER). This work was supported by the National Natural Science Foundation of China (nos. 41230744 and 41271355), The Major Projects on Control and Rectification of Water Body Pollution (2014ZX07104-006), and USA National Science Foundation Grants No. ENG/CBET 0826819 and 1230543 and DEB 1240851 Dimensions in Biodiversity.

References

- Agusti S, Duarte CM, Canfield DE (1990) Phytoplankton abundance in Florida lakes: evidence for the frequent lack of nutrient limitation. *Limnol Oceanogr* 35(1):181–188
- Bergquist A, Carpenter S (1986) Limnetic herbivory: effects on phytoplankton populations and primary production. *Ecology* 67(5):1351–1360
- Brookes JD, Carey CC (2011) Resilience to blooms. *Science* 334:46–47
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85(7):1771–1789
- Canfield DE, Glazer AN, Falkowski PG (2010) The evolution and future of Earth's nitrogen cycle. *Science* 330(6001):192–196
- Chen Y, Qin B, Teubner K, Dokulil MT (2003) Long-term dynamics of phytoplankton assemblages: microcystis-domination in Lake Taihu, a large shallow lake in China. *J Plankton Res* 25(4):445–453
- Chen B, Xu Z, Zhou Q, Chen C, Gao Y, Yang S, Ji W (2010) Long-term changes of phytoplankton community in Xiagu waters of Xiamen, China. *Acta Oceanol Sin* 29(6):104–114
- Chisholm SW (1992) Phytoplankton size. Primary productivity and biogeochemical cycles in the sea. Plenum, 213–237
- Conley JD, Paerl HW, Howarth RW, Boesch DF, Seitzinger SP, Havens KE, Lancelot C, Likens GE (2009) Controlling eutrophication: nitrogen and phosphorus. *Science* 323(5917):1014–1015
- Cyr H, Curtis JM (1999) Zooplankton community size structure and taxonomic composition affects size-selective grazing in natural communities. *Oecologia* 118(3):306–315
- Downing JA, Watson SB, McCauley E (2001) Predicting cyanobacteria dominance in lakes. *Can J Fish Aquat Sci* 58(10):1905–1908
- Edwards KF, Klausmeier CA, Litchman E (2011) Evidence for a three-way trade-off between nitrogen and phosphorus competitive abilities and cell size in phytoplankton. *Ecology* 92(11):2085–2095
- Elser JJ, Bracken ME, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10(12):1135–1142
- Fenchel T (1974) Intrinsic rate of natural increase: the relationship with body size. *Oecologia* 14(4):317–326
- Hu HJ, Li Y, Wei H, Zhu J (1980) Freshwater algae in China. Shanghai Science and Technology Press, Beijing
- Jensen J, Jeppesen E, Orlík K, Kristensen P (1994) Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. *Can J Fish Aquat Sci* 51(8):1692–1699
- Keams KD, Hunter MD (2001) Green algal extracellular products regulate antialgal toxin production in a cyanobacterium. *Environ Microbiol* 2(3):291–297
- Kjørboe T (1993) Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Adv Mar Biol* 29(1):1–72
- Knoechel R, Kalf J (1975) Algal sedimentation: the cause of a diatom-blue-green succession. *Verhandlungen Internationale Vereinigung Limnologie* 19:745–754
- Li M, Zhu W, Gao L, Lu L (2013) Changes in extracellular polysaccharide content and morphology of *Microcystis aeruginosa* at different specific growth rates. *J Appl Phycol* 25(4):1023–1030
- Litchman E, Klausmeier CA, Schofield OM, Falkowski PG (2007) The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecol Lett* 10(12):1170–1181
- Ma J, Brookes JD, Qin B, Paerl HW, Gao G, Wu P (2014) Environmental factors controlling colony formation in blooms of the cyanobacteria *Microcystis* spp. in Lake Taihu, China. *Harmful Algae* 31:136–142
- Marañón E, Cermeño P, López-Sandoval DC, Rodríguez-Ramos T, Sobrino C, Huete-Ortega M, Blanco JM, Rodríguez J (2013) Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use. *Ecol Lett* 16(3):371–379
- Morita RY (1975) Psychrophilic bacteria. *Bacteriol Rev* 39(2):144–167
- Munoz R, Guieysse B (2006) Algal-bacterial processes for the treatment of hazardous contaminants: a review. *Water Res* 40(15):2799–2815
- Oliver RL, Hamilton DP, Brookes JD, Ganf GG (2012) Physiology, blooms and prediction of planktonic cyanobacteria. *Ecology of Cyanobacteria II*. Springer, pp. 155–194
- Paerl HW, Hall NS, Calandrino ES (2011a) Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. *Sci Total Environ* 409(10):1739–1745
- Paerl HW, Xu H, McCarthy MJ, Zhu G, Qin B, Li Y, Gardner WS (2011b) Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): the need for a dual nutrient (N & P) management strategy. *Water Res* 45(5):1973–1983
- Paerl HW, Xu H, Hall NS, Zhu G, Qin B, Wu Y, Rossignol KL, Dong L, McCarthy MJ, and Joyner AR (2014) Controlling cyanobacterial blooms in hypertrophic Lake Taihu, China: will nitrogen reductions cause replacement of non-N₂ fixing by N₂ fixing taxa? *PLoS One* (In Press)
- Pápišta Ě, Acs E, Böddi B (2002) Chlorophyll-a determination with ethanol—a critical test. *Hydrobiologia* 485(1):191–198
- Pick FR, Lean DR (1987) The role of macronutrients (C, N, P) in controlling cyanobacterial dominance in temperate lakes. *N Z J Mar Freshw Res* 21(3):425–434
- Reynolds C (1988) Functional morphology and the adaptive strategies of freshwater phytoplankton. Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge, pp 388–433
- Reynolds CS (2006) The ecology of phytoplankton. Cambridge University Press
- Reynolds CS, Oliver RL, Walsby AE (1987) Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. *N Z J Mar Freshw Res* 21(3):379–390
- Scheffer M, Rinaldi S, Gagnani A, Mur LR, van Nes EH (1997) On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology* 78(1):272–282
- Smith VH (1986) Light and nutrient effects on the relative biomass of blue-green algae in Lake Taihu. *Can J Fish Aquat Sci* 43(1):148–153
- Steinberg C, Hartmann H (1988) Planktonic bloom-forming Cyanobacteria and the eutrophication of lakes and rivers. *Freshw Biol* 20(2):279–287
- Tilman D (1976) Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science* 192(4238):463–465
- Trimbee AM, Prepas E (1987) Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta lakes. *Can J Fish Aquat Sci* 44(7):1337–1342
- Watson S, McCauley E, Downing JA (1992) Sigmoid relationships between phosphorus, algal biomass, and algal community structure. *Can J Fish Aquat Sci* 49(12):2605–2610
- Wilson AE, Kaul RB, Sarnelle O (2010) Growth rate consequences of coloniality in a harmful phytoplankton. *PLoS One* 5(1):1–8
- Wu X, Kong F (2009) Effects of light and wind speed on the vertical distribution of *Microcystis aeruginosa* colonies of different sizes during a summer bloom. *Int Rev Hydrobiol* 94(3):258–266
- Xu H, Paerl HW, Qin B, Zhu G, Gao G (2010) Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. *Limnol Oceanogr* 55(1):420–432
- Yamamoto Y, Shiah F-K, Chen Y-L, (2011) Importance of large colony formation in bloom-forming cyanobacteria to dominate in eutrophic ponds. *Annales de Limnologie-International Journal of Limnology*. Cambridge Univ Press, pp. 167–173