RESEARCH ARTICLE

Effects of N and P enrichment on competition between phytoplankton and benthic algae in shallow lakes: a mesocosm study

Xiufeng Zhang · Xueying Mei · Ramesh D. Gulati · Zhengwen Liu

Abstract Competition for resources between coexisting phytoplankton and benthic algae, but with different habitats and roles in functioning of lake ecosystems, profoundly affects dynamics of shallow lakes in the process of eutrophication. An experiment was conducted to test the hypothesis that combined enrichment with nitrogen (N) and phosphorus (P) would be a greater benefit to phytoplankton than benthic algae. The growth of phytoplankton and benthic algae was measured as chlorophyll a (Chl a) in 12 shallow aquatic mesocosms supplemented with N, P, or both. We found that enrichment with N enhanced growth of benthic algae, but not phytoplankton. P enrichment had a negative effect on benthic algal growth, and no effect on the growth of phytoplankton. N+P enrichment had a negative effect on benthic algae, but enhanced the growth of phytoplankton, thus reducing the proportion of benthic algae contributing to the combined biomass of these two groups of primary producers. Thus, combined N+P enrichment is more favorable to phytoplankton in competition with benthic algae than enrichment with either N or P alone. Our study indicates that combined enrichment with N+P promotes the dominance of phytoplankton over benthic algae, with consequences for the trophic dynamics of shallow lake ecosystems.

Keywords Benthic algae · Phytoplankton · Nutrient · Resource competition · Shallow lakes · Eutrophication

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X. Zhang (✉) · X. Mei · Z. Liu
Department of Ecology and Institute of Hydrobiology, Jinan University, Guangzhou 510632, China
e-mail: wetlandxfz@163.com

X. Zhang · Z. Liu
State Key Laboratory of Lake Science and Environment, Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, China

X. Mei
College of Resources and Environment, Anhui Agricultural University, Hefei 230036, China

R. D. Gulati
Department of Aquatic Ecology, The Netherlands Institute of Ecology, 6708 PB Wageningen, The Netherlands

Introduction

Shallow lakes can shift from a clear state to turbid state as a result of increased nutrient loading (Moss 1990; Scheffer et al. 1993, 2001). The turbid water state is often characterized by a dominance of phytoplankton (Timms and Moss 1984; Moss 1990), whereas benthic algae may, like submerged macrophytes, be beneficial in maintaining or increasing lake water clarity (Genkai-Kato et al. 2012; Zhang et al. 2013).

Phytoplankton and benthic algae coexist in shallow lakes, where they compete for nutrients (N and P) and light (Pasternak et al. 2009). The major differences between these two classes of primary producers focus on their habitats and roles in the functioning of lake ecosystems. Free-floating phytoplankton have direct access only to nutrients present in the water column, while benthic algae growing on sediment surfaces are able to exploit nutrients from both sediment and overlying water (Carlton and Wetzel 1988; Hansson 1988).

Nutrient loading can stimulate the growth of both phytoplankton and benthic algae (McDougal et al. 1997; Faithfull et al. 2011). However, the growth of phytoplankton leads to increased light attenuation. If light attenuation within the water column is severely reduced, light becomes a limiting factor for the benthic algae beneath (Hansson 1988), leading to poor growth and declining abundance. Loss of benthic algae further promotes the growth of phytoplankton through reduced competition for nutrients and enhanced nutrient release from the sediment (Zhang et al. 2013). This positive

feedback is among the leading mechanisms facilitating the shift from clear to turbid water states in shallow lakes (Søndergaard et al. 2003). Benthic algae decrease the availability of nutrients for phytoplankton in the overlying water column (Carlton and Wetzel 1988) by consuming the resources they require for growth and, indirectly, by oxidizing the top layer of sediment and thus immobilizing nutrients within (Hansson 1990; Wetzel 2001; Zhang et al. 2013). In shallow lakes or in the shallow areas of deep lakes where light can penetrate to the bottom, the competitive influence of benthic algae can substantially reduce growth of phytoplankton and contribute to maintaining clear water conditions (Genkai-Kato et al. 2012; Zhang et al. 2014). Thus, competition between phytoplankton and benthic algae can be important in maintaining either of the two alternative regimes in shallow lakes.

In shallow lakes, however, this competition is influenced by the availability of essential nutrients, either nitrogen (N) or phosphorus (P) or both N and P. N enrichment often has a stimulatory effect on benthic algae (Havens et al. 1996; Kniffin et al. 2009), while enrichment with P has been shown to cause the decline and even loss of benthic algae (McCormick et al. 2001; Gaiser et al. 2006). N+P enrichment can dramatically promote the growth of phytoplankton (Smith et al. 2006). Several studies have been carried out on the effects of various nutrients on the competition between algae (Hansson 1988; Vadeboncoeur et al. 2003; Pasternak et al. 2009). Despite the fact that phytoplankton and benthic algae coexist in most shallow lakes, the specific influence of N, P, and N+P on the competition between these two major groups is not well understood. The likely competitive outcomes of individual and combined addition of N and P to shallow lake water remain unclear. Since any shift in the dominance of primary producers resulting from changing competitive advantage is likely to have extensive effects on lake dynamics (Havens et al. 1999; Vadeboncoeur et al. 2003), research in this area is urgently required.

In the present study, a mesocosm experiment was designed to evaluate the effects of separate and combined enrichment with N+P on the competition between phytoplankton and benthic algae. It was hypothesized that combined N and P enrichment would be more conducive to the growth of phytoplankton during competition with benthic algae than either N or P enrichment alone since systems enriched by one nutrient are likely to be limited by the other (Elser et al. 2007; Harpole et al. 2011). To test this hypothesis, mesocosms mimicking shallow aquatic ecosystems were constructed. N and P were added individually and in combination at the rates of 1.5 mg/L/week (N) and 0.1 mg/L/week (P). Samples of benthic algae developing on the sediment surface and phytoplankton in the overlying water were collected every 2 weeks to measure biomass and assess taxonomic composition. The main aim of this study was to evaluate the influence of N and P, both separately and together, on the competition between phytoplankton and benthic algae in shallow lakes.

Materials and methods

Experimental setup

The experiments were carried out in 12 plastic mesocosms (upper diameter=54 cm, bottom diameter=40 cm, and height=60 cm) containing sediments and water. Sediments [total N (TN), 1.13 ± 0.04 mg/g DW; total P (TP), 0.56 ± 0.01 mg/gDW] obtained from Ming Lake, a eutrophic shallow water body in Guangzhou City, were air dried, powdered, and sieved through a stainless sieve (mesh size, 0.5 mm) to remove coarse debris and clumps. The homogenized sediment was added as a ~10 cm thick layer to each mesocosm. These mesocosms were then filled with Ming Lake water filtered by a plankton net (mesh size 0.064 mm). Other parameters for the filtered water were as follows: TN, 2.15 mg/L; TP, 0.06 mg/L; and chlorophyll a (Chl a), 19.1 ± 0.6 μg/L. The mesocosms were exposed to natural sunlight and allowed to acclimatize for 2 weeks. Thereafter, nutrient concentrations in the mesocosms were the following: TN, 2.41 ± 0.42 mg/L, and TP, 0.14 ± 0.01 mg/L. The Chl a concentration in the water at the end of acclimatization period was 31.1 ± 0.3 μg/L.

After the acclimatization period, an artificial substrate (a 2×2 cm plastic gauze with a mesh size of 2×2 mm) was carefully placed onto the sediment as a substrate on which benthic algae could grow. Triplicate mesocosms were dosed with N and P separately and with N+P together. The remaining three mesocosms received no nutrients and served as controls (Table 1). The calculated doses of N (sodium nitrate), P (sodium dihydrogen phosphate), and N+P were added as solutions and prepared by dissolving nutrient compounds in distilled water, which were then stirred into the mesocosms to ensure complete mixing. The mesocosms were topped up with more filtered lake water as required to maintain a constant water level during the entire experiment. The experiment was run from August 21, 2010 to October 16, 2010.

Table 1 Design of the mesocosm experiment

Treatment	Description	Replicates
Control	No nutrient added	3
N	KNO_3 added weekly at a rate of 1.50 mgN/L	3
P	NaH_2PO_4 added weekly at a rate of 0.10 mgP/L	3
N+P	Both P and N added at the above rates	3

Sampling and analysis

Phytoplankton The samples for phytoplankton analyses were collected from the mesocosms using clean 500-ml glass bottles every 2 weeks during the period of experiment prior to each nutrient addition. As a measure of phytoplankton biomass, Chl *a* levels were determined spectrophotometrically after ethanol extraction of the filtered material on cellulose acetate membrane filters at room temperature (Jespersen and Christoffersen 1987). The dominant phytoplankton taxa were identified by microscopy using the method of Hu and Wei (2006).

Benthic algae The artificial substrata and any attached benthic algae were removed every 2 weeks from each mesocosm after sampling of phytoplankton and replaced immediately by fresh gauzes. The biomass of benthic algae was measured as Chl *a* by spectrophotometry as above, and the dominant taxa of benthic algae were identified. Prior to the sampling of benthic algae, light intensity in the water layer just above the sediment surface was measured every week between 09:00 and 12:00 hours using an underwater irradiance meter (ZDS-10W).

Biomass calculation Biomass data for the two primary producer groups studied ware calculated as follows: total phytoplankton biomass (total Chl *a*, mg)=volume of water column in the mesocosm (L)×phytoplankton biomass (Chl *a*, μg/L)/1000; total benthic algal biomass (total Chl *a*, mg)=surface area of sediment in the mesocosm (m^2)×benthic algal biomass (Chl *a*, mg/m^2); and total biomass of the two groups of primary producers (total Chl *a*, mg)=total phytoplankton biomass (Chl *a*, mg)+total benthic algal biomass (Chl *a*, mg).

Statistical analyses

Repeated measurement analysis of variances (ANOVAs) were used to test for significant differences in algal biomass, light intensity, and temperature, with time as the repeated factor under different enrichments. Where a significant difference was determined, a least significant difference (LSD) test was used to detect treatments that differed. One-way ANOVA was performed to detect differences in biomass on each date among treatments. If the difference was significant, an LSD test was used to detect which treatments differed. All results are presented as mean values±SD.

Results

Light intensity

The light reaching the sediment surface varied between treatment groups (repeated measurements ANOVAs, treatment effect, $p < 0.05$). The light intensities observed in the N-enriched groups ranged from 5.9 to 98.0 μmol/m^2/s but did not differ from the control range of 5.3 to 89.7 μmol/m^2/s. Light intensity was higher ($p < 0.05$) in P-enriched mesocosms, ranging from 7.5 to 143.2 μmol/m^2/s and lower ($p < 0.05$) in N+P-enriched mesocosms at 4.6 to 26.5 μmol/m^2/s than in the controls (Fig. 1).

Biomass of phytoplankton

Differences were observed between enrichment treatments in terms of biomass of phytoplankton measured as Chl *a* (repeated measurements ANOVAs, treatment effect, $p < 0.05$).

Chl *a* concentrations between the control mesocosms and the mesocosms enriched with either N or P alone did not differ significantly ($p > 0.05$). However, Chl *a* levels in the treatment with N+P enrichment were significantly higher than in either of the single nutrient treatments or the controls ($p < 0.05$). Thus, enrichment with N+P was seen to stimulate the growth of phytoplankton. In the controls, Chl *a* concentrations of phytoplankton samples ranged from 7.7 to 34.5 μg/L during the experiment, with mean±SD to be 20.2±11.0 μg/L (upper panel in Fig. 2). In the N+P-enriched treatments, Chl *a* ranged from 29.6 to 71.4 μg/L, with mean±SD to be 45.9± 20.0 μg/L.

Levels of phytoplankton Chl *a* also varied significantly with time (repeated measurements ANOVAs, time effect, $p < 0.05$). Analyses of the effects of nutrient treatments on each date revealed that Chl *a* concentration was higher on September 4 and October 16 in mesocosms with N+P enrichments than in the controls (one-way ANOVA, treatment effect, $p < 0.05$; upper panel in Fig. 2).

Biomass of benthic algae

The Chl *a* concentration of benthic algae varied dramatically between treatment groups (repeated measurements ANOVAs,
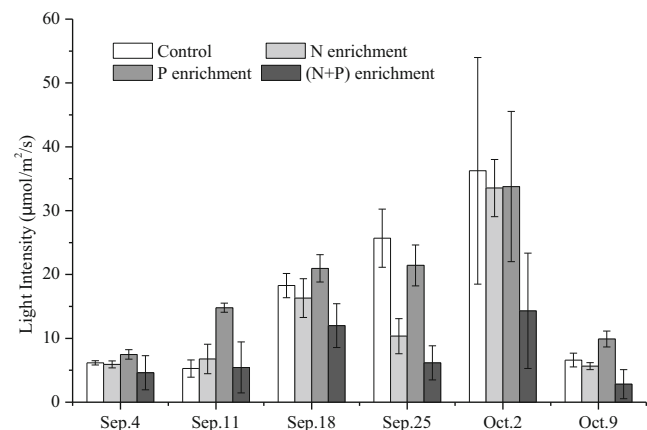

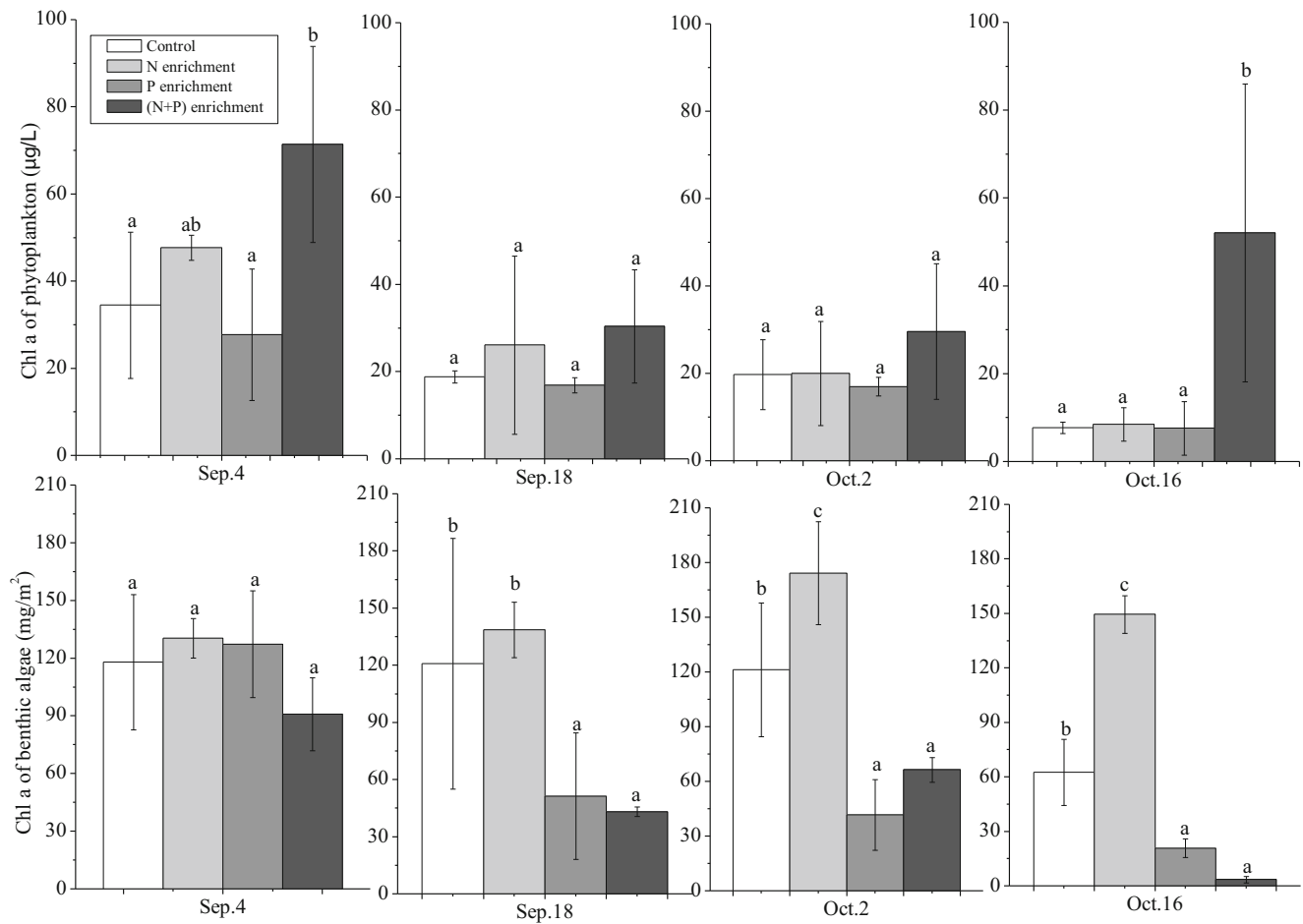**Fig. 1** Light intensity under different treatments (mean±SD)

Fig. 2 Chl *a* of phytoplankton and benthic algae under different treatments (mean±SD). *Upper panel*: phytoplankton, *lower panel*: benthic algae. *Different letters* indicate significant (*p*<0.05) differences of Chl *a*. Chl *a* that are statistically equal share a common letter

treatment effect, *p*<0.05). In the controls, Chl *a* levels ranged from 62.6 to 121.0 mg/m^2, with mean±SD to be 105.7± 28.8 mg/m^2 (lower panel in Fig. 2). In treatments with N enrichment, Chl *a* was higher than in the control mesocosms (*p*<0.05), ranging from 130.4 to 174.2 mg/m^2, with mean± SD to be 148.2±19.0 mg/m^2, indicating that N enrichment stimulates the growth of benthic algae. In contrast, Chl *a* was lower in mesocosms enriched with P and N+P than in the controls (*p*<0.05). In the P-enriched mesocosms, Chl *a* levels ranged from 20.8 to 127.3 mg/m^2 (with mean±SD to be 60.2±46.5 mg/m^{-2}). In the N+P treatment, Chl *a* ranged from 3.5 to 91.0 mg/m^2 (with mean±SD to be 51.0±37.2 mg/m^2).

Chl *a* concentrations also changed significantly over time (repeated measurements ANOVAs, time effect, *p*<0.05). The Chl *a* levels were higher on October 2 and October 16 in the N enrichment groups than in the control groups (one-way ANOVA, treatment effect, *p*<0.05). In the P- and N+P-enriched treatments, Chl *a* concentrations were generally lower than the controls,

except on September 4 (one-way ANOVA, treatment effect, *p*<0.05; lower panel in Fig. 2).

Relative biomass of phytoplankton and benthic algae

The total biomass (total Chl *a*) of each class of primary producers varied between treatment groups (repeated measurements ANOVAs, treatment effect, *p*<0.05). The total biomass was elevated in N-enriched treatments but reduced in the P- and N+P-treated mesocosms compared to the controls (*p*<0.05, Fig. 3).

In addition to changes in overall abundance, the relative proportions of phytoplankton and benthic algae to total algal biomass also varied between treatments (Fig. 4). N enrichment appeared not to affect the relative proportions of phytoplankton and benthic algae compared with controls, whereas P enrichment boosted phytoplankton growth and decreased the contribution of benthic algae to total primary producer biomass. N+P enrichment had the greatest effect, resulting in an enhanced contribution of

Fig. 3 Total Chl *a* of phytoplankton and benthic algae under different treatments (mean ±SD)
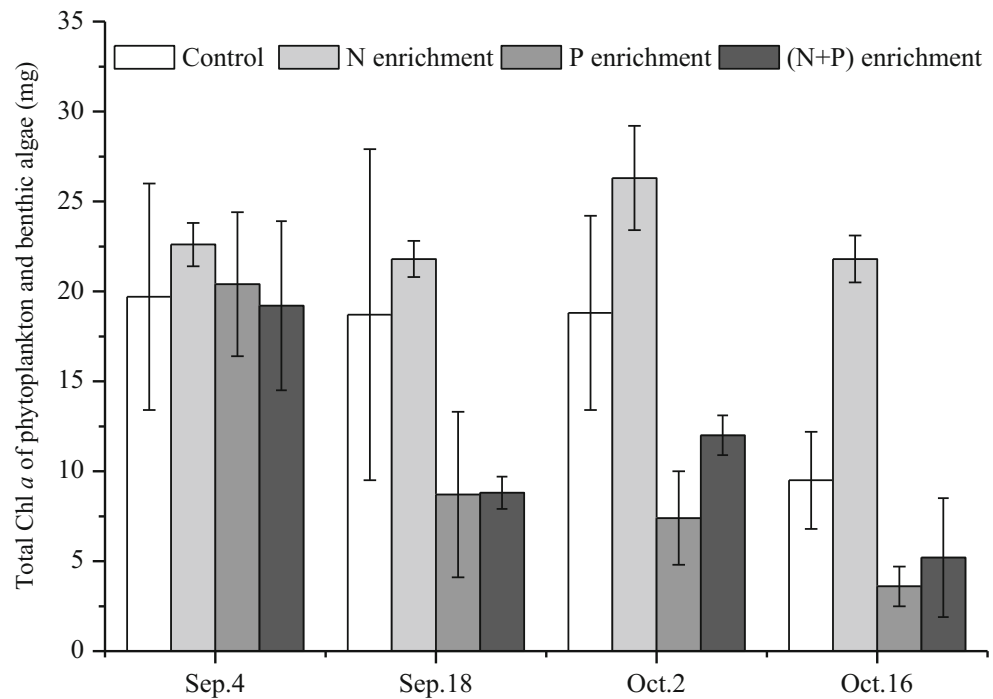
planktonic algae to the total biomass compared with either N- or P-enriched treatments, and a reduced proportion of benthic algae relative to mesocosms enriched separately with either N or P.

Discussion

The biomass of benthic algae, but not of phytoplankton, increased with N enrichment compared with the controls, leading to greater combined primary producer biomass. The

stimulatory effect of N on benthic algal growth is already known (Havens et al. 1996; Kniffin et al. 2009). The increased growth rate probably enables these algae to outcompete phytoplankton for resources.

In contrast to N enrichment, the addition of P depresses the biomass of benthic algae relative to the controls. Although declines and even losses of benthic algae have been previously reported in response to P enrichment (McCormick et al. 2001; Gaiser et al. 2006), the mechanism of this decline is unclear (Gaiser et al. 2006). In our study, the decline of benthic algae led to an increased relative contribution of

Fig. 4 Proportion of phytoplankton and benthic Chl *a* to total biomass under different treatments
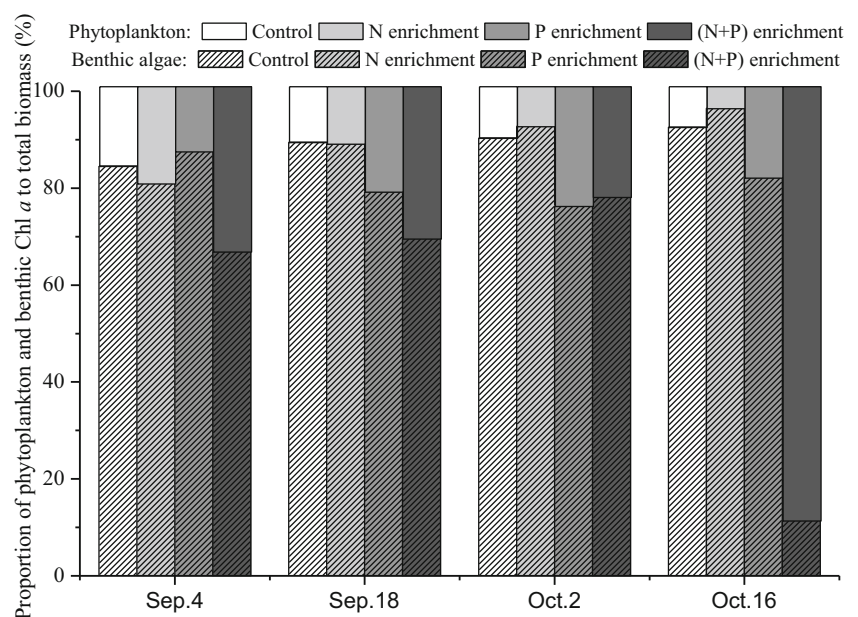
phytoplankton to overall primary production because the level of phytoplankton Chl *a* was not significantly altered by P enrichment. This probably enabled phytoplankton to benefit disproportionately from excess P, thereby imparting a competitive advantage over benthic algae.

Our study also demonstrates that combined enrichment with N+P boosts the biomass of phytoplankton (Fig. 2) while reducing that of benthic algae (Fig. 2) relative to the controls, causing an increase in the relative contribution of phytoplankton to the total biomass of primary producers (Fig. 4). A similar negative relationship between production of phytoplankton and benthic algae has been reported by Stevenson et al. (1985), Hansson (1988), and Blumenshine et al. (1997), and numerous other studies (Sand-Jensen and Borum 1991; Blumenshine et al. 1997; Smith et al. 2006) have shown that phytoplankton growth and biomass increase with nutrient enrichment. Excessive growth of phytoplankton in the surface waters of nutrient-enriched lakes impacts negatively on benthic algae through shading. Our study fits with generally accepted conceptual models of eutrophication (Sand-Jensen and Borum 1991; Duarte 1995; Valiela et al. 1997), which predict that with increased nutrient loading, enhanced phytoplankton production and biomass will cause increased shading in the water column, limiting light conditions for the production of benthic algae and thus decreasing their biomass. The decline, death, and decay of benthic algae increase the efflux of nutrients from the sediment to the water column (Zhang et al. 2013), thereby further stimulating phytoplankton growth. Such positive feedback loops for phytoplankton increase the availability of nutrients via internal loading and act to perpetuate eutrophic conditions (Cerco and Seitzinger 1997). In this study, the declining intensities of underwater light due to the shading by phytoplankton boosted by N+P enrichment (Fig. 1) were followed by the decline of benthic algae.

In this study, different nutrient enrichment regimes resulted in taxonomic shifts in both phytoplankton and benthic algal communities. For example, by the end of the experiment on October 16, *Dactylococcopsis* sp. and *Cryptomonas* sp. were dominant phytoplankton genera in the control mesocosms. In the N-enriched mesocosms, the dominant phytoplankton genera were *Dactylococcopsis* sp., and *Chlorella* sp. P-enriched mesocosms were dominated by *Cryptomonas* sp. and *Chlorella* sp. However, mesocosms with N+P enrichment are dominated by *Scenedesmus* sp. and *Cryptomonas* sp. The dominant genera of benthic algae were *Ulotrichales* sp. and *Synedra* sp. in the controls. In the N-enriched treatment, *Closterium* sp. and *Ulotrichales* sp. dominated the benthic algal community. *Ulotrichales* sp. was the sole dominant genera of benthic algae in both the P- and N+P-enriched mesocosms. Thus, the experimental nutrient treatments distinctly affected the composition of phytoplankton and benthic algae, though some of the algae found in our benthic samples

such as *Synedra* sp. are primarily planktonic and likely settled from the water column to the bottom. The shifts in the nutrient-enriched mesocosms and the genera succession observed during the course of the experiment suggest that the nutrient enrichment changes the outcome of competition between phytoplankton and benthic algae, with the nature of the change dependent on the type of enrichment (N or P or both N and P together).

The consequences of interactions between phytoplankton and benthic algae under enriched conditions are interesting from an ecological viewpoint. Given that human activities profoundly affect the global biogeochemical cycles of both N and P (Vitousek et al. 1997; Elser et al. 2009; Ashley et al. 2011), the loading of either or both elements into aquatic ecosystems in excessive amounts can alter the outcome of competition between phytoplankton and benthic algae. Shifts in the composition and dominance of primary producer communities can markedly alter both the structural and functional characteristics of an ecosystem, affecting the flow of energy from primary production to higher trophic levels. Much greater attention is required to identify the specific impacts of N and P when loaded separately and in combination on competition between phytoplankton and benthic algae. This is especially true for shallow lakes where nutrient recycling is rapid and availability less restricted than in deeper water bodies.

In conclusion, combined enrichment N and P is more conducive to the growth of phytoplankton than benthic algae and thereby promotes the dominance of phytoplankton over benthic algae, thereby increasing the pace of eutrophication in shallow lakes.

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