Fundam. Appl. Limnol. Vol. 184/4 (2014), 247–260
Stuttgart, July 2014

Article

Trophic state mediates the effects of a large colonial cyanobacterium on phytoplankton dynamics

Cayelan C. Carey[1, 2, *], Kathryn L. Cottingham[3], Nelson G. Hairston, Jr.[1] and **Kathleen C. Weathers[4]**

With 4 figures, 1 table and 2 appendices

Abstract: Although cyanobacterial blooms are typically found in eutrophic lakes, where they are able to exert inhibitory effects on other plankton, they are also reported from oligotrophic and mesotrophic lakes. Here, we explored whether trophic state mediates the effects of *Gloeotrichia echinulata* blooms in freshwater ecosystems. This taxon is a large, colonial cyanobacterium that may be increasing in low-nutrient lakes in northeastern North America. We manipulated *Gloeotrichia* presence in mesotrophic and eutrophic mesocosms and measured its effects on phosphorus, nitrogen, phytoplankton growth in two size fractions (< 30 µm, and total fraction), and zooplankton. In mesotrophic mesocosms, *Gloeotrichia* stimulated the growth of smaller-sized phytoplankton, potentially through significantly higher total nitrogen and phosphorus concentrations than in non-*Gloeotrichia* controls, although nearly all measured soluble nutrient concentrations were below method detection limits. In contrast, the growth of smaller-sized phytoplankton was inhibited in eutrophic mesocosms, where concentrations of total nitrogen and phosphorus were significantly lower in the presence of *Gloeotrichia* in comparison to controls. The *Gloeotrichia* colonies likely inhibited phytoplankton growth in the eutrophic mesocosms by creating scums that decreased light availability, although other mechanisms may be involved. The positive or negative effect of *Gloeotrichia* did not cascade to higher trophic levels: zooplankton biomass was significantly higher in the eutrophic than mesotrophic mesocosms, but not affected by *Gloeotrichia* presence. In summary, trophic state determined if the effects of *Gloeotrichia* on smaller-sized phytoplankton were stimulatory or inhibitory, likely due to several interacting mechanisms.

Key words: bloom, context-dependency, eutrophic, facilitation, *Gloeotrichia echinulata*, inhibition, mesotrophic, zooplankton.

Introduction

Aquatic habitats are critically threatened worldwide by eutrophication and the accompanying degradation of water quality (MEA 2005). One of the most profound and visible symptoms of eutrophication is cyanobacterial blooms, which can be harmful to humans because of their floating scums, noxious odors, and toxin production (Paerl et al. 2001, Hudnell 2008). In the past three decades, the geographic range and frequency of such blooms has increased, and this trend is predicted to continue under current climate change scenarios (Paerl & Huisman 2009, Brookes & Carey 2011).

Authors' addresses:

[1] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA

[2] Current address: Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia 24061 USA

[3] Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA

[4] Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA

* Corresponding author: cayelan@vt.edu

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www.schweizerbart.de
DOI: 10.1127/1863-9135/2014/0492
1863-9135/14/0492 $ 3.50

Cyanobacterial blooms typically occur in eutrophic systems, where they are considered to be inhibitory to ecosystem functioning and trophic dynamics (reviewed by Paerl et al. 2001). Modeling and experimental studies have demonstrated that cyanobacterial blooms in high-nutrient systems decrease other phytoplankton (e.g., Paerl 1988, Huisman et al. 1999). This may be due to the numerous eco-physiological adaptations that allow cyanobacteria to outcompete other phytoplankton: they have been shown to produce surface scums that limit light penetration (Reynolds et al. 1987), excrete allelopathic chemicals and toxins (Leflaive & Ten-Hage 2007), store luxury phosphorus (P; Healey 1982), and fix nitrogen (N; Stewart 1967). By decreasing the density of other phytoplankton, cyanobacteria can reduce the flow of energy and nutrients to higher trophic levels, including zooplankton and fish (Rondel et al. 2008). In addition, cyanobacteria can inhibit zooplankton by mechanically interfering with grazing (Lampert 1987), producing toxins (Rohrlack et al. 2005, but see Tillmanns et al. 2008), and because they lack certain fatty acids, sterols, and nutrients (Brett et al. 2006).

Although much less studied, cyanobacterial blooms and scums also occur in oligotrophic and mesotrophic lakes, where bloom densities appear to have increased in the past decade in North America and Europe (e.g., Ernst et al. 2009, Winter et al. 2011, Carey et al. 2012). We sought to explore whether lake trophic state – and the concomitant differences in nutrient limitation, light availability, and trophic dynamics that result from eutrophication (Wetzel 2001) – would result in fundamental differences in how cyanobacterial blooms affect plankton food webs.

No studies we know of have measured the effects of cyanobacterial blooms on other plankton in freshwater systems while also manipulating trophic state. Most experimental studies that have tested the effects of freshwater cyanobacteria have created blooms in mesocosms by adding nutrients to stimulate growth or by adding cyanobacteria in a culture media matrix, thereby conflating the effect of the cyanobacteria and nutrients (Ghadouani et al. 2003, Rondel et al. 2008). Here, we report the results of a mesocosm study in which cyanobacteria were manipulated separately from nutrients, making possible an independent comparison of the effects of cyanobacteria on plankton food webs in systems of different trophic state.

We analyzed the effects of *Gloeotrichia echinulata*, a large colonial cyanobacterium that can occur at high densities in oligotrophic and mesotrophic lakes in the northeastern USA (Carey et al. 2012), as well as in eutrophic lakes in the USA and Europe (Barbiero & Welch 1992, Karlsson-Elfgren et al. 2003). Because *Gloeotrichia* produces large colonies visible without a microscope (1–3 mm in diameter; Carey et al. 2008), colony densities can be easily manipulated without contaminating mesocosms with added nutrients.

We explored whether trophic state can mediate the effect of *Gloeotrichia* on freshwater ecosystems. This taxon has the ability to fix N (Stewart 1967) and to take up and store P in excess of its immediate metabolic needs (Istvánovics et al. 1993, Pettersson et al. 1993). In low-nutrient lakes, these nutrients may be released into the water column via leakage, cell lysis, or grazing, which could then provide a nutrient subsidy to other phytoplankton (Healey 1982, Ray & Bagchi 2001). Although zooplankton may occasionally exhibit inhibitory effects from some cyanobacteria (e.g., Rohrlack et al. 2005), zooplankton may be able to benefit indirectly from *Gloeotrichia* in a low-nutrient system if *Gloeotrichia* stimulated smaller-sized phytoplankton that zooplankton can generally graze. In contrast, in high-nutrient lakes, where nutrients are typically less limiting than light (Wetzel 2001), and where the additional nutrients provided by *Gloeotrichia* would also be a smaller proportion of the total available N and P, it is unknown if *Gloeotrichia* would still stimulate smaller-sized phytoplankton. To explore these ecosystem dynamics, we manipulated *Gloeotrichia* presence and trophic state in mesocosms.

Methods

Experimental design and set-up

We conducted a fully factorial 2 × 2 mesocosm experiment that crossed nutrient concentrations (Nutrients: Ambient vs. Enriched) with the presence and absence of *Gloeotrichia* (+*Gloeotrichia* vs. –*Gloeotrichia*). Every treatment had four randomly-assigned replicates (n = 16 total). The mesocosms consisted of 1136 L (total volume) cattle tanks (Rubbermaid, Wooster, OH, USA), each filled with 800 L of water and situated away from tree cover in an old field in Etna, New Hampshire, USA (43° 41′ N, 72° 13′ W). The experiment ran for 37 days from 7 July to 13 August 2010.

In late May 2010, we acid-washed the inside of each mesocosm with 1 N hydrochloric acid and immediately covered it with 1 mm fiberglass mesh to prevent invasion by insects. We added a mesh bag to each mesocosm containing 200 g of dead leaves as a carbon source for the plankton communities before filling the mesocosms with groundwater from a well in mid-June. Every bag contained 50 g (dry weight) each of sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), white pine (*Pinus strobus*), and American beech (*Fagus grandifolia*) leaves collected from near our field site. The groundwater was slightly basic, with a pH of 8.7.

We established the different nutrient levels immediately after the mesocosms were filled with water. N and P were added in a concentrated solution of KH_2PO_4 and NH_4NO_3 to the Enriched mesocosms twice every week throughout the experiment at daily loading rates of 1 µg P L^{-1} and 20 µg N L^{-1} (molar N:P ratio = 44.2). Ambient mesocosms received the same volume of reverse osmosis water. These loading rates approximate the N:P ratio observed in nearby lakes (Appendix 1).

We created phytoplankton communities in all of the mesocosms in mid-June by adding 2 L of unfiltered water collected from the top 0.5 m of eight nearby lakes (16 L total of lake water per mesocosm; Appendix 1).

We let the phytoplankton community develop for two weeks before establishing zooplankton communities in the mesocosms. At four of the eight lakes where we collected phytoplankton, we also collected zooplankton in 2 m vertical hauls with a 100 µm mesh plankton net. We visually inspected each haul sample and manually removed *Gloeotrichia* colonies, large predatory zooplankton, and macroinvertebrates before adding the contents of one haul from each lake to each mesocosm.

We allowed the zooplankton communities to develop for one week and then added *Gloeotrichia* to the appropriate mesocosms. We collected *Gloeotrichia* colonies from oligotrophic Lake Sunapee (43° 24′ N, 72° 20′ W, Sunapee, New Hampshire) and mesotrophic Lake Morey (43° 55′ N, 72° 8′ W, Fairlee, Vermont) with the goal of creating a +*Gloeotrichia* treatment that matched the highest *Gloeotrichia* density observed in an oligotrophic or mesotrophic northeastern USA lake (250 *Gloeotrichia* colonies L^{-1}; Carey et al. 2012).

We collected colonies at each lake by towing a plankton net (0.5 m diameter, 100 µm mesh) for ~25 m just below the water's surface. We rinsed the contents of each tow into separate 1-L white plastic bottles that were kept in the shade until transport back to the laboratory. We cleaned the *Gloeotrichia* colonies from each tow separately: one bottle at a time, we rinsed the colonies three times with 1.2 µm-filtered (GF/C Whatman) Lake Sunapee water, individually inspected the colonies with a dissecting microscope, removed any remaining adhered debris or plankton with micro-scalpels and probes, discarded *Gloeotrichia* colonies that were missing trichomes or were not buoyant, and placed the cleaned colonies into a new bottle. We then randomly assigned an equal number of bottles of cleaned *Gloeotrichia* from each lake to every +*Gloeotrichia* mesocosm. Visual inspection of *Gloeotrichia* colonies from Lakes Sunapee and Morey with a dissecting microscope indicated that the colonies from both lakes were identical in both size and coloration. We added colonies to the +*Gloeotrichia* mesocosms in four pulses on the 1st, 4th, 14th, and 22nd days of the experiment because we were unable to collect enough colonies in one day to reach our target density (250 colonies L^{-1}, i.e., 2×10^5 colonies per mesocosm).

We sampled the mesocosms 24 h before the first *Gloeotrichia* addition and every 3–4 days thereafter. On each sampling day, we measured the mesocosm water level, recorded water temperature and dissolved oxygen at 0.5 m depth in the mesocosms (Yellow Springs Inc. model 556 MPS, Yellow Springs, Ohio, USA), and removed insect invaders with a dip net. To evaluate light availability, we examined the extent of the phytoplankton scum covering the surface of each mesocosm on each sampling day on a scale from 0 to 100 % cover. The same observer assigned the percent scum cover for every mesocosm throughout the experiment to ensure that the ranks were consistent.

Manipulated variables: Nutrients and *Gloeotrichia*

We sampled each mesocosm weekly using a separate integrated tube sampler (0.5 m long, 5.1 cm diameter) for chemical and zooplankton analyses. We retained 125 mL for TN and TP analyses, and filtered 500 mL through 0.7 µm Whatman GF/F filters for ammonium (NH_4^+), nitrate (NO_3^-), and soluble reactive P (SRP) analyses. We froze all total and soluble nutrient samples until analysis. Both P fractions (TP and SRP) were analyzed using Method 4500-P (American Public Health Association 1980) with an acidic persulfate digestion for TP samples. We analyzed TN samples with a spectrophotometric method after basic persulfate digestion (Crumpton et al. 1992). NO_3^- and NH_4^+ samples were analyzed on a Lachat QuikChem 8000 (Lachat Instruments, Loveland, Colorado, USA) according to the QuikChem Phenate method #10–107–106–1-J and QuikChem Cadmium Reduction method #10–107–04–1-A, respectively.

We sampled *Gloeotrichia* weekly by filtering 7 L of water from each mesocosm through 80 µm mesh and preserving the sample in 70 % ethanol. The filtered water was returned to the mesocosms. We counted *Gloeotrichia* colonies with a dissecting microscope.

Response variables: Phytoplankton and Zooplankton

Two samples were collected for phytoplankton biomass (as chlorophyll-*a*) from each mesocosm every 3–4 d. One sample was vacuum-filtered directly onto a 1.2 µm pore size Whatman GF/C filter (for total chlorophyll-*a*), while the second was prefiltered through a 30 µm Nitex mesh before being collected on a GF/C filter. This smaller fraction (< 30 µm) of phytoplankton excluded *Gloeotrichia* colonies and represented a size fraction of phytoplankton that zooplankton are generally able to graze (Lampert et al. 1986), with some exceptions (e.g., Hambright et al. 2007). All chlorophyll-*a* samples were frozen for at least 24 h, extracted with methanol, and analyzed with a fluorometer (Turner Designs TD 700, Sunnyvale, California, USA) according to Arar & Collins (1997).

We sampled zooplankton weekly from each mesocosm as described above for *Gloeotrichia*, and returned the filtered water to the mesocosms. We counted and identified zooplankton to genus on a dissecting microscope and calculated total zooplankton biomass and total *Ceriodaphnia* biomass from established length-mass regressions (Downing & Rigler 1984). Log-transformed weights were calculated individually from each log-transformed length and back-transformed to original units before calculating the mean weight and size of a taxon.

Statistical analyses

We conducted several analyses to determine if the treatments worked as planned and then whether nutrients mediated the effect of *Gloeotrichia* on the response variables, all at $\alpha = 0.05$. We first examined if there were significant main effects and interactions of our two factors (Nutrients and *Gloeotrichia*) on TN, TP, *Gloeotrichia* density, total zooplankton biomass, and *Ceriodaphnia* biomass using two-way repeated measures

ANOVA in SAS PROC MIXED (SAS v. 9.2, SAS Institute, Cary, North Carolina, USA). We chose a covariance structure for each repeated measures ANOVA using AIC. We analyzed total zooplankton biomass and *Ceriodaphnia* biomass separately because they were highly correlated (on each sampling day, $r > 0.80$) and MANOVA is not recommended for variables with high collinearity (Quinn & Keough 2002).

More than half of the NH_4^+ and NO_3^- concentrations and approximately half of the SRP concentrations measured in the mesocosms were below the method limit of detection (9.7 µg L^{-1} for NH_4^+ and NO_3^-, 1.2 µg L^{-1} for SRP), and therefore we could not use repeated measures ANOVA to assess treatment effects. For these nutrients only, we calculated for each mesocosm the proportion of all samples collected after the first *Gloeotrichia* addition that had concentrations above the method detection limit and analyzed the resultant data to determine the effects of Nutrients and *Gloeotrichia* with two-way ANOVA using JMP statistical software (JMP v. 9.0.2, SAS Institute, Cary, North Carolina, USA).

Because smaller-sized and total chlorophyll-*a* were significantly higher in the Enriched mesocosms than the Ambient mesocosms even before *Gloeotrichia* addition (two-way ANOVA, both $F_{1,14} \geq 9.48$, $p \leq 0.01$), we analyzed the rate of change in these variables over time by calculating the growth rate, r, between successive samples as: $r = [\ln(X_2/X_1)]/(t_2 - t_1)$, where r (d^{-1}) is the per capita growth rate of smaller-sized or total chlorophyll-*a*, X_2 is the concentration of smaller-sized or total chlorophyll-*a* on sampling day t_2, and X_1 is the concentration of smaller-sized or total chlorophyll-*a* on the preceding sampling day t_1. We analyzed the effect of Nutrients and *Gloeotrichia* on smaller-sized and total chlorophyll-*a* growth rate with two-way repeated measures ANOVA as described above. In addition, we analyzed all pairwise comparisons of the four repeated measure treatment means for the smaller-sized chlorophyll-*a* growth rate, with a Bonferroni-corrected α (Maxwell 1980).

To determine if different levels of Nutrients resulted in positive or negative interactions between *Gloeotrichia* and smaller-sized phytoplankton, we subtracted the mean growth rate of smaller-sized phytoplankton in all four *–Gloeotrichia* mesocosms from each of the corresponding *+Gloeotrichia* mesocosms, on each sampling day. We interpreted values greater than 0 as indicating positive interactions, or facilitation (i.e., *Gloeotrichia* increased the growth rate of smaller-sized phytoplankton relative to *–Gloeotrichia*), and values less than 0 as indicating negative interactions, or inhibition (i.e., *+Gloeotrichia* decreased the growth rate of smaller-sized phytoplankton relative to *–Gloeotrichia*). We tested if the differenced growth rates for the Ambient and Enriched mesocosms, respectively, were significantly different from 0 with one-sample t-tests in JMP.

Results

Limnological characteristics during the experiment

Averaged over the experimental period, mean total N (TN) and total P (TP) concentrations in the control (*–Gloeotrichia*) Ambient mesocosms were mesotrophic (359 ± 29 (1 S.E.) µg TN L^{-1} and 15 ± 1 µg TP L^{-1}), and the control Enriched mesocosms were eutrophic (700 ± 70 µg TN L^{-1} and 53 ± 7 µg TP L^{-1}) using the trophic criteria established by Nürnberg (1996; mesotrophy defined by 350 µg $L^{-1} \leq$ TN $\leq$ 650 µg L^{-1} and 10 µg $L^{-1} \leq$ TP $\leq$ 30 µg L^{-1}; Fig. 1). In the control treatments, mean total and smaller-sized fraction chlorophyll-*a* concentrations throughout the experiment were 6.7 (± 1.4) µg L^{-1} and 4.2 (± 0.8) µg L^{-1}, respectively, in the Ambient mesocosms, and 28.8 (± 4.7) µg L^{-1} and 5.5 (± 0.8) µg L^{-1}, respectively, in the Enriched mesocosms. In the *+Gloeotrichia* treatments, the mean total and smaller-sized fraction chlorophyll-*a* concentrations throughout the experiment were 16.1 (± 2.7) µg L^{-1} and 9.1 (± 1.3) µg L^{-1}, respectively, in the Ambient mesocosms, and 14.7 (± 4.1) µg L^{-1} and 9.5 (± 2.6) µg L^{-1}, respectively, in the Enriched mesocosms.

Ambient and Enriched mesocosms also exhibited different physical characteristics. Enriched mesocosms exhibited significantly lower temperatures (by $\leq$ 0.5 °C) at 0.5 m depth throughout the experiment (repeated measures ANOVA; $F_{1,12} = 8.22$, $p = 0.01$). The temperature in all of the mesocosms, regardless of treatment, was consistently between 20.8 and 24.7 °C (minimum observed temperature = 18.4 °C, maximum observed temperature = 27.0 °C), with a median temperature of 22.2 (± 2.2) °C (1 S.D.). Scum cover in the control (*–Gloeotrichia*) Ambient mesocosms was generally ~10 %, while scum cover in the control Enriched mesocosms averaged ~30 % throughout the experiment, with three Enriched mesocosms exhibiting > 80 % scum cover by the end of the sampling period (Fig. 2).

There was no significant effect of *Gloeotrichia* on the time series of scum cover or temperature (both repeated measures ANOVA effects: $p \geq 0.31$); however, when the sampling days were examined separately, the Nutrient and *Gloeotrichia* treatments significantly interacted to influence scum cover. After the third addition of colonies, the Ambient *+Gloeotrichia* mesocosms had higher scum cover than the Ambient controls, whereas the Enriched controls had higher scum cover than the Enriched *+Gloeotrichia* mesocosms (two-way ANOVA, $F_{1,14} = 5.23$, $p = 0.04$). The Enriched mesocosms exhibited consistently higher scum cover than the Ambient mesocosms on each day, corresponding to the repeated measures time series analysis, but no other significant effects were observed. Other than described above, we did not detect effects of the Nutrient and *Gloeotrichia* treatments on the time series of temperature or dissolved oxygen concentrations (all $p \geq 0.08$; dissolved oxygen concentrations were typically at or just above saturation).

Manipulated variables: Nutrients and *Gloeotrichia*

Consistent with our experimental design, TN and TP were higher in the Enriched than the Ambient mesocosms (Fig. 1; Table 1). We observed significant effects of Nutrients × *Gloeotrichia*, *Gloeotrichia* × time, Nutrients, and time on TN (all $p \leq 0.02$; Fig. 1; see Table 1 for all repeated measures ANOVA statistics). The +*Gloeotrichia* mesocosms generally exhibited higher TN concentrations than the –*Gloeotrichia* mesocosms at Ambient nutrients, while the –*Gloeotrichia* mesocosms exhibited higher concentrations than the *Gloeotrichia* mesocosms at Enriched nutrients ($p = 0.002$). The TP concentrations exhibited a similar interaction

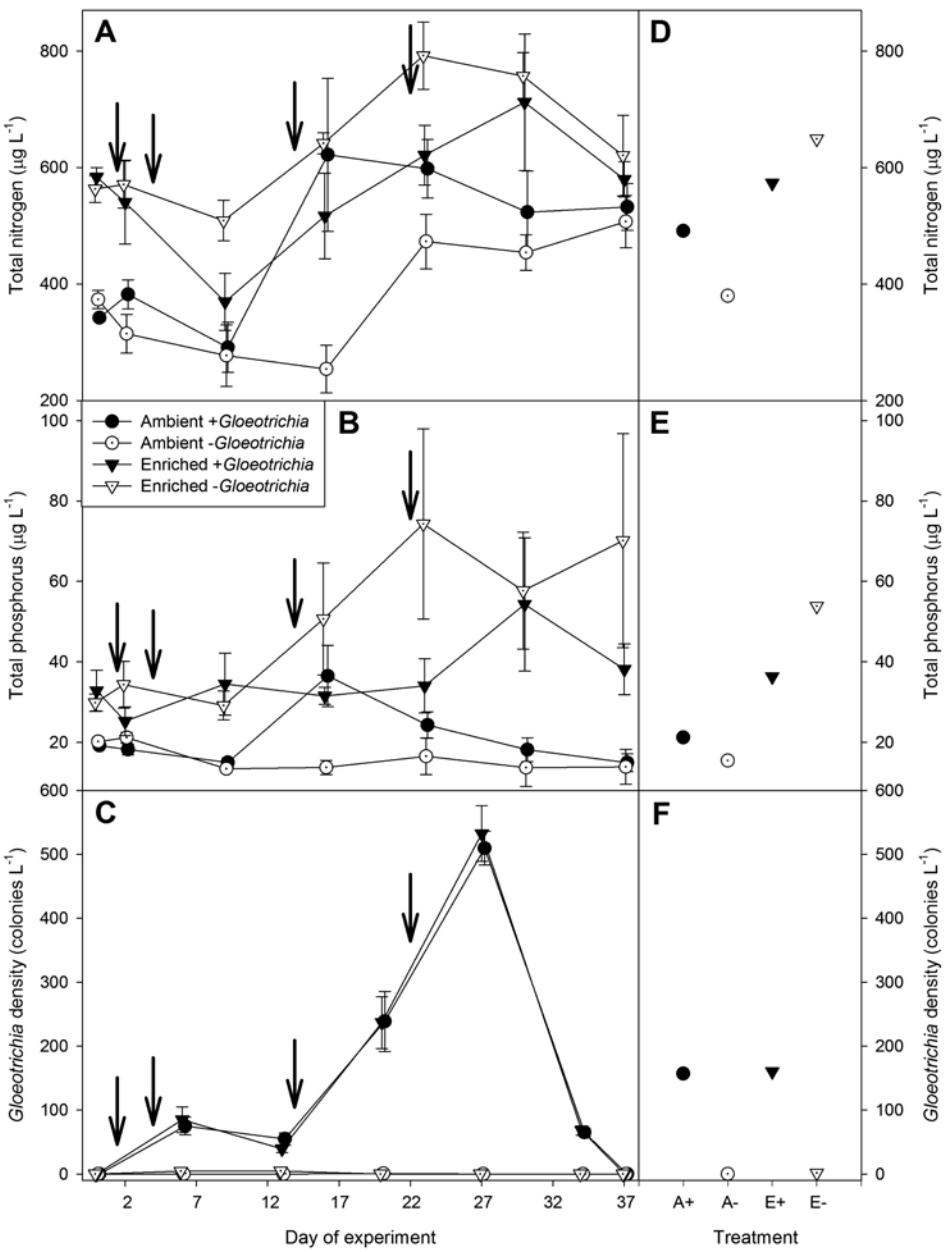

Fig. 1. (A) The mean (± 1 S.E.) total nitrogen concentrations, **(B)** total phosphorus concentrations, and **(C)** *Gloeotrichia* densities in the Nutrients × *Gloeotrichia* treatments over time. The arrows refer to the days of *Gloeotrichia* addition. **(D)** The mean total nitrogen concentrations, **(E)** total phosphorus concentrations, and **(F)** *Gloeotrichia* densities in the Nutrients × *Gloeotrichia* mesocosms, calculated from averaging all observations on all sample days within a treatment after the first *Gloeotrichia* addition. A+ refers to the Ambient +*Gloeotrichia* treatment, A- is the Ambient –*Gloeotrichia* treatment, E+ is the Enriched +*Gloeotrichia* treatment, and E- is the Enriched –*Gloeotrichia* treatment.

between Nutrients and *Gloeotrichia* that was also mediated by time (Fig. 1, Table 1).

Most of the NH_4^+ and NO_3^- samples (75 % and 61 %, respectively) and 43 % of the SRP samples in the mesocosms were below the method detection limit. The Enriched mesocosms exhibited a significantly higher proportion of detectable NH_4^+, NO_3^-, and SRP than the Ambient mesocosms after the first *Gloeotrichia* addition (two-way ANOVA: all $F_{1,14} \geq 5.76$, $p \leq 0.03$; Appendix 2). However, the soluble nutrient concentrations were quite low: when the concentrations below the detection limit were omitted, the mean concentrations were only slightly higher (18 µg NH_4^+ L^{-1}, 15 µg NO_3^- L^{-1}, and 2 µg SRP L^{-1}) than the detection limit. There were no significant effects or interactions of *Gloeotrichia* on any of the soluble nutrients (all $p > 0.41$).

Consistent with the treatments, *Gloeotrichia* densities were significantly higher in the +*Gloeotrichia* mesocosms than in the –*Gloeotrichia* mesocosms ($p < 0.0001$; Fig. 1, Table 1). The *Gloeotrichia* density in the Ambient +*Gloeotrichia* and Enriched +*Gloeotrichia* treatments peaked at 510 (± 27) colonies L^{-1} and 532 (± 44) colonies L^{-1}, respectively, on the 27th day of the experiment after four *Gloeotrichia* additions. The small difference in maximum *Gloeotrichia* density between the two levels resulted in a significant Nutrients × *Gloeotrichia* × time effect ($p = 0.04$). We also observed significant changes in *Gloeotrichia* density with time (Table 1).

Response variables: Phytoplankton and zooplankton

Nutrients and time mediated the effect of *Gloeotrichia* on the growth rate of smaller-sized phytoplankton (see Methods; $p < 0.0001$; Fig. 3, Table 1). In Ambient mesocosms, on average, *Gloeotrichia* increased the growth rate of smaller-sized phytoplankton in comparison to the –*Gloeotrichia* controls, whereas in Enriched mesocosms, *Gloeotrichia* decreased the smaller-sized phytoplankton growth rate relative to –*Gloeotrichia* controls. Smaller-sized phytoplankton growth rate was generally higher in Ambient mesocosms than in Enriched mesocosms, resulting in significant Nutrients × time, *Gloeotrichia* × time, Nutrients, and time effects (all $p \leq 0.01$); results were very similar for total phytoplankton growth rate (Table 1, Fig. 3). In both cases, the interaction was driven primarily by significant differences between the Ambient +*Gloeotrichia* and Enriched +*Gloeotrichia* treatments (smaller-sized growth rate pairwise comparison, $p = 0.001$) and the Enriched +*Gloeotrichia* and Enriched –*Gloeotrichia* treatments ($p = 0.004$). All other pairwise comparisons were not significant ($p \geq 0.01$). Finally, the difference in smaller-sized phytoplankton growth rates between the Ambient +*Gloeotrichia* and the Ambient –*Gloe-*

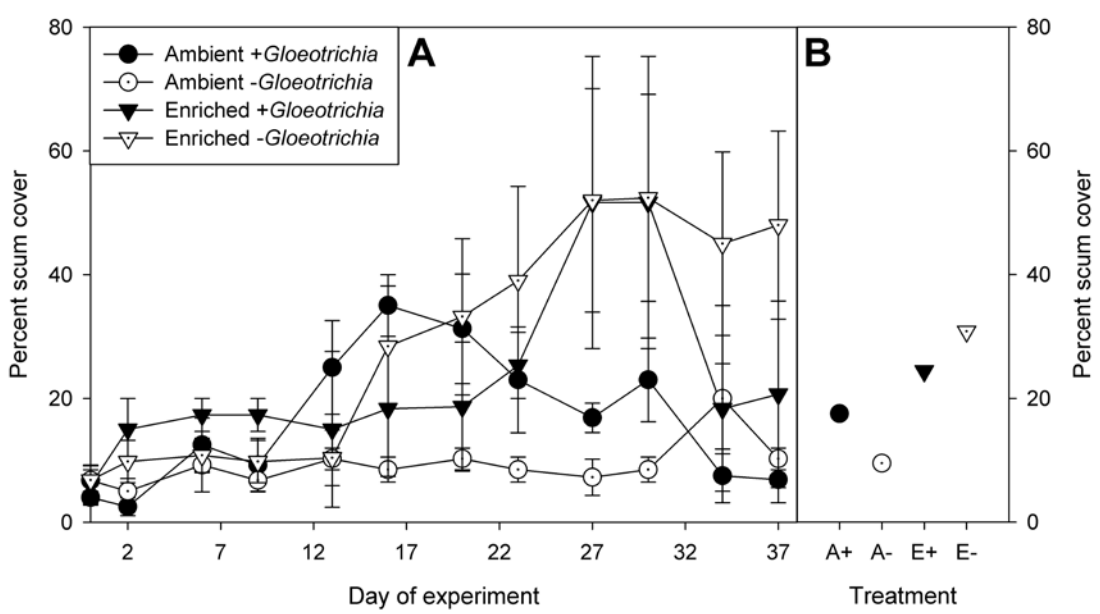

Fig. 2. (A) The mean (± 1 S.E.) percent scum cover in the Nutrients × *Gloeotrichia* treatments over time. **(B)** The mean percent scum cover in the Nutrients × *Gloeotrichia* mesocosms, calculated from averaging all observations on all sample days within a treatment after the first *Gloeotrichia* addition. A+ refers to the Ambient +*Gloeotrichia* treatment, A- is the Ambient –*Gloeotrichia* treatment, E+ is the Enriched +*Gloeotrichia* treatment, and E- is the Enriched –*Gloeotrichia* treatment.

Table 1. Statistical results from the two-way repeated measures ANOVA testing the effects and interactions of Nutrients and *Gloeotrichia* on the manipulated variables: total nitrogen (μg L^{-1}), total phosphorus (μg L^{-1}), and *Gloeotrichia* density (colonies L^{-1}); and the response variables: smaller-sized phytoplankton (chlorophyll-*a*) growth rate (d^{-1}), total phytoplankton (chlorophyll-*a*) growth rate (d^{-1}), total zooplankton biomass (μg L^{-1}), and *Ceriodaphnia* biomass (μg L^{-1}) in mesocosm experiments conducted in NH, USA. DF denotes degrees of freedom, and significant effects ($p \leq 0.05$) are in bold.

		Repeated measures ANOVA	DF	F-value	*p*-value
Manipulated variables	Total nitrogen	**Nutrients**	**1,12**	**42.61**	**< 0.0001**
		Gloeotrichia	1,12	0.13	0.73
		Time	**5,12**	**28.93**	**< 0.0001**
		Nutrients × *Gloeotrichia*	**1,12**	**15.89**	**0.002**
		Nutrients × Time	5,12	2.04	0.14
		***Gloeotrichia* × Time**	**5,12**	**4.14**	**0.02**
		Nutrients × *Gloeotrichia* × Time	5,12	2.44	0.095
	Total phosphorus	**Nutrients**	**1,12**	**9.86**	**0.009**
		Gloeotrichia	1,12	0.41	0.54
		Time	5,12	1.91	0.17
		Nutrients × *Gloeotrichia*	1,12	1.77	0.21
		Nutrients × Time	**5,12**	**3.42**	**0.04**
		***Gloeotrichia* × Time**	**5,12**	**4.74**	**0.01**
		Nutrients × *Gloeotrichia* × Time	**5,12**	**3.07**	**0.05**
	Gloeotrichia density	Nutrients	1,12	0.06	0.80
		Gloeotrichia	**1,12**	**337.67**	**< 0.0001**
		Time	**4,12**	**220.92**	**< 0.0001**
		Nutrients × *Gloeotrichia*	1,12	0.01	0.93
		Nutrients × Time	4,12	2.42	0.11
		***Gloeotrichia* × Time**	**4,12**	**229.91**	**< 0.0001**
		Nutrients × *Gloeotrichia* × Time	**4,12**	**3.56**	**0.04**
	Percent scum cover	**Nutrients**	**1,12**	**4.32**	**0.05**
		Gloeotrichia	1,12	0.01	0.91
		Time	10,12	1.60	0.35
		Nutrients × *Gloeotrichia*	1,12	0.13	0.31
		Nutrients × Time	10,12	0.65	0.74
		Gloeotrichia × Time	10,12	1.06	0.55
		Nutrients × *Gloeotrichia* × Time	10,12	0.89	0.61
Response variables	Smaller-sized chlorophyll-*a* growth rate	**Nutrients**	**1,12**	**8.34**	**0.01**
		Gloeotrichia	1,12	2.29	0.16
		Time	**10,12**	**34.75**	**< 0.0001**
		Nutrients × *Gloeotrichia*	**1,12**	**12.80**	**0.004**
		Nutrients × Time	**10,12**	**68.90**	**< 0.0001**
		***Gloeotrichia* × Time**	**10,12**	**17.65**	**< 0.0001**
		Nutrients × *Gloeotrichia* × Time	**10,12**	**28.82**	**< 0.0001**
	Total chlorophyll-*a* growth rate	**Nutrients**	**1,12**	**5.83**	**0.03**
		Gloeotrichia	1,12	1.73	0.21
		Time	**10,12**	**41.37**	**< 0.0001**
		Nutrients × *Gloeotrichia*	**1,12**	**9.89**	**0.009**
		Nutrients × Time	**10,12**	**20.42**	**< 0.0001**
		***Gloeotrichia* × Time**	**10,12**	**7.08**	**0.001**
		Nutrients × *Gloeotrichia* × Time	**10,12**	**19.71**	**< 0.0001**
	Total zooplankton biomass	**Nutrients**	**1,12**	**22.46**	**0.0005**
		Gloeotrichia	1,12	0.60	0.45
		Time	**4,12**	**8.39**	**0.002**
		Nutrients × *Gloeotrichia*	1,12	0.06	0.81
		Nutrients × Time	4,12	3.06	0.06
		Gloeotrichia × Time	4,12	0.61	0.66
		Nutrients × *Gloeotrichia* × Time	4,12	1.00	0.45
	Ceriodaphnia biomass	**Nutrients**	**1,12**	**23.60**	**0.0004**
		Gloeotrichia	1,12	0.20	0.66
		Time	**4,12**	**13.44**	**0.0002**
		Nutrients × *Gloeotrichia*	1,12	1.55	0.24
		Nutrients × Time	**4,12**	**4.39**	**0.02**
		Gloeotrichia × Time	4,12	0.26	0.90
		Nutrients × *Gloeotrichia* × Time	4,12	0.76	0.57

otrichia treatments was significantly greater than zero (one-sample t-test, $t_{32} = 1.87$, $p = 0.03$), indicating facilitation, whereas the difference in smaller sized growth rates between the Enriched +*Gloeotrichia* and the Enriched –*Gloeotrichia* treatments was significantly less than zero ($t_{32} = -1.75$, $p = 0.04$), indicating inhibition.

The zooplankton communities that developed in the mesocosms were similar among treatments and composed predominantly of *Ceriodaphnia*. The biomass of the cladoceran *Ceriodaphnia* was significantly higher in the Enriched than the Ambient mesocosms (Fig. 4), resulting in significant or marginally significant effects of Nutrients × time, Nutrients, and time (total zooplankton biomass: all $p \leq 0.06$; total *Ceriodaphnia* biomass: all $p \leq 0.02$). On average, the Enriched mesocosms exhibited 429.8 (± 49.6) µg L^{-1} higher total zooplankton biomass and 304.5 (± 41.6) µg L^{-1} higher *Ceriodaphnia* biomass than the Ambient mesocosms. Despite the increase of smaller-sized phytoplankton growth rate in the Ambient +*Gloeotrichia* treatment, there was no significant effect or interaction of *Gloeotrichia* on either total zooplankton or *Ceriodaphnia* biomass (all $p \geq 0.24$).

Discussion

Although many studies have focused on the inhibitory effects of cyanobacteria, recent research has in-

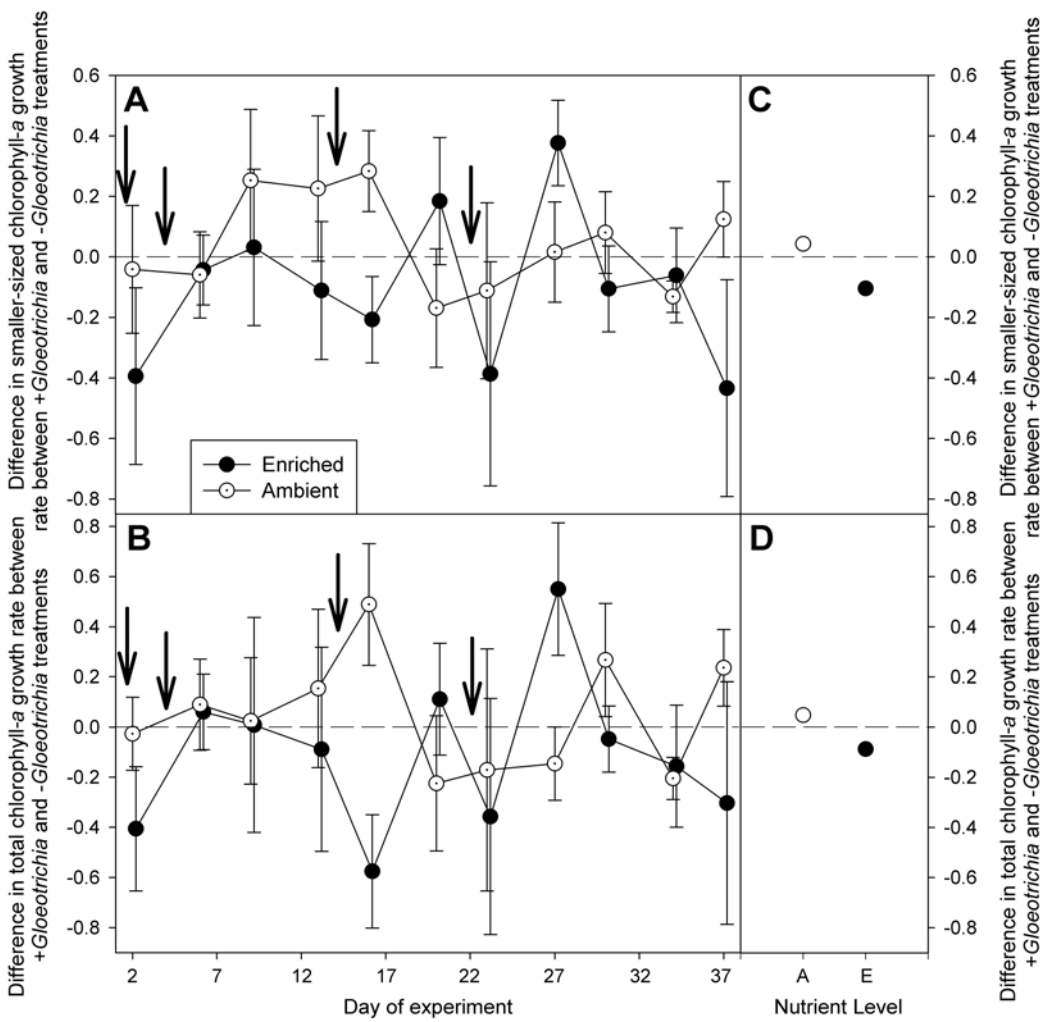

Fig. 3. (A) The mean difference (± 1 S.E.) in smaller-sized phytoplankton (< 30 µm fraction of chlorophyll-*a*) growth rate and **(B)** total phytoplankton (total chlorophyll-*a*) growth rate in d^{-1} between +*Gloeotrichia* and –*Gloeotrichia* mesocosms over time. The arrows refer to the days of *Gloeotrichia* addition. **(C)** The mean difference in smaller sized phytoplankton (chlorophyll-*a*) growth rate and **(D)** total phytoplankton (chlorophyll-*a*) growth rate, calculated from averaging all observations across all sample days. A refers to the Ambient nutrient level, and E is the Enriched nutrient level.

dicated that the effects of cyanobacterial blooms are more complex and context-dependent than previously realized (Ibelings et al. 2008). A growing number of studies indicate that cyanobacteria can stimulate the growth and division of smaller-sized phytoplankton (Carey & Rengefors 2010, Neisch et al. 2012). While it is not possible to determine why the effects of cyanobacterial blooms are sometimes inhibitory and sometimes stimulatory, we note that the majority of the studies finding inhibitory effects of cyanobacteria have been conducted in eutrophic and hypereutrophic systems, primarily using laboratory monocultures (reviewed by Hudnell 2008). We propose that studies of natural phytoplankton communities in less nutrient-rich systems may be more likely to demonstrate the incidence of stimulatory effects of cyanobacteria on smaller-sized phytoplankton, as found in this study and by Suikkanen et al. (2005).

Our experimental data further indicate that trophic state can play a role in mediating the effect of *Gloeotrichia* on the smaller-sized phytoplankton community. Although there was variability in the smaller-sized phytoplankton growth rate over time, *Gloeotrichia* generally facilitated smaller-sized phytoplankton at Ambient nutrient concentrations, and inhibited smaller-sized phytoplankton at Enriched concentrations.

The incidence of facilitation may have been higher in the Ambient mesocosms than Enriched mesocosms because *Gloeotrichia* significantly increased water column total N and P. Our data indicate that nutrients were likely more limiting for phytoplankton in

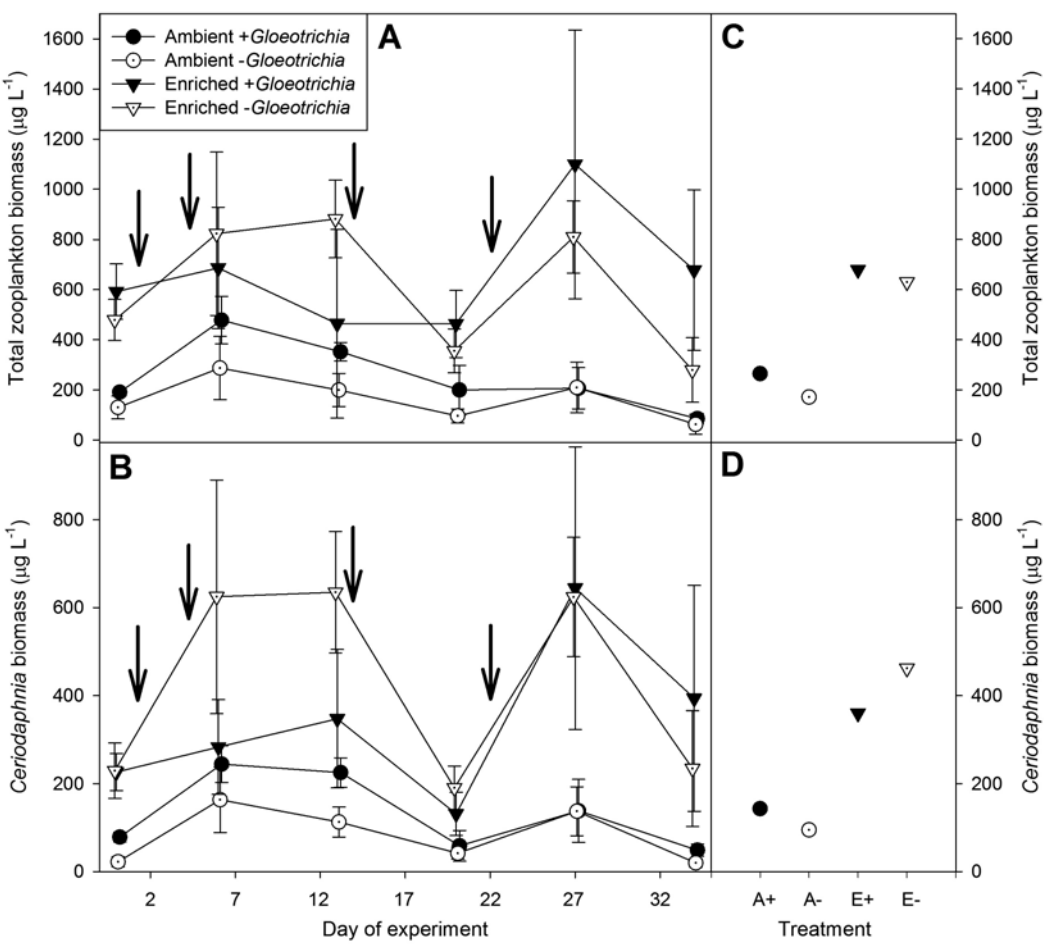

Fig. 4. (A) The mean (± 1 S.E.) total zooplankton biomass and **(B)** *Ceriodaphnia* biomass concentrations in the Nutrients × *Gloeotrichia* treatments over time in the mesocosms. The arrows refer to the days of *Gloeotrichia* addition. **(C)** The mean total zooplankton biomass and **(D)** *Ceriodaphnia* biomass concentrations, calculated from averaging all observations in all sample days after the first *Gloeotrichia* addition within the Nutrients and *Gloeotrichia* treatments. A+ refers to the Ambient +*Gloeotrichia* treatment, A- is the Ambient –*Gloeotrichia* treatment, E+ is the Enriched +*Gloeotrichia* treatment, and E- is the Enriched –*Gloeotrichia* treatment.

the Ambient mesocosms than in the Enriched mesocosms: TN and TP concentrations were significantly higher in the Enriched mesocosms than in the Ambient mesocosms throughout the experiment. In addition, the Enriched mesocosms exhibited significantly higher proportions of samples with NH_4^+, NO_3^-, and SRP concentrations above the method detection limit. Finally, the Ambient +*Gloeotrichia* mesocosms exhibited significantly higher TN and TP concentrations than Ambient –*Gloeotrichia* mesocosms, which we have documented in other experiments with this cyanobacterium in oligotrophic systems (Carey et al. 2014). Although we do not have definitive evidence from this study, *Gloeotrichia* may release some of its nutrients into the water column through senescence, zooplankton grazing, or leakage, which can potentially stimulate phytoplankton growth, as has been observed in Loch Antermony, Scotland (Pitois et al. 1997), Lake Peipsi, Estonia (Nõges et al. 2004), and oligotrophic mesocosms (Carey et al. 2014). However, because of the lack of soluble N and P data above the method detection limit, we are unable to test if nutrient limitation was the primary mechanism driving *Gloeotrichia*'s stimulatory effect. Other cyanobacterial taxa, including *Anabaena*, *Microcystis, Nodularia,* and *Oscillatoria,* also release nutrients into the water column (Ray & Bagchi 2001, Agawin et al. 2007), especially in low-nutrient systems, where the nutrient diffusion gradients are greater (Wetzel 2001).

The increase in TN and TP concentrations in the Ambient +*Gloeotrichia* treatment is most likely due to N and P bound within the colonies that were added to the mesocosms. Several studies have demonstrated that *Gloeotrichia* transports a considerable amount of P from the sediments into the water column during the recruitment stage of its life cycle (Istvánovics et al. 1993, Pettersson et al. 1993). In our study, we collected *Gloeotrichia* colonies from the water column after recruitment, so presumably the colonies contained a substantial amount of P. Estimates for the total amount of P in a *Gloeotrichia* colony range from 0.018–0.08 µg P colony^{-1} (Pettersson et al. 1993, Tymowski & Duthie 2000), and by multiplying these estimates by the observed molar N:P ratio of *Gloeotrichia,* 5.7 ± 0.7 (Vuorio et al. 2006), the amount of N in a colony likely ranges from 0.10–0.46 µg N colony^{-1}. On the 27th day of the experiment, when the +*Gloeotrichia* mesocosms exhibited their highest colony density, the TP concentrations in the Ambient +*Gloeotrichia* mesocosms were 7.8 ± 1.3 µg TP L^{-1} higher than in the Ambient –*Gloeotrichia* mesocosms. By multiplying the Ambient +*Gloeotrichia* density on experiment day 27 (510 ± 27 colonies L^{-1}) by the colony P concentration, we estimate that the amount of P that was added to the Ambient +*Gloeotrichia* mesocosms within *Gloeotrichia* colonies was between 8.7–43.0 µg P L^{-1}, which is similar to the observed increase in TP concentrations. Similarly, the amount of N that may have been added to the Ambient +*Gloeotrichia* mesocosms within colonies was 51–235 µg N L^{-1}, which brackets the observed increase of 125 ± 40 µg N L^{-1} in the mesocosms. It is also possible that N fixation by *Gloeotrichia* contributed to higher N concentrations in the Ambient +*Gloeotrichia* mesocosms, further alleviating nutrient limitation for other phytoplankton. While we did not measure N fixation in this study, Stewart et al. (1967) found that *Gloeotrichia* exhibited one of the highest rates of acetylene reduction observed among the eight cyanobacterial taxa tested.

It is unclear what factors were responsible for the inhibitory effects of *Gloeotrichia* on smaller-sized phytoplankton in the Enriched mesocosms. It may be possible that *Gloeotrichia* decreased light availability in mesocosms that were already light-limited. In eutrophic systems, light is often more limiting to phytoplankton growth than nutrients (Wetzel 2001, Reynolds 2006). Although we did not measure light attenuation directly, it is probable that the Enriched mesocosms had lower light availability throughout the experiment because the Enriched mesocosms had higher nutrients, total chlorophyll-*a* concentrations, and scum cover than the Ambient mesocosms. Furthermore, the Enriched mesocosms exhibited cooler temperatures at 0.5 m depth than the Ambient mesocosms, indicating that more light was attenuated in the surface waters. *Gloeotrichia* additions may have further reduced light availability in the Enriched mesocosms, but our scum cover data are inconclusive. In eutrophic Lake Erken, Sweden, *Gloeotrichia* forms large scums that substantially decrease light availability, resulting in lower littoral periphyton growth (Liess et al. 2006). Cyanobacteria can outcompete other phytoplankton under conditions of low light and can also create a higher turbidity per unit of P than any other phytoplankton group (Scheffer et al. 1997); thus, *Gloeotrichia* in our study may have also decreased smaller-sized phytoplankton by limiting light availability, but additional studies are needed to definitively test this hypothesis, as well as examine other mechanisms, such as allelopathy and toxin production, that may be acting in concert.

Although the Enriched mesocosms had significantly higher overall TN and TP concentrations than the Ambient mesocosms, Enriched +*Gloeotrichia* me-

socosms exhibited lower TN and TP concentrations relative to the Enriched –*Gloeotrichia* mesocosms. It is possible that the loss of TN and TP from the water column was due to senesced phytoplankton that settled to the bottom of the mesocosms. Alternatively, the TN and TP concentrations may have decreased because those nutrients went into zooplankton or *Gloeotrichia* production; however, there were no significant main or interaction effects of *Gloeotrichia* on total zooplankton or *Ceriodaphnia* biomass or nutrient effects on *Gloeotrichia* density.

Total zooplankton and *Ceriodaphnia* biomass concentrations were primarily driven by the manipulation of Nutrients, not *Gloeotrichia*. It is possible that the zooplankton biomass did not respond to *Gloeotrichia* addition because grazing of *Gloeotrichia*, as has been observed for other cyanobacteria, decreased zooplankton feeding rates (Lampert 1987). However, despite the many negative effects that cyanobacteria are known to exert on zooplankton survival and fecundity, it is clear that zooplankton biomass did not decrease in response to *Gloeotrichia*.

Synthesis

We propose that trophic state may determine whether the effect of *Gloeotrichia* on smaller-sized phytoplankton is inhibitory or stimulatory. In the Ambient mesocosms, *Gloeotrichia* had a stimulatory effect on smaller-sized phytoplankton, presumably because of increased total N and P, as has been observed in other low-nutrient systems (Carey et al. 2014). In the Enriched mesocosms, it is not as clear what factors may be responsible for *Gloeotrichia*'s inhibitory effect on smaller-sized phytoplankton. Although *Gloeotrichia* likely released nutrients in both the Ambient and Enriched mesocosms, those nutrients would have been only a small contribution to already high levels, and smaller-sized phytoplankton in the Enriched mesocosms did not increase, indicating that other factors, such as light availability or allelopathy, may have been important. Additional studies are needed to determine what mechanisms were responsible for *Gloeotrichia*'s inhibitory effects in eutrophic mesocosms.

Nutrient pollution is increasing in many lakes globally (e.g., Carpenter et al. 1998). Simultaneously, cyanobacterial blooms are increasing in oligotrophic, mesotrophic, and eutrophic systems (Ernst et al. 2009, Winter et al. 2011, Carey et al. 2012). Understanding how cyanobacteria in general, and *Gloeotrichia* in particular, affect phytoplankton and zooplankton communities has substantial implications for ecosystem functioning. Our data suggest that increasing nutrient loads to lakes may alter the role of *Gloeotrichia*, as it transitions from a facilitator of smaller-sized phytoplankton growth in low-nutrient lakes to an inhibitor of smaller-sized phytoplankton growth in high-nutrient lakes.

Acknowledgments

We thank J. A. Brentrup, N. M. Ruppertsberger, H. A. Ewing, R. Q. Thomas, S. B. Fey, E. Traver, D. Schmidt, M. Vomela, and L. Grapel for assistance with field and laboratory analyses. R. Kurmayer, P. C. Hanson, A. S. Flecker, and anonymous reviewers provided very helpful comments on this manuscript. This work was supported by a National Science Foundation (NSF) Graduate Research Fellowship to C.C.C., NSF Doctoral Dissertation Improvement Grant DEB-1010862 to C.C.C. and N.G.H.; NSF DEB-0749022 to K.L.C., K.C.W., and H. A. Ewing; NSF EF-0842267 to K.L.C.; NSF EF-0842112 to H. A. Ewing; NSF EF-0842125 to K.C.W.; and grants to C.C.C. from the Cornell Biogeochemistry and Biocomplexity Program, Andrew W. Mellon Foundation, Kieckhefer Adirondack Foundation, and NSF Biogeochemistry and Biocomplexity IGERT. The preparation of this manuscript was facilitated by NSF CDI-0941510 to P. C. Hanson.

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Submitted: 02 April 2013; accepted: 19 May 2014.

Appendix 1. The eight New Hampshire, USA lakes from which we collected unfiltered lake water to create phytoplankton communities. The asterisks (*) denote lakes from which we collected zooplankton.

Lake name	Latitude	Longitude	Total phosphorus (µg L^{-1})	Total nitrogen (µg L^{-1})	Nutrient data source
Lake Sunapee*	43° 24′ N	72° 20′ W	5	175	C.C.C., unpubl.
Goose Pond	43° 42′ N	72° 5′ W	5	179	A.C. Dawson & K.L.C., unpubl.
Post Pond*	43° 50′ N	72° 09′ W	8	215	A.C. Dawson & K.L.C., unpubl.
Boston Lot Reservoir	43° 40′ N	71° 17′ W	10	251	A.C. Dawson & K.L.C., unpubl.
4 A Pond	43° 29′ N	71° 58′ W	23	145	A.M. Siepielski, unpubl.
Deweys Pond*	43° 39′ N	72° 24′ W	54	552	A.M. Siepielski, unpubl.
Occum Pond*	43° 43′ N	72° 17′ W	117	.	C.C.C., unpubl.
Broken Tank Pond	43° 41′ N	72° 13′ W	437	3007	C.C.C., unpubl.

Appendix 2. The mean (± 1 S.E.) proportion of all (Top) NH_4^+, (Middle) NO_3^-, and (Bottom) SRP samples collected after the first *Gloeotrichia* addition that were above the method detection limit in the Nutrients and *Gloeotrichia* treatments. Enriched treatments exhibited significantly higher NH_4^+ ($F_{1,14} = 10.19$, $p = 0.008$), NO_3^- ($F_{1,14} = 5.76$, $p = 0.03$), and SRP ($F_{1,14} = 20.76$, $p < 0.0001$).