Increases in phosphorus at the sediment-water interface may influence the initiation of cyanobacterial blooms in an oligotrophic lake

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Introduction

Freshwater cyanobacteria have been implicated as both indicators and agents of ecosystem change (WETZEL 2001). *Gloeotrichia echinulata* is a nuisance cyanobacterium common in meso- to eutrophic systems that has recently begun to bloom in oligo- to mesotrophic lakes across northern New England, USA (CAREY et al. 2008). Between 2002 and 2006, at least 27 outbreaks of *G. echinulata* were confirmed in oligotrophic lakes across Maine and New Hampshire that do not normally experience algal blooms. These blooms are of particular concern because *G. echinulata* produces the toxin microcystin-LR (CAREY et al. 2007) and can transport a considerable amount of phosphorus (P) from the sediment into the water column (ISTVANOVICS et al. 1993).

At present, little is known about the mechanisms that have stimulated *G. echinulata* blooms in oligotrophic systems. We hypothesized that increased P concentrations in lake sediments may be responsible, in part, for *G. echinulata* blooms in low-nutrient lakes. Many oligotrophic lakes have low concentrations of P in their water, but high concentrations of P in their sediments (MAASSEN et al. 2005), potentially due to increasing external P loads (WETZEL 2001). Interestingly, many of the lakes in Maine that are now experiencing *G. echinulata* blooms had been classified as "at risk from new watershed development" (MAINE DEPARTMENT OF ENVIRONMENTAL SERVICES, unpublished), indicating that those lakes may be subject to increased sediment P. Thus, one hypothesis is that the recent *G. echinulata* blooms may be occurring in response to increased P concentrations in lake sediment: "eutrophied" sediment in an oligotrophic lake.

Phosphorus plays a major role in *G. echinulata*'s complex life cycle. Overwintering akinetes, or resting cells, must absorb a substantial amount of phosphate from the sediment pore water during a germination and growth phase on the lake sediment before recruitment into the water column (PETTERSSON et al. 1993, KARLSSON 2003, KARLSSON-ELFGREN et al. 2004), which takes ~2.5–4 weeks after the initiation of germination. Phosphorus absorbed in the sediments fuels planktonic cell division; *G. echinulata*'s P uptake in the water column is thought to be negligible (ISTVANOVICS et al. 1993, TYMOWSKI & DUTHIE 2000). Because of the large pool of sediment P that exists, even in oligotrophic lakes (MAASSEN et al. 2005), and *G. echinulata*'s apparent demand for P from the sediment, we hypothesized that akinetes would exhibit increased germination and recruitment when exposed to increased concentrations of sediment P. We used an *in situ* nutrient-diffusing substrate experiment to test this hypothesis in an oligotrophic lake while simultaneously monitoring *G. echinulata* recruitment and P at the sediment-water interface.

Key words: cyanobacterial blooms, eutrophication, *Gloeotrichia echinulata*, Lake Sunapee, sediment phosphorus

Methods

Study site

We studied *G. echinulata* in Lake Sunapee, an oligotrophic system of glacial origin in central New Hampshire, USA, at 43°24'N, 72°2'W. Humans have used the watershed since the 1800s when logging and clear-cutting for crop cultivation and pasturing was dominant. Present land use/land cover changes are primarily due to human development, especially along the shoreline. Lake Sunapee's mean water column total P concentration is <5 µg/L, mean summer Secchi depth is 8–10 m, and mean summer chlorophyll *a* concentration is <2 µg/L (CAREY et al. 2008). The lake has a surface area of 16.55 km^2, a volume of 1.88×10^8 m^3, a mean depth of 11.4 m, and a maximum depth of 34 m (LAKE SUNAPEE PROTECTIVE ASSOCIATION, unpublished data). Most of the lake stratifies thermally from mid-June to early October and is covered with ice from December to mid-April.

We conducted our monitoring and in-lake experiment at a site in southern Herrick Cove (HC South), a large bay in the northeastern area of Lake Sunapee where *G. echinulata* colonies were first identified in the water column in July 2003.

Field monitoring

During summer 2006 we monitored *G. echinulata* recruitment in the littoral zone at HC South with recruitment traps consisting of an inverted transparent glass funnel (diameter = 8.57 cm) attached to a 250-mL plastic collection bottle and hung ~10 cm above the sediment to trap migrating colonies (CAREY et al. 2008). On each sampling date, the recruitment trap funnel unit was stoppered underwater, emptied into a collection bottle at the water surface, preserved with Lugol's iodine, and returned to the same location. All *G. echinulata* colonies were identified and enumerated with a Leica MZ12 dissecting microscope. We calculated *G. echinulata* recruitment rate as the number of *G. echinulata* colonies migrating into the water column between sampling dates (colonies · cm^{-2} of lake sediment · d^{-1}).

We placed 3 traps over organic-rich sediment at 2 m depth and sampled *G. echinulata* abundance in traps and total dissolved phosphorus (TDP) at the sediment-water interface adjacent to each trap every 3–9 days from 22 June to 18 September. We estimated sediment TDP by collecting samples from the sediment-water interface adjacent to each trap; procedures were as described in CAREY et al. (2008) except that total P was determined following VAN VELDHOVEN & MANNEARTS (1987).

Nutrient-diffusing substrate experiment

In August 2006 we conducted a field experiment to measure the response of *G. echinulata* recruitment to P enrichment *in situ*. The experiment contrasted 2 treatments, a control and a P nutrient-diffusing substrate (NDS), at 5 sites located 10–50 m from the HC South monitoring site. Protocols for this experiment followed FLECKER et al. (2002); the agar contained 0.5 M phosphorus as NaH_2PO_4.

We initiated the experiment on 2 August 2006. To measure the response of *G. echinulata* recruitment to the +P and control substrates, we placed 2 recruitment traps over sediment ~10 cm away from the +P substrates and one recruitment trap ~10 cm away from the control substrates (~1.4 m from the +P substrates) at each site. All substrates were gently embedded into the top of the lake sediment, agar side down, at ~2 m water depth; sites were separated by at least 5 m.

We quantified *G. echinulata* recruitment rate in each trap by sampling every 3–9 days for 39 days. We tested the hypothesis that *G. echinulata* recruitment rates increase with *in situ* P addition by comparing the recruitment rate in the 10 +P traps with the 5 control traps on each sampling date using a 2-sample median test.

Using a fixed-step model for saturated homogenous porous medium (OGATA & BANKS 1961, FREEZE & CHERRY 1979), we estimated that P diffused through the top 2 cm of lake sediment from the +P substrates to the sediment below the 2 +P recruitment traps in <2 days. In contrast, the minimum time needed for phosphate to diffuse from the +P substrates to the sediment below the control recruitment traps was >35 days.

Results

G. echinulata recruited into the water column of Lake Sunapee from 22 June to 18 September 2006 at a mean rate of 0.02 ± 0.005 (1 SE) colonies · cm^{-2} · d^{-1}. Although mean sediment TDP declined through the summer, there were short-term increases in late June and
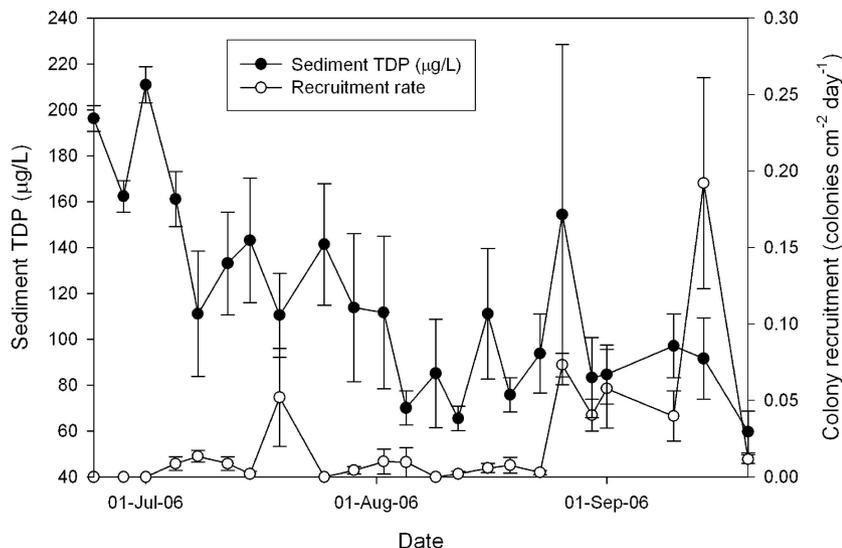

Fig. 1. Mean *G. echinulata* recruitment rate (colonies · cm^{-2} · d^{-1}) and mean sediment TDP (µg P/L) in southern Herrick Cove, Lake Sunapee, NH, over time in June–September 2006. Error bars demarcate 1 SE.

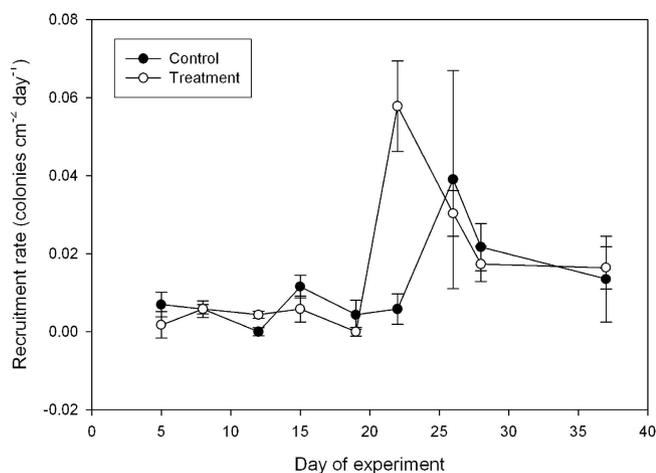**Fig. 2.** The effect of P enrichment on median *G. echinulata* recruitment rate (colonies · cm^{-2} · d^{-1}) in comparison to the control treatment (n = 5) in the nutrient-diffusing substrate experiment.

August (Fig. 1). Mean recruitment rate appeared to increase following these increases in mean sediment TDP: peaks in sediment TDP on 29 June and 24 August were followed by peaks in *G. echinulata* recruitment 18 and 19 days later, respectively (Fig. 1).

In the field, experimental P addition significantly increased the rate of *G. echinulata* recruitment 22 days after the start of the experiment (Fig. 2; 2-sample median test, P = 0.03). On 24 August the median recruitment rate was 0.057 ± 0.007 colonies · cm^{-2} · d^{-1} higher (587 %) in the +P treatment than the control treatment. There were no other dates with significantly different recruitment between the +P traps and controls (all P > 0.10).

Discussion

Lake Sunapee experienced *G. echinulata* blooms in late August and early September in 2006. The maximum recruitment of colonies in Lake Sunapee (0.32 colonies bull cm^{-2} · d^{-1}) was far lower than the maximum *G. echinulata* recruitment documented in eutrophic lakes (~36 colonies · cm^{-2} · d^{-1} in Green Lake in 1989, Barbiero 1993; ~1520 colonies · cm^{-2} · d^{-1} in Lake Erken in 1993, Forsell & Pettersson 1995), and about one-third of the recruitment measured in Lake Sunapee in 2005 (1.13 colonies · cm^{-2} · d^{-1}; Carey et al. 2008).

Our combined field results indicate that increased sediment TDP concentrations may have influenced *G. echinulata* recruitment in Lake Sunapee. First, our field monitoring data indicate that a pulse of sediment TDP was typically followed by an increase in *G. echinulata* 18–19

days later; this time lag corresponds to the amount of time *G. echinulata* needs to germinate (1–7 d) and absorb P from the sediment (2–3 wk) before recruiting into the water column (Tymowski & Duthie 2000, Karlsson 2003). We also noted an increase in *G. echinulata* recruitment ~3 weeks after an increase in sediment TDP in Lake Sunapee during 2005 (Carey et al. 2008). Second, *G. echinulata* recruitment responded positively to *in situ* P additions after 22 days. Assuming that diffusion from +P substrates occurred within 1–2 days, akinetes in this treatment exhibited a 20–21 day lag from phosphate enrichment to recruitment, similar to the lag period observed in the field observations. Additional laboratory and field experiments with different P concentrations and rates of addition are needed to elucidate the potential mechanisms behind these results: for example, is *G. echinulata* germination accelerated by a discrete pulse of P, or because P exceeds a certain threshold (as proposed by Pettersson et al. 1993)?

Our results indicate that sediment P may play a role in influencing *G. echinulata* blooms in oligotrophic lakes such as Lake Sunapee. However, several other drivers are likely involved in triggering *G. echinulata* recruitment, including light and temperature (e.g., Karlsson-Elfgren et al. 2004). Understanding how multiple drivers, biotic and abiotic, interact to influence *G. echinulata* represents the next frontier for studies of how and why this organism is increasing in oligotrophic lakes.

Acknowledgements

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