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Occurrence and toxicity of the cyanobacterium *Gloeotrichia echinulata* in low-nutrient lakes in the northeastern United States

Cayelan C. Carey · Holly A. Ewing · Kathryn L. Cottingham · Kathleen C. Weathers · R. Quinn Thomas · James F. Haney

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Abstract To date, most research on cyanobacterial blooms has focused on high-nutrient, not low-nutrient lakes. We investigated reports of the cyanobacterium *Gloeotrichia echinulata* in lakes with low concentrations of nitrogen and phosphorus across the northeastern United States by surveying selected oligotrophic and mesotrophic lakes during four summers. *G. echinulata* is a large (1–3 mm diameter) colonial cyanobacterium that may have substantial effects on low-nutrient lakes used for drinking water and recreation because it can produce the toxin microcystin-LR. We found *G. echinulata* in the water column of 27 out of 37 lakes we sampled in Maine, New Hampshire, New York, and Vermont. *G. echinulata* densities were typically low (<5 colonies L^{-1}), but occasionally at surface scum-producing levels (up to 250 colonies L^{-1}). *G. echinulata* colonies from the survey lakes exhibited detectable microcystin-LR concentrations ranging from 58 to 7,148 ng microcystin-LR g^{-1} dry weight colonies. If *G. echinulata* densities increase to bloom levels observed in eutrophic systems, our data suggest that the microcystin-LR concentrations attributable to *G. echinulata* may reach levels known to influence aquatic organisms and pose human health risks.

Keywords Bloom · Mesotrophic · Microcystin · Oligotrophic · Phytoplankton

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C. C. Carey (✉) · R. Q. Thomas
Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA
e-mail: ccc99@cornell.edu

H. A. Ewing
Program in Environmental Studies, Bates College, Lewiston, ME 04240, USA

K. L. Cottingham
Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA

K. C. Weathers
Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA

J. F. Haney
Center for Freshwater Biology, Department of Biological Sciences, University of New Hampshire, Durham, NH 03824, USA

Introduction

Cyanobacterial blooms in freshwater lakes have long been considered problematic because of their toxins, foul odors, and harmful effects on aquatic food webs (Paerl 1988; Paerl et al. 2001). Blooms are typically associated with eutrophic lakes, yet phytoplankton records indicate that cyanobacteria can also bloom and form scums in oligotrophic and mesotrophic lakes (Downing et al. 2001; Padisák et al. 2003; Lepisto et al. 2005; Galvao et al. 2008; Ernst et al. 2009; Vareli

et al. 2009). Cyanobacterial blooms in low-nutrient systems have not engendered much discussion among limnologists (e.g., there is no text on the topic in Wetzel 2001 or Kalff 2002), despite the fact that cyanobacterial blooms in a water column characterized by low nutrients are puzzling.

In the past three decades, scientists have observed an increase in cyanobacterial blooms in eutrophic (Hallegraeff 1993; Van Dolah 2000; Anderson et al. 2002; Paerl and Huisman 2008, 2009) as well as oligotrophic and mesotrophic systems (Boyer 2008; Ernst et al. 2009; Winter et al. 2011), highlighting the importance of understanding bloom dynamics, especially in lakes used for drinking water, irrigation, and recreation. Although many of the recent blooms in the oligotrophic and mesotrophic lakes are attributed to increasing nutrient concentrations (e.g., Winter et al. 2011), their water column nutrient concentrations still meet the established criteria for oligotrophic (mean summer epilimnion total phosphorus (TP) concentration <10 μg L^{-1}) or mesotrophic (10 μg $L^{-1} \leq$ TP $\leq$ 30 μg L^{-1}) systems (Nürnberg 1996). Understanding the effects of cyanobacterial blooms in these systems is important for understanding changes in lake ecosystem functioning, as well as determining whether there are potential consequences to human health.

Gloeotrichia echinulata (J.E. Smith) P. Richter 1894, a nitrogen-fixing cyanobacterium that forms large (1–3 mm diameter) filamentous colonies, may be increasing in low-nutrient systems in the northeastern United States and Canada (Carey et al. 2008, 2009; Winter et al. 2011). Monitoring data from watershed and state organizations indicate that *G. echinulata* was not common in the past few decades in lakes in the northeastern United States (AWI; LSPA; ME-DEP; NH-DES-VLAP; VT-DEC-VLMP). However, the number of reports of *G. echinulata* blooms is increasing (ME-IWQAR 2006, 2008, 2010; NH-DES-VLAP). Because phytoplankton monitoring in the northeastern United States is limited both spatially and temporally, the distribution of lakes in which *G. echinulata* is present and its abundance in the water column are unknown.

G. echinulata has been well studied in high-nutrient systems (e.g., Barbiero 1993; Jacobsen 1994; Karlsson-Elfgren et al. 2003), but until recently, much less was known about *G. echinulata* dynamics in low-nutrient systems. The cause of its increase in northeastern US nutrient-poor lakes is uncertain. However, higher temperatures (Karlsson-Elfgren et al. 2004) or increasing phosphorus (P) concentrations in the lake sediment, perhaps linked to watershed development (Carey et al. 2009), may be implicated. Regardless of the cause, many of the systems that are now experiencing increased *G. echinulata* densities have not exhibited high levels of cyanobacteria in the recent past, raising the question of what consequences *G. echinulata* might have for water quality.

G. echinulata has several physiological attributes that may cause it to have significant effects on ecosystem functioning in low-nutrient lakes. First, *G. echinulata* has a meroplanktonic life history in which akinetes (dormant cells) are formed that overwinter on the lake sediment (Roelofs and Oglesby 1970; Karlsson 2003). In response to increased light and temperatures, the akinetes germinate and grow on the lake sediment, take up luxury concentrations of P from pore water, and then recruit into the water column via gas vesicles, translocating stored P with them (Carr and Whitton 1982; Istvánovics et al. 1993; Pettersson et al. 1993; Tymowski and Duthie 2000). In eutrophic Lake Erken, Sweden, and Green Lake, Washington, United States, *G. echinulata* recruitment from the sediments can contribute up to two-thirds of the total summer internal P load (Barbiero and Welch 1992; Istvánovics et al. 1993). Second, *G. echinulata* is able to fix atmospheric nitrogen (N; Stewart et al. 1967; Roelofs and Oglesby 1970; Carr and Whitton 1982). Some of *G. echinulata*'s fixed N and stored P may become available to other phytoplankton in the water column (Pitois et al. 1997; Nõges et al. 2004; Fey et al. 2010). Third, *G. echinulata* produces a low concentration of microcystin-LR (MC-LR; Carey et al. 2007), which can have adverse effects on phytoplankton (e.g., Christoffersen 1996; Kearns and Hunter 2001), macrophytes (Pflugmacher 2002; Romanowska-Duda and Tarczynska 2002), zooplankton (Fulton and Paerl 1987; DeMott et al. 1991; Rohrlack et al. 2001; Rohrlack et al. 2005), and fish (Malbrouck and Kestemont 2006; El Ghazali et al. 2010), as well as humans, livestock, and pets (Miura et al. 1991; Jochimsen et al. 1998; Wiegand and Pflugmacher 2005; Hernández et al. 2009). *G. echinulata* is also known to cause skin irritation for swimmers (Backer 2002; Serediak and Huynh 2011). Because the concentration of MC-LR in *G. echinulata* has only been reported from one lake (Carey et al. 2007), and even low concentrations of microcystins can exert

substantial negative effects on food webs (reviewed by Babica et al. 2006), it is important to determine *G. echinulata*'s toxin production in other systems.

To examine the distribution, abundance, and MC-LR concentrations of *G. echinulata* in the northeastern United States, we conducted a survey of *G. echinulata* in low-nutrient lakes in summer 2006 and continued sampling some of those lakes and others in 2008, 2009, and 2010. We measured *G. echinulata* MC-LR concentrations from a subset of these lakes in 2008.

Methods

In summer 2006, we conducted an initial survey of 14 lakes in Maine and New Hampshire. We targeted low-nutrient lakes that had incidental reports of increased cyanobacteria (LSPA; ME-DEP; NH-DES-VLAP) as well as nearby lakes that were logistically feasible to sample. In summer 2008, we resampled many of the lakes in the 2006 survey and expanded our survey to additional lakes in Maine, New Hampshire, New York, and Vermont. We continued sampling a subset of the 2006 and 2008 lakes in 2009 and 2010. In total, we sampled 37 lakes across 4 years for a combined 193 observations from June to September (Table 1), the summer period in which *G. echinulata* has been observed in the water column in other lakes (Barbiero 1993; Karlsson-Elfgren et al. 2003).

At each lake, we sampled the littoral zone at its state-designated boat launch and noted lake conditions (e.g., if a scum was a present). We sampled *G. echinulata* surface density by collecting plankton from the top 1 m of the water column with an 80-μm plankton net and always used the same site for repeat samplings to compare *G. echinulata* densities over time. When the water level was low, the resulting vertical plankton tow was <1 m, but given the distributed pattern of colonies in the water column at nearly all observations (i.e., absence of a scum), we have no evidence that these lower volume collections were biased with respect to measures of colonies L^{-1}. We also collected water samples in 250-mL acid-washed polyethylene bottles from 0.5 m depth for total N (TN) and TP analysis in 2006 and 2008. *G. echinulata* samples were immediately preserved with Lugol's solution, and nutrient samples were frozen until they were processed in the laboratory. We analyzed TN samples with spectrophotometric methods after a basic persulfate digestion (Crumpton et al. 1992), and TP samples were analyzed colorimetrically according to Van Veldhoven and Mannaerts (1987) with an acidic persulfate digestion. Method detection limits were 74 μg L^{-1} for TN and 7.8 μg L^{-1} for TP.

We counted *G. echinulata* colonies with dissecting microscopes to determine *G. echinulata* densities (colonies L^{-1}). Following the procedures of previous studies (e.g., Barbiero 1993; Istvánovics et al. 1993; Pettersson et al. 1993; Forsell and Pettersson 1995; Tymowski and Duthie 2000; Hyenstrand et al. 2001; Karlsson-Elfgren et al. 2003; Eiler et al. 2006), we enumerated colonies instead of filaments because colonies were the "natural unit" of *G. echinulata* biomass that we observed in the net samples (following Cottingham et al. 1998). We evaluated a colony as a central core with a mucilaginous sheath surrounded by vegetative cells (Karlsson 2003).

To determine whether there was a time of the summer consistently associated with high *G. echinulata* density across sites, we analyzed differences in *G. echinulata* density among months and 10-day periods with one-way Welch ANOVA (which accounted for unequal variance) in JMP (v. 8.0). We chose 10 days as an appropriate interval because *G. echinulata* akinetes typically take <12 days for germination and recruitment (Karlsson 2003). We repeated the analysis for all ten possible 10-day groupings of sampling days throughout the summer (i.e., the first 10-day period of the first grouping was June 1–10, the first 10-day period of the second grouping was June 2–11, etc.) to ensure that our groupings did not bias our analysis. Significance (α) was initially set at $p \leq 0.05$, and a sequential Bonferroni procedure was performed to adjust α for multiple comparisons (Hochberg 1988).

In August 2008, we collected *G. echinulata* colonies to determine their MC-LR concentration from the 18 sample lakes that exhibited sufficient colony biovolume for analysis. From each lake, we used a dissecting microscope to isolate two samples of 100 colonies each, thoroughly rinsed the colonies ten times with reverse osmosis water, and estimated the mean colony biovolume from radius measurements of 25 different colonies. We froze these samples and transported them to the Center for Freshwater Biology Analytical Laboratory at the University of New Hampshire for analysis by enzyme-linked immunosorbent assay (ELISA). Suspensions of *G. echinulata*

Table 1 Summary geographical information and water quality parameters for each of our study lakes in the northeastern United States, grouped by whether or not *G. echinulata* colonies were observed in the lake on sampling visits

Lake	Latitude	Longitude	US State	Total nitrogen (μg L^{-1})	Total phosphorus (μg L^{-1})	Chlorophyll *a* (μg L^{-1})	pH	Number of *G. echinulata* samples	Number of sample years	Ref.
Lakes that exhibited G. echinulata on sampling visits										
Androscoggin	N 44°21′	W 70°4′	Maine	260 (1)	16 ± 13 (51)	4.7 ± 1.3 (3)	7.1 ± 0.2 (2)	11	4	a,b
Auburn	N 44°9′	W 70°13′	Maine		7 ± 1 (5)	3.2 ± 0.8 (5)	7.3 (1)	20	3	b
Champlain-St. Albans Bay	N 44°48′	W 73°10′	Vermont, New York	390 ± 83 (64)	28 ± 9 (70)	9.3 ± 7.1 (75)	8.4 ± 0.4 (58)	2	1	c
Colby	N 44°21′	W 74°9′	New York	245 (1)	14 ± 4 (20)	4.5 ± 2.8 (20)	7.4 ± 0.3 (20)	2	1	a,d
Crescent	N 43°57′	W 70°28′	Maine	125 (1)	11 ± 4 (3)	3.2 (1)	7.3 (1)	5	2	a,b
Echo	N 44°27′	W 70°1′	Maine	200 (1)	5 ± 2 (3)	2.5 ± 0.1 (2)*	7.3 (1)	6	1	a,b
Fairlee	N 43°53′	W 72°14′	Vermont	160 (1)	17 ± 5 (46)	4.9 ± 2.8 (92)		2	1	a,e
Flower	N 44°19′	W 74°8′	New York	405 (1)	19 ± 3 (5)	6.0 ± 1.3 (5)	6.6 ± 0.1 (5)	2	1	a,d
Great	N 44°31′	W 69°52′	Maine	320 (1)	12 ± 5 (7)	5.6 ± 1.4 (3)	7.1 (1)	8	4	a,b
Little Ossipee	N 43°36′	W 70°43′	Maine	160 (1)	6 ± 3 (12)	2.8 (1)	6.9 (1)	4	2	a,b
Long Lake	N 43°58′	W 70°36′	Maine	155 (1)	7 ± 2 (101)	2.9 ± 0.7 (71)	6.8 ± 0.1 (59)	9	3	a,b
Long Pond	N 44°31′	W 69°55′	Maine	180 (1)	9 ± 3 (21)	4.6 ± 1.5 (7)	7.1 ± 0.1 (5)	8	4	a,b
Lower Saranac	N 44°19′	W 74°10′	New York	170 (1)	16 ± 3 (3)	4.9 ± 1.1 (13)	6.9 ± 0.3 (13)	2	1	a,d
Messalonskee	N 44°29′	W 69°47′	Maine	185 ± 28 (2)	13 ± 8 (22)	4.7 ± 0.6 (4)	7.2 ± 0.1 (3)	11	4	a,b
Middle Range	N 44°2′	W 70°22′	Maine	145 (1)	8 ± 2 (8)	3.9 ± 1.2 (6)	7.0 ± 0.3 (5)	11	3	a,b
Panther	N 43°54′	W 70°28′	Maine	140 (1)	5 ± 4 (2)*	2.5 ± 0.1 (2)*	7.2 (1)	4	2	a,b
Parker	N 44°31′	W 70°1′	Maine	155 (1)	8 ± 3 (6)	3.0 ± 0.8 (4)*	7.2 (1)	3	1	a,b
Pleasant	N 44°0′	W 70°31′	Maine		6 ± 3 (6)	3.7 ± 0.1 (2)	7.0 ± 0.1 (2)	9	4	b
Sabattus	N 44°7′	W 70°6′	Maine		50 ± 15 (18)	27.5 ± 21.5 (16)	7.2 ± 0.3 (10)	2	1	b
Sebago	N 43°54′	W 70°28′	Maine	165 (1)	4 ± 1 (2)	1.6 ± 0 (2)*	7.1 ± 0 (2)	8	4	a,b
Square	N 43°34′	W 70°52′	Maine		8 ± 3 (4)	2.0 (1)	7.2 (1)	2	1	b
Sunapee	N 43°25′	W 72°2′	New Hampshire	170 ± 41 (427)	6 ± 1 (15)	2.0 ± 0.5 (15)	6.6 ± 0 (3)	30	4	a,f,g
Thomas	N 43°55′	W 70°30′	Maine	165 (1)	15 ± 8 (4)*	2.5 ± 0.3 (2)*	7.4 ± 0 (2)*	5	2	a,b
Thompson	N 44°1′	W 70°28′	Maine	145 (1)	5 ± 2 (16)	3.7 ± 5.2 (16)	6.8 ± 0.2 (11)	11	4	a,b
Togus	N 44°19′	W 69°39′	Maine		16 ± 14 (5)	15.8 ± 17.3 (2)	7.3 (1)*	2	1	b
Upper Saranac	N 44°14′	W 74°19′	New York	170 (1)	14 ± 5 (34)	4.6 ± 2.2 (34)	7.3 ± 0.5 (33)	2	1	a,h
Winnipesaukee	N 43°28′	W 71°14′	New Hampshire	250 (1)	5 ± 0 (9)	1.4 (1)	7.1 (1)	2	1	a,i

Table 1 continued

Lake	Latitude	Longitude	US State	Total nitrogen (μg L^{-1})	Total phosphorus (μg L^{-1})	Chlorophyll *a* (μg L^{-1})	pH	Number of *G. echinulata* samples	Number of sample years	Ref.
Lakes that did not exhibit G. echinulata on sampling visits										
Brettuns	N 44°23′	W 70°15′	Maine		9 ± 5 (5)*	3.9 ± 2.5 (2)*	7.2 ± 0 (2)	1	1	[b]
Chapel	N 44°8′	W 73°45′	New York	230 (1)	7 ± 3 (8)*	2.3 ± 1.2 (8)*	6.7 ± 0.5 (8)*	1	1	[a,d]
East	N 44°36′	W 69°46′	Maine		16 ± 5 (98)	9.7 ± 12.9 (83)	7.1 ± 0 (2)*	1	1	[b]
Goose	N 43°43′	W 72°6′	New Hampshire		7 (1)	13 (1)	5.1 (1)	1	1	[i]
Mascoma	N 43°38′	W 72°9′	New Hampshire		10 ± 4 (3)	3.9 ± 0.5 (3)	7.0 ± 0.3 (3)	1	1	[i]
Placid	N 44°18′	W 73°59′	New York	230 (1)	6 ± 1 (2)			1	1	[a,j]
Pleasant	N 43°25′	W 71°57′	New Hampshire		5 ± 1 (14)	4.1 ± 2.6 (14)	6.4 ± 0.4 (10)	1	1	[i]
Salmon	N 44°31′	W 69°48′	Maine		21 ± 31 (49)	6.6 ± 1.0 (4)	7.7 ± 0.3 (3)	1	1	[b]
Squam	N 43°44′	W 71°35′	New Hampshire		5 ± 3 (6)†	2.9 ± 1.6 (6)†	6.7 ± 0.3 (6)†	1	1	[i]
Upper Cascade	N 44°13′	W 73°53′	New York	240 (1)	8 ± 7 (2)		7.3 (1)	1	1	[a,j,k]

Mean summer total nitrogen, total phosphorus, and chlorophyll *a* concentrations and pH values for 2006–2010 (our study period) are listed with one standard deviation, with the number of samples in parentheses. Asterisks (*) denote means that include 2000–2010 data, crosses (†) denote means that include 1988–2010 data

[a] Total nitrogen (TN): our measurements

[b] Chlorophyll *a*, total phosphorus (TP), and pH: KB

[c] Chlorophyll *a*, TN, TP, and pH: VT-DEC-LC

[d] Chlorophyll *a*, TP, and pH: AWI

[e] Chlorophyll *a* and TP: VT-DEC-VLMP

[f] Chlorophyll *a* and TP: NH-DES-VLAP

[g] pH: NH-DES-LWQR

[h] Chlorophyll *a*, TP, and pH: USLA

[i] Chlorophyll *a*, TP, and pH: NH-DES-LWQR

[j] TP: our measurements

[k] Chlorophyll *a* and pH: ALSC

were treated with three freeze–thaw cycles followed by sonification to disrupt the cells and release microcystins. Immediately before analysis, the samples were passed through a 13-mm, 0.2-μm Whatman PTFE syringe filter to remove particulates (Sasner et al. 2001).

ELISA analyses were performed using instructions for Microcystin 96-Well-Plate Kits (EnviroLogix, Portland, ME), with a method detection limit of 2.5 pg MC-LR mL^{-1}. We calculated the mean MC-LR concentration attributable to *G. echinulata* (i.e., the MC-LR concentration within colonies, which may be potentially released to the water column) in each survey lake using the equation:

$$\left(\frac{\mu g\ MC-LR}{L}\right) = \left(\frac{ng\ MC-LR}{g}\right) \times \left(\frac{g}{mL}\right) \times \left(\frac{mL}{colony}\right) \times \left(\frac{colony}{L}\right) \times \left(\frac{0.001\ \mu g}{1\ ng}\right) \quad (1)$$

where μg MC-LR L^{-1} refers to the mean water column MC-LR concentration attributable to *G. echinulata*, ng MC-LR g^{-1} is the mean colonial MC-LR concentration determined by ELISA, g mL^{-1} is the specific gravity of an individual *G. echinulata* colony (assumed to be 1 g mL^{-1}; Reynolds 2006), mL colony^{-1} is the mean colony biovolume determined by 25 radius measurements, and colony L^{-1} is the mean water column *G. echinulata* density in each lake. We repeated the calculations for the minimum and maximum MC-LR concentration attributable to *G. echinulata* using the minimum and maximum values of MC-LR g^{-1} colonies, colony biovolume, and water column *G. echinulata* density for each lake.

Results

We observed *G. echinulata* in low-nutrient lakes throughout the northeastern United States during multiple years (Figs. 1, 2, 3). In 2006, all 13 of the Maine lakes we sampled (Androscoggin, Crescent, Great, Little Ossipee, Long Pond, Messalonskee, Panther, Pleasant, Sebago, Square, Thomas, Thompson, and Togus; Table 1) and the single New Hampshire lake (Sunapee) exhibited low, but nonzero, *G. echinulata* water column densities (ranging from 0.004 to 11 colonies L^{-1}).

In 2008, we sampled all of the lakes surveyed in 2006 (except for Togus) and found that the lakes again all exhibited nonzero *G. echinulata* concentrations. In addition, we observed nonzero, and some quite high (up to 51 colonies L^{-1} in Auburn), densities in five additional Maine lakes (Auburn, Echo, Long Lake, Middle Range, and Parker), one additional New Hampshire lake (Winnipesaukee), four additional New York lakes (Colby, Flower, Lower Saranac, and Upper Saranac), and two additional Vermont lakes (Champlain and Fairlee). In 2008, we also visited ten more lakes—three in Maine (Brettuns, East, and Salmon), four in New Hampshire (Goose, Mascoma, Pleasant, and Squam), and three in New York (Chapel, Upper Cascade, and Placid)—but did not observe any visible *G. echinulata* in their water columns. Those lakes were only visited once and were not visited again in future years.

In 2009 and 2010, we resampled a subset of the lakes that exhibited *G. echinulata* when surveyed in 2006 and 2008, as well as Sabattus Pond (Maine). *G. echinulata* was present in the water column on at least one sampling date during both 2009 and 2010 for all of the lakes visited and densities ranged from 0.007 colonies L^{-1} (Androscoggin) to 250 colonies L^{-1} (Long Pond), which exhibited a surface scum.

Overall, *G. echinulata* was present in the water column in 174 out of 183 samples from the 27 lakes that exhibited *G. echinulata* on at least one sampling date. During the four years of surveys, we observed a mean nonzero density of 2.8 ± 19 *G. echinulata* colonies L^{-1} (±1 S.D.) and a median density of 0.21 colonies L^{-1}. For all lakes combined, we did not observe a significant difference in *G. echinulata* density among years (Welch one-way ANOVA, $F_{3,179} = 0.54$, $p = 0.66$) or months (Welch one-way ANOVA, $F_{2,180} = 2.11$, $p = 0.13$). However, when we partitioned the summer sampling months into 10-day periods, we found that samples at the end of August consistently exhibited higher *G. echinulata* densities than any other period during the summer, regardless of how the 10-day groupings were chosen (seven out of ten 10-day groupings exhibited significant differences: Welch one-way ANOVA, $F_{7,175} > 3.68$, Bonferroni-corrected $p < 0.01$; for the three nonsignificant groupings: $F_{7,175} \leq 2.58$, $p \geq 0.05$).

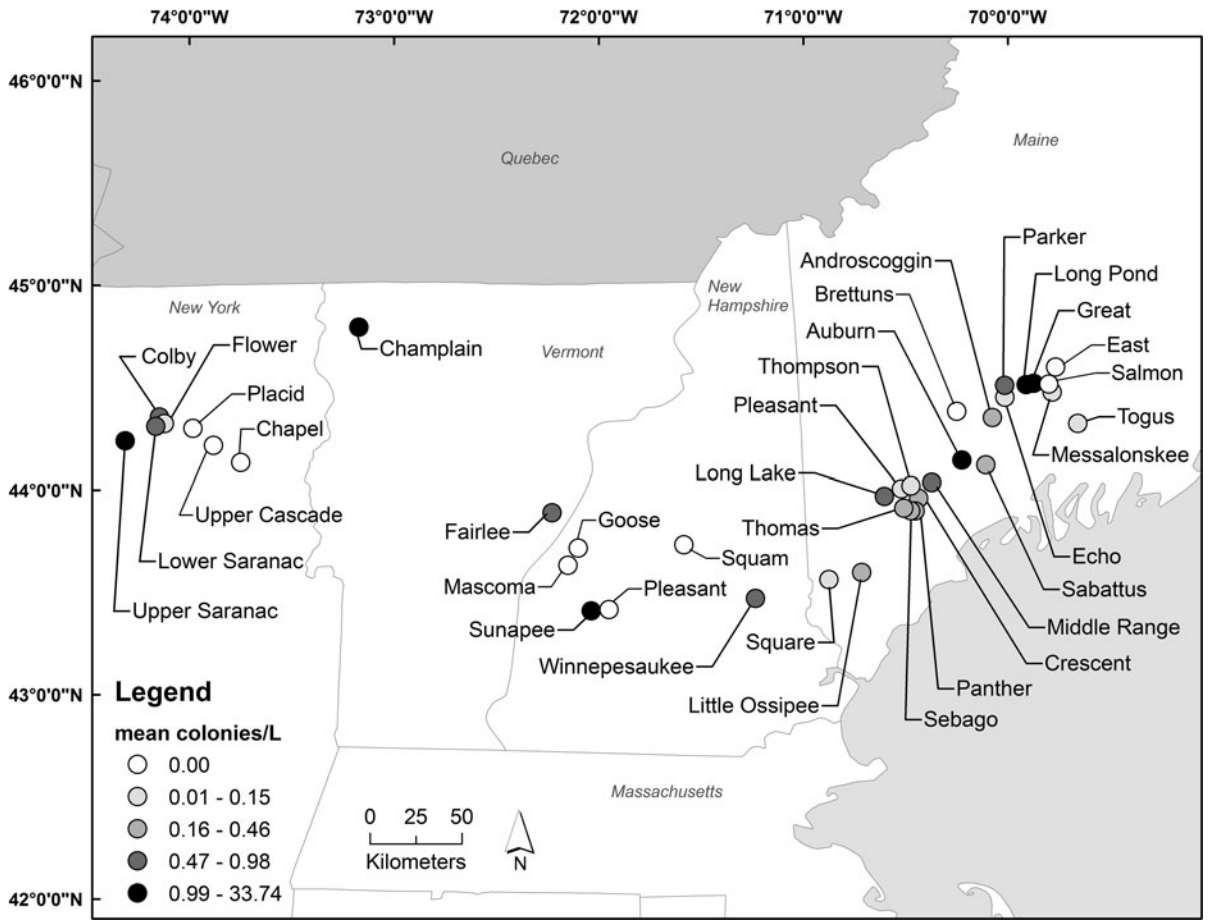


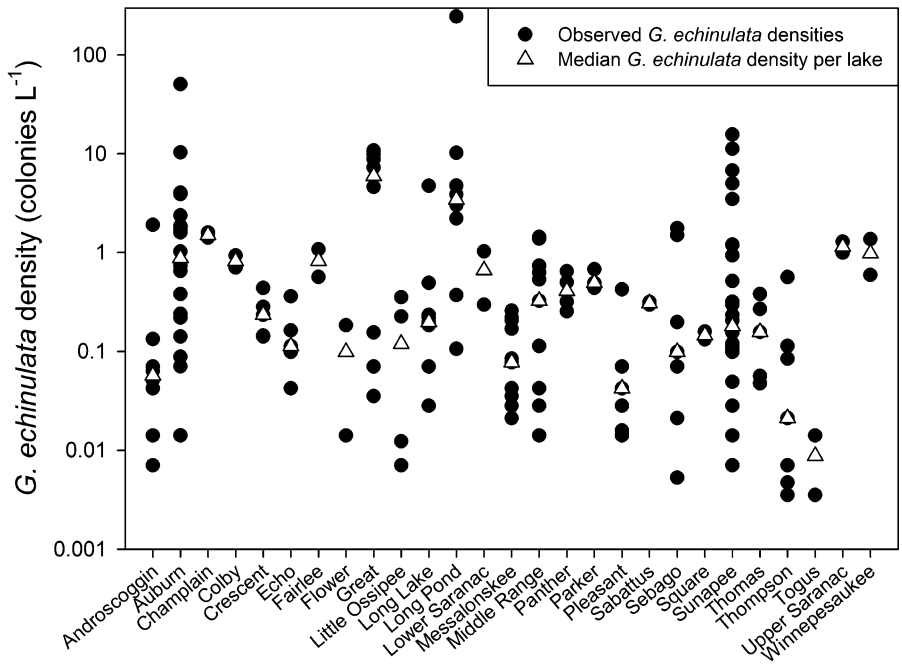
Fig. 1 Map of the 37 lakes in the northeastern United States sampled during surveys in 2006–2010, with the mean *G. echinulata* density from all observations for each lake color-coded by density range. The observed densities were divided into quartiles with *white* representing no observed *G. echinulata* colonies and *black* representing the highest observed mean densities. Lake descriptions with water quality parameters are given in Table 1

In 2008, *G. echinulata* colonies exhibited low, but detectable, MC-LR concentrations in every lake where *G. echinulata* was in sufficient density to collect a sample for MC-LR analysis (Fig. 4). *G. echinulata* MC-LR concentrations varied considerably among lakes, ranging from a low in Great Pond of 58.5 ± 4.2 ng MC-LR g^{-1} d.w. (±1 S.D.) to 7,148.1 ± 1,521.5 ng MC-LR g^{-1} d.w. in Panther Pond (Table 2). When the ranges of *G. echinulata* water column densities and biovolumes we measured for each lake were taken into account, the estimated mean concentration of MC-LR in the water column attributable to *G. echinulata* colonies was between four and seven orders of magnitude below the 1 μg MC-LR L^{-1} World Health Organization (WHO) drinking water guideline (WHO 1998; Table 2). The maximum MC-LR concentrations for each lake, as determined by the upper bound of the observed MC-LR concentration, *G. echinulata* colonial biovolume, and water column *G. echinulata* density, were at least three orders of magnitude below the WHO guideline.

Discussion

G. echinulata in northeastern US lakes

Our survey data indicate that *G. echinulata* may be widespread in lakes throughout the northeastern United States, corresponding to reports from state officials and watershed groups (LSPA; ME-DEP; NH-DES-VLAP). Strikingly, all but one (Sabattus) of the



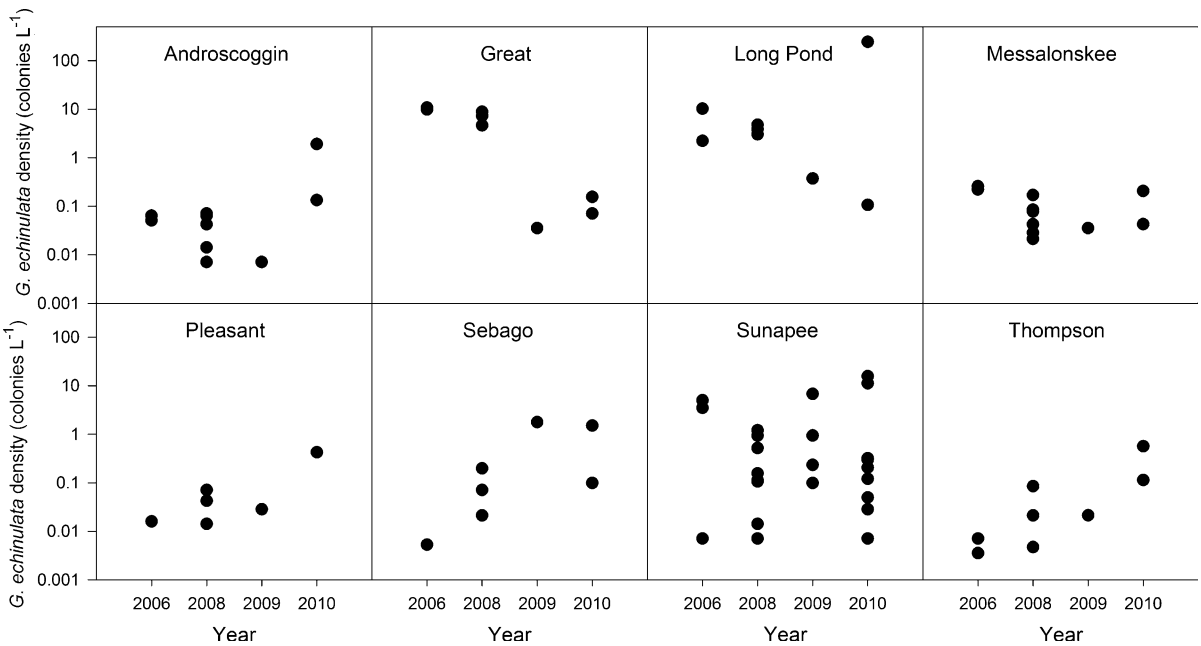


Fig. 2 Individual observations of *G. echinulata* water column density (colonies L^{-1}) for each lake (*filled circles*) and median densities for each lake (*open triangles*) during our surveys in 2006–2010. *Note* that the *y*-axis is a logarithmic scale

Fig. 3 Individual observations of *G. echinulata* density (colonies L^{-1}), shown by year for all eight lakes sampled in every year of the study. *Note* that the *y*-axis is a logarithmic scale

27 lakes in which we found *G. echinulata* would be characterized as low-nutrient systems (Nürnberg 1996): 14 were oligotrophic (TP < 10 μg L^{-1}) and 12 were mesotrophic (TP ≤ 30 μg L^{-1}). Most research on cyanobacteria, including the majority of the published studies on *G. echinulata* (e.g., Barbiero 1993; Jacobsen 1994; Karlsson-Elfgren et al. 2003), is from high-nutrient systems, though there is evidence from

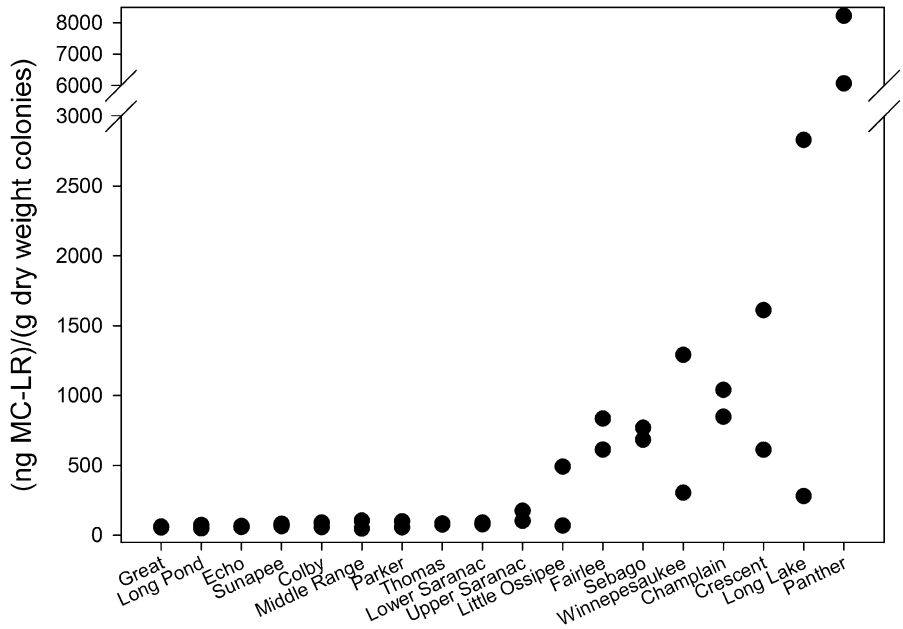


Fig. 4 The microcystin-LR (MC-LR) concentrations (ng MC-LR g^{-1} dry weight colonies) from survey lakes ($n = 2$ measurements per lake) sampled in August 2008. The lakes are listed in order of increasing mean MC-LR concentrations. *Note* the break between 3,000 and 6,000 ng MC-LR g^{-1} dry weight

paleoecological work that *G. echinulata* may be a common species early in the eutrophication process (Bunting et al. 2007). While a randomized sampling of lakes is needed to determine the relative abundance of *G. echinulata* at the landscape scale, our data suggest that *G. echinulata* may be more common in low-nutrient systems in the northeastern United States than previously thought.

Twenty-seven of the 37 lakes we sampled had *G. echinulata* colonies in their water column. Given the limited data provided by our "snapshot" sampling, we are unable to determine why *G. echinulata* was present in some lakes but not others. The 10 lakes we visited that did not have detectable *G. echinulata* were not significantly different from the lakes in which *G. echinulata* occurred in water column nutrient concentrations, chlorophyll *a*, and pH (Welch *t* test, all $t \leq 1.80$, $p \geq 0.09$; see Table 1). In addition, no patterns were observed with *G. echinulata* and no-*G. echinulata* lakes using a principal components analysis of the data in Table 1. It is possible that *G. echinulata* may be dispersal-limited, as has been observed for other large colonial cyanobacteria (Reynolds 2006). Alternatively, *G. echinulata* may have been present in the 10 lakes in which we did not find colonies, but in densities too low to detect with our procedures or because we were unable to observe them in the part of the lake or the particular day that we sampled. For example, we found no *G. echinulata* in the water column in Androscoggin, Pleasant, Sebago, Sunapee, and Thompson on at least one sampling visit, even though these lakes had detectable *G. echinulata* densities on other dates.

We found substantial within- and among-lake variation in *G. echinulata* densities (Fig. 2). This heterogeneity may exist because both recruitment from the sediments and currents that drive redistribution in the water column are spatially and temporally variable. *G. echinulata* surface populations are heavily subsidized (up to 50 %) by recruitment from the sediments, which has been shown to be extremely variable both temporally (over a summer) and spatially (at different sites) within the same lake (Barbiero and Welch 1992; Barbiero 1993; Forsell and Pettersson 1995; Karlsson-Elfgren et al. 2005; Carey et al. 2008). The combination of factors that drive recruitment is still unknown, but a number of factors may be important, including sediment P (Carey et al. 2008, 2009), nitrate (Chang 1979), light (Roelofs and Oglesby 1970; Barbiero 1993; Forsell and Pettersson 1995; Karlsson-Elfgren et al. 2004), temperature (Barbiero 1993; Forsell and Pettersson 1995; Karlsson-Elfgren et al. 2004), dissolved oxygen (Barbiero 1993), sediment bioturbation (Pierson et al. 1992; Karlsson-Elfgren et al. 2004), and depth (Karlsson-Elfgren et al. 2004). Each of these factors may vary

Table 2 The mean *G. echinulata* colony biovolumes (mm^3; $n = 25$ for each lake), microcystin-LR (ng MC-LR g^{-1} dry weight; $n = 2$ for each lake) concentrations in *G. echinulata* colonies, and the estimated mean MC-LR concentration attributable to *G. echinulata* in the water column (μg MC-LR L^{-1}; $n = 2$ for each lake), calculated with the mean, minimum, and maximum *G. echinulata* MC-LR concentrations, colony biovolumes, and *G. echinulata* water column densities (see "Methods")

Lake	Mean *G. echinulata* colony biovolume (mm^3), with the range of observed biovolumes in parentheses	*G. echinulata* MC-LR concentration (ng MC-LR g^{-1} d.w.)	Mean lake MC-LR concentration attributable to *G. echinulata* (μg MC-LR L^{-1})	Range of lake MC-LR concentrations attributable to *G. echinulata* (μg MC-LR L^{-1})	
				Minimum	Maximum
Champlain*	0.047 (0.011–0.15)	944.0	6.7×10^{-5}	1.4×10^{-5}	2.5×10^{-4}
Colby*	0.038 (0.011–0.18)	74.3	2.3×10^{-6}	4.7×10^{-7}	1.5×10^{-5}
Crescent	0.082 (0.022–0.20)	1111.5	3.9×10^{-5}	1.9×10^{-6}	4.3×10^{-4}
Echo	0.075 (0.0059–0.41)	62.1	1.4×10^{-6}	1.5×10^{-8}	2.9×10^{-5}
Fairlee*	0.011 (0.0032–0.028)	723.5	6.4×10^{-6}	1.1×10^{-6}	2.6×10^{-5}
Great	0.038 (0.0084–0.14)	58.5	1.4×10^{-5}	6.6×10^{-9}	1.2×10^{-4}
Little Ossipee	0.026 (0.0039–0.13)	279.6	1.1×10^{-6}	1.9×10^{-9}	2.3×10^{-5}
Long Lake	0.045 (0.0099–0.18)	1554.6	6.2×10^{-5}	2.3×10^{-7}	2.4×10^{-3}
Long Pond	0.032 (0.0059–0.085)	61.3	6.8×10^{-5}	3.1×10^{-8}	1.5×10^{-3}
Lower Saranac	0.042 (0.0039–0.18)	84.3	2.3×10^{-6}	9.1×10^{-8}	1.7×10^{-5}
Middle Range	0.021 (0.0084–0.052)	75.9	1.3×10^{-6}	5.5×10^{-9}	2.3×10^{-5}
Panther	0.030 (0.0084–0.21)	7148.1	1.5×10^{-4}	1.3×10^{-5}	2.7×10^{-3}
Parker*	0.039 (0.0059–0.15)	78.3	2.5×10^{-6}	1.7×10^{-7}	2.0×10^{-5}
Sebago*	0.035 (0.015–0.16)	726.0	3.8×10^{-6}	5.5×10^{-8}	7.3×10^{-5}
Sunapee*	0.34 (0.16–0.76)	73.2	4.1×10^{-5}	7.2×10^{-8}	9.7×10^{-4}
Thomas	0.045 (0.0071–0.092)	80.3	7.4×10^{-7}	2.6×10^{-8}	3.0×10^{-6}
Upper Saranac*	0.060 (0.011–0.33)	138.8	9.6×10^{-6}	1.2×10^{-6}	7.4×10^{-5}
Winnipesaukee*	0.029 (0.0048–0.11)	797.6	2.3×10^{-5}	8.8×10^{-7}	2.0×10^{-4}

For reference, the World Health Organization guideline for drinking water is 1 μg MC-LR L^{-1} (WHO 1998). Asterisks (*) denote lakes that are drinking water sources

considerably among lakes during the summer. Hence, it is not surprising that *G. echinulata* surface concentrations in neighboring lakes are so variable.

In spite of this variability, however, *G. echinulata* densities across all lakes were significantly higher in late August than any other time of year, which may be coincident with a regional cue, such as changes in light or temperature. This finding is in contrast to *G. echinulata* dynamics in eutrophic systems in Estonia, Sweden, and Washington (United States), where peak *G. echinulata* densities are observed earlier in the summer (e.g., Barbiero 1993; Karlsson-Elfgren et al. 2003, 2005; Nõges et al. 2004).

Although the variability we observed in *G. echinulata* densities may have been amplified by sampling only the littoral zone in one part of each lake, *G. echinulata* densities within many of the lakes showed less variation year to year within the same lake than among lakes (Fig. 3). For example, lakes that typically exhibited water column *G. echinulata* densities >1 colony L^{-1} consistently exhibited higher than median *G. echinulata* densities in other years (e.g., Long Pond, Sunapee; Fig. 3), despite being sampled at different times. This may be due to a substantially larger akinete pool in those lakes' sediments (Pettersson et al. 1993; Forsell 1998); a shallow lake bathymetry (Karlsson-Elfgren et al. 2003; Karlsson-Elfgren et al. 2004); an organic, non-rocky lake sediment substrate (Carey et al. 2008); or other persistent environmental conditions that may promote higher recruitment rates. Similarly, lakes with low *G. echinulata* water column densities (e.g., Messalonskee, Pleasant, Thompson) consistently exhibited lower densities (Fig. 3).

G. echinulata's microcystin-LR concentrations and possible toxic effects

All of the *G. echinulata* samples tested exhibited detectable concentrations of MC-LR. We observed a large range of colonial MC-LR concentrations among lakes (Fig. 4), which may be because our data only represented samples collected on 1 day, rather than an integrated sample of colonies collected throughout a summer. However, the mean MC-LR concentration for Lake Sunapee samples collected in August 2008 (73.2 ± 11.8 μg MC-LR g^{-1} dry weight colonies, ±1 S.D.) was similar to the mean concentration in August–September 2005 (97.07 ± 7.78 μg MC-LR g^{-1} dry weight colonies; Carey et al. 2007). MC-LR production in other cyanobacteria can vary depending on light (Utkilen and Gjolme 1992; Wiedner et al. 2003; Tonk et al. 2005), temperature (van der Westhuizen and Eloff 1985), nutrients (Kotak et al. 2000; Lee et al. 2000; Downing et al. 2005), pH (Eloff and van der Westhuizen 1981), and other environmental conditions, causing large variation in MC-LR concentrations spatially and temporally within the same system (e.g., Makarewicz et al. 2009). These factors may be important drivers of among-lake variation in MC-LR, although we did not observe any correlations between nutrients (TN and TP) and MC-LR concentrations in our survey lakes (untransformed, log–log, and Spearman's rank correlations: $r \leq 0.17$, $p \geq 0.48$).

Our calculations of the MC-LR concentration in lake water attributable to *G. echinulata*, which take into account the range of measured colonial MC-LR concentrations, *G. echinulata* biovolumes, and *G. echinulata* surface densities, indicate that *G. echinulata*'s MC-LR concentrations are at least two orders of magnitude below levels that affect food webs. However, an increase in *G. echinulata* densities to the maximum level observed in this study (250 colonies L^{-1}) could result in MC-LR concentrations that are associated with ecological effects if those toxins are released in the water column. For example, exposure to low levels of MC-LR (0.1–0.5 μg MC-LR L^{-1}) over short time periods (24 h) has inhibited growth and photosynthesis for macroalgal, emergent macrophyte, and submerged macrophyte species (Pflugmacher 2002). Similarly, Pietsch et al. (2001) found that photosynthesis by the green alga *Scenedesmus armatus* was inhibited after exposure to 0.25 μg MC-LR L^{-1} for 1 h. Since blooms of *G. echinulata* can last for >2 weeks (Karlsson-Elfgren et al. 2003), it is possible that macrophytes and algae in northeastern lakes could be exposed to MC-LR for longer periods if the MC-LR is released from *G. echinulata* colonies to the water column.

Low concentrations of MC-LR may also affect higher trophic levels. While there are few studies examining the effect of low MC-LR levels on food webs as a whole, Kotak et al. (1996) surveyed phytoplankton, macroinvertebrates, zooplankton, and fish for 3 years in four Canadian lakes where maximum water column MC-LR concentrations during the sample period were ≤0.34 μg L^{-1} and mean concentrations were less than half that (~0.12 μg L^{-1}). They found that all food web levels except for fish exhibited detectable concentrations of MC-LR accumulated in biomass, and that low MC-LR concentrations may be linked to shifts in zooplankton community structure (Kotak et al. 1996). We hypothesize that if *G. echinulata* density were to increase and their MC-LR was released to the water column, it could reach levels that affect plankton in northeastern US lakes.

While the MC-LR concentrations in northeastern lakes attributable to *G. echinulata* could approach levels that affect food webs, current *G. echinulata* densities are low enough that it is unlikely that there is a toxicity concern for drinking water quality. However, if *G. echinulata* densities in the northeastern United States increased while the MC-LR concentrations per colony stayed constant, MC-LR attributable to *G. echinulata* could become more of a public health concern. For example, if densities increased to the bloom levels observed in Lake Erken, Sweden (5,000 colonies L^{-1}; Eiler et al. 2006), three lakes (Crescent, Panther, and Long Lake) would exhibit MC-LR concentrations exceeding the World Health Organization drinking water guideline of 1 μg L^{-1}, and 8 lakes would exhibit MC-LR concentrations between 0.1 and 1.0 μg L^{-1} (Champlain, Echo, Fairlee, Little Ossipee, Sebago, Sunapee, Upper Saranac, and Winnipesaukee). If *G. echinulata* densities in Panther Pond increased to the maximum density we observed in Long Pond (250 colonies L^{-1}), Panther MC-LR concentrations could be as high as 0.4 μg L^{-1}. It is important to note that these estimates are based on littoral *G. echinulata* densities and may not represent pelagic MC-LR concentrations attributable to *G. echinulata* because wind and currents can accumulate

colonies in downwind coves, as has been found for other cyanobacteria (Wynne et al. 2011).

Even at current *G. echinulata* surface densities, MC-LR concentrations attributable to *G. echinulata* should be monitored. There have been reports of swimmers developing rashes after exposure to low levels of *G. echinulata* (Backer 2002; Serediak and Huynh 2011), suggesting that *G. echinulata* may be a recreational nuisance even at low densities. All of our survey lakes are used for swimming or other recreation and nine of the 27 lakes in which we observed *G. echinulata* are public or commercial drinking water sources (FTP 2008; JBS 2008; LCA; LCBP; ME-DWP; NH-DWSPP; USLA). Given that the long-term effects of chronic exposure to low-level microcystins are unknown (WHO 1998), we recommend monitoring MC-LR concentrations in any lake that exhibits visible surface densities of *G. echinulata*.

Conclusions

Phytoplankton records from monitoring organizations indicate that *G. echinulata* has not been common during the past decade or longer in lakes in the northeastern United States (AWI; AWSD; LSPA; ME-DEP; NH-DES-VLAP; VT-DEC-VLMP), but may now be increasing (ME-IWQAR 2006, 2008, 2010; NH-DES-VLAP). For example, in-depth phytoplankton monitoring in five of our Maine lakes (Androscoggin, Great, Long Pond, Messalonskee, and Sebago) during 1971–1973 did not find *G. echinulata* (Davis et al. 1978). *G. echinulata*'s large colonies (up to 3 mm in diameter) are easy to see, so we expect that limnological monitoring would have detected the species if it had been present in the water column. The survey data indicate that some of our survey lakes may be exhibiting increasing *G. echinulata* densities (Fig. 3), and more temporally extensive monitoring at several sites in a lake would allow us to determine whether those are real trends.

Our data provide strong evidence that cyanobacteria *can* reach nuisance concentrations (e.g., up to 250 colonies L^{-1}) in low-nutrient lakes, systems in which cyanobacterial blooms are not traditionally studied. Cyanobacterial toxicity is primarily assessed in eutrophic lakes (Chorus and Bartram 1999); however, *G. echinulata*'s abundance in low-nutrient systems indicates the need for monitoring MC-LR concentrations in oligotrophic and mesotrophic lakes. We found that *G. echinulata* persists in the same lakes from year to year, even when lakes are sampled in different months (Fig. 3). This finding suggests that once *G. echinulata* is established in a low-nutrient lake, it may become a consistent part of the phytoplankton assemblage. As such, the cyanobacterium's MC-LR production may allow it to exert substantial effects on food webs and ecosystem functioning if *G. echinulata* densities increase in low-nutrient northeastern US lakes.

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