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Spatial and temporal variability in recruitment of the cyanobacterium *Gloeotrichia echinulata* in an oligotrophic lake

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Abstract: Recruitment from dormant stages in the benthos can provide a critically important inoculum for surface populations of phytoplankton, including bloom-forming cyanobacteria. For example, water-column populations of the large (1–3-mm diameter) colonial cyanobacterium *Gloeotrichia echinulata* (Smith) P. Richter can be strongly subsidized by benthic recruitment. Therefore, understanding controls on recruitment is essential to an investigation of the factors controlling *Gloeotrichia* blooms, which are increasing in low-nutrient lakes across northeastern North America. We quantified surface abundances and recruitment from littoral sediments at multiple near-shore sampling sites in oligotrophic Lake Sunapee, New Hampshire, USA, during the summers of 2005–2012 and used this data set—the longest known record of cyanobacterial recruitment—to investigate potential drivers of interannual differences in *Gloeotrichia* recruitment. We found extensive spatiotemporal variability in recruitment. Recruitment was higher at some sites than others, and within seasons, recruitment into replicate traps at the same site was generally more similar than recruitment at different sites. These data suggest that local factors, such as substrate quality or the size of the seed bank, may be important controls on recruitment. Benthic recruitment probably accounted for <4%, but possibly up to 8%, of pelagic populations, within the range observed in previous studies. Across years, higher seasonal recruitment rates were associated with greater lake mixing during August, including deeper thermoclines, lower Schmidt stability, lower minimum air temperatures, and greater variability in water temperature. Taken together, our data suggest that interannual variation in *Gloeotrichia* recruitment may be related to regional climatic variability.

Key words: benthic–pelagic coupling, akinetes, phytoplankton, lake stratification, climate change, dormancy

Cyanobacteria can impair the functioning of freshwater lakes via toxicity, scums, and adverse effects on planktonic food webs (reviewed by Paerl 1988, Havens 2008). Therefore, knowledge about drivers of cyanobacterial populations is important for understanding foodweb dynamics and forecasting and controlling the occurrence of blooms, especially because cyanobacteria are increasing in high- and low-nutrient lakes worldwide (Hallegraeff 1993, Anderson et al. 2002, Boyer 2008, Paerl and Huisman 2008, Ernst et al. 2009, Brookes and Carey 2011, Winter et al. 2011, Carey et al. 2012a, Paerl and Paul 2012, Sinha et al. 2012).

Two major processes by which populations of planktonic cyanobacteria increase are recruitment from dormant stages in the benthos and division in the water column (Reynolds 2006). Many cyanobacterial species produce dormant cells, such as akinetes or vegetative cells, in response to adverse environmental conditions (Nichols and Adams 1982, Adams and Duggan 1999, Kaplan-Levy et al. 2010), thereby creating a seed bank. Akinetes can remain viable

in the sediments for years to decades (Livingstone and Jaworski 1980, Wood et al. 2009) and germinate in response to increased light, temperature, dissolved O_2, or a combination of factors (reviewed by Kaplan-Levy et al. 2010). After dividing and growing on the lake sediments, mature cells and colonies recruit into the water column actively by production of gas vesicles or passively via physical processes, such as entrainment (MacIntyre and Melack 1995, Hansson 1996).

For some cyanobacterial species, active recruitment from the benthos via gas vesicles can substantially subsidize pelagic populations. Based on cyanobacterial recruitment rates measured with inverted sedimentation traps (sensu Hansson 1995), pelagic populations of many taxa, including *Anabaena*, *Aphanizomenon*, *Coelosphaerium*, *Gomphosphaeria*, *Gloeotrichia*, *Lyngbya*, *Merismopedia*, *Microcystis*, *Oscillatoria*, and *Spirulina*, are subsidized by such recruitment (see Table S1 for a list with taxonomic authorities and references). Recruitment rates for *Aphanizomenon flos-aquae* and *Gloeotrichia echinulata* can be very high and contribute up to ~60 and ~50% of the surface population, respectively, during peak recruitment (Trimbee and Harris 1984, Barbiero and Welch 1992, Forsell and Pettersson 1995, Carey et al. 2008).

Except for a 5-y study in Green Lake, Washington, USA (Sonnichsen et al. 1997), nearly all cyanobacterial recruitment studies have typically lasted 1 to 2 summers (Table S1). These studies were primarily designed to elucidate the drivers of recruitment within a summer (e.g., Barbiero 1993, Rengefors et al. 2004, Carey et al. 2009). However, understanding changes in recruitment *among* seasons also is important, especially given the considerable interannual variability in the timing and magnitude of cyanobacterial blooms among years (e.g., Lathrop et al. 1996, Stumpf et al. 2012). The extent to which these fluctuations are driven by responses of recruitment to changes in environmental factors, such as precipitation-driven inputs from watersheds; water temperature; and the timing, extent, and strength of stratification; is unknown. Investigators have not explored temporal variability in recruitment, its contribution to the development of pelagic populations, and the drivers of recruitment across many consecutive years in the same system.

We quantified the recruitment dynamics of *Gloeotrichia echinulata* (Smith) P. Richter in an oligotrophic lake in New Hampshire, USA, over 8 summers. *Gloeotrichia* recruitment dynamics are of particular interest because this species seems to be increasing in low-nutrient lakes across the northeastern USA and Canada (Winter et al. 2011, Carey et al. 2012a) and it has a number of interesting life-history traits (Barbiero 1993, Karlsson 2003). *Gloeotrichia* produces akinetes that overwinter on the lake sediment and germinate to form large colonies (up to 1–3 mm in diameter; Karlsson 2003, Karlsson-Elfgren et al. 2003, Carey

et al. 2008). These colonies recruit from the sediments to the water column via gas vesicles and can form dense surface scums (blooms) in the summer (Roelofs and Oglesby 1970, Barbiero 1993, Karlsson-Elfgren et al. 2003). During recruitment, *Gloeotrichia* can transport substantial amounts of P acquired from the sediment into the water column (Istvánovics et al. 1993, Pettersson et al. 1993). *Gloeotrichia* also can fix N (Stewart et al. 1967) and produce the toxin microcystin-LR (Carey et al. 2007, 2012a). Moreover, *Gloeotrichia* has one of the highest levels of recruitment-dependency observed among cyanobacterial taxa (Barbiero and Welch 1992, Barbiero 1993, Forsell and Pettersson 1995, Karlsson-Elfgren et al. 2003, Carey et al. 2008).

We used our 8-y record to test the hypothesis that climatic variables might be particularly important to interannual variability in recruitment. Specifically, we investigated associations with ice-out date, which affects the length of the growing season (reviewed by Magnuson et al. 1997); regional precipitation, which affects nutrient inputs and turbidity (Reed-Andersen et al. 2000, Bennett et al. 2001, McClain et al. 2003); air temperature, which drives water temperature (Livingstone and Lotter 1998, Livingstone and Dokulil 2001); water temperature, which affects biological rates (Reynolds 2006), including recruitment (Barbiero 1993, Forsell and Pettersson 1995, Karlsson-Elfgren et al. 2004); and lake stratification, which affects mixing (Adrian et al. 2009, Read et al. 2011) and nutrient availability (Soranno et al. 1997, Nürnberg 1998).

METHODS
Study site

We monitored *Gloeotrichia* recruitment, surface abundance, and selected abiotic variables in Lake Sunapee, New Hampshire, USA, during the summers of 2005–2012 (Fig. 1). Lake Sunapee (lat 43°24′N, long 72°2′W) is an oligotrophic system with surface area = 16.55 km², volume = 1.88×10^8 m³, mean depth = 10 m (Carey et al. 2008), and maximum fetch = 9.1 km. Most of the lake stratifies thermally from mid-June to late September at ~6 to 8 m depth based on data from a chain of thermistors deployed from the Lake Sunapee Protective Association's (LSPA; lakesunapee.org) Global Lake Ecological Observatory Network (GLEON, gleon.org) buoy near a deep hole in the lake. Temperature and other variables are measured every 10 min (LSPA, unpublished data). The buoy was first deployed in late 2007 and collected data from April to October in most years. The lake typically is covered with ice from December or January through March or April. During the study period, Lake Sunapee's near-shore mean summer (June–September) concentration of total P (TP) was 7.4 ± 0.6 μg/L (mean ± 1 SE), total N (TN) was 170 ± 141 μg/L, and chlorophyll *a* was 1.6 ± 0.2 μg/L (KLC, CCC, KCW, and HAE, unpublished data); in the open water, mean Secchi depth was
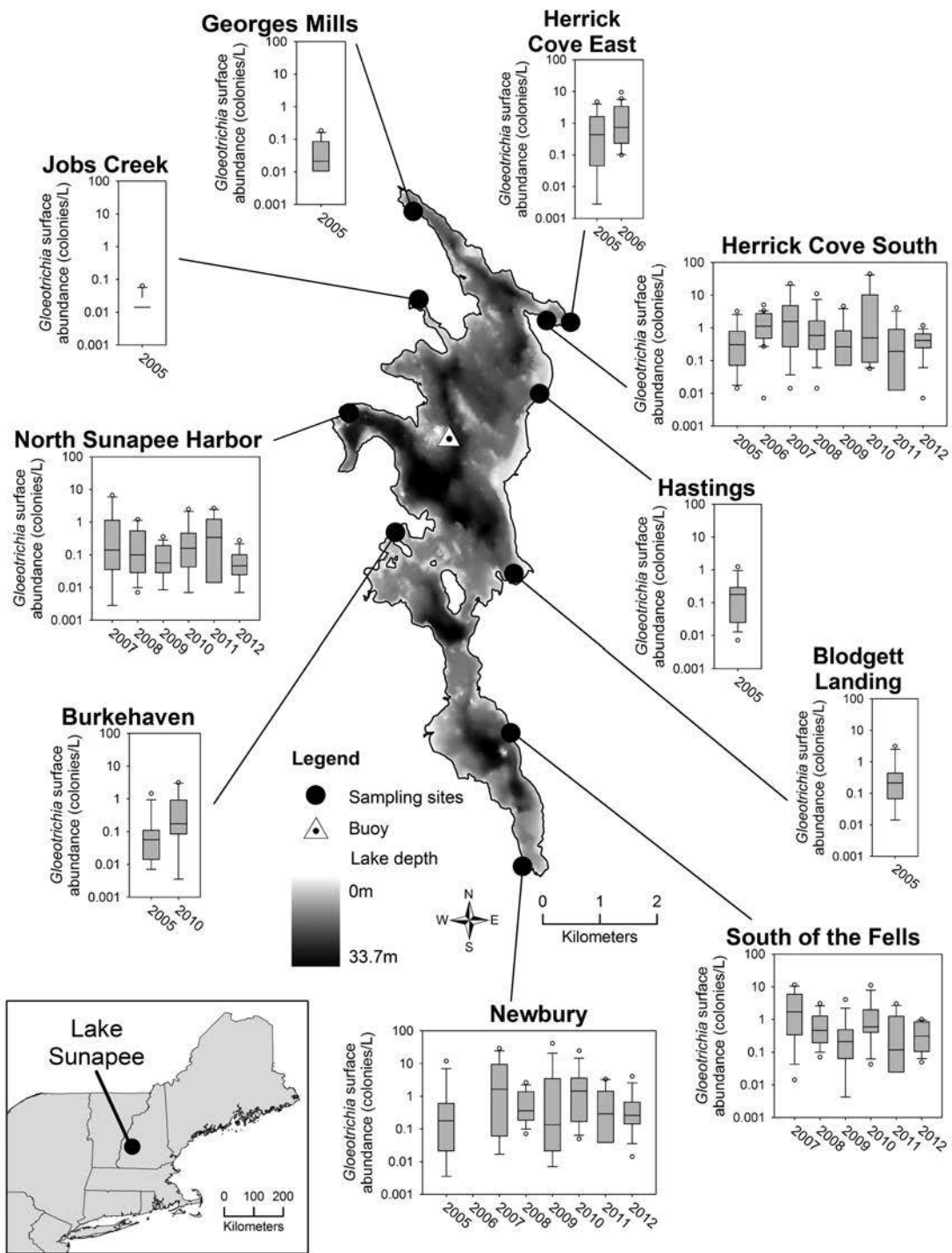
Figure 1. Location, bathymetry, and all near-shore sampling sites visited in Lake Sunapee, New Hampshire, USA, for ≥1 season during 2005–2012. Box plots summarize the observed surface abundances of *Gloeotrichia echinulata* at each study site during the indicated sample years. All box plots have the same $\log_{10}$-scaling to facilitate comparisons across sites. Zero values are not visible in the panels. Lines in boxes are medians, box ends are quartiles, whiskers show values within 1.5× the interquartile range (1.5×IQR) of the quartiles, and dots show outliers (values >1.5×IQR beyond the quartiles). Bathymetry courtesy of the Lake Sunapee Protective Association.

8.0 ± 0.1 m (LSPA-Volunteer Lake Assessment Program, unpublished data).

Gloeotrichia recruitment and water temperature

We sampled *Gloeotrichia echinulata* recruitment throughout the study period with downward-facing, transparent glass funnels attached to plastic collection bottles (Carey et al. 2008). The funnels hung ~10 cm above the sediment surface from masts resting in plastic crates and were designed to prevent lateral transport of colonies into traps (Barbiero and Welch 1992, Hansson 1995). During sampling, a snorkeler stoppered each funnel unit underwater and brought it back to shore, where trap contents were filtered through 80-μm Nitex mesh and preserved with Lugol's iodine (target concentration 2–3%) in an opaque plastic bottle.

Trap sites and spatiotemporal sampling scales differed between 2005–2006 and 2007–2012. In 2005–2006, we placed traps over organic-rich sediment thought to be favorable to *Gloeotrichia* recruitment (Carey et al. 2008, 2009). In 2007–2012, we placed traps in representative habitat at each site (see Table S2 for site characteristics). In 2005, we sampled ~2×/wk at 8 sites at 2-m depth around Lake Sunapee, including duplicate traps at the 2 Herrick Cove sites (Carey et al. 2008; Fig. 1). In 2006, we placed 3 traps at each Herrick Cove site and sampled ~2×/wk, but we did not sample elsewhere in the lake.

Beginning in 2007, we adopted a sampling strategy that remained consistent through 2012. We sampled recruitment traps weekly at 4 sites positioned on the northern, eastern, southern, and western sides of the lake (Herrick Cove South, South of the Fells, Newbury, and North Sunapee Harbor, respectively; Fig. 1). At each site, we placed 2 crates at 1.5–2.0-m depth at the beginning of the season. Each crate supported 2 funnels hung from opposite corners of the crate, for a total of 4 traps/site (Fig. S1). Traps on the same crate were ~1.4 m apart (Carey et al. 2009). Crates were positioned 1 to 10 m apart depending on site and year, but typically within 2 to 3 m of each other. This sampling design enabled us to quantify the variability among sites, among crates at a site, and between replicate traps hung from the same crate. In 2010 only, we included a 5th site (in Burkehaven Cove) that also had 2 crates and 4 traps.

We removed crates from the lake at the end of each season, so crate locations within sites changed from year to year (within a few meters) to avoid sediment that was disturbed during trap removal. From 2006–2012, we attached an Onset Optic StowAway temperature logger (Onset Computer Corporation, Pocasset, Massachusetts) to 1 crate at each site during deployment. This logger recorded temperatures at funnel height at 1-h intervals throughout the sampling period.

We enumerated *Gloeotrichia* with the aid of a Leica MZ12 dissecting microscope (Leica, Buffalo Grove, Illinois). In 2005–2006, we recorded only the total number of colonies encountered, regardless of morphology. Beginning in 2007, we separated counts into colonies (those with an intact central core and filaments throughout the phycosphere) and 'filament bundles' (colonies that lacked filaments filling the full phycosphere; Fig. S2; Karlsson 2003). Filament bundles were found in <4% of all recruitment samples from 2007–2012, so we report total colonies for this period.

We evaluated temporal dynamics in recruitment within a season based on samples taken once or twice each week by calculating the mean daily *Gloeotrichia* recruitment rate during each trap deployment as the number of colonies collected divided by the area of the funnel used in the trap (initial funnels were 8.57-cm diameter, replacement funnels were 8.5–9.0-cm diameter) and the number of days that trap had been deployed. We report daily recruitment rates as colonies m^{-2} d^{-1}, consistent with previous studies (Barbiero and Welch 1992, Karlsson-Elfgren et al. 2003).

Gloeotrichia surface abundance

At every site and on each trap sampling day, we sampled *Gloeotrichia* in the top 1 m of the water column by pooling 2 hauls from 1 m to the surface of a 30-cm-diameter, 80-μm-mesh plankton net (Wildlife Supply Co., Yulee, Florida). We washed *Gloeotrichia* from the net into the collection vessel, rinsed it into an opaque plastic bottle, and preserved it in Lugol's iodine. We counted all colonies in a surface sample without subsampling as described for recruitment samples. We converted counts to densities by dividing the total number of colonies by the volume sampled (170.2 L). We quantified *Gloeotrichia* surface abundance as colonies/L, rather than biovolume, following the precedent set in earlier studies of *Gloeotrichia* (Roelofs and Oglesby 1970, Barbiero and Welch 1992, Karlsson-Elfgren et al. 2005).

Data analyses

We plotted the time series of recruitment rates by site within years and statistically summarized spatial and temporal variability in recruitment and its contributions to the surface population of *Gloeotrichia*. To make comparisons among years as similar as possible, we focused on the solar summer, day-of-year (doy) 173 (22 June in non-leap years) to 265 (22 September). We have solar summer data for 2006–2012. In 2005, monitoring began later in June.

Variability within a year Starting in 2007, our nested sampling design allowed us to evaluate the relative con-

tributions of different spatial scales (among sites, among crates at a site, and between traps on a crate) to temporal variability in daily recruitment rates. We used these data to quantify the temporal coherence (sensu Kratz et al. 1987, Magnuson et al. 1990) between all possible pairs of recruitment time series by calculating the Spearman rank correlations (as done for 2005 by Carey et al. 2008; the Pearson correlation coefficient assumes linearity and was not appropriate for most pairings). In our study, 120 comparisons were possible in each year. We grouped these comparisons into categories labeled 'different sites' (D; traps from different locations around the lake, $n = 96$), 'same site' (S; traps at the same site but on a different crate, $n = 16$), and 'same crate' (C; traps at the same site and on the same crate, but on different masts, $n = 8$). For each year, we calculated a 1-way analysis of variance (ANOVA) comparing mean Spearman rank correlations among these 3 categories to assess the spatial scale at which recruitment fluctuated most synchronously. When we rejected the null hypothesis of equal means, we used Tukey's Honestly Significant Difference to identify the means that differed. We also compared the correlations among years to evaluate whether the degree of coherence changed through time.

Variability among years   To compare recruitment rates among years (2005–2012), we calculated an integrated, summer-long measure of recruitment (integrated recruitment rates) from the total number of *Gloeotrichia* colonies captured in a particular trap during the entire summer (22 June–22 September), divided by the trap area and total number of days of trap deployment to yield colonies $m^{-2}d^{-1}$. Most sites sampled in 2005 and 2006 did not have replicate traps or crates, so we focused on differences among sites in this analysis. We then evaluated the relative contributions of site and year to variability in this integrated recruitment rate with a 2-way ANOVA with an interaction term. We $\log_{10}(x)$-transformed the summer-long recruitment rates to equalize variance among treatments and years before analysis.

Drivers of interannual variability in recruitment

We explored whether precipitation, air and water temperature, stratification, and ice-out date were associated with interannual variability in integrated recruitment rates by comparing the integrated recruitment rate for each year to summary statistics for these abiotic drivers. We used several metrics to summarize *Gloeotrichia* recruitment in initial exploratory analyses, but settled on the median integrated recruitment rate as the metric that best captured central tendencies for a process as highly dynamic in space and time as *Gloeotrichia* recruitment. Results were generally similar for means. We were unable to analyze the

effects of wind speed and direction on *Gloeotrichia* recruitment because of intermittent anemometer sensor malfunction during the study period (LSPA, unpublished data).

Precipitation and air temperature   We obtained records of precipitation (daily total; mm) and air temperature (daily minimum, daily maximum, and at time of observation [~0800 h]; °C) for Newport, New Hampshire, USA (GHCND:USC00275868) from 2005–2012 from the National Climate Data Center website (ncdc.noaa.gov/cdo-web/search). For precipitation, we calculated monthly totals, the number of large precipitation events (>25.4 mm of rain in a 24-h period) per month, and cumulative precipitation: 1) during the winter (January, February, and March), 2) from 1 January through ice-out, and 3) from 1 January through the 1st day of each month from May through September. We summarized each air-temperature variable as the median and 1st and 3rd quartiles (Q1 and Q3, respectively) within each calendar month.

Water temperature   For 2006–2012, we used hourly water temperature data from data loggers placed near the sediment–water interface to derive thermal metrics for each site and a cross-site average. We truncated the time series to be shorter than those used for recruitment to maximize the number of years of record: doy 181 to 260 (30 June–17 September in non-leap years). Summary metrics included the mean, standard deviation (SD), and maximum temperature observed during this time period; the cumulative number of degree days across the period; the number of days/season when the mean temperature was >20, 21, 22, 23, 24, 25, and 26°C; and mean and SD of temperature for the calendar months July and August and the first 17 d of September.

Stratification and ice-out date   We derived stratification indices for Lake Sunapee from the high-frequency data collected by the LSPA GLEON buoy, following Read et al. (2011). We used 10-min temperature-profile data to calculate thermocline depth and Schmidt stability (resistance to mechanical mixing; Idso 1973) with Lake Analyzer, a MATLAB (R2012b; Mathworks, Natick, Massachusetts) program designed to calculate high-frequency mixing and stratification metrics (Read et al. 2011; lakeanalyzer.gleon.org). We calculated the median thermocline depth (m) and Schmidt stability (J/m^2) through the summer season (June–September) and within each calendar month for which the buoy was operating reliably for ≥15 d. Using medians reduced the influence of errors caused by occasional sensor failure. Our use of calendar months facilitated comparisons across years because buoy operation was intermittent in some years. We obtained the date of ice-out from Town

of Sunapee records (town.sunapee.nh.us/Pages/SunapeeNH _Clerk/ice).

Statistical comparisons with integrated recruitment rate

We wrote a MATLAB program to compare the median integrated *Gloeotrichia* recruitment to the full suite of abiotic variables systematically using scatterplots and the Spearman rank correlation (to account for potential nonlinearity in associations). Our maximum sample size in any comparison was 8 y (2005–2012), which is too small for reliable *p*-values for ρ. Because we did thousands of comparisons during data exploration, we focused on visual inspection of scatterplots for which ρ > 0.5. We paid particular attention to August and September because *Gloeotrichia* abundances tend to peak in late summer in lakes in the northeastern USA (Carey et al. 2012a), and we focused on biologically plausible associations for which the visual pattern resulted from all data points rather than 1 or 2 highly influential values.

Contribution of recruitment to surface abundances

We estimated the contribution of recruiting *Gloeotrichia* colonies to pelagic populations over time by the methods of Carey et al. (2008) and Karlsson-Elfgren et al. (2003). Because we monitored recruitment at different sites in 2005, 2006, and 2007–2012 and we wanted a comparable metric among years, we restricted our calculations to Herrick Cove South, which was the only site monitored during the summer of all years. Herrick Cove is a semiclosed basin because of its bathymetry (Fig. 1). Thus, we expected it to be one of the better locations in the lake to assess the relationship between recruitment and pelagic populations.

For each year, we estimated how many colonies recruiting from the sediment subsidized the observed maximum surface population. We used the most conservative of the procedures detailed by Carey et al. (2008). First, we used our surface-sampling data and the known volume of the 0- to 2-m stratum to estimate the total number of colonies in the top 2 m of Herrick Cove on the day of highest surface density. Second, we estimated the total number of potential recruits from the 0- to 2-m sediment stratum daily over a 14-d moving window preceding the day of maximum surface density. We made separate estimates based on the minimum, Q1, median, Q3, and maximum number of colonies caught in our traps (see Karlsson-Elfgren et al. 2003, Carey et al. 2008). We restricted the area of the lake sediment suitable for recruitment to 25% of the available area because Lake Sunapee's littoral zone has considerable rocky substrate (Carey et al. 2008). Last, we divided the estimated number of recruited colonies by the number of colonies in the water column to calculate the recruitment-dependency of the pelagic population.

RESULTS

Spatial and temporal variability in *Gloeotrichia* recruitment

Variability within a year   Recruitment of *Gloeotrichia* from the shallow sediments into the water column was highly variable in space and time (Fig. 2). Daily recruitment rates were often very low, with late-season pulses in most years (Fig. 2). The maximum daily recruitment rate varied >2 orders of magnitude among years, from lows of ∼600 colonies m^{-2} d^{-1} in 2011 and 2012 to >10,000 colonies m^{-2} d^{-1} in 2005, 2007, and 2010 (Fig. 2). Daily recruitment rates tended to be higher and more variable among years at Herrick Cove South (red lines in Fig. 2) and Newbury (blue lines in Fig. 2) than at North Sunapee Harbor and South of the Fells.

In most summers, the pulses of recruitment occurred synchronously among multiple traps (Fig. 2), but the degree of synchrony varied among years and with the distance between traps (Fig. 3, Table 1). Daily recruitment rates generally peaked after doy 230 (18 August). Early-season peaks in *Gloeotrichia* recruitment occurred in the 2 y with the latest ice-out dates, 2007 and 2008 (Fig. 2), which led to a tendency for the peak daily recruitment rate to occur *later* when the ice went out early (ρ = –0.74). The late-summer peak occurred earlier in 2008 and 2010 (between doy 230 and 245) than in most other years (after doy 245). Temporal coherence among traps within a site was most striking in 2010, when recruitment to all traps at Newbury peaked 1 wk before recruitment to 3 of the traps at Herrick Cove South (Fig. 2). Recruitment dynamics were least coherent in 2008, when negative correlations between sites (Fig. 3) arose from strongly asynchronous fluctuations in recruitment (Fig. 2).

Overall, D traps (those at different sites) tended to be least coherent and C traps (those at the same crates) tended to be most coherent, as evidenced by an increasing pattern moving from left to right within years in Fig. 3. In all years but 2012, the temporal coherence of traps differed among spatial scales (Table 1). Mean coherence of S traps did not differ (i.e., the crate from which a trap hung did not matter), but mean correlations between S traps and D traps differed significantly in 2008, 2009, and 2011 (Table 1).

Variability across years   Integrated recruitment rates varied from >10 colonies m^{-2} d^{-1} at North Sunapee Harbor in 2012 to nearly 3000 colonies m^{-2} d^{-1} at Herrick Cove South during 2010 (Fig. 4). Mean log$_{10}(x)$-transformed integrated recruitment rates depended strongly on site, year, and their interaction (2-way ANOVA, year: $F_{5,72}$= 58.8, site: $F_{3,72}$= 133.1, year × site: $F_{15,72}$= 5.7; all $p < 0.0001$, R^2= 0.92). Some sites and years had very high integrated recruitment rates (e.g., Herrick Cove South and Newbury during 2007 and 2010; Fig. 4), whereas others had low
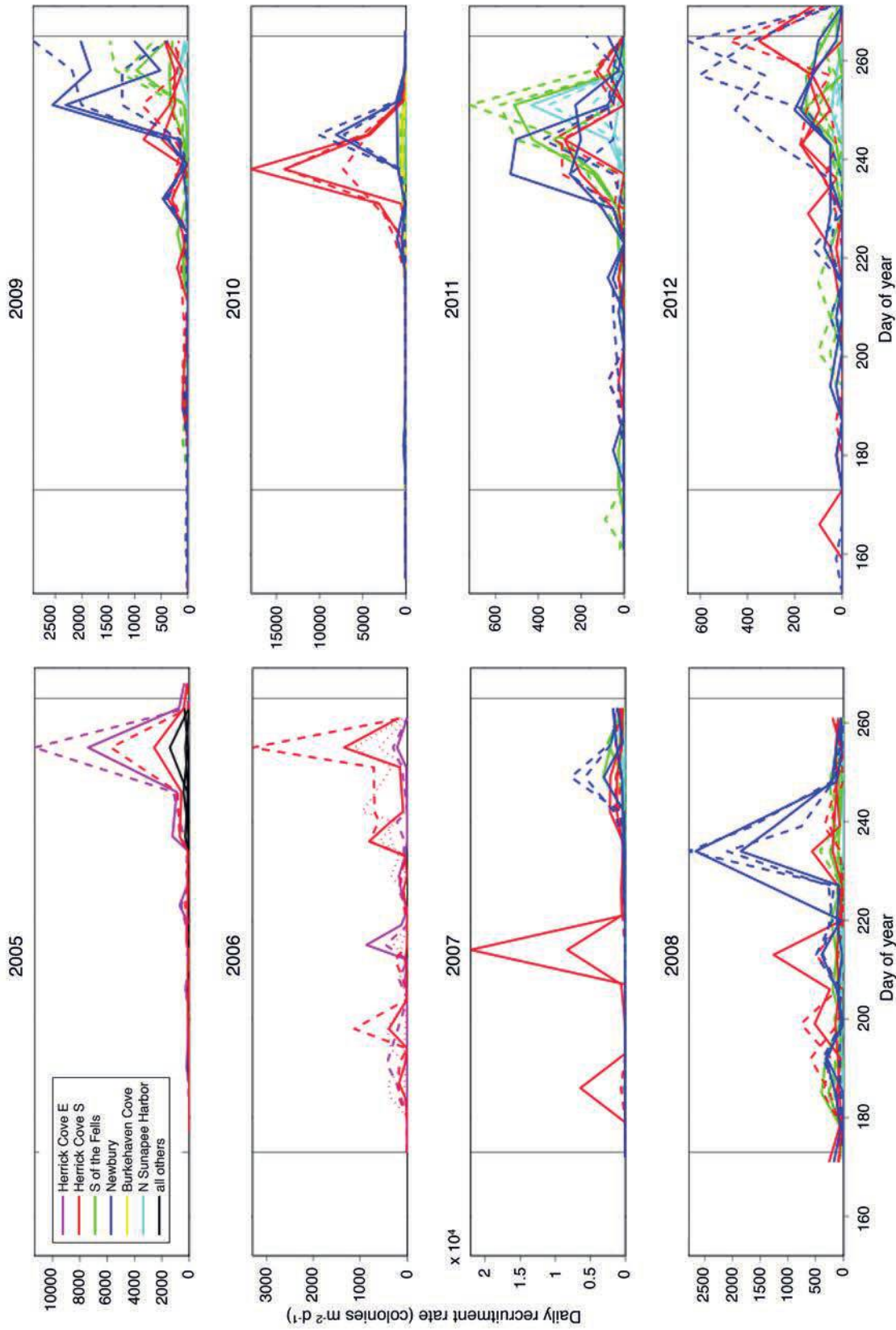
Figure 2. Daily recruitment of *Gloeotrichia echinulata* (colonies m^{-2} d^{-1}) into funnel traps at multiple sites in Lake Sunapee, New Hampshire, USA, for summers 2005–2012. The vertical black lines indicate the period during which statistics were calculated (days of the year 173–265 [22 June–22 September in non-leap years]). Sites sampled only with a single trap in 2005 are indicated with solid black lines. Otherwise, colors denote traps at the same site within the lake and line types indicate traps on the crate at a site, such that the same color and same line type indicate traps on the same crate at the same site. Note different *y*-axes on each panel.
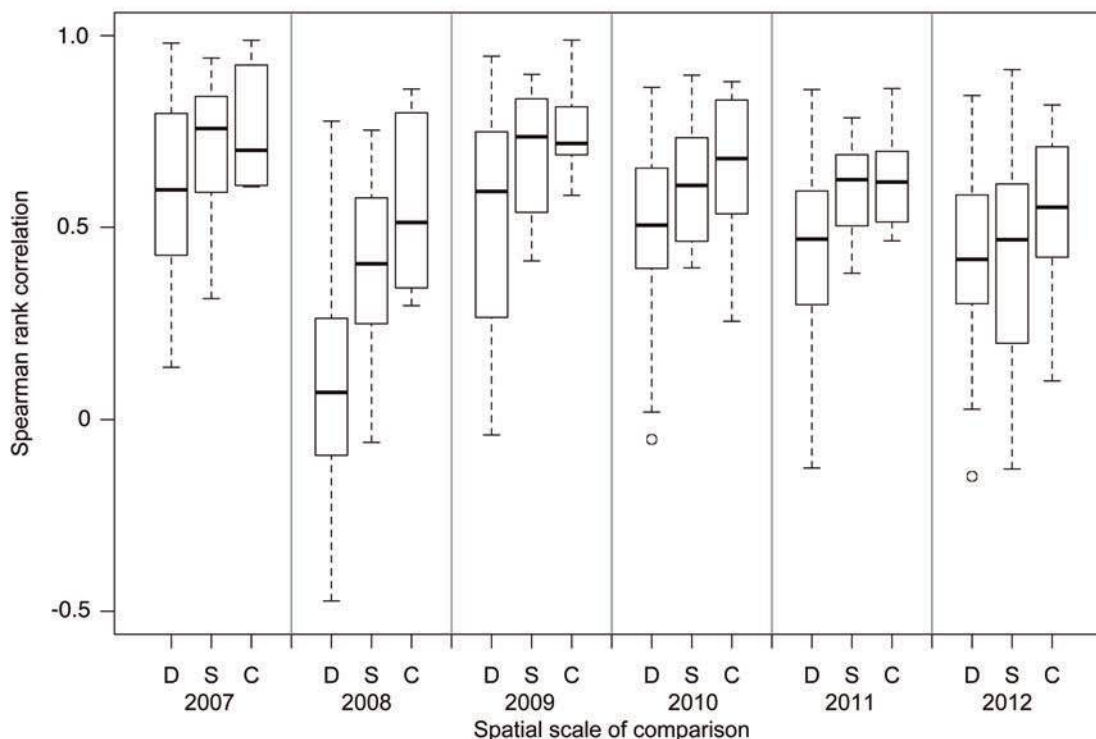
Figure 3. Outlier boxplots summarizing the pairwise temporal coherence (indicated by Spearman rank correlation) of *Gloeotrichia echinulata* recruitment into funnel traps deployed in Lake Sunapee, New Hampshire, USA, from 2007–2012. Boxplots drawn as described in Fig. 1. Coding indicates different sites within the lake (D), at the same site but different crates (S), and at the same crate within a site (C).

recruitment rates (e.g., North Sunapee Harbor in 2008, 2009, 2011, and 2012). Overall, the North Sunapee Harbor site tended to have the lowest integrated recruitment rates, whereas Herrick Cove South and Newbury had the highest (Fig. 4). In many sites, the integrated recruitment rates declined through time, reflecting in part the lower rates observed in 2011–2012 (Fig. 4).

Drivers of interannual variability in recruitment Summarized at monthly to summer-long time scales, the focal abiotic drivers fluctuated during the period from 2005–

2012 (Fig. S3). Cumulative annual precipitation ranged from 862.7 mm in 2012 to 1424.8 mm in 2005. Tropical Storms Irene and Lee in late August and early September 2011 marked a high point in precipitation (Klug et al. 2012) relative to a general decline over the study period. In August, when *Gloeotrichia* recruitment was high (Fig. 2), minimum daily air temperatures (Q1) increased ~3°C from 2005 to 2012 (Fig. S3). Mean water temperatures were ~23°C in most years, but lower in 2008 (22.0°C) and higher in 2012 (24.3°C), whereas SDs declined from a high of 2°C in 2006 to a low of 0.8°C in 2012. Median

Table 1. Mean temporal coherence of *Gloeotrichia echinulata* recruitment at different spatial scales in each year from 2007–2012 in Lake Sunapee, New Hampshire, USA. The F-test for the null hypothesis of no difference among spatial scales is indicated by F (df = 2,117 for all years) and the p-value. When $p < 0.05$, we used Tukey's Honestly Significant Difference (HSD) test to run multiple comparisons. ND = no difference detected, D = different sites, S = same site but different crate, C = same crate.

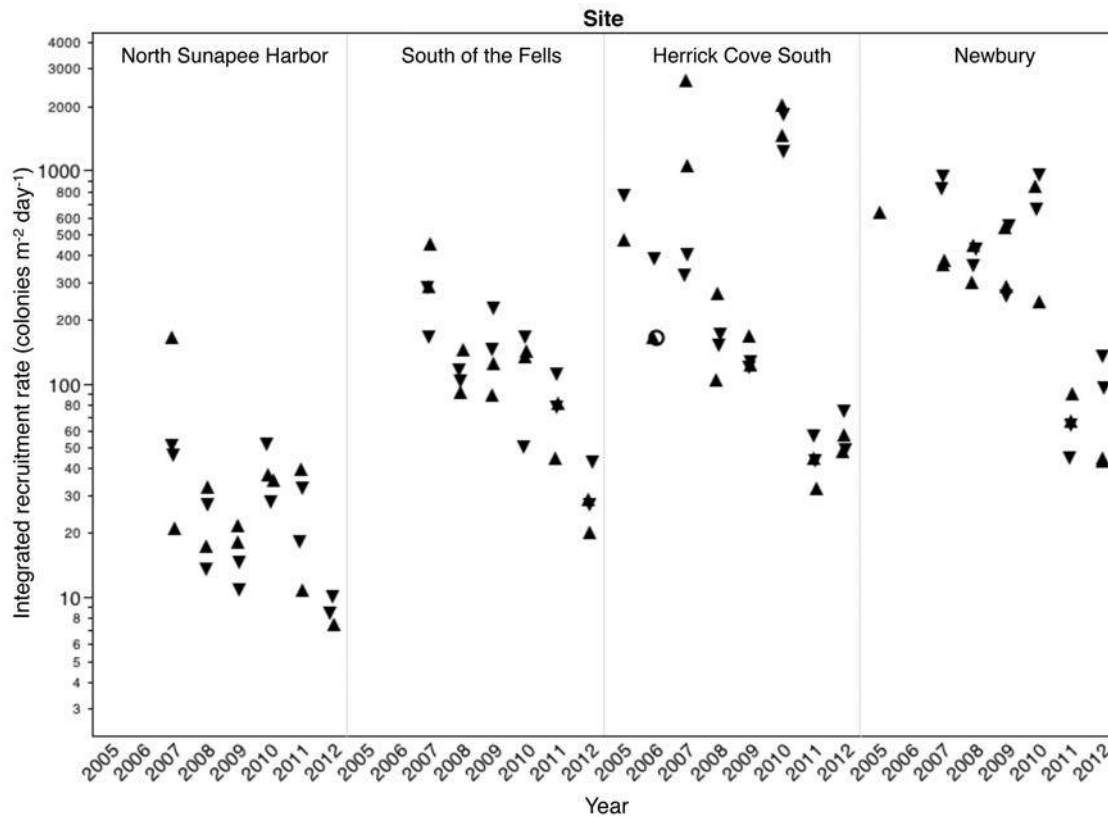| Year | Mean Spearman rank correlation | | | ANOVA | | | |
	Different sites	Same site	Same crate	F	p	Tukey's HSD	R^2
2007	0.60	0.71	0.76	3.83	0.02	ND	0.06
2008	0.08	0.40	0.56	23.01	<0.0001	D < S = C	0.28
2009	0.51	0.69	0.75	6.17	0.0028	D < S = C	0.10
2010	0.50	0.62	0.65	4.28	0.0160	ND	0.07
2011	0.45	0.60	0.62	6.64	0.0019	D < S = C	0.10
2012	0.43	0.42	0.54	0.80	0.4507	–	0.01

Figure 4. Integrated, summer-long recruitment rates for *Gloeotrichia echinulata* at the 4 core sampling locations in Lake Sunapee, New Hampshire, USA, from 2005–2012. Within each year, each point represents the total recruitment into 1 trap during the summer (total colonies caught divided by the total number of days of trap deployment multiplied by the area of the trap to yield colonies m^{-2} d^{-1}). Symbols indicate unique crates that held replicate traps. The *y*-axis is represented on a log$_{10}$-scale to facilitate comparisons across years.

thermocline depth was much deeper in 2010 (>10 m) than in 2011 and 2012 (<7 m), and Schmidt stability was highest in 2011 and 2012. Ice-out date varied from 22 March 2012 (doy 82), the earliest since monitoring began in 1869, to 24 April 2007 and 23 April 2008 (doy 114), 1 d later than the long-term mean from 1869–2012 (doy 113).

Despite explorations of thousands of pairwise comparisons, we found few robust associations between median integrated recruitment rate and ice-out date, regional precipitation, air and water temperatures, and lake stratification. There was no association with precipitation (Fig. 5A) or mean water temperature (Fig. 5C). However, higher median integrated recruitment rates were associated with periods of greater mixing in mid-to-late summer, evidenced by lower minimum air temperatures during August (Fig. 5B), greater variability in July (not shown) and August water temperatures (Fig. 5D), deeper thermocline depths (Fig. 5E), and lower Schmidt stability (Fig. 5F). We detected no associations with ice-out date or precipitation summary statistics (Fig. S3).

Contribution of recruitment to surface abundances Near-shore densities of *Gloeotrichia* in the top 1 m of the lake varied among sites and years (Fig. 1). Median densities within a summer were generally low (≤1 colony/L; Fig. 1), but densities >10 colonies/L were observed in ≥1 location in 2005 and 2007–2010. Abundances tended to be highest in Herrick Cove South and Newbury, the same 2 sites for which recruitment rates tended to be highest. During our study, *Gloeotrichia* colonies recruited from the sediments contributed a small proportion of the surface population maxima in Herrick Cove (median: ~0.2–4%, maximum: 8.2% in 2008; Fig. 6).

DISCUSSION

Gloeotrichia echinulata is a large, colonial cyanobacterium readily visible to the naked eye and, hence, the public. Concern is growing about increases in cyanobacteria, including *Gloeotrichia*, in low-nutrient lakes across northeastern North America (Winter et al. 2011, Carey et al. 2012a). Cyanobacterial population dynamics can depend critically on recruitment from sediment resting stages (e.g.,
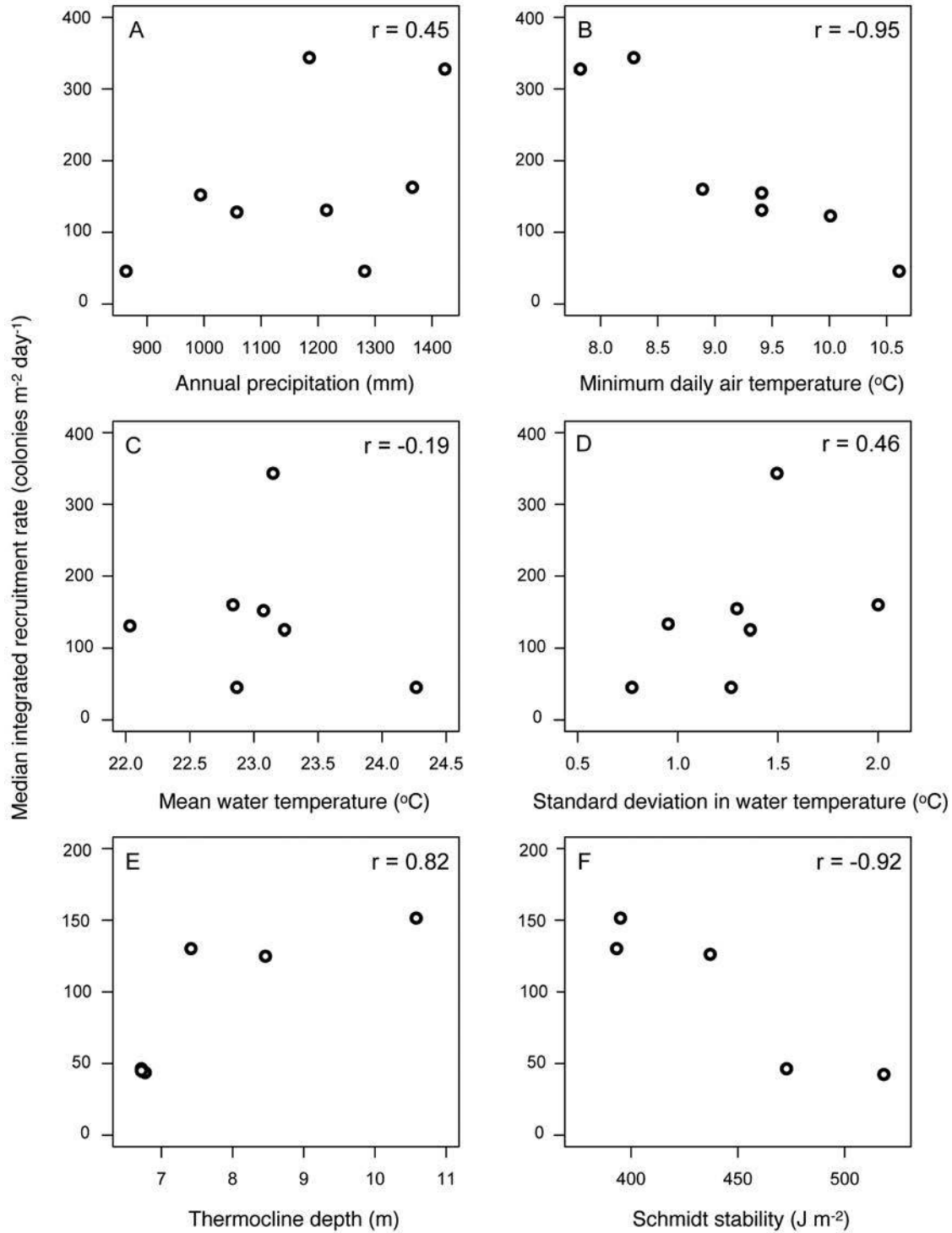
Figure 5. Scatterplots showing the association between integrated, summer-long *Gloeotrichia echinulata* recruitment in Lake Sunapee, New Hampshire, USA, and annual precipitation (A), minimum daily air temperature (B), mean (C) and standard deviation (D) in water temperature, thermocline depth (E), and Schmidt stability (F) during August of each year. The standard Pearson correlation coefficient *r* is presented because all associations were linear.
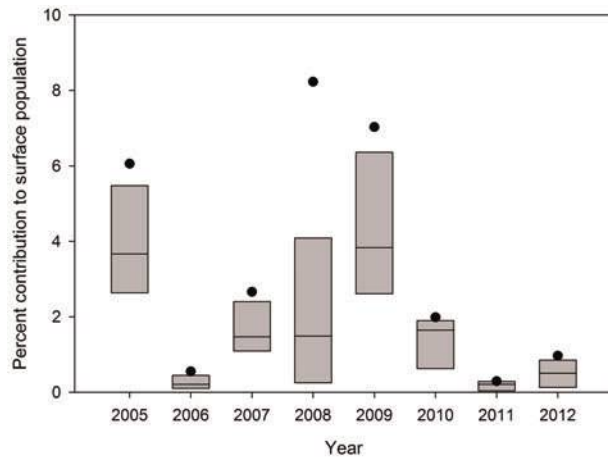
Figure 6. Contributions of recruitment to surface abundances of *Gloeotrichia echinulata* at Herrick Cove, Lake Sunapee, New Hampshire, USA during 2005–2012. Lines in boxes show the recruitment contribution based on the median recruitment rates, box ends show recruitment contributions calculated from the 1st and 3rd quartiles of the recruitment rate data, respectively, and circles indicate the recruitment contribution derived from the maximum recruitment rates.

Trimbee and Harris 1984, Barbiero and Welch 1992), so we investigated the potential drivers of variability in *Gloeotrichia* recruitment across space and time. To the best of our knowledge, our data set constitutes the longest continuous record of coupled recruitment and surface-abundance data in 1 lake for any cyanobacterial taxon, and it provides valuable information about the factors influencing recruitment for this species.

Spatial variability in recruitment We found substantial variability in *Gloeotrichia* recruitment among sites within and among years. *Gloeotrichia* recruitment rates and surface abundances were consistently higher at Herrick Cove South and Newbury than the other sites, and within a season, recruitment dynamics were more synchronous within a site than between sites. These observations indicate that local, microhabitat characteristics may affect the relative rates and timing of recruitment among sites, consistent with results of short-term laboratory experiments and field studies. Others have shown that, within a season, recruitment dynamics may be driven in part by local abiotic factors, such as depth (Karlsson-Elfgren et al. 2004), sediment chemistry and substrate type (Carey et al. 2008, 2009), and dissolved O_2 (Barbiero 1993). Biotic factors, such as the size of the akinete bank (Forsell 1998), bioturbation (Pierson et al. 1992, Karlsson-Elfgren et al. 2004), and grazing (Rengefors et al. 1998), also can be important.

Individual biotic and abiotic factors often are controlled by environmental characteristics at a broader spatial scale than site. In this case, lake morphometry, the

location and types of coves, watershed land use and land cover, and the orientation of the lake relative to prevailing winds may be particularly important controls on local factors, such as the amount of sediment habitat at a particular water depth, the accumulation of sediment of any given type or chemistry, and the distribution of the akinete bank. For example, buoyant cyanobacteria, such as *Gloeotrichia*, are susceptible to redistribution in the lake by wind and currents (Wynne et al. 2011). Redistribution can lead to high surface abundances (and potentially greater akinete accumulation) at downwind sites. The Herrick Cove South and Newbury sites are both in long, narrow coves (Fig. 1) that collect and trap wind-displaced colonies from other areas of the lake (Carey et al. 2008). The maximum possible fetch is 3.6 km for Herrick Cove and 6.6 km for Newbury and provides substantial opportunity for colonies to collect in these coves when the winds blow from the west or north, respectively. These sites are likely to accumulate fine, organic-rich sediment for the same reason, and the bathymetry of the lake is such that both locations have sizable habitat within the depths from which recruitment has been observed. Consistently higher recruitment in more sheltered coves, thought to be a consequence of wind redistribution, also has been observed in Lake Erken, Sweden (Forsell and Pettersson 1995, Karlsson-Elfgren et al. 2003).

Temporal coherence differed among sites in most years, but we did not detect an effect of spatial scale on recruitment during 2012. The very low recruitment in 2012 could simply indicate that relatively little signal was present with which to compare coherence across sites, although the signal itself may have been controlled by factors operating at a broader spatial scale. We hypothesize that the 2 extreme storms experienced in August and September 2011 (Klug et al. 2012) may have disturbed the akinete bank in ways that inhibited subsequent recruitment, e.g., by washing viable akinetes in surface sediments from littoral coves into deeper areas of the lake. Alternatively, the meager ice cover in winter 2011–2012 and the early ice-out date in 2012 may have compromised the viability of *Gloeotrichia* akinetes in the following spring and summer, as has been observed for *Microcystis* sp. vegetative cells (Brunberg and Blomqvist 2002).

Variability in recruitment and its importance to surface populations

Regardless of the difference in the magnitude of recruitment among sites, recruitment was predictably highest in late August and early September (Fig. 2), consistent with observations of maximum pelagic *Gloeotrichia* abundances in low-nutrient lakes in the northeastern USA (Carey et al. 2012a). This pattern could be the result of a lake-wide cue, such as a change in photoperiod or temperature. *Gloeotrichia* recruitment and surface abundance peak in early to

mid-summer in most eutrophic lakes (e.g., Barbiero 1993, Karlsson-Elfgren et al. 2003, Nõges et al. 2004, Karlsson-Elfgren et al. 2005), a pattern suggesting that germination and recruitment cues for *Gloeotrichia* akinetes might differ between low- and high-nutrient lakes, perhaps because of differences in late-summer light availability.

Gloeotrichia has been reported as having one of the highest levels of recruitment-dependency observed among cyanobacterial taxa, considerably higher than some observations of *Anabaena*, *Gomphosphaeria*, *Lyngbya*, or *Oscillatoria* (Trimbee and Harris 1984, Barbiero and Welch 1992, Hansson 1996, Head et al. 1999, Karlsson-Elfgren and Brunberg 2004). In Lake Sunapee, recruitment contributed less to water-column *Gloeotrichia* densities than we had anticipated based on our initial study in 2005 (Carey et al. 2008). Over the 8-y study, median recruitment contribution estimates for Lake Sunapee were ~0.2 to 4%, an order of magnitude smaller than those we reported previously (21–45%; Carey et al. 2008). We think the lower contribution is the result of our decision to make the most conservative calculations (e.g., restrict surface abundance to the top 0–2 m of the water column, reduce the area of potential habitat, and consider only a 14-d pelagic residence time for each colony), and to focus solely on Herrick Cove, rather than the entire lake. Herrick Cove is downwind of prevailing winds, making it a likely location for accumulation of colonies from throughout the lake, thus, minimizing the apparent importance of recruitment from the benthos. We think it likely that we underestimated the whole-lake recruitment contribution to surface populations of *Gloeotrichia* in Lake Sunapee during 2005–2012. Nevertheless, our estimates from Herrick Cove are bracketed by estimates from eutrophic Lake Erken, Sweden, and Green Lake, Washington, USA. In Lake Erken, Karlsson-Elfgren et al. (2003) found that recruitment contributed <5% to pelagic populations, whereas in Green Lake, Barbiero and Welch (1992) observed up to ~50% contribution to surface abundances. Both groups of investigators found similar contributions in 2 summers of monitoring, results suggesting that recruitment subsidies within a lake may be fairly consistent over time, as we observed for Lake Sunapee (Fig. 6).

The relatively small contribution of recruitment to pelagic populations suggests that examining the factors governing colony division in the water column will be an important next step in understanding *Gloeotrichia* population dynamics. However, in ice-covered, north temperate lakes, recruitment is by far the most important mechanism for *initiating* a bloom of this species and other cyanobacterial taxa.

Drivers of interannual variability in recruitment

In some years (e.g., 2007 and 2010), daily and integrated recruitment rates were ≥1 order of magnitude higher than in other years (e.g., 2011 and 2012). These fluctuations might be the result of differences in trap placement at each site. Changing crate sites from year to year may have led to placement of traps over better microhabitats in some years than in others, especially at Herrick Cove South and Newbury, where patches of organic-rich substrate are present (Table S2). However, our analyses suggest that the fluctuations largely reflected real interannual differences in environmental conditions. First, the spatial differences among sites were generally robust in that some sites consistently produced higher *Gloeotrichia* recruitment rates every year. Second, higher recruitment rates in some years usually were consistent among multiple traps at each site. Third, the differences between low and high recruitment sites were similar among years: i.e., maximum recruitment rates occurred during the same years at all sites regardless of whether a site typically had high or low recruitment rates.

We do not know with confidence the drivers of these interannual differences, but our analyses suggest that abiotic factors that affect lake mixing—especially thermocline depth, Schmidt stability, and minimum air temperatures—play a key role in interannual recruitment dynamics (Fig. 5). The most striking associations in our record were between integrated recruitment rates and variables associated with open-water or near-shore mixing in August, when recruitment rates were high and germination rates probably were highest. An ~3-wk lag exists between initiation of germination on the sediments and recruitment into the water column (Tymowski and Duthie 2000, Karlsson 2003, Carey et al. 2009), so we think that the peak recruitment observed in September in most years was cued in August. It follows that abiotic triggers for *Gloeotrichia* recruitment were more important in August than at other times of year.

Experimental and field data support the hypothesis that mixing may affect recruitment. In laboratory studies, *Gloeotrichia* recruitment increased when surface sediments were gently mixed at regular intervals (Karlsson-Elfgren et al. 2004). This phenomenon has been observed for *Anabaena* and *Microcystis* (Stahl-Delbanco and Hansson 2002, Misson and Latour 2012). Substantial convective mixing from littoral to pelagic areas can occur overnight because of greater cooling in shallow than in deep waters (Horsch and Stefan 1988, Stefan et al. 1989, James and Barko 1991a, b), particularly during periods of decreasing air temperatures (James and Barko 1991b). As overnight air temperatures decrease in late summer, greater convective mixing may cue *Gloeotrichia* germination and recruitment (Karlsson-Elfgren et al. 2004) or transport of colonies from the sediments into the water column (MacIntyre and Melack 1995). Near-shore mixing is correlated with variability in water temperature, evidenced by larger SDs of August water temperatures during years of higher recruitment (Fig. 5D). Thus, the association between integrated, summer-long recruitment rate and minimum August air

temperatures may indicate an important role of convective mixing in late-summer *Gloeotrichia* recruitment.

Pelagic stratification as a driver was initially puzzling because we measured recruitment from shallow sediments (1.5–2.0 m), well above the Lake Sunapee thermocline depth (6–8 m). Moreover, peak abundances of pelagic cyanobacteria (i.e., blooms) usually are associated with periods of strong stratification, high levels of irradiance, high temperatures, and minimum wind (Reynolds 2006). Thus, we wondered why cyanobacterial recruitment and lake stratification might be associated. We were unable to analyze relationships between wind speed and recruitment, but we think that the stratification indices calculated from the LSPA GLEON buoy near the deep hole of the lake are a proxy for a lake-wide, integrated signal of increased mixing.

Deeper thermoclines might signal increased entrainment and greater P availability in the water column (Pierson et al. 1992, Soranno et al. 1997). If *Gloeotrichia* responds positively to an increase in water-column nutrients, then it may take advantage of higher P concentrations in the water column by increasing recruitment rates. Water-column *Gloeotrichia* populations benefit from additional P and other nutrients in the water column (Karlsson-Elfgren et al. 2005), and luxury uptake of P from the sediment occurs at the time of germination (Istvánovics et al. 1993), suggesting that increased recruitment in response to greater P availability may be possible.

Unexpectedly, we did not detect associations between integrated recruitment rate and other abiotic factors, including water temperature and precipitation. The absence of strong associations may mean that these drivers interact with mixing or other factors (as has been concluded from shorter-term studies; e.g., Barbiero 1993, Karlsson-Elfgren et al. 2004), possibly with time lags, in ways that cannot be untangled without many more years of data on biotic responses (i.e., *Gloeotrichia* recruitment) and potential abiotic drivers. Alternatively, it may simply mean that the role of abiotic factors in *Gloeotrichia* recruitment requires investigation at a finer temporal resolution than weekly sampling of recruitment traps or the monthly-to-seasonal summaries for abiotic variables.

Regional climate forecasts predict increased air temperatures and increases in the number and magnitude of large precipitation events (Hayhoe et al. 2007, 2008). Higher air temperatures are expected to favor water-column cyanobacteria via the direct effects of higher water temperature and the indirect effects of stronger stratification (Jöhnk et al. 2008, Paerl and Huisman 2008, Carey et al. 2012b). However, if recruitment of *Gloeotrichia* is reduced by stronger stratification, water-column populations may not become established in early spring or summer, at least in lakes where populations of cyanobacteria cannot be maintained in the water column through the winter. On the other hand, more storms may lead to greater winds (which increase mixing, especially in shallow areas), greater stream inflow (and thus, mixing where streams enter the lake), and more nutrient and sediment inputs, all of which would be expected to stimulate *Gloeotrichia* recruitment. Therefore, linked drivers associated with climate change may dictate future trends in *Gloeotrichia* population dynamics. Whether similar predictions might hold for other highly recruitment-dependent taxa, such as *Aphanizomenon flos-aquae* (Trimbee and Harris 1984, Barbiero and Kann 1994), or for *Gloeotrichia* in other lakes remains to be seen.

If we hope to anticipate and manage cyanobacterial blooms, we will need to understand key drivers of recruitment and of pelagic division, which contributes the vast majority of growth in *Gloeotrichia* surface populations in Lake Sunapee. A comprehensive understanding of in-lake microsite characteristics and regional-to-local influences on watersheds will be fundamentally important for predicting the long-term likelihood of initiation of cyanobacterial blooms by recruitment in the future.

LITERATURE CITED

Adams, D. G., and P. S. Duggan. 1999. Tansley Review No. 107. Heterocyst and akinete differentiation in cyanobacteria. New Phytologist 144:3–33.

Adrian, R., C. M. O'Reilly, H. Zagarese, S. B. Baines, D. O. Hessen, W. Keller, D. M. Livingstone, R. Sommaruga, D. Straile, E. Van Donk, G. A. Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnology and Oceanography 54:2283–2297.

Anderson, D. M., P. M. Glibert, and J. Burkholder. 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries and Coasts 25:704–726.

Barbiero, R. P. 1993. A contribution to the life-history of the planktonic cyanophyte, *Gloeotrichia echinulata*. Archiv für Hydrobiologie 127:87–100.

Barbiero, R. P., and J. Kann. 1994. The importance of benthic recruitment to the population development of *Aphanizomenon flos-aquae* and internal loading in a shallow lake. Journal of Plankton Research 16:1581–1588.

Barbiero, R. P., and E. B. Welch. 1992. Contribution of benthic blue-green algal recruitment to lake populations and phosphorus translocation. Freshwater Biology 27:249–260.

Bennett, E. M., S. R. Carpenter, and N. F. Caraco. 2001. Human impact on erodable phosphorus and eutrophication: a global perspective. BioScience 51:227–234.

Boyer, G. L. 2008. Cyanobacterial toxins in New York and the lower Great Lakes ecosystems. Pages 153–165 *in* H. K. Hudnell (editor). Cyanobacterial harmful algal blooms: state of the science and research needs. Springer, New York.

Brookes, J. D., and C. C. Carey. 2011. Resilience to blooms. Science 334:46–47.

Brunberg, A. K., and P. Blomqvist. 2002. Benthic overwintering of *Microcystis* colonies under different environmental conditions. Journal of Plankton Research 24:1247–1252.

Carey, C. C., H. A. Ewing, K. L. Cottingham, K. C. Weathers, R. Q. Thomas, and J. F. Haney. 2012a. The occurrence and toxicity of the cyanobacterium *Gloeotrichia echinulata* in low-nutrient lakes in the northeastern United States. Aquatic Ecology 46:395–409.

Carey, C. C., J. F. Haney, and K. L. Cottingham. 2007. First report of microcystin-LR in the cyanobacterium *Gloeotrichia echinulata*. Environmental Toxicology 22:337–339.

Carey, C. C., B. W. Ibelings, E. P. Hoffmann, D. P. Hamilton, and J. D. Brookes. 2012b. Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. Water Research 46:1394–1407.

Carey, C. C., K. C. Weathers, and K. L. Cottingham. 2008. *Gloeotrichia echinulata* blooms in an oligotrophic lake: helpful insights from eutrophic lakes. Journal of Plankton Research 30:893–904.

Carey, C. C., K. C. Weathers, and K. L. Cottingham. 2009. Increases in phosphorus at the sediment-water interface may accelerate the initiation of cyanobacterial blooms in an oligotrophic lake. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 30:1185–1188.

Ernst, B., S. J. Hoeger, E. O'Brien, and D. R. Dietrich. 2009. Abundance and toxicity of *Planktothrix rubescens* in the prealpine Lake Ammersee, Germany. Harmful Algae 8:329–342.

Forsell, L. 1998. Migration from the littoral zone as an inoculum for phytoplankton. Archiv für Hydrobiologie Special Issues: Advances in Limnology 51:21–27.

Forsell, L., and K. Pettersson. 1995. On the seasonal migration of the cyanobacterium *Gloeotrichia echinulata* in Lake Erken, Sweden, and its influence on the pelagic population. Marine and Freshwater Research 46:287–293.

Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32:79–99.

Hansson, L. A. 1995. Diurnal recruitment patterns in algae: effects of light cycles and stratified conditions. Journal of Phycology 31:540–546.

Hansson, L. A. 1996. Algal recruitment from lake sediments in relation to grazing, sinking, and dominance patterns in the phytoplankton community. Limnology and Oceanography 41:1312–1323.

Havens, K. 2008. Cyanobacteria blooms: effects on aquatic ecosystems. Pages 733–748 *in* H. K. Hudnell (editor). Cyanobacterial harmful algal blooms: state of the science and research needs. Springer, New York.

Hayhoe, K., C. Wake, B. Anderson, X.-Z. Liang, E. Maurer, J. Zhu, J. Bradbury, A. DeGaetano, A. M. Stoner, and D. Wuebbles. 2008. Regional climate change projections for the Northeast USA. Mitigation and Adaptation Strategies for Global Change 13:425–436.

Hayhoe, K., C. P. Wake, T. G. Huntington, L. Luo, M. D. Schwartz, J. Sheffield, E. Wood, B. Anderson, J. Bradbury, A. DeGaetano, T. J. Troy, and D. Wolfe. 2007. Past and future changes in climate and hydrological indicators in the US Northeast. Climate Dynamics 28:381–407.

Head, R. M., R. I. Jones, and A. E. Bailey-Watts. 1999. An assessment of the influence of recruitment from the sediment on the development of planktonic populations of cyanobacteria in a temperate mesotrophic lake. Freshwater Biology 41:759–769.

Horsch, G. M., and H. G. Stefan. 1988. Convective circulation in littoral water due to surface cooling. Limnology and Oceanography 33:1068–1083.

Idso, S. B. 1973. On the concept of lake stability. Limnology and Oceanography 18:681–683.

Istvánovics, V., K. Pettersson, M. A. Rodrigo, D. Pierson, J. Padisak, and W. Colom. 1993. *Gloeotrichia echinulata*, a colonial cyanobacterium with a unique phosphorus uptake and life strategy. Journal of Plankton Research 15:531–552.

James, W. F., and J. W. Barko. 1991a. Estimation of phosphorus exchange between littoral and pelagic zones during nighttime convective circulation. Limnology and Oceanography 36:179–187.

James, W. F., and J. W. Barko. 1991b. Littoral-pelagic phosphorus dynamics during nighttime convective circulation. Limnology and Oceanography 36:949–960.

Jöhnk, K. D., J. Huisman, J. Sharples, B. Sommeijer, P. M. Visser, and J. M. Stroom. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. Global Change Biology 14:495–512.

Kaplan-Levy, R. N., O. Hadas, M. L. Summers, J. Rucker, and A. Sukenik. 2010. Akinetes: dormant cells of Cyanobacteria. Pages 5–27 *in* E. Lubzens, J. Cerda, and M. S. Clark (editors). Dormancy and resistance in harsh environments. Springer, Heidelberg, Germany.

Karlsson, I. 2003. Benthic growth of *Gloeotrichia echinulata* cyanobacteria. Hydrobiologia 506:189–193.

Karlsson-Elfgren, I., and A. K. Brunberg. 2004. The importance of shallow sediments in the recruitment of *Anabaena* and *Aphanizomenon* (Cyanophyceae). Journal of Phycology 40:831–836.

Karlsson-Elfgren, I., P. Hyenstrand, and E. Rydin. 2005. Pelagic growth and colony division of *Gloeotrichia echinulata* in Lake Erken. Journal of Plankton Research 27:145–151.

Karlsson-Elfgren, I., K. Rengefors, and S. Gustafsson. 2004. Factors regulating recruitment from the sediment to the water column in the bloom-forming cyanobacterium *Gloeotrichia echinulata*. Freshwater Biology 49:265–273.

Karlsson-Elfgren, I., E. Rydin, P. Hyenstrand, and K. Pettersson. 2003. Recruitment and pelagic growth of *Gloeotrichia echinulata* (Cyanophyceae) in Lake Erken. Journal of Phycology 39: 1050–1056.

Klug, J. L., D. C. Richardson, H. A. Ewing, B. R. Hargreaves, N. R. Samal, D. Vachon, D. C. Pierson, A. M. Lindsey, D. M. O'Donnell, S. W. Effler, and K. C. Weathers. 2012. Ecosystem effects of a tropical cyclone on a network of lakes in northeastern North America. Environmental Science and Technology 46:11693–11701.

Kratz, T. K., R. B. Cook, C. J. Bowser, and P. L. Brezonik. 1987. Winter and spring pH depressions in northern Wisconsin lakes caused by increases in pCO2. Canadian Journal of Fisheries and Aquatic Sciences 44:1082–1088.

Lathrop, R. C., S. R. Carpenter, and L. G. Rudstam. 1996. Water clarity in Lake Mendota since 1900: responses to differing levels of nutrients and herbivory. Canadian Journal of Fisheries and Aquatic Sciences 53:2250–2261.

Livingstone, D., and G. H. M. Jaworski. 1980. The viability of akinetes of blue-green algae recovered from the sediments of Rostherne Mere. British Phycological Journal 15:357–364.

Livingstone, D. M., and M. T. Dokulil. 2001. Eighty years of spatially coherent Austrian lake surface temperatures and their relationship to regional air temperature and the North Atlantic Oscillation. Limnology and Oceanography 46:1220–1227.

Livingstone, D. M., and A. F. Lotter. 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with paleolimnological implications. Journal of Paleolimnology 19:181–198.

MacIntyre, S., and J. M. Melack. 1995. Vertical and horizontal transport in lakes: linking littoral, benthic, and pelagic habitats. Journal of the North American Benthological Society 14:599–615.

Magnuson, J. J., B. J. Benson, and T. K. Kratz. 1990. Temporal coherence in the limnology of a suite of lakes in Wisconsin, USA. Freshwater Biology 23:145–159.

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield region. Hydrological Processes 11:825–871.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, W. H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312.

Misson, B., and D. Latour. 2012. Influence of light, sediment mixing, temperature and duration of the benthic life phase on the benthic recruitment of *Microcystis*. Journal of Plankton Research 34:113–119.

Nichols, J. M., and D. G. Adams. 1982. Akinetes. Pages 387–412 *in* N. G. Carr and B. A. Whitton (editors). The biology of Cyanobacteria. University of California Press, Berkeley, California.

Nõges, T., I. Tonno, R. Laugaste, E. Loigu, and B. Skalalski. 2004. The impact of changes in nutrient loading on cyanobacterial dominance in Lake Peipsi (Estonia/Russia). Archiv für Hydrobiologie 160:261–279.

Nürnberg, G. K. 1998. Prediction of annual and seasonal phosphorus concentrations in stratified and polymictic lakes. Limnology and Oceanography 43:1544–1552.

Paerl, H. W. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. Limnology and Oceanography 33:823–847.

Paerl, H. W., and J. Huisman. 2008. Blooms like it hot. Science 320:57–58.

Paerl, H. W., and V. J. Paul. 2012. Climate change: links to global expansion of harmful cyanobacteria. Water Research 46:1349–1363.

Pettersson, K., E. Herlitz, and V. Istvánovics. 1993. The role of *Gloeotrichia echinulata* in the transfer of phosphorus from sediments to water in Lake Erken. Hydrobiologia 253:123–129.

Pierson, D. C., K. Pettersson, and V. Istvánovics. 1992. Temporal changes in biomass specific photosynthesis during the summer: regulation by environmental factors and the importance of phytoplankton succession. Hydrobiologia 243:119–135.

Read, J. S., D. P. Hamilton, I. D. Jones, K. Muraoka, L. A. Winslow, R. Kroiss, C. H. Wu, and E. Gaiser. 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. Environmental Modelling and Software 26: 1325–1336.

Reed-Andersen, T., S. R. Carpenter, and R. C. Lathrop. 2000. Phosphorus flow in a watershed-lake ecosystem. Ecosystems 3:561–573.

Rengefors, K., S. Gustafsson, and A. Stahl-Delbanco. 2004. Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from littoral and profundal sediments. Aquatic Microbial Ecology 36:213–226.

Rengefors, K., I. Karlsson, and L. A. Hansson. 1998. Algal cyst dormancy: a temporal escape from herbivory. Proceedings of the Royal Society of London Series B: Biological Sciences 265:1353–1358.

Reynolds, C. S. 2006. Ecology of phytoplankton. Cambridge University Press, New York.

Roelofs, T. D., and R. T. Oglesby. 1970. Ecological observations on planktonic cyanophyte *Gleotrichia* [*sic*] *echinulata*. Limnology and Oceanography 15:224–229.

Sinha, R., L. A. Pearson, T. W. Davis, M. A. Burford, P. T. Orr, and B. A. Neilan. 2012. Increased incidence of *Cylindrospermopsis raciborskii* in temperate zones. Is climate change responsible? Water Research 46:1408–1419.

Sonnichsen, J. D., J. Jacoby, and E. B. Welch. 1997. Response of cyanobacterial migration to alum treatment in Green Lake. Archiv für Hydrobiologie 140:373–392.

Soranno, P. A., S. R. Carpenter, and R. C. Lathrop. 1997. Internal phosphorus loading in Lake Mendota: response to external loads and weather. Canadian Journal of Fisheries and Aquatic Sciences 54:1883–1893.

Stahl-Delbanco, A., and L.-A. Hansson. 2002. Effects of bioturbation on recruitment of algal cells from the "seed bank" of lake sediments. Limnology and Oceanography 47:1836–1843.

Stefan, H. G., G. M. Horsch, and J. W. Barko. 1989. A model for the estimation of convective exchange in the littoral region of a shallow lake during cooling. Hydrobiologia 174:225–234.

Stewart, W. D., G. P. Fitzgerald, and R. H. Burris. 1967. *In situ* studies on N_2 fixation using the acetylene reduction technique. Proceedings of the National Academy of the Sciences of the United States of America 58:2071–2078.

Stumpf, R. P., T. T. Wynne, D. B. Baker, and G. L. Fahnenstiel. 2012. Interannual variability of cyanobacterial blooms in Lake Erie. PLoS ONE 7:e42444.

Trimbee, A. M., and G. P. Harris. 1984. Phytoplankton population dynamics of a small reservoir: use of sedimentation traps to quantify the loss of diatoms and recruitment of summer bloom-forming blue-green algae. Journal of Plankton Research 6:897–918.

Tymowski, R. G., and H. C. Duthie. 2000. Life strategy and phosphorus relations of the cyanobacterium *Gloeotrichia echinulata* in an oligotrophic Precambrian Shield lake. Archiv für Hydrobiologie 148:321–332.

Winter, J. G., A. M. DeSellas, R. Fletcher, L. Heintsch, A. Morley, L. Nakamoto, and K. Utsumi. 2011. Algal blooms in Ontario, Canada: increases in reports since 1994. Lake and Reservoir Management 27:107–114.

Wood, S. A., K. Jentzsch, A. Rueckert, D. P. Hamilton, and S. C. Cary. 2009. Hindcasting cyanobacterial communities in Lake Okaro with germination experiments and genetic analyses. FEMS Microbiology Ecology 67:252–260.

Wynne, T. T., R. P. Stumpf, M. C. Tomlinson, D. J. Schwab, G. Y. Watabayashi, and J. D. Christensen. 2011. Estimating cyanobacterial bloom transport by coupling remotely sensed imagery and a hydrodynamic model. Ecological Applications 21: 2709–2721.