








# “New” cyanobacterial blooms are not new: two centuries of lake production are related to ice cover and land use

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**Abstract.** Recent cyanobacterial blooms in otherwise unproductive lakes may be warning signs of impending eutrophication in lakes important for recreation and drinking water, but little is known of their historical precedence or mechanisms of regulation. Here, we examined long-term sedimentary records of both general and taxon-specific trophic proxies from seven lakes of varying productivity in the northeastern United States to investigate their relationship to historical in-lake, watershed, and climatic drivers of trophic status. Analysis of fossil pigments (carotenoids and chlorophylls) revealed variable patterns of past primary production across lakes over two centuries despite broadly similar changes in regional climate and land use. Sediment abundance of the cyanobacterium *Gloeotrichia*, a large, toxic, nitrogen-fixing taxon common in recent blooms in this region, revealed that this was not a new taxon in the phytoplankton communities but rather had been present for centuries. Histories of *Gloeotrichia* abundance differed strikingly across lakes and were not consistently associated with most other sediment proxies of trophic status. Changes in ice cover most often coincided with changes in fossil pigments, and changes in watershed land use were often related to changes in *Gloeotrichia* abundance, although no single climatic or land-use factor was associated with proxy changes across all seven lakes. The degree to which changes in lake sediment records co-occurred with changes in the timing of ice-out or agricultural land use was negatively correlated with the ratio of watershed area to lake area. Thus, both climate and land management appeared to play key roles in regulation of primary production in these lakes, although the manner in which these factors influenced lakes was mediated by catchment morphometry. Improved understanding of the past interactions between climate change, land use, landscape setting, and water quality underscores the complexity of mechanisms regulating lake and cyanobacterial production and highlights the necessity of considering these interactions—rather than searching for a singular mechanism—when evaluating the causes of ongoing changes in low-nutrient lakes.

**Key words:** agriculture; basin morphometry; cyanobacteria; eutrophication; *Gloeotrichia*; ice-out; land use; Maine; New Hampshire; paleoecology; sediment chemistry; watershed.

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## INTRODUCTION

Eutrophication and phytoplankton blooms are commonly identified as primary concerns in aquatic systems (Carpenter et al. 1998). In freshwater lakes, it is well documented that both nutrient loading from watersheds and warmer conditions favor phytoplankton growth and, particularly in eutrophic lakes, the development of extensive cyanobacterial blooms (Brookes and Carey 2011). These blooms negatively impact recreation, property values, drinking water, and the health of people, domesticated animals, and wildlife (Walker et al. 2008, Dodds et al. 2009, Carmichael and Boyer 2016, Mueller et al. 2016). Management of lakes for recreation or drinking water could be more focused if we better understand both potential lake sensitivity to trophic change and the proximal drivers of such trophic shifts (Cowing and Scott 1980).

However, because a series of nested factors operating at different scales may be responsible for trophic changes in lakes (Soranno et al. 1999, Leavitt et al. 2009, Soranno et al. 2015), separating these factors is challenging and remains a key management goal. Regionally, climate (Arnott et al. 2003, Rühland et al. 2003) and atmospheric deposition (Kopáček et al. 2015) can be responsible for changes in water quality while changes in land use, particularly agriculture (Bunting et al. 2007, Levine et al. 2012) and urban point sources of nutrients including wastewater (Levine et al. 2012, Moorhouse et al. 2018), may have major effects at the watershed scale. Regional coherence of change in species assemblages, phytoplankton abundance, or water quality is commonly interpreted as stemming from regional drivers such as climate (Magnuson 1990, Patone and Leavitt 2006, Moorhouse et al. 2018). However, even lakes in close proximity may exhibit asynchronous patterns of change in the abundance of phytoplankton species due to site-specific differences in chemistry or morphometry that control the abundance of cyanobacteria (Patoine and Leavitt 2006) or the ways climate impacts lakes (Moorhouse et al. 2018).

Multi-decadal data from paleoecological studies may help answer questions about the extent and timing of trophic-state change in lakes. Because various proxies of trophic state may respond differently to changes in influx of energy

and mass (Leavitt et al. 2009, Vogt et al. 2011), comparison of the historical changes in contrasting proxies can help identify the underlying mechanisms of change (e.g., Bunting et al. 2007). Similarly, application of these fossil analyses to the landscape-scale may be necessary to evaluate how diverse forcing mechanisms themselves vary over decadal-to-millennial and local-to-subcontinental scales (Tonn et al. 1990, Maheaux et al. 2016, Moorhouse et al. 2018). In particular, comparison of paleolimnological records across multiple sites can help untangle the influence of watershed- and lake-specific characteristics (Patone and Leavitt 2006, Taranu et al. 2015, Maheaux et al. 2016), as well as regional variation stemming from landscape position, climate, and anthropogenic forcing agents (Magnuson et al. 1990, Soranno et al. 1999, Arnott et al. 2003).

Low-nutrient lakes in the northeastern United States are among those with the highest water quality (USEPA 2017), but recent cyanobacterial blooms in these (Carey et al. 2012a) and similar low-nutrient lakes in Canada (Winter et al. 2011) have raised concerns about incipient eutrophication. Among the potential indicators of impending trophic-state change are blooms of *Gloeotrichia echinulata*, a large, colonial cyanobacterium, that have been increasingly reported in low-nutrient lakes of eastern North America (Winter et al. 2011, Carey et al. 2012a). This taxon is capable of fertilizing surface waters with both nitrogen (N) and (P); it fixes N<sub>2</sub> (Stewart 1967, Roelofs and Oglesby 1970, Carr and Whitton 1982) and can translocate substantial amounts of P from the sediment to the water column when it recruits from sediments (Barbiero and Welch 1992, Istvánovics et al. 1993). The P loading can account for up to two-thirds of internal P loading in eutrophic lakes (Barbiero and Welch 1992, Istvánovics et al. 1993) and amounts comparable to the external loading from smaller riverine tributaries entering an oligotrophic lake (Cottingham et al. 2018). Moreover, high densities of *Gloeotrichia* were associated with significantly higher N concentrations and increased abundance of other phytoplankton in laboratory and mesocosm experiments (Carey et al. 2014b). Thus, *Gloeotrichia* has the potential to not only act as an indicator of lake transition but also to catalyze eutrophication and state change (Cottingham et al. 2015).

Given considerable inter-annual variability in water-quality proxies (e.g., Secchi depth, TP, chlorophyll), and the reality that most water-quality monitoring began in the 1970s, we took a paleoecological approach to disentangle the regional and local mechanisms regulating cyanobacterial and lake production in the north-eastern 1850 over the past 200 yr. Specifically, we used diverse sedimentary, climatic, and land-use proxies to quantify how past lake production has changed in response to historical variation in climate and anthropogenic drivers across seven lakes in Maine and New Hampshire, USA. All sites currently experience blooms of *Gloeotrichia* or other cyanobacteria, yet differ in their current trophic state, watershed land use, and morphometry—all characteristics which we predicted would structure historical changes in lake production. We collected sediment cores covering the period from before European settlement began (c. 1750 CE) to present to investigate: (1) whether *Gloeotrichia* is a recent addition to these phytoplankton assemblages; (2) whether there is evidence that *Gloeotrichia* facilitates the growth of other phytoplankton; (3) the extent to which different proxies for trophic status indicate similar timing of changes in water quality; and (4) whether the timing of changes in these lakes co-occurs with climatic and watershed changes. We also investigated whether variation among lakes in the answers to these questions was related to watershed and lake morphometry.

## METHODS

### Study sites and field sampling

The seven lakes in this study were located across south-central Maine and New Hampshire, USA, and vary in size, morphometry, and recent trophic state (Fig. 1; Table 1). These lakes were selected to represent a gradient in current trophic state from oligotrophic to eutrophic; additionally, they have had modern water-quality data collected to support active management of the lake and watershed or to document recent blooms of *Gloeotrichia* or other cyanobacteria. All basins had shoreline development but largely forested watersheds, were important recreationally, and experienced blooms of one or more cyanobacterial taxa in the last decade (Carey et al. 2012a). Two lakes were sources for municipal domestic

water use (Table 1), and all lakes were personal water sources for some homeowners (Ewing, *personal observation*; Lake Stewards of Maine, *personal communication*). Sediment cores were collected through the ice at each lake in the winters between 2007 and 2012 (Appendix S1: Table S1). Cores were collected with a square-rod piston corer fitted with an 8.3 cm internal diameter polycarbonate tube attached to the core head. This apparatus collects a large volume of sample and insures that the sediment–water interface remains intact. All cores were collected at the deepest part of the lake except in instances where lake depth exceeded equipment capability and then cores were collected in water as deep as was feasible (Appendix S1: Table S1).

Cores were kept upright and in the dark during transport to the laboratory, where they were extruded vertically at 1-cm intervals. As each core was extruded, sediment from the center of the core was transferred to opaque containers and immediately frozen ( $-20^{\circ}\text{C}$ ) until shipped on dry ice to the University of Regina, Regina, Canada, for elemental composition, stable isotope ratio, and pigment analyses. Remaining sediment from each interval was bagged and refrigerated at  $4^{\circ}\text{C}$  until freeze-dried or subsampled for further analyses. Macrofossils encountered during extrusion were saved for identification and  $^{14}\text{C}$  radiocarbon dating.

### Laboratory analyses

Subsamples of each interval were analyzed for water content (percentage of dry mass), organic content (as mass loss-on-ignition at  $550^{\circ}\text{C}$  for 2 hr), elemental composition (percentage of dry mass as C or N), stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), past lake production (as fossil pigments), and cyanobacterial bloom intensity (the number of senescent colonies of *Gloeotrichia*). Water and organic contents were calculated from the mass loss of a subsample dried at  $105^{\circ}\text{C}$  for 12 h and at  $550^{\circ}\text{C}$  for 2 h, respectively.

Stable isotope ratios and elemental composition were determined on whole sediment samples following standard procedures as described in Savage et al. (2004). Samples were analyzed using a ThermoQuest Delta Plus XL isotope ratio mass spectrometer equipped with a continuous flow (Con Flo II) unit and an automated Carlo Erba elemental analyzer as an inlet device. Stable

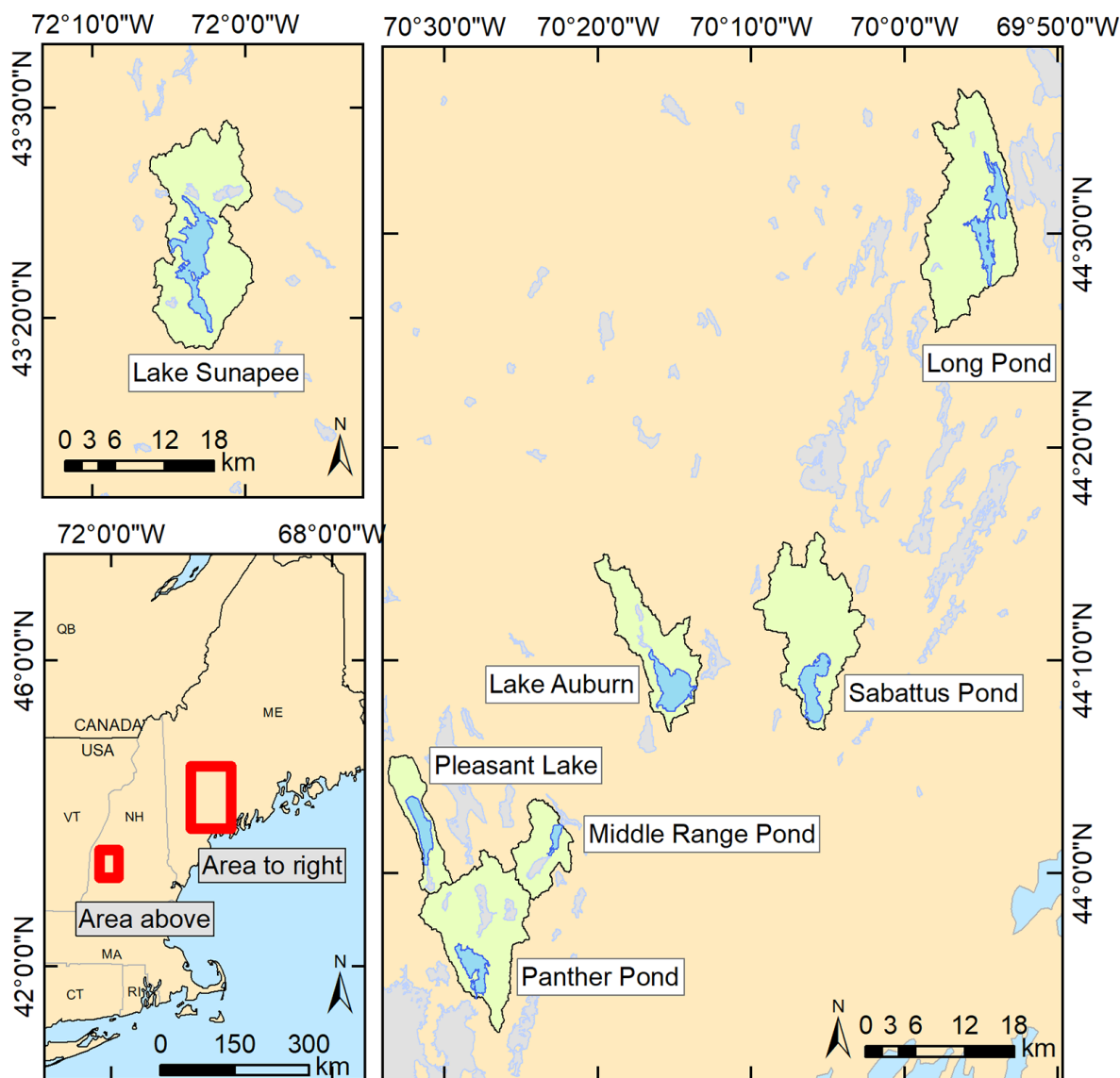


Fig. 1. Area of study in the northeastern United States. Sediment cores were collected from the lakes outlined and labeled. Watershed area of each lake is highlighted in green.

N ( $\delta^{15}\text{N}$ ) and C ( $\delta^{13}\text{C}$ ) isotopic composition were expressed in the conventional  $\delta$ -notation in units of per mil (‰) deviation from atmospheric  $\text{N}_2$  and an organic C standard which had been calibrated with authentic Vienna Pee Dee Belemnite. Sample reproducibility was within 0.25‰ and 0.10‰ for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively. Carbon isotope values were adjusted for changes in  $\delta^{13}\text{C}$  in the atmosphere (Suess effect), according to the equation in Schelske and Hodell (1995).

Pigments were used to reconstruct changes in abundance and composition of phototrophic assemblages of algae and cyanobacteria (Leavitt and Hodgson 2001). Pigments from aliquots of freeze-dried samples were extracted, and individual compounds were separated and quantified on filtered extracts via high-performance liquid chromatography (HPLC) using an Agilent 1100 series quaternary pump equipped with an autosampler, reversed phase column, and



Table 1. Characteristics of study lakes and their watersheds.

Characteristic	Auburn†	Long	Middle Range	Panther	Pleasant	Sabattus	Sunapee‡
Residence time (years)	4.8‡	0.31§	1.05¶	1.06#	5	0.66††	3.3‡‡
Lake area (km <sup>2</sup> )§§	9.25	10.3	1.52	5.74	5.39	7.94	16.7
Maximum lake depth (m)¶¶	35.9	31.6	19.1	21.3	18.7	4.91	33.7
Watershed area (km <sup>2</sup> )§§	41.2	94.7	25.1	72	20.2	74	104
Percent agricultural land in watershed##	11.2	5.39	6.27	3.5	4.32	16.1	4.47
Percent developed land in watershed##	6.14	2.29	4.99	4.13	5.27	6.9	6.34
Percent forested land in watershed##	73.3	86.7	79	81.5	80	65.6	77.6
Mean total phosphorus (µg/L)	12.33	8.1	6.93	7	4.75	52.83	5.17
Mean chlorophyll a (µg/L)	5.98	5.93	3.86	4.2	3.03	42.9	1.91

† Lake is used as a municipal drinking water supply.

‡ Dudley (2004).

§ MEDEP (2008).

¶ Public communication, Maine Department of Environmental Protection. ([https://www.lakesofmaine.org/data/2017\\_Lake\\_Reports/3762\\_1.html](https://www.lakesofmaine.org/data/2017_Lake_Reports/3762_1.html)).

# Public communication, Maine Department of Environmental Protection. ([https://www.lakesofmaine.org/data/2017\\_Lake\\_Reports/3694\\_1.html](https://www.lakesofmaine.org/data/2017_Lake_Reports/3694_1.html)).

|| MEDEP (2009).

†† MEDEP (2004).

‡‡ Public communication, New Hampshire Volunteer Lake Assessment Program Lake Sunapee 2012 Annual Report. ([https://www.des.nh.gov/organization/divisions/water/wmb/vlap/annual\\_reports/2012/lake-reports.htm](https://www.des.nh.gov/organization/divisions/water/wmb/vlap/annual_reports/2012/lake-reports.htm)).

§§ USGS National Hydrography Dataset (USGS 2015) HUC12 classification was used for Auburn, Sabattus, and Sunapee; for the other lakes, pour points were established at the outlet of the lake; and the Flow Direction, Flow Accumulation, and Watershed tools were used within ArcGIS 10, Spatial Analyst extension.

¶¶ Bathymetry layer produced in ArcGIS from ME DEP lake depth point data (MEDEP and MEDIFW 2011) and 1 arc-second DEM rasters (USGS 2017); high-resolution bathymetry files for Auburn, Panther, and Sunapee provided by local organizations.

## Maine data originated from the GIS layer for the Maine Land Cover Database (MELCD) (ME Office of GIS, 2006), and land cover for Sunapee's watershed originated from the New Hampshire Land Cover GIS layer (NHLC) (Complex Systems Research Center, 2002). All percentages are for the terrestrial portion of the watershed only.

|||| Maine lake data originate from the Volunteer Lake Monitoring Program, (public communication, Maine lakes water quality—total phosphorus (by date), <http://www.gulfofmaine.org/kb/2.0/record.html?recordid=9212> and Maine lakes water quality—chlorophyll (by date), <http://www.gulfofmaine.org/kb/2.0/record.html?recordid=9211>). These values are the mean of summer (Day of Year 173–267) integrated samples (whole epilimnion) 2006–2015. Sunapee data originate from the Lake Sunapee Protective Association's Long-term Monitoring Program. This value is the mean of summer (Day of Year 173–267) epilimnetic grab samples 2006–2015.

photodiode array (PDA) detector, following Bunting et al. (2016). The HPLC was calibrated using commercial pigment standards from DHI (Denmark). Analysis included chemically stable, taxonomically diagnostic carotenoids representing total algal production ( $\beta$ -carotene), cryptophytes (alloxanthin), colonial cyanobacteria (canthaxanthin), all cyanobacteria (echinenone), mainly diatoms (diatoxanthin), and the degradation products pheophytin *a* and *b*, as well as less-stable pigments indicating total algae and plants (chlorophyll *a*); dinoflagellates, diatoms, and chrysophytes (fucoxanthin); and, for Long Pond only, photosynthetic dinoflagellates, diatoms, chrysophytes, cryptophytes (diadinoxanthin) (Leavitt and Hodgson, 2001). Lutein (chlorophytes) and zeaxanthin (cyanobacteria) were incompletely separated on the HPLC system and are presented as a combined marker of bloom-forming phytoplankton.

Because of their large size and ability to withstand degradation (Forsell 1998), *Gloeotrichia* colonies in the sediments provide a useful proxy of their water column abundance. Hence, the abundance of *Gloeotrichia* through time was assessed by counting the number of senesced colonies in 5 cm<sup>3</sup> of sediment (dispersed with deionized water) under a Nikon SMZ 1500 stereoscope (Melville, New York, USA) at magnifications ranging from 20 $\times$  to 120 $\times$ . In general, senescent *Gloeotrichia* colonies appeared as intact colonies though with much reduced filament lengths relative to those sampled from the water column (Appendix S1: Fig. S1).

### Dating

Chronologies were developed primarily through <sup>210</sup>Pb-dating protocols. Wet sediment was freeze-dried and shipped to the St. Croix Watershed Research Lab to estimate <sup>210</sup>Pb and

daughter isotope activities. At 15–20 depth intervals in each core,  $^{210}\text{Pb}$  was measured through its grand-daughter product  $^{210}\text{Po}$ , with  $^{209}\text{Po}$  added as an internal yield tracer (modified from Eakins and Morrison 1978). Ages and sedimentation rates were determined using the constant rate of supply (CRS) calculation (Appleby 2001). Across lakes, the oldest intervals with sufficient radioactivity for dating ranged from 1809 to 1870 (Appendix S1: Table S1). Only two macrofossils suitable for radiocarbon dating were found over all cores; therefore, ages of the lower portion of all cores were approximated by linear extrapolation of the sedimentation rate from the bottom two  $^{210}\text{Pb}$  dates. Ages from the two radiocarbon-dated macrofossils confirmed lower sedimentation rates in sediments below the  $^{210}\text{Pb}$  interval, therefore suggesting that our extrapolations protocol likely underestimated the true age of sediments before c. 1840 CE. The calendar ages of the two macrofossils were established using Oxcal 4.2 (Appendix S1: Table S1).

#### *Comparative data on watershed characteristics, land-use history, and climate*

For all study lakes, quantitative estimates of watershed, land use, and bathymetric parameters were developed using a geographic information system (ArcGIS 10). Data layers from the USGS and New Hampshire and Maine governmental GIS offices were used for digital elevation models (USGS 2017), land cover (Complex Systems Research Center 2002, ME Office of GIS 2006), and basic depth soundings (MEDEP and MEDIFW 2011). These data were complemented with higher quality bathymetric maps made by local management groups for Sunapee (*personal communication* Lake Sunapee Protective Association), Auburn (*personal communication* Auburn Water District), and Panther lakes (*personal communication* Panther Pond Association). Watersheds from the USGS National Hydrography Dataset (USGS 2015) HUC12 classification were used for Auburn, Sabattus, and Sunapee, but for the other lakes, the outlet of the lake was substantially upstream of the base of the HUC12 watershed. For these lakes, pour points were established at the outlet of the lake and the Flow Direction, Flow Accumulation, and Watershed tools were used within ArcGIS 10, Spatial Analyst extension.

Land-use history within the watersheds was derived from public documents. We used changes in agricultural land use (a combination of area of land in farms and populations of sheep and dairy cows) and the size of the human population as proxies for the land-use changes most likely to impact water quality. Town settlement and incorporation dates for Maine towns were obtained from the Maine Encyclopedia (*public communication*, <http://maineencyclopedia.com>, e.g., <https://maineencyclopedia.com/auburn/>) and for New Hampshire from the New Hampshire Community Profiles database (*public communication*, <http://www.nh.gov/elmi/products/cp>). Human populations were estimated from town-level census data (United States Bureau of the Census 1790) from 1790 to 2010 (where town is a subdivision of a county rather than a specific urban site). Estimates of the areal extent of farmland, as well as the sizes of the sheep and cow populations, came from the county-level census of agriculture (United States Bureau of Census 1850–1992, Ahn et al. 2002, National Agricultural Statistics Service 1997–2012). Estimates of total farmland area designated as total land in farms, improved or unimproved, were available starting in 1850. For years with incomplete data on the proportion of the land that was improved (cropland plus pasture) or unimproved (farm-associated woodlands, brushland, rough or stony land, or swampland), missing values were calculated by difference or summation of subcategories. When an agricultural census value for sheep, cows, or land was completely missing (less than 10% of the time for each record), we interpolated between neighboring census values.

Estimates for human population size and agricultural activity in each watershed were calculated from GIS-derived data of the proportion of each town (population) or county (agricultural land, sheep, and cows) in each watershed. Given constraints of available data, we assumed that the proportion of a given town's population within a lake's watershed was equal to the proportion of the town that was in the watershed. The resulting population sizes (in integer values) for each proportion of town were then summed to estimate the total population within the watershed. The same process was used with the agricultural data at the county level.

We used the timing of ice-out as an index for historical changes in regional climate. This metric integrates variation in irradiance, air temperature, and local hydrology (Dröscher et al. 2009, Sharma et al. 2019). Further, reliable records of ice-out were available for this region beginning in the early 1800s. Compilations of these data through 2008 came from Hodgkins (2010), with more recent data supplemented by the State of Maine's Bureau of Parks and Lands historical ice-out data (*public communication*, [https://www.maine.gov/dacf/parks/water\\_activities/boating/ice\\_out\\_dates.shtml](https://www.maine.gov/dacf/parks/water_activities/boating/ice_out_dates.shtml)), the Auburn Water District/Lewiston Water Division (*personal communication*), and the Town Clerk's office in Sunapee, NH (*public communication*, Lake Sunapee Ice Out Dates 2019, <https://www.town.sunapee.nh.us/town-clerk-tax-collector>). Continuous annual data were available for Sunapee; however, many of the other lakes had incomplete ice-out records. The analyses required a continuous record, and year-to-year variation is large, making interpolation inappropriate. Hence, we used the Sunapee record on its own and assigned each of the Maine study lakes to one of three regional groupings that included neighboring lakes with more continuous ice-out records (Appendix S1: Fig. S2). Annual ice-out values for each regional group of lakes were averaged to obtain continuous ice-out records. Prior analysis of these ice-out records has revealed significant temporal coherence of ice out among lakes (Hodgkins et al. 2002, Patterson and Swindles 2015). The Spearman rank correlation between the regional-average record used here and the observed ice-out record at each lake was 0.97 or greater, except at Panther Pond where only six years of data were available and the correlation was 0.89.

#### Data analysis overview

Most analytical techniques for comparison of temporal data across metrics either require that all datasets have the same time points across all metrics (e.g., temporal coherence among systems; Magnuson et al. 1990, Rusak et al. 1999) or are suitable only for one type of response variable at a time (e.g., generalized additive models could be used for the pigments or stable isotopes, but not both in the same model; Simpson 2018). However, most of our proxies for trophic state contained multiple metrics (e.g., different

pigments) and our questions necessitated examination of their collective behavior and relationship to drivers that also could contain multiple metrics (i.e., land-use associated metrics). Furthermore, the data from sediment trophic proxies, watershed land-use and human population, and ice-out were on different time steps.

To address these issues, we performed a four-step analysis. First, we examined the synchrony of changes among individual metrics of trophic state within each lake core via a series of pairwise comparisons using Spearman rank correlation. Second, we quantified the timing of transitions in (a) groups of trophic-state proxies that might be expected to behave similarly (i.e., pigments, C, N, and *Gloeotrichia*) and (b) potential watershed-level drivers of change (i.e., human population, agricultural land use, and ice-out date) using stratigraphically constrained cluster analysis (CONISS; Grimm 1987). Third, we compared the timing of the transitions identified in step two, specifically (a) among trophic-state proxies and (b) between trophic-state proxies and external drivers of change. Fourth, we evaluated the relationship between catchment morphometry and the percentage of transitions that were coincident between trophic-state proxies and external drivers of change. Details of all steps are provided below.

This analytical approach accounted for the temporal autocorrelation of paleoecological time series, as well as variable sediment accumulation rates and temporal resolution in both sedimentary and driver variables. Prior to analysis, all sediment core records were truncated at c. 1770, the age of the youngest core, a date that also corresponds to the beginning of European settlement in this region. This date preceded the start of the reliable  $^{210}\text{Pb}$  record by a few decades, but all zone breaks fell within the period of the  $^{210}\text{Pb}$  dating; the matching of in-lake events with potential drivers was as good as sedimentation rates allowed.

Four steps of analyses.—

*Correlations.*—To examine the temporal coherence among individual metrics within each core (e.g.,  $\%C$ ,  $\delta^{15}N$ , individual pigments, *Gloeotrichia*), we used Spearman rank correlations and a threshold for importance of  $>0.6$  or  $<-0.6$ . Results were not qualitatively different when thresholds were set at either  $0.5(-0.5)$  or  $0.7$

(−0.7), as 68% of correlations presented below were >0.7 or <−0.7. It was not possible to bring the complete sediment records into alignment with the driver data by combining multiple stratigraphic intervals (Patoine and Leavitt 2006) or working with confidence intervals around  $^{210}\text{Pb}$  dates (Das et al. 2008), so this step focused only on the metrics from the cores (e.g., %C,  $\delta^{15}\text{N}$ , select pigments).

*Stratigraphically constrained cluster analyses.*—We used the standard stratigraphically constrained cluster analysis (CONISS) of Grimm (1987) to identify the timing of transitions between periods of relative stasis in which the proxy records had similar characteristics (i.e., zones). This technique identifies groups of samples that are similar to each other in multidimensional space. Samples are tested for membership in clusters with the requirement that they join only those that are temporally adjacent (Grimm 1987). The number of significant zone breaks (boundaries between high-level clusters) for each analysis was determined from a broken-stick model (Birks 2012). Each of the breaks between zones is a statistical description of a significant transition in the system, as determined by the group of metrics (e.g., individual pigments) that make up the proxy (e.g., pigments) in a given cluster analysis, rather than a determination of a specific trophic state.

Zones were established for each lake individually and included related metrics as a part of each trophic-state proxy and potential watershed-level driver. The C proxy included the percentage of C and  $\delta^{13}\text{C}$  value of that sedimentary interval. For the N proxy, we included the percentage of N and  $\delta^{15}\text{N}$  value. For the pigment proxy, we used five chemically stable biomarkers that represent a diversity of phytoplankton taxonomic groups: alloxanthin (cryptophytes), canthaxanthin (colonial cyanobacteria), lutein + zeaxanthin (chlorophytes and cyanobacteria), diatoxanthin (diatoms), and echinenone (total cyanobacteria) following Leavitt and Hodgson (2001). The agricultural land-use proxy included the areal extent of improved and unimproved land and the population density of sheep and dairy cow populations within the watershed. A few cluster analyses were based on one parameter alone: *Gloeotrichia* was estimated as the number of senesced colonies (akinetes) per gram of dry sediment while the human

population was estimated as the number of people in the watershed, and ice-out date was the calendar day of year (DOY) when the lake became ice-free, where 1 January is DOY 1.

Prior to analysis, each proxy time series was Z-transformed to account for the considerable differences in absolute magnitude among metrics. These standardized values were used in a Euclidean distance model to find the timing of transitions identified as significant zone breaks. We implemented this procedure in R with the *rioja* package (Juggins 2015).

*Comparison of proxy zone breaks.*—After we determined the timing of transitions for each proxy using CONISS, we made pairwise comparisons among proxies across all of the zone breaks in each lake (Appendix S1: Fig. S3). For comparisons between proxy pairs (e.g., pigments and *Gloeotrichia*), zone breaks were considered contemporaneous (a match) when the zone break occurred in the same year for each trophic-state proxy. For comparison of trophic-state proxies and potential external drivers, zone breaks were considered contemporaneous when the interval containing the break in an external driver overlapped with the date range for the sediment interval containing a zone break for the trophic-state proxy. To compare the frequency of zone-break matches among the different proxy groups, we expressed each set of comparisons (e.g., *Gloeotrichia*-to-pigments or pigments-to-ice-out) as a percentage of the observed number of zone-break matches relative to the number of possible matches between that proxy pair.

These comparisons retained the zone boundaries defined using CONISS, but allowed for differences in resolution of individual time series (e.g., annual ice-out vs. decadal population) as well as compression of sediments with age that changes the number of years represented in each centimeter of sediment. Given the differences in sedimentation rate both with time and across lakes, these analyses did not consider the extent of lags between changes in watershed and climatic drivers and sedimentary records of trophic state. Additionally, no comparison of timing of change across lakes was made.

*Relationship to watershed and bathymetric characteristics.*—Finally, we examined whether the degree of similarity in zone breaks across proxies was related to watershed and bathymetric



characteristics. Specifically, we calculated the Spearman rank correlation between the percentage of zone-break matches in pairs of paleorecords (e.g., percentage of matching zone breaks between pigments and ice-out date) and watershed area, lake area, and lake volume as well as ratios of metrics such as watershed-to-lake area (WA:LA) and watershed area-to-lake volume (WA:LV) that are indicative of the relative influence of watershed inputs to the lake (Klug et al. 2012, Hayes and Vanni 2018).

## RESULTS

### *Historical change in metrics of lake trophic status*

All lakes showed evidence of change in primary production over the historical record. The magnitude of change in these records, however, varied both among lakes and metrics (Figs. 2–4). Most often, the generalized biogeochemical signals, including the elemental percentages and isotopic values for C and N, were the least temporally variable (Fig. 2), while the pigment concentrations and abundance of senesced *Gloeotrichia* colonies exhibited greater variation through time (Figs. 3, 4).

Historical changes in C and N signatures (as percentage of dry mass and isotopic values) were largely monotonic but did not show the same patterns across lakes (Fig. 2). Within the individual lake records, C and N percentages varied by 2–5% and <1%, respectively, and generally increased through time toward present-day values. Changes in isotopic values ranged from 1.5‰ to 2‰ for  $\delta^{13}\text{C}$  and 1–3‰ for  $\delta^{15}\text{N}$ . Values of  $\delta^{13}\text{C}$  decreased in most lakes, although they were relatively constant at Panther Pond and increased at Sabattus Pond. Changes in sedimentary  $\delta^{15}\text{N}$  were most often positive and were largest in eutrophic Sabattus Pond, although three sites showed little change (oligotrophic Pleasant and mesotrophic Long and Panther) and one showed a recent depletion after multiple decades of enrichment (mesotrophic Auburn). The stratigraphically constrained cluster (CONISS) analysis identified between one and three zone breaks for both C and N in all lakes, and in all but two lakes (Long and Panther), at least one of the breaks was contemporaneous in the C and N records.

In five of seven lakes (exceptions were Panther and Sunapee), there were recent increases

in pigment concentrations that were substantial enough to be identified with a significant zone break in CONISS analysis (Fig. 3). These increases appeared to be a function of increased primary production (as indicated by stable pigments), but may also reflect changes in the preservation environment (as indicated by chlorophyll *a*:pheophytin *a* ratios) at Auburn, Pleasant, and Sabattus (Appendix S2: Fig. S1). The number of zone breaks identified by the stratigraphically constrained cluster analysis varied from one to five across study lakes.

*Gloeotrichia* colonies were found historically in all lakes, although the abundance of colonies through time varied greatly across lakes and followed four general patterns (Fig. 4). First, there was a recent (post-1950) monotonic increase in fossil abundance (Long Pond). Second, there was elevated abundance of *Gloeotrichia* during or immediately following the time of greatest European land clearance between 1780 and 1860 CE (Auburn, Middle Range, Pleasant). Third, there was a high abundance of this colonial cyanobacterium long before European land clearance expanded c. 1750 CE (Sunapee and Panther). Finally, there was one lake with few *Gloeotrichia* preserved in the sediment during the past 1000 yr, despite current large populations of other cyanobacteria (Sabattus Pond; Appendix S1: Table S1 for  $^{14}\text{C}$  dating). All sedimentary records had between one and three breaks in the *Gloeotrichia* record except Sabattus Pond, where the rarity of *Gloeotrichia* led to no significant breaks.

### *Relationships among metrics of trophic status and identification of zone breaks*

Within-lake correlations for the trophic metrics were strongest between %C and %N and among the pigments, but were variable in terms of both strength and direction for other pairwise comparisons (Fig. 5). Percentages of C and N were strongly positively correlated in four lakes, whereas elemental percentages were rarely correlated with changes in  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$ . Pigment abundances were often positively correlated within individual cores, although the diatom pigment diatoxanthin did not regularly co-vary with other pigments. Pigments were positively correlated with %C,  $\delta^{13}\text{C}$ , %N, and  $\delta^{15}\text{N}$  values

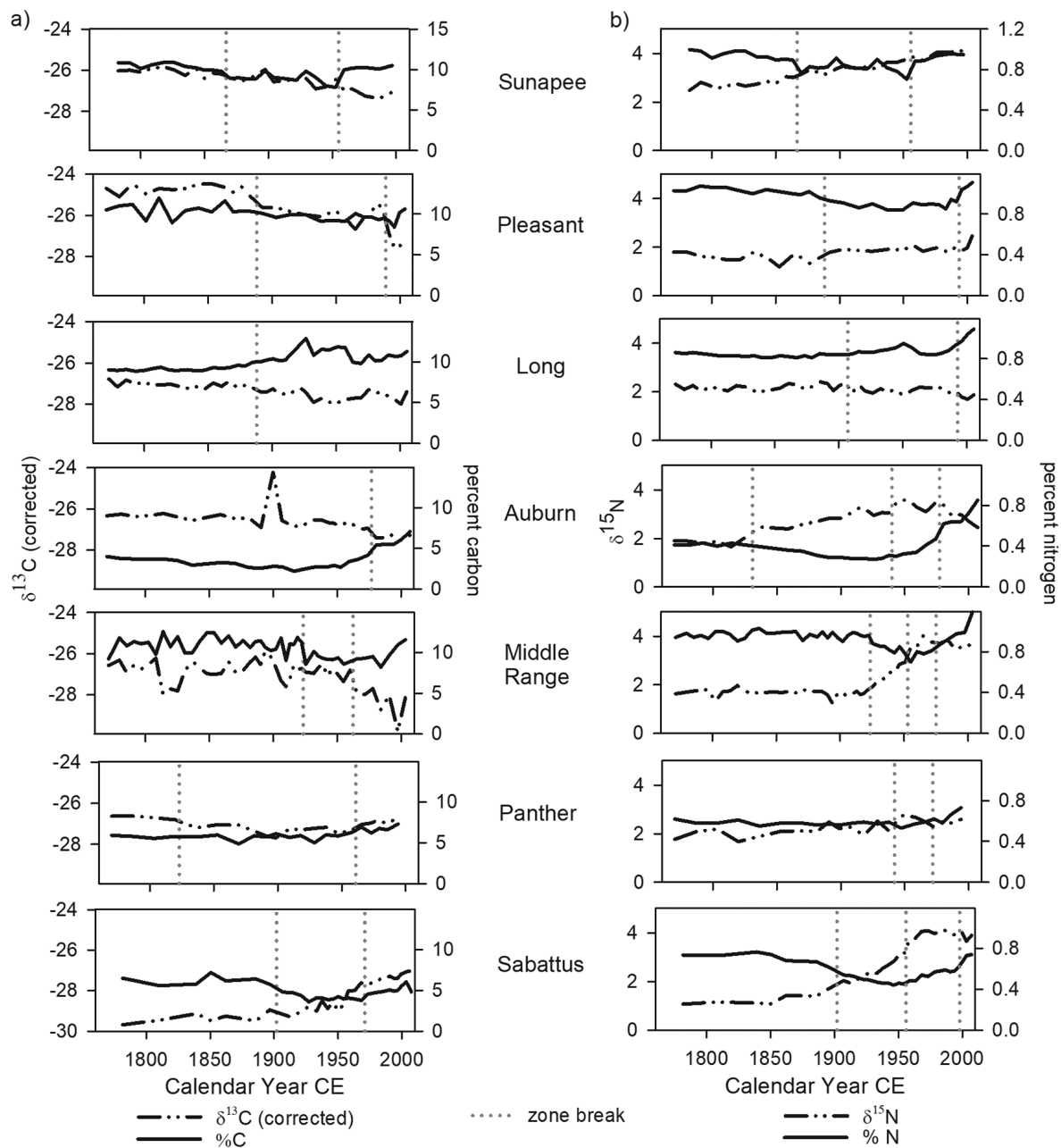


Fig. 2. Records of carbon (C) and nitrogen (N) across study lakes in Maine and New Hampshire, USA. Vertical dotted lines designate shifts in the record identified by statistically significant zone breaks within stratigraphically constrained cluster analysis; see text for details. Lakes increase in current trophic state from top to bottom (Sunapee and Pleasant are oligotrophic, Sabattus is eutrophic, and the others are mesotrophic). (a) Percentage of C in bulk sediment and  $\delta^{13}\text{C}$  (corrected for the Suess effect). (b) Percentage of N in bulk sediment and  $\delta^{15}\text{N}$ . Records reveal small changes in C and N percentages and isotopic values over the study period, with most dramatic changes happening in the last 50 yr. Patterns vary asynchronously and with different patterns across sites.

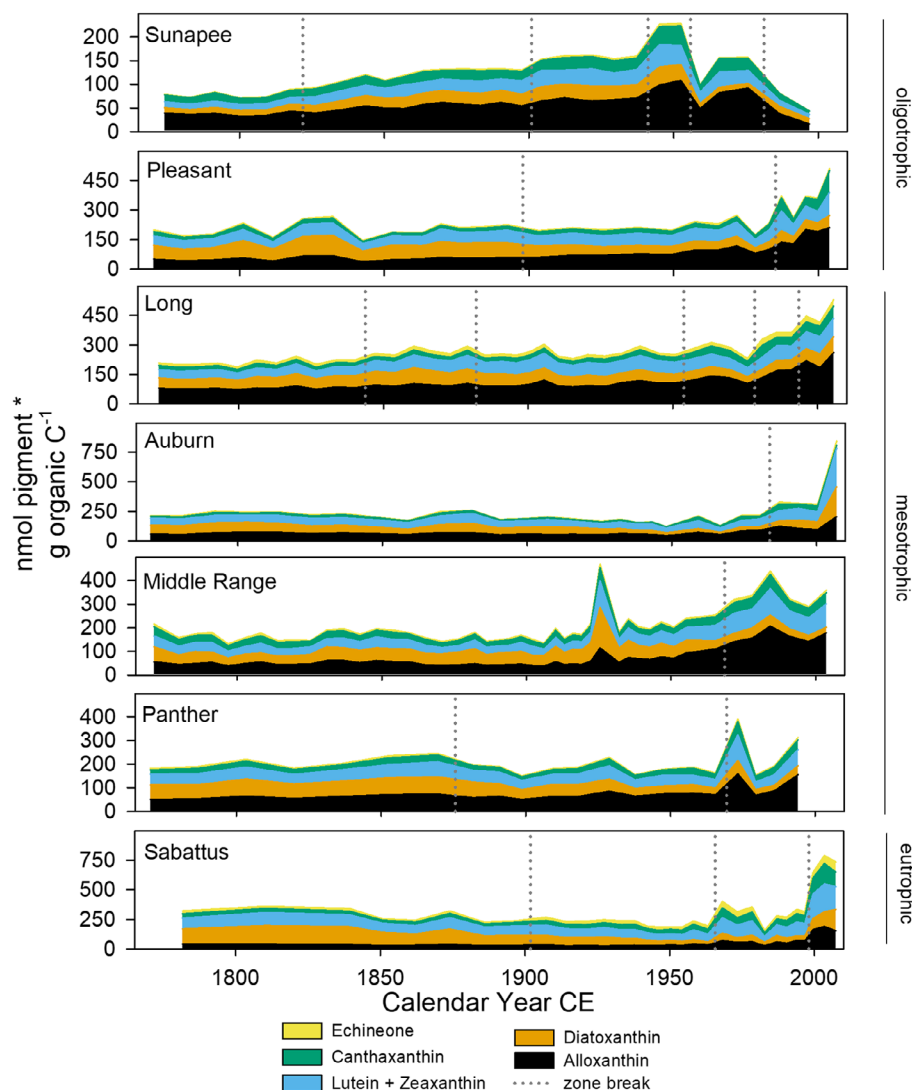


Fig. 3. Records of common stable biomarker pigments across study lakes in Maine and New Hampshire, USA; note lake-specific y-axes. Vertical dotted lines designate shifts in the assemblage identified as statistically significant zone breaks within stratigraphically constrained cluster analysis; see text for details. Pigments include alloxanthin (cryptophytes), canthaxanthin (colonial cyanobacteria), diatoxanthin (mainly diatoms), echinenone (cyanobacteria), and lutein + zeaxanthin (incompletely separated in analysis so combined as a measure of bloom-forming phytoplankton including chlorophytes and cyanobacteria). Details about taxonomic origin come from Leavitt and Hodgson (2001). Pigments suggest increased productivity recently at many, but not all, lakes. Differences among records in the pigments that have changed over time suggest that the taxa that have responded most over time vary.

in the most eutrophic lake (Sabattus) and also in some of the mesotrophic lakes (Auburn, Long, and Middle Range). At mesotrophic Long Pond, the abundance of *Gloeotrichia* was strongly and positively correlated with all pigments except

diatoxanthin. In contrast, only diatoxanthin was correlated with *Gloeotrichia* within the core from mesotrophic Lake Auburn.

The four in-lake proxies of trophic status (C, N, pigments, *Gloeotrichia*) provided slightly

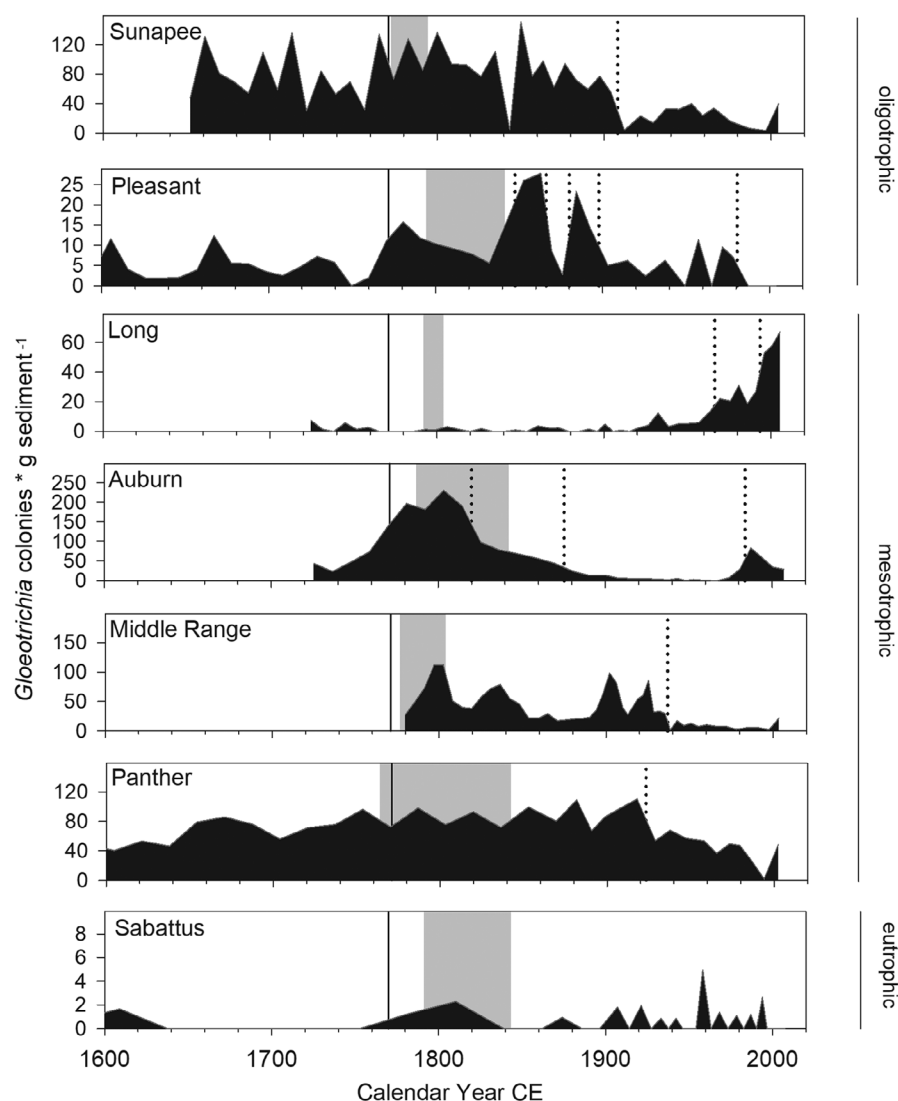


Fig. 4. Complete records of *Gloeotrichia* abundance across study lakes in Maine and New Hampshire, USA; note the lake-specific y-axes. Vertical dotted lines designate shifts in abundance identified as statistically significant zone breaks within stratigraphically constrained cluster analysis; see text for details. Records were truncated at c. 1770 CE (heavy vertical line), the length of the shortest record, for quantitative comparisons. Current trophic state is noted to the right of the lake panels. Gray shading within the lake panels indicates the time range of incorporation of the various towns within each watershed (Sunapee 1772–1794, Pleasant 1796–1841, Long 1792–1804, Auburn 1786–1842, Middle Range 1774–1803, Panther 1762–1841, Sabattus 1788–1840). Forest clearance for homesteading likely began a decade or more before town incorporation (Barton et al. 2012). Logging in the Lake Auburn watershed likely began earlier yet (c. 1750), because of its hydrologic connection to the Androscoggin River, a major route for running timber during early European wood extraction (Barton et al. 2012).

different estimates of when significant ecosystem transitions occurred, as identified with zone breaks in the CONISS analysis (Figs. 2–4). All detected zone breaks were after 1800, in the

range of the  $^{210}\text{Pb}$  dating on the cores. For C, N, and pigments, nearly all records showed transitions after ca. 1950 CE. Zone breaks in the general biogeochemical proxies C and N co-occurred



in approximately half of the instances, whereas approximately a quarter of the transitions identified by pigments and *Gloeotrichia* were concurrent (Appendix S2: Fig. S2). Beyond this, transitions in the group of proxies within each lake appeared to occur independently as indicated by proxy zone breaks that were generally offset in time (Figs. 2–4).

#### *External drivers of trophic change*

Records of human population size, agricultural land use and livestock density, and ice-out showed directional trends over the period of record in most of the watersheds (Appendix S2: Figs. S3–S5). The records were quite similar across watersheds, but varied with the intensity of urban and agricultural change in each watershed.

In general, townships in the watersheds were established by European colonists in the late 1700s or early 1800s. Human population increased slowly until c. 1850 in most watersheds. In all watersheds except Lake Auburn, the population then either remained steady or decreased slightly until c. 1950, when there were dramatic increases. Lake Auburn is near the major industrial mill towns of Lewiston and Auburn, where human population increased rapidly during 1850–1950 before a plateau after 1950 when the mills shut down (Appendix S2: Fig. S3). Population records in most lakes had a single zone break in the 1970s or 1980s, though Lake Auburn had two—both earlier in time—and Long Lake had none.

The area of land in agriculture and the density of sheep and dairy cows were generally highest between 1850 and 1910, but declined thereafter (Appendix S2: Fig. S4). The stratigraphically constrained cluster analysis identified at least two zone breaks in all three records. One break was in the late 1800s, when sheep populations and till agriculture declined. The other consistent zone break was around 1950, when there was a major decrease in agricultural land use. Zone breaks occurred at slightly different times in each watershed, as a result of differences in rates of agricultural decline (Appendix S2: Fig. S4).

The ice-out records had substantial inter-annual variability, but the overall trend was toward earlier ice-out over time, with a change of nearly three weeks over the period of record (Appendix S2: Fig. S5). The stratigraphically

constrained cluster analysis identified this decline as having three zones in the Maine records and two at Sunapee. In all systems, a break occurred in the early 1980s, and in the Maine records, an earlier break was identified at the start of the 20th century. In Lake Auburn, where there is a 65-yr record of ice duration, there was both earlier ice-out and a reduced duration of ice cover (Appendix S2: Fig. S5b).

#### *Relationships between in-lake changes and potential external drivers of change in trophic state*

Temporal patterns of the four lake trophic proxies—C, N, pigments, and *Gloeotrichia*—differed from patterns in timing of ice-out, watershed population, and agricultural land use—the three external drivers investigated herein (Fig. 6). Nevertheless, synchronous changes in these records, assessed as the match in the timing of zone breaks between lake and watershed records, occurred in at least one lake for each of the pairs of potential watershed drivers and in-lake proxies (Fig. 6). Coherence among changes in proxies tended to be greater if we provided a more generous window for matching zone breaks (Appendix S2: Fig. S6). For human population in the watershed, usually only one zone break was identified, so the matches in zone breaks between population and the in-lake proxies tended to be either 100% or 0%, with matches most often occurring in the pigment and N records. Zone breaks in the agricultural record were most commonly associated with zone breaks in C, N, and *Gloeotrichia* records. However, in the two oligotrophic lakes, all sediment proxies had at least some zone-break matches with those in agricultural land use. Zone breaks in the ice-out record were most commonly contemporaneous with breaks in the pigment record and, secondarily, with those in the N record. At mesotrophic Lake Auburn and eutrophic Sabattus Pond, zone breaks in the ice-out record had at least one match for all available trophic proxies.

#### *Relationship of in-lake changes to morphometry*

The ratio of watershed area to lake area (WA:LA) was the basin characteristic that best explained the percentage of zone-break matches between internal metrics of lake trophic status

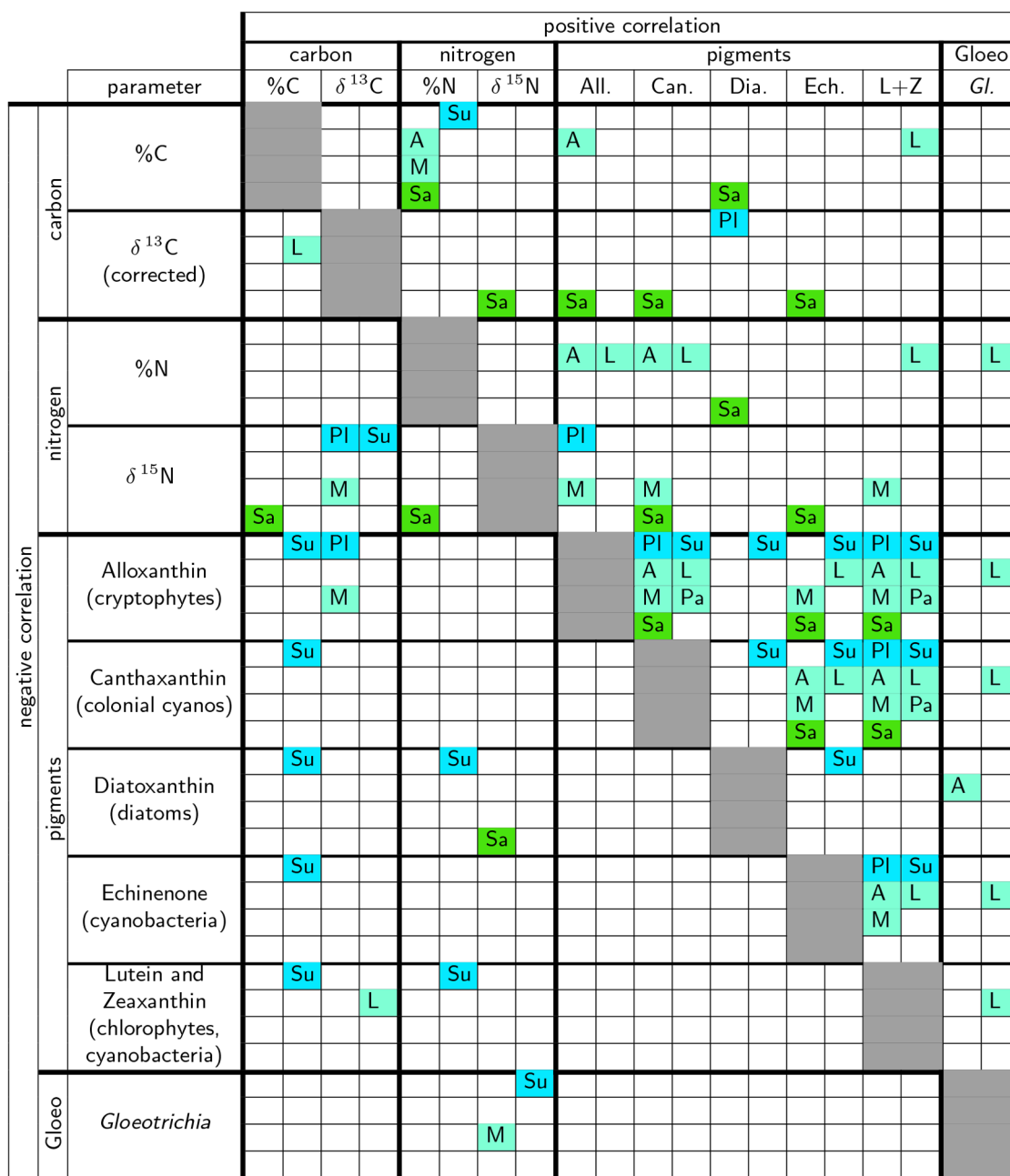


Fig. 5. Pairwise Spearman rank correlations among paleoecological metrics in study lakes in Maine and New Hampshire, USA. Colored cells indicate lakes for which either a positive ( $r_s > 0.6$ , above the diagonal) or negative ( $r_s < -0.6$ , below the diagonal) association existed between the two metrics. Weighted black horizontal and vertical lines separate the groups of metrics used in the stratigraphically constrained cluster analyses. Colors indicate current trophic state of the lake, oligotrophic (blue), mesotrophic (blue-green), or eutrophic (dark green), and letters are abbreviations for lake names (A, Auburn; L, Long; M, Middle Range; Pa, Panther; PI, Pleasant; Sa, Sabattus; Su, Sunapee). Pigment concentrations were commonly positively associated with each other and also with C and N metrics in the eutrophic lake and some mesotrophic lakes. Negative correlations among metrics were generally less common except between pigments and C and N metrics in oligotrophic Lake Sunapee.

potential driver	trophic proxy	oligotrophic		mesotrophic				eutrophic
		Pleasant	Sunapee	Auburn	Long	Middle Range	Panther	Sabattus
population	carbon				n/a			
population	nitrogen				n/a			
population	pigments				n/a			
population	<i>Gloeotrichia</i>				n/a			n/a
agriculture	carbon							
agriculture	nitrogen							
agriculture	pigments							
agriculture	<i>Gloeotrichia</i>							n/a
ice	carbon							
ice	nitrogen							
ice	pigments							
ice	<i>Gloeotrichia</i>							n/a

Key	
	100% zone-break matches
	67% zone-break matches
	50% zone-break matches
	0% zone-break matches
n/a	No zone breaks in one of the series, no comparison possible

Fig. 6. Percentage of zone breaks—points of transition in the record as identified by stratigraphically constrained cluster analysis—occurring in records of each of the driving factors (human population, agricultural land use, and ice-out) that match with zone breaks from the in-lake metrics of trophic state (carbon, nitrogen, pigments, and *Gloeotrichia*). Each cell indicates the percentage of zone breaks that matched between the potential external driver and the in-lake trophic proxy (Appendix S1: Fig. S3) for each of the Maine and New Hampshire, USA, study lakes.

and potential external drivers of change (Fig. 7). In particular, there was a strong negative relationship between the degree of coherence in zone transitions between pigment and ice-out records and the WA:LA ratio ( $r_s = -0.94$ ). Lakes with smaller WA:LA ratios typically exhibited concordant timing of changes in ice-out date and changes in the pigment record. In contrast, lakes with relatively large WA:LA ratios had no common zone breaks. For the *Gloeotrichia* record, where agricultural land use was the most common external driver to have zone-break matches, there was a moderate negative association between the WA:LA ratio and the zone-break matches between the in-lake proxy and external driver ( $r_s = -0.68$ ); lakes

with the smallest WA:LA ratio typically had 50% or 100% zone-break matches between agricultural and *Gloeotrichia* records, while the lakes with the largest WA:LA ratio had no matches. These patterns were qualitatively similar when we allowed a more generous window for zone-break matching, and, for the concordance of *Gloeotrichia* changes with those in agricultural records, the relationship was stronger ( $r_s = -0.84$ ), particularly for currently oligotrophic lakes (Appendix S2: Fig. S7).

## DISCUSSION

At the broadest scale, all seven lakes showed changes in trophic state and external drivers

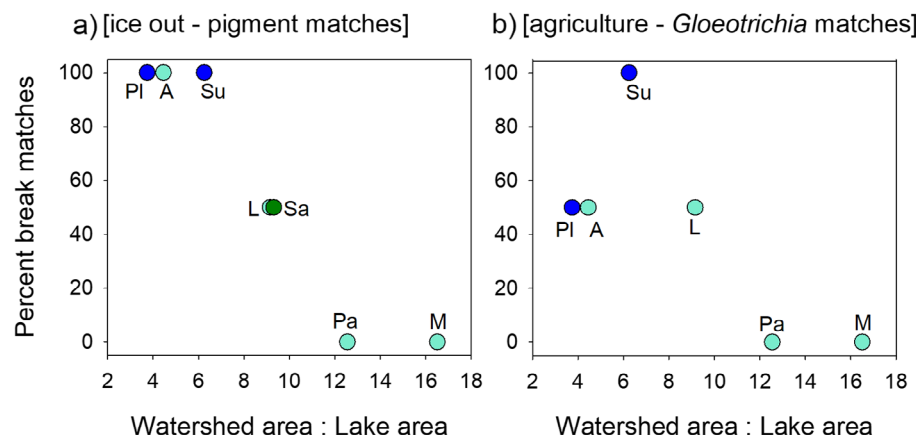


Fig. 7. Association of change in external drivers and measures of trophic state in each lake's paleoecological record and the morphometry of each lake basin (ratio of the watershed area to lake area, WA:LA). Letters are abbreviations for lake names (A, Auburn; L, Long; M, Middle Range; Pa, Panther; PI, Pleasant; Sa, Sabattus; Su, Sunapee), and colors indicate current trophic status (blue, oligotrophic; light green, mesotrophic; dark green, eutrophic). (a) The percentage of zone breaks in the ice-out record that aligns with zone breaks in the pigment record for each lake declines with increased WA:LA ( $r_s = -0.94$ ). (b) The percentage of zone breaks in the agricultural land-use record that match with zone breaks in the *Gloeotrichia* record is lowest at high WA:LA ( $r_s = -0.68$ ). In the lakes with the largest WA:LA, zone breaks in the measure of trophic state did not co-occur with changes in either the ice-out or agricultural records.

consistent with some degree of cultural eutrophication (Figs. 2–4 and Appendix S2: Figs. S3–S5). In the period since European land clearance began to expand c. 1750 CE, all lakes experienced climate change in the form of earlier ice-out, agricultural expansion and contraction, and a continuous increase in human population in the watershed (Appendix S2: Figs. S3–S5). While any of these changes could facilitate lake eutrophication, the timing and extent of inferred change in trophic state differed across lakes and among the paleoecological metrics (Figs. 2–4). Nevertheless, high concentrations of the cyanobacterium *Gloeotrichia* in sediment records consistently revealed that the recently reported blooms of *Gloeotrichia* (Winter et al. 2011, Carey et al. 2012a) are likely not a new phenomenon (Fig. 4). Among-lake variation in the correlations among fossil markers of trophic state and their relationship to external drivers and lake morphometry (Figs. 5–7) underscore the importance of considering how the effects of climate or watershed change may be influenced by watershed-specific characteristics (Blenckner 2005, Leavitt et al. 2009).

#### Within-lake indicators of trophic change

*Carbon, nitrogen, and pigments.*—While this paleoecological study did not reconstruct numerical values for metrics like Secchi depth, nutrients, or water column chlorophyll concentration that are typically used to specify trophic state (e.g., Carlson 1977), all seven lakes had sedimentary evidence of eutrophication. The increases in many lakes in sedimentary %C and %N and concentrations of pigments from green algae, cryptophytes, and cyanobacteria (Figs. 2, 3)—taxa that tend to increase with eutrophication (e.g., Cottingham et al. 1998)—were the most consistent evidence of lake eutrophication. Stratigraphically constrained cluster analyses identified these changes as having occurred primarily in the last 30–50 yr, consistent with many studies highlighting the last half-century as a period of intense cultural acceleration of biogeochemical cycles (e.g., Taranu et al. 2015). The observation of eutrophication itself was not surprising, given the profound landscape modifications that have occurred since European settlement began c. 1750 CE and the continuing and substantial climate change occurring since at least the mid-



1800s. However, variation in timing of changes in each proxy also suggested that assessment of the degree of past eutrophication will depend on the proxy used and will be most easily interpreted in a multi-proxy framework (cf. Bunting et al. 2016).

The dissimilarities in timing of eutrophication derived from the different proxies are consistent both with studies that focus on the role particular nutrients or assemblages play in a lake, as well as prior assessments of the utility of various taxa as indicators. The stronger associations among C, N, and pigments, rather than between these metrics and *Gloeotrichia* (Fig. 5), are similar to findings in modern studies of temporal coherence in which aggregated metrics tend to be more synchronous than more taxonomically resolved, species-level parameters (e.g., Vogt et al. 2011, Angeler and Johnson 2012). This pattern might logically result from the co-occurrence of C and N in bulk organic matter and the importance of N for phytoplankton production. Further, the strong correlations between sediment N parameters and the abundance of pigments from cryptophyte and Nostocales cyanobacteria in a number of lakes (Fig. 5) reinforce the finding that these taxa may be particularly good indicators of increased nutrient availability (Cottingham et al. 1998).

*Gloeotrichia*.—Patterns of *Gloeotrichia* fossil abundance varied tremendously through time and among lakes but clearly demonstrated that this taxon is not new to these ecosystems (Fig. 4). Unexpectedly, *Gloeotrichia* was historically common in lakes of differing current trophic state (e.g., both oligotrophic Sunapee and mesotrophic Panther) and yet rare in other ecosystems (e.g., oligotrophic Pleasant and mesotrophic Long Pond). Among the study lakes, only eutrophic Sabattus Pond exhibited little *Gloeotrichia* in past centuries (Fig. 4), perhaps because *Gloeotrichia*'s need for light for germination (e.g., Karlsson-Elfgren et al. 2004) cannot be met in turbid, eutrophic ecosystems like Sabattus Pond. Given the long-term abundances of *Gloeotrichia* in most of these sediment records, we infer that recently observed increases of *Gloeotrichia* are not due to their recent arrival in these systems.

Although reports of the apparent expansion of *Gloeotrichia* in low-nutrient lakes (Winter et al. 2011, Carey et al. 2012a) led us to expect

pronounced increases in its abundance in the most recent decades associated with climate or land-use changes, this pattern occurred only in Long Pond (Fig. 4). Other paleoecological studies have identified *Gloeotrichia* as an important taxon during intermediate times of ecosystem transition (Bottema and Sarpaki 2003, Bunting et al. 2007, Levine et al. 2012), but we did not see strong evidence of *Gloeotrichia* abundance increasing concomitantly with fossil pigment concentrations in recent decades. In fact, we observed fossil *Gloeotrichia* densities to be correlated consistently with concentrations of algal and cyanobacterial pigments only at Long Pond (Fig. 5). We have good experimental evidence that *Gloeotrichia* can be associated with increases in the abundance of other phytoplankton (Carey and Rengefors 2010, Carey et al. 2014a,b), and modeling results illustrate how *Gloeotrichia*'s translocation of nutrients to the water column could tip a lake into a more eutrophic state (Cottingham et al. 2015). However, our paleoecological data suggest that whole-lake evidence of such facilitation may occur only in particular cases.

The abundance of *Gloeotrichia* relative to other primary producers during eutrophication appears to differ across lakes. Short-term laboratory experiments have suggested that *Gloeotrichia* may stimulate the abundance of the diatom *Cyclotella* sp. (Carey and Rengefors 2010), but in these New England lakes, the long-term outcome of interspecific interactions appears more complex. For example, *Gloeotrichia* abundance was not correlated with the diatom pigment diatoxanthin at Long Pond despite significant correlations with other pigments, whereas diatoms changed in concert with *Gloeotrichia* at Lake Auburn (Fig. 5). Lake Auburn also currently has blooms of *Dolichospermum* (formerly *Anabaena*) during and following *Gloeotrichia* blooms (Ewing, *unpublished data*), a result consistent with the laboratory evidence of enhanced *Dolichospermum* growth in cultures containing *Gloeotrichia* (Carey and Rengefors 2010). Given that phytoplankton community composition is governed by many different factors, such as zooplankton dynamics, macro- and micronutrient concentrations, light availability, thermal structure, and other factors that vary over multiple temporal scales,

it is not surprising that *Gloeotrichia*'s co-occurrence with other phytoplankton varied both within and among lakes.

#### *Climatic and watershed influence on changes in lake systems*

*Timing of ice-out.*—Coeval changes in lake production and ice-out date (Fig. 6) are consistent with process-based studies that demonstrate a synchronizing effect of climate on regional lake phenology (Magnuson et al. 1990, Arnott et al. 2003, Vogt et al. 2011). Strong correspondence between changes in the ice-out record and the pigment record, rather than between ice-out and *Gloeotrichia* records, suggests that primary producer abundance estimated from ubiquitous pigments may better reflect the effects of climate change (as ice-free season) than do individual cyanobacterial taxa.

That neither *Gloeotrichia* nor the cyanobacterial biomarkers canthaxanthin and echinenone were particularly responsive to changes in timing of ice-out in nutrient-poor lakes is unsurprising, as these taxa typically bloom only later in the summer. However, cyanobacteria are predicted to do particularly well in warmer, more thermally stratified lakes (Paerl and Huisman 2008, Carey et al. 2012b), conditions that are favored by longer ice-free periods (e.g., O'Reilly et al. 2015, Woolway and Merchant 2019) such as those these lakes are experiencing (Appendix S2: Fig. S5). Importantly, these effects may differ as a function of lake trophic state; Rigosi et al. (2014) suggest that effects of warming temperature on cyanobacteria may occur in eutrophic—but not oligotrophic—lakes. Consistent with this pattern, eutrophic Sabattus Pond exhibited important contributions of cyanobacteria to production, particularly in the most recent decades which also had the shortest periods of ice cover (Fig. 3).

Across most study lakes, vernal and autumnal taxa such as cryptophytes (as alloxanthin), diatoms (diatoxanthin), and secondarily chlorophytes (in part lutein + zeaxanthin) were most responsive to eutrophication (Fig. 3). This pattern suggests that the extended periods of low light, high turbulence, and abundant nutrients in spring and fall resulting from shorter periods of ice duration may be particularly important to overall changes in productivity, including differences in the synchrony of changes among lakes

(Dröscher et al., 2009, Vogt et al. 2011). This is also consistent with studies concluding that ice cover plays a key role in composition and abundance of planktonic assemblages (Riual and Mackay 2005, Smol et al. 2005, Katz et al. 2015, Hampton et al. 2017).

The extent of zone-break matches between ice-out and pigment records was strongly associated with the watershed-to-lake area ratio (WA:LA; Fig. 7, Appendix S2: Fig. S7). Where WA:LA ratios are high, hydrologic inputs from the watershed can more easily result in either hydrological disturbances (Klug et al. 2012) or substantial nutrient influx (Horppila et al. 2019 and references therein) that may override the effect of ice cover on lake production. In contrast, in lakes with lower WA:LA ratios, the proportional importance of watershed hydrology would be expected to be reduced, favoring closer correspondence between changes in phototrophic production (pigments) and changes in the ice-free period. This scenario is consistent with idea that influxes of energy (irradiance, heat) induce stronger temporal coherence among lakes, whereas influx of mass (water, solutes, particles) can override effects of energy (Leavitt et al. 2009, Vogt et al. 2011). It also further supports arguments from both recent (Brookes and Carey 2011, Rigosi et al. 2014) and paleolimnological (Leavitt et al. 2009) perspectives that both temperature and nutrient loading are likely to control lake productivity.

*Watershed land use.*—Changes in anthropogenic drivers related to watershed land use (human population and agricultural activities) sometimes co-occurred with those in sedimentary proxies of trophic state (Fig. 6). In the case of human population, changes were coeval with those of trophic proxies during the 1970s (Figs. 2–4 and Appendix S2: Fig. S3). During this period, tourism and land subdivision for second homes in Maine increased dramatically (Condon and Barry 1995), so these nearshore changes may be particularly important for both N loading and overall productivity as N and pigment proxies most commonly changed in concert with population (Fig. 6 and Appendix S2: Fig. S6). In contrast, correspondence between changes in trophic-state proxies and agricultural activities occurred particularly for C and *Gloeotrichia* records, supporting other studies pointing to the

importance of watershed nutrient additions in regulating primary production (Brookes and Carey 2011, Rigosi et al. 2014, Taranu et al. 2015). These latter patterns appeared particularly pronounced in currently oligotrophic lakes (Fig. 6) where all trophic-state proxies had some correspondence to changes in agricultural land use, and patterns were even stronger when more allowance was made for uncertainty in dates (Appendix S2: Figs. S6, S7).

*Gloeotrichia* abundance was greatest in five of our focal lakes around or immediately following the time of maximal European land clearance (c. 1780–1860) and declined as agricultural land use was reduced (Fig. 4). For example, peak abundance of *Gloeotrichia* in Lake Auburn occurred during initial European land clearance and was followed by a decline coinciding with the end of the most intense period of deforestation in this region (Barton et al. 2012) and the initial expansion of sheep production (Connor 1921) in Maine's history (~1780–1810 CE). Watershed clearance, soil disturbance, and introduction of livestock (Appendix S2: Fig. S4) likely resulted in significant nutrient influxes, as seen globally (Carpenter et al. 1998), and as suggested as a stimulus for *Gloeotrichia* in previous paleoecological studies (Van Geel et al. 1996, Bottema and Sarpaki 2003, Bunting et al. 2007). Consistent with studies in nearby Vermont (Levine et al. 2012), the introduction of livestock may be particularly important agents of initial change in lake water quality. Here, the only low-nutrient lake that did not show an increase in *Gloeotrichia* during European land clearance was Long Pond—also the only site with few sheep and cows in its catchment relative to land area (Appendix S2: Fig. S4).

The extent to which changes in watershed agricultural land use corresponded to those in the *Gloeotrichia* record was inversely related to WA:LA, as lakes with lower ratios were more likely to exhibit coherence in break patterns (Fig. 7), especially when more allowance was made for possible error in the dating (Appendix S2: Fig. S7). While this observation seems to run counter to the expectation that lakes with high WA:LA are likely to have proportionally larger inputs in times of high flow, it matches recent empirical work showing that cyanotoxin concentrations are higher in lakes with low WA:LA

(Hayes and Vanni 2018) and that nutrient limitation varies as a function of water input (Hayes et al. 2015). In particular, Hayes et al. (2015) point to the importance of the interaction between precipitation and watershed land use for bloom development and note that lake residence time may be functionally important behind the WA:LA relationships (Hayes and Vanni 2018). In our study lakes, water residence times are sufficiently long (Table 1) that it is unlikely that they limit *Gloeotrichia* bloom development, although it remains possible that pelagic populations are disturbed through mixing resulting from storm events in systems with large WA:LA ratios (as in Klug et al. 2012).

We also note that lakes with lower WA:LA ratios have a larger fraction of the watershed land in close proximity to the lake, suggesting that the effects of nearshore agricultural activity—especially those historically involving livestock (Appendix S2: Fig. S4)—may have been particularly important to *Gloeotrichia* and its recruitment from the littoral zone. The absence of consistent historical data across all sites limits our ability to test this hypothesis. However, the rich historical record of the area around Lake Auburn reveals the close proximity of substantial agricultural activity to the lake (Emil 2017), and an oral history describes stocking densities on properties near the lake that were several orders of magnitude greater than that in the county as a whole (L'Hommedieu 2002). These historical records and studies documenting greater housing development immediately around lakes than across the landscape as a whole (Schnaiberg et al. 2002) support this inference and highlight the importance of future investigation of the impacts of spatially variable patterns of land use on water quality.

### Synthesis

Collectively, these paleoecological records demonstrate that regional eutrophication can be variably expressed among individual lakes (cf. Maheaux et al. 2016) and yet reveal insights about cyanobacterial populations not easily ascertained from limnological studies spanning shorter time periods. First, the cyanobacterium *Gloeotrichia* is not new to the New England lakes we studied but rather was present before European settlement c. 1750 CE. Second, while there

is evidence in one lake for *Gloeotrichia* as a potential driver of eutrophication, it appears that *Gloeotrichia* abundance is more often related to watershed land use, particularly in systems with small ratios of watershed area to lake area (WA:LA). Hence, the recent increase in *Gloeotrichia* seen in contemporary studies (Winter et al. 2011, Carey et al. 2012a) may be a function of intensification of nearshore land uses. Third, various manifestations of trophic change—overall organic matter production, patterns of isotopic fractionation, and the abundance of various taxa or groups of taxa, seen here through different proxies—may differ in the story they tell of the timing of shifts even within a single lake. Further, even with similar regional drivers such as climate and broadly similar land-use changes, lakes differ in both the magnitude and nature of response of individual metrics that are related to trophic change. Fourth, the duration of ice cover and the extent of agricultural activity are important drivers of lake trophic change, particularly in systems with smaller WA:LA. Together, these records suggest that single metrics of change in lake trophic state are insufficient and that even aggregate metrics may respond differently across lakes under similar pressures. Hence, attention to the intersection of changes in climate and watershed land use in the context of basin morphometry is necessary to understand how lakes respond to multiple stressors, and lake management will need to attend to this intersection to keep these low-nutrient lakes in the clear-water state.

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