



# Climate variability promotes unprecedented cyanobacterial blooms in a remote, oligotrophic Ontario lake: evidence from paleolimnology

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**Abstract** Dickson Lake, located in Algonquin Provincial Park, Ontario, is a remote, oligotrophic lake, where cyanobacterial blooms of the genus *Dolichospermum* (Ralfs ex Bornet & Flahault) P. Wacklin, L. Hoffmann and J. Komárek were reported for the first time in the fall of 2014, and subsequently in the late spring of 2015. To investigate the potential environmental triggers of these bloom events, we assessed long-term trends in water quality using a multi-proxy paleolimnological approach, examining sedimentary diatoms, chironomids, cladocerans, spectrally inferred chlorophyll *a*, and cyanobacterial akinetes preserved in a <sup>210</sup>Pb-dated sediment core. Assemblage changes were modest in all biological

proxies. A subtle increase in the abundance of warm-water chironomid taxa ( $T_{opt} > 15\text{ }^{\circ}\text{C}$ ) commences in the year  $\sim 2000$ , with further increases in the most recent years of the sediment record ( $\sim 2013\text{--}2015$ ). End-of-summer volume-weighted hypolimnetic oxygen concentrations (CI-VWHO), inferred from chironomid remains, reveal a decline in oxygen concentrations over the last two decades coincident with the highest levels of sedimentary chlorophyll *a* and cyanobacterial akinetes in the sediment record. These paleolimnological findings corroborate observed reports of the onset of cyanobacterial blooms in Dickson Lake in late 2014 and are consistent with increasingly favourable bloom-forming conditions over the past few decades that are related to warmer air temperatures, sharp declines in wind speed, and a lengthening of the ice-free season by 2 weeks since 1975. It is plausible that late ice-out and a quick onset

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to stratification in 2014 may have resulted in incomplete spring mixing, early onset of hypolimnetic anoxia, and increased internal nutrient loading, that, occurring during a period when climate conditions were particularly ideal for cyanobacterial proliferation, may have fueled the unprecedented algal blooms in this remote lake. Collectively, the factors causing algal blooms in remote lakes such as Dickson Lake are not yet fully understood, and it is worrisome that with continued warming the triggering conditions may become a more common feature of Algonquin Park and other minimally impacted Boreal Shield lakes in the coming years.

**Keywords** Blue-green algae · Cyanobacteria · Climate change · Primary production · Hypoxia · Akinetes

## Introduction

Over the past several decades, the extent of nuisance algal blooms, as well as public concern over putative environmental degradation, has grown in Canada and globally (O'Neil et al. 2012; Taranu et al. 2015; Pick 2016). Algal blooms pose an environmental hazard because they may negatively impact water quality by increasing turbidity, depleting deep-water oxygen concentrations, and producing a variety of toxic compounds—all of which can affect and alter aquatic food webs (Paerl et al. 2001). In Ontario specifically, the Ministry of the Environment, Conservation and Parks (MECP) has noted a significant increase in both the number of confirmed algal bloom reports each year between 1994 and 2009, as well as the number of these blooms where cyanobacteria were dominant (Winter et al. 2011). This increasing trend has persisted to at least 2018 (MECP, unpubl. data). Fall cyanobacterial blooms have also been noted since 2001 in oligotrophic-to-mesotrophic lakes in Western Québec (Leblanc et al. 2008; Pal et al. 2015), indicating that this is a widespread phenomenon.

Affected Ontario lakes vary in total phosphorus concentrations, with many (26%) being classified as oligotrophic (Winter et al. 2011). Therefore, cultural eutrophication alone cannot explain the rise in nuisance blooms. Over the past two decades the length of the bloom-reporting period has also increased, with

recent cyanobacterial blooms being reported later into the fall than in the 1990s (Winter et al. 2011; MECP, unpubl. data), suggesting a link to climate change. Additionally, a longer ice-free period (Futter 2003; Minns et al. 2012), enhanced thermal stratification (Stainsby et al. 2011; Hadley et al. 2014), and warmer midsummer epilimnia (King et al. 1999) have all been observed in the region over the last few decades and indicate that climate change is a potentially important contributing factor to these algal blooms.

With rare exceptions, most lakes in Ontario do not have continuous, long-term monitoring records, making paleolimnological studies valuable for establishing baseline (or natural) and pre-disturbance conditions (Smol 2008). Algal blooms have been interpreted from the paleolimnological record using proxies such as sedimentary pigments (McGowan et al. 1999) and akinetes (van Geel et al. 1994; Bunting et al. 2016). Akinetes are perennating structures produced by many heterocystous cyanobacteria under adverse environmental conditions. Akinetes have a thick hyaline cell wall which allows them to remain viable in sediments for centuries (Ellegaard and Ribeiro 2017) and for their structure to preserve for millennia (van Geel et al. 1994). In temperate lakes, akinete production coincides with the stabilization of the water column, the accumulation of planktonic populations during the formation of dense blooms, and often proceeds rapidly and extensively in response to conditions unfavourable to vegetative growth (Fay 1983). The majority of akinetes settle to the sediment surface where, if not brought back into suspension the following spring by water mixing and turbulence, they become incorporated into the sediment record.

In this study, we explore the main putative causes of cyanobacterial blooms: increased nutrients, decreased deep-water oxygen leading to greater internal nutrient loading from the sediments, changes in grazing pressure, warmer surface waters, and enhanced thermal stratification. Climate warming is resulting in a longer open water period, with warmer air and water temperatures, and greater summer thermal stability. When nutrients are sufficient, enhanced thermal stability can favour cyanobacteria, which possess several traits that give them a distinct competitive advantage over eukaryotic phytoplankton. These traits include the ability to fix nitrogen, possession of gas vesicles providing buoyancy, and having maximum growth rates at elevated water temperatures (Huisman

et al. 2018). Trends over the past  $\sim 250$  years in these bloom-forming factors are examined using subfossil diatoms (to indicate nutrient levels and thermal stability), chironomids (to indicate hypolimnetic dissolved oxygen concentrations and water temperature), and cladocerans (for top-down effects) to better understand why cyanobacterial blooms have recently been observed in remote, oligotrophic, Dickson Lake (Algonquin Provincial Park, Ontario). Additionally, changes in overall primary production inferred from sedimentary chlorophyll *a*, and cyanobacterial abundance inferred from subfossil akinetes, are used to assess whether the blooms in the study lake are unprecedented over the past  $\sim 250$  years. Long-term trends in these variables are critical in evaluating whether the observed cyanobacterial blooms, and conditions amenable for them, have occurred in Dickson Lake in the past, or whether they are a new phenomenon. Additionally, we investigate whether regional warming and associated changes in lake properties are potential causal factors.

#### Site description

Dickson Lake (45°47'40.1"N, 078°12'46.8"W), situated in the interior of Algonquin Provincial Park, Ontario, has a surface area of 10.02 km<sup>2</sup>, a drainage area of 58.4 km<sup>2</sup> and a maximum depth of 18.6 m (Fig. 1). Dickson Lake lies in the Georgian Bay Ecoregion (5E) of Ontario (Crins et al. 2009), which is situated on the southern portion of the Precambrian Shield and extends from southeastern Lake Superior in the west to the central portion of the Ottawa Valley in the east. Land cover is composed of mixed forest (32.0%), deciduous forest (22.2%), coniferous forest (12.1%), and sparse forest (11.3%) (Crins et al. 2009). The climate of the Georgian Bay Ecoregion is cool-temperate and humid. From 1971 to 2000 the mean annual temperature in Algonquin Park was 4.5 °C and the mean annual precipitation was 949.0 mm (McKenney et al. 2010). From 2011 to 2040 it is expected that mean annual air temperature for the Park will increase to 6.1 °C, and the mean annual precipitation will increase to 961.0 mm, with trends continuing upwards in subsequent decades (McKenney et al. 2010; McDermid et al. 2015).

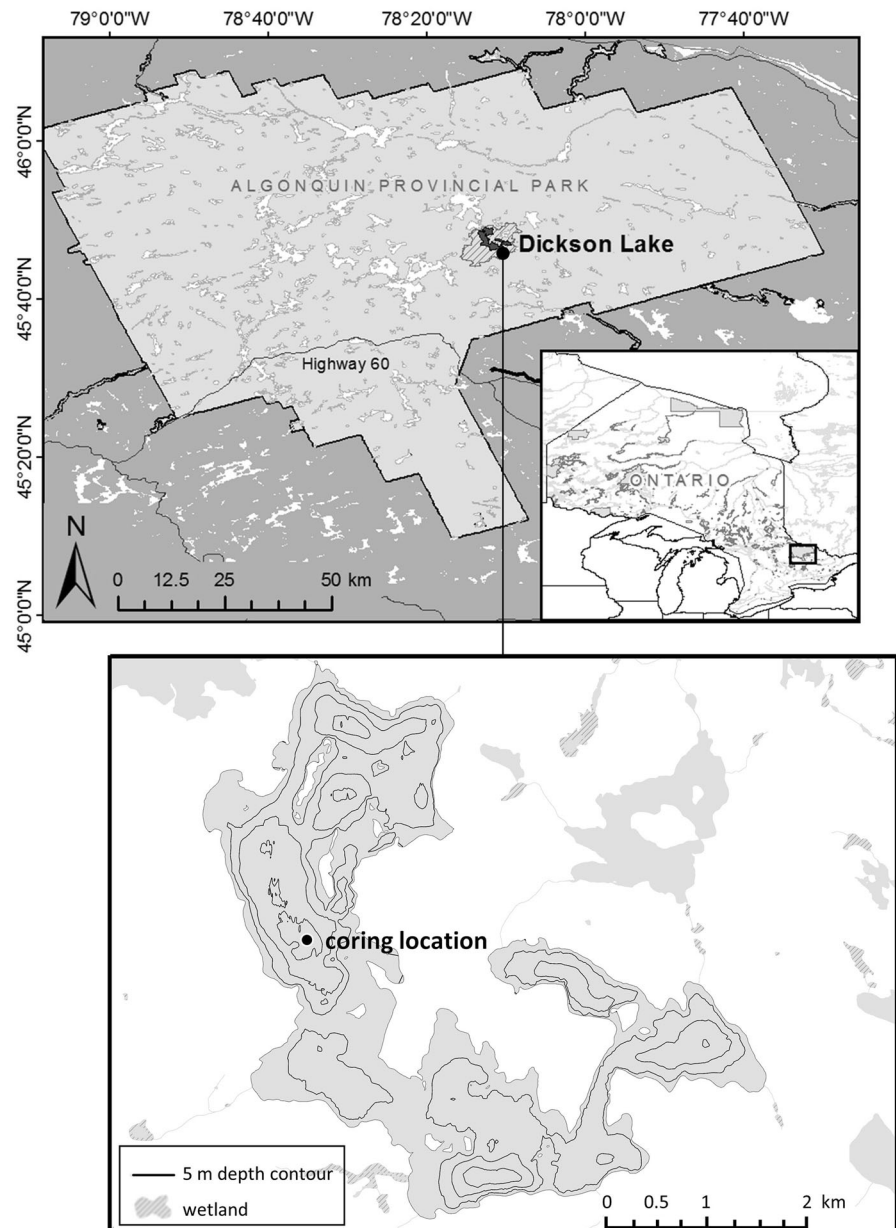
Anthropogenic nutrient sources to Dickson Lake are minimal since there is no industrial, agricultural, or residential development on the shoreline or in the

catchment. Present-day direct human impacts on the lake include backcountry canoeing and camping, as well as logging operations, mostly in the western edge of the catchment and in the surrounding area, which are managed by the Algonquin Forestry Authority (Cumming 2010). Water chemistry data for Dickson Lake, sampled by the MECP from 1980 to 1987 as well as in 2015 and 2016 (Table 1), indicate conditions typical of lakes on the Canadian Shield and in Algonquin Park, with low concentrations of nutrients and ions, and a circumneutral pH. It is especially notable that the mean total phosphorus concentration in the surface water of Dickson Lake (9.95  $\mu\text{g L}^{-1}$ ) declined from mesotrophic levels in the 1980s (13.00  $\mu\text{g L}^{-1}$ ) to oligotrophic levels in 2015 and 2016. Dickson Lake is dimictic, with a thermocline depth between 6 and 10 m during the peak stratification period in late July to early September (MECP, unpubl. data). The mean August Secchi depth of Dickson Lake in the 1980s was 4.4 m ( $n = 15$ ,  $SD = 0.48$ ), but was as low as 1.8 m in 2015 during the *Dolichospermum* bloom (MECP, unpubl. data).

In the early fall of 2014, an extensive lake-wide bloom of nitrogen-fixing cyanobacteria (genus *Dolichospermum*) formed in Dickson Lake (Fig. 2), evidently for the first time, although algal records from the 1980s show the presence of filamentous blue-green algae in low abundance (MECP, unpub. data). Mass spectrometry analysis (LC–MS/MS) to identify algal toxins determined that this bloom produced concentrations of microcystin congeners (MC-LA, MC-LY, and MC-LR) that were below the Ontario Drinking Water Quality Standard for MC-LR (i.e.,  $< 1.5 \mu\text{g L}^{-1}$ ). Microcystins have high acute and chronic toxicities and their production can cause liver, digestive and neurological diseases when ingested by animals and humans (Bláha et al. 2009; Merel et al. 2013). A second bloom of the same genus was reported the following open-water season, beginning in late-June of 2015 and persisting throughout the summer. As a precaution to protect visitor health, park authorities closed Dickson Lake, and downstream Lake Lavieille (Hardy Bay), to overnight camping.

Algonquin Park contains one of the world's highest concentrations of natural brook trout (*Salvelinus fontinalis*) lakes, with Dickson Lake supporting natural brook trout and lake trout (*Salvelinus namaycush*) populations (Quinn et al. 1994). The severity of the cyanobacterial blooms on Dickson Lake has resulted

**Fig. 1** Upper: Dickson Lake is situated in the interior of Algonquin Provincial Park, in central Ontario, Canada (black box in inset represents extent). The catchment of Dickson Lake is indicated by the line-filled area. Lower: Bathymetry and coring location within Dickson Lake (base data from Land Information Ontario (LIO) and bathymetric data provided by Harkness Laboratory of Fisheries Research)



in public concern about the future of the recreational fishery on the lake, which is an important economic stimulus for the Park. It is currently too early to establish whether recent changes in water quality are having an impact on native fish populations, and whether the lake's first experience with algal blooms over two consecutive years is part of a regime shift in which bloom events will become a common occurrence in the future.

## Materials and methods

### Instrumental and historical climate records

Long-term temperature records (spanning years 1915–2016) were available for the Algonquin Park region from the Madawaska climate station ( $45^{\circ}30'00.0''\text{N}$ ,  $77^{\circ}58'48.0''\text{W}$ ), located  $\sim 40$  km southeast of Dickson Lake (Adjusted and Homogenized Canadian Climate Data, AHCCD; <https://www.>

**Table 1** Selected water chemistry parameters for Dickson Lake. Values indicated are arithmetic means of at least three sampling times in different months during the ice-free season (April–October) for each year in the specified range, apart from 1980 and 2016 which only had sampling from 2 months of the open-water period available

	1980–1987	2015–2016
Gran alkalinity (mg L <sup>-1</sup> )	7.48	9.62
Ca (mg L <sup>-1</sup> )	3.69	2.88
Cl (mg L <sup>-1</sup> )	0.35	0.28
Conductivity (μS cm <sup>-1</sup> )	48.89	34.27
DIC (mg L <sup>-1</sup> )	1.93	2.30
DOC (mg L <sup>-1</sup> )	3.69	4.43
Fe (μg L <sup>-1</sup> )	118.53	65.00
K (mg L <sup>-1</sup> )	0.73	0.58
Mg (mg L <sup>-1</sup> )	1.51	1.22
pH	6.93	6.99
TIN (μg L <sup>-1</sup> )	41.80	55.33
TP (μg L <sup>-1</sup> )	13.00	9.95
SiO <sub>3</sub> (mg L <sup>-1</sup> )	0.62	0.71
SO <sub>4</sub> (mg L <sup>-1</sup> )	9.71	4.29

*DIC* dissolved inorganic carbon, *DOC* dissolved organic carbon, *TIN* total inorganic nitrogen, *TP* total phosphorus



**Fig. 2** *Dolichospermum* bloom on Dickson Lake in September 2014. Photo courtesy of Alison Lake, Ontario Ministry of Natural Resources and Forestry

[ec.gc.ca/dccha-ahccd/](http://ec.gc.ca/dccha-ahccd/)). Total precipitation records for the years 1916–2000 were also obtained from the Madawaska climate station, whereas more recent records were unavailable from this location and data for 2005–2016 were therefore retrieved from the Algonquin Park East Gate climate station (45°32'N,

78°16'W), located ~ 50 km south of Dickson Lake and ~ 24 km southwest of the Madawaska station (<http://climate.weather.gc.ca>). Data for annual and seasonal means of daily wind speed were acquired from both the North Bay and Muskoka Airport stations (46°21'36.0"N, 79°25'12.0"W and 44°58'12.0"N, 79°18'00.0"W, respectively), which are equidistant from the study lake, located ~ 115 km northwest and ~ 125 km southwest of Dickson Lake, respectively. Trends in average wind speed from these two stations are closely correlated ( $R = 0.611$ ,  $p < 0.001$ ) and are available from the AHCCD. Daily wind speed data were also obtained from the Algonquin Park East Gate climate station for the years 2005 to 2017. Historical lake ice data were available for Lake of Two Rivers (45°34'42.0"N, 78°28'54.9"W; located ~ 30 km southwest of Dickson Lake), including both ice-on and ice-off dates recorded since 1975 (R. Tozer, unpubl. data). Linear regressions were applied to temperature, wind speed, precipitation, and ice records to determine the rate of change over the time series. Locally estimated scatterplot smoothing (LOESS) were applied to these data to highlight the general trends and to reduce noise, with appropriate span determined in R 3.1.3 (R Core Team 2015) using general cross validation with the fANCOVA package (Wang 2010).

### Core collection

A sediment core was taken from under the ice in March 2015 at the deepest point of Dickson Lake using a Glew (1989) gravity corer with an inner core tube diameter of 7.62 cm. The 30-cm-long core was then sectioned on site using a Glew (1988) extruder at a 0.5 cm resolution throughout. Following the second algal bloom in 2015, a confirmatory core was retrieved in October 2016 from the same location in the study lake using the same coring equipment. The first two centimeters of the core, as well as an interval at 25 cm, were sectioned at 0.25 cm resolution to obtain the highest possible temporal resolution and verify similarity to baseline conditions revealed in the initial core. Sediment samples were kept in coolers until they were placed in the cold room at PEARL (~ 4 °C) for storage prior to analyses.

## $^{210}\text{Pb}$ dating

Preparation of samples for  $^{210}\text{Pb}$  dating followed Schelske et al. (1994). In brief, 20 sedimentary intervals were strategically selected over the 30-cm long core, freeze-dried, placed into gamma tubes to a height of about 2.5 cm, and sealed using 2-ton epoxy above a silicone septum. A germanium crystal detector was then used to measure the gamma activity of radioisotopes  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$ . Concentrations of unsupported  $^{210}\text{Pb}$  were then used to estimate age, based on the constant rate of supply (CRS) model described by Appleby (2001). Ages of sediment intervals that were not analyzed for gamma activities were estimated by using straight-line interpolation between pairs of dated samples.

## Spectrally inferred chlorophyll *a*

Concentrations of sedimentary inferred chlorophyll *a*, as well as its isomers and main degradation products, were determined by visible reflectance spectroscopy, which provides a fast, reliable, and non-destructive method for analysis of trends in fossil pigments and serves as a proxy for whole lake primary production (Michelutti and Smol 2016). Methods followed those outlined in Michelutti et al. (2010). Briefly, small amounts of freeze-dried sediment from each interval were sieved through a 125  $\mu\text{m}$  screen, placed into glass scintillation vials, and then analyzed for spectral absorbance in the range of 650 and 700 nm using a FOSS NIR System Model 6500 Rapid Content Analyzer. The wavelength-absorbance plot was then used to calculate an inferred chlorophyll *a* value since wavelength absorption and chlorophyll *a* concentration are linearly correlated (Wolfe et al. 2006; Michelutti et al. 2010).

## Preparation and analyses of biological indicators

### *Akinetes*

In this study, akinetes are used in a comparative way through time, and as supporting data for temporal trends in algal production obtained from sedimentary chlorophyll *a*, rather than as a measure of cyanobacteria population size. Akinete preparation and analyses were completed at Phycotech, Inc. (St. Joseph, Michigan, U.S.A.). Briefly, subfossil akinetes were

isolated from ten strategically selected intervals of freeze-dried sediment and prepared for microscopy following a modified protocol of Crumpton (1987). Sediment samples ( $\sim 0.1$  g freeze-dried) were diluted with distilled water and homogenized. Aliquots ( $\sim 0.10$  mL) were removed from these samples and fossils were filtered onto a 0.45  $\mu\text{m}$  pore membrane filter. Filters were mounted on cover slips using hydroxypropyl-methacrylate (HPMA) resin, air dried for 24 h, and permanently mounted onto glass microscope slides with HPMA resin. For each sample,  $\sim 200$  cells (including cyanobacterial akinetes, chlorophytes, chrysophyte cysts, and pollen grains) were identified to genus or species level, using Komárek (2013) as a taxonomic guide, and enumerated (at 400X magnification) by counting random fields using an Olympus BX51 compound microscope equipped with Nomarski and phase-contrast optics and epifluorescence illumination (blue, green and UV Excitation). Akinete microfossil concentration was calculated as the number of cyanobacterial akinetes  $\text{g}^{-1}$  dry mass of sediment, a metric that is linearly correlated to phytoplankton densities (Bunting et al. 2007).

### *Diatoms*

Sediment preparation for diatom analyses generally followed methodology described in Battarbee et al. (2001). Approximately 0.2 g of wet sediment was digested with a 50:50 molar ratio of concentrated sulphuric and nitric acid to remove the organic content of the sediment and leave the siliceous material intact. The samples were then placed into a hot water bath set at 80 °C for at least two hours to accelerate the reaction. The diatom slurries were allowed to settle for  $\sim 24$  h, then aspirated and rinsed with deionized water. This procedure was repeated until a circum-neutral pH was reached ( $\sim 6$  rinses). The slurries were then strewn onto coverslips at four different dilutions and allowed to evaporate at room temperature. Using Naphrax<sup>®</sup> as a mounting medium, the coverslips were affixed onto microscope slides. Diatoms were examined using a Leica DMR HC light microscope under oil immersion (at 1000X magnification) fitted with differential interference contrast optics. Diatom identification was accomplished using multiple taxonomic references including Krammer and Lange-Bertalot (1986–1991), Camburn and

Charles (2000), and Fallu et al. (2000). A minimum of 350 diatom valves was counted for each sample.

### *Cladocerans*

Replicate microscope slides for 16 sediment sections were prepared following the techniques outlined in Korhola and Rautio (2001). Approximately 0.1 g of freeze-dried sediment was deflocculated in 150 mL of 10% KOH solution at a temperature of 70 to 80 °C for 30 min, while providing gentle mixing using a glass stirring rod. The sediment was then passed through a 37 µm sieve and rinsed with deionized water until all small particulate matter had washed through. Residue retained on the sieve was transferred to a small vial using deionized water. Subsequently, two to three drops of ethanol were added to prevent fungal growth, and two to three drops of safranin-glycerin solution were added to stain the cladoceran remains. Finally, two to four 50 µL aliquots were pipetted onto slides (allowing drying between aliquots using gentle heat from a slide warmer), and permanent slides were made using glycerine jelly containing a small amount of safranin stain and ethanol. Taxonomic identifications of fossil cladocerans followed Frey (1959), Smirnov (1996), Taylor et al. (2002), Sweetman and Smol (2006), Szeroczyńska and Sarmaja-Korjonen (2007), and Korosi and Smol (2012a,b). A minimum of 100 cladocerans were enumerated per sample (Kurek et al. 2010) using a Nikon Eclipse 80i light microscope with bright field optics (10–40 × objective, 15 × ocular lens). All cladoceran remains (e.g., carapaces, head-shields, ephippia, and postabdominal claws) were tabulated separately. For each taxon, the most abundant remain was used to calculate the number of individuals (Frey 1986).

### *Chironomids*

Chironomid head capsules were analyzed following standard procedures outlined in Walker (2001). To summarize, starting with 1.5 g, and working upwards to achieve a minimum of 50 head capsules per interval (Quinlan and Smol 2001a), wet sediment was heated in a 5% KOH solution for 20 min at about 80 °C to deflocculate the samples. The samples were then rinsed through a 95 µm sieve with distilled water. Midge remains were then hand-picked from the sediment concentrate using a Bogorov counting tray

(Gannon 1971), plated and mounted onto microscope slides, using Entellan® as a binding agent. Chironomid taxonomic identification followed references including Wiederholm (1983) and Brooks et al. (2007).

### Statistical techniques for biological groups

The most common taxa recorded for diatom, chironomid, and cladoceran proxies were displayed stratigraphically as percent relative abundance, with ecologically similar taxa grouped to better highlight the trends. For statistical analyses, all taxa (species and varieties) were kept distinct. To summarize and compare biological trends, principal component analysis (PCA) was used on diatom, chironomid, and cladoceran species data using CANOCO version 5 for Windows (ter Braak and Šmilauer 2002). Relative abundance data were square-root transformed prior to analysis to equalize the variance among taxa. Down-core PCA sample scores, with analyses performed on all taxa and without down-weighting of rare taxa, were used to graphically summarize the major patterns of variation for each biological proxy over time. Zones of similar assemblages for diatoms and chironomids were delineated by stratigraphically constrained incremental sum of squares (CONISS) cluster analysis performed in R 3.1.3 (R Core Team 2015) using the vegan (Oksanen et al. 2015) and rioja (Juggins 2017) packages, and with Euclidean distance as the dissimilarity coefficient (Grimm 1987). A broken stick model was subsequently used to determine the number of important zones within each stratigraphy (Bennett 1996).

An end-of-summer volume-weighted hypolimnetic oxygen (VWHO) inference model from the Muskoka-Haliburton region of south-central Ontario (Quinlan and Smol 2010) was applied to the Dickson Lake downcore chironomid data. The VWHO inferences are based on the optima and tolerances of modern chironomid assemblages across a measured lake water gradient from near-saturation to anoxic. This model uses weighted averaging with tolerance down-weighting and inverse deshrinking and is comprised of 45 midge taxa, including *Chaoborus*, from 54 lakes, and has a cross-validated model error of 1.98 mg L<sup>-1</sup> O<sub>2</sub> and a jackknifed coefficient of determination ( $r^2$ ) of 0.60 (Quinlan and Smol 2010).

## Results

### Instrumental climate data trends

Linear regressions revealed that annual means of daily minimum air temperatures from the Madawaska climate station have increased by 2.26 °C over the 100-year record, with the largest increases occurring in the summer (June, July, and August; 3.64 °C) and fall (September, October, and November; 2.90 °C) seasons (Fig. 3a–c). Increasing trends in mean annual and seasonal air temperatures were also observed (Electronic Supplementary Material 1), however daily minimum temperature increases are more pronounced across Canadian weather stations (Vincent et al. 2012) and are projected to continue to increase in Ontario (McDermid et al. 2015). Mean annual air temperature increases in Algonquin Park of 1.07 °C over the 100-year record are greater than the global average of 0.55–0.80 °C since the preindustrial period (Hawkins et al. 2017), but less pronounced than those of ~ 1.5 °C recorded further northwest in Ontario around Sault Ste. Marie (E.J. Favot, unpubl. data) and Kenora (Rühland et al. 2010). Here we present annual means of daily minimum temperatures, since we are looking for environmental triggers for cyanobacterial blooms, and it is the minimum temperatures that show the greatest amount of change over the time series. North Bay and Muskoka Airport stations both record a decrease in mean annual wind speed of 1.54 and 2.93 km h<sup>-1</sup>, respectively, over the 61-year record (Fig. 3d). At the Muskoka station, decreases were most pronounced in the fall and spring (March, April, and May), with declines of ~ 3.28 km h<sup>-1</sup> and ~ 3.09 km h<sup>-1</sup>, respectively, and at the North Bay station decreases were most pronounced in the winter and spring, with declines of ~ 1.77 km h<sup>-1</sup> and ~ 1.73 km h<sup>-1</sup>, respectively. Total annual precipitation at the Madawaska climate station decreased from 1916 to 1933, followed by an increasing trend to present day, with ~ 240 mm more precipitation annually over the past 83 years (Fig. 3e). This increasing trend was most prominent in fall precipitation (data not shown), which has increased by ~ 85 mm since 1933. The length of the ice-free season recorded from nearby Lake of Two Rivers (~ 30 km SW of Dickson Lake) shows an increase of 14.6 days since 1972 (Fig. 3f). Means of daily data for temperature and wind speed

during the 2 weeks after ice-out between 2005 and 2016 show that 2014 was an unusual year, with a relatively late ice-out, above average temperature and lower wind speed than other years (Fig. 4).

### Radiometric dating

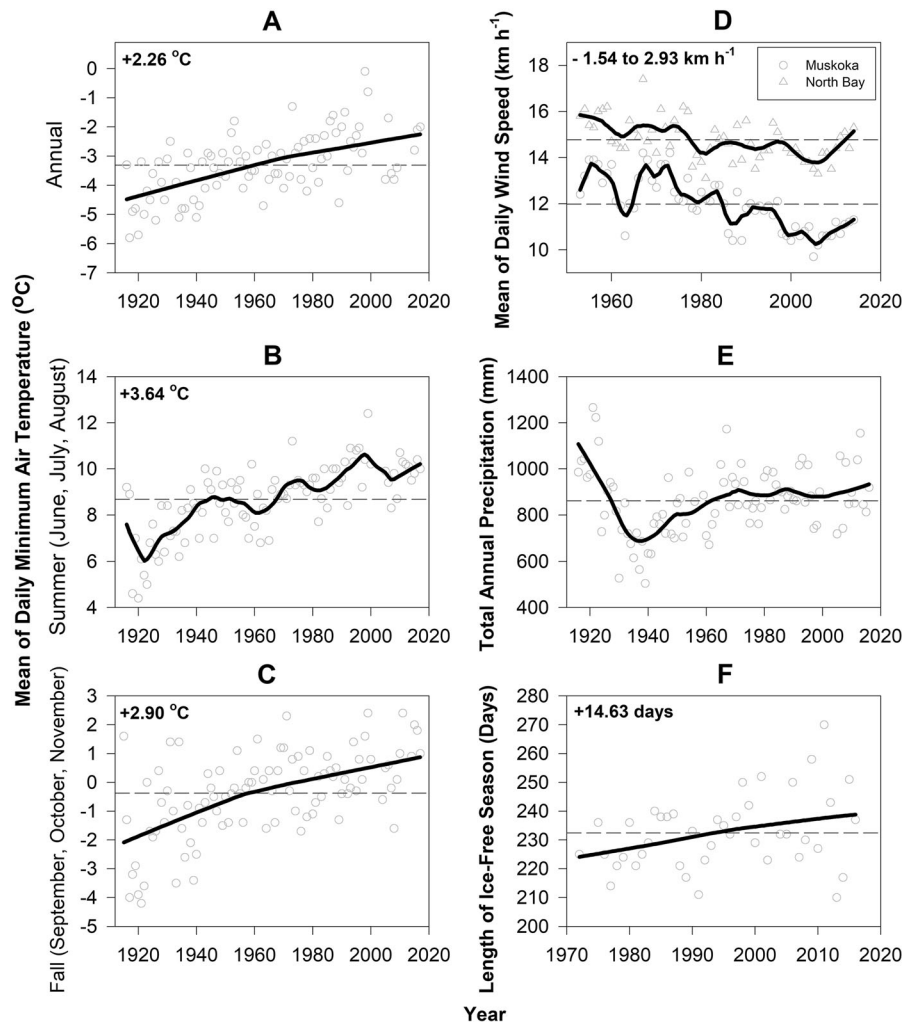
The radiometric dating profile generally follows an exponential decline in <sup>210</sup>Pb activity with depth and reaches background levels (as represented by mean <sup>214</sup>Bi) between 22 and 25 cm (Fig. 5). However, a slight flattening of the <sup>210</sup>Pb activity profile versus core depth occurs above 10 cm. Although such a profile might be interpreted as evidence of possible sediment mixing, marked changes in proxy data between adjacent intervals in this area of the core indicate no significant mixing. Instead, the flattened profile in the upper core is more likely due to an increase in sedimentation rate (Appleby 2001) in recent years. The low level of <sup>210</sup>Pb activity in the upper ~ 2 cm of the core may be the result of steep redox gradients across the uppermost few centimeters of sediment (Flett 2012). As is often the case in organic-rich sediments, the <sup>137</sup>Cs data shows no clear peak associated with maximum atmospheric fallout prior to a worldwide moratorium placed on atmospheric testing of nuclear weapons in ~ 1963.

### Sedimentary chlorophyll *a* and cyanobacterial akinetes

Spectrally inferred trends in chlorophyll *a* indicate a decline in overall primary production from ~ 1840 to ~ 1930, followed by a steady increase to the highest levels on record in sediment intervals corresponding to the last decade (Fig. 6). Cyanobacterial akinetes in the recent sediments markedly increased in density and deposition rate (Fig. 6). Akinetes began to increase in the ~ 1970s, increased further in sediment at 0.5-cm depth in the core (<sup>210</sup>Pb-dated ~ 2013–2014), and then spiked with a threefold increase at the surface of the core (~ 2014–2015) relative to the 0.5-cm interval (Fig. 6). Interestingly, in a surface sediment sample taken in late 2016, a year in which no cyanobacterial blooms were observed in the lake, the number of akinetes were found to be at pre-bloom (2013–2014) levels (Fig. 6). All cyanobacterial akinetes observed in the sediment were from the order Nostocales Borzi and primarily of the family



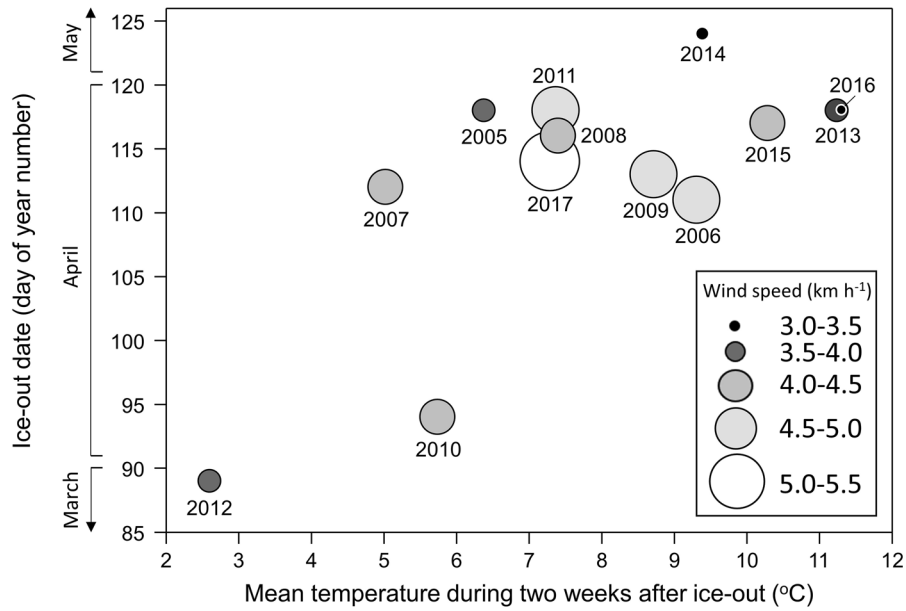
**Fig. 3** Annual (a), summer (b) and fall (c) mean of daily minimum air temperature has increased by 2.26–3.64 °C over the last ~ 100 years at the Madawaska climate station. Mean annual wind speed (d) from the Muskoka and North Bay climate stations show declining trends. Total annual precipitation (e) recorded from Madawaska and Algonquin Park East Gate climate stations has also increased since the 1930s, and length of the ice-free season in the region (f) has increased over the last four decades (from Lake of Two Rivers). Thick black lines represent LOESS trends and dashed grey lines represent time series means



Nostocaceae Eichler, and to a lesser degree from the family Rivulariaceae Bornet & Flahault (specifically multi-filament *Gleotrichia echinulata* (Smith) Richter at samples from 12 and 16 cm in the core). Within the Nostocaceae family, akinetes were primarily the single non-motile cells of the genus *Dolichospermum* (including *D. lemmermannii* (Richter) P. Wacklin, L. Hoffmann and J. Komárek, *D. flos-aquae* (Brébisson ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek and *D. circinale* (Rabenhorst ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek). Also present from the Nostocaceae family were filamentous *Dolichospermum planctonicum* (Brunthaler) P. Wacklin, L. Hoffmann & J. Komárek and multi-filamentous *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault.

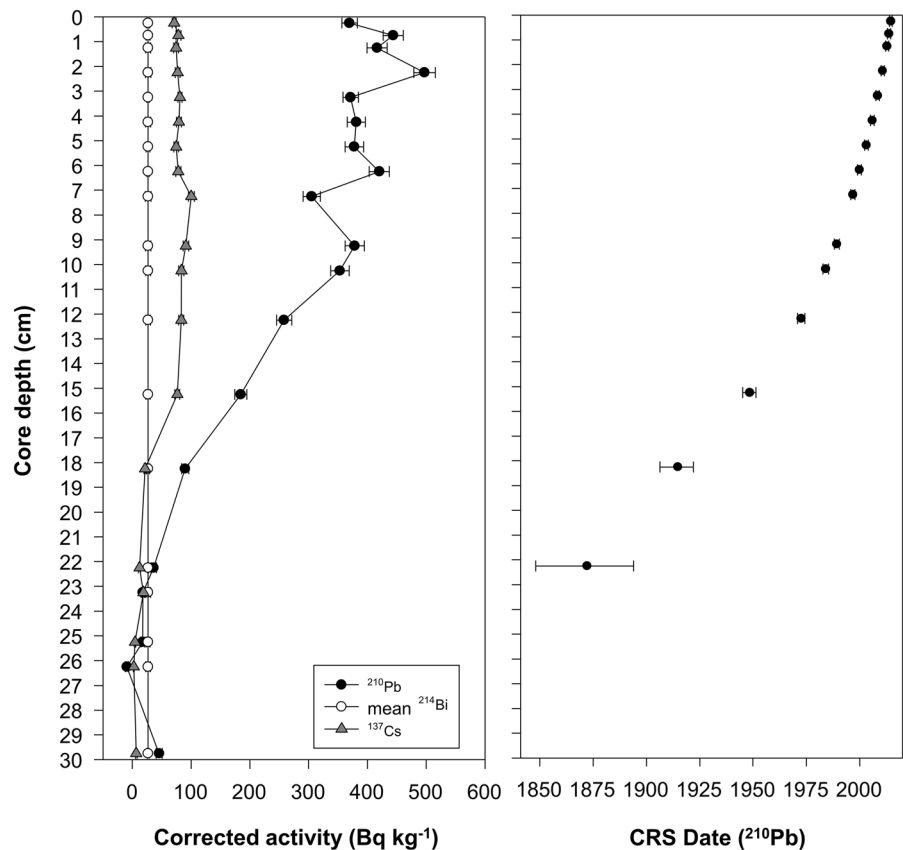
### Multi-proxy analyses

In the Dickson Lake sediment core, we recorded 26 genera and 165 species and varieties of diatoms, 38 species of cladocerans, and 77 genera and 113 species and types of chironomids. Changes in species relative abundances for all proxies were generally subtle. This was summarized by individual species trends described in the following sections and using Principal Component Analysis (Electronic Supplementary Material 2). A CONISS cluster analysis and subsequent broken stick modelling performed in R did not identify any important transitions for the diatom or chironomid assemblages.

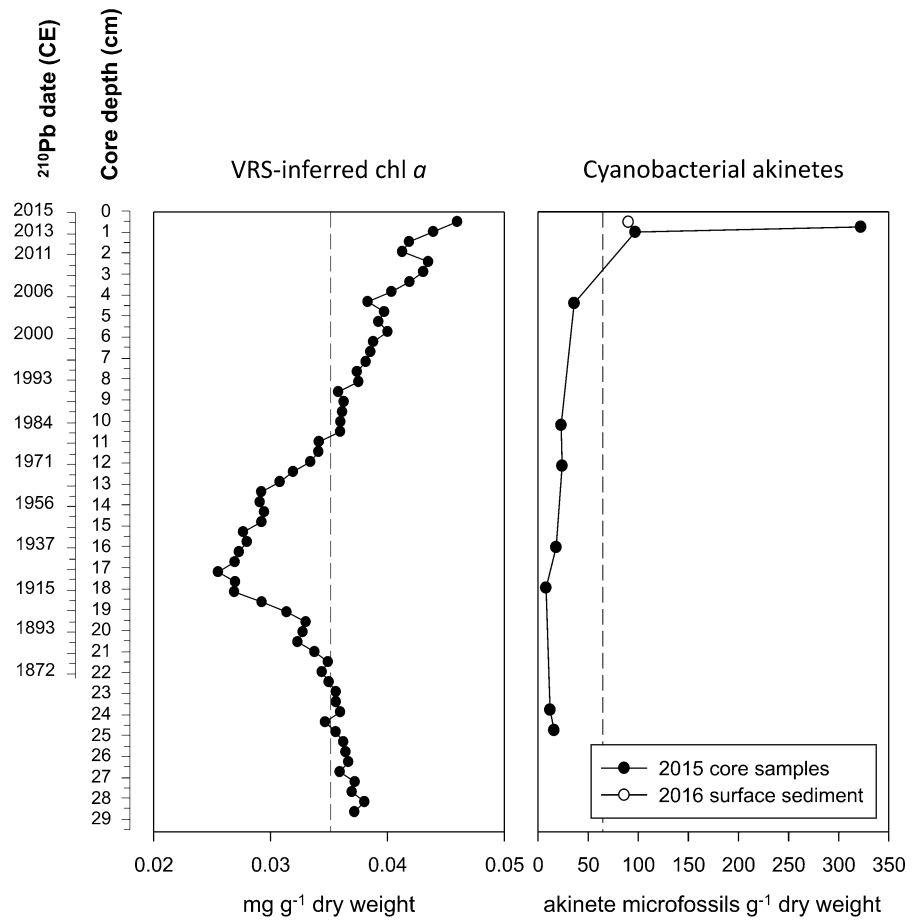


**Fig. 4** Average temperature during the 2 weeks after ice-out versus ice-out date, with size of symbol representing average wind speed during this period. Note that 2014 was characterized by warm temperatures and low wind speed following a late ice-out date

**Fig. 5** Activities for radioisotopes <sup>210</sup>Pb, <sup>137</sup>Cs, and mean <sup>214</sup>Bi versus core depth in the sediment core for Dickson Lake, as well as the estimated CRS <sup>210</sup>Pb date versus core depth profile



**Fig. 6** Spectrally inferred sedimentary chlorophyll *a* trends (including its main diagenetic products) and abundance of cyanobacterial akinetes scaled by core depth (with secondary axis of estimated <sup>210</sup>Pb dates). Note that the open circle in the akinete profile represents abundance in 2016 surface sediments. Dashed lines represent times series means



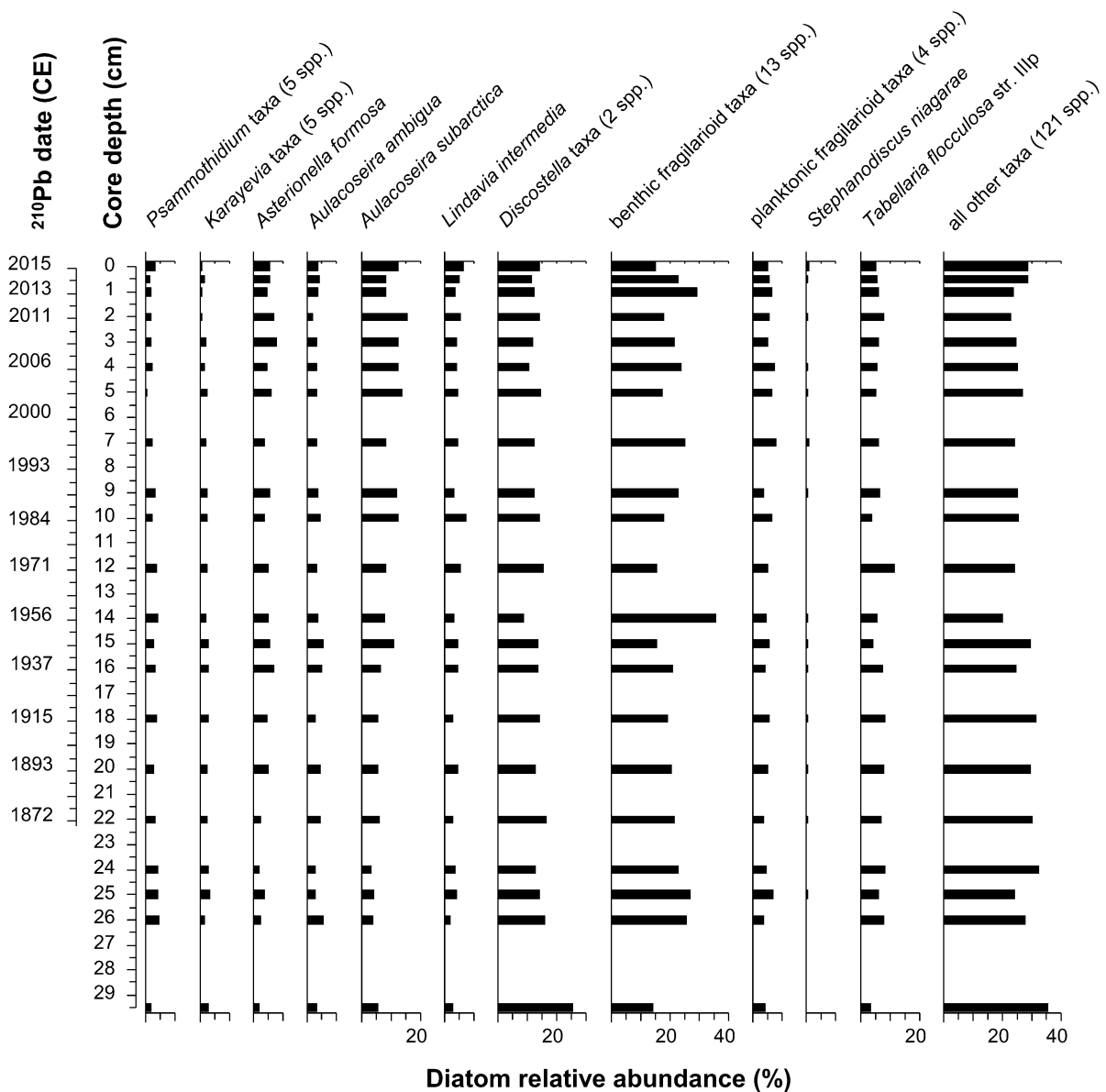
*Diatoms*

Diatom taxa were deemed “rare” if they were below 4% relative abundance in all intervals and these rare taxa were grouped as “All other taxa” for the figure (Fig. 7). The diatom record exhibits little change over time. For the entire diatom record, the assemblages are dominated by small benthic fragilaroid taxa (15 to 30% relative abundance), comprised predominantly of *Staurosirella pinnata* (Ehrenberg) D. M. Williams & Round, *Pseudostaurosira brevis-triata* (Grunow) D. M. Williams & Round, and *Staurosira construens* (Ehrenberg) D. M. Williams & Round, in order of prominence. Centric planktonic taxa *Discostella stelligera* (Cleve and Grunow) Houk and Klee 2004, *Discostella pseudostelligera* (Hustedt) Houk and Klee 2004 and members of the genus *Aulacoseira* Thwaites are also a prominent feature in the sediment record ranging from ~ 8 to 25% and ~ 7 to 17% relative abundance for *Discostella*

spp. and *Aulacoseira* spp., respectively (Fig. 7). Tychoplanktonic *Aulacoseira subarctica* (Otto Müller) E. Y. Haworth increases from < 5% relative abundance at the beginning of the record until ~ 1870 to 8 to 16% relative abundance from ~ 1940 to present day (Fig. 7). Elongate planktonic *Asterionella formosa* Hassall valves increase slightly around the same time, with < 3.5% relative abundance prior to ~ 1890 and from ~ 4 to 8% relative abundance thereafter (Fig. 7). These increases are concurrent with slight decreases in *Psammothidium* L. Bukhtiyarova & Round and *Karayevia* Round & L. Bukhtiyarova ex Round taxa. The relative abundances of all other taxa are either stable throughout the record or are variable with no discernable trends (Fig. 7).

*Cladocerans*

Assemblages throughout the record are dominated by bosminids. Like the diatoms, sedimentary cladocerans



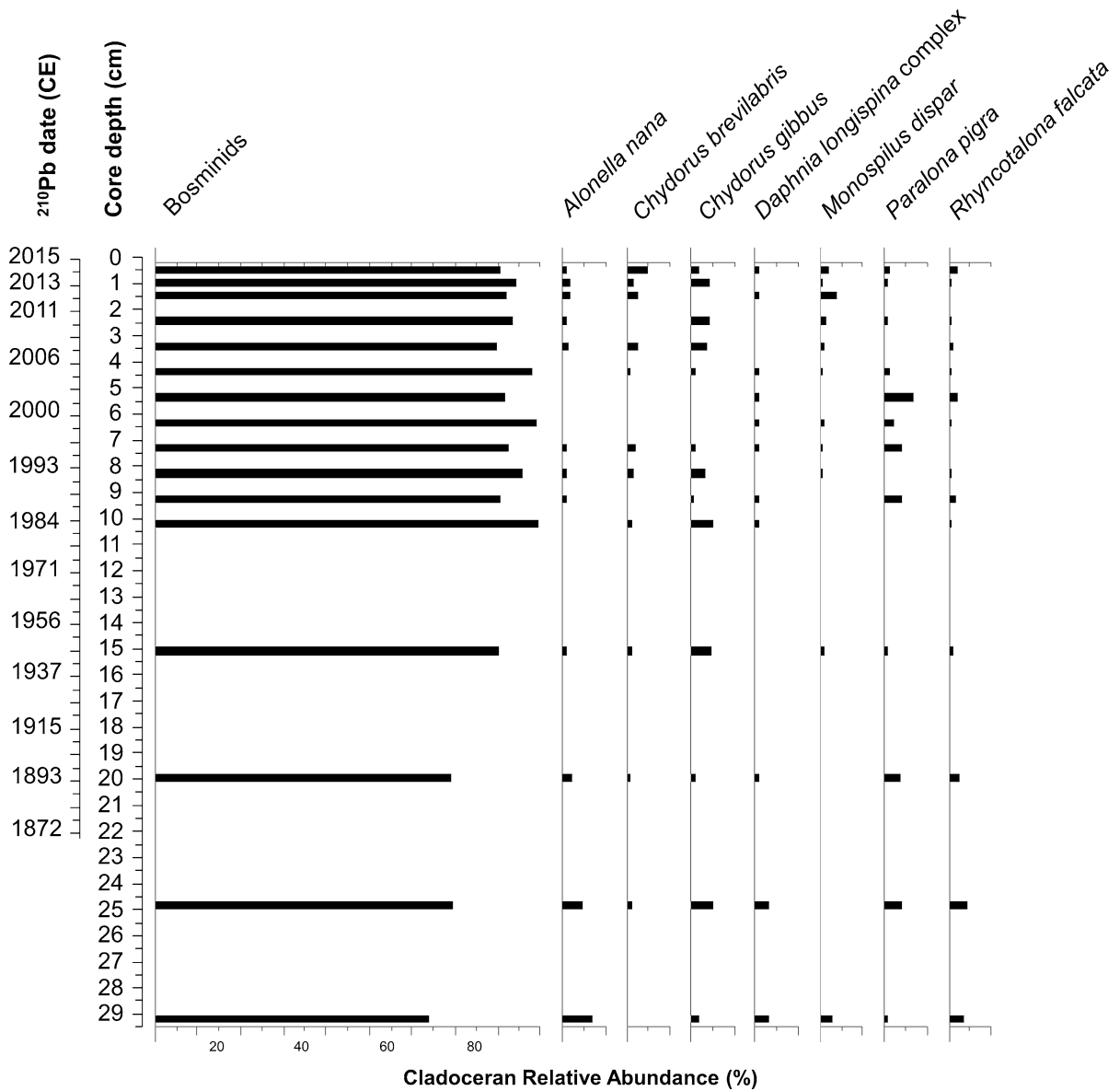
**Fig. 7** Diatom assemblage changes scaled by core depth (with secondary axis of estimated  $^{210}\text{Pb}$  dates) showing relative abundance of the most common taxa; the number of species within each complex is shown in brackets

undergo subtle changes throughout the sediment record (Fig. 8). The most notable change is a gradual increase in bosminids from  $\sim 65\%$  relative abundance at the beginning of the record to  $\sim 80\%$  abundance by the  $\sim 1950\text{s}$  and remaining elevated thereafter (Fig. 8). The increase in bosminids is accompanied by decreases in the less abundant *Alonella nana* Baird (from  $\sim 7$  to  $\sim 1\%$ ),

*Rhynchotalona falcata* Sars (from  $\sim 3$  to  $\sim 1\%$ ) and the *Daphnia longispina* complex (from  $\sim 3$  to  $< 1\%$ ).

#### Chironomids

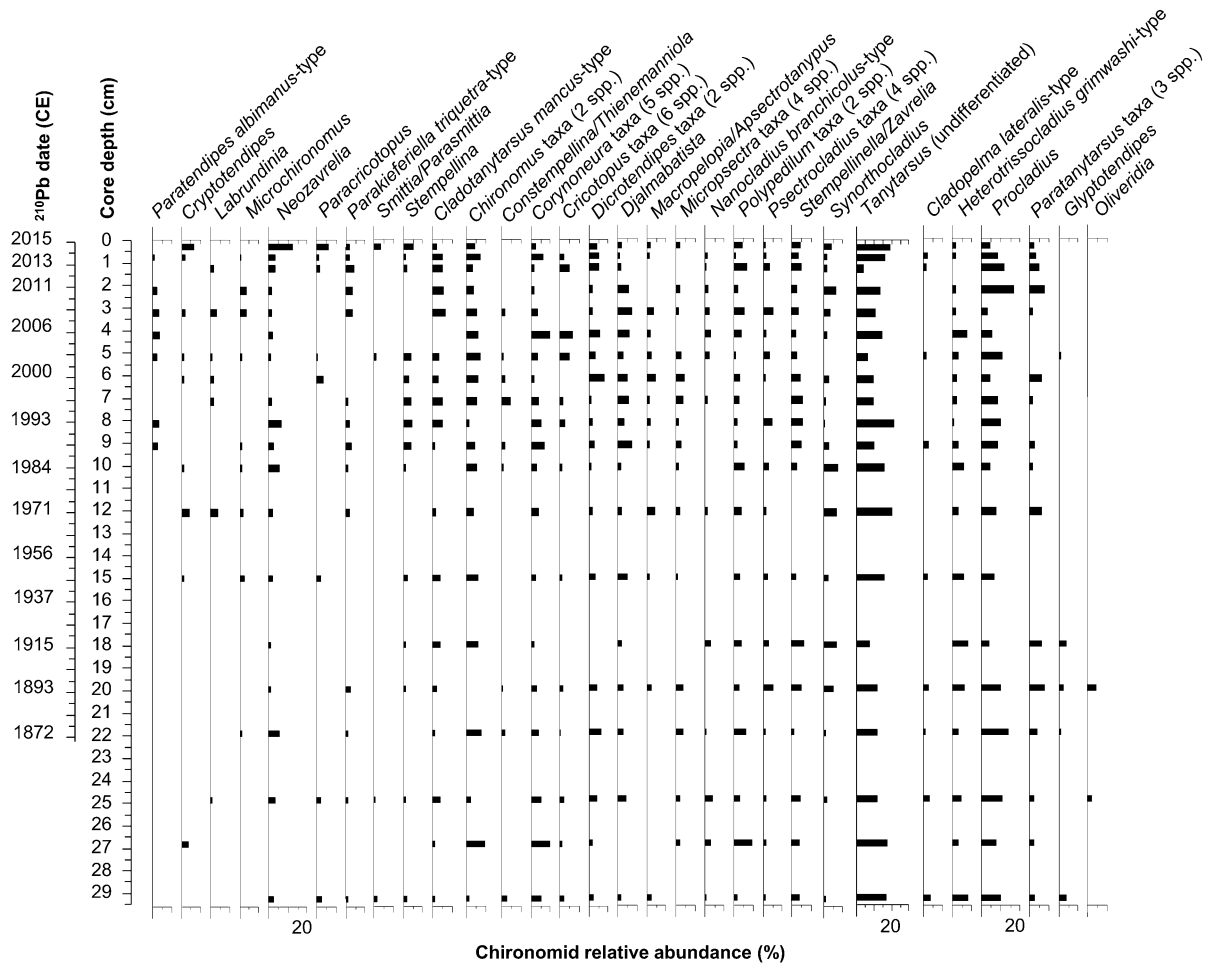
Chironomid assemblages undergo more pronounced changes in composition over the past  $\sim 200$  years



**Fig. 8** Cladoceran profile scaled by core depth (with secondary axis of estimated <sup>210</sup>Pb dates) showing relative abundance of taxa that occurred in at least two samples with a relative abundance of at least 2%

relative to the subtle changes in both diatom and cladoceran assemblages (Fig. 9). The most common taxa observed were undifferentiated *Tanytarsus* van der Wulp species, followed by *Procladius* Skuse (Fig. 9). Most taxa present are often found in mesotrophic or oligotrophic lakes. Taxa often associated with relatively warm and mesotrophic waters, such as *Labrundinia* Fittkau (Brodin 1986) and *Microchironomus* Kieffer (Kansanen 1985; Brodin 1986; Brooks et al. 2007), appear and become a

consistent feature of assemblages in the post-1950 sediments. *Paratendipes albimanus*-type also appears in assemblages for the first time at ~ 1989 and remains in notable abundances to the present. Recent increases after ~ 1985 occur in *Cryptotendipes* Lenz ( $T_{opt}$  24.0 °C; Laroque and Rolland 2006) and *Cladotanytarsus mancus*-type, which has been found to occur in warm waters of the littoral zone ( $T_{opt}$  17.9 °C; Laroque and Rolland 2006), as well as *Stempellina* Thienemann & Bause, a warm stenotherm



**Fig. 9** Chironomid profile scaled by core depth (with secondary axis of estimated  $^{210}\text{Pb}$  dates) showing relative abundance of taxa that occurred in at least two samples with a

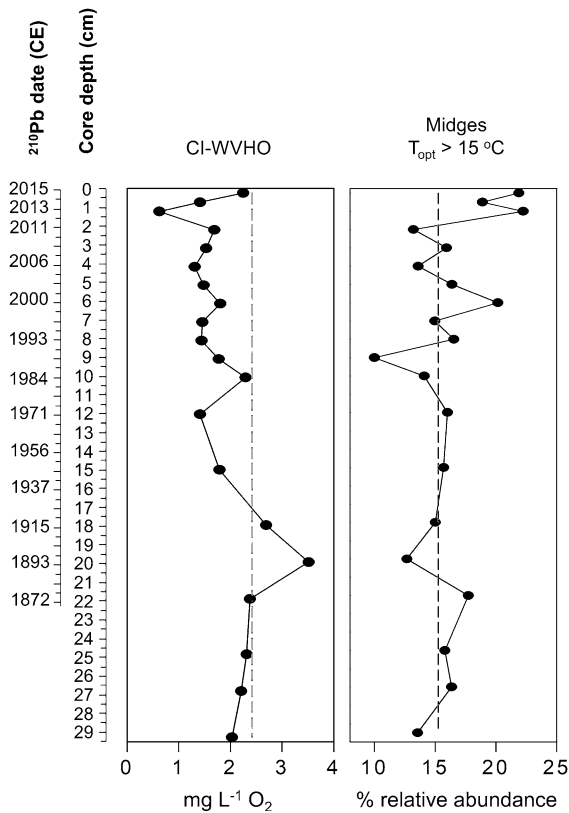
relative abundance of at least 2%, and at least one sample with a relative abundance of at least 4%; the number of species within each complex is shown in brackets

(Brundin 1949; Walker et al. 1991) found in oligotrophic lakes (Brundin 1949; Brodin 1986) ( $T_{\text{opt}}$  17.9 °C, Laroque and Rolland 2006) (Fig. 9). Trends towards higher relative abundances of warm-water taxa, summarized by grouping species with a thermal optimum of greater than 15 °C, indicate a subtle shift beginning around 1990 and becoming slightly more pronounced in the last 2 years of the record (2013–2015) (Fig. 10). The CI-VWHO model applied to the Dickson Lake core indicated that end-of-summer hypolimnetic oxygen values were historically hypoxic, around 2.0–3.5 mg L<sup>-1</sup> until ~ 1950, with peak concentrations of the sampled intervals being > 3.5 mg L<sup>-1</sup> in the late nineteenth century (Fig. 10). After this time, the mean volume-weighted

hypolimnetic oxygen concentration is consistently inferred to be even lower at < ~ 1.8 mg L<sup>-1</sup> (Fig. 10). The lowest inferred oxygen levels on record of 0.63 mg L<sup>-1</sup> occur in the sediment sample from 1 to 1.5 cm (2012–2013, estimated  $^{210}\text{Pb}$  dates), shortly before the first reported bloom in 2014 (Fig. 10).

## Discussion

Our multi-proxy paleolimnological analysis of remote, oligotrophic, cyanobacterial bloom-affected Dickson Lake indicates that changes in subfossil diatom, chironomid, and cladoceran assemblages over the past ~ 200 years are muted. Based on our data,



**Fig. 10** Chironomid-inferred end-of-summer volume-weighted hypolimnetic oxygen concentration (CI-VWHO), and percent relative abundance of warm midge taxa ( $T_{opt} > 15\text{ }^{\circ}\text{C}$ ) scaled by core depth (with secondary axis of estimated  $^{210}\text{Pb}$  dates). Dashed lines represent pre-1950 means

there is no clear “smoking-gun” indicating why cyanobacterial blooms were observed in the lake beginning in 2014. Nevertheless, through a process of elimination and a weight-of-evidence approach, we discuss the likely contributions that various environmental factors may have had on bloom formation in the study lake.

Are the recent blooms unprecedented?

The most noteworthy change of the five proxies analyzed in this study is the persistent increase of spectrally inferred primary production since ~ 1930, with post-1980 estimates surpassing the highest levels previously recorded in the sedimentary sequence (Fig. 6). This increase in aquatic primary production in a lake that has not experienced cultural eutrophication suggests the importance of factors other than

allochthonous nutrient additions in prompting excessive algal growth. Regional warming, a longer ice-free period, and declines in wind speed (Fig. 3) can bolster whole-lake primary production, even in the absence of increases in catchment derived nutrients, as has been observed in many other lakes (Michelutti et al. 2005; Weyhenmeyer and Broberg 2014; O’Beirne et al. 2017; Paterson et al. 2017). The striking increase in sedimentary cyanobacterial akinete microfossils around 2014 suggests that the observed cyanobacterial blooms in this year were in fact unprecedented in Dickson Lake (Fig. 6). The ~ 2014 peak in akinete microfossils was followed by a return to lower akinete abundance in a surface sediment sample collected in 2016, consistent with the absence of a bloom in that year. These results are consistent with historical records, as there are no known accounts of blooms in Dickson Lake, apart from those in 2014 and 2015, since the establishment of the Park in 1893.

Have nutrient levels changed?

Dickson Lake is remote and the catchment is isolated from direct anthropogenic nutrient sources such as urban development and agriculture. However, nutrients could plausibly deviate from natural variability due to fluctuations in lake water levels, export of naturally occurring phosphorus from the catchment, or in the amount of internal nutrient loading from the sediments. Measured total phosphorus (TP) concentrations from surface waters of Dickson Lake indicate a decline from mesotrophic to oligotrophic levels since the 1980s (Table 1). This decrease is consistent with trends seen in other Ontario Shield lakes that have recorded declines in phosphorus concentrations since the 1970s (Eimers et al. 2009; Palmer et al. 2011). Although total inorganic nitrogen (TIN) concentrations appear to have increased in Dickson Lake since the 1980s (Table 1), despite a declining trend in atmospheric deposition observed in the region (Kothwala et al. 2011; Vet et al. 2014; Sivarajah et al. 2016), the cyanobacterial taxa that have produced blooms in Dickson Lake (*Dolichospermum*) are diazotrophic and are therefore not limited by lake water inorganic nitrogen (Molot 2017). Moreover, the TIN:TP ratios at the time of data collection suggest that P is the limiting nutrient (i.e. TIN:TP > 3.4; Bergström 2010). There is also no indication of nutrient enrichment in the paleolimnological record, with diatom taxa indicative

of higher nutrient levels, such as *Stephanodiscus niagarae* Ehrenberg, remaining in trace abundances throughout the sedimentary sequence (Fig. 6).

However, Dickson Lake is on the higher end of the nutrient gradient among Algonquin Park lakes, and may therefore be primed to support, or be more susceptible to, cyanobacterial blooms than nearby lakes. Of 55 Algonquin Park lakes sampled in August 2015, Dickson Lake had the second highest measured TP concentration at  $10.2 \mu\text{g L}^{-1}$  (Rampone 2018). Interestingly, cyanobacterial blooms have also occurred in a few other Algonquin Park lakes in recent years with lower TP concentrations than Dickson (Lake of Two Rivers, Opeongo Lake, Merchant Lake, all with measured August 2015 TP concentrations of  $\sim 4.8$  to  $5.7 \mu\text{g L}^{-1}$ ).

#### Has hypolimnetic dissolved oxygen declined?

Anoxic hypolimnetic waters generate redox conditions in which phosphorus and ferrous iron (an important micronutrient that can limit cyanobacteria; Sorichetti et al. 2014) can be released from the sediments into the water column, potentially fueling subsequent algal growth (Molot et al. 2014). This mechanism has therefore been considered a potential trigger for bloom events. As previously discussed, there is no evidence that nutrient levels have increased in Dickson Lake, and it is therefore unlikely that the relative contribution of external nutrient loading in Dickson Lake has changed. However, water chemistry data have been primarily collected from surface waters (composite samples collected through the Secchi depth) and therefore may not capture an internal nutrient loading signal. Moreover, since internal nutrient loading is coupled with anoxia, it tends to peak near the end of summer, when lakes have been stratified for a few weeks to months. Cyanobacteria can access these nutrients from the hypolimnion during stratification (Cottingham et al. 2015), prior to their redistribution during fall overturn. Since diatoms commonly dominate during mixing periods in the spring and fall, the sedimentary diatom record may not be responsive to increases in internal nutrient loading that occur in late summer when the nutrients can be scavenged by cyanobacteria.

Subfossil chironomid assemblages provide useful information on levels of hypolimnetic oxygen at the end of summer, and therefore are reliable indicators of

the potential for internal phosphorus and ferrous iron loading. The observed declines in oxic *Heterotrissocladius grimwashi*-type beginning around 1990 (Fig. 10) are likely associated with declines in hypolimnetic dissolved oxygen (Quinlan and Smol 2001b). In the two years prior to the 2014 cyanobacterial bloom, end-of-summer CI-VWHO registers the lowest oxygen conditions of the sedimentary record, following initial declines post- $\sim 1950$ . Declines in hypolimnetic oxygen in Dickson Lake since the mid-twentieth century may be indirectly attributable to recent warming that also likely triggered the simultaneous increase in aquatic primary production indicated by spectrally inferred chlorophyll *a* (Fig. 6), as well as longer open-water periods (Fig. 3f) and enhanced thermal stratification.

#### Have there been changes in grazing pressure?

Many softwater lakes in Ontario have been experiencing calcium declines as a legacy effect of base cation depletion from acidification in the early- to mid-1900s, as well as repeated cycles of deforestation, resulting in a decline of calcium-rich daphniids relative to other cladoceran taxa (Korosi et al. 2012; Jeziorski et al. 2014; Jeziorski and Smol 2017). In some cases, this lakewater calcium decline has been linked to increases in algal production through food web interactions (Korosi et al. 2012). Despite a decline in the measured calcium concentrations in Dickson Lake between the 1980s and 2015–2016 (Table 1), concentrations remain well above critical thresholds (i.e.  $1.5 \text{ mg L}^{-1}$ ) necessary for survival and reproduction of daphniids (Jeziorski et al. 2008). Therefore, the observed gradual  $\sim 15\%$  increase in the relative abundance of calcium-poor bosminids and concurrent  $\sim 2\%$  decline in calcium-rich daphniids prior to  $\sim 1950$  in Dickson Lake (Fig. 8) is likely not attributable to calcium decline. Nonetheless, bosminids are less effective grazers than other cladoceran species and their increase in the post- $\sim 1930$  sediments, at the expense of more efficient zooplankton grazers (i.e. daphniids), could be considered a top-down control linked to increasing whole-lake primary production at this time (Fig. 6). However, this shift in cladoceran assemblage composition is subtle and therefore unlikely to be a major driver of increasing algal production in Dickson Lake.



## Is climate warming a contributing factor to the recent blooms?

Regional meteorological records indicate pronounced changes in climate metrics over the past century, with air temperatures and precipitation exceeding the record mean around the mid-1960s. Additionally, the ice-free growing season has increased by  $\sim 15$  days, and wind speeds have declined by  $\sim 1.5$  to  $3 \text{ km h}^{-1}$  and fall below the record mean at around 1980 (Fig. 3). However, there are no anomalies or extremes observed in any of these annually-resolved variables between 2013 and 2015 that would explain the manifestation of the recent blooms in Dickson Lake.

The arrival and/or increase in small planktonic diatom taxa in the sedimentary record (at the expense of heavier-celled taxa and/or small, benthic fragilaroid taxa) is often associated with a response to warming-related changes in the water column (especially fast-growing *Discostella* spp.; Rühland et al. 2015). In Dickson Lake, *Discostella* spp., benthic fragilaroid taxa as well as *Aulacoseira* taxa have co-occurred in relatively stable and modest relative abundances throughout the diatom record, suggesting that conditions were favourable to support these ecophysiological different taxa (e.g. periods of strong mixing and periods of thermal stratification). There is no evidence for a substantial change in the thermal regime of this lake over the past  $\sim 200$  years, despite climate conditions becoming favourable for enhanced thermal stability (i.e. longer ice-free period, warmer temperatures and reduced wind). Indeed, a recent top–bottom assessment of diatom assemblages in 53 Algonquin Park lakes, including Dickson Lake, indicates that regionally there is a subtle diatom response to warming in Algonquin Park although this is not the case in every lake (Rampone 2018). Specific reasons for the lack of a diatom response to climate in Dickson Lake (and some other Algonquin Park lakes), whilst other lakes under similar climate warming conditions have pronounced responses, remain unclear.

Cladoceran assemblages can be summarized as undergoing gradual and directional change, as observed in PCA Axis 1 sample scores throughout the sediment sequence (Electronic Supplementary Material 2). Specifically, increases in pelagic bosminids and corresponding declines in littoral *Alonella nana* and *Rhyncotalona falcata* (albeit subtle) in the

cladoceran assemblages of Dickson Lake is consistent with trends reported from the Experimental Lakes Area (Jeziorski et al. 2014), Ontario's Ring of Fire region (Jeziorski et al. 2015), the East Coast of Canada (Korosi et al. 2012), and other Algonquin Park lakes (A.M. DeSellas, unpubl. data) in response to anthropogenic warming. This may be due to the relatively small body size of bosminids allowing them a competitive advantage over larger-bodied cladocerans under a warming climate (Daufresne et al. 2009).

Similar to the cladoceran assemblages, chironomid assemblages may also show a subtle response to warming, beginning in the mid-1900s, with the appearance of warm-water taxa including *Cryptotendipes* (Laroque and Rolland 2006), *Labrundinia* (Matthews-Bird et al. 2016), *Microchironomus* (Brooks et al. 2007), and *Stempellina* (Brundin 1949; Walker et al. 1991; Laroque and Rolland 2006). The appearance of *Paratendipes albimanus*-type during this period may also be an indication of warmer water temperatures based on optimal growth rate in mesocosm studies at  $20 \text{ }^{\circ}\text{C}$  (Reynolds and Benke 2005). In the 1990s, an increase in the relative abundances of dipteran taxa with thermal optima greater than  $15 \text{ }^{\circ}\text{C}$  is observed (Fig. 10), with further increases in the most recent sediment intervals corresponding to 2013–2015, indicating warmer water temperatures in recent years in response to regional warming.

## The possible role of short-term climate variability as an explanation for the 2014 bloom

While it is clear that the long-term climatic and limnological conditions have changed in a manner that is favourable to cyanobacteria, shorter-term climate variability (i.e. meteorology) may have been important in triggering the 2014 bloom in Dickson Lake. For example, despite long-term increases in air temperature and precipitation, decreases in wind speed, and earlier ice-off, 2014 stands out as anomalous to these trends in at least one respect: an unusually late ice-out. This late ice-out date in 2014 was immediately followed by above average air temperatures and low wind speeds in the subsequent 2 weeks (Fig. 4). These factors could have produced unusual limnological conditions in Dickson Lake during the spring of 2014, such as a rapid onset to thermal stratification resulting in a very short spring overturn period (i.e., less than a week), as was observed in other lakes in the region in

May, 2014 (MECP, unpubl. data). In turn, this may have resulted in incomplete spring mixing and oxygen replenishment in the water column, resulting in lower than normal hypolimnetic dissolved oxygen concentrations at the beginning of the summer. The decline recorded in our midge-inferred hypolimnetic oxygen concentration data around 2014 corroborates this hypothesis. These conditions could have exacerbated internal nutrient loading of phosphorus and iron into the hypolimnion over the course of the growing season. Cyanobacteria have the means to access these hypolimnetic nutrients through buoyancy regulation and vertical migration (Cottingham et al. 2015).

An ultimate driver and a proximate cause

Although recent changes in climate are not well expressed in the diatom record from Dickson Lake, the weight-of-evidence from our other proxies does support changes in regional climate metrics being the ultimate driver for the onset of cyanobacterial blooms in 2014 and 2015. In addition to being able to exploit increases in internal nutrients, warmer temperatures, a longer growing season and weaker water column mixing (i.e. reduced wind speed) provide conditions favourable for cyanobacterial proliferation (Paerl and Huisman 2008, 2009).

By eliminating elevated catchment-derived nutrients and changes in grazing pressure as potential causes, and adding additional evidence of subtle declines in hypolimnetic dissolved oxygen and increases in warm-water chironomid taxa and small-bodied cladoceran taxa, we conclude that increasing whole-lake primary production since ~ 1930, and ultimately the manifestation of the 2014 and 2015 cyanobacterial blooms, were most likely a result of accelerated climate change leading to ideal bloom conditions.

An anomalously late ice-out in 2014 (paired with elevated temperatures and low wind speeds) may have contributed as a proximate cause for the blooms in Dickson Lake by reducing the spring mixing period resulting in intensified end-of-summer anoxia and internal nutrient loading. Future monitoring of hypolimnetic DO, P and Fe concentrations, especially in the fall, winter, and spring prior to late summer bloom events, would be useful to substantiate our interpretations. Despite a thorough examination of five paleolimnological indicators in a sediment core

spanning two centuries, we hypothesize, but are unable to definitively point to specific limnological factors that could account for the cyanobacterial blooms observed in Dickson Lake in 2014 and 2015. This is worrisome and emphasizes the challenges in understanding what triggers cyanobacterial blooms in remote lakes and the unpredictability of environmental interactions with continued anthropogenic climate change. Acknowledging that we lack the measured data to unequivocally determine the cause, we suggest a combination of long-term trajectories in air temperature and wind speed, paired with unusual weather conditions in the spring of 2014, leading to heightened hypolimnetic anoxia and subsequent internal nutrient loading, as the most likely explanation for the recent development of cyanobacterial blooms in Dickson Lake.

## Conclusions

Our analysis of a  $^{210}\text{Pb}$ -dated sediment core from remote Dickson Lake revealed that the observed 2014 *Dolichospermum* bloom was likely the unprecedented response to climate-mediated changes in lake properties (both long-term change and short-term variability). The subsequent 2015 bloom may have been a direct result of the 2014 bloom itself, which would have provided a large supply of resting cells to the sediment to act as an inoculum for cyanobacterial population growth in 2015. Our paleolimnological data corroborate this hypothesis showing that, even in the absence of increased nutrients, the past few years have experienced the lowest midge-inferred bottom-water oxygen levels, increases in warm-water chironomid taxa, the highest whole-lake primary production, and the highest abundance of cyanobacterial akinetes of the ~ 250-year sedimentary record. Pronounced changes in climate metrics that affect bloom formation are on a trajectory that is advantageous for cyanobacterial proliferation. Our results highlight the complexity of biological responses to anthropogenic warming and that the factors responsible for bloom formation in remote, oligotrophic lakes are not yet fully understood. This is troubling, particularly in light of the forecasts of future climate scenarios for Ontario (McKenney et al. 2010; McDermid et al. 2015) that are anticipated to result in increased severity and frequency of bloom events in the future, even in lakes

with low direct anthropogenic impact such as Dickson Lake.

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