

# Tracking the long-term responses of diatoms and cladocerans to climate warming and human influences across lakes of the Ring of Fire in the Far North of Ontario, Canada

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**Abstract** The extensive peatlands and lakes of the Far North of Ontario warrant committed scientific attention given their status as a significant carbon sink. Economic interest in this region has recently increased due to the discovery of vast mineral deposits (mainly chromite and nickel) known as the “Ring of Fire”. Mineral exploration and infrastructure planning are underway, but environmental monitoring is only beginning. Detailed baseline ecological information is required to assess the impacts of future resource extraction within the context of multiple environmental stressors (including recent regional climate warming). Here we use sediment cores from two relatively deep lakes ( $Z_{\max} \sim 10$  m) and two shallow lakes ( $Z_{\max} \sim 2$  m), all located in the vicinity of the Ring of Fire, to examine biotic responses to warming prior to

the commencement of mining activities. Our data show that, over the past  $\sim 150$  years, diatom and cladoceran sedimentary assemblages have transitioned from dominance by littoral/benthic forms to greater abundances of planktonic cladoceran (an increase of  $\sim 3$  to 34 %) and diatom taxa (an increase of  $\sim 3$  to 22 %). Increased relative abundances of planktonic taxa are consistent with warming-induced changes in lake properties including longer ice-free periods and increased production by planktonic algae. The response of diatom assemblages in shallow lakes to warming preceded the deeper lakes by  $\sim 45$  to 60 years, and substantial increases in aquatic production ( $\sim 4$  to 15 times higher than in sediments deposited prior to 1900) were observed in the shallow lakes, in agreement with previous analyses demonstrating the heightened sensitivity of shallow systems to climate warming. These data provide important information necessary to distinguish potential ecological impacts related to resource extraction from natural

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variation and the ongoing responses to regional climate warming.

**Keywords** The Far North of Ontario · Ring of Fire · Climate change · Diatoms · Cladocerans

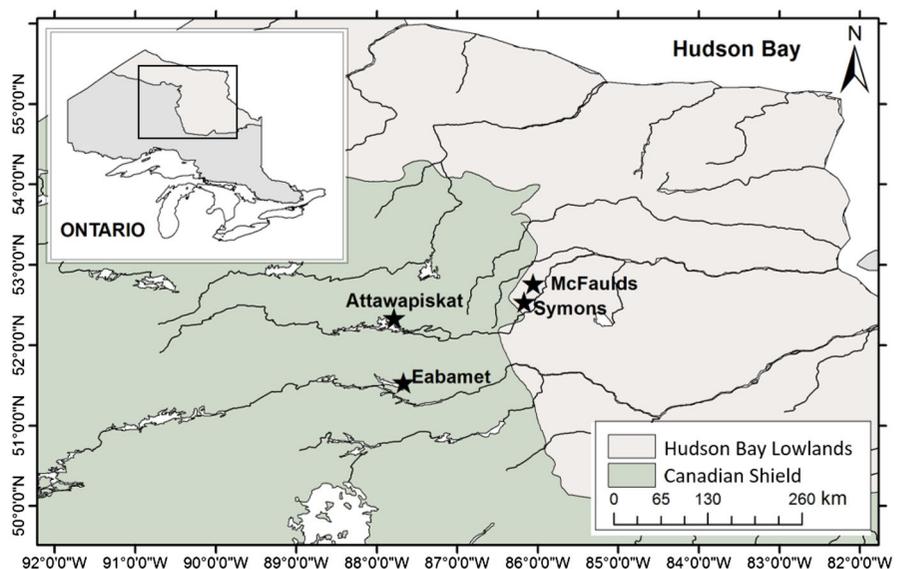
## Introduction

The Far North of Ontario ( $\sim 50$  to  $57^\circ\text{N}$ ,  $79$  to  $94^\circ\text{W}$ ; Fig. 1), Canada, is a region of increasing ecological and economic significance. Vast amounts of carbon ( $>35$  Gt C; Far North Science Advisory Panel 2010) are stored within the largest, continuous peatland in North America (second largest globally). Three of Canada's largest rivers cross the region and  $>10\%$  of the landscape is covered by lakes and rivers, representing a significant freshwater resource (Cox 1978; Far North Science Advisory Panel 2010). The substantial stores of carbon, potential value as a carbon sink, and abundant water resources warrant further research and collection of baseline ecological data. Air and sea surface temperatures on Hudson Bay have risen substantially since the mid-1990s (Hochheim and Barber 2014) suggesting that disruptions to the negative feedbacks that maintain the cool regional climate will have consequences for carbon storage and the persistence of sporadic discontinuous permafrost.

In northern Ontario, mining exploration, land claims, development proposals, and future plans for mineral extraction have recently intensified due to the discovery of extensive mineral deposits (e.g., chromite, gold, zinc, nickel, copper and platinum; Dyer and Burke 2012). Unpatented mining claims are particularly concentrated along the Attawapiskat River at the boundary between the Canadian Shield and the Hudson Bay Lowlands (HBL), a region of Ontario that has become known as the "Ring of Fire". The Ring of Fire is estimated to contain one of the largest chromite deposits on Earth (Hjartarson et al. 2014); therefore, the proposed mining and infrastructure developments required for extraction are of great economic importance. Balancing future resource development and conservation of these sensitive northern wetlands and lakes will require a detailed understanding of the regional ecology. Prior to the onset of mining and development in the Ring of Fire, there is an opportunity to proactively use paleolimnological techniques to identify baseline ecological conditions and the impacts of recent warming on these northern environments.

The Ring of Fire is situated at a latitude of  $52^\circ\text{N}$  and  $\sim 300$  to  $400$  km inland from Hudson Bay, where its cooling influence may be lessened, and where continental effects play a role in local climate (Crins et al. 2009). It is unknown whether the coastal marine climate could have sheltered Ring of Fire lakes from

**Fig. 1** Location of the four study lakes in the Far North of Ontario, Canada, with the Hudson Bay Lowlands and the Canadian Shield delineated



the impacts of early twentieth century warming, as was found in lakes closer to the Hudson Bay coast near the Sutton River (Rühland et al. 2013), approximately 200 km north of the Ring of Fire. The regional climate of the Far North of Ontario is primarily influenced by large-scale cold air masses that originate over Hudson Bay, along with land-sea breezes that impose cold air temperatures on the adjacent terrestrial environment (Martini 2006). In contrast with the pronounced warming trend across most of the Canadian Arctic that began as early as the middle of the nineteenth century (Smol et al. 2005), the subarctic HBL maintained stable and relatively cool conditions from 1960 to the mid-1990s (Rouse 1991; Gough et al. 2004; Macrae et al. 2014). Although the spatial extent of the cooling influence of Hudson Bay is not known precisely, modeling has suggested that a significant maritime effect could extend up to ~650 km inland at a latitude of 54°N (Rouse 1991).

In regions close to the coastline, the moderating effect of Hudson Bay sea ice on regional climate has diminished substantially over the last ~20 years due to changes in land surface air temperatures, Hudson Bay sea surface temperatures, sea ice thickness and extent, and sea ice phenology (Gough et al. 2004; Hochheim and Barber 2014). In contrast with the Ring of Fire, in the Sutton River region, a rapid, threshold-type response of HBL lake and river ecosystems to warming temperatures has occurred including: a large-scale fish die-off event from abnormally warm conditions in the Sutton River in 2001 (Gunn and Snucins 2010); evaporation and desiccation of lakes following low snowfall winters (Bouchard et al. 2013); and abrupt algal community changes and increased primary production as a result of warming and shorter duration of lake ice cover (Rühland et al. 2013, 2014, 2015; Friel et al. 2014). Trends towards warmer air temperatures and longer ice-free seasons on Hudson Bay are projected to continue and accelerate (Gough et al. 2004; Hochheim et al. 2010; McKenney et al. 2010), likely promoting further biological changes within lakes in the Far North of Ontario.

Diatoms (Bacillariophyceae) are often used as biomonitoring tools to track direct and indirect anthropogenic impacts such as nutrient and mining pollution (Dixit et al. 1992; Greenaway et al. 2012). In lakes of the HBL, and across the globe, diatoms have responded to changes in limnological conditions

linked to climate warming, including a reduction in seasonal ice cover, a longer open water and growing season, changes in the duration and strength of thermal stratification, and development of more complex substrates and aquatic habitats for the growth of diatoms (Lotter and Bigler 2000; Winder and Hunter 2008; Rühland et al. 2013, 2014, 2015; Friel et al. 2014; Weckström et al. 2014). Cladoceran subfossils are also widely used paleolimnological indicators that may respond to different ecological cues than diatoms, as the Cladocera occupy a mid-trophic position, and thus are major consumers of primary producers, benthic detritivores, and serve as prey items for planktivorous fish and invertebrate predators (Korhola and Rautio 2001; Korosi et al. 2010). Cladoceran communities are also strongly influenced and structured by ice cover (Catalan et al. 2013), habitat changes, and longer growing seasons that may place pressure on larger-bodied species (Bruce et al. 2010; Adamczuk 2014; Nevalainen et al. 2014). The response of cladocerans to recent changes in temperature is well described in central and northwestern European lakes (Lotter et al. 1997; Kattel et al. 2008), which share similar latitudinal gradients and temperate climates with Ontario lakes.

The responses of aquatic biota to regional climate warming in the Ring of Fire has yet to be described, as this is a remote and relatively understudied region of Ontario. The Ring of Fire is a heterogeneous landscape because it includes a major physiographic boundary (i.e. distinct change in geology), varied topography, variation in the degree of permafrost development, and, because of its vast wetlands, lake catchments contain large quantities of trapped carbon and water. The landscape is hydrologically complex and lakes across the region also vary in the degree of connectivity to other water bodies and in morphometry, including lake depth, which may contribute to highly variable responses to climate warming. Our objectives were to evaluate the responses of diatom and cladoceran communities to recent environmental changes in lakes in the Ring of Fire region to address the following questions: (1) Have the diatom and cladoceran assemblages of lakes located in the Ring of Fire changed in ways that are often induced by warmer air temperatures, such as changes in aquatic habitat availability and physical changes in the water column? (2) If so, when did these responses to warmer temperatures occur? (3) Do deeper lakes (~9 to 10 m in depth) and

shallow lakes (~1 to 2 m in depth) exhibit similar biological responses to environmental and climate change? (4) How do the ecological responses to regional climate warming within lakes in the Ring of Fire compare with lakes closer to the Hudson Bay coast, or to more southern, temperate Ontario lakes?

### Study site

The Ring of Fire lies on the boundary between two physiographic regions, the Canadian Shield and the HBL (Fig. 1). The Canadian Shield is dominated by an irregular topography underlain by Precambrian igneous and metamorphic rocks, and the relatively flat HBL is underlain by sedimentary rocks of Paleozoic and Mesozoic age covered by loose glacial and marine deposits (Martini 2006; Far North Science Advisory Panel 2010). Regional surveys of >50 lakes across the Ring of Fire have noted little differences between the chemistry of lakes located on the Canadian Shield and in the HBL (MacLeod 2014; Jeziorski et al. 2015). Small distinctions in lake water chemistry (e.g., elevated nutrients in McFaulds Lake) are attributed to variations in surficial cover (i.e. thick glacial till and peat deposits in catchments, degree of permafrost development) rather than the underlying bedrock (MacLeod 2014; Jeziorski et al. 2015).

The two relatively deep study lakes (Eabamet and Attawapiskat lakes) are located in the Canadian Shield and the two shallow lakes (McFaulds and Symons lakes) are in the HBL (Fig. 1). However, from previous studies, we do not anticipate that the change in physiographic region across the study sites will solely yield distinct differences in water chemistry and biota, and rather morphological differences are more important in structuring aquatic communities and responses to climate. These four lakes were selected to capture the most common and important lake types within the boundary of Ring of Fire unpatented mining claims. For instance, large, shallow lakes are a common landscape feature within the Ring of Fire (which currently extends ~50 km into the HBL) and deeper, fluvial lakes, although less common, are important to First Nations communities within the Far North of Ontario.

### *Ring of Fire shallow lakes*

McFaulds Lake (52°47′15.304″N, 86°3′10.384″W; Table 1) is located at the approximate center of the

Ring of Fire (Fig. 1), and was isolated from human activity until mining prospecting camps were recently established on the lake's perimeter. The lake is situated within the HBL, close to the transition zone between the HBL and the Canadian Shield. It is part of the Attawapiskat watershed and ~270 km from the Hudson Bay coast. McFaulds Lake is ~6 km long, ~14 km in perimeter, and shallow (coring depth = 2 m) and therefore is predominantly littoral habitat. Low relief organic peat deposits and bogs characterize the surrounding landscape (Riley 2011). Symons Lake (52°32′57.043″N, 86°9′3.393″W; Table 1) is located ~22 km to the south of McFaulds Lake (Fig. 1), and thus shares similar geology and catchment characteristics. The lake is the smallest of the four study lakes (2.3 km long and 7 km in perimeter), the shallowest (coring depth = 1.8 m), and has had the least human disturbance. Both McFaulds and Symons lakes are situated within a region classified as having sporadic discontinuous permafrost (10–50 % of region underlain by ground ice; Far North Science Advisory Panel 2010).

### *Ring of Fire deep lakes*

Eabamet Lake (51°31′11.661″N, 87°51′6.868″W) is located ~185 km to the SW of McFaulds Lake and is situated on the Canadian Shield (Fig. 1). It is considerably larger (~30 km long and ~80 km in perimeter) and deeper (coring depth = 9.0 m) than McFaulds and Symons lakes, and is closely connected to the Albany River, which may influence the lake's water levels. The lake is important to the community of Fort Hope and the Eabametoong First Nation, situated along its northern shoreline as both a drinking water source and a cool-water fishery. Attawapiskat Lake (52°11′40.711″N, 87°45′58.730″W), located ~40 km north of Eabamet Lake, is ~18 km long, >100 km in perimeter, and deep (10.4 m at coring depth) (Fig. 1). Attawapiskat Lake forms the headwaters to the Attawapiskat River, which flows through the center of the Ring of Fire (i.e., where the highest concentration of unpatented mining claims have been made). The Neskantaga First Nation community is situated on the shores of Attawapiskat Lake and the Lansdowne House climate station (Environment Canada, <http://climate.weather.gc.ca>) is located at the community airport. Both Eabamet and Attawapiskat lakes are southwest of the permafrost zones of northern Ontario (i.e. permafrost is not present). Compared to the shallow lakes, both of these fluvial, deeper lakes have

**Table 1** Geographical coordinates, physical variables, and water chemistry measurements including calcium (Ca), total phosphorus (TP), total Kjeldahl nitrogen (TKN), dissolved organic carbon (DOC), and dissolved oxygen (DO) for the four Ring of Fire study lakes

	McFaulds	Symons	Eabamet	Attawapiskat
Coordinates	52°47′15.304″N 86°3′10.384″W	52°32′57.043″N 86°9′53.393″W	51°31′11.661″N 87°51′6.868″W	52°11′40.711″N 87°45′58.730″W
Date of sampling	July 12, 2012	July 12, 2012	July 15, 2012	July 11, 2012
Distance to James Bay coast (km)	281	305	415	395
Coring depth (m)	2.0	1.8	9.0	10.4
Secchi depth (m)	1.4	1.4	2.8	1.5
pH	7.4	7.6	7.8	7.7
Ca (mg L <sup>-1</sup> )	7.2	9.0	14.0	12.8
TP (µg L <sup>-1</sup> )	18.0	11.2	8.6	10.6
TKN (µg L <sup>-1</sup> )	509	346	336	381
DOC (mg L <sup>-1</sup> )	12.0	13.0	10.9	14.0
Specific conductivity (µS cm <sup>-1</sup> )	46.2	61.8	96.4	87.6
DO at surface (mg L <sup>-1</sup> )	8.3	8.0	8.2	7.9
DO at bottom (mg L <sup>-1</sup> )	8.3	8.0	7.7	7.1

had several decades of direct human influence, and thus the biotic assemblages may also track changes related to human pressures (e.g., water level changes from damming, fishing pressure, erosion and nutrient enrichment). In 1890, the Hudson Bay Company built a trading post on the shores of Eabamet Lake. In 1905, 500 people signed the James Bay Treaty No. 9 to establish the Fort Hope Band and Fort Hope Indian Reserve, which included the First Nations of both Fort Hope and Lansdowne House. In 1969, construction of a generating system commenced in Fort Hope and in 1980 a forest fire destroyed most of the community infrastructure and the village was temporarily evacuated (<http://eabametoong.firstnation.ca/history-of-eabametoong-first-nation/>). The new community of Eabametoong was established in 1982, and as of the last regional census in 2006, the population was approximately 1144, whereas Lansdowne House is considerably smaller with a population between 265 and 414 people.

## Methods

### Water chemistry and sediment core collection

Sediment cores and water chemistry samples for the study lakes were collected in July 2012. Sediment cores were collected using either a Glew (1989)

gravity corer (for Attawapiskat and Eabamet lakes) or a Glew and Smol (2016) push corer designed for retrieving sediment from shallow lakes, and sectioned at 0.25-cm intervals using a Glew (1988) extruder. At each lake, efforts were made to sample within, or near, the deepest depositional basin of the lake determined from local knowledge for Eabamet Lake (Xavier Sagutch, personal communication) or through visual inspection from aerial surveys. At each lake, temperature and oxygen readings were taken at 1-m intervals throughout the water column using a YSI 58 Dissolved Oxygen Meter. For water chemistry analyses, an integrated sample of the lake water column was collected from the Secchi disk depth to the surface, following standard Ontario Ministry of the Environment and Climate Change (OMOECC) protocols (Ingram et al. 2013). All chemical analyses were performed at the OMOECC Dorset Environmental Science Centre laboratory.

### Radiometric dating

A chronology was determined for each core using an EG&G Ortec High Purity Germanium Gamma Spectrometer to measure the activity of radioisotopes (e.g., <sup>210</sup>Pb, <sup>137</sup>Cs, <sup>214</sup>Bi) (Schelske et al. 1994; Appleby 2001). For each core, approximately 15–20 sedimentary intervals were prepared for radiometric dating

following Schelske et al. (1994). Dates for each sample were determined using the constant rate of supply (CRS) model applied to the unsupported fraction of the  $^{210}\text{Pb}$  activity (Binford 1990; Schelske et al. 1994).

### Diatom preparation

Sediment samples were prepared for diatom analyses following standard procedures outlined in Battarbee et al. (2001). Briefly,  $\sim 0.5$  g of wet sediment from every 0.25-cm interval was treated with a 1:1 molar ratio of concentrated sulphuric ( $\text{H}_2\text{SO}_4$ ) and nitric ( $\text{HNO}_3$ ) acids to digest the organic content of the sediment and isolate the siliceous material. The rinsed siliceous slurries were pipetted onto cover slips, dried, and mounted on glass microscope slides using Naphrax<sup>®</sup>. A minimum of 400 diatom valves were counted for each sedimentary interval using a Leica DMRB light microscope fitted with differential interference contrast optics at  $1000\times$  magnification. Diatoms were identified to the lowest taxonomic level possible using a selection of taxonomic references (Krammer and Lange-Bertalot 1986–1991; Camburn and Charles 2000).

The prepared diatom samples contained an excess of siliciclastic material and very low concentrations of diatom valves below 5.5 cm in the Eabamet Lake core and below 4 cm in the Attawapiskat Lake core. To attain sufficient diatom counts for analysis, excess clastic material was removed and diatom valves were concentrated on the microscope slide by treating with a density gradient separation technique using the heavy liquid, sodium polytungstate (SPT) (Tapia and Harwood 2002) at a density of  $2.3 \text{ g cm}^{-3}$ .

### Cladoceran preparation

The preparation of cladoceran samples was adapted from Korhola and Rautio (2001). Approximately 1.0 g of wet sediment from each 0.25-cm interval was deflocculated in a 10 % potassium hydroxide solution and heated to  $80^\circ\text{C}$  for  $\sim 20$  min. Sediment slurries from each interval were then sieved using a  $38\text{-}\mu\text{m}$  mesh. To aid identification, chitinous remains were stained with a safranin-glycerol solution, and a few drops of ethanol were added to the slurry to inhibit fungal growth. Identification of cladoceran subfossils followed Korosi and Smol (2012a, b). A minimum of

$\sim 70$  to 100 cladoceran individuals were identified from each interval to obtain a representative sample of the sedimentary assemblage (Kurek et al. 2010).

### Chlorophyll-*a* analysis

The analyses of sedimentary chlorophyll-*a*, a proxy for overall aquatic primary production, largely followed the methods of Michelutti et al. (2005, 2010). The chlorophyll-*a* analysis resolution for each core depended upon the availability of sedimentary material and were as follows: (1) Attawapiskat for every interval except 4.5 and 5.5 cm; (2) Eabamet for every interval; (3) Symons for every interval until 5.5 cm, then every 1-cm; and (4) McFaulds at 0.25, 1.0, 1.5–3.5 cm continuously, then every 1 cm from 3.5–10 cm. Freeze-dried sediment was sieved through a  $125\text{-}\mu\text{m}$  screen onto weigh paper and added to vials that were then run through a spectrophotometer using Visible Near-Infrared Spectroscopy (NIRS) to infer chlorophyll-*a* concentrations. As wave absorption and chlorophyll-*a* concentrations are linearly correlated (Michelutti et al. 2005), the NIRS output of absorbance was used directly to calculate inferred chlorophyll-*a*. This was done by calculating the area under the 650–700-nm wavelength peak of a wavelength-absorbance plot (Wolfe et al. 2006). This technique is robust as the chlorophyll-*a* inferences are not affected by diagenetic processes or changes in chlorophyll-*a* sources (i.e., the inferences incorporate all algal production, including isomers and post-depositional degradation products) (Wolfe et al. 2006; Michelutti et al. 2010).

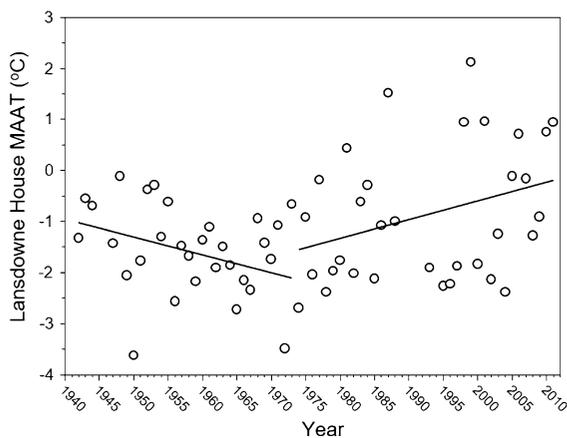
### Statistical analyses

Mean annual air temperatures (MAAT) from  $\sim 1943$  to 2011 (length of the instrumental record, missing data from 1989 to 1992 and 1994) were obtained from the Lansdowne House Climate Station (<http://climate.weather.gc.ca>). A 2-segment piecewise regression analysis (Toms and Lesperance 2003) was used to determine the timing of greatest change in measured regional air temperature in the Ring of Fire (Fig. 2). To examine temperature trends across the HBL, comparisons were made between the Lansdowne House MAAT and MAAT from Churchill, Manitoba, the nearest, continuous temperature record in the HBL. Direct comparisons and correlations between

long-term data sets and sediment records require sediment accumulation rates to be sufficiently rapid to allow precise matching with observational data (Battarbee et al. 2012). Correlation analysis between temperature records and summarized diatom and cladoceran data was not performed because the slow sediment accumulation rates of these northern Ring of Fire lakes inhibited the number of sedimentary intervals that could potentially be compared to annually resolved temperature records (i.e. relatively low temporal resolution as more time is captured within each sedimentary interval).

Species assemblage data from each core were expressed as percent relative abundances. For each proxy, biostratigraphic zones were identified by cluster analysis using constrained incremental sum of squares (CONISS) (Grimm 1987) with the number of zones determined with the broken stick model (Bennett 1996) via the “vegan” package (Oksanen et al. 2014) for the R software environment (R Development Core Team 2012). To characterize the timing of chlorophyll-*a* increases, piecewise linear regression models were applied (Toms and Lesperance 2003). A linear relationship with a single breakpoint was assumed, and a two-segmented model was used.

Although diatom taxa were identified to the level of species and often variety, several diatoms were grouped so that trends could be more easily visualized in the figures. However, all diatom taxa were kept



**Fig. 2** Mean annual air temperature (MAAT) (<http://climate.weather.gc.ca>) for Lansdowne House climate station (located at Attawapiskat Lake) with break-point identified at 1973 (straight solid lines). This climate station is missing data from 1989 to 1992 and 1994

distinct (i.e. not grouped) and the full diatom species assemblages were used for all statistical evaluations including cluster analysis (CONISS). The complete list of diatom taxa encountered in the 4 cores and their authorities are given in ESM 1. Species were only grouped if their % relative abundance showed no trend or similar trends (i.e. an increase or decrease) through time. Also, species have only been grouped if they share similar life strategies (e.g., planktonic, tycho-planktonic, benthic, epiphytic, etc.). Grouping taxa in this manner allowed us to display diatom, cladoceran and chlorophyll-*a* changes for each lake on the same stratigraphy. This highlighted the timing of changes within each proxy as they could be more easily compared. All bosminids were grouped together as *Bosmina* spp., as the amount of fragmentation and the large amount of debris that made it through the digestion process impeded our ability to differentiate between *Bosmina* and *Eubosmina* taxa with any confidence. In the shallow study lakes, both *Daphnia pulex* and members of the *Daphnia longispina* complex were present, and have been grouped as *Daphnia* spp., whereas in the deeper lakes, only members of the *D. longispina* complex were found.

## Results

McFaulds Lake (52°47′15.304″N,  
86°3′10.384″W)

McFaulds Lake is shallow ( $Z_{\max} = 2.0$  m) and circum-neutral (pH = 7.4). Nutrient concentrations were elevated compared to the other study lakes (total phosphorus (TP) = 18.0  $\mu\text{g L}^{-1}$ ; total Kjeldahl nitrogen (TKN) = 509  $\mu\text{g L}^{-1}$ ); however, conductivity was the lowest of the four study lakes (Table 1). The radiometric profile showed low initial  $^{210}\text{Pb}$  activity at 0.25 cm which subsequently increases to  $\sim 1100$   $\text{bq kg}^{-1}$  at 3 cm, and then  $^{210}\text{Pb}$  activities show a general exponential decay with depth to  $\sim 5.25$  cm (Fig. 3a). McFaulds Lake had the lowest sedimentation rate of the study lakes with a mean sedimentation rate of 0.0058  $\text{g cm}^{-2} \text{ year}^{-1}$ . Radioisotope  $^{210}\text{Pb}$  analysis and application of the CRS model identified a date of  $\sim 1850$  at a depth of 5.25 cm. Sedimentary chlorophyll-*a* concentrations in McFaulds Lake were below the detection limit of 0.01  $\text{mg g}^{-1}$  dry weight of sediment until  $\sim 1870$ , and

increased thereafter (Fig. 4a). Breakpoint analysis identified an increase in inferred chlorophyll-*a* beginning at ~1870. The chlorophyll-*a* at 2012 is ~15 times higher than concentrations prior to ~1870, representing the most pronounced increase in primary production recorded in any of the study cores.

The cluster analysis identified that the greatest change in the McFaulds Lake diatom assemblages occurred at ~1910 (4.5 cm, Fig. 4a). Diatom Zone 1 was composed mainly of larger (>40 µm) benthic diatom taxa including *Sellaphora* Mereschowsky complex, *Kobayasiella jaagii* (Meister) Lange-Bertalot, *Navicula reinhardtii* (Grunow) Grunow, *Neidium* Pfitzer spp., *Pinnularia* Ehrenberg spp., and *Stauroneis* Ehrenberg spp. (ESM 1). These diatom assemblages were almost entirely replaced in the modern sediments by diatom assemblages dominated by a combination of diatoms with a variety of life-strategies including epipsammic (*Achnanthes* Bory *sensu lato* complex), epilithic (fragilarioid taxa), epiphytic (*Brachysira neoexilis* Lange-Bertalot) and planktonic (*Fragilaria tenera* (W.Smith) Lange-Bertalot, *Asterionella formosa* Hassall) taxa (Fig. 4a). Of the diatom assemblages represented in Zone 1, only the *Sellaphora* complex is present in low abundances in the modern sediments.

The cluster analysis of the cladoceran sedimentary assemblages identified two main zones within the stratigraphy, the first major split occurring in the mid-2000s (~2 cm), separating Zone 1 and Zone 2 and a secondary split within Zone 1 occurring in the early 1900s (4.25 cm; ~1930), yielding Zone 1a and 1b (Fig. 4a). A total of 22 cladoceran taxa were recorded from the McFaulds Lake sediment core with *Bosmina* spp. and *Chydorus brevilabris* dominating the assemblages (Fig. 4a). Early in the record, cladoceran Zone 1a represents an assemblage composed almost entirely of *C. brevilabris* with ~83 % relative abundance compared to *Bosmina* which accounts for ~10 % of the relative abundance. The transition from Zone 1a to Zone 1b at ~1930 represents a substantial increase in *Bosmina* spp., and a concurrent decline in *C. brevilabris*. As well, both pelagic *Daphnia* spp. and littoral, acidophilous *Acantholeberis curvirostris* (Potts and Fryer 1979) appear for the first time in the sedimentary record and their presence continues to the top of the core. The transition from cladoceran Zone 1a to Zone 1b at 1930 lags the main diatom assemblage shift from Zone 1 to Zone 2 by ~20 years. Zone

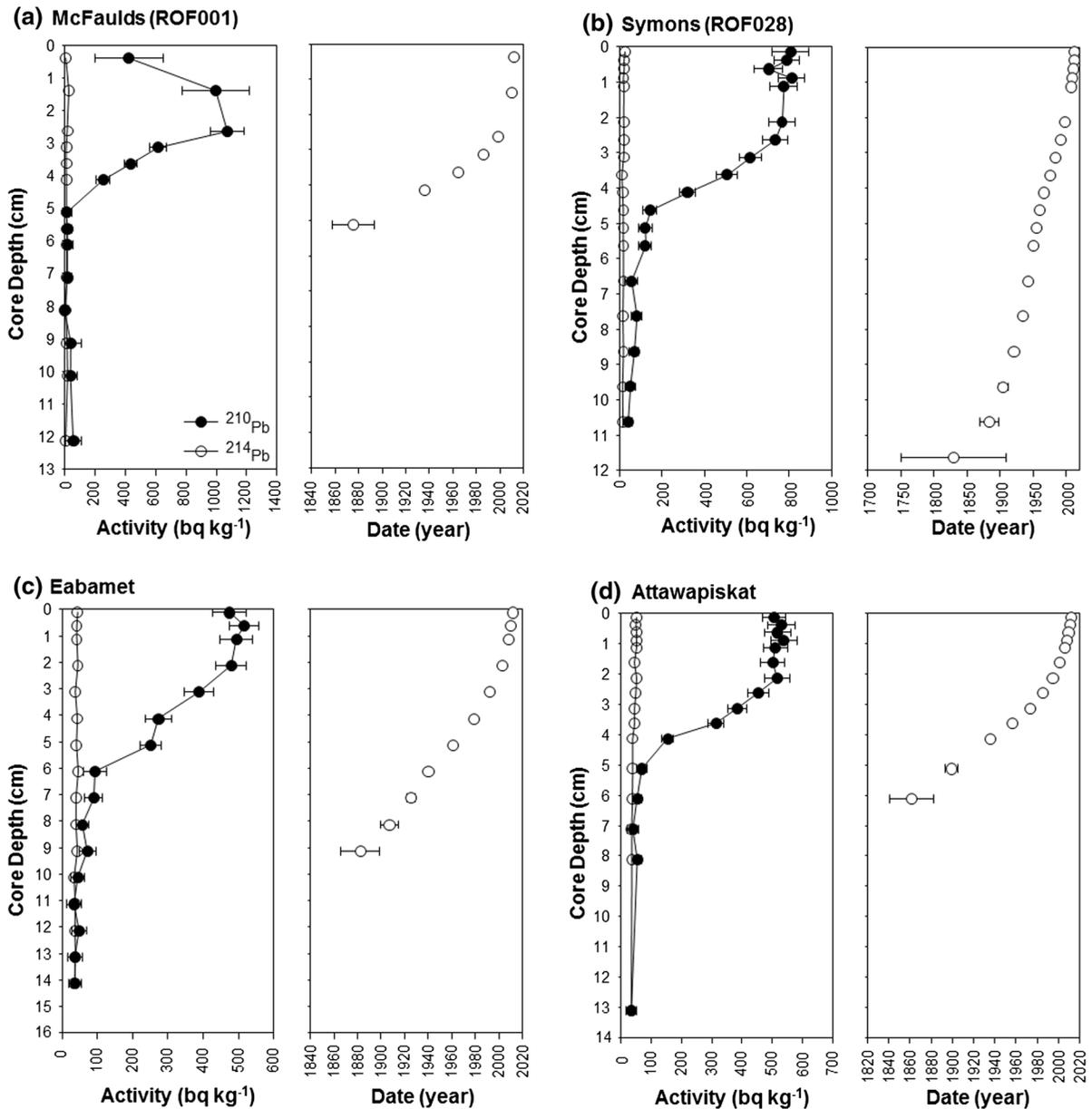
2 represents a further increase in *Bosmina* spp. (from 10 to 40 %) and a decline in *C. brevilabris* (from 83 to 35 %) throughout the core.

Symons Lake (52°32′57.043″N, 86°9′53.393″W)

Symons Lake is a shallow ( $Z_{\max} = 1.8$  m) lake that is chemically the most similar to McFaulds Lake. The lake is circum-neutral (pH = 7.6) and borderline mesotrophic (TP = 11.2 µg L<sup>-1</sup>; TKN = 346 µg L<sup>-1</sup>) (Table 1). The CRS model yielded a mean sedimentation rate of 0.0144 g cm<sup>-2</sup> year<sup>-1</sup> and the radiometric profile shows a <sup>210</sup>Pb date of ~1904 at a depth of 9.5 cm (Fig. 3b). Breakpoint analysis identified the greatest change in primary production occurred ~1965 when chlorophyll-*a* concentrations increased above the detection limit (>0.01 mg g<sup>-1</sup> dry weight).

CONISS identified two main diatom zones, with the greatest change occurring at ~1980 (3.25 cm) establishing Zone 1 and Zone 2 (Fig. 4b). There is a subsequent secondary split within each zone, at ~1960 (separating Zone 1a and 1b) and at ~2000 (splitting Zone 2a from Zone 2b). Common diatom taxa encountered in Symons Lake were epilithic fragilarioid taxa, largely from the genera *Staurosira* Ehrenberg and *Staurosirella* D.M. Williams and Round (Fig. 4b). These taxa contribute greater than 60 % of the diatom assemblages in Zone 1. A subtle increase in *Achnanthes sensu lato* complex and *Nitzschia* Hassall taxa distinguish Zone 1a and Zone 1b. The transition from diatom Zone 1 to Zone 2 is marked by substantial increases in the relative abundances of many *Nitzschia* taxa (e.g., *N. palea* (Kützing) W.Smith, *N. perminuta* (Grunow) M. Peragallo, *N. dissipata* (Kützing) Rabenhorst; ESM 1) and planktonic diatoms (e.g., *Fragilaria tenera*, *F. crotonensis* Kitton, *Asterionella formosa*). Planktonic taxa occurring in Symons Lake transition from a relative abundance of 0 % at the end of the nineteenth century to an average of ~7 % relative abundance within the twenty-first century (a subtle but notable change). The secondary split in Zone 2 is marked by the continued increase in planktonic taxa and *Nitzschia* spp., concurrent with a decline in benthic fragilarioid taxa.

Unlike the other study lakes, Symons Lake records very subtle cladoceran taxonomic changes (Fig. 4b), and therefore CONISS and broken stick analyses were not performed on this core. The sedimentary



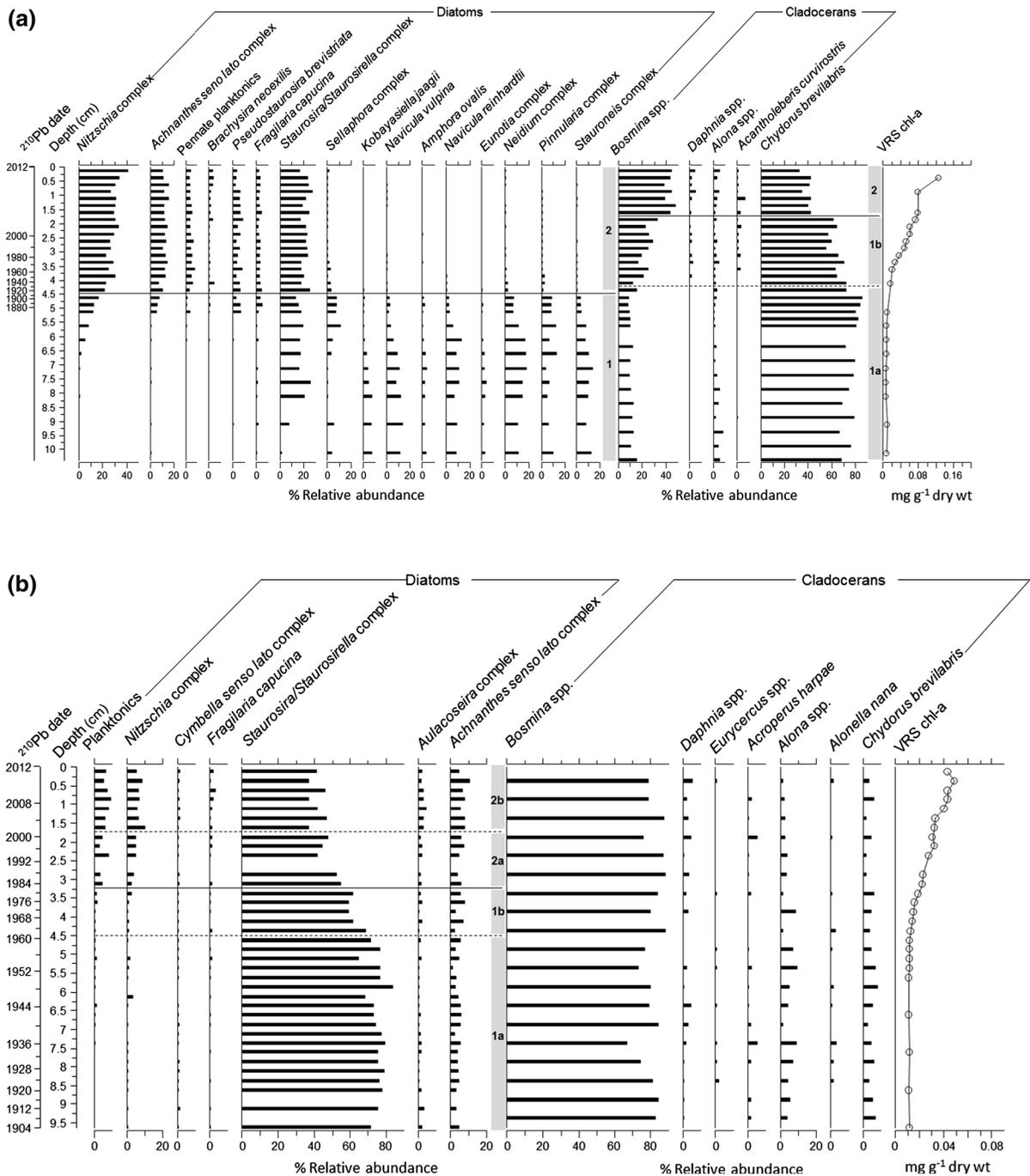
**Fig. 3**  $^{210}\text{Pb}$  (solid circles) and  $^{214}\text{Pb}$  (hollow circles) activities and estimated ages of sediment based on the constant rate of supply (CRS) model (Appleby 2001) for: **a** McFaulds,

**b** Symons, **c** Eabamet, and **d** Attawapiskat lakes. Error bars indicate 1 standard deviation in  $^{210}\text{Pb}$  activity and sediment age

cladoceran assemblage of Symons Lake is dominated by *Bosmina* spp. for the past ~150 years fluctuating between 74 and 88 % of the species relative abundance (Fig. 4b). Over the period of the cladoceran record there are small changes in relative abundances of *Daphnia* spp. with an increase by ~5 %, and decline in relative abundance of *C. brevilabris* by ~4 %.

Eabamet Lake (51°31'11.661"N, 87°51'6.868"W)

The two deep lakes are oligotrophic, with Eabamet Lake having the lowest nutrient (TP = 8.6  $\mu\text{g L}^{-1}$ , TKN = 336  $\mu\text{g L}^{-1}$ ) and dissolved organic carbon (DOC) concentrations, but the highest specific conductivity of all the study lakes (Table 1). The



**Fig. 4** Combined diatom and cladoceran profiles, scaled by depth (with secondary axis of estimated <sup>210</sup>Pb year), showing relative abundances of the most common taxa and species complexes for: **a** McFaulds Lake, **b** Symons Lake, **c** Eabamet Lake, and **d** Attawapiskat Lake. Diatom and cladoceran results for the constrained incremental sum of squares (CONISS) are also shown (solid horizontal lines indicate the primary zonation,

dashed lines, if present, indicate secondary zonations). Sedimentary chlorophyll-*a* analysis is plotted to the right of the species profiles on the same y-axis (and approximately same scale for all cores). Sodium polytungstate (SPT) was used to concentrate diatom valves in Eabamet Lake for the region highlighted in grey

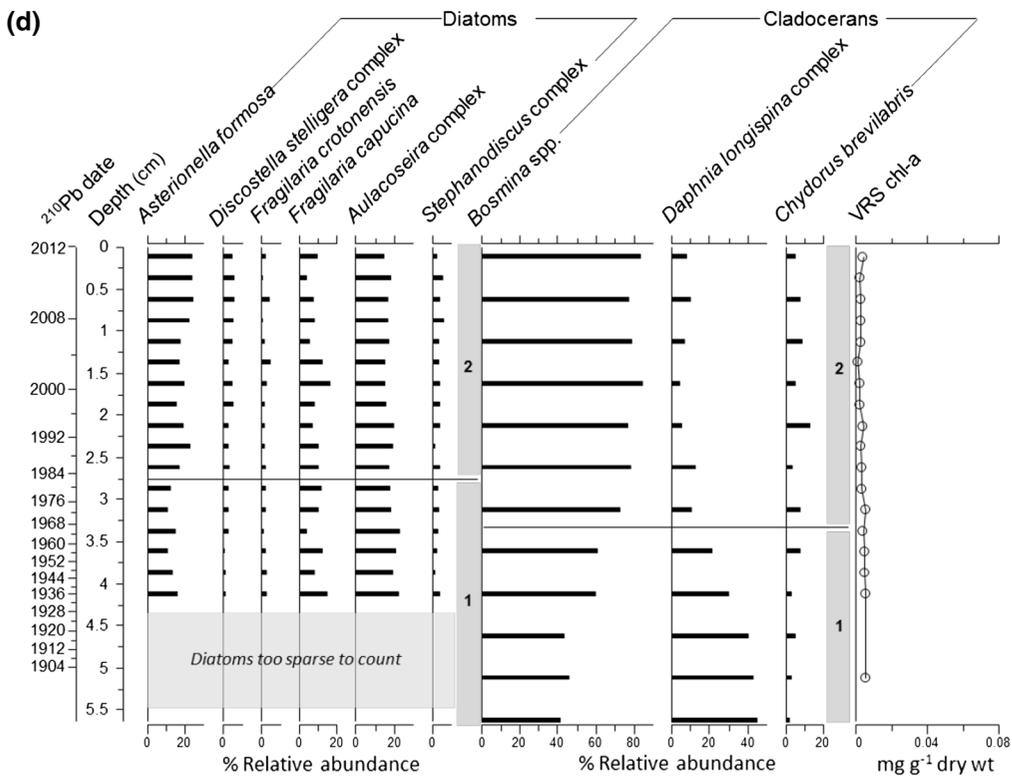
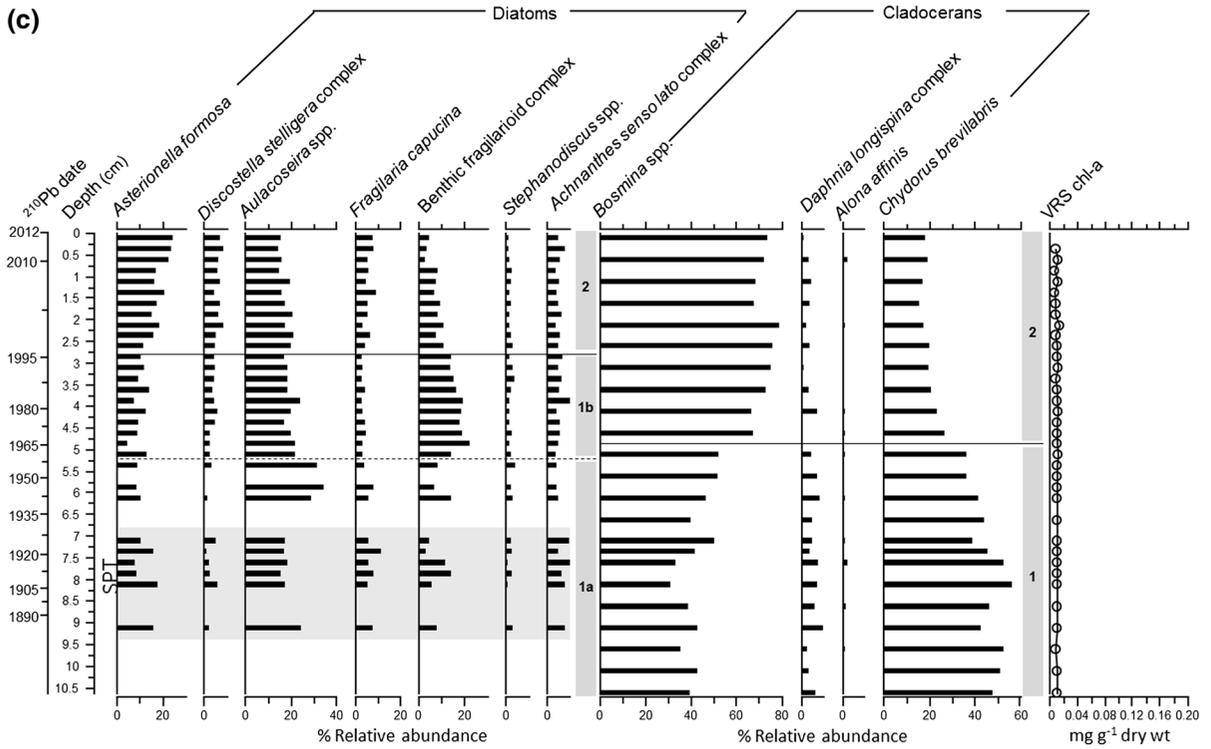


Fig. 4 continued

radiometric profile for Eabamet Lake shows a general exponential decline in  $^{210}\text{Pb}$  activities with a  $^{210}\text{Pb}$  date of  $\sim 1850$  at a depth of 10 cm (Fig. 3c). The sedimentation rates ranged between  $0.0124$  and  $0.0301 \text{ g cm}^{-2} \text{ year}^{-1}$  with a mean rate of  $0.0217 \text{ g cm}^{-2} \text{ year}^{-1}$ . Inferred chlorophyll-*a* concentrations in Eabamet Lake were all below the detection limit of  $0.01 \text{ mg g}^{-1}$  dry weight, and so no trend was recorded (Fig. 4c).

The cluster analysis identified a primary change in the diatom assemblages of Eabamet Lake at  $\sim 2000$  (2.25 cm). Within Zone 1, there is a secondary split at  $\sim 1963$  ( $\sim 5$  cm). In Zone 1a, below  $\sim 6$  cm ( $\sim 1945$ ), the samples became increasingly difficult to count due to a high concentration of siliciclastic material. For these intervals, obtaining counts greater than 400 diatom valves was difficult. Treatment of these samples with SPT resulted in concentrating the diatom sample and the removal of much of the clastic materials, enabling an additional six intervals to be counted and extending the diatom record to  $\sim 1880$ . Unlike the HBL lakes, planktonic diatoms dominate the diatom sedimentary record of deeper Eabamet Lake (Fig. 4c). Planktonic *Asterionella formosa* and *Discostella stelligera* (Cleve and Grunow) Houk and Klee, gradually increase in relative abundance through time and peak at the top of the core ( $\sim 2012$ ) at  $\sim 24$  and  $7\%$  relative abundance, respectively. Diatom Zone 1 is characterized by higher abundances (relative to Zone 2) of heavily silicified tycho planktonic *Aulacoseira* spp. (mainly *A. ambigua* (Grunow) Simonsen, *A. islandica* (Otto Müller) Simonsen, and *A. subarctica* (Otto Müller) E.Y. Haworth; ESM 1) and benthic fragilarioid species. Diatom Zone 2 ( $\sim 2000$ ; 2.25 cm) is established by the marked decline in the relative abundance of these tycho planktonic and benthic diatom species and increases in *A. formosa* and *D. stelligera*. In Zone 2, these planktonic diatoms are on average  $\sim 15\%$  higher in relative abundance than in Diatom Zone 1.

The CONISS analysis for Eabamet Lake indicated that the greatest change in cladoceran assemblages occurred  $\sim 1965$ , represented by the transition from *C. brevilabris* to *Bosmina* spp.-dominated assemblages. Although CONISS identified the primary split between Zone 1 and Zone 2 at  $\sim 1965$ , the onset of notable changes occurred  $\sim 30$  years prior. Similar to McFaulds Lake, assemblages were dominated by *Bosmina* spp. and *C. brevilabris* with

notable abundances of *Daphnia* spp. (up to  $10\%$ ) (Fig. 4c). The remaining cladoceran taxa represented less than  $2\%$  of the sedimentary assemblages. Cladoceran Zone 1 consists of  $48\%$  *C. brevilabris* and  $40\%$  *Bosmina* spp. in species relative abundances. In Zone 2, *Bosmina* spp. increases to  $74\%$  relative abundance and *C. brevilabris* decreases to  $18\%$  relative abundance.

Attawapiskat Lake ( $52^{\circ}11'40.711''\text{N}$ ,  $87^{\circ}45'58.730''\text{W}$ )

With moderate nutrient concentrations (TP =  $10.6 \mu\text{g L}^{-1}$ , TKN =  $381 \mu\text{g L}^{-1}$ ), Attawapiskat Lake was dystrophic with the highest DOC concentration ( $14.0 \text{ mg L}^{-1}$ ) of the study lakes, and the lowest Secchi disk depth of 1.5 m, which may be indicative of higher turbidity and/or colour from DOC. Although it is the deepest of the study lakes (coring depth = 10.4 m), Attawapiskat Lake was not stratified on the day of sampling (Table 1). Attawapiskat Lake had sedimentation rates ranging between  $0.0085$  and  $0.0324 \text{ g cm}^{-2} \text{ year}^{-1}$  with a  $^{210}\text{Pb}$  date of  $\sim 1900$  at a depth of 5.25 cm (Fig. 3d). Attawapiskat Lake sedimentary chlorophyll-*a* concentrations are below detection limits throughout the sedimentary record and no breakpoint was identified (Fig. 4d).

For Attawapiskat Lake, the concentration of siliciclastic material increases below a core depth of 4 cm ( $\sim 1936$ ), and it was not possible to obtain adequate diatom counts even after treatment with SPT. This yielded a diatom record that was  $\sim 80$  years shorter than for the cladocerans, which extends back to  $\sim 1850$ . CONISS identified the main change in the diatom assemblage record  $\sim 1980$  (2.75 cm), separating diatom Zone 1 and Zone 2. A planktonic assemblage of *Asterionella formosa*, *Discostella stelligera*, tycho planktonic *Aulacoseira* spp. (largely *A. subarctica* and *A. ambigua*), and low abundances of *Stephanodiscus* spp. (largely *S. minutulus* (Kützing) Cleve and Möller, *S. niagarae* Ehrenberg) were present throughout the sediment core of Attawapiskat Lake (Fig. 4d). *Fragilaria capucina* Desmazières was also present at modest relative abundances (i.e.,  $\sim 10\%$  mean abundance) throughout the sedimentary record. Subtle increases in the relative abundances of *A. formosa* and *D. stelligera* and a concurrent decline in the *Aulacoseira* complex occurs at the transition from Zone 1 to Zone 2, with total planktonic diatoms

increasing by ~16 % from the bottom assemblage of Zone 1 to the top assemblage of Zone 2.

Cladoceran assemblages of Attawapiskat Lake were co-dominated by *Bosmina* spp. and the *Daphnia longispina* complex at the start of the record, Zone 1 (41 % *Bosmina* spp. and 45 % *D. longispina* mean abundance through Zone 1) through to the middle of the twentieth century (Fig. 4d). A switch from co-dominance to full dominance by *Bosmina* spp. (73 % abundance) occurred ~1970 (3.25 cm) and was identified as a zonation break by the cluster analysis. The modern assemblage contains 84 % *Bosmina* spp., and only 8 % *D. longispina* complex. Compared to the other study lakes, *C. brevilabris* made up a smaller proportion of the species assemblage in Attawapiskat Lake, fluctuating between 2.9 and 13 % in species relative abundances over the length of the cladoceran record.

## Discussion

A common trend across the diatom and cladoceran profiles of the Ring of Fire study lakes was increased abundances of planktonic/pelagic biota relative to benthic and littoral taxa. However, there was a distinct difference in the nature and timing of biological changes in the deeper, oligotrophic lakes compared to the shallower, more nutrient-rich lakes. In the deeper lakes, planktonic diatoms were present throughout the sedimentary records, but showed a clear increase in relative abundance in the past few decades concurrent with declines in tychoplanktonic and benthic diatom taxa. In addition to a relative increase in planktonic diatom taxa in the two deeper lakes, there was a switch in the dominant cladoceran taxa in Attawapiskat Lake from the *Daphnia longispina* complex to more generalist *Bosmina* spp. In contrast, the two shallow lakes register the appearance of planktonic diatom taxa for the first time in the sedimentary record in the early 1900s (McFaulds), and in the 1960s (Symons), that reach maximum abundances in the most recent sediments. In these shallow lakes, generalist *Bosmina* spp. becomes increasingly dominant through time to 2012. Concurrent with the relative increases of these open-water taxa, there were marked decreases in benthic diatom taxa and littoral cladocerans, and a notable increase in sedimentary chlorophyll-*a* from previously low and stable concentrations. Consistent

with other studies (Battarbee et al. 2012), evidence for warming-induced changes is confounded in the deeper lakes of our study by a history of human interaction (including shoreline development, river diversion and enhanced fishing pressure activities), and therefore, climate warming was best expressed in the shallow Ring of Fire lakes.

Lansdowne House annual air temperature records over the past ~70 years indicate that warming in the Ring of Fire region began in the mid-1970s (Fig. 2). Farther north, climate warming in subarctic HBL began in the mid-1990s, lagging the continental Canadian Shield region by ~20 years, after which both regions show accelerated and synchronous increases in mean annual temperatures (Rühland et al. 2013; Macrae et al. 2014). Many of the biotic assemblage changes across the four Ring of Fire lakes co-occur with these temperature increases, with an initial assemblage change during the 1970s becoming more pronounced in the 2000s (particularly in Eabamet and Symons lakes). The Ring of Fire is situated at a latitude of 52°N and ~300 to 400 km inland from Hudson Bay, where its cooling influence may be lessened, and where continental effects play a role in local climate (Crins et al. 2009). In contrast with the pronounced warming trend across most of the Canadian Arctic that began as early as the middle of the nineteenth century (Smol et al. 2005), the subarctic HBL maintained stable and relatively cool conditions from 1960 to the mid-1990s (Rouse 1991; Gough et al. 2004; Macrae et al. 2014). In our Ring of Fire study region we capture the biota of lakes responding to warming earlier than coastal Hudson Bay lakes (Rühland et al. 2013), but later than high Arctic lakes. The timing of biotic changes in the Ring of Fire region is most similar to temperate lakes further south in Ontario, such as Lake of the Woods, which show pronounced and similar diatom assemblage shifts in response to climate warming beginning in the 1970s (Rühland et al. 2010).

The diatom, cladoceran and chlorophyll-*a* trends from McFaulds Lake show the most striking changes of all four lakes with an almost complete species turnover in the diatom assemblages and a striking shift in the cladoceran assemblages. However, this change occurs at the turn of the twentieth century and it is not entirely clear why the biological records change ~30 to 50 years earlier than the other three Ring of Fire lakes, including the nearby shallow Symons Lake that is ~20 km away. The earlier proxy changes here are

consistent with the timing of biological response to climate warming recorded in many Arctic and Subarctic lakes throughout the world (Smol et al. 2005; Rühland et al. 2015), as well as in some lakes in the Canadian Shield in northwestern Ontario (Wiltse 2014). These aquatic changes in McFaulds Lake may be signs of early Arctic warming (~1850 to 1900) in this continental region of northern Ontario. This is in contrast to locations closer to Hudson Bay where cooling effects of Hudson Bay sea ice maintained stable temperatures until ~1990s. Although the two shallow HBL lakes show similar taxonomic changes, differences in the timing of response could potentially be accounted for by the sporadic nature of permafrost in this region (i.e. not all lakes are surrounded by permafrost and permafrost extent is likely lake-specific). It may be that changes in localized catchment processes triggered changes in the littoral and planktonic habitat of McFaulds Lake late in the nineteenth century that was not observed in nearby Symons Lake. Local changes in hydrology including permafrost thawing and changes in connectivity to other water bodies could have potentially caused an expansion in lake size. For example, McFaulds Lake may have undergone large catchment-scale changes in localized, ice-rich permafrost as temperatures initially increased at the turn of the twentieth century. The thawing of ground ice may release and mobilize inorganic nutrients, previously immobilized in permafrost soil horizons, which then stimulates biogeochemical processes in the receiving waters (Vincent et al. 2013). This scenario is consistent with the moderately elevated nutrient concentrations measured at McFaulds Lake (TP = 18  $\mu\text{g L}^{-1}$ ; TKN = 509  $\mu\text{g L}^{-1}$ ) relative to other lakes in the region (MacLeod 2014). This may have resulted in the development and/or increase in aquatic macrophytes and mosses and other littoral habitat alterations at McFaulds Lake leading to a diatom assemblage turnover from large benthic naviculoid taxa in the earlier sediment to epipsammic *Achnanthes sensu lato* species and epiphytic *Nitzschia* species, which have been found to respond to increases in nutrients in other Arctic regions (Keatley et al. 2009; Stewart et al. 2014).

#### Diatom assemblage responses to warming

Across the Ring of Fire lakes, changes in the frequency of planktonic diatoms relative to benthic fragilarioid

diatoms, heavily-silicified, tychoplanktonic *Aulacoseira* taxa, and large (>40  $\mu\text{m}$ ) benthic naviculoid *sensu lato* taxa were observed. Small, benthic fragilarioid taxa are considered to be pioneering diatoms, often present in lakes with simple rock and sediment substrates (Michelutti et al. 2003; Smol and Douglas 2007). Conditions can be unfavourable for the success of more diverse diatom assemblages, such as low-light from extended periods of ice-cover in cold environments (Lotter and Bigler 2000). This group of opportunistic species has broad chemical tolerances and can live in a wide variety of limnological conditions (e.g., low to high nutrients, circum-neutral to alkaline conditions, Finkelstein and Gajewski 2008; Bennion et al. 2010). Their dominance in the early sediments of all four lakes may be due to their ability to successfully grow during prolonged periods of ice-cover, short growing seasons, limited resources (light and nutrients), and under a limited variety and availability of aquatic habitats.

Pennate planktonic diatoms, such as *Asterionella formosa*, across all the study lakes exhibit one of the greatest changes, increasing between ~3 and ~15 % from ~1910 to ~2012. Additionally, the *Discostella stelligera* complex increased by ~5 % in relative abundance from the base of the record to the surface in the two deeper lakes. This shift towards a higher abundance of planktonic diatoms in the recent sediments is consistent with longer open water periods, enhanced thermal stability and water column changes related to warming (Rühland et al. 2015; Sivaraajah et al. 2016). For example, in lakes across the subarctic, increases in both centric and pennate planktonic diatoms have been linked to recent warming (Rautio et al. 2000; Smol et al. 2005; Solovieva et al. 2008; Rühland et al. 2013, 2015; Thienpont et al. 2013). Due to the large surface area to volume ratios of pennate planktonic diatoms, these taxa have one of the lowest sinking velocities of all freshwater planktonic diatoms (Spaulding and Edlund 2009). Warmer winter and spring temperatures, a prolonged growing season, and increased lake thermal stability could favour the growth of planktonic diatoms.

Over the past four decades, warmer air temperatures, as recorded at the Lansdowne House climate station (Fig. 2), may have led to increases in the length of the growing season, opening up previously ice-covered pelagic habitat and potentially allowing greater time for planktonic taxa to bloom in these

four study lakes. Over the ~70-year climate record, increases in air temperatures began in the mid-1970s, with an escalation in the 1990s to the present (Fig. 2). Notably, planktonic taxa in the deeper Attawapiskat Lake increase from ~1980 to the present with a median planktonic increase of 12 % relative abundance. Interestingly, shallow Symons Lake records the greatest change in diatom assemblage at this time (~1980) with the first appearance of planktonic taxa. This synchrony in timing of temperature changes, algal compositional changes and increased primary production suggests these substantially warmer annual temperatures may have triggered changes in the water column properties of lakes in the region. Further increases in planktonic diatoms in Eabamet Lake in the mid-1990s and early-2000s in Symons Lake are consistent with the accelerated increases recorded in regional air temperatures at this time, as is a pronounced increase in the pelagic cladocerans of McFaulds Lake. However, diatom changes at McFaulds Lake occurred much earlier, and causes for these assemblage changes are difficult to pinpoint as they occur prior to establishment of climate monitoring at Lansdowne House.

Both shallow lakes track changes in littoral habitat, as well as increases in planktonic habitat availability. Given that these shallow lakes are ~2 m in depth and light penetrates to the bottom of each lake (Table 1), the lakes littoral habitat is important to the biotic assemblages, and therefore would be expected to respond to a longer and warmer open water period. Indeed, the epiphytic *Nitzschia* complex increased from trace abundances to ~8 % from the 1990s to the present in Symons Lake and notably increased at McFaulds Lake at the turn of the twentieth century to the present (37 %). In both lakes these changes were concurrent with the arrival and increase in planktonic diatoms (Fig. 4a–b). With warming, a reduction in the duration of ice-cover and a lengthened growing season allow mosses and aquatic macrophyte habitat to establish and/or expand, and thus epiphytic diatoms that grow attached to these substrates flourish (Smol and Douglas 2007; Rühland et al. 2013, 2015).

Additionally, enhanced nutrient export from the catchment related to climatic influences on weathering rates, precipitation, run-off, and terrestrial primary productivity (Smol and Douglas 2007; Adrian et al. 2009) may occur, increasing the relative abundances of diatom taxa commonly linked to higher nutrient

influxes (e.g., *Nitzschia* spp.; Keatley et al. 2008, 2009; Stewart et al. 2014). Therefore, in the Ring of Fire lakes, not only is a change in ice-cover influencing the diatom and cladoceran assemblages, but many interrelated processes linked to climate change are likely promoting both littoral and pelagic habitat alterations. The development of these periphytic diatom assemblages is indicative of the expansion of aquatic plants and increased habitat availability, consistent with changes reported in lakes and ponds throughout the Canadian High Arctic (Antoniades et al. 2005; Smol et al. 2005), and the Canadian subarctic (Rühland et al. 2013). Similar to the trends recorded in deeper subarctic HBL lakes near the Sutton River (Rühland et al. 2013), the first appearance of planktonic diatoms and the expansion of periphytic taxa in our two shallow lakes coincide with an exponential increase in sedimentary chlorophyll-*a*.

#### Cladoceran assemblage responses

Whereas diatom assemblages are largely influenced by bottom-up controls such as water chemistry and physical lake changes, Cladocera may be influenced by and respond to both bottom-up and top-down controls, such as fish and invertebrate predation. Additionally, given the increased fishing pressure on the deeper study lakes, changes among Cladocera may not be temporally synchronous with warming or diatom changes in these lakes. Indeed, our results show differential response times and magnitudes of change within the cladoceran assemblages of each lake. For instance, the trend through time in the relative abundance of *Daphnia* spp. varies in direction across the Ring of Fire lakes. In shallow McFaulds Lake, pelagic *Daphnia* spp. and *Bosmina* spp. increase in relative abundance coincident with a decline in littoral species that is likely a response to an increase in the availability in pelagic habitats. Here, a lengthened ice-free period has potentially allowed a pelagic cladoceran assemblage with both *Bosmina* spp. and *Daphnia* spp. to develop and flourish, which was previously inhibited by shorter growing seasons. This main change in the McFaulds Lake cladoceran assemblage in the early 2000s occurs with substantial temperature increases across the Ring of Fire region, as inferred at both the Lansdowne House and Churchill climate station, suggesting that the

cladocerans of this shallow lake are sensitive to an increase in the length of the growing season and associated changes in aquatic habitats.

Across all the Ring of Fire study lakes there is a general trend towards increasing pelagic cladocerans, although minimal changes were observed in Symons Lake. Occupying a trophic position higher than diatoms, it is also possible that cladocerans have not yet had time to fully respond to climate-induced lake changes, especially the accelerated regional warming that began in the 1990s. Many studies have demonstrated that diatoms respond faster to climate warming than invertebrates, as diatoms are often only strongly influenced by bottom-up controls whereas cladoceran communities are influenced by both bottom-up and top-down controls (Sweetman et al. 2008; Rühland et al. 2014). Differences in the magnitude of change between diatom and cladoceran assemblages across the Ring of Fire lakes suggest that these two indicator groups may not be strongly coupled.

In the deeper study lakes, there is a shift among pelagic taxa with *Daphnia* relative abundances decreasing in tandem with the success of *Bosmina* spp. One potential explanation for this trend is that *Daphnia* taxa are more vulnerable to size-selective predation by planktivorous fish than small-bodied *Bosmina*, and therefore a switch between these two pelagic species can occur in response to natural changes in fish densities or to fish stocking (Nevalainen et al. 2014). With a longer open water season on deep Ring of Fire lakes, predation pressure from planktivores may be enhanced, reducing the overall biomass of zooplankton communities (Jeppesen et al. 2014) and favouring smaller taxa (e.g., the pelagic taxa *Bosmina* spp.). This generally occurs because planktivorous fish tend to selectively consume the larger, more visible cladocerans (e.g., *Daphnia*), whereas smaller taxa (e.g., *Bosmina*) are a less efficient source of food (de Bernardi et al. 1987). Additionally, communities located on the shores of Eabamet and Attawapiskat lakes have harvested piscivore populations (e.g., whitefish, walleye) since the late 1800s and more actively since the 1960s when the present settlements began to expand in size (<http://eabametoong.firstnation.ca/history-of-eabametoong-first-nation/>). As the communities and their fishing pressure have grown, predation pressure on planktivorous fish may have been lessened, thus increasing predation on large-bodied zooplankton. This may have

played a role in the recent success of small-bodied *Bosmina*.

To date, the isolated location of lakes in the Far North of Ontario has precluded the region from direct impacts from development activities. However, the west Albany River network has a history of water management for hydropower generation that may have impacted the downstream waters of the most southern study lake, Eabamet Lake. In 1957, Ontario Hydro diverted water from Lake St. Joseph (headwaters of the Albany River) westward to meet the electricity demands of mines at Lynn Lake and Thompson, Manitoba. This project, termed the 'Root River diversion', allowed Lake St. Joseph to flow into Lac Seul, increasing the flow of the English and Winnipeg rivers, and yielding a reduction and fluctuation in the flow of the Albany River (Long 2010; Mishkeegogamang Ojibway Nation). However, it has been documented that during this period of river diversion at the end of the 1950s, the community on Eabamet Lake experienced large-scale flooding. The primary change in cladoceran assemblages in Eabamet Lake occurs ~1960, with a transition from a littoral *C. brevilabris* dominated assemblage to an assemblage dominated by pelagic *Bosmina* spp. The timing of this cladoceran shift, prior to the largest change in regional warming, is also similar in timing to modest changes seen in the diatom assemblages. Given a lack of water level monitoring on Eabamet Lake, it is difficult to conclude whether the Root River diversion resulted in overall lower or higher water levels on Eabamet Lake; however, the timing of diatom and cladoceran changes suggest that the project did influence the lake's aquatic biota. An assemblage with greater pelagic cladocerans indicates that water levels may have increased from the connectivity between Albany River and Eabamet Lake.

Differences in the timing of biological responses across Ring of Fire lakes

The timing of aquatic primary production and taxonomic shifts across the study lakes is spatially asynchronous, with the response recorded in the shallow lakes predating the deep lakes by ~45 to 60 years. Given the location of the two shallow lakes, ~100 km closer to the Hudson Bay coast than our two Canadian Shield lakes, one might first expect that the cooling effect of sea ice would have resulted in a later

diatom response to regional warming in the shallow lakes than within the two deeper lakes farther inland. However, the paleoclimate responses are earlier and most pronounced in the shallow lakes, further demonstrating the high sensitivity of shallow lakes to climatic and other environmental changes (Smol 2016). The more pronounced biological response of the shallow lakes within the Ring of Fire can be explained by their physical properties (e.g., high surface area to volume ratios and low water volumes). The water column of shallow high latitude lakes and ponds warm substantially faster than the water columns of the deeper lakes, which can result in increased production and large changes in biotic communities (Smol and Douglas 2007; Chen et al. 2014; Macrae et al. 2014; White et al. 2014). For example, Chen et al. (2014) found that deeper lakes tempered the responses of the subarctic aquatic ecosystems to climate change in the presence of regional cryogenic cooling. Specifically, they compared lakes with different morphometries but similar proximities to regional ice fields, and observed that the shallow lake registered a more pronounced biotic response than that deeper lake. Similar to the study, these shallower systems responded earlier than deeper lakes, but once the deeper lakes crossed thermal thresholds (Rühland et al. 2015), they can be equally as responsive to climate change as shallow lakes.

## Conclusions

A change from simple benthic assemblages to more complex planktonic and epiphytic diatom assemblages across the four study lakes, as well as increases in sedimentary-inferred primary production in the shallow lakes, are an early indication of regional warming in lakes across the Ring of Fire region. Each lake record tracks a change in aquatic habitat structure and availability over the past ~100 years, which may be linked to warmer regional air temperatures and a subsequent reduction in ice cover length, as well as direct human influences on the deep lakes. While, Eabamet Lake, as well as Symons Lake, track a later response, comparable to changes recorded in lakes located proximal to Hudson Bay, where warming occurred a few decades later in the mid-1990s (Rühland et al. 2013; Friel et al. 2014). The early timing of biotic changes in shallow McFaulds Lake is most

similar to shallow High Arctic lakes and ponds that first began detecting signs of climatic change in the mid-nineteenth century (Smol et al. 2005). However, it is plausible that this lake has experienced local changes in hydrology including permafrost thawing and changes in connectivity to other water bodies potentially causing an expansion in lake size. Increases in aquatic primary production are pronounced in the sedimentary records of the two shallow lakes and marginally precede a response in the diatom assemblages; however, no change in primary production has yet to be detected in either of the deep lakes. Together with catchment-specific differences, local variation in lakes across the Ring of Fire yields differences in the timing of biotic responses to climatic change. An earlier response across multiple proxies to climatic changes in the shallow lakes in the Ring of Fire highlights the sensitivity of shallow lakes and ponds for tracking environmental changes. If regional air temperatures continue to increase, vertical lake mixing will likely weaken and thermal stratification may become more frequent and prolonged in the deeper lakes, which could potentially lead to a stronger biological response in the near future. This study highlights conclusions from previous studies (Rühland et al. 2015) that regional and site-specific differences in lakes (e.g. degree of permafrost development, soil development, morphometry, depth) can influence the timing and magnitude of biological response to recent climate change.

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