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Diatom-based evidence of regional aridity during the mid-Holocene period in boreal lakes from northwest Ontario (Canada)

Moumita Karmakar, Kathleen R Laird and Brian F Cumming

Abstract

Boreal regions and their freshwater ecosystems may be susceptible to future climate change under projected warmer conditions. Northwest Ontario is a boreal region adjacent to the climatically sensitive prairie-forest ecotone (PFE). Pollen records spanning the Holocene from near the Manitoba/Ontario border to lakes up to ~300 km east of the PFE indicate a warmer and possibly wetter mid-Holocene period across northwest Ontario from ~8000 to 4500 cal. yr BP. To date, only one Holocene-scale record of changes in effective moisture, as indicated through diatom-inferred changes in lake level (Experimental Lakes Area (ELA) Lake 239), is available from this region. Our study expands the regional context of Holocene climate changes, with the analysis of diatom assemblages in sediment cores from two additional lakes, which span a distance of over 200 km across the present-day boreal forest, from 80 km west of ELA Lake 239 to ~150 km to the northeast. In cores from both lakes, benthic taxa predominate in the early-to-mid-Holocene period, with a low abundance of planktonic taxa, suggesting lower lake levels by ~2–5 m. Increases in the abundance of planktonic taxa to >50% occurred in both lakes beginning ~4500–4000 cal. yr BP suggesting positive water balance over the last 4000 years in comparison with the mid-Holocene period. This new evidence supports a regional mid-Holocene period of aridity, with reduced water levels across the boreal region of northwest Ontario. If future climate change results in lower effective moisture, then conditions could become similar to the mid-Holocene period aridity, leading to real challenges for the management of water resources across the region.

Keywords

boreal region, diatom assemblages, lake-level fluctuations, mid-Holocene period, northwest Ontario, prairie-forest ecotone

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Introduction

Boreal regions are globally significant biomes containing over 60% of the fresh surface water on the planet and more than half of the carbon stored in forested regions (Schindler and Lee, 2010). Boreal regions and their freshwater ecosystems may be extremely vulnerable to climate change, especially boreal regions situated adjacent to ecotonal regions (Frelich and Reich, 2010). One such region is northwest Ontario, a boreal region located adjacent to the semi-arid Canadian prairies to the west. Projections from General Circulation Models, using several emission scenarios, suggest that the temperatures in northwest Ontario will increase by a mean of ~2°C by 2020, and by >3°C by 2050 (Chiotti and Lavender, 2008). It is widely expected that warming will lead to the prairie biome shifting to the northeast, displacing the existing forest (Frelich and Reich, 2010). Warming will likely increase the occurrence and magnitude of fires, winds, insects and disease, which would further fragment the land scape and lead to a reduction in the extent of the boreal forest (Frelich and Reich, 2010).

Given the climatic sensitivity of ecotonal regions, it is important to understand how aquatic systems and water balance have changed over time in response to a changing climate. Fortunately, changes in climate over the Holocene period are relatively well known from studies of pollen from trees, shrubs and grasses preserved in lake sediments. In a synthesis of pollen data across the prairie-forest ecotone (PFE) in central Canada and the north-central United States, a rapid eastward expansion of prairie occurred between 10,000 and 8000 cal. yr BP, with the prairie reaching its maximum extent by 6000 cal. yr BP (Williams et al., 2009). Well-dated sediment cores that have been analyzed for pollen are sparse in northwest Ontario. However, the few sites in this region indicate changes to a more open forest (parkland) during the early-to-mid-Holocene period (Björck, 1985; Lewis et al., 2001; McAndrews, 1982; Moos and Cumming, 2011). Pollen-based inferences from the Experimental Lakes Area (ELA) Lake 239 in northwest Ontario suggest conditions were wetter and approximately 1–2°C warmer than today during the mid-Holocene period (~8000–4500 cal. yr BP). A synthesis of available pollen-based records from the North American Pollen Database, which span the Canadian prairie-boreal forest ecotone, indicate changes in vegetation at eight sites (Moos and Cumming, 2011). However, there were differences in the species changes dependent on lake location; the prairie lakes indicate changes in Poaceae and *Ambrosia* during

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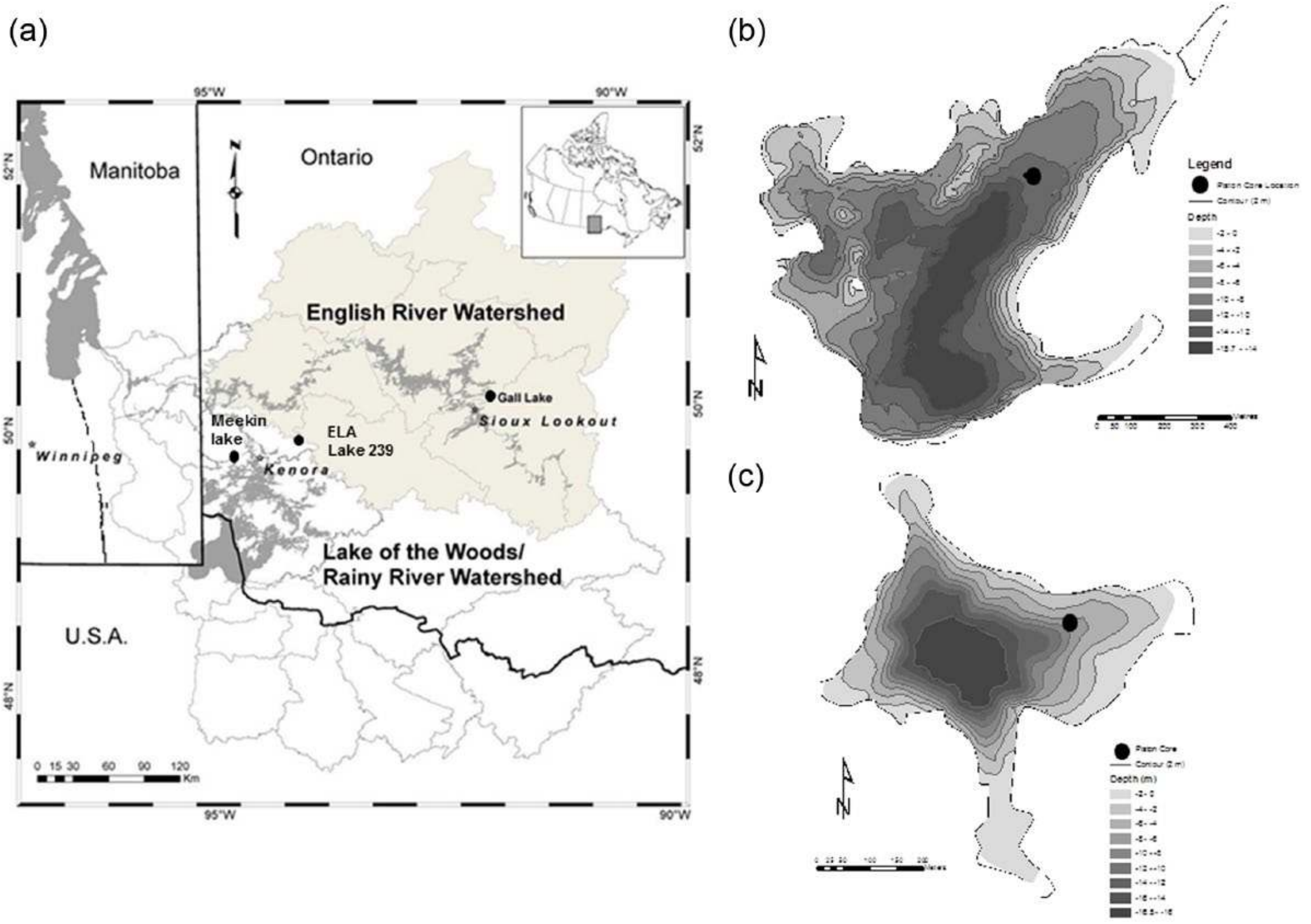

Figure 1. (a) Map showing the location of the three study lakes (Meekin, ELA Lake 239, and Gall Lake) that are located within the Winnipeg River Drainage Basin. Black dash line is the modern-day prairie-forest boundary (Teed et al., 2009). Meekin Lake is located in the Lake of the Woods/Rainy River Watershed, whereas Lake 239 and Gall Lake are located in the English River Watershed. (b) Bathymetry map of Meekin Lake showing changes in lake depth (2 m contour intervals) and the coring location (black circle). (c) Bathymetry of Gall Lake showing changes in lake depth (2 m contour intervals) and the coring location (black circle). Please see text for rationale of near-shore coring locations.
ELA: Experimental Lakes Area.

the mid-Holocene period, whereas changes in Cupressaceae and *Ambrosia* are more apparent in the boreal region.

There is a scarcity of Holocene-scale records of hydrologic conditions from boreal regions, particularly in northwest Ontario (Laird and Cumming, 2008; Moos et al., 2009). This paucity of long-term hydrological changes largely reflects the difficulty in detecting changes in effective moisture from sedimentary evidence in drainage lakes, those with a surface outlet (Smol and Cumming, 2000). Currently, the only Holocene-scale record of effective moisture is from ELA Lake 239, a drainage lake within the Winnipeg River Drainage Basin (WRDB), a watershed that is ~120,000 km^2 in surface area. This record is based on a modified Digerfeldt approach, which is summarized in Laird et al. (2011). This approach identifies sensitive coring locations from near-shore regions with high rates of sediment accumulations to reconstruct changes in lake level from drainage lakes based on the diatom assemblages preserved in the lake sediments.

A primary focus of this study was to investigate the changes in sediment cores from two additional northwest Ontario lakes to assess whether the trends in water levels at ELA Lake 239 were representative of the region, with inferred low levels throughout the mid-Holocene period and a transition to higher water levels for the last ~4000 years. A secondary focus was to determine whether there was a west-to-east gradient in the timing or magnitude of change as was seen in the northern US prairies in the early to mid-Holocene period (Williams et al., 2010). The two study lakes, Meekin Lake and Gall Lake, were chosen from six previously studied unregulated low-order lakes in northwest Ontario that were investigated for changes in water level over the past ~2000 years (Laird et al., 2012). The rational for choosing these two lakes was that these two lakes maximized the west-to-east moisture gradient across the boreal region in northwest Ontario, with Meekin Lake closest to the modern-day prairie–boreal forest ecotone and Gall Lake ~200 km to the northeast situated in present-day boreal forest (Figure 1a).

Study sites

Meekin Lake (N 49°49′, W 94°46′) is located in the western portion of the WRDB (in the Lake of the Woods/Rainy River Watershed) just 22 km northwest of Kenora, and ~100 km away from the modern-day PFE boundary (Figure 1a). The watershed is mostly forested with minimal anthropogenic activities in the catchment (Kingsbury et al., 2012). The predominant vegetation around Meekin Lake is balsam fir (*Abies balsamea*), poplar (*Populus* spp.), white birch (*Betula papyrifera*), with some red maple (*Acer rubrum*) and black ash (*Fraxinus nigra*). Meekin Lake is a relatively large (surface area = 78 ha, maximum depth = 13 m), first-order circumneutral lake (pH = 6.5) that is oligotrophic (total phosphorus (TP) = 9.7 µg/L) and moderately colored (dissolved organic carbon (DOC) = 7.7 mg/L; Kingsbury et al., 2012). Importantly, this lake had a gently sloping eastern basin (Figure 1b), from which the near-shore core was taken from a depth chosen based on changes in modern diatom assemblages (Laird et al., 2011).

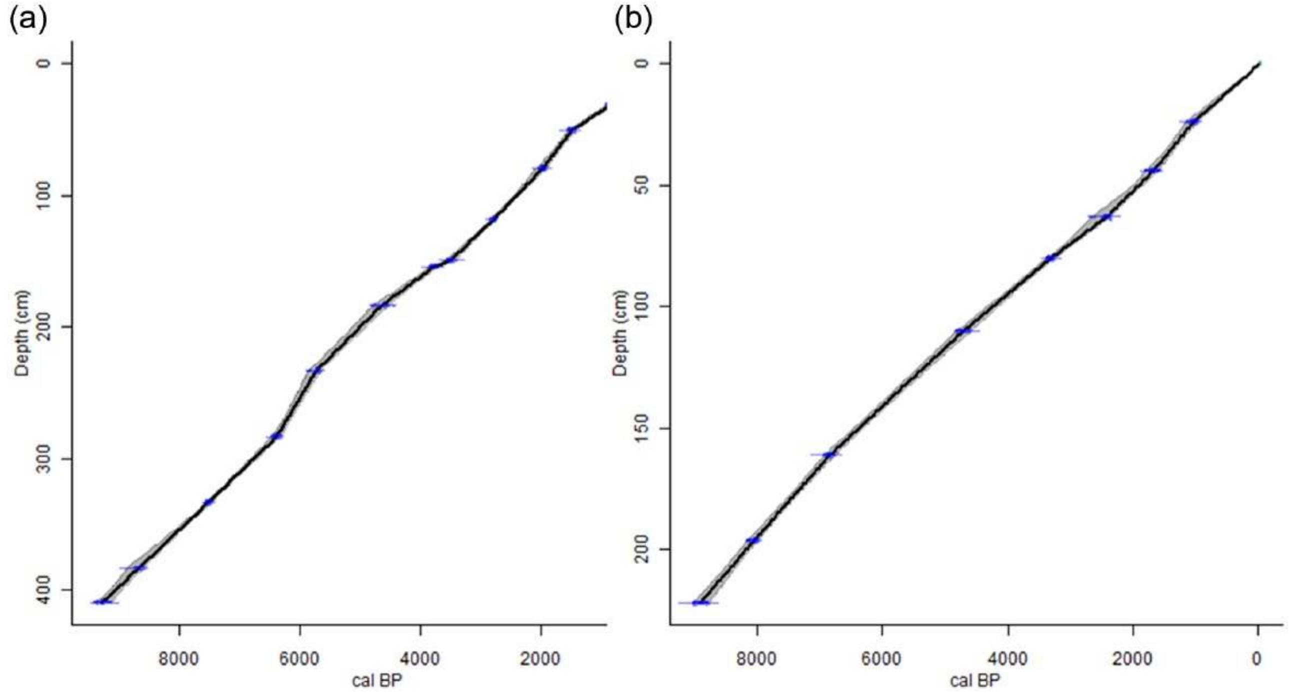

Figure 2. Age–depth model for (a) Meekin Lake and (b) Gall Lake, based on calibrated ^{14}C dates (Table 1), obtained by the *clam* software (Blaauw, 2010). Dates and errors are shown in blue. The gray area shows 95% confidence intervals based on 1000 iterations.

Gall Lake (N 50°14′, W 91°27′) is located within the eastern region of the WRDB (in the English River Watershed), approximately 20 km northwest of Sioux Lookout, and ~250 km away from the PFE boundary (Figure 1a). Similar to Meekin Lake, the watershed of Gall Lake is mostly forested with minimal anthropogenic activities in the catchment (Kingsbury et al., 2012). However, the vegetation is quite different being dominated by black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and poplar, with lesser amounts of white birch, balsam fir, and larch (*Larix* spp.). Gall Lake is also a first-order lake with a smaller surface area (19 ha), but with a greater maximum water depth (18 m) than Meekin Lake. Gall lake is slightly acidic (pH = 5.9), oligo-mesotrophic (TP = 12.3 µg/L), with a relatively high concentration of DOC (15.8 mg/L; Kingsbury et al., 2012). Similar to Meekin Lake, Gall Lake has an eastern basin that is gently sloping (Figure 1c), which allowed sufficient sediment accumulation and assessment of changes in the present-day distribution of diatom assemblages, and enabled the identification of a sensitive coring location (Laird et al., 2011).

Methods

Field sampling and core location

Prior to coring, high-resolution sub-bottom profiling was used to identify near-shore areas in each lake with high sediment deposition. Sub-bottom profiling was accomplished using a Knudsen 320 M marine sounder with 200 and 28 kHz transducers. A square-rod Livingston piston corer (ID − 5.1 cm), a corer designed to recover sediment in 1-m increments (Glew et al., 2001), was used to collect cores from each of the study lakes. The piston cores were wrapped in 1-m sections on site and subsequently sectioned into ~0.25-cm intervals in the lab.

Our modified Digerfeldt approach is outlined in detail in Laird et al. (2011), but is briefly described here. The sediment cores used in this study were located ~1.5 m deeper than the modern-day benthic-to-planktonic (B-P) diatom boundary (Kingsbury et al., 2012; Laird et al., 2011), as a means of determining a sensitive location to interpret lower lake levels in drainage lakes, in comparison with deep center cores which have been shown to be much less sensitive to variations in lake level (Haig et al., 2013; Laird and Cumming, 2009; Ma et al., 2013). The B-P diatom boundary is the water depth where there is a distinct change in the present-day diatom assemblage from primarily benthic diatoms to an assemblage dominated primarily by planktonic diatoms as water levels increase and is based on a within lake surface-sediment calibration across the depth gradient (Kingsbury et al., 2012; Laird et al., 2011). As lake level declines, the B-P boundary will move towards the center of the lake and move back towards the lake shore with a rise in lake level (Laird et al., 2011). Retrieval of a core near this boundary provides a means of tracking this movement and inferences of changes in lake level. The depth of the B-P diatom boundary in both of our study lakes was established by Kingsbury et al. (2012) and occurs at a depth of ~10 m in Meekin Lake and a depth of ~6 m in Gall Lake, the difference thought to be related to the greater light transparency in Meekin Lake (Kingsbury et al., 2012). Consequently, the targeted depths for coring were set at 11.5 m for Meekin Lake and a depth of 7.5 m for Gall Lake. We compare our results with the previously published Holocene sedimentary record from ELA Lake 239 (Laird and Cumming, 2008), in which the depth of the diatom B-P boundary was ~10–12 m and core retrieved at ~13 m.

Geochronology

The chronology for the sediment cores for Meekin Lake and Gall Lake were primarily based on accelerator mass spectrometry (AMS) estimates of age based on ^{14}C dating (Figure 2), as well as measurements of ^{210}Pb activities on the uppermost samples from each lake. Briefly, 8–12 AMS ^{14}C dates were obtained along the cumulative depth of the sediment cores from Meekin and Gall lakes (Table 1). The AMS ^{14}C age estimates were based on the carbon from pollen isolated from lake sediments (Brown et al., 1989), which was subsequently measured at the Lawrence Livermore National Laboratory. Radiocarbon dates were calibrated (using IntCal09, Reimer et al., 2009, under *clam* package), and age–depth models were created using 'classical' age–depth modeling (Blaauw, 2010). To determine the age at the top interval of

Table 1. Summary of the ^{14}C dating results on pollen isolated from selected intervals from the sediment cores from Gall Lake and Meekin Lake. All analyses were performed based on pollen isolated at the Limnological Research Center at the University of Minnesota, and dated at Lawrence Livermore National Laboratory.

Lake name, core number and section	Sample depth (cm)	Cumulative depth (cm)	^{14}C Age (±1 SD)	Calibrated ^{14}C age (±2 sigma) calendar years BP (*clam*)	No. of CAMS
Gall,C2S1	24–24.5	24–24.5	1125 ± 53	958–1092	149,853
Gall,C2S1	44–44.5	44–44.5	1760 ± 35	1567–1740	149,831
Gall,C2S1	63–63.5	63–63.5	2380 ± 30	2342–2489	149,832
Gall,C2S1	80–80.5	80–80.5	3110 ± 30	3239–3385	149,833
Gall,C2S2	27–27.5	110–110.5	4155 ± 30	4582–4769	157,795
Gall,C2S2	77–77.5	161–161.5	6005 ± 35	6750–6767	157,796
Gall,C2S3	21–21.5	196–196.5	7525 ± 30	7968–8068	157,797
Gall,C2S3	47–47.5	222–222.5	8045 ± 40	8763–9030	157,798
Meekin, C1S1	30.25–31	30.25–31	895 ± 30	737–834	149,837
Meekin, C1S1	50–51	50–51	1605 ± 30	1413–1552	147,807
Meekin, C1S2	10.25–11	79.5	2020 ± 30	1894–2051	149,838
Meekin, C1S2	50–50.5	118–118.5	2670 ± 30	2747–2808	147,808
Meekin, C1S2	80–81	149–149.5	3270 ± 40	3437–3579	147,809
Meekin, C1S2	85.25–85.5	154–154.5	3505 ± 30	3696–3859	147,835
Meekin, C1S3	25–25.5	183.5–184	4110 ± 30	4225–4709	157,808
Meekin, C1S3	75–75.5	233–233.5	4995 ± 30	5650–5758	157,809
Meekin, C1S4	25–25.5	283–283.5	5620 ± 30	6313–6453	157,810
Meekin, C1S4	75–75.5	333–333.5	6640 ± 30	7407–7575	157,811
Meekin, C1S5	25–25.5	383–383.5	7885 ± 30	8592–8777	157,812
Meekin, C1S5	50–50.5	409–409.5	8280 ± 35	9137–9405	157,813

the piston core, total ^{210}Pb was measured in the uppermost sediment in the first section of the piston cores from each lake. This activity was compared with a dated gravity core retrieved at the same depth as the piston core. The unsupported activity of ^{210}Pb, along with percent organic matter and diatom assemblage data, was used to determine the overlap between the gravity and piston cores in each lake (Laird et al., 2012).

Laboratory

Diatom slides were prepared and enumerated at 4-cm intervals in the piston cores from both lakes. Briefly, a 50:50 molar mixture of concentrated sulfuric and nitric acid was added to approximately ~0.2–0.3 g of wet sediment in a 20-mL glass vial, which was subsequently heated in a water bath at ~80°C for a period of 6–7 h. After allowing the sample to settle for a period of 24 h, the acid above the sample was removed by suction into a flask, and then rinsed with deionized water. This procedure was repeated until the sample reached the same pH as the deionized water (around 8 rinses). The sample was then drawn down to a height of ~5 mL at which time a known volume of microsphere solution (concentration – 2.0×10^7 spheres/mL) was added. A pipette was used to remove a small volume of the sample into a test tube, which was subsequently diluted with deionized water, before being pipetted onto a coverslip. In total, four successive dilutions from each slurry were made. The slurries on the coverslips were allowed to air dry (~12 h) on a warming tray, at which point the coverslips were heated on a hotplate to remove any remaining moisture, before being permanently mounted onto glass microscope slides using Naphrax®.

Diatoms were enumerated using a Leica DMRB microscope with a 100× fluotar objective (NA = 1.3) and differential interference contrast optics at 1000× magnification. For each sample, a minimum of 400 diatom valves were counted along transects on the coverslip. Diatoms were identified down to the species level or lower using the following taxonomic references: Camburn and Charles (2000), Cumming et al. (1995), Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), and Lange-Bertalot and Metzeltin (1996). Chrysophyte scales were also enumerated, but not identified to the species level. Estimates of the percent of organic matter in the sediments from both lakes were carried out every 4 cm in each of the cores following the methods outlined by Dean (1974). The chrysophyte scale-to-diatom index was calculated using the following formula: (number of scales/(number of scales + number of diatom valves)) × 100. Calculation of the concentration of diatoms is based on the addition of known concentration of microspheres and follows methods outlined in Battarbee and Kneen (1982).

Numerical analysis

To assess and summarize the changes in diatom assemblages over the Holocene, a number of techniques were used. First, both the relative abundance and concentration of individual diatom taxa were assessed. Second, to summarize the main diatom assemblages, taxa with a relative abundance > 5% in at least two samples were plotted, and taxa with lower abundances were grouped into larger taxonomic categories (such as *Achnanthes* sensu lato, *Navicula* sensu lato, *Fragilaria* sensu lato, etc.). Third, a commonly used constrained clustering technique (CONISS, using a squared Euclidean distance as a measure of similarity) was undertaken with the aid of the computer program Tilia v. 2.02 (Grimm, 1987) to define the major periods of similar diatom assemblages. Fourth, the main trends in diatom assemblages were summarized and compared by two ordination techniques using square-root transformed species data: Correspondence Analysis (CA) and nonmetric multidimensional scaling (nMDS). Analyses were based on taxa ≥ 2% in one sample (including grouped categories). The computer program CANOCO v. 5 was used to calculate the CA and nMDS (Ter Braak and Šmilauer, 1998). This comparative approach between ordination methods provided an opportunity to assess the robustness of the two approaches. While nMDS has not been as commonly used to summarize paleolimnological data as principal component analysis (PCA) or CA (Legendre and Birks, 2012), nMDS has fewer assumptions on the structure of species data, on the interrelationship between the samples and can generally represent assemblage relationships in low-dimensional space (Clarke and Warwick, 2001). nMDS also provides the ability to choose the

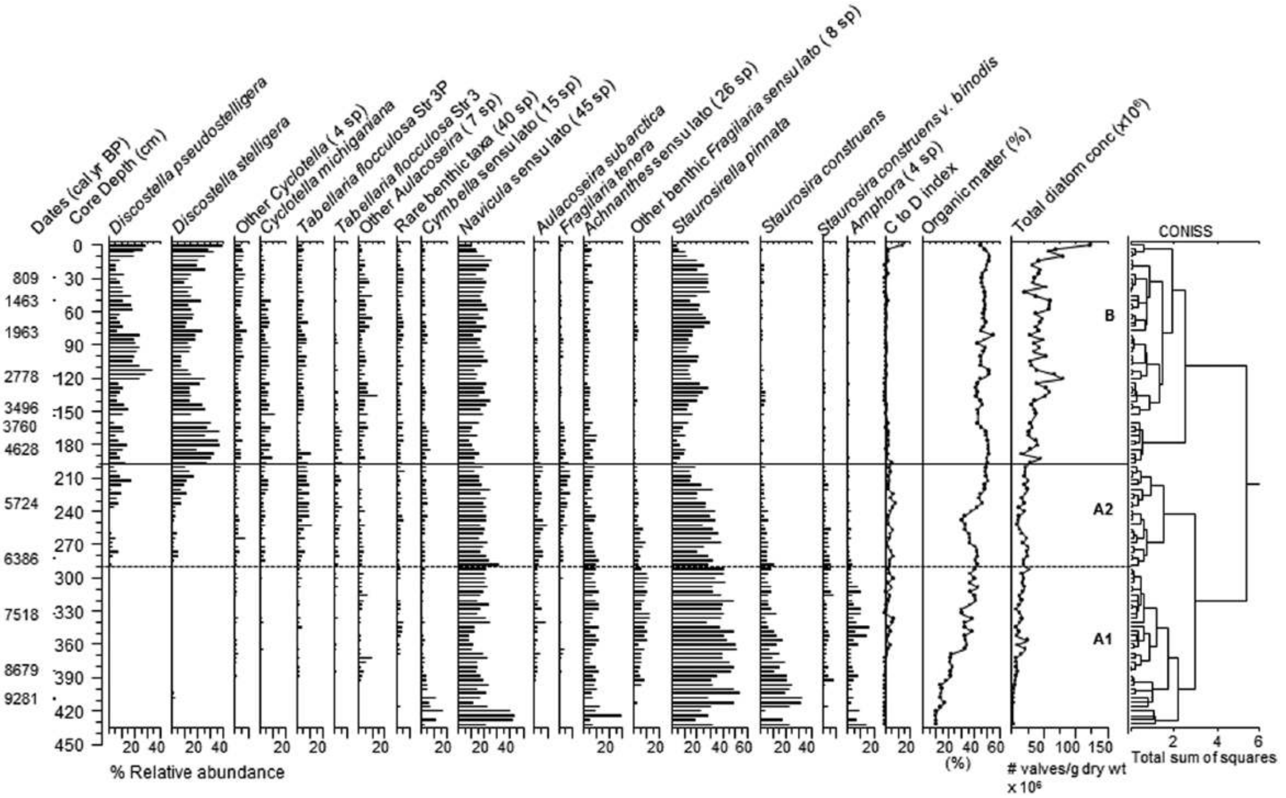

Figure 3. The dominant (>5%) diatom taxa found in a near-shore (depth = 11.4 m) sediment core from Meekin Lake versus cumulative core depth. ^{14}C-estimated dates are indicated to the left. The diatom taxa are arranged by Correspondence Analysis (CA) axis-1 scores so that the changes in diatom assemblages across time are clearly shown. The chrysophyte scale-to-diatom index (C to D index), total diatom concentration, and percent organic matter are also plotted. The zones and subzones are indicated, as defined by the constrained cluster analysis.

Bray-Curtis dissimilarity measure which is very suitable for data sets with lots of zeros (Clarke and Warwick, 2001). Finally, a regional summary is provided by a comparison of the results from the two new study lakes (Meekin and Gall) with those from the previously published near-shore core from ELA Lake 239 (Moos et al., 2009) using graphics in Origin ver. 6.1 (Origin, 2000).

Results

Piston cores were obtained from a depth of 11.4 m in Meekin Lake in June 2009, and from a depth of 7.5 m in Gall Lake in June 2010. The cumulative length of the sediment cores were 440 and 230 cm for Meekin Lake and Gall Lakes, respectively, and in both cases, gray clays were present in the bottommost sections. The activities of ^{210}Pb in the upper intervals of the piston cores from Meekin Lake (0–0.5 cm interval) and Gall Lake (2.5–3 cm interval) corresponded to the years 1960 and 1975, respectively, based on the dated gravity cores from the same depth (Laird et al., 2012). A total of 12 and 8 pollen extracts were analyzed for ^{14}C activity in the sediment cores from Meekin Lake and Gall Lake, respectively (Table 1; Figure 2). Good correspondence between pollen-based radiocarbon dates to those derived from macrofossils from the same sediment levels of lakes in northwest Ontario supports the utility of using pollen as the carbon source for ^{14}C analysis (Haig et al., 2013; Laird and Cumming, 2008; Moos et al., 2009). Based on the *clam* age–depth models, the analysis of diatom assemblages at a 4-cm interval in the cores represents an approximate centennial-scale resolution for both lakes (~120-year resolution for Meekin Lake and 150-year resolution for Gall Lake).

Meekin Lake

A total of 190 diatom taxa were identified from the sediment core from Meekin Lake over the last ~9500 years. The zonation estimated by a constrained cluster analysis (Grimm, 1987) provides a framework to discuss the major changes in diatom assemblages that occurred over the Holocene (Figure 3). Broadly, changes in the diatom assemblages showed differentiation into two main periods: an early-to-mid-Holocene (~9600–4800 cal. yr BP) period that was dominated by benthic diatom taxa (Zone A) and a post-4800 cal. yr BP period that was characterized by a dominance of a planktonic diatom assemblage (Zone B). Trends in these two periods are elaborated below.

Zone A (~9500–4800 cal. yr BP) early-to-mid-Holocene period in Meekin Lake. The earliest part of subzone A1 (~9600–8600 cal. yr BP) was characterized by the lowest concentrations of organic matter (<20%) and low concentrations of diatoms (Supplemental Figure 1, available online) that were dominated by a diverse assemblage of benthic diatom taxa, including *Staurosirella pinnata* (Ehrenberg) Williams and Round, *Staurosira construens* (Ehrenberg) Williams and Round, *Navicula* sensu lato, *Cymbella* sensu lato, other benthic *Fragilaria* sensu lato, and *Amphora* species (Figure 3). The chrysophyte-to-diatom index was low and stable. The remainder of subzone A1 (~8600–6400 cal. yr BP) was characterized by an almost doubling of organic matter to ~40% and increased abundances and doubling of the concentrations of a number of the benthic taxa, with the noted exception of *S. construens* which experienced declines in both relative abundance (Figure 3) and concentration (Supplemental Figure 1, available online).

Subzone A2 (~6500–4800 cal. yr BP) was characterized by declines in many of the benthic taxa and increases in the relative abundances and concentrations of a number of planktonic taxa that achieved their highest relative abundances and concentrations, including *Tabellaria* spp., *Aulacoseira subarctica* (O'Muller) Haworth, and *Fragilaria tenera* (W. Smith) Lange-Bertalot. This zone was also characterized by the initial appearance of

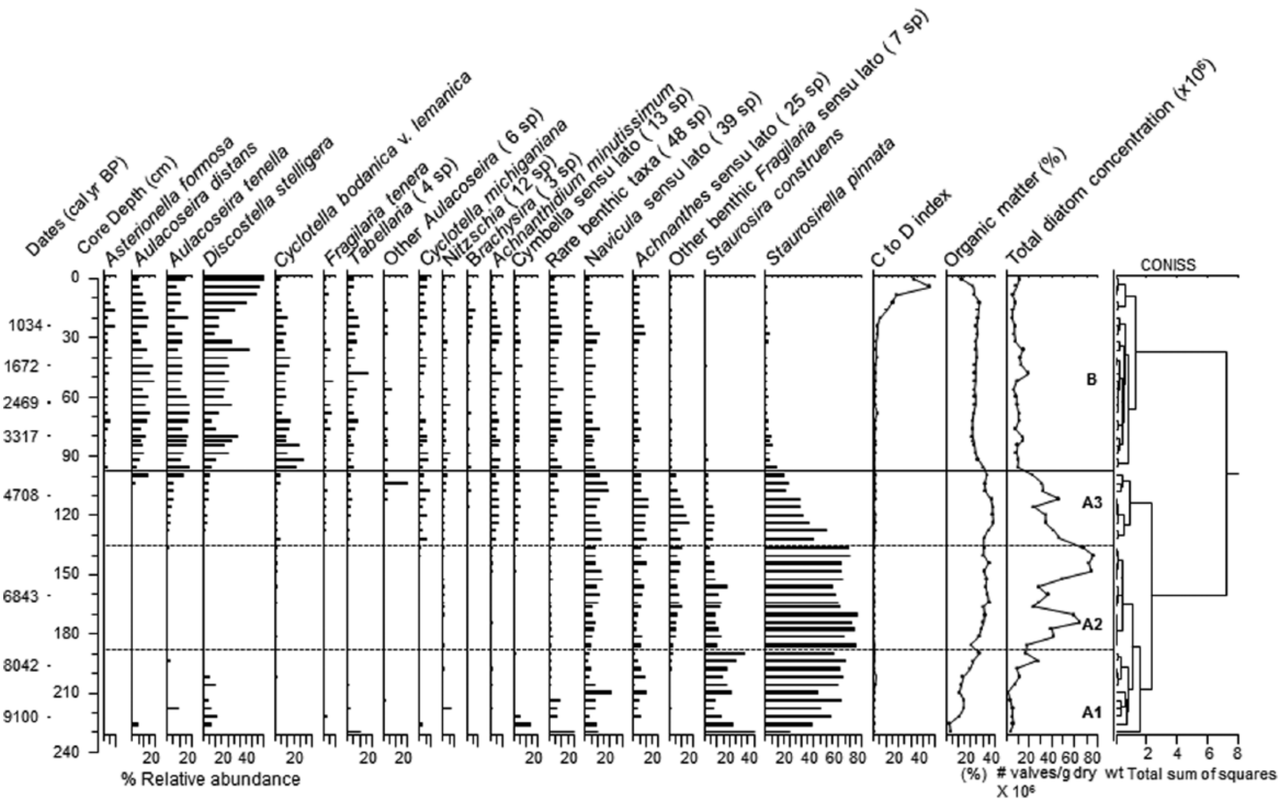

Figure 4. The dominant (>5%) diatom taxa found in a near-shore (depth = 7.5 m) sediment core from Gall Lake versus cumulative core depth. ^{14}C-estimated dates are indicated to the left. The diatom taxa are arranged by Correspondence Analysis (CA) axis-1 scores so that the changes in diatom assemblages across time are clearly shown. The chrysophyte scale-to-diatom index (C to D index), total diatom concentration, and percent organic matter are also plotted. The zones and subzones are indicated, as defined by the constrained cluster analysis.

Discostella stelligera (Cleve and Grunrow) Houk and Klee and *Discostella pseudostelligera* (Houk and Klee) initially at low abundances which then increase to over 10% by ~4800 cal. yr BP. Percent organic matter increased gradually over this period from ~40% to 50%, and the chrysophyte-to-diatom index remained low and variable throughout most of this subzone, decreasing to essentially zero by ~4800 cal. yr BP.

Zone B (~4800 cal. yr BP to present) mid-to-late Holocene in Meekin Lake. The mid-to-late Holocene in Meekin Lake was characterized by large increases in the relative abundances and concentrations of *D. stelligera* and *D. pseudostelligera* reaching combined relative abundances of ~40–75% (Figure 3; Supplemental Figure 1, available online). The planktonic taxa, *Tabellaria flocculosa* strains 3p and 3 (*T. flocculosa* (Roth) Kutz strains (sensu Koppen), *A. subarctica*, and *F. tenera*, declined in both relative abundance and concentrations in Zone B, whereas the planktonic taxa *Cyclotella michiganiana* and other *Aulacoseira* (mainly *A. distans humilis* (Ehrenberg)) increased. The relative abundance and concentrations of *S. pinnata* reached a record low at the beginning of this period, but then fluctuated between ~15% and 30% over the last ~4600 years.

Gall Lake

A total of 163 diatom taxa were identified from the sediment core from Gall Lake over the last ~9200 years. The zonation estimated by a constrained cluster analysis (Grimm, 1987) provides a framework to discuss the major changes in diatom assemblages that occurred over the Holocene (Figure 4). Similar to the changes seen in the sediment core from Meekin Lake, changes in the diatom assemblages show differentiation into an early-to-mid-Holocene period (~9200–4000 cal. yr BP) that was dominated by benthic diatom taxa (Zone A) and a post-4000 cal. yr BP period that was characterized by a dominance of a planktonic diatom assemblage (Zone B). Trends in these two periods are elaborated on below.

Zone A (~9200–4000 cal. yr BP) early-to-mid-Holocene period in Gall Lake. The early-to-mid-Holocene period was composed of three distinct subzones (A1, A2, and A3; Figure 4). Subzone A1 (~9200–8000 cal. yr BP) was characterized by low concentrations of organic matter that increased from <5% to ~25% by ~7800 cal. yr BP. From ~9200–8200 cal. yr BP, low abundances and concentrations of planktonic taxa, including *D. stelligera* and *Tabellaria*, and some *Aulacoseira* taxa, co-existed with low concentrations of benthic taxa (*S. construens, S. pinnata, Navicula* sensu lato, *Achnanthes* sensu lato., and *Cymbella* sensu lato) followed by increases in the concentration and relative abundance of *S. pinnata* (Figure 4; Supplemental Figure 2, available online). The chrysophyte-to-diatom index was very low throughout Subzone A1.

Subzone A2 (~8000–5700 cal. yr BP) was characterized by an initial increase in the organic matter to ~30% which then remained relatively constant. *S. pinnata* increased in relative abundance and concentration, as did many of the other benthic *Fragilaria* sensu lato (mainly *Staurosirella leptostauron* (Ehrenberg) Williams and Round, Figure 4; Supplemental Figure 2, available online). Total concentration of diatom valves increased throughout this zone, which was reflected primarily in increased concentrations of *S. pinnata*, other benthic *Fragilaria* sensu lato, *Achnanthes* sensu lato, and *Navicula* sensu lato (Supplemental Figure 2, available online). The chrysophyte-to-diatom index remained very low in this zone.

Subzone A3 (~5700–4000 cal. yr BP) was characterized by declines in the previously common benthic taxa (*S. pinnata*, other benthic *Fragilaria* sensu lato, *Achnanthes* sensu lato, and *Navicula* sensu lato) that were replaced by other benthic taxa (e.g. *Achnanthidium minutissimum* (Kutzing) Czarnecki, *Brachysira,*

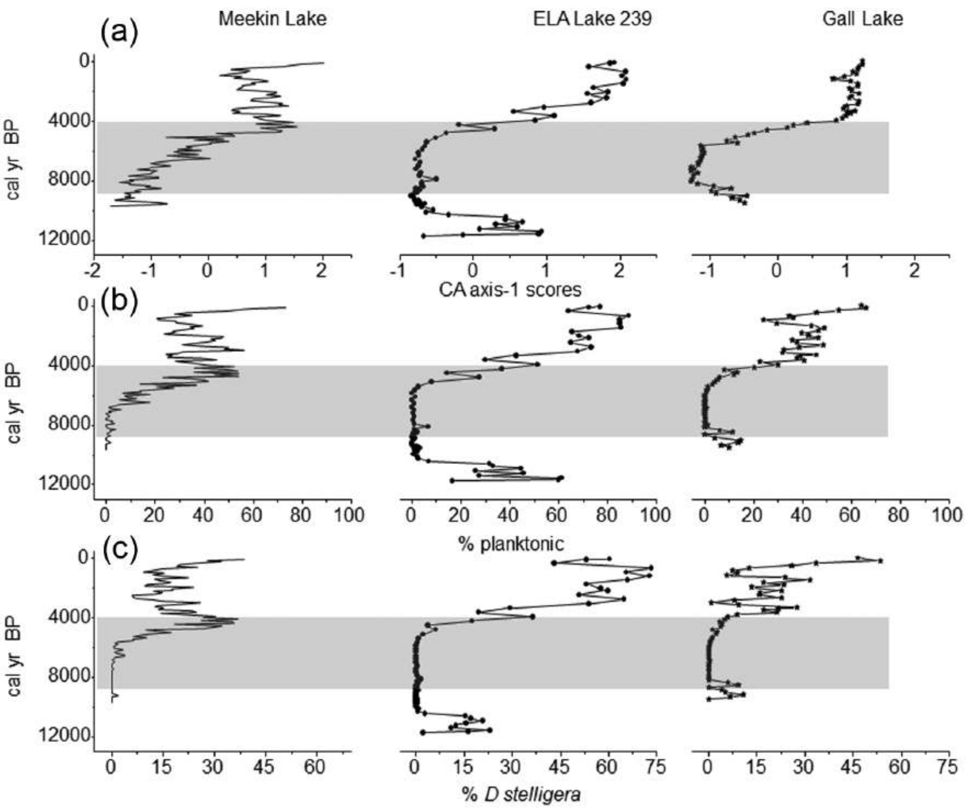

Figure 5. Summary of the changes in diatom assemblages in sediment cores of the three lakes (Meekin, ELA Lake 239, and Gall Lake) arranged in geographic position from west to east. Three metrics are shown to summarize the changes over the Holocene: (a) Correspondence Analysis (CA) axis-1 scores, (b) percent (%) planktonic taxa, and (c) percent abundance of the dominant planktonic taxon in all cores, *Discostella stelligera*.
ELA: Experimental Lakes Area.

Nitzschia, Cymbella sensu lato), as well as some planktonic taxa, including *C. michiganiana* and small abundances of other planktonic taxa (e.g. *Aulacoseira tenella* (Nygaard) Simonsen, *D. stelligera*, and *Tabellaria*; Figure 4; Supplemental Figure 2, available online). Percent organic matter remained high, reaching a peak of just over 30%. Total concentration of all diatoms decreased, and the chrysophyte-to-diatom index remained very low.

Zone B (~4000 cal. yr BP to present) mid-to-late Holocene in Gall Lake. The mid-to-late Holocene in Gall Lake was characterized by large increases in the relative abundances and concentrations of planktonic taxa, including *Asterionella formosa* (Hassall) Houk et Klee., *Aulacoseira distans* (Ehrenberg) Simonsen, *A. tenella, D. stelligera, Cyclotella bodanica* v. *lemanica*, and *Tabellaria* spp. (Figure 4; Supplemental Figure 2, available online). Although the relative abundance of *C. michiganiana* remained constant, the concentration of this taxon declined somewhat from the previous zone (Figure 4; Supplemental Figure 2, available online). Most of the benthic taxa that increased in Subzone A3 (e.g. *A. minutissimum Brachysira, Nitzschia, Cymbella* sensu lato) remained relatively constant in both relative abundance and concentration in Zone B. Peak abundances of *D. stelligera*, the dominant planktonic taxon, were reached in the uppermost three samples. Total concentration of all diatoms was lower throughout Zone B, and the chrysophyte-to-diatom index remained very low, but increased slightly until the last 1000 years, where this index greatly increased.

Regional patterns in diatom assemblages

Changes in the diatom assemblages in well-dated sediment cores over the Holocene along a west-to-east gradient across the boreal region (Meekin Lake, ELA Lake 239, and Gall Lake) were summarized by three metrics: changes in the main direction of variation in the diatom assemblages (CA axis-1 scores), changes in the percentage of planktonic diatoms, and changes in the dominant planktonic diatom in all three cores, *D. stelligera* (Figure 5). Concentrations and percent abundance of *D. stelligera* showed very similar patterns across all three lakes (Figure 5 and Supplemental Figure 3, available online). The CA axis-1 scores captured 56.8% (Meekin Lake), 66.8% (ELA Lake 239), and 69% (Gall Lake) of the variance, and the patterns in all three metrics were similar. *D. stelligera* is the dominant planktonic taxon in all three lakes and the percent abundance significantly correlated with the percent abundance of planktonic taxa for all three lakes (Meekin, $r = 0.9$, $n = 109$, $p = <0.05$; Lake 239, $r = 0.96$, $n = 72$, $p = <0.05$; Gall, $r = 0.88$, $n = 60$, $p = <0.05$). In ELA Lake 239 and Gall Lake, the early-Holocene diatom assemblages initially contained planktonic taxa but at low concentration (Figure 4; Moos et al., 2009) that quickly changed to dominance by benthic taxa by the mid-Holocene period. For the last ~4000 years, the diatom assemblages in all lakes reached high and relatively stable abundances of planktonic taxa, which were dominated by *D. stelligera*. Transition out of the dominance of the diatom assemblage by benthic taxa and the low-lake levels of the mid-Holocene began much earlier in Meekin Lake with increasing percentages of planktonic taxa starting *c*. 6500 cal. yr BP (Figure 5). Whereas the initial increase in percent planktonic taxa occurred later and with similar timing at *c*. 5700 cal. yr BP in ELA Lake 239 and Gall Lake (Figure 5).

Changes in the diatom assemblages within three broad time periods were summarized by a two-dimensional nMDS plot (Figure 6). The time periods used were (1) the period of deglaciation to ~8000 cal. yr BP; (2) the mid-Holocene warm period (~8000–4000 cal. yr BP), and (3) the neoglacial period (~4000 cal. yr BP to present). In general, the three periods were distinct in

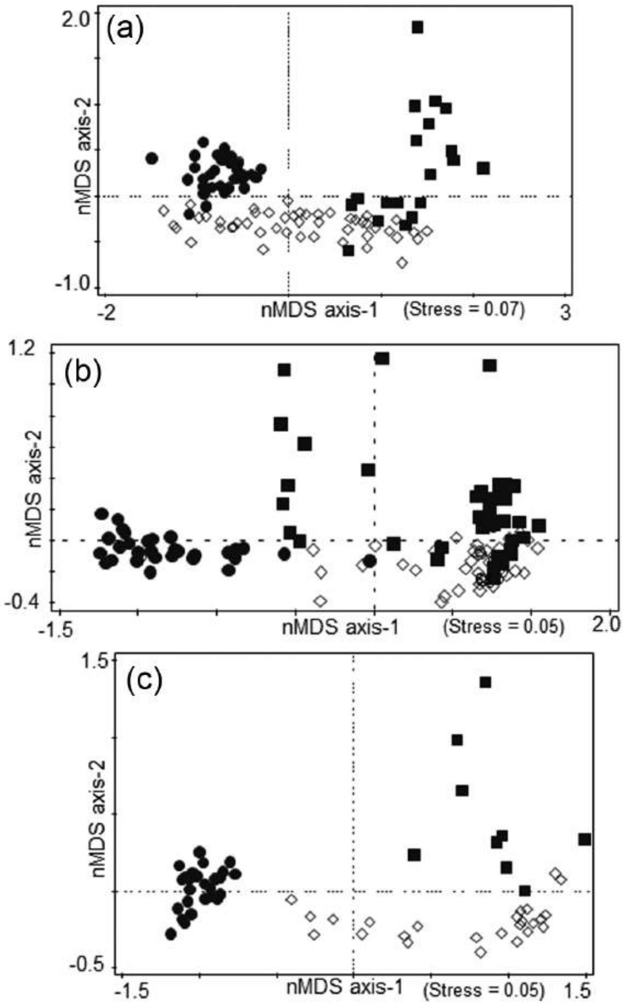

Figure 6. Non-metric multidimensional scaling (nMDS) plot of diatom assemblages over the Holocene in (a) Meekin Lake, (b) ELA Lake 239, and (c) Gall Lake. Three time periods are indicated: (1) deglaciation to ~8000 cal. yr BP is shown by solid square, (2) the mid-Holocene warm period (~8000–4000 cal. yr BP) is shown by open diamond, and (3) the late Holocene (~4000 cal. yr BP to present) is shown by solid circle).
ELA: Experimental Lakes Area.

their assemblages in each of the lakes as there is little overlap of the groups in ordination space (Figure 6). The exception to this is the overlap between the early and mid-Holocene period in Meekin Lake and Lake 239, as our generalized time periods do not exactly correspond to the assemblage zones of the individual lakes (Figures 3 and 4). In addition, in Lake 239, the initial assemblage after deglaciation had similar percentages to the early part of the late Holocene (albeit much lower concentrations, Figure 5 and Supplemental Figure 3, available online) of some planktonic taxa (i.e. *D. stelligera*) and as a consequence these early-Holocene samples ordinate closer to the late Holocene assemblages. In Meekin Lake and Gall Lake particularly, the mid-Holocene period is a period of gradual change of transition between the early and late Holocene assemblages, as represented by the broad placement of samples across nMDS axis space. Across all lakes, the late Holocene assemblages were very distinct from the other two periods and had the most similar composition within the period as represented by the tight cluster of samples (Figure 6).

Discussion

The WRDB is an important source of water for ecosystems and human activities. Future climate projections for this region include temperature increases in excess of 2°C over the next 20 years (Chiotti and Lavender, 2008). Instrumental records show that WRDB has experienced droughts during the 1930s, 1950s, and 1980s, but these droughts have been spatially asynchronous across climate stations in northwest Ontario (Laird et al., 2012). However, periods of synchronous aridity have occurred across this region over the past 2000 years, as indicated by the regional drought during the Medieval Climate Anomaly (MCA; Laird et al., 2012). Given this climatic sensitivity over the last 2000 years, the goal of this study was to assess whether synchronous changes in water balance have occurred over longer timeframes, especially in the mid-Holocene period, a time when temperatures have been inferred to be at least 1–2°C warmer than present in the WRDB (Moos and Cumming, 2012). The impact of extreme aridity over the Holocene has been well studied on the northern prairies from loess records (Miao et al., 2005; Wolfe et al., 2006), pollen and other proxy records (Grimm et al., 2011), and from lake records (Laird et al., 2007), whereas changes in water balance over the Holocene in boreal regions is less studied. The recent synthesis of pollen records in the WRDB (Moos and Cumming, 2012) indicates a distinct change in the vegetation in the mid-Holocene period to a more open canopy forest with increased temperatures (particularly in the winter) and increased evapotranspiration (reduced effective moisture).

The impact of these inferred changes in effective moisture on lake ecosystems in the WRDB is poorly known. Influences of lake-level changes are mainly known from various proxies on one lake sediment record, ELA Lake 239, in northwest Ontario (Laird and Cumming, 2008; Moos and Cumming, 2011, 2012; Moos et al., 2009). The lack of studies to date on lake-level fluctuations in boreal regions is largely because of the problem of investigating hydrologic changes in drainage lakes (Laird and Cumming, 2008; Smol and Cumming, 2000). Our modified Digerfeldt approach for ELA Lake 239 (Laird and Cumming, 2008) was applied to the Holocene records from Meekin Lake and Gall Lake to provide a more regional assessment of the changes in lake level in the WRDB. The estimated ages of sediments in the cores from Meekin Lake and Gall Lakes based on AMS ^{14}C dating of pollen provide strong evidence of continuous sedimentation and strong chronological control in the cores (Figure 2). Consequently, changes in the diatom assemblages in Meekin and Gall lake cores, in conjunction with the previous record from Lake 239, enabled two important findings: (1) the predominance of benthic diatom assemblages throughout the early-to-mid-Holocene period are consistent with prolonged declines in effective moisture inferred from pollen analysis in this region, and (2) the dominance of planktonic taxa over the last ~4000 years indicate that lake water levels have been much higher during this period which is consistent with cooler conditions inferred from the pollen inference in this region (Moos and Cumming, 2012).

Early to mid-Holocene changes in effective moisture

The dominance of benthic diatom assemblages from at least ~8000 to 5000 cal. yr BP in all three lakes strongly suggests persistently low water levels across the region during the mid-Holocene warm period (Figure 5), indicating that the pollen-inferred warmer temperatures and increased evapotranspiration resulted in a negative water balance in this region. The consistency between sites, which span a gradient of over 300 km through the present-day boreal forest, suggests the importance of extrinsic climate forcing (Williams et al., 2011).

The aridity of the mid-Holocene period (~8000–4000 cal. yr ago) is well documented in the northern prairies of North America as well as regions to the west in the Rocky Mountains (Laird et al., 1996; Lewis et al., 2001; Shuman et al., 2009), with similar timing to those seen in our sites in northwest Ontario. The inferred declines in effective moisture had a large impact on lake levels within the region. Laird and Cumming (2008) suggest that ELA Lake 239 declined by at least 8 m during the mid-Holocene period. The consistently high percent abundance and concentrations of benthic taxa in Meekin Lake and Gall Lake strongly suggests much lower water levels than present between ~8000 and 5000 years ago (Figure 5), likely by as much as 2–3 m in Meekin Lake and 3–5 m in Gall Lake based on the modern distribution of *S. pinnata*, other benthic taxa, and *D. stelligera* (Laird and Cumming, 2008; Laird et al., 2011; Kingsbury et al., 2012). The nMDS ordination also clearly showed that the diatom assemblages of the mid-Holocene period were unique in all three lakes in comparison with the early-Holocene and late-Holocene periods (Figure 6).

The dominance of *Discostella* taxa today in both Meekin Lake and Gall Lake and the presence of unique mid-depth assemblages (Kingsbury et al., 2012) preclude the usefulness of modern surface sample calibrations to provide adequate quantitative estimates of depth down core, because of the presence of several benthic taxa at higher abundances than those of the modern surface samples. For example, in Meekin Lake, the present-day abundance of *S. pinnata* reaches a maximum abundance of ~20% in the surface samples between a modern depth of 8 and 9 m (Laird et al., 2011). However, this taxon achieved a sustained and high relative abundance of greater than 40% in the early-to-mid-Holocene period. Similarly, the maximum abundance of *S. construens* is only ~5% in the surface samples, but the relative abundance in the core was consistently greater than ~20%. The same situation is present in Gall Lake in the early-to-mid-Holocene period, where the modern maximum of *S. pinnata* is ~30% occurring between 2 and 4 m depth (Laird et al., 2011), whereas in the core, abundances greater than 60% were common. This lack of adequate analogs is in part the result of models being based on percent diatom taxa, a constrained metric in which if one taxon increases, others have to decrease. Other influences on analogs may be related to different physical and chemical conditions along the depth gradient today in comparison with the past. However, while specific benthic and planktonic taxa may differ between the present and past, the B-P boundary appears to be a robust metric highly related to depth.

Several variables within a lake vary with depth and influence the spatial distribution of diatom taxa, including substrate type, disturbance regime, temperature, nutrients, and light availability (Laird et al., 2011 and citations within). Wave disturbance and light availability have been found to be two of the primary factors that characterize the vertical zonation of the diatom community across the depth gradient, whereas the location of the B-P boundary is primarily influenced by changes in water depth and light availability (Laird et al., 2011). In the analysis of diatoms along three depth transects in Worth Lake, northwest Ontario, from different portions of the basin that had different wind orientations and wave disturbance, as well as varying complexity in bottom profiles and degree of slope, the estimated B-P boundaries were the same (Laird et al., 2010). Basin morphometry, and changes in water depth, can influence the sources of benthic and planktonic taxa to the sediments and their ratios, particularly in complex basins (Stone and Fritz, 2004). Here, we chose lakes with relatively simple basin morphometry and cored in the part of the basin with a gentle slope to minimize these influences. Degree of light transparency can also change with changes in depth and turbulence; however, the analysis of invertebrate remains (which are not influenced by light) in Gall Lake shows similar trends to the diatoms over the last two millennia, suggesting that changes in depth is one of the primary influences on both proxies (Karmakar et al., 2014).

The few other Holocene studies of lake level in adjacent regions to the WRDB suggest similar magnitude changes during the mid-Holocene period as estimated in our study lakes. In two Minnesota lakes, estimated lake-level declines were between ~1 and 15 m (Cohen et al., 2006), and declines of up to ~10 m were estimated in Rocky Mountains lakes (Shuman et al., 2009). In the Canadian prairies, Lake Winnipeg was a closed-basin lake from ~4.5 to 8.2 cal. yr BP, with the southern basin desiccated (today this basin has a maximum depth of ~11 m) and the parkland border much further to the east (Lewis et al., 2001). The return to an open-lake system and rising lake levels in Lake Winnipeg is similar to the timing of increasing planktonic taxa in Meekin Lake, our site closest to the PFE.

late Holocene changes in effective moisture

In all cores, planktonic taxa increase in abundance (by at least 4000 years ago) and remain abundant until today (Figure 5). Modern-day diatom assemblages from all of our study lakes show a dominance of planktonic taxa in deep waters. In all lakes, *D. stelligera* and *D. pseudostelligera* reach their modern-day maximum abundances of ~40–60% at depths greater than 10–12 m (Laird and Cumming, 2008; Kingsbury et al., 2012). In Meekin Lake, high abundances of *D. stelligera* and *D. pseudostelligera*, combined with abundances of many other planktonic taxa, suggest high and maintained water levels, of at least the depth of coring (11.5 m) over the past 4000–5000 years. Similarly, at Gall Lake and ELA Lake 239, many planktonic taxa were dominant post-4000 years ago (Figure 5). In the Gall Lake Holocene record, *D. stelligera* exceeded abundances of ~35–40%, abundances observed at water depths > 8 m in the calibration set (Kingsbury et al., 2012), suggesting water levels have been at their highest at the coring site, over the past few hundred years and during other periods over the past 4000 years.

The sites in northwest Ontario suggest that high lake levels were clearly established by ~4000 cal. yr BP. This is similar to the broad-scale syntheses of lake-level conditions over the Holocene in North America to generally cooler, moister conditions which generally begin ~6000–5000 cal. yr BP, with 'modern' conditions in some lakes not established until ~3000–2000 cal. yr BP (Ritchie and Harrison, 1993; Thompson et al., 1993). More recent studies suggest a similar timing to the onset of moisture conditions with the onset of higher lake levels generally by ~3000 cal. yr ago in the Great Lakes region (Booth et al., 2002) and in the Rocky Mountains by ~3000–4000 cal. yr BP (Shuman et al., 2009). However, changes in aridity have not been static over the past 4000 years. Higher-resolution studies (decadal-scale analysis) from near-shore cores from Gall Lake indicate that a significant period of lower lake levels, much greater than any instrumental droughts, occurred during the MCA indicated by both diatoms (Haig et al., 2013) and invertebrates (Karmakar et al., 2014). A synthesis across the WRDB also indicates a regional period of aridity during the MCA (Laird et al., 2012). Similarly, peatland records in the western Great Lakes region suggest several extreme drought events over the past 2000 years, including the MCA period (Booth et al., 2006). However, the low-lake levels of the mid-Holocene period are clearly more extreme than during the last 2000 years.

West to east gradient in effective moisture

Holocene shifts in the PFE have been extensively studied beginning with the classic work of McAndrews (1966), and the more recent syntheses of other studies (Nelson and Hu, 2008; Williams et al., 2009). These recent syntheses support Umbanhowar et al. (2006) that the timing and rates of the PFE shifts were heterogeneous, with many records indicating an abrupt early-Holocene transition from forest to grassland, but a more gradual reforestation during the late Holocene. A west to east time-transgressive response to aridification was also documented with the early shift in the PFE (Williams et al., 2010). Williams et al. (2011) suggest this may be because of more arid sites being nearer to a threshold than less arid sites. The length of our early-Holocene records varies, with only ELA Lake 239 recording the very early Holocene. Potentially, the larger size and depth of Lake 239 enabled greater accumulation of sediments in the near-shore locations in the earliest history of the lake. The Lake 239 sedimentary record clearly records an abrupt transition into the lower lake levels of the mid-Holocene period. This is only somewhat evident in the Gall Lake record, but timing of at least the lowest lake levels is much later. All three lakes do indicate a more gradual transition to the higher lake levels of the late Holocene.

Variability in the timing of low-lake levels in the mid-Holocene period and transition to rising lake levels in the late Holocene varies within and between regions across much of North America (Laird et al., 1996; Shuman et al., 2009; Thompson et al., 1993). Our records also show variability in the timing of the transition to planktonic diatom taxa after the mid-Holocene low stands dominated by benthic taxa, with the earliest changes occurring in Meekin Lake ~1 millennia earlier than seen in ELA Lake 239 and Gall Lake (Figure 5). Spatial and temporal variability in sediment records can be attributable to many factors, including spatial variability in climate and individual responsiveness of the lakes. Potentially, the more western and closer location of Meekin Lake to the PFE explains the earlier onset of higher lake levels, whereas there may have been a lag in the response in the more northern site, as seen in Teed et al. (2009). However, the timing of the transition to higher lake levels is similar between Lake 239 and Gall Lake, thus physical characteristics of the lakes, and local geological and vegetational settings, may have played more of a role in lake response than geographical position. The magnitude of change also does not have a clear west to east signal. We expected Meekin Lake to have the highest magnitude change and longest duration with its closer proximity to the modern PFE. However, the magnitude of change in percent planktonic composition is similar across all lakes, and the estimated decline in lake level is similar between Meekin Lake and Gall Lake. There also was not a clear west to east signal of the low-lake levels of the MCA in either timing or magnitude of six study lakes in the WRDB (Laird et al., 2012). However, the overall similarity in the direction and magnitude of response, and generally similar timing on both time scales (last ~2000 years and Holocene), suggests that a broad-scale forcing factor such as climate is likely a major driver of these changes (e.g. Williams et al., 2011).

Conclusion

Collecting sediment cores adjacent to the B-P boundary appears to be a sensitive method to track changes in aridity from present-day drainage lakes. As such, this approach can provide a method to estimate changes in effective moisture in comparison with conditions today, in more humid regions from where such data have been difficult to acquire. Empirical evidence of the low water levels during the mid-Holocene period across northwest Ontario during a time when climate was warmer by 1–2°C warmer than today has important implications for mitigation and adaptation in this region. Increasing trends in precipitation over the last 100 years across northwest Ontario suggest that water scarcity may not be an issue in the near future (St. George, 2007). However, this study and other studies (Laird et al., 2012) suggest that northwest Ontario has experienced periods of synchronous aridity in the past, and thus, future warming could result in droughts across the region, similar to those of the past. What the future climate holds for regions of North America because of global warming is unclear, but a return to the aridity of the mid-Holocene period would bring significant ecological, environmental, and social challenges.

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