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Complex responses of phototrophic communities to climate warming during the Holocene of northeastern Ontario, Canada

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Abstract

Although the Holocene climate of North America has been generally well-studied, high regional variability can obscure understanding of mechanisms underlying large-scale and long-term variability. To address such a shortcoming, historical changes in Holocene climate in northeastern Ontario were quantified using analysis of sedimentary pollen, diatoms, and pigments in a small boreal lake. Modern Analog Technique (MAT) based on pollen was used to reconstruct average temperature over the Holocene record of Charland Lake and showed average temperature was ~2 °C warmer than present conditions ~7800–4500 cal yr BP, a time period which we define as the Holocene Thermal Maximum (HTM). Further investigation of pollen data suggests a two-phase HTM: warm and dry conditions followed by warm and wet conditions based on the occurrence of *P. strobus* and Cupressaceae (*Thuja*) pollen. Concomitant changes in landscape features affected the sedimentological and phycological nature of the lake, as diatom assemblages reflect delayed stabilization of the landscape following the draining of Glacial Lake Ojibway ~8200 cal yr BP. In contrast, during a Post-HTM period, which was warmer than today but cooler than the HTM, diatom and pigment data appear to be more influenced by indirect effects of climate, such as lake-water thermal stratification and changes in plankton seasonality. This study suggests that while climate greatly influenced regional forest ecology, landscape, hydrological, and indirect climate effects were more influential on the phytoplankton communities during the Holocene in northeast Ontario. These findings may provide insight into how freshwater environments will respond to future anthropogenic warming in the region.

Keywords: *Thuja, pollen,* thermal stratification, landscape dynamics, diatoms, sedimentary pigments

Introduction

The Holocene Thermal Maximum (HTM) was a period of enhanced warmth that occurred during the early and middle Holocene (Viau et al., 2006; Renssen et al., 2009, 2012). This warming has been well recorded and well-studied in the mid-to-high latitudes of the Northern Hemisphere that experienced major climatic alterations following the last glacial maximum (LGM) and deglaciation (Whitlock and Bartlein, 1997; Carlson et al., 2008). The cause of the HTM has largely been attributed to an increase in solar insolation, due to orbital variation, which maximized at ~10 ka BP (thousand years before present) (Ritchie et al., 1983; Bond et al., 2001). Despite the overall maximum solar insolation occurring at this time, the specific regions of North America may not have experienced maximum warmth at the same time or to the same degree (Renssen et al., 2009, 2012). In general, regions at higher latitudes experienced greater amounts of warming than those at lower latitudes (Renssen et al. 2009, 2012; Briner et al., 2016) and the western portion of the continent warmed earlier than the east, likely due to downwind cooling effects of the melting Laurentide Ice Sheet (LIS) (Carlson et al., 2008; Viau and Gajewski, 2009). Alongside the variation in onset, duration, and magnitude of warmth experienced during the HTM in North America, reconstructions of Holocene precipitation levels suggest a climatic dipole in which the west of the continent was dry while the east was wet during the HTM (Shuman and Marsicek, 2016). To date, however, these studies have focused on the continental United States and the Arctic or subarctic regions (Viau and Gajewski, 2009; Briner et al., 2016; Shuman and Marsicek, 2016) and relatively little is known regarding the nature of the HTM in the boreal region of east-central Canada (e.g., northern Ontario).

The boreal forest of northern Ontario spans ~1500 km, is one of the largest continuous forests globally, and contains abundant fresh water in its wetlands, rivers, and innumerable small lakes. Despite its size, the region is susceptible to anthropogenically-forced climate change

(Price et al., 2013). Therefore, a characterization of landscape responses to analogs of past climates may be useful for predicting effects of atmospheric warming and changes in regional hydrology (Klemm et al., 2016; Navarro et al., 2018; Teller et al., 2018). Atmosphere-ocean-vegetation models have suggested that the HTM in northern Ontario was ~2–3 °C warmer than the modern climate (Renssen et al., 2009, 2012). Recent work from northwest Ontario (~1200 km to the west of our study site) reveals that the HTM occurred from ~8500–4500 cal yr BP (calendar years before present) and was ~2 °C warmer than present conditions. This estimate was calculated using a modern analog technique (MAT) calibration based on fossil pollen and a regional set of modern pollen and climate data (Moos and Cumming, 2011). Associated dryer conditions resulted in lower lake levels, increased algal production, an eastward shift of the prairie-forest ecotone, and an increase in fire activity (Moos et al., 2009; Moos and Cumming, 2011, 2012; Karmakar et al., 2015a, 2015b). Despite this research, there has been little work examining the HTM of northeastern Ontario, Canada, which is a problem this paper seeks to address.

Only one Holocene-scale palynological study has documented Holocene climate variability in northeast Ontario (Liu, 1990). This study examined three sediment cores in a north-south transect of eastern Ontario. One of these sites, Lake Six, is 6 km away from our study site so comparisons to Liu (1990) refer to the Lake Six record. In Liu (1990), the author showed a delayed, but protracted HTM period occurring from ~7–2.5 ka BP at Lake Six. This was defined by increases in *Pinus strobus*, a typical taxon of the warm Great Lakes-St. Lawrence forest, and in Cupressaceae. Liu (1990) interpreted the presence of Cupressaceae pollen as belonging to *Thuja* based on its co-occurrence with *Thuja* macrofossils within the sediment core. These data suggest that the HTM of northeast Ontario was wet, agreeing with studies at similar longitudes to the south (Viau et al., 2006; Shuman and Marsicek, 2016). A similar interpretation has been made by Carcaillet et al. (2001) who used charcoal analysis to infer that low fire activity during the this time in western Quebec was due to enhanced water availability. Unfortunately, Liu's (1990) climatic results from Lake Six are supported by only three radiocarbon dates. With these few data points there is likely considerable error regarding the temporal boundaries of HTM warming and it is likely that the upper boundary (~2.5 ka BP) is overestimated based on studies from northwest Ontario (Moos and Cumming, 2011, 2012). Improved geochronology, as well as replicate sites in the region, are important to better define the onset and duration of the HTM in northeast Ontario, as well as its effects on lake ecosystems.

This paper attempts to quantify changes in climate systems in northeastern Ontario using robust analysis of fossil pollen to reconstruct climatic and vegetation characteristics, as well as fossil diatoms and pigments from aquatic phototrophs to quantify the effects of climate variability on lake production and community composition. Diatoms are ideal for these objectives, as certain species have well-documented optima for nutrients and other physical and chemical limnological characteristics (water-depth, pH, salinity, stratification regime, etc.). By examining changes in diatom species which are known to be nutrient-controlled, changes in nutrient levels can be inferred (Douglas and Smol, 1999; Lotter et al., 1999; Rühland and Smol, 2005; Cumming et al., 2015). Similarly, fossil pigments (chlorophylls, carotenoids, derivatives) often preserve after the loss of morphological remains of non-siliceous phytoplankton and phytobenthos, and are used to estimate historical changes in the abundance of primary producers, as well as their gross community composition (Leavitt et al., 1994a, 1997; Hodgson et al., 1998; Hall et al., 1999). Taken together, analysis of these proxies are can be used to answer three questions related to the HTM: a) when and for how long did the HTM take place in northeast

Ontario; b) what was the degree of warming that occurred during the HTM of this region and was the warmer climate wet or dry, and; c) what was the response in algal production to this warmer climate?

Methods

Study area

Charland Lake (N 48°34' 50.8", W 80°53' 46.5) (Figure 1**)** is located east of Timmins, Ontario, Canada, immediately west of Kettle Lake Provincial Park and is located within 6 km of Lake Six, site of the only other study of Holocene climate in northeast Ontario (Liu, 1990). Charland Lake, like other basins in the region, formed when Glacial Lake Ojibway drained off the landscape of northeastern Ontario ~8200 cal yr BP (Veillette, 1994; Carlson et al., 2008; Roy et al., 2015; Margold et al., 2018). The lake is small (~20 ha), 16 m deep, and 274 m above sea level. The climate of the region is humid continental (Koppen Dfb) which is characterized by wet summers and long, cold winters. Average temperature is ~1.8 °C (Environment Canada, 2019).Modern boreal forest in the area is composed mainly of white (*Picea glauca*) and black spruce (*Picea mariana*) in lowlands with jack pine (*Pinus banksiana*) and white birch (*Betula papyrifera***)** on upland sites. Charland Lake occurs in the 'Great Clay Belt' of northern Ontario. The bedrock is composed of metamorphosed Precambrian granites and granodiorites which are overlain by Quaternary glacial landforms and extensive glaciolacustrine clay deposits laid down by Glacial Lake Ojibway (Veillette, 1994; Roy et al, 2011, 2015). [insert Figure 1.]

Figure 1. (A) Bathymetric map of Charland Lake with 2 m contours. The black star represents the location of the piston core that was taken from a depth of ~16 m. (B) A reference map of

Ontario with the Charland Lake coring site indicated by a black star.

Sample collection

Bathymetric data points were collected from Charland Lake using a Garmin GPS-Map Sounder 238 connected to a Toughbook computer with Bathymetric Automated Survey System (B.A.S.S.) software, v 2.4 (Levec, 2001). These data points were converted to shape files and used to produce the bathymetric map in ArcMap 10.5 (Esri, 2016). A 473 cm long sediment core was collected from a depth of ~16 m on 19 June 2014 using a 1-m square-rod Livingstone piston corer with an internal diameter of 5.1 cm (Wright, 1967; Wright et al. 1984; Glew et al., 2001). Approximately 10 cm of material from the top of the core was lost during horizontal extrusion in the field. To assure collection of an undisturbed sediment-water interface, and to be able to accurately date the top of the piston core, a gravity core (internal diameter 7.62 cm) was taken at the same site using a modified gravity corer (Glew 1989) and was sectioned into 0.5 cm intervals in the field. The piston core exhibited distinct units, with organic gyttja 0–313 cm, grey clays from 313–337 cm, organic-rich material from 337–417 cm, and basal clay deposition below that level. In this paper, we refer to these clay layers in order of deposition, making the clay deposit from 417–473 cm ‘the first clay layer’ and the deposit from 313–337 cm ‘the second clay layer’. The piston core was wrapped in 1-m sections on site and transported in a cooler to the Paleoecological Environmental Assessment & Research Laboratory (PEARL) at Queen’s University where they were stored horizontally in a cold room at ~4° C. Half of the core was then sectioned into 1 cm intervals, while the other half was archived.

Analyses

Chronology

The top 13 cm of the gravity core were dated by using a constant rate of supply (CRS) model applied to ^{210}Pb gamma activity of the sediments. This was done to assess the date of the top of the piston core as the sediment-water interface was lost during extrusion. The ^{14}C chronology for the piston core was determined by dating a concentrated sample of pollen grains from eight sediment samples with accelerator mass spectrometry (AMS). Pollen grains were isolated from lake sediments by LacCore using a procedure similar to Brown et al. (1989) and measured for ^{14}C at the Lawrence Livermore National Laboratory. An age-depth relationship based on these radioisotopic data was constructed using Bayesian age modeling with the *BACON* (v. 2.2) modeling package in R (R Core Team, 2015) with the IntCal13 ^{14}C calibration curve (Blaauw and Christen, 2011; Reimer et al., 2013). Default settings outlined by Goring et al. (2012) were used to determine the gamma distribution of the accumulation rate, which were in agreement with the posterior distribution of activities (Blaauw and Christen, 2011). The prior memory was set to a mean of 0.3 and shape of 25 to accommodate small shifts in accumulation rates. The sensitivity of prior memory parameters was tested and changes in mean and shape did not result in large changes to the model.

Dry mass and organic matter

Dry mass and percent organic matter was determined through standard loss-on-ignition procedures (Heiri et al., 2001) on 60 intervals throughout the sediment core.

Pollen

Pollen samples were prepared at every 8 cm (60 samples total) using a modification of the method of Bennett and Willis (2001). Sediment samples were spiked with two exotic Lycopodium tablets (batch no. 1031) and digested with 10% hydrochloric acid and 10% potassium hydroxide before being sieved through a 10 μm mesh. The remaining sediment was further digested in 40% hydrofluoric acid and then acetolyzed, deflocculated with 10% sodium metaphosphate, stained with Safranin, and mounted on microscope slides in silicon oil. Pollen grains were counted with a Leica light microscope with a 40x differential-interference-contrast objective. A minimum of 400 pollen grains were counted per sample except those in which pollen concentration was low and multiple coverslips needed to be counted. In those cases, a minimum of 300 grains were counted. Pollen grains were identified to the lowest possible taxonomic resolution based on published references (Bassett et al., 1978; McAndrews et al., 1978; Kapp et al., 2000).

Pigments

Subsamples of wet sediment were used for determination of photosynthetic pigment concentrations from 59 intervals throughout the core at the University of Regina's Institute of Environmental Change and Society (IECS). Sedimentary pigment analysis was undertaken following procedures outlined in Leavitt and Hodgson (2001). Pigment concentrations are reported as nmoles pigment g^{-1} gram organic matter, a unit which is linearly proportional to the standing stock of phytoplankton in decadal-scale monitoring programs (Leavitt et al., 1994a). An Agilent model 1100 high-performance liquid chromatography (HPLC) system with photodiode array detector was calibrated using commercial pigment standards from DHI (Denmark). Analysis included the main *a*- and *b*-phorbins (chlorophyll, pheophytin), as well as chemically-stable, taxonomically-diagnostic pigments representing total algal abundance (β-carotene), cryptophytes (alloxanthin), total cyanobacterial (echinenone), colonial cyanobacteria (myxoxanthophyll), Nostocales cyanobacteria (canthaxanthin), chlorophytes (Chl *b*), chlorophytes + cyanobacteria (lutein-zeaxanthin), siliceous algae (fucoxanthin), mainly diatoms (diatoxanthin), and anaerobic purple sulfur bacteria (okenone) following Leavitt and Hodgson, (2001). Historical changes in the lacustrine preservation environment were recorded as changes in the ratio of labile precursor (Chl *a*) to stable products (pheophytin *a*), both ubiquitous pigments used to estimate total phototrophic abundance (Leavitt and Hodgson, 2001).

Diatoms

Diatom samples were prepared using ~0.2–0.3 g of wet sediment, taken every 8.0 cm, for a total of 59 subsamples. Samples were digested in a 1:1 molar solution of concentrated nitric and sulphuric acids before being brought to a slightly acidic pH through repeated rinses with double-deionized water. Diatom slurries were reduced to a volume of ~5 ml by aspiration following sedimentation, and spiked with a solution of microspheres of known concentration equivalent to 4 ml of a 2.0×10^7 spheres/ml solution for organic samples and 0.2 ml of a 2.0×10^7 for clay-rich samples. Samples were plated on coverslips in a series of four dilutions and then mounted to slides using Naphrax®. Diatoms valves were identified and enumerated using a Leica DMRB microscope under a 100× Fluotar objective (NA of objective = 1.3) and differential interference contrast optics at 1000× magnification. For most diatom samples a minimum of 400 valves were counted, or, if the concentration of valves was exceptionally low, until five transects were completed. Diatoms were identified to species or lower taxonomic units using the standard references (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Cumming et al., 1995). Chryosphyte scales were enumerated alongside diatoms, but were not taxonomically identified.

Numerical analyses

Fossil pollen, pigment, and diatom data were plotted using the computer program Tilia v.2.0.2 (Grimm, 2004). Pollen taxa present at greater than 2% abundance in at least two samples and diatom species with greater than 5% abundance in at least three samples were included in the plots. Pollen concentration was calculated with the formula: (exotic Lycopodium spores added x fossil pollen counted) / exotic Lycopodium spores counted (Bennett and Willis, 2001) and standardized to dry mass. A depth-constrained cluster analysis (CONISS) (Grimm, 1987) was performed on the pollen assemblage to identify major differences in the pollen assemblage. The statistical significance of zones delineated by CONISS were validated with a broken-stick model by *rioja* package in R (Juggins, 2015; R Core Team, 2015).

Modern Analog Technique (MAT) was used to quantitatively reconstruct mean annual temperature over the Holocene record of Charland Lake using the C2 software program (Juggins, 2003). Modern pollen taxa and climate data were collected from the North American pollen database (Whitmore et al., 2005; Williams et al., 2006) to form a regional calibration set. A total of 305 samples between 45–60 °N and 75–90 °W were selected to form the calibration set which captured the transition between the boreal and mixed-wood forests to the south of Charland Lake. The fossil pollen from Charland Lake are well represented in the modern pollen dataset so it is likely that this group of sites should provide strong analogs for the assemblages found in the Charland Lake sediment core over the Holocene. Cupressaceae pollen was removed from the reconstruction model as this pollen type can represent both *Juniperus* and *Thuja* which have very different climatic preferences (Yu, 1997). Annual average temperature was reconstructed using the five closest analogs compared to fossil pollen interval with squared-chord measurement of similarity (Overpeck et al., 1985; Viau et al., 2006; Viau and Gawjewski, 2009) and bootstrap cross-validation (bootstrapped $r^2 = 0.95$, root-mean-square-error-of-prediction (RMSEP) = 0.88). The 305 site calibration set was tested against itself using the same method described above to discern the distribution of dissimilarities among the analogs used for the temperature reconstructions. Each of the five closest analogs used for each fossil interval was within the 20th percentile of the 305 sites. The majority were within the 10th percentile. This resulted in average dissimilarity values to be less than 30% which corresponds to the top 10th percentile for each reconstructed site.

Pigments were restricted to common sedimentary compounds of known chemical stability (see above). Analysis of similarities (ANOSIM) using a Bray-Curtis similarity coefficient and 999 permutations, were used to test the null hypothesis that there was no difference in diatom and pigment composition between the pollen-inferred climate zones (Clarke and Warwick, 1994). Analyses were performed using both non-transformed and square-root transformed species data. ANOSIM tests were performed on diatom relative abundance and concentration and pigment concentration data. ANOSIM tests were calculated using the PAST 3 software package (Hammer et al., 2001; Hammer and Harper, 2006). The sample from a depth of 440 cm was determined to be an outlier and was removed prior to any statistical analyses. Following the ANOSIM analysis, SIMPER tests (also performed in PAST), were used to calculate the contribution of each species to the average dissimilarity between the two groups. *Post-hoc* t-tests assuming unequal variance were performed to identify the significant difference between the pollen-inferred climate zones for individual sedimentary pigments using Microsoft Excel. The index of chrysophyte scales to diatom frustules (scale-to-diatom index) was calculated using the formula: scales/ (diatoms + scales) × 100 (Moos et al., 2005).

Results

Age model

The activity of ^{210}Pb in the Charland Lake gravity core was adequate to produce an age-depth model for the top 12 cm of sedimentation (Supplemental Figure 1). Background levels of ^{210}Pb were reached below that depth. Approximately 10 cm were lost from the first section of the piston core during extrusion. Based on our CRS model , this would mean the top of the piston core would correspond to an age of 0 cal yr BP with BP = 1950.

Concentrated pollen samples from eight sediment intervals were dated using AMS (Table 1). Bayesian modeling of the depth-^{14}C age relationship revealed a relatively constant rate of deposition over the period of study (Figure 2). Overall, the errors of the inferred ages for intervals in the sediment core were relatively low (±30–40 years). The calibrated ^{14}C dates increased in age with increasing depth and follows an approximately linear trend with cumulative core depth. [insert Figure 2.]

Table 1. Summary of the ^{14}C-dating results on pollen isolated from selected intervals from the sediment cores from Charland Lake. All analyses were performed based on pollen isolated at the LacCore Facility at the University of Minnesota, and dated at Lawrence Livermore National Laboratory. The mean age of the distribution is presented in “Cal yr BP”. The top date was generated through ^{210}Pb dating and a CRS model.

Core	Cumulative depth in piston core (cm)	δ^{13}C	^{14}C Age ± SD	Cal yr BP	2-σ cal yr BP range (min-max)	CAMS #
C2S1	0	N/A	N/A	0	-6–28	N/A
C2S1	45.5	-28	1170 ± 30	1081	976–1187	171192
C2S2	143.5	-28	2505 ± 40	2623	2451– 2749	171205
C2S2	178.5	-28	3035 ± 30	3260	3133–3360	171201
C2S3	204-206	-28	3480 ± 30	3762	3649–3863	176019
C2S3	262.5	-28	4400 ± 30	4925	4846–5037	171194
C2S4	305-306	-28	4560 ± 35	5390	5238–5570	176020
C2S4	401.5	-28	6235 ± 30	7159	6999–7272	171206
C2S5	437.5	-28	6995 ± 40	7815	7670–7947	171202

Figure 2. Age-depth model run for the Charland Lake core using BACON (Version 2.2). Top left panel: Markov Chain Monte Carlo model iterations. Top middle panel: Prior (heavy line) and posterior (solid) distribution of accumulation rate. Top right panel: Prior (heavy line) and posterior (solid) distribution of model memory. Bottom panel: calibrated ^{14}C dates and the age-depth model. The outer dotted lines indicate 95% confidence intervals. The central dotted line is the ‘best’ model based on the weighted mean age.

Pollen

Four statistically-significant pollen zones were identified in the Charland Lake core through CONISS and validated with the broken stick model (Figure 3; Supplemental Figure 2). CONISS analysis demonstrated that breaks between zones occur at cumulative depths of 85, 253, and 445 cm. Reconstructed average temperature showed major changes in line with these boundaries and we labelled the zones as the Pre-HTM, HTM, Post-HTM, and Modern climate zones (Figure 3). Standard error for the temperature reconstructions were generally low and on average did not exceed 0.5 °C above or below the estimate (Figure 4). Error is larger in the Pre-HTM zone, but even considering the upward limit of the error there is still a large and noticeable increase in temperature when entering the HTM zone (Figure 4).

The Pre-HTM zone occurred from 473–445 cm (~8200–7800 cal yr BP) and showed mixed dominance of *Picea* and *Pinus; P. bankisana and P. resinosa* could not be distinguished. This zone also included a relatively low abundance of arboreal pollen compared to rest of the core, as well as more abundant spores and pollen from *Sphagnum*, fern, and Cyperaceae. Reconstructed average temperature was approximately -0.5–0 °C in this zone. The HTM zone occurred from 445–253 cm (~7800–4500 cal yr BP) and showed a major increase in reconstructed temperature (Figure 3, Figure 4). Average temperatures of ~2–3 °C were consistent across this zone, but there appears to be two distinct floral assemblages within the warm period. The first was marked by an increase in the *P. banksiana/resinosa* and the second with an increase in *Pinus strobus* and Cupressaceae. Organic sedimentation also began in this zone, concomitant with pollen concentration rapidly increasing before falling substantially at the onset of the second clay layer. The Post-HTM period (253–85 cm, ~4500–1700 cal yr BP) showed an increase in *Picea*, *P. banksiana/resinosa*, and *Betula* pollen, as those of *P. strobus* and Cupressaceae declined. This is reflected in the MAT reconstruction as average temperature fell by ~1 °C. Pollen concentration was variable in this zone but generally increased during the earlier portion before declining after ~3300 cal yr BP. The Modern Zone (85–0 cm, ~1700–0 cal yr BP) showed a general decrease in pollen concentration and further decreases of *P. strobus*. *Picea* became predominant in this zone with *P. banksiana/resinosa* and *Betula* experiencing minor decreases compared to the Post-HTM zone. Reconstructed average temperature slowly declined by ~0.5 °C throughout this zone. The concentration of pollen types was also plotted and can be found in the supplemental materials (Supplemental Figure 3).

[insert Figure 3]

Figure 3. Relative abundance of abundant (>2% found in 2 sections of the core) pollen taxa in Charland Lake. Total pollen concentration is also shown. Darker zones in Sediment Type represent organic sedimentation in the piston core. Layered zones represent clay deposits. Climate Zones are derived through CONISS. Reconstructed average temperature was estimated through Modern Analog Technique calibration (bootstrapped $r^2 = 0.95$, RMSEP = 0.88).

[insert Figure 4]

Figure 4. Reconstructed average temperature with error bars and percent dissimilarity of the analogs used in the MAT temperature reconstruction of the Charland Lake record. Percent dissimilarity refers to the mean dissimilarity of the five closest analogs used to reconstruct annual temperature for each fossil interval. Zones are the CONISS-derived climate zones from Figure 3.

Pigments

The pollen climate zones were used as a framework to assess the relationship between climate change and variation in pigment assemblages (Figure 5). Overall, preservation of pigments was poor in the Pre-HTM zone, with fossil concentrations below detection limit in most samples. A similar absence of fossil pigments in the second clay layer suggests that the near absence of sedimentary organic matter favored complete decomposition of carotenoids and chlorophylls, irrespective of their inherent chemical lability, similar to patterns seen in glacially-fed alpine lakes (Bunting et al., 2010). In contrast, concentrations of ubiquitous pigments (β-carotene, Chl *a*, pheophytin *a*), and those from cryptophytes (alloxanthin), diatoms (diatoxanthin), total cyanobacteria (echinenone), Nostocales cyanobacteria (canthaxanthin), chlorophytes (pheophytin *b*) and chlorophytes+cyanobacteria (lutein-zeaxanthin) all increased markedly at the base of the HTM zone, whereas more labile compounds (fuxoxanthin, Chl *b*) did not. These patterns reflect the increase in okenone from obligate anaerobic purple sulfur bacteria, an indicator of anoxia in deep-waters or sediment. Transition from the HTM to Post-HTM zone was marked by significant increases in the concentration of most fossil pigments (Table 2, Figure 6). The Post-HTM zone was characterized by elevated concentrations of most pigments, often to a historical maximum relative to other zones (e.g., β-carotene, lutein-zeaxanthin, okenone, and canthaxanthin). In the Modern zone (0–85 cm; ~1700–0 cal yr BP), pigment assemblages were marked by the first appearance of myxoxanthophyll from colonial cyanobacteria, increases in concentrations of compounds from Nostocales cyanobacteria (canthaxanthin) and secondarily total cyanobacteria (echinenone), and historical maxima of less chemically-stable pigments from diatoms (fucoxanthin, diatoxanthin) and chlorophytes (Chl *b*). In contrast, fossil levels of ubiquitous β-carotene and the mixed chlorophyte-cyanobacterial indicator, lutein-zeaxanthin, declined slightly in the most recent zone. Relative to individual pigments, the ratio of labile chlorophyll *a* to stable phaeophytin *a* (indicating the preservation environment) remained relatively constant through the core, with some variance within and between the clay bands of the Pre-HTM and HTM zones (Figure 5). [insert Figure 5.]

Figure 5. Concentration of photosynthetic pigments (nmoles per gram organic matter) in Charland Lake sediment core over time (cal yr BP). The ratio of chlorophyll *a* to phaeophytin *a,* an indicator of preservation, and organic matter (%) are also shown. Darker zones in Sediment Type represent organic sedimentation in the piston core. Layered zones represent clay deposits. The dotted lines indicate the pollen-derived climate zones from Figure 3.

Table 2. Summary table of the results from a series of two sample post hoc t-tests assuming unequal variance conducted to identify significant differences in pigment concentrations between the HTM, Post-HTM, and Modern zones for sedimentary pigments. Bold cells indicate significance.

Zones	Canthaxanthin	Echinenone	Okenone	Alloxanthin	β-carotene
HTM, Modern	***t*** **(22) -8.7 =** ***p*** **= <0.01**	***t*** **(12) -2.5 =** ***p*** **= 0.03**	***t*** **(21) = -6.3 =** ***p*** **= <0.01**	***t*** **(26) -5.1 =** ***p*** **= <0.01**	*t* (21) = -1.9 *p* = 0.07
HTM, Post-HTM	***t*** **(44) -5.0 =** ***p*** **= <0.01**	***t*** **(43) = -4.5** ***p*** **= <0.01**	***t*** **(42) = -4.2 =** ***p*** **= <0.01**	***t*** **(31) -4.2 =** ***p*** **= <0.01**	***t*****(43) = -4.1** ***p*** **= <0.01**
Post-HTM, HTM	**t (23) -4.2 = p = <0.01**	*t* (11) = -0.8 *p* = 0.44	***t*** **(25) = -2.2 =** ***p*** **= 0.04**	*t* (32) -1.4 = *p* = 1.69	*t* (24) = 1.7 *p* = 0.1
	Lutein-zeaxathin	*Myxoxanthopyll*	*Fucoxanthin*	*Chlorophyll b*	*Diatoxanthin*
HTM, Modern	***t*** **(32) -2.5 =** ***p*** **= 0.02**	***t*****(10) -3.3 =** ***p*** **= <0.01**	***t*** **(16) -19.4 =** ***p*** **= <0.01**	***t*** **(10) -8.4 =** ***p*** **= <0.01**	***t*** **(25) -10.7 =** ***p*** **= <0.01**
HTM, Post-HTM	***t*** **(36) -4.4 =** ***p*** **= <0.01**	N/A	***t*** **(25) -6.3 =** ***p*** **= <0.01**	***t*** **(22) -3.1 =** ***p*** **= <0.01**	***t*** **(41) -6.4 =** ***p*** **= <0.01**
Post-HTM, Modern	***t*** **(25) 2.3 =** ***p*** **= 0.03**	***t*** **(10) -3.3 =** ***p*** **= <0.01**	***t*** **(31) -4.6 =** ***p*** **= <0.01**	*t* (26) 0.3 = *p* = 0.77	***t*** **(19) -6.0 =** ***p*** **= <0.01**

One-way pair-wise ANOSIM tests confirmed that there were significant differences in pigment concentration among the three most recent zones. Specifically, the null hypothesis of no difference between pigment concentrations among zones was rejected in comparisons of the

HTM and Post-HTM zones, and between the Post-HTM and Modern zones (Table 3). A SIMPER test identified lutein-zeaxanthin as the predominant pigment contributing to ~40% of the difference in composition between the HTM and Post-HTM zones (Table 4), and ~29% of the difference in composition seen between Post-HTM and Modern zones (Table 4). [insert Figure 6].

Figure 6. Boxplots of pigment concentrations (nmol/g OM) within the *a priori* defined pollen-derived climate zones (HTM (n= 24), Post-HTM (n= 21), Modern (n= 11)). ANOVA tests were run to test for significant differences between zones for A) β -carotene (F(2, 53) = 8.2, p-value < 0.01) B) lutein-zeaxanthin (F(2, 53) = 7.6, p-value < 0.01) C) alloxanthin (F(2, 53) = 11.4, p-value < 0.01) D) echinenone (F(2, 53) = 7.3, p-value < 0.01) E) okenone (F(2, 53) = 10.1, p-value < 0.01) F) canthaxanthin (F(2, 53) = 26.8, p-value < 0.01) G) chlorophyll *b* (2 outliers removed in the Post-HTM zone) (F(2, 53) = 6.5, p-value < 0.01) H) fucoxanthin (F(2, 53) = 52.1, p-value < 0.01) I) diatoxanthin (F(2, 53) = 47.1, p-value < 0.01) J) myxoxanthophyll (F(2, 53) = 22.9, p-value < 0.01). Asterisks indicate zones that are significantly different based on post-hoc t-tests (Table 2). Pre-HTM zone omitted due to the small number of samples in this zone.

Table 3 Summary of the one-way ANOSIM pair-wise tests (Bray-Curtis dissimilarity) on Charland Lake diatom relative abundances, diatom concentrations, and HPLC data between the pollen-derived climate zones. Significance levels indicated in brackets. Bold cells indicate significance (999 permutations).

	Diatom Relative Abundance	Diatom Relative Abundance (sqrt)	Diatom Concentration	Diatom Concentration (sqrt)	HPLC concentration	HPLC concentration (sqrt)
Global R	0.25 (0.001)	0.28 (0.001)	0.23 (0.001)	0.24 (0.001)	0.23 (0.001)	0.31 (0.001)
Modern, Post-HTM	0.02 (0.294)	0.08 (0.12)	**0.21 (0.008)**	**0.27 (0.003)**	**0.39 (0.001)**	**0.58 (0.001)**

Modern, HTM	**0.35 (0.002)**	**0.37 (0.001)**	**0.3 (0.002)**	**0.27 (0.002)**	0.12 (0.1)	**0.21 (0.017)**
Post-HTM, HTM	**0.34 (0.001)**	**0.33 (0.001)**	**0.22 (0.001)**	**0.24 (0.001)**	**0.21 (0.001)**	**0.27 (0.001)**

Table 4. Summary of the one-way SIMPER tests (Bray-Curtis dissimilarity) on Charland Lake diatom relative abundances, diatom concentrations, and HPLC data between pollen-derived climate zones. Percent contribution of driving taxa indicated in brackets.

	Diatom Relative Abundance	Diatom Relative Abundance (sqrt)	Diatom Concentration	Diatom Concentration (sqrt)	HPLC concentration	HPLC concentration (sqrt)
Modern, Post-HTM	*S. minutulus* (32.8%)	*D. stelligera* (18.8%)	*S. minutulus* (46.2%)	*S. minutulus* (26.7%)	Lutein (29.0%)	Myxoxanthophyl (17.4%)
Modern, HTM	*S. minutulus* (29.7%)	*S. minutulus* (17.1%)	*S. minutulus* (46.0%)	*S. minutulus* (26.3%)	Lutein (27.9%)	Diatoxanthin (17.4%)
Post-HTM, HTM	*S. minutulus* (22.8%)	*S. minutulus* (14.6%)	*S. minutulus* (27.7%)	*D. stelligera* (17.8%)	Lutein (40.2%)	Lutein (22.3%)

Diatoms

Application of pollen climate zones to the diatom assemblages of Charland Lake showed that diatom concentrations were low in both the Pre-HTM zone and the second clay band, but increased in the organic layer between the clay bands during the HTM to ~23 x 10^8 valves per gram dry weight (Figure 7). Diatom concentrations also increased after the second clay band and remained relatively stable between 284–145 cm (range ~9 to 21 x 10^8 valves per gram dry weight). The scale-to-diatom index was low within both clay bands, with an increase in scaled chrysophyte abundance in the intervening organic layer. The abundance of scaled chrysophytes increases during the second clay band and continued to increase throughout the HTM and Post-HTM zones. After a Post-HTM zone peak, scaled chrysophyte abundance declined into the Modern zone and remained low to the top of the core (Figure 7). [insert Figure 7.]

Figure 7. Relative abundance of dominant (>5% found in 3 sections of the core) diatom taxa in Charland Lake arranged by age (cal yr BP). The diatom taxa are arranged by their weighted-average optima based on cumulative depth in the core. The scale-to-diatom index and total diatom concentrations (valves/g dry weight x 10^8) are also shown. Darker zones in Sediment Type represent organic sedimentation in the piston core. Layered zones represent clay deposits. The dotted lines indicate the pollen-derived climate zones from Figure 3.

The largest shift in diatom assemblages occurred after the second clay band, before the boundary of the HTM and Post-HTM zones. Prior to this point, the Pre-HTM and HTM zones were predominated by benthic taxa, while the Post-HTM and Modern zones were composed mainly of planktonic taxa. Only one sample from the Pre-HTM zone contained enough diatoms for enumeration so this zone was removed from the analysis.

HTM taxa prior to the second clay band included *Staurosira construens* and *Staurosirella pinnata*. *Lindavia intermedia* appeared as an important taxon immediately before and after this clay band. After the resumption of organic sedimentation, *Stephanodiscus minutulus* was the predominant taxon for the remainder of the zone. The importance of *S. minutulus* increased in the Post-HTM -zone and remained common until ~220 cm when relative abundance of *Discostella stelligera* increased. This pattern was reversed at ~105 cm. Diatom assemblages within the Modern zone were composed largely of *S. minutulus* and *Stephanodiscus parvus*; however, *D. stelligera* abundance increased again at ~70 cm until it became a subdominant species at the top of the core (Figure 7).

The difference in diatom assemblages between the four pollen-derived climate zones were assessed using ANOSIM tests. The null hypothesis of no difference between diatom assemblages in the HTM, Post-HTM, and Modern zones was rejected in two of the pair-wise tests comparing the HTM zone to the Post-HTM zone and the HTM zone to the Modern zone (Table 3). SIMPER tests identified *S. minutulus* as the predominant species contributing to ~23% of the difference in species composition between the HTM and Post-HTM zones (Table 4). Similarly, there was a significant shift in species composition between the HTM and Modern zones with *S. minutulus* driving species change and contributing to ~30% of the difference in species composition (Table 4).

Discussion

The HTM in northeast Ontario took place from ~7800–4500 cal yr BP based on large changes in pollen data that suggest elevated temperatures. Average temperature reconstructions from the pollen assemblages in Charland Lake showed that the climate was ~1.5–2.0 °C warmer than the modern day. In this context, the 'modern day' refers to the top of our piston core which corresponds to ~1950. All discussion referring to 'the modern day' or 'present day' relate to this time frame. Algal response to climate change over the Holocene of this region was variable and somewhat unexpected as the warm HTM zone did not experience the greatest amount of algal abundance. Instead, the cooler Post-HTM and Modern zones showed increased algal production which may be related to various indirect climate and landscape effects. These effects, along with more thorough interpretations of pollen and algal data, are discussed in the forthcoming sections.

Pollen as a climate proxy in northeastern Ontario

Pre-HTM zone (~8200–7800 cal yr BP)

The climate during this interval was cooler than present as is shown in the temperature reconstruction (Figure 3). This inference of cooler temperatures arises because of the predominance of *Picea* pollen, combined with a relatively low amount of *Pinus sp*. pollen. Thermophilous taxa, such as deciduous hardwood trees, were rare in the Pre-HTM zone, further contributing to the inference of cool conditions. In addition, the landscape was likely poorly developed with low vegetation cover and immature, highly inorganic soils, as inferred by the relatively high abundances of ferns and other spore producing plants. It is likely that the boreal forest had not completely colonized the watershed of Charland Lake so soon after the draining of Glacial Lake Ojibway ~8200 cal yr BP (Liu, 1990; Prentice et al., 1991).

HTM zone (~7800–4500 cal yr BP)

Reconstructed temperature shows a sharp increase by ~2 °C at the onset of this zone ~7800 cal yr BP. This climate shift is most driven in the decline of *Picea* and the increase in *P. banksiana/resinosa*, followed by increases in *P. strobus* and Cupressaceae at ~6000 cal yr BP. This is similar to patterns recorded in the mid-Holocene of Lake Six as described by Liu (1990). This two-phase HTM likely represents an increase in precipitation levels after ~6000 cal yr BP as inferred by increase of Cupressaceae.

Interpretation of the Cupressaceae peak is difficult, as this pollen morphotype cannot be easily distinguished between *Juniperus* and *Thuja* based on morphological characteristics alone (McAndrews, 1973; Yu, 1997). As *Juniperus* and *Thuja* are indistinguishable as pollen types, and the two genera have differing climatic optima, we have elected to remove Cupressaceae from our temperature reconstructions. It is for this reason as well, that we did not attempt to reconstruct annual precipitation over the Holocene based on the pollen in the Charland Lake core. *Juniperus* is known to prefer dry habitats, while *Thuja* prefers wetter conditions (Johnston, 1990; Yu et al., 1996; Yu 1997). Nonetheless, we infer that Cuppressaceae were composed mainly of *Thuja* at Charland Lake due to the presence of *Thuja* stomata observed on pollen slides. This interpretation agrees with that of Liu (1990) who inferred that *Thuja* represented most Cupressaceae pollen at Lake Six based on the occurrence of fossil *Thuja* seeds. Carcaillet et al. (2001) also inferred the presence of *Thuja* rather than *Juniperus* because charcoal analysis shows that forest fire frequency did not increase in the area during the HTM which would be consistent with a wetter, *Thuja*-rich environment.

Pinus strobus, which increased in relative abundance alongside Cupressaceae likely expanded northward from the mixed Great Lakes-St. Lawrence forest as average temperature increased (Terasmae and Anderson, 1970; Richard, 1980; Bartlein et al., 1984, Liu, 1990; Hall et al., 1994). Concomitant changes in *P. strobus* and Cupressaceae during the HTM also argues for the presence of *Thuja*, as competition for the drier upland areas would not have allowed the coexistence of *Juniperus* and *P. strobus* (Liu, 1990). *Thuja* would have had minimal habitat competition with *P. strobus*, allowing the species to coexist (Fowells, 1965; Liu, 1990). It is therefore likely that *Thuja* proliferated in the widespread wetlands of the Clay Belt lowlands, while *P. strobus* occupied dry upland sites (Liu, 1990).

We infer that the HTM manifested in two phases in the Charland Lake region. The first phase, from ~7500–6000 cal yr BP, saw the increase of *Pinus banksiana/resinosa* and increased average temperature ~2 °C compared to the previous zone. The second phase occurred from ~6000–4500 cal yr BP and experienced increases in *P. strobus*, a large increase in *Thuja*-inferred Cupressaceae, and a further increase in temperature by ~0.5–1.0 °C to a maximum of ~3 °C. This reconstruction makes the maximum HTM temperature ~1.5–2.0 °C warmer than current conditions, a value which is in line with temperature estimates provided by climatic modelling for this region (Renssen et al., 2009, 2012). We also postulate that the second phase of the HTM was wetter than present in this region, as *Thuja* would have inhabited widespread wetlands which developed during this time. This interpretation is consistent with Prentice et al. (1991) whose precipitation reconstructions of the Holocene of eastern North America shows an increase in annual precipitation in northeast Ontario after ~6000 cal yr BP.

The Post-HTM zone (~4500–1700 cal yr BP)

The Post-HTM zone was a transitional time between the warmer HTM and cooler modern climate regimes. The reconstructed temperature shows a decline in temperature from the maximum Holocene value of ~3.0 °C at ~5000 cal yr BP to ~1.5 °C ~4500 cal yr BP. Average temperature remained around 1.5 °C for the majority of this zone. Floristically, this zone saw clear decreases in *P. strobus* and Cupressaceae and increases in *Picea* and *Pinus banksiana/resinosa*. In addition, the observed increase in *Betula* may suggest increased fire activity and drier conditions which in turn would not allow for the continued high abundance of *Thuja* after ~3700 cal yr BP (Carcaillet et al., 2001) which is shown in the concentration diagram (Supplemental Figure 3).

Modern zone (~1700–0 cal yr BP)

During the Modern interval, *Picea* increased, while *P. strobus* declined further, contributing to the inferred decrease in average temperature to ~1.0 °C. *Betula* and other common and uncommon arboreal tree types remained largely unchanged throughout this period.

It is quite likely that this climate zone experienced an increase in precipitation as represented by the increased abundance in *Picea* and decrease in *P. banksiana/resinosa* (Liu, 1990; Prentice et al., 1991).

Lake and algal responses to Holocene climate change

Definition of climate zones based on historical changes in terrestrial vegetation allows us to evaluate both how regional climate variation may have affected the linkage between land and water, and the responses of past changes in the production and community composition of aquatic primary producers. Here we evaluate changes in community composition of phototrophs (using fossil pigments and diatom assemblages) better understand changes in climate on aquatic environments.

Pre-HTM zone (~8200–7800 cal yr BP)

Northeastern Ontario was inundated by Glacial Lake Ojibway during the early Holocene. This glacial lake deposited thick clay layers which form the Great Clay Belt in the Cochrane District of northern Ontario before draining into the Tyrrell Sea ~8200 cal yr BP (Veillette, 1994; Roy et al., 2011, 2015) resulting in the formation of Charland Lake. Algal production (both pigments and diatoms) was too low to be detected or analyzed statistically in the Pre-HTM zone. This may be due to the deposition of the first clay layer during this time. Clastic or mineral-rich sedimentation is common in the early ontogeny of post-glacial boreal lakes (Liu, 1990; Teller et al., 2018) and is known to interrupt fossil preservation and signals of algal abundance when sedimentary organic matter is extremely low (Leavitt and Hodgson, 2001; Bunting et al., 2010).

HTM zone (~7800–4500 cal yr BP)

The climate rapidly warmed at the onset of this zone as shown in the temperature reconstruction based on pollen (Figure 3), but pollen data suggests a two-phase warming event; first warm and dry conditions followed by warm and wet conditions. Charland Lake continued to experience major clastic input at the beginning of this zone, although microfossils from algae and cyanobacteria begin to appear at this time. High abundance of *S. construens* and *S. pinnata* during the early HTM suggests low-light or turbid conditions (Haworth, 1976; Bradshaw et al., 2000; Fritz et al., 2004) consistent with high clastic influx. These benthic diatoms are known to be tolerant of low-light environments (Punning and Puusepp, 2007; Kingsbury et al., 2012) which, along with the low concentrations of both diatoms and pigments, suggests an unproductive and light-limited environment. Influx of clastic material in Charland Lake may reflect high rates of terrestrial erosion from the undeveloped landscape. The young forest surrounding Charland Lake was likely open during the early HTM, favoring high rates of weathering and transport of clay particles to the lake (Dearing, 1983; Dearing and Foster, 1986; Almquist-Jacobson, 1992).

Deposition of organic matter begins in the HTM, although algal fossils remain rare until ~7000 cal yr BP (Figure 5). The appearance of fossil pigments from many but not all groups was likely a response to HTM warming, soil development, and the influx of organic matter which would have created anoxic sediments which provided a better environment for pigment preservation (Leavitt, 1993; Leavitt and Hodgson, 2001; Leavitt et al., 2003). Consistent with this pattern, the ratio of chlorophyll *a* to phaeophytin *a* suggests a high degree of pigment preservation (Leavitt and Hodgson, 2001) following the period of high clastic influx. Lower light penetration during the final period of fine inorganic matter influx may have reduced photo-oxidation of pigments and favoured elevated fossil concentrations (Furlong and Carpenter, 1988; Hurley and Armstrong, 1990, 1991; Leavitt, 1993). Finally, inferred low water-levels (based on the high abundances of benthic diatoms) may have favoured development of benthic mats of chlorophytes and cyanobacteria (as canthaxanthin). Typically, labile pigments (such as Chl *a*) are preserved better if they are produced in benthic mats (Leavitt et al., 1994b; Leavitt et al., 2003).

At ~6000 cal yr BP, *Thuja*-inferred Cupressaceae increases rapidly, signifying the onset of wet conditions (Figure 3). Several major phycological and sedimentological changes coincided with this wetter climate. First, elevated organic matter sedimentation persisted until ~6100 cal yr BP and was characterized by increased pigment concentrations, elevated relative abundance of planktonic diatoms, and an increase in chrysophyte scales indicative of deeper lake conditions (Zeeb and Smol, 2001; Figure 5, 7). Contemporaneous with increased temperatures and lake-levels, landscape stabilization was occurring, as indicated by a hiatus in clastic sedimentation which suggests forest closure and reduced erosion (Liu, 1990). The transition to gyttja-based sediments also suggests the presence of soluble nutrients leaching from fresh, organic soils (Liu, 1990).

Organic sedimentation was interrupted by the deposition of the second clay layer ~6000–5500 cal yr BP, at which time concentrations of phototrophic fossils declines and diatom assemblages reverted to benthic taxa. Paradoxically, high Cupressaceae pollen abundance suggests a wet climate and high lake-levels. We propose that water levels increased sufficiently to let Charland Lake join with surrounding aquatic ecosystems, including nearby Fredrick House Lake, a site which is only ~2 m below the study basin. As Fredrick House Lake is turbid, conjoined waters may have introduced clastic material from the Fredrick House Lake catchment into Charland Lake. Aquatic conditions in this second clay band were similar to those seen in the early HTM period, where diatom assemblages were composed mainly of benthic species and pigment and frustule concentrations were low.

After ~5500 cal yr BP, organic sedimentation resumed with no noticeable change in pollen assemblages. In contrast, diatom assemblages rapidly shifted to planktonic taxa, similar to that observed within the organic layer between clay bands, but with elevated abundance of the eutrophic taxon *Stephanodiscus minutulus*. *Stephanodiscus* taxa are common in productive waters (Cumming et al., 2015) and compete for silica better than other planktonic species (Mechling and Kilham, 1982). Past research has associated higher water levels with lower Si:P ratios and an associated dominance of *Stephanodiscus* (Kilham and Kilham, 1990). The eutrophication may reflect increased internal loading of nutrients from anoxic sediments, as indicated by the presence of okenone, a pigment from purple sulfur bacteria. These prokaryotic taxa are obligate anaerobes and are present only when light penetrates to anoxic environments (see Leavitt et al., 1989). Regardless of the mechanism, the increase in nutrients must have been relatively minor, as neither frustule concentration nor that of most pigments suggests a strong increase in primary production during this period.

Post-HTM zone (~4500–1700 cal yr BP)

Reconstructed average temperature shows that this zone experienced a cooler climate than the HTM but was still warmer than modern conditions. Algal groups responded to these climate changes; both diatom frustules and pigment concentrations increased moderately, possibly signaling an overall increase in primary production. The eutrophic *S. minutulus* continued to dominate the diatom assemblage until ~3900 cal yr BP when it was replaced by the more oligotrophic *Distostella stelligera* (Figure 7). Presently, we are uncertain whether observed changes in fossil patterns reflect direct effects of climate, or indirect variation in lake structure and function, such as a change in thermal stratification. For example, increased abundance of *D. stelligera* has been shown to correspond with a longer period of stratification (Dean et al., 1994; Bradbury et al., 2002; Wiltse et al., 2016) and a shallow mixing depth (Saros et al., 2012). This interpretation is supported by changes in the chrysophyte scale-to-diatom index, as chrysophytes have a competitive advantage over diatoms when the water column is strongly stratified (Eimers et al., 2009). An increase in the abundance of chrysophytes has also been related to less eutrophic conditions, which agrees with an increase in *D. stelligera* (Reynolds, 1988; Brabury et al., 2002).

Despite a trend towards oligotrophication as suggested by diatoms, interpretation of fossil pigment data suggests an increase in algal production during this period. Several mechanisms could underlie this pattern. First, increased thermal stratification can lead to the formation of metalimnetic blooms which tend to be over-represented in lake sediments (Leavitt et al., 1989; Leavitt and Hodgson, 2001). Alternately, changes in the seasonality of lake stratification could favor production of phototrophic groups other than diatoms. For example, both lutein-zeaxanthin, a stable indicator of green algae and cyanobacteria, and alloxanthin, a stable indicator of cryptophytes, had significantly higher concentrations (Figure 6) during this period compared to the HTM zone. Lower concentrations of other pigments from cyanobacteria (e.g., echinenone, canthaxanthin, myxoxanthophyll) suggest limited contributions of those taxa to the lutein-zeaxanthin signal (Brock et al., 2006). Both cryptophytes and chlorophytes (together ‘flagellates’) tend to replace negatively buoyant diatoms during periods of thermal stratification, due to their motility (Hickman, 1974; Reynolds, 1984). As such, higher concentrations of these algal groups suggest a longer period of thermal stratification during the Post-HTM period and, perhaps, reduced diatom recruitment, which favoured growth of other phytoplankton groups, such as cryptophytes and chlorophytes.

Modern zone (~1700–0 cal yr BP)

At Charland Lake, the Modern period of northeastern Ontario was characterized by a cold and wet environment based on the decrease of *P. strobus* and the dominance of *Picea*. However, algal proxies from Charland Lake suggest the onset of more eutrophic conditions as concentrations of diatoms, and pigments characteristic of diatoms (fucoxanthin, diatoxanthin), were highest during this period. Statistical analyses of individual pigments revealed that canthaxanthin and okenone increased significantly (Figure 6), indicating an abundance of colonial cyanobacteria and purple sulfur bacteria, respectively (Leavitt and Hodgson, 2001). Given that the Chl *a*:pheophytin ratio declined slightly prior to the Modern period (Figure 5), but okenone increased, we infer that these changes may reflect in part a minor change in the preservation environment at Charland Lake. However, because this interval is also marked by the first occurrence of chemically-robust myxoxanthophyll, a ubiquitous compound in colonial cyanobacteria, we infer that the Modern zone has also been more productive than previous periods.

The movement towards colder conditions during this period may have also promoted more lake mixing and less-stable thermal stratification, allowing some algal species, such as *S. minutulus*, to proliferate (Reynolds and Reynolds, 1985; Kilham et al., 1986; Makulla and Sommer, 1993; Bradbury et al., 2002). Growth requirements of *Stephanodiscus* species may have been largely satisfied by the regeneration of phosphorus from nutrient-dense water to the photic zone during spring circulation, resulting in large blooms of *S. minutulus* and *S. parvus* (Kilham and Kilham, 1978; Bradbury et al., 2002). The inference of extended periods or vigorous lake-mixing is also supported by the decrease in the chrysophyte scale-to-diatom index, further suggesting less stratification (Reynolds, 1984; Rott, 1984).

Interpretation of the influence of climate on canthaxanthin (Nostocales cyanobacteria) and okenone (purple sulfur bacteria) is not straightforward, as both of these algal groups would be expected to decrease under cooler and wet conditions (Lami et al., 2009). Okenone is found in anaerobic purple sulfur bacteria which prefer the oxic-anoxic interface in lakes (Massé et al., 2002), hence higher concentrations of okenone can be related to seasonal anoxia in lakes (Maheux et al., 2016). On the other hand, low concentrations of purple sulfur bacteria have been related to cool conditions, likely coupled with increased mixing of the water column (Schmidt et al., 2002). Overall, concentrations of okenone are much lower than those seen in meromictic or strongly stratified ecosystems (Leavitt et al., 1989) and suggests the presence of only seasonal (summer) anoxia, perhaps restricted to deep littoral sediments. Furthermore, canthaxanthin, an indicator of Nostocales cyanobacteria, is often associated with high nutrients in the water column (Kleppel et al., 1988; Lami et al., 2009), but can also be a marker of N_2 fixation (Hayes et al., 2018). One possibility is that the Modern period experienced in an influx of dissolved organic matter (DOM) which would have helped proliferate the heterotrophic growth of the cyanobacteraial groups (Stevenson et al., 2016). Regardless it seems likely that factors other than climate must be considered to understand how limnologic conditions became ideal for these groups in the Modern period.

Conclusions

Pollen data from Charland Lake suggests that the HTM in northeast Ontario took place from ~7800–4500 cal yr BP. The onset of warmth is ~1000 years later than recorded in northwest Ontario (Moos et al., 2009; Moos and Cumming, 2011, 2012; Karmakar et al., 2015a, 2015b). Differences between our findings and Liu's (1990) may be due to the more rigorous carbon dating model used in our study as our pollen analysis agrees with Liu's (1990) quite well. Analysis of fossil pollen showed that the HTM in northeastern Ontario was warm and dry from ~7500–6000 cal yr BP and then become wet from ~6000–4500 cal yr BP as indicated by the high abundance of *Thuja*-inferred Cupressaceae pollen. Algal abundance was variable over the Holocene, as inferred from both fossil pigment and diatom concentrations, apparently responding mainly to variation in the linkage between land and water.

This work represents one of the first investigations in northeast Ontario to assess the relationship between climate and in-lake production during the Holocene Epoch. Overall, the interaction between climate and limnological conditions were complex within Charland Lake, providing a striking comparison with lakes in northwest Ontario at millennial time scales. In general, we demonstrate that limnological conditions were more optimal for algae over the last ~4500 years than in the preceding millennia. This pattern is in stark contrast to those seen in lakes from northwest Ontario, where paleolimnological studies have linked the warmer HTM to enhanced lake-water production (Moos and Cumming, 2009; Karmakar et al., 2015b). In Charland Lake, such changes were evident, but small in comparison, and did not indicate the warmer temperatures of the HTM directly influenced lake-water production. These findings suggest indirect climate effects, such as changes in thermal stratification and mixing, may be more influential on algal production in some lakes in northeast Ontario. If this were broadly true, it suggests that lakes in northeast Ontario may respond differently to future climate change compared to lakes elsewhere in northern Ontario, and that the response and susceptibility of lakes to climate change can vary across an ecozone.

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Supplemental figure 1. A) Activity of ^{210}Pb, ^{214}Pb, ^{214}Bi, and ^{137}Cs in the Charland Lake gravity core. B) Constant Rate of Supply (CRS) model inferred ages for the Charland Lake gravity core.

Supplemental figure 2. Broken stick model based on a constrained cluster analysis (CONISS) of abundant pollen taxa (>1% in two or more intervals) from Charland Lake.

Supplemental figure 3. Total concentration of pollen grains (x10^4) from Charland Lake. Darker zones in Sediment Type represent organic sedimentation in the piston core. Layered zones represent clay deposits. Climate Zones are derived through CONISS from Figure 3.