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

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1 Complex responses of phototrophic communities to climate warming during the Holocene of
2 northeastern Ontario, Canada
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31 **Abstract**

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

51

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

54

55 **Introduction**

56

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

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

80 (Price et al., 2013). Therefore, a characterization of landscape responses to analogs of past
81 climates may be useful for predicting effects of atmospheric warming and changes in regional
82 hydrology (Klemm et al., 2016; Navarro et al., 2018; Teller et al., 2018). Atmosphere-ocean-
83 vegetation models have suggested that the HTM in northern Ontario was ~2–3 °C warmer than
84 the modern climate (Renssen et al., 2009, 2012). Recent work from northwest Ontario (~1200
85 km to the west of our study site) reveals that the HTM occurred from ~8500–4500 cal yr BP
86 (calendar years before present) and was ~2 °C warmer than present conditions. This estimate was
87 calculated using a modern analog technique (MAT) calibration based on fossil pollen and a
88 regional set of modern pollen and climate data (Moos and Cumming, 2011). Associated dryer
89 conditions resulted in lower lake levels, increased algal production, an eastward shift of the
90 prairie-forest ecotone, and an increase in fire activity (Moos et al., 2009; Moos and Cumming,
91 2011, 2012; Karmakar et al., 2015a, 2015b). Despite this research, there has been little work
92 examining the HTM of northeastern Ontario, Canada, which is a problem this paper seeks to
93 address.

94 Only one Holocene-scale palynological study has documented Holocene climate
95 variability in northeast Ontario (Liu, 1990). This study examined three sediment cores in a north-
96 south transect of eastern Ontario. One of these sites, Lake Six, is 6 km away from our study site
97 so comparisons to Liu (1990) refer to the Lake Six record. In Liu (1990), the author showed a
98 delayed, but protracted HTM period occurring from ~7–2.5 ka BP at Lake Six. This was defined
99 by increases in *Pinus strobus*, a typical taxon of the warm Great Lakes-St. Lawrence forest, and
100 in Cupressaceae. Liu (1990) interpreted the presence of Cupressaceae pollen as belonging to
101 *Thuja* based on its co-occurrence with *Thuja* macrofossils within the sediment core. These data
102 suggest that the HTM of northeast Ontario was wet, agreeing with studies at similar longitudes to

103 the south (Viau et al., 2006; Shuman and Marsicek, 2016). A similar interpretation has been
104 made by Carcaillet et al. (2001) who used charcoal analysis to infer that low fire activity during
105 the this time in western Quebec was due to enhanced water availability. Unfortunately, Liu's
106 (1990) climatic results from Lake Six are supported by only three radiocarbon dates. With these
107 few data points there is likely considerable error regarding the temporal boundaries of HTM
108 warming and it is likely that the upper boundary (~2.5 ka BP) is overestimated based on studies
109 from northwest Ontario (Moos and Cumming, 2011, 2012). Improved geochronology, as well as
110 replicate sites in the region, are important to better define the onset and duration of the HTM in
111 northeast Ontario, as well as its effects on lake ecosystems.

112 This paper attempts to quantify changes in climate systems in northeastern Ontario using
113 robust analysis of fossil pollen to reconstruct climatic and vegetation characteristics, as well as
114 fossil diatoms and pigments from aquatic phototrophs to quantify the effects of climate
115 variability on lake production and community composition. Diatoms are ideal for these
116 objectives, as certain species have well-documented optima for nutrients and other physical and
117 chemical limnological characteristics (water-depth, pH, salinity, stratification regime, etc.). By
118 examining changes in diatom species which are known to be nutrient-controlled, changes in
119 nutrient levels can be inferred (Douglas and Smol, 1999; Lotter et al., 1999; Rühland and Smol,
120 2005; Cumming et al., 2015). Similarly, fossil pigments (chlorophylls, carotenoids, derivatives)
121 often preserve after the loss of morphological remains of non-siliceous phytoplankton and
122 phytobenthos, and are used to estimate historical changes in the abundance of primary producers,
123 as well as their gross community composition (Leavitt et al., 1994a, 1997; Hodgson et al., 1998;
124 Hall et al., 1999). Taken together, analysis of these proxies are can be used to answer three
125 questions related to the HTM: a) when and for how long did the HTM take place in northeast

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

129

130 **Methods**

131

132 *Study area*

133

134 Charland Lake (N 48°34' 50.8", W 80°53' 46.5) (Figure 1) is located east of Timmins,
135 Ontario, Canada, immediately west of Kettle Lake Provincial Park and is located within 6 km of
136 Lake Six, site of the only other study of Holocene climate in northeast Ontario (Liu, 1990).
137 Charland Lake, like other basins in the region, formed when Glacial Lake Ojibway drained off
138 the landscape of northeastern Ontario ~8200 cal yr BP (Veillette, 1994; Carlson et al., 2008; Roy
139 et al., 2015; Margold et al., 2018). The lake is small (~20 ha), 16 m deep, and 274 m above sea
140 level. The climate of the region is humid continental (Koppen Dfb) which is characterized by wet
141 summers and long, cold winters. Average temperature is ~1.8 °C (Environment Canada,
142 2019). Modern boreal forest in the area is composed mainly of white (*Picea glauca*) and black
143 spruce (*Picea mariana*) in lowlands with jack pine (*Pinus banksiana*) and white birch (*Betula*
144 *papyrifera*) on upland sites. Charland Lake occurs in the 'Great Clay Belt' of northern Ontario.
145 The bedrock is composed of metamorphosed Precambrian granites and granodiorites which are
146 overlain by Quaternary glacial landforms and extensive glaciolacustrine clay deposits laid down
147 by Glacial Lake Ojibway (Veillette, 1994; Roy et al, 2011, 2015). [insert Figure 1.]

148

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

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

152

153 *Sample collection*

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

172

173 *Analyses*

174 *Chronology*

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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.

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195 *Dry mass and organic matter*

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

198

199 *Pollen*

200 Pollen samples were prepared at every 8 cm (60 samples total) using a modification of
201 the method of Bennett and Willis (2001). Sediment samples were spiked with two exotic
202 Lycopodium tablets (batch no. 1031) and digested with 10% hydrochloric acid and 10%
203 potassium hydroxide before being sieved through a 10 µm mesh. The remaining sediment was
204 further digested in 40% hydrofluoric acid and then acetolyzed, deflocculated with 10% sodium
205 metaphosphate, stained with Safranin, and mounted on microscope slides in silicon oil. Pollen
206 grains were counted with a Leica light microscope with a 40x differential-interference-contrast
207 objective. A minimum of 400 pollen grains were counted per sample except those in which
208 pollen concentration was low and multiple coverslips needed to be counted. In those cases, a
209 minimum of 300 grains were counted. Pollen grains were identified to the lowest possible
210 taxonomic resolution based on published references (Bassett et al., 1978; McAndrews et al.,
211 1978; Kapp et al., 2000).

212

213 *Pigments*

214 Subsamples of wet sediment were used for determination of photosynthetic pigment

215 concentrations from 59 intervals throughout the core at the University of Regina's Institute of
216 Environmental Change and Society (IECS). Sedimentary pigment analysis was undertaken
217 following procedures outlined in Leavitt and Hodgson (2001). Pigment concentrations are
218 reported as nmoles pigment g⁻¹ gram organic matter, a unit which is linearly proportional to the
219 standing stock of phytoplankton in decadal-scale monitoring programs (Leavitt et al., 1994a). An
220 Agilent model 1100 high-performance liquid chromatography (HPLC) system with photodiode
221 array detector was calibrated using commercial pigment standards from DHI (Denmark).
222 Analysis included the main *a*- and *b*-phorbins (chlorophyll, pheophytin), as well as chemically-
223 stable, taxonomically-diagnostic pigments representing total algal abundance (β -carotene),
224 cryptophytes (alloxanthin), total cyanobacterial (echinenone), colonial cyanobacteria
225 (myxoxanthophyll), Nostocales cyanobacteria (canthaxanthin), chlorophytes (Chl *b*),
226 chlorophytes + cyanobacteria (lutein-zeaxanthin), siliceous algae (fucoxanthin), mainly diatoms
227 (diatoxanthin), and anaerobic purple sulfur bacteria (okenone) following Leavitt and Hodgson,
228 (2001). Historical changes in the lacustrine preservation environment were recorded as changes
229 in the ratio of labile precursor (Chl *a*) to stable products (pheophytin *a*), both ubiquitous
230 pigments used to estimate total phototrophic abundance (Leavitt and Hodgson, 2001).

231

232 *Diatoms*

233 Diatom samples were prepared using ~0.2–0.3 g of wet sediment, taken every 8.0 cm, for
234 a total of 59 subsamples. Samples were digested in a 1:1 molar solution of concentrated nitric
235 and sulphuric acids before being brought to a slightly acidic pH through repeated rinses with
236 double-deionized water. Diatom slurries were reduced to a volume of ~5 ml by aspiration
237 following sedimentation, and spiked with a solution of microspheres of known concentration

238 equivalent to 4 ml of a 2.0×10^7 spheres/ml solution for organic samples and 0.2 ml of a $2.0 \times$
239 10^7 for clay-rich samples. Samples were plated on coverslips in a series of four dilutions and then
240 mounted to slides using Naphrax[®]. Diatoms valves were identified and enumerated using a Leica
241 DMRB microscope under a 100× Fluotar objective (NA of objective = 1.3) and differential
242 interference contrast optics at 1000× magnification. For most diatom samples a minimum of 400
243 valves were counted, or, if the concentration of valves was exceptionally low, until five transects
244 were completed. Diatoms were identified to species or lower taxonomic units using the standard
245 references (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Cumming et al., 1995).
246 Chryosphyte scales were enumerated alongside diatoms, but were not taxonomically identified.

247

248 *Numerical analyses*

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

258 Modern Analog Technique (MAT) was used to quantitatively reconstruct mean annual
259 temperature over the Holocene record of Charland Lake using the C2 software program (Juggins,
260 2003). Modern pollen taxa and climate data were collected from the North American pollen

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

278 Pigments were restricted to common sedimentary compounds of known chemical
279 stability (see above). Analysis of similarities (ANOSIM) using a Bray-Curtis similarity
280 coefficient and 999 permutations, were used to test the null hypothesis that there was no
281 difference in diatom and pigment composition between the pollen-inferred climate zones (Clarke
282 and Warwick, 1994). Analyses were performed using both non-transformed and square-root
283 transformed species data. ANOSIM tests were performed on diatom relative abundance and

284 concentration and pigment concentration data. ANOSIM tests were calculated using the PAST 3
285 software package (Hammer et al., 2001; Hammer and Harper, 2006). The sample from a depth of
286 440 cm was determined to be an outlier and was removed prior to any statistical analyses.
287 Following the ANOSIM analysis, SIMPER tests (also performed in PAST), were used to
288 calculate the contribution of each species to the average dissimilarity between the two groups.
289 *Post-hoc* t-tests assuming unequal variance were performed to identify the significant difference
290 between the pollen-inferred climate zones for individual sedimentary pigments using Microsoft
291 Excel. The index of chrysophyte scales to diatom frustules (scale-to-diatom index) was
292 calculated using the formula: $\text{scales} / (\text{diatoms} + \text{scales}) \times 100$ (Moos et al., 2005).

293

294 **Results**

295

296 *Age model*

297

298 The activity of ^{210}Pb in the Charland Lake gravity core was adequate to produce an age-
299 depth model for the top 12 cm of sedimentation (Supplemental Figure 1). Background levels of
300 ^{210}Pb were reached below that depth. Approximately 10 cm were lost from the first section of the
301 piston core during extrusion. Based on our CRS model, this would mean the top of the piston
302 core would correspond to an age of 0 cal yr BP with BP = 1950.

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

309 *Table 1.* Summary of the ^{14}C -dating results on pollen isolated from selected intervals from the
 310 sediment cores from Charland Lake. All analyses were performed based on pollen isolated at the
 311 LacCore Facility at the University of Minnesota, and dated at Lawrence Livermore National
 312 Laboratory. The mean age of the distribution is presented in “Cal yr BP”. The top date was
 313 generated through ^{210}Pb dating and a CRS model.
 314

| Core | Cumulative depth in piston core (cm) | $\delta^{13}\text{C}$ | ^{14}C Age \pm 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 \pm 30 | 1081 | 976–1187 | 171192 |
| C2S2 | 143.5 | -28 | 2505 \pm 40 | 2623 | 2451–2749 | 171205 |
| C2S2 | 178.5 | -28 | 3035 \pm 30 | 3260 | 3133–3360 | 171201 |
| C2S3 | 204-206 | -28 | 3480 \pm 30 | 3762 | 3649–3863 | 176019 |
| C2S3 | 262.5 | -28 | 4400 \pm 30 | 4925 | 4846–5037 | 171194 |
| C2S4 | 305-306 | -28 | 4560 \pm 35 | 5390 | 5238–5570 | 176020 |
| C2S4 | 401.5 | -28 | 6235 \pm 30 | 7159 | 6999–7272 | 171206 |
| C2S5 | 437.5 | -28 | 6995 \pm 40 | 7815 | 7670–7947 | 171202 |

315

316

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

323

324 ***Pollen***

325

326

Four statistically-significant pollen zones were identified in the Charland Lake core

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

335 The Pre-HTM zone occurred from 473–445 cm (~8200–7800 cal yr BP) and showed
336 mixed dominance of *Picea* and *Pinus*; *P. banksiana* and *P. resinosa* could not be distinguished.
337 This zone also included a relatively low abundance of arboreal pollen compared to rest of the
338 core, as well as more abundant spores and pollen from *Sphagnum*, fern, and Cyperaceae.
339 Reconstructed average temperature was approximately -0.5–0 °C in this zone. The HTM zone
340 occurred from 445–253 cm (~7800–4500 cal yr BP) and showed a major increase in
341 reconstructed temperature (Figure 3, Figure 4). Average temperatures of ~2–3 °C were consistent
342 across this zone, but there appears to be two distinct floral assemblages within the warm period.
343 The first was marked by an increase in the *P. banksiana/resinosa* and the second with an
344 increase in *Pinus strobus* and Cupressaceae. Organic sedimentation also began in this zone,
345 concomitant with pollen concentration rapidly increasing before falling substantially at the onset
346 of the second clay layer. The Post-HTM period (253–85 cm, ~4500–1700 cal yr BP) showed an
347 increase in *Picea*, *P. banksiana/resinosa*, and *Betula* pollen, as those of *P. strobus* and
348 Cupressaceae declined. This is reflected in the MAT reconstruction as average temperature fell
349 by ~1 °C. Pollen concentration was variable in this zone but generally increased during the

350 earlier portion before declining after ~3300 cal yr BP. The Modern Zone (85–0 cm, ~1700–0 cal
351 yr BP) showed a general decrease in pollen concentration and further decreases of *P. strobus*.
352 *Picea* became predominant in this zone with *P. banksiana/resinosa* and *Betula* experiencing
353 minor decreases compared to the Post-HTM zone. Reconstructed average temperature slowly
354 declined by ~0.5 °C throughout this zone. The concentration of pollen types was also plotted and
355 can be found in the supplemental materials (Supplemental Figure 3).

356 [insert Figure 3]

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

362 [insert Figure 4]

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

368

369

370 ***Pigments***

371

372 The pollen climate zones were used as a framework to assess the relationship between
373 climate change and variation in pigment assemblages (Figure 5). Overall, preservation of

374 pigments was poor in the Pre-HTM zone, with fossil concentrations below detection limit in
375 most samples. A similar absence of fossil pigments in the second clay layer suggests that the
376 near absence of sedimentary organic matter favored complete decomposition of carotenoids and
377 chlorophylls, irrespective of their inherent chemical lability, similar to patterns seen in glacially-
378 fed alpine lakes (Bunting et al., 2010). In contrast, concentrations of ubiquitous pigments (β -
379 carotene, Chl *a*, pheophytin *a*), and those from cryptophytes (alloxanthin), diatoms
380 (diatoxanthin), total cyanobacteria (echinenone), Nostocales cyanobacteria (canthaxanthin),
381 chlorophytes (pheophytin *b*) and chlorophytes+cyanobacteria (lutein-zeaxanthin) all increased
382 markedly at the base of the HTM zone, whereas more labile compounds (fucoxanthin, Chl *b*) did
383 not. These patterns reflect the increase in okenone from obligate anaerobic purple sulfur bacteria,
384 an indicator of anoxia in deep-waters or sediment. Transition from the HTM to Post-HTM zone
385 was marked by significant increases in the concentration of most fossil pigments (Table 2, Figure
386 6). The Post-HTM zone was characterized by elevated concentrations of most pigments, often to
387 a historical maximum relative to other zones (e.g., β -carotene, lutein-zeaxanthin, okenone, and
388 canthaxanthin). In the Modern zone (0–85 cm; ~1700–0 cal yr BP), pigment assemblages were
389 marked by the first appearance of myxoxanthophyll from colonial cyanobacteria, increases in
390 concentrations of compounds from Nostocales cyanobacteria (canthaxanthin) and secondarily
391 total cyanobacteria (echinenone), and historical maxima of less chemically-stable pigments from
392 diatoms (fucoxanthin, diatoxanthin) and chlorophytes (Chl *b*). In contrast, fossil levels of
393 ubiquitous β -carotene and the mixed chlorophyte-cyanobacterial indicator, lutein-zeaxanthin,
394 declined slightly in the most recent zone. Relative to individual pigments, the ratio of labile
395 chlorophyll *a* to stable phaeophytin *a* (indicating the preservation environment) remained

396 relatively constant through the core, with some variance within and between the clay bands of
 397 the Pre-HTM and HTM zones (Figure 5). [insert Figure 5.]

398
 399 *Figure 5.* Concentration of photosynthetic pigments (nmoles per gram organic matter) in
 400 Charland Lake sediment core over time (cal yr BP). The ratio of chlorophyll *a* to phaeophytin *a*,
 401 an indicator of preservation, and organic matter (%) are also shown. Darker zones in Sediment
 402 Type represent organic sedimentation in the piston core. Layered zones represent clay deposits.
 403 The dotted lines indicate the pollen-derived climate zones from Figure 3.

404
 405 *Table 2.* Summary table of the results from a series of two sample post hoc t-tests assuming
 406 unequal variance conducted to identify significant differences in pigment concentrations between
 407 the HTM, Post-HTM, and Modern zones for sedimentary pigments. Bold cells indicate
 408 significance.

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

410
 411 One-way pair-wise ANOSIM tests confirmed that there were significant differences in
 412 pigment concentration among the three most recent zones. Specifically, the null hypothesis of no
 413 difference between pigment concentrations among zones was rejected in comparisons of the

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

419
 420 *Figure 6.* Boxplots of pigment concentrations (nmol/g OM) within the *a priori* defined pollen-
 421 derived climate zones (HTM (n= 24), Post-HTM (n= 21), Modern (n= 11)). ANOVA tests were
 422 run to test for significant differences between zones for A) β -carotene (F(2, 53) = 8.2, p-value <
 423 0.01) B) lutein-zeaxanthin (F(2, 53) = 7.6, p-value < 0.01) C) alloxanthin (F(2, 53) = 11.4, p-
 424 value < 0.01) D) echinenone (F(2, 53) = 7.3, p-value < 0.01) E) okenone (F(2, 53) = 10.1, p-
 425 value < 0.01) F) canthaxanthin (F(2, 53) = 26.8, p-value < 0.01) G) chlorophyll *b* (2 outliers
 426 removed in the Post-HTM zone) (F(2, 53) = 6.5, p-value < 0.01) H) fucoxanthin (F(2, 53) = 52.1,
 427 p-value < 0.01) I) diatoxanthin (F(2, 53) = 47.1, p-value < 0.01) J) myxoxanthophyll (F(2, 53) =
 428 22.9, p-value < 0.01). Asterisks indicate zones that are significantly different based on post-hoc
 429 t-tests (Table 2). Pre-HTM zone omitted due to the small number of samples in this zone.

430

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

435

| | 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) |

436

437 *Table 4.* Summary of the one-way SIMPER tests (Bray-Curtis dissimilarity) on Charland Lake
438 diatom relative abundances, diatom concentrations, and HPLC data between pollen-derived
439 climate zones. Percent contribution of driving taxa indicated in brackets.
440

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

441

442

443 *Diatoms*

444

445 Application of pollen climate zones to the diatom assemblages of Charland Lake showed

446 that diatom concentrations were low in both the Pre-HTM zone and the second clay band, but

447 increased in the organic layer between the clay bands during the HTM to $\sim 23 \times 10^8$ valves per

448 gram dry weight (Figure 7). Diatom concentrations also increased after the second clay band and

449 remained relatively stable between 284–145 cm (range ~ 9 to 21×10^8 valves per gram dry

450 weight). The scale-to-diatom index was low within both clay bands, with an increase in scaled

451 chrysophyte abundance in the intervening organic layer. The abundance of scaled chrysophytes

452 increases during the second clay band and continued to increase throughout the HTM and Post-

453 HTM zones. After a Post-HTM zone peak, scaled chrysophyte abundance declined into the

454 Modern zone and remained low to the top of the core (Figure 7). [insert Figure 7.]

455

456 *Figure 7.* Relative abundance of dominant (>5% found in 3 sections of the core) diatom taxa in
457 Charland Lake arranged by age (cal yr BP). The diatom taxa are arranged by their weighted-
458 average optima based on cumulative depth in the core. The scale-to-diatom index and total
459 diatom concentrations (valves/g dry weight x 10⁸) are also shown. Darker zones in Sediment
460 Type represent organic sedimentation in the piston core. Layered zones represent clay deposits.
461 The dotted lines indicate the pollen-derived climate zones from Figure 3.

462

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

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

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

486

487 **Discussion**

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

498

499 *Pollen as a climate proxy in northeastern Ontario*

500 *Pre-HTM zone (~8200–7800 cal yr BP)*

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

510

511 *HTM zone (~7800–4500 cal yr BP)*

512 Reconstructed temperature shows a sharp increase by ~2 °C at the onset of this zone
513 ~7800 cal yr BP. This climate shift is most driven in the decline of *Picea* and the increase in *P.*
514 *banksiana/resinosa*, followed by increases in *P. strobus* and Cupressaceae at ~6000 cal yr BP.
515 This is similar to patterns recorded in the mid-Holocene of Lake Six as described by Liu (1990).
516 This two-phase HTM likely represents an increase in precipitation levels after ~6000 cal yr BP
517 as inferred by increase of Cupressaceae.

518 Interpretation of the Cupressaceae peak is difficult, as this pollen morphotype cannot be
519 easily distinguished between *Juniperus* and *Thuja* based on morphological characteristics alone
520 (McAndrews, 1973; Yu, 1997). As *Juniperus* and *Thuja* are indistinguishable as pollen types,
521 and the two genera have differing climatic optima, we have elected to remove Cupressaceae
522 from our temperature reconstructions. It is for this reason as well, that we did not attempt to

523 reconstruct annual precipitation over the Holocene based on the pollen in the Charland Lake
524 core. *Juniperus* is known to prefer dry habitats, while *Thuja* prefers wetter conditions (Johnston,
525 1990; Yu et al., 1996; Yu 1997). Nonetheless, we infer that Cupressaceae were composed
526 mainly of *Thuja* at Charland Lake due to the presence of *Thuja* stomata observed on pollen
527 slides. This interpretation agrees with that of Liu (1990) who inferred that *Thuja* represented
528 most Cupressaceae pollen at Lake Six based on the occurrence of fossil *Thuja* seeds. Carcaillet et
529 al. (2001) also inferred the presence of *Thuja* rather than *Juniperus* because charcoal analysis
530 shows that forest fire frequency did not increase in the area during the HTM which would be
531 consistent with a wetter, *Thuja*-rich environment.

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

541 We infer that the HTM manifested in two phases in the Charland Lake region. The first
542 phase, from ~7500–6000 cal yr BP, saw the increase of *Pinus banksiana/resinosa* and increased
543 average temperature ~2 °C compared to the previous zone. The second phase occurred from
544 ~6000–4500 cal yr BP and experienced increases in *P. strobus*, a large increase in *Thuja*-inferred
545 Cupressaceae, and a further increase in temperature by ~0.5–1.0 °C to a maximum of ~3 °C. This

546 reconstruction makes the maximum HTM temperature $\sim 1.5\text{--}2.0$ °C warmer than current
547 conditions, a value which is in line with temperature estimates provided by climatic modelling
548 for this region (Renssen et al., 2009, 2012). We also postulate that the second phase of the HTM
549 was wetter than present in this region, as *Thuja* would have inhabited widespread wetlands
550 which developed during this time. This interpretation is consistent with Prentice et al. (1991)
551 whose precipitation reconstructions of the Holocene of eastern North America shows an increase
552 in annual precipitation in northeast Ontario after ~ 6000 cal yr BP.

553

554 *The Post-HTM zone ($\sim 4500\text{--}1700$ cal yr BP)*

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

564

565 *Modern zone ($\sim 1700\text{--}0$ cal yr BP)*

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

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

572

573 **Lake and algal responses to Holocene climate change**

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

580

581 *Pre-HTM zone (~8200–7800 cal yr BP)*

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

591

592 *HTM zone (~7800–4500 cal yr BP)*

593 The climate rapidly warmed at the onset of this zone as shown in the temperature
594 reconstruction based on pollen (Figure 3), but pollen data suggests a two-phase warming event;
595 first warm and dry conditions followed by warm and wet conditions. Charland Lake continued to
596 experience major clastic input at the beginning of this zone, although microfossils from algae
597 and cyanobacteria begin to appear at this time. High abundance of *S. construens* and *S. pinnata*
598 during the early HTM suggests low-light or turbid conditions (Haworth, 1976; Bradshaw et al.,
599 2000; Fritz et al., 2004) consistent with high clastic influx. These benthic diatoms are known to
600 be tolerant of low-light environments (Punning and Puusepp, 2007; Kingsbury et al., 2012)
601 which, along with the low concentrations of both diatoms and pigments, suggests an
602 unproductive and light-limited environment. Influx of clastic material in Charland Lake may
603 reflect high rates of terrestrial erosion from the undeveloped landscape. The young forest
604 surrounding Charland Lake was likely open during the early HTM, favoring high rates of
605 weathering and transport of clay particles to the lake (Dearing, 1983; Dearing and Foster, 1986;
606 Almquist-Jacobson, 1992).

607 Deposition of organic matter begins in the HTM, although algal fossils remain rare until
608 ~7000 cal yr BP (Figure 5). The appearance of fossil pigments from many but not all groups was
609 likely a response to HTM warming, soil development, and the influx of organic matter which
610 would have created anoxic sediments which provided a better environment for pigment
611 preservation (Leavitt, 1993; Leavitt and Hodgson, 2001; Leavitt et al., 2003). Consistent with
612 this pattern, the ratio of chlorophyll *a* to phaeophytin *a* suggests a high degree of pigment
613 preservation (Leavitt and Hodgson, 2001) following the period of high clastic influx. Lower light

614 penetration during the final period of fine inorganic matter influx may have reduced photo-
615 oxidation of pigments and favoured elevated fossil concentrations (Furlong and Carpenter, 1988;
616 Hurley and Armstrong, 1990, 1991; Leavitt, 1993). Finally, inferred low water-levels (based on
617 the high abundances of benthic diatoms) may have favoured development of benthic mats of
618 chlorophytes and cyanobacteria (as canthaxanthin). Typically, labile pigments (such as Chl *a*) are
619 preserved better if they are produced in benthic mats (Leavitt et al., 1994b; Leavitt et al., 2003).

620 At ~6000 cal yr BP, *Thuja*-inferred Cupressaceae increases rapidly, signifying the onset
621 of wet conditions (Figure 3). Several major phycological and sedimentological changes
622 coincided with this wetter climate. First, elevated organic matter sedimentation persisted until
623 ~6100 cal yr BP and was characterized by increased pigment concentrations, elevated relative
624 abundance of planktonic diatoms, and an increase in chrysophyte scales indicative of deeper lake
625 conditions (Zeeb and Smol, 2001; Figure 5, 7). Contemporaneous with increased temperatures
626 and lake-levels, landscape stabilization was occurring, as indicated by a hiatus in clastic
627 sedimentation which suggests forest closure and reduced erosion (Liu, 1990). The transition to
628 gyttja-based sediments also suggests the presence of soluble nutrients leaching from fresh,
629 organic soils (Liu, 1990).

630 Organic sedimentation was interrupted by the deposition of the second clay layer ~6000–
631 5500 cal yr BP, at which time concentrations of phototrophic fossils declines and diatom
632 assemblages reverted to benthic taxa. Paradoxically, high Cupressaceae pollen abundance
633 suggests a wet climate and high lake-levels. We propose that water levels increased sufficiently
634 to let Charland Lake join with surrounding aquatic ecosystems, including nearby Fredrick House
635 Lake, a site which is only ~2 m below the study basin. As Fredrick House Lake is turbid,
636 conjoined waters may have introduced clastic material from the Fredrick House Lake catchment

637 into Charland Lake. Aquatic conditions in this second clay band were similar to those seen in the
638 early HTM period, where diatom assemblages were composed mainly of benthic species and
639 pigment and frustule concentrations were low.

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

653

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

655 Reconstructed average temperature shows that this zone experienced a cooler climate
656 than the HTM but was still warmer than modern conditions. Algal groups responded to these
657 climate changes; both diatom frustules and pigment concentrations increased moderately,
658 possibly signaling an overall increase in primary production. The eutrophic *S. minutulus*
659 continued to dominate the diatom assemblage until ~3900 cal yr BP when it was replaced by the

660 more oligotrophic *Distostella stelligera* (Figure 7). Presently, we are uncertain whether observed
661 changes in fossil patterns reflect direct effects of climate, or indirect variation in lake structure
662 and function, such as a change in thermal stratification. For example, increased abundance of *D.*
663 *stelligera* has been shown to correspond with a longer period of stratification (Dean et al., 1994;
664 Bradbury et al., 2002; Wiltse et al., 2016) and a shallow mixing depth (Saros et al., 2012). This
665 interpretation is supported by changes in the chrysophyte scale-to-diatom index, as chrysophytes
666 have a competitive advantage over diatoms when the water column is strongly stratified (Eimers
667 et al., 2009). An increase in the abundance of chrysophytes has also been related to less
668 eutrophic conditions, which agrees with an increase in *D. stelligera* (Reynolds, 1988; Brabury et
669 al., 2002).

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

683 algal groups suggest a longer period of thermal stratification during the Post-HTM period and,
684 perhaps, reduced diatom recruitment, which favoured growth of other phytoplankton groups,
685 such as cryptophytes and chlorophytes.

686

687 *Modern zone (~1700–0 cal yr BP)*

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

701 The movement towards colder conditions during this period may have also promoted
702 more lake mixing and less-stable thermal stratification, allowing some algal species, such as *S.*
703 *minutulus*, to proliferate (Reynolds and Reynolds, 1985; Kilham et al., 1986; Makulla and
704 Sommer, 1993; Bradbury et al., 2002). Growth requirements of *Stephanodiscus* species may
705 have been largely satisfied by the regeneration of phosphorus from nutrient-dense water to the

706 photic zone during spring circulation, resulting in large blooms of *S. minutulus* and *S. parvus*
707 (Kilham and Kilham, 1978; Bradbury et al., 2002). The inference of extended periods or
708 vigorous lake-mixing is also supported by the decrease in the chrysophyte scale-to-diatom index,
709 further suggesting less stratification (Reynolds, 1984; Rott, 1984).

710 Interpretation of the influence of climate on canthaxanthin (Nostocales cyanobacteria)
711 and okenone (purple sulfur bacteria) is not straightforward, as both of these algal groups would
712 be expected to decrease under cooler and wet conditions (Lami et al., 2009). Okenone is found in
713 anaerobic purple sulfur bacteria which prefer the oxic-anoxic interface in lakes (Massé et al.,
714 2002), hence higher concentrations of okenone can be related to seasonal anoxia in lakes
715 (Maheux et al., 2016). On the other hand, low concentrations of purple sulfur bacteria have been
716 related to cool conditions, likely coupled with increased mixing of the water column (Schmidt et
717 al., 2002). Overall, concentrations of okenone are much lower than those seen in meromictic or
718 strongly stratified ecosystems (Leavitt et al., 1989) and suggests the presence of only seasonal
719 (summer) anoxia, perhaps restricted to deep littoral sediments. Furthermore, canthaxanthin, an
720 indicator of Nostocales cyanobacteria, is often associated with high nutrients in the water column
721 (Kleppel et al., 1988; Lami et al., 2009), but can also be a marker of N₂ fixation (Hayes et al.,
722 2018). One possibility is that the Modern period experienced an influx of dissolved organic
723 matter (DOM) which would have helped proliferate the heterotrophic growth of the
724 cyanobacterial groups (Stevenson et al., 2016). Regardless it seems likely that factors other than
725 climate must be considered to understand how limnologic conditions became ideal for these
726 groups in the Modern period.

727

728 **Conclusions**

729 Pollen data from Charland Lake suggests that the HTM in northeast Ontario took place
730 from ~7800–4500 cal yr BP. The onset of warmth is ~1000 years later than recorded in
731 northwest Ontario (Moos et al., 2009; Moos and Cumming, 2011, 2012; Karmakar et al., 2015a,
732 2015b). Differences between our findings and Liu’s (1990) may be due to the more rigorous
733 carbon dating model used in our study as our pollen analysis agrees with Liu’s (1990) quite well.
734 Analysis of fossil pollen showed that the HTM in northeastern Ontario was warm and dry from
735 ~7500–6000 cal yr BP and then become wet from ~6000–4500 cal yr BP as indicated by the high
736 abundance of *Thuja*-inferred Cupressaceae pollen. Algal abundance was variable over the
737 Holocene, as inferred from both fossil pigment and diatom concentrations, apparently responding
738 mainly to variation in the linkage between land and water.

739 This work represents one of the first investigations in northeast Ontario to assess the
740 relationship between climate and in-lake production during the Holocene Epoch. Overall, the
741 interaction between climate and limnological conditions were complex within Charland Lake,
742 providing a striking comparison with lakes in northwest Ontario at millennial time scales. In
743 general, we demonstrate that limnological conditions were more optimal for algae over the last
744 ~4500 years than in the preceding millennia. This pattern is in stark contrast to those seen in
745 lakes from northwest Ontario, where paleolimnological studies have linked the warmer HTM to
746 enhanced lake-water production (Moos and Cumming, 2009; Karmakar et al., 2015b). In
747 Charland Lake, such changes were evident, but small in comparison, and did not indicate the
748 warmer temperatures of the HTM directly influenced lake-water production. These findings
749 suggest indirect climate effects, such as changes in thermal stratification and mixing, may be
750 more influential on algal production in some lakes in northeast Ontario. If this were broadly true,
751 it suggests that lakes in northeast Ontario may respond differently to future climate change

752 compared to lakes elsewhere in northern Ontario, and that the response and susceptibility of
753 lakes to climate change can vary across an ecozone.

754

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765

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1084 *Supplemental figure 1.* A) Activity of ^{210}Pb , ^{214}Pb , ^{214}Bi , and ^{137}Cs in the Charland Lake gravity
1085 core. B) Constant Rate of Supply (CRS) model inferred ages for the Charland Lake gravity core.
1086

1087 *Supplemental figure 2.* Broken stick model based on a constrained cluster analysis (CONISS) of
1088 abundant pollen taxa (>1% in two or more intervals) from Charland Lake.
1089

1090 *Supplemental figure 3.* Total concentration of pollen grains ($\times 10^4$) from Charland Lake. Darker
1091 zones in Sediment Type represent organic sedimentation in the piston core. Layered zones
1092 represent clay deposits. Climate Zones are derived through CONISS from Figure 3.