Complex responses of phototrophic communities to climate warming during the Holocene of 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 Paleoecological 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*

Chronology
175
176   The top 13 cm of the gravity core were dated by using a constant rate of supply (CRS)

177   model applied to ^{210}Pb gamma activity of the sediments. This was done to assess the date of the

178   top of the piston core as the sediment-water interface was lost during extrusion. The ^{14}C

179   chronology for the piston core was determined by dating a concentrated sample of pollen grains

180   from eight sediment samples with accelerator mass spectrometry (AMS). Pollen grains were

181   isolated from lake sediments by LacCore using a procedure similar to Brown et al. (1989) and

182   measured for ^{14}C at the Lawrence Livermore National Laboratory. An age-depth relationship

183   based on these radioisotopic data was constructed using Bayesian age modeling with the *BACON*

184   (v. 2.2) modeling package in R (R Core Team, 2015) with the IntCal13 ^{14}C calibration curve

185   (Blaauw and Christen, 2011; Reimer et al., 2013). Default settings outlined by Goring et al.

186   (2012) were used to determine the gamma distribution of the accumulation rate, which were in

187   agreement with the posterior distribution of activities (Blaauw and Christen, 2011). The prior

188   memory was set to a mean of 0.3 and shape of 25 to accommodate small shifts in accumulation

189   rates. The sensitivity of prior memory parameters was tested and changes in mean and shape did

190   not result in large changes to the model.

191

193

194

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

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

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 Gawjewski, 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: scales/ (diatoms + 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 ($\pm$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)	$\delta^{13}C$	[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

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. bankisana 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 (fuxoxanthin, 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

16

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.
409

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**

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	*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%)

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 ~23 x 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 x 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 10^8) 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

3

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 Cuppressaceae 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 ~1.5–2.0 °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 (~4500–1700 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 (~1700–0 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

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 N_2 fixation (Hayes et al.,

722 2018). One possibility is that the Modern period experienced in an influx of dissolved organic

723 matter (DOM) which would have helped proliferate the heterotrophic growth of the

724 cyanobacteraial 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

766   **References**
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1083

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 (x10^4) 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.