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Enhanced algal abundance in northwest Ontario (Canada) lakes during the warmer early-to mid-Holocene period

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ABSTRACT

This study investigates regional changes in primary producers in boreal head-water lakes during the warmer early-to-mid-Holocene (EMH) period, across the present-day boreal forest in northwest Ontario, a region that is adjacent to the prairie-forest ecotone. We quantified changes in algal abundance and composition over the Holocene period using pigments, spectrally-inferred chlorophyll *a* and diatom assemblages in well-dated sediment cores from three lakes. All three indicators showed a coherent pattern of enhanced primary producers in two of the study lakes (Gall Lake and Lake 239) during the EMH, whereas only diatom assemblages suggested higher levels of nutrients in Meekin Lake. Overall, this study supports a regional pattern of enhanced primary producers during the EMH, likely as a function of lower water-levels and warmer temperatures. Elevated concentrations of cyanobacterial pigments also occurred in two of the three lakes during the EMH, whereas pigments from purple-sulphur bacteria provide evidence of enhanced deep-water anoxia in one lake. These findings suggest that future climatic warming in boreal regions could include regional eutrophication and associated increases in cyanobacteria.

1. Introduction

Temperatures have increased an average of 0.8 °C (1.4 °F) across the northern hemisphere since 1900, and climate models predict an additional increase between 0.3 and 4.8 °C by the end of the 21st century relative to the 1986–2005 reference period (Collins et al., 2013). Under future warming scenarios, scientists, governments and industry have been tasked to understand the risk of climatic warming on water resources. The direct and indirect mechanisms that could cause changes to lakes in a warmer world are numerous. For example, changes in the surface-water temperature of lakes can result in changes to mixing regimes and thermal stability (Adrian et al., 2009; Read et al., 2014). Changes in physical characteristics may also have cascading effects on nutrient, oxygen and biotic assemblages (Adrian et al., 2009). Further, it is well known that climate influences the length of the ice-free periods (Schindler et al., 1996a; Rodriguez et al., 2001; Diehl et al., 2002; Smol et al., 2005) and many studies have demonstrated an increase in ice-free conditions as air temperatures have increased (Mcknight et al., 1996; Livingstone and Dokulil, 2001; Magnusson et al., 2000; Williams and Stefan, 2006). Climatic warming can also increase water-residence times in lakes, through decreases in stream flow (Schindler et al., 1996a; Rippey et al., 1997). Declines in stream flow can result in lower lake-levels, but also a lower inputs of nutrients and dissolved organic carbon (DOC) from the catchment, with resultant increases in lake-water transparency, and changes in thermocline depth (Schindler et al., 1996a, 1996b). Nutrient concentration can also be affected by the internal processes related to changes in the thermal structure and/or primary production (Jeeppesen et al., 2005; Wilhelm and Adrian, 2008). Warmer climatic conditions also favour cyanobacterial blooms (Paerl and Huisman, 2008), a change that is widely acknowledged as a threat to water quality in many regions (O'Neil et al., 2012), because many species are toxic (Carmichael et al., 1988). The growth rates of many cyanobacteria are higher relative to eukaryotic

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phytoplankton at higher temperatures (Robarts and Zohary, 1987), which also increase the buoyancy of many cyanobacteria (Kromkamp et al., 1988; Reynolds, 2006; Carey et al., 2012). In addition to temperature, high concentrations of nutrients are also important predictors of cyanobacteria blooms (Jöhnk et al., 2008; Kosten et al., 2012; Taranu et al., 2012), which can also change in a warmer climate. In summary, many physical, chemical and biological factors can influence the abundance and composition of primary producers, often in complex and unexpected ways (Findlay et al., 2001), and the response of lakes to climatic change can vary between lakes with different characteristics (Adrian et al., 2006; Read et al., 2014). Given this complexity, it is often hard to predict how primary producers in lakes will change under a warmer climate.

Long-term studies are important to understand how past periods of warmer conditions have influenced algal abundance. Unfortunately, long-term records of changes in algal abundance are rare, especially during prolonged periods of enhanced warmth. Fortunately, records of past periods that were warmer than present do exist, thereby allowing the opportunity to examine how primary producers changed in the past under warmer conditions. Such changes can be investigated using paleolimnological approaches, by examining changes in sedimentary pigments, inferences of chlorophyll *a*, and changes in diatom assemblages in well-dated sediment cores (e.g. Hall et al., 1999; Garrison and Wakeman, 2000; Reavie et al., 2006). To date, climate-related changes in lake trophic status during warmer periods on the Holocene scale are available from few lakes (e.g., Fietz et al., 2007; Lake Baikal; Kirilova et al., 2009; central European Lake; Hickman et al., 1990; Baptiste Lake, Alberta), with a particular absence of relatively small boreal lakes.

In this paper, we quantify past changes in the abundance and composition of algae in sediment cores from three boreal lakes to evaluate how the warmer early-to-mid-Holocene (EMH) period affected primary producers. This study builds on previous research from a core from Lake 239, that indicated nutrient-rich planktonic diatom taxa were most abundant during the EMH period (c. 8500 – 4500 cal yr BP) (Moos et al., 2009). The EMH period in northwest Ontario was characterized as a more open boreal forest (McAndrews, 1982; Björck, 1985; Lewis et al., 2001; Moos and Cumming, 2011) based on a low abundance of spruce pollen, and increases in non-arboreal pollen including Cupressaceae, *Artemesia*, and *Ambrosia*. Pollen-based inferences of the EMH period suggest that temperatures were warmer than present conditions by approximately 2–3 °C (Moos and Cumming, 2012). During the EMH, lake levels were regionally low in comparison with the last 4–5 thousand years (Karmakar et al., 2015), and in conjunction with the pollen, suggests both warm and arid conditions (Karmakar et al., 2015). We use these established changes to address two questions: a) is enhanced algal abundance in lakes a common phenomenon in head-water lakes in northwest Ontario during the EMH period in comparison with earlier and later in the Holocene; and b) did cyanobacterial assemblages become more abundant during the EMH?

2. Study sites

The boreal region of northwest Ontario is located approximately 200-km east of the modern-day prairie-forest ecotone, a climatically-sensitive ecotone (Umbanhowar et al., 2006). All of our study lakes are located within the Winnipeg River Drainage Basin (WRDB), a large catchment (150,000 km^2) located primarily in northwest Ontario (Fig. 1). Instrumental records from the WRDB are limited, but show a warming trend of 1–2 °C over the past century, and spatially-asynchronous droughts on a sub-decadal scale (Laird et al., 2012). We selected three lakes to study within the WRDB that span a spatial transect of over ~200 km (Fig. 1) across the boreal region. This region consists of rolling topography of hills and valleys located on crystalline bedrock with shallow soils (McAndrews, 1982). The easternmost site, Gall Lake is located in the English River Watershed (50° 14′N, 91° 27′W) whereas the westernmost site, Meekin Lake (49°49′N, 94°46′W) is located ~100 km from the modern-day prairie-forest ecotone. Lake 239 (49°40′N, 93°44′W) was included as the changes in the diatom assemblages during the EMH was the motivation for this study (Moos et al., 2009) and is located centrally between the other two study sites.

The study lakes are all relatively small (Gall Lake: surface area = 19 ha, maximum depth = 18 m, fetch = 0.85 km; Lake 239: surface area = 56 ha, maximum depth = 31 m, fetch = 1.1 km; Meekin Lake: surface area = 78 ha, maximum depth = 13 m, fetch = 1.5 m), slightly acidic (pH = 5.9 – 6.5), dimictic, first-order lakes, with gentle sloping bathymetry in at least one basin (Kingsbury et al., 2012). These lakes represent presently oligotrophic (Meekin Lake and Lake 239) to slightly mesotrophic nutrient condition (Gall Lake) (Kingsbury et al., 2012), and contain few macrophytes. The vegetation near Gall Lake is dominated by black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and poplar (*Populus* spp.), along with white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), and larch (*Larix* spp.). Similarly, the boreal forest around Lake 239 consists mainly of black spruce, jack pine and some poplar. Further to the west, the vegetation around Meekin Lake consists of balsam fir, poplar, white birch with some black ash (*Fraxinus nigra*) and red maple (*Acer rubrum*).

A synthesis of available pollen-based records, which span the Canadian prairie-boreal forest ecotone, clearly indicate EMH warmth (Moos and Cumming, 2011). However, changes in pollen species were dependent on lake location, with the prairie lakes showing increases in grasses and *Ambrosia* spp. during the EMH, whereas changes in Cupressaceae and *Ambrosia* are more apparent in the boreal region.

3. Materials and methods

In June 2011, a piston core was collected from the deepest region of the central basin in Gall and Meekin lakes using a Livingstone square-rod piston corer, with an internal diameter of 5.1 cm (Glew et al., 2001). A piston core was also removed from the deep central basin of Lake 239 in July 2004 (Moos et al., 2009). The total core lengths were ~5, 11 and 9 m of sediment from Gall Lake, Lake 239 and Meekin Lake, respectively. In the lab, each core was sectioned at 0.5 cm intervals into 10 oz Whirlpak® bags. A total of 10 (Gall Lake), 8 (Lake 239, Moos et al., 2009) and 13 intervals (Meekin Lake) were sampled, and analysed along the length of both cores, for radiocarbon dates (Table 1). AMS ^{14}C age estimates were based on analysis of carbon from pollen isolated at the Limnological Research Center at the University of Minnesota using the procedures of Brown et al. (1989), after which they were analysed for ^{14}C activity at the Lawrence Liverpool National Laboratory. Radiocarbon dates were calibrated (using IntCal, Reimer et al., 2009) and age-depth models for sediment cores from Gall and Meekin lakes were created using 'classical' age-depth modelling (*clam*; Blaauw, 2010). The age-depth model for the Lake 239 sediment core was based on a simple polynomial (Fig. 3 in Moos et al., 2009). To determine the age at the top interval of the piston core for cores from Gall and Meekin lakes, total ^{210}Pb and ^{137}Cs were measured in the uppermost sediment in the first section of the piston cores from each lake and matched to the activities measured in a dated gravity core retrieved at the same depth as the piston core (e.g., Laird et al., 2012; Haig et al., 2013; Ma et al., 2013).