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ORIGINAL PAPER

Biological and geochemical changes in shallow lakes of the Hudson Bay Lowlands: a response to recent warming

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Abstract The Hudson Bay Lowlands (HBL) region of the far north of Ontario (Canada) is expected to undergo considerable physical, chemical and biological change as a result of ongoing climatic change. Previous research in the region has shown marked limnological changes during the past ~ 20 years in relatively deep lakes that have been attributed to increased air temperatures and changes in sea ice phenology in Hudson Bay since the mid-1990s. Here, we present diatom assemblage, primary production and geochemical data from lake sediments documenting recent limnological change in two shallow subarctic lakes in the Sutton River region of the HBL. Both lakes recorded increased whole-lake production and diatom diversity changes that are consistent with a longer ice-free period and growing season. Changes in diatom composition at Wolfgang Lake were characterized by a response amongst benthic/periphytic taxa whereas a modest increase in planktonic diatoms was observed at Sam Lake. Geochemical changes ($\delta^{15}N$, C/N and %N) were temporally coherent with diatom assemblage changes, but showed different responses in the two study lakes. Thus, although the biological and geochemical changes were consistent with recent warming, differences in the nature and timing of these shifts illustrate the heterogeneous nature of shallow lakes, and suggest that local (catchment-specific) factors are important determinants of the trajectory of limnological change in these sensitive systems.

Keywords Diatoms · Climate change · Stable isotopes · Chlorophyll *a* · Paleolimnology · Lake sediments

Introduction

As a result of the moderating role of Hudson Bay sea ice on the regional climate, the northern Hudson Bay Lowlands (HBL) registered minimal warming throughout the mid- to late-twentieth century (Chapman and Walsh 1993; Gough et al. 2004). However, since the mid-1990s, the Hudson Bay region has

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experienced marked warming, associated with decreased sea ice cover and changes in sea ice phenology (Hochheim and Barber 2010, 2014). The effects of warming during the past two decades are well documented in the Hudson Bay marine ecosystem, with changes to the productivity of the marine food web (Hoover 2010), declines in polar bear body condition, reproduction, survival, and abundance in several sub-populations (Obbard et al. 2006; Regehr et al. 2007), and marked changes to sea bird populations and their prey (Mallory et al. 2010; Gaston et al. 2012). There is also concern that warming may alter carbon dynamics in the region's extensive peatlands, with possible global consequences (Tarnocai 2006; Dunn and Freeman 2011; McLaughlin and Webster 2014).

Climate change may also alter fundamental water column properties and nutrient dynamics in lakes in several ways, with implications for biota. Increases in surface water temperatures (O'Reilly et al. 2015), longer and warmer ice-free seasons (O'Beirne et al. 2017), and increased thermal stability in stratified lakes (Stainsby et al. 2011; Hadley et al. 2014) have been linked to long-term changes in phytoplankton communities and sedimentary diatom assemblages in temperate, sub-arctic, and Arctic lakes (Sorvari et al. 2002; Smol et al. 2005; Rühland et al. 2008; Weckström et al. 2016; Bramburger et al. 2017; Reavie et al. 2017; Roberts et al. 2017). Increases in aquatic production, as inferred from sedimentary chlorophyll *a*, have also been observed with recent warming (Michelutti and Smol 2016), even in lakes with stable or declining nutrient concentrations (Paterson et al. 2017). In part, this may be attributed to a longer growing season that allows more time for the development of algal populations (Nelligan et al. 2016).

Limnological changes with 1990s warming have been documented in relatively deep lakes in the northern HBL. In a detailed analysis of diatom assemblages from four deep lakes within the HBL (all lakes > 10 metres maximum depth), diatom species assemblage changes were recorded in the mid-1990s, including an increase in species richness, and significant increases in the relative abundances of planktonic taxa that were coherent with increases in mean annual and seasonal air temperatures (Rühland et al. 2013). Similarly, in a comparison of diatom assemblages between recent and pre-industrial sediments in the HBL (i.e., using a "top–bottom" paleolimnological approach), Rühland et al. (2014) reported higher diatom diversity in modern sediments, which they attributed to a longer ice-free period (and thus longer growing season), and the development of new aquatic habitats.

In general, less is known about long-term biological trajectories in shallow lakes in the northern HBL, despite their importance and prevalence in the region. However, recent research suggests that these shallow water bodies may be quite sensitive to 20th century climate change. In the Churchill region of northwestern HBL, for example, changes to hydrological connectivity and enhanced evaporation with warming have been linked to periods of hydrological instability in shallow freshwater tundra ponds. In some cases, declining snowmelt runoff has led to pond desiccation (Bouchard et al. 2013). It is apparent that biological (Shinneman et al. 2016) and hydrological (Wolfe et al. 2011) responses to warming can be quite variable in shallow lakes, as these responses are moderated by catchment-scale differences in landscape variables and vegetation. Moreover, shallow lakes may also show a heightened sensitivity and more pronounced biological response to warming, relative to deeper water bodies, because of their higher surface to volume ratios and lower water volumes (Roberts et al. 2015; Hargan et al. 2016; Smol 2016).

Here, we present diatom assemblage data and reconstructions of past primary production from lake sediment cores from two shallow lakes in the Sutton River region of the HBL. In light of evidence for recent changes in air temperature, and observed biological changes in nearby deeper lakes, our primary objective was to determine how the algal communities of shallow lakes in the HBL may have responded to a warming climate. In addition, we present detailed geochemical data (δ^{15}N, C/N and %N) from the same sediment cores to explore the possible influence of the long-range deposition of atmospheric nitrogen as an alternative, synergistic, or confounding explanation for the recent algal changes. These data were then compared to results from four nearby relatively deep lakes (Rühland et al. 2013), as well as 13 lakes from a regional "top–bottom" paleolimnological survey (Rühland et al. 2014). We argue that increased nitrogen deposition is not responsible for these assemblage changes and that the paleolimnological data are consistent with recent climate warming in this region. However, we also note that the biological and geochemical responses varied between the study lakes, suggesting that trajectories of change are moderated by local and catchment-scale factors.

Study lakes

Sam and Wolfgang (unofficial names) lakes are relatively small (32 and 157 ha, respectively), shallow (Z_{max} = 1.7 and 1.2 m, respectively) waterbodies located in the Sutton River region of the HBL, located 53 and 43 km south of the Hudson Bay coast (Fig. 1). The northern HBL is considered to be sub-arctic, with regional climate strongly influenced by circulation patterns and ice dynamics within Hudson Bay (Martini 2006). For most of recorded history, air temperatures in this region have remained relatively stable, suggesting a lack of twentieth century warming. This is supported by paleoecological studies from the Hudson and James Bay region that show minimal biological changes over the past two centuries (Laing et al. 2002; Paterson et al. 2003) to millennia (Ponader et al. 2002; Fallu et al. 2005). However, beginning in the mid-

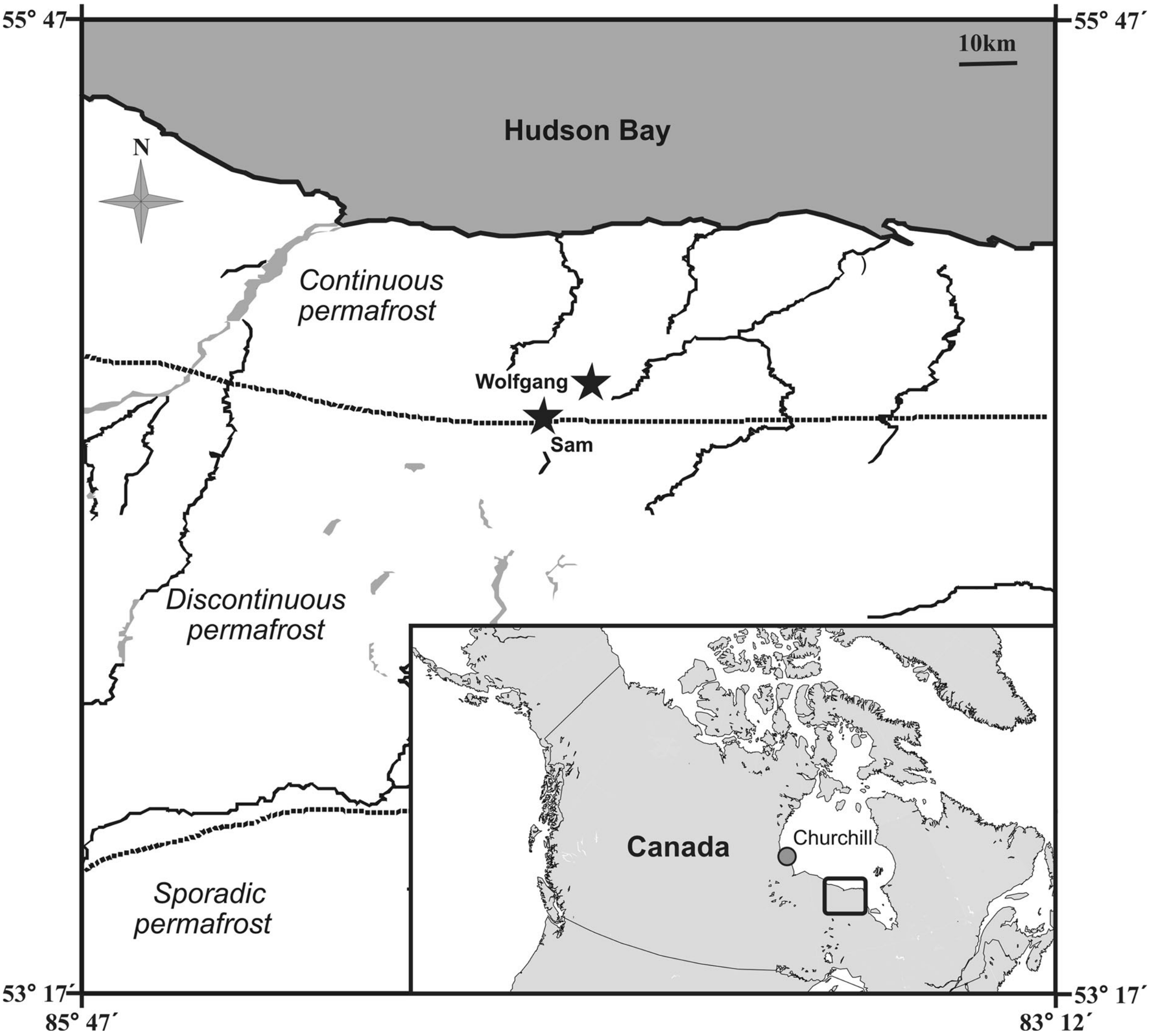

Fig. 1 Regional map showing the location of the lakes surveyed in the Sutton River region of the Hudson Bay Lowlands, and the location of the climate station at Churchill, MB, Canada (inset map). Sam and Wolfgang lakes (unofficial names) are highlighted (stars). The approximate location (determined using GIS) of the boundaries between continuous, discontinuous, and sporadic permafrost are also indicated (dashed lines)

1990s, mean annual air temperature increases of 0.5–1.0 °C per decade were documented at Churchill, Manitoba, and at other HBL stations (e.g., Winisk/Peawanuck climate station) with shorter monitoring records. These changes in regional air temperature have resulted in altered sea ice dynamics, including delayed freeze-up (1.6–2.4 weeks) and earlier spring break-up (1.5–2.5 weeks) (Hochheim and Barber 2014).

The study lakes are alkaline and oligo-mesotrophic, with water chemistry influenced by the underlying limestone bedrock, calcareous till, the proximity of the sites to Hudson Bay, and the degree of permafrost development (Table 1; Paterson et al. 2014). Sam Lake is located very close to the continuous-discontinuous permafrost boundary, recognizing that the precise position of this boundary is based on very few sampling points.

Materials and methods

Field sampling

Water chemistry data for Sam and Wolfgang lakes were collected once per year in August, 2010 and 2011. At the coring location, a composite bottle was lowered and raised through the water column, from the surface to the Secchi disk depth (Ingram et al. 2013). Samples for water chemistry were analyzed at the Ontario Ministry of the Environment and Climate Change (OMOECC) Dorset Environmental Science Centre using standard OMOECC protocols (Ontario Ministry of the Environment 1983). A more detailed description of the limnological sampling and analyses is presented by Paterson et al. (2014).

Sediment cores were collected in August, 2011 from the deepest basin of each lake using a 7.6-cm internal-diameter Glew (1989) gravity corer, and sectioned at 0.5-cm intervals on site using a Glew (1988) vertical extruder, following standard paleolimnological protocols. Core lengths for Wolfgang and Sam lakes were 26.5 and 48.5 cm, respectively. The sediment samples were stored in Whirlpak® bags and refrigerated in the dark until analysis.

Laboratory analyses

^{210}Pb dating

Sediment cores were dated using gamma spectroscopy to detect radio isotope activities of ^{210}Pb, ^{137}Cs and ^{214}Bi, following Schelske et al. (1994). The Constant Rate of Supply model (CRS, Appleby 2001) was applied to determine sediment age based on unsupported ^{210}Pb concentrations. Approximately 0.3–0.7 g of freeze-dried sediment was prepared for age determinations. Sediment was placed into plastic test tubes and sealed with 2-Ton Epoxy® to ensure equilibrium between ^{226}Ra and ^{214}Bi prior to gamma counting. Activities were collected for 13 samples per core, and ^{210}Pb dates were estimated for the past ~ 100–150 years.

Diatoms

Sediment preparation for diatom analysis followed standard paleolimnological procedures (Battarbee et al. 2001). Briefly, 0.2–0.3 g of wet sediment was digested in a 50:50 molar mixture of concentrated nitric and sulphuric acid, and rinsed repeatedly with deionized water until a neutral pH was achieved. Diatom slurries were then dried onto coverslips and permanently mounted on microscope slides using Naphrax® mounting medium. Diatom microfossils were counted at 1000 × under oil immersion, using a Nikon Eclipse 80i microscope with differential interference contrast optics. A minimum of 400 diatom

Table 1 Selected limnological data for Sam and Wolfgang lakes, presented as 2-year means (2010–2011)

Lake name	Decimal Degree		Distance to sea (km)	Lake depth (m)	Area (ha)	pH	Conductivity (µS/cm)	SiO_3 (mg/L)	TP (µg/L)	TIN (µg/L)	DOC (µg/L)
	Lat (N)	Long (W)									
Sam	54.76	− 84.60	53	1.7	32	8.1	160.5	0.5	8.0	21.0	6.7
Wolfgang	54.85	− 84.47	43	1.2	157	7.9	146.0	0.8	15.2	32.0	9.1

valves were counted for each sample and diatoms were identified using Krammer and Lange-Bertalot (1986–1991) and Antoniades et al. (2008).

Spectrally inferred chlorophyll a

To track temporal changes in whole-lake production of these lakes, we used spectral analysis to infer trends in sedimentary chlorophyll *a* concentration (Michelutti et al. 2010). Briefly, this analysis infers chlorophyll *a* based on a unique trough found in the 650–700 nm range of the spectral profile of the sediments. The area of this trough has been correlated to the concentration of chlorophyll *a* and its major derivatives in the sediment, providing a rapid, non-destructive method for estimating primary production. Following the development of this technique, research has demonstrated the applicability of the method in both temperate and Arctic environments (Michelutti et al. 2010), as reviewed by Michelutti and Smol (2016). Sedimentary spectral profiles were obtained using a FOSS NIRSystems Model 6500 series Rapid Content Analyzer, operating over the range of 400–2500 nm.

Elemental and isotope composition

Bulk organic carbon and nitrogen elemental and isotope composition were measured at 0.5-cm sediment intervals for both lakes. Samples were prepared for analysis following standard methods described by Wolfe et al. (2001). 1 M hydrochloric acid (8–10% by volume) was applied to samples in order to remove any carbonate material. The supernatant of the samples was then aspirated and samples were rinsed repeatedly with de-ionized water until a neutral pH was obtained. The samples were then freeze-dried and sieved to < 500 µm to remove macrofossil plant debris. The remaining fine fraction was then analysed for organic carbon and nitrogen elemental and isotope composition using a continuous flow isotope ratio mass spectrometer (CF-IRMS) at the University of Waterloo Environmental Isotope Laboratory. Carbon and nitrogen ratios were calculated using percent dry weight organic carbon and nitrogen contents. Stable nitrogen isotope ratios were reported as $\delta^{15}N$ (‰) relative to atmospheric nitrogen (AIR).

Statistical analyses

Principal components analysis (PCA) was used to detect major patterns of variation in the diatom data and to facilitate comparisons in the magnitude and timing of changes between the two cores. The default settings in Canoco version 4.5 (ter Braak and Šmilauer 2002) were used to generate PCA sample scores on square-root transformed species data. For each sedimentary interval, diatom species diversity was calculated using Hill's N2 (the number of very abundant taxa in a given sample) using Canoco version 4.5 (ter Braak and Šmilauer 2002). Stratigraphic zones in both the diatom and elemental/isotope data were determined by constrained hierarchical clustering, following the Constrained Incremental Sum of Squares (CONISS) methodology described in Grimm (1987), using the "rioja" package (Juggins 2009) in R v. 2.13.2.

Limnological changes were plotted against continuous temperature data (1943–2011) available from the Churchill meteorological station (Environment and Climate Change Canada: http://www.cccma.ec.gc.ca/hccd/). Churchill, Manitoba is the nearest climate station within the western HBL with a continuous climate record (located ~ 700 km from the study lakes) and, similar to our study sites, is located close to the Hudson Bay coast. Annual and seasonal temperature data from the Churchill record were significantly correlated to records from Winisk, ON, which is located much closer to the study sites (~ 90 km away), but where the climate record was interrupted and the station was re-located farther inland to Peawanuck in the 1980s because of flooding. Direct comparisons between annually resolved time series data and lake sediment proxy data are always difficult, as the time period represented by each sediment interval may vary with core compression and varying sedimentation rates. To help align these datasets, air temperature data were averaged to match the period of accumulation for each sediment interval based on ^{210}Pb dates, with 6–8 years of instrumental data averaged per sediment interval. Correlations of mean annual and seasonal air temperature anomalies with biological indices were performed using a Spearman rank correlation using the "rcorr" function of the "Hmisc" package (v. 3.9-2; Harrell Jr 2012) in R 2.13.2. Seasonal time periods were defined as: spring (March, April, and May); summer (June, July, and

August); fall (September, October, and November); and winter (December, January, and February). Following Rühland et al. (2013), the Churchill annual and spring air temperature data are plotted as anomalies from the long-term (1971–2000) baseline.

Results

^{210}Pb dating

Background ^{210}Pb activities, estimated as the mean ^{214}Bi concentration from all dated samples, were reached at core depths of ~ 24 cm and ~ 15 cm in Wolfgang and Sam lakes, respectively (Figs. 2, 3). Neither lake followed an ideal exponential decline curve for ^{210}Pb. The dating profile for Wolfgang Lake (Fig. 2) showed a flattening of the ^{210}Pb activity curve from core depths of 8–20 cm, with a corresponding increase in inferred sedimentation rates. In Sam Lake (Fig. 3), the upper 3 cm of the sediment core showed variable ^{210}Pb activity, indicating possible physical or biological mixing near the sediment–water interface in this shallow lake (Appleby 2001). However, relatively well resolved peaks in the ^{137}Cs activity profiles from both cores provide independent support for the age-depth models, with ^{137}Cs peaks observed at inferred ages of ~ 1966 and 1969 for Wolfgang and Sam lakes, respectively.

Wolfgang Lake

Diatoms from both sediment cores were well preserved in all intervals counted with no obvious signs of silica dissolution or valve breakage. Prior to a marked taxonomic shift in the mid-1990s, diatom assemblages in Wolfgang Lake were dominated (up to 60%) by small benthic fragilarioid taxa (Fig. 4). Beginning in the mid-1990s, we recorded a concurrent increase in whole-lake primary production (approximated as chlorophyll *a* concentration) and diatom species diversity (Hill's N2), which included increases in relative abundances of several periphytic taxa (from the genera *Cymbella* (sensu lato), *Brachysira*, *Achnanthes* (sensu lato) and *Nitzschia*; Fig. 4). Based on CONISS and broken-stick analysis, the diatom species assemblage change in the mid-1990s (4 cm) was the only notable taxonomic change recorded throughout the sediment core.

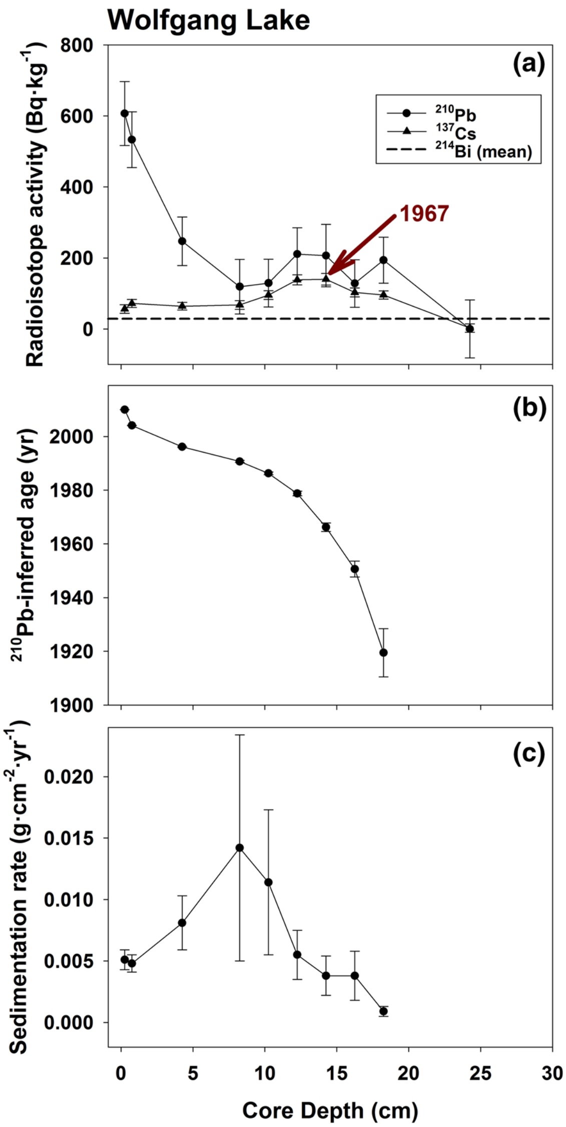

Fig. 2 Radiometric dating analysis of lake sediments from Wolfgang Lake showing **a** ^{210}Pb, ^{137}Cs activities (in Bq kg^{-1}), and the mean ^{214}Bi activity from all dated sections (dashed vertical line), plotted against core depth, **b** ^{210}Pb inferred year plotted against core depth, with dating errors associated with each dating interval, and **c** sedimentation rate (in g cm^{-2}year^{-1}) plotted against core depth, with estimated errors shown

In Wolfgang Lake, δ^{15}N and C/N records were stable throughout the duration of the sediment core (Fig. 6a). There was a gradual decline in %N in Wolfgang Lake, which began at a core depth of ~ 9 cm (ca. late 1980s).

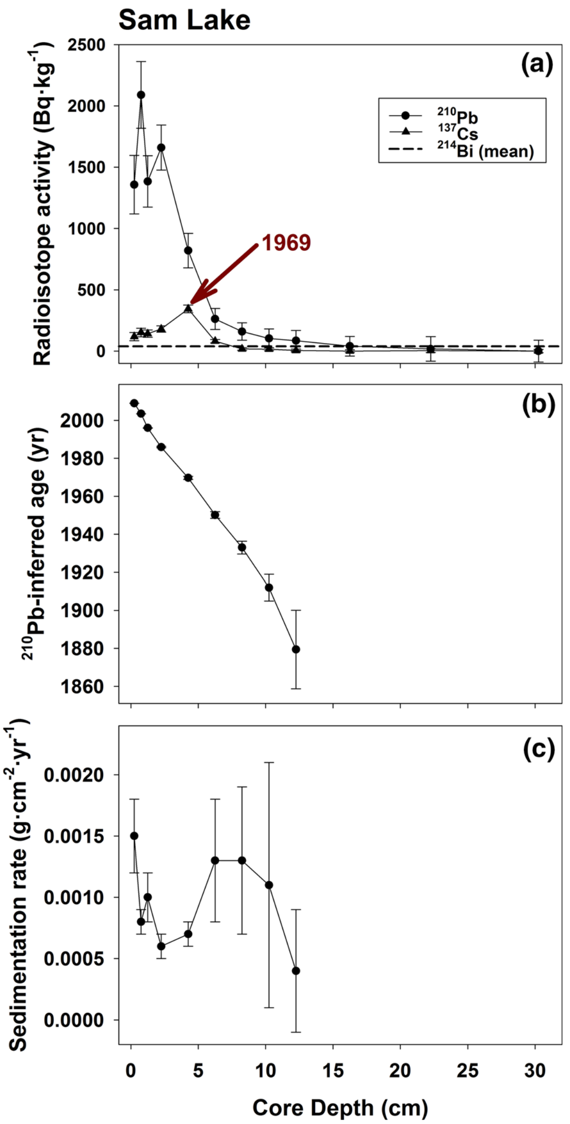

Fig. 3 Radiometric dating analysis of lake sediments from Sam Lake showing **a** ^{210}Pb, ^{137}Cs activities (in Bq kg^{-1}), and the mean ^{214}Bi activity from all dated sections (dashed vertical line), plotted against core depth, **b** ^{210}Pb inferred year plotted against core depth, with dating errors associated with each dating interval, and **c** sedimentation rate (in g cm^{-2}year^{-1}) plotted against core depth, with estimated errors shown

Sam Lake

Diatom species assemblage changes in Sam Lake were clear but muted relative to those described in Wolfgang Lake, with no apparent directional trend in species diversity (Fig. 5). The most pronounced taxonomic shift, as identified by CONISS, occurred at ~ 4 cm depth in the sediment core (early 1970s) and was characterized by a decline in the relative abundance of several *Navicula* (*sensu lato*) taxa [e.g., *Eolimna minima* (Grunow) Lange-Bertalot and *Sellaphora pupula* (Kützing) Mereschovsky] and contemporaneous increases in *Brachysira vitrea* (Grunow) R. Ross, *Encyonopsis falaisensis* (Grunow) Krammer and Lange-Bertalot, and several planktonic taxa [*Discostella stelligera* (Cleve and Grunow) Houk and Clee, *Asterionella formosa* Hassall, and *Fragilaria crotonensis* Kitton; Fig. 5]. Concurrent with the ca. 1970 shift in the diatom species assemblage, we documented an increase in whole-lake primary production. However, a marked decline in spectrally-inferred chlorophyll *a* concentration occurred ca. 1980 and persisted until the most recent sediment interval (ca. 2011), at which time chlorophyll *a* increased sharply (Fig. 3). This decline in chlorophyll *a* coincides with variable ^{210}Pb activity noted near the surface of the Sam Lake core.

In Sam Lake, geochemical changes occurred in both the pre-industrial sediments (at ~ 40 cm core depth), and then again in the recent sediments (Fig. 6b). In the pre-industrial sediments, these changes were characterized by a ~ 1.25 ‰ increase in δ^{15}N along with a concurrent decrease in sediment %N. Since ca. 1970, %N has increased and δ^{15}N decreased, returning to levels observed in pre-industrial sediments (at core depths of > 40 cm) (Fig. 6b).

Inter-lake comparisons and climate correlations

In Wolfgang Lake, we observed significant correlations between the mean annual air temperature anomaly (relative to a 1970–2000 baseline) and increases in primary production ($r = 0.66$, $p < 0.01$; Fig. 7a) and diatom species diversity ($r = 0.56$, $p = 0.01$; Fig. 7a). We also found significant correlations between diatom assemblage changes (i.e., PCA axis 1 scores) and the mean annual ($r = 0.66$, $p < 0.01$; Fig. 7a), mean fall ($r = 0.56$, $p < 0.01$), and mean winter ($r = 0.59$, $p < 0.01$) air temperature anomalies.

Similarly, we found significant correlations between the changes observed in the diatom species assemblage of Sam Lake and recent climate change metrics. Specifically, we noted a positive correlation between diatom PCA axis 1 sample scores and the mean spring air temperature anomaly at Churchill

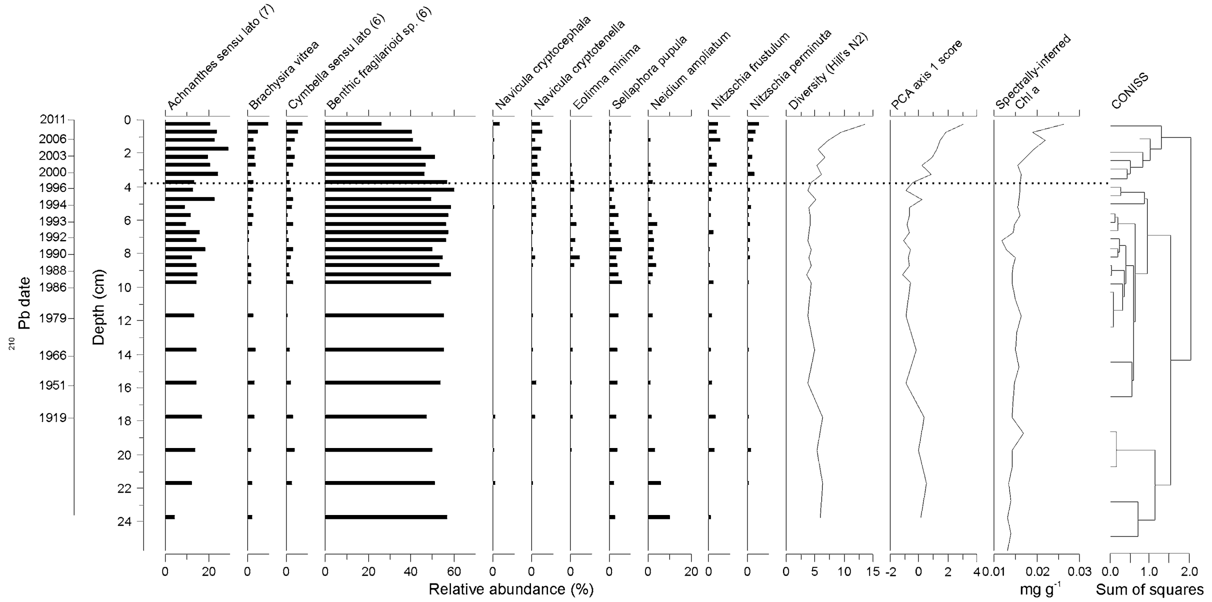

Fig. 4 Horizontal dashed line depicts zonation determined through constained incremental sum of squares (CONISS) and deemed important by broken stick analysis. Diversity (as Hill's N2), diatom species assemblage shifts (PCA axis 1 sample scores), and spectrally inferred chlorophyll *a* are also shown. The Benthic fragilarioid sp. category includes *Fragilaria capucina*, *F. capucina* var. *vaucheriae*, *Pseudostaurosira brevistriata*, *Staurosira construens* var. *venter*, *Staurosirella pinnata*, and *S. pinnata* var. *intercedens*. *Cymbella* sensu lato includes *Encyonema hebridicum*, *E. minutum*, *Encyonopsis cestaii*, *E. descripta*, *E. microcephala*, and *E. falaisensis*. *Achnanthes* sensu lato includes *Achnanthes saccula*, *Achnanthidium minutissimum*, *A. macrocephalum*, *A. rosenstockii*, *Encocconeis flexella*, *Psammothidium curtissimum*, and *Rossithidium petersenii*

(r = 0.68, $p < 0.01$, Fig. 7b). No significant correlations were observed between the biological metrics and annual or the other seasonal (summer, fall and winter) air temperature anomalies. However, an examination of the relationship between changes in planktonic diatom species and the mean spring air temperature anomaly revealed a significant correlation (r = 0.70, $p < 0.01$, Fig. 7b), as has been reported for deeper lakes in the HBL (Rühland et al. 2013; mean planktonic relative abundance versus mean annual air temperature anomaly).

Discussion

Changes in diatom assemblages

Our paleolimnological analyses provide evidence of biological and geochemical responses to recent warming in shallow sub-arctic lakes. However, consistent with previous studies (Smol and Douglas 2007a, b; Rühland et al. 2015), variability in the magnitude and nature of the proxy changes was related to site and catchment-specific differences between these two shallow lakes. In Wolfgang Lake we documented an increase in the complexity and diversity of benthic/littoral taxa in the modern sediments, characterized by higher relative abundances of a number of periphytic forms, that was temporally coherent (mid-1990s) with increases in mean annual air temperature. These taxonomic changes, from a simple benthic assemblage towards a diversified and complex benthic community, coincided with increased primary production (i.e., spectrally inferred chlorophyll *a*). Diatom assemblage changes observed in Wolfgang Lake were consistent, taxonomically and temporally, with floristic changes observed in other shallow lakes in the HBL (Rühland et al. 2014), and throughout the Arctic where climate warming has resulted in increased availability and variety of littoral habitat (Douglas et al. 1994; Smol et al. 2005; Smol and Douglas 2007a; Roberts et al. 2015; Rühland et al. 2015).

Clear changes in relative abundances of benthic taxa were observed in the upper sedimentary intervals

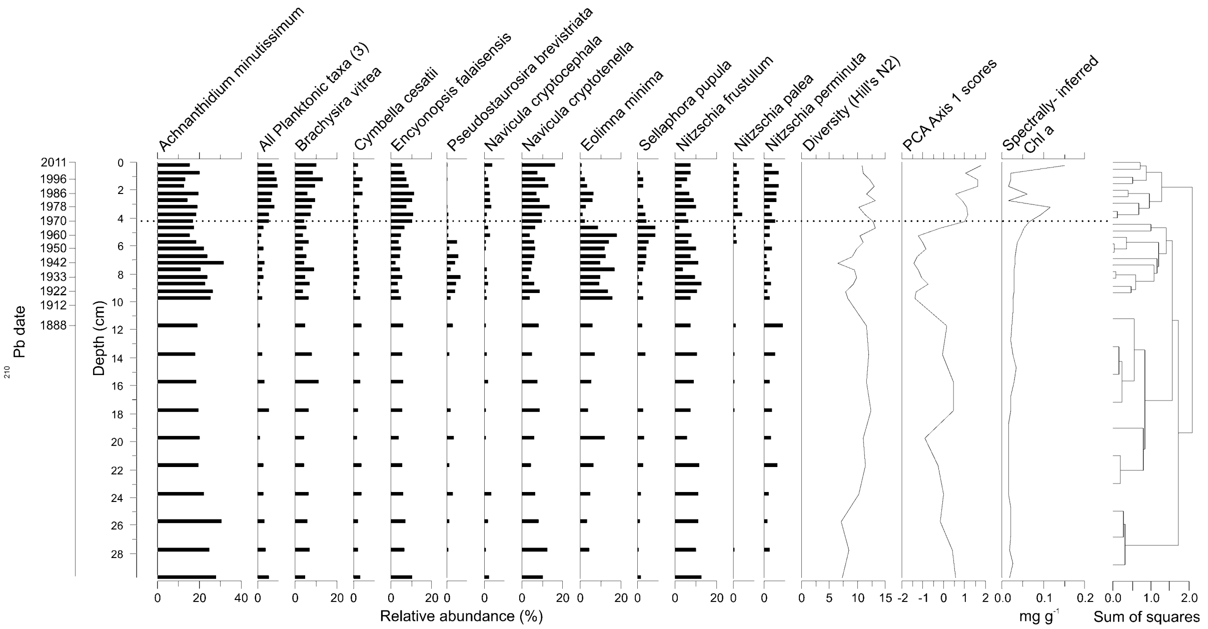

Fig. 5 Horizontal dashed line depicts zonation determined through constained incremental sum of squares (CONISS) and deemed important by broken stick analysis. Diversity (as Hill's N2), diatom species assemblage shifts (PCA axis 1 sample scores), and spectrally inferred chlorophyll *a* are also shown. The Planktonic taxa group included *Discostella stelligera*, *Asterionella formosa*, and *Fragilaria crotonensis*

of Sam Lake, with some similarity to the taxonomic changes recorded in Wolfgang Lake. For example, both lakes underwent an increase in relative abundance of several periphytic forms [e.g., *Cymbella* (sensu lato), *Nitzschia* and large *Navicula*, and *Brachysira* taxa]. These benthic diatoms are commonly found attached to a variety of substrates (mud, rocks, mosses and macrophytes). Concurrent with these increases, declines in species reported as epipelic/epilithic (e.g., *Eolimna minima*, *Sellaphora pupula*: Mann et al. 1999; Cho 2000) were observed in both lakes. With climate warming, reduced ice cover and a lengthening of the growing season may promote the establishment and expansion of aquatic mosses and plants (Smol 1988), thus facilitating the diversification and growth of the epiphytic taxa that we have documented here. Similar taxonomic changes have also been observed in the Canadian High Arctic (Smol et al. 2005; Smol and Douglas 2007a, b), in other shallow lakes in the HBL (Stuart, Billbear, Julison, and Cassie lakes; Rühland et al. 2014), and elsewhere (Roberts et al. 2015; Rühland et al. 2015).

Contemporaneous with benthic species changes, planktonic diatom taxa in Sam Lake doubled in relative abundance to $>5\%$, a change that was significantly correlated with trends in spring air temperature (Fig. 7b). Although this change was not observed in Wolfgang Lake, an increased importance of planktonic taxa in these polymictic, shallow systems is consistent with findings from other shallow lakes in the HBL. For example, Paterson et al. (2014) found evidence of blooms of planktonic algae in shallow HBL lakes when sampling phytoplankton during particularly warm temperatures in mid-summer, including relatively high biovolumes of the diatoms *Cyclotella* (sensu lato) and *Asterionella formosa*, and the presence of *Mallomonas*, a genus of unicellular, planktonic chrysophytes (Siver 1991). Likewise, a recent "top–bottom" paleolimnological survey of lakes in this HBL region, which included Sam and Wolfgang lakes, found higher relative abundances of several planktonic taxa in the modern sediments of all lakes studied including nine shallow lakes (Rühland et al. 2014). In the "Ring of Fire" region, $\sim$ 250 km farther south but still within the HBL, Hargan et al. (2016) also reported the first arrival and increase in the relative abundances of planktonic diatoms during the past few decades in two shallow lakes ($Z_{\max} \sim 2$ m), that were attributed to recent warming. Thus, while benthic taxa clearly dominate

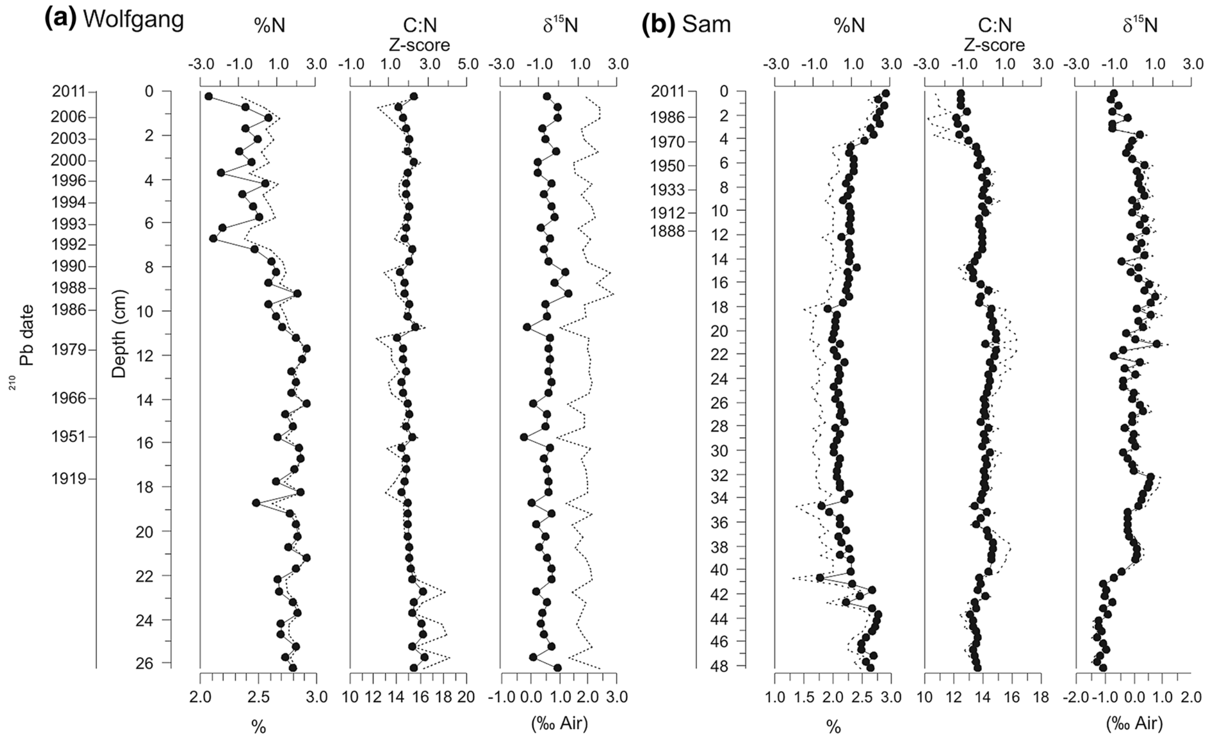

Fig. 6 Results of sedimentary elemental and isotope analysis (%N, C:N and δ^{15}N) from **a** Wolfgang Lake and **b** Sam Lake presented as stratigraphic profiles against both sediment depth and age (based on ^{210}Pb dating). Data are summarized as both measured values (black circles and solid lines) and standardized scores (dotted lines)

the diatom assemblages of shallow lakes in the HBL, widespread increases in the relative importance of planktonic taxa are now being reported in many lakes, indicating these changes are ecologically important. As reported elsewhere (Taranu et al. 2012), it is possible that these polymictic systems stratify for short periods of time (hours to days) during warm periods, allowing for the rapid proliferation of planktonic taxa.

Changes in geochemistry

Similar diatom responses to those we have documented in Sam Lake (i.e., the increased relative abundance of cyclotelloid and pennate planktonic taxa) have been attributed to the long-range transport and deposition of anthropogenic contaminants in some lakes (Wolfe et al. 2003, 2006). For example, in two ponds on Baffin Island, Wolfe et al. (2006) partially attributed diatom species changes to ^{15}N depletion and increased %N. They suggested that these isotopic signatures were indicative of nutrient enrichment from atmospheric nitrogen deposition, which has increased globally by as much as 10% annually in the 20th century as a result of fertilizer production, cultivation of nitrogen-fixing legumes, and the release of nitrogen oxides associated with the burning of fossil fuels (Sheldrick 1987; Matthews 1994). However, global assessments by Vet et al. (2014) indicate that atmospheric nitrogen deposition in the HBL region is very low, and geochemical data from the Sam and Wolfgang Lake sediment cores offer little evidence that atmospheric nitrogen deposition is responsible for the diatom changes we document here (Fig. 4). In Wolfgang Lake, where notable changes in diatom assemblages have occurred since the mid-1990s, we document no directional change in δ^{15}N or C/N ratio. Furthermore, rather than an increase in %N that would be expected with increased inputs from deposition, we observed a decline since the mid-1990s (Fig. 3a). In Sam Lake, the geochemical changes throughout the core are subtle with current values falling within the range of long-term variability recorded in the sediment core, and representing a return to pre-industrial levels

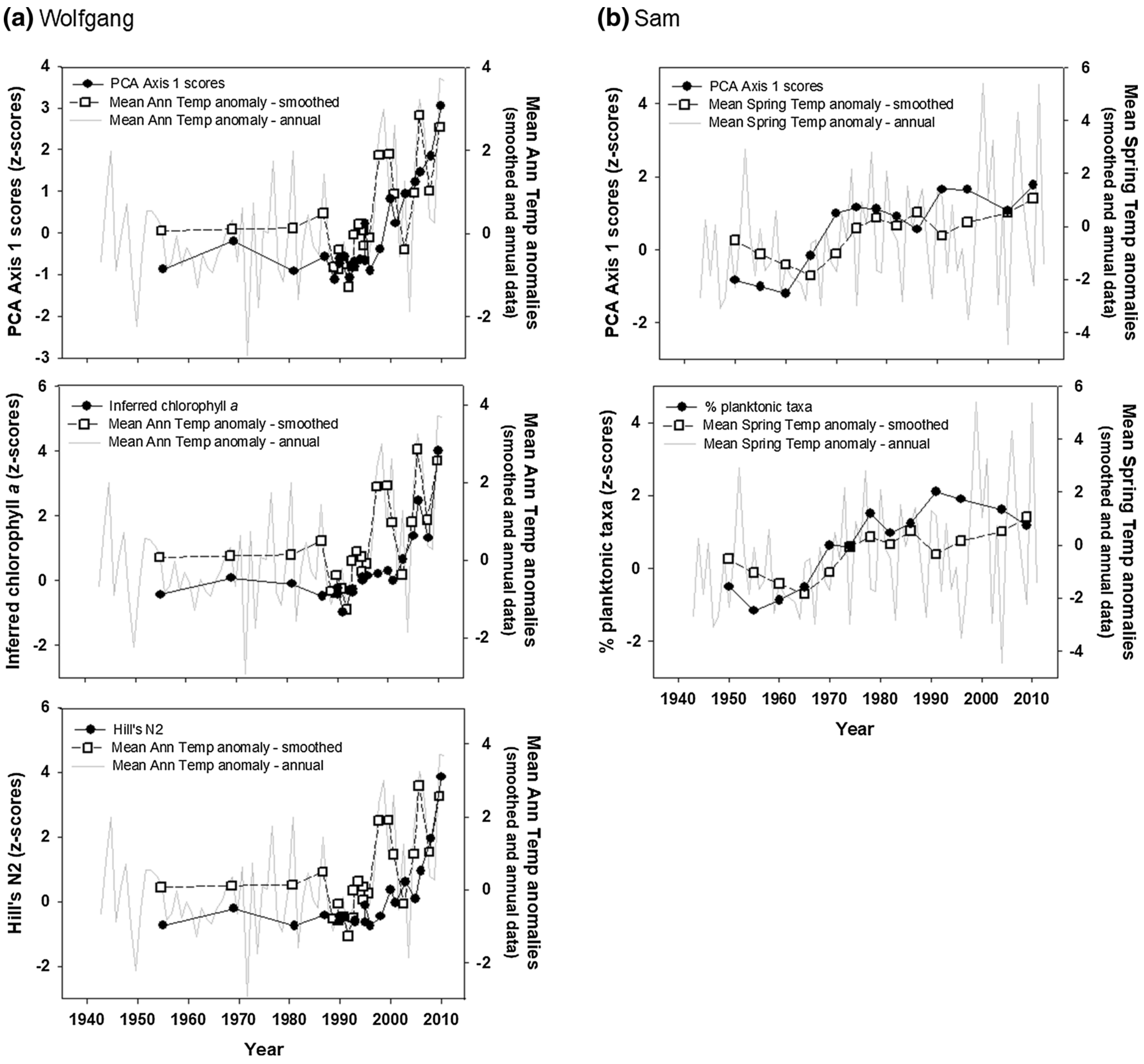

Fig. 7 **a** Trends in diatom assemblage composition (PCA axis 1 scores), primary production (inferred chlorophyll *a*, standardized as z-scores) and species diversity (Hills N2, standardized as z-scores) from Wolfgang Lake, plotted against mean annual temperature anomalies. Temperature anomalies are presented as both adjusted (open squares) and annual (solid grey line) data. **b** Trends in diatom assemblage composition (PCA Axis 1 scores), and % planktonic taxa (standardized as z-scores) from Sam Lake, plotted against mean spring temperature anomalies. Temperature anomalies are presented as both adjusted (open squares) and annual (solid grey line) data. Mean annual and mean spring air temperature anomalies were calculated relative to a 1971–2000 baseline, using data from the Churchill (Manitoba) climate station from 1953 to 2011

(Fig. 3b). Furthermore, nitrogen isotope changes in Sam Lake (ca. 1970) post-date the timing expected under an atmospheric deposition scenario.

With minimal supporting data in this remote region, it would be speculative to comment on the specific reasons for the differing geochemical signals over time in the study lakes, although it is worth noting that the timing of these changes correlates well with diatom assemblage changes, suggesting a common driver. As described below, a number of factors may have contributed to differences in the observed geochemical signals, including differences in the organic matter supply related to variations in catchment vegetation and permafrost extent (Wolfe et al. 1999; Talbot 2001). Furthermore, lake-specific differences in hydrological connectivity may have contributed to variability in the delivery of organic matter, and to the relative importance of precipitation in the lakes' water and nutrient budgets (Wolfe et al. 2011).

Variability in shallow lakes: local factors moderate biological and geochemical responses to warming

Diatom species assemblage changes in Sam Lake predated those observed in Wolfgang Lake by approximately two decades. The shift to an assemblage characterized by more planktonic taxa was comparable to changes reported for deeper lakes of the Sutton River region of the HBL, where temperature anomalies (both annual and seasonal) were significantly correlated to increased relative abundances of planktonic taxa, increased species diversity (Hill's N2) and increased primary production (i.e., chlorophyll *a* concentration) (Rühland et al. 2013). Similar increases in planktonic taxa have also been noted in shallow lakes in the Ring of Fire, where the first records of planktonic species in McFaulds Lake and Symons lakes were recorded in the 1900s and the 1960s, respectively (Hargan et al. 2016). Temporal variation in the response of planktonic taxa in Wolfgang, Sam and other northern Ontario lakes suggest that local scale factors such as morphology, permafrost dynamics and hydrological connectivity likely mediate threshold responses to climate in these systems, and in shallow lakes in general.

For example, important morphometric differences exist between Sam and Wolfgang lakes. Wolfgang Lake is substantially larger than Sam Lake in both surface area (157 ha vs. 32 ha) and fetch (approx. 1.6 km vs. 0.6 km). These properties may significantly influence the thermal regimes of lakes, altering the strength and duration of thermal stratification (Gorham 1964; Timms 1975; Hanna 1990; Rühland et al. 2015). As noted above, it is possible that the smaller Sam Lake may be more thermally stable for longer periods in the summer as a result of its smaller fetch. This may account for the differences we observe in the nature (i.e., the presence of planktonic taxa in Sam Lake) and earlier timing of the diatom species assemblage changes.

In addition, previous research has also shown that the degree of permafrost development (continuous versus discontinuous) may influence the water chemistry of lakes in the HBL region (Paterson et al. 2014) that, in turn, may have contributed to differences in diatom assemblage changes and geochemistry in Sam and Wolfgang lakes. These lakes reside very near the boundary between continuous and discontinuous permafrost and thus it is possible that recent climate change has altered permafrost conditions at a local scale. For example, it is well documented that the presence or absence of permafrost affects the infiltration of surface water and groundwater flow (MacLean et al. 1999; Carey 2003; Kawahigashi et al. 2004; Jones et al. 2005; O'Donnell and Jones 2006), and may result in the release of previously bound nutrients (Vincent et al. 2013); however, given the lack of ground-truthed data for our isolated lakes, we can only speculate on possible differences in their hydrological connectivity and permafrost dynamics within their surrounding catchments.

Climate and hydrological connectivity

As well as direct and indirect impacts on physical and chemical properties of lakes, climate warming may also alter the hydrology of sub-arctic freshwater systems. For example, changes in hydrological connectivity attributed to thawing permafrost and increased surface water-groundwater interaction likely contributed to divergent hydrological responses to recent warming in four HBL ponds near Churchill (Wolfe et al. 2011). Limnological characteristics of ponds in this region are likewise influenced by climatic and hydrological conditions (Bos and Pellatt 2012; White et al. 2014).

Visual inspection (Google Earth®; 2005 image) may further illustrate potential variability in limnological responses associated with hydrological connectivity. By constructing a simple schematic of water bodies around Sam and Wolfgang lakes, Sam Lake appears to currently be relatively isolated, while Wolfgang Lake is surrounded by several shallow water bodies within 250 m of its shoreline (Fig. 8). Thus, we speculate that some of these small ponds may become hydrologically connected to Wolfgang Lake during the ice-free season. In the northwestern HBL, hydrological connectivity in ponds, both temporary and permanent, has been shown to result in higher suspended sediment and total nitrogen concentrations, while lakes without connectivity generally show rising alkalinity and ionic content as evaporative concentration dominates the lake water balance

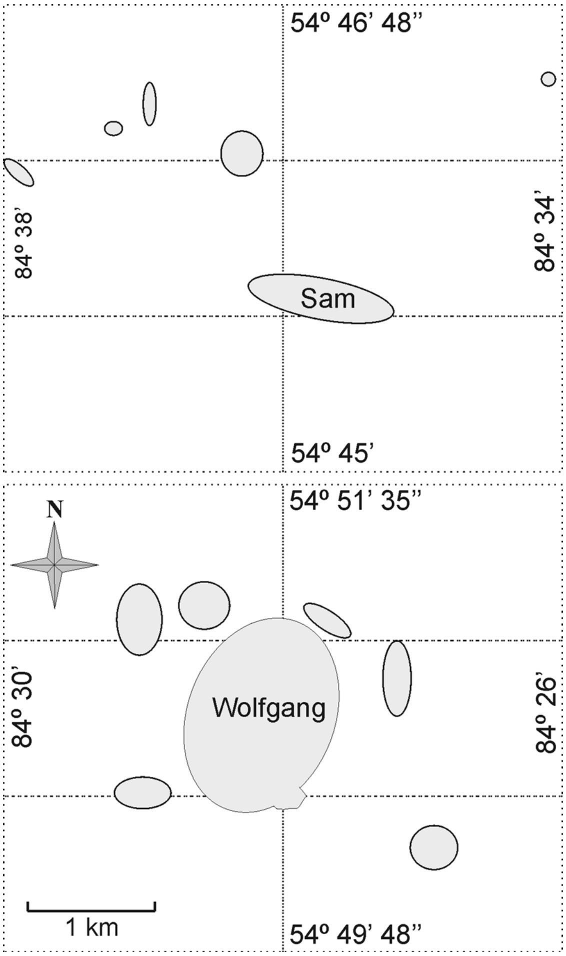

Fig. 8 Schematic diagram of Sam and Wolfgang lakes, showing the surrounding water bodies. The image is transcribed from a 2005 Google Earth™ image

(White et al. 2014). While it is not possible to determine the extent of hydrological connectivity in our study lakes with the information available, water chemistry data record higher nutrient concentrations in Wolfgang Lake, consistent with connectivity. Similarly, higher conductivity in Sam Lake (despite being 10 km farther inland from Hudson Bay) is consistent with potential evaporative concentration associated with its relative isolation (Table 1). A significant correlation between diatom species assemblage shifts (as PCA axis 1 scores) and spring precipitation in Sam Lake ($r = -0.65$, $p = 0.02$), which were not present in Wolfgang Lake, also suggests that it has responded to historical fluctuations in precipitation and may be less influenced by groundwater inputs. Furthermore, Wolfgang Lake has a much higher sediment deposition rate than Sam Lake based on ^{210}Pb dating, supporting the notion of increased hydrological inputs.

Conclusions

Evidence provided by recent limnological and paleolimnological surveys of the HBL suggests that relatively deep lakes in this region have been altered by 20th century climate warming (Paterson et al. 2014; Rühland et al. 2013, 2014). We have presented detailed paleolimnological and geochemical results for two shallow sub-arctic lakes in the Sutton River region of the HBL. In both lakes we record abrupt, albeit subtle, shifts among benthic diatom taxa from assemblages predominantly associated with sediments to more diverse assemblages that include an increased abundance of epiphytic diatoms. In Wolfgang Lake, we recorded increases in whole-lake production and diatom diversity, changes that are consistent with a longer-ice free period and longer growing season. Unlike Wolfgang Lake, Sam Lake registered an increase in planktonic diatoms in the upper sediments that is similar to changes recorded in deeper lakes of this region (Rühland et al. 2013). The timing of limnological change in Wolfgang Lake supports other regional evidence (Rühland et al. 2014) that warming during the past ~ 20 years has led to notable biological responses in these aquatic systems. The timing of the limnological changes in Sam Lake pre-dates perturbations in mean annual temperature by ~ 20 years and suggests that a more complex mechanism, and seasonal warming, may be important. We speculate that differences in hydrological connectivity and permafrost dynamics, in part influenced by climate change, combined with differences in lake morphometry, likely contributed to the observed differences.

The paleolimnological examination of only two shallow lakes in the Sutton River region limits our ability to make broad statements about regional limnological change in the HBL, particularly given the temporal variability in the responses we have documented. Nevertheless, it is clear that the biological and geochemical responses to warming in shallow lakes may vary because of differences in local, catchment-scale factors, including permafrost extent and vegetation (Shinneman et al. 2016). This is true of lakes located in the same geographic region and experiencing similar climatic forcing, emphasizing the need to understand the local context when interpreting long-term trends.

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