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Changes in diatom assemblages since pre-industrial times in 40 reference lakes from the Experimental Lakes Area (northwestern Ontario, Canada)

Mihaela D. Enache · Andrew M. Paterson · Brian F. Cumming

Abstract Diatom assemblages in recent versus pre-industrial sediments were examined in 40 relatively undisturbed lakes from the Experimental Lakes Area (ELA). The ELA region of northwestern Ontario receives low amounts of acidic deposition and the lakes have been minimally disturbed by watershed development or other human activities. Consequently, this region represents an important location to detect possible changes in lakes due to climate change. In over half of the lakes, planktonic taxa (especially *Discostella stelligera*) increased between 10 and 40% since pre-industrial times. Changes in diatom assemblages are consistent with taxa that would benefit from enhanced stratification and a longer ice-free season. We hypothesized that there should be a relationship between stratification and measured chemical and physical characteristics of the study lakes. Multiple correlation analysis was undertaken to see the relationship between planktonic taxa and *D. stelligera* since pre-industrial times and the physical and chemical characteristics of the study lakes. Lake depth was consistently identified as an important variable. The timing of the increase in planktonic taxa within cores from these lakes will be needed to rule out other possible regional changes that may also be occurring in the ELA region.

Keywords Diatoms · Climate · Lake · Experimental Lakes Area · Paleolimnology · Reference lakes

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Introduction

Changes in climatic conditions can have important and complex effects on lacustrine ecosystems (Smol and Cumming 2000). Climate is an important factor driving changes in physico-chemical properties of lake water such as water temperature and transparency (Blenkner et al. 2007), pH, nutrient cycling, which in turn may affect lake biota (Schindler et al. 1990; Snucins and Gunn 2000; Winder and Schindler 2004). For example, shifts in diatom species have been attributed to recent climatic warming in arctic (Smol and Douglas 2007), subarctic (Sorvari et al. 2002; Rühland et al. 2003), alpine (Karst-Riddoch

et al. 2005), and temperate regions (Harris et al. 2006; Rühland et al. 2008). The lake-specific response of ecosystems to climatic forcing, including the degree of ecological change that occurs, is complex and may be modulated by differences in seasonality and/or related changes in thermal structure and mixing regimes (Gerten and Adrian 2001). Furthermore, changes related to human disturbance, such as alterations to lake-water pH and nutrient concentrations complicate our ability to isolate the relative importance of individual stressors on lake ecology.

In part, the complication of having to disentangle multiple environmental stressors may be overcome by studying comparatively undisturbed lakes in relatively remote regions (Rühland et al. 2008). For example, reference lakes in the Experimental Lakes Area (ELA) of northwestern Ontario, Canada have received minimal impact from human activities (Findlay and Shearer 1992). Most of these lakes are oligotrophic and circumneutral, and their physical, chemical, and biological processes, including nutrient cycling and primary production are very sensitive to climatic change (Xenopoulos and Schindler 2001). For example, the ELA reference lakes experienced an increase in lake temperature during the warmer and drier decades of the late-1970s and 1980s (Schindler et al. 1996; Fee et al. 1996; Xenopoulos and Schindler 2001). Warmer and drier conditions can result in limnological changes that include: enhanced water clarity, deeper thermoclines (Schindler et al. 1990, 1996), increased lake stability (Findlay et al. 2001; Winder and Schindler 2004), and changes in nutrient levels (Magnuson et al. 1997) and hypolimnetic dissolved oxygen concentrations (Blumberg and Di Toro 1990). Moreover, measurable changes occurred in lake biota at ELA, including an increase in algal biomass and number of phytoplankton species, with greater abundances of dinoflagellates and large chrysophytes (Findlay et al. 2001).

Sedimentary diatom assemblages from climate-sensitive lakes can provide an extended temporal record of environmental conditions, including changes related to variations in climate (Smol and Cumming 2000). Variations in temperature and precipitation may result in changes in lake depth, mixing regimes, salinity and nutrients, which can influence the specific composition and abundance of diatom assemblages (Bradbury et al. 2002; Fritz et al. 2010). Indeed, changes in diatom assemblages have been attributed to recent climatic warming in subarctic and alpine lakes (Sorvari et al. 2002; Rühland et al. 2003; Karst-Riddoch et al. 2005), and temperate regions (Forrest et al. 2002; Harris et al. 2006). In relatively undisturbed lakes, increases of at least 5% in planktonic *Cyclotella* taxa were present in 84 of 105 lakes, concurrent with declines in thickly silicified *Aulacoseira* and/or benthic *Fragilaria* taxa (Rühland et al. 2008).

An examination of diatom assemblages in recent versus pre-European settlement times from sediment cores (known as the 'top–bottom paleolimnological approach'; Cumming et al. 1992) can provide a rapid assessment of regional environmental change in aquatic ecosystems (Smol 2008). Diatoms present in the uppermost lake sediments (top sample, 0–0.25⁻cm of sediment cores) represent present-day conditions, while diatoms preserved in deeper sediments (generally > 20 cm in Canadian Shield lakes) represent pre-industrial times, and can be considered to be a measure of natural lake conditions (Cumming et al. 1992; Rühland et al. 2003; Smol 2008).

The primary goal of this study is to determine if and how the relative abundance of diatom species have changed from pre-industrial to modern times in relatively undisturbed lakes from the ELA. In most temperate freshwater ecosystems, climate-related changes may be masked by direct anthropogenic stressors, such as eutrophication and acidic deposition. Lakes located in remote regions, such as the ELA from northern Ontario, have been minimally impacted by such anthropogenic stressors (Findlay and Shearer 1992) and can be considered "reference sites" (Schindler et al. 1996; Findlay et al. 2001). Such lakes should be useful in simplifying the number of anthropogenic stressors impacting lakes, and maximize the importance of climate and/or other potential regional stressors on diatom communities. We hypothesize that 'reference' lakes from the ELA should display changes in diatom assemblages that are similar to those observed in the meta-analysis of relatively undisturbed sites examined by Rühland et al. (2008) (i.e., an increase in planktonic diatoms, particularly small *Cyclotella* species). Although Rühland et al. (2008) examined dated cores from 105 'relatively' undisturbed lakes, small to medium-sized lakes from north-western Ontario and the ELA were poorly represented. A secondary goal of this paper was to determine if the physio-chemical

characteristics of ELA lakes can be used to predict change in diatom assemblages since pre-industrial times. If recent warming is an important causal mechanism for the observed changes in diatom assemblages, we hypothesize that deeper lakes (i.e., lakes that are more prone to exhibit thermal stratification), should display a stronger impact from recent increases in temperature (*sensu* Gerten and Adrian 2001), as these lakes should show larger changes in heat storage capacity, water column stability, and variation in the strength and period of mixing with climatic warming in comparison to shallower lakes.

Study area and sampling

The 40 study lakes are located within the Experimental Lakes Area (ELA), northwestern Ontario (Fig. 1). The area is situated on the Canadian Shield

with the bedrock constituted from Precambrian granites and gneisses (Findlay and Shearer 1992). The lakes ranged from 2 to 30 m in maximum depth and their watersheds consist of thin, poorly developed soils that are dominated by *Picea mariana* (black spruce) and *Pinus banksiana* (jack pine) forests. Duplicate sediment cores were sampled from all 40 lakes in June, 2006. Sediment cores were retrieved from the deepest basin of the lakes using a Glew corer (internal diameter 7.62 cm) ensuring that the sediment–water interface was preserved (Glew et al. 2001). Sediment samples from the top (0–0.25 cm, representing sediments recently accumulated or modern samples) and from the bottom of each core (20–20.25 cm, representing pre-industrial sediments) were analyzed to allow comparisons between modern and pre-industrial diatom species composition. The advantage of the so called 'top–bottom' approach is that it allows the investigator to quickly determine if

Fig. 1 Map showing the location of the ELA study lakes (study lakes are in *bold*)
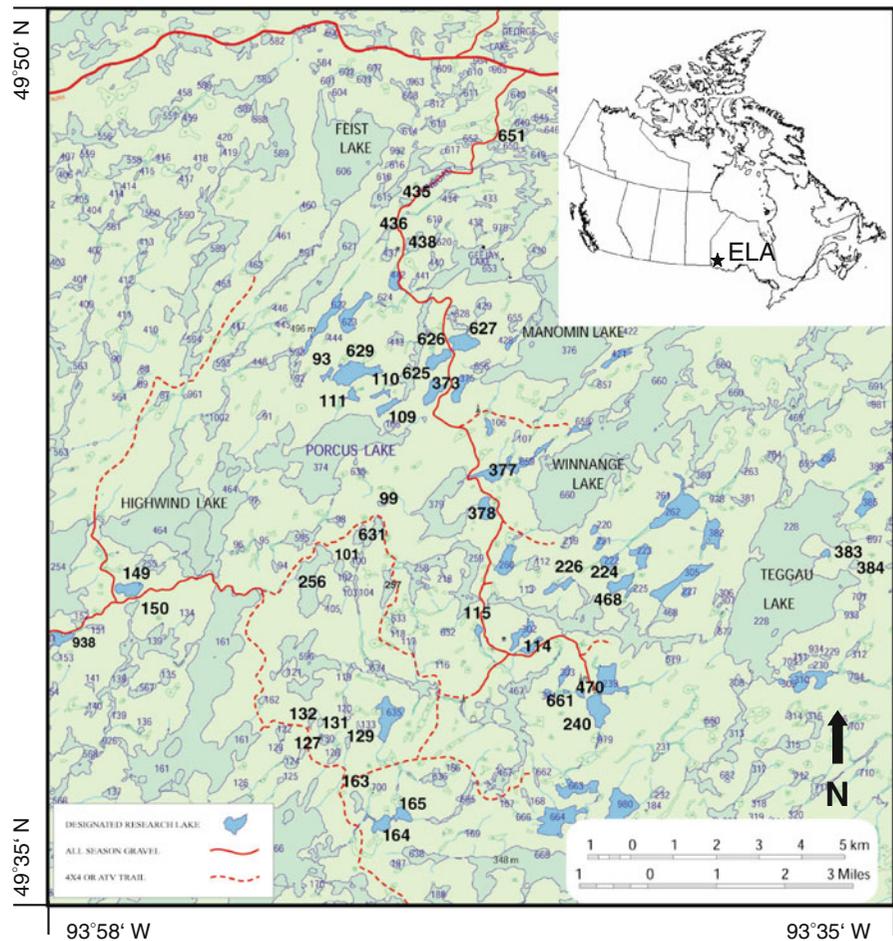
consistent ecological changes have occurred across a region, which would be worthy of more detailed analyses. However, because the 'top' and 'bottom' sediment intervals vary slightly in the amount of time they represent (e.g., the 'bottom' sample will typically represent more time than a similarly sized interval from the top), it is possible that a change could emerge that is due to temporal differences between 'top' and 'bottom' samples. However, in practice, results from the 'top–bottom' approach have been verified by complete core analyses (Cumming et al. 1992, 1994; Ginn et al. 2007a, b). Although the specific dates of individual bottom sediment samples from the 40 lakes were not dated, full-core ^{210}Pb profiles from 17 lakes from ELA show that supported ^{210}Pb activity is reached at core depths of ∼20 cm (mean and median = 20 cm; SD = 6; n = 17) (Cumming et al. Department of Biology, Queen's University, Kingston, ON, unpublished data). Based on these results and the relatively high unsupported ^{210}Pb in these cores, we are confident that a depth of 20 cm represents pre-industrial conditions in the majority of the study lakes. As mentioned above, the length of time represented by a sediment interval can also be important. Based on cores collected to date from northwestern Ontario, typically the 0.25-cm interval would represent between 1 and 2 years, whereas a sample between 20 and 20.25 cm would represent between 1 and 5 years. These results are similar to ^{210}Pb dating results from many published studies of cores taken from lakes on the southern Canadian Shield (Mills et al. 2009) and in northwestern Ontario (Paterson et al. 2002), including Lake 239 from the Experimental Lakes Area (Laird and Cumming 2008).

Methods

Water chemistry

Water samples were collected from 35 of the 40 study lakes and analyzed at the Ontario Ministry of the Environment's Dorset Environmental Science Centre using standard MOE protocols (Ontario Ministry of the Environment 1983). The five lakes not sampled for water chemistry are sampled regularly by ELA staff as reference lakes, and consequently spot samples from these systems were deemed unnecessary at the time. Chemical analyses included concentrations of chloride, sulphate, sodium, potassium, magnesium, calcium, NH_4/NH_3, NO_2/NO_3, total Kjeldahl nitrogen (TKN), total phosphorus (TP), dissolved organic carbon (DOC), reactive silicate (SiO_3), specific conductivity, and true colour. Lake-water pH was measured in the field using a Fisher-Accumet pH meter (model 925). Of the study lakes, ELA lakes 110, 114, and 226 have been experimentally manipulated. In 1993, northern pike were introduced to Lake 110. Lake 114 was manipulated for epilimnetic acidification (1979–1986), including the addition of aluminum in 1984. Experiments conducted in Lake 226 include epilimnetic fertilization from 1973 to 1980, epilimnetic addition of radioisotope tracers (1977–1978; 1989) and metals (1987), and the lowering of water levels from 1995 to 1997. The watersheds of the study lakes have been minimally impacted by recent human disturbances, but in the past (between 1970 and 1980), some of the watersheds were partially logged (ELA lakes: 114, 115, 149, 164, 165, 373, 377, 378, 626, 627, 629, and 938), and some have experienced fires. Low-impact bait fishing and angling has likely occurred in many of the study lakes, as these activities are restricted but not monitored closely.

Diatom preparation and enumeration

Slides for diatom analysis were prepared using standard techniques (Cumming et al. 1992) for the top (0–0.25 cm) and the 20–20.25-cm sediment intervals. A small amount of wet sediment was suspended in a 50:50 (molar) mixture of sulfuric and nitric acid in a 20-ml glass vial for 24 h prior to being submersed in a 70°C water bath for approximately 5 h. The remaining sedimentary material was settled for a period of 24 h, at which time the acid above the sample was removed. The sample was rinsed with distilled water and allowed to settle once again for 24 h. The rinsing with distilled water was repeated approximately 8 times until the sample was neutral (litmus test). The samples were settled onto coverslips in a series of four 100% dilutions, which when dry, were mounted onto glass slides using Naphrax®, a high-resolution mounting medium. For each sample, at least 400 diatom valves were enumerated with a Leica DMRB microscope equipped with DIC optics at 1000× magnification (Numerical Aperature of oil

objective and condenser top lens = 1.3 and 1.4, respectively). The diatom taxonomy was based on the references of Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Camburn and Charles (2000), Cumming et al. (1995) and Tanaka (2007). Resting cysts of diatoms were not often encountered and consequently not enumerated.

Statistical analyses

To determine the main directions of variation in the water chemistry and physical variables within the ELA study sites, a principal component analysis (PCA), using inter-sample distances on a correlation matrix of log-transformed values, was run using the computer program CANOCO v. 4.5 (ter Braak and Šmilauer 1998).

Diatom species counts for the 'top' and 'bottom' samples were converted to relative abundance measures for each lake, and changes in the relative abundance of diatom taxa that achieved >5% relative abundance were examined. To summarize the main direction of variation in the diatom assemblages of the study lakes, a correspondence analysis (CA) with downweighting of rare taxa was performed using CANOCO v. 4.5 for each of the modern and preindustrial diatom assemblages. For summary purposes, diatom taxa were also grouped into functional groups (planktonic, tychoplanktonic and benthic taxa) based on the literature (Krammer and Lange-Bertalot 1986, 1988, 1991a, b). To assess if significant differences in dominant diatom taxa and functional groups existed between all modern versus all pre-industrial samples, ANOVAs and paired t-tests were used.

Multiple correlations with Bonferoni correction were performed to assess if: (1) changes in planktonic diatom species; and (2) changes in the dominant species *D. stelligera* could be related to the measured limnological variables, or the environmental PCA axis scores of the environmental data. As mentioned previously, the goal of these analyses was to determine if biological changes were related to a unique combination of limnological variables, that could then give insight into possible mechanism for the observed changes (i.e., are the changes larger in lakes that would be more susceptible to lake stratification). Six lakes were eliminated from the PCA and correlation analyses. These lakes included lakes that

lacked adequate information on maximum depth (Lake 224, Lake 631 and Lake 651), and/or lakes that were experimentally manipulated (Lake 110, Lake 114, and Lake 226). Experimentally manipulated lakes were also excluded from ANOVAs, because diatom species may reflect changes related to lake recovery after manipulation rather than to natural conditions. ANOVAs, t-tests, and multiple correlations were performed using the program JMP v. 7.0 (SAS Institute Inc.).

Results

Physical and chemical characteristics of study lakes

The study lakes from north-western Ontario (Fig. 1) can be broadly characterized as small (mean depth = 9.3 m; median depth = 8 m; range = 2–30 m), low-conductivity (mean specific conductivity = 18.5 μS/cm; median = 16.4 μS/cm; range = 11–42 μS/cm), low-alkalinity (mean = 5 mg/L, median = 4.5 mg/L; range = 1.5–11.3 mg/L), acidic-to-circumneutral (mean pH = 6.7; median pH = 6.7; range = 5.4–7.2) oligotrophic (mean total phosphorus = 6.9 μg/L; median = 5.1 μg/L, range = ~1–21 μg/L) lakes with moderate to high concentrations of DOC (mean DOC = 7.3 mg/L; median DOC = 6.9 mg/L; DOC range = 3–15 mg/L) (Table 1). A PCA of the water chemistry was used to identify the largest limnological gradients in this dataset. The first two axes explained 78% of the variance in the study lakes, with lake-water pH and DOC being the most important variables contributing to the first axis. Lake depth, nutrients (TP and TKN), and specific conductivity contributed equally to define the first and second axes (Fig. 2). Generally, higher-pH lakes (e.g., lakes 435, 373 and 163) had lower concentrations of DOC, whereas lower-DOC lakes were more acidic (e.g., lakes 661, 470, 115, 131; Fig. 3). Similarly, nutrients were inversely correlated to lake depth (Fig. 2).

Diatom assemblages

From the 40 study lakes, 271 diatom species were identified from both 'top' and 'bottom' sediment samples. Most of the species were rare and consisted of less than 1% of the total relative abundance of

Table 1 Physical and chemical variables from the study lakes

Lake	Chloride (mg L⁻¹)	Sulphate (mg L⁻¹)	Sodium (mg L⁻¹)	Potassium (mg L⁻¹)	Magnesium (mg L⁻¹)	Calcium (mg L⁻¹)	TP (µg L⁻¹)	NH₄/NH₃ (µg L⁻¹)	NO₃/NO₂ (µg L⁻¹)	TKN (µg L⁻¹)	SiO₃ (mg/L)	DOC (mg/L)	True colour (TCU)	Alkalinity (mg L⁻¹)	pH	Conductivity (µS cm⁻¹)	Depth (m)
ELA 101	0.16	1.60	0.69	0.40	0.53	1.62	18.60	34.00	8.00	573.00	0.72	5.90	12.80	4.97	6.48	16.40	3
ELA 109	0.20	1.35	0.66	0.38	0.57	1.70	3.10	30.00	42.00	295.00	0.36	5.50	6.20	4.91	7.01	16.40	10
ELA 110	0.13	1.35	0.53	0.31	0.46	1.10	2.00	30.00	16.00	323.00	0.42	6.20	12.40	2.56	6.56	11.60	11
ELA 111	0.18	2.05	0.63	0.35	0.59	1.52	0.70	24.00	4.00	253.00	0.86	7.00	18.60	3.16	6.76	15.40	30
ELA 115	0.15	1.80	1.08	0.35	0.54	1.22	15.30	42.00	10.00	627.00	0.46	11.30	58.80	2.94	6.11	15.80	4
ELA 127	0.19	2.50	0.68	0.24	0.37	0.90	9.10	24.00	2.00	430.00	0.22	5.70	13.00	1.82	6.30	11.80	5
ELA 129	0.14	1.55	0.86	0.26	0.57	1.34	8.30	24.00	2.00	465.00	0.32	9.60	41.60	3.47	6.52	14.80	6
ELA 131	0.13	2.05	0.55	0.26	0.37	0.86	21.30	40.00	2.00	470.00	0.10	6.80	16.00	1.47	6.14	10.60	2
ELA 132	0.22	1.80	0.61	0.33	0.35	1.30	7.30	30.00	4.00	348.00	0.10	5.20	9.40	2.54	6.44	13.00	8
ELA 149	0.30	1.95	1.29	0.45	0.79	2.52	13.00	52.00	12.00	700.00	0.46	8.00	18.40	8.32	7.02	25.60	4
ELA 150	0.31	1.90	1.42	0.44	0.91	3.38	7.80	24.00	2.00	830.00	0.70	8.10	27.00	11.30	7.12	31.00	2
ELA 163	0.18	1.70	1.00	0.36	0.79	2.76	4.40	12.00	2.00	258.00	0.18	4.50	6.40	9.96	7.12	25.60	8
ELA 164	0.18	1.75	0.85	0.31	0.59	1.76	5.10	22.00	2.00	334.00	1.02	8.80	45.40	4.50	6.71	17.00	7
ELA 165	0.21	1.70	0.84	0.29	0.61	1.86	7.40	24.00	2.00	391.00	1.06	9.30	57.00	4.82	6.64	17.40	5
ELA 240	0.24	2.25	0.95	0.41	0.69	2.28	3.60	18.00	2.00	299.00	1.38	6.40	15.20	6.41	6.90	21.80	11
ELA 256	0.27	2.60	0.87	0.44	0.61	2.36	4.40	20.00	4.00	237.00	0.16	3.30	2.00	7.27	6.68	23.00	25
ELA 257	0.15	1.65	0.77	0.31	0.50	1.64	11.00	30.00	56.00	361.00	1.30	9.10	52.20	3.25	6.29	15.80	9
ELA 373	0.21	2.05	0.77	0.39	0.67	2.86	1.20	24.00	4.00	177.00	1.28	3.60	3.40	8.10	7.16	23.00	15
ELA 377	0.22	2.15	0.95	0.39	0.61	2.16	4.00	14.00	6.00	260.00	0.94	4.80	10.00	5.98	7.15	20.20	16
ELA 378	0.19	1.85	0.89	0.36	0.56	1.80	3.50	8.00	4.00	300.00	1.26	6.90	13.20	4.83	7.00	17.60	16
ELA 383	0.12	1.80	0.67	0.32	0.58	1.74	3.80	26.00	4.00	369.00	0.42	8.40	21.40	4.29	6.72	16.40	9
ELA 384	0.12	1.45	0.76	0.29	0.51	1.58	5.70	18.00	4.00	389.00	1.00	9.40	24.20	3.96	6.57	14.60	3
ELA 435	4.60	2.70	3.28	0.59	1.04	3.16	1.60	24.00	4.00	214.00	0.80	4.70	11.40	8.94	7.19	42.20	13
ELA 436	0.20	1.35	0.62	0.50	0.74	1.28	12.00	20.00	6.00	529.00	0.36	8.30	21.00	4.34	6.79	15.40	2
ELA 438	0.17	1.40	0.59	0.41	0.80	1.84	11.10	358.00	50.00	917.00	0.10	9.20	27.20	6.02	6.67	21.20	3
ELA 468	0.33	2.25	0.93	0.54	0.61	2.78	4.30	34.00	252.00	321.00	0.20	5.00	6.80	6.21	6.96	25.60	15
ELA 470	0.12	1.45	0.67	0.30	0.54	1.16	8.80	30.00	6.00	496.00	0.12	11.70	64.60	2.04	5.75	13.20	3
ELA 625	0.43	1.80	0.76	0.40	0.59	1.68	1.60	32.00	2.00	318.00	0.78	5.90	14.80	4.39	6.89	16.60	25
ELA 626	0.18	1.50	0.65	0.32	0.55	1.54	3.40	18.00	18.00	304.00	0.36	5.50	6.40	4.64	7.10	15.40	12
ELA 627	0.15	1.65	0.64	0.29	0.55	1.48	5.20	26.00	10.00	330.00	0.60	5.80	7.60	4.16	6.90	15.00	8
ELA 629	0.21	2.05	0.62	0.36	0.59	1.58	2.10	20.00	2.00	286.00	0.56	7.80	23.00	3.75	6.76	15.60	15
ELA 661	0.01	0.80	0.57	0.28	0.55	1.40	13.70	34.00	10.00	526.00	0.40	15.30	134.00	2.24	5.38	13.60	2
ELA 93	0.23	1.85	0.70	0.30	0.57	1.36	4.40	28.00	6.00	353.00	1.48	8.40	30.60	3.14	6.54	14.60	9
ELA 938	0.26	2.75	0.98	0.49	1.06	3.08	4.00	16.00	2.00	535.00	0.64	5.20	10.20	10.20	7.17	29.60	5

Table 1 continued

Lake	Chloride (mg L⁻¹)	Sulphate (mg L⁻¹)	Sodium (mg L⁻¹)	Potassium (mg L⁻¹)	Magnesium (mg L⁻¹)	Calcium (mg L⁻¹)	TP (µg L⁻¹)	NH₄/NH₃ (µg L⁻¹)	NO₃/NO₂ (µg L⁻¹)	TKN (µg L⁻¹)	SiO₃ (mg/L)	DOC (mg/L)	True colour (TCU)	Alkalinity (mg L⁻¹)	pH	Conductivity (µS cm⁻¹)	Depth (m)
ELA 99	0.14	0.85	0.77	0.39	0.42	1.34	9.70	32.00	16.00	551.00	0.10	8.90	20.20	4.85	6.44	13.80	6
Min	0.01	0.80	0.53	0.24	0.35	0.86	0.70	8.00	2.00	177.00	0.10	3.30	2.00	1.47	5.38	10.60	2
Max	8.19	2.75	5.85	0.65	1.21	3.42	21.30	358.00	252.00	917.00	1.48	15.30	134.00	11.30	7.19	54.60	30
Mean	0.54	1.83	1.00	0.37	0.63	1.87	6.80	35.28	16.17	407.39	0.61	7.31	24.71	5.12	6.70	19.48	9.34

Water samples were collected as mixed layer composites in June, 2006. Depth is a measure of coring depth, taken from the deepest basin of each study lake
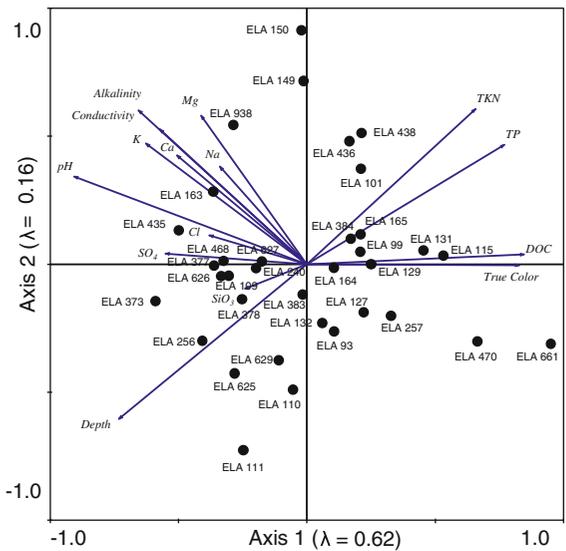
Fig. 2 PCA biplot based on a correlation matrix showing the position of the ELA study lakes in relation to measured environmental variables. Lakes with missing environmental data (i.e., lakes ELA 114, 224, 226, 631, 651) were excluded from the ordination

diatom species. Diatom taxa with relative abundance >5% in either a 'top' or 'bottom' sample are ordered in Fig. 3 according to the 'present-day' (top) species and lake scores in a CA analysis. A clear pattern is displayed with planktonic and tychoplanktonic taxa on the left-hand side of the figure (e.g., *Urosolenia eriensis* (Smith) Round et Crawford ex Round, Crawford et Mann, *Cyclotella ocellata* Pantocsek, *Synedra delicatissima* Smith, *Aulacosiera* taxa, *Discostella stelligera* (Hustedt) Houk et Klee, *Tabellaria floculosa* (Roth) Kützing, and *Fragilaria tenera* (Smith) Lange-Bertalot) and benthic taxa on the right-hand side (e.g., taxa from the genera *Achnanthidium, Brachysira, Cymbella, Eunotia, Navicula, Nitzschia, Pinnularia, Staurosira*) (Fig. 3). The planktonic *D. stelligera* complex (including *D. glomerata* (Bachmann) Houk et Klee, *D. stelligera*, and *D. pseudostelligera* (Hustedt) Houk et Klee) was the most abundant taxonomic group, with relative abundances up to 70% in modern sediments and up to 60% in pre-industrial sediments (Fig. 3). The next most abundant taxon, was the tychoplanktonic species *Aulacoseira ambigua* (Grunow) Simonsen with abundances of ∼30% in lakes 164 and 257, in both modern and pre-industrial sediments. *Aulacoseira subarctica* (Müller) Haworth was less abundant
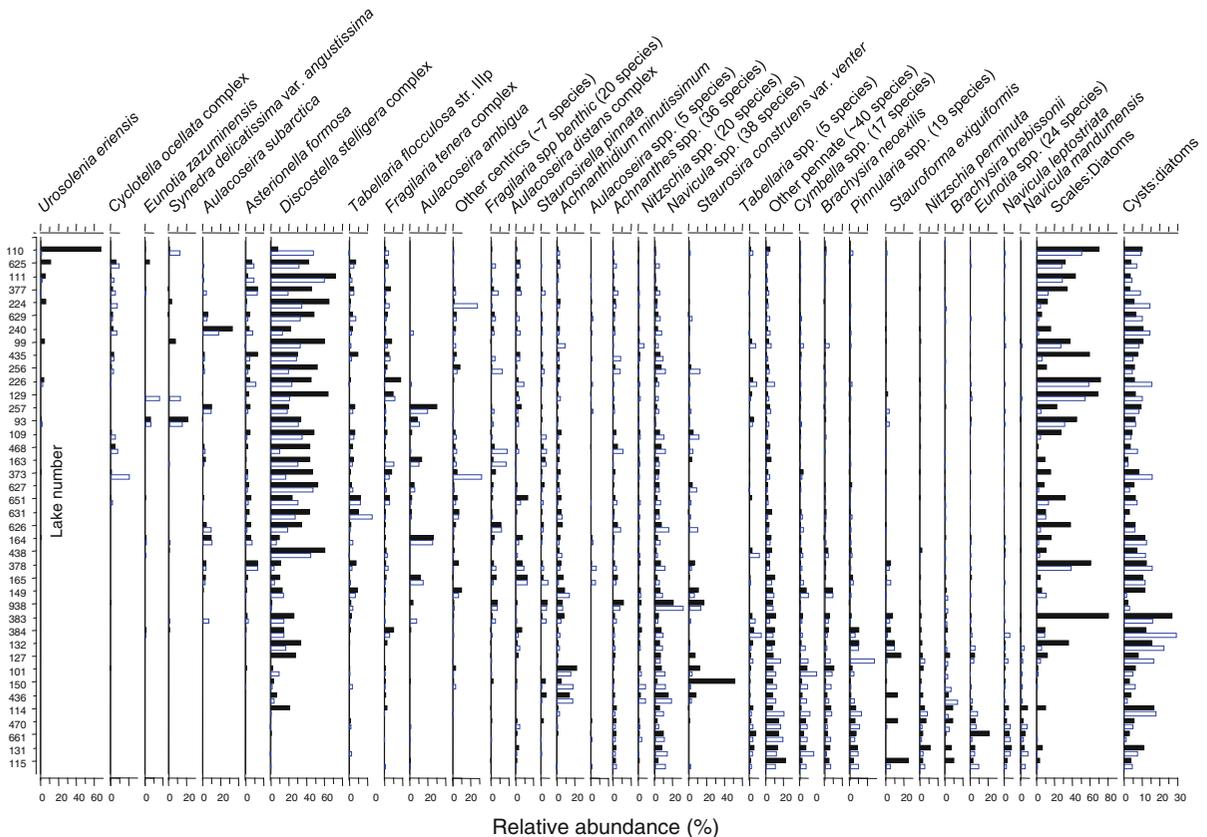
Fig. 3 Relative abundances of diatom species in modern (*solid bars*) and pre-industrial (*open bars*) sediments in 40 study ELA lakes. Diatom taxa and lakes are arranged according to the first-axis species scores and site scores, respectively, of a correspondence analysis (CA). Lake codes are those of the Experimental Lakes Area

reaching a maximum abundance of 33% in Lake 240. In the remaining lakes, species of *Aulacoseira* (including *A. ambigua*, *A. subarctica*, and the *A. distans* (Ehrenberg) Simonsen complex) were present at relative abundances of less than 10%. The uppermost sediments of Lake 110 were dominated by *U. eriensis* (65%) which only reached a maximum of 5% in six other lakes.

The lakes towards the bottom of the figure are dominated by benthic taxa, with smaller abundances of *D. stelligera* (Fig. 3). In lakes 938, 115, 661, 131, 470, *D. stelligera* complex was absent or very rare. Diatoms from these lakes were represented by diverse assemblages with benthic species of *Achnanthoids*, *Brachysira brebissonii* Ross, *B. vitrea* (Grunow) Ross, *Navicula mandumensis* Jørgensen, *N. leptostriata* Jørgensen, *Nitzschia perminuta* Grunow, *Cymbella* spp., *Eunotia* spp., occasionally *Stauroforma exiguiformis* (Lange-Bertalot) Flower, Jones et

Round, and small abundances of the *A. distans* complex and *T. flocculosa* (Fig. 3).

Changes in modern versus pre-industrial diatom assemblages

Over half of the lakes displayed increases in the relative abundance of planktonic taxa since pre-industrial times (Fig. 4). In sixteen lakes the increase in planktonic species (including *Discostella* spp., *Cyclotella* spp., *Tabellaria* spp., *Eunotia zasuminensis* (Cabejszekowna) Körner, *Asterionella formosa* Hassal, *Fragilaria nanana* Lange-Bertalot, *F. tenera*, *S. delicatissima* var. *angustissima* Grunow, and *U. eriensis*) was between 10 and 40% in modern versus pre-industrial sediments (Fig. 3). A change of less than 5% relative abundance of planktonic species is displayed by the rest of the lakes with the exception of Lake 373 which had a decrease in planktonic taxa
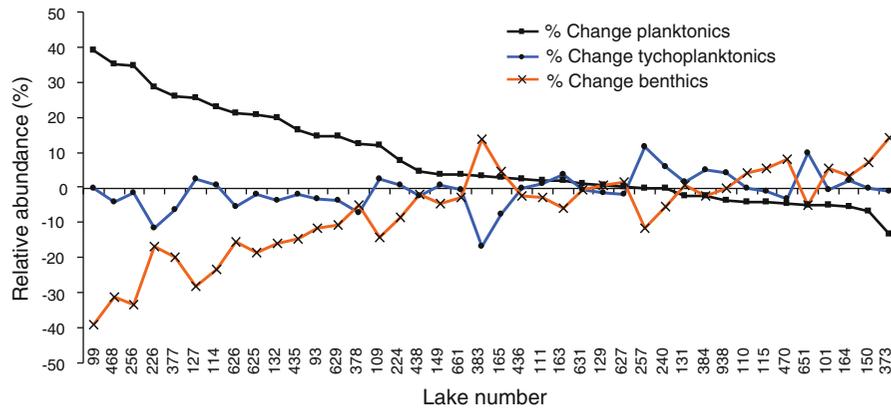
Fig. 4 Percent change in planktonic, tychoplanktonic, and benthic diatom species in modern versus pre-industrial sediments in the 40 study ELA lakes. Lakes are arranged from the greatest positive change to the greatest negative change in the relative abundance of planktonic taxa since pre-industrial times

of >10%. Based on a pairwise t-tests with Bonferroni correction, the average change in relative abundances of *D. stelligera* between pre-industrial and modern times was statistically significant ($p < 0.05$). In other lakes, changes in diatoms species displayed different patterns. For example, in Lake 110, the dominant diatom taxa changed from *D. stelligera* complex in pre-industrial times to a modern assemblage dominated by *U. eriensis* (Fig. 3).

Tychoplanktonic *Aulacoseira* spp. (*A. ambigua*, *A. subarctica*, *A. distans* complex, *A. perglabra floriniae* (Camburn) Haworth, *A. italica* (Ehrenberg) Simonsen, *A. lacustris* (Grunow) Krammer, *A. lirata* (Ehrenberg) Ross, *A. nygaardii* Camburn) are less abundant in present-day sediments by 0.3–19% than in pre-industrial sediments with the exception of lakes 257, 240, 651, 384, 938 where abundances increased by more than 5% (Fig. 4). In terms of planktonic diatom species, the highest increase in relative abundance in modern sediments is recorded by the *D. stelligera* complex while many benthic species, such as *Achnanthidium minutissimum* (Kützing) Czarnecki, *Brachysira neoexilis* Lange-Bertalot, *Staurosirella pinnata* (Ehrenberg) Williams et Round decreased in relative abundance in comparison to pre-industrial sediments (Fig. 3).

In general, the benthic diatom species occurred at higher relative abundances in pre-industrial sediments relative to modern samples. Based on a pairwise t-tests with Bonferroni correction, the average decrease in relative abundances in *A. minutissimum*, *S. pinnata,* and *S. exiguformis* between pre-industrial and modern times were statistically significant ($p < 0.05$). However, in a small number of samples, benthic species increased in modern sediments (e.g., *Staurosira construens* var. *venter* (Ehrenberg) Hamilton in Lake 150, and *S. exiguiformis* in lakes 115, 127, 436, 383, 470).

Patterns in limnological characteristics and relationships to changes in diatom species

Multiple correlations were performed to assess if the amount of change in planktonic, benthic and tychoplanktonic groups between the top and bottom samples, could be significantly related to measured environmental variables (i.e., coring depth, pH, TKN, TP, SiO_3, DOC, true colour). The change in planktonic species was positively correlated to lake depth ($R = 0.44$; $p = 0.01$). Conversely, the change in benthic species was correlated negatively to lake depth ($R = 0.45$; $p = 0.008$) and positively to lake silica concentration, but with very low correlation coefficient and marginally significant. No significant correlation was found between the amount of change of tychoplanktonic species and the measured environmental variables.

Multiple correlations were also used to investigate if the amount of change of dominant diatom species (*D. stelligera*, *Aulacoseira* spp., *Tabellaria* spp., *A. formosa* and sum of small *S. pinnata* and *S. construens* var. *venter*) could be related to measured environmental variables. The strongest correlation was found between the percent change

of *D. stelligera* and lake depth ($R = 0.4$; $p = 0.01$), and true colour ($R = -0.5$; $p = 0.003$). The percent change of *A. formosa* was correlated to lake depth ($R = -0.3$; $p = 0.05$) while *Tabellaria* spp. and *S. pinnata* and *S. construens* var. *venter* were both correlated to TKN ($R = -0.5$; $p = 0.005$; and $R = 0.48$; $p = 0.005$, respectively). Multiple correlations performed between the amount of change of select diatom species and the PCA axis-one scores, revealed that PCA axis-one site scores is significantly correlated with the change in *D. stelligera* ($R = 0.4$; $p = 0.01$) and *Tabellaria* spp., ($R = -0.35$; $p = 0.04$).

Discussion

Variations in diatom composition and abundance from lacustrine ecosystems have consistently been shown to be strongly related to changes in water physico-chemical properties, such as pH, nutrient concentration, transparency, and lake stratification (Smol and Cumming 2000). Changes in diatom species composition in time and space have been attributed to natural (e.g., geological factors, climate, fire) and anthropogenic factors (e.g., acidification, nutrient enrichment, climate). In this study, we choose a region and study lakes where the impacts from direct watershed disturbance, and the impacts of acidic deposition would be minimal, so that the impact of other potential regional stressors could be assessed. As detailed in the introduction, the ELA lakes used in this study are located in an area that is minimally impacted by human activities (e.g., no agriculture or industrial activities, and limited forestry), and is a region that receives low amounts of acidic deposition (Findlay and Shearer 1992).

The most apparent taxonomic shift that occurred in the ELA study lakes is a significant increase of the relative abundance of planktonic taxa in modern sediments, especially the *D. stelligera* complex, while the abundance of many benthic species, such as *A. minutissimum*, *S. pinnata*, *Brachysira* spp., *Navicula* spp., *Cymbella* spp. *sensu lato*, *Pinnularia* spp., have decreased since pre-industrial times (Figs. 3, 4). Large increases in *Cyclotella* taxa have been reported in lakes from arctic and temperate regions (Rühland et al. 2008). For example, studies across the Arctic have shown marked increases of the

small *Cyclotella* species in the recent lake sediments (Sorvari et al. 2002; Rühland et al. 2003; Rühland and Smol 2005; Rühland et al. 2008). Similar changes have also been reported from temperate regions in Ontario (Forrest et al. 2002) and eastern Canada (Harris et al. 2006) and from high-elevation lakes (Karst-Riddoch et al. 2005). The increase in the relative abundances of the planktonic *Discostella* and *Cyclotella* species, especially *D. stelligera*, has been previously linked to a lengthening of the ice-free season and enhanced lake stratification (Sorvari et al. 2002; Rühland et al. 2003), a phenomenon that can be induced by increasing temperature (Smol et al. 2005; Rühland et al. 2008). Increases in *D. stelligera* and other planktonic diatom taxa since pre-industrial times from the ELA may be an indication of changes in the thermal characteristics of these lakes. Records of temperature and precipitation are available from the ELA meteorological station since 1970 and from the nearby town of Kenora, Ontario since the beginning of the 20th century (Fig. 5). A strong correlation was found between data recorded at both stations since 1970 ($r = 0.98$ for mean annual temperature and $r = 0.80$ for annual precipitation), indicating that the climate record from Kenora is representative of climatic conditions at the ELA (Moos et al. 2005). Mean annual temperatures measured at Kenora display a steady and significant increase of 0.01°C per year over the last century, with a total increase of ~2.5°C since 1899, and the largest increases recorded in the winter months (Dec–Feb: 0.025°C year^{-1}). Concurrently, records of the duration of the ice-free season from Lake 239 show an increasing rate of ~0.3 days year^{-1} since 1969 (Fig. 5). At ELA the duration of the ice-free season has increased at Lake 239 by ~2 weeks since 1969 ($r = 0.35$, $p < 0.05$, Fig. 5), with both earlier ice-off dates and later ice on.

Changes in seasonality are also now occurring in larger lakes in north-western Ontario. In a nearby, but much larger waterbody (Whitefish Bay of Lake of the Woods), there has been a reported increase of ice-free days (Rühland et al. 2008). Evidence of the effects of climatic change on small lakes in the Northern Hemisphere is clearly shown with ice-on and ice-off data (Magnuson et al. 2000). The length of the ice-free season is increasing in many small, mid-latitude lakes, as well as some of the Great Lakes (Austin and Colman 2007), due to later freezing and earlier
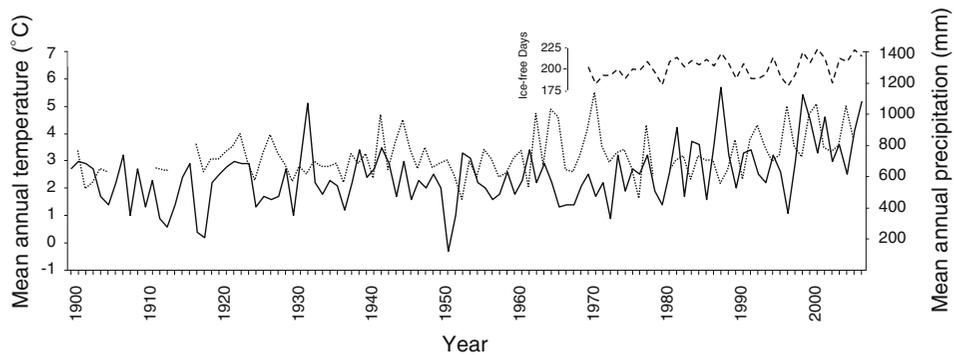
Fig. 5 Mean annual temperature (°C) (*solid line*) and total annual precipitation (mm) (*dotted line*) recorded at Kenora airport, Ontario, Canada. Also shown is the duration of the ice-free period in days recorded at ELA Lake 239. Climate data are from http://www.cccma.bc.ec.gc.ca/hccd

breakup dates. Changes in seasonality can have significant impacts on the thermal regime of lakes. In a number of the Great Lakes, summer stratification has been increasing largely due to an earlier onset of stratification (Austin and Colman 2007). Changes to the thermal structure of a lake have implications for many in-lake processes, including nutrient recycling, primary production, and late-summer hypolimnetic oxygen levels, which in turn have biological impacts for many aquatic organisms.

Long-term monitoring of lakes from ELA has documented limnological changes due to climate in the 1980s. Prolonged dry periods combined with generally higher temperatures in the late 1980s resulted in a small decrease in lake depth, and increased lake transparency and light transmission in a number of ELA lakes (Schindler et al. 1996). The rapid spring warming and decreases in DOC inputs resulted in deeper thermoclines and increased thermal stability in the ELA reference lakes (Schindler 2001). Examination of algal communities from four oligotrophic lakes from the ELA between 1968 and 1998 revealed noticeable shifts in phytoplankton species composition and abundance during drought periods, including an increase in the biomass of diatoms (Findlay et al. 2001), providing further evidence that ELA lakes are climatically sensitive. Long-term monitoring data from Lake Tahoe, USA, provide additional evidence that climate warming may favour smaller diatoms over larger forms during periods of enhanced stratification (Winder et al. 2008). Winder et al. (2008) argues that reduced vernal mixing and increased thermal stability that occurs with climatic

warming may alter cell sinking velocities, and the rate at which nutrients are redistributed in the water column, ultimately favouring smaller taxa such as small species of *Cyclotella*.

The results of the multiple correlation analysis are also consistent with some of the variation in diatom assemblages being related to a recent change in climate. They suggest that lake depth is the most important variable correlated with changes in planktonic, benthic and *D. stelligera* between the 'pre-industrial' and 'modern' sediment samples. According to our results, lake depth may be a strong predictor explaining the increase of *D. stelligera* among lakes. Shallow lakes generally displayed a smaller increase in *D. stelligera*, and they exhibited increases in the relative abundance of other planktonic taxa (e.g. *A. formosa*, Lake 240) or benthic species (e.g., Lake 127). The role of lake characteristics in modulating a climate signal is also supported by the correlation between PCA axis one scores of the environmental data, representing environmental gradients of pH, DOC, True Colour, and lake depth (Fig. 2), and variation associated with changes in the relative abundance of *D. stelligera* and *Tabellaria* species. The multiple correlation results also show that increases in *A. formosa* occurred more commonly in shallower lakes (<10 m maximum depth), while deeper lakes recorded shifts towards increases in *D. stelligera* complex. In general, shallower lakes were more highly coloured and higher in nutrient concentrations than the deeper, dimictic lakes. Thus, it appears that the specific biological response to climate warming varies among lakes, depending on

lake morphometry and pre-existing water quality. Changes in planktonic taxa were not just limited to increases in *D. stelligera*. In Lake 110, *D. stelligera* decreased dramatically in favour of an abrupt increase of *U. eriensis*; however, dissolution of *U. eriensis*, a lightly-silicified taxon, in deeper sediments cannot be ruled out.

The modulation of lake response by lake morphometry in response to climate warming has been reported elsewhere (Adrian et al. 1999; Gerten and Adrian 2001). Gerten and Adrian (2001) demonstrated that the influence of climatic warming can vary substantially among lake types and that water temperature regimes are expected to show more impact in deep, dimictic lakes. In contrast, shallow, well-mixed lakes have a low heat-storage capacity with relatively short-term effects on water temperature regimes, and implicitly with a reduced impact on the plankton community (Adrian et al. 1999). Similar findings have also been reported from arctic and subarctic regions where deeper, stratified lakes displayed the highest increase in *D. stelligera* and decrease of benthic species, whereas changes in isothermal lakes were typically among benthic species (Sorvari et al. 2002; Rühland et al. 2003; Smol et al. 2005). Changes in diatom assemblages reported at ELA suggest that deeper lakes may be the most responsive to recent climatic warming, with a longer growing season, increased water transparency, and more persistent thermal stability. However, *D. stelligera* and other planktonic species also increased in some of our shallow study lakes (e.g., ELA lakes 114, 99, 132, 129). A possible explanation is that the seasonal position of the thermocline is not only dependent climate conditions, but also on other variables such as lake area, fetch, and water clarity (Fee et al. 1996; Mazumder et al. 1990; Xenopoulos and Schindler 2001).

While lake depth is an important variable in predicting differences in the response of diatoms to climatic change across the landscape, it is unlikely that the biological changes we observe within lakes are a result of increasing lake depth since pre-industrial times. For example, changes in lake level have been shown to be minimal since the mid-to-late 1800s to present at the ELA (Laird and Cumming 2008). Furthermore, the frequency of drought, an important determinant of changes in lake level, have not increased significantly since AD 1783 in the Winnipeg River Basin, according to reconstructions from a network of 54 tree-ring sites (St. George et al. 2008). Finally, marked increases in *Cyclotella* sensu lato species have been shown in a sediment core from Lake of the Woods, a large international lake ~100 km from the ELA (Rühland et al. 2008), during a period of minimal change in lake level (1980-present) (Lake of the Woods Control Board, http://www.lwcb.ca). Thus, the changes in diatom species from the ELA study lakes are consistent with recent warming, but the influence on individual lakes is modulated by lake-specific factors.

Acidic deposition can be ruled out as a factor responsible for the observed changes. As mentioned earlier, the ELA region is also located in an area with a low-deposition of sulphate. Although there are significant changes in diatom species composition over time, circumneutral taxa dominate both pre-industrial and present-day assemblages. The primary shift to planktonic taxa, such as *D. stelligera* (a circumneutral taxon; Findlay and Shearer 1992), is not consistent with biological changes resulting from lake acidification (Battarbee et al. 2010).

The observed changes in diatom taxa since pre-industrial times at ELA are also not consistent with known watershed disturbances, including logging and fires. Although some forest harvesting has occurred, it has been of limited intensity. The observed changes are also not consistent with increases in eutrophic taxa, as might be expected with more severe or sustained changes in land-use (Hall and Smol 2010). The main, albeit small, watershed disturbance has been some forest harvesting, but only from a small subset of the study lakes. Previous studies have shown that the impact from logging is minimal on diatom species if forests are allowed to regenerate (Laird and Cumming 2001; Laird et al. 2001), or may be masked by regional changes in climate (Paterson et al. 1998, 2000).

Long-term changes in nutrient deposition (e.g., nitrogen) warrant further examination, but are generally not consistent with the observed changes in diatom assemblages in the study lakes. Several studies have shown that increases in *D. stelligera* abundances are not necessarily coeval with changes in nutrient deposition (e.g., increasing N deposition), or to changes in nutrient concentrations in lakes (Fritz et al. 1993; Sorvari and Korhola 1998; Rühland et al. 2003, 2008; but see Wolfe et al. 2001, which shows

abrupt decrease in *D. stelligera* in the post-industrial era). Rühland et al. (2008) examined the relationship between long-term changes in diatom species and inorganic N deposition in Lake of the Woods and concluded that there was no significant relationship between long-term diatom species changes and inorganic N deposition. However, Rühland et al. (2008) note that changes in inorganic N deposition may be correlated to climatic changes, indirectly through changes in precipitation. Thus, a synergistic relationship between climate and nutrient dynamics may exist in the ELA region, and may provide a partial explanation of the observed biological changes.

Changes in temperature and seasonality are likely explanatory factors for the observed trends in diatom taxa in the ELA region, recognizing that the 'top'/'bottom' approach is limited, and does not allow for a full assessment of causes of the observed species changes. Future studies of dated sediment cores should be applied to assess the timing of changes in planktonic taxa, synchronicity of the changes among lakes, and to more fully assess the biological changes relative to measured changes in climate and other regional stressors.

In conclusion, we believe that the changes we observe in the modern diatom assemblages from the ELA lakes, punctuated with an increase in the relative abundance of *D. stelligera* complex in deeper lakes, are consistent with enhanced summer stratification, a longer ice-free season and increased thermal stability in recent decades. The ELA lakes have been minimally impacted from anthropogenic disturbances in comparison to lakes in other regions of the Precambrian Shield (e.g., south-central Ontario; Yan et al. 2008), and thus we conclude that recent warming provides the strongest explanation for the observed species changes. The biological changes were greater in deeper, thermally stratified, and nutrient poor lakes, although a few of the shallower lakes also showed similar changes.

Detailed paleolimnological studies are necessary from the ELA region to further assess when planktonic taxa increased, so that the relationship between climate change and other potentially important regional factors can be evaluated further.

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