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ORIGINAL PAPER

Diatom assemblages reveal regional-scale differences in lake responses to recent climate change at the boreal-tundra ecotone, Manitoba, Canada

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Abstract The direction of pan-Arctic ecosystem shifts in response to climate warming is relatively well understood; however, landscape-level linkages among terrestrial, wetland, and lake ecosystems significantly influence the dynamics of each, making it difficult to generalize about lake responses to warming across the Arctic, and at times difficult to interpret paleoclimate records from lake sediments. To investigate differences in lake responses to recent climate change at the boreal-tundra ecotone, we conducted a 2-year survey of diatom assemblages from lakes with varying catchment characteristics in northern Manitoba, Canada. We investigated whether catchment geomorphology and landscape, including slope and vegetative cover, result in characteristic water chemistries and hence diatom assemblage signatures, which could then be used in paleolimnological studies to infer past changes in the catchment. Forty-four lakes were sampled for water chemistry and catchment vegetation was characterized using Landsat Imagery. Lake catchments were generally small (median 702 ha) and dominated by peat (*Sphagnum*) with or without lowland forest (*Picea-Larix)*, or open tundra, with different amounts of exposed rock/till, upland forest/woodlands, and burn recovery area. Lakes were generally nutrient-poor, with lower nutrient and DOC concentrations in tundra-dominated catchments, and higher nutrients and DOC in catchments with greater forest cover. A diatom-based transfer function for pH ($R^2 = 0.72$, $R^2_{boot} = 0.54$) was developed and compared with diatom assemblage turnover and sediment geochemistry in cores from eight lakes to reconstruct limnologic conditions over the past ~200 years. Most cores showed similar increases in biogenic silica and carbon burial, beginning around AD 1880 in the tundra lakes and about 1920 in the more forested catchments, likely in response to regional warming. In contrast to lakes in other Arctic regions, our lakes showed only minor pH changes in recent decades. The shift, however, was more pronounced in higher-latitude lakes with less forest cover, suggesting small-scale

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watershed influence on lake response to climate, even on short time scales. Diatom assemblages did not follow previously published models of climate-linked community change seen in circum-Arctic and sub-Arctic lakes. Translating local changes detected in the paleolimnological record to the regional level requires an understanding of how different catchment properties mediate the response of lakes, and their diatom assemblages, to climate change.

Keywords Diatoms · pH transfer function · Sub-Arctic · Ecotone · Manitoba · Climate change

Introduction

There is strong consensus that climate is changing rapidly in the Arctic, as evidenced by a 0.4 °C per decade rise in temperature over the past 40 years (McBean et al. 2005; Christensen et al. 2007). Physical and ecological responses to this recent warming, including increased lake productivity, decreased duration of ice cover, thawing of permafrost, northward shifts in the sub-Arctic tree line and expansion of shrub vegetation, have been documented in Arctic regions and are predicted to continue across the Arctic with future warming (Zhang et al. 1997; Pastor et al. 2003; Camill 2005; Fallu et al. 2005; Hinzman et al. 2005; Smol et al. 2005; Prowse et al. 2006; Tape et al. 2006; Walker et al. 2006; Osterkamp 2007; Umbanhowar et al. 2013; O'Reilly et al. 2015).

The limnology of Arctic lakes can vary widely within and among regions (Antoniades et al. 2003; Rühland et al. 2003a, b; Keatley et al. 2007; Onda et al. 2007; Westover et al. 2009). Differences in biogeochemical variables such as dissolved organic carbon (DOC), pH, and nutrients have been linked to bedrock/till geology, connections to surface or groundwater, lake morphometry and vegetation. In the sub-Arctic, the boreal forest to tundra transition may be associated with decreases in nutrients, major ions and DOC (Pienitz and Smol 1993; Rühland et al. 2003a). Uncertainty remains as to whether Arctic lakes are more strongly controlled by catchment factors or direct forcing by climate (Michelutti et al. 2007; Anderson et al. 2008; Fritz and Anderson 2013), and in particular how past and future lake responses to climate may be understood in the context of modern biogeochemical gradients.

Diatoms represent a major component of primary productivity in high-latitude lakes, and previous Arctic and sub-Arctic studies have demonstrated that modern diatom assemblages reflect regional and historical differences in DOC, pH, and nutrients (Gregory-Eaves et al. 1999; Ponader et al. 2002; Lim et al. 2007). Studies of diatoms in sediment cores (Smol et al. 2005; Rühland et al. 2008) highlight widespread changes, beginning in the nineteenth century, in relative abundances of cyclotelloid (*Cyclotella* and *Discostella*), *Aulacoseira*, and several benthic diatom species groups across large spatial and ecoregional gradients (Arctic, Alpine, Tundra, Boreal). In larger, deeper lakes these changes have been interpreted as responses to lake warming that result in reduced ice cover and/or strengthened lake stratification (Smol et al. 2005; Rühland et al. 2008). However, duration of ice cover may also reflect local differences in the physical (depth or surface area) and chemical limnology of lakes (Keatley et al. 2008a; Devlin and Finkelstein 2011), resulting in varied diatom responses to warming. Similarly, differences among lakes in DOC, pH, and nutrients that stem from differences in catchment geology, morphometry, or vegetation cover, potentially mediate diatom responses to warming.

In this study, we focused on lakes in a relatively small region at the tundra-forest border of northern Manitoba (Fig. 1) where Umbanhowar et al. (2014) described DOC and pH as two major, nearly orthogonal gradients of variability in lake water chemistry. The goal of this study was to better understand the impacts of local factors on regional lake responses to past and future climate change in the sub-Arctic. Our work focused on three principal questions. First, to what extent are differences in the modern distribution and abundance of diatom assemblages in these 44 lakes correlated with measured landscape and lake chemical and physical characteristics, including DOC and pH? Second, for a subset of eight cored lakes, how have diatom assemblages changed over the past ~200 years and to what extent can these changes be understood in terms of differences and similarities in the local characteristics of the lakes? We paid special attention to changes in the abundances of *Cyclotella/Discostella, Aulacoseira*, and other species highlighted by Smol et al. (2005), Rühland et al. (2008, 2015) and Saros and Anderson (2015) as being sensitive indicators of climate warming. Finally, we

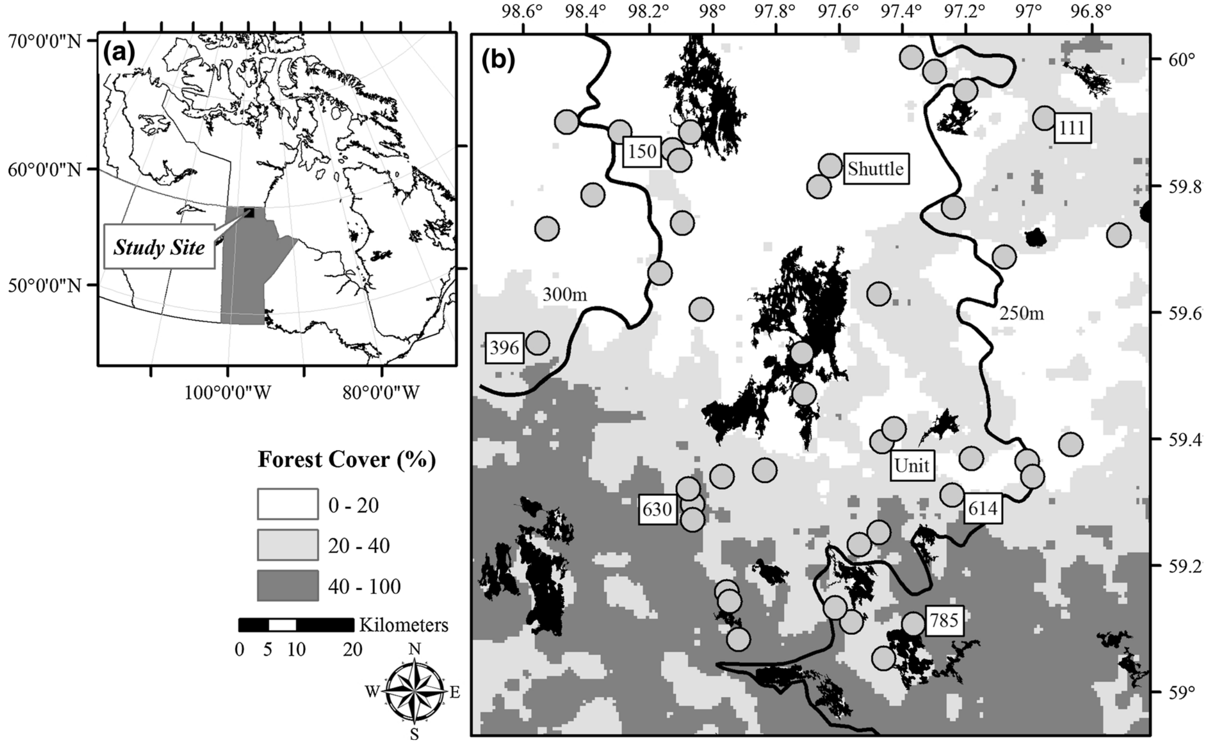


Fig. 1 Map of the study region *shaded* by percent forest cover (based on Landsat imagery). All lakes in the calibration set are marked, cored lakes are labeled

asked if past changes in diatom assemblages and community turnover can be linked to possible shifts in lake pH and productivity based on reconstruction of diatom-inferred pH, changes in the concentration of sediment Ca, and calculated biogenic silica and carbon burial rates. Understanding the response of lakes and modern diatom communities to modern biogeochemical and landscape gradients, and to changes over the past 200 years, will inform more nuanced interpretations of past climate influences on sub-Arctic lakes.

Study region

The study region represents a portion of the forest-tundra ecotone in northern Manitoba (Fig. 1) and is part of a much larger transitional region extending from Alaska to Newfoundland in North America (Payette et al. 2001). The forest-tundra ecotone is a mosaic of woodland, forest, and shrub tundra with many lakes and wetlands interspersed. Average temperatures in the region range from −25 to −30 °C (winter) and 10 to 15 °C (summer) and monthly precipitation ranges from 15 to 30 mm (winter) to 30–60 mm (summer) (Plummer et al. 2006). Models of future climate change suggest increases in both summer and winter temperatures of 3–4 °C over the 1961–1990 average and a shift in growing season from 118 to 142 days by 2100 (Price et al. 2013).

The area north of tree-line is dominated by low- and high-shrub tundra and is a mixture of lowland drainage areas rich in peat and uplands dominated by ridges, small hills and eskers with exposed till (Umbanhowar et al. 2014). Approximately 21 % of the landscape is covered by water. The tree-line region includes patchy stands of predominantly *Picea* and *Larix*. The area is underlain by Archean granitic bedrock (Anderson et al. 2005). Till parent materials in the area are generally sandier, and have only one third to half the concentration of cations, including calcium and magnesium, than similar transitional areas in northwestern Canada and Alaska (Timoney et al. 1993). The region is largely considered a zone of continuous permafrost, with a few scattered patches of extensive discontinuous (50–90 %) coverage (National Atlas Information Service 1993). Soils are thin and poorly developed. Extensive areas of unvegetated bedrock and frostheaved and frost-shattered bedrock blocks are exposed at the surface (Anderson et al. 2005).

Materials and methods

Site selection

A total of 44 lakes were chosen using existing Digital Elevation Models (DEMs), recent Landsat 7 imagery (Global Land Cover Facility) and 1:60,000-scale photography (Canadian National Air Photo Library); stratified sampling was used to include a range of upland and lowland sites, forested and non-forested areas, lakes with and without adjacent peatlands, and lakes with and without surrounding exposed till. Final site selection was made from the air, and lakes were ultimately included or excluded based on the feasibility of access by float plane. Sites were sampled in July 2008 and 2009.

Land cover and lake-catchment characteristics

Lake and land cover determinations were based on analysis of a 2002 Landsat image mosaic (ETM Mosaic, N-14-55) downloaded from the University of Maryland Global Land Cover Facility, and are described in more detail by Umbanhowar et al. (2014). For the 44 lakes sampled, surface area and perimeter were delimited by hand from the 2002 Imagery using ArcGIS 9.2. Feature extraction (ENVI EX 4.8) was used to identify water bodies and a total of eleven cover types (Table 1) based on ground-truthing of over 60 sites with on-ground surveys and low-altitude aerial photography. Catchments were delineated using the ArcHydro extension for ArcGIS and the total cover of each of the 11 cover types was tabulated for each catchment (for details, see Umbanhower et al. 2014). Slope within 200 m was calculated from DEMs based on the average within buffers of each delineated lake.

Water chemistry

Thirty-three water chemistry and morphological variables were measured on 44 lakes: lake elevation, lake area, lake depth, catchment size, slope within 200 m of the lake, temperature, Secchi depth, conductivity (EC), oxidation–reduction potential (ORP), dissolved oxygen (DO), pH, Fe, Ca, Mg, K, Na, Al, Cl, SO_4, dissolved Si, particulate Si, chlorophyll-a, pheophytin, dissolved organic carbon (DOC), specific ultraviolet absorbance (SUVA), Color440, total dissolved nitrogen (TDN), ammonia, nitrate, total phosphorus (TP), total dissolved phosphorus (TDP), volatile suspended solids (VSS), and total suspended solids (TSS).

At each lake, a YSI 556 multi-meter water quality sonde was used to determine pH, conductivity, DO, and redox potential. Two-liter water samples were collected from ~30 cm below the water surface. Filtering (0.45-µm pore size) was done in the field, and all samples (preserved or not) were stored at 4 °C. Water was divided among four different acid-washed, amber polypropylene bottles for (a) dissolved silica (filtered and chilled), (b) DOC, TDN, and TDP (filtered and preserved with H_2SO_4, $pH < 2$), (c) cations (filtered and preserved with HNO_3, $pH < 2$), and (d) TP (unfiltered, and preserved with H_2SO_4, $pH < 2$). Filtered (0.7-µm pore size) water samples were scanned for optical density across the UV–Vis–NIR spectrum (200–900 nm) with a Cary 300 spectrophotometer within 12 h of collection. Measurements of optical density were converted to absorbance. Specific ultraviolet absorbance (SUVA) was calculated by dividing absorbance at 254 nm by DOC concentrations (mg/L) of each sample. Color was calculated using absorbance at 440 nm as outlined by Cuthbert and Del Giorgio (1992). DOC was analyzed using a Shimadzu TOC-VCSN. Cations (Na, Ca, Mg, Fe, K, Al) were analyzed using a Horiba Jobin–Yvon Ultima 2 OES-ICP. A persulfate digestion was used for total P in water, and P was analyzed colometrically using a Lachat QC8000 autoanalyser (Liao 2002). Nitrate was measured on a Lachat QC8000 autoanalyser (Hach Co., Loveland, CO, U.S.A.) using a cadmium reduction method modified for freshwater from Sechtig (2001). Ammonia was analyzed using a fluorometric method developed by Holmes et al. (1999) on a Turner Designs Trilogy Fluorometer (Turner Designs, Inc., Sunnyvale, CA, U.S.A.).

Initial evaluation of pH data, including comparison between our measurements from this study and past unpublished data, suggested that our in-field pH measurements were too low. A depression in pH associated with stirring or movement during sampling of low-EC water (<20 µS cm^{-1}) has been noted in the literature (Hoenicke et al. 1991). Using an experimental approach in the lab (Umbanhowar et al. 2014),

Table 1 Landscape cover for the lakes. Percent cover data do not include the area of the catchment that is surface water, consequently sums are <100 %

Site	Lake elevation (m)	Lake area (ha)	Catchment area (ha)	Slope within 200 m of lake (°)	Lowland forest	Peat	Bare till	Dry tundra	Sedge peat	Moist-wet tundra	Dry shrub tundra	Upland forest/woodland	Burn recovery	Rock
1	272	13,204	142,344	1.8	7.1	25.1	0.4	28.3	3.4	7	7.23	2.1	0	0
2	265	32,976	453,643	1.7	9.3	24.9	0.3	20.1	3.6	5.9	6.67	3.6	1.4	0.2
3	265	2099	461,709	1.7	8.7	23.1	0.3	18.7	3.3	5.6	6.12	3.3	1.3	0.2
29	221	21	141	3.3	8.8	23	0	45.7	1.7	6.6	11.78	4.1	0	0
66	262	53	331	2.3	10	40.2	0.1	19.2	6.5	4.7	6.92	0.9	0	0
79	262	56	2420	1.9	12.6	33.3	0.1	9.6	6.6	6.9	3.31	0.9	0	0
94	243	35	158	1.3	15.2	32.6	0.1	20.9	4.3	10.4	8.77	0.2	0	0
111	225	131	434	0.9	20.8	31.4	0	3.3	9	22	0.74	0.3	0	0
116	305	106	1164	1.4	13.5	23.7	0.1	35.7	2.4	10.6	9.92	2.6	0	0
125	293	61	1208	1.2	5.1	23.3	0.2	41.3	2.9	5.4	8.09	3.9	0	0
150	299	40	304	2.7	6	24.6	0	47.8	1.4	7.5	14.91	2.4	0	0
160	278	425	21,884	1.8	8.7	23.3	0.2	29	2.8	6.5	8.63	2.7	0	0
165	276	96	313	0.6	4.7	36.8	0.1	26.9	6.5	10.4	10.52	1.6	0	0
197	270	110	240	0.8	5.4	44.3	0.1	21.8	7.9	7.1	8.92	4	0	0
205	313	41	2415	2.9	3.9	22.7	0.3	35.2	3.1	4.2	9.59	4.7	0	0
224	243	57	3162	1.1	5.9	32.2	0.2	28.8	6.1	3.3	7.96	2.3	0	0
228	292	98	383	0.6	14.2	26.7	0	33.8	3.2	11.5	12.08	4.4	0	0
260	315	88	657	0.9	11.8	29.6	0	26.6	2.9	9.8	7.77	3.3	0	0
264	195	101	935	1.6	4.6	15.2	2.5	0.8	7.9	0.5	0.3	0.8	59.8	2.8
270	237	132	537	1.2	18.6	38.8	0	7.9	5.4	11.7	6.33	0.6	0	0
299	294	73	2334	0.8	7.5	29.9	0.2	26.7	3.9	3.8	9.33	1.9	0	0
315	282	115	709	1.3	22.7	32.8	0.2	19.6	3.3	8.4	7.91	3.2	0	0
350	317	101	500	0.6	31.7	29.5	0	3.1	3.6	14.6	1.93	0.3	0	0
373	279	80	240	0.6	15.2	37.7	0.1	17.9	5.5	7.2	10.07	2.5	0	0
396	296	84	311	1.2	5.6	25.3	1.2	26.3	6.9	1.4	5.8	13.6	7.2	3.3
513	294	69	138	0.9	3.2	21	0.4	49.2	1.3	8.9	13.8	2	0	0
528	277	59	137	1.2	8.9	29.4	0.2	37	1.3	6.8	12	2.9	0	0
551	243	68	964	1	12	25.9	0.1	24.6	2.9	9.2	10.61	1.8	0	0
554	275	59	731	1.3	18.4	25.6	0.1	27.4	2.5	12.5	10.12	2.3	0	0
578	287	126	1586	1.9	7.7	26.1	0.9	21.2	3.8	4.7	6.99	15.6	0	0
583	263	44	295	1.4	7.3	30.7	0	17	3.8	5.2	5.78	20.5	0	0.5

Table 1 continued

Site	Lake elevation (m)	Lake area (ha)	Catchment area (ha)	Slope within 200 m of lake (°)	Lowland forest	Peat	Bare till	Dry tundra	Sedge peat	Moist-wet tundra	Dry shrub tundra	Upland forest/woodland	Burn recovery	Rock
584	268	106	220	1.7	3.2	27.9	0.3	33.3	4	5	13.33	4.2	0	0
599	274	70	2703	3.1	12.1	26.7	0	6.1	5.6	3.2	3.16	15.6	2.3	0.5
614	271	46	1609	3.8	19.9	25.1	0.1	15.3	1.6	15.9	9.28	2.4	0	0
615	267	22	15,141	2.3	10	23.7	0.2	7.7	4.2	3.6	4.33	14.3	12	0.9
630	260	91	3569	3.1	10.3	25.6	0	6.8	5	3	3.6	20.3	2	0
677	262	58	934	1	29.1	26.6	0	9.1	4.3	9.6	4.72	4.7	1.6	0.1
687	266	54	564	1.4	22.7	34.1	0	11.7	3.5	8.9	6.83	7.3	0	0.1
741	259	62	158	0.9	4.8	36.8	0	5.9	1.9	3.1	3.53	43.1	0	0
754	237	63	1559	2	15	29.1	0	3.5	7.3	5.2	1.72	13.1	15.5	0.6
764	247	71	2443	1.9	13.9	29.9	0.1	8.1	4	7.1	4.53	16	0.3	0.4
781	234	61	294	1.4	17	32	0	6.6	2.2	11.2	4.31	25.6	0	0
785	264	65	696	1.1	43.8	23.9	0.3	3.3	3	8.2	1.77	2.4	0	0
813	239	37	116	0.9	23.2	38.6	0	4	4.6	6.2	0.9	20	0	0

we found a nearly identical pH depression of 0.65 units (SD = 0.22, n = 12) for two new YSI 5565 pH probes in stirred solutions, with motion similar to that of our sampling from the float of a plane. Therefore, all reported pH values were adjusted upwards by 0.65 units to account for the observed depression.

Diatom sampling

Surface sediments were collected from each lake with a HTH (Pylonex, Umeå, Sweden) gravity corer and the top 0.5-cm section was used as the modern sample. Selection of the coring site within each lake was based on assessment of a combination of aerial reconnaissance, basin topography and depth soundings to identify centrally located and flat depositional sites. Diatom samples were processed using standard preparation techniques (Renberg 1990) and 300 diatoms per slide were identified using regional floras (Camburn and Charles 2000; Fallu et al. 2000; Moser et al. 2004) as well as standard reference materials (e.g. Patrick and Reimer 1966; Krammer and Lange-Bertalot 1986–1991).

Sediment cores

Longer sediment cores from eight lakes were collected with a clear polycarbonate piston corer (6.5-cm diameter). Cores were sectioned in the field at 0.5-cm intervals, transferred to polycarbonate cups and put in dark storage at 4 °C for later analysis. Age-depth models were based on ^{210}Pb dating. ^{210}Pb was measured through its granddaughter product ^{210}Po (Eakins and Morrison 1978), and the constant rate of supply model (Appleby 2001) was used to estimate age, with confidence intervals calculated by first-order error analysis of counting uncertainty (Binford 1990; Fig. 2).

Diatoms were extracted from these cores and slides prepared and counted as described above for surface sediments. Biogenic silica (bSi) was used as a proxy for plankton productivity. We extracted silica from ~30 mg of freeze-dried sediment using a weak Na_2CO_3 solution. Concentrations of bSi were determined colorimetrically on 3-, 4-, and 5-h digests (Conley 1998) using a Lachat QC 8000 FIA system (method 10-114-27-1-A) and slope-corrected or averaged across the three measurements. For seven of eight lakes (sediment was no longer available for Shuttle

Lake), calcium was measured at the University of Minnesota Duluth using the Large Lakes Observatory's ITRAX X-ray fluorescence (XRF) core scanner (Cox Analytical Instruments) and expressed as a fraction of titanium. Calcium for Shuttle was calculated as a concentration (mg cm^{-3}) based on dry bulk density × mass loss at 1000 °C as $CaCO_3$ × 0.4004 (Ca as percent of $CaCO_3$). Carbon was estimated based on LOI at 550 °C (Dean 1974), assuming a correction factor of 0.469 to convert from organic matter loss to carbon. Carbon and bSi accumulations are both expressed as focusing-corrected burial rates (Hobbs et al. 2013).

Data analysis

Many prior studies in Arctic and sub-Arctic ecosystems have examined the influence of pH, nutrients, and DOC on diatom assemblages, and these variables have been established as the main gradients of variability in the study lakes (Umbanhowar et al. 2014). These three variables were therefore the focus of transfer function development and testing. Additionally, Canonical Correspondence Analysis (CCA) was performed individually on all landscape variables to identify those variables that were significantly ($p \leq 0.05$) related to diatom community composition. Manual forward selection among individually significant landscape variables was conducted using ANOVA, with 200 unrestricted Monte Carlo permutations to determine those variables with significant explanatory power. To assess whether each individually significant variable explained a unique fraction of the variance in the diatom assemblages, a CCA was run for each variable individually and with other significant variables as conditional co-variables. This enabled separation of the unique explanatory power of each variable of interest. Unless noted, all ordination and cluster analyses were run in R software, with rare species down-weighted before analysis using default functions in the vegan package of R (R Development Core Team 2011).

Transfer functions were developed and the predictive ability assessed using a weighted-averaging approach with bootstrap error estimation in C2 software (version 1.4; Juggins 2003). The strength of each model was assessed using the coefficient of determination (R^2) and the root mean square error (RMSE). Because the same data were used to generate and evaluate the model, these assessments were not entirely independent, and the validation step of bootstrapping with 1000 cycles was used to generate a bootstrapped coefficient of determination (R^2 boot) and a root mean square error of prediction (RMSEP), which more realistically portrayed error estimates (Fritz et al. 1999). Transfer functions were developed using a weighted-averaging calculation with classic de-shrinking; both classic and inverse de-shrinking were evaluated and gave very similar R^2 and RMSEP values. De-shrinking corrects the overestimation of low values and underestimation of high values caused by averaging in both the regression and calibration steps of model development.

Down-core reconstructions of pH were assessed using a ratio of the first axis scores from a Redundancy Analysis (RDA) constrained by diatom-inferred pH (DI-pH; λR) to the first axis scores of an unconstrained PCA (λP) on the down-core assemblage data (Juggins et al. 2013). Detrended Correspondence Analysis (DCA) on core samples was also evaluated as a measure of β-diversity turnover of species over time (Hill and Gauch 1980; Hobbs et al. 2016). Constrained hierarchical clustering of the diatom assemblages was carried out constrained to time, and based on the Bray-Curtis dissimilarity between samples. Clusters were evaluated against a random broken-stick model to infer significance (Jackson 1993).

Results

Modern lake and catchment characteristics

Lake depths ranged from <1–15 m (Table 2), with most lakes shallow (<5 m) and relatively small (<100 ha). Dominant land cover surrounding the lakes was either open Peat and/or Dry Tundra (Table 1).

Lowland or Upland forests were present in most catchments, but only dominant at three sites. One catchment was mainly characterized as Burn Recovery (Table 1). There was not a significant relationship between the skewness or kurtosis in the landscape distribution data and latitude, indicating that the landscape is equally "patchy" moving north, from peat and lowland forest closer to treeline, to tundra at higher latitudes.

Lakes were dilute (5.0–51.3 μS cm^{-1}) and oligotrophic to mesotrophic. Corrected lake pH ranged

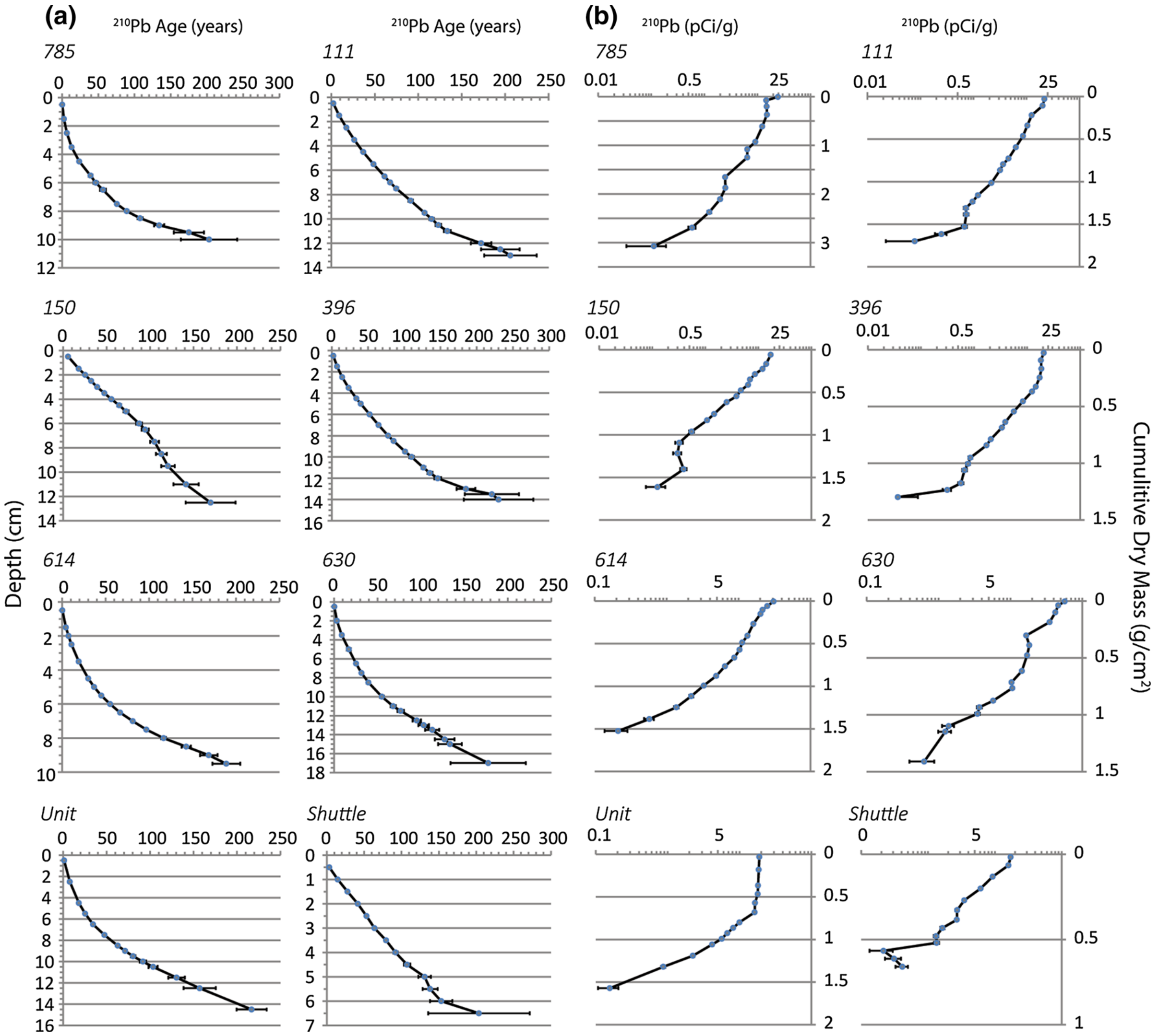


Fig. 2 ^{210}Pb dating; **a** Age versus depth and **b** unsupported ^{210}Pb activity versus cumulative dry mass

from 4.4 to 7.0 (Table 2). Consistent with the findings of Umbanhowar et al. (2014), a PCA of water chemistry data with land cover data passively fit to the plot (Fig. 3), showed DOC and nutrients increased, and SO_4 decreased, along a gradient toward increased lowland vegetation, especially Lowland Forest, but also Peat and, to a lesser extent, Moist-Wet tundra. Tundra categories fell along the low-pH, low-conductivity end of the gradient. Bare till, rock (Exposed), and Burn Recovery areas were associated with higher ionic concentrations, higher pH, and increased silica in the lakes, although the overall area with these characteristics was small (Table 1). Lakes dominated by tundra vegetation had lower pH, nutrients, and DOC. Increased slope was also associated with the exposed areas in the catchment (Fig. 3).

Diatom communities and relationships with water chemistry and landscape variables

Nearly 400 diatom taxa were found in the 44 lakes; 186 met abundance criteria and were included in further analyses (Table 3). Benthic and tychoplanktonic diatoms were most common, dominating the diatom flora in most lakes. Common genera included many fragilarioid species (*Staurosira*, *Staurosirella*, *Pseudostaurosira*) and a high diversity of *Eunotia* species. Cyclotelloid (*Cyclotella* spp., *Discostella* spp.) and *Asterionella* spp. were also common, with the highest abundances in the deepest lakes. Lakes with high pH and ionic concentrations (and associated with open and dry, or wooded catchments) were dominated by *Aulacoseira* species, with some *Tabellaria* species, and a mix of benthic groups including *Gomphonema* and *Amphora* species in the relatively deeper lakes compared with greater dominance of benthic fragilarioid species in shallower lakes.

Using CCA, we first tested whether there were distinct diatom assemblages in lakes located in catchments with different vegetation and geomorphology. All landscape variables (10 land cover types, catchment size, and slope within 200 m of shore) were tested individually; five catchment variables (catchment size, slope within 200 m of the lake shore, % Lowland Forest, % Upland Forest, and % Peat in the catchment) were significantly ($p \leq 0.05$) related to diatom distributions. Using the same method, we also tested variables of specific interest based on known lake chemistry-landscape relationships; pH, DOC, and TP were tested to assess their potential utility for down-core reconstructions; pH and TP had significant ($p \leq 0.05$) relationships with diatom assemblages. DOC explained 20 % of variance, but was not statistically significant ($p = 0.20$) at $p \leq 0.05$. Utilizing pCCA, each of the individually significant landscape and lake chemistry variables was assessed for significance with the remaining individually significant variables in both data sets used as conditional co-variables; only pH and TP had significant independent relationships with diatom distributions (Table 4). No landscape variables showed independent and significant relationships with diatom distributions. Optima and tolerances for each species were calculated and transfer functions were examined for both pH and TP. Bootstrapped comparisons of estimated and observed values gave relatively weaker correlations for the TP model ($R^2 = 0.51$; $R^2_{boot} = 0.21$); correlations between estimated and observed values were higher for pH ($R^2 = 0.72$; $R^2_{boot} = 0.54$) (Fig. 4).

Changes over the past 200 years

Diatom taxa in core samples were well represented in the modern data with a minimum of 52 % (Lake 630) of fossil taxa present in the modern set. DCA axis 1 scores in all eight lakes followed a common trajectory, with constrained cluster analysis showing a zone division at 1840–1890 for higher-latitude/less forested lakes (111, 150, Shuttle [165], 396), whereas in the lower latitude lakes (614, 630, 785) the zone boundary falls around 1920 (Fig. 5). None of the zones were different from a random model; however, there is a common regional zonation defined by the analysis.

Although DCA axis 1 scores followed a common trajectory, there was little evidence of similar changes in individual taxa or groups of taxa across the eight lakes. For example, the relative abundance of phytoplankton increased in three of eight lakes, decreased in another, and showed little change in the remaining four (Fig. 6). Taxa identified as indicators of climate change show similar ambiguous patterns (Fig. 6), with three lakes showing decreased *Aulacoseira* abundance (lakes 150, 111, and Unit-528), and four lakes showing increased *Aulacoseira* abundance (lakes 165 [Shuttle], 396, 614, 785). Cyclotelloid diatoms showed increased abundance in only two lakes (150, 396) and two other lakes showed decreased cyclotelloid abundance (lakes 614, Unit-528).

The transfer function for pH was applied to all cores and results showed subtly different patterns of change among lakes over the past approximately 200 years. The ratio of variance explained by DI-pH (λ_R) to the total variance explained (λ_P) was low and diatom-inferred pH changes were small for the lowest latitude, forest-dominated catchments. The λ_R/λ_P was higher for lakes with less forest cover (Table 5), and three of these cores had DI-pH changes outside of model error (Lakes 396, 150, Unit [528]; Fig. 5), with all three lakes showing increases in pH in the later decades of the twentieth century. A greater portion of the explained variance in diatom communities (Juggins et al. 2013) appears to be caused by changes in pH in the tundra-lakes compared to more forested catchments.

In the three lowest-latitude lakes (614, 630, 785) biogenic silica and carbon burial increase from the mid-1900s to present; DCA Axis 1 scores in these lakes are synchronous with these increases (Fig. 5). In lakes 150, 396, Shuttle and Unit (all high-latitude and with low forest cover), bSi and carbon also increase at least slightly toward the top of the cores; however, in contrast to the lower-latitude lakes these changes do not occur synchronously with DCA scores or at stratigraphic boundaries defined by constrained cluster analysis (Fig. 5). In Lake 111, which is located at high

Table 2 Select water chemistry and physical data for 44 northern Manitoba lakes

Site	Lat N (dd)	Long W (dd)	Depth (m)	Area (ha)	Secchi (m)	Conductivity	pH	DOC (mg L^{-1})	TDN (mg L^{-1})	TDP (μg L^{-1})
1	59.96	−98.02	14.3	13,204	3.2	11.4	5.6	3.7	0.18	0.9
2	59.57	−97.77	15.7	32,976	3.1	15.7	6	3.0	0.21	9.5
3	59.45	−97.73	11.2	2099	2.5	13.6	5.6	2.9	0.16	7.8
29	59.4	−96.91	1.6	21	1.6	6.7	5.2	5.4	0.17	3.5
66	60.01	−97.37	1.6	53	1.6	11.9	5.4	9.8	0.19	1.0
79	60.01	−97.37	2.3	56	2.1	6.9	5.3	5.7	0.21	5.5
94	59.96	−97.21	2.6	35	2.5	9.8	5.7	5.6	0.2	6.2
111	59.92	−96.96	3.4	131	2.7	6.8	5	5.3	0.18	5.6
116	59.92	−98.48	2.7	106	2.5	11.5	5.7	5.1	0.19	5.2
125	59.9	−98.29	2.3	61	2.3	8.7	5.7	3.9	0.14	3.7
150	59.88	−98.13	5.5	40	2.5	8.8	4.9	4.9	0.22	20.8
160	59.84	−98.12	5.7	425	2.5	10.0	5.7	3.8	0.25	2.6
165	59.85	−97.63	2.8	96	2.6	6.2	4.9	3.4	0.16	1.7
197	59.81	−97.68	5.6	110	4.6	7.5	5.5	3.8	0.25	2.5
205	59.8	−98.38	8.8	41	3.9	6.4	5.2	3.7	0.15	7.8
224	59.78	−97.26	1.9	57	1.9	9.6	5.3	4.6	0.17	2.0
228	59.76	−98.11	3.2	98	2.8	7.6	5.7	4.1	0.14	1.1
260	59.75	−98.53	2.7	88	1.9	8.9	5.3	6.1	0.19	6.2
264	59.73	−96.74	11.8	101	3.5	13.3	6	5.1	0.21	7.9
270	59.7	−97.1	2.7	132	1.5	11.1	6.1	7.4	0.45	7.0
299	59.69	−98.18	2.3	73	2.1	7.7	5.1	4.8	0.26	6.1
315	59.62	−98.05	4.5	115	2.4	8.2	5.4	5.5	0.29	9.9
350	59.57	−98.56	1.8	101	1.7	9.9	5.9	7.9	0.3	12.2
373	59.64	−97.5	1.2	80	1	8.6	4.9	7.4	0.42	6.7
396	59.43	−97.45	7.3	84	4.1	15.3	5.9	3.0	0.15	8.1
513	59.41	−97.49	4.7	69	4.5	5.3	5	2.8	0.14	3.8
528	59.38	−97.22	7.5	59	3.5	14.6	5.8	3.2	0.15	5.8
551	59.37	−97.05	1.8	68	1.8	14.1	5.7	5.7	0.19	10.4
554	59.36	−97.86	1.9	59	1.9	11.3	5.7	7.1	0.22	3.7
578	59.36	−97.99	3.9	126	2.4	17.4	6.3	3.6	0.14	7.3
583	59.35	−97.03	3.1	44	3.1	5.0	4.4	5.2	0.16	6.9
584	59.32	−97.29	9	106	8.7	5.7	5.3	2.8	0.3	2.0
599	59.34	−98.09	3.3	70	2.2	15.9	5.9	4.8	0.24	12.3
614	59.31	−98.09	13.8	46	2.2	51.3	7	7.6	0.24	7.2
615	59.29	−98.08	1.9	22	1.9	17.9	5.9	4.8	0.2	11.4
630	59.26	−97.51	10.5	91	2.2	15.0	6	4.9	0.19	3.8
677	59.25	−97.57	4.5	58	1.8	10.0	5.1	9.0	0.32	3.7
687	59.18	−97.98	4.5	54	2	11.4	5.6	7.8	0.32	3.8
741	59.16	−97.97	3	62	3	10.2	6.4	4.4	0.22	8.1
754	59.15	−97.65	14.8	63	2.4	12.7	5.9	8.2	0.21	7.0
764	59.12	−97.6	1.5	71	1.5	18.5	6	7.8	0.28	9.3
781	59.12	−97.4	1.8	61	1.8	8.9	5.3	6.8	0.38	1.7
785	59.1	−97.95	12.6	65	1.7	17.5	6.1	9.3	0.3	5.6
813	59.06	−97.5	1.4	37	1.3	12.4	5.5	9.8	0.32	15.1

Site numbers are as in Fig. 1

latitude, but is locally more forested, the bSi and carbon burial increases are also synchronous with changes in diatom assemblages.

Changes over time in diatom-inferred pH and Ca are synchronous in the high-latitude lakes (150, Shuttle, 396, 111) and not synchronous in lower-latitude lakes. In the higher-latitude and less-forested lakes the DI-pH and DCA axis 1 scores are synchronous, whereas in the lower-latitude/more-forested lakes the DCA axis 1 scores are more synchronous with changes in productivity, as measured by bSi and C.

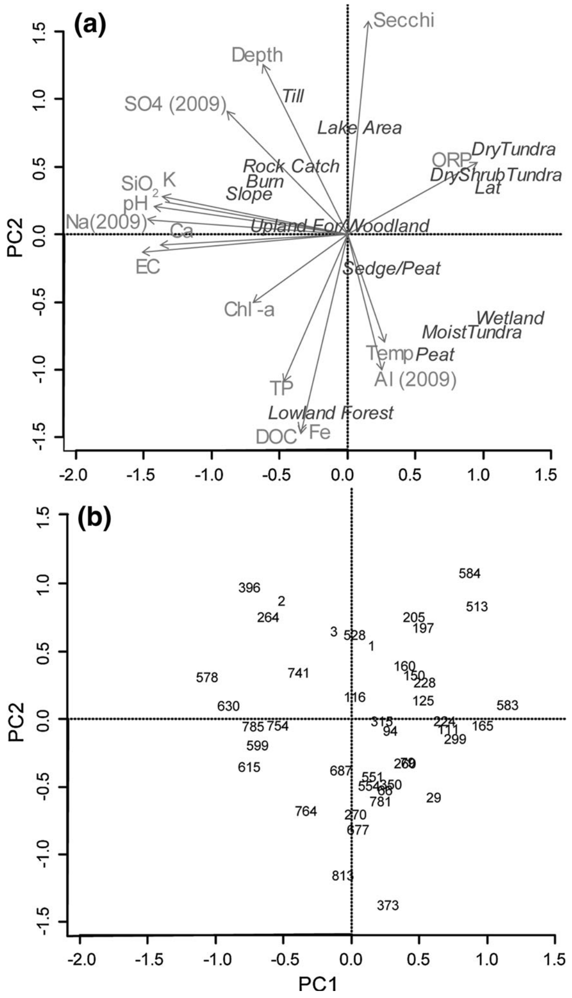


Fig. 3 Both panels based on a PCA using all water chemistry variables. **a** Only those water chemistry variables with a significant relationship to diatom distributions; landscape variables are passively plotted in the ordination space. **b** The relationship among sites. Variables are averages of 2008 and 2009 data unless noted as 2009 only

Discussion

Lake water chemistry and biotic communities are affected directly by climate (e.g. temperature, mixing, ice cover) and indirectly by the effects of climate on the catchment (e.g. changes in weathering rates, climate-driven changes in terrestrial vegetation; Leavitt et al. 2009). To understand how local factors influence diatom responses to climate change, we first examined the idea that diatom assemblages would reflect an integrated response to a suite of chemical and related landscape variables. The multivariate analyses in this study demonstrate that diatom distributions were most strongly related to water chemistry, in particular pH, whereas links between diatoms and landscape/vegetation were relatively weak. We found that diatom assemblages, based on DCA Axis 1 scores, changed increasingly rapidly in the late nineteenth and early twentieth century (Fig. 5), but the species patterns varied widely among lakes and assemblage changes were not driven by changes in *Cyclotella*/*Aulacoseira* abundance as reported elsewhere (Fig. 6; Rühland et al. 2008, 2015; Saros and Anderson 2015). Regional and locally constrained changes in the biogeochemistry of the lakes are highlighted by a slight decrease in diatom-inferred pH and Ca concentrations in some lakes, as well as increasing bSi and carbon burial rates in all lakes (Fig. 5).

Diatom assemblages showed the strongest statistical relationship with pH, although the suite of lakes represents a fairly limited pH gradient. The granite bedrock and prevalent *Sphagnum* likely account for the low pH values across the study area (Timoney et al. 1993). Species with optima for low pH include typical acidophiles, including *Frustulia* species and abundant *Eunotia* species (Camburn and Charles 2000). Developing a transfer function for pH is consistent with the results of similar work in other Arctic and sub-Arctic regions where change in lake pH is a known response to environmental and climate drivers, and pH often shows a strong relationship with diatom assemblages (Weckstrom et al. 1997; Korhola et al. 1999; Keatley et al. 2008b).

Past studies have shown that DOC is tightly linked to catchment vegetation (Pienitz and Smol 1993) and that the shift from forest to tundra is often accompanied by decreased DOC (Rühland and Smol 1998), a finding that was supported in this region by Umbanhowar et al. (2014). Similarly the amount of forest

Table 3 Maximum percent abundance and number of occurrences in the 44-lake dataset for the most commonly occurring diatom species (those found in at least half of surveyed lakes)

Species	Code	Maximum %	# of occurrences
Achnanthes sp. 1	ACEMB1	4	24
Achnanthes sp. 2	ACEMB2	3	21
Achnanthes sp. 3	ACEMB4	1	21
Achnanthidium minutissimum	ACHMINUT	6	40
Adlafia minuscula v. *muralis*	NAVMINMU	14	43
Aulacoseira ambigua	AULAMBIG	32	23
Aulacoseira distans v. *nivaloides*	AULDISNI	19	30
Aulacoseira perglabra	AULPERGL	11	23
Aulacoseira subarctica	AULSUBAR	11	21
Brachysira brebissonii	BRABREBI	3	28
Brachysira microcephala	BRAMICRO	4	23
Cavinula pseudoscutiformis	CAVPSEUD	4	33
Cymbella schubartoides	CYMSCHUB	7	33
Discostella pseudostelligera	DISPSEUD	14	22
Encyonema gracile	CYMGRACI	4	35
Encyonema hebridicum	CYMHEBRI	12	27
Eunotia meisteri	EUNMEIST	2	28
Eunotia vanheurckii	EUNVANHE	3	31
Fragilaria nanana	FRANANAN	7	35
Frustulia rhomboides	FRURHOMB	2	22
Frustulia rhomboides v. *saxonica*	FRURHOSA	4	26
Kobayasiella okadae	NAVHOEFL	6	27
Navicula leptostriata	NAVLEPTO	10	42
Neidium affine v. *amphirhynchus*	NEIAFFAM	2	27
Nitzschia gracilis	NITGRACI	5	37
Nitzschia inconspicua	NITINCON	8	40
Nitzschia palea	NITPALEA	11	36
Nitzschia perminuta	NITPERMI	6	41
Pinnularia interrupta	PININTEP	9	37
Pinnularia microstauron	PINMICRO	2	35
Psammothidium levanderi	ACELEVAN	13	41
Psammothidium subatomoides	ACEDETHA	6	39
Pseudostaurosira brevistriata v. *inflata*	PRABREIN	5	21
Rossithidium linearis	ACELINEA	3	20
Rossithidium nodusum	ACENODOS	9	32
Sellaphora cf. *auldreekie*	SELCAULD	3	21
Sellaphora difficillima	NAVDIFFI	24	33
Sellaphora pupula	SELPUPUL	3	34
Sellaphora seminulum	NAVSEMIN	13	29
Stauroforma exiguiformis	FRAEXIGU	18	38
Stauroneis anceps	STAANCEP	2	29
Stauroneis anceps v. *gracilis*	STAANCGR	3	29
Staurosira construens v. *venter*	SRACONVE	37	43
Staurosirella pinnata	SLLPINNA	29	33
Tabellaria fenestrata	TABFENES	5	26
Tabellaria flocculosa f. III	TABFLOC3	3	22
Tabellaria flocculosa f. IIIp	TABFLO3P	4	22
Tabellaria flocculosa f. IV	TABFLOC4	11	40

cover can also be a good predictor of diatom assemblages (Fallu et al. 2002). However, the statistical relationship between diatoms and DOC was relatively weak in our dataset, which can be expected along such a short gradient (Bennion et al. 2001), and likewise, the relationship of forest cover to diatom assemblages was weakly supported, but not independently robust enough to use in statistical prediction. Links have also been drawn between DOC and slope in lake catchments (Rasmussen et al. 1989; D'Arcy and Carnigan 1997). Lakes in our dataset with steeper slopes were weakly associated with higher pH and ion concentrations, and were not strongly correlated with DOC (Fig. 3). Even if DOC were not strongly correlated with our diatom assemblages, Juggins et al. (2013) recently cautioned that interpreting the effect of DOC on diatoms is often confounded by other variables.

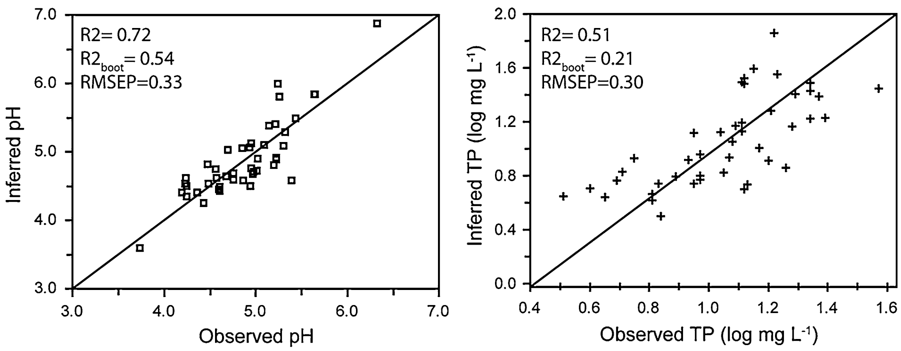
Duration of ice cover in Arctic and sub-Arctic regions can also influence diatom diversity and assemblage composition (Douglas and Smol 1999; Keatley et al. 2008a; Rühland et al. 2015), with ice cover linked to changes in light penetration, mixing, and productivity, though the effect of ice cover duration on diatom assemblages may also be related to lake depth (Smol 1983, 1988; Douglas and Smol 1999; Keatley et al. 2008a). Although we did not have an independent measure of ice duration on the surveyed lakes, we recognize the possibility that some of the relationship between lake depth and diatom assemblages may also reflect duration of ice cover or other linked variables. The overall increase in productivity in the lakes, as recorded by bSi and carbon burial, may be related to direct climate impacts, including overall warmer temperatures in the lakes and/or a longer ice-free season (Brown and Duguay 2011).

Table 4 Total (for each variable individually) and unique (for each variable when others are considered as conditional co-variables) variance explained for each of the most significant variables

	% Variance explained	Significance
pH		
Total	9.7	<0.005
Unique	3.9	<0.005
TP		
Total	4.4	<0.005
Unique	3.50	=0.01

Landscape variables were evaluated for their direct relationship with diatoms based on the idea that diatoms may integrate the average conditions in a lake over a year, or several years, as opposed to single measurements of water chemistry, and may therefore be more reflective of the effect of landscape and vegetation during a growing season than are water chemistry data. Such metrics that link diatom assemblages to indirect, integrated watershed variables have been developed elsewhere (Reavie et al. 2008); however, the gradients of landscape disturbance in those studies are much larger than the subtle variability among catchments in this data set. DOC is positively correlated with cover of forested wetlands (Umbanhowar et al. 2014), but as noted above, does not explain significant variability in modern diatom communities. Weak correlation of lake pH with open tundra or bare ground may simply reflect difficulties with remote sensing and classification of these cover types, the latter often occurring in small patches with potentially large impacts on cation delivery to lakes (Kokelj et al. 2005).

Fig. 4 Transfer functions for the independently significant water chemistry variables



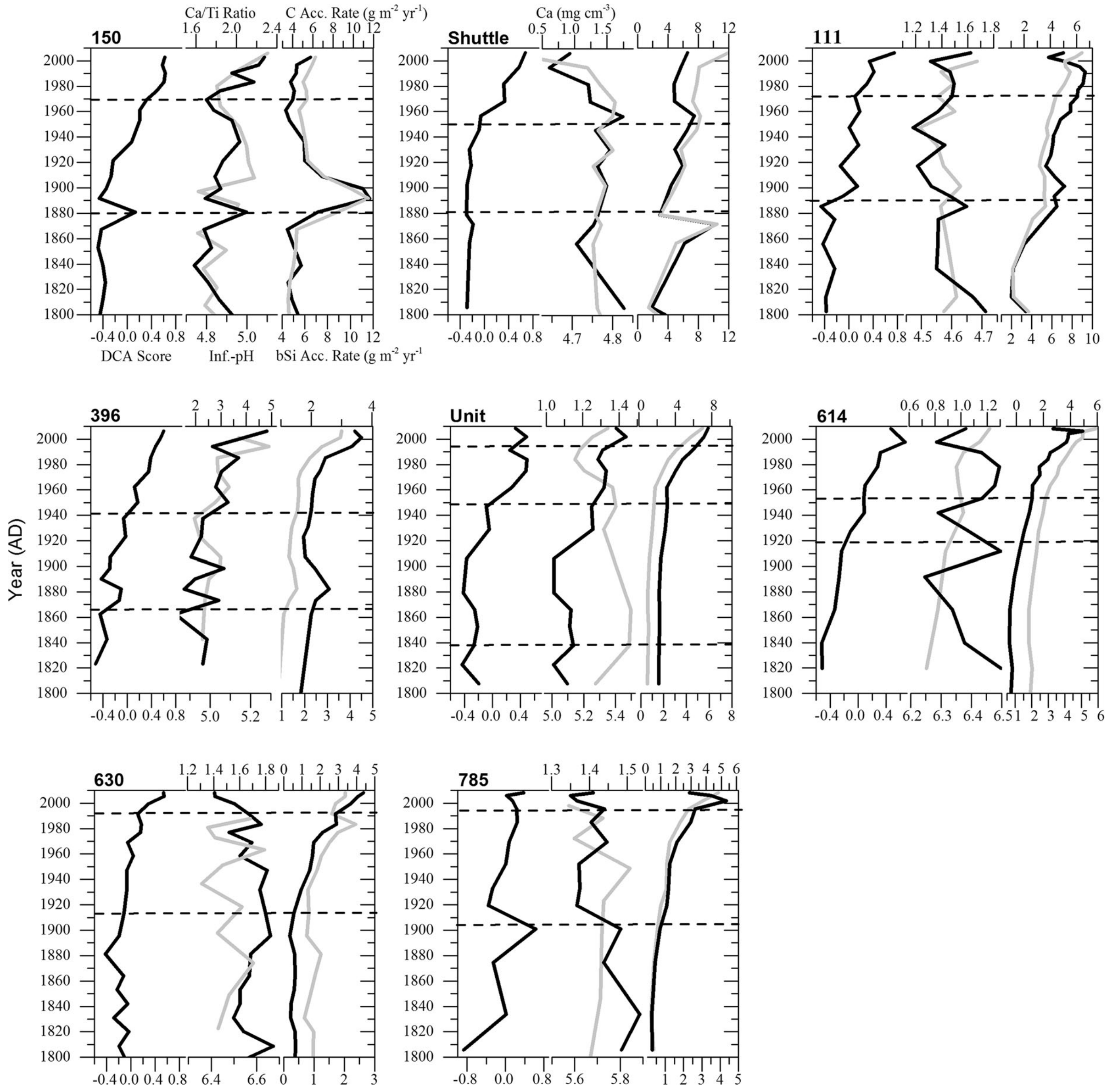


Fig. 5 Summary of changes in DCA axis scores, diatom-inferred pH (*black line*) concentration of Ca (*grey line*), and focusing-corrected biogenic silica (*black line*) and carbon (*grey line*) accumulation rates. Ca data for Lake 150 given as Ca/Ti ratio (see text). *Dashed lines* represent location of boundaries between three main clusters of diatom assemblages in each lake using hierarchical constrained cluster analysis. None of the clusters were significantly different based on a random broken-stick model to infer significance (Jackson 1993)

Landscape effects on variability in proximal paleorecords

Over the twentieth century, Manitoba experienced increasing temperatures, especially in winter, increased snowfall, and loss of permafrost (Camill 2005). The eight lakes we present here across the forest-tundra ecotone are no more than 100 km apart and experience similar changes in regional climate. Although changes in diatom assemblages and diatom-inferred changes in pH over the past 200 years were small, there was notable coherency in the changes related to landscape. DCA Axis 1 scores, bSi, and carbon burial increased in all lakes over this time

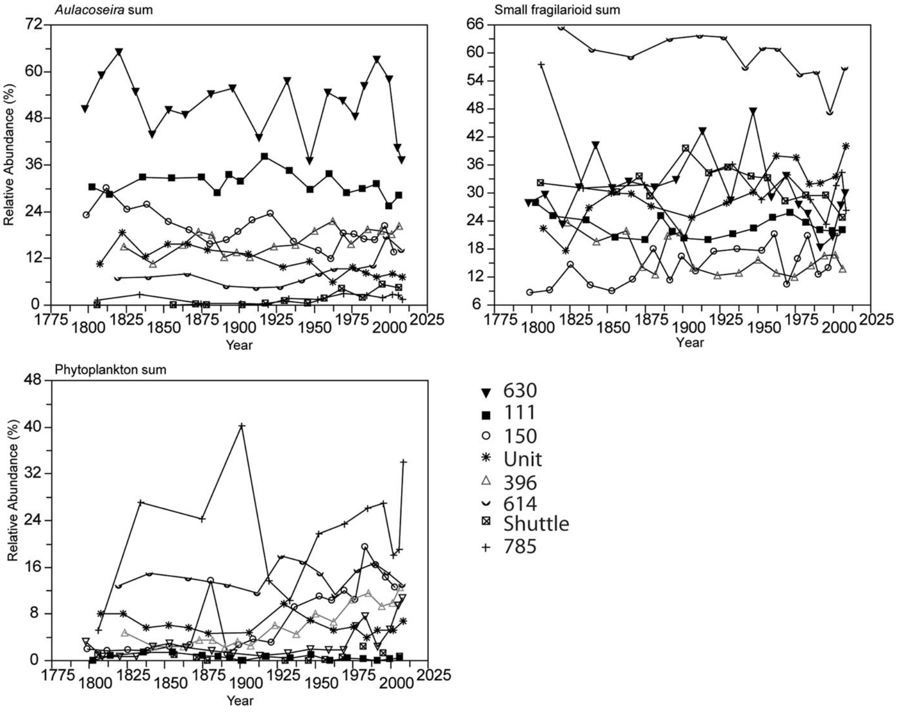


Fig. 6 *Aulacoseira* sum, small fragilarioid sum, and total phytoplankton sum over time. No clear trends or patterns of change are apparent over time, in contrast to other Arctic and sub-Arctic regions (Rühland et al. 2008)

Table 5 The ratio of the first axis scores from a Redundancy Analysis (RDA) constrained by diatom-inferred pH (λ_R) to the first axis scores of an unconstrained PCA (λ_P) on the downcore assemblage data

Lake	λ_R/λ_P
Shuttle (165)	0.57
396	0.67
150	0.58
Unit	0.61
111	0.38
630	0.59
614	0.38
785	0.61

period; higher-latitude/less-forested lakes (lakes 150, Shuttle [165], 396, Unit) record earlier changes in DCA scores than lower-latitude lakes (lakes 614, 630, 785) by several decades. In the higher-latitude/less-forested lakes there is a secondary shift in DCA Axis 1 scores between 1950 and 1970 that is absent in the two lakes with the most-forested catchments (lakes 620 and 785; Fig. 5). Lakes with >10 % Lowland Forest in the catchment (lakes 785, 630, 614, 111), regardless of latitude, showed little to no change in inferred pH, whereas three of the four lakes with <10 % Lowland Forest (lakes 150, 396, Unit [528]) in the catchment had larger changes in pH. Changes in DI-pH and changes in Ca are also synchronous in the higher-latitude lakes and the diatom-inferred pH changes explained a larger fraction of the variation in these lakes than lakes in lowland forest regions (Table 5). Synchrony of Ca with pH in the higher-latitude lakes may reflect changes in the export of bicarbonate from soils caused by changes in weathering and depth of the active layer (Tank et al. 2012). This synchrony may not be evident at lower-latitude, lowland, forest-dominated lakes because lowland forest soils have higher carbon concentration, lower pH, and higher Ca concentrations than tundra soils (Umbanhowar et al. 2014) resulting, potentially, in greater buffering. Although differences between less-forested and more-forested lakes on this time scale are small, noting the fact that catchment-level differences can outweigh latitude in influencing lake response may be significant when interpreting longer-term changes detected in sub-Arctic paleolimnological records.

Earlier work in High Arctic and other northern regions not directly impacted by human activities has shown a strong shift in diatom assemblages in recent decades, primarily linked to a longer ice-free season and stratification (Smol et al. 2005; Rühland et al. 2008, 2015). In the High Arctic, diatom communities in shallow lakes shifted between AD 1850 and 1950 toward species that are indicative of littoral or mossy habitats and are associated with longer growing periods. In deeper lakes, there was a shift toward greater planktonic cyclotelloid (*Cyclotella* and *Discostella*) species, in conjunction with decreases in *Aulacoseira* and benthic fragilarioid (e.g. *Staurosira*, *Staurosirella*, *Pseudostaurosira*) and "*Achnanthes*" species, in response to reduced ice cover and more stable stratification. Across broader regions, a meta-analysis by Rühland et al. (2008) synthesized over 200 paleolimnological records from Arctic, sub-Arctic, boreal, alpine and north temperate lakes that were characterized by $\mathrm{pH} > 6$ and total phosphorus concentrations <20 ppb. They showed consistent ecological shifts toward greater abundance of planktonic *Cyclotella* and decreased abundance of *Aulacoseira* and benthic fragilarioids beginning between 1850 and the late 1900s. Similar shifts were seen in >50 % of lakes studied in the Experimental Lakes Area of northwestern Ontario (Enache et al. 2011). Although we captured the range of lake types in this understudied sub-Arctic region, the northern Manitoba lakes contrast with lake regions that have been included in previous high-latitude paleolimnological syntheses. The median and mean pH of lakes in our region are 5.6 and 5.5, respectively, and median and mean TP concentrations are 18.5 and 23.1 ppb. Diatom community changes in northern Manitoba during the past two centuries were centered on significant shifts around AD 1900, but were of smaller magnitude compared with those in other high-latitude regions with documented climate change (Rühland et al. 2008; "Appendix"). The timing of change in northern Manitoba lakes does adhere to the broader pattern of changes shown by Rühland et al. (2008), where shifts in 15 high-latitude and Arctic lakes were centered on AD 1870, and shifts in lower-latitude north temperate lakes ($n = 60$) were centered on AD 1970.

More surprising was that species-level shifts in diatom communities were highly variable among our cored lakes. Whereas Rühland et al. (2008) found that >80 % of lakes showed greater than 5 % increases in abundance of cyclotelloids (*Cyclotella* and *Discostella*), only two (lakes 150, 396) of our eight lakes showed that pattern, and two other lakes showed decreased cyclotelloid abundance (lakes 614, Unit-528). Similarly, consistent patterns of decrease in *Aulacoseira* and fragilarioid species reported from other studies (Smol et al. 2005; Rühland et al. 2008, 2015) were ambiguous in the northern Manitoba lakes, with three lakes showing decreased *Aulacoseira* abundance (lakes 150, 111, and Unit [528]), but four lakes showing increased *Aulacoseira* abundance (lakes 165 [Shuttle], 396, 614, 785). The changes in diatom assemblages were subtle and highly variable among lakes and suggest a muted response to recent climate change in central Canada as compared to other High and Low Arctic, boreal, and north temperate systems with circumneutral pH and lower productivity (Fig. 6; "Appendix").

Potential for pH reconstruction on longer time scales

Our transfer function for pH has comparable R^2 (0.72), R^2_{boot} (0.54), and error values ($\mathrm{RMSEP} = 0.33$) to others developed for Arctic and sub-Arctic regions (Korhola et al. 1999; Keatley et al. 2008b; Hadley et al. 2013). Although we have a robust transfer function for pH and expected to see strong in-lake responses to regional warming, thawing permafrost, and vegetation changes over the past ~40 years (Camill 2005; Mamet and Kershaw 2012, Umbanhowar et al. 2013), individual lake responses differed, with only three lakes showing significant increases in pH during the twentieth century. In the highest-latitude lakes, λ_R/λ_P were higher and the inferred changes in pH tracked Ca changes well, indicating that changing ion input from the catchment could be acting as a driver for pH change. In the lower-latitude lakes with less forest cover, the λ_R/λ_P was low and DI-pH was not synchronous with changes in sediment chemistry and DCA axis 1 scores, indicating that pH inferences are likely less reliable in these cores.

Application of this pH transfer function to a longer core from Unit Lake may provide some insights into regional climate response. We estimated much larger pH changes in the cores during more pronounced and longer periods of climate change, for example a pH decrease during the Holocene Thermal Maximum (HTM; Camill et al. 2012). This may be related to longer-term, more extensive vegetation changes in the watershed. Over time scales long enough to see climate change drive a substantial shift in treeline, the treeline migration and soil development may affect lakes in several ways including pH decreases as *Picea*/*Pinus* enter the catchment area and/or *Sphagnum*-peat develops in warmer-wetter conditions, as is seen in Unit Lake during the HTM (Camill et al. 2012). Lowland forest increases may, alternatively, buffer pH changes because of higher Ca concentrations in the soils and/greater inputs of DOC, particularly when treeline is composed of more woodland/forest species. Although these terrestrial and wetland changes may significantly alter the lakes over the course of the Holocene, there is less significant impact on lakes over a 200-year time scale. On this shorter time scale, soil composition, erosion rates, and in-lake processes are likely more important. A variety of in-lake mechanisms may also increase pH over short time scales, including higher productivity and a longer growing season with warmer temperatures. The three lakes that show the most significant changes in diatom-inferred pH, range in maximum depth from 5.5 to 7.5 m and are potentially highly susceptible to climate-induced changes in stratification and mixing regime (Gorham and Boyce 1989; Rühland et al. 2015; Vonk et al. 2015). As climate-mediated changes in catchment vegetation are likely to occur and impact lakes in this region over time scales longer than 200 years (but see Umbanhowar et al. 2013), application of this landscape approach to longer core records should be explored further (Camill et al. 2012) and may help disentangle the relative contributions of direct and indirect impacts of climate changes on small regional scales, including across ecotones.

Conclusions

Paleolimnological studies have played an important role in understanding modern and historical ecological responses to climate change in the Arctic (Smol et al. 2005; Rühland et al. 2008; Camill et al. 2012). Ecotones are thought to be especially sensitive to climate change and have been targeted in the development of paleoclimatological and paleoecological records to examine the effects of past climate shifts on various ecosystems (Umbanhowar et al. 2006). Our diatom records reflected a broad regional change starting in 1900, which appears to be more pronounced in higher-latitude lakes. Small increases in pH were apparent in some cores in the past several decades, a response that, in contrast, appears to be more similar among lakes with similar, poorly forested catchments, regardless of latitude. However, changes on these time scales are small. We were unable to directly attribute the pH increases to an indirect climate-related mechanism such as landscape variation; the link between diatom assemblages and landscape variables was weak at small regional scales across landscapes characterized by short environmental gradients. Although using diatoms to directly assess lake response to vegetation composition in the catchment was inconclusive on short time scales, catchment characteristics may prove helpful for interpretations dealing with longer time scales, where climate-mediated changes in catchment vegetation are more influential (Camill et al. 2012), or in broader regional comparisons among lakes. Catchment-scale differences should be taken into account when interpreting paleolimnological records; however, multi-proxy approaches are necessary, as diatom-based transfer functions may not be sensitive enough across such small gradients and short time scales to be useful for interpreting these subtle watershed effects and identifying indirect mechanisms of climate response. Comparison with larger studies and meta-analysis from neighboring regions demonstrates the need for further work to understand muted and variable biological responses in low-Arctic versus high-Arctic lakes, in response to documented warming in recent decades.

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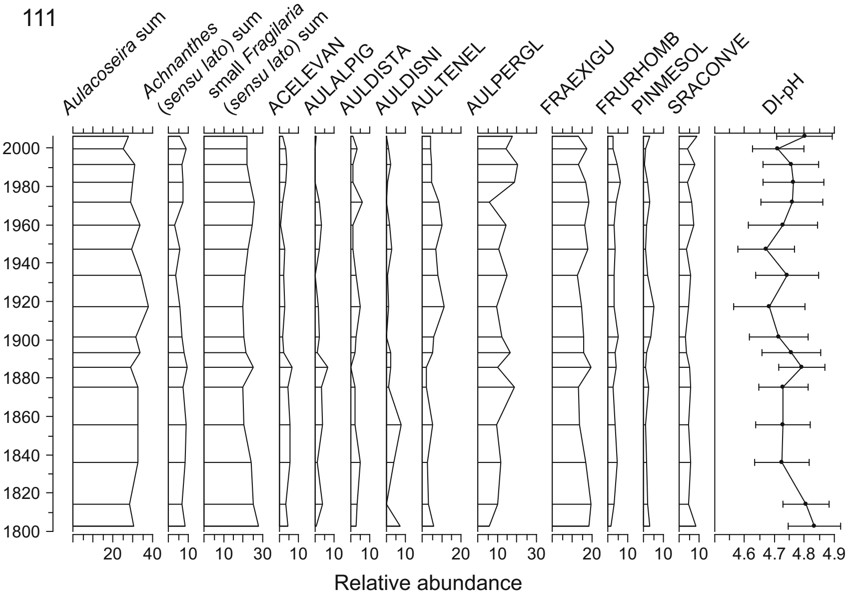
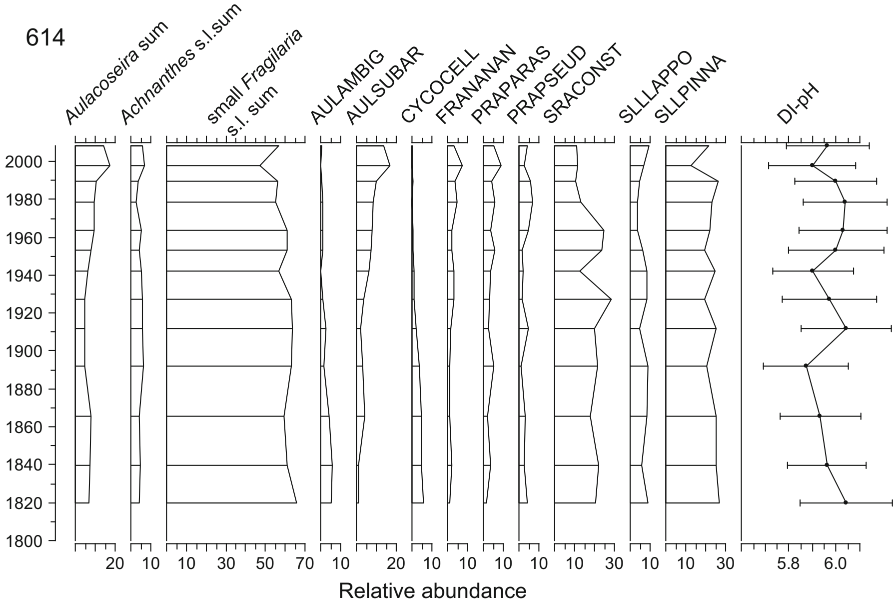
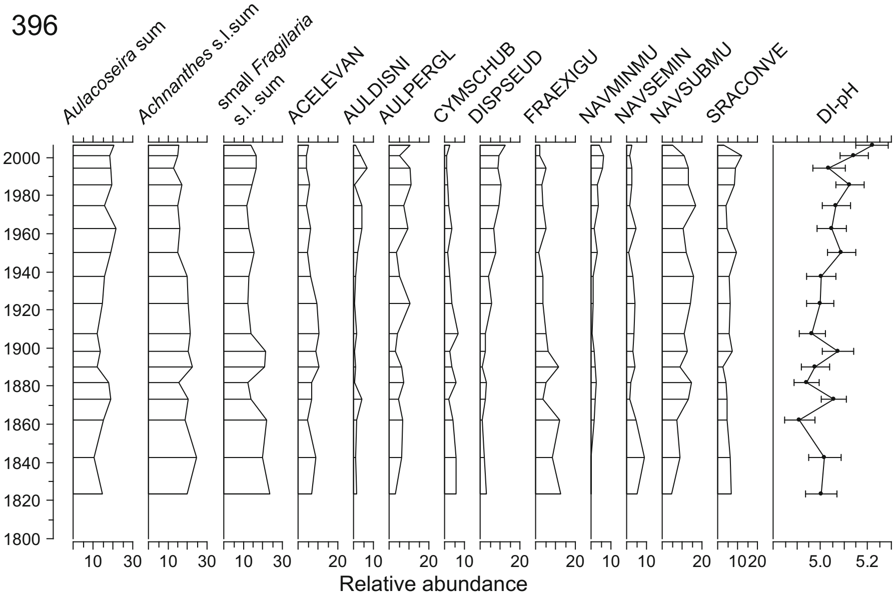
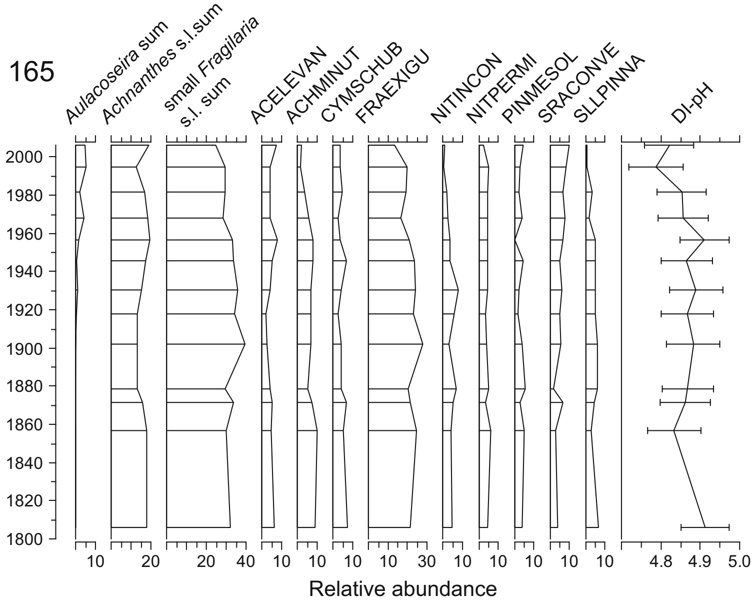
Appendix

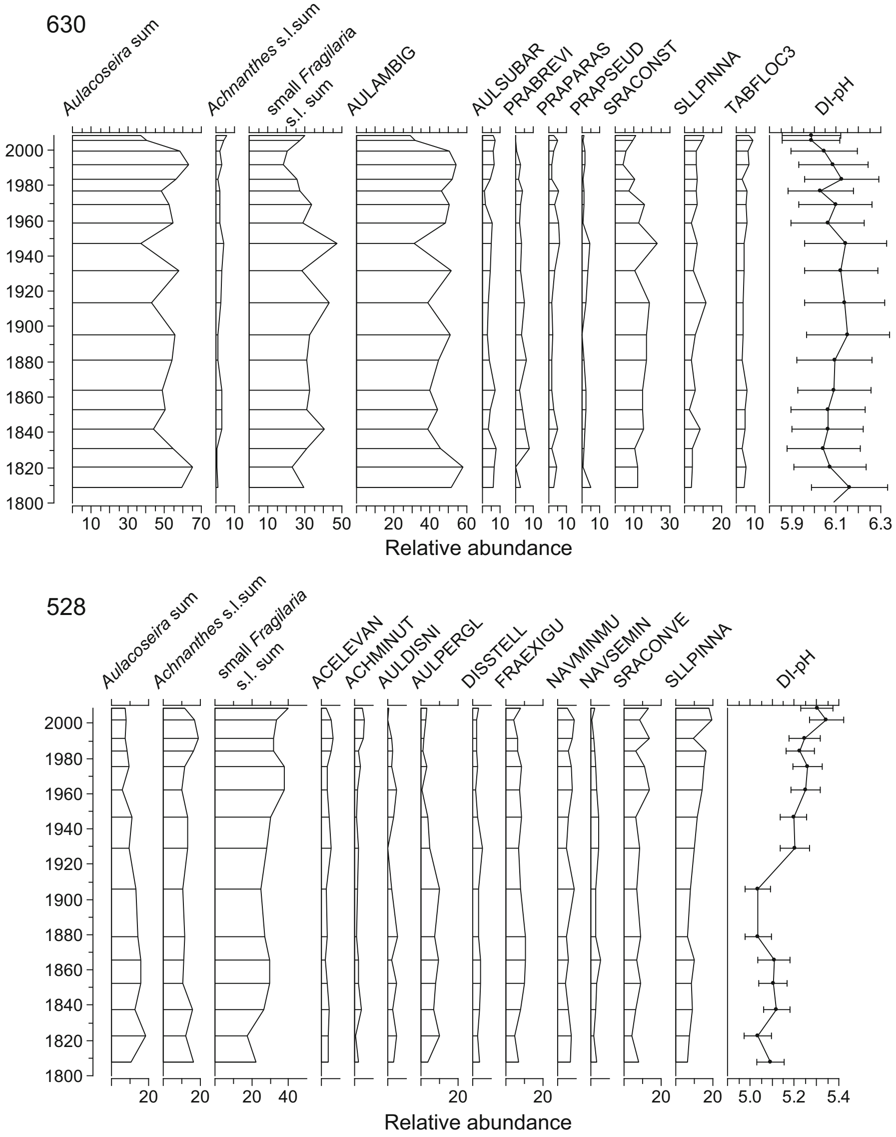
Relative abundance of the most common diatom species in all lakes






396
Aulacoseira sum
Achnanthes s.l.sum
small Fragilaria s.l. sum
ACELEVAN
AULDISNI
AULPERGL
CYMSCHUB
DISPSEUD
FRAEXIGU
NAVMINMU
NAVSEMIN
NAVSUBMU
SRACONVE
DI-pH
2000
1980
1960
1940
1920
1900
1880
1860
1840
1820
1800
10 30 10 30 10 30 20 10 20 10 20 20 10 10 20 1020 5.0 5.2
Relative abundance


165
Aulacoseira sum
Achnanthes s.l.sum
small Fragilaria s.l. sum
ACELEVAN
ACHMINUT
CYMSCHUB
FRAEXIGU
NITINCON
NITPERMI
PINMESOL
SRACONVE
SLLPINNA
DI-pH
2000
1980
1960
1940
1920
1900
1880
1860
1840
1820
1800
10 20 20 40 10 10 10 10 30 10 10 10 10 10
4.8 4.9 5.0
Relative abundance


630
Aulacoseira sum
Achnanthes s.l.sum
small Fragilaria s.l. sum
AULAMBIG
AULSUBAR
PRABREVI
PRAPARAS
PRAPSEUD
SRACONST
SLLPINNA
TABFLOC3
DI-pH
2000
1980
1960
1940
1920
1900
1880
1860
1840
1820
1800
10 30 50 70
10
10 30 50
20 40 60
10
10
10
10
10 30
20
10
5.9 6.1 6.3
Relative abundance
528
Aulacoseira sum
Achnanthes s.l.sum
small Fragilaria s.l. sum
ACELEVAN
ACHMINUT
AULDISNI
AULPERGL
DISSTELL
FRAEXIGU
NAVMINMU
NAVSEMIN
SRACONVE
SLLPINNA
DI-pH
2000
1980
1960
1940
1920
1900
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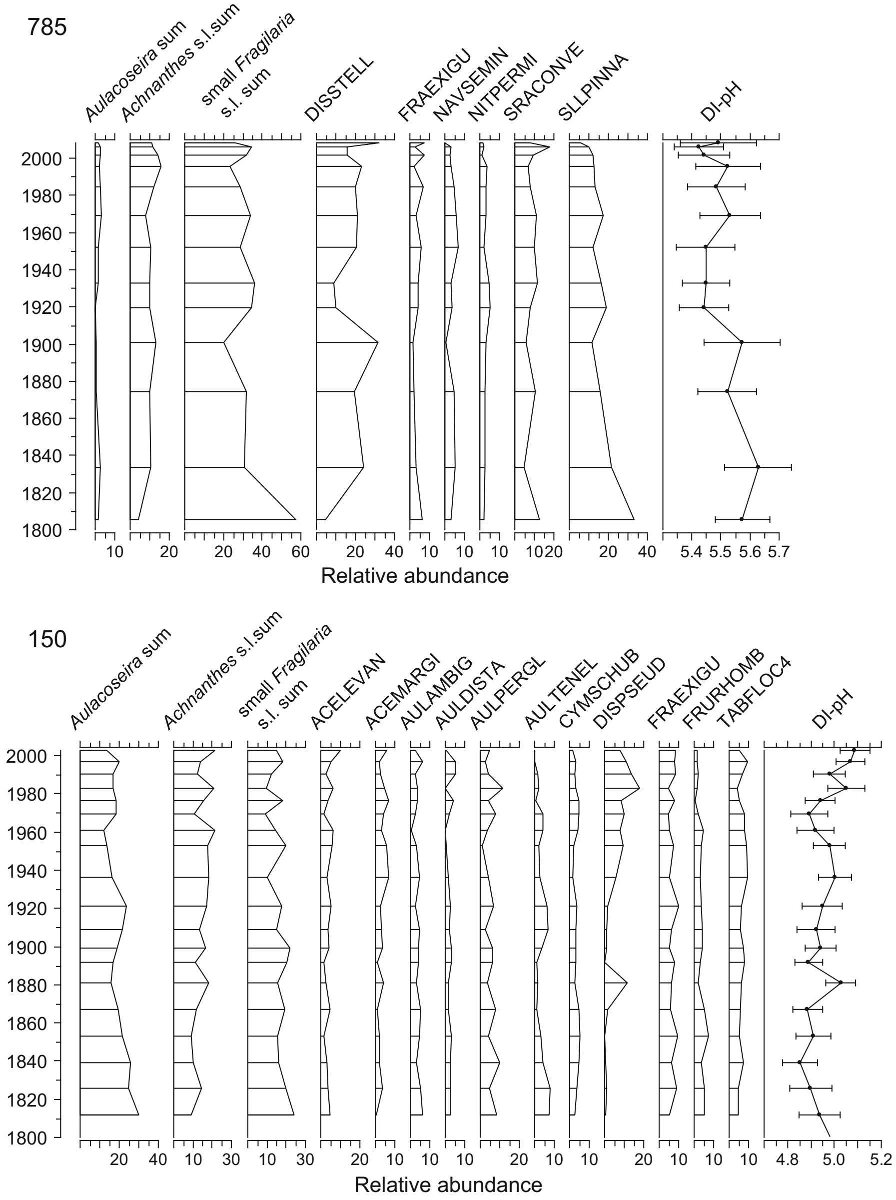
20
20
20 40
20
20
20
20
5.0 5.2 5.4
Relative abundance



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