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Evidence for temporally coherent increases in the abundance of small *Discostella* (Bacillariophyceae) species over the past 200 years among boreal lakes from the Experimental Lakes Area (Canada)

Brendan Wiltse · Graham R. Mushet · Andrew M. Paterson · Brian F. Cumming

Abstract Increased relative abundances and accumulation rates of the small, centric diatom *Discostella* have been recorded in numerous paleolimnological investigations of north temperate lakes that span the last century. Yet, conflicting observations in the seasonal succession of small *Discostella* from monitoring studies, and opposite patterns in their abundance in sediment cores from some nearby lakes have prevented consensus on the mechanisms responsible for this trend. Differences in lake and catchment characteristics that filter biological responses to regional environmental changes have likely played a role in this variability. We present detailed sub-fossil diatom data in dated sediment cores from eight small lakes in the undisturbed Experimental Lakes Area of northwest Ontario, Canada. These lakes were chosen because they experienced large (> 25%) increases in relative abundance of small *Discostella* taxa since preindustrial times, enabling a clearer assessment of their change over time and linkages with climate. Our data showed increased abundances of small *Discostella* in all lakes, with changes in the majority of lakes beginning in the mid-1800s. Application of a hierarchical generalized additive model structure provided statistical evidence that this pattern was shared among all lakes, although lake-specific departures from this trend were also apparent. Based on the coincidence of trends with historical temperature records and results from previous phytoplankton monitoring studies in the ELA, we suggest that the observed recent increases in the proportion of *Discostella* may be related to earlier ice-off and extended periods of spring mixing, and that the small amount of between-lake variability is attributable to differences in lake morphometry.

Keywords *Discostella* · Hierarchical generalized additive models · Climate · Paleolimnology · Experimental Lakes Area

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Introduction

Twentieth century increases in small, planktonic diatom taxa in temperate and sub-Arctic lakes are a prominent feature of numerous recent paleolimnological investigations (Rühland et al. 2015; Saros and Anderson 2015) and have led to efforts to try and understand proximate mechanisms responsible for this trend. The microscopic ($\sim$ 4–15 μm), centric *Discostella* species such as *D. stelligera* and *D. pseudostelligera* are often important taxa that contribute to this pattern. Proliferation of these taxa has been documented in dated lake-sediment cores from diverse physiographic regions, including boreal temperate (Harris et al. 2006; Rühland et al. 2008; Enache et al. 2011), high-elevation (Karst-Riddoch et al. 2005; Rühland et al. 2008; Saros et al. 2012), sub-Arctic and Arctic (Sorvari et al. 2002; Smol et al. 2005; Rühland et al. 2008), and equatorial (Michelutti et al. 2015) areas. Given that these patterns are geographically widespread, the forcing mechanisms are usually considered to be regional in nature. Although extended open-water seasons and/or enhanced thermal stratification as a result of twentieth century warming is frequently invoked as an explanation, authors have proposed the possible importance of other regional stressors such as enhanced atmospheric deposition of reactive nitrogen (Saros and Anderson 2015) and altered light dynamics as a result of changes in the delivery of terrestrial particles and solutes driven by climate and/or reductions in acid deposition (Brown et al. 2017).

An important obstacle to understanding small *Discostella* ecology and bloom dynamics has been disparate observations in both the timing and direction of change in *Discostella* relative abundances in nearby lakes. For example, Saros and Anderson (2015) noted that two lakes in the central Rocky Mountain region, situated $\sim$ 30 km apart, showed opposite trends in abundance over the twentieth century. Inconsistent patterns in *Discostella* abundances have also been documented in lakes across the state of Maine (Boeff et al. 2016), and in large, boreal lakes in central North America (Saros and Anderson 2015). Monitoring studies have also provided data that are difficult to reconcile, with some lakes showing peak water-column abundances of small *Discostella* taxa during spring and fall mixing (Catalan et al. 2002; Köster and Pienitz 2006; Thackeray et al. 2008; Wiltse

et al. 2016) and others showing peak abundances during summer thermal stratification (Winder and Hunter 2008; Saros et al. 2012). In some cases, the same lake can show variable patterns in the seasonal abundance of *Discostella* in different years (Malik et al. 2018).

Temporal variability in *Discostella* abundances between nearby lakes is likely caused, at least in part, by lake and catchment characteristics that vary across a landscape and act to filter biotic responses to regional stressors. Lake elevation, catchment size, vegetation and soil characteristics, lake morphometry, and lake-specific foodweb structure are examples of lake and catchment variables (Blenckner 2005). Given this heterogeneity among lakes, it follows that algal communities respond differently to regional environmental stressors (Patoine and Leavitt 2006), especially between lake districts or systems from different physiographic regions (Arnott et al. 2003; Magnuson et al. 2004). Therefore, selecting study lakes to maximize signals of species of interest is an important step in assessing regional and temporal coherence (which we define as similarity in the timing, direction, and variability of change in the abundance of a species among lakes), and understanding linkages with regional climate. In this study, we present detailed sub-fossil diatom assemblages from eight study lakes in the Experimental Lakes Area (ELA), a region of northwest Ontario, Canada, that has remained relatively undisturbed from urban and industrial activity. Lakes were selected to have experienced large ($\geq$ 25%) increases in the relative abundance of small *Discostella* taxa since pre-industrial (pre-1850) times, based on results of a previous top-bottom paleolimnological study of sub-fossil diatom assemblages in 40 ELA lakes (Enache et al. 2011). This approach allowed us to be confident we were analyzing the appropriate lake types that support small *Discostella*, enabling a clearer assessment of their change over time and response to regional stressors. Specifically, we used detailed diatom data coupled with newly described hierarchical generalized additive models (HGAMs) to address three questions: (i) is there statistical support for coherence in changes in small *Discostella* abundances over the past 200 years in this region; (ii) when did abundances begin to change; and (iii) do these changes correspond to changes in climate?

Materials and methods

Study area

The eight study lakes are in the Experimental Lakes Area (ELA), a ∼ 550-km² region of northwest Ontario that encompasses 58 lakes and their watersheds that were selected for whole-ecosystem experiments and long-term environmental and ecological monitoring (Fig. 1). This region has a low population density and no urban or industrial development, which makes it a suitable location to study lakes and streams with minimal influence from local anthropogenic stressors (Blanchfield et al. 2009). Detailed descriptions of catchment and climate characteristics of the region can be found in Mushet et al. (2018). Briefly, the landscape is typical of the Ontario Shield, with Precambrian Shield (granite) bedrock, thin soils, and coniferous forests. Climate is continental, with cold winters and hot summers. Mean annual air temperature (MAAT) and precipitation (MAP) recorded in nearby Kenora (∼ 55 km from the ELA field station)
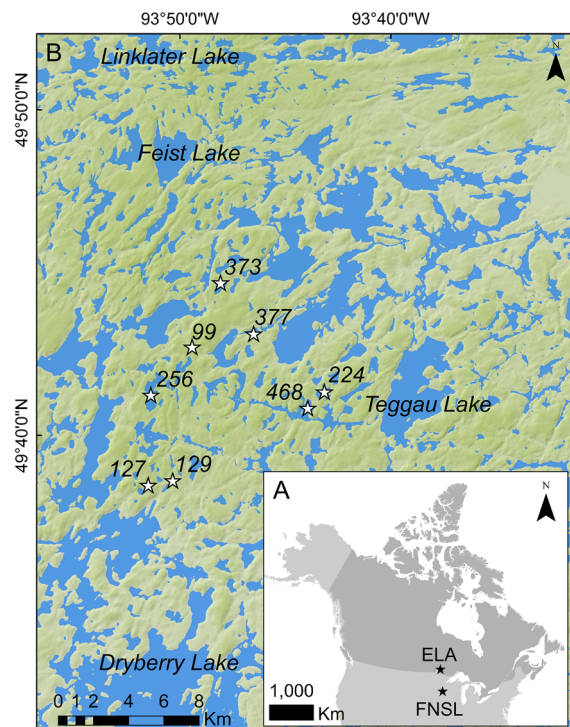
Fig. 1 A Location of the Experimental Lakes Area (ELA; Ontario, Canada), and Fort Snelling (FNSL; Minnesota, USA), relative to Canada and the USA. **B** Location of the eight study lakes within the ELA

are 3.3 °C and 794 mm, respectively, for the period 1980–2015.

The study lakes are relatively small, with surface areas (SA) < 150 ha (except for Lake 468 [290 ha]) and water depths ≤ 25 m (Table 1). Water chemistry measurements taken as mixed layer composites in June 2006 indicated the lakes are oligotrophic (total phosphorus < 10 μg L⁻¹ in all lakes), slightly acidic to circumneutral (pH range 6.3–7.2) and have low-to-moderate concentrations of dissolved organic carbon (range 2.9–8.9 mg L⁻¹). None of the study sites had experienced experimental manipulations for unrelated studies prior to the date of core collection (Enache et al. 2011; Mushet et al. 2018).

Sample collection and core chronologies

Sediment cores were collected from the deepest basin of each lake in June 2006, using a Glew gravity corer with an internal core tube diameter of 7.62 cm (Glew et al. 2001). Cores were extruded and sectioned on site at 0.5-cm intervals. Samples were transported to Queen's University where they were kept in cold storage (4 °C) until processed for analysis. Water samples were collected at the time of coring using an integrated water sampler, and were later analyzed using standardized protocols at the Ontario Ministry of the Environment, Conservation and Parks' Dorset Environmental Science Centre (Ontario Ministry of the Environment 1983). Lake 224 was not sampled at that time because it was a regularly monitored lake at the ELA.

Chronologies of the cores are based on ²¹⁰Pb activities that were measured using gamma spectroscopy at the Paleoecological Environmental Assessment and Research Laboratory (PEARL), following procedures and instrumentation described in Schelske et al. (1994). Dates for intervals that were selected for ²¹⁰Pb analysis were estimated using the constant rate of supply (CRS) model applied to the unsupported fraction of ²¹⁰Pb activity (Binford et al. 1990). Undated intervals were interpolated using a monotonic cubic spline (Simpson 2018), and these models were also used to extrapolate dates to ∼ 1800 CE, when necessary. All dates are presented in years Common Era (CE) hereafter.

Table 1 Physicochemical characteristics of the study lakes

Lake	TP (μg L^{-1})	NO$_3$/NO$_2$ (μg L^{-1})	SiO$_2$ (mg L^{-1})	DOC (mg L^{-1})	pH	Specific conductance (μS cm^{-1})	Depth (m)	Surface area (ha)	Elevation (m)
ELA 99	9.7	16	0.10	8.9	6.4	13.8	6	7	438
ELA 127	9.1	2	0.22	5.7	6.3	11.8	5	5	427
ELA 129	8.3	2	0.32	9.6	6.5	14.8	6	5	402
ELA 224	5.0	10	0.20	2.9	7.0	18.0	25	25	410
ELA 256	4.4	4	0.16	3.3	6.7	23.0	25	120	426
ELA 373	–	4	1.28	3.6	7.2	23.0	15	28	423
ELA 377	4.0	6	0.94	4.8	7.2	20.2	16	27	390
ELA 468	4.3	252	0.20	5.0	7.0	25.6	15	290	403

Water samples were collected as mixed-layer composites in June 2006. Water chemistry data from Lake 224 are from ELA monitoring records for 6 June 2006 and represent a surface-water sample. Depth is water depth at the coring location, which occurred at the center of the deepest basin within each system

Diatom analysis

Sub-fossil diatoms were analyzed at either 1-cm or 0.5-cm resolution, depending on sedimentation rate, over the past $\sim$ 200 years in each core. For each sample, approximately 0.2–0.3 g of wet sediment was placed in a 20-mL glass vial and digested in a 50:50 (molar) mixture of concentrated nitric (HNO$_3$) and sulfuric (H$_2$SO$_4$) acid. Samples were kept in a hot-water bath ($\sim$ 75 °C) for 8 h to accelerate the digestion of organic matter. The samples were then allowed to settle for 24 h prior to being aspirated to a volume of $\sim$ 5 mL and diluted with double-deionized water. The process of aspiration, dilution and settling was repeated daily until they reached the pH of the deionized water (7–8 rinses). The samples were then aspirated to a volume of $\sim$ 5 mL, and a known volume of microsphere solution (2.0 $\times$ 10^7 spheres mL^{-1}) was added to each sample to enable the calculation of diatom concentrations. Four successive dilutions for each sample were pipetted onto coverslips, allowed to dry overnight, and mounted onto glass slides using Naphrax®. At least 400 diatom valves were enumerated from slides for each sample to the lowest possible taxonomic unit, using a Leica DMRB microscope fitted with a 100$\times$ Fluotar objective with differential interference contrast optics at 1000$\times$ magnification. Taxonomic identification followed Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), and Lange-Bertalot and Metzeltin (1996).

Numerical analysis

To determine if there was statistical support for coherence in small *Discostella* abundances through time in our cores, we utilized the hierarchical generalized additive model (HGAM) framework described in Pedersen et al. (2019). HGAMs can be seen as an integration of the hierarchical generalized linear model (HGLM), which are often used to allow linear relationships between predictor and response to vary across a grouping level, and the generalized additive model (GAM), which are used to model flexible relationships between a response variable and covariate(s). The flexible nature of the HGAM framework is ideal for paleoecological data, where we have a priori defined grouping levels, but do not necessarily expect a linear relationship between proxy data and sediment age.

Within the HGAM framework, group-level smooths can have varying degrees of departure from a "common" (global) trend, such as differences in shape and how quickly a function changes (i.e., wiggliness/complexity; Pedersen et al. 2019), though departures from the common trend are penalized to be close to the mean function. The degree of information shared between groups (i.e., intergroup variability) is controlled in each model formula. Using the *mgcv* package (Wood 2020) in R (R Core Team 2018), this is accomplished through the use of either factor smooth interactions, which allows a separate smooth for each level of a factor, but with the same smoothing parameter for all smooths, or via the use of the "by"

argument, whereby each level of the by factor gets its own smoothing parameter [allowing each group-specific smoother to have its own complexity (Wood 2020)].

In all models, grouping levels are included as a random effect, to enable group-specific intercepts. For each of the eight lakes, the HGAMs were run on three separate response variables: (1) the accumulation of small *Discostella*; (2) the relative abundance of small *Discostella*; and (3) principal curve (PrC) scores that summarize the changes in the diatom assemblages for each core (Simpson and Birks 2012). These response variables were modeled as a function of age (^{210}Pb date) and lake I.D. (i.e., the grouping level in this study). Following Pedersen et al. (2019), we produced three separate models, each one with progressively less information shared among individual lakes. Model 1 assumed one common smooth for the response variable for all eight lakes, testing the hypothesis that a single temporal trend was present across all eight lakes [model G in Pedersen et al. (2019)]. Model 2 tested the hypothesis that some inter-lake variability was present, by including the global smooth term (as in Model 1), but also allowing individual lakes to deviate from the common trend in terms of both shape (by penalizing functions that are too far from the average) and complexity [Model GI in Pedersen et al. (2019)]. Model 3 tested the hypothesis that the response was strongly lake-specific, by allowing response shape and complexity to be unrelated between lakes by removing the global smooth term [Model I in Pedersen et al. (2019)]. Model formulae and descriptions are shown in Table 2.

Restricted maximum likelihood (REML) was used as the smoothness selection method, and in all models, observational weights (the number of years represented by each sample) were used to help account for heteroscedasticity in the response variables, a characteristic common to paleolimnological data, caused by changing sedimentation rates and sediment dewatering with depth in the core (Simpson 2018). In the case of accumulation data, error distributions from the gamma family with a log-link function were used, and for relative abundances, error distributions from the beta family (and logit link) were used, which is appropriate for data confined to the interval (0,1). The Akaike information criterion (AIC) was used as evidence for model parsimony, to assess which

model(s) best fit the data (Burnham and Anderson 2002).

To determine when accumulations of small *Discostella* taxa began to change in the dated cores from the eight ELA lakes, we applied additional GAMs in which the response was modeled individually within cores, with ^{210}Pb age as the sole covariate. The individual models enabled the identification of periods of significant change, as identified by the first derivative of the estimated trend, when evaluated at regularly spaced time-steps over the length of each record. Where the derivative and its confidence interval was non-zero, that time point is considered to be undergoing significant change (either increasing or decreasing). This procedure was carried out as described in Simpson (2018). Smoothness selection, basis spline type, choice of error distribution family, and inclusion of observational weights were the same as described above for the HGAMs. Finally, we also applied individual GAMs to recorded climate data from nearby Kenora (~ 55 km northwest of the ELA), and a long-term temperature record from Fort Snelling, MN (Fig. 1; Baker et al. 1985), which is one of the few temperature records that pre-dates the beginning of the 20th century, to compare trends with changes in *Discostella*. Because the Fort Snelling record extends only to 1980, we estimated post-1980 air temperature values for this site using a linear regression with overlapping temperature data (for the period 1895–1982) recorded in nearby Farmington, MN, 30 km south of Fort Snelling. All statistical analyses were carried out using R (R Core Team 2018), with packages *mgcv* (Wood 2020) and *analogue* (Simpson 2020).

Results

Sediment core chronologies

Cores from all eight lakes had high activities of total and unsupported ^{210}Pb, and a characteristic exponential decay of total ^{210}Pb with core depth (ESM Fig. 1), with an R^2 for a first order exponential decay ranging from 0.91 to 0.97. Linear models fit to cumulative dry mass and log unsupported ^{210}Pb also showed excellent fits (R^2 from 0.85 to 0.98). The high unsupported activities and exponential profiles enabled development of core chronologies with relatively low

Table 2 Hierarchical generalized additive model (HGAM) formulae

Model number	Model formula	Model description	Evidence for temporal coherence
1	$g(\mu_i) = b_j + f(age_i)$	Single common smoother (Global smoother)	High
2	$g(\mu_i) = b_j + f(age_i) + f_j(age_i)$	Global smoother + group-level smoothers with differing complexity	Medium
3	$g(\mu_i) = b_j + f_j(age_i)$	Group-specific smoothers of differing complexity	Low

$g(\mu_i)$ is an inversible monotonic link function, b_j is the intercept for the jth lake, $f(age_i)$ is the global smooth of age, and $f_j(age_i)$ represents the smooth of age for the jth lake [i.e., defined using the "by" argument in *mgcv* (Wood 2020), which characterizes the departure from the common trend]. Model specifications follow those presented in Pedersen et al. (2019)

uncertainties. Background (supported) ^{210}Pb was reached at core depths ranging from $\sim$ 10 cm (Lake 373), between 10 and 15 cm (Lakes 224 and 468), between 15 and 20 cm (Lakes 99, 127, 129, 377), and > 20 cm (Lake 256) (ESM Fig. 1). For modeling the diatom data to $\sim$ 1800 CE, some extrapolation of ^{210}Pb dates was necessary, although only the final 1–4 data points are based on extrapolation, except for Lakes 224 and 256, for which the bottommost 5 and 8 samples have extrapolated ages, respectively. Diatom enumeration at 1-cm resolution in cores from all lakes (except Lake 373, analyzed every 0.5 cm) resulted in approximately decadal-scale resolution between samples in most lakes, ranging from $\sim$ 7 years in Lake 256 to $\sim$ 14 years in Lake 468.

Diatom assemblages

Diatom assemblages in cores from all lakes were relatively diverse, containing between 91 and 164 taxa. Importantly, small *Discostella* spp. (*D. stelligera* + *D. pseudostelligera*) were an important component of the planktonic community in all lakes, and on average accounted for 40% (range 12–50%) of the assemblage across all lakes during the post-1900 period, whereas they accounted for 24% on average (range 1–40%) during the period between 1800 and 1900 (Fig. 2). Other planktonic taxa present in the cores included additional species from the group *Cyclotella sensu lato* such as *Cyclotella bodanica* v. *lemanica*, *Lindavia ocellata*, *Lindavia tripartita*, and *D. stelligera* v. *robusta*, in addition to some pennate planktonic taxa such as *Tabellaria flocculosa*, *Asterionella formosa*, and *Fragilaria tenera* (ESM Figs. 2–9). Most lakes also had diverse benthic

communities, with benthic taxa accounting for, on average, between 25 and 45% of the assemblage, except for Lake 127, which consisted of $\sim$ 80% benthic taxa on average (ESM Figs. 2–9). A trend towards a smaller proportion of benthic taxa over the past 200 years was evident in all lakes (ESM Fig. 10). It is important to note that in the subsequent numerical analysis of changes in small *Discostella* over time, we excluded *D. stelligera* v. *robusta*, as it is often larger (> $\sim$ 15 μm) and much more heavily silicified than the nominate variety (Houk and Klee 2004; Flower 2006).

Hierarchical generalized additive models (HGAMs)

Within the HGAM framework, we ran all three response variables twice to assess the sensitivity to different time frames, using the dataset to 1850 CE (little to no extrapolation of ^{210}Pb dates), and the dataset to 1800 CE (some extrapolation of ^{210}Pb dates required). Regardless of the timeframe used, Model 2 (inclusion of global smooth, but with group-level smoothers of differing complexity) provided the best fit to all three response variables analyzed, based on AIC (Table 3, ESM Table 1). Hence, we focus our results and discussion on the $\sim$ 200-year dataset. Among all three response variables, there was strong support that Model 1 (single global smooth) did not allow sufficient among-lake variability and was always the weakest model. Model 3 is equivalent to Model 2 without the addition of a global smooth. Given that Model 3 provided the second-best fit for all three metrics and had a much lower delta AIC compared to Model 1, it highlights the importance of
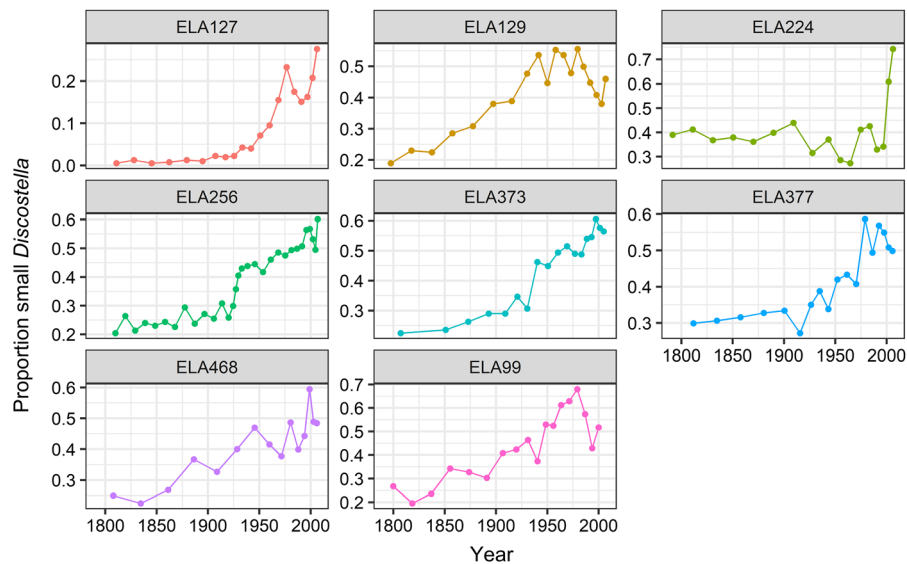
Fig. 2 Proportion of small *Discostella* (*D. stelligera* + *D. pseudostelligera*) over the last ∼ 200 years in eight lakes from the Experimental Lakes Area (ELA)

allowing smooth complexity to vary between individual lakes, as well as variation in individual lake response shape. In summary, the HGAMs provide strong support for allowing inter-lake variability in temporal trends for all response variables, but also that a shared trend is an important characteristic of the data.

When small *Discostella* abundances were predicted using Model 2, a trend towards higher values over the period of record was evident in all lakes with respect to accumulations (valves cm^{-2} yr^{-1}, Fig. 3), and in all lakes except for Lake 224 with respect to relative abundances (ESM Fig. 11). Indeed, this was reflected in the similar global trend for both metrics (Fig. 4). The similarity between the accumulation and relative abundance data indicates that we can interpret the increases in relative abundances as increases in the production of these taxa. Model 2 predictions indicated that *Discostella* accumulations began to increase in most of the lakes after ∼ 1860 (Fig. 3), coinciding with the available temperature records, particularly the longer record from Fort Snelling, Minnesota (Fig. 4), which we were able to extend to 2010 based on a high degree of correlation with the Farmington, MN record (ESM Fig. 12). Departures from the common trend, however, were evident in some cases. For example, Lakes 129 and 99 showed subsequent declines in accumulations

after ∼ 1970, whereas Lake 256 remained at stable values after ∼ 1950 (Fig. 3). When PrC scores were modeled, the common trend had a slightly different shape compared to the accumulation data and showed a gradual increase in PrC scores beginning at ∼ 1825 (Fig. 4). Lake-specific departures from the common trend were most pronounced in Lakes 224 and 377 (ESM Fig. 13).

Timing of the initial changes in small *Discostella* (individual GAMs)

Individual GAMs of the small *Discostella* accumulations (with ^{210}Pb age as the sole covariate) fit well, explaining at least 80% of the variation in individual time series. The derivatives of these individual models indicate where the rate of change is non-zero (i.e., significantly increasing or decreasing), with the results from most lakes showing an initial significant increase between 1850 and 1860, with the exception of Lake 256, in which it occurred at ∼ 1890 (Fig. 5). Only two of the lakes (Lakes 127 and 468) showed continuous significant increases until present, whereas lakes 224, 373, and 377 experienced little change during the early-to-mid 1900s, before showing a second period of significant increase at ∼ 1950. Lakes 99 and 129 showed brief (∼ 10 years) significant declines

Table 3 Results of hierarchical generalized additive models (HGAMs) run on the three metrics of interest using the extended dataset (i.e., extrapolated to 1800)

| Model	Model description	df	Deviance explained (%)	AIC	delta AIC
Small *Discostella* accumulations					
1	Single common smoother	13	86.8	4564	247
2	**Global smoother + group-level smoothers with differing complexity**	**65**	**98.6**	**4317**	**0**
3	Group-specific smoothers of differing complexity (no global smoother)	55	98.2	4350	33
Small *Discostella* relative abundance					
1	Single common smoother	11	89.6	− 426	206
2	**Global smoother + group-level smoothers with differing complexity**	**55**	**98.6**	**− 632**	**0**
3	Group-specific smoothers of differing complexity (no global smoother)	38	97.5	− 575	57
PrC scores					
1	Single common smoother	11	73	534	215
2	**Global smoother + group-level smoothers with differing complexity**	**59**	**96.6**	**319**	**0**
3	Group-specific smoothers of differing complexity (no global smoother)	43	94.4	361	42

Models in bold are those suggested to be the best fit based on AIC
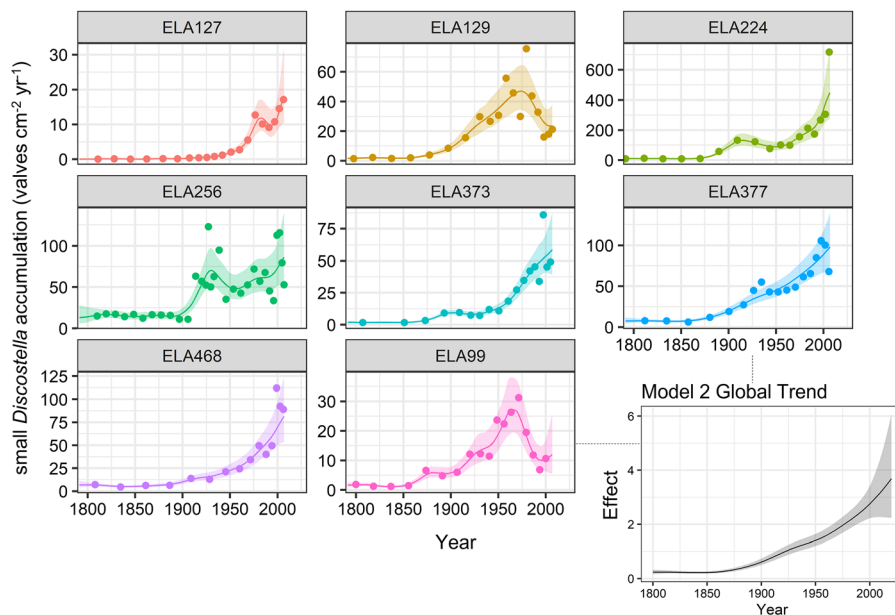
Fig. 3 Trends in the accumulation of small *Discostella* species for eight lakes from the Experimental Lakes Area (ELA) over the past ∼ 200 years, as predicted by Model 2 within the hierarchical generalized additive model (HGAM) framework. The shaded bands in each plot represent the 95% confidence intervals. The global trend is also shown
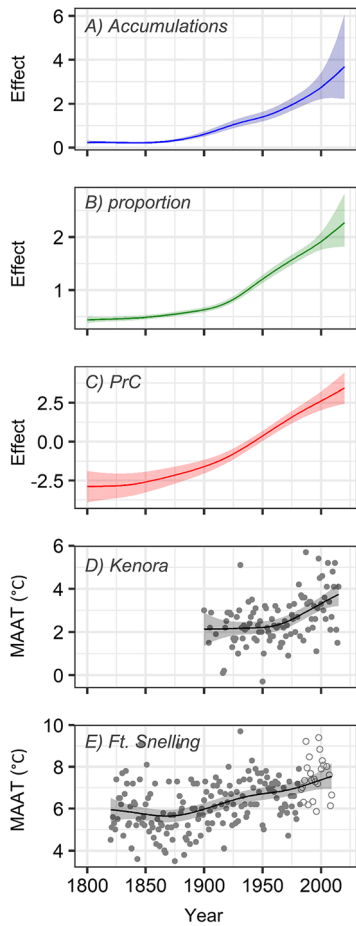
Fig. 4 Synthesis of global trends (i.e., the mean effect of age on the centred variable of interest) extracted from Model 2 within the hierarchical generalized additive model (HGAM) framework for (**A**) small *Discostella* accumulations, (**B**) proportion of small *Discostella*, and (**C**) principal curves representing overall diatom assemblage change. Regional temperature records for (**D**) Kenora, Ontario, and (**E**) Fort Snelling, Minnesota are also shown (open points represent mean annual air temperatures estimated based on a regression with overlapping data recorded in nearby Farmington, MN). The shaded bands in each plot represents the 95% confidence intervals

beginning in 1970. After ∼ 1975, Lake 256 showed little change in *Discostella* accumulation.

Discussion

Our analysis of subfossil diatom assemblages in sediment cores from eight lakes, which span the last ∼ 200 years of sedimentation, revealed coherent patterns in assemblage change, characterized by

mid-nineteenth century increases in small *Discostella* species. Application of a hierarchical generalized additive model (HGAM) structure provided statistical evidence that this pattern was shared among all lakes, although lake-specific departures from this trend were important, which we speculate were a consequence of differences in lake morphometry. Although a possible secondary influence of indirect impacts from low-level acid deposition in the region cannot be ruled out, correspondence between the common trend and the temperature record from Fort Snelling (Minnesota, USA) provides strong evidence for regional climate control on *Discostella*. Based on monitoring records and synthesis of climate data in the ELA, we suggest these patterns are related to earlier ice-off and extended spring mixing conditions (Wiltse et al. 2016). However, definitive identification of the mechanism(s) associated with increased small *Discostella* production remains difficult, largely because of disparate observations in the seasonal succession of these taxa among regions and lakes, and even among years within lakes.

Consistent trends in *Discostella* among lakes

Coherence in trends of small *Discostella* abundances over the past ∼ 200 years, determined from the HGAM framework, suggests a regional stressor as an important process behind these changes, and the similar global trend extracted from the accumulation data and PrC scores (Fig. 4) indicates that changes in *Discostella* represent an important gradient of change in the lakes. Numerous studies indicate that enhanced thermal stability, as a result of atmospheric warming, favours small planktonic diatoms such as *Discostella*, because of their high surface area (SA) to volume (V) ratios and ability to remain suspended in the water column for longer periods of time, compared to larger and more heavily silicified diatoms (e.g., some *Aulacoseira* taxa; Winder and Hunter 2008; Winder et al. 2009; Rühland et al. 2015). The high SA:V of small *Discostella* taxa also enables efficient nutrient uptake as surface waters become nutrient-depleted as summer thermal stratification progresses. Indeed, recent experimental work provides support for this hypothesis in high-latitude and high-elevation lakes (Saros et al. 2012, 2016).

In the ELA lakes, however, an alternative mechanism, related to changes in seasonality, may be
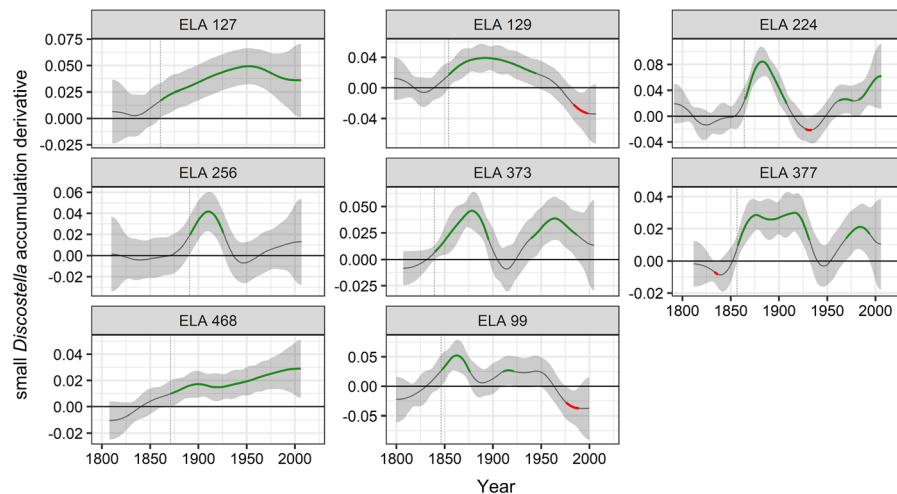
Fig. 5 Derivatives of individual generalized additive models (GAMs) fit to small *Discostella* accumulations in each lake over the past ∼ 200 years. The thick green line represents periods of significant increase, whereas the thick red line represents periods of significant decrease. The horizontal line in each plot represents where the rate of change is zero, and hence where little-to-no change is occurring in the accumulation data. The vertical line marks the date of first significant increase in each record. The shaded bands in each plot represent the 95% confidence intervals

responsible for the observed patterns. Bi-weekly monitoring of two lakes in the ELA indicated that small *Discostella* species were more common in the spring and early summer (April–June), when the lakes were well-mixed and nutrient concentrations were at their highest (Wiltse et al. 2016). These observations are consistent with additional monitoring studies that have also shown peak abundances of small *Discostella* taxa during spring (Thackeray et al. 2008) and fall (Köster and Pienitz 2006) mixing periods in some lakes. Although these disparate explanations are difficult to reconcile, they likely arise from the complex interaction of limnetic properties including light, nutrients, and mixing depth (Rühland et al. 2015; Saros and Anderson 2015), all of which are subject to change with climate. For example, Malik et al. (2018) showed that peak abundances of *Discostella* were associated with the spring maximum in nutrient concentrations in a monitoring study of a small lake in Maine, USA (although they did persist at lower abundances throughout the summer months). Additional experimental work has shown that sufficient nutrients may be an important prerequisite for initiating responses to enhanced light and temperature, although response type (positive or negative) may further depend on the composition of the ambient phytoplankton community (Malik et al. 2016).

A recent synthesis of climate and lake temperature trajectories since 1970 at the ELA indicated that the summer season (as defined by the development and breakdown of the 15 °C isotherm) has not become longer, but has shifted later into the year, although the spring period (defined as the period from ice-off to development of surface temperatures ≥ 15 °C) did lengthen over the period of record (Guzzo and Blanchfield 2016). This is consistent with extended spring conditions as a driver of small *Discostella* abundances at ELA (Wiltse et al. 2016), and not enhanced summer thermal stratification as has been observed in other investigations (Winder and Hunter 2008). This is also supported by the observation that in Lakes 99, 224, and 373, rises in small *Discostella* occurred at the expense of *C. bodanica* v. *lemanica* (ESM Figs. 2, 5, and 7), a planktonic taxon that has consistently been identified as a late summer bloomer (Bradbury 1988; Interlandi et al. 1999; St. Jacques et al. 2009). We note that although the complex and sometimes contradictory observations related to ideal conditions for *Discostella* populations preclude identification of a single mechanism responsible for the observed trends at the ELA, the correspondence between Model 2 global trends, the timing of significant increases in *Discostella* accumulations, and the long-term temperature record from Fort Snelling, Minnesota, USA (Figs. 4, 5) are

consistent with changes in climate, potentially as it relates to the length of the spring season, as an important driver of *Discostella* abundances in this region.

Indirect biogeochemical consequences of widespread low-level acid deposition that began in the late 1800s and peaked in the 1960s may have also influenced historical phytoplankton assemblages in the ELA. Whereas deposition rates of sulphate (SO_4^{2-}) in northwest Ontario were only a fraction of those in regions farther east in close proximity to major industrial sources (e.g., Sudbury, Ontario, Canada > 22.7 kg SO_4^{2-} ha^{-1} yr^{-1}, 1990–1998; Whiteface Mountain, northeast New York, USA, 55.1 kg SO_4^{2-} ha^{-1} yr^{-1}, 1986–1995; Watmough et al. 2005), recent work has shown that indirect effects of acid deposition can influence dissolved organic carbon (DOC) in lakes. Meyer-Jacob et al. (2019) presented spectrally inferred DOC concentrations in sediment cores from eight ELA lakes that spanned the last $\sim$ 200 years of sedimentation. These records suggested the onset of reduced lake-water DOC at $\sim$ 1880, subsequent recovery to pre-1880 levels by $\sim$ 1930, followed by concentrations that exceeded pre-1880 values by $\sim$ 1970. These trends were attributed to response and recovery related to low-level acid deposition, in addition to changes in temperature and precipitation. Indeed, DOC has a strong control over water transparency in Boreal lakes (Pérez-Fuentetaja et al. 1999), creating the possibility for cascading effects on lake structure and function (Williamson et al. 2015). Given that experimental work has shown small *Discostella* species may respond positively to increased light (although this may depend on enhanced nutrient availability; Saros et al. 2012; Malik et al. 2018), and small *Discostella* taxa tend to bloom in the spring and early summer in the ELA lakes when nutrient concentrations are higher (Wiltse et al. 2016), increased light could provide conditions favourable for their growth. Increased transparency, however, would also be expected to enhance growth of benthic taxa (Laird et al. 2011), a trend that we did not observe in the study lakes (ESM Fig. 10), and thus our data do not support water clarity as a predominant driver of historical diatom assemblages. Additionally, the declines in inferred DOC occurred $\sim$ 2–3 decades after most study lakes showed an initial significant increase in *Discostella*. Although this does not preclude the possibility of an interactive effect between climate-related mechanisms and low-level acid deposition, it does suggest that indirect biogeochemical consequences related to low-level acid deposition likely did not initiate the proliferation of *Discostella*.

Departures from the common trend

Whereas the HGAM framework repeatedly suggested that Model 2 was most parsimonious (incorporating a common smooth), this model also enables the response between lakes to vary in both complexity and shape, indicating that departures from the common trend are an important characteristic of the data. Differences in shape were most evident in Lakes 99, 129, and 256 (Fig. 3). Post-1970 declines in small *Discostella* accumulations occurred in Lakes 99 and 129, a time when inferred DOC in several ELA lakes began to surpass pre-industrial concentrations (Meyer-Jacob et al. 2019). These lakes are two of the smallest in our dataset, possibly making them more susceptible to declines in water clarity because of increased DOC delivery from the catchment (Rasmussen et al. 1989; Houle et al. 2020). This is consistent with Meyer-Jacob et al. (2019), who showed that the largest post-1970 increases in inferred DOC in the ELA occurred in the two smallest lakes investigated (Lakes 127 and 129).

Some degree of lake-specific response was also evident when examining the timing of significant change in *Discostella* accumulations (Fig. 5). For example, Lakes 256 and 468 showed a later response, at $\sim$ 1890 and 1871, respectively. These two lakes are the largest in the dataset in terms of surface area, and both are relatively deep (Table 1). Because Wiltse et al. (2016) showed that spring conditions were important for *Discostella* populations in the ELA, we considered the potential influence that lake morphometry would have on the timing of spring ice-off. Some studies have shown that larger lakes undergo ice-off later in the spring compared to smaller systems (Gao and Stefan 1999; Duguay et al. 2003; Arp et al. 2013), possibly attributed to differences in lateral ice decay. Therefore, it is possible that the spring mixing period may have become sufficiently long for the proliferation of small *Discostella* in the smaller lakes first. In contrast, others have shown that air temperature is the most important determinant of ice-off timing, and lake morphometry has only a weak control over timing of

ice-off compared to the timing of ice-on (Williams and Stefan [2006]; Hewitt et al. [2018]). An alternative explanation may be that the larger, deeper lakes are also more susceptible to changes in thermal stability under a changing climate (Kraemer et al. [2015]), such that earlier set-up of stratification in these lakes delayed the amount of time it took for early ice-out to influence the length of the spring mixing period. Although we cannot test these inferences with the available data, lake morphometry may contribute to the small amount of inter-lake heterogeneity we observed in our dataset, possibly modulating both early-season mixing and changes in light dynamics. Both would require additional investigation to fully understand these processes.

The post ~ 1850–1860 increases in *Discostella* that we documented in the ELA occur substantially earlier than others have documented in temperate lakes. In a meta-analysis of 60 temperate lakes across the northern hemisphere, Rühland et al. ([2008]) showed that the median timing of increased small *Cyclotella* was 1970, including Whitefish Bay in nearby Lake of the Woods (~ 45 km southwest of the ELA field station), which coincided with an abrupt increase in MAAT recorded in Kenora. In contrast, the median response in *Cyclotella* for Arctic and sub-Arctic lakes occurred at 1870, like our eight lakes at the ELA. Hence, the small, dilute, oligotrophic lakes in this undisturbed region of northwest Ontario appear to be more sensitive to regional environmental change, compared to lakes in other areas at similar latitudes. We do note, however, that some temperate lakes showed an early increase in *Cyclotella*, such as Emmett Lake (~ 1880; Werner et al. [2005]) in south-central Ontario, and Indian Lake (~ 1880; Forrest et al. [2002]) in southeast Ontario. Elsewhere, Michelutti et al. ([2015]) showed abrupt increases in *Discostella stelligera* over the past ~ 50 years in three high-elevation lakes from the southern sierra of Ecuador. These differences highlight the complexity that landscape and lake filters introduce to temporal variability in phytoplankton response to environmental stressors, and the need for long-term records of limnological change which will ultimately help to address this knowledge gap.

Conclusions

Our detailed paleolimnological analyses of eight lakes in the ELA, which were selected because they had experienced large increases in small *Discostella* taxa since pre-industrial times, showed similar temporal patterns in the abundance of these taxa. Application of a recently described hierarchical generalized additive model (HGAM) framework, as well as individual GAMs and their associated derivatives, provided statistical evidence for coherent increases in small *Discostella* abundance in our lakes that began at ~ 1850–1860 CE. Coupled with corresponding trends in a long-term temperature record from Fort Snelling, Minnesota, our results suggest that the paramount process controlling small *Discostella* in our study region is related to climate, possibly the timing of spring ice-off. Models also suggested, however, that lake-specific departures from the common trend are an important characteristic of the data, and we suggest that lake morphometry played an important role in this variability. Moreover, we cannot fully rule out a possible secondary control on late nineteenth and twentieth century *Discostella* abundances, related to changes in light dynamics as an indirect effect of low-level acid deposition and changes in precipitation in the region. Additional experimental work in the ELA would be needed to fully understand ideal conditions for small *Discostella* taxa, and refinement of the pathways by which climate regulates them.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Arp CD, Jones BM, Grosse G (2013) Recent lake ice-out phenology within and among lake districts of Alaska, U.S.A. Limnol Oceanogr 58:2013–2028

Arnott SE, Dillon PJ, Yan N, Paterson M, Findlay D (2003) Using temporal coherence to determine the response to

climate change in Boreal Shield lakes. Environ Monit Assess 88:365–388

Baker DG, Watson BF, Skaggs RH (1985) The Minnesota long-term temperature record. Clim Change 7:225–236

Binford MW (1990) Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project lakes sediment cores. J Paleolimnol 3:253–267

Blanchfield PJ, Shearer JA, Schindler DW (2009) Johnson and Vallentyne's legacy: 40 years of aquatic research at the Experimental Lakes Area. Can J Fish Aquat Sci 66:1831–1836

Blenckner T (2005) A conceptual model of climate-related effects on lake ecosystems. Hydrobiologia 533:1–14

Boeff KA, Strock KE, Saros JE (2016) Evaluating planktonic diatom response to climate change across three lakes with differing morphometry. J Paleolimnol 56:33–47

Bradbury JP (1988) A climatic-limnologic model of diatom succession for paleolimnological interpretation of varved sediments at Elk Lake, Minnesota. J Paleolimnol 1:115–131

Brown RE, Nelson SJ, Saros JE (2017) Paleolimnological evidence of the consequences of recent increased dissolved organic carbon (DOC) in lakes of the northeastern USA. J Paleolimnol 57:19–35

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York

Catalan J, Pla S, Rieradevall M, Felip M, Ventura M, Buchaca T, Camarero L, Brancelj A, Appleby PG, Lami A, Grytnes JA, Agustí-Panareda A, Thompson R (2002) Lake Redó ecosystem response to an increasing warming in the Pyrenees during the twentieth century. J Paleolimnol 28:129–145

Duguay CR, Flato GM, Jeffries MO, Ménard P, Morris K, Rouse WR (2003) Ice-cover variability on shallow lakes at high latitudes: model simulations and observations. Hydrol Process 17:3465–3483

Enache MD, Paterson AM, Cumming BF (2011) Changes in diatom assemblages since pre-industrial times in 40 reference lakes from the Experimental Lakes Area (northwest Ontario, Canada). J Paleolimnol 46:1–15

Flower RJ (2006) Validation of Discostella stelligera var. microrobusta Flower var. nov., A new name for Cyclotella stelligera var. microrobusta Flower. Diatom Res 21:463–464

Forrest F, Reavie ED, Smol JP (2002) Comparing limnological changes associated with 19th century canal reconstruction and other catchment disturbances in four lakes within the Rideau Canal system, Ontario, Canada. J Limnol 61:183–197

Gao S, Stefan HG (1999) Multiple linear regression for lake ice and lake temperature characteristics. J Cold Reg Eng 13:59–77

Glew JR, Smol JP, Last WM (2001) Sediment core collection and extrusion. In: Last WM, Smol JP (eds) Tracking Environmental Change Using Lake Sediments, Volume 1: Basin analysis, Coring, and Chronological techniques. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 73–105

Guzzo MM, Blanchfield PJ (2016) Climate change alters the quantity and phenology of habitat for lake trout (Salvelinus namaycush) in small Boreal Shield lakes. Can J Fish Aquat Sci 74:871–884

Harris MA, Cumming BF, Smol JP (2006) Assessment of recent environmental changes in New Brunswick (Canada) lakes based on paleolimnological shifts in diatom species assemblages. Can J Bot 84:151–163

Hewitt BA, Lopez LS, Gaibisels KM, Murdoch A, Higgins SN, Magnuson JJ, Paterson AM, Rusak JA, Yao H, Sharma S (2018) Historical trends, drivers, and future projections of ice phenology in small north temperate lakes in the Laurentian Great Lakes Region. Water 10:70

Houk V, Klee R (2004) The Stelligeroid taxa of the genus Cyclotella (Kützing) Brébisson (Bacillariophyceae) and their transfer into the new genus Discostella gen. nov. Diatom Res 19:203–228

Houle D, Khadra M, Marty C, Couture S (2020) Influence of hydro-morphologic variables of forested catchments on the increase in DOC concentration in 36 temperate lakes of eastern Canada. Sci Total Environ 747:141539

Interlandi SJ, Kilham SS, Theriot EC (1999) Responses of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem. Limnol Oceanogr 44:668–682

Karst-Riddoch TL, Pisaric MFJ, Smol JP (2005) Diatom responses to 20th century climate-related environmental changes in high-elevation mountain lakes of the northern Canadian Cordillera. J Paleolimnol 33:265–282

Köster D, Pienitz R (2006) Seasonal diatom variability and paleolimnological inferences-a case study. J Paleolimnol 35:395–416

Kraemer BM, Annevill O, Chandra S, Dix M, Kuusisto E, Livingstone DM, Rimmer A, Schladow SG, Silow E, Sitoki LM, Tamatamah R, Vadeboncoeur Y, McIntyre PB (2015) Morphometry and average temperature affect lake stratification responses to climate change. Geophys Res Lett 42:4981–4988

Krammer KH, Lange-Bertalot (1986) Bacillariophyceae. Teil 1. Naviculaceae. In: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa, vol 2/1. Gustav Fischer Verlag, Stuttgart

Krammer KH, Lange-Bertalot (1988) Bacillariophyceae. 2. Teil: Bacillariaceae, Epithmiaceae, Surirellaceae. In: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa, vol 2/2. Gustav Fischer Verlag, Stuttgart/New York

Krammer KH, Lange-Bertalot (1991) Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. In: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa, vol 2/3. Gustav Fischer Verlag, Stuttgart/Jena

Krammer KH, Lange-Bertalot (1991) Bacillariophyceae. 4. Teil: Achnanthaceae. In: Ettl H, Gärtner G, Gerloff J, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa, vol 2/4. Gustav Fischer Verlag, Stuttgart/Jena

Laird KR, Kingsbury MV, Lewis CFM, Cumming BF (2011) Diatom-inferred depth models in 8 Canadian boreal lakes: inferred changes in the benthic:planktonic depth boundary and implications for assessment of past droughts. Quat Sci Revs 30:1201–1217

Lange-Bertalot H, Melzeltin D (1996) Indicators of oligotrophy. 2 Iconographia Diatomologica. Koeltz Scientific Books, Königstein

Magnuson JJ, Benson BJ, Kratz TK (2004) Patterns of coherent dynamics within and between lake districts at local to intercontinental scales. Boreal Environ Res 9:359–369

Malik HI, Saros JE (2016) Effects of temperature, light and nutrients on five *Cyclotella sensu lato* taxa assessed with *in situ* experiments in arctic lakes. J Plankton Res 38:431–442

Malik HI, Warner KA, Saros JE (2018) Comparison of seasonal distribution patterns of *Discostella stelligera* and *Lindavia bodanica* in a boreal lake during two years with differing ice-off timing. Diatom Res 33:1–11

Meyer-Jacob C, Michelutti N, Paterson AM, Cumming BF, Keller W, Smol JP (2019) The browning and re-browning of lakes: Divergent lake-water organic carbon trends linked to acid deposition and climate change. Sci Rep 9:16676

Michelutti N, Wolfe AP, Cooke CA, Hobbs WO, Vuille M, Smol JP (2015) Climate change forces new ecological states in Tropical Andean Lakes. PLoS ONE 10(2):e0115338

Mushet GR, Flear K, Wiltse B, Paterson AM, Cumming BF (2018) Increased relative abundance of colonial scaled chrysophytes since pre-industrial times in minimally disturbed lakes from the Experimental Lakes Area, Ontario. Can J Fish Aquat Sci 75:1465–1476

Ontario Ministry of the Environment (1983) Handbook of analytical methods for environmental samples vol 1 and 2. Laboratory Services Branch,Ontario Ministry of the Environment and Energy, Sudbury, ON

Patoine A, Leavitt PR (2006) Century-long synchrony of fossil algae in a chain of Canadian Prairie lakes. Ecology 87:1710–1721

Pérez-Fuentetaja A, Dillon PJ, Yan ND, McQueen DJ (1999) Significance of dissolved organic carbon in the prediction of thermocline depth in small Canadian Shield lakes. Aquat Ecol 33:127–133

Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7:e6876

R Core Team (2018) R: a language and environment for statistical computing; https://www.r-project.org/

Rasmussen JB, Godbout L, Schallenberg M (1989) The humic content of lake water and its relationship to watershed and lake morphometry. Limnol Oceanogr 34:1336–1343

Rühland KM, Paterson AM, Smol JP (2008) Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Glob Change Biol 14:2740–2754

Rühland KM, Paterson AM, Smol JP (2015) Lake diatom responses to warming: reviewing the evidence. J Paleolimnol 54:1–35

Saros JE, Anderson NJ (2015) The ecology of the planktonic diatom *Cyclotella* and its implications for global environmental change studies. Biol Rev 90:522–541

Saros JE, Northington RM, Anderson DS, Anderson NJ (2016) A whole-lake experiment confirms a small centric diatom species as an indicator of changing lake thermal structure. Limnol Oceanogr Lett 1:27–35

Saros JE, Stone JR, Pederson GT, Slemmons KEH, Spanbauer T, Schliep A, Cahl D, Williamson CE, Engstrom DR (2012) Climate-induced changes in lake ecosystem structure inferred from coupled neo- and paleo-ecological approaches. Ecology 93:2155–2164

Schelske CL, Peplow A, Brenner M, Spencer CN (1994) Low-background gamma counting: applications for ^{210}Pb dating of sediments. J Paleolimnol 10:115–128

Simpson GL (2018) Modelling palaeoecological time series using generalised additive models. Front Ecol Evol 6:149

Simpson GL (2020) Analogue: analogue and weighted averaging methods for paleoecology. https://cran.r-project.org/web/packages/analogue/index.html

Simpson GL, Birks HJB (2012) Statistical learning in palaeolimnology. In: Birks HJB, Lotter AF, Juggins S, Smol JP (eds) Tracking Environmental Change Using Lake Sediments, Data Handling and Numerical Techniques. Springer, Dordrecht, pp 249–327

Smol JP et al (2005) Climate-driven regime shifts in the biological communities of arctic lakes. Proc Natl Acad Sci 102:4397–4402

Sorvari S, Korhola A, Thompson R (2002) Lake diatom response to recent Arctic warming in Finnish Lapland. Glob Change Biol 8:171–181

St. Jacques JM, Cumming BF, Smol JP (2009) A 900-yr diatom and chrysophyte record of spring mixing and summer stratification from varved Lake Mina, west-central Minnesota, USA. The Holocene 19:537–547

Thackeray SJ, Jones ID, Maberly SC (2008) Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. J Ecol 96:523–535

Watmough SA, Aherne J, Alewell C, Arp P, Bailey S, Clair T, Dillon P, Duchesne L, Eimers C, Fernandez I, Foster N, Larssen T, Miller E, Mitchell M, Page S (2005) Sulphate, nitrogen and base cation budgets at 21 forested catchments in Canada, the United States and Europe. Environ Monit Assess 109:1–36

Werner P, Chaisson M, Smol JP (2005) Long-term limnological changes in six lakes with differing human impacts from a limestone region in southwestern Ontario, Canada. Lake Reserv Manage 21:436–452

Williams SG, Stefan HG (2006) Modeling of lake ice characteristics in North America using climate, geography, and lake bathymetry. J Cold Reg Eng 20:140–167

Williamson CE, Overholt EP, Pilla RM, Leach TH, Brentrup JA, Knoll LB, Mette EM, Moeller RE (2015) Ecological consequences of long-term browning in lakes. Sci Rep 5:18666

Wiltse B, Paterson AM, Findlay DL, Cumming BF (2016) Seasonal and decadal patterns in *Discostella* (Bacillariophyceae) species from bi-weekly records of two boreal lakes (Experimental Lakes Area, Ontario, Canada). J Phycol 52:817–826

Winder M, Hunter DA (2008) Temporal organization of phytoplankton communities linked to physical forcing. Oecologia 156:179–192

Winder M, Reuter JE, Schadlow SG (2009) Lake warming favours small-sized planktonic diatom species. Proc R Soc B 276:427–435

Wood S (2020) *mgcv*: mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation. https://cran.rproject.org/web/packages/mgcv/index.html