LETTER

A whole-lake experiment confirms a small centric diatom species as an indicator of changing lake thermal structure

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Abstract

In many lakes across the Northern Hemisphere, paleolimnological records have revealed that the relative abundances of small centric diatoms, such as the cosmopolitan species Discostella stelligera, have changed over the past century. Such changes have been thought to be a result of climate change based on inferences from small-scale experiments and contemporary observational studies. However, there have been no whole-ecosystem tests of the mechanisms underlying such changes in diatoms. This study provides evidence from a whole-lake experiment that shows the importance of water column stratification on D. stelligera, thus providing a mechanistic link between climate and observed patterns in lake fossil records.

Scientific Significance Statement

In many lakes across the Northern Hemisphere, paleolimnological records have revealed that the relative abundances of small centric diatoms, such as the cosmopolitan species Discostella stelligera, have changed over the past century. Such changes have been thought to be a result of climate change based on inferences from small-scale experiments and contemporary observational studies. However, there have been no whole-ecosystem tests of the mechanisms underlying such changes in diatoms. This study provides evidence from a whole-lake experiment that shows the importance of water column stratification on D. stelligera, thus providing a mechanistic link between climate and observed patterns in lake fossil records.

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Author contribution statement: JES developed the research question and designed the experiment with input from NJA. JES and RMN conducted the fieldwork and experiment, and RMN and DSA analyzed samples and processed data. JES wrote the manuscript with input from all co-authors.

Data availability statement: Data are available in the NSF Arctic Data Center repository (https://arcticdata.io/catalog/#view/doi:10.18739/A2435B).

Additional Supporting Information may be found in the online version of this article.

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Introduction

Monitoring and remote sensing approaches have documented climate-driven changes in many lake ecosystems over recent decades, with effects ranging from increasing surface water temperatures (Schneider and Hook 2010) and altered lake thermal structure (Kraemer et al. 2015) to changing delivery of organic and inorganic materials from watersheds (Strock et al. 2016) and shifts in phenology (Berger et al. 2010). Our primary tool, however, for assessing longer-term effects of climate change on lakes and for understanding patterns of natural variability in lake ecosystems remains the paleolimnological record. This underscores the importance of developing reliable proxies and fossil indicators of climate-driven change that are preserved in lake sediments.

Fossil diatom assemblages are often used to reconstruct chemical (Fritz et al. 1991; Anderson and Rippey 1994) and habitat (Stone and Fritz 2004) changes in lakes over centennial to millennial timescales. These inferences rest on relationships established from contemporary ecological studies of current distribution patterns and, to a lesser extent, experimental results. The links between climate-driven lake ecosystem changes and diatom community structure, however, have been more difficult to decipher (Saros and Anderson 2015). This is due in part to the myriad effects of climate on lakes and hence diatom communities, as well as the often limited spatial (e.g., one integrated sample, no vertical resolution) and temporal (e.g., once or twice per year) resolution of diatom distribution assessments. Pairing experimental approaches with these contemporary distribution assessments becomes necessary to identify controlling factors and mechanisms.

The relative abundances of the small centric diatom Discostella stelligera (Cleve and Gronow) Houk and Klee have undergone widespread increases in alpine, boreal, temperate, and particularly arctic areas since 1850 (Smol et al. 2005; Rühland et al. 2008; Perren et al. 2009; Saros et al. 2012), with these shifts often used as indicators of warming-induced changes in lakes. It is important to note, however, that D. stelligera has also declined over the same time frame in many lakes experiencing warming (Perren et al. 2009; Hobbs et al. 2010; Saros et al. 2012), raising questions about the mechanisms involved. Correlative studies suggest positive effects of longer ice-free seasons on this species (Rühland et al. 2008), but given the highly coherent nature of changing ice off dates across lakes in a region (Magnuson et al. 1990; Arp et al. 2013), it remains unclear how this would lead to variable response of this species across a landscape.

Many studies using surveys and small-scale experiments have now provided evidence for the importance of greater water column stability and/or shallower epilimnion thickness for the success of small centric diatom taxa (Carney et al. 1988; Winder et al. 2009), including D. stelligera (Saros et al. 2012, 2014). Because of regional variability in how increasing air temperatures alter surface winds and delivery of materials from the watershed that affect lake water transparency, changes in water column stability and mixing depths may vary across regions experiencing similar warming and lead to different patterns in D. stelligera sedimentary profiles across lakes (Perren et al. 2009; Saros et al. 2012; Saros and Anderson 2015). The response of this opportunistic species, however, can also be complex and variable (Saros and Anderson 2015), with interactive effects between light and nutrients on this species often apparent (Saros et al. 2014; Malik and Saros 2016). This suggests the need for a direct, whole-ecosystem scale test of thermal structure effects on the response of this important and widely used indicator species.

We conducted a whole-lake mixing manipulation in a remote arctic lake that normally has relatively shallow thermal stratification and abundant D. stelligera populations during the summer. We employed a “Before-After-Control-Impact” (BACI) design (Stewart-Oaten et al. 1986), with an experimental lake and a control lake. Lake thermal structure and diatom populations were monitored in both lakes in summer 2013 without manipulating either lake, and again in summer 2014 when the experimental lake was manipulated to achieve deeper mixing depths. We predicted that shallower mixing depths would favor D. stelligera in this region, and that the relative abundance of this species would decline during the manipulated period of deeper mixing.

Methods

Site description

Two arctic lakes near Kangerlussuaq, southwest Greenland (67.01°N, 50.69°W) were selected for this experiment (Fig. 1) because D. stelligera is common and abundant in many lakes in this area (Perren et al. 2009), and the remote nature of the area ensured no direct disturbance from human activity. Lakes across this area are generally dilute and oligotrophic.

Lake SS16 was selected as the experimental lake for this study for four reasons. Previous research indicated that D. stelligera is the dominant diatom in this lake (Perren et al. 2009), making up more than 40% of diatom assemblages deposited in lake sediments over the past century. The lake is also relatively small (surface area of 0.033 km², maximum depth of 13 m), making it a manageable size for a whole-lake thermal manipulation. The lake thermally stratifies during summer with a mixing depth of 4 m. Finally, an unnamed lake in close proximity to Lake SS16 is similar in all three features, providing an ideal “control” system to which to compare the manipulated Lake SS16. We refer to this second, unmanipulated lake as Control Lake (surface area of 0.022 km², maximum depth of 9.8 m), and hereafter refer to Lake SS16 as Experimental Lake.

The two lakes are situated at approximately 66.91°N, 50.44°W, in an area only accessible by helicopter. The two lakes are hydrologically connected early in the summer by
very low surface flow from Control Lake to Experimental Lake; in this semi-arid region (total annual precipitation < 200 mm yr\(^{-1}\)) there is generally very little surface flow connecting lakes. Both lakes are circumneutral and dilute (conductivity of 70–80 \(\mu\)S cm\(^{-1}\)) with low to moderate total phosphorus (<12 \(\mu\)g L\(^{-1}\)). Concentrations of dissolved organic carbon (DOC) are about 10 mg L\(^{-1}\) in both lakes. The *D. stelligera* populations in both lakes have cell sizes that range from 4 \(\mu\)m to 6 \(\mu\)m; these cells have the features of *D. stelligera* as opposed to *D. pseudostelligera*. Both lakes contain populations of the planktivorous three-spined stickleback (*Gasterosteus aculeatus*), and hence zooplankton communities of both lakes are dominated by rotifers (primarily *Asplanchna* and *Polyarthra* taxa), with no cladocerans and only copepod nauplii observed.

**Whole-lake experiment**

A BACI design was used to assess whether deeper mixing affects the relative abundances of *D. stelligera*. Data from Experimental Lake and Control Lake during Year 1 (2013) serve as the “Before” data, while data collected from both lakes in Year 2 (2014) during the manipulation of Experimental Lake serve as the “After” data. Control Lake, not manipulated at any point, provides the “Control” data, while Experimental Lake undergoing manipulation provides the “Impact” data.

During both years, lakes were monitored with automated instrumentation for a 4-week period, starting shortly after ice off and spanning many weeks of thermally stratified conditions. The period of observation extended only to late July to avoid the initial stages of thermocline erosion that typically begin in August. Ice off on Experimental Lake was 13 June in 2013 and 12 June in 2014. A string of temperature probes (Onset HOBO Pendant) recording at hourly resolution was deployed in each lake at 1-m intervals from the lake surface to 9 m to assess stratification patterns. Rotating sediment traps (Technicap PPS 4/3) were deployed in each lake to determine planktic diatom community structure. Sediment traps were used because they provide a more integrated plankton sample over time compared to water column samples, and they allowed for automated, unattended collection at this remote site. The trap in Experimental Lake was deployed at 8-m depth, while the trap in Control Lake was at 7 m due to the shallower maximum depth of this lake. A new collection bottle in the trap rotated into position every 5 days, providing six 5-day composite samples from 19 June to 19 July in both years for both lakes. Rotation dates of the traps were kept the same in both years. We relied on the short duration of the experiment and low temperatures (4–5\(^{\circ}\)C) at trap depth for sample preservation; more than 2 \(\times\) 10\(^6\) \(\mu\)m\(^3\) mL\(^{-1}\) trap material of soft-bodied algae also accumulated in each trap, with larger quantities measured in the first two traps of each season. Microscopic examination indicated no signs of degradation across samples.

We returned to the site briefly on 24 June 2013 and 26 June 2014 to collect epi-, meta-, and hypolimnion plankton samples in each lake to verify the presence and assess the vertical distribution of *D. stelligera*.

Water column measurements of light, chemistry and chlorophyll were conducted manually twice each summer, shortly after ice off and at the end of the sampling period. While the timing of the early season sampling is the same in both years, the timing of the late season sampling differs between years owing to logistical constraints (i.e., timing of
availability of air transportation; occurred 31 July 2013 and 15 August 2014). Conductivity was measured with a multi-parameter sonde (Hydrolab MS5). Vertical attenuation of photosynthetically active radiation (PAR) was measured with a radiometer (Biospherical Instruments BIC). Water samples for total and dissolved nutrients, DOC, and chlorophyll a (Chl a) were collected from the epilimnion (at 2 m) using a van Dorn horizontal sampling bottle.

In Year 2 (2014), the thermal structure of Experimental Lake was manipulated using a solar-powered hydraulic lift system (Medora Corporation SolarBee 10000v18), which pumps water up from a selected depth and redistributes it to the surface. This is the same system used in other whole-lake manipulations that assessed the biological effects of changing thermocline depth (Cantin et al. 2011; Jobin and Beisner 2014; Sastri et al. 2014). The SolarBee was deployed by helicopter into the deep area of the lake on 15 June 2014. The intake hose for the system was set to 8 m, the target depth for deepened mixing. Once the system was anchored, adjusted, and properly positioned, it was started (evening of 17 June). The first plankton sample began collecting in the sediment traps at 12:01 a.m on 19 June.

Sample processing

Each sediment trap bottle was homogenized before an 8-mL sub-sample was removed with an electronic pipet. Sub-samples were treated with 30% hydrogen peroxide to remove organic material and a known concentration of microspheres was added to each processed sample to calculate absolute abundances of each diatom taxon. A minimum of 300 diatom valves were counted for each sample under oil immersion at a magnification of 630X.

From the early and late season manually collected water samples, nutrients and DOC were measured as described in Burpee et al. (2016). Chl a was extracted in acetone and analyzed with a spectrophotometer (Varian Cary50). We used an average of early and late season light attenuation coefficients for each lake to calculate average light intensities in the epilimnion (as in Tilzer and Goldman (1978)) for each 5-day period.
The response of *D. stelligera* to the thermal manipulation was assessed with a two-factor analysis of variance (ANOVA), with treatment (i.e., lake) and year as the two factors. A significant \( p < 0.05 \) interaction between these two factors would indicate an effect of the 2014 manipulation in Experimental Lake on *D. stelligera* population size. Cell densities were log-transformed to meet the assumptions of normality.

**Fig. 3.** Response of Control Lake and Experimental Lake in both years, with neither lake manipulated in 2013 and only Experimental Lake manipulated in 2014: (a, b) epilimnion thickness; (c, d) average epilimnetic temperature; (e, f) calculated average light intensity experienced by a cell circulating in the mixed layer; (g, h) cell densities of *Discostella stelligera* in sediment traps (note log scale of y-axis). Data are shown as spline curves; values in panels a through d are based on averages from each 5-day sediment trap interval, matching the sampling resolution of the primary response variable (*Discostella stelligera* cell densities).
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Table 1. Water column data collected early (mid-June) and late (late July 2013 or mid-August 2014) summer each year in both lakes. Neither lake was manipulated in 2013; only Experimental Lake (Exp Lake) was manipulated in 2014, with the “late” samples being the post-manipulation data (denoted by shading). Chemical parameters are measured from samples collected at a depth of 2 m.

|                | Control lake | Exp lake | Control lake | Exp lake |
|----------------|--------------|----------|--------------|----------|
|                | Early        | Late     | Early        | Late     |
| Conductivity (µS cm⁻¹) | 65          | 67       | 69           | 71       |
| TP (µg L⁻¹)     | 8           | 11       | 8            | 7        |
| TN (µg L⁻¹)     | 580         | 610      | 480          | 443      |
| DIN (µg L⁻¹)    | 6           | 5        | 3            | 6        |
| DOC (mg L⁻¹)    | 11          | 12       | 11           | 12       |
| Chlorophyll (µg L⁻¹) | 5.2       | 3.5      | 4.5          | 2.9      |
| 1% PAR (m)      | 6.02        | 6.85     | 5.83         | 6.44     |

The responses of four other diatom taxa common to both lakes in both years were also tested with this approach. In all ANOVA analyses (regardless of taxon), the number of degrees of freedom was 12 (16 total data points - 1 (treatment) - 1 (year) - 1(trt x year) - 1 (intercept)). With sediment traps collecting over the same time intervals and dates each year, sample period should not be an issue with this design but we tested its effect by adding it as a term in the ANOVA for D. stelligera and found that it was not significant (p=0.75).

Results

From 19 June to 19 July 2013, epilimnion thickness varied between 2 to 4 m in both Experimental Lake and Control Lake (Figs. 2, 3). In 2014, epilimnion thickness in Control Lake again varied from 2 to 4 m, being similar to but often slightly shallower than in 2013. This shallower mixing in Control Lake was likely due to the higher air temperatures in 2014 compared to 2013 (Danish Meteorological Institute, http://www.dmi.dk/groenland/arkiver/vejrarkiv/), resulting in higher July surface water temperatures in 2014 in both lakes (Figs. 2, 3). In the manipulated Experimental Lake in 2014, epilimnion thickness began similarly to that in 2013 (between 2-3 m depth from 19 to 23 June both years), but then deepened to vary between 4 and 8 m between 24 and 28 June 2014. On 29 June, stratification broke down and the lake mixed until 5 July; stratification redeveloped and between 6 and 19 July, varied largely between 6 m and 7 m, with occasional days at 5 m.

Water column metrics collected in early and late summer each year revealed no difference in lake water chemistry as a consequence of the thermal manipulation in Experimental Lake (Table 1). The 1% PAR depth deepened over the summer in all cases except the manipulated Experimental Lake in 2014, in which it remained the same from early to late summer (Table 1). The water column plankton samples collected 6-8 d into the monitored period revealed maximum D. stelligera cell densities in the metalimnia of both lakes on 24 June 2013, and epilimnetic maxima in both lakes on 26 June 2014 (Supporting Information Fig. S1).

Calculated average light intensities in the mixed layer ranged from 30% to 50% of surface irradiance in both lakes over summer 2013 (Fig. 3). In 2014, they ranged from 40% to 55% of surface irradiance in Control Lake. Once deeper mixing began (25 June) in Experimental Lake in 2014, average light intensities in the mixed layer ranged from 16% to 24% of surface irradiance.

Cell densities of D. stelligera in Experimental Lake declined during the period of manipulated, deeper mixing (p = 0.0025 for treatment x year interaction; Fig. 3). During the first ten sampling days of each year, cell densities of this species in Experimental Lake sediment traps were comparable. From 29 June to 19 July when consistently deeper mixing was achieved, cell densities ranged from 4 to 40 times lower (absolute densities lower by 1,300 cells mL⁻¹ to 6,300 cells mL⁻¹ trap material) in 2014 compared to 2013. In contrast, in Control Lake, cell densities in the traps were higher in 2014 compared to 2013 (p = 0.01).

Four other diatom taxa were common to both lakes in both years: Fragilaria tenera v. nanana (Lange-Bertalot) Lange-Bertalot and S. Ulrich, Stauroforma exiguiformis (Lange-Bertalot) R.J. Flower, V.J. Jones and Round, Fragilaria capucina v. gracilis (Oestrup) Hustedt, and Tabellaria flocculosa (Roth) Kütz. strain III sensu Koppen (Fig. 4). The treatment x year interaction was not significant for F. tenera v. nanana (p = 0.17), S. exiguiformis (p = 0.23), or T. flocculosa (p = 0.75), but was significant for F. capucina v. gracilis (p = 0.01). This interaction resulted from the positive effect of deeper mixing in 2014 on this species in Experimental Lake. We note, however, that this species was abundant both years in the stratified Control Lake, leaving the relationship, if any, between mixing and this species unclear.
Discussion

The results of this whole-lake experiment are consistent with those of surveys and small-scale experiments (Winder et al. 2009; Saros et al. 2012, 2014) and support the importance of lake thermal structure for the success of *D. stelligera* populations. In these lakes as well as others (Winder et al. 2009; Saros et al. 2012), multiple lines of evidence continue to support the use of increasing relative abundances of *D. stelligera* in lake sediment records as an indicator of shallower mixing depths. In our study, ice off occurred at essentially the same time both years, yet deeper mixing in Experimental Lake in 2014 resulted in lower *D. stelligera* densities. Furthermore, average epilimnetic temperatures in mid-July were higher in both lakes in 2014 than in 2013, yet *D. stelligera* declined in Experimental Lake, suggesting that direct temperature effects on this species are not the primary control on its success. With early and late season sampling indicating no apparent changes in water chemistry in this case, our results suggest that altered average light exposure as a result of deeper mixing may be one of the main mechanisms by which changing thermal structure affected *D. stelligera* densities in this lake.

Multiple factors, including water transparency, water temperatures, and wind strength, affect mixing depths and the strength of thermal stratification in lake ecosystems (Fee...
et al. 1996; Kraemer et al. 2015). Widespread changes in lake thermal structure have been occurring over recent decades (Kraemer et al. 2015; Williamson et al. 2015) and are driven to varying degrees by these multiple factors, resulting in different patterns (e.g., deeper thermocline depth, increasing strength of stratification) across systems. These differences in lake thermal response are consistent with the variable patterns observed in *D. stelligera* sedimentary profiles across lakes (reviewed by Saros and Anderson 2015). For example, since the late 1800s, *D. stelligera* increased in relative abundance in the sediments of a small alpine lake experiencing warming, advancing treeline, and likely increasing DOC concentrations, factors that would promote shallower stratification (Saros et al. 2012). In contrast, this species decreased in relative abundance over the same time frame in the sediments of a large lake on Isle Royale in Lake Superior experiencing increasing wind speeds, a factor that would promote deeper mixing depths (Saros et al. 2012).

Our results support the use of *D. stelligera* as an indicator of changing mixing depths in some lake ecosystems. Of the five diatom taxa found in both lakes in both years, *D. stelligera* was the only species showing a consistent, positive response to shallower thermal stratification. Changes in the abundances of other taxa, such as *F. tenera v. nanana* and *T. flocculosa*, were not linked to stratification patterns in these lakes, suggesting that these species were affected by other factors. We do reiterate, however, the cautions advised in Saros and Anderson (2015). *Discostella stelligera* responds to the interactive effects of light and nutrients (Saros et al. 2012, 2014; Malik and Saros 2016), which likely influence how and why it responds to lake thermal structure. As a result, while this species is more abundant during thermally stratified conditions in many lakes (Winder et al. 2009; Saros et al. 2012), there are some lakes in which this species is more abundant during periods of turnover (Köster and Pienitz 2006; Boeff et al. 2016). When possible, the site-specific seasonal distribution patterns of *D. stelligera* should be assessed before applying this tool to a lake sediment core (as in Boeff et al. 2016).

Changes over recent decades in the factors affecting lake stratification are well documented, as are the implications of these changes for plankton production and diversity in lakes (Berger et al. 2010; Cantin et al. 2011). What remains less clear, however, is how recent changes in lake thermal structure compare to longer-term variability. We are already learning more about this longer-term variability through the use of this indicator species in lake sediment records spanning back hundreds (Smol et al. 2005; Rühland et al. 2008; Saros et al. 2012) to thousands (Wang et al. 2008; Stone et al. 2016) of years. The results of this whole-lake experiment provide an important step in confirming the use of this inference tool when coupled with contemporary pelagic sampling of seasonal distributions of this species. The broader application of this tool will yield greater insight into longer-term variability in the response of lake ecosystems to climate.

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Acknowledgments

We are sincerely grateful to Benjamin Burpee, Rachel Fowler, Hamish Greig, Emily Rice, Kristin Strock, and Kathryn Warner for extraordinary field assistance, and to our helicopter pilots Gregor Beer and Petrus Nobreus. CH2M Hill Polar Services provided logistical support for this project; in particular, Geoff Miller provided extensive assistance with the assembly and transport of the Solar Bee. We thank Corey Siminovich of the Medora Corporation for modifying the design of the Solar Bee to meet our requirements. Benjamin Burpee, Johanna Cairns, Jeffery Stone and Nora Theodore provided photos and figure elements. Brian McGill provided assistance with statistical analyses. This research was funded by the Arctic System Science program of the US National Science Foundation (grant #1203434 to JES).

Submitted 14 March 2016
Revised 24 May 2016
Accepted 11 July 2016