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# Climate-induced changes in lake ecosystem structure inferred from coupled neo- and paleoecological approaches

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# Climate-induced changes in lake ecosystem structure inferred from coupled neo- and paleoecological approaches

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**Abstract.** Over the 20th century, surface water temperatures have increased in many lake ecosystems around the world, but long-term trends in the vertical thermal structure of lakes remain unclear, despite the strong control that thermal stratification exerts on the biological response of lakes to climate change. Here we used both neo- and paleoecological approaches to develop a fossil-based inference model for lake mixing depths and thereby refine understanding of lake thermal structure change. We focused on three common planktonic diatom taxa, the distributions of which previous research suggests might be affected by mixing depth. Comparative lake surveys and growth rate experiments revealed that these species respond to lake thermal structure when nitrogen is sufficient, with species optima ranging from shallower to deeper mixing depths. The diatom-based mixing depth model was applied to sedimentary diatom profiles extending back to 1750 AD in two lakes with moderate nitrate concentrations but differing climate settings. Thermal reconstructions were consistent with expected changes, with shallower mixing depths inferred for an alpine lake where treeline has advanced, and deeper mixing depths inferred for a boreal lake where wind strength has increased. The inference model developed here provides a new tool to expand and refine understanding of climate-induced changes in lake ecosystems.

**Key words:** climate; *Cyclotella*; lake stratification; mixing depth; paleoecology.

## INTRODUCTION

In many lake ecosystems around the world, water temperatures increased over the 20th century (Austin and Colman 2008, Hampton et al. 2008, Schneider and Hook 2010). While evidence suggests that climate-induced changes to lake thermal structure are occurring (Livingstone 2008), the long-term patterns of change in thermal structure and mixing remain unclear across lakes. A physical feature of key importance to the structure and function of lake ecosystems is the thickness of the surface mixed layer (i.e., the epilimnion). This feature is determined by climate via wind strength, solar radiation, and inputs of terrestrially derived dissolved organic material (Fee et al. 1996). Understanding the biological effects of climate-induced changes in lake mixing depths has thus become a key focus in lake ecology over the last decade (Diehl et al. 2002, Jäger et al. 2008, Berger et al. 2010). At present, however, we lack sufficient understanding about how trends and variability in climate have actually altered

lake mixing depths over time due to the limited spatial and temporal extent of lake monitoring programs. To address this issue, we developed a paleoecological tool using pelagic organisms to infer past changes in lake mixing depths.

Isolating the specific response of pelagic organisms to climate-induced changes can be challenging given the extent of human activity around many lakes. Plankton are sensitive to climate change and nutrient loading, making it notoriously difficult to disentangle the degree to which either driver (e.g., warming or enhanced nutrient loading) is involved in an observed change, especially as we lack explicit ecological information for many of these taxa. One approach to address this is to focus on common pelagic species that exhibit widespread changes across remote lakes that are sensitive to climate, such as arctic and alpine lakes. The phytoplankton assemblages of many of these oligotrophic lakes are dominated by diatoms (Bacillariophyceae), unicellular photoautotrophic algae that are highly sensitive to changes in physical and chemical features of lakes. Fossil diatom profiles in the sediments of numerous arctic and alpine lakes share a common feature: the relative abundances of species in the genus *Cyclotella* have changed dramatically over the last 150 years (Smol et al. 2005, Hobbs et al. 2010). *Cyclotella*

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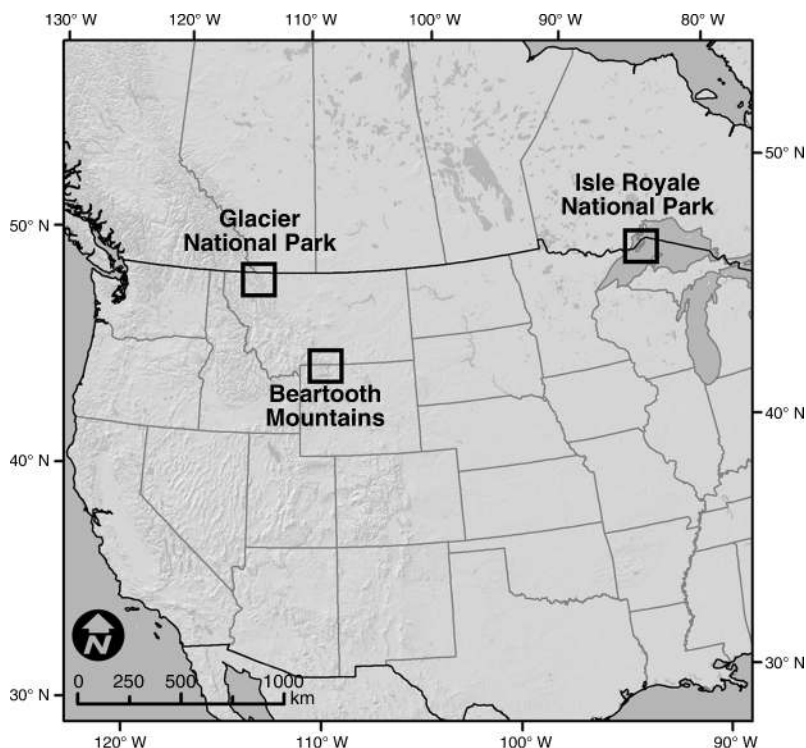


FIG. 1. Overview map of the study areas, with the inference model developed from lakes in the Beartooth Mountains and Glacier National Park, and the model applied to sediment records from Glacier National Park (Hidden Lake) and Isle Royale National Park (Siskiwit Lake).

species are common members of the phytoplankton not only in arctic and alpine lakes, but also in temperate and boreal lakes, hence an inference model focused on these species has potential for broad application. Increases in the relative abundances of small *Cyclotella* species are often interpreted as signals for warming-induced changes in the length of the ice-free season or depth of the mixed layer (Rühland et al. 2008, Winder et al. 2009). However, the relationships between specific physical parameters and any of these species remain unclear due to a lack of species-specific, mechanistic information to reconcile sometimes conflicting observations on population distributions (Thackeray et al. 2008, Winder et al. 2009). In addition, synergistic interactions between water column stability and nutrients on *Cyclotella* populations are suggested by some experiments and long-term data sets (Jäger et al. 2008, Winder et al. 2009).

To establish better species-specific mechanisms underlying observed changes in pelagic population distributions and thereby understand long-term changes in lake thermal structure, we have coupled results from in situ ecological experiments with fossil-based lake records spanning multiple centuries. Specifically, we coupled contemporary ecological observations and experiments to decipher how changes in three key *Cyclotella* taxa (*Discostella stelligera* (Cleve and Grunow) Houk and Klee, *Cyclotella comensis* Grunow, and *Cyclotella bodanica* Grunow) are related to nutrient

availability (i.e., nitrogen and phosphorus) and lake thermal structure. The relationships among these three species and lake mixing depth were then used as rationale for developing an inference model, which we applied to sedimentary diatom profiles from two lakes, one alpine and one boreal, both situated in areas with increasing air temperatures over the 20th century but experiencing different consequences as a result of this change. Treeline has advanced around the alpine lake (Roush et al. 2007), largely due to decreasing regional snowpack and increasing mid-elevation temperatures (Pederson et al. 2010), while wind speeds have increased around the boreal lake (Desai et al. 2009). Our results suggest that these species can be used to infer climate-induced change in lake thermal structure in lakes meeting specific nutrient criteria.

## METHODS

### Study sites

Contemporary ecological observations and experiments were conducted in the central Rocky Mountains of North America, in both the Beartooth Mountains and Glacier National Park (Fig. 1). Lake sediment records were collected from Hidden Lake (48°40'53" N, 113°44'34.5" W), an alpine lake situated at 1943 m above sea level in Glacier National Park, and Siskiwit Lake (48°00'02" N, 88°47'45" W), a boreal lake situated at 220 m above sea level in Isle Royale

National Park (Fig. 1). Additional maps of these sites are provided in Appendix A.

### Experiments

The effects of nutrient enrichment and incubation depth on the growth rates of each target species were determined in a  $2 \times 2$  factorial experiment. The experimental containers and incubation approach followed that used previously (Doyle et al. 2005). Experiments were conducted in Hidden Lake, where sampling in 2007 revealed that this lake contains all three target species. At present, compared to 25 other lakes across the central Rockies (Saros et al. 2010), Hidden Lake has similar low total phosphorus (TP;  $1 \mu\text{g/L}$ ) and moderate nitrate ( $25 \mu\text{g/L}$ ).

Lake water and phytoplankton assemblages for the experiments were collected from the lake in July 2009. Whole lake water was collected with a van Dorn bottle from the depth of the chlorophyll maximum, 23 m, and pre-screened through 100- $\mu\text{m}$  Nitex mesh (Sefar America, New York, New York, USA) to remove zooplankton. Subsamples of this water were collected and preserved with Lugol's iodine solution to determine initial cell densities for each species. Nutrient treatments were created in triplicate, with either no added nutrients (control) or N + P enrichment ( $8 \mu\text{mol/L N} + 1 \mu\text{mol/L P}$ ). Nitrogen was added in the form of  $\text{NaNO}_3$ ; P was added in the form of  $\text{NaH}_2\text{PO}_4$ . The amended water was added to 500-mL liquid-tight specimen bags (Bitran Series S; Com-Pac International, Carbondale, Illinois, USA) and incubated in the lake for 8 days on racks previously described (Doyle et al. 2005), except that all bags were only covered with bird netting to hold them in place. One set of bags (control and enriched) was incubated in the epilimnion at 5 m (photosynthetically active radiation [PAR] irradiance of  $700 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , ultraviolet B radiation between 1% and 10% of surface irradiance), and another set in the hypolimnion at 15 m (PAR irradiance of  $190 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , which was still above the 10% attenuation depth). The temperature at 5 m was  $14^\circ\text{C}$ , and at 15 m was  $11^\circ\text{C}$ .

At the end of the experiment, duplicate 50-mL subsamples were collected from each bag after homogenizing the contents, preserved with Lugol's iodine, and counted as described in *Lake survey*, with a minimum of 500 individuals enumerated in each sample. One subsample was counted from each bag, and then cell counts were averaged across the three bags in each treatment.

### Lake survey

To develop the inference model, oligotrophic lakes with the target species present were selected from both the Beartooth Mountains and Glacier National Park. Lakes in both regions have very low total phosphorus (TP) and moderate to high soluble reactive silica, while nitrate concentrations vary across lakes (Saros et al. 2010). Seventeen lakes were sampled in July 2007 for environmental parameters related to water column structure

(epilimnetic temperature, mixing depth, 1% PAR) and nutrient concentrations (nitrate, TP) as well as for diatom assemblages from both the water column and surface sediments. While 17 lakes is a relatively low number for a calibration set, we note that this set is used in conjunction with mechanistic experiments that are designed to clarify relationships, and that very few calibration sets are accompanied by such experiments. Water column profiles of temperature and PAR were collected with a BIC submersible profiling radiometer (Biospherical Instruments, San Diego, California, USA) and 1% attenuation depths of PAR were calculated. Temperature profiles were used to determine the mixing depth (i.e., depth of the surface mixed layer: the epilimnion) and the average temperature of this layer. Water samples were collected for determination of nutrients using standard methods, as described in Saros et al. (2010).

Diatom assemblages were determined in both water column and surface sediment samples, all collected the same day as the environmental parameters. Three subsamples of lake water from each depth were preserved with Lugol's iodine solution and phytoplankton were counted on an inverted microscope (Nikon TS100; Nikon Instruments, New York, New York, USA) with 400 $\times$  magnification after settling 50 mL in Utermöhl-style chambers. Surface sediments were collected from a depth of at least 15 m in each lake using a Hongve gravity corer. A minimum of 500 diatom valves was counted in the top 0.5-cm increment of each core under oil immersion at a magnification of 1000 $\times$  using an Olympus BX51 microscope (Olympus America, Center Valley, Pennsylvania, USA) with differential interference contrast.

### Fossil analysis

Sedimentary diatom profiles extending back several centuries were determined for Hidden and Siskiwit lakes. Select characteristics of the lakes are provided in Appendix B. These two lakes were chosen because surface sediments contained all three species of interest, and because of their contrasting sizes and climate settings. Spring air temperatures have increased, snowpack has declined, and the number of frost days has decreased during the 20th century in the region in which Hidden Lake is situated (Pederson et al. 2010). The Hidden Lake watershed has undergone substantial treeline advance during this time (Roush et al. 2007). We also note that a moraine of Little Ice Age origin is situated at the head of the watershed, suggesting a small ice mass was present within the basin for some duration of time since 1850 AD. Siskiwit is a large ( $>1600$  ha) boreal lake situated on Isle Royale in Lake Superior, with a fetch that runs west to east along the island. Air temperatures have also increased during the 20th century in the Lake Superior region (Austin and Colman 2008), with Lake Superior summer water temperatures increasing more rapidly over that time than air temperatures (Desai et al. 2009). As a result of this

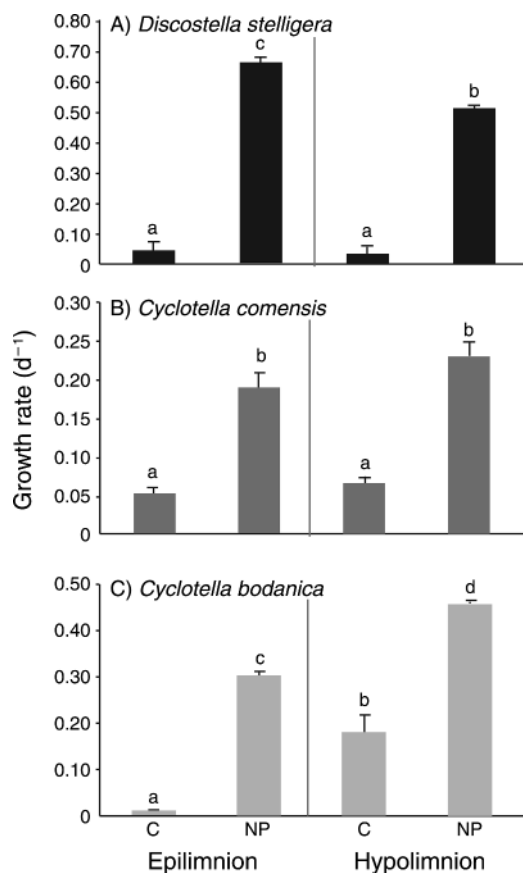


FIG. 2. Growth rates in the incubation experiments under control (C) and nutrient enrichment (NP) conditions at the two different incubation depths (epilimnion and hypolimnion) for: (A) *Discostella stelligera*, (B) *Cyclotella comensis*, and (C) *Cyclotella bodanica*. Lowercase letters above bars indicate significant differences ( $P < 0.05$ ) based on Tukey's post hoc analysis.

differential heating, instrumental records that extend back to 1985 reveal that, contrary to trends over many terrestrial areas, wind speeds have been increasing over Lake Superior (Desai et al. 2009).

A 65-cm sediment core was collected from the deepest basin of Hidden Lake with a rod-operated piston corer in July 2007. A 30-cm gravity core was collected from the deepest spot in Siskiwit Lake in July 2010. Both cores were subsampled in the field in continuous 0.5-cm increments, and dated from <sup>210</sup>Pb activities counted by gamma ray (Hidden) or alpha (Siskiwit) spectroscopy methods, as described in Saros et al. (2011). Chronology was based on the constant rate of supply (CRS) model. Diatom assemblages were determined in each subsample as described above, except 300 valves were counted in each sample.

#### Numeric analysis

In the experiments, growth rates for each species were determined using a standard growth rate equation, as

described in Michel et al. (2006), and were compared across treatments using a two-way ANOVA with Tukey's post hoc comparison (using Mathematica 7; Wolfram Research, Champaign, Illinois, USA).

From the lake surveys, we chose to primarily use the surface sediment samples in our analysis for two key reasons: (1) they integrate assemblages from the entire water column over some portion of the open-water season, rather than plankton samples that capture discrete depths on the day collected and thus provide more variable representation across lakes; and (2) identification of the smaller *Cyclotella* taxa is difficult and often unreliable in plankton samples as cells still contain chlorophyll. Plankton samples allowed us to confirm the presence of *Cyclotella* taxa during stratified conditions.

Spearman's rank correlation analysis was used to determine relationships between environmental parameters and the percent relative abundance of each species (using JMP 7; SAS Institute, Cary, North Carolina, USA). A Bonferroni correction (0.05/5 variables) was applied in determining the significance of each variable ( $P \leq 0.01$ ). Multiple linear regression was used to model the influence of multiple environmental variables on species abundance ( $P \leq 0.01$ ). Parameters were transformed to meet assumptions for normality, linearity, and constant variance.

The optimum mixing depths for *D. stelligera* and *C. comensis* were determined from their distribution in surface sediment samples using weighted averaging with bootstrap error estimation (Birks 2010) in the program C2 (Juggins 2007). Because one of the target species (*C. bodanica*) was sparse in surface sediment samples, we estimated its optimum mixing depth and standard error by fitting a Gaussian curve (using the program JMP) to cell densities measured in plankton samples. Unlike the other two taxa, this species is easily identified in plankton samples.

For the Hidden and Siskiwit sedimentary diatom profiles, detrended correspondence analysis (DCA) was used to quantify the dominant pattern of down-core assemblage variability. DCA was performed on all diatom taxa with down-weighting of rare species (using Canoco 4.5; Microcomputer Power, Ithaca, New York, USA). Mixing depths were reconstructed by applying calculated optima to the relative abundances of the three target species (within the full assemblages) with a weighted-averaging equation (Birks 2010; Appendix C). Error was estimated using the root mean square error of prediction based on comparisons of measured to reconstructed mixing depths for the 17 study lakes.

#### RESULTS

In the experiments, all three species exhibited positive growth (Fig. 2); full results of the two-way ANOVA are provided in Appendix D. Incubation depth and nutrient addition had an interactive effect on the growth of *D. stelligera* ( $P < 0.001$ ), with a greater increase in growth



rates with nutrient enrichment in the epilimnion compared to the hypolimnion (Fig. 2A). Based on post hoc comparisons, the incubation depth alone (i.e., without nutrient additions) had no effect on the growth rates of this species (group a in Fig. 2A).

For *C. comensis*, nutrients stimulated growth ( $P < 0.001$ ), and had an equally positive effect at both depths (group b in Fig. 2B). Based on post hoc comparisons, depth alone had no effect on the growth of this species (group a in Fig. 2B), but when control and nutrient treatments were pooled from each depth, growth rates were higher in the hypolimnion ( $P = 0.001$ ).

The growth rates of *C. bodanica* were the only ones affected by incubation depth alone (group a vs. b in Fig. 2C), with higher growth rates in the hypolimnion ( $P < 0.001$ ). Nutrients had an equally positive effect on growth rates at both depths ( $P < 0.001$ ).

The 17 lakes spanned gradients in mixing depth, epilimnetic temperature, 1% PAR, and nitrate, while there was little variation in TP (Appendix E). The relative abundances of *D. stelligera* and *C. comensis* in surface sediments varied among lakes; those of *C. bodanica* were never more than 5% across lakes, so correlations for this species were not tested.

The relative abundances of *D. stelligera* exceeded 5% in seven of the lakes. The distribution of this species was correlated only with mixing depth ( $\rho = -0.64$ ,  $P = 0.006$ ), indicating that this species was more abundant in lakes with shallower mixing depths (correlations for all variables provided in Appendix F). Multiple linear regression revealed that the distribution of this species was both negatively correlated with mixing depths and positively correlated with nitrate concentrations ( $\log[\text{percent } D. stelligera] = 3.7 - 2.1[\text{sqrt}(\text{mixing depth})] + 0.35[\text{sqrt}(\text{NO}_3)]$ , where sqrt is square root;  $r^2 = 0.50$ ,  $P \leq 0.01$ ,  $n = 17$  lakes), with *D. stelligera* exceeding 10% of surface sediment assemblages only in lakes with both moderate to high nitrate and mixing depths  $\leq 5$  m (Fig. 3A).

The relative abundances of *C. comensis* exceeded 5% in six of the lakes. The distribution of this species was positively correlated with mixing depth ( $\rho = 0.58$ ,  $P = 0.01$ ) and nitrate ( $\rho = 0.60$ ,  $P = 0.01$ ), and negatively correlated with TP ( $\rho = -0.65$ ,  $P = 0.002$ ) (Appendix F). No significant multivariate models were found using multiple linear regression. The relative abundance of *C. comensis* exceeded 10% of assemblages in lakes with a mixing depth of 5 m and moderate nitrate (25  $\mu\text{g/L}$ ), or those with mixing depths  $> 5$  m and moderate to high nitrate ( $> 50 \mu\text{g/L}$  nitrate; Fig. 3A).

Weighted-averaging analysis of surface sediment assemblages revealed a mixing depth optimum of  $4 \pm 2.5$  m (mean  $\pm$  SE) for *D. stelligera*, and  $9 \pm 4.8$  m for *C. comensis*. Using a Gaussian fit to cell densities from plankton samples (Fig. 3B), an optimum mixing depth of 14 m was estimated for *C. bodanica*. For the mixing depth inference model, the root mean square error of prediction was 3.8 m, with an  $r^2$  of 0.26. Comparing

measured mixing depths to diatom-inferred mixing depths across the 17 lakes (Appendix G), diatom-based inferences almost always overestimated mixing depths, suggesting that these inferences may reflect the average mixing state (i.e., length of spring and fall turnover times plus depth of summer stratification). This suggestion is further supported by the observation that the alpine lakes with the greatest overestimate of mixing depth are those dominated by *C. bodanica* (Appendix G), which likely blooms in some lakes close to or during turnover periods due to its deeper mixing depth optimum, in contrast to species with shallower mixing depth optima that could sustain populations during stratified periods (which often last longer than turnover periods). Model performance is discussed in more detail in Appendix G.

Over the last few centuries (dating models for cores provided in Appendix H), the relative abundances of the three taxa fluctuated in both Hidden and Siskiwit, but in different directions (Fig. 4). In Hidden Lake, *Cyclotella comensis* comprised  $\sim 20\%$  of the total diatom assemblage until 1850 AD, after which the relative abundances of this species increased to 30–40% during 1850 AD to  $\sim 1940$  AD, and then sharply rose to 50 to 60% since  $\sim 1940$  AD. The relative abundances of *C. bodanica* dropped from 10–15% prior to 1750 AD (data not shown) to 5–10% through the end of the 19th century, and then rapidly disappeared after the early 20th century. *Discostella stelligera* made up less than 10% of diatom assemblages throughout the core, but its relative abundance increased after  $\sim 1940$  AD. In contrast, in Siskiwit Lake, *D. stelligera* comprised 20–40% of assemblages from the 18th century up until about 1960 AD, and then steadily declined to less than 10% at the top of the core. Collectively, *C. bodanica* and *C. comensis* made up 10% or less of assemblages from the 18th century up until about 1920 AD. After 1920 AD, *C. bodanica* increased substantially, and today makes up more than 50% of the modern assemblage. *Cyclotella comensis* steadily increased after 1940 and peaked at about 20% of the assemblage in 1970, after which it steadily declined to about 10% at the top of the core.

Lake survey data from both Hidden and Siskiwit Lakes indicate that these lakes are P-limited and have some measurable ( $> 1 \mu\text{g N/L}$ ) nitrate (Appendix B), making them suitable for the application of the inference model. Diatom-inferred mixing depth (DIMD) based on the relative abundances of the three target species suggests changes in mixing depth occurred in both lakes over the last few centuries, but in different directions (Fig. 4). We note that DIMD patterns in both lakes mirror first-axis DCA scores for the entire diatom assemblage (Fig. 4). In Hidden Lake, DIMD varied between 9.5 and 10.25 m from 1750 AD to 1850 AD. From 1880 AD to  $\sim 1940$  AD, DIMD steadily became shallower from 9 to 8.5 m, with the 8.5 m DIMD then sustained for the rest of the 20th century. Patterns in DIMD for Hidden Lake mirror tree-ring inferred air

temperature for the region (Luckman and Wilson 2005; Fig. 4A), with deeper mixing depths during cooler periods (1750–1850 AD) and shallower mixing depths during the warmer 20th century. In contrast, diatom-inferred mixing depths in Siskiwit Lake suggest progressively deepening mixed layers during the 20th century (Fig. 4B), deepening from about 5 m in 1900 to 1912 m at the top of the core. The Lake Superior water temperature anomaly for most of the 20th century is plotted for comparison, as wind strength over Siskiwit Lake is strongly controlled by Lake Superior water temperatures (Desai et al. 2009).

#### DISCUSSION

While many diatom-based inference models rely on the entire community, a focus on ecologically relevant taxa in this case (i.e., planktonic species for which previous research suggested that mixing depths might affect their distributions) distills the complexity of sedimentary diatom records to permit inference of changes in lake thermal structure. The two lakes in which thermal structure is reconstructed are located in contrasting climate settings. Patterns in reconstructed mixing depth are opposite in the two lakes, yet both depart dramatically from their previous range in variability, with changes starting after 1880 AD in the alpine lake and after 1920 AD in the boreal lake. This suggests that most historical lake data are too brief to capture the full range of variability in lake thermal structure. The diatom-based inference model developed here can expand both the spatial and temporal scales of our understanding of climate-induced change in this ecologically important feature of lakes. Further development of such fossil-based thermal models may prove useful as a high-resolution climate proxy for areas lacking other paleoclimatic information (e.g., ice cores, tree rings).

The results presented here suggest that these three diatom species—important members of the phytoplankton in many oligotrophic lakes around the world—can be used to infer climate-driven changes in lake stratification patterns in P-limited lakes with some measurable nitrate. Results from both the survey and experimental approaches indicate that mixing depth affects these three species, and that nutrient conditions play a role in this relationship to varying degrees for these three taxa. The opposite trends in mixing depth inferred for these two lakes, with Siskiwit situated in a region with documented increases in wind strength in recent decades, further supports the use of these species to infer climate-driven change in certain lake types. This study thus provides a more mechanistic and enhanced ecological foundation to interpret and clarify climate-driven change in lake ecosystems.

Our experimental results and comparative lake sampling indicated interactive effects between depth and nutrients for *D. stelligera*, which is consistent with other studies that demonstrate the importance of light

for this species (Williamson et al. 2010) or similar species (*Cyclotella glomerata*; Carney et al. 1988), and its potential interactions with moderate nutrient concentrations (Anderson et al. 1997). While we did not explicitly test which physical factors altered diatom growth rates in the depth manipulation, differences in light (PAR irradiance of 700 vs. 150  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  between the two incubation depths) were much greater than differences in temperature (14°C vs. 11°C), suggesting that interactions between light and nutrients are at the root of the response. Small centric diatoms such as *Discostella stelligera* are commonly used as indicators of warming-induced changes in lakes (e.g., Rühland et al. 2008, Winder et al. 2009). However, our results suggest that nutrient conditions are an important component in the response of this species to changes in lake mixing depths. Interestingly, *D. stelligera* is either absent or has declined over the last century in sediment records from other small lakes in Glacier National Park without glaciers present within their watersheds (Saros et al. 2011), and hence lacking associated nitrogen subsidies (Saros et al. 2010).

For *C. comensis*, we found that either mixing depth or nutrients were important for this species, although its distribution with respect to mixing depths did vary with nitrate concentrations, such that it was more abundant at deeper depths when nitrate concentrations were higher. We note that the negative correlation between this species and TP is likely a function of the high nitrate lakes having lower TP, since the range in TP concentrations is comparably small across the lakes in this study. The relative abundances of this species increased in both sediment cores at some point during the last two centuries (after 1850 AD in Hidden and 1940 AD in Siskiwit). At present, both lakes have comparable, moderate, nitrate concentrations, and their sediment records do not reveal increases in diatom taxa indicative of N enrichment over the 20th century (Saros et al. 2011), hence we infer that the primary driver of changes in the abundance of this species in these two phosphorus-limited lakes is mixing depth. We suggest that nitrate concentrations and the presence of N indicator taxa in sediment records should be determined when making inferences from *C. comensis*.

While the approach used to determine the optimum mixing depth for *C. bodanica* relied on a small data set, experimental evidence supported the positive effect of greater depth on this species. Interlandi et al. (1999) also found that this species bloomed in P-limited conditions in oligotrophic lakes of the Greater Yellowstone Ecosystem when mixing depth was between 10 and 15 m, consistent with our results here. At present, few lakes in our data set mix deeply during summer, which may explain the low relative abundance of *C. bodanica* in surface sediment samples. It may be that this species blooms only during or just prior to turnover events, which are fairly short in duration compared to the rest of the open water season, resulting in a small contribution of this species to modern sedimentary



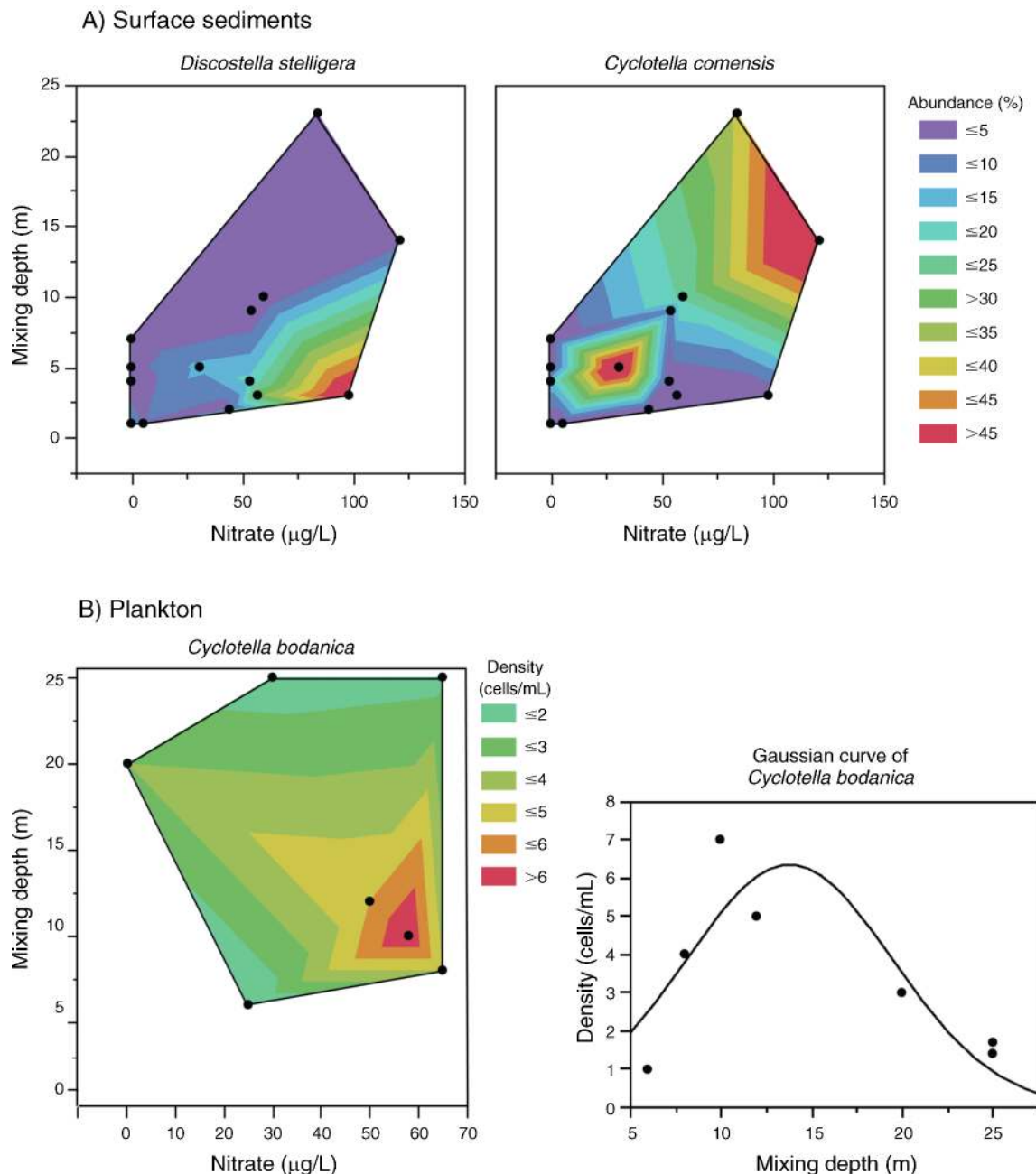


FIG. 3. Distributions of the three diatom taxa in relation to mixing depth and nitrate concentrations. Panel A depicts data from surface sediment samples for *Discostella stelligera* and *Cyclotella comensis*. Panel B is based on water column samples for *Cyclotella bodanica*, with distribution in relation to nitrate and mixing depth and Gaussian fit to cell densities in relation to mixing depth.

diatom assemblages. *Cyclotella bodanica* currently dominates diatom assemblages in Siskiwit Lake, with a mixing depth of 9 m during the summer.

The fairly consistent overestimation of mixing depth across modern samples, including the surface samples of the two cored lakes (Hidden, measured mixing depth of 6 m, DIMD of 8.5 m; Siskiwit, measured mixing depth of 9 m, DIMD of 12 m) suggests that, as expected, sedimentary diatom assemblages will integrate the

average mixing state of a lake, including the length of turnover time in spring and fall as well as the depth of summer stratification. Hence, the reconstructed trends in mixing state, rather than absolute values of summer mixing depth, are the key information provided by this approach. While the current estimates of error are relatively large, these may be improved in the future with an expanded data set that continues to include nutrient conditions as a factor.

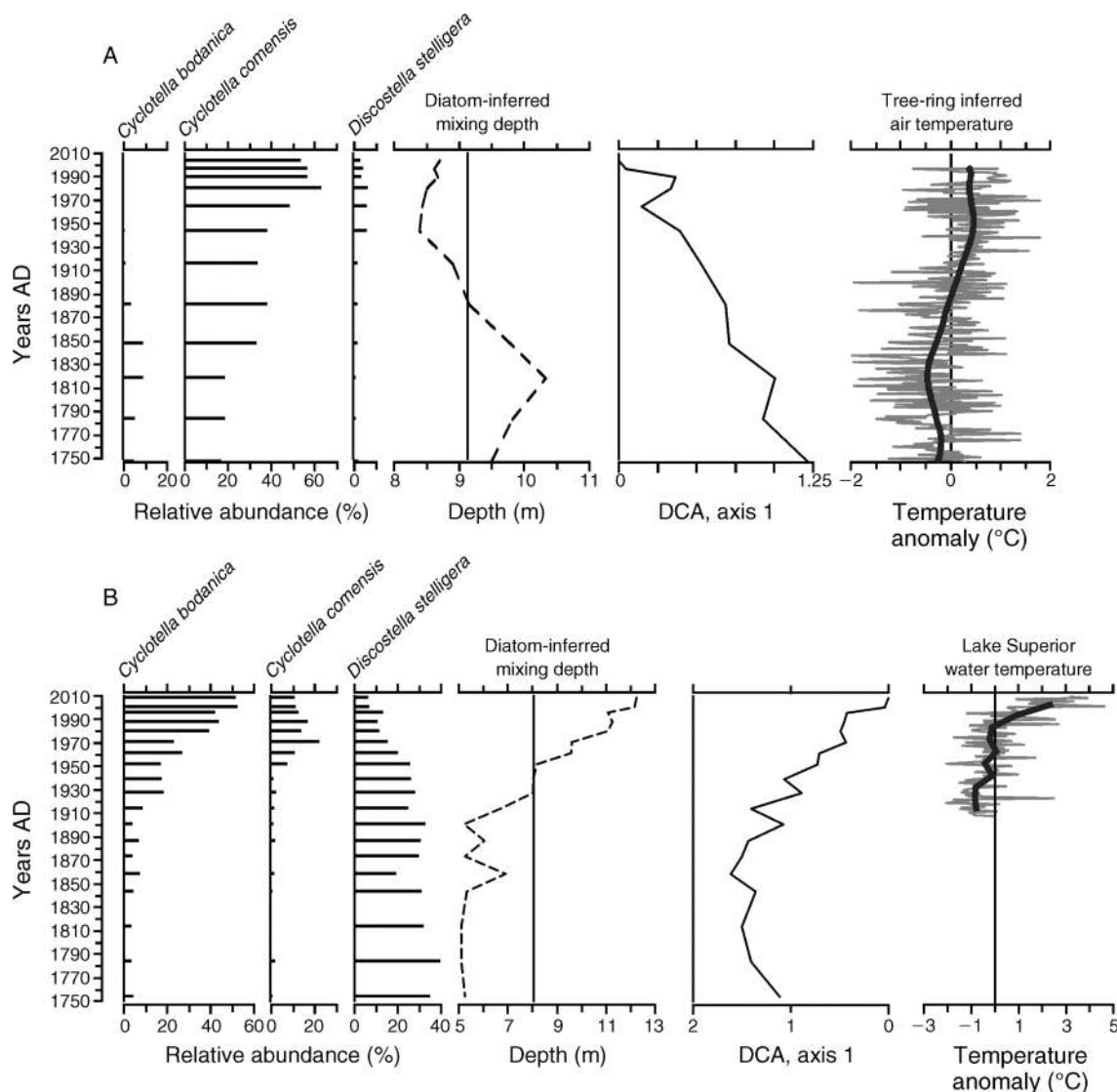


FIG. 4. Sedimentary profiles of the relative abundances of the three diatom taxa in two sediment cores along with mixing depth values inferred from these three species plus detrended correspondence analysis (DCA) of the entire diatom assemblages. Vertical lines on mixing depth plots and on temperature anomalies are the average for the record: (A) Hidden Lake, with tree-ring inferences of air temperature (at annual resolution smoothed with a 20-year spline; Luckman and Wilson 2005) plotted for comparison; (B) Siskiwit Lake, with Lake Superior water temperature anomaly (Austin and Colman 2008) plotted for comparison; wind strength over Siskiwit Lake is strongly controlled by Lake Superior water temperatures.

The opposite historic trends found between Hidden and Siskiwit are likely due to differences in the effects of increasing air temperatures on key factors that affect lake mixing depths. Hidden Lake is a moderately sized lake, in which water clarity and to a lesser extent wind strength determine mixing depths (Fee et al. 1996, von Einem and Grinneli 2010). The shallower mixing depths inferred for this lake during the 20th century may be the result of tree establishment and infilling around Hidden Lake during this time period, which are attributed to increasing air temperatures during the 20th century

(Rousch et al. 2007). Such changes may have in turn increased inputs of dissolved organic carbon to the lake, reducing water clarity and leading to shallower mixing depths. McVicar et al. (2010) also found that near-surface wind speeds have declined more rapidly at higher elevations relative to lower ones during the second half of the 20th century. Without wind or water transparency records over the 20th century from this area, the extent to which changing dissolved organic carbon concentrations or wind speeds are driving mixing changes in this lake remain unclear. Siskiwit is a large lake with a long

fetch, with wind strength controlling mixing depths in this type of lake (Fee et al. 1996). The documented increases in wind strength over Lake Superior in recent decades (period of record over lake only back to 1985; Desai et al. 2009) are consistent with our diatom-based inferences of progressively deeper mixing depths over this time period.

While the direction of change in thermal structure differs between the two lakes, the inferred depths of the upper mixed layer in both records begin to depart dramatically from their previous range in variability sometime between 1880 and 1920 AD, and are sustained during the 20th century. These changes are suggestive of broad unidirectional changes in temperature and/or wind strength during this time that may have altered the thermal structure of many lakes across these regions.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Figures showing the locations of the lakes used in this study (*Ecological Archives* E093-204-A1).

### Appendix B

A table showing select characteristics of Hidden and Siskiwit lakes (*Ecological Archives* E093-204-A2).

### Appendix C

Equations used for weighted averaging inference model and error estimates as root mean square error of prediction (*Ecological Archives* E093-204-A3).

### Appendix D

Results of two-way ANOVA of growth rate experiment for each species (*Ecological Archives* E093-204-A4).

### Appendix E

A table showing select physical and chemical characteristics of the 17 study lakes, along with the percentage relative abundance of the three target species in surface sediment samples (*Ecological Archives* E093-204-A5).

### Appendix F

A table showing Spearman's rank correlation coefficients of distribution patterns for *Discostella stelligera* and *Cyclotella comensis* across the 17 lakes (*Ecological Archives* E093-204-A6).

### Appendix G

Analysis of model performance (*Ecological Archives* E093-204-A7).

### Appendix H

A figure showing  $^{210}\text{Pb}$  dating results for Hidden and Siskiwit lakes (*Ecological Archives* E093-204-A8).