J Paleolimnol (2016) 56:33–47
DOI 10.1007/s10933-016-9889-z

ORIGINAL PAPER

Evaluating planktonic diatom response to climate change across three lakes with differing morphometry

Kelsey A. Boeff · Kristin E. Strock · Jasmine E. Saros

Received: 9 July 2015 / Accepted: 24 March 2016 / Published online: 2 April 2016

Abstract We applied a diatom-based thermal stratification index to sediment cores from three lakes in the northeast USA to evaluate the influence of lake morphometry and within-lake processes on diatom responses to climate change. The three lakes all had surface area $>5\ \mathrm{km}^2$ and experienced the same regional declines in wind speed and progressively earlier ice-out dates, but differed in morphometry, particularly surface area and mean depth. We coupled this paleolimnological approach with contemporary ecological measurements to validate the use of two indicator species (*Aulacoseira subarctica* (O. Müller) Haworth and *Discostella stelligera* (Cleve & Grunow) Houk & Klee) in the stratification index. *D. stelligera* was abundant during stratified conditions in Tunk Lake and Sebago Lake, but not in Lobster Lake. Diatom-inferred stratification shifted to shallower and/or longer duration in Tunk Lake starting in the late nineteenth century, and continued to become shallower over much of the twentieth century. A shift to shallower and/or longer duration was also apparent in Sebago Lake starting around 1850, after which the index suggested little change, even though ice-out occurred 30 days earlier in 2000 than in 1807 and wind speed began to decline in the 1960s. This lake has very slow sedimentation rates, experiences regular seiches, and has *D. stelligera* present during circulation and stratified periods. These factors may smooth stratification-driven diatom responses. Contemporary ecological measurements did not support the application of the stratification index in Lobster Lake because *D. stelligera* bloomed only during spring turnover. In Lobster Lake, the relative abundances of *D. stelligera* in the sediment record showed some variation over time, were generally lower in periods with earlier ice-out in the region, and have been lower since the 1980s. Our results highlight the different responses recorded in the sediments of three large lakes in the same region to climate-driven changes and support the use of indicator species in reconstructing lake thermal stratification patterns when paired with site-specific morphometric and ecological data.

Keywords *Discostella* · *Aulacoseira* · Climate · Wind · Ice-out · Stratification

Introduction

Sedimentary diatom profiles from many lakes in the northern hemisphere have revealed that the relative

---

K. A. Boeff (✉) · J. E. Saros
Climate Change Institute, School of Biology and Ecology,
University of Maine, 137 Sawyer Environmental Sciences
Center, Orono, ME 04469, USA
e-mail: kaboeff@gmail.com

K. E. Strock
Environmental Studies Department, Dickinson College,
112 Kaufman Hall, Carlisle, PA 17013, USA

abundances of small centric taxa, particularly *Discostella stelligera*, have increased since 1850 (Smol et al. 2005; Rühland et al. 2008). These changes have been attributed to warming that occurred over this time frame. Although warming has generally been pervasive across the northern hemisphere (IPCC 2014), changes in small centric taxa have not been coherent across lakes within regions of North America (Hobbs et al. 2010; Saros et al. 2011, 2012) or West Greenland (Perren et al. 2009; Hobbs et al. 2010). As a result, despite the implication that ice-out dates were the driver of these species changes (Rühland et al. 2015), the strong coherence in ice-out dates among lakes within a region (Magnuson et al. 2005) challenges this inference.

Recently, linkages among warming, lake thermal structure and *D. stelligera* relative abundances have become clearer through water-column sampling (Winder et al. 2009; Saros et al. 2012) and experiments (Saros et al. 2012, 2014). This research indicates that, in many lakes, *D. stelligera* densities are higher when the epilimnion is shallower (i.e. thinner), or in experiments when populations were incubated in the epilimnion compared to deeper waters in the photic zone. In all cases, interactive effects with nutrients are also apparent, with increased nutrient availability strongly stimulating this species, particularly when growing in the epilimnion (Saros and Anderson 2015).

This relationship between the relative abundances of *D. stelligera* and epilimnion thickness has been used to reconstruct lake thermal structure from sedimentary diatom profiles (Wang et al. 2008; Saros et al. 2012). An increase in *D. stelligera* indicates periods of shallower and/or longer duration of stratification in some lake ecosystems. For larger lakes (surface area >5 km^2), where wind is the primary determinant of lake thermal structure (Fee et al. 1996), increasing wind strength will deepen the thermocline, and should reduce the relative abundance of *D. stelligera*. The opposite pattern will result with declining wind strength. Integrating the relationship between *D. stelligera* and epilimnion thickness, with an understanding of factors that control lake thermal structure (i.e. wind strength for larger lakes), has helped to clarify the spatial variability in *D. stelligera* profiles across lakes, with local differences in wind strength playing an important role in reducing coherence across records (Saros et al. 2012; Saros and Anderson 2015).

Although our ability to reconstruct thermal structure changes in large lakes has been improved from a better understanding of *D. stelligera* ecology, the extent to which within-lake processes may modify these signals remains unclear. Changes in wind-driven thermal stratification patterns should be fairly consistent across large lakes in a region, because predictions suggest that climate-mediated changes in energy, such as changes in wind speed, result in coherent trends within a region (Leavitt et al. 2009; Pham et al. 2009). Lake morphometry, however, modifies the thermal response of lakes (Kraemer et al. 2015). The thermal stratification of deeper lakes has responded more strongly to warming over recent decades, with thermocline depth deepening in some large, deep systems (Kraemer et al. 2015). Lake depth may also modify species responses to changing thermal structure, owing to generally greater light and nutrient availability in the water columns of shallow (<10 m mean depth), compared to deep lakes. As a result, species responses to changing thermal structure in shallow lakes may be damped because these physical changes will have less of an effect on altering light and nutrient availability. Another within-lake process that becomes relevant for lakes larger than 50 km^2 is the development of seiches (Fee et al. 1996). These oscillations create variability in the depth of the thermocline, and may consequently smooth the response of planktonic diatoms to externally forced changes in lake thermal structure.

Although our understanding of the ecology of *D. stelligera* has improved in recent years, the response of this small, opportunistic species can still be quite variable across systems, as reviewed by Saros and Anderson (2015). For example, in shallow Bates Pond (maximum depth 3.6 m), Köster and Pienitz (2006) found that the abundances of *D. stelligera* peaked during fall turnover as opposed to shallow, stratified conditions (Saros et al. 2012). In both studies, the abundances of *D. stelligera* were positively correlated with nitrate concentrations. This suggests that the seasonal patterns of *D. stelligera* distributions should be assessed when using this species to reconstruct thermal structure from sediment records.

We evaluated diatom-inferred lake stratification patterns over recent centuries in three large lakes (surface area >5 km^2) in Maine, USA. All three lakes experienced the same regional declines in wind speed (Pryor et al. 2009) and progressively earlier ice-out dates (Hodgkins et al. 2002), but differ in morphometry. This allowed us to assess whether within-lake processes in these large lakes influence the links between climate and diatom responses. We coupled this paleolimnological approach with periodic water-column sampling during the ice-free season to validate the application of the index to each of our study lakes.

Study site

The three lakes chosen across the state of Maine for this study were: (1) Lobster Lake in the northern interior, (2) Tunk Lake in the central coastal area, and (3) Sebago Lake in the southern coastal area (Fig. 1). These lakes were selected because their surface areas exceed 5 km^2, but they vary with respect to other key morphometric variables (Table 1). Tunk Lake and Lobster Lake are both moderately large (surface areas of 8 and 14 km^2, respectively), but differ in mean and maximum depths. Tunk Lake has a maximum depth of 68 m, and a mean depth of 22 m, whereas Lobster Lake has a deep hole of 32 m, but much of the basin is substantially shallower, with a mean depth of 9 m. Like Tunk Lake, Sebago Lake is quite deep, with a maximum depth of 94 m and mean depth of 31 m, but the surface area of this lake is much larger, at 116 km^2. The large size of this lake allows for frequent development of seiches during the summer (N. Whalen, Portland Water District, pers. commun.).

In other key features, the lakes are quite similar to one another. All three lakes are located in watersheds that are 67–71 % forested, with Sebago Lake having the largest percentage of developed land, at 6 % (Table 1). Lobster and Tunk Lakes have never been dammed. Sebago Lake has an eel weir dam that was installed during the early half of the nineteenth century. This can alter lake depth by 1.5–2 m over the course of the year, but given the great depth of the lake, this is unlikely to affect planktonic habitat. The long axes of these lakes are all oriented north–south,

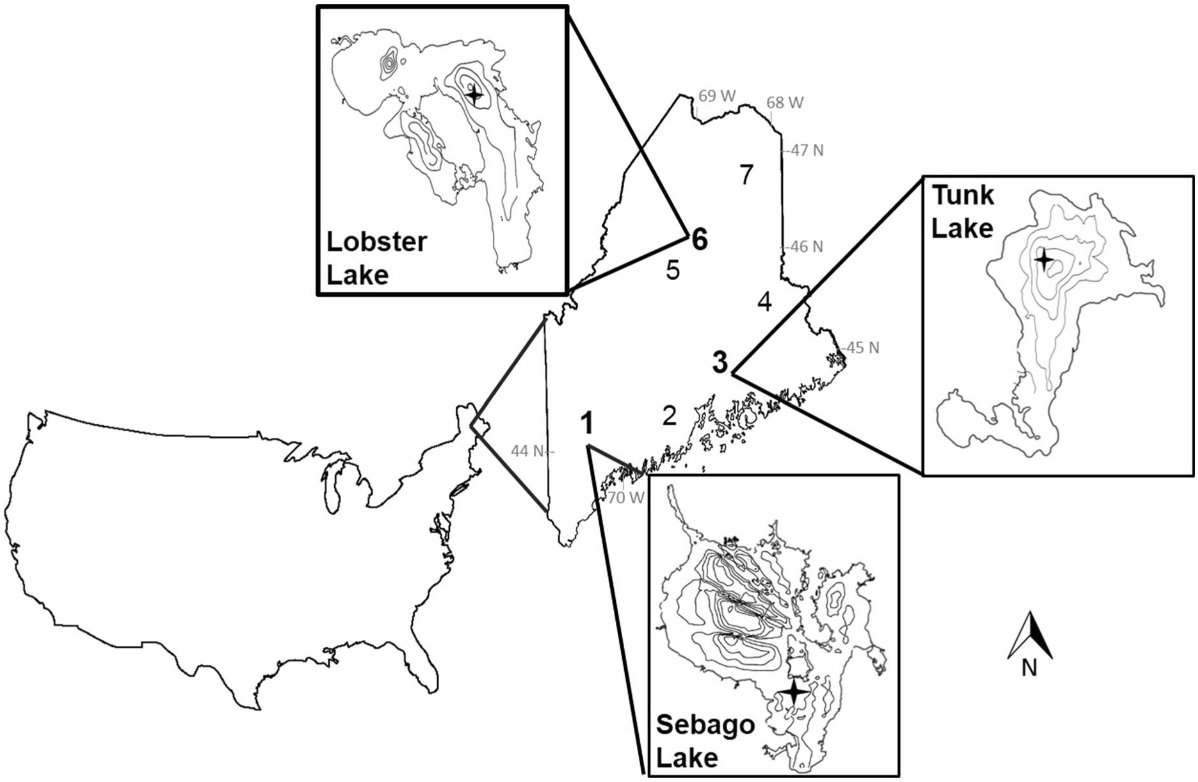


Fig. 1 Locations of three study lakes (bolded) in Maine, USA. Lake bathymetry with 20-m contours for Sebago Lake and Tunk Lake, and 5-m contours for Lobster Lake. The *star symbol* designates the location of limnological sampling and coring. The *map* highlights the locations of the lakes that have long-term historical ice-out data. These lakes include Swan Lake (*2*), West Grand Lake (*4*), Moosehead Lake (*5*), Portage Lake (*7*)

Table 1 Select lake characteristics of the study lakes

Lake name	Lake area (km^2)	Average depth (m)	Max depth (m)	Fetch (km)	Watershed characteristics				Average TP (μg L^{-1})	August epilimnion thickness (m)
					Size (km^2)	Open water (%)	Forested (%)	Developed (%)		
Tunk Lake	8	22	68	5	20	23	70	1	4	8
Sebago Lake	116	31	94	16	1147	17	67	6	3	8
Lobster Lake	14	9	32	6	172	9	71	<1	4	7

Watershed characteristics are delineated from National Hydrography Dataset shape files from the National Land Cover Dataset 2006 (version 1)

Source: lakesofmaine.org

and prevailing summer winds in Maine come from the southwest, suggesting the lakes should be similarly affected by wind.

Declining wind strength has been observed during the last few decades across terrestrial habitats in North America, with the strongest declines observed in the Midwestern and Eastern United States (Pryor et al. 2009). Yearly average wind speeds were compiled for three weather stations near each lake (Fig. 2; data from NOAA National Weather Service), and all three lakes are situated in areas with declining average wind speeds from 1940 to 2013 (Fig. 2). The strongest decline in wind speed is in Bar Harbor (15.5 miles south of Tunk Lake; Fig. 2d) (linear regression; $n = 38$, $R^2 = 0.799$, $p < 0.001$), although we note that there is a temporal gap in the data that may influence the strength of this relationship. Wind speed also declined in Portland (20 miles from Sebago Lake; Fig. 2e) and Millinocket (43 miles from Lobster Lake; Fig. 2f) over the recorded period (linear regression; $n = 66$, $R^2 = 0.203$, $p = 0.001$ and $n = 50$, $R^2 = 0.352$, $p < 0.001$, respectively). The wind record from the Blue Hill Observatory Science Center near Boston, Massachusetts extends back to the 1880s and also shows a similar decline in wind speeds beginning in the 1940s (Iacono 2009).

Ice-out date records, or the date of ice break-up, are available (http://me.water.usgs.gov/iceout.html) for Sebago Lake and lake pairs in the vicinities of Tunk Lake (West Grand Lake and Swan Lake) and Lobster Lake (Moosehead Lake and Portage Lake). Nonparametric correlation reveals coherence in ice-out trends for all pairs of the five lakes across the state (ρ ranging from 0.42 to 0.86, $p < 0.001$), with lakes in the same region having the strongest coherence with each other (Fig. 2). Although coherent across the state, the records show some variation in the timing of major changes. Starting in the late 1800s, ice-out dates occurred progressively earlier for Sebago Lake, and are about 30 days earlier (Hodgkins et al. 2002), with the greatest decline between 1875 and 1930 (Fig. 2). From 1900 to 1980, average decadal ice-out dates for West Grand Lake and Swan Lake showed no directional change, after which they became earlier. Ice-out on Moosehead Lake shifted to 9 days earlier between 1850 and 2000, with the most rapid advances in date occurring from 1875 to 1900 and 1968 to 2000 (Hodgkins et al. 2002). The timing of spring ice-out in Maine lakes is related to the number of accumulated freezing and melting degree-days in January–February (Beyene and Jain 2015).

Materials and methods

Water column sampling

In each lake, distributions of key diatom taxa were measured along with physical and chemical variables four times during the course of 2013: spring mixing or early stratification, mid-summer, late summer, and early fall. Samples were taken from the same location, marked with a buoy, during each sampling period. Lake transparency was measured using a Secchi disk, and these values were converted to photic zone depth by doubling the Secchi depth. The temperature profile was measured with a Yellow Springs Instruments (YSI) temperature probe at every meter to the lake bottom or a depth of 25 m. To assess variability in lake thermal structure owing to seiches in Sebago Lake, a

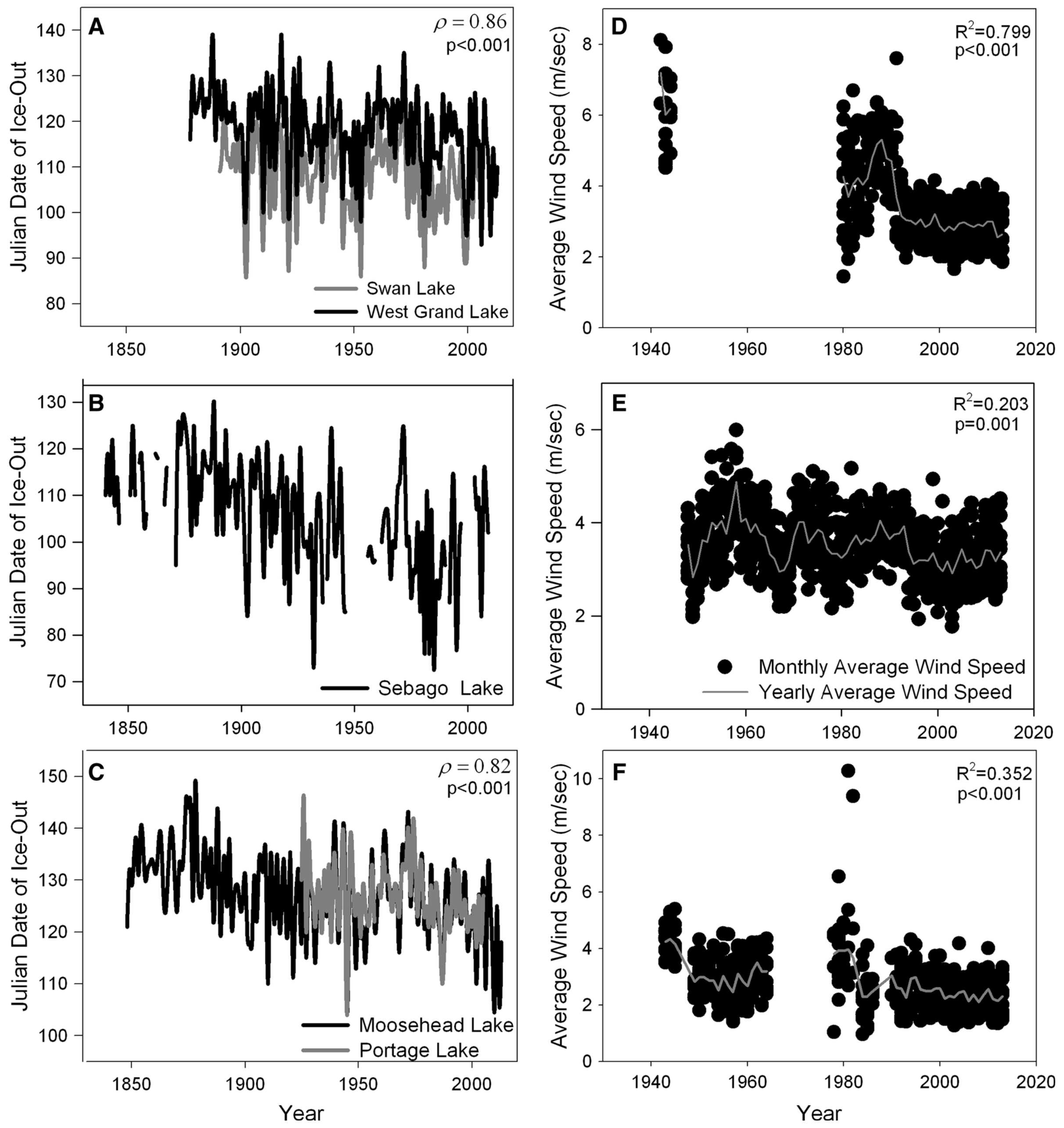


Fig. 2 Long-term ice-out dates and wind speeds for the study and nearby lakes. **a**–**c** The Julian date of ice-out is shown for Swan Lake and West Grand Lake (near Tunk Lake), as well as the study lake Sebago, and Moosehead Lake and Portage Lake (near Lobster Lake). For the Sebago Lake plot after 1900, years with no data shown are those in which the lake did not completely freeze. Coherence between lake pairs in each area (based on Spearman's correlation analysis) is indicated by ρ and *p* value on the plots. **d**–**f** monthly average wind speeds from the 1940s to 2013 from weather stations near the three study lakes: **d** Tunk Lake, **e** Sebago Lake, and **f** Lobster Lake. The *grey lines* show annual average wind speeds. All show statistically significant declines in wind speed (linear regression; $p \leq 0.001$)

string of temperature probes (Onset HOBO Pendant Data Logger) was deployed at every meter from 3 to 20 m for the ice-free season.

Water was collected with a van Dorn bottle from the epilimnion, metalimnion, and hypolimnion for the following chemical analyses: dissolved inorganic nitrogen (DIN, including nitrate and ammonium), total phosphorus (TP), dissolved organic carbon (DOC) and chlorophyll *a*. Dissolved nutrient samples were syringe-filtered through a polycarbonate membrane into 125-mL acid-washed bottles and refrigerated until processed. Nitrate was measured using the cadmium reduction method, and ammonium was measured with the phenate method (APHA 2000). Whole water samples were collected in 125-mL acid-washed bottles for TP. These were digested using persulfate, then analyzed by the ascorbic acid colorimetric procedure, following standard methods (APHA 2000). Ratios of DIN:TP were calculated as indicators of nutrient limitation status (Bergström 2010). A sample for DOC was collected from the epilimnion water, and filtered with a 0.7-µm-pore-size GF/F filter into a glass vial. These samples were stored in a refrigerator until analyzed on a Shimadzu Total Organic Carbon Analyzer. The water collected for chlorophyll analysis was filtered through a 0.7-µm-pore-size GF/F filter. Filters were frozen and analyzed within 2 weeks. Chlorophyll *a* was extracted from the filters in acetone, following standard methods (APHA 2000), with modifications as outlined in Saros et al. (2005), and quantified with a Varian 50 Bio UV–visible spectrophotometer.

Phytoplankton were sampled at increments of two meters (Lobster Lake) and three meters (Tunk Lake and Sebago Lake) from the surface to right above the lake bottom (increments varied depending on lake depth). Samples were collected in duplicate, placed in 50-mL centrifuge tubes, and preserved with Lugol's iodine solution. Phytoplankton species composition was determined by settling 50-mL aliquots overnight in an Utermöhl-style chamber. Transects of the slides were counted on a Nikon Eclipse TS100 inverted microscope and phytoplankton were identified to the species level. Transects were counted until a minimum of 300 cells per slide was reached.

Paleolimnological sampling

Sediment cores were collected using a gravity corer deployed from a boat in the deep area of each lake (Fig. 1). The length of each core extruded was: 11.5 cm for Sebago Lake, 29 cm for Tunk Lake, and 26 cm for Lobster Lake. Cores were sectioned in the field into 0.5-cm increments. Sediment profiles were dated using ^{210}Pb activity, counted with a high-purity germanium well detector with a low-background graded lead shield at the University of Maine in Orono, and the chronology was based on the constant rate of supply model (Appleby and Oldfield 1978).

Sediments were processed for diatoms following methods outlined by Battarbee et al. (2001). A minimum of 300 diatom valves were counted per slide using an Olympus BX51 compound microscope at a magnification of 600×. Diatom taxonomy was based on Krammer and Lange-Bertalot (1986, 1988, 1991a, b) and Camburn and Charles (2000).

Statistical analyses

A detrended correspondence analysis (DCA) was applied to the percent relative abundance of all diatom species using a square root transformation, to evaluate diatom community turnover down core (R version 2.15.1, package vegan). Lake stratification conditions were reconstructed by applying a stratification index, similar to that used by Wang et al. (2008) and Stone et al. (2016): a ratio of *Aulacoseira subarctica* to *D. stelligera*. The ratio is lower when *D. stelligera* dominates, indicating shallower stratification and/or longer seasons of stratified conditions.

The relative abundances of both of these taxa in each sediment core were also compared to ice-out dates using Spearman's nonparametric correlation analysis, with $p \leq 0.05$ suggesting coherent changes in ice-out and diatom relative abundances. As mentioned above, there is an ice-out record for Sebago Lake; for Tunk Lake, the ice-out record from nearby Swan Lake was used, whereas for Lobster, the ice-out record from nearby Moosehead Lake was used.

Results

Water column sampling

Epilimnion thicknesses varied throughout the sampling period in 2013 for all three lakes. In May, there was not an established epilimnion for Sebago Lake or Lobster Lake (Table 2). This was also the case for Lobster Lake in September. Tunk Lake was stratified during all sampling periods. On the two sampling dates for each lake during the summer months, epilimnion thickness was between 5 and 8 m (Table 2). Thermistor data from Sebago Lake indicated that, from late June to the end of August, the epilimnion thickness fluctuated between 7 and 14 m, often changing by 1–5 m from one day to the next.

Chlorophyll concentrations varied during the summer, but were generally low (Table 2). Lobster Lake had higher DOC concentrations (7 mg L^{-1}) than Sebago and Tunk Lakes (both 3 mg L^{-1}; Table 2). Consequently, Lobster Lake had the lowest photic zone depth (between 6 and 9 m), whereas Tunk Lake and Sebago Lake had photic zones more than twice that of Lobster Lake. However, when considered as a proportion of the mean depth, the photic zone in the summer extended to more than 90 % of the water column in Lobster Lake, and 60–72 % in Sebago and Tunk Lakes. DIN:TP ratios indicated P limitation for all lakes (Table 2).

Asterionella formosa Hassall, *Tabellaria flocculosa* (Roth) Kützing, *A. subarctica, Cyclotella comensis* Grunow, and *D. stelligera* were part of the spring assemblages in all three lakes; however, seasonal phytoplankton dynamics varied across the three lakes (Fig. 3). *Discostella* taxa were only abundant in the water column of Lobster Lake during the spring, when the lake was not stratified. In contrast, it was more abundant in the water columns of both Tunk Lake and Sebago Lake during both samplings of summer stratified conditions, although *D. stelligera* was also present during spring turnover in Sebago Lake. *A. formosa* and *T. flocculosa* were abundant during summer stratified conditions in Tunk Lake, and during unstratified and stratified conditions in Sebago Lake. *T. flocculosa* was abundant during unstratified and stratified conditions in Lobster Lake.

Paleolimnological sampling

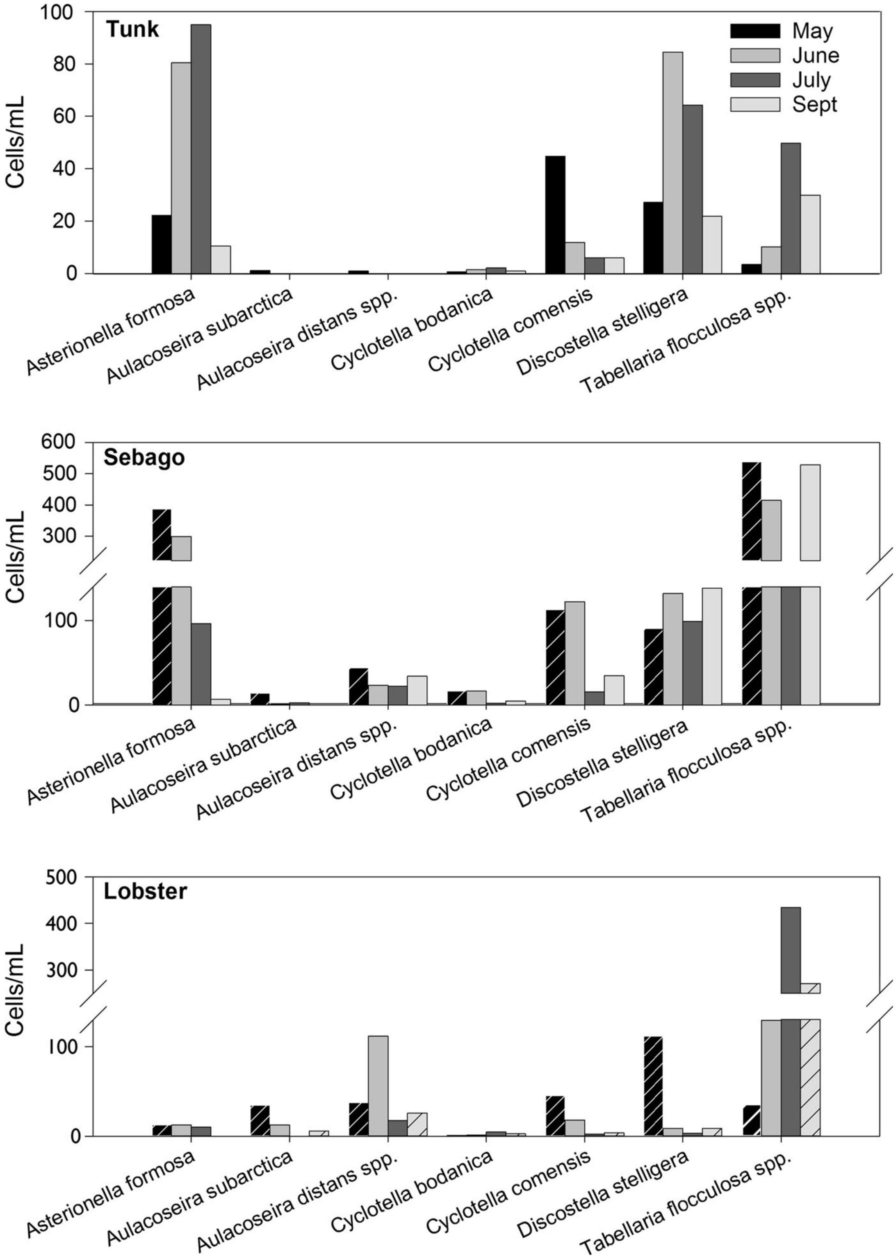
^{210}Pb activities declined exponentially in Tunk and Sebago (Fig. 4). Deviation from exponential decline in Lobster Lake indicates possible mixing or a change in sedimentation rate towards the surface of the core. The sedimentation rates for Lobster Lake and Tunk Lake were approximately 0.05–0.15 cm $year^{-1}$ with each sample depth integrating approximately 5–10 years. The sedimentation rate for Sebago Lake was lower, at 0.02 cm/year; each sediment section integrated an approximate 20-year period.

Table 2 Water column data for each lake and sampling period

	Tunk Lake	Sebago Lake	Lobster Lake
Epilimnion thickness (m)			
May	6	None	None
June	6	6	5
Aug.	8	8	7
Sept.	10	13	None
Photic zone depth (m)			
May	21	18	6
June	15	19	8
Aug.	16	21	8
Sept.	23	18	9
Average Chlorophyll (μg L^{-1})			
May	2.3	1.3	1.3
June	3	3	3.6
Aug.	2.2	1.8	2.7
Sept.	1.9	0.8	2.4
DIN:TP in epilimnion			
May	29	47	1.8
June	6.9	18	4.2
Aug.	10	6.9	6.6
Sept.	2.7	11	14
DOC (mg L^{-1})			
Average	3	3	7

Photic zone depth estimated by doubling the Secchi disk depth. DIN:TP stands for dissolved inorganic nitrogen:total phosphorus

Fig. 3 Dominant diatom species in the water column for each of the four sampling periods, for Tunk Lake, Sebago Lake, and Lobster Lake. *Striped bars* indicate mixed conditions at time of sampling



The relative abundances of diatom taxa in the Tunk Lake record began to shift during the latter half of the nineteenth century (Fig. 5). At that time, *A. subarctica* declined from about 7 % of assemblages to 2 %, and *C. comensis* showed a temporary increase to 10 % of assemblages. In the early twentieth century, *D. stelligera* increased from 40 % to 55–60 % of assemblages while *A subarctica* further declined to 1 % or less of assemblages. This pattern was sustained until the 1970s, when *D. stelligera* declined to 40-50 % of assemblages and *A. subarctica* increased to 1–2 % of assemblages. The relative abundances of *T. flocculosa var. linearis* Koppen and *T. flocculosa* (*strain IIIp*) sensu *Koppen* (Roth) Kützing varied over time. Considering just *A. subarctica* and *D. stelligera*, the relative abundances of these taxa were not correlated with the timing of ice-out ($p > 0.90$ in both cases) (Fig. 6; comparison only shown for *D. stelligera*). The

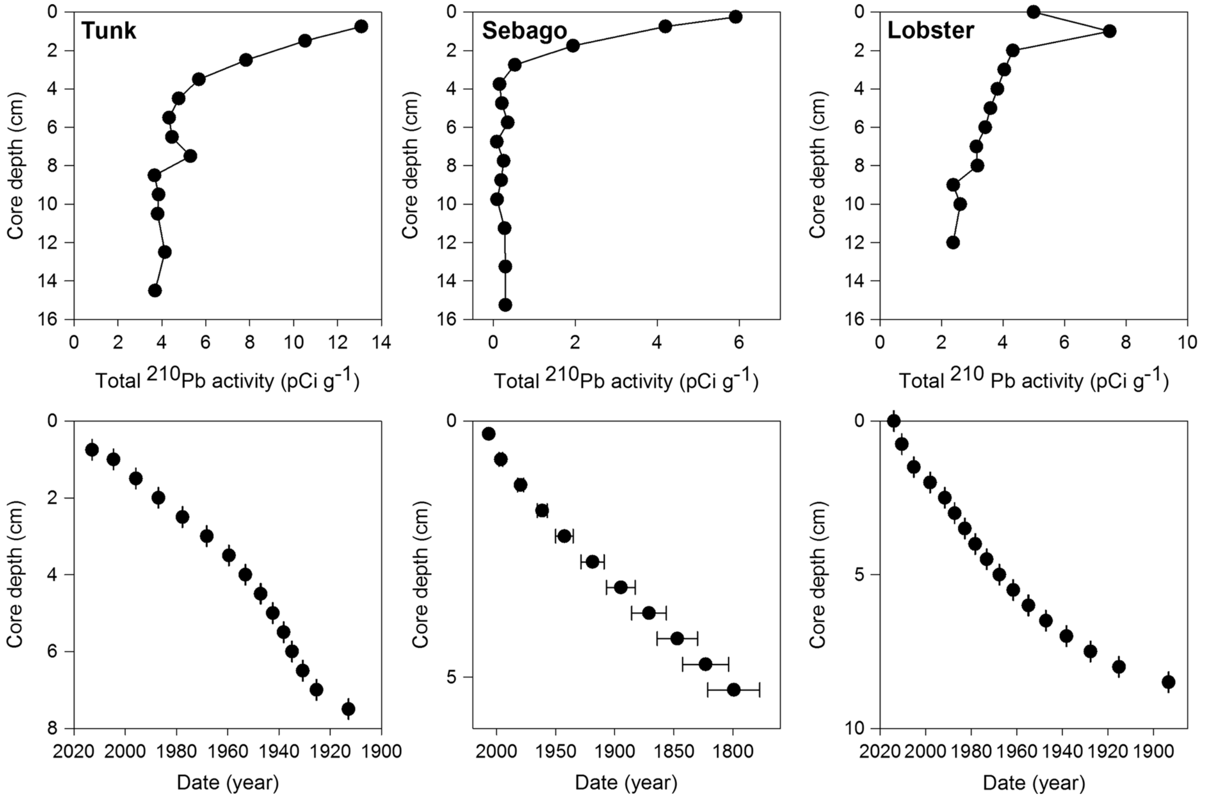


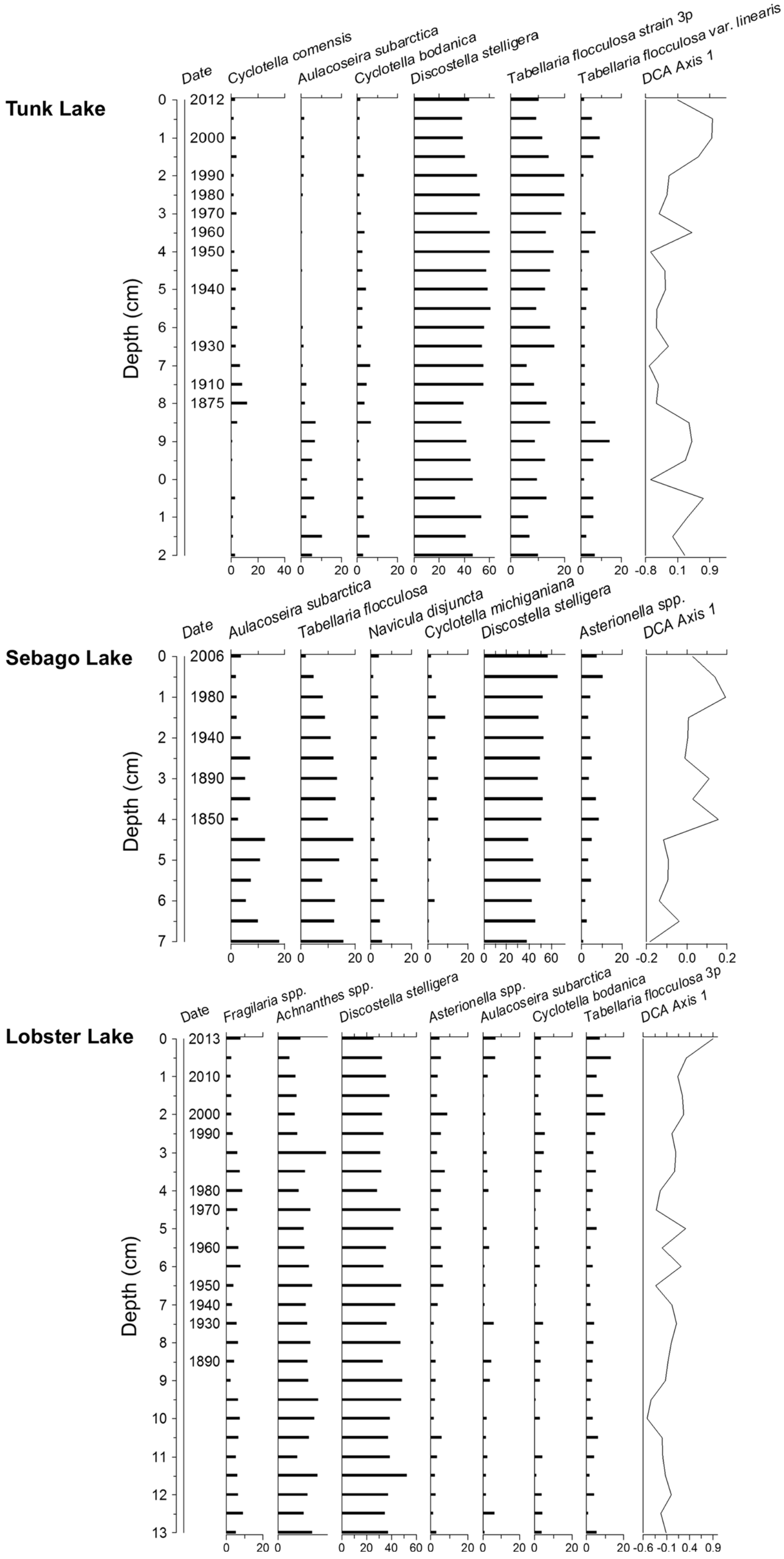
Fig. 4 ^{210}Pb activities (*top*) and inferred age (*bottom*)

stratification index suggests a shift towards shallower and/or longer periods of stratification at the end of the nineteenth century. The stratification index continues to decline over much of the twentieth century, but with a shift to possibly deeper mixing depths and/or shorter periods of stratification starting in the mid-1990s (Fig. 7).

The relative abundances of *A. subarctica* and, to a lesser extent, *D. stelligera* also changed over time in Sebago Lake (Fig. 5). Starting about 1850, the relative abundance of *A. subarctica* declined from about 10 to 3–7 % of assemblages; this species continued to decline over the twentieth century. *D. stelligera* was generally abundant throughout the record, with a small increase in relative abundance after 1850; this increase was sustained for the rest of the record. *T. flocculosa* declined after 1850, while *Cyclotella michiganiana* increased. Small, temporary increases in *Asterionella* species occurred around 1850, when the watershed experienced major land clearance for agriculture, as well as in the 1990s. Both of those increases in *Asterionella* taxa were accompanied by small increases in the relative abundances of *D. stelligera*. Based on DCA scores, it appears the rate of community turnover shifted in the mid-1800s (Fig. 5). Although ice-out day became about 30 days earlier over the period of record, there was no correlation with the relative abundances of either taxon ($p > 0.90$ in both cases) (Fig. 6; comparison only shown for *D. stelligera*). Diatom-inferred stratification shifted around 1850, to consistently shallower and/or longer periods of stratification during the twentieth century (Fig. 7).

Whereas the sedimentary diatom profiles of Tunk and Sebago Lakes showed shifts from the nineteenth to twentieth centuries, this was not apparent in the Lobster Lake record (Fig. 5). *A. subarctica* showed no directional change over the record. The relative abundances of *D. stelligera* were 40–50 % of assemblages until the 1980s, when they declined to about 30 %. *Asterionella* species began to increase around 1950, from about 1–2 % to about 5 % of assemblages, whereas around 1990, *T. flocculosa* (*strain IIIp*) began to increase and *Achnanthes* and *Fragilaria* species declined. Comparing ice-out day to the relative

Fig. 5 Fossil diatom records expressed as percent relative abundance of taxa comprising at least 5 % of the assemblage. *Downcore* detrended correspondence *axis-1* scores are also depicted



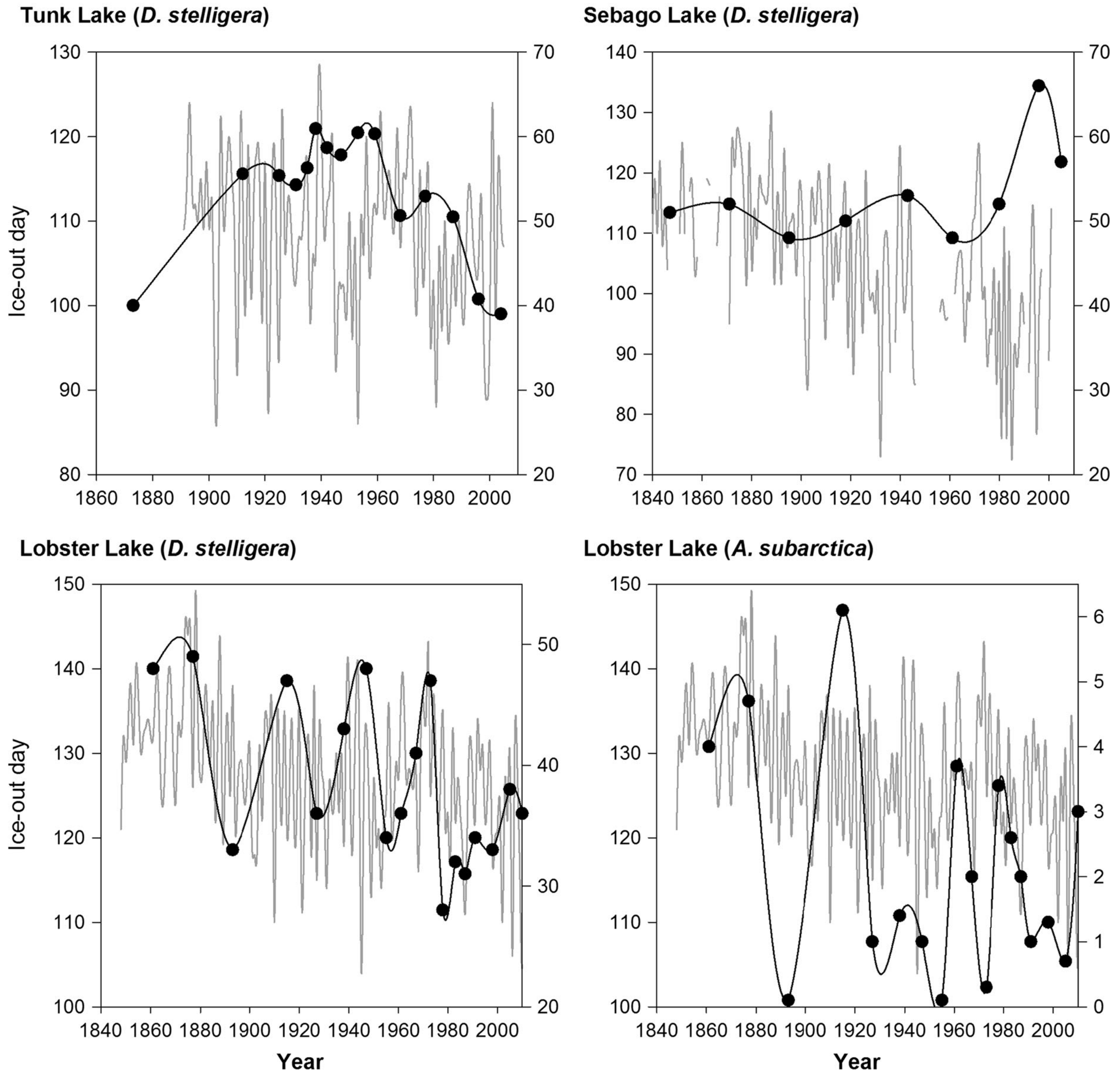


Fig. 6 Julian date of ice-out (*gray lines*) and relative abundances of certain diatom taxa in lake sediments (*black circles* and *line*) over time. Secondary *y*-axis is percent relative abundance for indicated taxon. Ice-out day is shown for Swan Lake (near Tunk Lake), with Tunk Lake diatoms; Sebago Lake (after 1900, years with no data shown are those in which the lake did not completely freeze); and Moosehead Lake (near Lobster Lake), with Lobster Lake diatoms. Note change in scale for *x*- and *y*-axes

abundances of *A. subarctica* and *D. stelligera*, there was no correlation ($p > 0.55$ in both cases), although the changes in *D. stelligera* abundance over time suggest that this species was less abundant during earlier ice-out years (Fig. 6). The stratification index showed no directional change until the twenty-first century (Fig. 7), when the index increased, suggesting deeper and/or shorter periods of stratification; we note, however, that the results of the water-column sampling indicated that both species bloom during spring turnover in this lake, raising questions about what a changing ratio of *A. subarctica* to *D. stelligera* reveals in this lake.

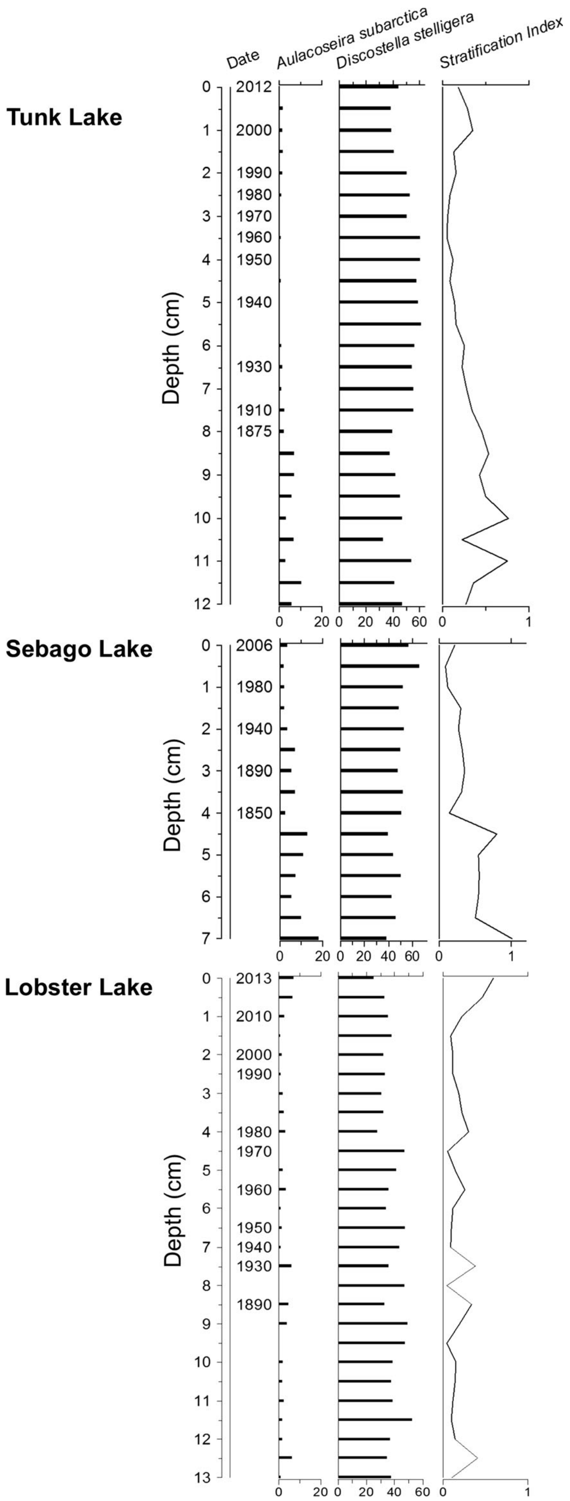


Fig. 7 Condensed diatom assemblage with species of interest. Percent relative abundance of *D. stelligera* and *A. subarctica* are shown along with the stratification index

Discussion

A diatom-inferred stratification index, which focuses on ecologically relevant taxa, was applied to three lake cores to evaluate the influence of lake morphometry on planktonic diatom responses to recent climate change in large lakes. This index was paired with modern ecological data to examine how the seasonal distribution of key diatom taxa affects our ability to use them to infer changes in lake thermal structure. Although all three of these large lakes have experienced similar declines in wind speed and earlier ice-out over the past two centuries, the responses of diatom communities varied across the sediment records. We attribute this to differences in lake morphometry and sedimentation rates, as well as variation in the timing of *D. stelligera* blooms.

The dominance of *D. stelligera* during stratified conditions in the contemporary water-column sampling of Tunk Lake supports the use of the stratification index to infer thermal-structure changes over time in this lake. The stratification index indicated a shift to shallower and/or longer stratification periods in this lake starting at the end of the nineteenth century and intensifying during the twentieth century. These changes began to occur as the Little Ice Age ended, and intensified during the period in which average wind speed declined in the region. There is a reversal, however, in the twenty-first century, with the stratification index suggesting deeper and/or shorter periods of stratification. These recent changes may be more strongly and directly driven by increasing air temperatures, resulting in a deepening thermocline as observed in some other deep lakes (Kraemer et al. 2015). Overall, the Tunk Lake diatom record suggests that lake stratification patterns have been changing in this area since the late nineteenth century, likely as a result of multiple effects of climate change (i.e. changing wind strength, increasing air temperatures).

In Sebago Lake, the validity of using the stratification index is less certain. In general, *D. stelligera* was more abundant during periods of stratification compared to turnover, but it was present during all samplings. In contrast, *A. subarctica* was only found in the water column during spring turnover. Together, this suggests that other factors, such as water transparency and/or nutrients, may be modifying the response of *D. stelligera* to stratification conditions in this lake (Saros and Anderson 2015). In the sediment core, *A. subarctica* declined and *D. stelligera* increased over time, with changes in both of these species beginning around 1850, only a few decades before those in Tunk Lake. These changes are sustained until the 1990s, when the relative abundances of *D. stelligera* increased again. This recent increase in *D. stelligera* is accompanied by an increase in *Asterionella* taxa as well, suggesting that this may reflect mild nutrient enrichment rather than, or in addition to, thermal change. Sebago Lake is deeper than Tunk Lake; we would not expect the thermal structure of these two lakes to respond differently to climate forcing in recent decades. Overall, the sediment record from Sebago Lake appears to integrate gradual, smoothed change over time, largely owing to the slower sedimentation rate and possibly to the less clear relationship between *D. stelligera* and thermal structure here. In addition, this lake has stronger internal wave dynamics compared to the other lakes in this study. This wave action results in high-frequency changes in epilimnion thickness, which appears to smooth diatom trends in the sediment record. Seiches may reduce the efficacy of using planktonic diatoms in sediment records to record shifts in lake thermal structure. Marcé et al. (2007) found that seiches and other internal lake dynamics can also result in a highly variable sedimentation pattern across a lake basin, and therefore concluded multiple cores should be collected from lakes that experience them.

In contrast to the other two lakes, the seasonal phytoplankton data from Lobster Lake do not support the use of *D. stelligera* as an indicator of stratified conditions, since it bloomed during spring turnover and was not abundant during stratified conditions. There are no planktonic species in this lake that bloomed solely during stratified conditions. In this lake, both *A. subarctica* and *D. stelligera* were most abundant during the spring sampling, yet they showed opposite patterns in the sediment record at some times. The relative abundances of these two species did not shift during the nineteenth century as in the other two lakes; rather, *D. stelligera* varied somewhat over time and consistently declined starting in the 1980s. In particular, the relative abundance of this species tended to decline in periods of earlier ice-out, though these trends were not significant. This is opposite to what others have found (Rühland et al. 2008, 2015), and raises questions about the mechanisms involved. Years with earlier ice-out may have less snowpack and hence, lower springtime nutrient pulses into lakes. Earlier ice-out may also negatively affect nutrient-light relationships for this species, with the spring nutrient pulse being delivered at a time of generally lower light availability when ice-out is earlier. In lakes with blooms of *D. stelligera* during turnover periods, future research that deciphers the ecology of this taxon under these conditions will improve our inferences.

With the different phytoplankton seasonal pattern in Lobster Lake, this highlights the importance of pairing modern phytoplankton studies with paleolimnological records to avoid erroneous conclusions. In both Tunk Lake and Sebago Lake, *D. stelligera* was present during periods of stratification in the modern ecological sampling, which is consistent with observations in other studies (Winder et al. 2009; Saros et al. 2012, 2014). However, the ecology of *D. stelligera* in Lobster Lake did not show similar environmental preferences. Other studies of shallow lakes observed similar trends in *D. stelligera* autecology. Köster and Pienitz (2006) found, in a shallow lake in Connecticut, that *D. stelligera* was present during fall turnover, a time when nitrogen was higher in the water column. The relationship between *D. stelligera* and thermal stratification is likely dependent on how mixing depth alters resource (light, nutrients) availability (Saros and Anderson 2015), and as such, nutrient and water transparency conditions in each lake will influence the strength of this relationship.

In Tunk and Sebago Lakes, we found little evidence to support the importance of ice-out timing as the primary driver of changing relative abundances of *D. stelligera* as other studies have suggested (Rühland et al. 2015). In addition, as described above, the potential pattern between ice-out date and *D. stelligera* in Lobster Lake (i.e. decline in relative abundance with earlier ice-out date) is opposite to what others have suggested. The relative abundances of this taxon were fairly stable and high in Tunk and Sebago Lakes from 1900 to 1960, despite changing ice-off dates over that time frame. The recent increase in this taxon in Sebago Lake happened at a time when ice-out date was occurring consistently earlier, but this increase in *D. stelligera* was also accompanied by other taxon changes that may suggest mild nutrient enrichment and hence multiple drivers of these community changes. In Sebago and Tunk Lakes, *D. stelligera* is generally more abundant in the water column during thermally stratified periods (i.e. summer), with thermal structure in large lakes like these shaped by factors such as wind strength and mean lake temperatures (Fee et al. 1996; Kraemer et al. 2015). Other factors, primarily January and February air temperatures, determine the timing of ice-out (Beyene and Jain 2015), suggesting that direct links between ice-out timing and summer stratification patterns should not necessarily be expected.

Results in this study further our understanding of mechanisms involved in spatial variability of pelagic diatom response to climate. All three lakes experienced similar changes in climate and ice-out over recent centuries. The sedimentary diatom profiles in both Tunk Lake and Sebago Lake indicated shifts to shallower and/or longer stratification starting in the mid- to late-nineteenth century. These changes became greater in Tunk Lake over the twentieth century while remaining stable in Sebago Lake. These differences may be attributed to within-lake processes, with Sebago Lake having strong internal wave dynamics and slow sedimentation rates that smooth diatom response to climate change. Autecological differences are also important, with *D. stelligera* in relatively shallow Lobster Lake exhibiting different timing in peak abundances compared to the other lakes, and a sedimentary diatom profile indicating more variability in *D. stelligera* abundances over time and a decline in this taxon starting in the 1980s in this lake. This study highlights the importance of pairing paleoecological reconstructions with contemporary water column sampling to provide refined insight into species distribution patterns and ultimately improve reconstructions.

Acknowledgments This project was funded by the Gokcen Fund and the Portland Water District. Funding for Tunk Lake dating was provided by the USEPA–USGS LTM project, funded by EPA CAMD to W. McDowell, J.S. Kahl and S.J. Nelson. The contents of this manuscript are solely the responsibility of the authors and do not necessarily represent the official views of the USGS. K. Boeff was supported as a graduate assistant by the Climate Change Institute and School of Biology and Ecology at the University of Maine while conducting this research. We are grateful for the field and lab assistance provided by R. Brown, K. Warner, D. Anderson, R. Northington, the Portland Water District, and the University of Maine Physics Department.

References

APHA (American Public Health Association) (2000) Standard methods for the examination of water and wastewater, 20th edn. APHA, Washington, DC

Appleby PG, Oldfield F (1978) The calculation of lead-210 dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. Catena 5:1–8

Battarbee RW, Jones VJ, Flower BP, Cameron NG, Bennion H, Carvalho L, Juggins S (2001) Diatoms. In: Smol J, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments. Kluwer, Dordrecht, pp 155–201

Bergström AK (2010) The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquat Sci 72:277–281

Beyene MT, Jain S (2015) Wintertime weather–climate variability and its links to early spring ice-out in Maine lakes. Limnol Oceanogr 60:1890–1905

Camburn KE, Charles DF (2000) Diatoms of low-alkalinity lakes in the Northeastern United States. Acad Nat Sci Phila Spec Pub 18:152

Fee EJ, Hecky RE, Kasian SE, Cruikshank D (1996) Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield Lakes. Limnol Oceanogr 41:912–920

Hobbs WO, Telford RJ, Birks HJB, Saros JE, Hazewinkel RRO, Perren BB, Saulnier-Talbot E, Wolfe AP (2010) Quantifying recent ecological changes in remote lakes of North America and Greenland using sediment diatom assemblages. PLoS One 5:e10026

Hodgkins G, James IC II, Huntington TG (2002) Historical changes in lake ice-out dates as indicators of climate change in New England, 1850–2000. Int J Climatol 22:1819–1827

Iacono MJ (2009) Why is the wind speed decreasing? Blue Hill Meterological Observatory. http://www.bluehill.org/climate/climate.html

IPCC Climate Change 2014: Synthesis Report (2014) Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. Core Writing Team, Pachauri RK, Meyer LA (eds). IPCC, Geneva

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

Kraemer BM et al (2015) Morphometry and average temperature affect lake stratification responses to climate change. Geophys Res Lett 42:4981–4988

Krammer K, Lange-Bertalot H (1986) Bacillariophyceae. I. Teil. Naviculaceae. In: Süsswasserflora von Mitteleuropa, Band 2/1

Krammer K, Lange-Bertalot H (1988) Bacillariophyceae. 2. Teil. Bacillariaceae, Epithemiaceae, Surirellaceae. In: Süsswasserflora von Mitteleuropa, Band 2/2

Krammer K, Lange-Bertalot H (1991a) Bacillariophyceae. 3. Teil. Zentrische Diatomeen, Diatoma, Meridion, Asterionella, Tabellaria, Fragilaria, Eunotia und Verwandte, Peronia und Actinella. In Süsswasserflora von Mitteleuropa, Band 2/4

Krammer K, Lange-Bertalot H (1991b) Bacillariophyceae. 4. Teil. Achnanthes, Navicula, Gomphonema, Kritische Nachtraege, Literatur. In Süsswasserflora von Mitteleuropa

Leavitt PR, Fritz SC, Anderson NJ, Baker PA, Blencker T (2009) Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnol Oceanogr 54:2330–2348

Magnuson JJ, Benson BJ, Jensen OP, Clark TB, Card V, Futter MN, Soranno PA, Stewart KM (2005) Persistence of coherence of ice-off dates for inland lakes across the Laurentian Great Lakes region. Verh Int Ver Limnol 29:521–527

Marcé R, Feijoó C, Navarro E, Ordoñez J, Gomà J, Armengol J (2007) Interaction between wind-induced seiches and convective cooling governs algal distribution in a canyon-shaped reservoir. Freshw Biol 52:1336–1352

Perren BB, Douglas MSV, Anderson NJ (2009) Diatoms reveal complex spatial and temporal patterns of recent limnological change in West Greenland. J Paleolimnol 42:233–247

Pham SV, Leavitt PR, Wissel BW, Wassenaar LI (2009) Spatial and temporal variability of prairie lake hydrology as revealed using stable isotopes of hydrogen and oxygen. Limnol Oceanogr 54:101–118

Pryor SC, Barthelmie RJ, Young DT, Takle ES, Arritt RW, Flory D, Gutowski WJ Jr, Nunes A, Roads J (2009) Wind speed trends over the contiguous United States. J Geophys Res. doi:10.1029/2008JD011416

Rühland K, Paterson A, Smol J (2008) Hemispheric-scale of 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, Michel TJ, Interlandi SJ, Wolfe A (2005) Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes. Can J Fish Aquat Sci 62:1681–1689

Saros JE, Clow DW, Blett T, Wolfe AP (2011) Critical nitrogen deposition loads in high-elevation lakes of the western U.S. inferred from paleolimnological records. Water Air Soil Pollut 216:193–202

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

Saros JE, Strock KE, McCue J, Hogan E, Anderson NJ (2014) Response of *Cyclotella* species to nutrients and incubation depth in Arctic lakes. J Plankton Res 36:450–460

Smol JP, Wolfe AP, Birks HJB, Douglas MSV, Jones VJ, Korhola A, Pienitz R, Rühland K, Sorvari S, Antoniades D, Brooks SJ, Fallu M, Hughes M, Keatley BE, Laing TE, Michelutti N, Nazarova L, Nyman M, Paterson AM, Perren B, Quinlan R, Rautio M, Saulnier-Talbot E, Siitonen S, Solovieva N, Weckström J (2005) Climate-driven regime shifts in the biological communities of arctic lakes. Proc Natl Acad Sci USA 102:4397–4402

Stone JR, Saros JE, Pederson GT (2016) Coherent late Holocene climate-driven shifts in the structure of three Rocky Mountain lakes. Holocene. doi:10.1177/0959683616632886

Wang L, Lu H, Liu J, Gu Z, Mingram J, Chu G, Li J, Rioual P, Negendank JFW, Han J, Liu T (2008) Diatom-based inference of variations in the strength of Asian winter monsoon winds between 17,500 and 6000 calendar years B.P. J Geophys Res. doi:10.1029/2008JD010145

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