Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes

KATHLEEN RÜHLAND*, ANDREW M. PATERSON† and JOHN P. SMOL*

*Paleoecological Environmental Assessment and Research Laboratory (PEARL), Department of Biology, Queen’s University, Kingston, ON, Canada K7L 3N6, †Dorset Environmental Science Centre, Ontario Ministry of the Environment, 1026 Bellwood Acres Road, Dorset, ON, Canada P0A 1E0

Abstract

A synthesis of over 200 diatom-based paleolimnological records from nonacidified/nonenriched lakes reveals remarkably similar taxon-specific shifts across the Northern Hemisphere since the 19th century. Our data indicate that these diatom shifts occurred in conjunction with changes in freshwater habitat structure and quality, which, in turn, we link to hemispheric warming trends. Significant increases in the relative abundances of planktonic Cyclotella taxa (P < 0.01) were concurrent with sharp declines in both heavily silicified Aulacoseira taxa (P < 0.01) and benthic Fragilaria taxa (P < 0.01). We demonstrate that this trend is not limited to Arctic and alpine environments, but that lakes at temperate latitudes are now showing similar ecological changes. As expected, the onset of biological responses to warming occurred significantly earlier (P < 0.05) in climatically sensitive Arctic regions (median age = AD 1870) compared with temperate regions (median age = AD 1970). In a detailed paleolimnological case study, we report strong relationships (P < 0.005) between sedimentary diatom data from Whitefish Bay, Lake of the Woods (Ontario, Canada), and long-term changes in air temperature and ice-out records. Other potential environmental factors, such as atmospheric nitrogen deposition, could not explain our observations. These data provide clear evidence that unparalleled warming over the last few decades resulted in substantial increases in the length of the ice-free period that, similar to 19th century changes in high-latitude lakes, likely triggered a reorganization of diatom community composition. We show that many nonacidified, nutrient-poor, freshwater ecosystems throughout the Northern Hemisphere have crossed important climatically induced ecological thresholds. These findings are worrisome, as the ecological changes that we report at both mid- and high-latitude sites have occurred with increases in mean annual air temperature that are less than half of what is projected for these regions over the next half century.

Keywords: climate, Cyclotella, ice-out, meta-analysis, Northern Hemisphere lakes, paleolimnology, planktonic diatoms

Introduction

Unequivocal evidence of pronounced warming in high latitude and high altitude regions beginning in the 19th century is well documented (Moritz et al., 2002; ACIA, 2004). Similarly, air temperatures in temperate latitudes of the Northern Hemisphere have increased over the last century, with an amplification of this warming trend over the past 30–40 years that is unprecedented in the last ~1300 years (Jansen et al., 2007).

The effects of recent temperature increases on freshwater ecosystems may be blurred at temperate latitudes, as these regions are typically subjected to multiple stressors that can mask or override climatic signals (Smol, 2008). However, in remote regions where extensive anthropogenic disturbances are diminished, the effects of climatic fluctuations on physical, biological and chemical processes of freshwater ecosystems are more clearly evident (Schindler et al., 1996; Gerten &
Adrian, 2002). Although the nature and magnitude of climate-driven responses may vary among freshwater systems, it is clear that a warmer climate will affect important lake properties and thus aquatic biota in a myriad of complex ways (Keller, 2007).

Analyses of spatial synchrony (i.e. temporal coherence) in lake ecosystem responses to climatic changes have rarely been examined at a regional or global scale. Given the wide range of differences in geographic settings, atmospheric circulation patterns and various feedback mechanisms, the temporal and spatial consistency of biological responses to these climatic changes is not expected. Furthermore, regional and site-specific differences in lakes (e.g. lake morphology, depth, bedrock geology) can result in a variety of responses, even under large-scale climatic changes. However, recent studies have reported strong correlations between plankton dynamics and climate variables (North Atlantic Oscillation, El Niño-Southern Oscillation Index) in lakes in North America and Europe (Straile & Adrian, 2000; Weyhenmeyer et al., 2002; Blenckner et al., 2007; Rusak et al., 2008). Thus, despite differences among lake settings and characteristics, regional climatic drivers may result in significant coherence among lakes within bioregions.

In many dimictic lakes, siliceous algae, particularly diatoms (Bacillariophyceae), are an important component of seasonal phytoplankton maxima, the timing of which may play a key role in the success of zooplankton populations (e.g. Winder & Schindler, 2004a; Adrian et al., 2006). Numerous climate-related physical properties in lakes, such as the length of the open-water season, the timing, duration and strength of thermal stratification, the timing and strength of the spring freshet, and the duration of spring overturn play critical roles in algal dynamics and community structure. These lake properties, in turn, affect water-column mixing processes, light availability and stability, and nutrient distribution (Smol, 1988). For example, warmer temperatures (quite notably winter temperatures) have resulted in earlier ice-out dates, earlier onset of thermal stratification, and earlier development of diatom blooms in both European (e.g. Adrian et al., 2006) and North American (e.g. Winder & Schindler, 2004b) lakes. Changes in the abundance and composition of primary producers in lakes can directly impact abundances of slower growing zooplankton taxa (Adrian et al., 2006), with important implications for cascading effects throughout aquatic foodwebs (Winder & Schindler, 2004b).

Recent increases in the relative abundances of small Cyclotella species, concurrent with decreases in heavily silicified Aulacoseira species and/or small, benthic Fragilaria taxa, were originally linked to warming-related changes in lakes from subarctic regions of Finland (Sorvari & Korhola, 1998; Sorvari et al., 2002) and Canada (Rühland et al., 2003; Rühland & Smol, 2005). Recently, paleolimnological studies from temperate regions across Canada (e.g. Werner et al., 2005; Harris et al., 2006) have likewise reported increases in planktonic Cyclotella species that we found to be strikingly similar to the above subarctic studies. However, a global synthesis of these trends has hitherto not been undertaken. The emergence of this recurring pattern in taxon-specific changes in lakes from diverse ecological settings prompted us to examine these trends more closely.

Plankton-based studies (e.g. sediment traps, water-column sampling, monitoring data, surface sediments) have added valuable insights into the seasonal dynamics of various plankton groups including species-level diatom trends. Although generally short in duration (typically 2 years or less), these empirical studies have found climate-related patterns in Cyclotella–Aulacoseira–Fragilaria diatom assemblages that may be related to the length of the ice-free season, the timing, duration and strength of thermal stratification, the depth of the epilimnion, the duration of the mixing period, and/or subsurface habitat development in relation to these factors (e.g. Fahnenstiel & Glieme, 1983; Kilham et al., 1996; Raubitschek et al., 1999; Lotter & Bigler, 2000; Rautio et al., 2000; Ptacnik et al., 2003; Chu et al., 2005; Forssström et al., 2005; Pannard et al., 2008). In general, these studies have concluded that warming-induced lakewater properties favor small Cyclotella species (Cyclotella comensis/gordonensis, Cyclotella stelligera/pseudostelligera/glomerata) over larger and heavier Aulacoseira species and/or small benthic Fragilaria diatom species. Longer-term monitoring data (~20–30 years) are rare, and when they exist rarely measure algal assemblages beyond coarse taxonomic groupings. While these studies clearly show that climate has played an important role in the composition of phytoplankton in freshwater lakes over the last few decades (e.g. Findlay et al., 2001), there is unfortunately little or no information on diatom seasonal dynamics at the species level.

In this paper, we provide a meta-analysis of more than 200 diatom-based paleolimnological studies that explores the geographic extent, spatial synchrony, and possible mechanisms for recent taxon-specific shifts (i.e. Cyclotella–Aulacoseira–Fragilaria species) recorded in a wide variety of Northern Hemisphere lakes. Specifically, we ask: (1) How many diatom-based paleolimnological profiles contain significant populations of Cyclotella species? (2) How many of these profiles record an increase or decrease in the relative abundance of Cyclotella species in recent sediments, and what do these lakes have in common? (3) Do studies that record increases in Cyclotella show concurrent decreases in Aulacoseira and/or Fragilaria species? (4) What is the geographic extent and timing of this increasing Cycle-
tella trend? (5) What are the most plausible mechanisms for this taxon-specific diatom shift? Furthermore, we examined a high-resolution diatom record from Whitefish Bay (Lake of the Woods, Ontario, Canada) in relation to long-term climate records, lake ice records, and atmospheric nitrogen deposition to elucidate the primary driver of this taxon-specific diatom shift (e.g. climate, habitat change, atmospheric contaminants). We conclude that nonacidified/nonenriched lakes from both circum-Arctic and temperate regions are showing remarkably similar warming-induced taxon-specific shifts since the 19th century. Diatom responses to warming were most sensitive in Arctic lakes but as temperature-related thresholds were exceeded at lower latitudes during the mid-20th century, this ecological reorganization is now evident throughout the Northern Hemisphere.

Methods

Paleolimnological studies containing Cyclotella species: meta-analysis

Biological proxy data preserved in lake sediments provide a reliable means for assessing ecological response to long-term environmental change (Smol, 2008). In particular, subfossil diatoms have been a mainstay for paleolimnological assessments because of their ability to respond rapidly to environmental change, their siliceous frustules preserve well, and their wide distribution among a diverse array of aquatic habitats (Stoermer & Smol, 1999). Dated, continuous lake-sediment sequences (i.e. lake-sediment records examined at close, consecutive intervals for the full core length) provide valuable records of the timing, magnitude, and direction of environmental change based on changes in diatom assemblages preserved in the sediment (Stoermer & Smol, 1999).

We recognize that not all lake types will support the particular diatom taxa examined in this study (i.e. Cyclotella–Fragilaria–Aulacoseira: Appendix S1) and, in addition to the genera considered here, other diatom species may also be sensitive to climatically induced limnological changes (e.g. see Smol et al., 2005). For example, recent studies from both the Russian Arctic, as well as in the Experimental Lakes Area (ELA; Ontario, Canada), have also reported increases in the relative abundances of planktonic diatoms, but these include genera such as Asterionella and Tabellaria with concurrent decreases in Aulacoseira taxa over the past few decades [Smol et al., 2005; Solovieva et al., 2005, 2008; M. Enache (National Academy of Sciences, Philadelphia, PA), personal communication]. These shifts may also be the result of recent warming with Asterionella and Tabellaria dominating the water column when stratification is strongest at the end of summer, and Aulacoseira taxa dominating in early spring with blooms occurring under ice (Solovieva et al., 2005). However, it was not practical for us to examine all available diatom records that elicit a response to climate. Rather, we have restricted our study to paleolimnological data that specifically contain the word ‘Cyclotella’ in published manuscripts, theses, or consultant reports, and that contain Cyclotella in recent sedimentary profiles (last ca. 200 years).

An important criterion for our meta-analysis was that lakes included in this study must not be profoundly disturbed by human activities so as to eliminate some of the more important confounding factors, such as high nutrient concentrations and low pH. For example, lakes in which concentrations of total phosphorus (TP) are > 20 μg L⁻¹ are more apt to experience cyanobacterial algal blooms than more oligotrophic lakes (MOE, 1994). Similarly, a pH level below 6 is found to be the point at which an ecological threshold is passed whereby acid-related aquatic community changes become measurable (e.g. Holt et al., 2003). Therefore, we categorized lakes as not being profoundly affected by cultural disturbances as having concentrations of TP 20 μg L⁻¹ or less and that pH levels must be 6.0 or higher. These criteria also included lakes that are currently showing a recovery from these impacts. For example, many lakes in both Europe and North America have undergone intensive remediation programs initiated in the early 1970s in response to eutrophication of freshwater systems from the addition of phosphorus and nitrogen compounds. As a result of these remediation efforts, many of these lakes are starting to show some recovery over the last decade or more. We rationalize that once these pollution stressors have been sufficiently removed, ambient climatic signals would become prevalent on the diatom assemblages from these systems.

All manuscripts included in our analysis were tabulated, irrespective of whether or not these studies registered increases, decreases or no trend in the relative abundances of small, planktonic Cyclotella taxa through time. Diatom-based paleolimnological studies that were included in this meta-analysis conformed to the following criteria. (1) All detailed diatom profiles had an established chronology (e.g. ²¹⁰Pb dating) for the last ca. 200 years; (2) all continuous diatom records contained at least 2% relative abundance of Cyclotella species in at least one sedimentary interval; (3) all detailed cores, as well as ‘top-bottom’ regional paleolimnological analyses, included lakes with present TP measurements below 20 μg L⁻¹ and pH above 6 (i.e. lakes unimpacted by anthropogenic nutrient enrichment or acid deposition). This criterion eliminated lakes with confounding factors as described above. (4) Diatom profiles were categorized as showing a rise in Cyclotella species if this
increase was greater than 5% above background relative abundances.

We examined differences in the timing of the diatom changes in lakes among regions [i.e. high latitude, high altitude, low latitude (temperate)] using an ANOVA on ranks followed by Dunn’s post hoc test to examine pairwise differences. Study lakes were categorized by region based on the original authors’ classifications; Arctic and subarctic lakes were considered to be high latitude. The approximate timing (year) of the change was determined from the authors’ interpretations, or by directly examining the published diatom stratigraphies and estimating the point at which the relative abundance of Cyclotella exceeded 5% above background levels (i.e. beyond the estimated percentage of possible error associated with diatom counting or chance alone; see Wolfe, 1997).

To examine trends over a relatively wide geographic range, we compared several regional datasets that used a technique known as the ‘top-bottom’ or ‘before and after’ paleolimnological approach, which has been successfully used to explore a large variety of environmental change issues (Smol, 2008). In brief, this approach compares environmental indicators from discrete sedimentary layers [top sediments: modern environment, and bottom sediments: preindustrial environment (before AD 1850)]. These broad-scale studies were included in our analysis to provide additional data to support our collection of detailed sediment core analyses, thereby adding to the geographic extent and reproducibility of the taxon-specific trend within a given region under examination. We acknowledge that the depth in the core of the bottom sample varies from lake to lake, as does the depth at which baseline (preindustrial) conditions would be reached. However, each regional dataset used in this paper consists of several 210Pb-dated and fully analyzed (whole core) sedimentary profiles that serve to substantiate that the bottom sediments represent preindustrial (pre-1850) diatom assemblages (Smol, 2008) for each region. For example, based on numerous dated cores, sediments from temperate North American lakes deposited below 20–30 cm typically represent pre-1850 lake conditions (e.g. Forrest et al., 2002; Harris et al., 2006; Smol, 2008; as well as the discussions in the original papers we cite).

For the ‘top-bottom’ portion of our synthesis, we have collected the results of studies from the Northwest Territories and Nunavut (Rühland et al., 2003), from New Brunswick (Harris et al., 2006), and from Ontario. The Ontario lake-set consists of three separate studies that we have combined into one representation of Ontario [South-central Ontario: collected 1992 (Hall & Smol, 1996); South-eastern Ontario: collected 1998 (Reavie et al., 2002); South-western Ontario: collected 1999 (Werner, 2003)]. To test whether the mean relative abundances of diatom species (i.e. Cyclotella, Fragilaria, Aulacoseira species) in the recent samples were significantly different from the preindustrial sediment samples, we used a nonparametric Wilcoxon Signed-Rank test for each regional lake set.

**Detailed paleolimnological case study**

To explore the primary mechanisms influencing the plankton increases, we analyzed a high-resolution fossil diatom record from Whitefish Bay, Lake of the Woods, Canada (49.38°N, 94.14°W), in conjunction with long-term climate-related instrumental and historical data. Lakes in northwestern Ontario, such as Whitefish Bay in the Lake of the Woods, are of particular interest as most have remained relatively isolated from long-term influences of direct human perturbations and are often considered 'reference' sites for local and regional impact studies (e.g. ELA; Schindler, 1997). In addition, climate records from northwestern Ontario have reported some of the highest rates of temperature increases in North America over the last few decades, particularly during the winter (Schindler, 1997; Chiotti & Lavender, 2008). Winter and spring snow fall has decreased significantly in this region with significant declines in streamflow since the 1970s (Chiotti & Lavender, 2008; Warren & Egginton, 2008). Although total annual precipitation has increased, it is likely insufficient to compensate for the rise in evaporation rates due to substantially warmer temperatures (Schindler, 1997; Warren & Egginton, 2008).

From a paleolimnological perspective, the exceptionally high temporal resolution of the Whitefish Bay sedimentary profile, the availability of long-term continuous climate data from the nearby town of Kenora, and the existence of a rare long-term lake ice record from this same site (Whitefish Bay) provided us with an ideal opportunity to directly examine relationships between diatom compositional changes and climate-related instrumental and historical data. In addition, to test the possibility that atmospheric nitrogen deposition may also have contributed to the recent increases in planktonic Cyclotella taxa, we examined the relationship between long-term nitrogen deposition data available from Lake 239 in nearby ELA and our Whitefish Bay diatom data. An examination of these relationships seeks to provide insights into some of the plausible triggers for this recent taxon-specific shift.

Kenora climate records dating back to 1899 were attained from the Historical Adjusted Climate Database for Canada available at the Environment Canada website (http://www.cccma.ec.gc.ca/hccd/). We examined monthly, seasonal, and annual temperature trends. The continuous Whitefish Bay Lake ice record (starting in
1964) was obtained from the Ontario Ministry of Natural Resources, Kenora, Ontario, Canada. We examined changes in the day in which ice formed on the lake (ice-on), the day in which ice left the lake (ice-out), as well as the number of ice-free days (ice-on day of year minus ice-out day of same year – in Julian days). Atmospheric inorganic nitrogen deposition data from 1970 to 2004 was collected at Lake 239 in the ELA and was measured as total annual delivery in precipitation to the lake surface (mg N m$^{-2}$) (data provided by Department of Fisheries and Oceans, Canada). Given the proximity of Lake 239 to Whitefish Bay (~40 km), similar nitrogen deposition rates are expected. Comparisons were made between each of these measured datasets and trends in the percent relative abundances of Cyclotella and Aulacoseira species. Running means were applied to the monitoring data, where appropriate, to ensure that these data were compared to the diatom data at a similar chronological interval.

Results

Meta-analysis: geographic extent of Cyclotella trend

Our meta-analysis included detailed diatom profiles from 170 lakes that contained at least 2% relative abundance of Cyclotella taxa in their sediments (Appendix S2). Twenty-six of these lakes (15%) did not have established chronologies (e.g. $^{210}$Pb dates) for the recent sediments and thus could not be included in our analysis. The remaining 144 diatom profiles met our first two criteria, of which 41 lakes showed a decrease in the relative abundance of Cyclotella species in the recent sediments. However, closer inspection revealed that 95% of the profiles that reported decreases in Cyclotella species were from lakes that had undergone cultural eutrophication or acidification in their recent history (e.g. Ek & Korsman, 2001; Lotter, 2001), and thus failed our third criterion. Therefore, 105 lakes met our first three criteria of which 84 lakes (80%) showed a >5% increase in the relative abundance of Cyclotella species since the mid-19th century (Fig. 1), 19 lakes (18%) did not register an increase above 5% relative abundance, and two lakes (2%) showed a decrease (Appendix S2).

Studies recording recent increases in Cyclotella species were almost exclusively found in naturally occurring, freshwater lakes from northern parts of North America (i.e. Canada and the northern USA) and western Europe, including both temperate and Arctic/alpine regions. Notably, increases in small Cyclotella taxa were commonly found in relatively pristine, nutrient-poor, nonacidified lakes (e.g. lakes that have averted, or recovered from, the effects of cultural eutrophication and acidification). An interesting result that became evident from our meta-analysis of studies containing diatoms from the species Cyclotella was the identification of gaps in the geographical distribution of paleolimnological research. In some parts of the Northern Hemisphere and in most of the Southern Hemisphere, there was a distinct lack of paleolimnological records focusing on recent sediments (with or without Cyclotella). For example, large sections of Russia (particularly Siberia) and Northern Eurasia remain largely unsampled for diatom-based paleolimnological analyses spanning the recent sediments (MacDonald et al., 2004). Perhaps, not surprisingly, much of the Southern Hemisphere did not yield paleolimnological studies suitable for the purposes of this study, primarily because naturally occurring freshwater lakes are not always abundant, human-made reservoirs are common, and nonimpacted lakes are generally rare.

A comparison of general trends in the timing of initial increases in Cyclotella species among the various bioregions (e.g. high latitude, high altitude and low latitude) clearly demonstrated that high latitude sites, although variable, recorded significantly earlier increases than low latitude sites (Fig. 2a–c; ANOVA on ranks, $H = 15.002, P < 0.001, df = 2$). The median years of change for high and low latitude sites were AD 1870 and 1970, respectively. The median age at which these changes occurred in high altitude sites (located both in temperate and in northern latitudes) was AD 1920. The least amount of variability in timing was recorded in temperate lakes, with 75% of the changes occurring post-1940 (Fig. 2b).

Although the results from our detailed, dated cores provided us with a large number of lakes (just under 100) that registered strikingly similar directional taxon-specific diatom shifts, the addition of several regional (i.e. top-bottom) diatom analyses gave us a more geographically extensive survey of the reproducibility of this trend within a given region. Similar to the detailed diatom profiles, top-bottom studies throughout Canada (see Fig. 1 for locations) recorded statistically significant ($P < 0.01$; Wilcoxon Signed-Rank test) taxon-specific changes in 120 out of 147 lakes (Fig. 3). Lakes from both the Canadian subarctic and from temperate regions of Canada, including New Brunswick and Ontario, showed similar, clear patterns of increasing Cyclotella species (Fig. 3a, c and e). Concurrent with these planktonic increases, small, benthic Fragilaria species, commonly found in lakes with short open-water seasons throughout circumpolar regions (Lotter & Bigler, 2000; Smith, 2002), recorded higher relative abundances in the preindustrial sediments of the subarctic lakeset (Fig. 3b), whereas heavily silicified Aulacoseira species were more commonly found at higher relative abundances in the preindustrial sediments of temperate lakes (Fig. 3d and f). However, both Fragilaria and Aulacoseira taxa were common to all latitudes.

© 2008 The Authors
Journal compilation © 2008 Blackwell Publishing Ltd, Global Change Biology, 14, 2740–2754
Detailed paleolimnological case study

The Whitefish Bay diatom record from the Lake of the Woods, Ontario (Fig. 4) shows a clear increase in small planktonic Cyclotella species beginning ca. AD 1980 with concurrent decreases in Aulacoseira subarctica (Fig. 1, inset). This marked diatom floristic change closely tracks an equally sharp rise in temperature recorded at the Kenora climate station over the same time period (Fig. 5a and b). A strong and significant positive corre-
Lake-ice records reveal that the ice-free period on Whitefish Bay has lengthened by 28 days since 1964 (Fig. 6) and is, not surprisingly, strongly related to increases in annual temperature recorded during this period at the Kenora climate station ($r = 0.77$, $P < 0.001$). The ice-out data show a strong inverse relationship to increases in *Cyclotella* taxa ($r = -0.57$, $P = 0.003$) (Fig. 7a), and equally striking positive relationship to decreases in *Aulacoseira* taxa ($r = 0.66$, $P < 0.001$) (Fig. 7b).

Trends in long-term inorganic nitrogen deposition in Lake 239 (ELA) revealed no significant relationship to our taxon-specific diatom trends. We found that total inorganic nitrogen deposition (TIN = NH$_4$ + NO$_3$, mg m$^{-2}$ yr$^{-1}$) at ELA was not significantly correlated to *Cyclotella* ($r = 0.28$, $P = 0.20$) or to *Aulacoseira* ($r = -0.28$, $P = 0.20$) relative abundance data in Whitefish Bay.

**Discussion**

The compilation of detailed diatom biostratigraphies throughout the Northern Hemisphere (Fig. 1), supplemented with regional paleolimnological (i.e. ‘top-bottom’) studies from various parts of Canada (Fig. 3), shows a strikingly coherent, yet geographically asynchronous large-scale pattern of ecological change. These data indicate that extensive reorganizations of algal community structure are evident in lakes across the Northern Hemisphere since the mid-19th century. Specifically, abrupt increases in planktonic *Cyclotella* species and concomitant decreases in heavily silicified *Aulacoseira* and/or small, benthic *Fragilaria* species are evident in regions where pronounced warming has been recorded (e.g. Chapman & Walsh, 1993).

The onset of the shift to higher relative abundances of *Cyclotella* taxa in Arctic lakes occurred significantly ($P < 0.05$) earlier (ca. AD 1870) than in lakes from temperate latitudes (ca. 1970) (Fig. 2c). The higher variability in the timing of this shift among high latitude lakes may be explained by the generally lower temporal resolution of Arctic sediment cores, and differences in the relative sensitivity of subarctic and high Arctic lakes, both of which were grouped together in this category. High altitude lakes, regardless of latitude (Arctic–subarctic–temperate), were intermediate in terms of the timing of this species change (ca. AD 1920). Despite the larger number of diatom profiles collected from temperate lakes than from high latitude/high altitude lakes for this meta-analysis, and large differences in lake characteristics across the temperate Northern Hemisphere, there was remarkable consistency in the timing of *Cyclotella* increases recorded in the biostratigraphic profiles from temperate lakes (i.e. low variance) with 75% of these studies recording this shift post-1940.
Fig. 3 The percent relative abundances of *Cyclotella* species, benthic *Fragilaria* species, and *Aulacoseira* species recorded in the top sedimentary intervals (modern) vs. the bottom sedimentary intervals (pre-1850) for regional datasets from (a) Northwest Territories and Nunavut in the Canadian subarctic, (Rühland et al., 2003), (b) New Brunswick, Canada, (Harris et al., 2006), and (c) combined datasets from Ontario including south-western Ontario, (Werner, 2003), south-central Ontario, (Hall & Smol, 1996), and south-eastern Ontario, (Reavie et al., 2002). All lakes in figure had a total phosphorus (TP) measurement < 20 µg L⁻¹ and/or did not record an increase in diatom-inferred TP. Changes between the diatoms preserved in modern (top intervals) and preindustrial (bottom intervals) for each lakeset were deemed significant using a Wilcoxon Signed-Rank test. *P* values indicate significance after correcting for the False Discovery Rate (Benjamini & Hochberg, 1995).
The response of aquatic organisms to climatically induced changes is typically abrupt and pronounced in the paleolimnological record when an ecological threshold is exceeded. Such a regime shift has been clear in high-latitude aquatic environments where a sharp increase in species turnover was reported among circumpolar lakes over the last ca. 200 years (Smol et al., 2005). Most of the Arctic and alpine sedimentary profiles we present in Fig. 1 (e.g. Catalan et al., 2002; Sorvari et al., 2002; Rühland & Smol, 2005; Karst-Riddoch et al., 2005) consist of diatom assemblages that have been relatively stable for millennia with the most pronounced changes starting in the 19th century. In all these studies, a marked and unprecedented shift to a diatom assemblage that is characterized by increases in the relative abundances of planktonic Cyclotella species suggests an abrupt transformation of aquatic habitat availability and quality.

In comparison to the well-documented sensitivity of high latitude/altitude environments to even moderate changes in climate, freshwater ecosystems in more southern (temperate) latitudes that experience longer ice-free periods and growing seasons will, understandably, take longer and/or require a greater increase in temperature before passing through climate-related ecological thresholds. This is consistent with the findings from our meta-analysis where the median age of increasing Cyclotella abundances recorded in temperate lakes (ca. AD 1970) lagged this same taxonomic shift in Arctic lakes by ~100 years (Fig. 2a–c). The timing of this change in temperate lakes of the Northern Hemisphere is concurrent with instrumental records that show a rise in air temperature post-1950 that is unprecedented in the last millennium (Jansen et al., 2007).

The nature and timing of the recent diatom changes recorded in our meta-analysis is consistent with warming that is associated with a shorter ice-cover period, a longer diatom growing season, changes in the aquatic light regime, increased nutrient cycling, and/or changes to the thermal and mixing properties of lakes. Changes in these lake water properties may provide favorable habitats for small, fast-growing planktonic Cyclotella species (Raubitschek et al., 1999; Rautio et al., 2000; Pannard et al., 2008). C. stelligera and C. comensis complexes, in particular, may exploit longer ice-free periods and/or deeper, subsurface habitats where nutrient concentrations are somewhat elevated and where light properties become more stabilized as thermal stratification develops (Fahnenstiel & Glime, 1983). For example, results from seasonal empirical studies suggest that, after the onset of thermal stratification, Cyclotella taxa (C. comensis, C. stelligera/pseudostelligera/glomerata) may bloom in the metalimnion (the layer of water below the mixed upper layer) where the
temperature gradient is steepest (Fahnenstiel & Glime, 1983; Raubitschek et al., 1999), and are the dominant taxa when the growing season is lengthened, spring overturn period is extended, hypolimnetic waters are warmer, and/or when water stability is at its peak during autumn (Rautio et al., 2000). In contrast, earlier sedimentary intervals from Arctic/alpine and temperate profiles were dominated by diatoms with life strategies linked to longer ice cover and/or greater turbulence. For example, large, thickly silicified diatoms, such as Aulacoseira taxa, require periods of resuspension through turbulence to maintain their position in the water column (Kilham et al., 1996), and thus commonly decrease in abundance during periods of strong stratification (Pannard et al., 2008). During colder periods with extended ice cover and/or greater turbulence. For example, large, thickly silicified diatoms, such as Aulacoseira taxa, require periods of resuspension through turbulence to maintain their position in the water column (Kilham et al., 1996), and thus commonly decrease in abundance during periods of strong stratification (Pannard et al., 2008).
In general, the results of our meta-analysis indicate that increases in small Cyclotella species were commonly found in relatively pristine, nutrient-poor, nonacidified lakes. This is consistent with previous studies that have found Cyclotella species to be notably absent from lakes that were directly impacted by anthropogenic activity, such as acids from industrial emissions (Battarbee et al., 1999), nutrients from agricultural and sewage runoff (Stoermer et al., 1985), metal toxicity from industrial effluents (Ruggiu et al., 1998), and the overdevelopment of shorelines (Little et al., 2000). Understandably, climate-related changes in temperate regions may be masked by direct anthropogenic stressors acting simultaneously on freshwater ecosystems. Therefore, in temperate regions, reliable test sites for this climate-related threshold response would logically be lakes that have been minimally impacted by direct human disturbance and/or other major stressors (e.g. eutrophication, acid deposition) (Schindler, 1997). Our detailed case study location, Whitefish Bay in the Lake of the Woods (Fig. 4), provides such a setting.

The sharp increase in the relative abundance of Cyclotella taxa and concurrent decrease in Aulacoseira taxa recorded in our detailed analysis of the Whitefish Bay sediment core (inset Fig. 1) are very similar in nature (although asynchronous, as expected) to diatom changes reported in both temperate (e.g. Fritz et al., 1993; Alefs & Müller, 1999; Marchetto et al., 2004; Harris et al., 2006) and circumpolar and alpine (e.g. Catalan et al., 2002; Sorvari et al., 2002; Rühland et al., 2003) regions of the Northern Hemisphere. The striking relationships observed between the Whitefish Bay diatom data and the Kenora temperature record (both visually and statistically) provide strong evidence that warming trends over the past few decades have played an important role in observed shifts in diatom community structure (Fig. 5a and b).

A decrease in the duration of ice cover with warmer temperatures, and associated changes in lakewater properties, have often been surmised as triggering the recent increases in planktonic Cyclotella species in subarctic/alpine lakes (e.g. Lotter & Bigler, 2000; Catalan et al., 2002; Sorvari et al., 2002; Rühland et al., 2003; Forström et al., 2005; Smol et al., 2005). It follows that long-term ice cover records could provide an ideal means of verifying the relationship between recent warming and increases in planktonic diatoms. For example, a rare, long-term ice cover record available from a river in Finland was used to indirectly corroborate recent changes in diatom assemblage composition recorded in several neighboring lakes (Sorvari et al., 2002). However, testing direct linkages between lake ice-cover duration and these taxon-specific changes (i.e. changes in the relative abundances of Cyclotella and Aulacoseira/Cyclotella taxa) has not, as of yet, been undertaken, understandably because continuous ice-out data for the same lakes where diatoms have been examined are extremely rare, particularly in remote Arctic and alpine regions.

An increase in the ice-free period by almost 30 days over the past ca. 40 years on Whitefish Bay is substantial and has undoubtedly played a critical role in determining the structure and distribution of plankton communities throughout the water column. For example, the strong and highly significant correlations between Whitefish Bay ice-out and diatom trends (Fig. 7a and b) suggest that recent increases in planktonic Cyclotella taxa (decreases in Aulacoseira taxa) are predominantly triggered by the lengthening of the ice-free period and related changes in lakewater properties. These Whitefish Bay data corroborate the premise that abrupt increases in Cyclotella species, concurrent with decreases in Aulacoseira and Fragilaria species reported throughout the Northern Hemisphere, can be primarily explained by climatically driven changes in lakewater properties. In particular, these taxon-specific diatom shifts were likely triggered by a warmer climate that commenced in the mid-1800s, and escalated to unprecedented highs over the last half century.

Other potential stressors and synergistic effects

The shift to planktonic diatom species, which we show is correlated with recent warming in temperate lakes, partly overlaps with a period of accelerated atmospheric deposition of anthropogenically derived contaminants and nutrients. Increased deposition of inorganic nitrogen, for example, has been cited as a possible trigger for these abrupt compositional turnovers (e.g. Stoermer et al., 1985; Fritz et al., 1993; Wolfe et al., 2003). However, we found no significant relationship between inorganic nitrogen deposition from nearby ELA and our diatom trends from Whitefish Bay. In fact, Cyclotella relative abundance and ice-out data from Whitefish Bay over this same time frame (i.e. 1974–2004) were significantly and negatively correlated (r = –0.45, P = 0.03), adding further support that climate-related factors are primarily responsible for recent taxon-specific diatom shifts. The relationships found in our case study are consistent with findings in nearby regions. For example, recent increases in the relative abundance of Cyclotella species have been reported in lakes in south-central Ontario since the early 1980s (Clerk et al., 2000; Quinlan et al., 2008) where significant increases in the duration of the ice-free period have been recorded in these lakes since the mid-1970s (Futter, 2003). However, no statistically significant trend has
been noted in nitrate or ammonium deposition over the past three decades (Schindler et al., 2006).

The lack of a strong relationship between recent diatom community reorganization and nitrogen deposition in our case study is also consistent with recent paleolimnological findings in the Arctic (Smol & Douglas, 2007; Keatley et al., 2008) where the effects of climatic change are first experienced. Aerially transported nutrients and contaminants would reach Arctic and alpine lakes decades after these pollutants would reach temperate lakes; however, the changes in diatom species occur decades earlier in the former. Therefore, the timing of these taxon-specific diatom shifts predating the onset of anthropogenic pollutants in Arctic lakes underscores that aerially transported nutrients and/or contaminants cannot explain the marked hemispheric-scale diatom shifts we describe.

Although we have found no support to link increases in Cyclotella species to nitrogen deposition, it is possible that a rise in inorganic nitrogen deposition may be linked to recent climatic changes. For example, in regions proximal to nitrogen sources, changes in precipitation could be important for the delivery of atmospheric inorganic nitrogen to nearby lakes (Macdonald, 2005). A comparison of Kenora precipitation data with the ELA TIN data resulted in a nonsignificant positive correlation (r = 0.33, P = 0.06). Although not conclusive, the possibility of a synergistic relationship exists. While it is clear that diatoms respond to a multitude of complex factors, it is equally clear that the nature, magnitude, and timing of these taxon-specific diatom shifts are best explained by recent warming and associated limnological changes.

Conclusions
The diatom data included in our meta-analysis of over 200 lakes provide a spatially coherent picture that climate-driven, taxon-specific changes are now evident across vast regions of the Northern Hemisphere representing a wide spectrum of lake ecosystems. Although the degree of ecological change may vary between lakes (as would be expected, based on morphometry and other limnological variables), the similarity in this diatom trend across a regional scale is striking. Freshwater ecosystems in the Northern Hemisphere have crossed ecological thresholds with changing climate that were initiated in the 19th century in Arctic and alpine regions, but typically only occurred in the mid-20th century in lakes from mid-latitude regions of North America and western Europe. The recurring and widespread trend of recent increases in the relative abundances of planktonic Cyclotella species is strongly correlated to recent increases in temperature and substantially longer ice-free periods. Synergistic effects between climate warming and other human-induced stressors also occur (Wolfe et al., 2006). However, based on the timing, magnitude, and nature of the diatom changes, we conclude that climatically induced change in lake-ice cover (and associated limnological changes) was the primary explanatory metric for hemispheric-scale increases in planktonic Cyclotella species over the last ca. 200 years. Our findings are particularly troubling given that the ecological changes we report are widespread, and have occurred with increases in mean annual temperatures that are substantially lower than levels projected by climate models for both high- and mid-latitude regions of the Northern Hemisphere. If this rate and magnitude of temperature increase continues, it is likely that new ecological thresholds will be crossed, many of which may be unexpected.

Acknowledgements
We thank R. Hall, A. Harris, E. Reavie, and P. Werner for kindly allowing the use of their data for producing Fig. 3, M. Stainton (Department of Fisheries and Oceans, Canada) for providing the sediments and dating the Whitefish Bay core, the Lake of the Woods District Property Owners Association for supporting field work for the Whitefish Bay core, and M. Turner (Department of Fisheries and Oceans, Canada) for providing nitrogen deposition data from ELA. We thank two anonymous reviewers for their thoughtful and constructive comments that helped to strengthen and clarify this paper. This work was supported by the Natural Sciences and Engineering Research Council of Canada (to J. P. Smol), and the Ministry of the Environment, Ontario.

References


Lotter AF, Bigler C (2000) Do diatoms in the Swiss Alps reflect the length of ice-cover? Aquatic Sciences, 62, 125–141.


Rühl KM (2001) Diatom assemblage shifts relative to changes in environmental and climatic conditions in the circumpolar treeline regions of the Canadian and Siberian Arctic. PhD thesis, Queen’s University, Kingston, Ontario, Canada, 265 pp.


Supplementary material

The following supplementary material for this article is available online:

Appendix S1. List of diatom taxa including taxonomic authorities, taxonomic synonyms, and the species complexes referred to in manuscript.

Appendix S2. Results of literature search for paleolimnological studies containing Cyclotella species. Lake names in bold indicate studies with suitable chronology and that reported increases in Cyclotella species $>5\%$. Rows shaded in grey indicate all studies that did not have suitable chronology. Studies without a suitable chronology but that had $>5\%$ relative abundance of Cyclotella taxa (i.e. 12 studies) were tallied in the chronology column. HL = high latitude; HA = high altitude; T = temperate lakes are sorted by author(s) in alphabetical order. Lakes in bold that had suitable chronology and that showed $>5\%$ increase in the relative abundance of Cyclotella taxa were plotted in Fig. 1. In general, lakes considered to be unpolluted had total phosphorus (TP) concentrations $<20\,\mu\text{g L}^{-1}$ and pH $>6.0$. w/ = with; w/o = without; ON = Ontario; BC = British Columbia; NW = Northwest; NS = Nova Scotia; NB = New Brunswick; QC = Quebec; USA = United States of America.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2486.2008.01670.x

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.