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FREY-DEEVEY INVITED REVIEW

Lake diatom responses to warming: reviewing the evidence

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Abstract Algae, the dominant primary producers in many aquatic ecosystems, are critical to global biogeochemical cycling, and changes in their abundance and composition can cascade throughout aquatic food webs. Diatoms often dominate the algal communities in many freshwater systems. Their population dynamics are affected by a variety of environmental variables, many of which are linked to changes in water column properties and habitat availability, which themselves can be linked to shifts in ice cover, length of the growing season, thermal stability and stratification, vertical mixing patterns, habitat alterations, and the availability of resources such as light and nutrients. Climate has strong moderating controls on all of these fundamental aquatic processes, which can directly and indirectly alter species composition, abundance and seasonal dynamics of both periphytic and planktonic diatoms. In this review, we examine the role that climate-mediated alterations in inter-related lake processes have played on diatom community composition, dynamics and size structure, with particular attention to the recent success of planktonic diatom species relative to heavier tychoplanktonic and small benthic diatoms. We focus primarily on paleolimnological records, but also reference a wide spectrum of limnological and physiological studies to review and discuss how climate-driven shifts in lake properties may affect diatom assemblage reorganization. Understanding the limnological and historical context of these often complex diatom changes is key to making scientifically defensible interpretations of paleolimnological records. We further evaluate the plausibility of alternative explanations (e.g. atmospheric nitrogen deposition) for the recent success of small cyclotelloid species by examining trends in these planktonic diatoms from a large number of sites. Using a weight-of-evidence approach, we conclude that recent climate change is the main driver that has led to ecological tipping points resulting in the recent success of small planktonic diatoms that have been reported in many aquatic systems.

Keywords Planktonic · *Cyclotella–Aulacoseira–Fragilaria* shift · Cyclotelloid · Pennate planktonic · Lake thermal properties · Mixing · Climate change · Ice cover dynamics · Thresholds · Nitrogen deposition · Paleolimnology

Introduction

Algae are primarily photosynthetic protists that occur in almost every marine and freshwater environment.

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As primary producers, they fix large amounts of atmospheric carbon dioxide through photosynthesis and generate a major fraction of the planet's oxygen. Global biogeochemical processes are inextricably linked to phytoplankton (planktonic algae) dynamics and community composition. Collectively, algae are the primary energy source for most aquatic ecosystems and are of global significance for biogeochemical cycling and climate regulation (Winder and Sommer 2012). Furthermore, changes in their abundance and composition may cascade throughout aquatic food webs (Adrian et al. 2006; Winder and Schindler 2004). Diatoms (Class Bacillariophyceae) are an especially important group of eukaryotic, siliceous algae that play a crucial role in ecosystem health, contributing between 20 and 25 % of global primary production, equivalent to all terrestrial rainforests combined (Falkowski et al. 1998; Saade and Bowler 2009).

In most freshwater lakes, diatom algae are often dominant primary producers, at times comprising the majority of a lake's phytoplankton biovolume. Diatoms are found across a broad range of limnological conditions. Their high taxonomic diversity and abundance in almost every conceivable aquatic environment is a testament to their remarkable competitive success in the ecological arena (Julius and Theriot 2010). Their growth habitat can generally be described by function including planktonic, tychoplanktonic and periphytic life strategies, but with wide variation within each functional group. However, changes in physical and chemical parameters within aquatic ecosystems can markedly alter the dominant diatom growth types (Julius and Theriot 2010). It should be no surprise, therefore, that diatoms respond sensitively (both directly and indirectly) to a wide range of environmental stimuli, including physical and chemical changes in their aquatic environment. Because many diatom taxa have well-defined preferences for a given micro-habitat type, they have the potential to track environmental and climate-mediated changes in lake properties (Smol 1988; Smol and Stoermer 2010). Studies worldwide have shown links between fluctuations in climate and ecological processes that affect phytoplankton (Gerten and Adrian 2002; Behrenfeld et al. 2006; Paerl and Huisman 2008; Paterson et al. 2008), and specifically diatom dynamics and species composition (Catalan et al. 2002a; Smol et al. 2005; Pannard et al. 2008; Winder and Hunter 2008; Rühland et al. 2008; Smol and Stoermer 2010). The details of these climate-driven aquatic ecosystem changes, and the factors that control diatom dynamics and species composition, are critical to understanding how aquatic ecosystems are affected by environmental change.

In this review, we examine the role that climate-mediated alterations in lake processes has contributed to algal compositional shifts in freshwater lakes, particularly the recent relative success of small-celled planktonic diatom species at the expense of heavier tychoplanktonic and small benthic species. We recognize that there are several uses of the term tychoplankton in the ecological literature. For the purposes of this review, we define tychoplankton as algae that are especially dependent on turbulence to remain in the water column, such as large *Aulacoseira* taxa. We focus primarily on paleolimnological records, but also reference a wide spectrum of limnological and physiological studies to review and discuss the intricacies of how climate-driven changes in lake properties may affect diatom assemblage reorganization. We draw heavily on examples from the Northern Hemisphere, not by design, but rather because this is where most of the research that is relevant to this review has thus far been published. To date, comparable diatom records from the tropics are rare, but we include several examples from the Southern Hemisphere when available. In this review, we start by examining how changes in climate and meteorological conditions are inextricably linked to fundamental aquatic ecosystem processes that affect diatom resource requirements and diatom species composition, highlighting the complexity of periphytic and planktonic diatom responses.

We further clarify why some ecosystems express an algal response more clearly and sensitively to climate change than others, and why some regions and ecosystems respond more quickly than others. Using paleolimnological records, we examine whether the changes we observe today are outside the realm of ecological changes that have occurred in the past. We explore these taxon-specific diatom shifts over a wide range of timescales, from physiological studies and annual monitoring data, to centennial and millennial-scale paleolimnological records. Furthermore, using modern sedimentary diatom samples from three sets of training lakes from temperate and subarctic Canada, we examine the relationships between *Discostella stelligera* (Cleve et Grunow) Houk et Klee and *D. pseudostelligera* (Hustedt) Houk et Klee relative abundances and measured water column nitrogen to evaluate the plausibility of alternative explanations to warming (e.g. atmospheric nitrogen deposition) for the recent success of small cyclotelloid species. In addition to increased relative abundances of small cyclotelloid diatoms, we also examine the recent success of elongate pennate planktonic diatoms that has been reported across a variety of lake settings and the role that multiple stressors have played in determining the nature of planktonic diatom response to climate.

The complexity of algal response to climate fluctuations

Algal dynamics are linked to a multitude of factors, including meteorological and climate-related variables such as fluctuations in temperature, ice cover dynamics, wind patterns, and solar radiation/cloudiness that affect fundamental lake processes such as strength, frequency and duration of lake mixing/turbulence and thermal stratification, and the availability of light and nutrient resources (Gerten and Adrian 2002; Reynolds et al. 2002; Smol and Douglas 2007; Adrian et al. 2009; Winder and Sommer 2012). Climate will thus have significant indirect effects on algal species composition through changes in fundamental aquatic ecosystem processes (Diehl et al. 2002; Smol et al. 2005), and the development of new aquatic habitats (Fig. 1). Not surprisingly, these changes exert a key control on algal growth, which can be linked to vertical mixing processes and attendant changes in resource availability, including nutrients and light (Salmaso 2005; Rühland et al. 2008; Winder and Sommer 2012). Recent anthropogenic warming and the linked chain of causal factors within a lake provide important controls on the seasonal development of phytoplankton (planktonic algae) growth, structure and competition (Diehl et al. 2002; Ptacnik et al. 2003; Huisman et al. 2004; Salmaso 2005; Wilhelm and Adrian 2008; Salmaso 2010). In all lakes, the response of algal communities is most evident and striking when climate-mediated ecological thresholds are passed (Smol et al. 2005; Smol and Douglas 2007). Climate change will: (1) directly affect the physical properties of lakes which, in turn, affect algal production and composition; and (2) indirectly affect the availability of algal resources including light and nutrients. In nature, it is the complex interaction of these important and linked factors that influence algal biomass, seasonality, and composition, and this may lead to variability in the nature and timing of the response among ecosystems.

Although some algal taxa may respond to changes in available resources by using alternate nutritional strategies, such as heterotrophy or phagotrohy (e.g. some chryosphyte taxa), all of the algal taxa that we discuss in this review ultimately require sufficient light for photosynthesis in order to maintain large populations. The survival of a planktonic population thus depends on its ability to remain in the photic zone, with the organization of the phytoplankton community ultimately related to the extinction of light in the water column (Margalef 1978). Several empirical studies have examined phytoplankton dynamics in relation to meteorological forcings (i.e. wind, rain, air temperature, solar radiation) and the effects of these forcings on the vertical structure of the water column (Huisman and Sommeijer 2002; McCausland et al. 2002; Ptacnik et al. 2003; Forsström et al. 2005; Pannard et al. 2008). Differences in the sinking rates or buoyancy of phytoplankton species across all algal groups provide competitive advantages and disadvantages, depending upon the strength of vertical mixing, with heavier diatoms often dominating during strong periods of mixing, and more buoyant phytoplankton such as cyanobacteria often dominating during more thermally stable periods (Huisman et al. 2002, 2004).

For diatoms, cell size, morphology and growth form (e.g. single-cell, colony-forming strategies) varies widely among taxa and can greatly affect sinking rates (Smol et al. 1984; Ptacnik et al. 2003; Rocha et al. 2012), as well as grazing vulnerability (Teubner 2003; Rocha et al. 2012), and the ability for efficient nutrient uptake and light harvesting (Lichtman et al. 2006; Winder et al. 2009; Rocha et al. 2012). For example, small-celled cyclotelloid diatoms with high surface area to volume ratios have: (1) small diffusion boundary layers enabling efficient nutrient uptake (Pasciak and Gavis 1974); (2) excellent light harvesting abilities (Round et al. 1990; Ptacnik et al. 2003; Lichtman et al. 2006; Winder et al. 2009); (3) relatively low sinking velocities (Round et al. 1990; Ptacnik et al. 2003; Litchman et al. 2006; Winder et al. 2009); and (4) are capable of prolific reproduction (Fahnenstiel and Glime 1983; Jewson 1992; Litchman et al. 2007; Winder and Hunter 2008). With warming, these ecophysiological traits often provide small, planktonic cyclotelloid diatoms the ability to outcompete large-

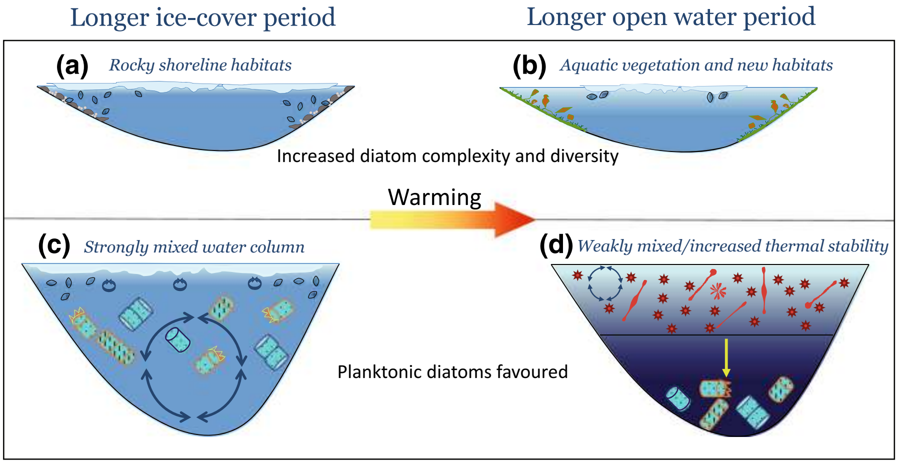


Fig. 1 A simplified schematic diagram illustrating some of the important effects of climate warming and decreased ice cover on lake properties and diatom composition. In Arctic ponds and shallow lakes, cooler temperatures and longer ice cover (*a*) tend to favour relatively simple diatom assemblages dominated by benthic fragilarioid taxa, whilst warmer temperatures and longer open-water periods (*b*) lead to the development of new habitats and associated changes in light and nutrient availability, which can be linked to increased diatom assemblage complexity and species richness, and other changes discussed in this review. In subarctic and more temperate regions, deeper lakes with extended ice cover and weakened, shorter periods of thermal stratification (i.e. with increased water column mixing) (*c*) favour heavier, tychoplanktonic diatoms, such as *Aulacoseira* taxa, whilst warming and less ice cover (*d*) may lead to increased thermal stability and longer periods of thermal stratification (i.e. with reduced water column mixing), as well as associated changes in light and nutrient availability, favouring planktonic diatoms such as small-celled *Cyclotella* (*s.l.*) taxa

celled diatoms that require more turbulence for the resuspension of nutrients and for maintaining their position in the photic zone (Kilham et al. 1996).

In addition to small, centric diatoms, the elongate shape of other planktonic diatoms and their ability to form, for example, stellate colonies also plays an important role in providing competitive advantages in reducing sinking velocity and competing for limiting light and nutrient resources. For example, the elongate cells of *Asterionella formosa* Hassal have high surface area to volume ratios and their competitive ability (decreased sinking rates, decreased grazing vulnerability) can be further aided by linking cells with mucilage pads to form star-shaped colonies (Round et al. 1990; Rocha et al. 2012). This species is considered to have one of the slowest sinking velocities of all freshwater diatoms (Spaulding and Edlund 2009). Other elongate planktonic diatoms have spines that can link cells to form ribbon-like colonies including *Fragilaria crotonensis* Kitton, *F. tenera* (W. Smith) Lange-Bertalot, *F. nanana* Lange-Bertalot (Morales and Rosen 2013; Morales et al. 2013) and zig-zag or stellate colonies for *Tabellaria* species (DeColibus 2013). If colonies are long enough, this growth form may alter their competitive ability for nutrients, light, and/or buoyancy in the open water.

Many studies that have examined responses within the broader phytoplankton community to environmental change have noted that certain diatom taxa consistently stand out as important to overall algal dynamics. For example, the diatom shift between large-celled tychoplanktonic *Aulacoseira* taxa (often favoured during periods of stronger vertical mixing) and small-celled cyclotelloid species (particularly successful during more thermally stable periods) were notable in limnological studies not primarily focused on diatom communities (McCausland et al. 2002; Ptacnik et al. 2003; Forsström et al. 2005; Pannard et al. 2008). Undoubtedly, the siliceous valves of diatoms make these algae heavy relative to all other phytoplankton (Fig. 2). However, as noted above, there are significant differences in the sinking rates and resource requirements (light and nutrients) among the large variety of diatom taxa (Smol et al. 1984; Ptacnik et al. 2003), and these diatom taxon-specific differences can be used to interpret climate-induced changes in aquatic systems over time.

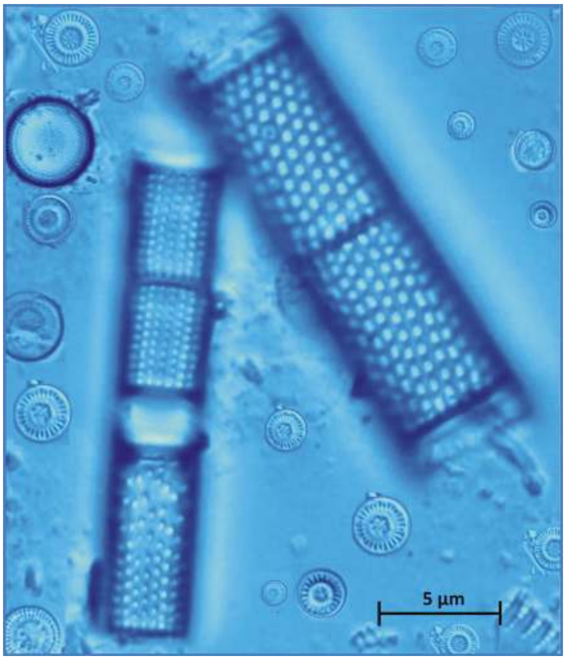


Fig. 2 A composite photomicrograph (to scale) showing the difference in cell-size and shape of fast-sinking, tubular-shaped *Aulacoseira* taxa and more buoyant, pancake-shaped cyclotelloid taxa

Shifts in diatom assemblage composition as a signal of climate change: context is key

Diatoms have been a key component of paleolimnological assessments for numerous reasons, including their well-preserved siliceous frustules, their ability to respond rapidly to changes in the environment, and their distribution among a diverse array of water quality gradients, aquatic habitats, and life history strategies (Smol 2008). Diatom assemblages (both periphytic and planktonic) can be especially sensitive to warming-induced changes in lake properties that favour, depending on the limnological setting, the growth of small, planktonic species with high surface area to volume ratios (Rühland et al. 2008; Winder and Sommer 2012), and/or the development of more complex and diverse periphytic diatom assemblages (Douglas et al. 1994; Smol et al. 2005; Douglas and Smol 2010).

Early paleolimnological studies on Arctic lakes suggested that shifts in the relative abundances between planktonic and periphytic diatoms (particularly small benthic fragilarioid taxa) may have been a response to changes in the duration of ice cover (Smol 1983, 1988; Smol and Douglas 2007; Douglas and Smol 2010). In shallow High Arctic lakes and ponds, a distinct shift in diatom composition is commonly observed from an assemblage dominated for millennia by benthic fragilarioid species to a more complex assemblage in recent sediments (onset post ~1850) of periphytic diatom taxa associated with littoral habitats and mossy substrates (Fig. 1a, b) (Douglas et al. 1994; Smol et al. 2005; Smol and Douglas 2007). This shift is consistent with warming-induced habitat expansion resulting from a shorter ice cover period and the associated multitude of interrelated lake property changes resulting from a longer growing season. Deeper lakes in subarctic regions also express a diatom response to warming that is consistent with a longer open water period, changes in the thermal properties of lakes and associated changes in resource availability (Sorvari et al. 2002; Rühland et al. 2003a, 2008). This shift in diatom life strategy is commonly characterized by increases in the relative abundances of small-celled, fast growing planktonic cyclotelloid taxa, often appearing in the record for the first time, with concurrent decreases in large-celled heavily silicified, tychoplanktonic *Aulacoseira* species and/or small, benthic fragilarioid taxa (Fig. 1c, d). These examples clearly show that linking recent taxon-specific diatom shifts to climate requires careful consideration of changes in composition of the entire diatom assemblage over time, as it is this shift in diatom life strategy, and not simply the expansion of planktonic or periphytic diatoms, that provides the proper context to assess these changes. These conclusions are reinforced by a strong foundation of field-based studies and observations, including over 30 years of Arctic phycological studies (Smol and Douglas 2007; Douglas and Smol 2010).

As noted in numerous publications from North America and Europe (Smol 1988; Lotter and Bigler 2000; Rühland et al. 2003a, 2008, 2013; Catalan et al. 2002b; Harris et al. 2006; Larsen et al. 2006; Winder and Hunter 2008; Winder et al. 2009; Douglas and Smol 2010; Devlin and Finkelstein 2011; Hobbs et al. 2011; De Senerpont Domis et al. 2013; Thienpont et al. 2013), it is important to clarify that recent diatom assemblage shifts are not direct responses to changes in air temperature and/or lake ice cover. Rather, these taxon-specific diatom shifts are in response to myriad indirect effects of changes in climate forcing on physical and chemical lake properties. These effects, in turn, may result from a change in the balance between thermal stratification and vertical mixing (King et al. 1997; Livingstone 2003; Huisman et al. 2004; Winder and Sommer 2012). Physical, climate-induced changes, such as decreased ice and snow cover and hence a lengthening of the growing season, increased intensity and duration of thermal stratification, and decreases in mixing strength and depth, also influence resource availability and distribution, such as light and nutrients, which are inextricably linked to phytoplankton/diatom production and species composition (Sorvari et al. 2002; Rühland et al. 2003a, 2008; Huisman et al. 2004; Winder et al. 2009; Winder and Sommer 2012).

An increase in air temperature by itself will not necessarily lead to an increase in thermal stability and a shift towards higher abundances of small, planktonic diatoms, as local factors must also be considered (such as orientation with respect to fetch, changes in windiness and mixing, light limitation, changes in acidity, nutrients, or colour). Furthermore, even in lakes that have rarely, if ever, experienced sustained periods of thermal stratification, such as many high latitude lakes, warmer conditions may result in weakened and less frequent mixing during the growing season. This may result in sustained, albeit short-lived, periods of stratification and increased thermal stability that favour planktonic diatoms (Rühland et al. 2013; Paterson et al. 2014). Planktonic diatoms, such as small *Cyclotella/Discostella* species that take advantage of these fundamental limnological changes, are often capable of prolific reproduction (Fahnenstiel and Glime 1983; Winder and Hunter 2008). What is clear is that the response of diatoms to climate-related changes in lake water properties is complex, and it is unlikely that a given diatom taxon would respond solely to any one of these variables in isolation. Rather, diatoms will be more (or less) competitive under a combination of environmental conditions. As discussed throughout this review, site-specific differences in lake characteristics and settings, and the composition of the initial diatom assemblage (not just the small cyclotelloid species), must be considered to make informed interpretations of recent diatom trends. Context is key.

Are all *Cyclotella/Discostella* taxa the same?

The cyclotelloid diatom group represents a diverse group of algae. It is important to acknowledge that not all cyclotelloid species are equally indicative of climate-induced water column changes, and that proper assessment of an assemblage shift requires an understanding of a study lake on an individual basis (including location, chemistry, disturbance history, etc.) together with a careful examination of the entire diatom record through time. Isolating the response of a single cyclotelloid species (such as an opportunistic and fast-growing *Discostella stelligera* or *Cyclotella comensis*) is not the best approach for understanding the most plausible mechanism for their increase (Rühland et al. 2010), as some species are able to compete across a range of nutrients and fare well with direct nutrient inputs (Saros et al. 2013). Additionally, not all *Cyclotella* taxa should be categorized in the same way. For example, an increase in the relative abundance of large, heavily silicified cyclotelloid species with lower surface area to volume ratios (e.g. *Cyclotella bodanica* Eulenstein *ex* Grunow and varieties, *Puncticulata radiosa* (Grunow) Lemmermann, *Thalassiosira minima* Gaarder) may respond similarly to heavy *Aulacoseira* taxa in some situations, with respect to changes in the physical structure of the water column, and therefore would be expected to have a different response to warming than small, fast-growing *Cyclotella* and *Discostella* taxa such as *C. comensis, D. stelligera, or D. pseudostelligera* (Rosén et al. 2009; Chipman et al. 2009; Guinder et al. 2010; Saros et al. 2012).

In climatically harsh environments such as the High Arctic, there are examples from deep, large lakes where large-celled cyclotelloid species appear in significant numbers for the first time in recent sediments concurrent with changes in ice cover dynamics (Doubleday et al. 1995; Perren et al. 2003; Antoniades et al. 2007). As noted earlier, in large, deep High Arctic lakes that have been perennially frozen for millennia, all diatoms (benthic and planktonic) may be nearly absent for most of the record (Doubleday et al. 1995; Perren et al. 2003; Antoniades et al. 2007; Besonen et al. 2008). With the onset of warming and reductions in ice cover, diatoms appear for the first time in notable abundances in these High Arctic records, with initial assemblages often dominated by benthic fragilarioid taxa. Once warming had advanced further and there was more open water, large-celled cyclotelloid species such as *Cyclotella bodanica* var. *lemanica* (Müller *ex* Schröter) Bachmann were observed to make a first appearance, at the expense of the once dominant pioneering benthic diatoms (Doubleday et al. 1995;

Perren et al. 2003). Further support for the powerful influence of climate and ice cover on diatom assemblages comes from another deep, High Arctic lake example from Ellesmere Island (Nunavut, Canada), which had the added advantage of having a high-resolution, varved sediment profile (Besonen et al. 2008). Here diatoms (*Campylodiscus noricus* Ehrenberg *ex* Kützing) appeared for the first time in the 0.75 cm (∼1998) interval of the core, and then continued to increase substantially to the surface sediments (∼2004). As expected, no planktonic diatoms have yet been reported, given the lake's ice regime. However, the authors suggested that the appearance of *Campylodiscus* is an early indicator of the onset of warming (less ice) and that the lake may be approaching a threshold in the development of a more complex and diverse diatom flora. It is unlikely that these deep High Arctic lakes have experienced periods of sustained thermal stability, but it is plausible that a longer open water period with 24 h daylight has increased light availability, while still allowing sufficient turbulence and deep mixing to favour these larger cyclotelloid species in these marginal environments. These are but a few examples that highlight the importance of carefully assessing the *Cyclotella–Aulacoseira–Fragilaria* shift within the context of the lake setting and of the entire composition of the diatom assemblage. When carefully considered, taxon-specific diatom shifts can potentially provide a powerful sentinel for climate-related regime shifts.

Do we see similar diatom shifts at different time scales?

Monitoring data: seasonal to decadal diatom records

Paleolimnological records are critical for establishing a temporal context for recent shifts in diatom assemblages; however, the details on the causal mechanisms for these changes are necessarily inferred (Winder et al. 2009). Exploring taxon-specific diatom shifts in paleolimnological records can provide insights, particularly when comparing empirically-derived, process-oriented data sets (Leavitt et al. 2009) with a relatively high degree of taxonomic precision, such as data collected at the species level. Although typically only a few years in duration, monitoring studies, including those using sediment traps, water column sampling, and surface sediments, have provided valuable insights into the seasonal dynamics of diatom assemblages. Similar to paleolimnological investigations, these monitoring studies have identified relationships between climate-mediated variables and patterns in *Cyclotella–Fragilaria–Aulacoseira* diatom assemblages that are often related to the phenology of lake ice and thermal stratification and mixing regimes, the depth of the epilimnion, and the development of subsurface habitats (Fahnenstiel and Glime 1983; Kilham et al. 1996; Raubitschek et al. 1999; Lotter and Bigler 2000; Rautio et al. 2000; Findlay et al. 2001; Ptacnik et al. 2003; Chu et al. 2005; Forsström et al. 2005; Pannard et al. 2008).

At the time of publication of the Rühland et al. (2008) meta-analysis, we wrote that longer-term monitoring data (∼20 to 30 years) were scarce, and that, when they existed, they rarely included algal assemblage data beyond coarse taxonomic groupings, providing little information on species-level diatom dynamics. However, within a few months of our 2008 publication, Winder and Hunter (2008) and Winder et al. (2009), using 30 years of measured species-level diatom data from Lake Tahoe (USA), provided particularly strong supporting evidence that a warmer climate and strengthening of thermal stratification (also calculated from long-term measured data) favours small-celled *Cyclotella/Discostella* taxa that have relatively high surface area to volume ratios. An increase in small-celled cyclotelloid species (≤∼5 μm) was observed in Lake Tahoe over the past decade (since ∼2005), with *Discostella glomerata* (Bachmann) Houk et Klee, *D. stelligera*, *Cyclotella comensis* Grunow/*gordonensis* Kling and Håkansson and other small cyclotelloid taxa becoming dominant over previously common, larger-celled diatoms (D. Hunter pers. comm). More recently, Guinder et al. (2010) provided evidence for warming-related diatom compositional shifts using ∼30 years of measured phytoplankton data including species-level diatom data from Bahía Blanca Estuary, Argentina. However, in this marine scenario, the recent occurrence of small-celled *Cyclotella* taxa replacing the previously dominant, large-celled *Thalassiosira curviseriata* Takano was found to be indirectly linked to rising temperatures through an advancement of the winter diatom bloom that resulted in a mismatch with peak abundances of zooplankton and consequent changes in zooplankton community structure.

The annual timing of planktonic diatom blooms vary substantially from region to region and from lake to lake (De Senerpont Domis et al. 2013), as well as from year to year within a region or a lake. These variations may be due to differences in the diatom species composition of a given lake and/or differences in regional and site-specific lake characteristics. Important information on the seasonality of planktonic diatom blooms can be gained by observational/empirical studies, particularly if these studies are over several years as the timing of the seasonal response may vary. Where data are available from contemporary studies, small cyclotelloid species have been shown to reach their maxima at various times during the open water season. For example, in four lakes with long-term monitoring at the Experimental Lakes Area (ELA) in Ontario (Canada), that have been sampled bi-weekly over the last two to four decades, small *Discostella* taxa consistently achieved their highest concentrations during the spring and early summer (April through June), with much lower concentrations in summer and autumn (Wiltse 2014). Other studies have observed a *Cyclotella/Discostella* peak in the metalimnion near the end of the summer, at the height of thermal stratification including in Lake Superior (Fahnenstiel and Glime 1983), in Lake Tahoe (Carney 1987; UC Davis (TERC) 2013), and in Lake Holzmaar (Raubitschek et al. 1999). Yet others have recorded peak abundances in the fall, before or during fall overturn in Finland (Rautio et al. 2000; Sorvari et al. 2002) and in the Spanish Pyrenees (Catalan et al. 2002b). Resource availability, mainly light and nutrient distribution, linked to the physical properties of the water column such as thermal stability, density gradients, and vertical mixing, is the likely mechanism giving a competitive advantage to these small planktonic diatoms. However, site-specific differences in lake setting, geography, meteorological factors and related water column properties are also likely important factors contributing to this variability in the timing of the seasonal peak of these planktonic diatoms.

Recent (past ~200 years) paleolimnological records of diatom assemblage shifts

While directly measured limnological data clearly provide a powerful means of understanding the mechanism of an observed change in the aquatic ecosystem, most monitoring data are of short duration (Smol 2008), and therefore paleolimnological records provide important temporal context for these recent changes. For example, recent *Cyclotella–Aulacoseira–Fragilaria* shifts, as well as increases in the complexity and diversity of benthic diatom assemblages in shallow high latitude lakes, have been reported in paleolimnological records from lakes across the Northern Hemisphere (Smol et al. 2005; Smol and Douglas 2007; Rühland et al. 2008, 2013; Thienpont et al. 2008; Hyatt et al. 2011; Enache et al. 2011; Hobbs et al. 2011; Medeiros et al. 2012; Panizzo et al. 2013). By providing a continuous record over the past few 100 years, paleolimnological profiles can establish whether the diatom changes observed today are outside of the realm of natural variability by establishing baseline conditions prior to the onset of anthropogenic disturbances.

Minimally disturbed lakes are preferred study sites when examining the biological response to climate in recent (i.e. ~200 years) paleolimnological records, as this time period often includes a history of multiple anthropogenic stressors that can mask or override a climate signal (Smol 2008). Not surprisingly, the effects of climate fluctuations on physical, biological and chemical processes of freshwater ecosystems are more distinct in remote regions (Gerten and Adrian 2002; Schindler and Smol 2006; Catalan et al. 2013). This is particularly evident in high latitude landscapes that are not only remote, but are also highly sensitive to changes in climate (Smol and Douglas 2007). Non-acidified, non-enriched lakes in temperate regions can also yield potentially clear diatom responses to climate (Rühland et al. 2008). The magnitude, timing and nature of diatom response to climate-related lake water changes are expected to vary across a wide range of geographical and climatic settings, with regional and site-specific differences affecting lake properties and aquatic biota in a range of complex ways. Once again, context is key.

Millennial-scale paleolimnological records in response to high-magnitude, cyclical shifts in climate

A rational question from a paleolimnological perspective is whether shifts between warmer and cooler periods in the distant past resulted in diatom compositional shifts similar to those observed under recent climate change scenarios. Undoubtedly, the complexity of diatom changes over past periods of warming such as the Holocene Thermal Maximum and the Medieval Climate Anomaly requires a more thorough examination than what is possible in this present review. Here, we restrict the discussion to examples of high-magnitude, cyclical shifts in climate resulting in nearly complete shifts in diatom species dominance that share similarities to the recent and widespread taxon-specific diatom shifts reported in paleolimnological records. Although not reported as frequently as diatom responses to recent warming, a surge of millennial-scale paleolimnological studies have reported striking and abrupt shifts in *Cyclotella–Aulacoseira–Fragilaria* species that are triggered by changes in lake properties linked to sharp shifts in high magnitude fluctuations in past climate from numerous regions of the world including China (Wang et al. 2008, 2012a, b), France (Ampel et al. 2010), Nepal (Lami et al. 2010), Austria (Huber et al. 2010; Schmidt et al. 2012), and Greece (Wilson et al. 2008; Jones et al. 2013). This pattern seems particularly strong in monsoon regions where climate change affects wind patterns and lake mixing trends. For example, pronounced shifts among small planktonic *Discostella stelligera* and large-celled *Aulacoseira taxa* tracked changes in the intensity of the East-Asian winter monsoon over the past ~1000 years (Wang et al. 2012a) and 15,000 years (Wang et al. 2012b) in northeast China, and from ~15,000 to ~6000 years in southeast China (Wang et al. 2008). The East Asian monsoon system controls prevailing climatic conditions that are strongly seasonal and, in turn, are tightly linked to the limnology of lakes in this region (Wang et al. 2012a). Seasonal shifts in dominance between relative abundances of *Discostella* and *Aulacoseira* species were used as a proxy for long-term changes in the strength of the winter monsoon winds, with strong monsoon periods (strong vertical mixing of the water column) dominated by *Aulacoseira* taxa, and periods of weak monsoon strength (strongly stratified water column) dominated by *Discostella* taxa (Wang et al. 2008, 2012a, b). These taxon-specific trends were supported further by a seasonal sediment trap study on the same lake where these dynamic taxonomic shifts were recorded (Wang et al. 2008).

In considerably longer paleolimnological records, such as from Les Echet (eastern France), several pronounced shifts in dominance between benthic fragilarioid and *Cyclotella* taxa were associated with Dansgaard-Oeschger cycles (36.2–31.7 k YBP) during the last glacial period (Ampel et al. 2010). During cool stadial periods, fragilarioid-dominated assemblages were prevalent, whereas during warmer interstadial periods, *Cyclotella*-dominated assemblages prevailed. The authors attributed this see-saw cycle in diatom life strategy to climate-mediated changes in the duration of ice cover and thermal stratification patterns during abrupt and pronounced stadial-interstadial transitions.

The above millennial-scale paleolimnological examples illustrate that a clear diatom response with almost complete shifts between small cyclotelloid species and *Aulacoseira*/fragilarioid taxa, can be driven by large magnitude, cyclical shifts in climate when they are strongly linked to the length of the open-water season, lake mixing regimes and/or thermal stability. However, not surprisingly, the magnitude, timing, and geographical extent of climate-induced changes in limnological properties and diatom assemblage shifts in lakes will vary considerably among climate regions (e.g. monsoon, continental, marine etc.), and over varying time scales (e.g. centennial, millennial, sub-millennial etc.). Climate characteristics (windiness, cloudiness, precipitation, etc.) and climate forcing mechanisms (including insolation, ice sheet distribution, sea level, aerosol and atmospheric greenhouse gas concentrations) will also vary temporally (Bigelow et al. 2003), further contributing to differences in diatom responses when comparing changes over time, or when comparing time periods (Fritz 2008; Catalan et al. 2013). Thus, careful consideration must be given when making comparisons between more recent diatom shifts with those reported in the distant past. As cautioned by Catalan et al. (2013), changes in these planktonic taxa (or any diatom taxa) should not be applied as a "lake thermometer" in paleolimnological records, particularly over long time periods. Nevertheless, regardless of differences in precise climatic mechanisms, if climate change strongly affects fundamental lake properties that are important for algal growth, threshold-type diatom responses can be similar to the recent taxon-specific diatom shifts reported throughout the Northern Hemisphere (Rühland et al. 2008), and now being reported in tropical regions such as the equatorial Andes (Michelutti et al. 2015).

Do we record similar diatom shifts at different latitudes and altitudes?

Seasonality, ice cover and lake thermal properties

The intricacy of climate-related changes among very different freshwater aquatic ecosystems is one of the most interesting challenges faced by researchers when attempting to interpret recent diatom assemblage shifts. The sensitivity of a given lake to climate change, both in terms of the magnitude and timing of the response of the biota, as well as differences in the nature of a given response, is a topic of considerable interest, importance, and complexity. In the previous section of this review, we highlighted the similarity of the responses of diatom assemblages to climate across different temporal scales; in this section we examine the spatial variability of this same diatom response during the 'Anthropocene' among and within regions. As noted below, the magnitude and coherence of the diatom response to climate-induced changes in water properties among lake records will understandably vary, often considerably, from region to region, and even among lake-types within regions.

Diatom responses to new climate regimes are particularly well expressed in regions where there is strong seasonality, such as in high latitude, temperate, and many high altitude regions (Smol 1988; Lotter and Bigler 2000; Catalan et al. 2002a, b; Karst-Riddoch et al. 2005; Smol and Douglas 2007). Changes in the duration of the ice season have been of particular interest for limnological research given the importance of global warming to lake ice phenology (Kirillin et al. 2012), and because of the strong relationship between warming and changes to the timing of onset of stratification, and end-of-season mixing patterns (Cahill et al. 2005). Understandably, a distinct switch in a lake's physical properties from completely snow and ice covered during the winter to the dynamics of ice-off and water column mixing in the spring, or to the establishment of a thermally stratified, relatively stable water column at the height of the summer, are some of the most important properties controlling aquatic biological communities (Catalan et al. 2002b, 2013; Smol and Douglas 2007).

Lakes in completely different geographic settings that experience a low degree of seasonality may be less sensitive to warming for very different reasons. For example, in latitudes where lakes are ice-free year-round, such as in Lake Tahoe, California (Winder and Hunter 2008), larger changes may be required to cross a climate threshold when compared to lakes with stronger seasonality that may be ice covered for a substantial period of the year. Similarly, deep High Arctic lakes that have been perennially frozen, or nearly so, also experience a low degree of seasonality. Therefore, lakes in the Canadian High Arctic such as Lower Dumbell Lake (Doubleday et al. 1995), Char Lake (Michelutti et al. 2003), and Ward Hunt Lake (Antoniades et al. 2007) will likely require larger and more extreme changes in climate, or a longer period of time before a threshold response is expressed in the diatom assemblages. In the sections below, we further explore these differences across and within regions to highlight some of the reasons for the variability in magnitude and timing of diatom responses to climate change.

Circumpolar lakes

Circumpolar regions are often the first to show signs of biological response to climatic change, as relatively small changes are amplified due to a variety of important feedback mechanisms. A synthesis of diatom trends collated by 26 co-authors from across the northern circumpolar regions of Canada, Finland, Russia and Spitsbergen concluded that the magnitude of diatom compositional change showed a generally increasing trend with latitude, highlighting the ecological sensitivity of Arctic systems to climate change (Smol et al. 2005). More recently, pronounced transitions in diatom community turnover were observed along a latitudinal gradient in the central Canadian Arctic islands, and were identified as diatom ecotone positions (Antoniades et al. 2014).

In shallow High Arctic ponds, where the ice-free period is very brief, a reduction in the degree and duration of ice cover (either completely ice-free or limited to a shallow, near-shore moat of open water) would increase the aquatic growing season and allow for the development of mosses in the littoral zone (Douglas and Smol 2010). This substantial expansion of aquatic habitat has led to a major reorganization of the algal communities, with a shift from very simple assemblages consisting of a few species of small, benthic diatoms towards a more complex, species-rich assemblage consisting of epiphytic diatom taxa associated with littoral habitats and mossy substrates that is consistent with warming-induced habitat expansion as ice cover is diminished (Douglas et al. 1994; Smol et al. 2005; Douglas and Smol 2010).

Clearly, however, the size of the water body and its geographic setting will affect its thermal inertia and this will result in different ecological responses. For example, in deeper circumpolar lakes, particularly in subarctic regions, pronounced increases in planktonic cyclotelloid species have been recorded, often appearing in the diatom record for the first time in millennia. These shifts are of similar magnitude to the periphytic diatom shifts recorded in Arctic ponds and shallow lakes (Smol and Douglas 2007), and are concurrent with declines in the abundances of benthic fragilarioid species or tychoplanktonic *Aulacoseira* taxa (Sorvari et al. 2002; Rühland et al. 2003a; Jones and Birks 2004; Solovieva et al. 2005; Antoniades et al. 2014). As noted previously, deep and higher latitude lakes, with more extensive ice cover, are often slower to respond to warming and, as predicted, consistently record a delayed diatom response in the more recent sediments (Doubleday et al. 1995; Michelutti et al. 2003; Perren et al. 2003; Antoniades et al. 2007). Also, not surprisingly, shallow lakes and ponds in subarctic regions do not typically show the near complete turnover in species composition among benthic diatoms (Rühland et al. 2003a) that are commonly reported in ponds of the High Arctic, likely because these lower latitude systems have long experienced completely ice-free periods during the summer and have long supported complex, species-rich benthic diatom assemblages. In subarctic regions, it appears that the sensitivity of the diatom response to recent warming is best expressed in deeper lakes (Sorvari et al. 2002; Rühland et al. 2003a). In these circumpolar regions, earlier ice-out, longer growing periods (often with near 24-h daylight), decreases in vertical mixing and increases in thermal stability during the summer season favour small planktonic diatoms (Rühland et al. 2008). During cooler periods with longer ice cover and stronger vertical mixing, *Aulacoseira* taxa and small benthic fragilarioid taxa fare better (Rautio et al. 2000; Smol et al. 2005; Forsström et al. 2007).

High elevation lakes

Air temperatures, particularly over the past few decades, have been increasing in mountainous regions, with an amplification of warming with elevation (O'Gorman and Singh 2013; Wang et al. 2014; Diaz et al. 2014). Climate warming in high altitude environments affects snowpack, streamflow patterns and terrestrial and aquatic ecosystem functioning (Diaz et al. 2003; IPCC 2007a, b; Parker et al. 2008; Vuille et al. 2008; Bradley et al. 2009; Gobiet et al. 2014). Similar to the sensitivity of high latitude lakes and ponds, high altitude systems in temperate, Arctic, and tropical regions are also showing a marked diatom response to recent warming (Lotter and Bigler 2000; Catalan et al. 2002a, b; Karst-Riddoch et al. 2005; Larsen et al. 2006; von Gunten et al. 2007; Parker et al. 2008; Hobbs et al. 2011; Saros et al. 2012; Chen et al. 2014; Michelutti et al. 2015). Alpine lakes above treeline share many limnological characteristics with high latitude lakes such as changes in ice cover extent, habitat availability, mixing processes, and thermal stability, and it is expected that the nature of a diatom response would also be somewhat similar (Karst-Riddoch et al. 2005). However, mountain lakes are located at many different latitudes and, unlike most high latitude regions, not all alpine locations can be considered remote, as many are proximal to, or are impacted directly by, human activities (Catalan et al. 2013). Such disturbances can blur the diatom-climate signal in the sediment record.

The median timing of a shift towards higher relative abundances of small cyclotelloid diatom taxa in alpine lakes from the Northern Hemisphere was found to occur about 70 years later than similar changes in Arctic lakes, but about 50 years earlier than in temperate low elevation lakes (Rühland et al. 2008). This is consistent with Arctic lakes registering a change earlier than other parts of the world (Smol and Douglas 2007) and supports evidence that mountain regions at lower latitudes may track an early response to warming (Battarbee et al. 2002; Hobbs et al. 2011; Catalan et al. 2013). Much like the changes observed in lakes at high latitudes, a distinct shift from benthic fragilarioid taxa to recent increases in the relative abundances of small planktonic *Cyclotella/Discostella* species has been observed in alpine paleolimnological records from various parts of the world (Lotter and Bigler 2000; Catalan et al. 2002a, b; Saros et al. 2003; Karst-Riddoch et al. 2005; Larsen et al. 2006; von Gunten et al. 2007; Hobbs et al. 2011; Chen et al. 2014; Michelutti et al. 2015).

In the Western Rocky Mountains of North America, regional air temperatures have increased considerably since the early nineteenth century, but this trend intensified in the mid- to late-1980s (Luckman and Wilson 2005; Parker et al. 2008). Substantial diatom assemblage shifts have been reported throughout the Rockies including in lakes from the southern Yukon, Canada (Karst-Riddoch et al. 2005), in Alberta, Canada (Parker et al. 2008; Hobbs et al. 2011), and in more southern areas including Colorado, Wyoming, Montana and Utah, USA. (Saros et al. 2003; Wolfe et al. 2003; Hobbs et al. 2010; Hundey 2014). In the more northern regions of the Western Rocky Mountains, recent increases in small cyclotelloid taxa were prevalent and attributed to twentieth century warming that was associated with changes in lake ice phenology, increased thermal stability, changes in stratification (Karst-Riddoch et al. 2005; Hobbs et al. 2011) and deepening of the thermocline (Parker et al. 2008). However, in the Rocky Mountains of the western United States, a region affected by large-scale industrial and agricultural activities (Fenn et al. 2003), recent warming and enhanced nitrogen deposition have been proposed as likely factors responsible for recent diatom assemblage shifts (Wolfe et al. 2003; Saros et al. 2005; Hobbs et al. 2010, 2011; Saros et al. 2011; Hundey et al. 2014). For example, Emerald Lake (Wyoming) shows an early diatom response with increases in the abundances of *Discostella stelligera* attributed to mid-nineteenth century regional warming, followed by a shift to dominance by *Asterionella formosa* after 1950, which the authors associated with nitrogen-enrichment (Hobbs et al. 2010). In the Uinta Mountains (Utah), Hundey et al. (2014) found increases in *Asterionella formosa* preceded regional temperature increases in the mid-1980s by a few decades, leading the authors to conclude that increasing deposition of nitrogen and phosphorus, as a result of regional population growth, increases in fossil fuel combustion, agricultural and mining activities, best explained the increase in this elongated planktonic diatom taxon, while noting that recent air temperature increases have exacerbated this assemblage change. Although increases in the availability of atmospheric nutrients has been evoked as the trigger for recent increases in *A. formosa* and other elongate pennate planktonic diatoms (such as planktonic *Fragilaria* and *Tabellaria* species) in the western US Rockies, it is interesting that non-alpine regions outside of this nitrogen hotspot have also reported similar increases in these elongate planktonic diatoms, concurrent with marked increases in regional air temperature, but where measured nutrients have not changed or have even declined (Solovieva et al. 2005; Rühland et al. 2010; Enache et al. 2011; Wang et al. 2012a; Hadley et al. 2013).

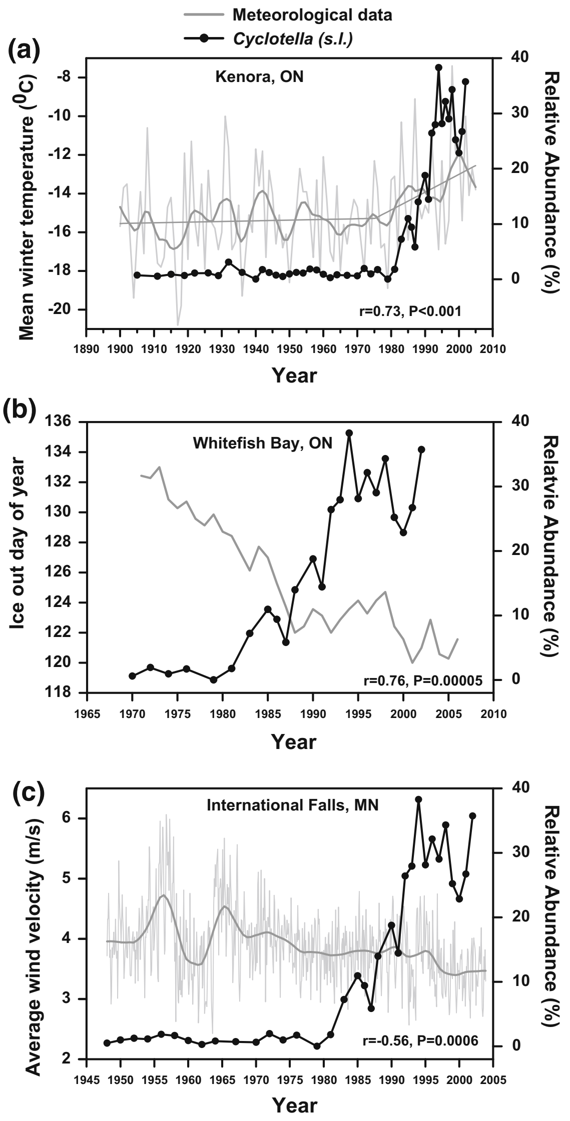
Although limnological and paleolimnological research is scarce for regions outside of the Northern Hemisphere, recent publications from equatorial and tropical regions are showing some similar and interesting trends in planktonic diatom shifts. In the tropical Andes, where the rate of warming has nearly doubled the global average in recent decades (Diaz et al. 2014), Michelutti et al. (2015) have reported striking and coherent shifts in diatom assemblage composition in three lakes in the southern Sierra of Ecuador. All lakes report an abrupt increase from trace abundances to dominance in the relative abundances of *Discostella stelligera*; these assemblage changes were synchronous with recorded temperature increases and declines in wind speed. The authors link these abrupt diatom shifts to warming and related changes in thermal stability and stratification. Unlike temperate and high latitude alpine regions, the lakes in the tropical Andes are exposed to minimal seasonality with winter ice cover a rarity. In contrast to Arctic and temperate lakes, which do experience strong seasonality, aquatic production (tracked using fossil chlorophyll *a* concentrations) in these Andean lakes has either remained stable or declined with warming. The authors speculate that enhanced thermal stability could impede the re-circulation of deepwater nutrients to surface waters resulting in declines in aquatic production and favouring the expansion of small cyclotelloid taxa. A subsequent paleolimnological study from the Peruvian Andes similarly reported recent increases in planktonic diatoms that were consistent with warming-induced lakewater changes (Michelutti et al. unpublished data).

Temperate lakes

Although lagging Arctic and alpine regions, temperate latitudes have likewise recorded substantial increases in air temperature over the past century, with a distinct amplification of this trend in the last 30–40 years (Mann et al. 2008). A growing body of scientific literature indicates that, similar to high latitude and alpine regions, temperate lakes are also showing strong signs of recent climate-induced biological changes (Adrian et al. 2006; Winder et al. 2009; Shimoda et al. 2011) including the aforementioned *Cyclotella–Aulacoseira–Fragilaria* shifts (Clerk et al. 2000; Holtham et al. 2004; Bradshaw et al. 2005; Werner et al. 2005; Harris et al. 2006; Ginn et al. 2008). The impacts of these recent climatic trends on ecosystems of more temperate latitudes are not always evident, mainly because these regions are typically subjected to multiple environmental stressors that can obscure a clear response to climatic change. However, in the absence of extensive anthropogenic disturbances, physical, biological and chemical processes of freshwater ecosystems in all regions of the world are principally regulated by climatic fluctuations (Gerten and Adrian 2002).

To examine potential drivers of *Cyclotella–Aulacoseira–Fragilaria* trends, a detailed diatom analysis from a dated sediment core retrieved from Whitefish Bay, Lake of the Woods (northwestern Ontario, Canada) was compared to instrumental and observational records (Rühland et al. 2008, 2010). The high-resolution diatom record provided an ideal opportunity to study this recent diatom shift, as northwestern Ontario is a region that has remained relatively isolated from direct human perturbations (Schindler 1997). Long-term continuous instrumental records are available from nearby weather stations, and a remarkably complete, continuous lake ice record exists from the same site where the sedimentary core was retrieved. Very similar in nature to the changes reported previously in circumpolar lakes, Whitefish Bay diatom assemblages underwent a pronounced and abrupt increase in the relative abundances of *Cyclotella* sensu lato (*s.l.*) taxa at the expense of heavily silicified *Aulacoseira* taxa. Pronounced temperature increases, particularly since the late-1970s, and a substantial lengthening in the ice-free period by almost 30 days in the past 40 years, were consistent with the timing of the taxon-specific shift observed in Whitefish Bay. Strong, significant relationships were observed between the *Cyclotella s.l.* trends and measured temperature and lake ice data (Fig. 3a, b), providing further convincing evidence that warming and other climate-related water column changes played an important role in influencing the diatom community re-organization.

Long-term records of wind speed from nearby International Falls (Minnesota, USA) indicate that wind velocity changed only minimally during this same period (Herb et al. 2005). However, this metric is also of potential interest, as a reduction in wind speed could contribute to reductions in mixing strength and depth, as well as to lake thermal stability (Saros et al. 2012). Wind speed, air temperature, and long- and short-wave radiation are all important determinants of water temperature and thermal stability in lakes (Hadley et al. 2014), with wind speed increasing in importance in larger waterbodies (>500 ha), where variability in summer mixing depths has been related to higher wind-induced mechanical energy (Fee et al. 1996). This indicates that, in the Lake of the Woods region, and in large lakes in general, changes in wind speed during the growing season may also affect fundamental lake processes, such as the strength, frequency and duration of lake mixing/turbulence and thermal stratification, and the availability of light and nutrient resources, possibly exacerbating the effects of warming alone on diatom assemblages. In Whitefish Bay, the slight decline in wind speeds over the past 50 years is significantly and negatively correlated with the relative abundance of *Cyclotella s.l.* species. (Fig. 3c). Of note, however, is that the period of ice cover in Whitefish Bay has clearly declined since the 1960s, despite evidence that declining wind speeds in other large lakes have facilitated a lengthening of the ice cover period (Kouraev et al. 2007), illustrating that the relationships between wind speed, ice dynamics and lake thermal properties are complex. Furthermore, the observed diatom assemblage changes we discuss here are also prevalent in smaller water bodies, including lakes in the nearby Experimental Lakes Area (Enache et al. 2011; Wiltse 2014), where the effect of wind speed on thermal stability is minimal (Fee et al. 1996), and in Lake of the Woods where air temperature and ice dynamics were more strongly correlated to recent diatom changes than wind speed (Fig. 3). Using such reasoning, warming, which was directly linked to an extension of the open water period and associated changes in lake thermal properties, was the most plausible explanation for the pronounced increase in small-celled cyclotelloid taxa at the expense of large-celled *Aulacoseira* taxa in the last few decades in Whitefish Bay (Rühland et al. 2010). These analyses clearly show that climate-related variables are primarily driving the recent diatom assemblage changes.



◀**Fig. 3** Comparison of *Cyclotella sensu lato* (*s.l.*) relative abundances from Whitefish Bay (Lake of the Woods, Ontario, Canada), and observational and instrumental meteorological data, including: **a** Mean winter air temperature recorded at Kenora (Ontario, Canada). A Loess smoother (span = 0.1) and a 2-segment piecewise linear regression was applied to highlight the trend. **b** Change in the day of ice off recorded from Whitefish Bay. **c** Monthly averaged wind velocity from 1948 to 2003 for International Falls (Minnesota, USA). A Loess smoother (span = 0.1) was applied to the monthly data to highlight the trend. The results of the correlation analysis are given in *each panel*. To enable comparisons between instrumental, observational, and diatom data for each sedimentary interval from Whitefish Bay, the average value (i.e. air temperature, wind speed and ice off day) during the period of diatom sedimentation was calculated, thereby aligning the meteorological and ice data with the diatom data (*sensu* Sorvari and Korhola 1998). The Kenora temperature data are available from http://www.ccma.bc.ec.gc.ca/hccd. Wind data from International Falls are courtesy of William Herb (University of Minnesota, St. Anthony Falls). Lake ice data from Whitefish Bay are from the Ontario Ministry of Natural Resources and Forestry, Kenora, Ontario

Comparisons in timing across ecoregions in the Northern Hemisphere: meta-analyses

The striking similarity of the *Cyclotella–Aulacoseira–Fragilaria* diatom shift in lakes from diverse ecological settings including high latitude, high altitude, and temperate regions, was examined in a synthesis of Northern Hemisphere paleolimnological diatom studies (Rühland et al. 2008). In the over 200 diatom records from non-acidified, non-enriched lakes that were analysed in this study, significant increases in the relative abundances of planktonic *Cyclotella s.l.* taxa were recorded, with concurrent and significant declines in both heavily silicified *Aulacoseira* taxa and small, benthic fragilarioid taxa. One of the key findings of this meta-analysis was that, although variable, the timing of initial increases in *Cyclotella s.l.* species in high latitude lakes (median age = AD 1870) significantly preceded initial increases in high altitude regions by ~50 years (median age = AD 1920) and preceded changes in lower latitude, temperate lakes by ~100 years (median age = AD 1970) (Fig. 4). This variation in timing among these different ecoregions is consistent with Arctic regions experiencing warming earlier, and so diatoms from Arctic lakes are recording an earlier response to warming than most other regions in the world (Smol et al. 2005; Smol and Douglas 2007).

The exact mechanism triggering the recent diatom shifts summarized above is difficult to infer from the paleolimnological records alone, but differences in timing would be expected, given the large variation in site-specific and regional characteristics. Nonetheless, a common feature reported for many of these studies is an increase in the open water season and periods of increased lake heat content and water column stability, and reduced vertical mixing. The later timing of this shift in temperate lakes would be predicted with warming, as lower latitude, temperate aquatic ecosystems that experience longer ice-free periods and growing seasons will understandably take longer and require a greater temperature increase to reach that tipping point than sensitive, circum-Arctic lakes.

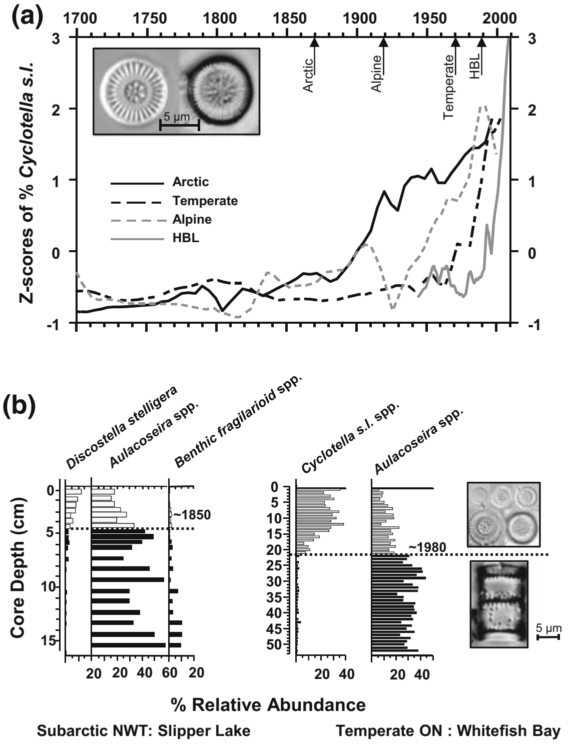


Fig. 4 The timing of change in small *Cyclotella sensu lato (s.l.)* species. **a** Photomicrographs (*inset*) of *Discostella stelligera* (*left*) and *Cyclotella comensis* (*right*).Timing of increased relative abundances (Z-scores) of *Cyclotella s.l.* taxa from a selection of lakes in Arctic (*black solid line*), alpine (*grey dashed line*), temperate (*black dashed line*) and the Hudson Bay Lowlands (HBL) (*solid grey line*) regions. *Arrows* demarcate the median timing of change in each region estimated from 82 diatom profiles from Rühland et al. (2008) and from four HBL diatom profiles from Rühland et al. (2013). **b** Diatom profiles typifying the nature of the *Cyclotella–Aulacoseira–Fragilaria* shift and the timing of this trend in subarctic (Slipper Lake) and in temperate (Whitefish Bay) regions. Photomicrographs (*inset*) of various small cyclotelloid taxa (*top*) and heavy *Aulacoseira* (e.g. *A. lirata*) taxa (*bottom*)

However, once that ecological threshold is passed, the response of temperate lakes can be equally abrupt and pronounced, as shown above for Whitefish Bay, Lake of the Woods.

Subsequent to the 2008 publication of the Rühland et al. meta-analysis, a large number of international studies have shown similar patterns of increasing relative abundances of small cyclotelloid diatom species at the expense of larger-celled diatoms across temperate and subarctic North America (Thienpont et al. 2008, 2013; Hyatt et al. 2011; Enache et al. 2011; Hawryshyn et al. 2012; Hobbs et al. 2011; Friel et al. 2014; Medeiros et al. 2012; Hadley et al. 2013), Europe (Guinder et al. 2010; Guilizzoni et al. 2012; Schmidt et al. 2012; Jones et al. 2013; Wilson et al. 2013), China (Wang et al. 2012; Panizzo et al. 2013) and Ecuador (Michelutti et al. 2015). The recent shift in diatom composition (*Cyclotella–Aulacoseira–Fragilaria*) reported from sites across a large geographic range, often registers the arrival of appreciable numbers of planktonic diatoms for the first time in millennia, suggesting that large-scale, threshold-induced, ecosystem shifts are underway (Smol et al. 2005; Axford et al. 2009).

Tropical lakes

Over the course of our literature search for publications on diatom responses to warming, it quickly became apparent that comparable limnological and paleolimnological data from regions outside of the Northern Hemisphere were scarce. As a result, this review is heavily weighted to studies in the Northern Hemisphere—this was not by our design, and not because diatoms are not responding to warming in other regions, but rather because, at the time of writing, published data were scarce. Unlike many lakes in the Northern Hemisphere, most tropical lakes do not experience seasonal ice cover and therefore differences in the nature and sensitivity of lake and diatom responses would be expected between these regions. Nevertheless, studies of recent diatom changes in African lakes share similarities to those reported throughout the Northern Hemisphere such as increases in elongated planktonic diatoms and decreases in heavily silicified *Aulacoseir*a taxa. In this section, we will highlight studies from African lakes that are interesting examples of diatom responses to recent warming-induced water column changes in tropical regions.

In tropical lakes where water temperatures are typically high, differences in the vertical temperature gradient are relatively small, but nonetheless strong density differences develop at these high water temperatures (Hutchinson 1957). Many of the large, deep Rift Valley lakes of East Africa, such as Lake Tanganyika and Lake Victoria, have undergone substantial limnological changes as a result of unprecedented warming in recent decades (Hecky 1993; O'Reilly et al. 2003; Verburg et al. 2003; Hecky et al. 2010; Tierney et al. 2010). Earlier observations report that Lake Victoria typically experienced a well-mixed water column (Talling 1966) but, following a general warming trend and periods of low wind stress since the 1970s (Verburg et al. 2003; Hecky et al. 2010), Lake Victoria became thermally stratified. This physical change in lake properties led to a new ecological state by triggering an increase in phosphorus and primary production (Hecky 1993; Hecky et al. 2010) and a switch from a diatom-dominated to a cyanobacteria-dominated system (Kling et al. 2001; Hecky et al. 2010).

The above transition to a new state in response to recent warming was confirmed by a paleolimnological study of recent diatom changes in Lake Victoria (Stager et al. 2009). Stager et al. (2009) used a shift from assemblages dominated by heavily silicified *Aulacoseira* taxa to assemblages dominated by long, thinly silicified planktonic *Nitzschia acicularis* (Kützing) W. Smith as an indication of eutrophication and reduced vertical mixing (increased thermal stability). The current dominance of diatom assemblages by long planktonic *Nitzschia* spp., and the near extirpation of the once dominant *Aulacoseira nyassensis* var. *victoriae* (O. Müller) Simonsen, was unprecedented in the ~15,000 year history of Lake Victoria (Stager et al. 2009). They suggested that the predominance of cyanobacterial blooms in this new ecological state have warmed surface waters further while shading the water column below, resulting in further reductions in vertical mixing and enhancement of thermal stratification. The authors proposed that these recent changes to Lake Victoria have made it difficult for less buoyant diatoms, such as *Aulacoseira* taxa, to capture sufficient light. Consequently, this has provided a competitive advantage to elongate planktonic *Nitzschia* taxa with its high surface area to volume ratio, enabling cells to better compete for light and nutrient resources as well as dissolved silica, which had undergone declines of ~80 % over the late twentieth century (Hecky 1993). Multiple stressors have been present in this lake for several decades, but warming and reductions in wind since the ~1970s have led to the tipping point triggering a new ecosystem state with changes in the food web, a highly productive algal community (Hecky et al. 2010), and a large increase in the percent relative abundance of elongate *Nitzschia* species in Lake Victoria (Stager et al. 2009).

Why are there differences in diatom responses to warming within a region?

In the previous section we outlined how differences in the timing and magnitude of diatom responses can be related to latitude and altitude. In nature, the responses of aquatic systems to environmental changes are not always straightforward and there are always exceptions to these generalizations. For example, the sensitivity of a given lake to respond to change within an ecoregion may differ among similar lake types with differing ice cover dynamics or because of differences in lake characteristics. Below we examine some of the more interesting exceptions.

Will latitude and ecoregion always determine the timing and magnitude of diatom shifts?

It is clear that latitude, in general, is an important factor to consider when examining the nuances of diatom responses to recent climate change. However, latitude *per se* does not necessarily determine the timing and sensitivity of a particular diatom compositional shift, as air temperature trends are not spatially uniform and can vary and be expressed differently across regions depending on regional and local lake characteristics. For example, unlike the typically pronounced warming trend reported throughout the circum-Arctic starting in the mid- to late-nineteenth century, the western subpolar North Atlantic region (Hudson Bay, northern Québec, and Labrador) did not experience a notable warming trend up until the mid-1990s due to negative climate feedback mechanisms related to persistent Hudson Bay sea ice (Chapman and Walsh 1993; Gagnon and Gough 2005; Rouse 1991). Consistent with this lack of warming, paleolimnological studies east of Hudson Bay have reported algal and invertebrate records with minimal biological change occurring over at least the past few centuries (Laing et al. 2002; Paterson et al. 2003), and likely since the onset of regional neoglacial cooling ~1500 years ago (Ponader et al. 2002; Pienitz et al. 2004; Fallu et al. 2005). However, in the past ~15–20 years, meteorological data from the region have shown marked air and sea surface temperature increases, from previously stable 30-year means, at a pace and magnitude that are exceptional even by Arctic standards (Hochheim and Barber 2010, 2014).

Using detailed diatom records retrieved from four lakes in the Hudson Bay Lowlands (HBL) of Ontario, Rühland et al. (2013) examined whether the algal communities have responded to this rapid and intense regional warming trend recorded only within the past ~15–20 years. The dated cores yielded an exceptionally high temporal resolution for Arctic and subarctic systems, providing an ideal opportunity to compare the diatom records to instrumental records and pinpoint the timing of ecological change. Based on earlier paleolimnological Arctic and subarctic work (Smol et al. 2005), Rühland et al. (2013) postulated that, if lake ice cover and other climate-related variables were the main drivers of assemblage changes in the HBL, then increases in planktonic diatoms and community complexity would be expected. However, these changes should occur much later (i.e. post-1990) given the late onset of warming in this region. Indeed, following their a priori predictions, Rühland et al. (2013) found coherent taxon-specific diatom shifts across all lakes, characterized by an increase in species diversity and complexity, and the first appearance of planktonic taxa beginning in the 1990s. These algal changes were concurrent with changes in Hudson Bay sea ice extent and phenology, and increases in regional air and sea surface temperatures. Nitrogen deposition was ruled out by the authors as a possible explanation for these changes given that this region experiences low fluxes of nitrogen to regional freshwater lotic systems (Howarth et al. 1996; Schindler et al. 2006) and, based on a global assessment by Vet et al. (2014), very low levels of atmospheric nitrogen deposition. Furthermore, the diatom taxa involved are not known to be nitrophilous (see detailed discussion below), and the diatom changes post-date the peak in long-range deposition of atmospheric nitrogen by several decades. Most importantly, the timing and nature of the algal changes were undeniably consistent with the later onset of known warming in the 1990s, and the new climate regime of the HBL. Moreover, the algal shifts recorded in lakes from the HBL are consistent and temporally coherent with other pronounced biological changes occurring in the Hudson Bay and James Bay regions. From top predators to the bottom of the food chain, there has been a variety of independent publications, including long-term studies on sea birds and their prey (Mallory et al. 2010; Gaston et al. 2012; Gaston and Elliott 2014), polar bears (Peacock et al. 2010), and orcas (Ferguson et al. 2010), that point to abrupt fundamental ecological changes occurring in the mid-1990s, and ultimately linked to a concurrent shift in the climate regime (Hochheim and Barber 2010, 2014). The diatom records in the HBL lakes clearly track these well-documented recent climatic changes.

High Arctic lakes with different characteristics and different ice regimes

Different lake types within the same geographic region would also be expected to vary in their response to regional warming, with different sensitivities and timings of diatom responses. For example, deep High Arctic lakes that maintain extensive ice cover even during the height of the short Arctic summer respond differently than shallow High Arctic lakes and ponds that have far more dynamic ice covers. In the nearly perennially frozen lakes in the High Arctic, diatoms were often virtually absent from the sedimentary record for millennia, presumably due to persistent ice cover (Doubleday et al. 1995; Perren et al. 2003; Antoniades et al. 2007; Perren et al. 2012). Even when the area first started to experience regional late-nineteenth century temperature increases, these deeper lakes remained largely ice covered over the short summer, thus delaying a diatom response due to a strong 'thermal inertia' (Michelutti et al. 2003). Unlike the dynamic diatom compositional shifts recorded in shallow lakes and ponds throughout the Arctic, often starting in the mid- to late-nineteenth century (Smol et al. 2005), these deeper High Arctic lakes did not register a change in diatom composition until warming was sufficient to effectively decrease lake ice cover during the height of the summer. For example, Char Lake, a deep High Arctic Lake on Cornwallis Island, was sampled for chemical, physical and biological variables from 1992 to 2000 (Michelutti et al. 2007). No notable differences in water quality variables, including nitrogen, were noted between these recent data and those collected 30 years earlier (1968–1972) as part of the International Biological Programme, indicating that Char Lake remained oligotrophic, dilute and slightly alkaline. However, the diatom assemblages initiated a modest ecological shift, from *Staurosirella pinnata* (Ehrenberg) Williams and Round dominating the record until ~1987 to a more diverse assortment of periphytic diatoms appearing during the warmest decade on record. In addition, small percentages of *Cyclotella* taxa were also recorded in the most recent sediments. The nature and timing of the diatom shifts are consistent with changing ice cover dynamics.

Paired High Arctic lakes with similar characteristics but different ice regimes

A powerful approach to explore the relative effects of climate-related variables such as ice cover duration on associated diatom changes is to find two lakes with nearly identical limnological characteristics, but different micro-climatic regimes, and then to compare their paleolimnological records. Understandably, such study sites are uncommon; however Keatley et al. (2008), working in the High Arctic, found such a paired set of lakes (within <20 m of each other), which had nearly identical physical and chemical characteristics but different ice cover dynamics. Observations since the 1960s confirmed that Skeleton Lake becomes ice-free weeks later than nearby EP2 Lake due to shading and protection from winds provided to Skeleton Lake by Blister Hill (Oliver and Corbet 1966). In contrast, EP2 Lake, which is not protected by Blister Hill, has a longer ice-free period. Detailed diatom analysis from these paired lakes showed that benthic *Staurosira construens* var. *venter* (Ehrenberg) Hamilton dominated the assemblages from both lakes, but only EP2 recorded a striking change in diatom composition in the recent sedimentary intervals that was consistent with warming. The *Staurosira construens* var. *venter*-dominated assemblages were quickly replaced with a more complex assemblage of benthic diatoms including *Pseudostaurosira brevistriata* (Grunow) Williams and Round as well as an assortment of periphytic diatom species, a trend commonly observed with warming in High Arctic lakes (Smol et al. 2005). In contrast, Skeleton Lake, with prolonged ice cover, showed minimal change with benthic fragilarioid species continuing to dominate to the present. Clearly these adjacent lakes with similar rocky catchments and lacking vegetation would have received the same aerial deposition of nutrients and pollutants. This condition was further confirmed by the near identical water chemistry analyses of the two sites (Keatley et al. 2008). This study provides strong evidence that changes in ice cover play a principal role in diatom composition and dynamics in High Arctic systems, and that the biological responses to climate will vary with local conditions.

Paired subarctic lakes with different characteristics and similar ice regimes

A paleolimnological comparison of two neighbouring subarctic lakes in the Yukon Territory (Canada), with similar limnological settings but with different lake depths, differed substantially in the response of diatoms and chironomids to recent warming (Chen et al. 2014). These high elevation lakes are located proximal to the Wrangell-St. Elias ice field, which exerts a negative feedback on the climate system. For example, despite similar locations relative to the ice field, deeper Howard Lake showed very little change in both diatoms and chironomids over the past ~300 years, whereas shallower St. Elias Lake showed notable compositional shifts in both proxy indicators. The presence of the ice field in this subarctic region resulted in deeper Howard Lake responding in a manner that is similar to deeper High Arctic lakes, such as Char Lake described above. Small benthic fragilarioid taxa dominated the assemblages of both lakes, but only in shallower St. Elias Lake was a compositional shift observed, with the first planktonic diatom (*Cyclotella bodanica* var. *lemanica*) making an appearance in notable abundances ~1970. This paired comparison of neighbouring lakes highlights the recurring observation that, although regional climate controls such as proximity to an ice field can dampen the biological response, site-specific differences are important in controlling the nature and timing of the biological response. In this case, shallower sites were more sensitive to changes in ice duration. These examples also highlight that lakes subjected to a lower degree of seasonality, regardless of being located in a climatically sensitive High Arctic environment, will require a higher magnitude of climate change and a longer period of time before a threshold response is expressed in the diatom assemblages.

Comparisons among similar lake types with different thermal regimes

In the previous section, we illustrated how larger and deeper High Arctic lakes tend to respond less sensitively than small and shallow High Arctic lakes and ponds due to 'thermal inertia' as a result of the perennially frozen nature of these lakes. We have also shown that in subarctic regions the opposite is often observed, with deeper subarctic lakes registering a pronounced shift in diatom life strategy from a predominantly benthic assemblage in the past to an assemblage that now includes small planktonic cyclotelloid species, often for the first time in the paleolimnological record. However, there are always exceptions to these trends, as we have illustrated with the paired Yukon subarctic lakes that do not behave like typical subarctic lakes due to the cooling effect of the nearby ice-field, resulting in these lakes being more akin to High Arctic aquatic systems. Once lakes are sufficiently ice-free and have warmed, such as in typical subarctic lakes, a new ecological threshold comes into play: a climate-mediated increase in thermal stability and increased frequency and strength of thermal stratification with concomitant declines in vertical mixing duration and strength.

The importance of ice cover and lake thermal properties to diatom assemblage composition in deeper subarctic lakes was illustrated in a study of lakes in subarctic Finland, where Sorvari et al. (2002) compared diatom records among lakes and revealed that, despite similarities in depth, these lakes registered very different sensitivities in their responses to recent warming. Deep lakes that experienced thermal stratification during the ice-free season registered a pronounced increase in small cyclotelloid species (most notably *Cyclotella comensis* and *Discostella glomerata*) and an overall increase in species richness. In contrast, deeper, isothermal lakes showed more muted changes among the benthic diatom taxa and no notable change in species richness. A comparison of the diatom shifts to mean annual air temperature data from the region showed significant correlations, although not completely linear. The authors suggested that slight variances between diatom and temperature trends were likely due to lake-specific internal thresholds that, once crossed, led to a rapid reorganization of the biological assemblages. The authors concluded that the expansion of small cyclotelloid taxa at the expense of benthic fragilarioid and/or *Aulacoseira* species was consistent with: (1) recent warming; (2) declines in the duration of lake ice cover; and (3) an increase in the growing season that likely led to the development of steep stratification and weakened mixing that these lakes currently experience.

Ecological considerations when interpreting the diatom record

When using biological indicators of environmental change, it is important that the ecology of the species and the historical context of a given system be carefully considered before exploring possible mechanisms for a given response. The approach should be as simple as possible, but no simpler. For example, using the *Cyclotella–Aulacoseira–Fragilaria* shift as a signal for climate change is relatively uncomplicated, but simplifying it further (such as coarse groupings of all planktonic diatoms and all benthic diatoms, or only considering changes in planktonic diatoms and not the entire assemblage) can introduce the risk of misinterpretation and overlooking important ecological and physical nuances. There are vast differences amongst planktonic diatoms in terms of physical shape such as the tubular shape of *Aulacoseira* taxa versus the pancake shape of *Cyclotella/Discostella*, *Cyclostephanos*, and *Stephanodiscus* taxa (Fig. 2), and their physical and chemical environmental optima and tolerances. Clearly, there are also ecologically important differences amongst the cyclotelloid species, which we discuss below. Understandably, the vast range in variation in natural systems over space and time would be anticipated to give rise to exceptions to the *Cyclotella–Aulacoseira–Fragilaria* trend. This is expected, but serves to remind us of the importance of considering the biology/ecology of these taxa when interpreting the paleolimnological records. For example, recent increases in the relative abundances of *Discostella stelligera* in a diatom record in which this small plankter has been a dominant member of the assemblage for centuries to millennia is quite different, in an ecological sense, than an abrupt change in the assemblage where this taxon makes its first notable appearance in the lake's history and signifies a shift in life strategy of the overall assemblage. A notable increase in the abundance of an already dominant taxon may not represent a "regime shift" *per se*, but is likely still a response to warming-induced water column changes (Lotter et al. 2002). Taking into account the entire diatom assemblage and understanding the ecology of an assemblage prior to a shift to higher abundances of small planktonic diatoms is important to making accurate interpretations. Again, context is key.

Can warming affect planktonic diatom cell size?

Many recent studies have presented evidence showing that warming favours smaller-sized organisms, including diatoms (Daufresne et al. 2009). Changes in the phenology, intensity and duration of thermal stratification and vertical mixing will also affect the sedimentation rates of phytoplankton cells (Gerten and Adrian 2002; Huisman et al. 2006; Winder and Sommer 2012), particularly non-motile and heavy cells of planktonic diatoms (Smayda 1970; Huisman and Sommeijer 2002; Falkowski and Oliver 2007). Therefore, thermal stratification and vertical mixing are important for determining the sinking velocities of diatoms and other phytoplankton, with increased thermal stability and decreased turbulence favouring small-celled species (Bopp et al. 2005). Increases in the duration and strength of thermal stratification and the corresponding depletion of nutrients in the epilimnion, and changes in the light regime, will also give a competitive advantage to smaller-sized species that are better competitors for nutrients (Litchman et al. 2006; Falkowski and Oliver 2007; Winder et al. 2009), and taxa that are better able to maintain a vertical position within the light gradient (Fahnenstiel and Glime 1983; Elliott et al. 2002; Huisman et al. 2004).

Planktonic diatom assemblages appear to be particularly responsive to warming, both in terms of compositional shifts towards smaller-celled species (Finkel et al. 2009; Winder et al. 2009), as well as intraspecific reductions in cell size (Selbie et al. 2011). However, in multiple-stressor systems, this trend in diatom cell diminution can be understandably unclear (Reavie and Barbiero 2013). Unlike terrestrial ecosystems, where temperature often has a direct effect on an organism's body size, phytoplankton size structure is partly driven by indirect temperature effects on aquatic systems such as thermal stability and nutrient distributions (Smol et al. 1984; Reavie and Barbiero 2013). Warming-related changes in water column properties tend to favour smaller-celled planktonic diatoms with a higher surface area to volume ratio over heavier diatoms that require vertical mixing to maintain a position in the photic zone.

Unlike planktonic diatoms that receive an ecological advantage from smaller cell size with warming (e.g. higher surface area to volume ratio, lower sinking velocities, and smaller diffusion boundary layers that enable more efficient nutrient uptake and light harvesting), it seems unlikely that benthic diatoms would realize the same benefit. Benthic taxa contain the widest diversity in diatom growth habits (Julius and Theriot 2010) and thousands of different benthic taxa are capable of becoming established on each of the numerous near-shore habitat types including rocks, sediment, mosses, macrophytes, etc. It seems more likely that indirect warming-mediated alterations to these benthic habitats, such as the development of aquatic macrophytes on a predominantly rocky substrate, would lead to a change in species composition that has been reported in numerous studies (Douglas et al. 1994; Smol et al. 2005, etc.), rather than cell diminution. Furthermore, small-celled planktonic diatoms, such as *Cyclotella* and *Discostella* species, are fast growing as they have shorter life cycles and increased growth rates (Jewson 1992; Litchman et al. 2007; Winder et al. 2009), in contrast to many benthic diatoms that may only undergo one cycle of sexual reproduction in a year (Edlund and Stoermer 1997; Vanden Byllaart and Cyr 2011).

Once again, it is important to note that most researchers, ourselves included, are not arguing that diatoms are responding to temperature directly. Rather, we emphasize that other key limnological variables will change with warming (depending on the setting), such as enhanced thermal stratification and an increase in the vertical density gradient, decreased turbulent mixing, changes in mixing depth, and associated changes in resource availability, that diminish the competitive advantage of larger-celled, heavy diatoms with low surface area to volume ratios (Smol 1988; Kilham et al. 1996; Finkel et al. 2009; Winder et al. 2009). Thus, the trend towards a smaller-sized planktonic diatom assemblage in response to warming is more complex than this seemingly simple relationship to the development of a density gradient in the water column. It is the myriad inter-related changes to water column properties associated with warming (such as changes in lake and ice phenology, changes in the duration and extent of open water, changes in the light regime and in nutrient cycling, changes in mixing strength, frequency and depth, wind strength and speed), coupled with the diversity of ecological preferences of individual diatom species, that will ultimately determine diatom assemblage composition. Through careful examination of the diatom data, this shift towards small, fast-growing, planktonic diatoms at the expense of larger-celled, heavier diatoms can provide a powerful paleolimnological fingerprint for climatic warming.

How do diatoms respond to climate in a multiple stressor system?

Freshwater ecosystems the world over are subjected to a wide range of environmental pressures; they are impaired by anthropogenic activities including land-use change, atmospheric pollution, shoreline development and the introduction of non-native species, to name but a few. How these various environmental stressors affect aquatic ecosystems will depend upon regional and site-specific differences, such as geographic setting, lake morphology, depth, bedrock geology, as well as lake water chemistry. It is clear that there are numerous combinations of these lake characteristics, settings and pressures that could characterize any given lake. However, what is common to all of these lake types and settings is that they are all, with very few exceptions, subjected to climate change pressures. Consequently, it would be expected that there will be variations in the timing, nature and sensitivity of a response to climate changes among these diverse lake types.

Are recent diatom shifts a response to recovery from pollution sources?

Diatoms respond to a wide range of environmental cues, and often to both physical and chemical triggers simultaneously (e.g. stratification and lower nutrients). Understandably, climatic signals are expressed more clearly in lakes that have experienced a minimal degree of disturbance, as opposed to lakes subjected to multiple environmental stressors (Smol 2010). However, it is also true that climatic pressures will be exerted on lakes whether or not an aquatic system is recovering from a previous stressor. Thus, it is likely that lakes that have undergone, or are currently undergoing, recovery from cultural eutrophication will elicit potential interactions between warming and a reduction in nutrients, as these are not always mutually exclusive (Guilizzoni et al. 2012). Increases in small cyclotelloid taxa are commonly recorded in nutrient-poor, non-acidified lakes including those that have not been affected by or have recovered from the effects of cultural eutrophication and acidification. Lakes in both Europe and North America have undergone intensive remediation programs, commonly initiated in the early 1970s in response to accelerated inputs of strong acids and nutrients into freshwater systems. As a result of these remediation efforts, many of these lakes are now showing chemical recovery. It can be rationalized that, once these aquatic systems have recovered sufficiently from these pollution stressors, climatic warming signals such as increases in the relative abundance of small-celled cyclotelloid taxa would likewise be expressed in these systems.

Importantly, while many of these systems have returned to pre-disturbance chemical conditions, the biological responses are more complex and these systems often contain communities that bear little resemblance to pre-disturbance assemblages (Quinlan et al. 2008; Smol 2010; Hobæk et al. 2012; Hadley et al. 2013; Barrow et al. 2014; Arseneau 2014; Cummings 2014). In many paleolimnological profiles, the recent increase in the relative abundance of small cyclotelloid species marks the first appearance of these plankters in any notable abundance over at least the past few millennia. Regardless of whether a lake is experiencing chemical recovery, this recent assemblage represents a very different environment than the pre-eutrophication environment, albeit equivalent with respect to baseline total phosphorus (TP) levels. This is perhaps not surprising as the current climate regime and environmental conditions are dissimilar to conditions observed in pre-industrial times. Despite strong evidence of chemical recovery, novel stressors, including recent warming, can result in limnological and biological conditions with no historical analogs.

The concept of warming during a period of chemical recovery is illustrated in a paleolimnological study (Forrest et al. 2002) of a suite of lakes within the Rideau Canal system in Ontario, Canada (Indian, Lower Rideau, Big Rideau and Otter lakes). These study lakes are naturally mesotrophic, but European settlement in the early nineteenth century and canal construction from 1826 to 1832 led to increasing nutrient enrichment. Like many lakes throughout North America and Europe, mitigation efforts were undertaken to reduce phosphorus levels in the 1970s. The reduction in phosphorus likely facilitated the striking appearance and increase in the relative abundances of small cyclotelloid species (*C. comensis,* *C.* aff. *gordonensis*, and *D. stelligera/pseudostelligera*) in all of these lakes starting ~1970. However, the nature of these particular diatoms, found to occur in lakes of lower nutrient concentrations, is consistent with recent warming trends experienced during this same period of phosphorus mitigation. In all four lakes, these small planktonic cyclotelloid species were not an important component of the diatom assemblages prior to ~1970 (i.e. <1 % relative abundance), but have hitherto become the dominant contributors to overall diatom assemblage composition with increases from 5 to 60 %. Therefore, even with a return to inferred pre-settlement phosphorus levels, the diatom assemblages in all of these lakes are currently very different than what they were during the pre-industrial intervals, suggesting they have undergone substantial re-organizations that have likely been triggered by recent warming over the last few decades.

Nutrients and climate: Are *Cyclotella/Discostella* taxa nitrophilous?

It is undeniable that atmospheric nitrogen deposition has increased since the advent of the industrial era. In particular, the most pronounced increases have occurred post-World War II with the accelerated application of the Haber–Bosch process that allows for mass synthesis of ammonia that was first used at an industrial scale in 1913. It is therefore a legitimate hypothesis to posit that the recent diatom assemblage shifts, particularly increases in planktonic species, are linked to increases in nitrogen, as this is a critical phytoplankton nutrient resource. However, evidence to support a causal link between increased atmospheric nitrogen deposition and the recent *Cyclotella–Aulacoseira–Fragilaria* shift remains elusive.

Diatoms respond to a multitude of complex environmental factors and, given that multiple-stressor environments may now be the rule rather than the exception (Smol 2010), it is increasingly important that paleolimnologists strive to understand the ecological implications underlying the changes observed in biological proxies. Exploring details of causal mechanisms underlying a given taxonomic shift using paleolimnological records can be challenging and requires insights into the often inter-related chemical and/or physical cues that trigger a response of a given diatom assemblage. As we have stressed throughout this review, context is key when making astute environmental interpretations using paleolimnological records of diatom assemblages. Detailed, species-level studies are necessary to explore a variety of potential drivers to explain the recent *Cyclotella–Aulacoseira–Fragilaria* shift including changes in grazing pressures (Sweetman et al. 2008), increases in UV exposure (Pienitz and Vincent 2000), increases in atmospheric nitrogen deposition (Wolfe et al. 2003; Saros et al. 2005), and how (or if) these stressors interact with climate changes. Below we use the evidence reviewed in this paper to assess whether increased nitrogen deposition provides an alternative explanation for the diatom shifts from benthic/tychoplanktonic to planktonic cyclotelloid recorded in lakes across a wide spatial and temporal range. These examples, together with the evidence for climate-mediated diatom responses we presented throughout this review, lead us to conclude that there is little evidence to support increased atmospheric nitrogen availability as a driver of recent *Cyclotella–Aulacoseira–Fragilaria* diatom shifts.

Evidence from long-term measured diatom data from Lake Tahoe, California

In deep, oligotrophic Lake Tahoe, regional warming, increased water temperatures, reduced mixing, and stronger thermal stratification have changed diatom size structure over 25 years of data collection. Intensified stratification in the last decade favoured the growth of small-celled cyclotelloid species since the year 2000, whereas large-celled diatoms dominated during stronger turbulent mixing conditions and decreased over the sampling record (Winder et al. 2009). Coincident with this diatom compositional and physiological shift, deep spring mixing did not occur in Lake Tahoe, drastically reducing nitrogen entrainment into the upper layers. The later onset of this shift relative to lakes in more temperate regions is likely due to the lack of strong seasonality, as Lake Tahoe is ice-free year-round and therefore it may take longer for the lake to cross a climate-related threshold.

Although cyclotelloid species were present in the diatom assemblages throughout the 25-year monitoring period, smaller-celled species (particularly *Cyclotella comensis/gordonensis, Discostella glomerata,* and *D. stelligera*; D. Hunter, pers. comm.) have become dominant in the past 10 years (UC Davis (TERC)

2013), contributing over 50 % of the total diatom biomass in most recent years (Winder et al. 2009). In addition, these small planktonic diatoms are now present year-round, dominating during the stratified period in the summer and sometimes extending into the fall (D. Hunter, pers. comm.). In fact, these small-celled cyclotelloid species are now the dominant algae (i.e. not just dominating the diatom community) in Lake Tahoe and their high abundances were largely responsible for recent reductions in summertime lake clarity (UC Davis (TERC) 2013). The recent dominance of these smaller-celled cyclotelloid species was significantly correlated to warming-induced strengthening of thermal stratification, reduced mixing, and notable reductions in regenerated nitrogen supplied from deeper waters to the euphotic zone (Winder and Hunter 2008; Winder et al. 2009). In many ways, this is not surprising as small-celled cyclotelloid diatoms are good competitors for nitrogen and often out-compete other diatoms when nutrient concentrations are lowered, as occurs during strong stratification periods (Carney 1987; Fahnenstiel and Glime 1983; Bradbury 1988; Tolotti et al. 2007). In summer, increases in small-celled cyclotelloid species in Lake Tahoe were particularly pronounced since 2000 CE, (Winder and Hunter 2008) in years when thermal stratification was strongly developed (Winder et al. 2009).

The high surface area to volume ratios of Lake Tahoe's small-celled centric diatoms contribute to a slower sinking velocity and more efficient light harvesting and nutrient uptake mechanisms, giving them a competitive advantage over larger-celled diatoms during increased thermal stratification and reduced water column nutrient redistribution (Winder et al. 2009). In contrast, stratification strength was found to be the only significant predictor of biovolume change for the largest sized diatom fraction from Lake Tahoe, with significantly higher biovolume in years with stronger turbulent mixing. Winder et al. (2009) argue that it is unlikely that the recent dominance of small-celled cyclotelloid taxa in Lake Tahoe was triggered by changes in external nutrient inputs because, had this been the case, diatom size structure would have remained unchanged in the deep water strata near the nitrocline where nutrient supply was sufficient (Winder et al. 2009). Phosphorus concentrations changed only slightly in Lake Tahoe during the monitoring period (with declines since the 1980s) and, although small-celled cyclotelloid taxa had, by far, the highest biovolume in the upper water strata of Lake Tahoe, smaller-sized diatoms also increased (albeit to a lesser degree) in the deeper layers, suggesting that external nutrient inputs were not important for this diatom shift (Winder et al. 2009). Furthermore, a significant negative relationship between water column nitrogen concentrations and small-celled cyclotelloid taxa indicates that the recent success of small-celled species of *Cyclotella/Discostella* in the past ~10 years cannot be explained by increased availability of nitrogen (internal or external), and must therefore be explained by other mechanisms (Winder et al. 2009). Based on their detailed analysis of 25 years of monitoring data, Winder et al. (2009) concluded that increases in small *Cyclotella/Discostella* taxa were related to warming-mediated changes in physical water properties and related limnological changes consistent with a growing body of research in the paleolimnological literature.

Nitrogen hot spots with minimal warming

If atmospheric nitrogen deposition is responsible for the recent taxon-specific shifts (i.e. *Cyclotella–Fragilaria–Aulacoseira*) reported in the literature, we would expect to see increases in small cyclotelloid taxa in regions where nitrogen deposition is reported to be high in so-called "hot spots", but where recent temperature increases have been dampened. However, multiple studies have shown that this is not the case. For example, the Tibetan Plateau is a region with relatively high levels of atmospheric nitrogen deposition and is considered sensitive to recent warming trends, but the complexity and heterogeneity of this mountain region results in high variability in its response to climate. In Dongerwuka Lake in the Nianbaoyeze Mountain region of eastern Tibet, minimal change over the past ~600 years was observed from a suite of paleoecological proxies (tree-rings, pollen, diatoms) as well as in instrumental records (Wischnewski et al. 2013). Dongerwuka Lake has a small watershed that is mainly fed by snow-melt and precipitation and is ice-free during the summer, and is therefore not cut off from the delivery of atmospheric inputs. This lack of change was consistent with the presence of localized cooling within south-eastern and eastern Tibetan Plateau. This same trend of little change over time was found in several diatom records from the eastern Tibetan Plateau (Wischnewski et al. 2013) and from the south-eastern Tibetan Plateau (Wischnewski et al. 2011a, b). Interestingly, all of these diatom records from this region have been dominated by *Cyclotella ocellata* Pantocsek throughout the entire record to the present, but with very little change in relative abundances. This lack of change in all independent proxies (diatoms, pollen and tree rings) is consistent with a lack of warming in this region. However, this is a region that is known to have experienced substantial increases in atmospheric nitrogen deposition in the latter half of the twentieth century as a result of increased agricultural activities and fossil fuel combustion (Liu et al. 2013; Jia et al. 2014). The minimal change in cyclotelloid species in eastern and southeastern Tibetan Plateau lakes, in spite of large increases in regional inorganic nitrogen deposition, provides strong evidence that nitrogen (even when added in large amounts) has not initiated a change in the relative abundances of cyclotelloid taxa

Examining trends in relative abundances of cyclotelloid species and measured nitrogen

We further explore the relationship between increases in small cyclotelloid diatom species and nitrogen by examining trends in the relative abundances of these taxa in modern lake sediments and measured nitrogen concentrations. We use data collected from lakes in the Canadian subarctic (Rühland et al. 2003b) and from south-central (Muskoka-Haliburton) (Hadley et al. 2013) and north-western (Enache et al. 2011) Ontario, Canada. In all lakes, the most prominent cyclotelloid species were *Discostella stelligera* and *D. pseudostelligera* (grouped into *D. stelligera* complex). The relative abundances of *D. stelligera* from all regions were plotted along gradients of measured total nitrogen (TN) and total inorganic nitrogen (TIN) to allow for comparisons within and among regions (Fig. 5). Nitrogen data were collected and analysed using standard Ontario Ministry of the Environment and Climate Change (temperate lakes) and Environment Canada (subarctic lakes) field and laboratory methods. TN and TIN were calculated as the mass sums of TKN and NO_3/NO_2, and NH_4/NH_3 and NO_3/NO_2, respectively

The distribution of *D. stelligera* across a gradient of measured TN from datasets in the Canadian subarctic, northwestern (ELA), and south-central Ontario shows a clear trend of higher *D. stelligera* relative abundances in lakes on the lower end of the nitrogen gradient, with the highest relative abundances found at TN concentrations $\sim 350\ \mu g\ L^{-1}$ (Fig. 5a). However, TN commonly includes a large organic fraction that may not be readily bioavailable, and thus it has been argued that TIN (or DIN) is a preferable measure when assessing nutrient requirements in algae (Bergström 2010). In contrast to TN, *D. stelligera* showed no relationship to TIN in lakes in these regions, with relative abundances exceeding 50 % in all regions, despite large difference in DIN concentration among and within regions (Fig. 5b). These spatial data suggest that cyclotelloid species may be insensitive to changing TIN concentrations, and recent increases in these planktonic diatoms are unrelated to changes in the availability of nitrogen (regardless of its source). Although we do not dispute that atmospheric nitrogen has played a role in determining the trajectory of some lake systems, there is little evidence to support increased atmospheric nitrogen availability as a driver of the recent *Cyclotella–Aulacoseira–Fragilaria* diatom shift.

Nutrients and climate: Increases in *Asterionella formosa* and other pennate planktonic diatoms

As we have mentioned in earlier sections, in addition to the recent success of small cyclotelloid species in non-acidified and non-enriched lakes worldwide, other planktonic diatoms have been observed to increase during the recent period of warming. Increases in pennate planktonic diatoms, including some *Asterionella*, *Fragilaria*, and *Tabellaria* taxa, have been reported from a variety of locations around the world including the North American Rocky Mountains (Baron et al. 2000; Wolfe et al. 2001, 2003; Saros et al. 2003, 2005; Hobbs et al. 2010; Hundey et al. 2014), the Spanish Pyrenees (Catalan et al. 2002b), the Polar Urals (Solovieva et al. 2005), temperate Canada (Rühland et al. 2010; Enache et al. 2011; Hadley et al. 2013), subarctic Canada (Rühland et al. 2013), the Canadian High Arctic (Stewart et al. 2008), Austria (Thies et al. 2012), Norway (Hobæk et al. 2012), Italy

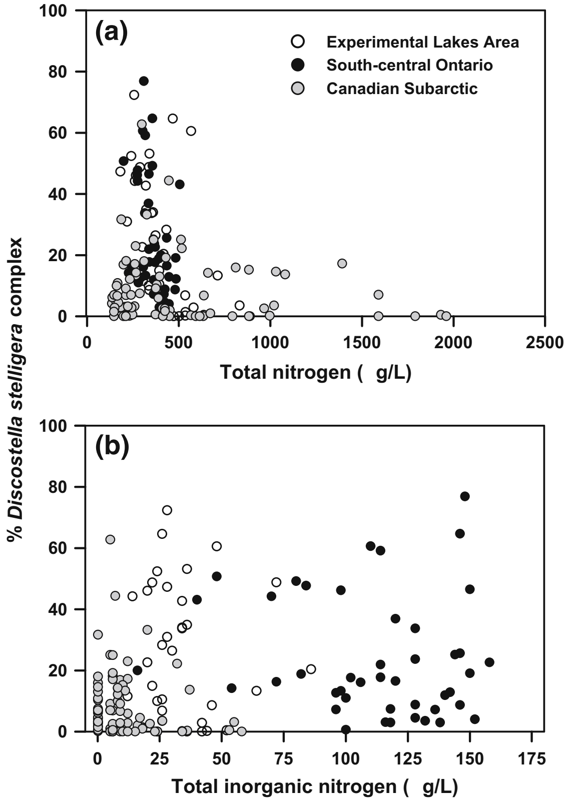


Fig. 5 Relationship between relative abundances of the *Discostella stelligera* complex (*D. stelligera* and *D. pseudostelligera*) with: **a** lakewater total nitrogen (TN) and **b** lakewater total inorganic nitrogen (TIN) concentrations from surface sediment (diatoms) and water chemistry datasets including the Experimental Lakes Area (northwestern Ontario) (Enache et al. 2011), south-central Ontario (Hadley et al. 2013), and the Canadian Subarctic (Rühland et al. 2003b)

(Guilizzoni et al. 2012), northeast China (Wang et al. 2012a; Panizzo et al. 2013), as well as the tropical Andes (Michelutti et al. 2015).

Asterionella formosa is commonly reported to be a spring and fall bloomer when turbulence and nutrient supplies in the water column are high (Ptacnik et al. 2003; Wang et al. 2012a; Morabito et al. 2012; De Senerpont Domis et al. 2013), with peaks in abundance often at the onset of thermal stratification and declines in growth thereafter as nutrients become limited. However, these taxa have also been observed to increase during the summer following thermal stratification (Becker et al. 2008), and may remain dominant until late autumn, residing in deeper water near the thermocline (Sommer et al. 1986; Rimet et al. 2009) where hypolimnetic nutrients can be more readily utilized. Although *Asterionella formosa* is commonly found in more nutrient-enriched lakes (Reynolds et al. 2002), it is also reported to have a wide range of nutrient tolerance (Rimet et al. 2009), and, as demonstrated in the examples below, increases in the relative abundance of *Asterionella formosa* and other pennate planktonic taxa may occur in the absence of nutrient enrichment.

The role of nitrogen in the US Rocky Mountains

Paleolimnological records from alpine lakes in the US Rocky Mountains that are proximal to large sources of pollution show striking, recent (post-1950) increases in pennate, planktonic diatoms, particularly *Asterionella formosa* (but also *Fragilaria crotonensis*), often replacing small cyclotelloid species that previously dominated the diatom assemblages (Wolfe et al. 2003; Saros et al. 2005; Hobbs et al. 2010; Saros et al. 2011). In a few lakes, this shift was at the expense of benthic fragilarioid and heavily silicified *Aulacoseira* taxa (Wolfe et al. 2003). Warmer temperatures at the turn of the century were believed to be a main factor explaining the dominance of small cyclotelloid taxa (Hobbs et al. 2010), but continued warming and the influx of nitrogen in the post-1950s was reported to be the main trigger for the shift to dominance of the newcomers *A. formosa* and *F. crotonensis* in the most recent sediments of these alpine lakes (Wolfe et al. 2003; Saros et al. 2005; Hobbs et al. 2010; Saros et al. 2011; Hundey et al. 2014). In these US Rocky Mountain lakes, recent sources for increased delivery of nitrogen included glacier meltwaters (Saros et al. 2010), and both atmospheric nitrogen and phosphorus as a consequence of increased agricultural and industrial pollution in the surrounding lower elevations (Hundey et al. 2014).

In the Uinta Mountains (Utah), population growth and intensified anthropogenic activity such as agriculture and mining in the surrounding lower elevations has resulted in recent increases in atmospheric deposition of both nitrogen and phosphorus in these high-elevation lakes (Hundey et al. 2014) that pre-date regional temperature increases by a few decades. Paleolimnological records from this alpine region reported highly variable diatom responses in terms of the nature and magnitude of change among six study lakes (Hundey et al. 2014). For example, in some lakes, *A. formosa* and small cyclotelloid species often appeared and increased at approximately the same time (~1980s). However, in other lakes, small cyclotelloid taxa dominated the assemblages and showed little change over time, whereas *A. formosa* appeared in notable abundances for the first time ~1950. In another lake, small cyclotelloid species were not present, but *A. formosa* was dominant throughout the core, with a subtle decline in abundance at the turn of the twentieth century. Finally, in another lake, *A. formosa* and *Fragilaria tenera* increased and replaced small cyclotelloid taxa as the dominant taxa in the post-1950 sediments (Hundey et al. 2014). The authors suggested that the differences in the sensitivity and the nature of diatom shifts reported from these lakes were likely related to differences in catchment characteristics (size, vegetation, etc.), as well as temporal and spatial differences in nutrient limitation among these oligotrophic lakes. Given the timing of warming versus increased nutrient deposition, the authors concluded that increased aquatic production and the onset of *A. formosa* in these Uinta Mountain lakes were initially driven by nutrient deposition, and that warming over the past few decades likely exacerbated these trends.

Increases in pennate planktonic diatoms that are unrelated to nutrient enrichment

Similar to the diatom trends observed in nitrogen-limited lakes from the US Rocky Mountains, increases in *A. formosa* and other pennate planktonic diatoms have also been found in relatively remote and undisturbed regions throughout the Northern Hemisphere (Catalan et al. 2002b; Solovieva et al. 2005; Rühland et al. 2010; Enache et al. 2011; Hyatt et al. 2011; Hadley et al. 2013; Rühland et al. 2013; Wang et al. 2012a, b; Panizzo et al. 2013) and from alpine regions of the Southern Hemisphere (Michelutti et al. 2015; Michelutti et al. unpublished data). In these examples, warming-related changes in lake properties have been suggested as a trigger for their appearance (Catalan et al. 2002b; Solovieva et al. 2005; Rühland et al. 2010; Enache et al. 2011; Hyatt et al. 2011; Hadley et al. 2013; Thies et al. 2012; Rühland et al. 2013; Wang et al. 2012a, b; Panizzo et al. 2013; Michelutti et al. 2015). Importantly, many of these studies have found little evidence to link the recent success of *A. formosa* to increased availability of atmospheric nitrogen (Solovieva et al. 2005; Rühland et al. 2010; Johnson et al. 2012; Wang et al. 2012a; Hadley et al. 2013), as nitrogen deposition has remained unchanged or has been declining over time in these systems. In contrast to the US Rocky Mountain lakes, some of these studies also documented increases in these pennate planktonic species concurrently with increases in cyclotelloid species taxa (Catalan et al. 2002b; Stewart et al. 2008; Rühland et al. 2010; Enache et al. 2011; Hadley et al. 2013; Michelutti et al. 2015). Other lakes show small cyclotelloid taxa replacing *Asterionella formosa* and *Fragilaria crotonensis* in the most recent years (Clerk et al. 2000; Little et al. 2000; Winder et al. 2009). Similar to increases in small cyclotelloid species, increases in these long, pennate planktonic diatoms are often at the expense of benthic fragilarioid taxa and heavily silicified *Aulacoseira* taxa.

Increases in pennate planktonic diatoms in higher nutrient lakes that have warmed

Many of the lakes reporting recent increases in *Asterionella formosa* and *Fragilaria crotonensis* are affected by multiple environmental stressors (Hyatt et al. 2011; Hadley et al. 2013), and their increase may be a response to a combination of stressors, of which climate plays an important role. For example, in Lake of the Woods (Ontario), nutrient loading (including atmospheric nitrogen) has remained unchanged or has declined during the period of substantial increases in air temperatures and declines in lake ice duration, concurrent with increases in *A. formosa* and *F. crotonensis* (Rühland et al. 2010; Hyatt et al. 2011). However, in bays with naturally higher nutrient concentrations, the response to warming was characterized by increases in both pennate planktonic taxa and small cyclotelloid taxa, whereas small cyclotelloid taxa increased more markedly in the oligotrophic Whitefish Bay. Similarly, widespread increases in both *A. formosa* and *F. crotonensis* were reported across lakes in south-central Ontario, but were of larger magnitude in the more nutrient-rich lakes from the region (Enache et al. 2011; Hadley et al. 2013).

In summary, the recent and widespread occurrence of *Asterionella formosa* and other pennate planktonic diatoms can perhaps be best explained by both higher nutrients, such as reported in oligotrophic lakes of the US Rocky Mountains, as well as by warming-related changes to lake properties, as is reported in regions where there is no evidence of nutrient increases. What is common to the examples cited above is that these taxa are able to out-compete other species for light and nutrient capture when they are limited, and that they are more competitive under thermally stable conditions, provided that nutrient concentrations are sufficient. The emerging trend of increases in elongate planktonic diatoms from such a variety of lakes and lake settings, over the period of recent climatic warming but also in a period of multiple environmental stressors, is certainly an important area for future research that may challenge some commonly held views on the ecology and distributions of these important taxa.

Conclusions

The responses of planktonic and periphytic diatoms to warming are often complex. Assessing possible mechanisms for a given assemblage shift requires careful consideration of the ecology and physiology of the species involved, as well as an understanding of the historical and limnological context of the aquatic system being investigated. We conclude that warming-mediated changes in lakes throughout the Northern Hemisphere, including changes to the ice regimes and the thermal structures of water columns, have led to major diatom community reorganizations. Based on the weight-of-evidence approach used in this review, we conclude that anthropogenic climate change is the main driver that has led to crossing important ecological thresholds, resulting in the recent success of small planktonic diatoms in many non-enriched, non-acidified lakes. When considered carefully, taxon-specific diatom shifts can potentially provide a powerful fingerprint for climate-related regime shifts. In summary, we conclude that:

- Climate has significant direct and indirect effects on algal species composition, facilitated through changes in fundamental aquatic ecosystem processes.
- Recent anthropogenic warming, and the linked chain of causal factors, such as strength, frequency and duration of lake mixing/turbulence and thermal stratification, and/or the availability of light and nutrient resources, have played a key role in influencing diatom community composition and dynamics, as well as diatom size structure in lakes.
- In general, diatom responses to warming occur earlier in sensitive Arctic ponds, but as temperature-related thresholds are exceeded at lower latitudes, algal community turnover can be equally pronounced in temperate lakes.
- The nature and timing of diatom responses to climate change may vary spatially by latitude and altitude, with differences in the sensitivity of a given lake to environmental change also dependent (and explainable) on lake type, as well as site-specific, local, and regional characteristics.
- Direct monitoring data, downcore paleolimnological trends and surface-sediment calibration data from the majority of studies reviewed do not support the notion that recent increases in cyclotelloid species are related to increased availability of atmospheric nitrogen.
- Recent increases in elongate planktonic diatoms, especially *Asterionella formosa*, can perhaps be explained by both the addition of nutrients, such as in some oligotrophic lakes of the US Rocky Mountains, as well by warming-related changes to lake properties, as reported in regions where there is no evidence of nutrient increases, because both of these scenarios may enhance this taxon's competitive abilities for light and nutrient capture under thermally stable conditions, provided that nutrient availability is sufficient.
- Climatically-induced ecological thresholds have already been crossed in many lakes, but if the rate and magnitude of change continues, it is likely that new, and often unexpected, ecological thresholds will be surpassed.
- We are entering unchartered territory as we encounter new climate regimes, the effects of which can cascade throughout the entire ecosystem. Climate change is the new threat multiplier (Smol 2010), and therefore lake managers must consider the synergistic, additive or antagonistic effects of a warming climate when assessing other environmental stressors.

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