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The power of the past: using sediments to track the effects of multiple stressors on lake ecosystems

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SUMMARY

1. One of the greatest challenges faced by limnologists, as well as most ecologists and environmental scientists, is finding data with time scales appropriate to their questions. Because of the general lack of reliable long-term monitoring data, it is often difficult to determine the nature and timing of ecosystem changes. In lieu of direct monitoring data, palaeolimnologists have developed a variety of physical, chemical and biological approaches to track past changes in aquatic ecosystems using proxy data archived in lake and river sediments. This article summarises a few of our recent palaeolimnological programs that have studied the effects of multiple stressors on lake ecosystems and demonstrates how palaeolimnological approaches can circumvent this common problem of data availability.
2. Lakewater calcium concentrations are declining in many softwater lake regions because logging and acid precipitation have lowered calcium levels in soils. In many cases, however, the onset of lakewater calcium decline predates direct observation, and so documenting the effects on freshwater ecosystems may be complex. By combining laboratory, field and palaeolimnological approaches, it is now evident that keystone taxa (e.g. *Daphnia* spp.) have been severely affected by these calcium declines.
3. Some of the most common complaints received by lake managers concern the smell and taste of water. Although the root causes of taste and odour problems vary, compounds released by certain species of algae are often responsible. In nutrient-poor or mesotrophic lakes, colonial chrysophytes are often the culprits, including scaled taxa of the genus *Synura*. Palaeolimnological approaches can be used to assess the various multiple stressors that influence the abundance of these phytoplankton.
4. *Thematic implications*: recent climatic warming is affecting a wide range of lake ecosystems in diverse and often complex ways across vast geographical regions, and this has added to the complexities of limnological responses to other stressors. As more palaeolimnological studies are completed, meta-analyses of sedimentary profiles can now be used to help disentangle the effects of climate warming from other environmental variables to determine how various components of lake ecosystems are responding to these multiple stressors.

Keywords: calcium, climate change, contaminants, lake sediments, long-term environmental change, multiple stressors, palaeolimnology

Introduction

Water is essential to life, yet it is widely recognised that aquatic resources are under threat from multiple environmental stresses. We live in a constantly

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changing environment, where a plethora of impacts are affecting the quality, quantity and ecological integrity of our water supplies. Although a wide spectrum of environmental changes are attributed to natural causes, human activities have markedly altered our planet.

The study and management of lakes and rivers share many of the challenges faced by other branches of the ecological and environmental sciences, not least of which is the lack of meaningful long-term monitoring data. For example, typical questions posed by environmental scientists and managers include:

1. What were the pre-disturbance conditions (i.e. Is there really an environmental problem? If so, then what are realistic mitigation targets, or how should we best direct our efforts to address or adapt to this problem?)

2. What is the range of natural variability? (i.e. Are changes recorded in monitoring data really tracking a directional trend, or is it just 'environmental noise'?)

3. If conditions have changed, then by how much? How quickly? When? What are the causes of these changes?

Each of the earlier questions has a temporal component. However, having little or no monitoring data constantly challenges environmental scientists. In fact, in most cases, data collection only commences *after* a problem has been identified, thus constraining our ability to deal effectively with environmental issues. What little monitoring data may be available are often of insufficient length and quality for reliable assessments or interpretations. For example, my analysis of publications in an international journal dedicated to environmental monitoring and assessment revealed that about two-thirds of the articles based their conclusions on monitoring windows that were of 1 year or less in duration, whilst about 90% were under 3 years in duration (Smol, 2008). The scarcity of long-term data sets was reinforced by Rosenzweig *et al.* (2008), who concluded that there were fewer than 50 long-term (defined as >35 years) data sets available for freshwater systems globally. Such short-time frames are rarely adequate to address the numerous and complex environmental questions faced by society today.

Fortunately, a variety of natural archives (e.g. tree rings, ice cores and ocean corals) preserves indirect records (or proxy data) of past environmental and ecological changes (Bradley, 1999). This study focuses on palaeolimnology, which uses the physical, chemical and biological information stored in lake and, to a lesser extent, river sediments to reconstruct past environmental conditions, from which past trajectories of water quality and other environmental changes can be reconstructed.

Palaeolimnological approaches are now being used to address a wide spectrum of water quality issues (e.g. Smol, 2008), and such studies continue to be integrated into a diverse array of environmental assessments. For example, the European Water Framework Directive (WFD 2000/60/EC) is now the general policy document for European water management (European Commission, 2000, 2003). The goal of the Directive, established in 2000, is that European waterbodies should be returned to 'good ecological status' by the years 2015–27. According to the WFD, this goal of good ecological status is characterised by 'low levels of distortion resulting from human activity, but deviate only slightly from those normally associated with the surface water body type under undisturbed conditions'. Hence, the key term 'undisturbed conditions', and thus the identification of reference conditions becomes a cornerstone of this European Commission initiative. As summarised by Bennion & Battarbee (2007), palaeolimnological approaches have much to offer to these new initiatives, such as in defining reference points, assisting in the ecological classification and identification of reference sites and in monitoring. Palaeolimnological approaches can also be used to track recovery trajectories from, for example, acidification (e.g. Dixit, Dixit & Smol, 1989a, 1992a,b; Cumming *et al.*, 1994; Smol *et al.*, 1998). Many new research opportunities are on the horizon.

Just as researchers and managers continue to recognise the need for long-term data, there is also a growing appreciation of the complexity of environmental problems. Multiple anthropogenic stressors pose significant challenges to neolimnologists; similarly, palaeolimnologists must acknowledge and wrestle with the confounding influences of several environmental stressors occurring simultaneously. For example, climatic changes associated with global warming are now occurring in many regions of the planet; the effects of a warmer climate will influence water quality as well as any subsequent mitigation or adaptation strategies (e.g. Smol, 2008).

The overall palaeolimnological approach is based on a simple premise (Cohen, 2003; Smol, 2008). In most lake systems, sediments accumulate in a relatively coherent manner over time, with more recently deposited sediments overlying older ones. Of course, problems may occur in some basins, such as significant mixing of the sediment profile or differential preservation of certain indicators (reviewed in Smol, 2008). Nonetheless, in most systems, these problems can be identified and partly rectified using, for example, multiple indicators or re-assessing the temporal resolution available from the sediment profile being investigated. Incorporated in the sediment matrix is a surprisingly large and diverse library of morphological and biogeochemical information or proxy data which can be used to reconstruct past limnological conditions. Methodologies continue to improve but are now generally standardised (e.g. Last & Smol, 2001a,b; Smol, Birks & Last, 2001a,b; Francus, 2004; Leng, 2006), and meta-analyses of large palaeolimnological datasets are now possible (e.g. Smol *et al.*, 2005; Rühland, Paterson & Smol, 2008). Moreover, multi-disciplinary and multi-proxy approaches now dominate the palaeolimnological literature. In contrast to many other fields of science, where there appears to be a movement to smaller articles that attempt to publish the least publishable units, palaeolimnological studies have followed an opposite trend. For example, an analysis of the length of articles published in the international *Journal of Paleolimnology* shows that an average contribution to that journal has steadily increased in size over recent years, as multi-proxy studies have become the norm.

This overview will focus on applied biological palaeolimnology, which I broadly define as the use of sedimentary approaches to study the effects of human impacts on lake ecosystems. Of course, much progress has been made in many other aspects of palaeolimnology (Cohen, 2003), which are not the focus of this article. The three examples I have chosen reflect environmental problems at local to regional to global scales. The two overriding themes in the examples I cite are the challenges faced by palaeolimnologists who must deal with multiple stressors to set realistic mitigation targets (i.e. defining pre-disturbance conditions) and to reconstruct environmental trajectories (i.e. determining how humans have affected aquatic ecosystems over long time frames). In keeping with the overall theme of this conference and this special issue of *Freshwater Biology*, my examples will primarily reflect my perspectives and the work with which I am most familiar with. A simple perusal of any recent issue of, for example, the *Journal of Paleolimnology* will reveal many other diverse studies where the effects of multiple stressors are being investigated on broad spatial and temporal scales.

'Aquatic osteoporosis[1]': exploring the effects of long-term calcium declines on lake ecosystems

Many of the approaches currently used by applied palaeolimnologists were either developed or improved during the so-called 'acid rain debates' of the 1980s and the early-1990s. Lake acidification is a serious international problem, and the questions posed by scientists and policy makers almost always have temporal components and are therefore well suited for palaeolimnological investigation. For example, key questions included: have lakes acidified? If so, when and by how much? What were the 'critical loads' of acidic deposition (i.e. loads which would produce an unacceptable level of ecological damage, usually expressed as the percentage of lakes that would lose, or not be able to support, valued fish life)? Because the limnological effects of human-influenced acidic precipitation pre-dated most monitoring programs, there was an immediate need for the development and application of indirect proxy methods to reconstruct changes in lakewater pH (and related limnological variables).

Much has been written about the successful applications of palaeolimnological approaches to track lakewater pH trajectories (see Chapter 7 in Smol (2008) for a recent review), and several palaeo-acidification studies continue to the present day (e.g. Dixit ***et al.***, 2007; Guhrén, Bigler & Renberg, 2007; Quinlan *et al.*, 2008). Although the problem of acid rain is relatively well understood and represents at least a partial environmental success story, some serious and unexpected legacies of acidification are now becoming apparent. One such problem, which is at least partly related to acidification, is the long-term decline in lakewater calcium concentrations.

Calcium is a macronutrient that is required, to varying degrees, by all living organisms. Most

[1]The term 'aquatic osteoporosis' was coined by Michael Turner, a co-author on the Jeziorski *et al.* (2008a) paper.

limnological studies dealing with nutrients have understandably focused on phosphorus and nitrogen concentrations; however, recent monitoring data suggest that declining calcium levels warrant attention in some North American and Scandinavian softwater lakes (e.g. Stoddard *et al.*, 1999; Skjelkvåle *et al.*, 2005; Jeziorski *et al.*, 2008a; Watmough & Aherne, 2008) and likely elsewhere.

The main calcium reservoir for a lake is its catchment bedrock and soils (Fig. 1a), although airborne calcium-rich dust may supplement local sources (Driscoll *et al.*, 1989; Hedin *et al.*, 1994). The mechanisms associated with calcium depletion in lakes are driven by reductions in the exchangeable calcium levels of catchment soils (Likens, Driscoll & Buso, 1996) via a number of biogeochemical mechanisms, which may be linked to multiple stressors that vary regionally in importance. For example, if leaching induced by acidic deposition exceeds replenishment of calcium from weathering and atmospheric deposition, soil base cation concentrations will decrease, as is the case in many watersheds with thin soils underlain by weathering resistant bedrock (Watmough *et al.*, 2005). It is therefore likely that calcium levels actually increased in some lakes during the early stages of acidic deposition, because more calcium ions would have been released from the catchment at that time (Fig. 1b). However, with continued mobilisation and depletion of watershed calcium stores, export from the catchment will eventually diminish (Fig. 1c).

Acidic deposition is not the only stressor affecting lakewater calcium levels (Fig. 1c). Forest re-growth following timber harvesting can also place pressure on the exchangeable soil Ca pool, further diminishing the supply available for export to receiving waters (Watmough, Aherne & Dillon, 2003; Watmough *et al.*, 2005). Declines in calcium-rich dust may further exacerbate lakewater depletion (Hedin *et al.*, 1994).

For many lake regions, such as those draining calcareous bedrock and/or thick soils, lakewater calcium concentrations are above threshold levels for biota. However, for lakes on calcium-poor bedrock, such as the vast numbers of Canadian softwater lakes on the Precambrian Shield, as well as certain lake regions in the U.S.A. and Northern Europe, calcium deficiency is a serious threat. Once again, given the lack of long-term monitoring data, the investigation of calcium declines in lakes was an ideal candidate for

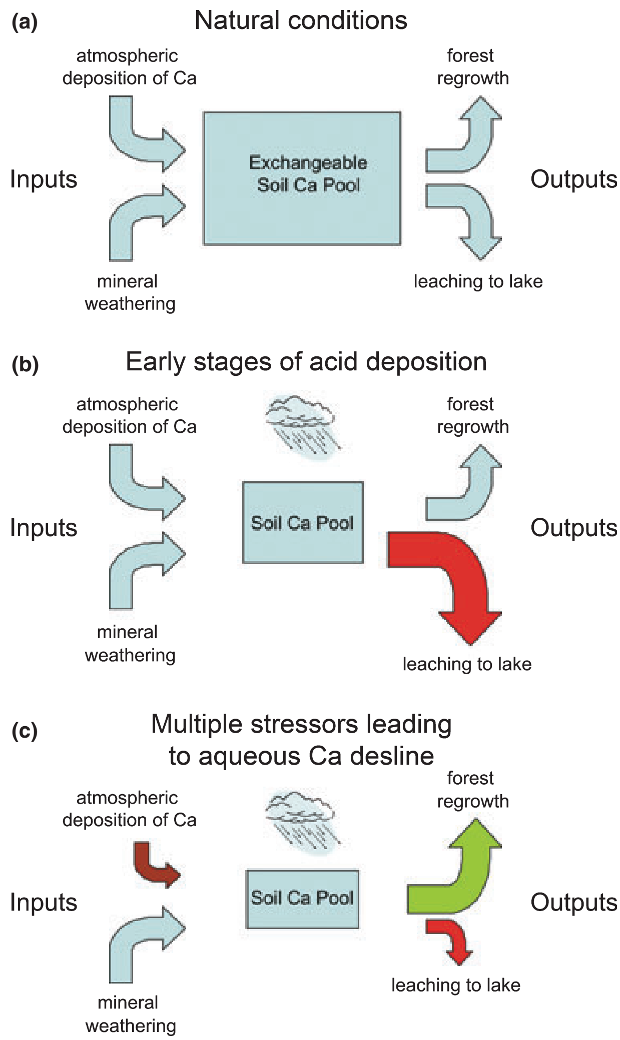

Fig. 1 Schematic diagram showing some of the multiple influences affecting calcium inputs and outputs. (a) Prior to human disturbances, mineral weathering and atmospheric deposition of calcium-rich dust contributed to the exchangeable soil cation pool. The major outputs were forest regrowth and leaching of calcium to lakes and rivers. (b) During the early stage of acidic deposition, leaching of calcium from the catchment would be accelerated, and the exchangeable soil cation pool would steadily be diminished. (c) Eventually, with continued acidic deposition, the calcium pool in granitic bedrock regions would be diminished to the point that calcium leaching is greatly reduced. In addition, the effects of multiple stressors would further diminish calcium supply to lakes. For example, with logging and timber removal, additional calcium is lost from the ecosystem, and as trees re-grow, more calcium is removed from the soil for tree growth. Also, as summarised by Hedin & Likens (1996), calcium-rich dust is now declining in many regions, as roads are paved, and agriculture is less prevalent in some regions, thus further exacerbating the problem.

palaeolimnological investigation, if suitable indicators could be identified.

Our palaeolimnological study of calcium depletion was based on a foundation of a decade of laboratory and more than three decades of field-based studies. The potential problem of calcium decline began to emerge from limnological surveys (e.g. Hedin *et al.*, 1994; Likens *et al.*, 1996; Stoddard *et al.*, 1999). Although calcium levels may have been dropping, the biological significance of these declines required further study. Within a broader analysis of metal levels in crustacean zooplankton, Yan, Mackie & Boomer (1989) first noted that calcium concentrations of daphniids were significantly higher than in other taxonomic groups. A decade later, Alstad, Skardal & Hessen (1999) used experimental approaches to study the calcification and calcium content of *Daphnia magna*. They suggested that this keystone pelagic herbivore may have been calcium limited in some systems, because they obtained the majority of their calcium directly from the lakewater and must replenish it throughout their life cycle, as little is reclaimed before moulting. Shortly afterwards, Hessen, Alstad & Skardal (2000) defined the threshold calcium levels required for the survival of *D. magna*, followed by Waervagen, Rukke & Hessen (2002) who completed a regional survey of Norwegian lakes and showed that aqueous calcium concentrations influenced the distribution of *Daphnia* species. These studies, combined with new observations of calcium declines in Ontario lakes (e.g. Keller, Dixit & Heneberry, 2001), prompted a new series of studies led by Norman Yan (York University, Ontario) to define the calcium thresholds of common cladoceran taxa from Canadian waters. First, Jeziorski & Yan (2006) completed a field study examining the calcium concentrations of eight crustacean zooplankton species from nine lakes on the Canadian Shield. They found species identity to be more important in determining crustacean zooplankton calcium concentration than either lakewater calcium concentration or seasonality. Once again, *Daphnia* spp. had much higher calcium levels than any of the other species examined (i.e. about an order of magnitude higher than *Bosmina* spp.). This was followed by a laboratory-based study (Ashforth & Yan, 2008) examining the calcium needs of *Daphnia pulex*, the species with the highest calcium content of the eight taxa examined in Jeziorski & Yan (2006). Ashforth & Yan (2008) identified a reproductive threshold of 1.5 mg Ca/L for this taxon under laboratory conditions. *Daphnia* taxa in general, and large species such as *D. pulex* in particular, were especially sensitive to low lakewater calcium concentrations.

It was becoming apparent that the species composition of fossil cladoceran assemblages might be a guide to tracking threshold changes in lakewater calcium concentrations. Not only did *Daphnia pulex* have a well-defined calcium threshold, but it also represented a keystone species in many North American lakes. Moreover, its laboratory-derived threshold value of 1.5 mg L^{-1} (Ashforth & Yan, 2008) was already higher than the calcium concentrations currently measured in many Ontario lakes (Jeziorski *et al.*, 2008a). Of course, many variables (e.g. predation, etc.) may affect cladoceran populations. However, with a careful choice of study lakes (e.g. comparing lakes with similar water chemistry characteristics but different predators) and using comparative palaeolimnological approaches, these confounding factors can be isolated and studied.

Like most environmental issues, the emerging problem of calcium decline was only identified after-the-fact as many softwater lakes had already passed critical biological thresholds. For example, a survey of 770 softwater Ontario lakes (Jeziorski *et al.*, 2008a) revealed that about 1/3 of the survey lakes were already below the 1.5 mg L^{-1} laboratory-based calcium threshold of *D. pulex* and 2/3 of these lakes were approaching that threshold (i.e. <2.0 mg L^{-1}). The next step would therefore be to try and track these important ecosystem changes and related them to historical conditions using palaeolimnological approaches.

An early attempt to measure calcium levels directly in fossil zooplankton resting eggs proved unsuccessful, because of low calcium concentrations in ephippia (Jeziorski *et al.*, 2008b). However, based on the work reviewed earlier, it was now evident that different cladoceran taxa had differing calcium thresholds. Notably, species such as *Daphnia pulex* and related taxa had especially low calcium thresholds and could potentially represent a limnological 'miner's canary', with declining numbers indicating low calcium levels in lakes. As chitinised cladoceran body parts are typically well preserved in lake sediments (Korhola & Rautio, 2001), we reasoned that palaeolimnological profiles could be used to determine when lakes crossed important ecological thresholds.

Jeziorski *et al.* (2008a) employed several lines of evidence to document ongoing biological damage because of 'aquatic osteoporosis' using a comparative palaeolimnological approach in strategically selected North American lakes. First, using ^{210}Pb-dated sediment cores, temporal changes in Ca-rich *Daphnia* species were examined in three widely separated, eastern North America lakes that currently have aqueous calcium concentrations near or below 1.5 mg L^{-1}, the threshold experimentally demonstrated by Ashforth & Yan (2008) to impede *Daphnia pulex* survival. However, each of the three study lakes had a different acidification history. Figure 2 summarises the major taxonomic shifts between the two dominant planktonic cladoceran genera in these lakes: the calcium-rich *Daphnia* and the Ca-poor *Bosmina* spp. Plastic Lake (45°11′N, 78°50′W) is a small softwater lake in south-central Ontario, which has been intensively studied by the Ontario Ministry of the Environment since the 1970s, and so these monitoring data could be used to 'ground truth' any changes recorded in the sedimentary record. The ice-free mean pH of Plastic Lake has been quite stable since the late-1970s at ~5.8, a pH value that has changed little from a diatom-inferred pH (5.7) predating the onset of modern human influence (Hall & Smol, 1996). Although pH has not changed markedly since pre-industrial times, calcium concentration measurements have recently fallen below the *D. pulex* threshold, from ~2.2 mg L^{-1} in 1980 to ~1.4 mg L^{-1} in 2006, with a period of steep decline occurring after 1991. Coincident with the measured decline in calcium, there has been a clear decrease in the relative abundance of daphniid sedimentary remains in Plastic Lake (Fig. 2). These data suggest that the critical calcium threshold in nature may actually be higher than the 1.5 mg L^{-1} value determined under laboratory conditions, thus making the extent of the problem even more widespread.

Jeziorski *et al.* (2008a) completed detailed palaeolimnological studies on two other lakes that presently have calcium concentrations near the 1.5 mg L^{-1} laboratory-based threshold, but which had markedly different acidification histories. A diatom-based palaeolimnological study of Little Wiles Lake (44°24′N, 64°39′W) from Nova Scotia indicated that it was naturally acidic (pH ~5.6) and that, similar to Plastic Lake, pH had remained relatively stable during the period of maximum acid deposition in the 1970s, but the lake had experienced declining calcium (Clair *et al.*, 2001). Meanwhile, a strikingly different acidification history was present in Big Moose Lake

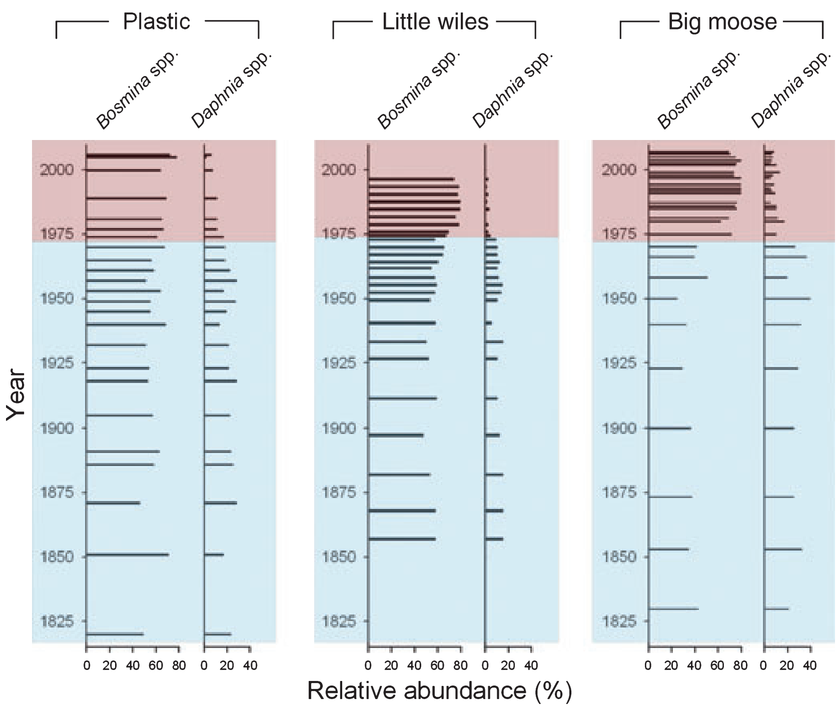

Fig. 2 Changes in the relative abundance (%) of the two dominant pelagic cladoceran zooplankton groups (Ca-poor *Bosmina* spp. and Ca-rich *Daphnia* spp.) among sedimentary zooplankton assemblages from Plastic Lake (Ontario, Canada), Little Wiles Lake (Nova Scotia, Canada) and Big Moose Lake (NY, U.S.A.). The red colouring marks the period of decline in the relative abundances of *Daphnia* spp. The *y*-axis denotes sediment age as estimated by ^{210}Pb analysis. Modified from Jeziorski *et al.* (2008a).

(43°49′N, 74°51′W), a well-studied lake in Adirondack Park (NY, U.S.A.), which had experienced marked acidification in the 1950s (to a pH of 4.6) (Charles *et al*., 1987) and then a subsequent recovery in pH to greater than 5.5 (Driscoll *et al*., 2003). Big Moose Lake continued to experience a decline in calcium, even though acidity levels have been decreasing.

Despite the strikingly different pH trajectories in the three study lakes, similar changes in fossil cladoceran assemblages were recorded in each site (Fig. 2). Calcium-sensitive daphniid remains in the Little Wiles Lake core dropped from ~15–0% during the mid-1970s, the period of calcium decline (Fig. 2) when acidic deposition peaked. A similar pattern of daphniid decline was detected in Big Moose Lake, and populations remain substantially below their pre-impact abundances despite a recovery of pH (Fig. 2). The depleted calcium levels may now represent a 'bottleneck' to the recovery process, preventing the return of daphniid populations despite clear increases in lakewater pH. The conclusions reached in these three detailed stratigraphic studies were supported by a regional 'top–bottom' palaeolimnological assessment of 43 Ontario lakes (DeSellas, 2006), where Jeziorski *et al.* (2008a) compared recent sedimentary cladoceran remains to those deposited prior to European settlement (~1850). The relative abundances of all daphniids have decreased in 60% of the lakes with present-day Ca <1.5 mg L^{-1} and 67% of the lakes with Ca <2.0 mg L^{-1}. Meanwhile, *Daphnia* spp. increased in relative abundances from pre-historical levels in all of the lakes that have a current Ca >2.5 mg L^{-1}. As discussed in Jeziorski *et al.* (2008a) and DeSellas (2006), these cladoceran changes could not be explained by changes in fish predation, nutrient levels or other confounding factors in this lake set. A weight-of-evidence approach strongly implicated lakewater calcium levels as the main causative factor.

Fossil cladoceran assemblages appear to be sensitive indicators of declining calcium levels. Although the mechanisms leading to calcium decline may differ among regions (e.g. acidification, logging; see Fig. 1c), the effects on biota are likely to be similar regardless of the cause. Ca-rich daphniids are some of the most abundant zooplankton in many lake systems, and their loss will significantly impact food webs. Furthermore, it is likely that calcium decline is of concern for other aquatic biota, not just daphniids (Cairns & Yan, 2009). Even some birds, which depend on aquatic biota for their dietary calcium requirements (Scheuhammer, 1991; Scheuhammer *et al*., 1997), may suffer from calcium decline, suggesting that ecological effects may transcend aquatic boundaries. It is quite possible that, rather than being the proverbial 'miner's canary', Ca-rich zooplankton may represent the first miner whose collapse has been noticed. Therefore, potential impacts on a variety of calcium-rich biota, such as mollusks, other crustaceans and vertebrates, warrant further scrutiny.

Exploring the influence of multiple environmental stressors on taste and odour causing chrysophytes

One of the most common complaints received by a lake manager is that the water smells and/or tastes 'bad', often referring to a 'dead fish' or cucumber taste or odour. There are a large number of potential sources for these problems (assuming of course that dead fish can be excluded from the list of culprits!), ranging from industrial pollutants to blooms of certain types of algae. Concerning the latter source, cyanobacteria are more commonly noted in phosphorus-enriched waters, whereas colonial chrysophytes, and especially *Synura petersenii*, dominate the list of problem taxa in nutrient-poor to mesotrophic systems (Nicholls & Gerrath, 1985; Nicholls, 1995). For reasons not fully understood, not all *Synura* blooms release compounds that result in taste and odour problems (Watson, 2004). However, a large population of this taxon is often a precursor to taste and odour problems, and because the factor(s) triggering these blooms are not always apparent, a better understanding of the dynamics of these algae is an important first step to dealing with this common water quality problem.

Complaints regarding taste and odour events are steadily increasing. Yet, without long-term monitoring data, it is not possible to determine whether the putative sources of these problems (e.g. *Synura petersenii* populations in many Ontario lakes) are in fact increasing or if these phytoplankton have bloomed naturally without any direct or indirect human influences. For example, it may be possible that the frequency of complaints is increasing, because cottagers are now frequenting areas that were previously unused, and/or are becoming more sensitive to algal bloom issues in general. In other words, *Synura* blooms may have occurred naturally in these waterbodies but were unwitnessed by potential complainants. Moreover, it is possible that people's standards concerning the smell and taste of water have become more stringent, as complaints are typically from cottagers who live most of the year in urban environments and are therefore more accustomed to, for example, municipal tap water or even bottled water.

Before any mitigation measures can be proposed, certain questions need to be answered, the first of which is simply to determine whether populations of colonial chrysophytes, and especially *Synura petersenii*, are actually increasing in size. If they are, then when did they begin to increase? And if these phytoplankton populations are changing, then can these shifts be linked to human activities, such as acidification, eutrophication, shoreline development, recent climatic change and/or other environmental stressors?

Chrysophytes such as *Synura* spp. are characterised by siliceous, morphologically species-specific scales that are well preserved in lake sediments (Smol, 1980), and so it is possible to reconstruct past population assemblages using palaeolimnological approaches (e.g. Dixit, Dixit & Smol, 1989b; Smol, 1995; Siver *et al.*, 1999). Paterson *et al.* (2004) first approached this multi-stressor problem related to taste and odour issues by examining fossil scale assemblages from a suite of 48 Muskoka-Haliburton (Ontario) Precambrian Shield lakes that were chosen to reflect a wide spectrum of water chemistry characteristics and degrees of human influence (Hall & Smol, 1996; Paterson *et al.*, 2001). The lake set also represented a region where taste and odour complaints had become common. Paterson *et al.*'s (2004) first objective was simply to determine whether the relative frequencies of colonial scaled chrysophytes, such as *Synura petersenii*, were increasing in these waters over the period of possible human impact (i.e. over the last ~150 years). Undertaking a detailed cm-by-cm palaeolimnological study of 48 lakes would require a herculean commitment of person-days and other resources. Therefore, Paterson *et al.* (2004) instead chose a regional 'top–bottom' palaeolimnological approach (similar to part of the Jeziorski *et al.*(2008a) study described earlier), whereby only two sediment samples were analysed for each lake. Chrysophyte scales preserved in the surface one-cm sediment slice were used to characterise current assemblages (i.e. the top sample), and a 1-cm interval of sediment at a minimum core depth of 20 cm was used to represent pre-disturbance conditions (i.e. the bottom sample). In regions such as Ontario, pre-disturbance conditions are often defined as sediments that were deposited before ~1850 AD, and thus pre-date the period of acidic deposition and other anthropogenic disturbances, such as European-style agriculture in most parts of the province. Such regional 'before and after impact' palaeolimnological assessments have been previously used to infer regional changes in acidification and eutrophication (e.g. Cumming *et al.*, 1992a; Dixit *et al.*, 1999; Leira *et al.*, 2006; Dixit *et al.*, 1992a,b; Reavie, Smol & Dillon, 2002; Quinlan & Smol, 2002; Ginn, Cumming & Smol, 2007), and in climate change research (Rühland, Priesnitz & Smol, 2003; Rühland *et al.*, 2008), as well as other applications (Smol, 2008).

Paterson *et al.* (2004) found that scaled chrysophytes, including *Synura petersenii*, have increased markedly since pre-industrial times in over 90% of the study lakes. Clearly, the potential biological source of many taste and odour complaints has been increasing over a time period that strongly suggested direct or indirect anthropogenic influences. The next step would be to search, from a large list of potential stressors, for one or more environmental triggers that could explain these population changes. The answer was not obvious from the top–bottom assessment, as colonial chrysophytes increased in such a wide variety of lakes. For example, historically acidified lakes recorded population increases in *Synura petersenii* and related taxa, but so did lakes that did not acidify. Lakes with intense cottage development had species changes, but so did lakes with no shoreline development that were only accessible using long portage routes. Similar changes were documented in lakes that have been invaded by exotic species such as the predatory Eurasian Cladoceran, *Bythotrephes*, but these same changes were also recorded in lakes with only native species present (Paterson *et al.*, 2004).

The major advantage of a top–bottom palaeolimnological approach is that only two samples are analysed for each sediment core (in addition to those used to assess sample variability), and so a large number of lakes can be studied with relatively little effort. The main disadvantage is that it is a 'snapshot' approach, with no indication of pattern or dynamics of changes between the two time slices being examined. To further explore the nature and timing of the chrysophyte changes, Paterson *et al.* (2004) undertook a detailed study of sediment cores from two lakes and showed that the changes in colonial chrysophytes and especially *Synura petersenii* began between the 1930s to the 1950s, with the most marked changes occurring since the 1980s (Fig. 3). Subsequent analyses of other Ontario sediment cores in our laboratory showed similar trends, including cores collected from the Experimental Lakes Area, in north-western Ontario (C. Chueng, unpubl. data), a region with minimal acidic deposition. It was now evident that the *Synura* increases were initiated in the 20th century and continued to the present time. As noted earlier, factors such as acidification, eutrophication and exotic species invasions were not the likely causes, nor was it likely that local stressors were responsible, given the

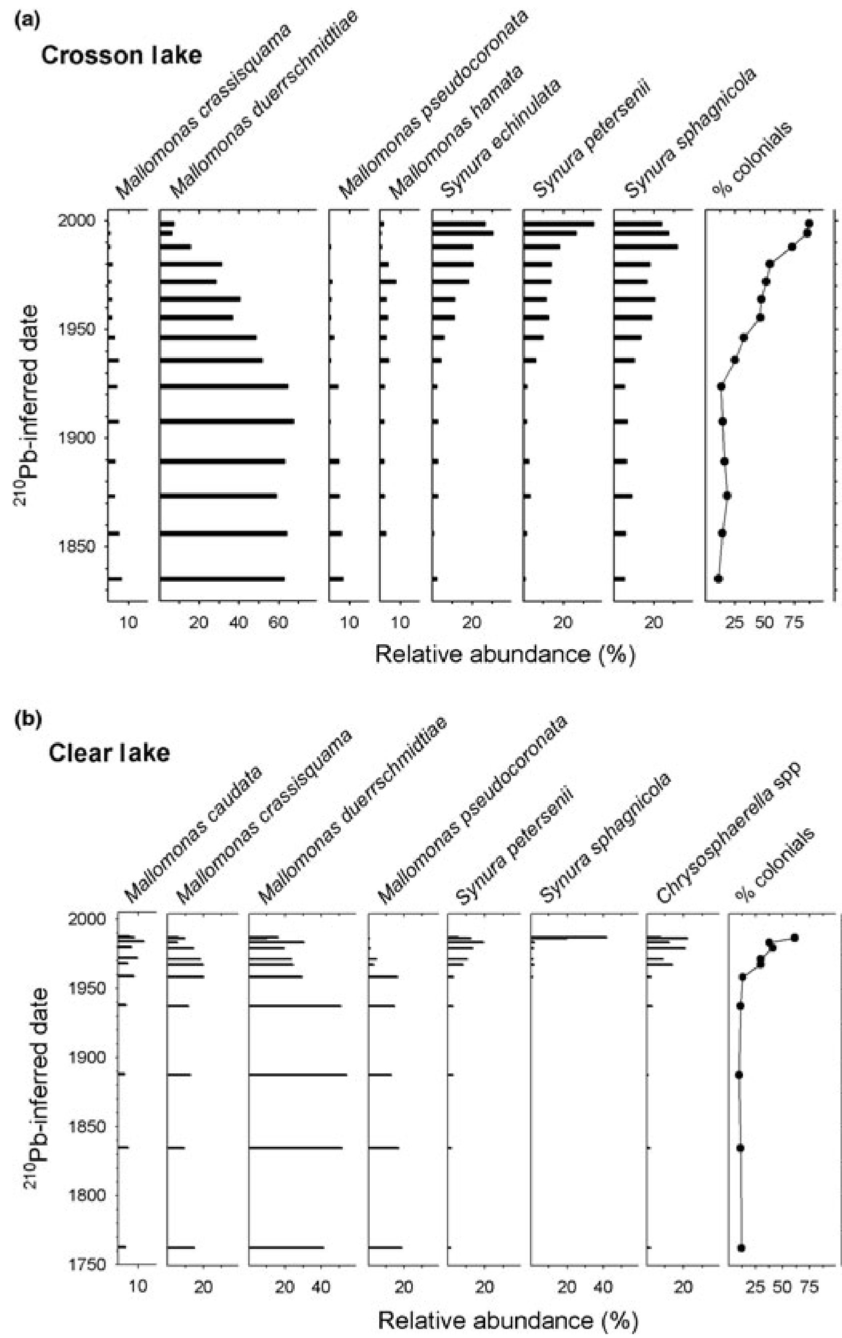

Fig. 3 Changes in the relative abundance (%) of the dominant scaled chrysophyte taxa in Crosson and Clear lakes (Ontario, Canada), showing the increase in colonial chrysophytes, including *Synura petersenii*, in the more recent sediments. The *y*-axis denotes sediment age as estimated by ^{210}Pb analysis. Using sedimentary biogenic silica concentrations, Paterson *et al.* (2004) showed that these were absolute increases in taste and odour causing chrysophytes, and not simply percentage changes between taxa. Reproduced from Paterson *et al.* (2004); used with permission.

regional scope of the species changes. A wider geographical assessment was necessary.

Building on the palaeolimnological and neolimnological work of scaled chrysophytes from Ontario lakes (e.g. Paterson *et al.*, 2001, 2004, 2008), Hyatt *et al.* (2010) examined the relationships between chrysophyte species assemblages and environmental variables from the sediments of over 200 lakes from three broad ecoregions of northeastern North America. When constrained to nine forward-selected environmental variables, canonical correspondence analysis (CCA) showed that lake water pH, ion concentrations and lake depth were the most important variables explaining the distribution of scaled chrysophyte species among the ecoregions. The pre-industrial species assemblages from Ontario were then plotted passively in CCA ordination space to determine the possible reasons for the observed increase in colonial taxa. Changes in species composition (which were dominated by increases in *Synura* taxa, and especially *S. petersenii*) were not closely linked to long-term changes in pH or ion concentrations. Instead, Hyatt *et al.* (2010) concluded that long-term changes in lake thermal properties associated with increasing air temperature, correlated to declines in total phosphorus and dissolved organic carbon concentrations, may have been responsible for the rise in the abundance of colonial chrysophyte species. Interestingly, a recent survey of scaled chrysophytes from the sediments of 52 Nova Scotia and New Brunswick lakes (Ginn *et al.*, 2009) further implicated thermal stratification as a potentially important factor influencing scaled chrysophyte abundances.

To summarise the earlier research, palaeolimnological studies clearly showed that colonial scaled chrysophytes have indeed been increasing in many lakes, over a time frame that suggested direct and/or indirect anthropogenic influences. Using a comparative palaeolimnological approach, various stressors could be evaluated as potential triggers for these changes. Acidification could not be the sole factor, as changes occurred in lakes that did not acidify, and similar (albeit smaller) species changes occurred in the Experimental Lakes Area, where deposition has been very low. Because similar species changes occurred in lakes with watersheds containing little or no anthropogenic activity, as well as in lakes with heavy shoreline development (e.g. agriculture, resort development), cultural eutrophication is not a likely candidate for these algal changes. Shifts in grazers, such as may occur with the arrival of invasive species, were similarly not a viable explanation. We have not fully assessed the aerial transport of pollutants, but contaminants are different across the lake regions we examined. Given the regional nature of the changes, direct or indirect effects of climate warming are currently the most viable explanations for these species changes. The fact that shifts in larger lakes typically occurred later than in smaller ones would be consistent with a climate warming scenario. Moreover, as colonial chrysophytes are highly competitive under conditions of higher thermal stability, recent warming may favour these taxa. Although the definitive cause has not yet been determined with certainty, palaeolimnological approaches have already played an important role in evaluating a number of potentially important stressors that may be affecting these algal populations.

Distinguishing the effects of recent climatic change from other potential stressors on lake ecosystem dynamics

Climate exerts an overriding influence on many lake processes. With recent climatic warming, lake ecosystems will be affected in diverse ways. Given that the period of recent climatic change overlaps the time period when a plethora of other potential environmental stressors have also affected ecosystems, it may be challenging to disentangle the effects of warming from those of other multiple stressors. Recently, several palaeolimnologists have been exploring these issues.

Some of the earliest palaeolimnological studies dealing with recent climatic change were conducted in the High Arctic. Because of a range of positive feedback mechanisms, polar regions are expected to show the first signs of climatic change and do so to the greatest degree, and polar lakes may be especially sensitive to some of these changes (Schindler & Smol, 2006). Biological indicators preserved in lake sediments can be used to track the effects of climate changes, at least in indirect ways (Smol & Cumming, 2000). Douglas, Smol & Blake (1994) conducted the first detailed palaeolimnological studies of recent environmental change in the High Arctic when they examined fossil diatom profiles from three ponds at Cape Herschel, Ellesmere Island (Nunavut, Canada).

Following several millennia of relatively stable diatom assemblages, the species shifts indicated marked ecological changes which they interpreted as indicating longer growing seasons with reduced ice cover. These conclusions, which came at a time before ideas concerning recent greenhouse-induced warming were well established, were repeatedly challenged in the following years, as researchers suggested alternative explanations for these marked species changes. Smol & Douglas (2007a) recently reviewed the 14 years of challenges that the conclusions of this article received, and the palaeolimnological studies that were completed to explore alternative mechanisms that could satisfactorily explain the biological changes initially reported by Douglas *et al.* (1994). For example, comparisons between palaeolimnological profiles from deep High Arctic lakes that still supported extensive ice covers even during the short Arctic summer and profiles from shallower sites with far more dynamic ice cover conditions showed that the deeper, more ice-covered lakes exhibited far subtler species assemblage changes (e.g. Michelutti, Douglas & Smol, 2003; Antoniades *et al.*, 2007). This is consistent with the hypothesis that the biological shifts were being primarily driven by warming-related changes in ice cover. To explore the potential influence of persistent organic pollutants, such as PCBs, on diatom and chrysophyte assemblages, palaeolimnological studies were completed on strategically selected lakes in coastal Labrador, one of the few sub-arctic regions where recorded temperature had not increased until the 1990s, but where some had experienced large loadings of PCBs from nearby abandoned military installations (Paterson *et al.*, 2003). No effect of the persistent organic pollutants could be discerned in the diatom and chrysophyte assemblages. The effects of nutrients were explored in various ways, including palaeolimnological studies on some of the few Arctic lakes that received sewage discharges (e.g. Douglas & Smol, 2000; Michelutti *et al.*, 2007). They showed that Arctic diatom assemblages responded quite differently to these nutrient additions compared to the marked changes in planktonic diatoms recorded in temperate lakes, presumably because the effects of ice cover and other climate-related variables partly overpowered those of fertilisation. To isolate the possible effects of other aerially transported nutrients or contaminants, Keatley, Douglas & Smol (2008) exploited the rare occurrence of two linked lakes with almost identical limnological characteristics. In this study, because of shading from a nearby hill, one of the paired lakes maintained a more extensive ice cover during the summer. If ice cover was a key controller of diatom assemblages in Arctic lakes, Keatley *et al.* (2008) hypothesised that the site with the extended ice cover should record more muted post-1850 diatom changes than the profile from the adjacent, un-shaded lake. The sedimentary records of these two lakes strongly supported this hypothesis.

Since the publication of the original Douglas *et al.* (1994) paper, many other studies have been completed, using very similar palaeolimnological approaches, throughout the circumpolar Arctic. This prompted Smol *et al.* (2005) to conduct a meta-analysis of 55 profiles from 44 sites from Arctic Canada, Finland, Svalbard and northern Russia, spanning 24° of latitude and over 170° of longitude. They concluded that Arctic regions that were expected to have warmed the most also showed the greatest degree of compositional change in diatoms and other palaeoindicators. Furthermore, they concluded that the ecological characteristics of the species changes were related primarily to climate warming, via direct and/or indirect mechanisms (e.g. changes in ice cover, thermal stability, etc.). Similar conclusions of recent climatic warming have also been gleaned from non-biological palaeolimnological indicators (reviewed in Smol & Douglas, 2007a; Hodgson & Smol, 2008).

One of the advantages of using polar lakes is that, because of their remote locations, most are relatively unaffected by local watershed disturbances, such as agriculture or extensive catchment modifications or from the effects of acidic deposition. However, there is no doubt that temperate lakes are also being affected by anthropogenic climate change (Keller, 2007), although currently to a lesser degree than those in polar regions. If such striking climate-related changes had occurred in the Arctic, can similar regime shifts be tracked in temperate lakes? Importantly, could any changes in the recent palaeolimnological record be attributed to climate warming, given that so many other potential stressors can affect temperate lake systems?

Rühland *et al.* (2008) decided to address the previously mentioned questions. One of the most obvious assemblage changes noted in at least the sub-arctic records summarised in Smol *et al.* (2005) was the marked increase in planktonic taxa such as *Cyclotella* diatoms, with compensatory declines in benthic species such as small *Fragilaria* taxa and/or heavier diatoms such as *Aulacoseira* taxa. These diatom changes were first studied in detail by Sorvari, Korhola & Thompson (2002) in Finnish Lapland and in the Canadian sub-arctic by Rühland *et al.* (2003) and Rühland & Smol (2005), who suggested that decreased ice cover and/or increased thermal stratification may have been the likely triggers for these marked assemblage shifts. It was becoming apparent, however, that similar types of diatom changes were being recorded in the most recent sediments of undisturbed temperate lakes.

It soon became evident that a large number of detailed diatom-based palaeolimnological profiles were available. Rühland *et al.* (2008) restricted their meta-analysis study to published manuscripts, theses or consultant reports that specifically contained the word '*Cyclotella*' in the text and included data on diatom changes in recent sedimentary profiles (last *c.* 200 years). However, to separate the effects of recent climate change from the influence of other multiple stressors, a pruning of the lake set was needed. An important criterion for this meta-analysis was that lakes must not be profoundly disturbed by other human activities so as to eliminate some of the more important confounding factors, such as cultural eutrophication and acidification. Rühland *et al.* (2008) therefore categorised lakes as not being profoundly affected by cultural disturbances if the current lake-water total phosphorus concentrations were less than 20 μg L^{-1} and that pH levels were 6.0 or higher. Over 200 palaeolimnological records met these criteria. Diatom profiles were further categorised as showing a rise in *Cyclotella* species if this increase was greater than 5% above background relative abundances.

The Rühland *et al.* (2008) study revealed remarkably similar taxon-specific shifts across the Northern Hemisphere since the 19th century. Significant increases in the relative abundances of planktonic *Cyclotella* taxa were concurrent with sharp declines in both heavily silicified *Aulacoseira* taxa and benthic *Fragilaria* taxa. They showed that this trend was not limited to Arctic and alpine environments, but that lakes at temperate latitudes were now showing similar ecological changes. In comparison with the sensitivity of high latitude environments to recent warming documented in Smol *et al.* (2005), freshwater ecosystems in temperate latitudes that experience longer open-water periods and growing seasons will understandably require a greater increase in temperature (and hence take longer) to cross climate-related ecological thresholds. This is consistent with the findings of Rühland *et al.* (2008) where the onset of biological responses to warming occurred significantly earlier in climatically sensitive Arctic regions (median age = AD 1870) compared to temperate regions (median age = AD 1970; Fig. 4a). A detailed palaeolimnological study of Whitefish Bay (Ontario), from Lake of the Woods, was used to further bolster their conclusions. Substantial increases in annual temperature recorded at the near-by Kenora climate station over the last few decades, particularly during the winter, were highly correlated with increases in *Cyclotella* species (r = 0.71) (Fig. 4b) and concurrent decreases in *Aulacoseira* species (see figures in Rühland *et al.*, 2008). Strongly related to this recent warming trend was an increase in the ice-free period by almost 30 days over the past *c.* 40 years that has been documented on Whitefish Bay; synchronous changes in the fossil diatom assemblages closely tracked these climate variables. For example, the ice-out data showed a strong inverse relationship to increases in *Cyclotella* species (r = −0.57) (Fig. 4c) and an equally strong positive relationship to decreases in the relative abundances of *Aulacoseira* taxa (r = 0.66; see additional figures in Rühland *et al.*, 2008). Rühland *et al.* (2008) assessed a wide spectrum of potential causes for the various diatom changes they described; however, climate-related variables, such as decreased ice cover and/or increased thermal stratification, provided the plausible explanation for the observed changes.

Although the Rühland *et al.* (2008) study was restricted to diatom changes, a longer open-water season and increased period of thermal stratification can have profound effects on other ecosystem functions and services. Rising water temperatures and a higher stability of the water column, for example, tend to favour blue-green algae (Paerl & Huisman, 2008). There are growing concerns in certain regions, such as Lake of the Woods, that algal blooms are increasing in severity and frequency. Traditionally, limnologists would immediately suspect additional nutrient inputs, and especially phosphorus, as the root cause of such blooms. Undoubtedly, cyanobacteria require a certain nutrient concentration to bloom, but if water temperatures increase and water column mixing has

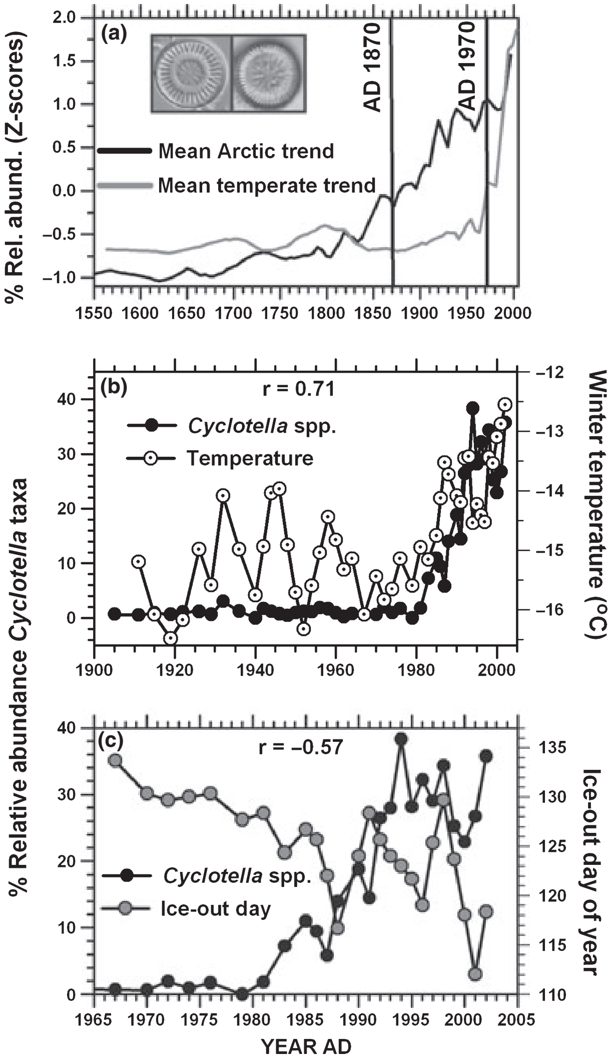

Fig. 4 Increases in the relative abundances of planktonic *Cyclotella* species from detailed palaeolimnological records throughout the Northern Hemisphere and relationships to climate metrics. Note that the *x*-axes of the three plots are on different scales. (a) Differences between the timing of sedimentary *Cyclotella* increases observed in a selection of six high latitude lakes (black lines) versus six temperate lakes (grey lines). Solid lines represent a loess smoothing curve fit through the mean % *Cyclotella* change (as z-scores). The vertical lines represent the median age of change calculated from all high latitude records (n = 15, median age = AD 1870) and all temperate records (n = 60, median age = AD 1970) used in the Rühland *et al.* (2008) meta-analysis. The timing of change between these two regions was significantly different (P < 0.05). Comparison between the per cent relative abundances of *Cyclotella* species from Whitefish Bay (Lake of the Woods, Ontario, Canada) and (b) mean winter temperature trend [Kenora (Ontario, Canada) climate station], (c) day of ice-out, Whitefish Bay. A 7-year mean was applied to the 100-year temperature record, and a 3-year mean was applied to the 35-year ice record to enable comparisons to the diatom data. A similarly strong relationship is evident if annual temperatures are used (r = 0.73). Figures modified from Rühland *et al.* (2008).

decreased with enhanced thermal stratification, blue-green algae may well be favoured (Jöhnk *et al.*, 2008; Paerl & Huisman, 2008), even if nutrient levels have not increased. There is undoubtedly a host of inter-relationships between various stressors and continued warming, with climate being the 'big threat multiplier'. The ecological, economic and aesthetic repercussions of these blooms can be considerable. The Rühland *et al.* (2008) findings are especially worrisome given that the widespread ecological changes which they reported have occurred with temperature increases that are substantially lower than those projected by climate models for both high- and mid-latitude regions of the Northern Hemisphere. With continued warming, which now seems inevitable, it is likely that many new and unexpected ecological thresholds will be crossed.

Conclusions and perspectives

Never before has there been a greater need for long-term data on the effects of human impacts on aquatic ecosystems. Although palaeolimnologists cannot conduct true experiments, by using carefully designed comparative approaches, they can make important contributions to the study of the effects of multiple stressors. Whilst this article focused on ecological approaches, lake sediments also archive a vast store of other types of proxy data. For example, all regions of our planet are affected, to varying degrees, by the long range transport of pollutants. There are multiple pathways for the delivery of most pollutants, and palaeolimnology can play a key role in determining the sources, fates and trajectories of past pollutants, including the exploration of under-studied pathways for pollution delivery, such as biovectors (Blais *et al.*, 2007). Sediments can therefore be used to study the distribution of pollutants both spatially (e.g. Blais *et al.*, 2005) and temporally (e.g. Michelutti *et al.*, 2009), and then, by using the biological records preserved in the same sediment profiles, palaeolimnology can also be used to assess the effects on past biota and community structure. Furthermore, given that a large number of high quality palaeolimnological profiles continue to be generated, using similar methods, it is now possible to undertake meta-analyses to assess regional trends on broad spatial and temporal scales. New approaches, such as investigations involving fossil DNA, are now being integrated into several research programs and can only strengthen ecological and environmental interpretations. The power of a trans-disciplinary approach is obvious, but also not without their challenges (Birks & Birks, 2006). My view is that palaeolimnologists are now more constrained by asking the best questions, rather than limitations imposed by inadequate methods and approaches.

Although palaeolimnology has enjoyed considerable success over recent years, much work remains. Whilst progress has been made to better understand the effects of environmental stressors, new problems are always being identified, further complicating assessments. Foremost amongst these stressors are the effects of recent climatic change, which often appears to be the great 'threat multiplier' or catalyst for change in aquatic ecosystem studies. Palaeolimnology continues to play a key role in documenting the various ecological thresholds that are being crossed over time frames that predate standard monitoring programs. As some of these thresholds include the disappearance of entire ecosystems (e.g. Smol & Douglas, 2007b), there is no time to waste.

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Conflicts of interest

The author has declared no conflicts of interest.

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