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Anomalous rise in algal production linked to lakewater calcium decline through food web interactions

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Increased algal blooms are a threat to aquatic ecosystems worldwide, although the combined effects of multiple stressors make it difficult to determine the underlying causes. We explore whether changes in trophic interactions in response to declining calcium (Ca) concentrations, a water quality issue only recently recognized in Europe and North America, can be linked with unexplained bloom production. Using a palaeolimnological approach analysing the remains of Cladocera (herbivorous grazers) and visual reflectance spectroscopically inferred chlorophyll *a* from the sediments of a Nova Scotia (Canada) lake, we show that a keystone grazer, *Daphnia*, declined in the early 1990s and was replaced by a less effective grazer, *Bosmina*, while inferred chlorophyll *a* levels tripled at constant total phosphorus (TP) concentrations. The decline in *Daphnia* cannot be attributed to changes in pH, thermal stratification or predation, but instead is linked to declining lakewater [Ca]. The consistency in the timing of changes in *Daphnia* and inferred chlorophyll *a* suggests top-down control on algal production, providing, to our knowledge, the first evidence of a link between lakewater [Ca] decline and elevated algal production mediated through the effects of [Ca] decline on *Daphnia*. [Ca] decline has severe implications for whole-lake food webs, and presents yet another mechanism for potential increases in algal blooms.

Keywords: palaeolimnology; lakewater calcium decline; Cladocera; chlorophyll *a*; trophic interactions

1. INTRODUCTION

Lakewater calcium (Ca) decline has emerged as a novel and a widespread threat to softwater lakes in eastern North America and Europe (and probably elsewhere), where decades of high acidic deposition and sustained logging cycles have depleted Ca pools in catchment soils, the main source of Ca to lakes [1]. Increases in Ca leaching from soils have not been accompanied by compensatory increases in bedrock weathering rates, resulting in significant, long-term declines in surface water Ca levels [2]. The biological implications of lakewater Ca decline are predicted to be extensive, because Ca is an essential nutritional element for many different types of aquatic biota [3]. In particular, many freshwater crustaceans such as *Daphnia* (Daphniidae, Anomopoda, Crustacea) require relatively large amounts of aqueous Ca for the development of Ca-rich exoskeletons, which must be regenerated following each moult [4].

Daphnia are an important component of the zooplankton community in many freshwater lakes. Like many crustaceans, they have relatively high amounts of Ca in their exoskeletons, and rely mainly on the uptake of aqueous Ca to fulfil their Ca requirements [4]. Only trace amounts of Ca are retained during moulting [5]. In low Ca environments, some daphniids must, therefore, expend large amounts of energy obtaining Ca from the water column, and are at a competitive disadvantage relative to smaller zooplankton species with lower Ca

requirements [3]. In fact, large declines in *Daphnia* populations, coincident with increases in less Ca-rich *Bosmina*, have been documented in softwater lakes in Ontario and Nova Scotia, Canada, and in Adirondack Park (New York, USA) when Ca levels fell below approximately 2 mg l^{-1} [1].

Substantial reductions in daphniid populations have the potential to dramatically affect lake food webs, as *Daphnia* are important herbivores in many freshwater systems. Owing to their larger body size, *Daphnia* are able to filter food particles at a much faster rate and graze a wider size-range of algae compared with *Bosmina* [6], a taxon that can withstand lower Ca levels [7]. As a result, in lakes with daphniid-dominated zooplankton assemblages, algal concentrations are often much lower than in bosminid-dominated lakes with comparable total phosphorus (TP) levels [8,9]. Species replacement of *Daphnia* by *Bosmina*, then, can potentially release phytoplankton from grazing pressure and lead to increased algal production. This presents problems for lake management programmes, as the link between TP and algal production becomes partly decoupled, limiting the use of nutrient-productivity model predictions [10]. Prior to this investigation, however, evidence of a link between lakewater [Ca] decline and increased algal production had not been documented.

In many lakes of Kings County, Nova Scotia (Canada), chlorophyll *a* (a common proxy for total primary production) has been steadily rising independently of TP since lake monitoring began in 1997 [11]. This includes Lake George, a popular recreational lake in the area
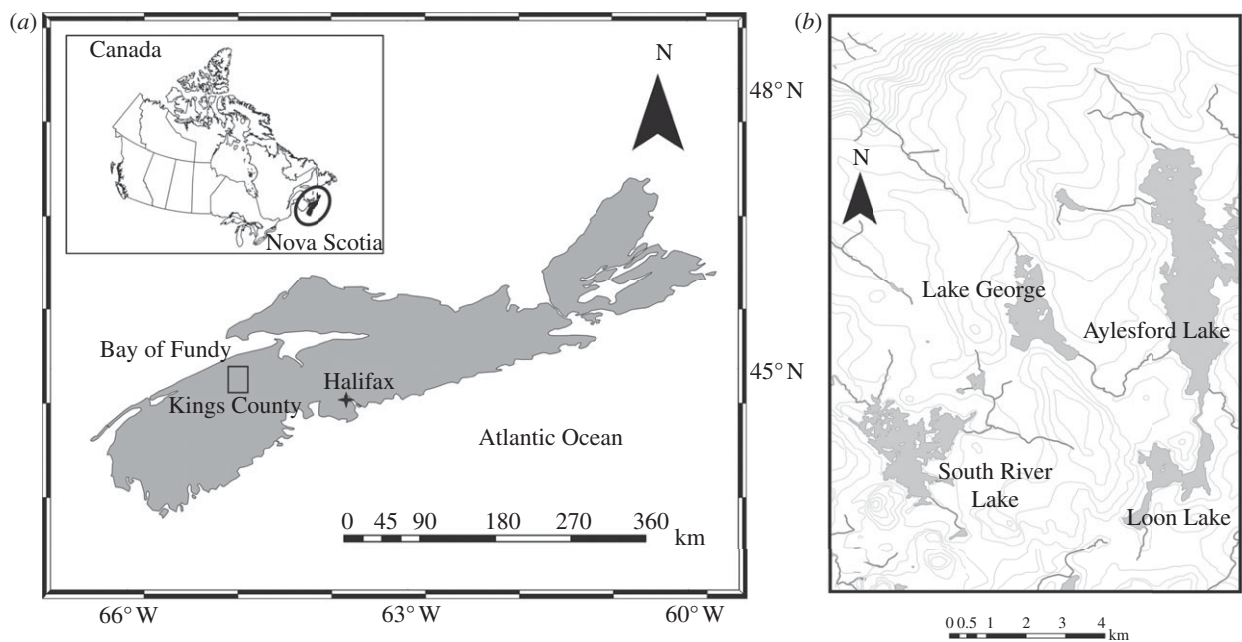
Figure 1. (*a*) Map showing the location of Lake George in Nova Scotia, Canada. Inset shows the location of Nova Scotia within Canada. (*b*) A hydrographic map of Lake George and neighbouring lakes and rivers (data from Natural Resources Canada CanVEC database).

where chlorophyll *a* levels are now approaching water quality guidelines (greater than $2.5 \, \mu g \, l^{-1}$) set by the Kings County Municipal Plan [11]. A previous diatom-based palaeolimnological study of Lake George did not record any diatom-inferred changes in TP or pH over the last approximately 100 years of the lake's history that can account for this increase in algal production, but do show changes in the diatom assemblage at approximately 1970 that are consistent with the timing of recent anthropogenic climate warming in this region [12]. The inferred timing of diatom assemblage changes related to warming, however, occurs too early to be considered a primary driver of recently documented increases in algal production in Lake George. Instead, these lakes are located on Ca-poor granitic bedrock in southwest Nova Scotia, where declines in lakewater [Ca] to very low levels have been documented [13]. We hypothesize, then, that in the absence of nutrient enrichment, elevated chlorophyll *a* in Kings County lakes may be related to top-down controls that were exacerbated by the effects of climate warming, and specifically that declines in *Daphnia* abundances, which could release phytoplankton from grazing pressure, may be occurring in these lakes related to [Ca] decline.

Since zooplankton monitoring data from the Maritimes are scarce (as they are in almost all regions), and the onset of environmental stressors such as acid deposition, Ca decline and shoreline development precede the beginning of the Kings County Lake Monitoring Programme, we use palaeolimnological techniques to reconstruct trends in zooplankton assemblages, and assess how trends in chlorophyll *a* and zooplankton species composition might be linked. We tracked changes in subfossil *Daphnia* and *Bosmina* (and other cladocerans) relative abundances, as well as sedimentary visual reflectance spectroscopically inferred chlorophyll *a* [14] levels in Lake George (figure 1), to assess whether changes in *Daphnia* abundances have occurred in the lake's history that coincide

with increases in algal production. This method measures *both* chlorophyll *a* and its post-depositional degradation products, and is therefore unaffected by diagenetic processes. To assess the role of changing predation regimes in any observed cladoceran community changes, we also measured *Bosmina* mucro length, as changes in mucro length recorded from lake sediments can be linked to changes in invertebrate and fish predation [15,16].

2. MATERIAL AND METHODS

Lake George (44°55′ N, 64°42′ W; figure 1) is a weakly stratified, circumneutral (pH = 6–7), oligo-mesotrophic (unfiltered TP = $5-20 \, \mu g \, l^{-1}$) lake located on the South Mountain in Kings County, Nova Scotia [11]. It has a mean depth of 9.0 m and a surface area of 153 ha, and drains into the Gaspereau River [11]. Its catchment is mid-Devonian granitic bedrock, and is comprised of mixed coniferous–deciduous forests [17]. It has a moderately developed shoreline with private cottages, homes, a trailer park, a public access beach and waterfront for the Lake George Provincial Park. Water chemistry for Lake George has been monitored monthly during the ice-free months since 1997 by the Kings County Lake Monitoring Programme [11], with some isolated measurements also available from 1993. Over the period of the monitoring record, a significant increase in chlorophyll *a* has been observed that cannot be explained by an increase in TP (figure 2*a*) [11].

A surface-sediment core was obtained from the deepest basin of Lake George in July 2005 using a Glew gravity corer with an internal diameter of 7.6 cm equipped with a 50 cm long Lexan core tube [18,19]. The core was sectioned into 0.5 cm intervals using a Glew vertical extruder [20], and then transferred to individual Whirl-Pak sample bags, and stored at 4°C at the Paleoecological Environmental Assessment and Research Lab (PEARL) at Queen's University in Kingston, Ontario. An additional water sample was taken in June 2010 following the protocols of the Ontario
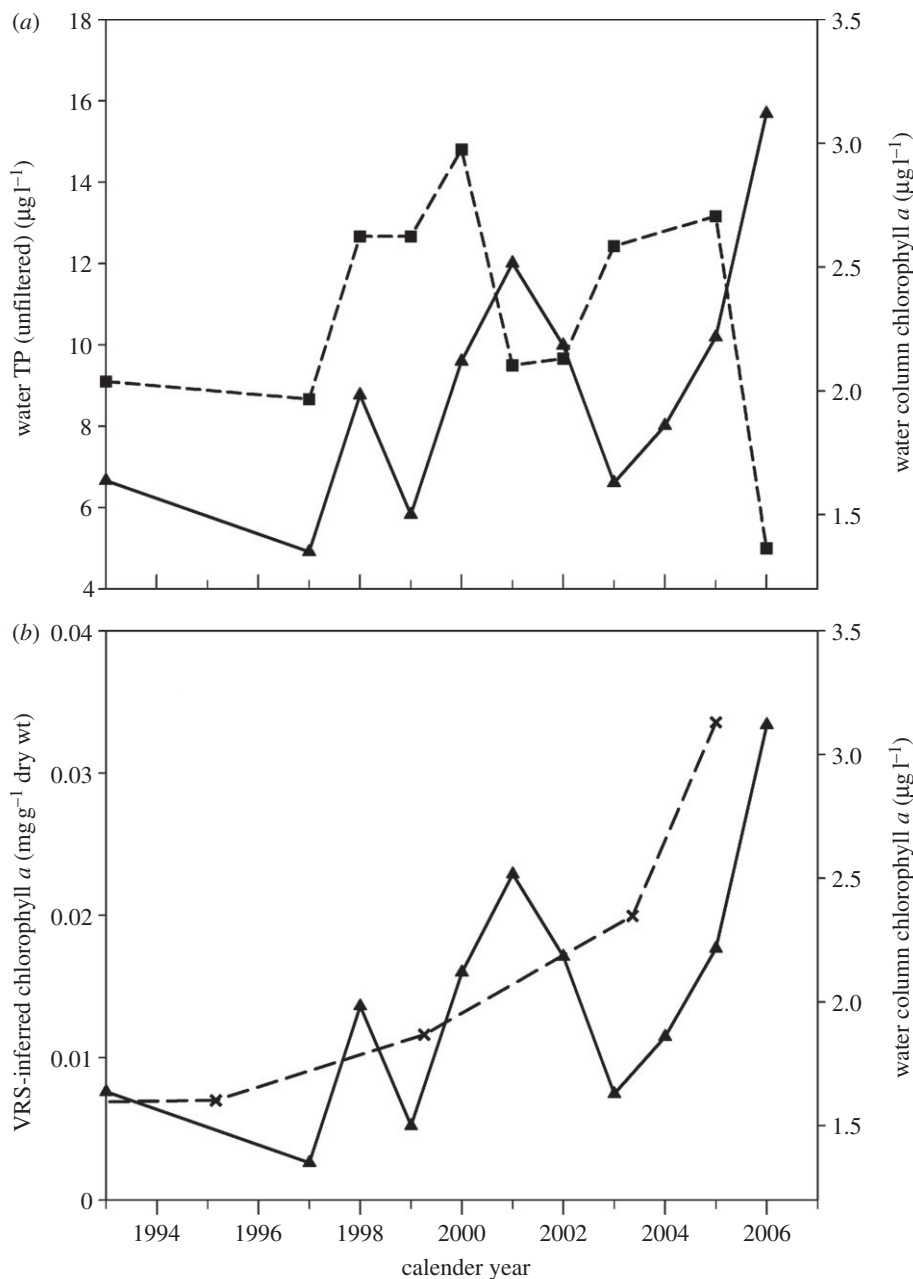
Figure 2. (*a*) Changes in average annual water column chlorophyll *a* and total phosphorus (TP) since 1993. The increase in chlorophyll *a* since 1993 is significant ($p = 0.02$). No trend exists for TP ($p = 0.49$), and chlorophyll *a* is not correlated with TP (pairwise Pearson correlation, $t_9 = -0.80$, *p*-value = 0.4). (*b*) Changes in VRS-inferred and measured water column chlorophyll *a*. Water chemistry data provided by the Kings County Lake Monitoring Programme [11]. Filled triangles with solid line, monitored water chlorophyll *a*; filled squares with dashed line, monitored water total phosphorous. (*b*) Crosses with dashed line, sedimentary VRS-inferred chlorophyll *a*; filled triangles with solid line, monitored water chlorophyll *a*.

Ministry of the Environment's Lake Partner Programme and analysed for Ca at the Dorset Environmental Science Centre (Dorset, Ontario).

The sediment core was dated using excess ^{210}Pb activities and ^{137}Cs, in an Ortec germanium crystal well detector following the procedures outlined by Schelske *et al.* [21] and Appleby [22]. Details of the dating of the Lake George sediment core can be found in Thienpont *et al.* [12]. The chronology was developed using the constant rate of supply programme developed by Binford [23].

For analysis of cladoceran remains, sediments were deflocculated in 10 per cent potassium hydroxide solution for approximately 30 min, then passed through a 37 µm sieve [24]. The material retained on the sieve was transferred to a vial using deionized water, and stained with safranin-glycerol

solution. A minimum of 100 individuals was enumerated per interval [25]. *Daphnia* were grouped into the *Daphnia pulex* complex based on the presence of stout spines on the middle comb of the post-abdominal claw, and in Lake George, this complex may consist of *Daphnia pulicaria* or *Daphnia catawba* (no remains belonging to the *Daphnia longispina* complex were identified). A total of 50 *Bosmina* remains were measured per interval using techniques outlined in Korosi *et al.* [26]. In order to estimate sedimentary chlorophyll *a* content, selected intervals were freeze-dried and sieved (125 µm), and then analysed for spectral reflectance using a FOSS NIRSystems Model 6500 rapid content analyser [27,28]. Since this technique detects *both* chlorophyll *a* and its derivatives (pheophytin *a* and pheophorbide *a*), which absorb in similar regions of the electromagnetic spectrum, visual reflectance
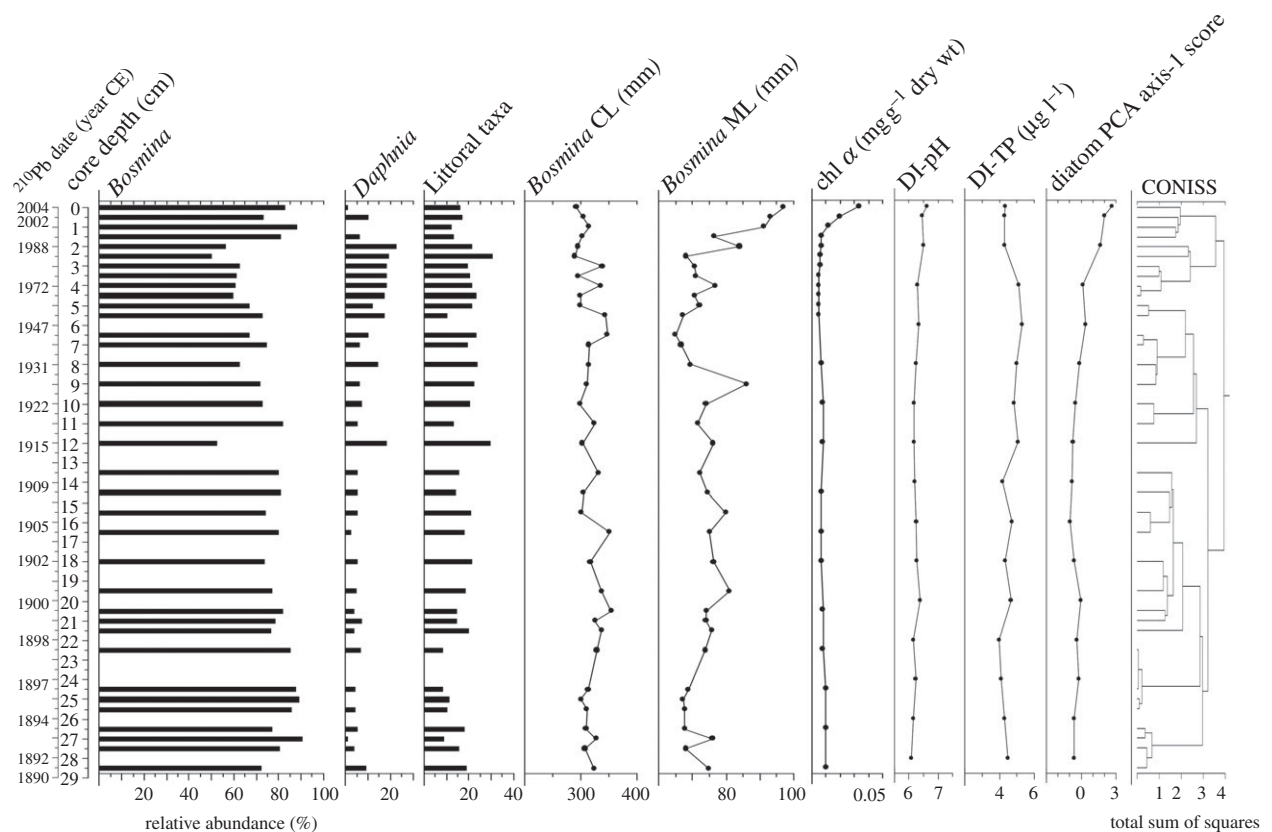
Figure 3. Stratigraphic diagram showing subfossil cladoceran taxon compositional changes occurring since the nineteenth century from Lake George Nova Scotia, as well as *Bosmina* mucro (ML) and carapace (CL) lengths, and VRS-inferred chlorophyll *a* (chl *α*) in a ^{210}Pb-dated sediment core. In addition, diatom-inferred pH and TP (DI-pH and DI-TP), and principal components analysis (PCA) axis 1 sample scores for diatoms are shown for comparison [12]. Results of the constrained incremental sum of squares (CONISS) cluster analysis are also shown.

spectroscopically (VRS)-inferred chlorophyll *a* are accurately tracking overall trends in lake production, and not simply diagenetic processes [14,28]. A stratigraphy was prepared, and a constrained incremental sum of squares (CONISS) cluster analysis was performed on the cladoceran relative abundance data (chlorophyll *a* and *Bosmina* measurements were not included) using the computer program TGVIEW v. 2.0.2 [29]. Pairwise Pearson correlations of select variables were conducted using the *stats* package for the R software environment [30].

3. RESULTS AND DISCUSSION

Chlorophyll *a* levels in the water column of Lake George have been steadily and inexplicably rising over 10 years of lake monitoring, indicating that phytoplankton production has increased (figure 2a) [11]. We used palaeolimnological techniques to determine whether these modern trends are a symptom of significant ecological changes occurring in the lake, or just natural variability in lake productivity. Similar to the modern limnological monitoring record, we observed an increase in VRS-inferred chlorophyll *a* (and its diagenetic products) in recent years, tripling in value between approximately 1990 and 2005, the year the sediment core was taken (figures 2b and 3). Prior to this, chlorophyll *a* levels had remained relatively unchanged over the last century. Therefore, we show that the elevated chlorophyll *a* values recorded by the Kings County Lake Monitoring Programme began in the early 1990s, and are

unprecedented over approximately 110 years of the lake's history. No significant changes in monitored lake-water or diatom-inferred TP and pH have occurred in Lake George that can account for this recent increase (figures 2a and 3) [11,12]. Instrumental temperature records from Halifax, Nova Scotia, have recorded an increase of 0.8°C in mean summer temperature since 1948, and recent changes observed in the diatom sedimentary assemblage are consistent with limnological changes related to climate warming [12]. While increased thermal stratification and growing season could account for increased lake productivity, the timing of diatom-inferred changes in lake thermal properties in Lake George are not consistent with the timing of changes in chlorophyll *a*, occurring more than a decade prior to the beginning of the rise in chlorophyll *a* (diatom principal components analysis axis 1 score on figure 3) [12]. Therefore, anthropogenic climate change alone cannot account for increased algal production in Lake George.

We hypothesized that changes in chlorophyll *a* might be linked to 'top-down' grazing control by *Daphnia* rather than 'bottom-up' influences, as the abundance of large-bodied *Daphnia* has been identified as an important predictor of lake production in previous studies [10,31,32]. In theory, a zooplankton assemblage dominated by *Daphnia* can graze a broader size-range of algae, filter food particles faster (filter-feeding rate is a function of body length), and recycle nutrients at a slower rate than a zooplankton assemblage of equal biomass dominated by *Bosmina*, ultimately leading to reduced algal
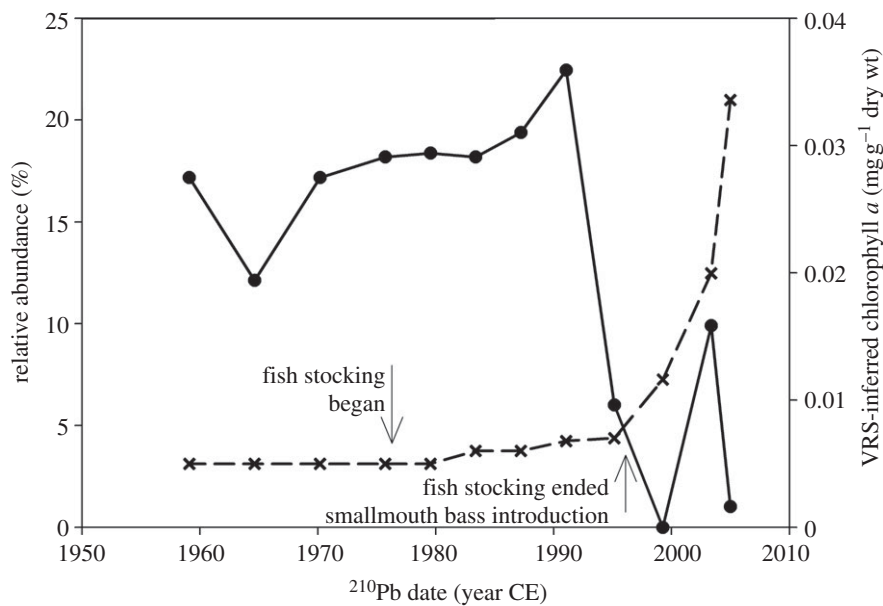
Figure 4. Changes in the relative abundances of *Daphnia* remains and sedimentary VRS-inferred chlorophyll *a* in Lake George, Nova Scotia, Canada over the last approximately 50 years (pairwise Pearson correlation, $t_{10} = -2.8$, *p*-value = 0.02). Circles with solid line, *Daphnia* relative abundance; crosses with dashed line, VRS-inferred chlorophyll *a*.

production [33]. We observed considerable changes in the pelagic cladoceran community of Lake George, which consisted almost entirely of *Bosmina* and *Daphnia* (figure 3). Prior to 1950, species of the *D. pulex* complex were present in the lake at relative abundances of 5–10% on average (figure 3). Above a core depth of 6 cm (approx. 1950), we observed a decrease in *Bosmina* relative abundance and an increase in *Daphnia* relative abundance to approximately 15–20%, nearly double background abundances (figure 3). Above a core depth of 2 cm (approx. 1990), however, *Daphnia* and *Bosmina* relative abundances returned to pre-industrial levels (figure 3). The most recent reduction in *Daphnia* relative abundance occurs immediately prior to the increase in VRS-inferred chlorophyll *a* (figure 4), and there is a significant negative relationship between *Daphnia* abundance and VRS-inferred chlorophyll *a* since 1960 ($t_{10} = -2.8$, $p = 0.02$). This supports our hypothesis of top-down control on algal populations, with *Daphnia* as more effective grazers on algae than smaller-bodied *Bosmina*. This is consistent with previous field and laboratory studies, which show that chlorophyll *a* yields at constant TP are substantially lower when *Daphnia* are abundant [8,9,34]. We conclude, then, that a decrease in grazing pressure by *Daphnia*, probably exacerbated by recent changes in lake thermal properties [12], have led to anomalous levels of algal production in Lake George without increased nutrient enrichment.

Similar to the chlorophyll *a* trends (whether they be VRS-inferred or monitored from the water column; figure 2*b*), changes in *Daphnia* cannot be explained by changing pH, TP or lake thermal structure in our lake, as discussed above. Owing to their larger body size relative to many other species of zooplankton, *Daphnia* are one of the preferred prey items for planktivorous fishes, and changes in predation intensity by planktivorous fishes can affect daphniid abundances [35]. Reduced predation by planktivorous fishes might be responsible for the increased

relative abundance of *Daphnia* observed at a core depth of 6 cm, although there is no corresponding increase in *Bosmina* mucro length (figure 3). Increases in the length of the mucro are an anti-predation strategy when predation by grasping copepod (and other invertebrate) predators is high, as a long mucro will make them more difficult to handle, providing them with increased opportunities of escape [36]. Predatory copepods, similar to *Daphnia*, are heavily preyed upon by planktivorous fishes owing to their large body size, and therefore increased mucro length can also indirectly infer reduced planktivorous fish predation [37]. Moreover, the increase in *Daphnia* relative abundance does not match known fish stocking records. Stocking of brook trout yearlings and fingerlings began in 1976, after *Daphnia* populations reached 15–20% abundance (figure 4) [38].

A strong increase in *Bosmina* mucro length is observed, however, above a core depth of 2 cm, with the average length reaching 100 μm in the uppermost sediments (figure 3). This matches well with the first-known record of smallmouth bass in Lake George in 1997 [38], a piscivorous fish, which often reduces the abundance of planktivorous fishes [39]. Fish predation, therefore, cannot explain the decrease in *Daphnia* observed above 2 cm. Furthermore, significant increases in dissolved organic carbon (DOC) have been measured in Lake George since 1993 [11], which impairs the visibility of planktivorous fishes and should provide further release for *Daphnia* from grazing pressure [35].

Lake George is located in a region of Nova Scotia that receives acidic deposition from long-range sources [40], and a few lakes in Kings County have acidified [12]. The timing of the increase in *Daphnia* abundances corresponds to the height of acid deposition before emission restrictions were implemented [41]. When acid deposition rates are high, Ca ions have been shown to leach into lakes at an increased rate, as hydrogen ions would replace base cations at soil-binding sites, leaving them free to wash

into lakes and rivers [42]. Lake George could probably have experienced elevated lakewater Ca levels in the 1950–1960s that may account for the observed increase in *Daphnia* relative abundances (figure 3). Eventually, following decades of increased leaching, soils become depleted in Ca, leading to long-term lakewater [Ca] declines that negatively impact *Daphnia* [3]. This has been demonstrated in nearby Little Wiles Lake (Bridgewater, Nova Scotia), where the loss of *Daphnia* in recently deposited lake sediments (similar to the trend observed in Lake George) was attributed to declining lakewater Ca levels [1]. Similarly, in 42 softwater, oligotrophic lakes in south-central Ontario, declines in *Daphnia* relative abundances and coincident increases in Ca-poor *Bosmina* since pre-industrial times were observed in lakes where modern Ca levels were less than $2 \, mg \, l^{-1}$, whereas in lakes with [Ca] greater than $2 \, mg \, l^{-1}$, *Daphnia* relative abundance increased owing to factors such as increasing DOC and the spread of smallmouth bass [43], changes that have also occurred in Lake George.

Unlike Little Wiles Lake, there are no long-term monitoring data on [Ca] for Lake George. At the time of sediment collection, alkalinity in Lake George was low ($2.8 \, mg \, CaCO_3 \, l^{-1}$), and [Ca] sampled from Lake George in June 2010 (5 years after the sediment core used in this study was collected) was $1.14 \, mg \, l^{-1}$, well below levels that have been shown to be detrimental to daphniid populations [3]. We conclude, based on the geology of the region and its history of acid deposition, that Lake George has also experienced declines in base cations similar to other lakes in southwest Nova Scotia that have been monitored for Ca [13], and that this decline in lakewater [Ca] is responsible for the decrease in *Daphnia* populations observed at a core depth of 2 cm. There can be considerable inter-annual variability in lakewater [Ca] levels related to climate variables that control the washing of ions into lakes [44], and the spike in *Daphnia* observed at 0.5 cm may be reflecting years when [Ca] was higher. Local climate records from nearby Greenwood, Nova Scotia, show that 2003, the approximate ^{210}Pb-inferred year the *Daphnia* spike occurred, was a wetter year than the decadal average [45], lending some support to this hypothesis. Interestingly, the long-term monitoring record for Lake George shows that lakewater chlorophyll *a* was also lower in 2003 (figure 2) when the *Daphnia* were more abundant, which was not detected by VRS in the sediment record, probably because it integrates material from several years.

4. CONCLUSIONS

We document a link between declines in *Daphnia* and elevated VRS-inferred chlorophyll *a* (a trend that matches closely with monitored lakewater chlorophyll *a*), where the decline in *Daphnia* cannot be attributed to changes in predation, TP, pH or lake thermal structure, but instead to a new environmental stressor: lakewater [Ca] decline. The decline in *Daphnia* is especially striking, as many of the known limnological changes that occurred in recent years in Lake George (e.g. increasing DOC, smallmouth bass introduction) should have favoured an increase in *Daphnia* abundances in the absence of [Ca] decline as a stressor. Indeed, *Daphnia* did increase as predicted in approximately 1950 in Lake George, until a

sudden reversal occurred in approximately 1990. The reversion of *Daphnia* and *Bosmina* back to pre-industrial relative abundances, combined with warmer surface water temperatures and a longer growing season, probably resulted in a striking rise in algal production as inferred from both sedimentary and measured lakewater chlorophyll *a* that is unprecedented over the last century.

The negative impacts of [Ca] decline on *Daphnia* in softwater lakes have recently been well established, and we provide, to our knowledge, the first evidence of a link between lakewater [Ca] decline and unusually high levels of algal production, implicating [Ca] decline as an additional mechanism for reductions in water quality related to increased algal production. This has become apparent in Lake George, where both modern limnological sampling and palaeolimnological data detect increasing chlorophyll *a* levels in the absence of nutrient enrichment, and complaints of episodic algal blooms may become more frequent in response to the combined effects of reduced grazing control by *Daphnia*, potential future nutrient enrichment from continued watershed development and anthropogenic climatic warming.

It is becoming increasingly clear that lakes are being affected by multiple stressors. As [Ca] decline in lakes can negatively affect keystone herbivores, we show that, through trophic linkages, this newly identified anthropogenic stressor may have complex, and potentially negative consequences for whole lake ecosystems.

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