

The influence of calcium decline and climate change on the cladocerans within low calcium, circumneutral lakes of the Experimental Lakes Area

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Abstract Calcium (Ca) concentrations of many softwater lakes on the Canadian Shield have been in decline for decades as a response primarily to regional acid deposition and repeated cycles of forest harvesting. These Ca declines are of ecological interest, as many lakes have fallen to Ca levels detrimental to the fitness of ecologically important Ca-rich cladoceran taxa such as *Daphnia pulex*. However, distinguishing the impacts of reduced Ca from acidification (i.e., decreasing pH) on Ca-demanding fauna has proven difficult due to strong correlations between pH and Ca in softwater lakes. Here, we examine cladoceran sedimentary assemblages from low Ca lakes (mean present-day Ca < 2.0 mg l⁻¹) in the Experimental Lakes Area (ELA) of Ontario, Canada, where Ca concentrations have declined since the 1980s, despite being closed to forestry and remote from (i.e., not downwind of) major sources of acid deposition.

Differences between present-day and pre-industrial cladoceran assemblages were greatest among planktonic taxa, including *Bosmina* spp. and *Holopedium glacialis*. However, daphniid remains were present in only three of the ten study lakes with minimal directional trends. Overall, in these ELA lakes, daphniid abundance was low historically, and impacts possibly attributable to Ca declines have been obscured by the effects of regional climate warming.

Keywords Lakes · Calcium (Ca) · pH · Cladocera · Zooplankton · Experimental Lakes Area (ELA)

Introduction

Declines in Ca concentration have been observed in large numbers of softwater lakes on the Canadian Shield (Stoddard et al., 1999; Jeziorski et al., 2008), and are generally attributed to depletion of the base cation reservoirs in watershed soils at rates faster than their replenishment via geochemical weathering of the underlying bedrock, as well as reduced leaching rates from these reservoirs (Kirchner & Lydersen, 1995; Houle et al., 2006). Two principal mechanisms are typically responsible for base cation depletion in the catchments of softwater boreal lakes: biomass removal via repeated timber harvesting cycles (Watmough & Dillon, 2003), and the mobilization of base cations by acid deposition (Likens et al., 1996). The impact of

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aqueous Ca decline on surface waters is a topic of concern, as reduced lakewater Ca availability may have profound ecological consequences should it fall below physiological thresholds of Ca-demanding organisms, including cladoceran members of the crustacean zooplankton (e.g., daphniids; Cairns & Yan, 2009). Due to their intermediate trophic position, changes within cladoceran communities can have far-reaching impacts, as they are often the dominant algal grazers and prey item of both fish and invertebrate predators (Brooks & Dodson, 1965; Wissel et al., 2003; Korosi et al., 2012).

The Experimental Lakes Area (ELA), located in a sparsely populated region of northwestern Ontario ~50 km from Kenora (Fig. 1), is a location well-suited to the study of the impacts Ca decline in the absence of its two principal causes. The site was established in 1968 by the Government of Canada for the study of boreal lakes (including whole-lake manipulation studies) in a region that was relatively undisturbed by human and industrial activity and has since remained distant (and due to the prevailing westerlies, is not downwind) from sources of acid deposition while experiencing minimal forest harvesting due to its protected status (Johnson & Vallentyne, 1971; Jeffries et al., 2003; Blanchfield et al., 2009). The extensive monitoring history of many small lakes within the ELA and the relatively pristine conditions of these systems have proven ideal over the past four decades for studying a wide variety of environmental stressors, including cultural eutrophication, experimental lake acidification, climate warming, and aquaculture (Blanchfield et al., 2009). Reconstructions of diatom-inferred lakewater pH in northwestern Ontario show little change throughout the mid-twentieth century (e.g., Dickman et al., 1988; Paterson et al., 2002) despite the high levels of industrial sulfur emissions in eastern North America (e.g., Keller, 2009). This relative stability in lakewater pH is of particular importance for our study, as it is often difficult to separate the relative impacts of lake acidification (i.e., declines in pH) and Ca decline upon cladoceran communities (Jeziorski et al., 2012a), and although pH and Ca are typically positively correlated, the acidification of some softwater lakes may have been accompanied by an increase in Ca due to the accelerated leaching of base cations (e.g., Watmough & Aherne, 2008). In the absence of either of the two principal mechanisms of Ca decline (i.e., acidification

and tree-harvesting), declining lakewater Ca concentrations have been documented in northwestern Ontario lakes (a mean decrease since the early 1980s of ~15% from 2.0 to 1.7 mg l⁻¹ in 92 lakes; Jeziorski et al., 2008). Although decreases in pH have accompanied decreases in Ca in some cases, the lakes have remained circumneutral (mean pH = 6.6; Table 1), with pH values above thresholds of zooplankton community change (i.e., pH > 6; Holt et al., 2003; Jeziorski et al., 2008). Mechanisms that may be responsible for the small Ca declines in northwestern Ontario include: reduced atmospheric particulate deposition of base cations (including Ca; Hedin et al., 1994) in response to increased soil conservation practices and adoption of erosion control in the prairies (Agriculture and Agri-Food Canada, 1997), and variation in drought and fire frequency altering the acid neutralizing capacity of runoff (Bayley et al., 1992; Schindler et al., 1996). However, although increases in drought and fire frequency will increase the export of acid anions relative to base cations in stream runoff, base cation concentrations in lakes will likely rise as total runoff decreases, due to an increased release of base cations from lake sediments associated with increased water renewal time (Schindler et al., 1996).

Irrespective of the cause, Ca declines observed in ELA lakes provide a “natural laboratory” for the study of Ca decline in the absence of acid deposition and associated pH changes. The declines are of interest due to the importance of ambient lakewater Ca concentration upon the distribution of Ca-rich herbivorous zooplankton taxa, and particularly members of *Daphnia* spp. (0.8–8% of dry body weight; Wærvågen et al., 2002; Jeziorski & Yan, 2006; Cairns, 2010). Laboratory analyses have identified Ca concentrations <1.5 mg l⁻¹ to be detrimental to daphniid growth, reproduction, and survival (Hessen et al., 2000; Ashforth & Yan, 2008; Tan & Wang, 2010) due in part to a poor ability to retain body Ca in low Ca environments (Tan & Wang, 2010), impairing processes such as the production of antipredator defenses (Riessen et al., 2012). Despite the accumulating evidence of the importance of Ca decline for Ca-rich cladoceran communities, interpretations of the indirect ecological effects of Ca decline have been complicated by the direct effects of acid deposition. The interdependence of lake pH and Ca concentration has had a confounding effect on determining the unique impacts of these environmental stressors

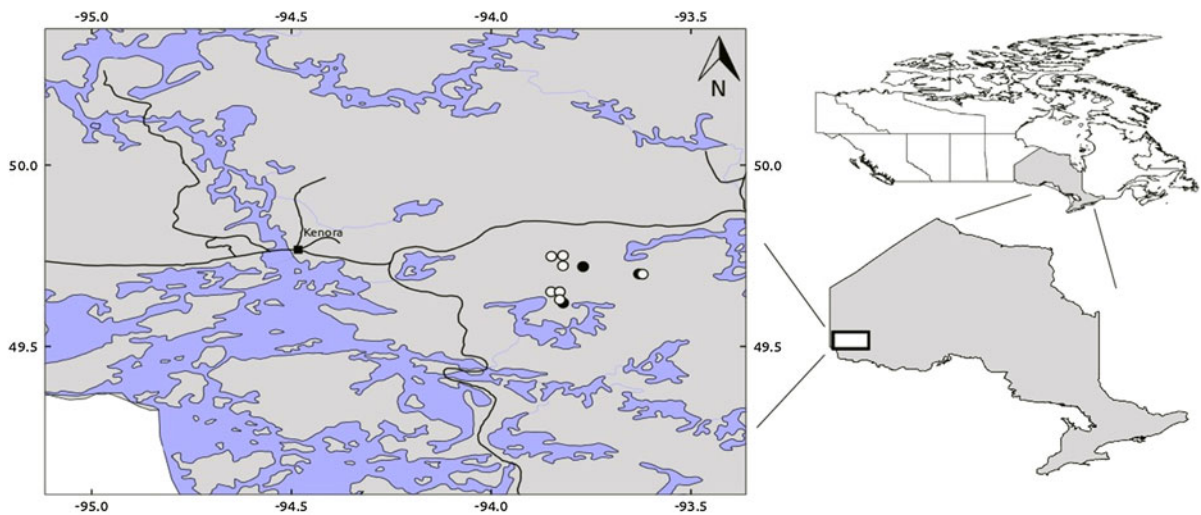


Fig. 1 Locations of the ten study lakes in northwestern Ontario, Canada. Three of the lakes (*black circles*) contained daphniid remains in their surface and pre-industrial sediments, and so full

sediment cores from these lakes were subsequently analyzed. Location of study area within Ontario and Canada

Table 1 Location and selected physical and water chemistry variables from the ten study lakes

Lake	Latitude	Longitude	1980s Ca (mg l^{-1})	Ca (mg l^{-1})	pH	SA (ha)	Depth (m)	SiO_3 (mg l^{-1})	Na (mg l^{-1})	NH_4 ($\mu\text{g l}^{-1}$)	TP ($\mu\text{g l}^{-1}$)	DOC (mg l^{-1})
93	49.75	-93.85	–	1.4	6.5	5.5	8.2	1.5	0.7	28	4.4	8.4
99	49.72	-93.82	2.0	1.3	6.4	6.5	6.7	0.1	0.8	32	9.7	8.9
110	49.75	-93.82	1.6	1.1	6.6	5.9	12.3	0.4	0.5	30	2.0	6.2
129	49.65	-93.83	2.3	1.3	6.5	4.5	14.5	0.3	0.9	24	8.3	9.6
132	49.65	-93.85	1.5	1.3	6.4	7.2	8.4	0.1	0.6	30	7.3	5.2
163	49.63	-93.83	2.7	2.8	7.1	15.7	4.5	0.2	1.0	12	4.4	4.5
164	49.62	-93.82	2.5	1.8	6.7	15.3	6.5	1.0	0.9	22	5.1	8.8
378	49.72	-93.77	–	1.8	7.0	24.3	18.1	1.3	0.9	8	3.5	6.9
383	49.70	-93.63	2.4	1.7	6.7	5.2	9.0	0.4	0.7	26	3.8	8.4
384	49.70	-93.62	1.4	1.6	6.6	6.3	3.0	1.0	0.7	18	5.7	9.4

The 1980s Ca measurements are adapted from Findlay & Shearer (1992), all other values were determined from water samples collected from the epilimnion of each lake in summer 2006

(Jeziorski et al., 2012a, b), as Ca is a major contributor to the alkalinity of lakes on the Canadian Shield. Furthermore, difficulties in distinguishing the effects of low pH from Ca limitation have been exacerbated by similar tolerances among some cladoceran taxa to both stressors (e.g., the relative sensitivity of *Daphnia pulex* to both low Ca availability and low pH contrasts strongly with the relative resilience of *Daphnia catawba* to these conditions; Malley & Chang, 1986; Ashforth & Yan, 2008; Cairns, 2010).

Here we use paleolimnological methods to examine cladoceran remains from the sediments of ten ELA lakes

that have present-day Ca concentrations near 1.5 mg l^{-1} (demonstrated in laboratory conditions to be detrimental to the growth and survival of Ca-rich daphniids; Hessen et al., 2000; Ashforth & Yan, 2008; Cairns, 2010; Tan & Wang, 2010). We test the hypothesis that the present-day and pre-industrial cladoceran sedimentary assemblages of these low Ca ELA lakes have changed significantly through time and investigate whether there is evidence of long-term changes among the most Ca-sensitive taxa (i.e., the daphniids) that are indicative of changes in Ca concentrations. Analysis of sediment intervals representing

modern-day and pre-industrial times using the so-called “top/bottom” paleolimnological approach (Smol, 2008) identified daphniid remains in three of the ten study lakes (lakes 164, 378, and 383). Sediment cores from these lakes were then radiometrically dated and analyzed in greater temporal detail to examine long-term changes in both daphniid populations and the broader cladoceran assemblage.

Methods

The ten ELA study lakes (Fig. 1) chosen for this paleolimnological analysis are a subset of 40 reference lakes used previously to examine changes in diatom assemblages in the ELA since pre-industrial times (Enache et al., 2011). Sediment cores were collected from each lake during the summer of 2006 using a Glew (1989) gravity corer, and sectioned on shore at a resolution of 0.5 cm using a Glew (1988) vertical extruder. The sediment cores were stored in a cold room at the Paleocological Environmental Assessment and Research Laboratory (Kingston, Canada) prior to analysis. The subset of lakes selected for cladoceran sedimentary analysis have modern-day Ca concentrations nearing levels identified as detrimental to daphniid fitness ($1.0 \text{ mg l}^{-1} < \text{Ca} < 2.75 \text{ mg l}^{-1}$; Hessen et al., 2000; Ashforth & Yan, 2008; Tan & Wang, 2010). To ensure that pH impacts would not confound the potential influence of Ca limitation, the subset was further restricted to lakes with measured pH above thresholds known to produce changes in crustacean zooplankton communities ($6.0 < \text{pH} < 7.2$; Holt et al., 2003). The lakes were also limited by maximum depth ($<20 \text{ m}$), area ($<25 \text{ ha}$), color ($6.25 < \text{TCU} < 50$), and total phosphorus (TP) concentrations ($<10 \text{ } \mu\text{g l}^{-1}$), to allow comparisons with prior investigations of the effects of Ca decline on cladocerans within south-central Ontario lakes (Jeziorski et al., 2012a, b). This screening procedure reduced the initial set of 40 lakes to ten (i.e., lakes 93, 99, 110, 129, 132, 163, 164, 378, 383, and 384; Table 1).

In our “top/bottom” paleolimnological analysis (the strengths and limitations of this approach are discussed in Smol, 2008) of the ten study lakes, we compared cladoceran remains present in recently deposited sediments (i.e., the “top” sample, sediment depth 1.5–2.0 cm) with deeper sediments (i.e., the

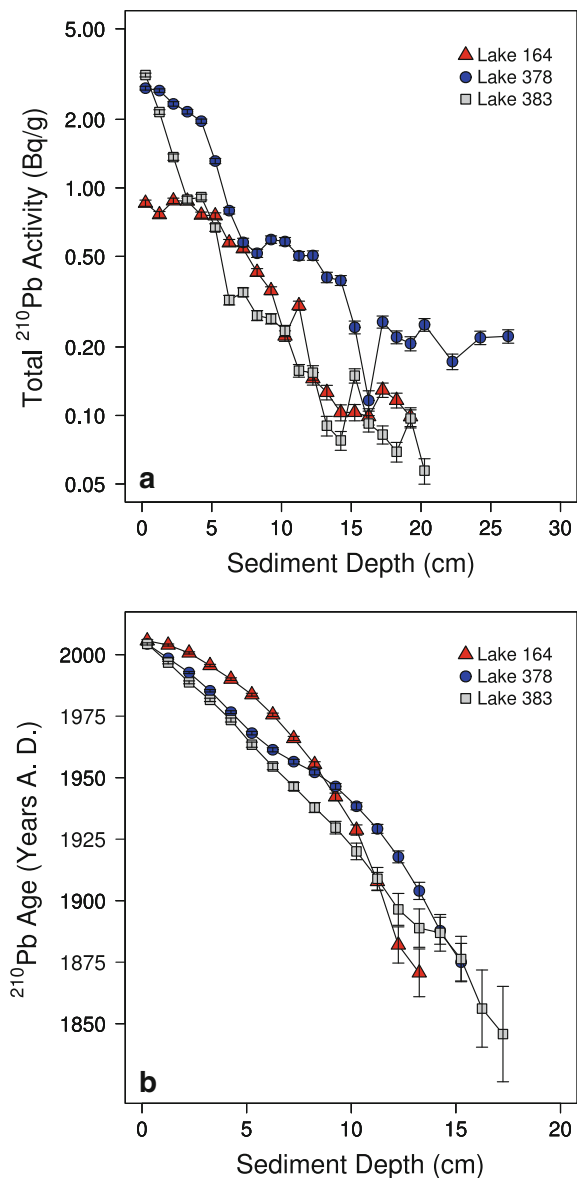


Fig. 2 ^{210}Pb radiometric dating analysis of sediment cores from lakes 164, 378, and 383. **a** Total ^{210}Pb activity versus sediment depth; **b** estimated age of sediment versus sediment depth. Error bars indicate 1 SD in sediment age

“bottom” sample, sediment depth 20.0–20.5 cm) representing pre-1900 (Enache et al., 2011), and deposited prior to the onset of acid deposition in eastern North America (Cogbill & Likens, 1974; Charles et al., 1990). For the three lakes in which daphniid remains were identified in both the “top” and “bottom” sediment samples (lakes 164, 378, and 383), sediments were analyzed in greater detail to determine

how cladoceran assemblages changed through time. Age–depth relationships were determined using ^{210}Pb radioisotopic techniques (Appleby, 2001) and gamma emission analysis (Schelske et al., 1994) by an Ortec[®] germanium-crystal well detector at the Paleoecological Environmental Assessment and Research Lab (Queen’s University, Kingston, ON, Canada). Dates were calculated using the constant rate of supply (CRS) model (Appleby & Oldfield, 1978; Binford, 1990), revealing similar activity profiles for each of the three lakes (Fig. 2). Background ^{210}Pb activities at a sediment depth of ~ 15 cm (corresponding to a calendar date of ~ 1875), validate that the deeper sediment depth considered in our “top–bottom” analysis (i.e., 20.0–20.5 cm) is representative of a period prior to major industrial development in eastern North America. Cladoceran analyses were performed on ~ 20 additional sediment intervals from each of these three sediment cores, providing a decadal-scale resolution over the past ~ 150 –200 years.

The preparation of microscope slides for the analysis of sedimentary cladoceran remains followed standard methods, as described in Korhola & Rautio (2001). Cladoceran remains (i.e., carapaces, headshields, post-abdominal claws, etc.) were tabulated separately and the total number of individuals present was calculated using the most abundant remain for each taxon (Frey, 1986). A minimum of 90 individual cladocerans (a sub-sample large enough for a representative estimation of the sedimentary cladoceran assemblage; Kurek et al., 2010) were identified from each sediment interval using a Leica DMRB light microscope with bright field optics (10–40 \times objective, 10 \times ocular lens). To remove the potential bias of a non-random distribution of remains, each slide was counted in its entirety.

The primary taxonomic resources used for identification of the cladoceran remains included Smirnov (1996), Sweetman & Smol (2006), Szeroczyńska & Sarmaja-Korjonen (2007), and Korosi & Smol (2012a, b). The postabdominal claws from *Daphnia* spp. were attributed to a species complex according to the presence/absence of stout middle pecten (Korosi et al., 2011): the *D. pulex* complex (stout pecten present) in this region may include the species *D. pulex*, *D. pulicaria*, *D. catawba*, and *D. minnehaha*; whereas the *D. longispina* complex (stout pecten absent) may include *D. mendotae*, *D. longiremis*, *D. dentifera*, *D. dubia*, and *D. retrocurva* (Keller & Pitblado, 1989; Hebert, 1995).

To first examine broad differences in the cladoceran assemblages between the two time periods, an analysis of similarity (ANOSIM) was performed using the vegan package (Oksanen et al., 2010) for the R software environment (R Development Core Team, 2011). ANOSIM is a non-parametric multivariate test used to examine a similarity matrix (of square-root transformed cladoceran relative abundances) comparing the samples (lakes) from the two a priori defined groups (i.e., the “tops” vs. the “bottoms”) by ranking them according to Bray–Curtis similarity, with minimal statistical assumptions (Clarke, 1993). The ANOSIM test determines whether average pair-wise similarity within groups is greater than average pair-wise similarity between groups. To then test whether the relative abundances of any individual taxa significantly differed between the modern and pre-industrial samples, we used a non-parametric Wilcoxon Signed-Rank test, again using the vegan package (Oksanen et al., 2010).

Ordination techniques were used to summarize the patterns of change in the modern and pre-industrial cladoceran assemblages of the ten study lakes. The percent relative abundance species data were square-root transformed prior to the analyses to equalize the variance among taxa. An initial detrended correspondence analysis (DCA) of the modern-day and pre-industrial species assemblages revealed relatively short gradient lengths (1.82 and 1.40 SD units for the first and second axes in the modern samples, and 1.58 and 1.52 SD units for the pre-industrial assemblages). Consequently the relationships between species assemblages were explored with principal component analysis (PCA) using the vegan package (Oksanen et al., 2010) for the R software environment (R Development Core Team, 2011). Both modern and pre-industrial samples were run in a combined ordination to allow modern and pre-industrial niche space to be observed in the PCA biplot, thus providing an assessment of change in the lakes over time.

The sediment cores from the three lakes with daphniid remains present in the “top/bottom” samples were examined in greater detail both for general trends over time in the crustacean zooplankton assemblages, and more rigorously using cluster analyses (constrained incremental sum of squares (CONISS); Grimm, 1987), with the number of zones determined via the broken stick model (Bennett, 1996). CONISS was performed using the vegan package (Oksanen

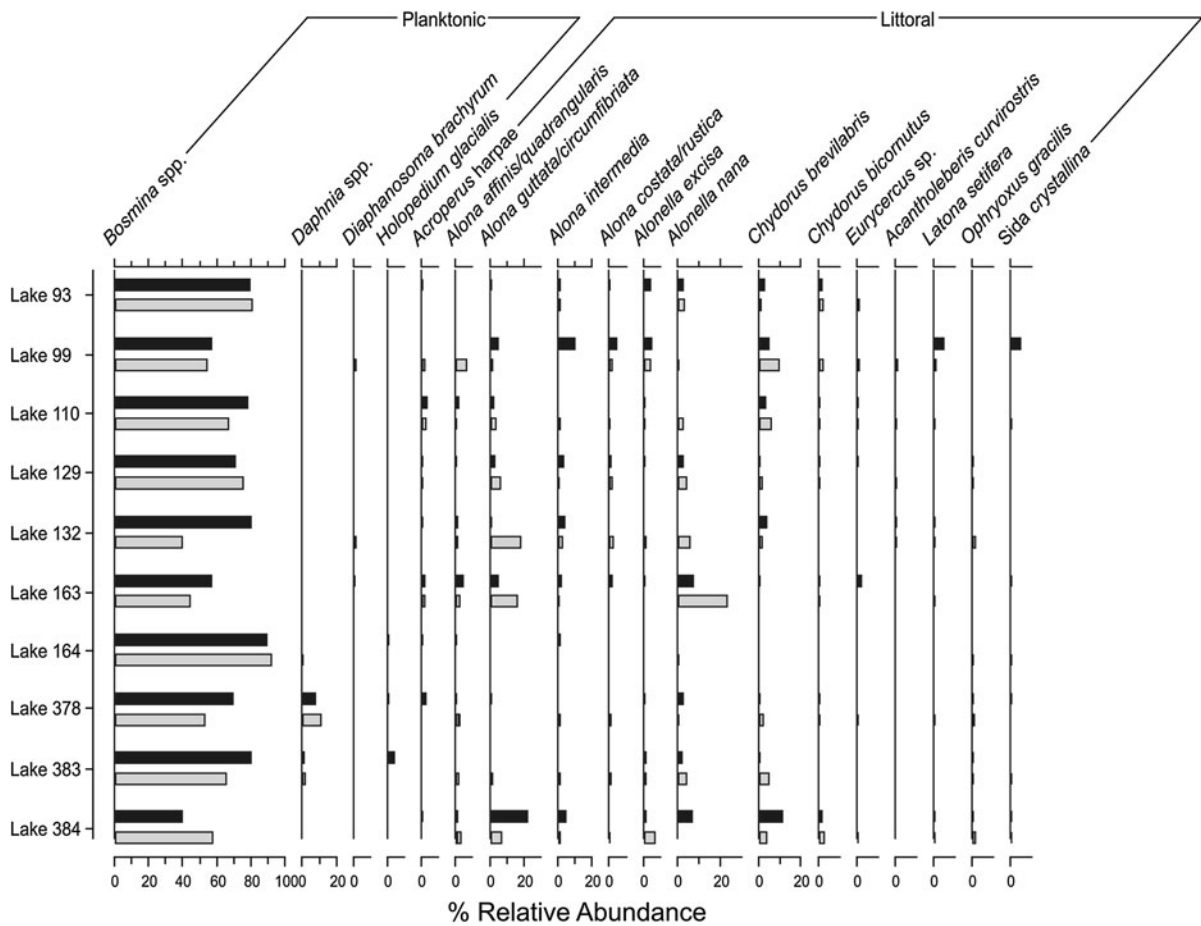


Fig. 3 Relative abundances of sedimentary crustacean zooplankton remains found in the modern-day (“top”; *black*) and pre-industrial (“bottom”; *gray*) sediments of the ten ELA study lakes. Daphniid remains were only observed in lakes 164, 378, and 383

et al., 2010) for the R software environment (R Development Core Team, 2011).

Results

The sedimentary cladoceran assemblages identified in the initial “top/bottom” analysis of the ten study lakes were broadly typical of softwater lakes on the Canadian Shield, with relatively simple assemblages dominated by the pelagic taxa *Bosmina* spp. and a diverse collection of littoral chydorid taxa (principally *Alona* spp. and *Chydorus* spp.; Fig. 3). The ANOSIM did not identify significant differences between the two time periods across the full dataset ($R = -0.01$, $P = 0.53$), nor did any individual taxa show significant directional changes through time across all lakes

in the Wilcoxon Signed-Rank tests. Differences between the two time periods were characterized by an increase in the relative abundances of *Bosmina* spp. of 10% or more in 5 of the 10 lakes, as well as smaller increases in *Alona intermedia*, and a coincident decrease in the other chydorid taxa (notably *Alona affinis/quadrangularis*; Fig. 4). As the ten study lakes were screened a priori to ensure similar physical and chemical environments, the modern-day crustacean zooplankton sedimentary assemblages were broadly similar, demonstrated by their similar site scores in the PCA biplot (47% of the variation present in the relative abundance data (square-root transformed) was captured by the first two ordination axes; Fig. 5).

Daphniid remains were recorded in only three of the ten lakes (164, 378, and 383; Fig. 3), albeit at small relative abundances: Lake 164 had daphniids present

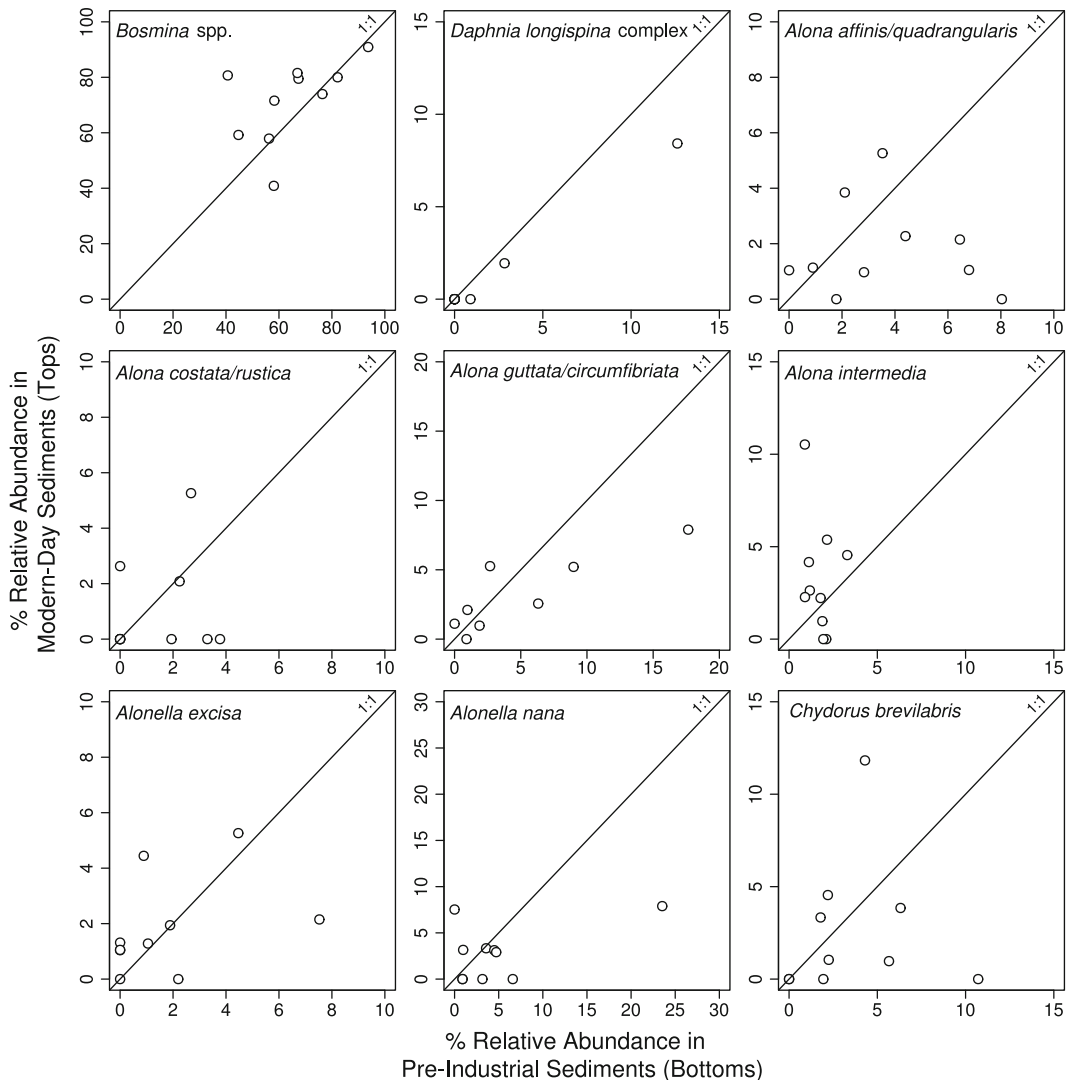


Fig. 4 Changes in the relative abundance between the “top” (surface) and “bottom” sediments (pre-industrial) for the major cladoceran taxa present in the ten ELA study lakes. The 1:1 line is also shown

in low ($\sim 1\%$) relative abundances in the “bottom” interval; Lake 378 had daphniids present in relatively high ($\sim 10\%$) abundances in the “top” and “bottom” intervals; and in Lake 383, daphniids were present in low ($\sim 2\%$) relative abundance in both the “top” and “bottom” intervals.

The down-core sedimentary cladoceran assemblages from Lake 164 remained stable throughout the core (Fig. 6). Bosminid remains dominated the assemblages ($\sim 90\%$ relative abundance) for the entire record, whereas daphniids (solely represented by the *Daphnia longispina* complex) were present only sporadically in low abundances. The most

notable changes were the appearance and gradual increase of *Holopedium glacialis* beginning in the 1960s, coinciding with the disappearance of *Alonella nana* from the littoral community. After performing the cluster analysis (CONISS), no “significant” zones were identified by the broken stick model (Bennett, 1996).

Lake 378 contained the most diverse assemblages of the three lakes (Fig. 7), with 31 species or groups identified. Although bosminid remains dominated the assemblages, daphniids (particularly members of the *D. longispina* complex) also comprised a sizable proportion ($\sim 10\%$) of the assemblage. Despite

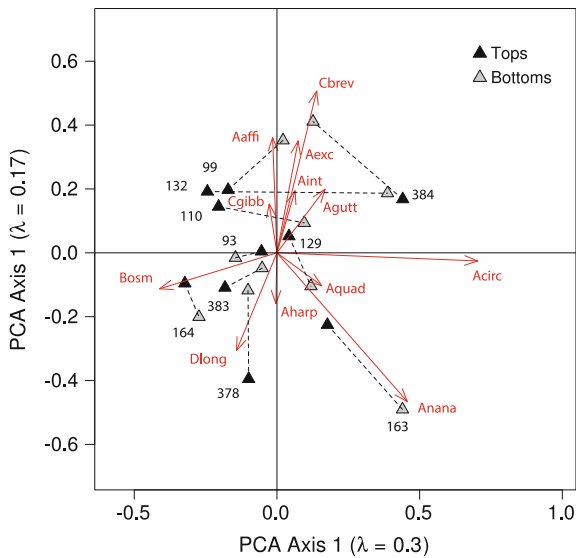


Fig. 5 Principal component analysis (PCA) biplot showing the relationship between species and site scores for the ten lakes of the “top/bottom” analysis (modern-day site scores, black triangles; pre-industrial site scores, gray triangles). Species names and associated symbols are *Acroperus harpae* (Aharp), *Alonella excisa* (Aexci), *Alonella nana* (Anana), *Alona affinis* (Aaffi), *Alona circumfimbriata* (Acirc), *Alona guttata* (Agutt), *Alona intermedia* (Aint), *Alona quadrangularis* (Aquad), *Bosmina* spp. (Bosm), *Chydorus brevilabris* (Cbrev), *Chydorus gibbus* (Cgibb), *Daphnia longispina* complex (Dlong)

variability among the littoral species, the assemblages have remained relatively stable throughout the last two centuries. After performing the cluster analysis (CO-NISS), no “significant” zones were identified by the broken stick model (Bennett, 1996).

Of the three lakes analyzed in detail, Lake 383 had the most pronounced changes in its crustacean zooplankton assemblages (Fig. 8). Bosminid remains were present in high abundances throughout the core; however, their dominance increased from ~65% in the late 1800s to ~80% at the start of the twentieth century. Remains from the *D. longispina* complex were present in low, but consistent abundances from the 1880s until the 1940s, at which point they were virtually eliminated from the sediments and subsequently only present in a few intervals at trace levels. Concurrent with the disappearance of the daphniids in the 1940s, *H. glacialis* appeared and has gradually increased in relative abundance in recent sediment intervals. The littoral community was dominated throughout the record by the combination of *A. nana* and *Chydorus* spp.; however, both have declined in

relative abundance since the beginning of the record, coincident with general increases in *Bosmina* spp. The only zonation identified as “significant” by the broken stick model (Bennett, 1996) occurs at ~1900.

Discussion

The water chemistry of the ELA study lakes is typical of softwater lakes located on the Canadian Shield; however, over the past several decades, there has been a regional decline in lakewater Ca concentration of ~15% while pH has remained circumneutral (a 2002 survey of 92 ELA lakes revealed 45% were <1.5 mg Ca l⁻¹, relative to only 21% 20 years earlier; Findlay & Shearer, 1992; Jeziorski et al., 2008). Eight of the ten study lakes (the exceptions were Lake 163 and Lake 378) examined in the “top/bottom” sediment analysis were included in the Canadian Wildlife Service helicopter surveys described by Jeziorski et al. (2008) and seven of these eight lakes have experienced declines of ~15–20% in aqueous Ca since the 1980s (presently all of the study lakes are below 2.8 mg l⁻¹ Ca; Table 1). However, despite declines in lakewater Ca, the sedimentary cladoceran assemblages have remained relatively stable (Figs. 3, 4), and radiometric dating of the three sediment cores (lakes 164, 378, and 383) revealed that background ²¹⁰Pb activity (i.e., ~1875; Binford, 1990) corresponded with a sediment depth of ~15 cm (Fig. 2), a shallower depth than was used for the “bottoms” of the “top/bottom” analysis (~15 vs. 20.0–20.5 cm). Despite this disparity, the assemblages from the “bottom” interval and the bottom of the dated sediments were very similar for each lake, further demonstrating the relative stability of these assemblages.

Small differences between the “top” and “bottom” cladoceran sedimentary assemblages were identified via PCA analysis, with the principal changes being an increase in the pelagic cladocerans, especially *Bosmina* spp. (Fig. 5). The lakes exhibiting the greatest changes over time (notably 132, 378, and 384) were those that had the greatest changes in *Bosmina* spp. since the pre-industrial period (Fig. 3). However, the accompanying changes in the relative abundances of the littoral taxa, *Alona* spp. and *Chydorus* spp., as well as the *D. longispina* complex, differ in both composition and direction among lakes, suggesting multiple factors may be responsible for the species shifts.

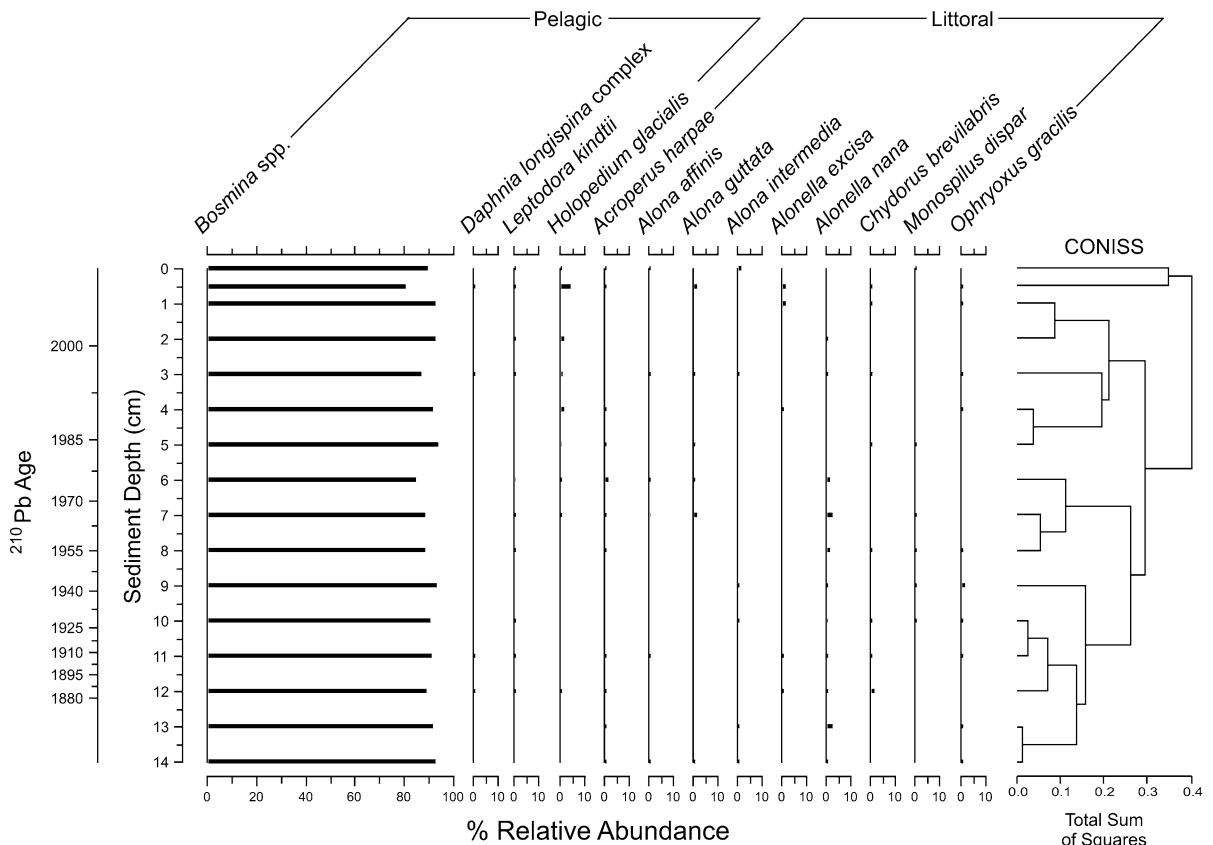


Fig. 6 Relative frequency diagram of the most common crustacean zooplankton remains found in the sediments of Lake 164. Sediments were radiometrically dated using ^{210}Pb . Results

of the constrained incremental sum of squares (CONISS) are also shown (no zonations were identified)

The general trend among cladoceran assemblages within both the “top/bottom” samples and the detailed cores were declines in littoral species (notably *Alona* spp. and *Chydorus* spp.) since the pre-industrial period and, in some cases, their complete disappearance from the assemblage. The dwindling abundances of littoral species resulted in the only zonation identified in the cluster analyses (at ~1900 in Lake 383; Fig. 8). The reduction in the relative abundances of littoral species is accompanied by a concurrent increase in *Bosmina* spp., pre-dating the changes in *Daphnia* spp. and *H. glacialis* relative abundance during the mid-twentieth century. The ELA’s location has kept it relatively undisturbed with respect to local anthropogenic stressors (the watershed of Lake 383 did experience a fire during 1974, but there is little evidence of its impact on the cladoceran sedimentary assemblage; Fig. 8), yet there has been some regional environmental changes over recent decades, including a

prolonged warm period during the 1970s and 1980s which resulted in lakes becoming warmer and clearer (Schindler et al., 1996). The decrease in stream export associated with this period of drought reduced chemical inputs to the lakes decreasing concentrations of dissolved organic carbon (DOC; Schindler et al., 1997), a change that may have increased the vulnerability of daphniids to visual predators relative to *Holopedium* (Wissel et al., 2003). However, the changes among the cladoceran sedimentary assemblages (i.e., in the early and mid-twentieth century; Figs. 6, 7, 8) pre-date this recent warm period and are more likely associated with an earlier climate response detected in paleolimnological analyses of ELA phytoplankton (Enache et al., 2011). Broad ecological shifts within the algal diatom communities of temperate lakes (i.e., increases in the relative abundances of pelagic taxa concurrent with decreases in littoral taxa) have been attributed to increases in the intensity of

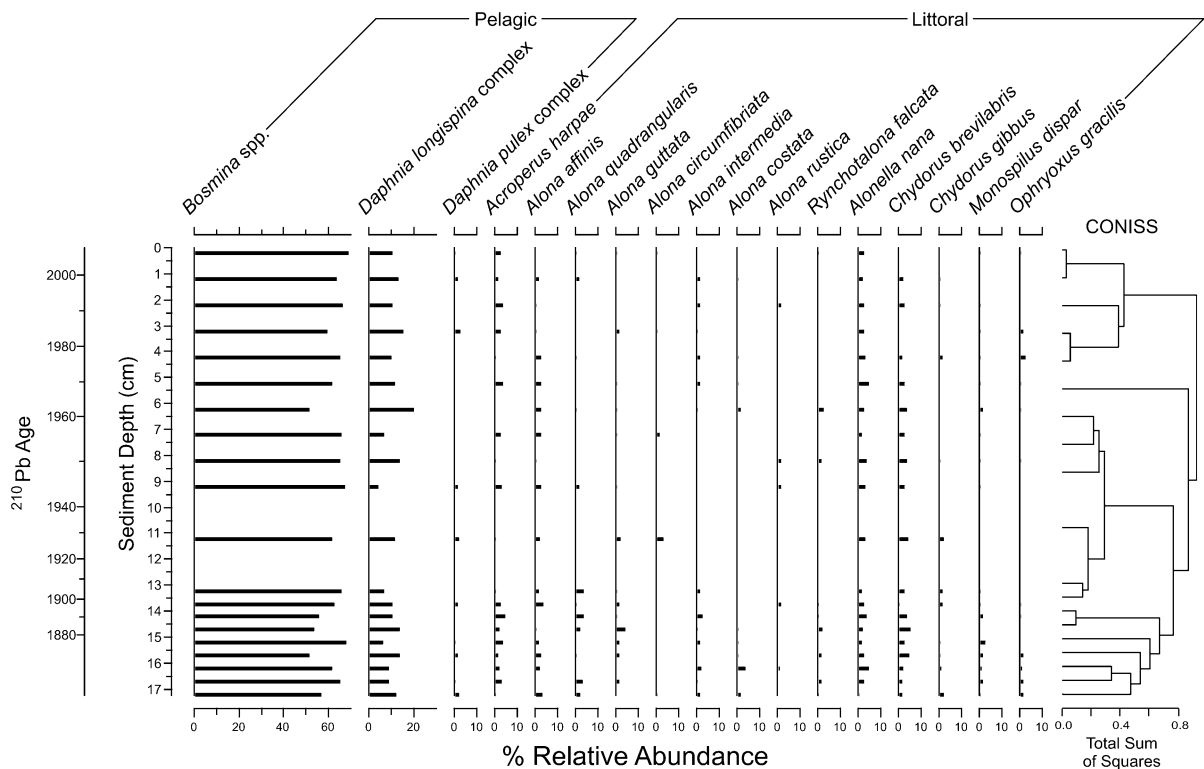


Fig. 7 Relative frequency diagram of the most common crustacean zooplankton remains found in the sediments of Lake 378. Sediments were radiometrically dated using ^{210}Pb . Results

of the constrained incremental sum of squares (CONISS) are also shown (no zonation was identified)

lake stratification and longer ice-free periods associated with regional climate warming (Rühdland et al., 2008), and the substantive modern-day increases in planktonic diatom abundances in lakes 99, 132, and 378 (Enache et al., 2011) coincide with some of the largest bosminid increases in the ten study lakes.

Although our intent was to examine lakewater Ca decline in circumneutral ELA lakes using changes in daphniid abundance, this objective was complicated by the absence or low relative abundance of daphniids in nine of the ten study lakes (Fig. 3). The relative scarcity of daphniids may be attributable to a focus on the extreme low end of daphniids' Ca range, as laboratory estimates of a 1.5 mg l^{-1} Ca limitation threshold for *D. pulex* (Ashforth & Yan, 2008) are substantially lower than recent field estimates of optimal Ca concentrations for many daphniid taxa common to softwater Shield lakes ($2.76\text{--}16.10 \text{ mg l}^{-1}$; Cairns, 2010). The daphniid remains identified in both the "top/bottom" (Fig. 5) and the detailed core analyses (Figs. 6, 7, 8) were almost exclusively from the *D. longispina* species complex (the

complex most sensitive to Ca limitation; Cairns, 2010; Jezierski et al., 2012a), with only a minimal presence of the *D. pulex* complex in the sediments despite historical records indicating the existence of *D. catawba* (a species tolerant of both low Ca and low pH conditions; Malley & Chang, 1986; Cairns, 2010) in low abundances in this region (Patalas, 1971). Of the three lakes containing daphniid remains, the greatest changes in daphniid relative abundance occurred in Lake 383 with a decrease from low, but consistent abundances ($\sim 2\%$) to near absence during the 1940s. Coincident with this daphniid decline/disappearance was the arrival and persistence of the planktonic taxon *H. glacialis*. Although little is known regarding the Ca requirements of the littoral Cladocera, three littoral taxa encountered in the "top/bottom" analyses (*Acroperus harpae*, *Alonella excisa*, and *Chydorus brevilabris*; Fig. 3) have been identified as having relatively low Ca content (i.e., % of dry body weight; Shapiera et al., 2011). However, none of these three species exhibited much directional change between the two time periods (Figs. 3, 4).

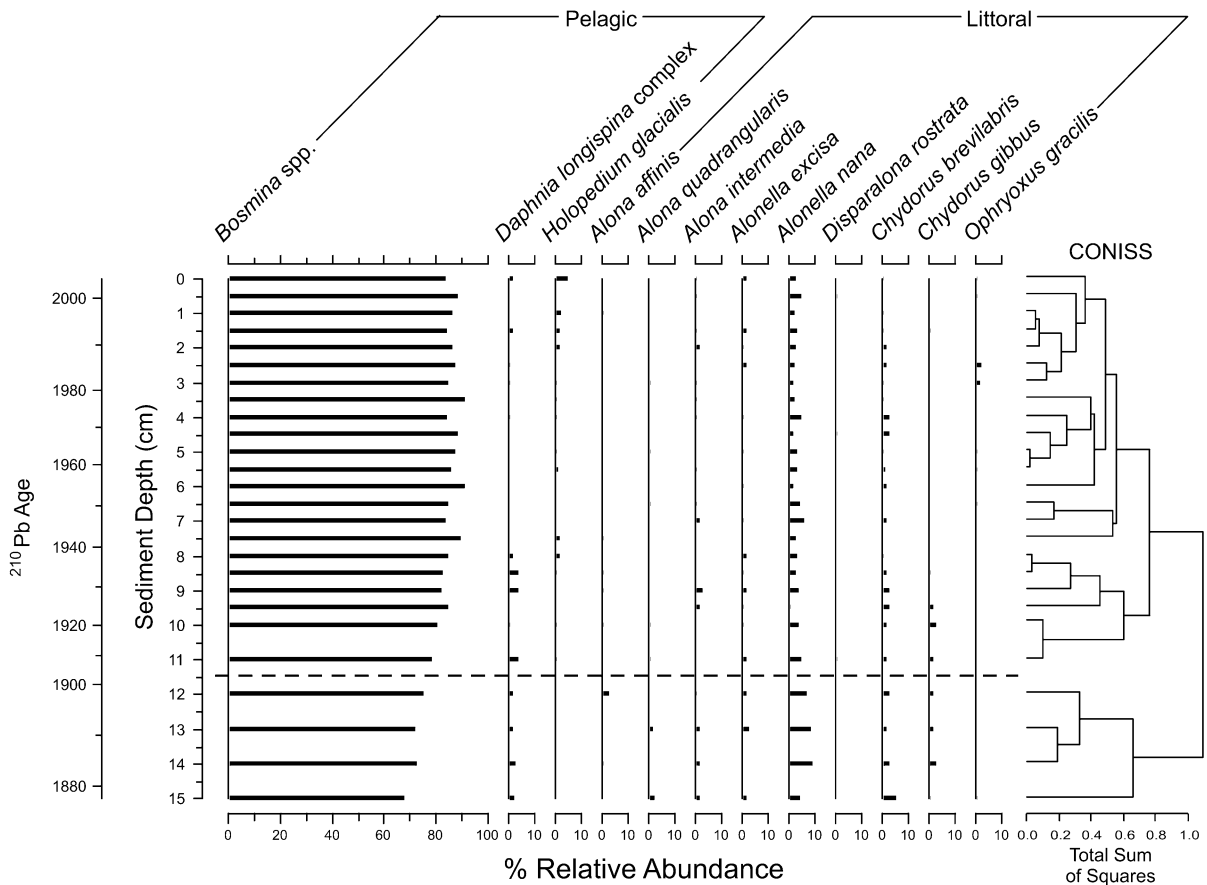


Fig. 8 Relative frequency diagram of the most common crustacean zooplankton remains found in the sediments of Lake 383. Sediments were radiometrically dated using ^{210}Pb . Results

Among pelagic cladocerans, there have been small ($\sim 0\text{--}5\%$) increases in *H. glacialis* since the mid-twentieth century in lakes 164 and 383, a decrease in the *D. longispina* complex since ~ 1940 in Lake 383, and an increase in *Bosmina* spp. in 383 since ~ 1900 . The rise of the Ca-poor taxa *H. glacialis* and *Bosmina* spp. (0.2–0.4% of dry body weight; Wærvågen et al., 2002; Jeziorski & Yan, 2006) at the expense of Ca-rich daphniid species (0.8–8% of dry body weight; Wærvågen et al., 2002; Jeziorski & Yan, 2006) in lakes 164 and 383 are changes consistent with reduced Ca availability, whereby taxa with low Ca requirements realize a competitive advantage. In other locations, the subtle changes since the 1940s in lakes 164 and 383 would likely be attributed to the onset of acid deposition (i.e., an increase in acid-tolerant taxa at the expense of acid-sensitive taxa). However, the ELA is remote from sources of industrial emissions

of the constrained incremental sum of squares (CONISS) are also shown (the horizontal dashed line marks the zonation identified by the broken stick model)

and the study lakes are presently circumneutral (Table 1), with no evidence to suggest that lake pH has been low enough to constitute a stressor for acid-sensitive crustacean zooplankton taxa either since the establishment of the ELA (Patalas, 1971; Enache et al., 2011) or in diatom-inferred pH reconstructions dating back to pre-industrial times (e.g., Dickman et al., 1988; Paterson et al., 2002).

Although changes in the relative abundances of cladoceran remains from pelagic species in the sediment records of lakes 164 and 383 provide limited evidence of Ca limitation impacts on aquatic communities in the absence of concurrent pH changes and timber harvesting, the changes in Ca-rich versus Ca-poor species are subtle, despite indications of a threshold response in laboratory conditions (Hessen et al., 2000; Ashforth & Yan, 2008; Tan & Wang, 2010). The relative stability of the cladoceran

assemblages (with the principal changes suggesting regional warming) and low daphniid abundances in most of the study lakes suggest that perhaps Ca limitation presents a competitive disadvantage prior to reaching lethal levels in natural environments, or that the poor taxonomic resolution of the daphniid species complexes in the sediment record is obscuring a progressive pattern of species replacement within the complex due to differing Ca thresholds (Cairns, 2010). As declines in lakewater Ca availability are expected to continue (Watmough et al., 2003) and the endpoints remain uncertain due to the site-specific nature of the issue, the next logical step in the development of the study of Ca decline using paleolimnological techniques will be to determine the taxa and/or communities that are benefitting from decreasing Ca availability (e.g., *H. glacialis*). Increasing our understanding of the broader response of aquatic communities in regions experiencing Ca declines will avoid the principal difficulties of recent observational studies focused upon daphniid changes (e.g., Jeziorski et al., 2012a). To take full advantage of the abundant information present in the sediment record, it is necessary to increase our knowledge of the Ca demands of a wider variety of fauna with remains that preserve well in sediments, and integrate this information with both direct monitoring programs in softwater regions and targeted sediment core analyses.

Conclusions

As neither acid deposition nor timber harvesting is present to any significant degree in the ELA region (limited logging occurred in the watersheds of selected ELA lakes between 1970 and 1980, including lakes 164 and 378), recent declines in lakewater Ca are most likely due to an alternate mechanism such as the reduced atmospheric deposition of Ca or increased stream acidity related to changes in drought (i.e., reduced base cation export) and forest fire frequency. Regardless of the underlying mechanism, Ca concentrations in some ELA lakes have fallen to levels that are detrimental to Ca-rich daphniids and although significant assemblage-wide differences among the sedimentary cladoceran remains were not observed, there have been subtle decreases in daphniid relative abundance and increases in their Ca-poor competitors (*Bosmina* spp. and *H. glacialis*). However, although

the shifts in daphniid fauna and Ca availability have occurred at circumneutral pH levels, the minor changes among the cladoceran sedimentary assemblages have likely been exacerbated by climate warming in recent decades. Due to the taxonomic limitations of daphniid sedimentary remains, future paleolimnological work examining the impact of Ca decline using cladocerans should focus on taxa such as *H. glacialis* that are likely to benefit from reduced Ca availability.

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