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Variation in calanoid copepod resting egg abundance among lakes with different acidification histories

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Abstract The maintenance of species and genetic diversity within zooplankton egg banks may be crucial to the re-establishment of zooplankton communities following historical disturbance, such as anthropogenic acidification which globally caused widespread damage to ecological communities. Despite this, no other study has described basic characteristics of zooplankton egg banks among lakes with different acidification histories, such as variation in resting egg concentration. Theoretically, habitats with frequent periods of harsh environmental conditions are expected to select for resting egg production or prolonged dormancy in zooplankton, which would increase the size of the resting egg bank in lake sediments. In this study, we compared abundances of viable and inviable calanoid copepod resting eggs among three freshwater lakes with different acidification histories. While Swan Lake underwent major chemical and biological changes from acid and metal deposition, Teardrop and Bat lakes were relatively unaffected by historical acidification and had comparatively constant, but different pH over time. We also tested the effect of age on the viability of resting eggs. As predicted, higher numbers of viable resting eggs were found in recent sediments from acid-recovering Swan Lake compared to study lakes with relatively temporally constant environments (Teardrop and Bat lakes) when the total number of eggs was held as a covariate. We detected this result in spite of similar pelagic abundances of *Leptodiaptomus minutus*, the dominant species in zooplankton communities of these lakes. This pattern did not necessarily hold for inviable egg concentrations since these eggs were more abundant in both Swan and Bat lakes compared to Teardrop Lake in older sediments (1939–1951, 1800s). Within study lakes, the abundance of viable resting eggs declined with increased egg age. Further study is required to test mechanisms underlying these patterns.

Keywords Acidification · Copepods · Freshwater lakes · Resting eggs

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Introduction

Zooplanktons are a key component of aquatic communities, and knowledge of how they cope with environmental stressors is important for understanding how the aquatic ecosystem as a whole will respond. Anthropogenic acidification caused widespread and long-lasting damage to biological communities in boreal lakes globally (Schindler, 1988). Along with increased acidity, many lakes faced additional stressors from metal contamination (Keller & Pitblado, 1986). Even with drastic reductions in smelter emissions and improvements in water chemistry in recent decades (Keller et al., 2003, 2004), full recovery of the crustacean zooplankton community has still not been observed in many lakes (Keller et al., 2002).

Many zooplankton, such as calanoid copepods, rely on the production of dormant resting or diapausing eggs to survive through periods of unsuitable physical or biological conditions (e.g,. increased predation, competition, low food availability, and seasonal change) (Brendonck & De Meester, 2003). Theoretically, the stability, predictability or frequency of periods of harsh environmental conditions in an organism's habitat determines whether diapause is a viable strategy or not (Gyllström & Hansson, 2004). For example, initiation of calanoid copepod resting egg production has been found to occur earlier in the season in temporary water bodies than permanent ones (Hairston and Van Brunt, 1994), and more frequently in temporary ponds compared to permanent ponds (Piercey & Maly, 2000). A declining trend in copepod resting egg production occurs toward the tropics, where seasonal fluctuations in environmental conditions (e.g., temperature, photoperiod, food availability, predation patterns) are relatively small compared to temperate regions (Dahms, 1995). It is not known if induction of resting egg production is linked to intra- or inter-annual variation in other environmental conditions, such as lake-water pH and metal concentrations. Temporal changes in pH occur during chemical recovery of acidified lakes and it is possible that there are differences in calanoid copepod resting egg production among lakes with different acidification histories.

Of the many factors that influence viability and hatching success of resting eggs (e.g., predation, disease, parasitism, degradation, and senescence), age appears to be particularly important (Brendonck & De Meester, 2003). Viable copepod eggs tend to be most abundant in the top 4–6 cm of lake sediments and decrease markedly with depth and age of sediment (Hairston & Van Brunt, 1994; Hairston et al., 1995). Despite the negative effects of age, resting eggs have the potential to remain viable for many decades or even centuries (Hairston et al., 1995). The maintenance of species and genetic diversity within egg banks may be crucial to the re-establishment of zooplankton communities following historical disturbance (Hairston 1996), such as acidification.

Despite their potential importance to the recovery of damaged lakes, few studies have addressed zooplankton egg banks in lakes recovering from anthropogenic acidification. No other study has described basic characteristics of zooplankton egg banks, such as variation in egg concentration, among lakes with different acidification histories. Other work on resting eggs from acidified lakes has examined factors controlling in-situ emergence (Arnott & Yan, 2002; Binks et al., 2005), genetically identified historical species assemblages (Pollard et al., 2003), and re-constructed historical ecological tolerances (Derry et al. unpubl.). In this study, we compared the abundance of calanoid copepod resting eggs among three lakes with different acidification histories. Swan Lake underwent major chemical and biological changes from acid and metal deposition associated with the Sudbury smelting activities (Dixit et al., 1989; Uutala & Smol, 1996). The other two study lakes, Teardrop and Bat lakes, were relatively unaffected by historical acidification and have had comparatively constant, but different pH environments over time (Uutala & Smol, 1996; Gunn et al., 2001). We predicted that adverse changes in environmental conditions caused by acidification would result in higher concentrations of viable and inviable resting eggs in the sediment egg bank of acid-recovering Swan Lake compared to Teardrop and Bat lakes. We also tested whether the abundance of viable resting eggs decreased with age.

Materials and methods

Study lakes

Swan Lake (46°22 N, 81°04 W) is a small lake (area, 5.8 ha; maximum depth, 8.8 m) with a high flushing rate (water renewal time of <1 year) that was affected by acid and metal deposition associated with metal smelting activities around Sudbury, ON, Canada (Dixit et al., 1989). The pH of Swan Lake was between 5.6 and 6.1 prior to the onset of lake acidification, but dropped to 4.0 and metal levels increased markedly during the 1970s (Fig. 1; Dixit et al., 1989). Low pH and increased heavy metal concentrations likely resulted in the disappearance of fish populations from Swan Lake during the 1950s (Uutala & Smol, 1996). With drastic reductions in smelter emissions from the local area, pH increased (Fig. 1) and metal concentrations declined between 1977 and 1987 (Keller et al., 1992). Chemical and biology recovery were interrupted by a drought-induced re-acidification event in 1988, which resulted in substantial decreases in pH, increases in metal levels and alterations to the plankton communities (Fig. 1; Keller et al., 1992; Arnott et al., 2001). While pH has since increased to 5.6 (Fig. 1), metal concentrations remain high (concentrations of copper and nickel were approximately 17 and 75 μg/l, respectively, in 2003; Keller et al., 2004). The hypolimnion of Swan Lake remains oxygenated throughout the summer (B. Keller, Ontario Ministry of the Environment, *unpublished data*). Species richness of the zooplankton community remains low (Arnott et al., 2001) and over the past decade, the crustacean zooplankton community has been dominated by a single calanoid copepod species, *Leptodiaptomus minutus* Lilljeborg (Arnott et al., 2001; S. McPhee for 2007 data pers. comm., Queen's University).

Teardrop Lake is a small lake (area, 3.4 ha; maximum depth, 16.6 m) located in Killarney Provincial Park, ON, Canada (46°2′ N, 81°24′ W). As a result of calcium diabase in its catchment, Teardrop Lake never acidified, but consistently maintained a circum-neutral pH of 6.5–6.8 from pre-industrial times to the present (Fig. 1; Gunn et al., 2001). During summer stratification, the hypolimnion of Teardrop Lake remains oxygenated Lake (B. Keller, Ontario Ministry of the Environment, *unpublished data*). Teardrop Lake has low metal levels (concentrations of aluminum, copper and nickel were 3.1, < 0.1 and 0.5 μg/l, respectively, in 1998; Gunn et al., 2001) and supports numerous species of phytoplankton, zooplankton, and fish (Snucins & Gunn, 1998). *Leptodiaptomus minutus* is also a dominant zooplankton species in Teardrop Lake (B. Keller, Ontario Ministry of the Environment, *unpublished data*).

Bat Lake is a small, oligotrophic kettle lake (area, 3.4 ha; maximum depth, 8.3 m) located in Algonquin Provincial Park, ON, Canada (45°35′ N, 78°31′ W). Bat Lake has been an acidic (pH 4.6), fishless, bog

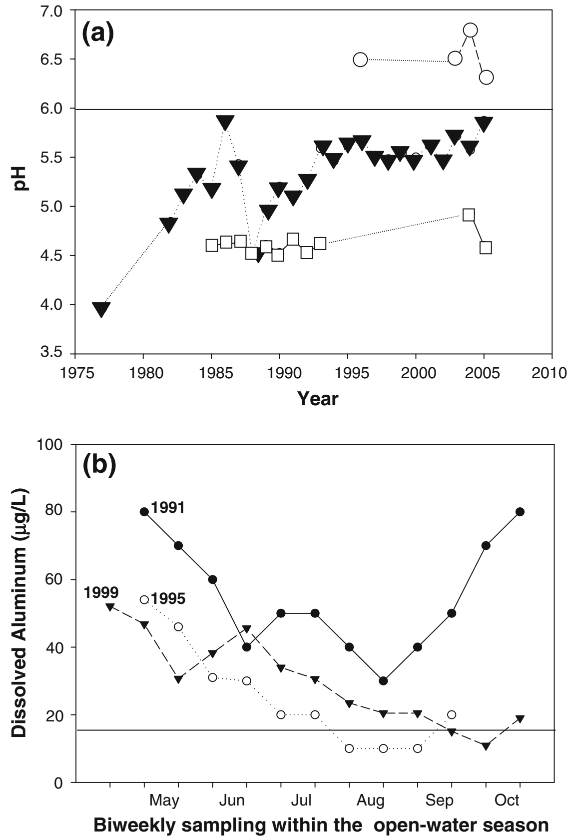

Fig. 1 (**a**) Annual change in lakewater pH in Swan, Teardrop, and Bat lakes between 1971 and 2006 (Sprules, 1975; M. Palmer, York University, *unpublished data*; A. Derry, Queen's University, *unpublished data*; B. Keller, Ontario Ministry of the Environment, *unpublished data*; B. Girard, Ontario Ministry of the Environment, *unpublished data*). Measurements were taken in the epilimnion during mid-summer. The horizontal line along pH 6.0 indicates the critical threshold for acid-sensitive species (Holt & Yan, 2003). Solid up-side-down triangles represent historically acidified Swan Lake. Open symbols represent lakes with historically stable lake-water pH: Teardrop (circles) and Bat (squares). (**b**) Seasonal variation in dissolved aluminum concentrations (μg/l) in Swan Lake in years spanning from 1991 to 1999 (biweekly sampling of the epilimnion from May to Oct.; B. Keller and J. Heneberry, Ontario Ministry of the Environment, *unpublished data*). The solid, horizontal line indicates an interim Ontario provincial water quality objective for aluminum at pH 4.5–5.5 (15 μg/l; MOEE, 1994)

lake for at least 200 years (Fig. 1; Uutala & Smol, 1996). Its distinctly low surface pH is likely due to the acidifying capability of *Sphagnum* moss surrounding the lake and seepage through coarse till, particularly during spring snow-melt and autumn rainfalls (Hoeniger, 1986). Bat Lake undergoes

Table 1 Comparison of sediment dates and age categories for Swan (Uutala and Smol, 1996), Teardrop (Dixit et al., 1989; S.S. Dixit, Environment Canada, *unpublished data*), and Bat (this study) lakes

Time Period	Swan Lake		Teardrop Lake		Bat Lake	
	Time (years)	Depth (cm)	Time (years)	Depth (cm)	Time (years)	Depth (cm)
1	Not available		Not available		2004–2006	0–2
2	1991–1997	1–2	1992–1999	7–9	1992–1999	7–9
3	1948–1966	7–10	1939–1951	14–16	1939–1951	14–16
4	1848–1867	23–27	mid-late 1800s	18–20	mid-late 1800s	18–20

periods of hypolimnetic anoxia in summer and winter (Nürnberg, 1995) and has low levels of toxic metals (concentrations of aluminum, arsenic, cadmium, and lead are 10, <1, <2, and <3 μg/l, respectively; Hoeniger, 1986). *Leptodiaptomus minutus* also dominates the crustacean zooplankton community in Bat Lake (Malkin et al., 2006).

Sediment coring and analyses of resting eggs

Sediment cores were collected from the deepest parts of the three study lakes using a gravity corer (diameter, 6.35 cm; length, 40 cm). A vertical extruding device was used to section each core into 1-cm intervals down to a maximum depth of 20 cm. Sediment sections were packed in Whirlpak bags, labeled and stored at 4°C in the dark until further processing. ^{210}Pb-dated chronologies were obtained from one core per study lake by gamma spectrophotometry in the Paleoecological Environmental Assessment and Research Laboratory (PEARL) at Queen's University, Kingston, Ontario. While Swan and Teardrop lakes were cored once during the summer of 2003, four cores were collected from Bat Lake during the summer of 2006. Otherwise, similar procedures were used to collect sediment cores from all of the study lakes. Dates corresponding to sediment depth intervals for Swan and Teardrop lakes were extrapolated from previously reported data (Dixit et al., 1989; S.S. Dixit, Environment Canada, *unpublished data*).

In order to extract resting eggs from sediment cores, each 1-cm sediment section was rinsed through an 80-μm sieve with distilled water to remove fine silt particles. The sediment remaining on the sieve was placed into 15 ml centrifuge tubes with a 50:50 sugar–water solution and centrifuged at 1,700 rpm for 7 min. After centrifugation, the supernatant containing resting eggs (~100 μm diameter) was washed through a 50-μm sieve with distilled water. The retained eggs were transferred to a scintillation vial containing 0.2-μm filtered Carlyle Lake water (pH ~ 6.2; collected from Killarney Park, Ontario) and wrapped in tin foil. In order to maximize egg collection, this process was repeated by re-suspending sediment left in centrifuge tubes with a 50:50 sugar–water solution and centrifuging at 1,700 rpm for another 10 min. All vials were stored at 4°C in the dark.

In order to examine the potential influence of lake-acidification history on resting egg concentration, abundances of viable and inviable copepod resting eggs were counted from sediment cores collected from Swan, Teardrop, and Bat lakes. Four sediment intervals were considered: mid to late 1800s, 1939–1951, 1991–1999, and 2004–2006 (Table 1). Subsamples of resting eggs from each 1-cm core section from Swan and Teardrop lakes and each 2-cm core section from Bat Lake were examined under a Leica MZ16 dissecting microscope (Leica Microsystems (Canada) Inc, Suite 400, 111 Granton Drive, Richmond Hill, ON, L4B 1L5 Canada). On the basis of external morphology, three egg categories were distinguished: viable, inviable, and other. Solid, smooth, dark reddish, or brownish eggs with an approximate diameter of 100 μm were classified as viable calanoid copepod resting eggs (Lohner et al., 1990). Deteriorated eggs with an approximate diameter of 100 μm (completely clear, clear-rimmed, or fuzzy) were considered inviable calanoid copepod resting eggs. Hatched eggs (clear, opened, and often in pieces) were not enumerated because these were few and we could not exclude the possibility of shell decomposition. Eggs that were grey, green, or black in color and/or had a diameter distinctly greater or less than 100 μm were classified as "other." Any dead or alive hatchlings found (hatched during the duration of storage or during examination of samples under the microscope) were placed in a separate nauplii category. Counts were converted to nauplii densities (no./cm^3 of dead and alive hatchlings), as well as densities of viable eggs (no./cm^3 of dead and live nauplii plus viable, unhatched eggs), and no./cm^3 of inviable eggs. Total eggs (no./cm^3) were counted as dead and live nauplii plus viable, unhatched eggs plus inviable eggs.

Methods for counting egg concentrations in Swan and Teardrop lakes were similar as for Bat Lake sediment cores, but with two notable exceptions. First, whereas four different sediment cores were used as replicates to estimate resting egg concentrations from Bat Lake, only one core was collected from each of Swan and Teardrop lakes. For Swan and Teardrop lakes, between 2 and 3 sediment sections (1.0 cm thickness), from time categories equivalent to Bat Lake within the same core were used as replicates. Secondly, up to 200 calanoid copepod resting eggs were identified and counted for each 2-cm section taken from Bat Lake, except in cases where the entire sample contained <200 eggs. In contrast, 200 eggs per 1-cm section were counted from Swan and Teardrop lakes. Egg concentrations from study lakes were standardized to no. per cm^3 for comparison.

Statistical analyses

We used ANCOVA to determine whether the number of viable resting eggs (log ($x + 1$)) differed between the three lakes and with time of deposition (egg age). Total resting egg density was used as a covariate. Since sampling of replicates was approached differently between Bat (in space) and Swan and Teardrop (in time) lakes, there were fewer replicate measurements available for Swan and Teardrop lakes for each age category (2–3 replicates per age category), which resulted in an unbalanced ANCOVA design. Therefore, averaged values of replicates within the same time period were substituted for missing values and degrees of freedom were adjusted accordingly. A two-way factorial ANOVA was used to compare inviable egg concentrations among lakes.

In order to examine the role of age on resting egg viability within lakes, simple linear regression was conducted on log ($x + 1$) transformed viable and inviable resting egg densities in Bat, Teardrop, and Swan lakes with mid-point date per sediment section as the predictor variable (intervals of 1-cm for Swan and Teardrop lakes and 2-cm for Bat Lake).

Statistica 6.0 software (Statsoft Inc., 2300 East 14th St, Tulsa, OK 74104) was used to conduct ANCOVAs and ANOVAs. Assumptions of normality and equal variance were tested using the Shapiro–Wilk *W*-test and Levene's test for homogeneity of variances, respectively. Log ($x + 1$) transformations were applied, if they were found to increase homogeneity of variance and normality. Post-hoc comparisons using Tukey's honestly significant difference (HSD) tests were conducted to assess individual differences when main effects and/or interactions were found to be significant.

Results

Comparison among lakes with different acidification histories

In support of our predictions, viable eggs recently deposited in sediments (4–15 years ago: 1991–1999) were more abundant in Swan Lake compared to Teardrop (Tukey test: $P < 0.01$) and Bat (Tukey test: $P < 0.05$) lakes after removing the influence of variation in total egg concentrations among lakes (Table 2, Fig. 2a). Concentrations of older, viable eggs, however, did not vary among the three lakes (viable eggs deposited 1939–1951 and in the 1800s; Fig. 2a). All ANCOVA assumptions were met, with the exception that the covariate (total resting egg density) was not independent from treatments (lake and egg age). This was not surprising, however, since total and viable egg densities co-varied with each

Table 2 Statistical results of an ANCOVA examining the effects of lake and egg age on viable calanoid copepod resting egg concentrations

Effect	df	*F*	*P*
Covariate (total eggs)	1	5.20	<0.05
Lake	2	1.79	>0.05
Age	2	13.11	<0.01
Lake × Age	4	5.03	<0.01
Error	18		

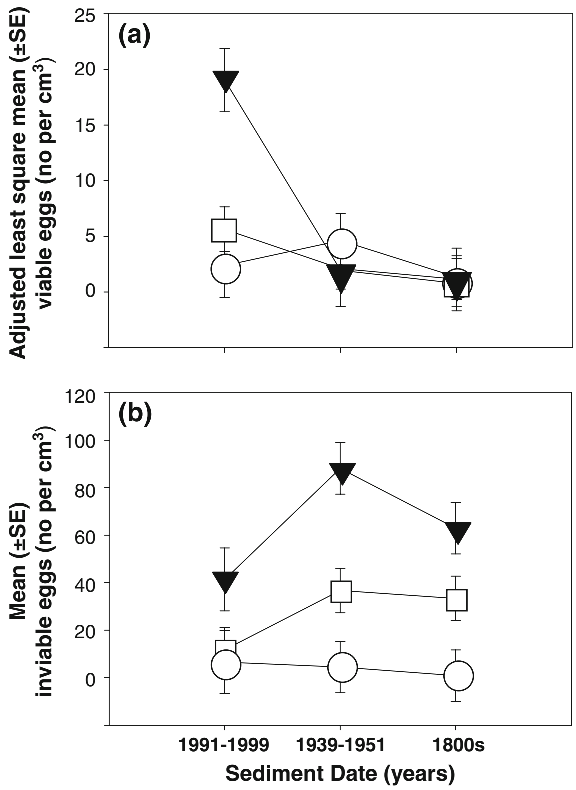

Fig. 2 Comparison of (**a**) adjusted least square mean (±SE) viable resting egg concentration (no./cm^3; total egg concentration is the covariate) and (**b**) inviable egg concentrations (no./cm^3) in Swan (solid up-side-down triangles), Teardrop (open circles), and Bat (open squares) lakes over three categories of egg age ranging from the mid-1800s to 1999. Note differences in the scales of *y*-axes in panels (**a** and **b**). Total egg concentrations were almost identical in pattern and quantity as inviable eggs and are not shown

other. The effect of violating this ANCOVA assumption was a greater risk of accepting a false null hypothesis (Type I error) (Rheinheimer and Penfield, 2001). We conducted a two-way factorial ANOVA on viable egg density ($\log(x + 1)$) without total eggs as a covariate and found that the ANCOVA results were supported by the ANOVA.

In support of our predictions, inviable egg concentration was greater in Swan Lake compared to Teardrop Lake across all categories of egg age (eggs deposited in 1991–1999, in 1939–1951, and in the 1800s) (Factorial ANOVA, lake × age interaction: df = 4, $F = 5.12$, $P < 0.01$; Tukey tests: $P < 0.01$; Fig. 2b). Also, inviable eggs recently deposited in Bat Lake (1991–1999) were as low in abundance as those in Teardrop Lake (Fig. 2b). However, old, inviable egg concentrations (deposited in 1939–1951 and in the 1800s) were similarly high in Bat Lake as in Swan Lake (Fig. 2b). Total eggs followed the same patterns and were detected in similar quantities as inviable eggs (Factorial ANOVA, lake × age interaction: df = 4, $F = 4.94$, $P < 0.01$; Tukey tests: $P < 0.01$).

Comparison within lakes through time

With increased egg age, viable resting egg concentrations declined in Swan (linear regression: $F_{1,13} = 26.56$, Adj. $R^2 = 0.65$, $P < 0.01$; Fig. 3a), Teardrop (linear regression: $F_{1,11} = 12.23$, Adj. $R^2 = 0.48$, $P < 0.01$; Fig. 3b), and Bat (linear regression: $F_{1,14} = 8.67$, Adj. $R^2 = 0.34$, $P = 0.01$; Fig. 3c) lakes. With increased egg age, inviable egg concentration increased marginally in Swan Lake (linear regression: $F_{1,13} = 4.23$, Adj. $R^2 = 0.19$, $P = 0.06$; Fig. 3a) and in Bat Lake (linear regression: $F_{1,14} = 9.46$, Adj. $R^2 = 0.36$, $P < 0.01$; Fig. 3c), but decreased in Teardrop Lake (linear regression: $F_{1,11} = 61.09$, Adj. $R^2 = 0.84$, $P < 0.01$; Fig. 3b).

Discussion

Viable resting eggs that were recently deposited (4–15 years ago: 1991–1999) were more abundant in acid-recovering Swan Lake compared to study lakes with relatively temporally constant, but different pH environments (Teardrop and Bat lakes). Recently deposited inviable egg concentration was also higher in Swan Lake compared to Teardrop Lake. However, old, inviable eggs (deposited 37–66 years ago and 200+ years ago) were more abundant in both Swan and Bat lakes compared to Teardrop Lake. Egg banks in all study lakes were limited by the effects of age as viability of resting eggs declined over time.

The greater abundance of viable resting eggs in Swan Lake compared to study lakes with relatively temporally constant environments (Teardrop and Bat lakes) may be related to the contrasting ecological histories of these lakes. Swan Lake has undergone dramatic shifts in lake-water pH (Fig. 1a) and heavy metal concentrations (Fig. 1b) associated with recovery from acidification. Theoretically, prolonged dormancy and/or increased resting egg production can occur as a response to variable habitat conditions

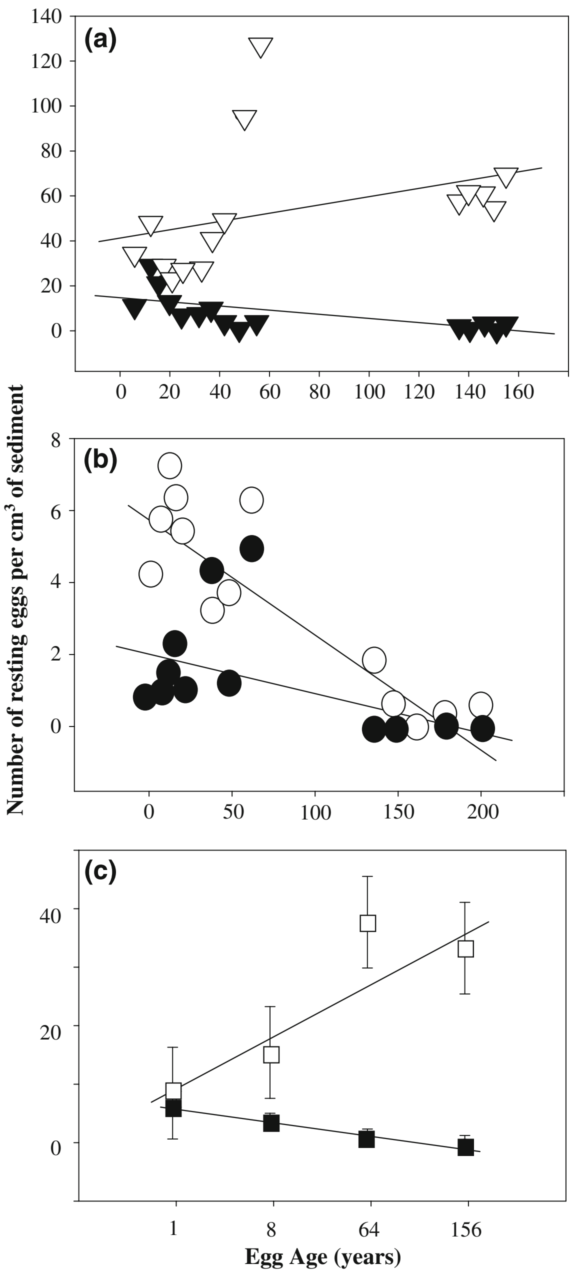

Fig. 3 Change in mean (±SE) viable (solid symbols) and inviable (open symbols) resting egg concentration (no./cm^3) within (**a**) Swan (up-side-down triangles) (**b**) Teardrop (circles), and (**c**) Bat (squares) lakes over time. Note differences in scales of *x*- and *y*-axes among panels

or environmental stress, increasing the size of the sedimentary egg bank for zooplankton (Gyllström & Hansson, 2004). Seasonally variable heavy metal concentrations, such as aluminum in Swan Lake (Fig. 1b), may pose a potential risk for recruitment in this species that could select for prolonged dormancy or increased resting egg production. *Leptodiaptomus minutus* appears to be sensitive to heavy metals because this species is often absent in metal-contaminated, acidified lakes compared to acidified lakes with low metal concentrations (Keller & Pitblado, 1984). Havens (1993) found that the survival of another calanoid copepod species, *Skistodiaptomus oregonensis*, depended on an interaction between pH and aluminum concentration. Acidity in absence of metals most likely did not directly influence differences in *L. minutus* viable egg density among lakes since Teardrop and Bat lakes had markedly different pH (Hoeniger, 1986; Gunn et al., 2001), but similar viable egg densities. Other studies have indicated that exposure to certain stressors, such as heavy metals, may reduce viability of zooplankton resting eggs in older lake sediments (Hairston et al., 1999; Kerfoot et al., 1999), but our results suggest otherwise. Direct and interactive effects of acidity and heavy metals on resting egg viability and hatchability remain to be experimentally tested.

Differences in resting egg numbers among study lakes did not appear to be related to variation in pelagic copepod abundance. From 1991 to 1999, when Swan Lake had higher overall viable egg density than Teardrop Lake (Fig. 2a), *L. minutus* abundance in the water column of Swan Lake was either similar or lower than in Teardrop Lake (Fig. 4). Similar pelagic *L. minutus* concentrations were detected in Swan and Bat lakes in 1987 (Fig. 4), but Swan likely had more viable and inviable eggs than Bat at this time (Fig. 2a). Swan Lake contained more of these copepods than Bat Lake in 2004 (Fig. 4). De Stasio (1989) presented evidence to support that egg density in sediments reflects freshwater calanoid copepod population size within a lake. However, this relationship may be less reliable when comparing between lakes, especially, if prolonged dormancy and/or increased resting egg production occurs in some lakes and not in others.

Within Swan Lake, there was a sharp increase in viable and inviable egg density between 1991–1999 and 1939–1951 (Fig. 2a) that was not observed in other study lakes. This increasing trend appeared to be related to the abundance of calanoid copepods in the water column. Calanoid copepods made up a notably small proportion of the total zooplankton community biomass in Swan Lake between 1977 and

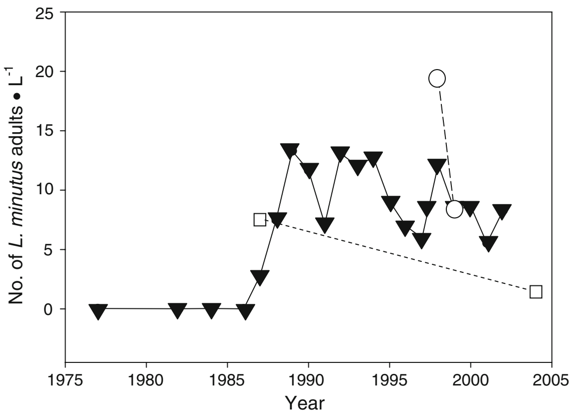

Fig. 4 Change in *L. minutus* abundance (no./L) in Swan (bold up-side-down triangles), Teardrop (open circles), and Bat (open squares) lakes between 1972 and 2005 (Sprules, 1975; Locke et al., 1994; Holt & Yan, 2003; J. Shead, Queen's University, *unpublished data*; M. Palmer, York University, *unpublished data*; B. Keller, Ontario Ministry of the Environment, *unpublished data*). Zooplankton samples were collected on a single date in mid-summer in the years shown at maximum lake depth by vertical hauls of the water column with tow nets. In cases where zooplankton were collected from epilimnion, metalimnion, and hypolimnion separately, *L. minutus* concentrations were summed across these strata

1987 (Arnott et al., 2001). *Leptodiaptomus minutus* is a dominant copepod species in many severely acidic lakes (Sprules, 1975), but is much less common in acidic lakes that are contaminated with metals (Keller & Pitblado, 1984). High metal concentrations in Swan Lake during the 1970s and early 1980s likely prevented successful establishment of this species, but with a decline in metal concentrations, *L. minutus* was able to establish in Swan Lake in 1987 (Arnott et al., 2001). The persistence of low resting egg numbers in Swan Lake sediments during the late 1980s likely resulted from egg bank depletion associated with drought-induced mass hatching (Arnott & Yan, 2002). Proliferation of *L. minutus* individuals living in the water column of Swan Lake during the 1990s likely primarily explain sharp increases in calanoid copepod resting egg concentrations in the sediments during this time. Other factors, such as prolonged dormancy or increased resting egg production per unit individual, possibly also influenced resting egg concentrations.

Although variation in sedimentation rates among lakes can influence exposure of resting eggs to the hatching cues, this was unlikely a factor that drove the among-lake differences in egg concentrations that we observed. More viable resting eggs can accumulate in lakes with high sedimentation rates and low mixing dynamics since a greater fraction of resting eggs become deeply buried before exposure to the proper hatching cues (e.g., oxygen, light, temperature) (Hairston & Kearns, 2002). Although Bat Lake had the highest sedimentation rate (0.484 cm/year) of the study lakes (Swan: 0.195 cm/year (Uutala and Smol, 1996); Teardrop: 0.149 cm/year (Dixit et al., 1989)), it had lower viable egg density compared to Swan Lake. Teardrop Lake is the deepest of study lakes (mean depth: 9.6 m) and may lose fewer viable eggs to hatch, if exposure to the hatching cues is limited in deep areas. Yet, Teardrop Lake had fewer recent viable eggs (deposited 4–15 years ago) compared to Swan Lake (mean depth: 2.8 m). ^{210}Pb dates of sediment cores taken from Swan (Uutala and Smol, 1996), Teardrop (Dixit et al., 1989), and Bat (this study) lakes indicated minimal sediment mixing.

Within all study lakes, the number of viable calanoid copepod resting eggs decreased with increasing egg age. These results were consistent with the findings of other studies (Hairston & Van Brunt, 1994; Hairston et al., 1995). This decline over time was likely the result of older eggs being exposed to adverse conditions (e.g., low oxygen levels, H_2S, extreme temperatures, parasitism, disease, predation) for longer periods of time (Brendonck & De Meester, 2003). Decreased viability over time could also result from gradual degradation of photosensitive compounds in the resting eggs, causing them to be less responsive to light cues, as has been observed for *Daphnia* sp. (De Meester et al., 1998). There is variation in the hatchability–age relationship. Calanoid copepod eggs could not be induced to hatch from Bat Lake after approximately 20 years of storage in the sediments, but 80-year-old resting eggs were hatchable from another acid-recovering lake, George Lake (Derry et al., unpubl.). Egg banks can act as a source of past genotypes and species to the active community, but their importance is likely limited by the effects of age on egg viability and the extent of this will vary among lakes.

A limitation of our study was the variation of replicates among study lakes (in space versus in time), especially since other studies have found heterogeneous spatial distributions of resting eggs (De Stasio, 1989; Hairston & Kearns, 2002). It would have been preferable to have had multiple cores from all four study lakes because increased numbers of replicates in space would have decreased variability in egg counts among replicates within lakes. In spite of this, we still found strong differences among study lakes in resting egg concentrations.

Conclusion

Our study provides evidence that in recent sediments, the calanoid copepod egg bank from an acid-recovering lake with elevated metal concentrations had greater numbers of viable resting eggs than lake ecosystems with relatively constant, but different pH environments (buffered and bog habitats). This result occurred in spite of similar pelagic abundances of *L. minutus*, the dominant species in zooplankton communities in these lakes. Studies examining the dormant stage are rare in comparison to the vast amount of research directed to the active stage (Gyllström & Hansson, 2004). Further study is required to test mechanisms underlying these patterns and their significance for recovery of zooplankton communities in disturbed lakes.

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