LOCAL FACTORS AND COLONIST DISPERSAL INFLUENCE CRUSTACEAN ZOOPLANKTON RECOVERY FROM CULTURAL ACIDIFICATION

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Abstract. We investigated the roles of local environmental conditions and dispersal limitation in zooplankton recovery from acidification in Swan Lake, Ontario, a historically acidified, metal-contaminated lake. We hypothesized that local environmental conditions (pH and the presence of resident, acid-tolerant zooplankton) would limit the establishment of several zooplankton colonist species. We tested this in a factorial mesocosm experiment that ran for 32 days during the mid summer. Ambient pH (5.6) reduced the abundance of two acid-sensitive cladoceran taxa, *Daphnia* spp. and *Ceriodaphnia lacustris* compared to elevated pH (6.5) but increased the abundance of cyclopoid copepod juveniles. The resident community suppressed *Skistodiaptomus oregonensis* and *Diacyclops bicuspidatus thomasi*, and to a lesser extent *Mesocyclops edax*, but slightly enhanced *Daphnia* spp. We also hypothesized that conditions in the sediments of acidified Swan Lake would limit zooplankton recruitment from diapausing eggs. We tested this by reciprocally transferring sediments containing eggs between Swan Lake and a nearby recovered lake, and incubating them for 15 weeks in 20-L emergence traps. Most zooplankton emerged from diapause in both lakes indicating that this mechanism contributes to the recolonization of acidified lakes once pH returns to normal. Some species, however, emerged in only one lake or the other, indicating that hatching cues such as light, temperature, oxygen, or appropriate pH may have been missing. Our experiments demonstrate that both local lake conditions and diapausing eggs can influence zooplankton recovery. Continued recovery may require additional management efforts to reduce and control regional acid emissions and active intervention in the form of food web manipulations.

Key words: acidification; diapause eggs; pH; recovery; species interactions; zooplankton.

INTRODUCTION

Past ecological research sought to explain community structure and biodiversity based on local-scale processes and species interactions with the biotic and abiotic environment (Dunson and Travis 1991). Ecologists, however, are limited in their ability to predict species assembly based solely on local processes. Biodiversity often fails to converge under similar environmental conditions and local diversity bears an imprint of regional diversity (Ricklefs 1987). Recent studies have demonstrated the importance of regional-scale processes, such as dispersal events, in shaping communities (Shurin 2000, Kneitel and Miller 2003). Jenkins and Buikema (1998) showed that different zooplankton communities developed in similar experimental ponds due to variation in colonization rates and sequences. Evidence suggests that both local and regional processes are important, but their relative contributions to community structure remain unknown (Ricklefs 2004).

The acidification and recovery of freshwater lakes provides a unique opportunity to study the role of local and regional processes in structuring or rebuilding communities. Large-scale acid deposition resulted in the acidification and subsequent loss of aquatic biodiversity in thousands of lakes across North America and Europe (Haines 1981, Schindler 1988). Fortunately, rates of acid deposition have decreased throughout the 1980s and 1990s in parts of North America and Europe (Stoddard et al. 1999), resulting in a corresponding reversal in surface-water acidity at national and regional scales (Jeffries et al. 2003). Although some biological recovery has been documented (Keller and Yan 1991), recovery is variable within regions (e.g., Holt et al. 2003). Many species are slow to return and the recovery is incomplete when compared to communities typical of non-acid lakes (Keller et al. 2002, Yan et al. 2004). The reason for this lag and the contribution of local and regional processes, such as dispersal, in controlling biological recovery are not well understood.

Yan et al. (2003) suggest that recovery is a multistep process, influenced by a number of local and dispersal-related processes. Local water quality must be suitable for the survival of potential colonists. In the case of acidification, pH 6 is often identified as a critical

threshold for sensitive species (Havens et al. 1993, Holt et al. 2003), although moderately sensitive species can colonize at lower pH (Keller et al. 2002). Colonists able to withstand the local abiotic conditions must also be able to survive and increase their population numbers in the face of biotic interactions. Predation by macroinvertebrate predators, which flourish in the absence of fish predation, can impair recovery of zooplankton communities (Eriksson et al. 1980, Keller et al. 2002). Studies have also considered the role of local biotic resistance in terms of founder effects (De Meester et al. 2002) and species interactions within the zooplankton community (Shurin 2000).

The availability of new colonists is probably determined by the severity and extent of the disturbance. Zooplankton colonists can arrive from three sources: (1) within-lake populations that are sustained in low numbers in habitat refuges, (2) historically deposited resting eggs or diapause stages in lake sediments (Hairston 1996), and (3) dispersal from nearby lakes via wind, animal, or human activities (Havel and Shurin 2004). Extensive regional damage to habitats may reduce the diversity of colonists available in the region whereas long-term damage can result in depleted relict populations and buried or nonviable diapause stages. However, the movement and mixing of lake sediments by water and burrowing animals, such as *Chaoborus* (Gosselin and Hare 2003), may bring ancient diapause eggs to the sediment surface, thereby providing a ready source of potential colonists. Genetic studies on zooplankton in Hannah Lake, an industrially acidified and metal-contaminated lake, however, suggested that the reappearance of *Daphnia mendotae* was the result of dispersal from neighbouring lakes, and not of colonization from the sediment egg bank (Pollard et al. 2003). It is not known, therefore, if acidified lake sediments contain viable resting stages and if they can provide a source of recolonizing species.

In this study, we investigated the role of local and regional factors in biological recovery of a small, historically acidified lake in Sudbury, Ontario, Canada. We hypothesized that two local factors—pH and the abundance of resident species—would affect the ability of nonresident zooplankton species to invade and persist, and tested this in a factorial mesocosm experiment in Swan Lake (effects of pH 5.6 and 6.5 and high/low abundance of resident species on survival of colonists from a nearby lake). We also hypothesized that dispersal from diapausing eggs historically deposited in sediments would contribute to zooplankton recovery, and tested this through a reciprocal transplant of sediment and diapausing stages between Swan Lake and a near-neutral lake using in situ emergence traps. We considered emergence from zooplankton diapausing stages within a lake to represent a regional process because the egg bank contains species that colonized from adjacent areas over long periods of time. Knowledge of the relative importance of both local and re-

gional processes is required for the management and restoration of disturbed habitats.

METHODS

Study sites

Swan Lake.—Mesocosm and emergence trap experiments were conducted in Swan Lake, a small (surface area 5.8 ha; maximum depth 8.8 m) fishless lake located on the Precambrian Shield in Sudbury, Ontario (46°22′ N, 81°04′ W). The preindustrial pH of Swan Lake was estimated to be between 5.6 and 6.1 (Dixit et al. 1989), but SO_2 emissions from nearby smelters caused a reduction in pH to 4.0 in 1977 (Keller et al. 1992). Since the 1970s, there has been a 90% reduction in SO_2 emissions and a steady increase in lake pH (Keller et al. 1992, 2003). Biological recovery started to occur, but was interrupted by a drought-induced reacidification event in 1988 (Arnott et al. 2001). Since then, the pH has increased to approximately 5.6, but the crustacean zooplankton community has remained dominated by a single acid-tolerant species, *Leptodiaptomus minutus* (Arnott et al. 2001). The fish community in Swan Lake was apparently extirpated during the 1950s with the onset of acidification (Uutala and Smol 1996) and has not recovered.

Carlyle Lake.—Emergence trap experiments were conducted in Carlyle Lake (surface area 157 ha, maximum depth 15 m) in Killarney Provincial Park, 55 km southwest of Sudbury, Ontario (46°04′ N, 81°17′ W). Carlyle Lake was acidified to 5.0 in 1971 (Sprules 1975), but has since recovered to a preindustrial pH of 6.3 (Keller et al. 2003). There is strong evidence of biotic recovery. The zooplankton community now consists of a diverse assemblage of species, including several taxa that disappeared in many lakes following acidification (*Daphnia ambigua*, *Daphnia retrocurva*, *Holopedium glacialis*, *Bosmina tubicen*, *Epischura lacustris*, *Tropocyclops extensus*; Snucins and Gunn 1998). Carlyle Lake supports a high diversity of fish species including both planktivores and piscivores (Snucins and Gunn 1998).

Kelly Lake.—Crustacean zooplankton colonists for the mesocosm experiment were obtained from Kelly Lake (surface area 339 ha, maximum depth 17 m), in Sudbury, Ontario (46°26′ N; 81°05′ W). During the past century, Kelly Lake received high atmospheric inputs of metals and sulphur dioxide as well as high nutrient inputs from private septic systems and municipal sewage plants. Although the lake remains eutrophic, the pH is currently neutral (~7.2) and contains diverse acid-sensitive zooplankton species including *Daphnia* spp. and *Skistodiaptomus oregonensis* (Table 1), as well as a high diversity of fish species (J. Gunn, *personal communication*).

Local factors experiment

We used an enclosure experiment to test the influence of local conditions (pH and the resident Swan Lake

TABLE 1. Zooplankton taxa found in Kelly and Swan Lakes, Ontario, Canada.

Taxon	Kelly Lake	Swan Lake	Acid tolerance
Acanthocyclops vernalis complex	x		t
Acroperus harpae	x		t
Ceriodaphnia lacustris	x		s
Cyclopoid copepodids	x		
Cyclopoid nauplii	x		
Daphnia spp.	x		s
Diacyclops bicuspidatus thomasi	x		t
Eubosmina (*Eubosmina*) *longispina*	x		t
Eucyclops agilis	x		t
Mesocyclops edax	x		t
Skistodiaptomus oregonensis	x		s
Calanoid copepodid	x	x	
Calanoid nauplii	x	x	
Chydorus spp.	x	x	t
Diaphanosoma birgei	x	x	t
Leptodiaptomus minutus	x	x	t
Sida crystallina	x	x	t
Simocephalus serrulatus	x	x	t
Bosmina (*Bosmina*) spp.	x	x	t

Notes: Colonist zooplankton groups are indicated in bold. Acid tolerance (t) and sensitivity (s) were based on previous lake surveys and included species rarely found in lakes with a pH below 6.0 (Brett 1989, Havens et al. 1993).

zooplankton community) on the establishment of zooplankton colonists. The experiment was arranged in a 2 × 2 factorial design with treatments being pH (ambient and elevated) and the concentration of resident (Swan Lake) zooplankton (high and low). The response variables were the abundances of zooplankton colonists transferred from Kelly Lake. The ambient pH of Swan Lake during the ice-free season of 2001 was approximately 5.6. The elevated pH of 6.5 was chosen because it is above the threshold pH 6 at which acid-sensitive zooplankton species could return (Holt et al. 2003). Each treatment had four replicates.

Plastic enclosures, 1 m in diameter and 5.5 m deep, were suspended from wooden frames in Swan Lake on 26 June 2001, a time when the abundance of fourth instar *Chaoborus*, a pelagic invertebrate predator, was low and would have little effect on the establishment and reproduction of colonizing species (Yan et al. 1991). The enclosures were filled with water from Swan Lake that was filtered through a 63-μm mesh to remove crustacean zooplankton but allow most algal species to pass. The following day, after the temperature of water in the enclosures had equilibrated with the lake temperature, a sodium bicarbonate solution was added to the appropriate treatments to raise the pH to a target of 6.5. Half of the enclosures were then stocked with resident zooplankton at ambient surface water concentration by taking vertical hauls from a depth of 2 m with a 25 cm diameter, 80-μm mesh net. The other enclosures received no resident zooplankton. On 30 June 2001, zooplankton colonists were collected from the top 2 m of Kelly Lake with the same net. Kelly Lake was chosen as a source of colonists because it

has a diverse assemblage of acid-sensitive zooplankton species and because it is a relatively large lake, located within 6 km of Swan Lake, we reasoned that Kelly Lake could be a potential source of overland dispersers. Colonists were added to all enclosures at 7% ambient Kelly Lake concentrations to simulate a colonizaton event. This level of colonization was chosen as a compromise between having a high probability of detecting the added colonists (which would require a large number of individuals) and simulating a realistic colonization event (which would result in low numbers of individuals arriving). However, considering the duration of our experiment, our level of colonization was probably not unrealistic. A study in Belgium indicated that zooplankton dispersal between a series of interconnected ponds contributed less than 1% of the target population per day (Michels et al. 2001). Some zooplankton species were common to both Swan and Kelly Lakes and hence the addition of colonists also added low numbers of some resident species to all enclosures. That is why we classified the Swan Lake zooplankton treatment as high and low concentrations of resident species rather than presence/absence. These species were not considered in the statistical analyses—only the seven most abundant taxa unique to Kelly Lake were considered colonists and treated as response variables (Table 1). Zooplankton in each enclosure were sampled once each week for 5 weeks by taking two vertical hauls from 5 m to the surface, with an 80-μm mesh net 15 cm in diameter and 50 cm in length. Zooplankton were preserved in a buffered 4% sugar–formalin solution for later enumeration.

Air-tight, opaque, Nalgene bottles were filled with surface water twice a week to monitor pH in the enclosures. The pH was measured in the laboratory using a PHM 80 portable pH meter (Radiometer, Copenhagen, Denmark) the day it was collected. Necessary adjustments were made the next day by adding either sodium bicarbonate or sulfuric acid to the enclosures. The pH in the ambient pH enclosures was not manipulated. Water chemistry, including metal, nutrient, and chlorophyll *a* concentration, was monitored every second week in each enclosure and in Swan Lake. Integrated water samples were collected from 5 m to the surface using a weighted 2.5 cm inner diameter Tygon tube. Samples for metal analysis were preserved with nitric acid. Water for chlorophyll *a* was filtered through 1.2-μm pore glass fiber filter paper and subsequently frozen for later spectrophotometric analysis. Water chemistry was analyzed at the Ministry of the Environment lab in Toronto, Ontario (Ontario Ministry of the Environment 1983).

Individuals were classified to species using Brooks (1957), Hebert (1995), Ward and Whipple (1959), Pennak (1989), Smith and Fernando (1978), and Balcer et al. (1984). *Daphnia* species were pooled, and to limit misclassification, chydorids were identified to genus and bosminids were identified to subgenus, following

the classification of Taylor et al. (2002). Subsamples of the total sample volume were enumerated at $40\times$ magnification using a Leica stereomicroscope (Leica Microsystems AG, Wetzlar, Germany). Individual crustacean zooplankton species were identified then measured using an automated zooplankton enumeration system (Zebra2; Allen et al. 1994). Several subsamples were counted, such that approximately 250 individuals were counted per sample with a target of 50 individuals per taxon, including copepodids, contributing to the total. A maximum of 30 calanoid and 30 cyclopoid copepod nauplii were counted per sample to enable the detection of less common species. The entire sample was scanned for *Daphnia* spp. after 250 individuals were counted because they typically occurred at low concentration but were a key acid-sensitive species used to assess the effects of Swan Lake water chemistry on colonizing zooplankton.

We recognize that results from this experiment apply in a strict sense only to the summer period when the enclosures were being monitored, and that colonists might have experienced different algal and zooplankton communities at other times of the year. We were constrained by the logistical challenges of mesocosm experiments, but feel our results are nevertheless representative of the process of recolonization of recovering lakes.

Statistical analysis.—A multivariate analysis of variance (MANOVA) was used to test for differences in water chemistry among treatments, using average concentrations across the two dates on which chemical data were collected. Residuals generated by the MANOVA were tested for normality using a Shapiro-Wilk *W* test. Equal variance was assessed for each dependent variable in all treatment groups using Bartlett's test for homogeneity of variances, and a correlation matrix was generated between all dependent variables to test the assumption of equal covariance (Zar 1999). MANOVA requires that the correlation between any two variables be the same in all groups. All parametric assumptions were violated for the water chemistry variables, but MANOVA is resistant to nonnormality and if the group sample sizes are equal, and departures from equal covariance have little effect on the type I error using the Pillai trace (Zar 1999, Quinn and Keough 2002).

We were unable to collect a zooplankton sample from each enclosure on the first day of the experiment to verify similarity in initial concentration of the colonist species from Kelly Lake across treatments—the first sample was collected on day three of the experiment. Since these data did not meet standard parametric assumptions, we used a permutation test (Edgington 1987) to evaluate whether initial colonist concentrations were uniform across pH and resident zooplankton treatments. Separate tests for each colonist species were carried out on log-transformed concentrations. No treatment effects for any species would indicate similar starting communities.

Repeated-measures MANOVA was done on log-transformed concentrations to test for an overall effect of pH and resident zooplankton on colonist concentration. Follow-up repeated-measures analyses of variance (RM-ANOVA) on log-transformed concentrations were used to investigate treatment effects on seven taxa present in at least three of the four replicates in any one treatment. A Bonferroni correction was applied to adjust for the total number of taxa tested ($P < 0.007$). Probability values reported for within-subjects were corrected for departure from sphericity using the Huynh-Feldt adjustment.

Because parametric assumptions of the RM-ANOVAs did not hold, the same permutation program was used to confirm our results by separately testing the effects of pH and resident zooplankton on the concentration of each colonist species for each week of the experiment (Edgington 1987). The *P* value produced in each test was compared to a *P* value generated by a two-factor ANOVA using the same data. Only five of 35 tests indicated discrepancies between permutations and ANOVAs, and on this basis we consider analyses to be rigorous despite non-parametric data. All statistical analyses were done in Statistica (Statsoft, Tulsa, Oklahoma, USA).

Regional factors experiment

A reciprocal transplant of lake sediments containing diapausing stages of zooplankton (eggs for cladocerans and calanoid copepods and juvenile stages for cyclopoid copepods) was done between Swan and Carlyle lakes to compare the viability of diapausing stages in an unrecovered (Swan Lake) and recovered (Carlyle Lake) lake and to evaluate the role of local environmental cues in emergence from diapause. Emergence traps were constructed using 20-L clear, plastic bottles, each with three holes in the side covered with 80-μm mesh to allow for water and oxygen exchange, and fit with a removable sample bottle at the top of the trap (Arnott and Yan 2002). Zooplankton emerging from diapause stages in the sediment that was placed at the bottom of the trap would swim up into the sample bottle and were trapped there until sample bottles were removed and exchanged. Swan Lake sediments were placed in emergence traps in both Swan and Carlyle lakes, and Carlyle Lake sediments were placed in emergence traps in both Carlyle and Swan lakes. A control treatment with no sediment was added to each lake to test for contamination of the emergence traps. Each treatment had four replicates for a total of 24 emergence traps.

Emergence traps were deployed on 2 April 2002, the day after ice-off. Surface sediments were collected with an Ekman dredge from several locations in each lake to compensate for heterogeneity in the distribution of diapause stages. Sediments from all sites within each lake were combined, mixed thoroughly, and equally distributed among emergence traps, such that each trap

received 1 L of sediment. Emergence traps were placed in shallow water (3.5 m depth) in both lakes because zooplankton have higher emergence in shallow water (Arnott and Yan 2002). Temperatures measured at this depth averaged 17.9°C over the experiment in Swan Lake and 17.1°C in Carlyle Lake. Dissolved organic carbon concentration was 2.4 mg/L in Swan Lake on 18 July and 1.2 mg/L on 24 July in Carlyle Lake, suggesting slightly lower light penetration at the incubation depth in Swan Lake.

Emerging zooplankton were sampled once each week for 15 weeks by removing and exchanging sample bottles on the top of the emergence traps. Emergence traps were carefully raised to just below the water surface. Sample bottles were removed and exchanged with one filled with water, leaving an air space at the top of the bottle. Accumulated detritus and algae were brushed off the traps and mesh screening, and the traps carefully lowered to their previous location. On shore, zooplankton in the samples bottles were filtered out using an 80-μm mesh filter, transferred into 100-mL bottles, and preserved in a buffered 4% sugar–formalin solution.

All samples for each of the 15 weeks were counted and individuals identified to species where possible. Usually, the entire sample was examined unless the total number of individuals exceeded 250. In this case, the same counting method used for the enclosure experiment was employed.

There was a risk that some individuals would not swim into the sample bottle and would be underestimated in the analysis or that they would remain in the emergence traps and reproduce, thus making it difficult to separate emergent individuals from those resulting from reproduction. To determine the extent to which individuals remained in the emergence traps, we filtered water from the emergence traps through an 80-μm mesh plankton net at the end of the experiment and preserved contents in buffered 4% sugar–formalin.

Four sediment samples from each lake were retained from the experimental setup to compare diapause egg concentrations between lakes (cladocerans and calanoid copepods only). Sediments were stored in the dark at 4°C until the diapause eggs could be separated and counted. Diapause eggs were collected on an 80-μm mesh sieve then separated from sediment by centrifuging 100-mL subsamples with a 50% sucrose solution (Cáceres 1998). Eggs were rinsed to remove sugar, then a subsample of approximately 250 diapause eggs was counted and classified into three categories based on their visual characteristics. Eggs with an embryo were considered viable, and diffuse or stippled eggs as potentially viable. The entire sample was then scanned for large cladoceran eggs, specifically *Daphnia* ephippia, because *Daphnia* spp. are generally acid sensitive and have not yet recolonized Swan Lake.

Statistical analysis.—Because emergence was low, the number of individuals of each taxon emerging from the sediments was summed across the 15 weeks of the experiment for each replicate emergence trap. Species were then pooled into functional groups based on body size, life history, and emergence characteristics (see Table 4). A permutation test was used to evaluate the effects of lake environment and sediment location on zooplankton hatching from diapause eggs.

RESULTS

Enclosure experiment: local factors

There were no differences in water chemistry (nutrients, DOC, base cations, metals) among treatments (MANOVA; pH, $F_{10,3} = 4.83$, $P = 0.11$; resident zooplankton, $F_{10,3} = 2.17$, $P = 0.28$; pH × resident zooplankton, $F_{10,3} = 0.26$, $P = 0.96$). We successfully established contrasting pH treatments since pH fluctuated between 6.53 ± 0.05 (mean ± SE) and 6.73 ± 0.06 in the elevated treatments and between 5.53 ± 0.01 and 5.70 ± 0.04 in the ambient treatments. The mean concentration of resident zooplankton species in treatments with high resident zooplankton was 7.9 ± 0.6 individuals/L and in low resident zooplankton treatments was 4.4 ± 0.7 individuals/L. However, these values are influenced by unusually high concentrations of *Chydorus* spp. and *Bosmina* spp. on the last date of the experiment. Without these values the corresponding numbers are 7.3 ± 0.6 and 2.2 ± 0.4 individuals/L, indicating that resident zooplankton were 3.3 times more abundant in the high than the low resident zooplankton treatments during the majority of the experiment. Permutation tests indicated no differences in starting concentrations for the colonist species across treatments except for *Daphnia* spp. and *C. lacustris* which were less abundant in the ambient than the elevated pH treatment ($P < 0.001$). This provides evidence that the initial community assemblages were similar among treatments. The observed differences in concentrations of *Daphnia* spp. and *C. lacustris* support the assertion that acidic conditions can have rapid effects on some acid-sensitive species (Locke 1991). At the beginning of the experiment, total zooplankton concentration averaged 35.7 individuals/L across all enclosures, of which 12.9 individuals/L were colonist species; at the end of the experiment, total zooplankton concentration was 115.5 individuals/L, of which 24.0 individuals/L were colonist species. Hence, the principal interactions experienced by the Kelly Lake colonists were with Swan Lake species rather than with Kelly Lake species. At the beginning of the experiment, the total zooplankton concentration in the lake (68.6 individuals/L) was almost double the mean concentration in the enclosures, probably reflecting low sampling efficiency when we stocked the bags. At the end of the experiment, the enclosures had more than twice the total concentration of zooplankton than the lake (45.4 individuals/L), probably the result of reduced invertebrate predation in the enclosures.

TABLE 2. Univariate between-subjects repeated-measures ANOVA and MANOVA for zooplankton responses to acidification and resident zooplankton in the enclosure experiment (species df = 1, MANOVA df = 7).

Species	pH		Resident		pH × Resident	
	F	P	F	P	F	P
Ceriodaphnia lacustris	68.20	<**0.01**	0.01	0.92	0.34	0.57
Cyclopoid copepodids	12.97	<**0.01**	1.60	0.23	1.08	0.32
Cyclopoid nauplii	1.23	0.29	<**0.01**	0.99	0.01	0.91
Daphnia spp.	25.19	<**0.01**	5.35	0.04	0.55	0.47
Diacyclops bicuspidatus thomasi	0.13	0.72	18.91	<**0.01**	0.62	0.45
Mesocyclops edax	1.38	0.26	5.16	0.04	1.31	0.28
Skistodiaptomus oregonensis	1.04	0.33	50.68	<**0.01**	0.10	0.75
Overall MANOVA	8.44	**0.01**	16.85	<**0.01**	0.73	0.66

Note: Bold P values indicate significance at the Bonferroni-corrected critical value of $P < 0.007$.

Colonist concentration was influenced by both biotic and abiotic components of the local environment. Results of the RM-MANOVA indicated an overall effect of pH and resident zooplankton, but no interaction between the two (Table 2). Two acid-sensitive taxa, *Daphnia* spp. and *C. lacustris*, were reduced at low pH (Fig. 1). Conversely, cyclopoid copepodids reached higher concentrations in the low pH treatment than in the treatment where pH was raised to 6.5 (Fig. 1), an unexpected result for this taxon. Two copepod taxa, *D. b.* *thomasi* and *S. oregonensis*, were reduced in the high resident zooplankton treatment (Table 2, Fig. 1). The concentration of *Daphnia* spp. increased in the high resident zooplankton treatment and the copepod *Mesocyclops edax* decreased but these trends were not statistically significant after Bonferroni corrections (Table 2). Cyclopoid copepod nauplii were unaffected by either treatment (Table 2); however, the population declined in the fourth week in the high resident zooplankton treatment (Fig. 1). Total chlorophyll averaged
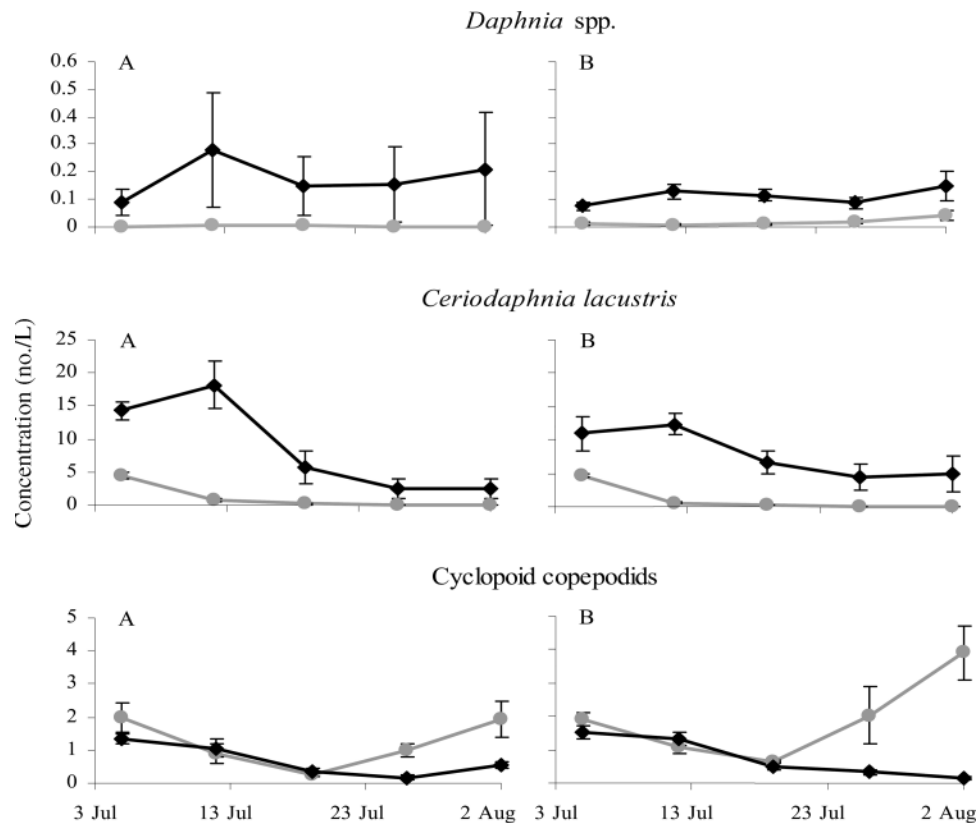

FIG. 1. Changes in mean concentration of colonist species with (A) high and (B) low resident zooplankton present at pH 5.5 (gray circles) and 6.5 (black diamonds) across the five-week enclosure experiment. Error bars (±SE) indicate the variability among the four replicates per treatment combination (some bars are too small to be visible).
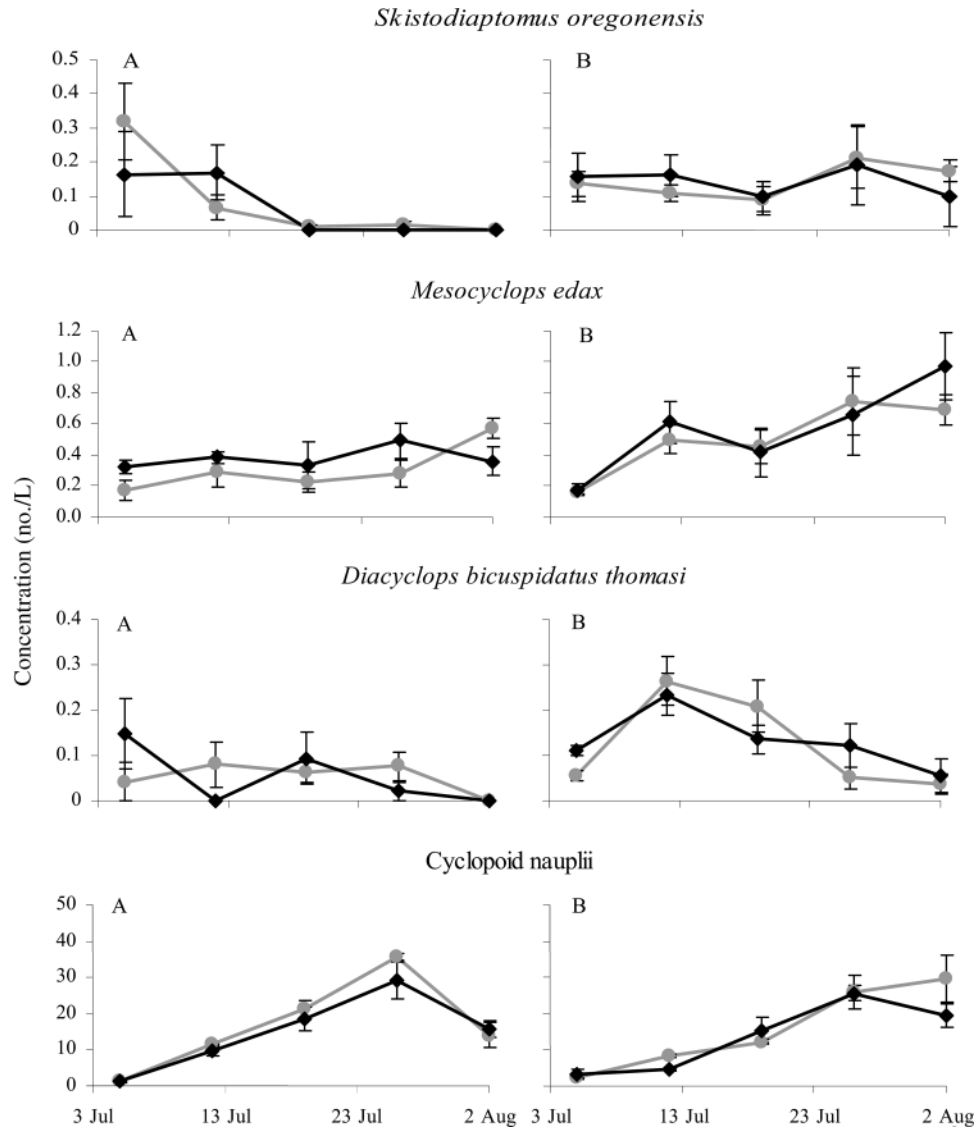
FIG. 1. Continued.

2.2 μ/L across all enclosures on 12 July near the beginning of the experiment and 1.5 μ/L on 26 July near the end indicating resources for the grazers declined by about 30% during the experiment.

Diapause stage experiment: regional factor

Alona spp. and *Bosmina* spp. were removed from analyses because high concentrations of these species were detected in the emergence traps at the end of the season. This suggests that their presence in the sample bottles did not reflect emergence patterns but may have resulted from reproduction in the emergence traps. *Sida crystallina* was also omitted from analyses because it was abundant in the control treatments throughout the experiment, indicating that this species may have also contaminated other treatments. Cyclopoid nauplii were assumed to result from reproduction and were not in-

cluded in the analyses because cyclopoids emerge from diapause as copepodids, a more advanced life stage.

The average emergence of diapausing zooplankton stages was low in all treatments and the variability within each treatment was high (Table 3). The greatest number of individuals of all species emerged from Swan sediments placed in Carlyle Lake, but, otherwise, emergent numbers were similar (Fig. 2). A total of 15 species emerged from Carlyle sediments placed in Carlyle Lake, 16 from Carlyle sediments placed in Swan Lake, nine from Swan sediments placed in Carlyle Lake, and 15 from Swan sediments placed in Swan Lake.

Most functional groups were unaffected by the experimental treatments (Table 4). Calanoid copepod emergence was influenced by incubation lake and littoral species were affected by sediment origin. Six of

TABLE 3. Total number of individuals collected in emergence trap samples from Swan Lake and Carlyle Lake.

| | Treatment | | | | | | | |
| | CC | | CS | | SC | | SS | |
Functional groups and species	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Calanoids (adults and juveniles)								
Leptodiaptomus minutus	0.0	0.0	8.3	2.0	0.0	0.0	2.5	1.2
Calanoid copepodids	0.3	0.3	11.3	1.9	0.8	0.3	4.0	1.3
Calanoid nauplii	121.0	38.9	83.3	60.2	10.0	3.7	19.3	5.1
Cyclopoids (adults and juveniles)								
Acanthocyclops vernalis complex	0.3	0.3	0.5	0.3	0.0	0.0	0.3	0.3
Diacyclops bicuspidatus thomasi	0.8	0.3	1.0	0.7	0.0	0.0	0.0	0.0
Eucyclops agilis	2.5	2.2	0.0	0.0	0.0	0.0	0.5	0.3
Macrocyclops albidus	0.0	0.0	0.3	0.3	4.8	4.1	42.5	25.1
Mesocyclops edax	0.5	0.5	0.8	0.3	0.0	0.0	0.0	0.0
Paracyclops affinis	0.0	0.0	0.0	0.0	0.5	0.5	3.3	3.3
Paracyclops poppei	0.0	0.0	1.3	0.5	0.0	0.0	0.0	0.0
Cyclopoid copepodids	7.0	1.2	3.0	1.8	14.0	11.0	21.3	12.2
Cyclopoid nauplii†	3.0	2.3	3.3	2.0	88.8	88.2	102.0	51.6
Large cladocerans								
Daphnia galeata mendotae	0.5	0.5	1.0	1.0	0.3	0.3	0.5	0.3
Holopedium glacialis	0.8	0.5	0.5	0.5	0.3	0.3	0.0	0.0
Littoral species								
Acantholebris curvirostris	28.5	20.9	13.0	8.2	247.1	184.5	20.5	20.2
Acroperus harpae	2.0	1.4	0.3	0.3	277.1	174.7	46.5	31.6
Alona sp.†	31.1	17.9	48.8	42.4	7.5	5.2	52.8	43.0
Chydorus spp.	13.0	13.0	1.3	1.3	0.0	0.0	1.5	0.5
Latona setifera	0.0	0.0	0.3	0.3	1.0	0.7	3.8	2.5
Sida crystallina†	0.3	0.3	17.5	2.5	0.0	0.0	24.5	6.9
Small cladocerans								
Ceriodaphnia lacustris	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Diaphanosoma birgei	0.3	0.3	0.0	0.0	0.0	0.0	3.5	2.8
Eubosmina (*Eubosmina*) *longispina*	55.8	33.7	66.3	59.1	0.0	0.0	0.8	0.5
Bosmina (Bosmina) spp.†	41.0	36.0	9.3	6.6	72.3	58.7	25.0	16.0

Note: Treatments are Carlyle sediments in Carlyle Lake (CC), Carlyle sediments in Swan Lake (CS), Swan sediments in Carlyle Lake (SC), and Swan sediments in Swan Lake (SS).

† Taxa were not analyzed.

the 17 species included in the analyses were found in both Carlyle and Swan lake sediments and had similar numbers of individuals hatch in Swan Lake, regardless of the sediment source. This suggests that they responded to emergence cues in a similar way. Of these six species, *L. minutus*, a calanoid copepod, was not detected in any of the emergence traps incubated in

Carlyle Lake, suggesting that the necessary cues to terminate diapause were not present. Two species, *Diaphanosoma birgei* and *Eucyclops agilis*, were detected in the sediments of both lakes, but only emerged when incubated in the lake of sediment origin. Several species, including *D. b. thomasi*, *M. edax*, *Paracyclops poppei*, and *C. lacustris*, emerged from Carlyle sediments but not from any of the Swan Lake sediments
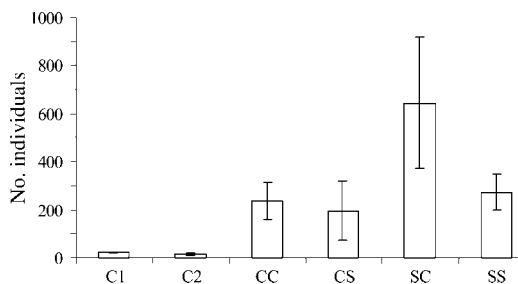

FIG. 2. Mean (±SE) total number of individuals that emerged in each treatment across the 15-week emergence trap experiment. Treatments: C1, control in Swan Lake; C2, control in Carlyle Lake; CC, Carlyle sediments in Carlyle Lake; CS, Carlyle sediments in Swan Lake; SC, Swan sediments in Carlyle Lake; SS, Swan sediments in Swan Lake.

TABLE 4. Results of permutation tests for zooplankton egg emergence responses to lake environment and sediment location.

Functional groups	Lake	Sediment
Calanoids	**0.001**	0.99
Calanoid copepodids, nauplii	0.57	1.00
Cyclopoids, cyclopoid copepodids	0.16	0.08
Large cladocerans	0.50	0.95
Littoral species	0.97	**0.02**
Small cladocerans	0.38	0.98
Total	0.89	0.09

Notes: Probabilities associated with the null hypothesis of no treatment effect are shown. Bold *P* values indicate significance at the Bonferroni-corrected critical value of $P < 0.007$.
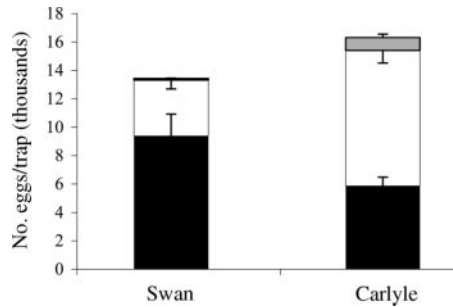
FIG. 3. Mean egg densities (across eight sediment subsamples) in Swan Lake and Carlyle Lake. Egg classifications are: embryo (black); diffuse or stippled egg (open); cladoceran species (gray). Standard errors are shown above or below the mean only for clarity.

(Table 3). This suggests that diapause stages for these species may not be present or viable in Swan Lake sediments.

Mean ($\pm$ SE) diapausing egg densities were slightly higher in Carlyle Lake sediments (16 304 $\pm$ 1053 eggs/L of sediment) than in Swan Lake (13 418 $\pm$ 2091) but this was not statistically significant (two-sample t test, $t = 1.23$, $P = 0.24$, df = 14). There were more embryo-filled calanoid copepod eggs in Swan Lake sediments than Carlyle Lake sediments (t test, equal variances, $t = 2.2$, $P = 0.02$, df = 14) but fewer cladoceran eggs (t test, unequal variances, $t = 3.13$, $P = <0.01$, df =7; Fig. 3).

DISCUSSION

Our experimental studies suggest that both local (pH and concentration of resident zooplankton species) and regional (dispersal from diapausing stages) processes play a role in the recovery of zooplankton communities following cultural acidification. Two acid-sensitive colonist species, *C. lacustris* and *Daphnia* spp., were reduced in the ambient pH enclosures but showed no or minimal response respectively to resident species. These species are thus vulnerable to local physical conditions in Swan Lake, and in fact are not found in Swan Lake. This could be a direct effect of low pH on survival, reproduction and physiological function (Brett 1989) or an indirect effect of low abundance or quality of algal prey (Fischer and Frost 1997). Chlorophyll *a* concentration was similar among all our experimental treatments and except for diatoms (Nicholls et al. 1992, Arnott et al. 2001) the phytoplankton assemblage of Swan Lake appears to have recovered. These observations suggest that sufficient resources were available for these acid-sensitive colonists and hence that direct effects of low pH are the most probable cause for their declines. *Daphnia* spp. emerged in low numbers from diapausing eggs in both Swan and Carlyle lakes, and one to two individuals were detected in the ice-free season in 2000, 2001, and 2002 (B. Keller, *unpublished data*). Despite the continual supply of this genus to the

acid environment of Swan Lake, enclosure results indicate such emergent individuals could not survive for long. *C. lacustris*, on the other hand, never emerged from Swan Lake sediment and only emerged from Carlyle Lake sediment placed in Carlyle Lake. This suggests that emergence cues are not appropriate in Swan Lake or that prolonged exposure in the acid environment of Swan Lake has reduced the viability of *C. lacustris* diapausing eggs. Arnott and Yan (2002) detected emergence of *C. lacustris* in Swan Lake, but primarily in sediments that had been previously dried, reinforcing the importance of environmental conditions. These two species are not likely to establish in Swan Lake until chemical conditions improve.

Three colonist species—*C. b. thomasi* and *S. oregonensis* and, to a lesser extent, *M. edax*—were not affected by the pH treatment in the enclosure experiment but were reduced in abundance by the resident zooplankton community indicating an effect of local biotic conditions. None of these species occurs in Swan Lake. *S. oregonensis* is herbivorous and since all local Swan Lake zooplankton species are also herbivorous (Table 1) we speculate that it was affected by competition with local zooplankton for algal resources. This species did not emerge from any of the sediments in our experiments suggesting some combination of absence of emergence cues or low numbers or viability of diapausing eggs. This species is present in lakes near Swan Lake, but Stemberger (1995) found little evidence for its dispersal beyond its postglacial distribution, making it a poor colonizing species that may take a long time to establish in Swan Lake even if conditions are suitable. *M. edax* and *C. b. thomasi* adults are predators on other zooplankton so it is less clear why they did poorly in the high resident species treatment. Furthermore, their juveniles (copepodids) were unaffected by resident zooplankton and actually increased at ambient pH, a surprising result given that cyclopoid copepods do not occur in the epilimnion of Swan Lake. Larval stages (nauplii) were affected by neither pH nor resident zooplankton so it appears that developmental stages of this group are differentially affected by local factors. Adults may be limited by a lower quality assemblage of prey in the relatively depauperate community of Swan Lake. Reasons for the increase of copepodids at ambient pH are unclear but it is possible that the enclosures released them from predation by surface-oriented invertebrates such as dytiscid larvae that normally control their abundance in Swan Lake (S. E. Arnott, A. Jackson, and Y. Alarie, *unpublished manuscript*). Several cyclopoid copepod individuals were detected 1 m off the bottom of the lake in 2001, but only one individual was detected in 2002 (B. Keller, *unpublished data*). The reestablishment of fish populations in Swan Lake may be necessary to control invertebrate predation, thus enabling the successful colonization of copepods. First- and second-instar larvae of *Chaoborus*, a predatory midge,

were present in the experimental enclosures but they feed primarily on algae and rotifers (Moore 1988) and hence probably did not influence species responses. *M. edax* and *C. b. thomasi* adults appeared from Carlyle Lake sediments placed in both lakes but never from Swan Lake sediment. However these adults can only arise from copepodids that form the diapausing stage; these cyclopoid copepodids emerged in greater numbers from Swan than Carlyle Lake sediments. Hence it would appear that diapausing copepodids are common in Swan Lake sediments and emerge into Swan Lake in reasonable numbers but disappear before they become adults. Combinations of factors, limited zooplankton prey for adults and effects of invertebrate predators on juveniles, may account for the absence of cyclopoid copepods from Swan Lake.

In addition to the colonist species, a number of others appeared in our emergence experiments and this deserves comment as patterns were quite variable as others have observed (Cáceres and Tessier 2003). For instance *H. glacialis* diapausing eggs are in Swan Lake sediments, indicating this species used to be in the lake, but emerged from Swan Lake sediments only when placed in Carlyle Lake. There was low emergence of *H. glacialis* from Carlyle Lake sediments placed in Swan Lake and one individual was detected in the water column of Swan Lake during routine sampling in 2001 (B. Keller, *unpublished data*). Current conditions in Swan Lake may limit emergence and subsequent survival of this species. Twelve species emerged from Swan Lake sediments placed in Swan Lake, indicating they were historically present in the lake and currently encounter appropriate emergence cues. Only three of these species, however, occurred in Swan Lake at the time of our study. Some emerged in low numbers and for those groups that are obligately sexual, such as copepods, recovery could be limited by density-dependent Allee effects—the requirement for a minimal number of propagules before a population can grow (Stephens et al. 1999, Sarnelle and Knapp 2004). *L. minutus* is very common in Swan Lake and was present in both Swan and Carlyle lake sediments, yet only emerged in the acid environment of Swan Lake. This is a widespread and common acid-tolerant species that must be able to emerge under a wide variety of physical and chemical conditions, so it is unclear why it did not emerge in near-neutral Carlyle Lake.

In summary, our experimental studies suggested that local and regional processes play a role in zooplankton community assembly. This indicates that a multifaceted management solution will be necessary for complete restoration of acidified ecosystems. Recovery of some taxa, such as *Ceriodaphnia* and *Daphnia*, will be impaired without further reductions in acid deposition and subsequent increases in lake pH. In southeastern Canada, it is estimated that, of 646 000 acid-sensitive lakes, ~76 000 will remain chemically damaged unless more stringent reductions in acid deposition are implemented

(Jeffries et al. 2000). Incomplete biological recovery is expected in lakes where the pH is currently below 6, a critical threshold for many sensitive taxa (Holt et al. 2003). To ensure the recovery of some species of copepods, active intervention in the form of large inocula from unacidified lakes may be required. Because they are obligately sexual, copepods may be subject to Allee effects and will require high colonization rates to ensure successful reestablishment of populations. Emergence of several acid-sensitive species from the Swan Lake egg bank was low, suggesting that recruitment from historically acidified lake sediments may be limited. Although there is evidence of overland dispersal by parthenogenic zooplankton (e.g., *Daphnia*; Pollard et al. 2003), some copepods are expected to be more restricted in their distribution because of Allee effects and overland dispersal limitation (Stemberger 1995). This will be particularly true in the many small, isolated, headwater lakes that occur throughout the Precambrian Shield. Our experiments also indicated that survival of some taxa was limited by biological resistance from the native species assemblage. Manipulations of higher trophic levels may ultimately be required to enable full recovery, especially in lakes where fish populations were extirpated during acidification. Previous studies have suggested that macroinvertebrates that proliferate in the absence of fish can influence zooplankton community structure (S. E. Arnott, A. Jackson, and Y. Alarie, *unpublished manuscript*). The extent to which invertebrate predation impairs crustacean zooplankton recovery is unresolved. Food web manipulations may be futile if current crustacean zooplankton communities are better adapted to the local environment and able to prevent reestablishment by other species. Ultimately, complete biological recovery from regional acidification may require intervention at local and regional scales to ensure that physical and biological barriers impeding biological recovery are overcome.

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