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# Recolonization of Acid-damaged Lakes by the Benthic Invertebrates *Stenacron interpunctatum*, *Stenonema femoratum* and *Hyalella azteca*

The recolonization of acid-damaged lakes in Killarney Park, Canada is described for 3 species of benthic invertebrates; 2 mayflies (*Stenonema femoratum*, *Stenacron interpunctatum*) and an amphipod (*Hyalella azteca*). Synoptic surveys of 119 lakes for amphipods and 77 lakes for mayflies were conducted between 1995 and 1997 and defined pH thresholds of 5.6 for *S. femoratum* and H. azteca and pH 5.3 for *S. interpunctatum*. In an intensive study of 2 acid-damaged lakes and 2 reference lakes from 1997 to 2002, reestablishment of *S. interpunctatum*, *S. femoratum* and *H. azteca* occurred, when timing of the events could be estimated, less than 4–8 years after pH thresholds for specific taxa were reached. Dispersal of *S. interpunctatum* to all habitat patches within a lake was completed 3 years after recolonization was detected in the smallest lake (11 ha). It is anticipated that dispersal throughout the largest lake (189 ha) will take much longer. The time lag from estimated pH recovery to reestablishment and subsequent dispersal of mayflies to all suitable habitats within a lake was as much as 11 to 22+ years. The density of *S. interpunctatum* increased in the recovering lakes to levels higher than in reference lakes, but stable endpoints have not yet been reached during 6 years of monitoring.

## INTRODUCTION

Chemical recovery of many anthropogenically acidified waters is occurring in Europe and North America in response to recent pollution reductions (1). These chemical improvements are particularly dramatic and well-described for the Sudbury, Ontario, Canada region including the lakes in Killarney Park (2, 3). From lakes in the Sudbury region there is also considerable evidence of natural recovery for a variety of biota including algae (4, 5), zooplankton (6, 7), and fish (8). This paper adds to this emerging body of literature on natural biological recovery by describing the recolonization of nearshore habitats by 3 benthic macroinvertebrate species; 2 mayflies (*Stenacron interpunctatum*, *Stenonema femoratum*) and an amphipod (*Hyalella azteca*). It is part of the Northern Lakes Recovery Study, a multidisciplinary investigation of the natural recovery of lake ecosystems from acidification (9).

**Table 1. Selected physical and chemical characteristics of synoptic survey lakes. Values are medians with range in parentheses. N = 119 for amphipod survey and N = 77 for mayfly survey.**

| | Amphipod survey | Mayfly survey |
|---|---|---|
| Latitude | (46°01'16" – 46°11'31") | |
| Longitude | (81°09'29" – 81°36'06") | |
| Surface area (ha) | 17.6 (0.8–810.1) | 24.1 (2–810.1) |
| Maximum depth (m) | 10.5 (1.5–61.0) | 14.0 (2.0–61.0) |
| Fish species richness | 3 (0–14) | 6 (0–14) |
| pH | 5.5 (4.3–7.6) | 6.1 (4.5–7.6) |

A unique feature of this study is the monitoring of recovery at the level of specific habitats within lakes. Other less spatially intensive studies of benthic invertebrate recovery in Sudbury area lakes indicate that species richness and densities of individual taxa tend to increase after water-quality improvement (10–12). However, by studying individual patches of habitat within lakes it was possible to quantify the time lag between chemical and biological responses, including within-lake dispersal. These types of quantitative data are required for future development of biological response models that link changes in biota to improvements in water chemistry.

## MATERIALS AND METHODS

### Synoptic Surveys

The distribution of *H. azteca* relative to lake pH was determined by means of a synoptic survey of 119 Killarney Park lakes (Table 1) between 1995 and 1997 during the months of June, July, and August (13). Nearshore areas were sampled by sweep netting and inspecting rocks and wood debris for 4–6 man-hours in each lake. A triangular (23 cm) 500 μm mesh sweep net was used and sampling was confined to depths < 1 m. Approximately equal periods of time were spent in each habitat type (e.g. detritus, rock, macrophytes, mud).

A second synoptic survey targeted *S. femoratum* and *S. interpunctatum* in 77 lakes (Table 1) during the month of May in 1996 and 1997 (13). The surveys were conducted early in the month because both species have adult emergence periods that begin in May and continue to the end of August (14). The field crews conducted searches by turning over and inspecting the underside of nearshore rocks, the habitat typically occupied by the nymphs of these species (15). The examination of rocks was done by 2 people at multiple sites for a total of 30 min on each lake.

### Intensive Survey

Between 1997 and 2002 we mapped in detail the distribution of all 3 species in 1 recovering acidified lake (George Lake: surface area 189 ha; maximum depth 36.6 m; shoreline perimeter 13.5 km) and one circumneutral reference lake (Low Lake: surface area 34 ha; maximum depth 28.4 m; shoreline perimeter 4.0 km). A second recovering acidified lake (Partridge Lake: surface area 11 ha; maximum depth 16.9 m; shoreline perimeter 1.6 km) was surveyed for all 3 species from 1998 to 2002, and a second circumneutral reference lake (Helen Lake: surface area 83 ha; maximum depth 41.2 m; shoreline perimeter 6.3 km) was surveyed for mayflies only in 2001 and 2002. All of the lakes contained native fish species and the number ranged from one in Partridge Lake to 14 in Low Lake. There were 11 species in each of George Lake and Helen Lake. The dominant fish species in the littoral zone, where the invertebrate studies were conducted, were rock bass (*Ambloplites rupestris*) and smallmouth bass (*Mircropterus dolomieui*), except in Partridge Lake where only yellow perch (*Perca flavescens*) was present. The shorelines in these glacially scoured lakes consist of a wide range of substrate types. The areas of coarse rock substrate where mayflies were collected are in discrete patches, often associated with windswept sites or at the base of cliffs where rocks have tumbled down. Proliferation of filamentous green algae typically occurs in Killarney lakes when they acidify (16), but the extensive growths tend to disappear as lakes recover and they were not observed in any of the intensive survey lakes.

All shoreline areas with coarse rock substrate were sampled in George Lake, Low Lake, and Partridge Lake, and a random subset of the available habitat was sampled in Helen Lake. The total numbers of sites surveyed for mayflies were 125 in George Lake, 42 in Low Lake, 12 in Partridge Lake, and 20 in Helen Lake. Sampling occurred in May at sites that had coarse rock habitat adjacent to shore and within easy reach (water < 60 cm deep) of people wading in the lake. Rocks were inspected for nymphs after removal from the water. Mayflies clinging to rocks were collected with the aid of forceps, identified and released alive. The rocks were then returned to their original location. The length of a habitat patch in these lakes ranged from 2.0 m to 323.7 m. Two people searched each patch for 11 minutes or, in smaller patches, until all rocks had been inspected. During the first 4 years the presence or absence of species was recorded. In 2001 and 2002 the catch-per-unit-effort (CPUE), the average number of mayflies captured by one person per minute of search, was also recorded.

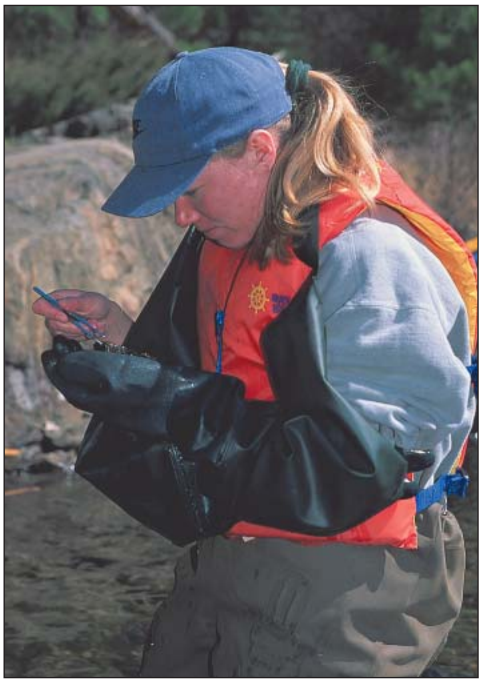
Amphipods were captured during the month of July by sweep-netting in water < 1 m deep below overhanging shoreline vegetation, in aquatic vegetation, and over fine and moderately coarse organic and inorganic substrates. Long continuous patches of habitat were sampled every 50 m. Two people searched each location for 4 minutes. Amphipods were preserved in 70% ethanol for later identification. Only presence or absence of *H. azteca* was recorded. Low Lake, the reference lake, was sampled at 30 sites in 1997, 1998, and 1999. George Lake was sampled annually at 68 sites in 1997–1998 and 2000–2002. Partridge Lake was sampled at 13 sites in 2000, 2001, and 2002.

The search times at each site, 11 minutes for mayflies and 4 minutes for amphipods, were selected to be greater than the maximum amount of time it took to find specimens at any given site in one of the reference lakes (Low Lake). On average, searchers found individuals of both mayfly species within 56 seconds (range 15–271 seconds) and *H. azteca* within 65 seconds (range 18–218 seconds) in Low Lake. The average time to find the first specimen of *S. interpunctatum* at a site in George Lake in 2001 ranged from 48 seconds (range 7–216 seconds) at sites colonized at least 5 years to 217 seconds (range 27–585 seconds) at sites colonized only one year. Thus, the 11 minute sampling effort appeared to be adequate for detecting this species.

## RESULTS

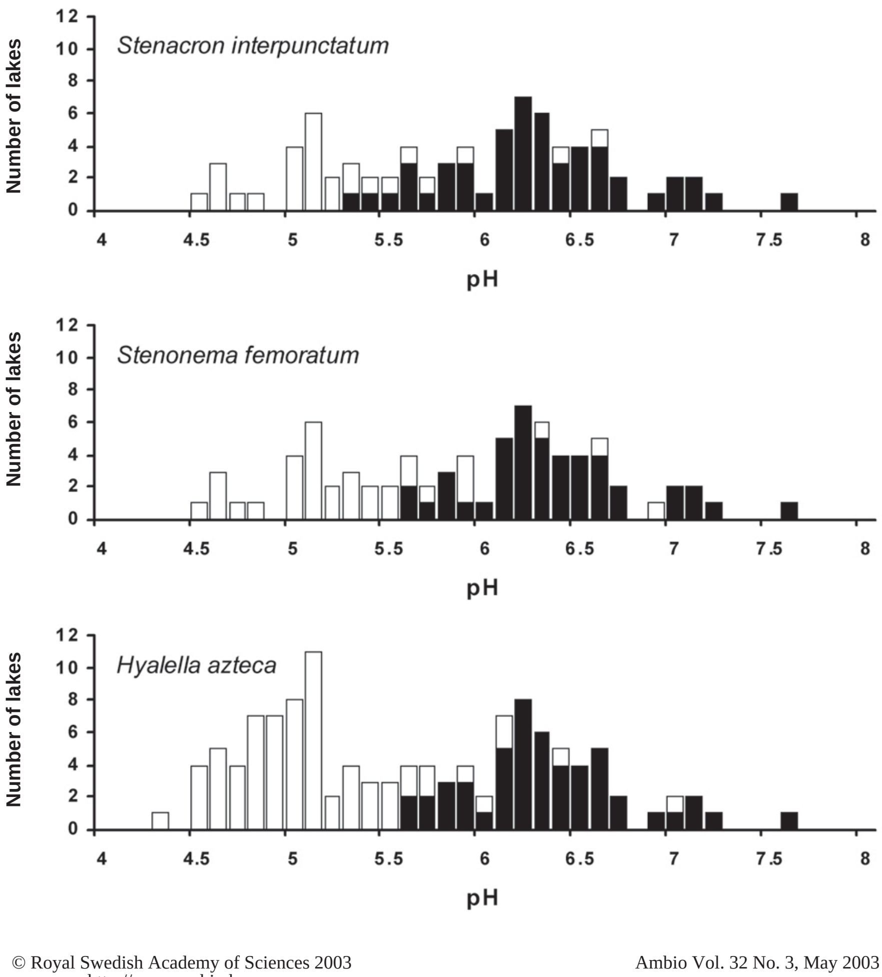
The springtime synoptic surveys (Fig. 1) captured *S. interpunctatum* in 53 lakes spanning a pH range of 5.3–7.6, and *S. femoratum* in 45 lakes spanning a pH range of 5.6–7.6. Two other mayfly taxa were found under rocks during the synoptic survey, *Eurylophella temporalis* in 43 lakes (pH 5.0–7.8) and *Leptophlebia* in 34 lakes (pH 5.0–7.6), but because of their acid-tolerance they were not included in further study. During the summertime sweep-netting survey of 119 lakes *H. azteca* were captured in 51 lakes spanning a pH range of 5.6–7.6.

The mayflies *S. interpunctatum* and *S. femoratum* and the amphipod *H. azteca* were found in all circumneutral Killarney lakes that contained suitable physical habitat for those species. Within the 2 reference lakes (Low and Helen), mayflies and



**Inspecting rocks for mayfly nymphs. Photo: E. Snucins.**

**Figure 1. The frequency by pH of synoptic survey lakes that contained *S. interpunctatum*, *S. femoratum*, and *A. azteca* (closed bars). Lakes from which species were absent are indicated by open bars.**



amphipods were found at all the individual sites that were sampled. These ubiquitously distributed species were not found in some acid-damaged lakes with apparently suitable pH and adequate physical habitat, presumably because recolonization had not yet occurred or because the organisms were not abundant enough to be detected. For example, all 3 species were known to be present in George Lake in 1996, but they were not found during the synoptic surveys. It was only during the intensive sampling that they were captured.

The intensive surveys of George Lake revealed that the number of sites occupied by *S. interpunctatum*, and to lesser extent by the other two species, increased with time (Fig. 2). In 1997 *S. interpunctatum* was found at 32 sites, *S. femoratum* was found at 2 sites, and *H. azteca* at 4 sites. By 2002 *S. interpunctatum* was found at 104 sites, *S. femoratum* was found at 4 sites, and *H. azteca* at 8 sites.

*S. interpunctatum* was first sampled in Partridge Lake in 1999 and so presumably established itself in that lake during 1998. By 2001 the species had spread to all 12 sites in the lake (Fig. 2). *H. azteca* was not captured in Partridge Lake during the synoptic survey in 1996, but the intensive surveys for amphipods conducted annually between 2000 and 2002 each captured individuals at 5 or 6 sites out of 13 inspected.

From the intensive study lakes it is possible to estimate the time to re-establishment of a species following water quality recovery. In George Lake *H. azteca* and *S. femoratum* were present at a small number of sites in 1997 about 4 years after their pH threshold (5.6) was reached and sustained in 1993 (Fig. 3). An estimate of establishment date following water-quality recovery is not possible for *S. interpunctatum* in George Lake because the species was already present at a large number of sites during the first survey in 1997. We lack continuous monitoring data for Partridge Lake, but if we assume a linear increase in pH between 1987 and 1996 the pH thresholds of 5.3 and 5.6 were reached in 1990 and 1994, respectively (Fig. 3). *S. interpunctatum* established itself in Partridge Lake in 1998, 8 years after the lake pH was estimated to have reached that species' threshold. *H. azteca* was detected in Partridge Lake in 2000, only 6 years after the lake pH was estimated to have reached the threshold for that species.

Not only did more sites get colonized, but the relative density of *S. interpunctatum* at a site also increased with time (Fig. 4). The CPUE in 2002 of *S. interpunctatum* on sites in George Lake that had been colonized for at least 6 years was significantly ($P < 0.05$; Mann-Whitney Test) higher than the CPUE in

**Figure 3. pH of George Lake (closed box) and Partridge Lake (open circle). Water samples collected at mid-lake during July in George Lake and during November in Partridge Lake. Species pH thresholds of 5.3 (*S. interpunctatum*) and 5.6 (*S. femoratum*, *H. azteca*) are indicated by the horizontal dotted lines.**

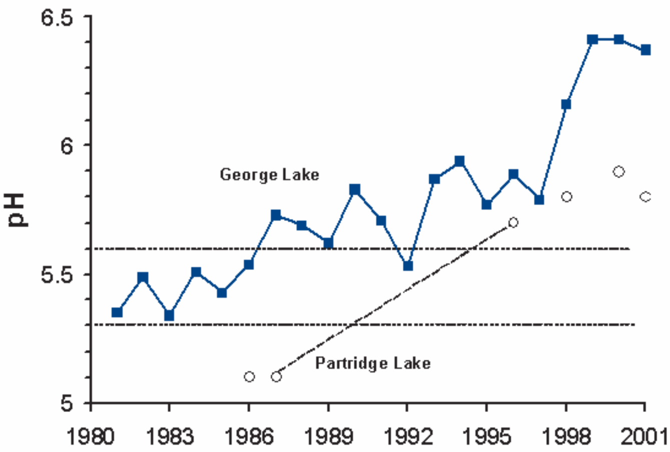



**Figure 2. Number of sites colonized by *Stenacron interpunctatum* (closed circle), *Stenonema femoratum* (open circle) and *Hyalella azteca* (open box) in George Lake and Partridge Lake between 1997 and 2002. The annual surveys of Partridge Lake began in 1998 for mayflies and in 2000 for amphipods. Total number of surveyed sites available for colonization indicated by dashed lines.**

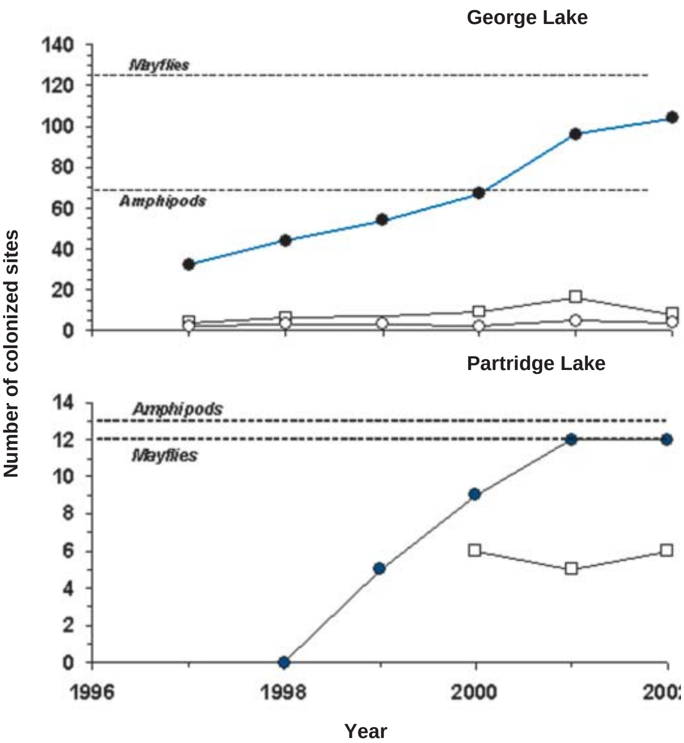
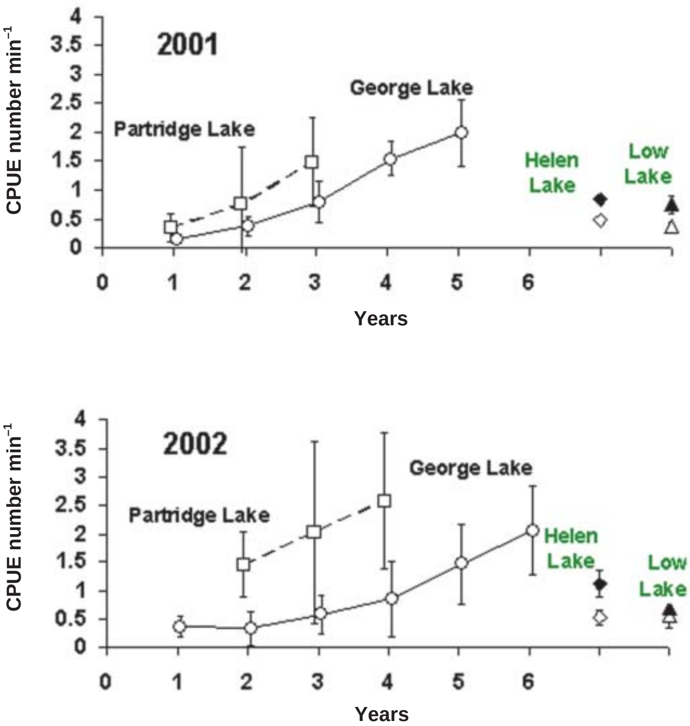



**Figure 4. Catch-per unit-effort (CPUE) in 2001 and 2002 of *S. interpunctatum versus* number of years since presence detected at sites in the 2 recovering lakes (Partridge and George). CPUE values from the 2 reference lakes (Helen and Low) are indicated for *S. Interpunctatum* (open symbols) and *S. femoratum* (closed symbols). Bars indicate 2 standard errors.**



the 2 reference lakes for that species. In the reference lakes the mean CPUE of *S. femoratum* was equal to or higher than the mean CPUE of *S. interpunctatum*.

## DISCUSSION

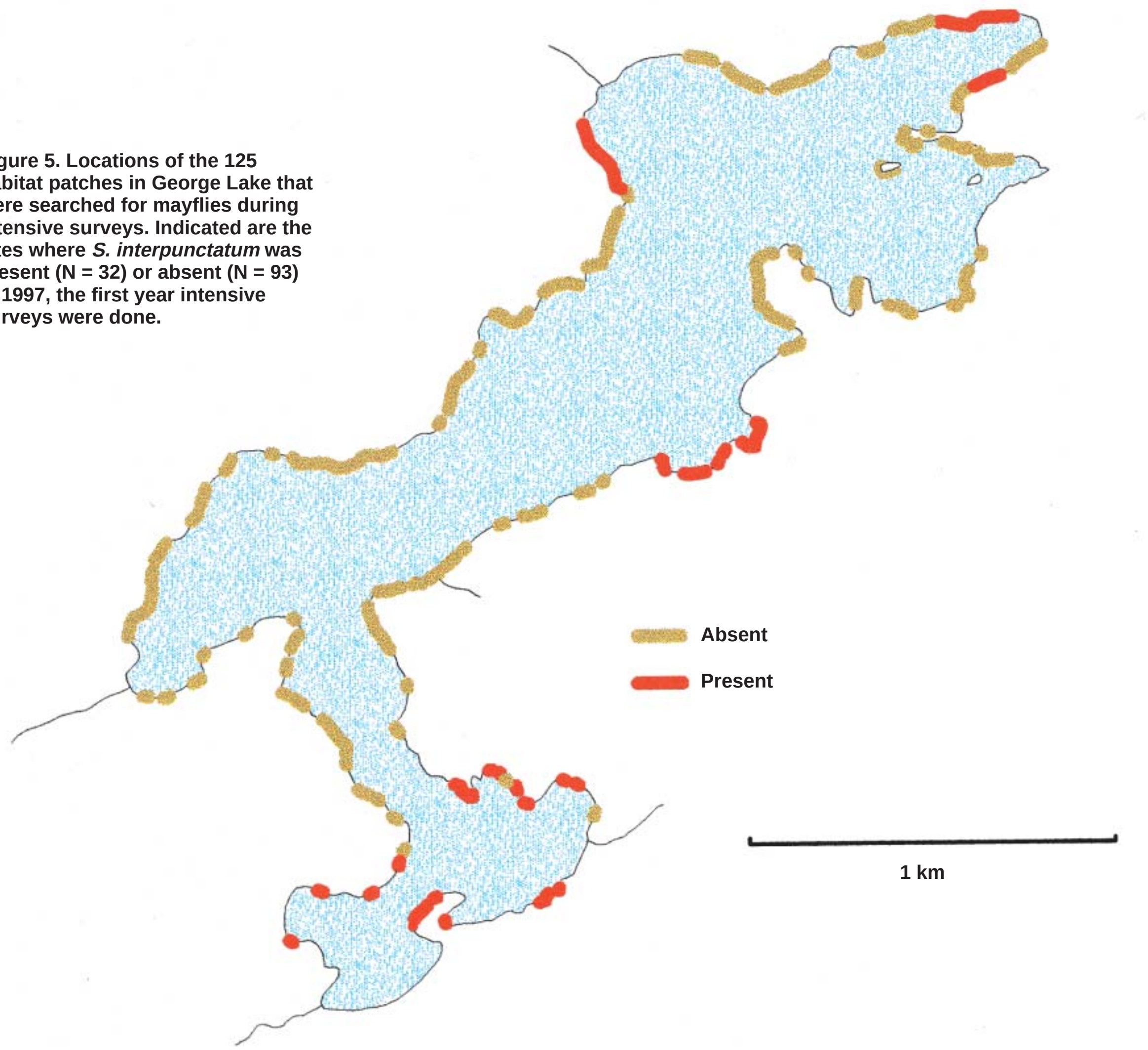
The synoptic surveys produced pH thresholds, of 5.6 for *H. azteca* and *S. femoratum* and 5.3 for *S. interpunctatum*. These thresholds are in close agreement with values from other field studies. In other surveys *H. azteca* has been identified as a good indicator species with a pH threshold of 5.6 (17–19). It could be considered the North American counterpart of the European amphipod *Gammarus lacustris*, an acid-sensitive indicator species that is affected below pH 6.0 (20). Other studies of the mayflies suggest pH minima of 5.3 for the genus *Stenonema* (21), 5.5 for *S. femoratum* and 5.4 for *S. interpunctatum* (22), and 5.3 for *S. interpunctatum* and 5.6 for *S. femoratum* (12).

The observation in this study of very limited movement of amphipods and mayflies within a lake during the earliest stages of recolonization has implications for monitoring of biological recovery. Re-establishment on the patchy habitats in these lakes began with very isolated settlements (Fig. 5) that could be missed if sampling effort is low. This observation suggests that sampling a small number of sites in a lake may not be sufficient to detect invertebrate recolonization in its earliest stages and may create a time lag between colonization and discovery of the new populations. This may be especially true for slow-dispersing species in large lakes.

Two potential sources of colonists of acid-damaged lakes are remnant populations inhabiting refuges within the lakes and populations migrating from nearby lakes. For example, refuge areas within a lake may consist of localized areas with well-buffered lake sediments (23, 24) or locations affected by circumneutral tributary streams or groundwater springs. In areas like Killarney with a wide variety of lakes in close proximity, colonists may also arrive from external sources. Our synoptic surveys revealed that sources of all 3 species exist in lakes that are only 1–4 km from the acid-damaged lakes (13), suggesting that inter-lake dispersal may occur quite quickly. Mayfly dispersal can occur by means of windblown females, perhaps windblown eggs, and possibly eggs attached to the feet or bodies of birds (25). Inter-lake dispersal of *H. azteca* can occur via animal vectors, including transport in the feathers of waterfowl or in the fur of animals (26, 27). Once barriers to dispersal between lakes are overcome, the number and rate of arrival of propagules, their generation time, fecundity of established colonizers, and interactions with resident species will determine whether or not new populations survive (28, 29). Establishment of a population can take decades if sources of colonists are distant, but could occur quite rapidly if nearby sources exist (28). Indeed, in this study populations were established quite rapidly, within less than 4 to 8 years after mid-lake pH reached thresholds of specific taxa.

During the early years of colonization the distribution of organisms in a lake appears to be very restricted (Fig. 5). Over time dispersal from the initial settlements, as well as perhaps new inoculations from external sources, allow the remaining habitat

**Figure 5. Locations of the 125 habitat patches in George Lake that were searched for mayflies during intensive surveys. Indicated are the sites where *S. interpunctatum* was present (N = 32) or absent (N = 93) in 1997, the first year intensive surveys were done.**



patches to become colonized. The rate of spread for a species in a lake is probably influenced by *i*) the size and distribution of optimal habitat patches; *ii*) the distance between patches; *iii*) species characteristics such as rate of growth and dispersal ability; and *iv*) the presence of predators and competitors (30). The potential mechanisms for dispersal within a lake include active migration by crawling across substrates and swimming, transport by wind-generated currents or by animals and, in the case of species with winged adults, dispersal of eggs to new locations during oviposition.

Dispersal of a newly arrived species to all available habitat patches within a lake can occur quite rapidly, especially in a small lake, but major lags can occur before the first successful colonization begins. For example, the dispersal of *S. interpunctatum* throughout Partridge Lake (11 ha) was complete within 3 years, but was estimated to have occurred up to 11 years after the lake pH reached the species' threshold. In George Lake (189 ha) *S. interpunctatum* was well-established during 1997 and complete dispersal throughout the lake had not yet occurred by 2002, a span of 6 years and an estimated 22 years after the species' threshold pH was reached in the recovering lake.

Uncertainties in the estimates of pH recovery are introduced by seasonal and spatial variability in lake pH. In this study species pH thresholds were characterized using midwinter water samples, but the estimated year of pH recovery was based upon water samples collected during summer and fall when pH values in Killarney lakes are typically higher than in winter (8). In addition, episodic pH depressions can occur at shallow depths in lakes during late winter and spring snow melt. However, the potential effect of these acid episodes on survival of benthic invertebrates is not clear because toxicity may be mitigated by physiological tolerance, population compensatory mechanisms, or by avoidance (31).

The more acid tolerant of the 2 mayflies (i.e. *S. interpunctatum*) dominates the communities in the recovering lakes, but it is uncertain whether it is the acid sensitivity of the lesser species (*S. femoratum*) or the order of colonization that affects the structure of the community. We observed that the densities of *S. interpunctatum* on the sites that have been occupied the longest in George Lake are higher than in the reference lakes. This may be because the carrying capacity of George Lake is higher than the reference lakes, but it could also be that the population in George Lake is overshooting the carrying capacity during this stage of recovery and that densities will decline with time. It is too early to predict if *S. femoratum* will achieve the densities in recovering lakes that it has in the unacidified reference lakes. Late-arriving species such as *S. femoratum* must also deal with more species-rich communities and it may be more difficult for them to succeed because of increased exposure to predation and competition (30) or changes in the availability or quality of food items.

The 6 years of monitoring described in this paper provide a unique data set on the recovery process and rates of dispersal for macroinvertebrates in acid-damaged lakes. However, important questions remain regarding final endpoints, and these should be addressed by continued monitoring. Niemi et al. (28) correctly stated that long-term studies are likely the only way to understand the dynamics of recovery of aquatic systems from disturbance.

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32. Jim Carbone provided valuable advice on mayfly taxonomy and sampling procedures. Constructive criticism of the manuscript was provided by John Gunn, Bill Keller, and the journal referees.



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