Effects of Changes in Acidity on Aquatic Insects in Rocky Littoral Habitats of Lakes Near Sudbury, Ontario

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Abstract

Benthic aquatic insects were collected from rocky nearshore areas (< 1 m deep) of 17 lakes near Sudbury, Ontario, with a pH range of 4.7–7.3 and a size range of less than 10 ha to over 10,000 ha. These insect communities were composed of taxa common to lake soft-sediments and streams. Direct and indirect effects of lake acidity appeared to be major controls on the structure of these communities, implying that several factors may be involved in restructuring during acidification or recovery. Declines in abundances of several taxa of Ephemeroptera at pH below 5.5 were attributable to acid toxicity, while increases in the abundances of Odonata and Diptera at pH below 5.5 were associated with the absence of fish predators and other indirect effects of acidity. The communities of two experimentally neutralized lakes restructured rapidly within 5 years, approaching but not achieving community structures typical of our near-neutral survey lakes. Neutralization led to recolonization or increased abundance of the acid-sensitive mayfly, *Stenacron interpunctatum*, and the dragonfly, *Boyeria grafiana*; however, recolonization by other taxa expected to be present in near-neutral lakes (*Stenonema femoratum*, *Eurylophella*, and *Basiaeshna janata*) was not observed. Consistent with results for the survey lakes, declines in the abundances of the dragonflies *Aeshna interrupta*, *Aeshna eremita*, and *Leucorrhinia glacialis* in the neutralized lakes were associated with reintroductions of *Salvelinus fontinalis* (aurora trout) and increased fish predation pressure, while reduced abundances of the dipterans Ceratopogonidae, *Psectrocladius*, and *Stackelbergina* may be related to indirect effects of acidity other than fish predation. Although community composition varied greatly across the acidity gradient, total species richness and abundance were not correlated with lake chemistry or number of fish species.

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Introduction

The acidification of lakes is a widespread phenomenon that has been extensively characterized in terms of chemical and biological changes (Dillon et al. 1979; Haines 1981; Keller & Pitblado 1984; Kelso et al. 1986; Schindler 1988; Stenson & Eriksson 1989). While much research exists on the effects of pH on biota such as fish and plankton, fewer studies have dealt with benthic invertebrate communities, especially those of the littoral zone. Reductions in benthic invertebrate richness with increasing acidity have been observed in some cases (Leivestad et al. 1976; Mossberg & Nyberg 1979; Raddum 1980; Harvey & McArdle 1986), but often, significant relationships did not exist between the abundance and/or richness of benthic invertebrates and pH (Dermott 1985; Dermott et al. 1986; Bradt & Berg 1987; McNicol et al. 1995). These differing conclusions likely depend on variations related to substrate type and depth, varying levels of taxonomy, and differences in the portion of the total benthic invertebrate community examined.

Although comprising a very common habitat type, the shallow, rocky area of lakes has been essentially neglected from study because it is difficult to sample quantitatively. It is extremely important, however, as a habitat and feeding ground for many fish species (Macan 1977), and it normally supports diverse assemblages of invertebrates (Whiteside & Lindegaard 1982). In attempts to characterize benthic invertebrate communities, the rocky littoral zone has been essentially ignored in favor of easily sampled, soft-sediment habitats, because common sampling techniques employ the use of various types of grab samplers or coring devices, which are poorly suited for sampling hard substrates. Consequently, some important groups of insects, such as odonates and ephemeropterans, may not have been adequately sampled (Roff & Kwiatkowski 1977; Griffiths & Keller 1992). Also, the level of taxonomic identification is often inadequate to provide information on effects at the level of species or even genus, and identification of indicator species is not possible. Since inferences of pH tolerances based on

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identification to higher classifications may be inappropriate, animals collected in this study were identified to species when possible. While recent surveys have investigated littoral benthos in Precambrian Shield lakes, these studies did not specifically target rocky habitats (Stephenson et al. 1994; Bendell & McNicol 1995).

The sampling of rocky littoral areas may be of substantial importance in the assessment of biological changes in acidifying or recovering systems. Because fine-grained sediments common to deeper zones may in fact ameliorate the effects of acidification on the benthos (Collins et al. 1981; Allard & Moreau 1987), studies of invertebrate communities inhabitating nearshore rocky areas that may show more extreme acidity, including episodic pH fluctuations (Gunn & Keller 1986), are more likely to demonstrate the effects of acidification.

In order to characterize the insect communities typical of rocky littoral areas, and to determine the effects of lake acidity, we surveyed communities in a group of Precambrian Shield lakes near Sudbury, Ontario, and examined their relationships to various environmental variables. The communities of two experimentally neutralized lakes were also assessed for a period of 5 years after liming to determine patterns in recovery following the removal of acid stress and reintroduction of fish.

Methods

Physicochemical Lake Characterization

Seventeen lakes within a 106-km radius of the Sudbury, Ontario, smelting operations were selected for study. The majority of the study lakes are within the zone of low-pH lakes (pH $<$ 5.5) determined by Keller et al. (1980) to be under the influence of acid deposition from the Sudbury smelters. Lakes in this area have been subjected to many years of atmospheric acid and metal loading, causing extensive damage to species across various trophic levels (Keller 1992). Recent emission reductions have resulted in improvement in water quality in many of these lakes (Keller et al. 1992*b*), and early signs of recovery of some of the aquatic biota have been observed (Keller et al. 1992*a*). Lakes sampled outside this area, (Apsey, Windy, Fairbank, Penage, and Geneva), were chosen to represent near-neutral pH environments.

We collected water samples for chemical analysis during the late summer and fall cage retrieval period using a standard non-volume-weighted tube composite sampling method (Ontario Ministry of the Environment 1979) through the epilimnion and metalimnion. Water samples were analyzed for various chemical variables by techniques outlined by the Ontario Ministry of the Environment (1981). All metals and phosphorus were analyzed as total concentrations.

Neutralization and Fish Stocking

In the fall of 1989, Whirligig and Little Whitepine lakes were neutralized by addition of powdered limestone ($CaCO_3$) to approximately pH 6.5. The pH of Little Whitepine Lake remained above 6.0 over the post-liming study period, but Whirligig Lake re-acidified to about pH 5.5 by 1992 and was relimed in the fall of 1993 (Fig. 1). Whitepine Lake was not manipulated, and its pH remained between 4.9 and 5.1. Although attempts to reintroduce native aurora trout, a rare color variant of *Salvelinus fontinalis* (brook trout), in acidic Whirligig Lake prior to liming were unsuccessful, restocking in 1990 was successful (Fig. 1); by the fall of 1990 a reproducing population had been established (Snucins et al. 1995). An abundant fish population estimated at 300 individuals with a biomass of 17 kg/ha was present by the fall of 1991. Little Whitepine Lake contained a small number of aurora trout that escaped from holding pens during experiments conducted in May 1990. Based on low catches and records of possible fish escapes from the experiments, less than 20–30 aurora trout inhabited Little Whitepine Lake after May 1990. Seven of the fish were captured and sacrificed in October 1993, and an intensive netting survey in 1995 captured only one fish. Whitepine Lake was stocked in 1991 with 247 5-year-old fish, but there is no evidence that any of the fish survived. The lake was stocked successfully in May 1994 with approximately 500 3-year-old fish, but densities in both Little Whitepine and Whitepine lakes were considered nil to low during the course of the study.

Fish data for all other lakes were compiled from standard Ministry of Natural Resources lake surveys (Ontario Ministry of Natural Resources 1987). Collection methods included standard gillnets, trap nets, minnow traps, and plexiglas traps. Since no comparable population data were available, only numbers of species present could be determined for each lake.

Aquatic Insect Collections

Benthic aquatic insects colonizing artificial substrate cages were collected from 17 lakes (survey lakes) during the period 1987–1989. During the initial survey period, one lake was sampled in 1987, four lakes were sampled in 1989, and the remainder were sampled in 1988. Sampling was conducted for an additional 5 consecutive years (1990–1994) in Whitepine, Whirligig, and Little Whitepine lakes (time-trend lakes).

Substrate cages were chosen as sampling gear in order to closely duplicate the existing bottom type, providing quantitatively comparable data than other samplers (Klemm et al. 1990) and yielding less-variable density estimates (Morin 1985). The sampling protocol was designed to sample by a standardized method a specific habitat common to all lakes. Substrate cages made of 4 cm^2 aper-

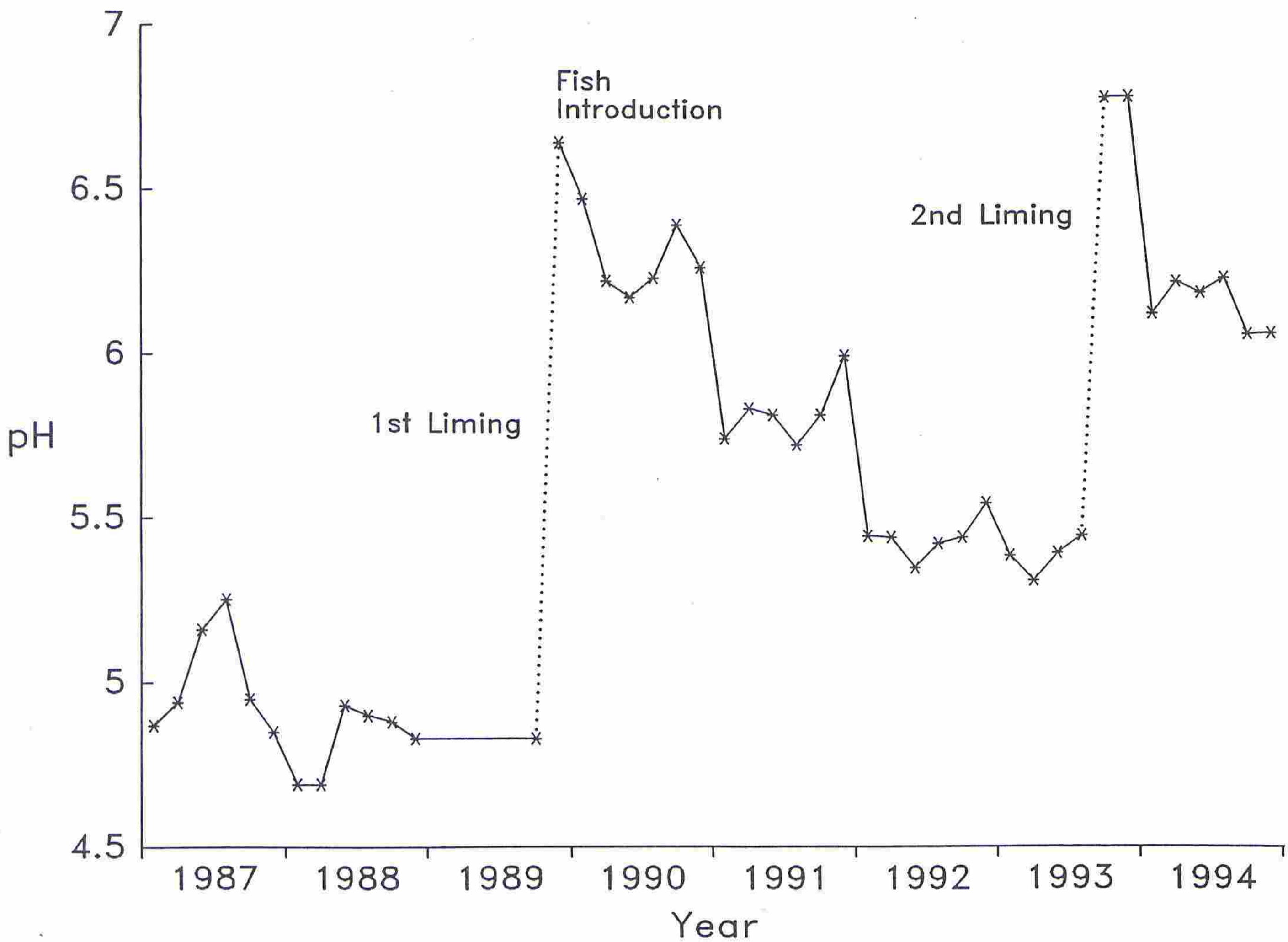

Figure 1. Timing of neutralizations and successful *Salvelinus fontinalis* (aurora trout) introduction in Whirligig Lake, 1987–1994.

ture steel mesh measuring 20 × 20 × 15 cm were filled with native rocks 5–15 cm in diameter to match the rocky, littoral substrate of the lakes. Five substrate cages were placed in shallow (< 1 m) areas of each lake, where such rocky habitat was prevalent. Cages were set in late summer (July/August) and retrieved in late fall (October) of each year, allowing a sufficient period of time (minimum 8 weeks) for colonization by benthic invertebrates (Clements et al. 1988). Cages were retrieved by lifting them from the substrate with a hook and pole and immediately inserting a net (0.6 mm aperture) beneath to catch any dislodged organisms. Cages and rocks were washed gently to remove any clinging organisms, and invertebrates lost from the cage but collected in the net beneath were picked and added to the sample.

In two of the near-neutral lakes, Geneva and Fairbank, invertebrates collected from the net and the cage proper were preserved and counted separately. The employment of nets beneath the cages at the beginning of retrieval significantly increased abundance estimates (paired t test; $p < 0.05$).

Invertebrates were sorted from debris and preserved in 70% ethanol. Insects were identified to species whenever possible. Chironomids were mounted on glass slides in a clearing medium, left for 24 hours at 60°C, then identified with a compound microscope; other insects were identified with a dissecting microscope. Taxonomic keys used for identifications were from Walker (1953, 1958), Walker & Corbet (1975), Bednarik & McCafferty (1979), Hilsenhoff (1981, 1984), Weiderholm (1983), and Merritt & Cummins (1984).

Data Analysis

Principal components analysis (PCA) of log(x + 1)-transformed species abundance data, averaged by lake, was used to identify factors explaining the variance in species abundance among the study lakes. Taxa were included in the PCA only if they were present in more than 20% of the survey lakes. The final species list for the PCA consisted of 24 taxa: 3 Trichoptera, 7 Odonata, 4 Ephemeroptera, and 10 Diptera. Component loadings were subsequently correlated with log-transformed limnological variables and untransformed pH to determine associations between taxonomic components and environmental characteristics. To assess recovery, comparison of component scores was used to provide an objective measure of the relative structure of insect communities in neutralized lakes and naturally neutral lakes.

One-way analysis of variance of $\log(x + 1)$-transformed data was used to test the differences in species abundances between 1987–1988 pre-neutralization communities and species abundances in portions of the post-neutralization period (1990–1992 and 1993–1994) in the time-trend lakes. Because inspection of the data indicated discontinuities in the distributions of many species at about pH 5.5, differences in species abundances, total abundance, and total species richness in lakes with pH greater and less than 5.5 were also tested by this method. Pearson correlation analyses were used to examine relationships between physicochemical and biological variables and relationships among physicochemical variables. All statistics were performed by means of SPSS/PC+ (SPSS, Inc. 1990).

Results

Lake Characteristics

The study lakes vary greatly in size and depth, with lake area and mean depth ranging from 4–11,660 ha and 4.7–18.3 m, respectively (Table 1). They are typical, although generally large, Precambrian Shield lakes: usually oligotrophic (total phosphorus ≤ 6 μg/L), dilute (conductivity < 87 μmho/cm), clear (dissolved organic carbon < 5 mg/L), and poorly buffered (total inflection point alkalinity < 18 mg/L). Exceptions are mesotrophic Whirligig and Apsey lakes (total phosphorus 11 and 12 μg/L, respectively). The lakes cover a wide range of pH values from 4.7 to 7.3. Metal concentrations were relatively low for nickel (≤ 17 μg/L) and copper (≤ 6 μg/L), but aluminum concentrations were elevated at low pH, ranging from 10 to 440 μg/L. The number of fish species ranged from 0 to 13, with most of the highly acidic lakes (pH < 5.0) having no fish populations. Fish species present were those common to northern Ontario lakes, such as *Salvelinus namaycush* (lake trout), *Perca flavescens* (yellow perch), *Micropterus dolomieui* (smallmouth bass), *Esox lucius* (northern pike), *Catostomus commersoni* (common white sucker), *Ictalurus nebulosus* (brown bullhead), and various minnow species.

Survey Lakes: Species Distributions and Abundances

The dominant groups of aquatic insects in the samples were Odonata, Ephemeroptera, Diptera, and Trichoptera, collectively comprising over 95% of the insect abundance in the study lakes (Tables 2 & 3). The number of taxa collected for the orders Odonata, Ephemeroptera, Diptera, and Trichoptera was 14, 6, 26, and 11, respectively. The mean total abundances per cage across the study lake set for the same orders were 4.4, 28.4, 11.8, and 8.2, respectively. Of the other orders of aquatic insects, Plecoptera and Megaloptera were rare, with the latter occurring

Table 1. Chemical, physical, and biological characteristics of the study lakes ($n = 17$).*

Lake Name	*I.D.*	*Latitude*	*Longitude*	*Area (ha)*	*Mean Depth (m)*	*pH*	*Alkalinity (mg/L)*	*Conductivity (umho/cm)*	*Copper (μg/L)*	*Nickel (μg/L)*	*Aluminum (μg/L)*	*DOC (mg/L)*	*Phosphorus (μg/L)*	*Number of Fish Species*
Wilderness	WIL	47°24′	80°38′	4.1	5.7	4.7	−1.10	36.0	2	4	180	0.8	3	0
Ruth Roy	RR	46°05′	81°15′	46.1	6.4	4.7	−0.89	32.8	4	17	440	0.9	2	0
Whirligig	WHG	47°23′	80°38′	11.4	4.7	4.8	−0.28	31.4	1	3	180	3.3	11	0
Whitepine	WP	47°23′	80°38′	77.8	7.6	4.9	−0.60	31.5	1	3	180	2.3	4	0
Chiniguchi	CHI	46°57′	80°42′	1,511.0	13.6	4.9	−0.60	36.4	3	12	170	0.5	2	3
Telfer	TEL	46°56′	80°47′	305.7	10.4	4.9	−0.62	36.5	4	13	180	0.6	2	0
Johnnie	JOH	46°05′	81°13′	395.4	7.9	5.3	−0.03	31.5	3	11	110	2.4	4	8
Little Whitepine	LWP	47°23′	80°39′	21.7	5.7	5.5	0.37	25.9	1	0	54	2.4	5	0
Bell	BEL	46°08′	81°12′	281.4	8.0	5.6	0.84	34.9	4	13	110	4.3	6	11
Tyson	TYS	46°07′	81°07′	1,142.7	11.9	5.6	0.72	34.7	4	10	78	3.4	5	9
Geneva	GEN	46°46′	81°33′	356.4	6.3	6.2	5.11	35.7	2	3	10	3.0	6	7
Joe	JOE	46°44′	81°01′	179.6	11.2	6.3	1.83	39.0	3	10	29	1.5	5	7
Nelson	NEL	46°44′	81°05′	316.1	11.2	6.4	1.83	36.2	2	5	10	2.0	5	5
Windy	WIN	46°36′	81°27′	1,112.0	10.7	6.5	2.21	53.0	2	11	14	2.1	6	12
Penage	PEN	46°15′	81°20′	11,659.9	14.7	6.9	7.52	74.2	6	16	15	3.4	6	12
Apsey	APS	46°13′	81°47′	289.7	6.0	6.9	17.24	86.5	1	0	14	4.7	12	13
Fairbank	FB	46°28′	81°26′	703.1	18.3	7.3	13.05	64.4	2	4	13	1.7	4	11
Mean				1,083.2	9.4	5.2	2.74	42.4	3	7.9	105.1	2.3	5.2	5.8

*Chemistry data for Whirligig and Little Whitepine lakes are prior to neutralization. I.D. = abbreviation of study lakes.

Table 2. Presence-absence data for aquatic insects in the survey lakes, arranged by pH, 1987–1989.[a]

Lake I.D.	WIL[b]	RR	WHG	WP	CHI[c]	TEL[c]	JOH	LWP	BEL	TYS	GEN	JOE	NEL	WIN	PEN[c]	APS[c]	FB
pH	4.7	4.7	4.8	4.9	4.9	4.9	5.3	5.5	5.6	5.6	6.2	6.3	6.4	6.5	6.9	6.9	7.3
Megaloptera																	
Chauliodes	*																
Sialis		*															
Coleoptera																	
Dineutus			*														
Dubiraphia											P						
Gyrinus	P									*							
Hydroporus									P						*		
Psephenus herricki															P		
Scirtes									*								
Stenelmis										*	*				*		
Hemiptera																	
Belostoma flumineum														*			
Hesperocorixa																*	
Notonecta	P	*	*					P									
Sigara			P	*		*											*
Trichoptera																	
Agrypnia		*									*						
Banksiola	*	P	*	*													
Ceraclea											P						*
Cheumatopsyche																	*
Lype diversa																	*
Nectopsyche															P		
Nyctiophylax			P	P			P	P		P	P	P	P	P			
Oecetis															*	*	
Oxyethira					*		*			*							
Polycentropus	P	*	P	P	P	*	P	P		P	P	P	P	P	P	P	P
Ptilostomis					*	*		*									
Odonata																	
Aeshna	*											*					
Aeshna eremita	*	P	P	*	*			P						*			
Aeshna interrupta	P		P	P	*	*		P									
Argia violacea?										P					P	P	P
Basiaeshna janata							P		*	*				P	*	P	
Boyeria grafiana									*				P	P	P		*
Chromagrion conditum	*						*										
Enallagma	P	P	P		P	*	P			P	P			*			
Epitheca spinigera										*				*			
Helocordulia uhleri											*						
Ladona julia							*										
Leucorrhinia glacialis	P	P	P	P	P												
Macromia illinoiensis														*			
Neurocordulia jamaskanensis										*							
Ephemeroptera																	
Caenis																P	
Eurylophella							P		P	P	P			*	*	P	*
Heptagenia																	P
Leptophlebia	P		P	*				P	P	P	P	P	*	P	P	P	*
Stenacron interpunctatum							P	P	P	P	P	P	P	P	P	*	P
Stenonema fermoratum										*	P	P	P	P	P	P	P
Plecoptera														*	P		
Diptera																	
Ablabesmyia	*		P			*											
Arctopelopia			P														
Ceratopogonidae	P	P	P	P	*	*	*	P							*		
Chironomus					P												
Conchapelopia			*	P	*		P	P		P	P	*	*	P			
Cryptochironomus						*											
Dicrotendipes				*		P	P	P		*	*					P	*
Empididae												*			*		

(continued)

Table 2. Continued.

Lake I.D. pH	WIL[b] 4.7	RR 4.7	WHG 4.8	WP 4.9	CHI[c] 4.9	TEL[c] 4.9	JOH 5.3	LWP 5.5	BEL 5.6	TYS 5.6	GEN 6.2	JOE 6.3	NEL 6.4	WIN 6.5	PEN[c] 6.9	APS[c] 6.9	FB 7.3
Diptera (cont.)																	
Endochironomus			P	P				P		*	P				*	*	
Glyptotendipes			*							*	P			*			
Heterotrissocladius																	
Hydrobaenus					*	P											
Meropelopia															P		
Micropsectra				*										*			
Microtendipes						*		*		P	*						*
Monopsectrocladius				*			*										
Paratanytarsus																*	
Polypedilum										P	*						
Procladius	*				*												
Psectrocladius (s.s.)	P	P	P	P		P	*	P	*	*	P		*				
Pseudochironomus											*	*			*	*	
Stackelbergina	P	*	P	P													
Tanytarsus					*	P											
Thienemannimyia																P	
Tribelos						*	*			*	P						
Zalutschia			*	P							*						

[a] All lakes sampled during 1998, except as indicated. P, present in more than one sample; *, present in only one sample. See Table 1 for abbreviations to study sites (Lake I.D.).
[b] Sampled in 1987.
[c] Sampled in 1989.

only in the two most acidic lakes, while Coleoptera and Hemiptera were uncommon but occurred across the pH range. Other groups of aquatic organisms, such as amphipods, isopods, molluscs, crayfish, leeches, and worms, were represented in the samples in low numbers and were not considered in further analyses.

Stenacron interpunctatum, *Leptophlebia*, *Stenonema femoratum*, and *Eurylophella* were the most common and abundant mayflies. The pH minima observed for occurrences of *Eurylophella*, *S. interpunctatum*, and *S. femoratum* were 5.3, 5.3, and 5.6, respectively, distinguishing *S. femoratum* as the most acid-sensitive mayfly (Table 2). All three taxa were more abundant ($p < 0.05$) in lakes of pH over 5.5 (Table 4). *Leptophlebia* is an acid-tolerant mayfly found in survey lakes of pH under 5.0, and abundances were not significantly different ($p > 0.05$) in lakes above and below pH 5.5.

The most common and abundant Odonata were *Enallagma*, *Leucorrhinia glacialis*, *Aeshna eremita*, and *Aeshna interrupta*. *L. glacialis*, *A. eremita*, and *A. interrupta* occurred only below pH 4.9, 5.5, and 6.5, respectively, although only a single specimen of *A. interrupta* was collected above pH 5.5 (Table 2). All three taxa were higher in abundance ($p < 0.05$) in lakes with pH below 5.5 (Table 4). *Enallagma* was found across the acidity gradient. Two other less common dragonflies, *Basiaeshna janata* and *Boyeria grafiana*, were not collected in lakes below pH 5.3 and 5.6, respectively (Table 2), but abundances were not significantly different ($p > 0.05$) in lakes above and below pH 5.5.

The most common and abundant Diptera were *Conchapelopia*, Ceratopogonidae, *Endochironomus*, and *Psectrocladius*. Occurrences of *Conchapelopia* and *Endochironomus* were distributed across the pH gradient, but abundances of Ceratopogonidae and *Psectrocladius* were higher ($p < 0.05$) in more acidic lakes. *Stackelbergina* occurred only in lakes with pH below 4.9 and was also more abundant ($p < 0.05$) in lakes below pH 5.5 (Table 4).

Polycentropus and *Nyctiophylax* were the most common and abundant caddisflies collected in the survey lakes, and their occurrences were distributed across the acidity gradient (Table 2). *Banksiola* was more abundant ($p < 0.05$) in lakes below pH 5.5 (Table 4).

Although marked shifts in the composition of the insect communities across the acidity gradient were apparent (Table 2), total species richness ($r = -0.04$) and abundance ($r = 0.37$) were not related to pH (Pearson correlations, $p > 0.05$). No significant difference ($p > 0.05$) between total species richness and abundance in lakes above and below pH 5.5 was found. The means of the total species richness in lakes above and below pH 5.5 were 13.1 and 13.8, respectively, and mean abundances above and below pH 5.5 were 65.4 and 40.1, respectively.

Survey Lakes: Principal Components Analysis

The first three principal components from the analysis of the common species accounted for 31.4%, 16.6%, and 11.1% of the variance in the data, respectively, for a to-

Table 3. Presence-absence data for aquatic insects in survey lakes (time-trend set), 1987–1994.*

Lake	*Whitepine*							*Whirligig*							*Little Whitepine*						
Year	*87*	*88*	*90*	*91*	*92*	*93*	*94*	*87*	*88*	*90*	*91*	*92*	*93*	*94*	*87*	*88*	*90*	*91*	*92*	*93*	*94*
pH	*5.1*	*4.9*	*4.9*	*5.0*	*5.0*	*5.1*	*5.1*	*5.0*	*4.8*	*6.3*	*5.8*	*5.4*	*5.4*	*6.1*	*5.6*	*5.5*	*6.5*	*6.7*	*6.3*	*6.5*	*6.3*
Megaloptera																					
Chauliodes																					
Sialis																					
Coleoptera																					
Dineutus								P													*
Dubiraphia																					
Gyrinus			*				*														*
Hydroporus																					
Psephenus herricki																					
Scirtes																					
Stenelmis																					
Hemiptera																					
Belostoma flumineum																					
Hesperocorixa																					
Notonecta	*		*				*		*							P					
Sigara		*	*	*					P	P		*	*				*	*		*	
Trichoptera																					
Agrypnia								*													
Banksiola		*							*												
Ceraclea																					
Cheumatopsyche																					
Lype diversa																					
Nectopsyche																					
Nyctiophylax	*	P		*			*	P	P	P		*			*	P	P				
Oecetis																					
Oxyethira																					
Polycentropus	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	*	P
Ptilostomis			*	P	*											*					
Odonata																					
Aeshna										*		*									
Aeshna eremita	P	*	P	P			*	P	P	*	*				*	P	P				*
Aeshna interrupta	P	P	P	P	P	P	*	P	P	P	P		P	P	P	P	P	P	P	P	P
Argia violacea?																					
Basiaeshna janata																					
Boyeria grafiana							*			P	P	P					P	*			*
Chromagrion conditum																					
Enallagma	*				*		*	*	P	P	P	P	P	P							*
Epitheca spinigera																					
Helocordulia uhleri					*																
Ladona julia																					
Leucorrhinia glacialis	P	P	*	*		P		P	P	*	*	*	*	*	*			P	*		
Macromia illinoiensis																					
Neurocordulia jamaskanensis																					
Ephemeroptera																					
Caenis																					
Eurylophella																					
Heptagenia																					
Leptophlebia	*	*		P	P		P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Stenacron interpunctatum					*					P	P	P	P	P	P	P	P	P	P	P	P
Stenonema femoratum																					
Plecoptera																					
Diptera																					
Ablabesmyia					*	*		P	P	P		P	P	*			P			*	P
Arctopelopia									P	*											
Ceratopogonidae	P	P	P	*	*			P	P		*					P					
Chironomus					*																
Conchapelopia	P	P	P				P	*	*	P		*	*	*		P	*				*
Cryptochironomus												*									

(continued)

Table 3. Continued.

Lake	*Whitepine*							*Whirligig*							*Little Whitepine*						
Year	*87*	*88*	*90*	*91*	*92*	*93*	*94*	*87*	*88*	*90*	*91*	*92*	*93*	*94*	*87*	*88*	*90*	*91*	*92*	*93*	*94*
pH	*5.1*	*4.9*	*4.9*	*5.0*	*5.0*	*5.1*	*5.1*	*5.0*	*4.8*	*6.3*	*5.8*	*5.4*	*5.4*	*6.1*	*5.6*	*5.5*	*6.5*	*6.7*	*6.3*	*6.5*	*6.3*
Diptera (continued)																					
Dicrotendipes		*											P			P		*	*	*	
Empididae																					
Endochironomus	P	P	P	P	P		P	P	P	P	P	P	*		P	P	P			*	*
Glyptotendipes							*		*					P							
Heterotrissocladius			P	P						P											
Hydrobaenus																					
Meropelopia																					
Micropsectra	*	*			P					P	*						*				
Microtendipes					P	*				*	*				*	*	*				P
Monopsectrocladius		*																			
Paratanytarsus			P	*	P		*														
Polypedilum																					
Procladius					*						*	*									
Psectrocladius (s.s.)	P	P	P	P	P	*	P	P	P	P	*	P		P	*	P	P				*
Pseudochironomus																					
Stackelbergina	P	P	P		*	*	*	P	P												
Tanytarsus											P	*	*								
Thienemannimyia																P	*				
Tribelos					*							*									
Zalutschia		P	*						*												

*P, present in more than one sample; *, present in only one sample.

tal of 59.2% of the explained variance. Any of the remaining components accounted for less than 10% of the variance in the data.

Component 1 was characterized by three mayflies (*S. interpunctatum*, *S. femoratum*, and *Eurylophella*) and a dragonfly (*B. janata*) that had high negative loadings and by three dragonflies (*A. eremita*, *A. interrupta*, and *L. glacialis*), three dipterans (*Psectrocladius*, *Stackelbergina*, and Ceratopogonidae), and one caddisfly (*Banksiola*) that had high positive loadings (Table 5). Component 1 was highly negatively correlated with number of fish species, area, pH, magnesium, alkalinity, potassium, calcium, sodium, and mean depth; it was positively correlated with aluminum (Table 6). It may best be described as an acidity factor represented by pH, because pH, related environmental variables, and number of fish species correlated well with component 1 scores (Table 6). A number of variables, including number of fish species ($r = 0.78$, $p < 0.001$), magnesium ($r = 0.86$, $p < 0.001$), calcium ($r = 0.85$, $p < 0.001$), alkalinity ($r = 0.95$, $p < 0.001$), and aluminum ($r = -0.77$, $p < 0.001$) were correlated with pH. Component 1 reflects the distribution of the most important species in our samples and is therefore considered to be of most use in describing the benthic community. A discontinuity at pH 5.5 was again apparent (Fig. 2), indicating a transition between more acid lakes

Table 4. Analysis of variance comparisons of $\log(x + 1)$ mean insect abundances per cage for survey lakes above and below pH 5.5.

Taxa	*pH < 5.5*	*pH > 5.5*
Banksiola	0.30*	0.00
Leucorrhinia glacialis	2.99*	0.00
Stackelbergina	0.69*	0.00
Ceratopogonidae	4.81*	0.03
Psectrocladius	2.72*	0.29
Aeshna eremita	0.85*	0.00
Aeshna interrupta	0.70*	0.02
Eurylophella	0.06	0.65*
Stenonema femoratum	0.00	11.27*
Stenacron interpunctatum	3.07	22.02*

*Significantly higher mean abundance ($p < 0.05$).

Table 5. Component 1 loadings for benthic insect taxa from survey lakes.

Taxa	*Component 1 "Acidity"*
Banksiola	0.86
Leucorrhinia glacialis	0.84
Stackelbergina	0.80
Ceratopogonidae	0.79
Psectrocladius	0.76
Aeshna eremita	0.74
Aeshna interrupta	0.70
Basiaeshna janata	−0.58
Eurylophella	−0.63
Stenonema femoratum	−0.72
Stenacron interpunctatum	−0.80

Table 6. Significant Pearson correlation coefficients of environmental variables with component 1 scores.

Parameter (units)	*Component 1*
Number of fish species	−0.90**
Area (ha)	−0.80**
pH	−0.76**
Magnesium (mg/L)	−0.76**
Alkalinity (mg/L)	−0.71*
Potassium (mg/L)	−0.69*
Calcium (mg/L)	−0.66*
Sodium (mg/L)	−0.60*
Mean depth (m)	−0.58*
Aluminum (μg/L)	0.73**

*$p < 0.01$.
**$p < 0.001$.

characterized by high abundances of dragonflies and dipterans (high positive scores) to near-neutral lakes characterized by high abundances of mayflies (high negative scores).

Results of the PCA agree well with the analysis of variance (ANOVA) comparisons for abundances of taxa in lakes above and below pH 5.5, with the exception of abundances of *B. janata*, which were not significantly different in the ANOVA (Table 4).

Component 2 was characterized by high positive loadings of *Conchapelopia*, *Nyctiophylax*, *Tribelos*, *Polycentropus*, *Microtendipes*, and *Enallagma* and was not correlated with the physicochemical or biological variables measured.

Leptophlebia and *Endochironomus*, taxa that loaded positively on component 3, were correlated with variables reflecting productivity (positively with total phosphorus, and negatively with Secchi depth); thus component 3 can be best described as a productivity factor.

Time-trend Lakes

When superimposed upon the survey lakes data, component 1 scores for Whitepine Lake were similar in all years, indicating little change in community composition over time under relatively constant low pH conditions (Fig. 2). In contrast, component 1 scores for both neutralized lakes (Whirligig and Little Whitepine) decreased dramatically toward the negative end of the component 1 scale after neutralization, related to increases ($p < 0.05$) in *S. interpunctatum* and *B. grafiana* abundances (Table 7). Whirligig Lake showed a larger decrease in component 1 scores than Little Whitepine Lake due to decreases ($p < 0.05$) in abundances of other taxa, including *A. eremita*, *A. interrupta*, *L. glacialis*, Ceratopogonidae, *Psectrocladius*, *Endochironomus*, and *Stackelbergina*, and increases ($p < 0.05$) in abundances of *Leptophlebia*. Even 5 years after manipulation, however, neither of the neutralized lakes achieved component 1 scores as low as those of the near-neutral survey lakes. The partial re-acidification of Whirligig Lake (Fig. 1) does complicate assessment of temporal recovery patterns in this lake. Although the abundances of most taxa changed rapidly in the short term (within 3 years of manipulation), several in Whirligig Lake continued to decline (*Endochironomus* and *B. grafiana*) or increase (*S. interpunctatum*) in abundance over the following 2 years (1993–1994; Table 7).

Discussion

Our study indicates that the nearshore insect communities of rocky littoral habitats are a combination of organisms commonly found in other habitats. Dipteran taxa common in the study lakes (*Psectrocladius*, *Conchapelopia*, and Ceratopogonidae) are typically found in fine-grained habitats in Precambrian Shield lakes (Dermott 1988; Keller et al. 1990; Griffiths & Keller 1992) and other oligotrophic, softwater lakes (Wiederholm & Eriksson 1977; Mossberg & Nyberg 1979; Whiteside & Lindegaard 1982). Other common taxa such as *Stenacron interpunctatum*, *Leptophlebia*, *Stenonema femoratum*, *Eurylophella*, and *Polycentropus* also inhabit stream habitats (Hall & Ide 1987; Giberson & Hall 1988; Smith et al. 1990); *Leptophlebia* and *S. femoratum* are common in nearshore areas (Dermott 1988); and *Leucorrhinia* is common in littoral, soft-sediment habitats (McNicol & Wayland 1992). *Stackelbergina* was commonly found in nearshore areas of our acid lakes, the first collection of this taxa in Ontario. *Boyeria grafiana* is common in rocky littoral areas of lakes (Walker 1958). Comparison of our data with data from the literature is difficult in some cases, however, due to the lack of species-level identifications in other studies.

Lake acidity clearly emerged as a major influence on community composition. Compared to near-neutral lakes, acidic lakes were generally characterized by increased abundances of dragonflies (*A. interrupta*, *A. eremita*, and *L. glacialis*), Diptera (*Psectrocladius*, *Stackelbergina*, and Ceratopogonidae), and the caddisfly *Banksiola*, and decreased abundances of three mayflies (*S. interpunctatum*, *S. femoratum*, and *Eurylophella*), and possibly a dragonfly (*Basiaeshna janata*; Table 5). These changes in community composition occurred at a pH of about 5.5 (Table 2; Fig. 2).

The effects of water chemistry and fish predation combine to structure the rocky littoral community. It is clear that certain mayflies are physiologically quite sensitive to increased acidity and are intolerant of low pH. Mayflies, other than the acid-tolerant *Leptophlebia* (Mossberg & Nyberg 1979; Hall & Ide 1987), do not appear to have the capacity to tolerate pH levels lower than about 5.0. Leivestad et al. (1976) and Harvey and McArdle (1986) also indicated that mayfly species generally decline or disappear below pH 5.0. The absence of the mayfly *S. interpunctatum* in lakes below pH 5.3 concurs

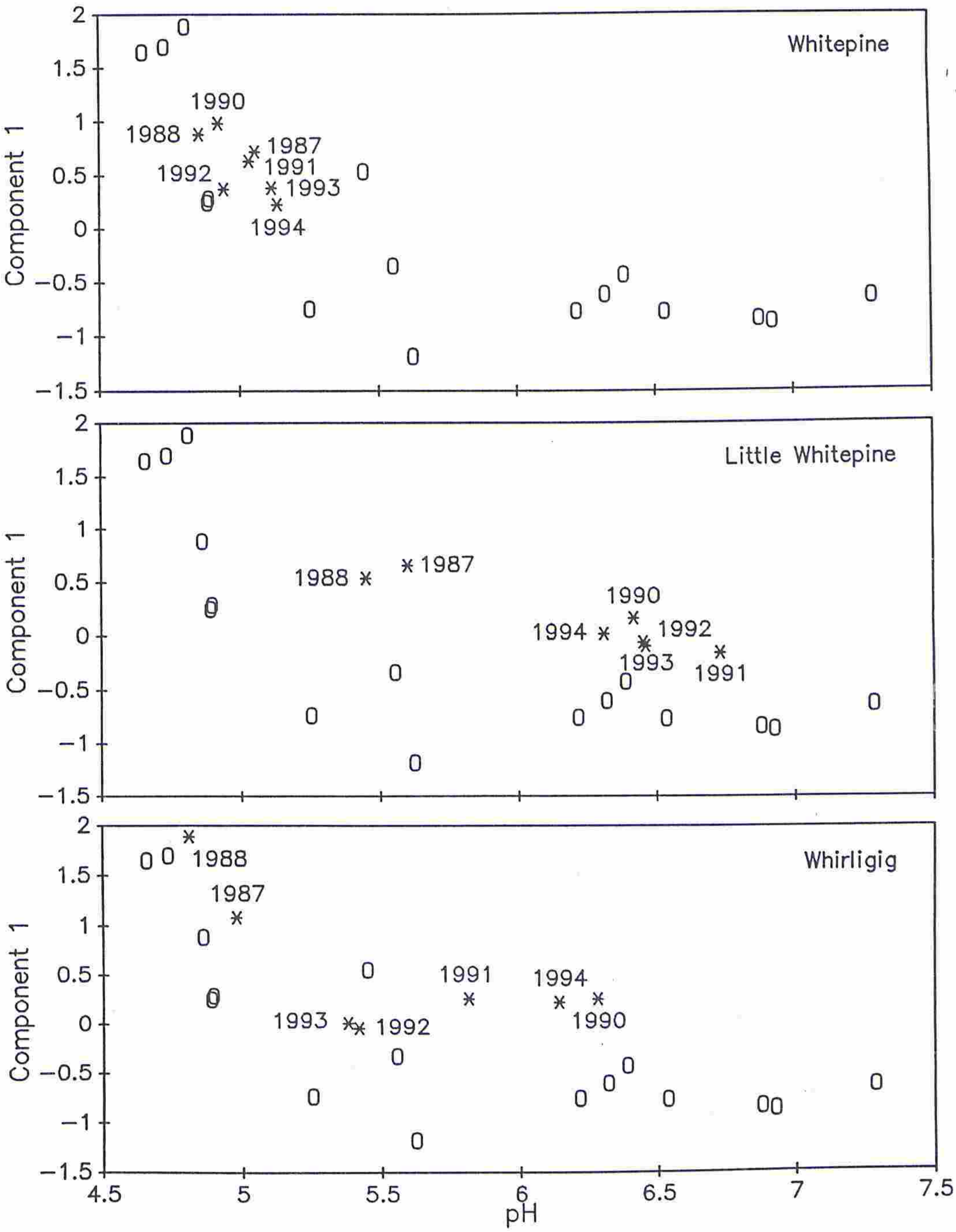

Figure 2. Component 1 scores versus pH for time-trend lakes (Whitepine, Little Whitepine, and Whirligig), 1987–1994, and for survey lakes (circles).

with its previous categorization in streams, as acid-sensitive to pH less than 5.0 (Hall & Ide 1987). *S. femoratum* was observed to be the most acid-sensitive species of mayfly in our study, not appearing at pH values below 5.6. *Eurylophella* was not found below 5.3, and certain species of this genus were also determined to be sensitive to low pH (Bell & Nebeker 1969; Hall & Ide 1987). Biological surveys of rocky littoral habitat provide valuable information for indicator species such as these mayflies that are not reported in surveys of deeper soft-sediment areas. *S. femoratum* in particular shows excellent potential as an acid-indicator species in Precambrian Shield lakes.

While the toxic effects of lake acidity directly influence the occurrence and abundance of certain acid-sensitive species, particularly mayflies, the indirect effect

Table 7. Analysis of variance comparisons of insect abundances of experimental lakes over various periods of study.*

	Whirligig		*Little Whitepine*	
Taxa	*Short term*	*Continued*	*Short term*	*Continued*
Leucorrhinia glacialis	—	0	0	0
Stackelbergina	—	0	0	0
Ceratopogonidae	—	0	0	0
Psectrocladius	—	0	0	0
Aeshna eremita	—	0	0	0
Aeshna interrupta	—	0	0	0
Endochironomus	—	—	0	0
Leptophlebia	+	0	0	0
Boyeria grafiana	+	—	+	0
Stenacron interpunctatum	+	+	+	0

*"Short term" indicates the pre-experimental period (1987–1988), compared to the 3-year period immediately after manipulation (1990–1992). "Continued" indicates the period immediately after manipulation (1990–1992), compared to the following 2 years (1993–1994).
+, significant increase in abundance ($p < 0.05$); —, significant decrease in abundance ($p < 0.05$); 0, no significant change in abundance ($p > 0.05$).

of lake acidity in controlling the degree of predation by benthivorous fish appears to be the dominant factor in determining the nearshore abundance of several dragonfly species. Dragonflies tend to be abundant at lower pH levels in these nearshore areas and, as a group, are generally considered tolerant to acidification (Mossberg & Nyberg 1979; Eilers et al. 1984; Pollard & Berrill 1992). The increase in abundances of dragonflies (*A. eremita*, *A. interrupta*, and *L. glacialis*) with increasing acidity and reduced numbers of fish species suggests that dragonflies in rocky littoral habitats are susceptible to fish predation and are therefore more successful in acidified lakes with depressed or absent fish populations. Similar conclusions have been reported for other lake environments (Mossberg & Nyberg 1979; Nilsson 1981; Morin 1984; Dermott 1988; Henrikson 1988; Gloss et al. 1989). Dragonflies such as *A. eremita* and *A. interrupta* are easy prey for fish because of their larger size (Pritchard 1964; Post & Cucin 1984), and *Leucorrhinia* is susceptible to predation because it is active by day and less inclined to hide in substrates than other species of Odonata (Eriksson et al. 1980).

The type of fish assemblage may also be important in structuring nearshore benthic invertebrate communities. Fish species that live and forage in these nearshore areas will have a greater impact than fish that inhabit more pelagic or profundal areas of the lake. Eriksson et al. (1980), Bendell and McNicol (1987), McNicol and Wayland (1992), and McNicol et al. (1995) also concluded that predator-prey interactions involving fish and invertebrates were important in determining community structures in acid lakes.

Fish predation alone, however, does not explain the distributions of all the common dragonfly taxa. The dragonfly species *B. janata* and *Boyeria grafiana* were restricted in occurrence to study lakes above pH 5.2 and 5.5, respectively, suggesting that they may be less susceptible to fish predation than other dragonfly species. Similarly, Pollard and Berrill (1992) found *B. janata* and *B. grafiana* to be restricted to lakes above pH 5.3 and 5.8, respectively. Although dragonflies are generally acid-tolerant, the absence of these species from acid, fishless lakes indicates that they may be acid-sensitive or, alternatively, they may be affected by negative interactions with other dragonfly species.

Diptera were also abundant in the rocky littoral zone at low pH (Table 2), in agreement with the findings of Mossberg and Nyberg (1979) and Bradt and Berg (1987). Ceratopogonidae were very abundant in the two most acid lakes, in contrast to the findings of Harvey and McArdle (1986), but Bradt and Berg (1987) and McNicol and Wayland (1992) also found Ceratopogonidae to increase in acid lakes. *Psectrocladius* abundances were higher in the acidic study lakes, further demonstrating the tolerance of this chironomid genus to acidity (Dermott et al. 1986; Fjellheim & Raddum 1988; Griffiths 1992; Stephenson et al. 1994). *Stackelbergina* was also common in acid lakes. Given the general acid tolerance of these taxa and the known importance of chironomids as fish prey (Post & Cucin 1984; Mittelbach 1988; Schofield et al. 1989; Griffiths & Keller 1992), increases in the abundances of chironomids in more acid lakes over near-neutral lakes may be related to a number of factors, including reduced fish predation, altered competitive interactions, or alterations in food resources.

The caddisfly *Banksiola* was also more abundant in acid lakes, agreeing with the findings of Bendell and McNicol (1995) and Stephenson et al. (1994).

In the neutralized lakes, the dramatic shifts in insect community composition demonstrate the ability of these communities to reestablish and restructure in response to changes in acidity, and they provide valuable insights into the recovery process. The temporal patterns observed largely confirm our inferences from the survey lakes about the mechanisms controlling insect community composition. The rapid decreases in the occurrence and abundance of dragonflies and Diptera and the increases of acid-sensitive mayfly species after neutralization of Whirligig Lake indicate that major changes can happen in a short time frame—within 5 years in our study lakes (Tables 3 & 7). The acid-sensitive mayfly *S. interpunctatum* increased dramatically in abundance in both Whirligig and Little Whitepine lakes after manipulation as a direct response to reduce acidity. The more acid tolerant taxon *Leptophlebia* increased in abundance in Whirligig Lake after neutralization, but abundances in Little Whitepine Lake did not increase because pH was already sufficiently high for an abundant population to be present. But the failure of species such as *S. femoratum*, *Eurylophella*, and *B. janata* to recolonize may be a result of limited recolonization sources, which could potentially include nearby near-neutral lakes and also rivers and streams, since some important nearshore species are common lotic organisms.

Declines in abundance of acid-tolerant Diptera (Ceratopogonidae, *Psectrocladius*, and *Stackelbergina*) in Whirligig Lake were observed after neutralization. In Little Whitepine Lake, however, without significant fish predation and with much higher pre-neutralization pH, these chironomids were low in abundance or absent, indicating that fish predation was not an important factor. This suggests that either direct chemical effects or indirect effects of acidity other than altered fish predation (e.g., food resources) are important.

The decrease in abundance of dragonflies (*A. eremita*, *A. interrupta*, and *L. glacialis*) in Whirligig Lake after neutralization (with concurrent increased predation pressure from introduced fish), in contrast to the lack of change in their abundance in Little Whitepine Lake (with little fish predation), further indicates that predation and not acidity controlled dragonfly abundance (Table 7). When lakes recover chemically (naturally or artificially) without the reestablishment of fish populations, the continued lack of fish predation pressure on predation-sensitive species may allow them to continue to thrive. This pattern has also been reported for zooplankton (Nyberg 1984). *B. grafiana*, a dragonfly found only in near-neutral study lakes, appeared abundantly in both Whirligig and Little Whitepine lakes after neutralization, again suggesting that it may be an acid-sensitive species and less susceptible to fish predation than other dragonfly taxa.

While significant shifts in community composition, both spatially and temporally, were observed, our study did not reveal overall changes in species richness and abundance related to acidity. The lack of significant general relationships between biological attributes (abundance and species richness) and chemical attributes (pH, alkalinity, conductivity, and metals) of benthic communities is not uncommon (Dermott 1985; Dermott et al. 1986; Bradt & Berg 1987; Degerman et al. 1995). Other studies have found significant positive correlations between pH and diversity, but not with abundance (Mossberg & Nyberg 1979; Harvey & McArdle 1986). The lack of a significant relationship between pH and species richness or total insect abundance in the study lakes can be attributed to concurrent changes in the occurrence and abundance of acid-intolerant and acid-tolerant species—species replacements within these nearshore assemblages.

Our data demonstrate that the rocky littoral zone of generally large Precambrian Shield lakes is an important habitat, supporting diverse benthic insect communities, many species of which are sensitive to changes in acidity. Lake acidification exerts a strong influence on these communities both directly, by elimination of acid-sensitive species, and indirectly, by altering predation pressure from fish populations and inducing other species interactions. As inferred from lake-neutralization experiments, some acid-sensitive taxa will recolonize rapidly in direct response to decreases in acidity, but populations of benthic insect taxa affected by fish predation will be restructured only after successful rehabilitation of fish populations. Therefore, varied factors are involved in defining the final composition of benthic insect communities in lakes subjected to significant changes in acidity. While we have shown that the direct and indirect effects of acidity are apparent for some species, the influence of other factors such as interspecific predation and competition and alterations in food sources on these insects is unknown. Further study of such relationships may lead us to a better understanding of the forces involved in shaping the assemblages of littoral insect communities in lakes during acidification and recovery.

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