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Use of littoral benthic invertebrates to assess factors affecting biological recovery of acid- and metal-damaged lakes

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Abstract. Biological recovery of aquatic ecosystems from acidification damage is a slow process. In lakes near the massive Cu and Ni smelters in Sudbury, Canada, the delays might be caused by residual metals, habitat damage, altered predator–prey interactions, or other persistent ecological stressors. Assessments of benthic invertebrate communities in 24 Sudbury lakes were conducted to evaluate the relative importance of these delaying factors. At the time of sampling, all lakes had chemically recovered to a pH >6.0, but they varied widely in the duration of time above this threshold and in current metal concentrations, watershed contributions of organic matter, littoral habitat composition, and fish community composition. A model developed with redundancy analyses (RDA) of 4 groups of environmental variables (i.e., water chemistry, fish communities, physical lake descriptors, and littoral habitat) accounted for 74.9% of the variance in benthic invertebrate community metrics across these environmental gradients. Fish species richness, duration of pH recovery, and % boulder habitat were the most significant variables and explained 22%, 9%, and 8% of the variance in benthic invertebrate community metrics, respectively. Damaged systems clearly need sufficient time to recover from severe disturbances. However, our study suggests that remediation techniques, such as manipulation of predator–prey interactions through fish introductions, might speed the recovery of benthic invertebrate communities.

Key words: biological recovery, littoral benthic invertebrates, damaged lakes, acidification, rapid bioassessment, redundancy analysis, variance partitioning.

Catastrophic damage following natural disasters, such as volcanic eruptions (Whittaker et al. 1989), severe wildfires (Morneau and Payette 1989, Galipeau et al. 1997), or floods creates important opportunities to study natural colonization processes and other aspects of biological recovery. Large-scale human disturbances present similar opportunities. For example, during >100 y of operation, the massive Cu and Ni smelters in Sudbury, Canada, once the largest point-source of sulfur dioxide emissions on earth, created a large industrial barren (~20,000 ha barren, 80,000 ha semibarren) and an extensively affected surrounding area that included >7000 acid-damaged lakes (Gunn et al. 1995). In recent decades, a 90% reduction in smelter emissions of sulfur dioxide and metal particulates has been achieved, and the chemical recovery of Sudbury's aquatic ecosystems has begun to occur (Keller et al. 1999a, b, 2003). Many of the formerly acidified lakes have now reached pH 6.0, a chemical threshold above which biological recovery is expected to occur (Neary et al. 1990, Keller et al. 1999a, Holt and Yan 2003).

Relatively rapid biological recovery has been documented for many components of the food webs of Sudbury lakes, including recovery of phytoplankton (Graham et al. 2007) and zooplankton communities (Keller et al. 1990, Holt and Yan 2003). However, recovery of higher-trophic-level organisms, such as fish and benthic invertebrates, has been a much slower process, possibly because of the initial severity of damage, dispersal constraints (Stephenson and Mackie

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1986, Snucins 2003, Yan et al. 2003, Blakely et al. 2006), or the effects of persistent contaminants (Nriagu et al. 1998, Arnott et al. 2001, Keller and Yan 1998, Yan et al. 2004, Keller et al. 2007). Interspecific competition and predation effects from tolerant species also have been suggested to hinder recolonization of sensitive taxa (Keller et al. 1999a, Snucins 2003, Frost et al. 2006, Szkokan-Emilson et al. 2009). For example, acid- and metal-tolerant fish, such as yellow perch (*Perca flavescens*), play a significant role in structuring existing benthic invertebrate communities via predator–prey interactions (Iles and Rasmussen 2005). In addition, the initial severity of damage to landscapes might have disrupted important trophic linkages between watersheds and aquatic systems that are slow to reestablish. Severe disturbances can affect these important linkages (France 1997, France et al. 2000). Allochthonous organic material from riparian and shoreline areas is an important energy source for many littoral invertebrates (Jones and Momot 1981) and helps sustain essential feeding guilds (Moran and Hodson 1990, Karlsson et al. 2003, Agren et al. 2008). In Sudbury, a general lack of allochthonous organic material might affect recovery of many littoral-zone benthic invertebrates.

Many hypotheses regarding recovery can be developed and tested within the recovering ecosystems surrounding the Sudbury smelters. For example, one hypothesis is that benthic invertebrate recovery in lakes is simply a function of time since a chemical threshold has been reached (Stephenson and Mackie 1986, Keller et al. 1999a, Snucins 2003). Other hypotheses are that residual metal concentrations regulate invertebrate communities or that recovery is related to within-lake habitat variables, such as availability of preferred substrate or organic matter. Other possible hypotheses include that dispersal of some recolonizing invertebrate taxa is regulated by geographic barriers to colonizers and that altered fish communities affect benthic invertebrate community composition through predator–prey interactions (Rasmussen et al. 2008).

The objectives of our study were to assess the factors that affect recovery of littoral benthic invertebrate communities in Sudbury lakes that have reached the minimum chemical criteria (pH > 6.0) but still exhibit a broad range of potential controlling factors.

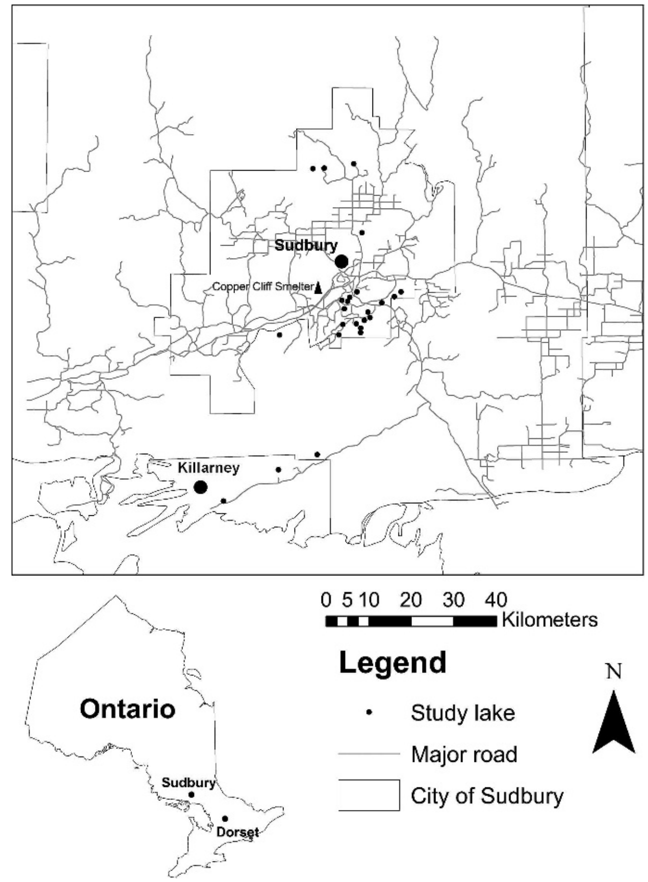

FIG. 1. Map of 24 study lakes in Sudbury and Killarney, Ontario, Canada, showing a wide spatial gradient across an acid- and metal-damaged region.

Methods

Selection of study lakes

Twenty-four lakes were chosen within the Sudbury and Killarney regions (Fig. 1). Sudbury lakes ($n = 21$) spanned gradients of high acid and metal damage and were all ~30 km from the Sudbury smelters, an area where many lake ecosystems were impacted by widespread deforestation of watersheds and soil erosion. Killarney lakes ($n = 3$) lengthened the spatial gradient of degradation and lie 45 to 60 km from the Sudbury smelters. These lakes have well forested watersheds and were not as heavily exposed to metal deposition. However, these lakes also underwent significant acidification and loss of biota (Keller et al. 2003). To reduce initial variation, all lakes chosen were relatively small (surface area <500 ha), oligo-mesotrophic (total P <20 μg/L), and dimictic (maximum depth >5 m). Twenty circumneutral reference lakes of similar size and trophic status also were sampled in the Dorset, Ontario, Canada, region (~250 km southeast of Sudbury) to characterize invertebrate communities in a less-impacted environment.

Site selection and benthic invertebrate collection procedure

Benthic invertebrates were sampled with the rapid bioassessment protocol of the Ontario Ministry of the

Environment (OMOE) (David et al. 1998, Somers et al. 1998). Invertebrates from Sudbury and Dorset lakes were sampled from mid-October to mid-November 2005 and Killarney lakes were sampled in mid-September 2007. To initiate site selection, each lake was first circumnavigated by boat to estimate whole-lake habitat and the distribution of substrate types within the littoral zone (maximum depth = 1 m). Five widely distributed sampling areas were selected with a stratified design based on the habitat proportions observed in the initial visual survey (David et al. 1998). Homogeneous areas of bedrock and sand were excluded from selection because invertebrates are scarce in such areas (David et al. 1998).

At each sample site, a D-frame kick net with 500-μm mesh was used for sample collection following the OMOE 10-min traveling-kick-and-sweep rapid bioassessment technique (David et al. 1998). The sampler was kicked along a transect perpendicular to shore out to a depth of ~0.75 m, and then was kicked along an adjacent transect back to shore. This process was repeated until 10 min had elapsed. At sites with fine debris, frequent stops were necessary to empty a clogged net.

Sample processing and identification

Each sample was stirred to homogenize its contents, and a random subsample was taken with a 75-mL scoop. The sample was spread out in a white tray, and all invertebrates were picked while alive and without the use of a microscope. A minimum of 100 organisms was picked per sample. If 100 organisms were not obtained in 1 subsample, subsequent subsamples were taken and picked completely to reach this minimum desired number. Invertebrates were preserved in 70% ethanol and were later identified to the family level, a level considered suitable for detection of recovery patterns in benthic invertebrate communities (Reynoldson et al. 2001, Jones 2008). However, Oligochaeta, Turbellaria, Hydracarina, and Nematoda were identified only to the order level. As a quality assurance/quality control check, 10% of the samples were recounted and identified by a 2nd researcher. If >5% error in identification or enumeration of invertebrates was detected by the 2nd researcher, then all samples were reidentified and enumerated until the acceptable error rate was achieved.

Biological summary metrics were calculated at the family level, and included Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness, Diptera richness, Ephemeroptera richness, Trichoptera richness, Shannon–Wiener diversity, Simpson diversity, % Ephemeroptera, Odonata, and Trichoptera (EOT), taxon richness, % dominant taxa, % shredders, % predators, and % scrapers (Barbour et al. 1999). Percent dominant taxa was chosen to demonstrate the range of community dominance of very few tolerant taxa within Sudbury's systems and was determined as the 4 most abundant taxa present in ≥70% of the study lakes. Dominant taxa included Chironomidae, Leptophlebiidae, Coenagrionidae, and Corixidae. Functional feeding guilds were assigned according to Pennak (1989), Peckarsky et al. (1990), and Merritt and Cummins (1996). Omnivorous amphipods, including Hyalellidae, Gammaridae, and Crangonyctidae were included as shredders because of their close association with breakdown of organic matter (Pennak 1989, Peckarsky et al. 1990). These metrics were chosen to incorporate estimates of community composition, sensitive taxa, and feeding guilds. Family richness for Ephemeroptera and Trichoptera, which are typically more sensitive taxa, also was included. In addition, EPT composite metrics were used to capture the representation of these relatively large-bodied organisms.

Environmental variables

Physical and chemical lake variables.—Physical lake and water-chemistry data were obtained from the OMOE (W. Keller, unpublished data) and Laurentian University's Cooperative Freshwater Ecology Unit (J. Gunn, unpublished data; see Table 1 for list of environmental variables measured for our study). Organic matter (measured as loss on ignition) in mid-lake surface sediments was sampled with a gravity corer. Percent organic matter content was measured from the 1st and 2nd cm of the sediment core, each representing ~10 y of deposition. Tree cover (presented as % buffer vegetation) in a 50-m band surrounding the lake was digitized and measured from aerial photographs. Time since reaching pH 6.0 was determined from annual pH averages of historical water-chemistry data (Table 2). In some cases, historical data were unavailable, so the earliest known year of chemical recovery (pH > 6.0) was used to estimate duration of improved water-quality conditions. Metals and other water-chemistry variables were measured as total concentration in solution. The Toxicity Binding Model (TBM; Tipping 1994) was used to reduce metal and pH data to a single toxicity variable (Ftox) expressed as a single lake value. The TBM uses the Windermere Humic Aqueous Model (WHAM; Tipping 1994) as a framework to account for Al, Ni, Cu, and Zn ion speciation and competition for binding sites in relation to pH (Tipping 1994). Ftox was calculated as the summed products of each available metal and their laboratory-determined toxi-

TABLE 1. All environmental variables measured and used in the principal components and redundancy analyses.

Variable	Abbreviation	Units
Physical lake descriptors		
Distance to smelter	Dist	km
Lake area (ha)	Area	ha
Maximum depth (m)	Dept	m
Secchi disk depth (m)	Secc	m
Time since pH 6.0	Time	y
% buffer vegetation	Veg	%
% organic matter (stratum 1)	Org1	%
% organic matter (stratum 2)	Org2	%
Water chemistry		
Al	Al	μg/L
Ca	Ca	mg/L
Cl	Cl	mg/L
Cu	Cu	μg/L
Dissolved organic C	DOC	mg/L
Ftox (see text for explanation)	Ftox	–
Fe	Fe	μg/L
Mg	Mg	μg/L
Mn	Mn	μg/L
Ni	Ni	μg/L
pH (2005)	pH	–
P	P	μg/L
K	K	mg/L
NA	Na	mg/L
SO_4	SO4	mg/L
Zn	Zn	μg/L
Littoral fish communities		
Benthivore biomass	Bent	g/net
Brown bullhead biomass	*Aneb*	g/net
Northern pike biomass	*Eluc*	g/net
Piscivore biomass	Pisc	g/net
Predator:prey	P:P	–
Prey biomass	Prey	g/net
Pumpkinseed biomass	*Lgib*	g/net
Smallmouth bass biomass	*Mdol*	g/net
Species richness	Fish	–
Total biomass	TBio	g/net
White sucker biomass	*Ccom*	g/net
Yellow perch biomass	*Pfla*	g/net
Littoral habitat		
% bedrock	BR	%
% boulder	B	%
% clay	CY	%
% cobble	CB	%
% detritus	DET	%
% gravel	GR	%
% macrophytes	MAC	%
% sand	SD	%
% silt	ST	%
% wood	WD	%

city coefficient, which ultimately relates the amount of bound metal to its potential toxic effect.

Fish community sampling and variables.—Fish community assessments were done for Sudbury lakes from July to September 2004 to 2006 and in the 3 Killarney lakes in September 2007. A Swedish standard sampling method modified for use on North American fishes (Morgan and Snucins 2005) was used as the netting protocol. This sampling technique, termed NORDIC Index Netting, used a stratified random sampling design in which sampling effort, or number of nets set, was determined by a volume-weighted design (Appelberg 2000). NORDIC Index Netting uses a 1.5-m-deep, 30-m-long gillnet composed of 12 interwoven panels of varying mesh size (5 mm–55 mm). Depth strata and location of net set were chosen randomly, and Nordic nets were fished for ~12 h (set between 1800 and 2000 h and lifted between 0600 and 0800 h). Measures of fish species richness and total biomass were summarized for all littoral (1.5–6 m) nets set. Biomass of each fish species and each functional group (benthivore, prey species, and piscivores) also was calculated. Benthivorous fish included white suckers (*Catostomus commersonii*), brown bullhead (*Ameiurus nebulosus*), burbot (*Lota lota*), pumpkinseed (*Lepomis gibbosus*), and yellow perch (*P. flavescens*). Prey species included minnows (Cyprinidae), darters (Percidae), and yellow perch. Piscivorous fish included northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreus*).

Invertebrate community habitat variables.—At each sample site, % composition of the littoral substrate was estimated for standard substrate categories (bedrock, boulder, cobble, gravel, sand, silt, and clay) (David et al. 1998). The sampler randomly selected five 1-m^2 quadrats of littoral habitat and approximate percentages of substrate type were estimated and recorded. Percent cover of macrophytes within all quadrats also was recorded.

Statistical analyses

All statistical analyses were done with STATISTICA (version 6.1; StatSoft Inc., Tulsa, Oklahoma) or CANOCO for Windows (version 4.5; Microcomputer Power, Ithaca, New York). All percentage data were arcsine$\sqrt{(x)}$-transformed. Environmental variables were $\log_{10}(x)$-transformed to approximate better the assumptions of normality. One-way analysis of variance was used to test for significant differences in invertebrate community metrics (n = 12) between Sudbury lakes and Dorset reference lakes. The Bonferroni correction method was used because of multiple comparisons (Howell 1987) and resulted in an adjusted alpha (α = 0.004) to reduce the chance of falsely rejecting a null hypothesis that in fact was true.

An initial Detrended Correspondence Analysis (DCA) was done to determine the suitable ordination

TABLE 2. Selected physical, chemical, and habitat variables from 24 Sudbury study lakes. Reference mean and standard error is also displayed. Distance to smelter denotes distance to the Vale INCO Copper Cliff complex. * denotes uncertainty in the value. NA = data not available.

Lake	Distance to smelter (km)	Time since pH 6.0 (y)	Area (ha)	pH	Ftox	Ca (mg/L)	Cu (µg/L)	Ni (µg/L)	% cobble
Baby	13	9*	12	6.45	3.02	3.5	10.8	91.0	2
Camp	11	10*	20	6.69	2.88	2.4	7.4	50.6	5
Clearwater	11	6	77	6.31	3.13	3.9	9.1	62.7	8
Crooked	6	2	26	6.09	3.42	4.1	26.5	173.0	1
Crowley	11	2	42	7.05	2.63	2.5	7.2	50.3	8
Daisy	13	6	36	7.44	2.59	3.0	7.2	68.7	4
Forest	10	15*	16	6.70	2.85	2.9	7.1	60.7	0
Hannah	3	30	27	6.84	2.83	9.4	19.2	117.0	2
Joe	23	24	216	6.14	3.13	2.5	1.7	6.4	8
Linton	13	2	27	6.55	2.94	2.8	8.4	59.8	11
Lohi	10	10	41	6.16	3.21	3.9	9.8	56.8	6
McFarlane	8	36	166	7.35	2.26	13.8	8.8	48.8	21
Middle	5	30	28	7.19	2.79	7.3	14.2	96.6	15
Nelson	28	29	316	6.64	2.73	2.2	2.1	4.6	2
Nepahwin	8	15*	128	7.42	2.32	16.8	10.2	44.9	2
Raft	12	15*	110	6.76	2.80	3.1	8.1	59.2	3
Richard	12	15*	84	7.04	2.45	9.5	6.6	60.1	9
Sans Chambre	28	8	15	6.27	3.06	1.7	2.0	5.7	2
St. Charles	5	15*	41	6.96	2.64	8.7	19.3	86.5	9
Tilton	11	11	52	6.63	2.81	3.3	6.7	42.5	7
Whitson	13	14	437	6.68	2.84	5.3	16.2	84.9	6
George	60	10	189	6.46	2.89	1.8	1.9	6.0	18
Johnnie	46	9	342	6.21	3.08	1.7	1.5	7.1	14
Bell	48	12	336	6.30	3.02	2.1	1.5	6.8	26
Reference mean	NA	NA	119.2	6.38	NA	2.1	0.4	1.2	7.2
Reference SE	NA	NA	25.5	0.05	NA	0.10	0.03	0.44	0.02

TABLE 3. Descriptive statistics and analysis of variance results for differences ($\alpha = 0.05$) in biological summary metrics between Sudbury study lakes ($n = 24$) and Dorset reference lakes ($n = 20$). $\alpha = 0.004$ after Bonferroni correction. EPT = Ephemeroptera, Plecoptera, Trichoptera. S–W = Shannon–Weiner, EOT = Ephemeroptera, Odonata, Trichoptera.

	Sudbury		Dorset			
Metric	Mean ± SE	Range	Mean ± SE	Range	F	p
Taxon richness	19.0 ± 0.6	14–29	24.9 ± 0.7	19–29	37.0	<0.001
Diptera richness	2.3 ± 0.2	1–5	2.2 ± 0.1	1–4	0.5	0.834
Ephemeroptera richness	2.5 ± 0.2	0–4	3.6 ± 0.2	1–5	14.5	<0.001
Trichoptera richness	2.9 ± 0.2	1–5	5.0 ± 0.3	3–7	31.0	<0.001
EPT richness	5.4 ± 0.3	1–9	8.6 ± 0.3	7–11	53.9	<0.001
S–W diversity	1.5 ± 0.1	1.0–2.3	2.0 ± <0.1	1.4–2.2	32.2	<0.001
Simpson diversity	0.7 ± <0.1	0.4–0.9	0.8 ± <0.1	0.6–0.8	19.1	<0.001
% EOT	31.8 ± 4.0	3.3–81.3	35.4 ± 3.0	8.4–61.7	0.8	0.391
% shredders	22.7 ± 4.5	0.2–60.9	35.6 ± 2.9	14.8–61.0	7.9	0.008
% predators	10.8 ± 1.1	3.1–19.5	11.6 ± 1.2	3.8–24.2	0.3	0.589
% scrapers	0.5 ± 0.1	0.0–1.6	2.3 ± 0.4	0.0–7.2	36.4	<0.001
% dominant taxa	57.4 ± 5.1	21.2–91.3	43.4 ± 2.7	20.7–62.1	5.6	0.027

method based either on linear or unimodal species response models. Gradient lengths (β diversity in community composition) were <4.0 standard deviations signifying that linear models were suitable for analysis (Leps and Šmilauer 2003).

Both Principal Components Analysis (PCA) and Redundancy Analysis (RDA) were used to examine variation among benthic invertebrate metrics and variation associated with environmental variables. PCA is an indirect gradient analysis approach that summarizes variability in taxonomic composition, whereas RDA is a direct gradient analysis approach that associates variation in taxonomic composition to environmental variables (ter Braak 1994, Leps and Šmilauer 2003). These methods do not assume a priori grouping of sites and are complementary, accounting for variability that might be missed by using one method alone (ter Braak and Šmilauer 2002, Leps and Šmilauer 2003). Ordination diagrams from these techniques were displayed with a 15% inclusion rule (i.e., only dependent variables with an $r^2 > 0.15$) to reduce clutter and show only variables that characterized the first 2 ordination axes.

RDA and partial RDA were done with forward-stepwise selection to uncover variability among the benthic invertebrate metrics associated with the environmental variables (water chemistry, fish community, physical lake descriptors, and littoral habitat). As an initial variable-reduction approach, only variables that had significant marginal effects were included in the stepwise model. Marginal effects, or variance that is explained by only a single variable, were assessed by performing a series of initial RDAs in which a single environmental variable was modeled alone (Zimmer et al. 2003). Full-model Monte Carlo permutation tests with 499 unrestricted permutations were used to determine statistical significance. Variables that were multicollinear (variance inflation value >20) were not included in the model (ter Braak and Šmilauer 2002, Zimmer et al. 2003).

An overall RDA was done on the benthic invertebrate metrics with all environmental variables (belonging to the 4 environmental groups) with significant marginal effects and no covariables to determine the total variation explained by all of the variables. Two additional sets of RDAs were done to determine variance explained by combinations of 2 and 3 groups of environmental variables with no covariables. Partial RDA was used to partition variation associated with the individual groups of variables (Borcard et al. 1992, Liu 1997). Fractions of variance explained by individual groups of variables were determined by a series of subtraction equations for 4 environmental variable groups (Oksanen et al. 2008).

Results

Invertebrate community differences and gradients

Seventy invertebrate taxa were identified across the 24 Sudbury lakes, and a broad range of values in the biological summary metrics was observed (Table 3). Comparisons with the Dorset reference lakes confirmed that recovery in the Sudbury lakes is incomplete with major differences in most metrics (Table 3). The most profound differences were significantly lower taxon richness and diversity in the Sudbury lakes than in the Dorset lakes (Table 3).

PCA axes 1 and 2 explained 39.0% and 17.2% of the variation in benthic invertebrate metric data in Sudbury lakes, respectively (Fig. 2). Negative relation-

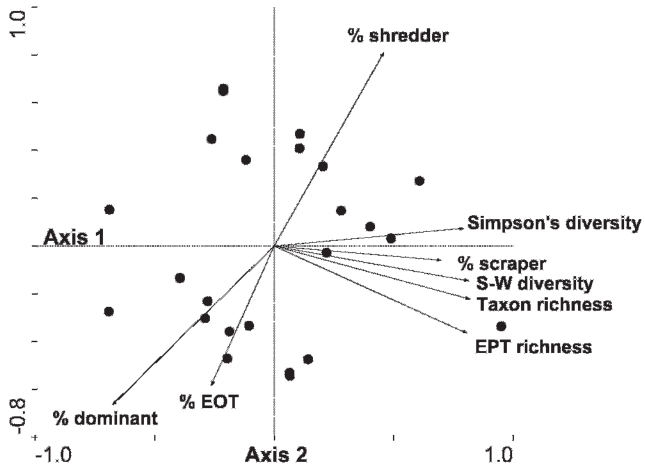

FIG. 2. Principal components analysis of benthic invertebrate summary metrics ($n = 12$). Length and direction of the arrows (invertebrate summary metrics) approximates the strength and relationship among correlation coefficients. Metrics with arrows in the same direction exhibit positive relationships, whereas metrics with arrows in the opposite direction exhibit negative. Solid circles represent study lakes. Only metrics that met 15% inclusion are displayed. EPT = Ephemeroptera, Plecoptera, Trichoptera, S–W = Shannon–Weiner, EOT = Ephemeroptera, Odonata, Trichoptera.

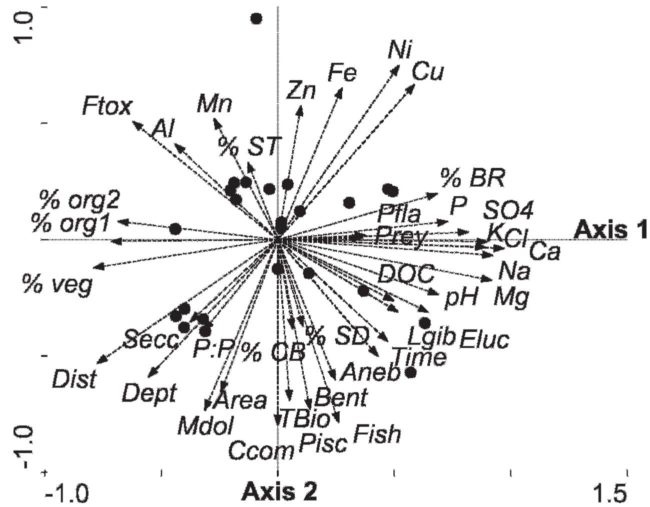

FIG. 3. Principal components analysis of environmental variables ($n = 46$). Only variables that met 15% inclusion are displayed. See Table 1 for an explanation of variable abbreviations.

ships were indicated between % dominant taxa, and taxon richness, diversity, and % shredder taxa (Fig. 2). Axis 1 showed a negative relationship between richness and diversity of invertebrate communities and the presence of dominant taxa. Axis 2 represents a gradient of changing feeding guilds, with a negative relationship between % dominant taxa (mostly collectors) and % shredder taxa.

Sudbury's environmental gradients

Lakes varied considerably in distance to Vale INCO's Copper Cliff smelter (3–60 km), lake surface area (12–437 ha), maximum depth (6.8–50.3 m), Secchi depth transparency (2.6–9.3 m), and lake sediment characteristics. Organic matter in mid-lake surface sediments varied from 14.2 to 51.6% in the most recently deposited layer (0–1 cm) and from 13.0–43.5% in slightly deeper (1–2 cm) sediments. Watersheds differed widely in their forest cover, from nearly barren to well forested and varied from 15 to 97% tree cover in the shoreline buffer areas. The varying effects of metal deposition, urbanization, and watershed disturbances also were evident in chemical variables, such as SO_4 (5.1–25.8 mg/L), dissolved organic C (DOC) (1.3–8.0 mg/L), Cl (0.3–125.0 mg/L), Na (0.7–75.4 mg/L), and total P (2.9–13.4 µg/L). Metals associated with the Sudbury smelters varied widely but declined with distance from the smelter. Cu and Ni exceeded provincial water-quality objectives (PWQO; Cu: 5 µg/L, Ni: 25 µg/L; MOEE 1994) in all lakes within 20 km of the smelter, despite an estimated 90% decline in metal deposition in recent decades. The fish communities (1–13 species) also varied in the study lakes. A summary of the fish community information for the study lakes is provided in Appendix 1.

PCA of all environmental variables showed that 26.9% and 18.1% of the variation within the environmental variable data set was explained by Axes 1 and 2, respectively (Fig. 3). Axis 1 represented a gradient of water chemistry, primarily base cations, and variables related to the surrounding watershed (i.e., DOC, sulfate, % buffer vegetation, % organic matter in lake sediments; Fig. 3). Axis 2 represented a toxicity and biological gradient with a negative relationship between metals and fish community variables.

Taxon–environmental variable relationships and variance decomposition

From initial RDAs, 14 environmental variables emerged with significant ($p < 0.05$) marginal effects (Table 4). An overall RDA on benthic invertebrate metric data incorporating the 14 environmental variables with significant marginal effects showed that 74.9% of the variance was explained by the 14 environmental variables. Littoral fish community richness, time since reaching pH 6.0, and % boulder emerged from the overall RDA with significant

TABLE 4. Results (conditional effects) of forward selection of 14 environmental variables with significant ($p < 0.05$) marginal effects. Lambda represents proportion of variance explained.

	Marginal effects	Conditional effects	
Variable	Lambda	Lambda	p
Fish richness	0.22	0.22	0.004
Time	0.13	0.09	0.038
Lake area	0.19	0.07	0.062
% cobble	0.12	0.05	0.104
Pumpkinseed biomass	0.12	0.05	0.210
Piscivore biomass	0.18	0.04	0.164
Sulfate	0.08	0.03	0.340
Ftox	0.06	0.03	0.302
% boulder	0.16	0.08	0.010
Smallmouth bass biomass	0.14	0.03	0.464
Ca	0.07	0.02	0.386
Mn	0.07	0.02	0.714
Sucker biomass	0.16	0.01	0.824
Pike biomass	0.11	0.01	0.882

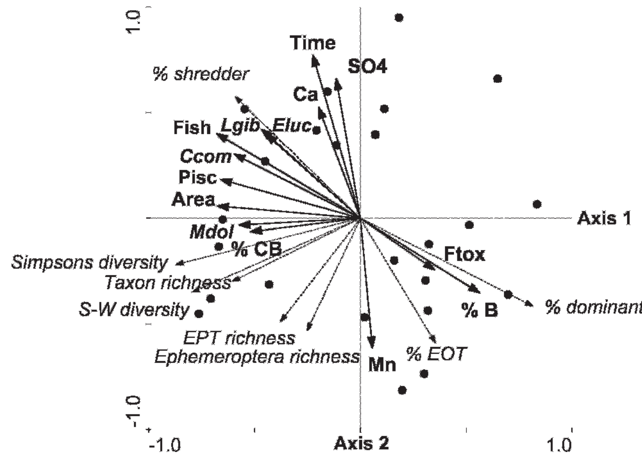

FIG. 4. Redundancy analysis triplot of invertebrate biological summary metrics (dashed arrows) and environmental variables (solid arrows) with significant marginal effects. Solid circles represent study lakes. Only metrics that met 15% inclusion and environmental variables with correlations of $r > 0.25$ are displayed. EPT = Ephemeroptera, Plecoptera, Trichoptera. S–W = Shannon–Weiner, EOT = Ephemeroptera, Odonata, Trichoptera, Taxon richness = invertebrate taxon richness. See Table 1 for an explanation of other variable abbreviations.

conditional effects and explained 39.0% of the total 74.9% of the variance explained by the 4 environmental data sets (Table 4). RDA Axes 1 and 2 explained 55.4% of the variance in the invertebrate metric data with eigenvalues of 0.395 and 0.159, respectively (Fig. 4). These axes also had taxon–environment correlations of 0.937 and 0.909, respectively, signifying a good fit of the benthic invertebrate metric data and environmental variables to the axes. The RDA ordination plots showed relationships in invertebrate metrics and environmental variables similar to those observed in the PCA ordination (Figs 3, 4). Axis 1 represented a diversity gradient and showed positive relationships among invertebrate taxon richness, diversity, and fish community variables, and negative relationships between % dominant taxa and all of the preceding variables. Axis 2 represents a possible temporal/chemical gradient and positive relationships between time since reaching pH 6.0 and invertebrate richness and diversity metrics.

Variance components for the 4 environmental variable groups and their interactions revealed significant sources of variance in the invertebrate community data (Fig. 5). Fish community variables explained the largest source of variance (36.3%) in the invertebrate community metrics. When controlling for shared variance, fish community variables explained the largest source of unique variance (19.9%; Fig. 5). Collectively, water chemistry explained the least amount of variance, but it was the 2nd-highest source of unique variance. Physical lake descriptors explained the 2nd-largest amount of variance in invertebrate community metrics, but the least amount of unique variance. The interaction between fish communities, physical lake descriptors, and littoral habitat explained the largest source of the total variance in the benthic invertebrate metric data set (7.7 %).

Discussion

What is Sudbury's recovery status and what insight do metrics give about biological recovery?

Clear deficits still exist in the recovery of Sudbury's littoral benthic invertebrate communities, even after lakes reach a chemical threshold (pH > 6.0). Invertebrate richness and diversity in Sudbury lakes are far from what is typical of Boreal Shield lakes (Table 3). Sudbury's lakes have higher proportions of tolerant individuals like Chironomidae, and lower richness of more sensitive, large-bodied invertebrates like Ephemeroptera and Trichoptera. High proportions of sensitive shredder taxa were present in some Sudbury lakes, but diversity within this shredder group is still very low and the high proportions might be driven by the abundance of a single family of amphipod, Hyalellidae. Diversity and, thus, complexity of the entire invertebrate community is limited by various

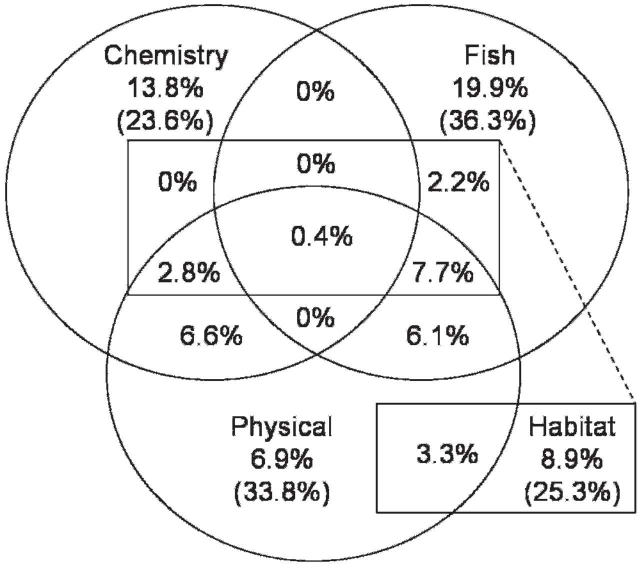

Fig. 5. Venn diagram of conceptual model displaying unique variance components for the 4 environmental variable groups and their interactions. Each circle or box represents variance explained by 1 of the 4 environmental variable groups. Areas that overlap represent shared variance between ≥2 environmental variable groups. The sum of all variance explained by a single environmental variable group is displayed in parentheses.

factors that shape biological recovery within these systems.

Our use of biological summary metrics produced a very powerful model in which the environmental variables explained a very large amount of variance in invertebrate communities. Biological summary metrics reduce much of the initial variation in raw benthic invertebrate abundance data, produce powerful ecological models (Schulenburg et al. 2007), and can be very useful for evaluating acidification of aquatic systems (Sandin and Johnson 2000). Littoral benthic invertebrate community metrics provide important insights into how recovery proceeds in such disturbed ecosystems. For example, measures of diversity, taxon richness, tolerance, and functional feeding composition help identify the reliance of taxa on food sources, habitat requirements and conditions, or interaction with general community composition. Sensitivity to pollution or water quality can show the effects of chemical stressors within a system, and the presence of functional feeding guilds like shredders show the importance of organic material and linkages between lakes and their adjacent terrestrial habitats. Metrics like taxon richness and diversity incorporate many processes that influence invertebrate communities, but appear to be very useful metrics when evaluating recovery.

What is the role of time and water chemistry in biological recovery?

Time is correlated with many interacting factors that affect biological recovery. For example, as time increases following pollution reduction, water chemistry generally improves, and species invasion, establishment of taxa at various trophic levels, and stabilization or improvement in the physical habitats continue to occur. Our results support this idea. Time since reaching pH 6.0 corresponded with an axis primarily associated with chemical factors and was strongly correlated with % shredder taxa (sensitive taxa). In an overview of case studies of recovery times in disturbed aquatic systems, Niemi et al. (1990) noted that time required for biological recovery increased in systems that had altered habitat, nutrient pathways, or reduced predators or competitors, as a result of press disturbances (i.e., disturbances characterized by long-term persistent ecological impacts like mining and acid deposition; Bender et al. 1984). Contrary to our expectation, negative correlations between time since reaching pH 6.0 and some metrics incorporating sensitive taxa, such as EPT richness, also were observed. This result might indicate that even these groups are dominated by a few tolerant taxa.

Recovery of Sudbury lakes might be affected by the continual inputs of stored metals and acid from watersheds (Nriagu et al. 1998, Arnott et al. 2001). PCA Axis 1 from ordination of environmental variables supports the idea that materials including metals or organic material stored in the watershed might influence Sudbury's lakes. RDA Axis 2 also upholds the link between water-chemistry variables and time since reaching pH 6.0. Nriagu et al. (1998) wrote that saturated catchments might sustain high levels of Cu and Ni in Sudbury lakes for well over 1000 y. Underlying bedrock, lake connectivity, and lake-flushing rate also can influence water chemistry (Mallory et al. 1998), and thus, recovery time. Results of our study showed that water-chemistry variables alone explained a large fraction of the variance in littoral benthic invertebrate communities. Undoubtedly, the effects of lingering metal toxicity are still limiting recolonization of sensitive taxa, and this assertion is supported in our data by negative relationships between invertebrate diversity and Ftox.

What possible roles do fish communities play in recovery of littoral benthic invertebrates?

The results of our study showed that littoral benthic invertebrate communities are highly correlated with fish communities in these lakes. This result might indicate that although invertebrate communities are beginning to overcome chemical barriers within these systems, they are affected by biological interactions like fish predation. Increased littoral benthic invertebrate taxon richness and diversity were observed in lakes with greater fish species richness. This finding is consistent with the suggestion by Niemi et al. (1990) that recovery time is increased by the loss of predators from a system. One possible mechanism is that abundant piscivorous fish species might reduce the predation pressure of benthivorous fish on littoral benthic invertebrates, thus providing more favorable conditions for recolonization and establishment of sensitive or vulnerable invertebrate taxa. Negative relationships between the abundant yellow perch and piscivorous fish were evident in PCA ordination of environmental variables. The positive relationships between piscivorous fish communities and the richness and diversity of littoral benthic invertebrate communities (Fig. 4) might be indicative of this mechanism. Post and Cucin (1984) showed that predation pressure on littoral benthic invertebrates by introduced yellow perch decreased biomass and body size in benthic invertebrate communities. Many other studies have shown the important interactions between fish and littoral benthic invertebrate communities (Diehl 1992, Carbone et al. 1998, Sherwood et al. 2002).

Fish can be efficient predators and are important in structuring invertebrate communities in aquatic ecosystems ranging from streams (Wooster 1994, Nilsson et al. 2008) to tropical reefs (Ayal and Safriel 1982, Dulvy et al. 2004). Benthivorous fish can alter the trophic structure of benthic invertebrate communities (Blois-Heulin et al. 1990, Iles and Rasmussen 2005, Nilssen and Waervagen 2002), and fish selectively forage for large-bodied invertebrates (Baumgartner and Rothhaupt 2005). Blois-Heulin et al. (1990) demonstrated the ability of benthivorous fish to efficiently eliminate large, active, predatory invertebrates, leaving more cryptic individuals to occupy their niche. In our PCA results, benthivorous fish biomass followed gradients of increased fish richness independent of yellow perch biomass even though yellow perch were included in this metric. This result indirectly shows the important role of yellow perch in structuring littoral benthic invertebrate communities.

An alternate, more parsimonious explanation exists for the large influence of fish communities on littoral benthic invertebrate communities. Fish might be responding to water-chemistry variables in much the same way as invertebrates, and therefore, would explain an inflated amount of variance because of collinearity. Multiple lines of evidence in our data suggest that fish communities influenced littoral macroinvertebrate communities. First, littoral fish community richness emerged as a significant variable explaining the largest amount of variance in invertebrate communities (Table 4). Second, fish communities explain the greatest amount of overall variance (36.6%) in littoral benthic invertebrate communities and the greatest amount of unique variance (19.9%; Fig. 5). In other words, nearly 20% of the variance in littoral benthic invertebrate communities was accounted for solely by fish communities, even after water-chemistry, littoral habitat, and physical lake descriptors were treated as covariables to remove their shared effects. Third, relationships between piscivorous fish, yellow perch, and littoral benthic invertebrate communities followed what has been reported in the literature. Reduced littoral fish species richness and reduced trophic structure within fish communities might indicate the loss of top-down controls on benthic invertebrate communities. These findings support the idea that fish communities might influence recovery of littoral benthic invertebrate communities in acid- and metal-damaged lakes.

Is littoral habitat a major factor in littoral benthic invertebrate recovery?

Littoral zones are dynamic habitats where biological, chemical, and physical interactions are intense, and many studies suggest that habitat complexity is an important factor in regulating zooplankton, benthic invertebrate, and fish communities in shallow lakes, wetlands, and littoral areas (Bendell and McNicol 1987, Carbone et al. 1998, Rennie and Jackson 2005, Meerhoff 2007, Helmus and Sass 2008). Predator avoidance by littoral benthic invertebrates might be influenced by habitat heterogeneity. In our data, diverse invertebrate communities were positively correlated with abundance of cobble substrates and negatively correlated with boulder habitat. These results might indicate that severe erosion of watersheds has led to the destruction or burial of important littoral zone habitats like cobble or coarse woody debris. The importance of macrophytes in providing refuge for littoral benthic invertebrates has been demonstrated by many studies (Diehl 1992, Cobb and Watzin 1998, Rennie and Jackson 2005). Macrophyte and other antipredator refuge structures, such as piles of coarse woody debris, typically are in low abundance in severely damaged Sudbury lakes, where shoreline forests have been absent for decades.

Is competition from dominant taxa an obstacle for recolonizing invertebrates?

The importance of dominant tolerant taxa in Sudbury's lakes was evident throughout our results and was manifested as negative relationships between a strong presence of tolerant dominant taxa and fish communities and invertebrate richness and diversity. The most damaged of Sudbury's lakes are dominated by tolerant taxa, a pattern that highlights the wide range of disturbance in these early recovering systems. However, without an experimental study design, any attempt to classify the patterns observed in the Sudbury systems in terms of one of the many hypotheses describing disturbance and species diversity (i.e., Intermediate Disturbance Hypothesis, see Connell 1978; Dynamic Equilibrium Model, see Huston 1979) would be speculative at best. Nonetheless, competitive dominance might be expressed by taxa like Chironomidae in these systems, where they might have superior abilities to tolerate adverse water-chemistry conditions, reproduce rapidly, and forage for food resources, with consequent poorer growth and establishment of other taxa. The Monopolization Hypothesis (De Meester et al. 2002) also might be consistent with processes in these systems, and this mechanism has been proposed as an important factor in the recolonization of 2 similar mayfly species in acid-damaged Boreal Shield lakes (Snucins 2003). Competitive interactions between dominant taxa and recolonizing invertebrate taxa are extremely hard to verify, but in the relatively homogenous Sudbury lakes, saturation of niches and monopolization of resources by dominant, persistent taxa might adversely affect recovery. Further studies are needed to investigate these mechanisms.

Conclusion

Sudbury's acid- and metal-damaged lakes remain in the early phase of recovery, and their littoral benthic invertebrate communities are far from recovered. Many lakes are still characterized by low invertebrate richness and diversity and are dominated by tolerant taxa at all trophic positions. For example, fish communities in most of the lakes are still heavily dominated by tolerant yellow perch. The results of our study showed that, among many possible mechanisms slowing recovery, altered fish communities might have the greatest influence on benthic invertebrate communities in Sudbury's biologically recovering lakes. Our results also demonstrate the importance of time and improved water chemistry for biological recovery. Manipulative experiments could be used to test further hypotheses and mechanisms related to recovery, including competition, the roles of fish predation, and the role of watershed inputs on littoral benthic invertebrate communities within Sudbury's systems. For example, stocking of piscivorous fish species to control yellow perch or perhaps the use of fencing or other fish exclusion devices could be used to test the role of fish communities, and nearshore tree planting and other habitat manipulations could be used to test linkages between watershed vegetation and recovery of invertebrate taxon richness, diversity, and functional feeding groups.

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APPENDIX 1. Selected fish community variables that were included in the overall redundancy analysis (RDA) model from Nordic netting of Sudbury and Killarney lakes. All fish community measures are for littoral zones (<6 m depth) only and all biomass measures are in grams/net.

Lake	Fish richness	Northern pike biomass	White sucker biomass	Pumpkinseed biomass	Smallmouth bass biomass	Piscivore biomass
Baby	8	147	301	1	0	147
Camp	2	0	0	0	0	0
Clearwater	3	0	0	6	0	0
Crooked	1	0	0	0	0	0
Crowley	1	0	0	0	0	0
Daisy	5	0	22	6	0	0
Forest	2	0	0	2	0	0
Hannah	5	40	0	18	0	40
Joe	4	0	1358	0	1159	1159
Linton	2	0	0	0	0	0
Lohi	2	0	0	16	0	0
McFarlane	13	391	1363	24	871	1715
Middle	3	0	0	27	0	0
Nelson	9	0	384	0	572	572
Nepahwin	11	95	461	60	558	654
Raft	8	0	917	149	0	0
Richard	7	259	75	8	0	682
Sans Chambre	2	0	0	0	1240	1240
St. Charles	5	655	0	19	0	788
Tilton	2	0	0	0	0	0
Whitson	7	476	701	0	10	1933
George	8	0	223	16	686	686
Johnnie	10	0	380	7	1620	1621
Bell	10	207	127	20	723	931