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RESEARCH ARTICLE

Restoration of Zooplankton Communities in Industrially Damaged Lakes: Influences of Residual Metal Contamination and the Recovery of Fish Communities

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Abstract

The Sudbury, Ontario, Canada area offers a unique opportunity to develop our understanding of biotic and abiotic lake recovery processes in industrially damaged natural systems. In recent decades, lakes in the Sudbury area have shown improvements in water quality due to decreases in sulfur (S) and metal emissions from area smelters, and reduced acid deposition from more distant sources. However, biological recovery is lagging and mechanisms controlling the lag are not yet clear. Our study examines the roles of two factors, residual metal contamination and altered fish predation, on zooplankton community recovery. Data collected over three decades on six study lakes were analyzed using redundancy analysis (RDA) and partial RDA's to assess historical and present relationships of water chemistry and fish abundance with zooplankton community recovery. Continuing metal toxicity appears to be the primary cause of the absence of some zooplankton species, particularly *Daphnia* spp. from metal-contaminated lakes. Conversely, once water quality is suitable and abundant planktivores reestablish, fish planktivory becomes a factor affecting *Daphnia* spp. establishment. The introduction of piscivores into these lakes may be necessary to facilitate the return of many *Daphnia* species. Further reductions in metal toxicity will also assist with the complete recovery of zooplankton communities. Studying natural systems over several decades allows us to better understand the intricate steps involved with recovery of industrially damaged lakes, and this knowledge will greatly benefit future restoration efforts in other industrially damaged systems.

Key words: **cladoceran, copepod, *Daphnia*, industrial disturbance, metal toxicity, piscivory, planktivory, water quality.**

Introduction

Historic atmospheric deposition of sulfur and metals from local copper (Cu) and nickel (Ni) smelting operations severely degraded lake water quality in many lakes in the Sudbury, Ontario, Canada region (Keller et al. 1999, 2007). Acidic lake conditions (pH < 6.0) and metal contamination had severe consequences for aquatic biota, causing the decline and disappearance of many aquatic species and leaving behind simplified communities (Conroy et al. 1976; Keller & Gunn 1995). Adverse effects on crustacean zooplankton, the communities we focused on in this article, have been particularly well documented for Sudbury area lakes (Sprules 1975; Keller & Pitblado 1984; Keller & Yan 1998). Zooplankton are a particularly important group of aquatic organisms, given their central position in aquatic food webs. As a group they also contain many valuable indicator species that show widely differing sensitivities to various environmental conditions (Keller & Pitblado 1984).

Of the many abiotic factors that are hypothesized to hinder the recovery of aquatic ecosystems in the Sudbury area, elevated metal concentrations are a major concern. In the past, numerous lakes in the region were affected by the atmospheric fallout of metals (Keller & Pitblado 1986). Many lakes close to the metal smelters (<30 km) continue to have concentrations well above Ontario's Provincial Water Quality Objectives (PWQO's) of 5 μg/L for Cu and 25 μg/L for Ni (MOEE 1994). Numerous laboratory experiments have shown that elevated concentrations of metals, such as Cu, lead to increased mortality, decreased growth rate, delayed maturity, and decreased brood size in many zooplankton species (Ingersoll & Winner 1982; Koivisto et al. 1992). Brix et al. (2001) found

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that cladoceran zooplankton are some of the most metal sensitive organisms in aquatic systems. Unfortunately, studies that examine zooplankton community responses to metal contamination in natural oligotrophic (total phosphorus <10 µg/L) systems with low ionic strength (<100 µs/cm), such as Sudbury area lakes, are very limited.

In addition to abiotic factors, there are also strong biotic food web linkages between fish, invertebrate predators, zooplankton, and phytoplankton in aquatic systems (Marmorek & Korman 1993). This implies that as lakes acidify, many biological changes may occur through mechanisms other than direct toxicity effects alone. During recovery, change may not occur in crustacean zooplankton communities until there is a reestablishment of a more balanced food web that includes planktivorous and piscivorous fish (Nyberg 1984). In lakes with residual fish populations, the complete recovery of zooplankton communities may be favored if recovery leads to the increase in abundance of piscivores such as lake trout (*Salvelinus namaycush*) and declines in planktivores such as yellow perch (*Perca flavescens*) (Gunn et al. 1988; Gunn & Keller 1990; Keller & Yan 1991).

A case in point for examining the combined effects of metal toxicity and fish predation is Yan et al.'s (2004) study of Middle Lake; a metal contaminated and historically acidic lake, located in Sudbury. Despite decades of near-neutral pH levels (pH > 6.0), cladoceran zooplankton, unlike the copepods, had not fully recovered. Middle lake supports a fish community strongly dominated by perch and has high metal concentrations. The researchers hypothesized that residual metal contamination and fish predation may be hampering recovery, but were unable to determine the relative roles of those two factors.

Previous work has examined the roles of metals and fish communities on the recovery of zooplankton on a spatial/landscape scale by comparing damaged Sudbury lakes to a set of reference lakes in a single year (Valois et al. 2010). The results of that study suggested that current crustacean zooplankton communities in many Sudbury area lakes are affected by both water quality conditions and fish populations. In contrast to the spatial analysis of Valois et al. (2010), our study examines the historical and recent roles of metals and fish communities as influences on zooplankton community structure, using long-term temporal data. Examining patterns in such long-term datasets allows scientists to gain empirical knowledge of the biotic and abiotic mechanisms important in the natural recovery of stressed lakes. Understanding these mechanisms is extremely valuable and this knowledge may be applied to current restoration efforts intended to assist in the recovery of industrially damaged aquatic ecosystems.

The specific objective of this study was to examine the roles of two local factors, residual metal contamination and altered predation from fish communities, on zooplankton recovery. A large, multi-lake, multi-year dataset was analyzed through variance partitioning to determine empirical relationships between temporal changes in zooplankton communities and changes in pH, metals, and fish communities. Partial redundancy analyses (pRDA's) were performed to determine how much of the variance in zooplankton community structure was explained by the chemistry variables compared to fish variables (Borcard et al. 1992). When two variable groups are analyzed using this method, one group is treated as a set of covariables, while the other group is used as explanatory variables.

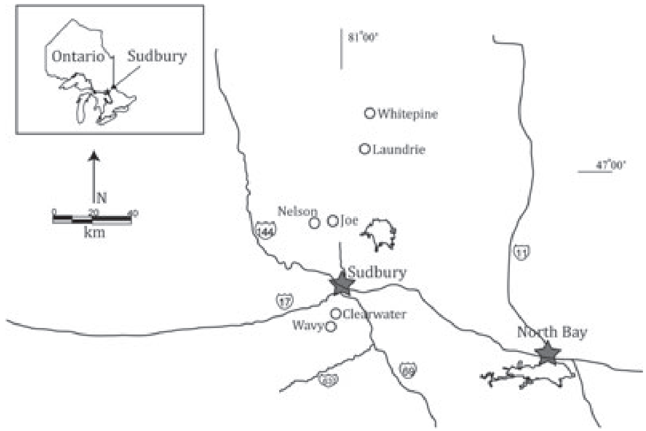

Figure 1. Map of the study area showing the locations of the study lakes.

The six study lakes examined (Fig. 1) span a wide gradient of historical and current conditions, largely related to their distance from the Sudbury smelters (Table 1). Some lakes close to the smelters were highly acidified and metal contaminated and residual metal contamination persists. Other lakes, further from the smelters were less impacted by acidification and metal contamination was minimal. Changes in fish communities also span a large gradient, including fishless conditions during the most severe contamination, very simple communities dominated by residual or reestablishing yellow perch populations, and communities dominated by lake trout where perch were greatly reduced after piscivore reestablishment. Collectively these lakes capture the range of chemical and biological changes in Sudbury area lakes, and the combined data series permits a broad analysis of the abiotic and biotic factors affecting lake recovery in the region. Lakes in the Sudbury area offer a very unique opportunity to increase the scientific understanding of important patterns and processes in lakes recovering from anthropogenic stressors.

Methods

Zooplankton and Chemistry Data

Zooplankton data and samples were assembled from previous studies conducted from 1974 to 2005. For our analysis, data from one sample per month taken in June, July, and August when available, for a total of three samples, were used to generate annual averages for subsequent analyses. Data from the next closest months were substituted when necessary (May–October). Sampling methods and the number of stations sometimes varied among lakes and years. When possible, we used data from one station per lake per year. In most cases, zooplankton were sampled using metered vertical net

Table 1. Location, morphometry, and selected chemical characteristics of the six study lakes.

Lake	Latitude	Longitude	Distance From Sudbury (km)	Area (ha)	Z_{max} (m)	pH 1980	pH 2006	Cu (µg/L) 1980	Cu (µg/L) 2006	Ni (µg/L) 1980	Ni (µg/L) 2006
Clearwater	46°22′	81°03′	13.0	77.0	21.5	4.5	6.6	64.0	7.7	198.0	72.7
Joe	46°44′	81°01′	28.0	180.0	34.0	5.7	6.7	3.0	2.0	14.0	7.0
Laundrie	47°07′	80°52′	80.0	364.0	27.0	5.1	5.8	2.0	1.0	7.0	3.3
Nelson	48°44′	81°05′	29.0	309.0	51.0	5.8	6.6	2.0	2.0	6.5	4.5
Wavy	46°18′	81°06′	21.0	255.0	34.0	4.4	5.4	9.0	6.0	58.0	52.0
Whitepine	47°17′	80°50′	89.0	67.0	22.0	5.5	6.3	1.5	<1.0	2.8	1.1

hauls. Other sampling methods included the use of non-metered vertical net hauls, and volume-weighted combined Schindler-Patalas Trap collections. In some cases sampling gear, mesh size and net mouth diameter changed over time; however, changes in methods are not expected to have caused any directional biases in the final data. To explore the consequences of changes in sampling methods, Yan & Strus (1980) compared data obtained from a Schindler-Patalas trap and a tow-net deployed in Clearwater Lake and found no significant difference between methods. They suggested that differences among sampling methods were small when compared with spatial and temporal variability. Other studies have also shown that Schindler-Patalas traps have performed as well as nets and had similar gear efficiency (Schindler 1969; Lewis 1978; Kankaala 1984). Johannssen et al. (1992) found that nets of different mesh size, mouth diameter, and length generally performed equally and few differences were found in species abundance data.

All zooplankton samples used in this study were processed using the Zooplankton Enumeration and Biomass Routines Program (ZEBRA2M); a semi-automated processing system for zooplankton. To ensure taxonomic accuracy, 10% of the total number of samples was reprocessed by another taxonomist using the same methodology.

Water chemistry data were assembled from previous studies conducted from May to October. From the available data, the average values for ice-free months were calculated for 15 chemical parameters (pH, Secchi depth, true colour, apparent colour, and the concentrations of Ni, Cu, aluminum [Al], zinc [Zn], calcium [Ca], magnesium [Mg], sulfate [SO_4], total phosphorus [TP], inorganic nitrogen [IN], total nitrogen [TN], and dissolved organic carbon [DOC]). As with the zooplankton data, sampling methods (surface grab and tube composite) and stations (1–4 per lake) varied somewhat among lakes and through time. For our analysis, data for one sample per ice-free month for a total of 6 months, taken at a single location near Z_{max} (lake maximum depth), were chosen and averaged when available.

Recent water chemistry samples were collected as non-volume weighted tube composites at all stations in June, July, and August of 2006 for Joe, Laundrie, Nelson, Wavy, and Whitepine lakes. A 2-cm diameter Tygon tube was used to collect water through the epilimnion and metalimnion during periods of stratification. Thermocline location was determined using an YSI58 Dissolved Oxygen and Temperature meter. Clearwater Lake water chemistry was collected as a whole-lake volume-weighted sample, based on lake morphometry, using a 2-L Van Dorn bottle. This method was used in our study to be consistent with the method employed in the long-term research program on this lake.

Previous studies have investigated differences in sampling methods (surface grab and tube composite) in Sudbury area lakes and found that there were no differences in concentrations of SO_4, Cu, and Ni. A significant difference ($p < 0.05$) between surface grabs and tube composites was found for pH, which was lower in tube composites (Keller & Pitblado 1986; Keller et al. 2006). However, observed absolute differences were generally small. Differences due to methods do need to be considered in interpretations of time series data. However, while there may have been slight changes of methods over time in our study, the effect of these on chemistry would be very small compared to the large changes that occurred with lake recovery.

Fish Data

Current fish communities were assessed using NORDIC multi-mesh gill netting, a sampling procedure based on stratified sampling. In addition, both quantitative and qualitative historical data were collected from fisheries surveys extending over the past few decades. Fish data were grouped at the family level into Percidae (yellow perch), Salmonidae (lake trout, and brook trout [*Salvelinus fontinalis*]), Centrarchidae (smallmouth bass [*Micropterus dolomieu*] and rock bass [*Amboplites rupestris*]), and Cyprinidae (various species). Previous relative abundance data were derived primarily from qualitative estimates by experienced fisheries biologists familiar with these lakes, but quantitative data were sometimes available. Relative abundance for each family was expressed numerically as a categorical variable for use in statistical analyses: high abundance (3); medium abundance (2); low abundance (1); and absent (0).

Statistical Analyses

Statistical analyses were carried out using STATISTICA 6.0 software (Statsoft, Inc. Tulsa, Oklahoma, U.S.A.) and CANOCO version 4.1 (Ter Braak & Smilauer 2002), at a significance level of $p = 0.05$. Environmental variables were $\log_{10}$ transformed and zooplankton species abundance data were $\log_{10}(x+1) + 0.2$ transformed to satisfy assumptions of normality and equal variance. The constant 0.2 was applied to further down weight the influence of uncommon species (Keller et al. 2002).

Given the demonstrated value of RDA in quantifying relationships between aquatic communities and different aspects of their habitats (Valois et al 2010), RDA was used to relate zooplankton assemblages to water chemistry variables and fish abundance data. All six study lakes were plotted together in ordination space. Zooplankton species that were not common across the lake dataset (occurring in <10% of the samples) were excluded. To determine how much of the variance in zooplankton community structure was explained uniquely by the chemistry variables compared to fish variables, pRDA's were performed (Borcard et al. 1992). Three RDA's were performed: water chemistry and fish variables, chemistry variables alone, and categorical fish variables alone.

Five other RDA tests and ensuing pRDA tests were performed. Data from the entire dataset were grouped based on year (1985 and prior, and 1990 and subsequent) and taxonomic level (copepod, cladoceran, and *Daphnia* spp.). Separate analyses based on period were used to detect whether the variation explained for zooplankton abundance by water chemistry, and fish alone changed through time. Analyses based on taxonomic level were used to detect which groups were most affected by water chemistry, or fish.

Results

Examination of the data indicated that the species richness of crustacean zooplankton communities increased with decreased metal concentrations. Few species were found at high metal concentrations; these included: *Cyclops vernalis*, *Chydorus sphaericus*, *Bosmina* sp., and *Polyphemus pediculus*. Species that were found in high abundances at high perch abundance were Tr*opocyclops extensus*, *Eubosmina tubicen*, and *Leptodiaptomus minutus*. A number of *Daphnia* species appeared with increasing pH, decreasing planktivore abundance, and increasing piscivore abundance (Fig. 2). *Daphnia mendotae* appeared to be a relatively metal-resistant species, which colonized and persisted in Sudbury area lakes when metal concentrations were still high (Cu 43 µg/L and Ni 170 µg/L). Other *Daphnia* species, which are apparently not as metal tolerant, did not persist in Cu concentrations above 3 µg/L, and Ni concentrations above 10 µg/L. Several *Daphnia* species colonized some study lakes on some occasions, but failed to persist when metals were above these threshold concentrations.

The RDA analysis for the six study lakes combined through the entire time period (Table 2), indicated that a number of chemistry and fish variables (Ni, DOC, Centrarchidae, Percidae, Ca, Cyprinidae, Salmonidae, pH, and Cu) explained 60.2% of the total variation in zooplankton composition. Unexplained variation was therefore 39.8%. Axis 1 explained 33.7% of the variation and was primarily an axis of water chemistry variables, separating high pH and low metal lakes from the low pH high metal lakes. Axis 2 explained 10.0% of the variation and was primarily an axis of fish community

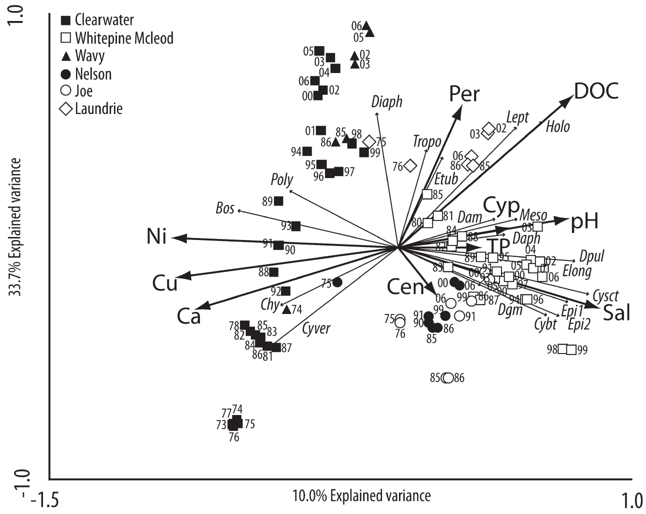

Figure 2. RDA triplot on zooplankton in the six study lakes. Environmental variables that were found significant by forward selection are shown by arrows; the length of the arrows indicates strength of the relationship. Variable abbreviations are: Per, percid abundance; DOC, dissolved organic carbon; Cyp, cyprinid abundance; pH, pH units; TP, total phosphorus; Sal, salmonid abundance; Cen, centrarchid abundance; Ca, calcium; Cu, copper; and Ni, nickel. The correlation of species with environmental variables is shown by thin arrows. Species abbreviations are: *Diaph*, *Diaphanosoma birgei*; *Tropo*, *Tropocyclops extensus*; *Etub*, *Eubosmina tubicen*; *Lept*, *Leptodiaptomus minutus*; *Holo*, *Holopedium gibberum*; *Dam*, *Daphnia ambigua*; *Meso*, *Mesocyclops edax*; *Daph*, *Daphnia* sp.; *Dpul*, *Daphnia_pulex*; *Elong*, *Eubosmina longispina*; *Cysct*, *Cyclops scutifer*; *Epi1*, *Epischura lacustris* copepodids; *Epi2*, *Epischura lacustris adults*; *Cybt*, *Cyclops bicuspidatus thomasi*; *Dgm*, *Daphnia mendotae*; *Cyver*, *Cyclops vernalis*; *Poly*, *Polyphemus pediculus*; *Bos*, *Bosmina* sp.; *and Chy*, *Chydorus scpphaericus*. Lakes are indicated by the following symbols: ■ Clearwater, □ Whitepine, △ Wavy, ● Nelson, ○ Joe, and ◇ Laundrie.

variables separating high planktivore/low piscivore lakes from low planktivore/high piscivore lakes.

Results of the pRDA analysis showed that water chemistry variables alone explained 19.8% of the total variation in species abundances. The significant variables were DOC, Ni, Ca, pH, and Cu. Of these variables, the two most important were DOC, explaining 8.0%, and Ni, explaining 6.0%. The other variables explained between 1.0 and 3.0% of the variation. Fish community data alone accounted for 10.2% of the total variation. The significant fish variables were Percidae, Centrarchidae, Cyprinidae, and Salmonidae. Of these variables the two most important were Centrarchidae explaining 4.0%, and Percidae explaining 3.0%.

When the RDA was based on pre-1985 data; DOC, pH, Cu, Salmonidae, and Ca were significant variables and explained 69.8% of the variation. So far the most important variable was DOC which explained 46.0% of the variation. The other variables explained between 2.0 and 7.0% of the variation. Results of the pRDA which covaried for fish indicated that DOC, pH, Cu, and Ca were significant variables and that water chemistry alone explained 26.8% of the variation. The two most important variables were DOC, explaining 10.0%, and

Table 2. Summary of the results of the pRDA's of zooplankton community composition with water chemistry and fish community variables.

Variation Explained		*Significant Variables*											
		Ni	*Cu*	*Ca*	*pH*	*TN*	*TP*	*DOC*	*Percidae*	*Centrarchidae*	*Cyprinidae*	*Salmonidae*	*% Variance Explained*
Total	All	**X**	—	X	X	—	—	X	X	X	X	X	60.2
	Years 1985 and before	—	X	X	X	—	—	**X**	—	—	—	X	69.8
	Years 1990 and after	—	—	X	X	X	—	X	X	X	—	**X**	67.4
	Cladocera	X	**X**	X	—	—	—	X	X	X	X	X	58.5
	Copepoda	**X**	X	X	X	—	X	X	X	—	X	X	63.3
	Daphnia	**X**	—	—	—	—	—	X	X	X	X	X	60.4
Water chemistry	All	X	X	X	X	—	—	**X**	—	—	—	—	19.8
	Years 1985 and before	—	X	X	X	—	—	**X**	—	—	—	—	26.8
	Years 1990 and after	—	—	**X**	X	X	—	X	—	—	—	—	21.1
	Cladocera	X	—	X	—	—	—	**X**	—	—	—	—	20.0
	Copepoda	X	X	X	**X**	—	X	**X**	—	—	—	—	20.0
	Daphnia	**X**	—	—	—	—	—	**X**	—	—	—	—	15.0
Fish community	All	—	—	—	—	—	—	—	X	**X**	X	X	10.2
	Years 1985 and before	—	—	—	—	—	—	—	—	—	—	**X**	5.5
	Years 1990 and after	—	—	—	—	—	—	—	**X**	X	—	X	10.4
	Cladocera	—	—	—	—	—	—	—	**X**	X	X	—	10.9
	Copepoda	—	—	—	—	—	—	—	X	X	**X**	**X**	10.9
	Daphnia	—	—	—	—	—	—	—	X	**X**	—	X	16.9

Variables deemed significant ($p < 0.05$) by forward selection are indicated. The variables explaining the greatest portion of the variation within each group are indicated in bold.

pH, explaining 7.0%. The other variables explained between 3.0 and 5.0% of the variation, respectively. Results of the pRDA which covaried for chemistry indicated that Salmonidae was the only significant variable and that fish data alone explained 5.5% of the variation. Salmonidae explained 3.0% of the total variation (Table 2).

Results of the RDA based on data from 1990 and on indicated that Salmonidae, Centrarchidae, DOC, Ca, Percidae, pH, and TN were significant variables and explained 67.4% of the variation. The two most important variables were Salmonidae, explaining 29.0%, and Centrarchidae, explaining 8.0%. The other variables explained between 1.0 and 6.0% of the variation. Results of the pRDA which covaried for fish indicated that Ca, TN, DOC, and pH were significant variables and that water chemistry alone explained 21.1% of the variation. The two most important variables were Ca, explaining 7.0%, and TN, explaining 5.0%. Results of the pRDA which covaried for water chemistry indicated that Percidae, Salmonidae, and Centrarchidae were significant variables and that fish data alone explained 10.4% of the variation (Table 2).

If the RDA analysis included only Cladocera then Cu, DOC, Centrarchidae, Percidae, Ca, Ni, Cyprinidae, Salmonidae, and pH were significant variables and explained 58.5% of the total variation. The three most important variables were Cu, explaining 28.0%, DOC, explaining 8.0%, and Centrarchidae, explaining 8.0%. The rest of the variables explained between 1.0 and 5.0% of the variation. Results of the pRDA, which covaried for fish, indicated that DOC, Ni, and Ca were significant variables and that water chemistry alone explained 20.0% of the variation. The two most important variables were DOC, explaining 8.0%, and Ni, explaining 7.0%. The rest of the variables explained between 1.0 and 3.0% of the variation. Results of the pRDA, which covaried for water chemistry, indicated that Centrarchidae, Percidae, and Cyprinidae were significant variables and that fish data alone explained 10.9% of the variation. The two most important variables were Percidae, explaining 5.0%, and Centrarchidae, explaining 4.0% of the variation.

An RDA based on copepods indicated that Ni, DOC, Salmonidae, Cyprinidae, pH, Percidae, TP, Ca, and Cu were all significant variables and explained 63.3% of the variation. The two most important variables were Ni, explaining 38.0%, and DOC, explaining 11.0%. The rest of the variables explained between 1.0 and 3.0% of the variation. Results of the pRDA, which covaried for fish, indicated that pH, Ni, DOC, TP, Cu, and Ca were significant variables and water chemistry alone explained 20.0% of the variation. The two most important variables were pH, explaining 9.0%, and Ni, explaining 4.0%. The rest of the variables explained between 1.0 and 3.0% of the variation. Results of the pRDA, which covaried for water chemistry, indicated that Cyprinidae, Salmonidae, Percidae, and Centrarchidae were significant variables and that fish data alone explained 10.9% of the variation. Both Cyprinidae and Salmonidae were important variables and each explained 3.0% of the variation.

Results of the RDA based on *Daphnia* sp. indicated that Ni, Centrarchidae, Percidae, Cyprinidae, Salmonidae, and DOC were significant variables and explained 60.4% of the variation. The two most important variables were Ni, explaining 31.0%, and Centrarchidae, explaining 18.0%. Results of the pRDA, which covaried for fish, indicated that Ni and DOC were significant variables and that water chemistry alone explained 15.0% of the variation. The most important variable was Ni which explained 11.0% of the variation. Results of the pRDA, which covaried for water chemistry, indicated that Centrarchidae, Percidae, and Salmonidae were significant variables and that fish data alone explained 16.9%

of the variation. The two most important variables were Centrarchidae, explaining 9.0%, and Percidae, explaining 2.0% of the variation.

Discussion

The overall goal of this study was to determine if there were detectable patterns of crustacean zooplankton community recovery from acid and metal damage, using lakes from the Sudbury area. In particular, we assessed the roles of two local factors, residual metal contamination and altered predation from fish communities, on zooplankton recovery. Results of this temporal study indicated that both abiotic (metals) and biotic (fish communities) factors have important influences on zooplankton recovery patterns, and must be considered in restoration planning.

The direct and indirect effects of metal contamination and fish communities on zooplankton community structure are complex. Zooplankton are strongly affected by planktivorous fish predators (Brooks & Dodson 1965), and planktivorous fish communities are in turn influenced by predation from piscivorous fish (Mills & Forney 1983). The history of fish community changes in the study lakes is complicated, and the mechanisms controlling fish recovery are often not clear. The reestablishment of viable lake trout populations followed management stocking in Laundrie Lake, enhanced natural recruitment in Nelson Lake, and both active stocking and resumption of natural recruitment of a remnant stock in Whitepine Lake. The establishment of brook trout in Joe Lake followed active stocking. Factors controlling the establishment of other species are not clear. Smallmouth bass were stocked in Nelson Lake, but have also appeared in Clearwater and Joe lakes with no records of any official stocking. The invasion of lakes by yellow perch and various cyprinids may have resulted from natural mechanisms; however, given the difficulties for fish dispersal to new habitats without water connections, it is very likely that many of these invasions resulted from unintentional introductions by anglers using them as bait.

Metal toxicity adds another level of complexity. Some zooplankton are strongly affected by increased metal concentrations (Brix et al. 2001). Furthermore, common piscivorous fishes of the Sudbury area (e.g. smallmouth bass and lake trout) are physiologically more susceptible to metal contamination than the metal tolerant planktivore, yellow perch (Beamish 1976; Taylor et al. 2003). An increase in metals is therefore associated with both direct stress on zooplankton, and indirect predation stress associated with increased perch planktivory as piscivores are reduced or eliminated. An important question for restoration ecology is how responsive zooplankton communities are to improvements in their abiotic and biotic habitat.

Effects of metal contamination on zooplankton vary considerably among species (Baudouin & Scoppa 1974) and taxonomic groups. In particular, *Daphnia* spp. have acute sensitivities to Cu; concentrations in the range of 20–30 μg Cu/L may hinder the long-term survival of many *Daphnia* species in Sudbury lakes (Biesinger & Christensen 1972; Winner & Farrell 1976; Yan et al. 2004). Interestingly, *D. mendotae* is apparently an exception; although its recovery is affected by metal concentration, this species can tolerate higher metal levels than other *Daphnia* (Yan et al. 2004). Valois et al. (2010) found that *D. mendotae* was able to tolerate Cu concentrations as high as 31 μg/L. Yan et al. (2004) also found that copepods appeared to be more sensitive to metal contamination than cladoceran zooplankton. Therefore, we expected to find that copepods and *Daphnia* spp. would be more sensitive to metal contamination than Cladocera in general, but that *D. mendotae* would be a resistant species.

As expected, *D. mendotae* appeared to be a relatively metal-resistant species, which colonized and persisted in Sudbury area lakes when metal concentrations were still relatively high while other *Daphnia* species did not persist. Several *Daphnia* species colonized some study lakes on some occasions, but failed to persist when metals were still elevated. Our results, and those of Valois et al. (2010), did not support the results of Yan et al. (2004), as copepods did not appear to be more sensitive to metal contamination than cladocerans.

Overall, metal contamination has had an important influence on zooplankton community structure in many Sudbury area lakes. The analyses of all the selected subsets of the long-term data series identified metals and variables affecting metal speciation and toxicity (pH, DOC, and Ca) as important explanatory variables.

Changes in direct predation by fish can also have dramatic effects on the abundance, size structure, and composition of crustacean zooplankton communities (Raess & Maly 1986; Mills et al. 1987). Cladoceran community composition is known to be much more vulnerable than is copepod composition to alterations in both vertebrate (Yan et al. 2004) and invertebrate (Boudreau & Yan 2003) predation. Fish predation forces zooplankton communities towards smaller-bodied species by selectively removing the larger-bodied forms (Brooks & Dodson 1965). Furthermore, the abundance of large *Daphnia* species is usually low in the presence of planktivorous fish (Brooks & Dodson 1965; Mills & Forney 1983). In one of the initially fishless study lakes (Clearwater), *Daphnia* spp. were recolonizing; however, as soon as perch colonized this lake and became abundant, *Daphnia* spp. were no longer collected. These results suggest that while established *Daphnia* populations can tolerate high-perch predation, early in the recovery process when *Daphnia* populations are first becoming established, abundant perch may be a barrier.

The results of the multivariate analyses for the entire data set and those of the post-1990 data set indicated that water chemistry alone explained approximately twice as much variation in the zooplankton assemblage than the fish community composition. Analysis of the pre-1985 dataset indicated that water chemistry alone explained approximately five times as much variation than the fish community composition. This suggests that for much of the recovery period to date, communities responded primarily to reduced acidification and metals. Conversely, now that metals have declined and perch are abundant, control by intensive fish predation may be limiting the complete recovery of zooplankton communities in some lakes.

The analyses based on cladoceran and copepod species indicated that both assemblages displayed similar trends to the whole dataset, with approximately twice as much variation explained by water chemistry as by fish community composition. The analysis based on *Daphnia* species, which are likely most susceptible to perch predation, indicated approximately equal amounts of variation explained by water chemistry and by the fish community composition. This suggests that once water quality thresholds are met, the fish community may still need to be restored in order to allow the complete recovery of the zooplankton community.

Implications for Practice

- Restoration plans for industrially damaged lakes must consider both the abiotic and biotic factors that affect the recovery of lake zooplankton communities.
- As acidity and metal concentrations decrease, fish planktivory may assume an increasing influence on zooplankton recovery. When populations of *Daphnia* spp. are first becoming established, the abundant perch characteristic of early fish population recovery can be a barrier to successful *Daphnia* colonization.
- Stocking of piscivorous fish species may be needed to control planktivores and aid the reestablishment of typical zooplankton communities in previously damaged lakes. Typical communities would be those currently existing in regional reference lakes that have not experienced industrial damage.

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LITERATURE CITED

Baudouin, M. F., and P. Scoppa. 1974. Acute toxicity of various metals to freshwater zooplankton. Bulletin of Environmental Contamination and Toxicology **12:**745–751.

Beamish, R. J. 1976. Acidification of lakes in Canada by acid precipitation and the resulting effects on fishes. Water, Air, and Soil Pollution **6:**501–514.

Biesinger, K. E., and G. M. Christensen. 1972. Effects of various metals on survival, growth, reproduction, and metabolism of *Daphnia magna*. Journal of Fisheries Research Board of Canada **29:**1691–1700.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology **73:**1045–1055.

Boudreau, S. A., and N. Yan. 2003. An introduced predator (*Bythotrephes*) reduces zooplankton species richness. Ecology Letters **5:**481–485.

Brix, K. V., D. K. DeForest, and W. J. Adams. 2001. Assessing acute and chronic copper risks to freshwater aquatic life using species sensitivity distributions for different taxonomic groups. Environmental Toxicology and Chemistry **20:**1846–1856.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150:**829–839.

Conroy, N. I., K. Hawley, W. Keller, and C. Lafrance. 1976. Influences of the atmosphere on lakes in the Sudbury area. Atmospheric contribution to the chemistry of lake waters. Journal of Great Lakes Research **2:**146–165.

Gunn, J. M., J. M. Casselman, M. J. McMurty, W. Keller, and M. J. Powell. 1988. Changes in the fish community of a limed lake near Sudbury, Ontario: effects of chemical neutralization or reduced atmospheric deposition of acids? Water, Air, and Soil Pollution **49:**113–136.

Gunn, J. M., and W. Keller. 1990. Biological recovery of an acid lake after reductions in industrial emissions of sulphur. Nature **345:**431–433.

Ingersoll, C. G., and R. W. Winner. 1982. Effect on *Daphnia pulex* of daily pulse exposures to copper or cadmium. Environmental Toxicology and Chemistry **1:**321–327.

Johannssen, O.E., M.A. Shaw, N.D. Yan, J.M. Filion, and D.F. Malley. 1992. A comparison of freshwater zooplankton sampling gear: nets, traps and submersible pump. Canadian Technical Report of Fisheries and Aquatic Sciences.

Kankaala, P. 1984. A quantitative comparison of two zooplankton sampling methods, a plankton trap and a towed net, in the Baltic. Internationale Revue der Gesamten Hydrobiologie **69:**277–287.

Keller, W., and J. R. Pitblado. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acid deposition. Water, Air, and Soil Pollution **23:**271–291.

Keller, W., and J. R. Pitblado. 1986. Water quality changes in Sudbury are lakes: a comparison of synoptic surveys in 1974–76 and 1981–83. Water, Air, and Soil Pollution **29:**285–296.

Keller, W., and N. D. Yan. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Canadian Journal of Fisheries and Aquatic Science **48:**1635–1644.

Keller, W., and J. M. Gunn. 1995. Lake water quality improvements and recovering aquatic communities. Pages 67–80 in J. M. Gunn, editor. Restoration and recovery of an industrial region: progress in restoring the smelter-damaged landscape near Sudbury, Canada. Springer-Verlag, New York.

Keller, W., and N. D. Yan. 1998. Biological recovery from lake acidification: zooplankton communities as a model of patterns and processes. Restoration Ecology **6:**364–375.

Keller, W., J. M. Gunn, and N. D. Yan. 1999. Acid rain: perspectives on lake recovery. Journal of Aquatic Ecosystems Stress and Recovery **6:**207–216.

Keller, W., N. D. Yan, K. M. Somers, and J. H. Heneberry. 2002. Crustacean zooplankton communities in lakes recovering from acidification. Canadian Journal of Fisheries and Aquatic Sciences **59:**726–735.

Keller, W., J. H. Heneberry, E. McLachlan, and S. MacPhee. 2006. Data Report: 25 years of Extensive Monitoring of Acidified Lakes in the Sudbury Area, 1981 to 2005. Cooperative Freshwater Ecology Unit, Sudbury, Canada.

Keller, W., N. D. Yan, J. M. Gunn, and J. H. Heneberry. 2007. Recovery of acidified lakes: lessons from Sudbury, Ontario, Canada. Water, Air, and Soil Pollution Focus **7:**317–322.

Koivisto, S., M. Ketola, and M. Walls. 1992. Comparison of five cladoceran species in short- and long-term copper exposure. Hydrobiologia **248:**125–136.

Lewis, W. M. Jr. 1978. Comparison of temporal and spatial variation in zooplankton of the lake by means of variance components. Ecology **59:**666–671.

Marmorek, D. R., and J. Korman. 1993. The use of zooplankton in a biomonitoring program to detect lake acidification and recovery. Water, Air, and Soil Pollution **69:**223–241.

MOEE. 1994. Water Management: Policies, Guidelines, Provincial Water Quality Objectives of the Ministry of the Environment and Energy, Toronto, Canada. ISBN: 0–7778–3494–4. Queen's Printer for Ontario.

Mills, E. L., and J. L. Forney. 1983. Impact on *Daphnia pulex* of predation by yellow perch in Oneida Lake, New York. Transaction of the American Fisheries Society **112:**154–161.

Mills, E. L., D. M. Green, and A. Schiavone. 1987. Use of zooplankton size to assess the community structure of fish populations in freshwater lakes. North American Journal of Fisheries Management **7:**369–378.

Nyberg, P. 1984. Impacts of *Chaoborus* predation on planktonic crustacean communities in some acidified and limed forest lakes in Sweden. Report/Institute of Fresh-water Research, Drottningholm **61:**154–166.

Raess, F., and E. J. Maly. 1986. The short-term effects of perch predation on a zooplankton prey community. Hydrobiologia **140:**155–160.

Schindler, D. W. 1969. Two useful devices for vertical plankton and water sampling. Journal of the Fisheries Research Board of Canada **26:**1948–1955.

Sprules, G. W. 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. Journal of Fisheries Research Board of Canada **32:**389–395.

Taylor, L. N., C. N. Wood, and D. G. McDonald. 2003. An evaluation of sodium loss and gill metal binding properties to explain species differences in copper tolerances. Environmental Toxicology and Chemistry **22:**2159–2166.

Ter Braak, C. J. F., and P. Smilauer. 2002. Reference manual and CanoDraw for Windows user's guide: software for canonical community ordinations (version 4.5). Microcomputer Power, Ithaca, New York.

Valois, A., W. Keller, and C. Ramcharan. 2010. Abiotic and biotic processes in lakes recovering from acidification: the relative roles of metal toxicity and fish predation as barriers to zooplankton re-establishment. Freshwater Biology **55:**2585–2597.

Winner, R. W., and M. P. Farrell. 1976. Acute and chronic toxicity of copper to four species of Daphnia. Journal of Fisheries Research Board of Canada **33:**1685–1691.

Yan, N. D., and R. Strus. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Canadian Journal of Fisheries and Aquatic Science **37:**2282–2293.

Yan, N. D., R. Girard, J. H. Heneberry, W. Keller, J. M. Gunn, and P. J. Dillon. 2004. Recovery of copepod, but not cladoceran, zooplankton from severe and chronic effects of multiple stressors. Ecology Letters **7:**452–460.