Analysis of Planktonic Rotifer Assemblages from Sudbury, Ontario, Area Lakes of Varying Chemical Composition

Hugh J. MacIsaac[1]

Department of Botany, University of Toronto, Toronto, Ont. M5S 1A1

Thomas C. Hutchinson

Department of Botany, University of Toronto, Toronto, Ont. M5S 1A1
and
Institute for Environmental Studies, Haultain Building, University of Toronto, Toronto, Ont. M5S 1A4

and W. Keller

Ontario Ministry of the Environment, 199 Larch Street, Sudbury, Ont. P3E 5P9

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Planktonic rotifer samples were collected from 47 Sudbury, Ontario, area lakes to determine factors influential to species distributions. The lakes ranged from highly acidic and metal contaminated to circumneutral with low metal concentrations. Median rotifer abundance was substantially higher in non-acid (pH > 5.2) than in acid (pH < 5.2) lakes, although differences in species distributions were evident. Application of detrended correspondence analysis to rotifer species densities revealed broad separation of communities from acid and non-acid lakes. Assemblages from acid lakes were highly similar in species composition and dominance, while those from non-acid lakes were generally much more heterogeneous. It was hypothesized that planktonic rotifer communities converged in species composition as a consequence of the stress of lake acidification, in a pattern similar to that previously described for planktonic crustaceans. Among the best predictors of rotifer community composition were lake pH and the concentrations of manganese and aluminum.

On a prélevé des échantillons de rotifères planctoniques dans 47 lacs de la région de Sudbury (Ontario) afin de déterminer les facteurs qui influent sur la répartition des espèces. Les eaux des lacs allaient de très acides et contaminées par des métaux à presque neutres avec de faibles concentrations de métaux. L'abondance médiane des rotifères était nettement plus élevée dans les lacs non acides (pH > 5,2) que dans les lacs acides (pH < 5,2) et des différences entre les répartitions spécifiques étaient évidentes. Une analyse factorielle de correspondance des densités des espèces de rotifères a révélé un important écart entre les communautés des lacs acides et non acides. Les assemblages des lacs acides étaient très semblables pour ce qui est de la composition et de la dominance spécifique tandis que, dans les lacs non acides, ils étaient généralement beaucoup plus hétérogènes. On formule l'hypothèse que les communautés de rotifères planctoniques ont fait l'objet d'une convergence touchant leur composition spécifique suite au stress de l'acidification lacustre et cela selon un régime semblable à celui décrit précédemment pour les crustacés planctoniques. Parmi les meilleures variables explicatives de la composition de la communauté des rotifères, ou compte le pH lacustre et les concentrations de manganèse et d'aluminum.

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Acidic precipitation is widely recognized as having adversely affected terrestrial and aquatic ecosystems in western Europe and eastern North America. In Canada, the Sudbury, Ontario, region has received considerable scientific attention since Gorham and Gordon (1960) first described chemical modifications of surface waters resulting from very large local smelter emissions.

Among the most intensively studied groups of biota in acid lakes are the zooplankton (Sprules 1975; Roff and Kwiatkowski 1977; Yan and Strus 1980; Malley et al. 1982; Keller and Pitblado 1984). Crustacean zooplankton diversity in acidic, metal-contaminated Ontario lakes is often impoverished relative to that in non-acidic lakes of similar morphometry. For example, in the La Cloche Mountains 60 km southwest of Sudbury, Sprules (1975) observed that crustacean zooplankton diversity was reduced in acid lakes, with the most acidic lakes containing only one species (*Diaptomus minutus*).

Rotifers may act as better indicators of exogenous stresses on plankton communities than crustaceans, since their diversity, abundance, and fertility frequently exceed comparable values

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[1] Current address: Department of Biological Sciences, Gilman Hall, Dartmouth College, Hanover, NH, 03755, USA

for crustaceans (Allen 1976; Roff and Kwiatkowski 1977; Gilbert 1985). Hydrogen ion concentration has long been considered to be an important determinant of rotifer community composition (see review in Pennak 1978), although several workers (Edmondson 1944; Hutchinson 1967) have cautioned that species distributions may be influenced by other chemical factors, especially by CO_2, HCO_3^-, Ca, and mineral salts. Siegfried et al. (1984) and Carter et al. (1986) observed that rotifer community composition in Adirondack Mountain lakes and New Brunswick – Nova Scotia lakes was related to pH and other related factors.

The relationship between lake acidity and total rotifer density is less clear. Synoptic studies have revealed that attendant with increased lake acidity, total abundance may increase (Malley et al. 1982; Schindler et al. 1985; Yan and Geiling 1985), decrease (Roff and Kwiatkowski 1977; Carter et al. 1986), or appear unaffected (Siegfried et al. 1984).

In this study we examine the planktonic rotifer communities from northeastern Ontario lakes of varying chemical composition in an attempt to determine factors governing species distributions. Additionally, we test the hypothesis that total rotifer abundance does not differ between acid and non-acid lakes.

Methods

Forty-seven lakes located within 175 km of Sudbury were selected for the study. Many of the lakes have been previously investigated by the Ontario Ministry of the Environment (MOE) (Keller and Pitblado 1984) and have been identified as having been affected by smelter emissions. The lakes are located primarily to the northeast and southwest of Sudbury along the prevailing wind directions.

Collections for chemical and zooplankton analyses were made between 16 July and 7 August 1984 from a central location in each lake. Access to 39 lakes was by fixed-wing aircraft, while the remaining 8 lakes were sampled by boat. Samples for chemical analysis were collected by immersing a tygon tube from the surface to the lower limit of the metalimnion (MOE 1979). All total inflection point (TIP) alkalinity and pH measurements were made using a Radiometer PHM 64 pH meter, while conductivity was determined and corrected to 25°C by a Radiometer CDM3 conductivity meter. Two protocols were followed in other chemical analyses. Briefly, for the 39 lakes sampled by floatplane, one sample for analysis of Mn, Al, Zn, Cu, Ni, Pb, and Fe was preserved with 0.5 mL of Analar-grade nitric acid for subsequent determination by atomic absorption spectroscopy (MOE 1981). A second sample was used for determination of Ca, Mg, K, Na, SO_4^{2-}, Cl, and SiO_3. Complete methods are outlined in MOE (1981). For the remaining eight lakes, concentrations of Mn, Al, Zn, Cu, Ni, Pb, Fe, Mg, Ca, and total S were determined using inductive coupled plasma (ICP) emission spectroscopy at the University of Toronto. A comparison of chemical methods is given in the Appendix. In general, there was good agreement between the methods, although in some instances ICP sulphur values were considerably lower than the sulphate values obtained using the first method (ion chromatography). Values for Na, K, Cl, and SiO_3 were obtained from 1983 data, as 1984 values were unavailable, while 1981 total P values were used for all lakes (W. Keller, unpubl. data).

Zooplankton samples were collected by a vertical haul from 1 m above bottom to the lake surface using a metered 44-μm Wisconsin-style net with a 12.5-cm-diameter mouth. Samples were preserved in a 5% sugar–formalin solution and later enumerated as subsamples following settling in sedimentation tubes for a minimum of 3 h. In general, a minimum of 300 individuals was counted per subsample, with additional subsamples being examined for rare species. All densities were corrected for filtration efficiency. The presence or absence of *Leptodora kindtii* and *Chaoborus* spp. was simply noted, since quantitative determinations of these organisms are difficult to make when collections are made during daylight hours.

Statistical Analysis

Chemical differences between acid ($pH < 5.20$; $N = 31$) and non-acid ($pH > 5.20$; $N = 16$) lake groups were examined with Student's *t*-tests, while differences in rotifer diversity and density were investigated using Mann–Whitney *U*-tests. Variability in community composition was analyzed using species densities and detrended correspondence analysis (DCA). DCA is an ordination procedure which allows for the projection of a multidimensional data swarm in low-dimensional space (Gauch 1982). Samples (lakes) with similar patterns of species composition and dominance have similar "loadings" or positions on DCA plots. DCA is generally considered to be superior to earlier ordination techniques because it "detrends" data, thereby preventing artificial "arch effects" and because it rescales each axis to uniform subdivision length (Gauch 1982).

Canonical correlation analysis was then used to explore the relationship between the DCA results (criterion set) and lake physical–chemical parameters (predictor set). The analysis was repeated using biotic variables (crustacean zooplankton species densities, *Leptodora* and *Chaoborus* presence/absence) as the predictor set. Between variable sets, canonical correlation coefficients (R^2) represent the variability of one set explained by the other. The significance of the correlations was tested using the *F*-test of Miller (1975).

Results

A large proportion (>65%) of the lakes had pH values below 5.2 and alkalinity values below 20 $\mu eq \cdot L^{-1}$ (Fig. 1a). While the concentrations of Al, Mn, and Zn were significantly higher ($p < 0.05$) in acid than in non-acid lakes (Fig. 1b, 1c, 1d), concentrations of Cu and Ni were not significantly different ($p > 0.05$; Fig. 1e, 1f). Acid lakes contained significantly higher ($p < 0.03$) levels of sulphate than non-acid lakes (Fig. 1g) and lower concentrations of Ca, Mg, and K ($p < 0.001$; Fig. 1h, 1i, 1j). Acid lakes were also more transparent ($p < 0.03$) and generally had lower total P values (Fig. 1k and 1l, respectively).

Thirty-seven rotifer species occurred in two or more lakes in the study (Table 1). The median number of species was significantly higher ($p < 0.001$) in non-acid (14.5) than in acid (8.0) lakes, despite the fact that sample depth was greater for the latter group (Table 2). Median rotifer density was significantly higher ($p < 0.05$) in non-acid (140.6 $ind. \cdot L^{-1}$) than in acid (67.2 $ind. \cdot L^{-1}$) lakes. However, a multiple regression model indicated that total P concentration was a better predictor of total rotifer density and that the effect of pH was indirect (Table 3).

The most frequently encountered species were *Gastropus* spp., *Keratella taurocephala*, *K. cochlearis*, *Polyarthra vulgaris*, and *Trichocerca multicrinis* (Table 1). Each of these species, excepting *T. multicrinis*, was dominant (>10% of total

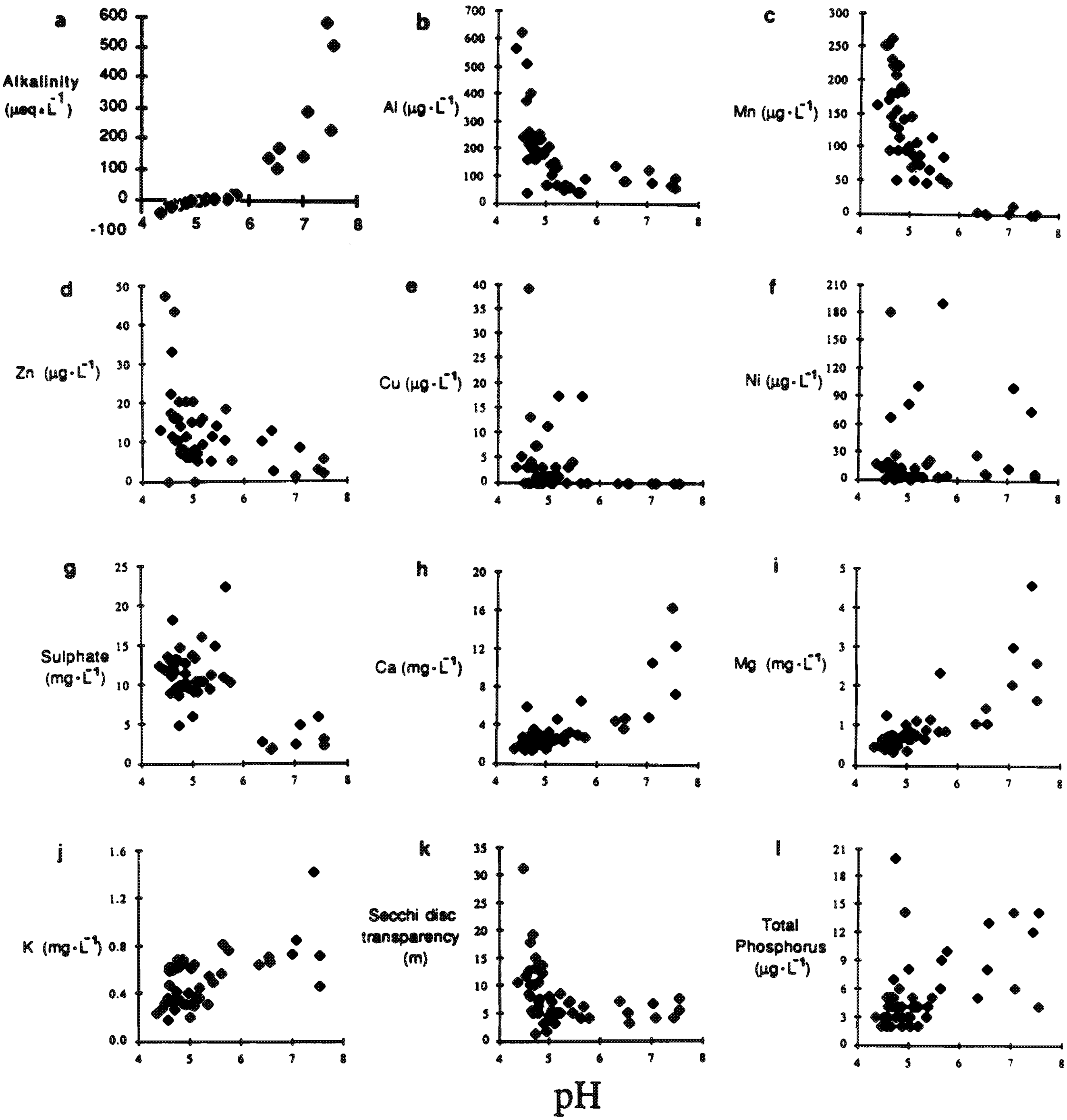

FIG. 1. Relationships between physical–chemical parameters and lake pH.

rotifer abundance) in more than 25% of the lakes. The relative abundance of many species appeared to be pH dependent; *K. taurocephala* and *Gastropus* together accounted for >70% of the total rotifer abundance in acidic lakes and <5% in non-acid lakes. In some acid lakes, *K. taurocephala* so dominated the rotifer fauna that the densities of all the other species combined accounted for <5% of total abundance. The dramatic decline in the abundance of *K. taurocephala* began at about pH 4.8, with the species being virtually absent from lakes with pH > 6.0 (Fig. 2).

While the overall distribution of *K. cochlearis* was nearly a mirror image of that for *K. taurocephala* (Fig. 2), its density in individual lakes was not correlated (Pearson's $r = -0.13$) with that of *K. taurocephala*. *Keratella cochlearis* was rarely found below pH 5.3, but it was a dominant member of the community in 88% of lakes with pH > 5.5. *Keratella cochlearis* and *P. vulgaris* together accounted for only 3.1% of total rotifer density in acid lakes and 75.9% in non-acid lakes. *Polyarthra vulgaris* and *P. remata* were frequently encountered species in the study (62 and 39% of lakes, respectively; Table 1). Both species were more abundant in non-acid than in acid lakes, and neither species occurred in lakes with pH < 4.5. Similarly, the predatory rotifer *Asplanchna priodonta* and its larger congener *A. herricki* occurred primarily in near-neutral lakes, although

TABLE 1. Occurrence and dominance of 37 rotifer species in the study lakes

Species	Occurrence		% of lakes in which dominant (>10%)
	Number of lakes	% of lakes	
Ascomorpha ecaudis	4	8.5	2.1
A. saltans	2	4.3	0
A. ovalis	7	14.9	2.1
Asplanchna priodonta	20	42.6	2.1
A. herricki	3	6.4	0
Conochilus unicornis	17	36.2	8.5
C. hippocrepis	2	4.3	2.1
Conochiloides natans	13	27.7	8.5
Euchlanis pellucida	2	4.3	2.1
Gastropus spp.	47	100	51.1
Kellicottia bostoniensis	14	29.8	4.3
K. longispina	14	29.8	2.1
Keratella cochlearis	31	66.0	25.5
K. crassa	20	42.6	2.1
K. earlinae	7	14.9	0
K. hiemalis	8	17.0	0
K. taurocephala	41	87.2	68.1
Lecane flexilis	3	6.4	0
L. mira	12	25.5	0
Lepadella acuminata	4	8.5	0
L. ovalis	4	8.5	0
Monostyla closterocerca	2	4.3	0
M. copeis	2	4.3	0
M. lunaris	14	29.8	0
M. obtusa	2	4.3	0
Ploesoma truncatum	19	40.4	0
Polyarthra major	7	14.9	2.1
P. remata	17	36.2	4.3
P. vulgaris	29	61.7	38.3
Synchaeta spp.	26	55.3	4.3
Testudinella parva	3	6.4	0
Trichocerca cylindrica	8	17.0	0
T. multicrinis	31	66.0	0
T. porcellus	3	6.4	0
T. rousseleti	3	6.4	0
T. similis	10	21.2	0
Trichocerca spp.	4	8.5	0

the distribution of *A. priodonta* extended into mildly acid waters.

DCA results are presented in Fig. 3 for the two primary axes of the species density ordination. These axes accounted for 47 and 27%, respectively, of the total variability in the ordination (Table 4). The grouping of the lakes along the axes of the figure (Fig. 3a) indicate that rotifer communities in acid lakes were relatively homogeneous in comparison with communities in circumneutral lakes. Specifically, acid lake communities characteristically were dominated by only a few species, most notably *K. taurocephala* and *Gastropus*, while non-acid lakes were dominated by a larger array of species, including *K. cochlearis*.

Application of canonical correlation analysis to DCA results demonstrated that chemical factors correlated best with DCA axis 1, while biological parameters (i.e. crustacean predictors) correlated most strongly with DCA axis 2. For example, canonical variate 1 (CV 1) of the physical–chemical data set was significantly correlated ($r = -0.921$; $p < 0.01$) with DCA axis 1 (Table 5). Negative correlations with CV 1 indicate that values for physical–chemical parameters increase with increasing DCA scores on axis 1. The best correlates of CV 1 included pH (Fig. 3a), Mn concentration (Fig. 3b), alkalinity (Fig. 3c), and Mg and Ca (Fig. 3d) concentrations (Table 5). Other physical–chemical variables which correlated with CV 1 included the concentrations of total P, K, and Al (Table 5). No significant correlations were observed between any other canonical variates for the physical–chemical data and the DCA axes.

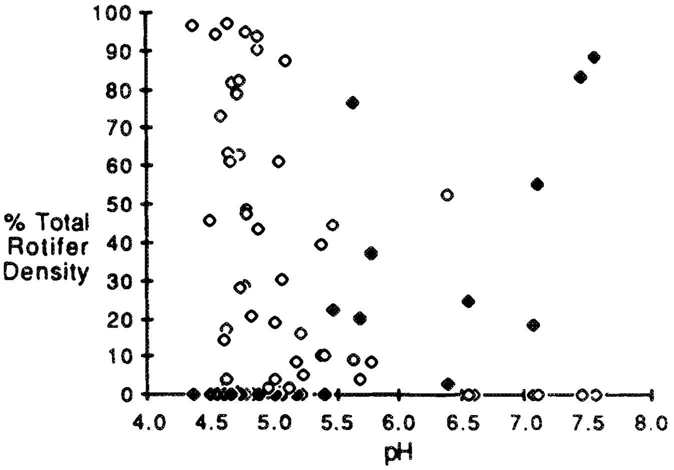

FIG. 2. Percent composition of the total rotifer density for *Keratella taurocephala* (◇) and *K. cochlearis* (◆) as a function of lake pH.

While the greatest amount of variation in the ordination of rotifer communities is accounted for by physical–chemical variables, variation along DCA axis 2 correlated best with CV 1 for the biotic variables ($r = -0.891$, $P < 0.01$; Table 6). In general, correlations between original crustacean densities and their corresponding canonical variates (intraset correlations; Table 6) were lower than those observed between physical–chemical parameters and their canonical variates (Table 5), possibly because it is more difficult to accurately determine animal densities than chemical concentrations in water. The highest correlations with CV 1 were obtained with the densities of *Diaptomus oregonensis* and *Daphnia* spp. (Table 6). However, many of the correlations between crustacean densities and CV 1 are perhaps spurious, as densities of many crustacean and rotifer species covary as a function of lake pH. In addition, assigning biological significance to correlations between CV 1 of the crustacean data set and the DCA axes is made difficult by the fact that separation of lakes on DCA axis 2 occurred mainly with non-acid lakes (Fig. 3a), of which there were a limited number in the study.

Discussion

The acidification of freshwater ecosystems represents a major ecological problem. Recent investigations have demonstrated that many groups of organisms, including planktonic rotifer communities, are affected by acidification related phenomena (Schindler et al. 1985; Carter et al. 1986, and references therein; MacIsaac et al. 1986). In the current study, median rotifer diversity decreased from 14.5 species in non-acid lakes to 8.0 species in acid waters. This finding corresponds well with results from previous studies in both Europe (Almer et al. 1974) and eastern North America (Roff and Kwiatkowski 1977; Bradt et al. 1984; Siegfried et al. 1984; Carter et al. 1986).

TABLE 2. Summary statistics for physical–chemical parameters of the study lakes.

Parameter	Lake group pH < 5.2 (31 lakes) Mean	 pH > 5.2 (16 lakes) Mean	t-statistic	$p <$
pH[a]	4.76	5.71	10.3	0.001
Alkalinity (μeq·L^{-1})	−15	136	4.6	0.001
Specific conductance (μS·cm^{-1})	37.5	71.6	3.2	0.003
Secchi disc transparency (m)	9.1	5.5	2.3	0.025
Mg (mg·L^{-1})	0.6	1.6	5.1	0.001
Ca (mg·L^{-1})	2.4	5.8	4.5	0.001
K (mg·L^{-1})	0.3	0.6	5.3	0.001
Na (mg·L^{-1})	0.7	3.3	2.6	0.012
Al (μg·L^{-1})	232.3	75.3	4.6	0.001
Mn (μg·L^{-1})	150.6	36.6	6.9	0.001
Zn (μg·L^{-1})	14.1	8.2	2.1	0.044
Fe (μg·L^{-1})	93.2	67.1	0.9	0.395
Cu (μg·L^{-1})	3.8	2.6	0.6	0.575
Ni (μg·L^{-1})	17.8	35.9	1.4	0.168
SO_4^{2-} (mg·L^{-1})	11.1	8.0	2.4	0.021
Cl (mg·L^{-1})	0.5	5.3	2.4	0.019
SiO_3 (mg·L^{-1})	0.9	1.3	1.0	0.331
Total P (μg·L^{-1})	4.7	6.6	1.6	0.112
Lake area (ha)	319	350	0.28	0.778
Lake depth (m)	21.0	20.0	0.2	0.839
Sample depth (m)	18.6	8.9	3.5	0.001
Distance from Sudbury (km)	72.4	41.2	3.1	0.003

[a] Based on [H^+] equivalents.

TABLE 3. Multiple regression analysis of total rotifer densities on lake pH and total P concentration for the survey lakes.

Source	df	SS	MS	F value	Pr > F
Model	3	464 177	154 726	9.69	0.0001
Error	43	686 517	15 966		
Total	46	1 150 694			

Source	df	Type 3	F value	Pr > F
pH	1	26 878	1.68	0.2014
phosphorus	1	65 114	4.08	0.0497
pH*phosphorus	1	117 626	7.37	0.0095

The effect of lake acidification on overall rotifer abundance is less clear. While our finding of decreased abundance in acid lakes agrees with the results of Roff and Kwiatkowski (1977), Brezonik et al. (1984), and Carter et al. (1986), they contrast with those of Yan and Miller (1984) and Schindler et al. (1985). Siegfried et al. (1984) found that clear, acid Adirondack lakes supported low rotifer populations, while humic, acid lakes supported higher densities. These disparate results may be reconciled in some instances by considering the productivity of the lakes involved (Carter et al. 1986) and the extent to which they have been contaminated by heavy metals. In the current study, total rotifer density correlated better with total P concentration than with the concentration of heavy metals and lake pH, indicating that lake productivity may well have been the primary determinant of total rotifer density.

Although overall rotifer density declined at low pH, species differences were evident. The predominant species in acid lakes included *K. taurocephala* and *Gastropus*. *Keratella taurocephala* has been observed in acid lakes over much of eastern North America (Roff and Kwiatkowski 1977; Malley et al. 1982; Bradt et al. 1984; Chengalath et al. 1984; Siegfried et al. 1984; Yan and Miller 1984; Carter et al. 1986). The species appears highly adapted to life in acid lakes since its large anterolateral spines may render it invulnerable to predation by invertebrates (e.g. *Chaoborus*; Moore and Gilbert 1987) which commonly occur in fishless acid lakes (MacIsaac 1986). Moreover, its body morphology minimizes sinking, and as a consequence, the energy expenditure required to remain in the plankton (R. S. Stemberger, Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, pers. comm.). As a result, *K. taurocephala* is able to live in relatively unproductive waters, such as those which might result as a consequencr of lake acidification where the total amount of edible phytoplankton is low (Havens and DeCosta 1985; Schindler et al. 1985; Stokes and Yung 1986).

Very little is currently understood regarding the factors which determine the distribution of *K. taurocephala* in relation to lake chemistry. Yan and Geiling (1985) and MacIsaac et al. (1986) reported large populations of *K. taurocephala* in an acidic (pH = 4.0) lake (Swan) located near Sudbury. However, it was not found in any acidic (pH < 4.0) ponds at the Smoking Hills, N.W.T., nor in Silver Lake, another highly acidic (pH = 4.1) Sudbury lake (H. MacIsaac, unpubl. data). The dominant species in both of these systems was *Brachionus urceolaris*, a species previously reported in highly acidic volcanic lakes in Japan (Masiko 1938) and in acid mine drainage lakes in Indiana (Smith and Frey 1971) and Missouri (Campbell et al. 1964). While the absence of *K. taurocephala* from the

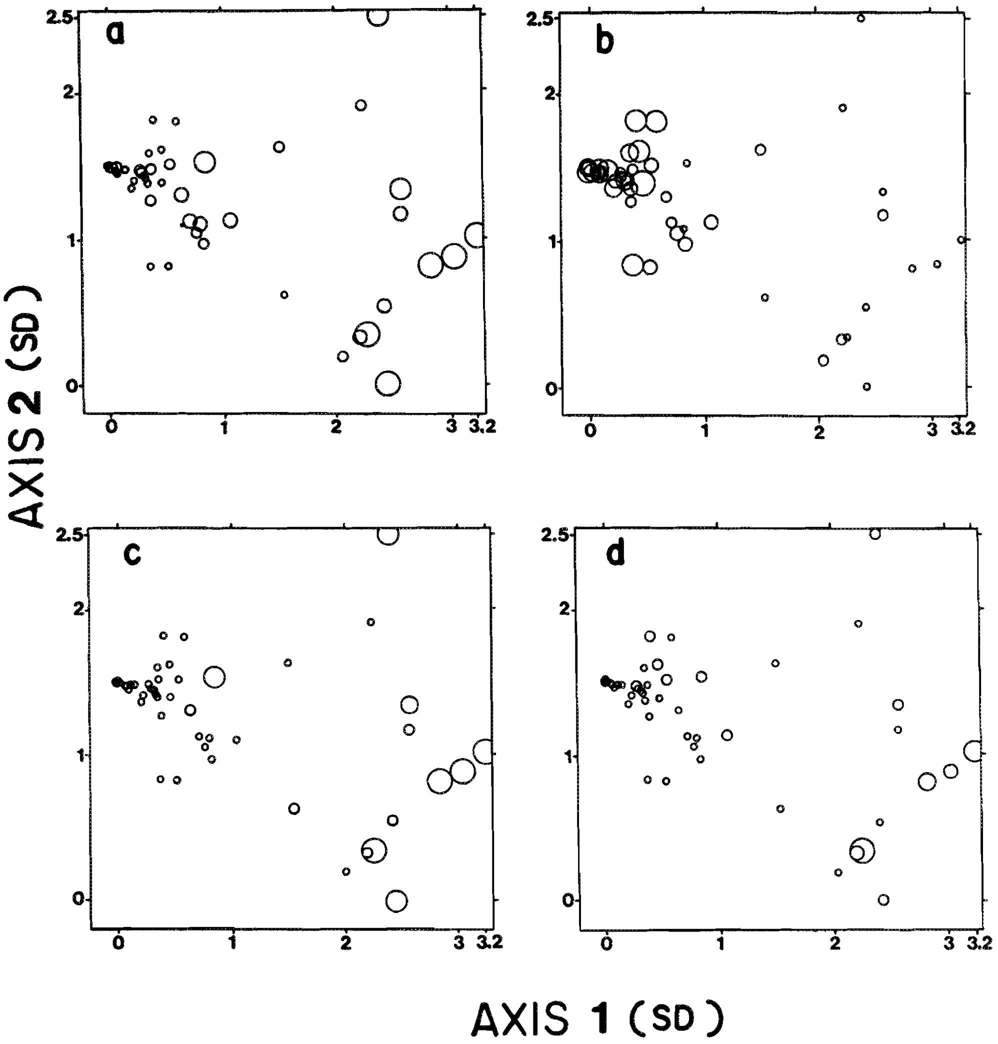

FIG. 3. Variability (standard deviations) in rotifer communities as determined by a detrended correspondence analysis model based on species densities (see text for further explanation). For each of the following, parameter value increases with circle: (a) pH, (b) total MN concentration, (c) TIP alkalinity, (d) Ca concentration. Maximum values: pH = 7.58, Mn = 260 $\mu g \cdot L^{-1}$, alkalinity = 585 $\mu eq \cdot L^{-1}$, Ca = 16.4 $mg \cdot L^{-1}$; minimum values: pH = 4.39, Mn ≤ 0.1 $\mu g \cdot L^{-1}$, alkalinity = −32 $\mu eq \cdot L^{-1}$, Ca = 1.3 $mg \cdot L^{-1}$.

TABLE 4. Species lists for rotifers that loaded most heavily onto the two primary DCA axes. Species at the high end of axis 1 are characteristic of non-acid lakes, while those at the low end are more characteristic of acidic waters. The middle 17 species (not shown) are considered nonpreferential. Beside each axis is the proportion of total variability in the ordination accounted for by that axis.

Axis 1 (47%)		Axis 2 (27%)	
Highest scores	Lowest scores	Highest scores	Lowest scores
Keratella cochlearis	*Trichocerca porcellus*	*Keratella earlinae*	*Asplanchna herricki*
Monostyla closterocerca	*Monostyla obtusa*	*Conochilus unicornis*	*Asplanchna priodonta*
Trichocerca rousseleti	*Keratella taurocephala*	*Ascomorpha ovalis*	*Ascomorpha ecaudis*
Conochilus hippocrepis	*Synchaeta* spp.	*Monostyla closterocerca*	*Ploesoma truncatum*
Asplanchna herricki	*Gastropus* spp.	*Euchlanis pellucida*	*Keratella crassa*
Keratella earlinae	*Ascomorpha saltans*	*Lecane flexilis*	*Polyarthra remata*
Trichocerca cylindrica	*Keratella hiemalis*	*Lepadella ovalis*	*Keratella hiemalis*
Kellicottia longispina	*Lepadella acuminata*	*Conochilus hippocrepis*	*Kellicottia longispina*
Keratella crassa	*Conochiloides natans*	*Trichocerca rousseleti*	*Polyarthra vulgaris*
Asplanchna priodonta	*Testudinella parva*	*Kellicottia bostoniensis*	*Lepadella acuminata*

TABLE 5. Loadings of physical–chemical variables on three canonical variates of the predictor set where rotifer DCA axes represent the criteria. Parenthetical numbers (canonical correlation coefficients) represent the amount of variation in the DCA axes explained by the canonical variates of the physical–chemical data set.

Variable	CV 1	CV 2	CV 3
Criteria (interset correlations)			
DCA axis 1	−0.921 (0.848)	0.162 (0.026)	0.126 (0.016)
DCA axis 2	0.563 (0.317)	−0.133 (0.018)	0.434 (0.188)
DCA axis 3	0.234 (0.055)	0.680 (0.462)	0.399 (0.159)
Predictors (intraset correlations)			
pH	−0.864.	0.066	0.133
Alkalinity	−0.698	−0.016	0.127
Mg	−0.685	0.019	−0.011
Ca	−0.664	−0.129	0.108
K	−0.570	0.162	−0.029
Na	−0.406	0.141	−0.158
Specific conductance	−0.487	0.001	−0.046
Mn	0.740	−0.234	0.012
Al	0.559	0.027	0.140
Zn	0.344	0.043	0.069
Cu	0.153	−0.329	−0.080
Ni	−0.143	−0.249	−0.049
Total P	−0.594	0.233	0.107
SO_4	0.462	−0.303	−0.166
Colour (Hazen)	−0.265	0.436	0.315
Secchi disc transparency	0.452	−0.038	0.107
Lake area	−0.165	0.172	0.030
Sample depth	0.393	0.033	−0.306
Lake depth	0.207	0.068	−0.211
Distance from Sudbury	0.202	0.081	−0.159

arctic ponds may be related to difficulties in dispersal, it is more difficult to explain its absence from Silver Lake, as the species occurs in many nearby lakes. Silver Lake and many of the arctic ponds are contaminated with extremely high levels of Al, Mn, Zn, Ni, and Cu (W. Keller, unpubl. data; Havas and Hutchinson 1983). In comparison, Swan Lake and the lakes in this survey have lower levels of heavy metal contamination (MacIsaac 1986; MacIsaac et al. 1986). Thus, the distribution of *K. taurocephala* may well be restricted at low pH by direct or indirect effects of toxic concentrations of heavy metals, rather than by hydrogen ion toxicity. Community composition may be expected to shift from *K. taurocephala* dominated *B. urceolaris* dominated when concentrations of heavy metals and hydrogen ion are greatly elevated.

The contribution to total rotifer density by *K. taurocephala* was very low in lakes with pH values > 5.5 (Fig. 3). A similar pattern has also been demonstrated with Adirondack Mountain lakes by Siegfried et al. (1984). Since metal levels are generally low in circumneutral waters, it is unlikely that metal toxicity affected the distribution of *K. taurocephala* in our near-neutral study lakes. It is also unlikely that predation had any direct effect on *K. taurocephala* abundance in these lakes; low densities of the species were frequently accompanied by higher densities of similar-sized members of the genus (*K. earlinae*, *K. crassa*, and *K. cochlearis*).

Two alternative hypotheses which may account for the decline in importance of *K. taurocephala* at high pH are competitive interactions and physiological intolerance. Although the evidence necessary to test the hypotheses is scant, competitive interactions between rotifers and other zooplankton have been demonstrated. Cladoceran zooplankters may effectively suppress rotifer populations either by interference (Gilbert and Stemberger 1985) or exploitative competition (Neill 1984; Gilbert 1985; H. MacIsaac, unpubl. data). Moreover, since non-acid lakes frequently support larger populations of both rotifers and herbivorous crustacean zooplankton than comparable acid lakes (Roff and Kwiatkowski 1977; Brezonik et al. 1984), the potential for competitive interactions may be greater in non-acid lakes. However, recent attempts to culture *K. taurocephala* clones from softwater New England lakes in competition- and predation-free environments at pH > 6.0 have been unsuccessful (R. S. Stemberger, pers. comm.). Thus, the available evidence is consistent with the hypothesis of physiological intolerance to non-acid conditions rather than competitive exclusion.

The distribution of *K. cochlearis* in relation to lake acidity is also very poorly understood. The species was found almost exclusively in lakes with low heavy metal concentrations and pH > 5.5 in our study. These results agree with its distribution as reported by Siegfried et al. (1984) for Adirondack Mountain lakes and by Carter et al. (1986) for lakes in New Brunswick and Nova Scotia. Furthermore, both Roff and Kwiatkowski (1977) and Bradt et al. (1984) described higher densities of *K. cochlearis* in non-acid lakes in their surveys of both acid and non-acid lakes. By contrast, Malley et al. (1982) reported dramatic increases in the density of *K. cochlearis* in an experimentally acidified northwestern Ontario lake, while Brezonik et al. (1984) found the species in both acid and non-acid Florida lakes. These incongruous results may possibly be explained by assuming that different varieties, with different ecological tolerances, from the *K. cochlearis* species complex were involved.

TABLE 6. Loadings of crustacean and insect variables on three canonical variates of the predictor set where rotifer DCA axes represent the criteria. Parenthetical numbers (canonical correlation coefficients) represent the amount of variation in the DCA axes explained by the canonical variates of the crustacean and *Chaoborus* data set.

Variable	CV 1	CV 2	CV 3
Criteria (interset correlations)			
DCA axis 1	0.587 (0.345)	−0.489 (0.239)	−0.481 (0.231)
DCA axis 2	−0.891 (0.793)	−0.230 (0.053)	−0.070 (0.005)
DCA axis 3	−0.027 (0.001)	−0.466 (0.217)	0.345 (0.119)
Predictors (intraset correlations)			
Chydorus sphaericus	0.419	0.064	0.033
Daphnia galeata mendotae	0.495	−0.192	0.029
D. retrocurva	0.499	0.000	0.020
Diaphanosoma brachyurum	0.314	−0.032	0.054
Bosmina longirostris	−0.034	0.147	−0.163
Eubosmina spp.	−0.103	−0.536	0.032
Holopedium gibberum	−0.131	0.129	0.175
Polyphemus pediculus	−0.232	0.180	0.047
Leptodora kindtii	0.389	−0.322	−0.085
Diaptomus minutus	−0.103	0.253	−0.018
D. oregonensis	0.572	−0.023	0.091
D. sicilis	0.120	0.022	−0.563
Epischura lacustris	0.433	−0.163	−0.204
Senecella calanoides	0.348	−0.165	0.085
Calanoid copepodids	−0.292	0.286	0.270
Cyclops scutifer	0.139	−0.329	0.099
C. bicuspidatus thomasi	0.318	−0.438	0.050
C. vernalis	0.125	−0.568	0.255
Tropocyclops prasinus mexicanus	−0.208	−0.481	−0.318
Cyclopoid copepodids	0.171	−0.435	−0.273
Total nauplii	0.077	−0.591	−0.267
Chaoborus spp.	−0.030	0.033	0.255

Alternatively, the results of Malley et al. (1982) and Brezonik et al. (1984) indicate that heavy metals may also influence *K. cochlearis* distributions. Acidic lakes in both studies were low in metal contamination, yet they contained sizeable populations of *K. cochlearis*. Thus, it is conceivable that the distribution of *K. cochlearis*, as well as that of other species such as members of the genus *Polyarthra*, may well have been determined more by elevated levels of metals than by hydrogen ion toxicity.

Using multivariate statistical procedures, Carter et al. (1986) found that while Labrador and Newfoundland lakes lacked any distinct zooplankton community structure associated with acidification, structure in lakes in Nova Scotia and New Brunswick was significantly related to acidification-related factors. In Labrador, where acidification is negligible, zooplankton species were almost independently distributed. In contrast, lakes in Nova Scotia and New Brunswick which were located on granitic and dioritic rock formations around the Bay of Fundy displayed distinct community types. Rotifers associated with non-acid waters included *K. crassa*, *K. cochlearis*, *T. cylindrica* and *A. priodonta*, while *K. taurocephala* was the predominant species in acid lakes. These findings bear very close resemblance to our results for northeastern Ontario lakes. In both models the primary factor (axis) associated with community composition correlated best with pH, alkalinity, Ca, Mg, and Al. Our model also designated Mn as a strong correlate of DCA axis 1 and hence of rotifer community composition. Mn has also been identified as a potentially important determinant of other small-bodied zooplankton assemblages in Ontario lakes (Sprules and Knoechel 1984), although unfortunately, very little work has been done to date to determine Mn toxicity thresholds for zooplankton species. It is possible, however, that Mn may appear to exert greater influence on plankton communities than it actually does, since its concentration is very closely related to lake acidity.

While biological indicators correspond poorly with the observed patterns in rotifer community composition in this study, they should not be discounted. Recent studies have demonstrated the potential for rotifer–crustacean (Gilbert 1985; Gilbert and Stemberger 1985) and rotifer–insect (Moore and Gilbert 1987) interactions. However, additional non-acid lakes need to be analyzed to determine the extent of these interactions.

We conclude that our results, when combined with those of Carter et al. (1986), indicate that rotifer community structure in eastern Canadian lakes subject to acidification becomes increasingly predictable as their assemblages become simpler. These patterns complement those previously established for crustacean zooplankton assemblages in acidic metal-contaminated Ontario lakes (Carter 1971; Sprules 1975). Thus, the response of rotifer communities does not appear to be unique. Circumneutral lakes in our study typically demonstrated greater diversity and heterogeneity than their acidic counterparts and as a result, recurrent patterns in species distributions in non-acid lakes were more difficult to discern and community structure was less clearly defined than in acid lakes.

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Appendix

Comparison of chemical parameters for two study lakes. Samples from 1981, 1982, and 1983 were analyzed by the Ontario Ministry of the Environment, while 1984 samples were analyzed at the University of Toronto using inductive coupled plasma (ICP) emission spectroscopy. All values are based on analysis of single samples (W. Keller, unpubl. data). —, not available.

	Clearwater			Tilton			
Parameter	Aug. 1981	July 1982	July 1984	Aug. 1981	Aug. 1982	Aug. 1983	July 1984
pH	4.52	4.48	4.65	5.00	5.11	5.08	5.23
Mg (mg·L^{-1})	1.5	1.4	1.3	1.2	1.2	1.1	1.1
Na (mg·L^{-1})	2.0	—	2.2	1.4	—	1.4	1.4
K (mg·L^{-1})	0.55	—	0.58	0.40	—	0.42	0.44
Ca (mg·L^{-1})	6.0	6.0	5.8	4.8	4.8	4.7	4.6
SiO_3 (mg·L^{-1})	1.35	—	0.85	0.60	—	0.50	0.26
SO_4 (mg·L^{-1})	20.0	19.4	18.1	17.5	15.5	17.5	16.0
Cu (μg·L^{-1})	46	58	39	28	35	21	17
Ni (μg·L^{-1})	190	230	180	140	150	120	100
Zn (μg·L^{-1})	28	35	33	19	28	18	16
Al (μg·L^{-1})	200	250	160	110	120	80	64
Mn (μg·L^{-1})	286	279	230	140	137	109	86
Fe (μg·L^{-1})	40	30	75	110	30	35	70