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## Zooplankton community structure in southwestern Québec lakes: the rôles of acidity and predation

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**Abstract.** The zooplankton community structure of 22 lakes with varying acidity and fish biomass, located southwest of the mining and smelting region of Rouyn/Noranda, Québec, was examined in July 1987. Lakes with dominant piscivorous fish communities could be discriminated from non-piscivorous communities using solely pH and *Chaoborus* abundance, demonstrating that modifications in the zooplankton community occurred concurrently with changes in the fish communities. Strong discontinuities in zooplankton species distributions were discerned in lakes with pH values <5.3; abundance ranges for several species could be semi-quantitatively related to lake morphology or chemistry. Small shallow kettle lakes with elevated heat budgets had high biomasses of small herbivorous organisms. The presence of >5 mg m<sup>-3</sup> of advanced *Chaoborus* instars (III and IV) was associated with reduced microcrustacean biomass in many lakes, particularly those with low fish biomass. There was little evidence for size-selective predation by fish in these oligotrophic lakes. Fish biomass/effort could be semi-quantitatively related to the biomass of *Leptodora kindtii* and the ratio of adult *Diaptomus minutus* to copepodite stage IV.

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### Introduction

Lake acidification results in a reduction of zooplankton species number and diversity (mainly cladocera) (Roff and Kwiatkowski, 1977; Almer *et al.*, 1978; Confer *et al.*, 1983), and a reduction in food web complexity (Havens, 1991). A shift to smaller crustaceans and rotifers in acidic metal-contaminated systems is often observed (Roff and Kwiatkowski, 1977; DeCosta and Janicki, 1978; Yan and Strus, 1980; Yan and Geiling, 1985; Tessier and Horwitz, 1990). However, hypotheses to explain these changes within a trophic framework have been few and limited to very acidic systems (pH = 4.5). Based on their studies in Clearwater lake, Yan and Strus (1980) hypothesized that the efficiency of energy transfer from primary to secondary trophic levels was reduced by acidification. They suggested that herbivory by *Bosmina longirostris* played a minor role in controlling the phytoplankton community and that the latter were constrained by the acid/metal tolerance of individual algal species. Pursuing this hypothesis, Havens and DeCosta (1985a) conclusively demonstrated that herbivores do not control phytoplankton community structure in acidic Cheat Lake, West Virginia, and suggested that the dominance of small herbivores was related to their greater tolerance to low pH rather than to the quality or size range of the grazeable algal species (Havens and DeCosta, 1985b). Thus, in highly acidic systems such as Clearwater and Cheat lakes, zooplankton species composition appears to be controlled by the physiological tolerance of individual species.

Many impacted Québec Shield lakes are presently in the intermediate pH range (5–6), where several questions remain unresolved. With the exception of Siegfried *et al.* (1988), there have been no studies relating acidification and

predation (invertebrate/vertebrate) to zooplankton community structure. Thus, the relative importance of individual species' physiological thresholds and/or predatory interactions in shaping zooplankton community structure, and the importance of size-selective predation (Hall *et al.*, 1976; Zaret, 1980), have not been fully evaluated in these oligotrophic systems. In addition, the lower limit of fish or invertebrate biomass which can modify zooplankton community structure is unknown, such that the contribution of predator-mediated changes to those attributed to direct physiological constraints has not been established. Our objective was to compare the midsummer zooplankton community structure in lakes of varying acidity and known abundances of vertebrate predators in an attempt to quantify some of the mechanisms described above.

### Study area

The Temiskaming region in southwestern Québec is in many ways similar to the Sudbury area in Ontario. Many remote headwater lakes have been impacted by acid and metal contaminants from mining and smelting operations in nearby industrial centres, Rouyn to the north and Sudbury to the southwest, respectively. However, in contrast to the Sudbury region, the surficial geology to the southeast of Rouyn is homogeneous over longer distances (<200 km) and representative of the pre-Cambrian Canadian Shield such that lakes of differing levels of acidity are available for study.

The drainage basin overburden of the lakes toward the southeast range consists of thin and well-drained till, and moraine deposits with occasional rock outcroppings. Coarser sands were sometimes present in overburden to the south (lakes 81, 90 and 99), while lake 15 close to Rouyn was influenced by locally derived fine glacio-lacustrine clay deposits. Unfortunately, except for aluminium, metal concentrations were not available for our study lakes. However, from an extensive 64 lake regional survey (Dupont, 1984; unpublished data) and the geographical position of our lakes, we expect that only lakes 14, 15, 16 and 17, which are within 90 km of the smelter, might be sufficiently metal impacted to significantly affect the planktonic community. Lakes located at greater distances typically had  $<5 \mu\text{g l}^{-1}$  Cu,  $<10 \mu\text{g l}^{-1}$  Zn and Ni and Mn varied between 10 and  $190 \mu\text{g l}^{-1}$ . Sediment cores examined in a subset of our lakes (2, 3, 4, 7, 8, 15 and 16; Carignan, 1989) revealed cumulative Cu and Pb loadings between 500 and  $800 \text{ g m}^{-2}$  for lakes within 90 km (15, 16), and 175 and  $525 \text{ g m}^{-2}$  for lakes within 150 km (2, 3, 4, 7, 8) from Rouyn. More importantly, Carignan and Tessier (1988) have shown that the buffering capacity of these lakes depends on the sediment iron oxyhydroxide reservoir, which in some lakes is diminished or exhausted. Since emissions from Rouyn are to be curtailed within the next 10–15 years, the biological characterization of existing communities is imperative to document the 'reversibility' of acidification in this region in future studies.

### Method

During mid-July 1987, we examined the zooplankton community structure of 22

lakes within the pH range of 4.7–6.3. Lake morphometry and bathymetry, water chemistry (Dupont, 1984; Frenette, 1986b), and fish species composition and biomass (Frenette, 1986a; Tremblay and Richard, 1990) had been studied during the previous year. The lakes were distributed along a southeast axis located from 44 to 186 km from Rouyn. From previous monitoring studies in the area, the lakes were selected on the basis of low colour (to exclude possible metal complexation with DOC) and a large range in both pH and fish biomass per unit effort (FBE) (Figure 1). Fish were captured using five gill nets of 46 m length, each composed of six panels corresponding to 25, 38, 51, 63, 76 and 89 mm stretched mesh. Minnow traps (five) and plexiglass trap nets (five) were used to capture smaller fish. This gear was active overnight, for at least 12 h in each lake. Fish biomass per unit effort is expressed in g per 12 h and is the product of the catch per unit effort and the mean weight for each fish species captured with a given type of gear summed over all gear. Details are given in Frenette (1986a) and Tremblay and Richard (1990). For our 22 lakes, the total effort was ~300 h per lake and FBE varied from 0 to 12 kg.

The lakes, mostly inaccessible by road, were sampled by float-plane. Using morphometric maps, the aircraft was positioned over the deepest area. A temperature profile was determined and to assess the total microbial resource base, an epilimnetic water sample for ATP analysis was obtained with a Van Dorn sampler 1 m below the surface. Samples (250 ml) were immediately filtered onto Nuclepore 0.4  $\mu\text{m}$  filters and plunged into a 3:1 mixture of DMSO–MOPS and placed in a cryogenic cooler containing dry ice. ATP was measured using the luciferase assay and an LKB-1219 luminometer according to Couture *et al.* (1987). Two replicate zooplankton samples were collected with a large (filtration area 1.45 m<sup>2</sup>), 0.5 m diameter 65  $\mu\text{m}$  plankton net. The net was lowered to within 0.5–1 m from the bottom and raised vertically to the surface. Although the net was unmetred, calibrations conducted in other similar oligotrophic lakes revealed that over net trajectories <20 m, the filtering efficiency is >80% (J.C. Auclair, unpublished). The samples were reduced to 100–200 ml and immediately preserved in 4% formalin. In the laboratory, the samples were size fractionated over seven sizes of netting (500, 363, 270, 202, 153, 102 and 63  $\mu\text{m}$ ) following Borgmann *et al.* (1979) and, after enumeration, where abundances permitted, individual organisms or copepodite life stages were grouped for the determination of dry weights for each lake and size class. Identification was carried out to species stage using Edmondson (1959) and Brooks (1959). Diaptomid copepodite stages II/III were separated from stage IV/V (designated as IV+ for the figure legends) based on the extent of development in the fifth leg. To ensure high precision during the enumeration stage, the abundance of each species in each size fraction was determined under a dissecting microscope according to Frontier (1972). A 10 ml subsample was withdrawn and placed into a gridded glass counting dish (Cuve de 'Dulfuss', MENU, S.A., Paris) containing 200 chambers. Each individual of a given species was tallied until 100 were counted. The total in the dish was obtained from the proportion of grids counted. For rarer species, a second 10 ml subsample was examined, so that the contents of 400 chambers were tallied. The

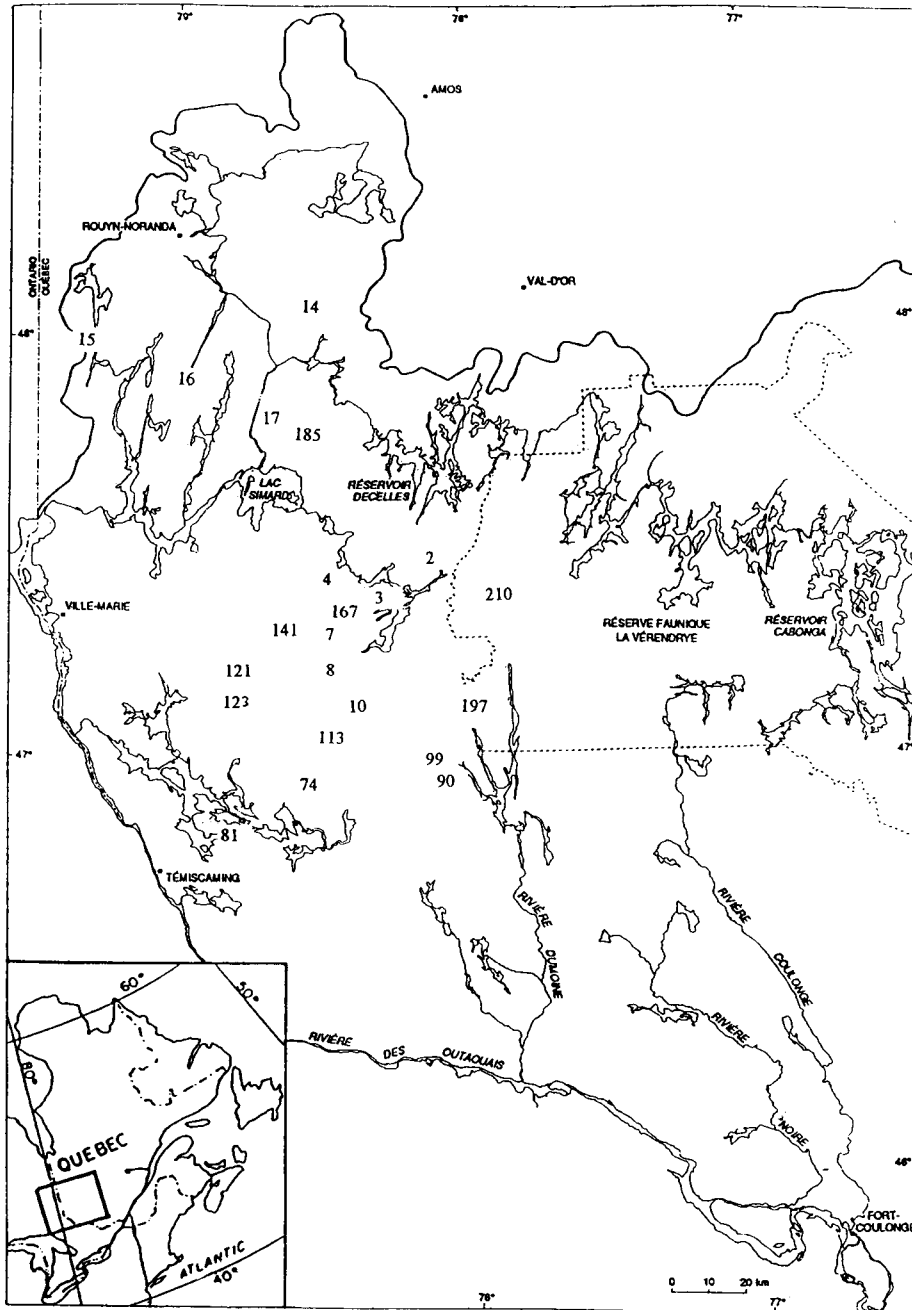


Fig. 1. Lake locations in southwestern Québec, Canada.

total in the original plankton sample was obtained from the proportion of the examined volume, usually 10–20%. The maximum subsampling error for any given size-fraction sample was  $\sim\pm 28\%$  (actually the error is asymmetrical: +31 and –26, cf. Frontier, 1972); however, the error on the total numbers for many species was lower since a given organism was often found in more than one size fraction.

Species weights for a given lake and size class were obtained by depositing 10–50 individuals on a pre-weighed glass fibre filter and drying for 24 h at 60°C. The filters were then weighed on a high-precision ( $10^{-6}$  g) analytical balance. The total biomass for each species in each size fraction was obtained from the product of the weights and the abundance. The total abundance and biomass for each species of life stage was then computed from the sum of the size fractions. For rare species, when it was impossible to pool enough organisms from a given size class in a given lake, a mean weight determined from other lakes was used. Rotifer and naupliar weights were taken from Yan and Strus (1980). Organisms were also classified by size–functional group according to Sprules (1980); group membership is indicated in Table III.

Watershed drainage and lake surface areas were digitized and calculated from topographical maps. Bathymetry was obtained from the Hydrographic Division, Environment Québec. Theoretical lake renewal rates were calculated using 10 year (1979–88) average annual precipitation (903 mm) and evapotranspiration (510 mm) values from nearby Kinojevis River, according to Brunskill and Schindler (1971). These values were compared to a second relative renewal estimate obtained from an empirical relationship derived from the total tributary area/lake volume ( $AV$ ) ratio and annual renewal rates determined for morphometrically similar ELA lakes in 1970 (Newbury and Beaty, 1980; renewal (years) =  $2.8/AV$  ( $m^{-1}$ ) – 0.1,  $r = 0.98$ ). Differences between the two estimates were within 10%, so the former estimates are reported in the results.

From temperature and bathymetric profiles, we calculated the volume weighted mean temperature ( $T_w$ ) and total heat content ( $\Theta_w$ ) for each lake according to Likens (1985). Epilimnetic volumes were computed from the thickness of the mixed layer and expressed as a percentage of lake volume.

To summarize lake ichthyology, we employed FBE as opposed to catch per unit effort because in a study of 74 lakes within this region, Tremblay and Richard (1990) were unable to find significant relationships between catch per unit effort and 18 measured limnological variables. However, FBE was significantly correlated to pH, alkalinity, calcium and mean lake depth. In addition, according to several published studies, biomass stability appears to be a conservative property of ecosystems (Kelso and Bagenal, 1977; Pimm, 1984), biomass distribution appears to be proportional among trophic levels (Gascon and Leggett, 1977) and appears to be independent of the number of fish species (Ryder *et al.*, 1974; Hanson and Leggett, 1985).

Based on the fish species composition (Frenette, 1986a; Tremblay and Richard, 1990) the lakes could be approximately classified into fishless (acidic lakes 14 and 16), non-piscivore- or piscivore-dominated lakes. In the absence of piscivores, lakes were mostly populated by Percidae (perch, *Perca flavescens*,

lakes 3, 4, 7, 15, 17 and 185; or darters, *Etheostoma nigrum*, lake 141), Cyprinidae (*Semotilus corporalis*, lake 123) or Catastomidae (*Catastomus commersoni*, lake 74). Piscivore-dominated lakes included lakes 2, 8, 10, 90, 121 and 167, where pike (*Esox lucius*) dominated in association with walleye (*Stizostedion vitreum*), white sucker (lakes 113 and 197) and/or whitefish (*Coregonus clupeiformis*, lakes 99 and 210). Lake 81 had the greatest number of captured species and was dominated by lake trout (*Salvelinus namaycush*) and white suckers.

## Results and discussion

### *Lake morphometry and chemistry*

Lake locations and variables derived from morphometry and temperature are summarized in Figure 1 and Table I, while lake chemistry (obtained from Dupont, 1984), ATP and fish biomass appear in Table II.

The chemical composition of the lakes was similar with only the bicarbonate system variables (pH, alkalinity, major cations) and SO<sub>4</sub> concentrations differing among lakes. The lattermost were higher in a group of shallow lakes (lakes 14–17) reflecting proximity to greater atmospheric deposition from smelter operations in Rouyn. Since most variables were highly correlated with pH, we assume that pH reflects the major difference among lakes and other aspects of lake chemistry were not analysed further.

Microbial biomass, as revealed by ATP analysis, was within the lower range for oligotrophic Shield lakes (Rudd and Hamilton, 1973). Concentrations were similar among lakes, indicating that by July most grazing had occurred and the lakes were within the 'clear water phase'. In hindsight, a more representative assessment of lake food supply would have been obtained following spring runoff in late May. Also, owing to higher zooplankton abundances observed elsewhere in Québec (J.C.Auclair, unpublished) during the warm summer of 1987 (a 'greenhouse' year), depression of microbial planktonic resources may have been unusually high.

To summarize morphological differences among lakes, lake volume, surface area, renewal rate and maximal depth were used to perform a cluster analysis using their unweighted pair average (UPGMA method) distances (Figure 2). The largest group was made up of eight lakes with surface areas <50 ha and located within 50 km of Rouyn. These lakes all had a pH <5.3, except lake 15 which, as mentioned above, was well buffered given its location within the glacio-lacustrine deposits. Coincidentally, these lakes were also geographically clustered.

A second cluster included five lakes with surface areas between 60 and 80 ha. Lake 123 is unique because of its greater maximal depth (38 m). All other clusters involved pairs of lakes: lakes 185 and 197 were the largest lakes (>100 ha), lakes 74 and 141 had the slowest renewal rates, followed by lakes 8 and 10 and, finally, lakes 113 and 210 formed a distinct cluster with almost identical sizes, maximal depths and renewal rates.

**Table 1.** Lake identification, position and variables derived from morphometry and temperature. Lake study (lake no.) and Environment Québec (MNR no.) numbers. Distance is from Rouyn, Québec. Drainage A(d) and lake A(l) areas, lake volume (vol in m<sup>3</sup>), percentage lake volume in epilimnion %Epi, mean Z(x), maximum Z(max) and thermocline Z(t) depths, ns = non-stratified. Renewal rate, Ren; T<sub>w</sub> and Θ<sub>w</sub>: mean volume weighted temperature and heat content (Likens, 1975)

Lake no.	MNR no.	Longitude (°W)	Latitude (°N)	Altitude (m)	Distance (km)	A(l) (ha)	A(d) (ha)	Vol × 10 <sup>6</sup> (m <sup>3</sup> )	%Epi (m)	Z(x) (m)	Z(max) (m)	Z(t) (m)	Ren years	T <sub>w</sub> (°C)	Θ <sub>w</sub> (cal cm <sup>-3</sup> )
2	77978	78°09	47°27	351	120	21	105	0.86	94	4.1	9.4	6.0	1.8	25.4	10.4
3	79398	78°18	47°23	381	122	29	161	1.80	70	6.2	16.5	6.0	2.5	23.1	14.3
4	79245	78°29	47°22	351	117	35	187	1.35	79	3.9	11.0	3.5	1.6	25.9	10.0
7	79269	78°29	47°17	351	128	32	138	1.61	36	5.0	12.2	2.0	2.5	24.0	11.9
8	78042	78°26	47°08	320	146	51	227	4.04	28	7.9	24.9	3.0	3.8	21.9	17.2
10	78097	78°22	47°05	335	155	35	123	2.25	53	6.4	17.1	4.0	3.8	24.2	15.5
14	18892	78°31	48°03	329	44	29	127	0.55	100	1.9	4.3	ns	0.9	26.0	4.9
15	96791	79°25	47°59	320	44	46	258	1.26	100	2.7	4.4	ns	1.1	28.1	7.5
16	96760	79°00	47°54	335	87	44	163	1.96	81	4.5	10.4	6.0	2.5	25.8	11.6
17	96814	78°41	47°46	305	64	30	124	1.29	100	4.3	12.6	ns	2.2	25.9	11.2
74	7222	78°33	46°55	329	172	84	181	5.30	72	6.3	16.7	5.0	5.4	24.2	14.9
81	7232	78°53	46°50	283	179	67	447	4.65	49	7.0	16.5	3.5	2.4	20.2	14.2
90	7255	78°03	46°53	360	186	75	284	3.93	60	5.2	14.1	4.5	2.9	24.6	12.9
99	7250	78°08	46°59	317	177	66	289	4.02	32	6.1	21.5	3.5	3.0	20.0	12.1
113	10497	78°32	47°13	317	133	60	624	2.45	42	4.1	14.5	2.0	0.9	24.9	10.1
121	10526	78°47	47°11	302	134	72	544	4.91	55	6.8	23.2	4.0	2.1	23.2	15.4
123	10529	78°47	47°06	314	144	78	788	8.57	21	11.0	38.7	3.0	2.6	18.4	17.9
141	10620	78°38	47°17	363	124	82	285	6.55	50	8.0	31.5	5.0	4.7	23.3	17.9
167	10681	78°26	47°19	347	124	61	400	3.74	53	6.2	19.9	3.0	2.1	22.1	13.6
185	10736	78°32	47°45	329	69	138	1872	3.80	80	2.7	14.5	5.0	0.5	27.1	7.6
197	10881	77°53	47°08	314	165	111	639	5.12	66	4.6	18.7	4.0	1.8	25.8	11.9
210	10908	77°54	47°21	329	140	65	700	2.59	74	4.0	13.2	4.0	0.9	26.5	10.5

**Table II.** Chemical composition, ATP, piscivore and total fish biomass/effort data for the Temiskaming lakes. Conductivity:  $\mu\text{S cm}^{-1}$ ; colour: Hazen units; alkalinity:  $\text{Alc mg CaCO}_3 \text{ l}^{-1}$ ; ATP:  $\mu\text{g l}^{-1}$ ; all remaining variables in  $\text{mg l}^{-1}$ .  $\text{Al}_f$ : filterable ( $0.2 \mu\text{m}$ ) aluminium. PBE and FBE: piscivorous and total fish biomass per unit effort (kg per 12 h)

Lake no.	Cond	Colour	DOC	Alc	pH	Ca	Mg	Na	K	Fe	Mn	$\text{NO}_2 + \text{NO}_3$	$\text{NH}_4$	$\text{SO}_4$	$\text{Al}_f$	ATP	PBE	FBE
2	23.5	2	1.4	0.7	5.2	1.6	0.4	0.5	0.3	0.04	0.05	0.04	0.07	8.0	0.07	0.10	2.43	2.43
3	28.5	4	1.0	0.1	4.9	1.6	0.4	0.6	0.4	0.11	0.13	0.03	0.03	8.5	0.03	0.14	0	0.05
4	24.2	17	4.0	0.2	5.0	1.6	0.5	0.6	0.4	0.21	0.07	0.05	0.03	8.0	0.16	0.05	0	0.12
7	21.5	14	3.4	0.2	5.2	1.5	0.4	0.6	0.3	0.21	0.06	0.06	0.05	7.0	0.08	0.13	0	0.41
8	27.5	5	2.8	2.4	6.2	2.6	0.7	0.8	0.6	0.03	0.00	0.03	0.02	9.0	0.02	0.08	4.10	4.10
10	29.2	2	3.0	1.3	6.2	2.6	0.7	0.9	0.6	0.01	0.02	0.04	0.03	9.5	0.03	0.04	2.60	2.62
14	31.1	20	4.0	0.1	4.8	1.2	0.6	0.5	0.4	0.69	na	0.11	0.16	8.5	0.14	0.06	0	0
15	44.8	7	4.0	2.8	5.9	3.6	1.3	1.4	0.5	0.06	0.04	0.06	0.03	15.0	0.07	0.04	0	2.27
16	29.2	6	3.0	0.2	5.2	1.9	0.7	0.7	0.4	0.12	0.12	0.03	0.04	10.0	0.10	0.05	0	0
17	30.3	3	2.4	0.9	5.3	1.8	0.8	1.2	0.4	0.04	0.05	0.06	0.11	11.5	0.10	0.04	0	0.55
74	21.5	4	2.0	0.9	5.3	1.8	0.5	0.6	0.3	0.07	0.06	0.06	0.04	6.0	0.04	0.06	0	0.20
81	44.2	12	4.2	6.4	6.4	4.1	1.1	1.0	1.0	0.13	0.18	0.14	0.01	9.0	0.01	0.03	1.11	3.70
90	25.1	5	2.0	2.5	6.2	2.2	0.6	0.9	0.5	0.05	0.01	0.17	0.04	6.5	0.01	0.09	6.32	7.34
99	26.6	25	5.8	2.1	6.0	2.5	0.7	0.9	0.5	0.20	0.02	0.14	0.02	6.5	0.05	0.05	4.17	6.62
113	32.4	21	5.2	3.4	6.3	3.1	0.8	0.9	0.7	0.16	0.02	0.11	0.06	7.5	0.05	0.04	4.04	6.41
121	21.8	11	3.6	1.7	6.0	1.8	0.6	0.7	0.4	0.14	0.03	0.05	0.01	5.5	0.05	0.08	2.74	3.19
123	26.0	20	4.6	0.8	5.6	2.2	0.6	0.7	0.3	0.17	0.05	0.05	0.02	7.5	0.14	0.05	0	1.12
141	27.5	7	2.4	0.2	4.8	1.8	0.5	0.6	0.4	0.08	0.07	0.10	0.04	6.5	0.07	0.04	0.72	0.73
167	24.3	14	4.2	0.7	5.3	2.0	0.5	0.7	0.3	0.13	0.05	0.05	0.04	7.0	0.12	0.04	0.46	0.50
185	34.0	10	3.4	0.1	4.7	1.4	0.5	0.8	0.2	0.15	0.08	0.15	0.07	8.5	0.28	0.07	0	0.47
197	25.5	13	4.2	2.7	6.2	2.5	0.5	0.9	0.6	0.08	0.02	0.08	0.05	6.0	0.05	0.04	5.26	6.05
210	25.7	19	5.0	2.9	6.1	2.1	0.7	1.0	0.6	0.15	0.02	0.10	0.07	5.0	0.07	0.03	11.96	12.33



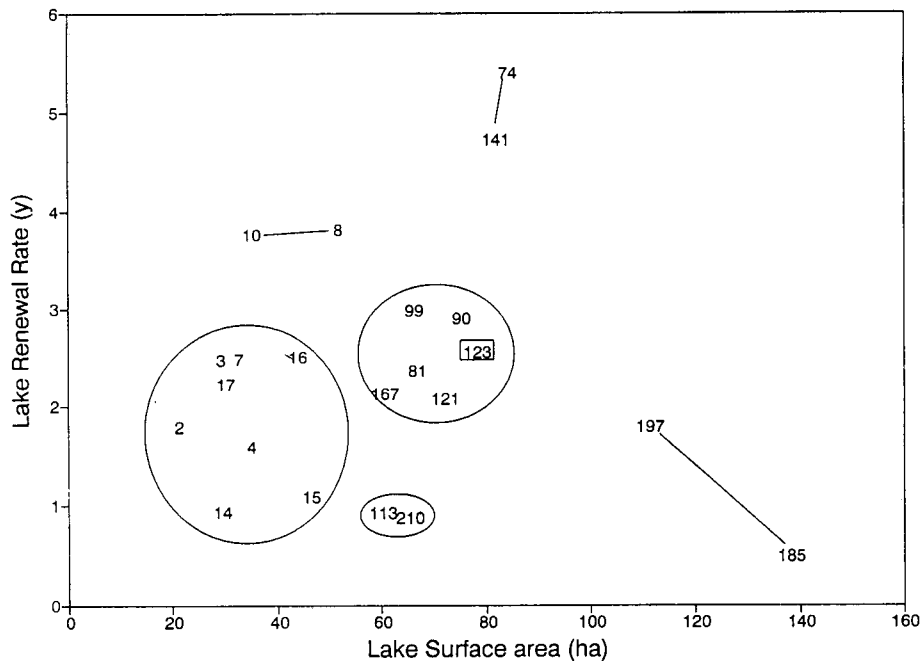


Fig. 2. Summary of the morphometric relationships; lake volume, surface area, renewal rate and maximal depth among the study lakes deduced from cluster analysis.

#### *Zooplankton and fish community structure: overview*

Inspection of the original lake by species/data matrix and scatter diagrams revealed strong discontinuities in species distributions with small groups or unique lakes possessing specific and interpretable biological characteristics (Table III). Asterisks in Table IV refer to 0.05 (\*), 0.01 (\*\*), and 0.001 (\*\*\*) significance levels. These are shown to indicate the approximate strength of association among variables, and are not intended for pair-wise *a posteriori* comparisons, since it is unlikely that their corresponding *z* transforms were sampled from a normally distributed population. Working from our complete matrix, we first sought to determine which variables could most powerfully discriminate piscivorous from non-piscivorous fish communities in our study lakes. The highest significance level in the canonical correlation ( $R = 0.84$ ,  $P < 3 \times 10^{-5}$ ) and optimal lake classification (all lakes correctly classified, except lake 2) was obtained using only pH and *Chaoborus* abundance; addition of other zooplankton species did not improve lake classification. Acidity was an overall determinant in the discriminant function score; all lakes with pH > 5.9 were piscivore dominated, while *Chaoborus* biomass was effective in separating lake 167, but not lake 2, from the other acidic non-piscivore-dominated lakes (Figure 3). There was a close relationship between piscivore biomass/effort and total fish biomass/effort ( $r^2 = 0.92^{***}$ ). That linear combinations of individual

**Table III.** Zooplankton species composition, percent and total biomass (mg m<sup>-3</sup>) in the Temiskaming region, Québec. Lakes are ordered on increasing pH

	SFG	Lake no.						
		185	14	141	3	4	2	7
pH		4.7	4.8	4.8	4.9	5.0	5.2	5.2
Species	SFG							
Rotifers	h1	2	5	<1	9	<1	<1	1
Nauplii	h1	4	16	9	2	2	2	24
Copepoda calanoids								
Copepodites III	h1	<1	13	<1	<1	<1	<1	2
Copepodites IV	h1	43	5	25	38	8	3	8
<i>Diaptomus minutus</i> (Lilljeborg)	h2	15	35	14	15	<1	4	
<i>Diaptomus spatulocrenatus</i> (Pearse)	c4	<1				<1	<1	20
<i>Epischura lacustris</i> (Forbes) cyclopoids	c3							
Copepodites	h1	<1	<1	1	<1	<1	<1	7
<i>Cyclops vernalis</i> (Fischer)	c2							<1
<i>Cyclops scutifer</i> (Sars)	c3	<1						
<i>C. bicuspidatus thomasi</i> (Forbes)	c2							
<i>Mesocyclops edax</i> (Forbes)	c2	5		13		3	<1	4
<i>Orthocyclops modestus</i> (Herrick)	c2			<1	<1	<1		5
Cladocera								
Immature <i>Daphnia</i>	h1	<1	<1	<1		<1	<1	<1
<i>Bosmina longirostris</i> (O.F.Muller)	h1	8	10	35	2	<1	<1	<1
<i>Diaphanosoma brachyurum</i> (Liévin)	h2	<1	11	<1	<1	<1	2	1
<i>Daphnia catawba</i> (Coker)	h3							10
<i>Daphnia dubia</i> (Herrick)	h3							
<i>D. galeata mendotae</i> (Sars-Birge)	h3					<1		
<i>Daphnia longiremis</i> (Sars)	h2	1	<1	<1	1	<1		6
<i>Daphnia pulex</i> (Leydig)	h4							
<i>Daphnia retrocurva</i> (Forbes)	h2							
<i>Holopedium gibberum</i> (Zaddach)	h4	2	4			66	62	2
<i>Leptodora kindtii</i> (Focke)	c4			<1				3
<i>Chaoborus</i> sp.		16	<1	<1	34	17	25	6
Total excluding <i>Chaoborus</i> sp.		26.6	136.8	30.5	11.4	69.8	90.6	18.3
Grand total		31.8	136.9	30.7	17.3	83.9	120.1	19.5
Functional and size classification								
Herbivore 1 (<0.30 mm)		59	50	71	51	11	8	42
Herbivore 2 (0.30–0.49 mm)		17	46	14	17	3	6	7
Herbivore 3 (0.50–0.84 mm)						<1		10
Herbivore 4 (0.85–1.19 mm)		2	4			66	62	2
Carnivore 2 (0.05–0.89 mm)		5		14	<1	3	<1	10
Carnivore 3 (0.90–1.19 mm)		<1						
Carnivore 4 (1.20–1.49 mm)		<1		<1		<1	<1	22

microcrustacean species among the zooplankton assemblage were not as efficient as pH in discriminating among lakes indicates that biological changes in both planktonic and fish communities must have occurred concurrently over time. However, as will be shown later, the abundance of several zooplankton species and life stages appeared to be related to fish biomass.

The major inter-lake differences in zooplankton species composition could be

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16	17	74	167	123	15	99	121	210	8	10	90	197	113	81
5.2	5.3	5.3	5.3	5.6	5.9	6.0	6.0	6.1	6.2	6.2	6.2	6.2	6.3	6.4
<1	2	<1	<1	1	<1	1	3	<1	2	<1	<1	<1	1	<1
27	8	6	2	36	15	6	8	24	17	4	6	15	53	8
<1	<1	<1	<1	2	<1	<1	11	1	<1	<1	1	<1	<1	
<1	36	8	2	12	5	17	7	3	7	4	2	<1	2	23
3	29	13	5	14	36	3	15	18	20	14	9	<1	6	1
	1	2		1	3	<1	<1	<1	<1				<1	<1
<1	<1	<1	<1	3	3	20	32	6	29	3	<1	1	3	2
			<1	<1		<1					<1	<1	1	
			1	9		10	4	13	5	<1	<1	<1	<1	<1
2	<1	18	2	<1	<1	1	2	4	3	<1	15	<1	3	11
<1					<1	2		<1	<1	<1	<1			
<1	<1	2	<1	<1	<1				<1	<1	<1			1
<1	6	<1	<1	1	30		2	<1	4	<1	<1	<1	<1	<1
<1	12	5	<1	2	<1	<1	<1	1	1	<1	2		<1	
								15		15				10
	<1	3	<1	1		4	2	9	1	2	13		1	8
													7	12
				4									<1	
2	5	41	1	9		7	10	<1	11	44	43	<1	18	14
		<1	<1	1	2		<1	3		1	<1		<1	
66	<1		85	<1		27	<1	1	<1	<1	2	81		8
31.4	227.8	41.6	18.5	19.3	46.2	12.1	6.2	34.8	24.6	61.5	44.2	9.7	23.8	7.9
91.3	227.8	41.6	122.3	19.4	46.2	16.6	6.2	35.3	24.7	61.6	45.2	52.0	23.8	8.6
28	52	18	5	55	56	45	62	35	59	13	10	18	60	36
3	41	21	5	21	37	6	18	28	22	16	24	<1	9	13
								15		15				17
2	5	41	1	9		7	10	<1	11	44	43	<1	25	14
2	<1	18	3	10	1	13	5	17	8	2	16	<1	5	11
			<1	<1		1	3	<1	<1	10	5		<1	<1
	1	2	<1	3	2		<1	3	<1	1	<1		<1	<1

attributed to the distance from Rouyn, and the presumed source of atmospherically derived acidity. For the total lake set, pH, piscivore biomass/effort and FBE were positively correlated to distance from Rouyn, while the correlations between distance and the morphometric variables (flushing rate, epilimnetic volume,  $T_w$  and  $\Theta_w$ ) reflected the proximity to Rouyn of small, shallow, non-stratified lakes 14–17 (Table IVa). All organisms, except the

**Table IV.** Correlation coefficients between selected lake parameters and zooplanktonic species. Upper right matrix (Table IVa) is for total lake set ( $n = 22$ ). Lower left matrix (Table IVb) is for lakes with  $\text{pH} < 5.3$ , ( $n = 12$ ).

	Distance	Flush rate	Epi. vol	$T_w$	$\Theta_w$	pH	Rotifers
Distance							
Lake flushing rate	0.710**	0.519*	-0.673***	-0.592**	0.628**	0.579*	-0.600**
Epilimnetic volume	-0.631*	-0.373	-0.400	-0.457	0.764***	0.028	0.255
$T_w$	-0.611*	-0.379	0.829***	0.803***	-0.695***	-0.418	0.505*
$\Theta_w$	0.761**	0.766**	-0.724**	-0.788**	-0.719***	-0.245	0.259
pH	0.487	0.278	-0.394	-0.585*	0.472	0.241	-0.472*
Rotifers	-0.742**	-0.362	0.563	0.332	-0.566	-0.257	-0.372
Nauplii	-0.647*	-0.213	0.405	0.274	-0.382	0.091	0.651*
Immature copepods III	-0.546	-0.346	0.386	0.228	-0.601*	-0.338	0.804**
Immature copepods IV	-0.460	-0.117	0.426	0.285	-0.140	0.090	0.518
<i>Diatomus minutus</i>	-0.668*	-0.243	0.57	0.325	-0.421	-0.029	0.902***
<i>Bosmina longirostris</i>	-0.634*	-0.061	0.425	0.289	-0.263	-0.326	0.808**
<i>Diaphanosoma brachyurum</i>	-0.610*	-0.209	0.561	0.329	-0.379	0.046	0.841***
Fish biomass/12 h	0.212	-0.385	-0.043	-0.788**	0.155	0.304	-0.265
Piscivore biomass/12 h	0.145	-0.004	0.192	0.062	0.011	0.042	-0.228
Planktivore biomass/12 h	0.121	-0.069	-0.489	-0.498	0.287	0.518	-0.053

Acidity/predation and zooplankton community structure

Table IV. Continued

	Nauplii	Cop. III	Cop. IV+	<i>D. min.</i>	<i>B. long.</i>	<i>D. brach.</i>	Tot. Fish	Piscivores	Planktivores
	-0.555**	-0.436*	-0.413	-0.615**	-0.730***	-0.503*	0.485*	0.463*	0.204
	-0.300	-0.269	-0.055	-0.182	-0.135	-0.136	-0.196	-0.144	-0.227
	0.400	0.360	0.395	0.566**	0.551**	0.502*	-0.223	-0.167	-0.248
	0.369	0.187	0.202	0.328	0.391	0.249	0.008	0.08	-0.241
	-0.437*	-0.504*	-0.132	-0.395	-0.376	-0.323	-0.025	0.014	-0.138
	-0.146	-0.297	-0.252	-0.258	-0.341	-0.265	0.740***	0.627**	0.574**
	0.624**	0.809***	0.563	0.894**	0.693***	0.855***	-0.282	-0.245	-0.197
	0.509	0.487*	0.341	0.596**	0.438*	0.565**	-0.101	-0.084	-0.083
	0.335	-0.064	-0.002	0.536*	0.468*	0.446*	-0.180	-0.14	-0.181
	0.625*	0.523	0.807**	0.804***	0.569**	0.879***	-0.246	-0.238	-0.092
	0.491	0.534	0.653*	0.853***	0.798***	0.968***	-0.243	-0.223	-0.131
	0.590*	0.414	0.868***	0.988***	0.811**	0.687***	-0.311	-0.336	0.002
	-0.303	-0.650	-0.018	-0.127	-0.099	-0.087	-0.243	-0.221	-0.14
	-0.278	-0.086	-0.146	-0.161	-0.067	-0.148	0.881***	0.961***	0.394
	-0.027	-0.228	0.27	0.084	-0.058	0.134	0.158	-0.327	0.126

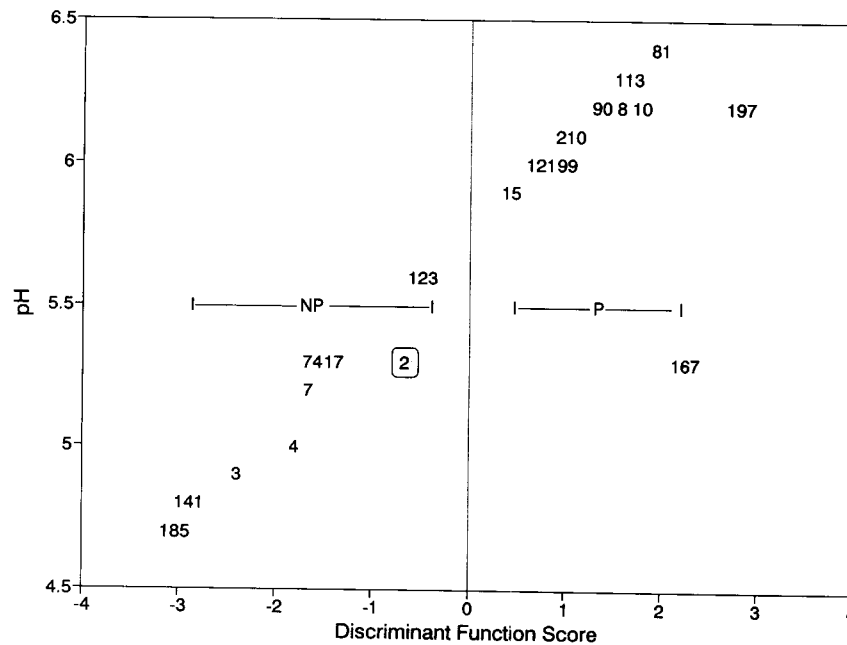


Fig. 3. Relationship between discriminant function score and pH. P and NP are piscivore and non-piscivore group centroids and associated 99% confidence intervals. Piscivore-dominated lake 2 (enclosed) was misclassified due to its low *Chaoborus* abundance.

copepodite IV+ group, comprising the herbivore 1 (h1: rotifers, nauplii, copepodite III, *B.longirostris*) and most herbivore 2 (h2: adult *Diaptomus minutus*, *Diaphanosoma brachyurum*) size-functional groups were highly negatively correlated to the distance from Rouyn (Table IVa). The positive correlation among these species and epilimnetic volume suggests that this assemblage was characteristic of shallow, weakly or non-stratified lakes (lakes 14, 15, 16, 17). The acid lake set (Table IVb) revealed even higher correlations among the herbivore 1 (h1) and 2 (h2) species groups driven by their high biomasses encountered in lakes 14, 16 and 17.

Since most lakes with pH < 5.6 had well-defined zooplankton species assemblages, these will now be examined in greater detail.

#### Lakes with a pH < 5.6

With the exception of lake 15, lakes with pH < 5.6 were either fishless (lakes 14 and 16) or had < 2.4 kg per 12 h (lake 2) of fish biomass. The communities were dominated by small herbivores and relatively high biomasses of *Chaoborus*.

Among the lakes within 50 km, two small non-stratified lakes (fishless lake 14 and lake 17) had 2-3 times the average zooplankton biomass of the acidic lake group (Table III and Figure 9). The zooplankton of fishless lake 16 and the very large and rapidly renewed lake 185 (FBE < 500) was dominated by *Chaoborus* sp. larvae and, consequently, had impoverished microcrustacean communities

comprised mostly of nauplii, copepodites and adults of *D.minutus*. Nearby, *Chaoborus* biomass was very low in the more buffered cyprinid-dominated lake 15 which had a similar h1- and h2-dominated zooplankton community (Table III). Thus, in addition to small lake size, intense planktivory may be responsible for the reduced abundance of larger micro-crustaceans in this lake.

Proceeding southward, three small lakes (2, 3 and 4) with reduced fish biomass (FBE < 2.5 kg per 12 h), within 120 km from Rouyn, also had very large abundances (17–34%) of *Chaoborus*. *Holopedium gibberum*, a species known to be resistant to predation by *Chaoborus* (Tessier, 1986), dominated the plankton of lakes 2 (*Chaoborus trivittatus*) and 4 (*Chaoborus flavicans*), while the most acidic lake 3 (*Chaoborus crystallinus*) was dominated by rotifers, and immature and adult calanoid copepods (Table III).

Communities in the two lakes having the longest renewal rates (lake 141, 4.7 years, pH = 4.8; lake 74, 5.4 years, pH = 5.3) had relatively high abundances of the large predator cyclopoid *Mesocyclops edax* (13% versus 18%) and the presence of the large predator cladoceran *Leptodora kindtii* (Table III). Large lake size, greater depth or low renewal rate may be important in the distribution of these two species. The lower pH in lake 141 was associated with high abundance of the acid-tolerant *B.longirostris* (35% versus 0.7%) and the diaptomid communities (39% versus 24%). Lake 123, a deep lake with an extensive hypolimnion (80% of lake volume), reflected a greater percentile abundance of hypolimnetic-dwelling organisms: nauplii (36%) and four species of cyclopoid copepods were encountered (Table III). Lake 167 had the greatest abundance of *Chaoborus* larvae, representing 85% of the zooplankton biomass and, consequently, as in the lakes discussed previously, the remaining crustacean biomass was considerably reduced. In contrast, *Chaoborus* was less abundant in lake 7 and the community structure was more diversified. Large inter-lake differences in *Chaoborus* biomass and larval instars were observed. *Chaoborus* biomass varied from 0 to 104 mg m<sup>-3</sup> in our lake survey. The presence of >5 mg m<sup>-3</sup> of advanced instars (3rd and 4th) was associated with greatly impoverished microcrustacean communities in lakes 3, 16, 99, 167, 185 and 197, and only the predation resistance of *H.gibberum* in lakes 2 and 4 'compensated' for a reduction in these lakes (Table III and Figure 9).

#### Lakes with pH > 5.9

Lakes with pH > 5.9, and located between 133 and 186 km from Rouyn, had more diverse zooplankton assemblages. Even in this small data set ( $n = 10$ ), rotifers and adult calanoid copepodites comprising the h1 functional group were significantly negatively correlated with lake surface area, and when *Chaoborus*-dominated lakes (99 and 197) were removed, the correlations were much higher (rotifers: -0.80; copepodites IV+: -0.81). These observations support the suggestion made above that small kettle-type lakes limit available niches and favours a high abundance of this h1 species assemblage. Similarly, on the basis of negative correlations between lake depth and phosphorus concentrations, as well as zooplankton biomass, Siegfried and Sutherland (1989) concluded that

shallow Adirondack lakes were more productive and could support greater zooplankton standing crop than deep lakes. Deep lakes ( $Z(\max) > 20$  m), within a narrow pH range of 6–6.2 (lakes 8, 99 and 121), and where *Chaoborus* biomass was  $< 5 \text{ mg m}^{-3}$ , had cyclopoid biomasses comprising  $> 33\%$  of the total. Reflecting this distribution, *M.edax* was positively correlated with lake flushing time ( $0.520, P < 0.05$ ).

Lake 113 was enigmatic, *Daphnia pulex* (7%) was observed, but  $> 53\%$  of the biomass consisted of nauplii (Table III). Intense predation from a recent emergence of *Chaoborus* larvae may have simplified this community.

#### Specific species distributions

In all our study lakes, high *H.gibberum* biomass appeared to be confined within a narrow range of mean-volume-weighted temperature ( $24\text{--}26^\circ\text{C}$ ; cf. Figure 4). This observation is strengthened by the high correlation between the percentage mass of *H.gibberum* and the percentage epilimnetic volume determined in a subset of 14 lakes ( $H.gibberum = 1.0804 \times \% \text{ epilimnetic volume} - 30.052, r = 0.83^{***}$ ), as well as the significant negative correlations with lake size ( $-0.45^*$ ) and lake depth ( $-0.41^*$ ). Most lakes which fell outside this relationship were extremely acidic (pH  $< 5.0$ ; 3, 14, 141, 185) or of very large surface area ( $A(l) > 100$  ha; lakes 197 and 210). In a biannual (1967–68) study of lac Bédard,

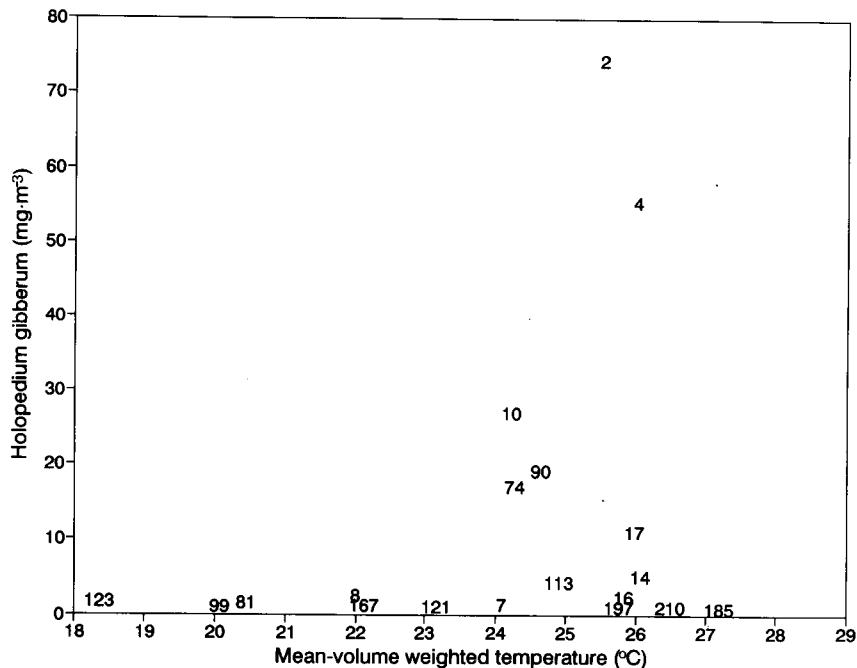


Fig. 4. Abundance of *H.gibberum* in lakes of differing mean volume-weighted temperatures ( $T_w, ^\circ\text{C}$ ).



Québec, Bernard and Lagueux, (1975) found that *H.gibberum* was much more abundant in 1968, when rapid warming of the lake occurred (Bernard and Lagueux, 1970). Thus, it appears that *H.gibberum* biomass develops in small rapidly heated lakes. The total biomass of *Daphnia* species was very low in lakes within 120 km of Rouyn (Figure 5) and was positively correlated with pH (0.454\*), fish biomass (0.523\*), and the abundance of *L.kindtii* (0.621\*\*) and *Epischura lacustris* (0.76\*\*\*). This assemblage of species was representative of most of our study lakes with a pH >5.9.

*Cyclops bicuspidatus thomasi* was mostly confined to the non-acid lakes, being encountered in only two acid lakes (123, 167), one of which was the deepest lake studied (123). Pinel-Alloul *et al.* (1989) also found that *Diacyclops bicuspidatus thomasi* was positively correlated to an alkalinity-hardness factor, and Havens and Heath (1989) showed that cyclopoid copepods (most of which were *C.bicuspidatus thomasi*) were very sensitive to acid and aluminium additions to mesocosms in East Twin Lake, Ohio. Interestingly, the biomass of *C.bicuspidatus thomasi* and *Leptodora* were significantly correlated (0.51\*), suggesting perhaps that *Leptodora* 'facilitates' (*sensu* Morin, 1987) *C.bicuspidatus thomasi*, perhaps by preying on larger copepods and cladocerans. In addition, this cyclopoid was highly correlated to both FBE (0.63\*\*) and piscivorous biomass per unit effort (PBE) (0.67\*\*\*); other individual zooplankton species did not reveal such a close association with fish biomass.

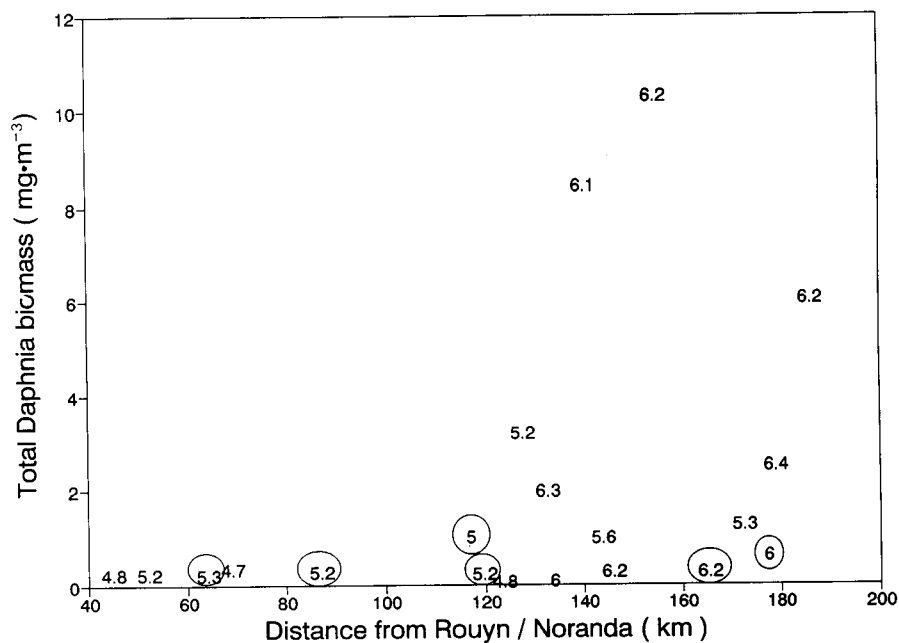


Fig. 5. Relationship between total biomass of *Daphnia* species and distance from Rouyn/Noranda. In circled lakes, *Chaoborus* biomass exceeded 16%. *Chaoborus*-dominated lakes 3 and 167, at 120 km from Rouyn, had negligible *Daphnia* biomass and were omitted for clarity.

The other dominant cyclopoid, *M.edax*, occurred over a larger pH and lake size range, however, it was dominant (11–18%) only in large lakes (>60 ha) with reduced *Chaoborus* biomass (lakes 74, 81, 90, 141). Siegfried *et al.* (1988) also found that *M.edax* dominated invertebrate predator standing crop in Adirondack lakes with planktivorous fish. Conversely, low biomasses (<5%) of *M.edax* were observed in the smaller lakes (lakes 2, 4, 7, 8, 10, 15, 16 and 17) and those having depressed total microcrustacean biomasses (lakes 99, 113, 121, 167 and 197).

The large crustacean predators *E.lacustris* and *L.kindtii* coexisted only in lakes with pH >5.9 (lakes 10, 15, 90, 113, 121 and 210). The pH dependence of *E.lacustris* distribution (Table III) is also well documented (Malley *et al.*, 1982; Confer *et al.*, 1983). *Leptodora kindtii* was absent in the low-pH lakes (lakes 2, 3, 4, 14, 16, 17 and 185) and was either reduced (121, 113, 90) or absent (8, 81, 99, 197) from lakes (except lake 210, see below) where the FBE exceeded 3 kg (box in the lower right corner of Figure 6; piscivore biomass >60% except in lake 81), presumably through intense fish predation. In the eight remaining lakes, within a narrow FBE range (200–2621), the biomass distribution of *L.kindtii* was enigmatic, but possibly related to pH (Figure 6). Lake 210 had the highest fish and piscivore biomass encountered in our study. Planktivory appeared to be severely curtailed, as this lake also had the highest proportion of large-sized zooplankters (*M.edax*, 4%; *Daphnia galeata mendotae*, 15%; *Daphnia longiremis*, 9%; *L.kindtii*, 3%). When all lakes were considered, both

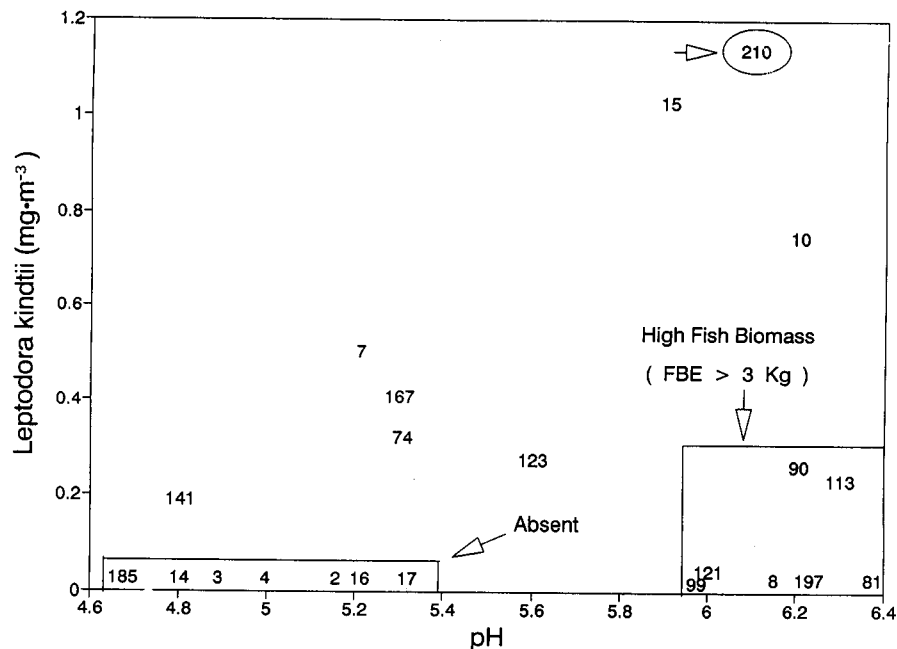


Fig. 6. Relationship between the biomass of *L.kindtii* and pH in lakes of differing fish biomass/unit effort.

FBE and PBE were positively correlated to distance from Rouyn (0.48\*, 0.46\*), pH (0.74\*\*\*, 0.63\*\*), the biomass of *C.bicuspidatus thomasi* (0.63\*\*, 0.67\*\*\*), *D.longiremis* (0.56\*\*, 0.58\*\*) and combined *Daphnia* sp. (0.52\*\*, 0.57\*\*).

#### *Calanoid copepod life stage, pH and FBE*

Lakes with the highest heat content (lakes 14, 16 and 17) also had the greatest biomass of copepod adults and nauplii (Tables I and III). Acid lakes 3, 4, 141 and 185 (pH < 5.0) all had higher abundances of the copepodite IV stage (Figure 7). This may reflect a slower development rate either due to decreased food availability and/or perhaps a physiological constraint related to the cost of ionic regulation at low pH.

The relationship between the biomass ratio of adult *D.minutus* to the copepodite IV stage and FBE was highly significant for all but six lakes (Figure 8;  $FBE = 1570.6 \times D.minutus/copepodite\ IV - 479.35$ ,  $r = 0.91$ ,  $n = 16$ ). The excluded lakes were either non-stratified (lakes 14–16) or *Chaoborus* dominated (lakes 81, 99, 197). This relationship probably reflects the combination of low predation pressure exerted on *D.minutus* and, perhaps, accelerated development times in the more productive lakes. Indeed, for the lakes with pH > 5.9, the significant correlations between adult *D.minutus* and *E.lacustris* (0.70\*), *L.kindtii* (0.77\*) and total biomass of *Daphnia* (0.82\*\*) suggest, perhaps, that the biomass of all these species was enhanced by greater food availability.

#### *Species weights and biomass distribution among size-functional groups*

As shown previously by Borgmann *et al.* (1979), we found Nitex fractionation to be unsatisfactory for separating cladocera by size; most were retained on the 500  $\mu\text{m}$  mesh. At high zooplankton densities, and particularly in the presence of the gelatinous *H.gibberum*, the passage of smaller organisms was sometimes occluded in the first two fractions. Thus, with the exception of the 270  $\mu\text{m}$  *D.minutus* fraction where the weight was inversely correlated with pH ( $r = -0.79$ ,  $P < 0.0001$ ,  $n = 18$ ), we did not find any significant trends between species weights and pH in the study lakes. However, many acid-tolerant species in a given size fraction had greater weights relative to the average weight in the two largest acid lakes: 141 [500  $\mu\text{m}$  *M.edax* (23.5 versus 5.5  $\mu\text{g}$ ), *B.longirostris* (500  $\mu\text{m}$ : 4.2 versus 0.94  $\mu\text{g}$ ) and *D.minutus* (500  $\mu\text{m}$ : 6.15 versus 2.40  $\mu\text{g}$ )] and lake 185 [500  $\mu\text{m}$ : *M.edax* (10.8 versus 5.5  $\mu\text{g}$ ) and *B.longirostris* (500  $\mu\text{m}$ : 1.72 versus 0.94  $\mu\text{g}$ )]. These observations are consistent with the idea that these species are all acid tolerant; their increased weight may be due to greater availability of resources as the more acid-sensitive species are eliminated from these large acid lakes.

#### *Distribution of the biomass among the size-functional groups*

The distribution of zooplankton biomass among six size-functional (no c1 organisms were found and c3 + c4 fractions have been combined; Figure 9) groups revealed two major patterns. In most lakes, the biomass was concen-

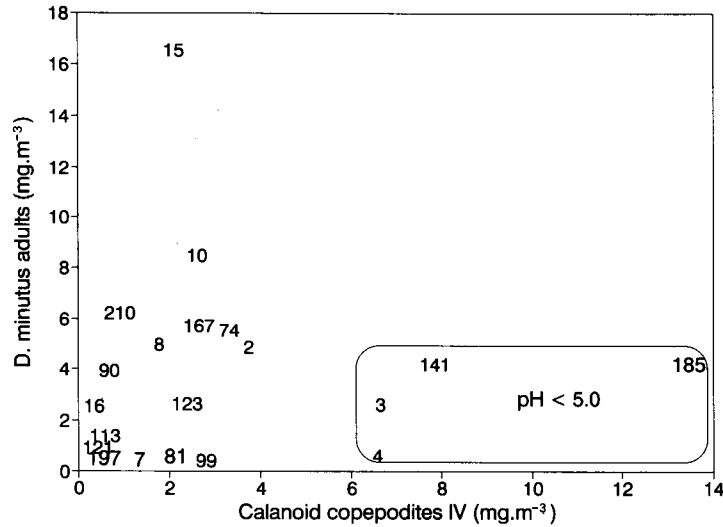


Fig. 7. Relationship between the biomass of adult *D.minutus* and the calanoid copepodite stage IV.

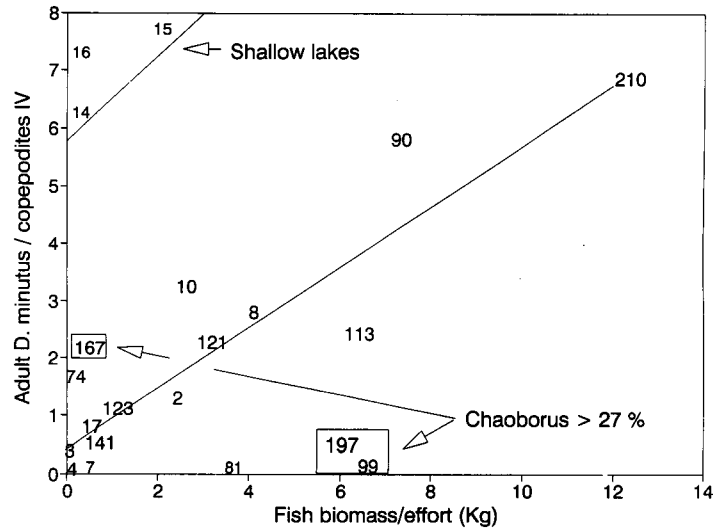


Fig. 8. The ratio of adult *D.minutus*/copepodite IV to fish biomass/effort. Lakes enclosed in boxes had *Chaoborus* biomass >16%. Lakes in the upper left quadrant were shallow and non-stratified.

trated in the h1 and h2 functional groups (*H.gibberum* in the h4 group dominated lakes 2 and 4). This was particularly important in lakes within 120 km of Rouyn (2, 3, 4, 14, 15, 16, 17, 141 and 185; cf. Figure 9) and/or lakes with a pH <5.0. Morphometrically identical lakes 14 and 15, which were separated by a 12.6-fold difference in [H<sup>+</sup>], had similar small herbivore-dominated com-

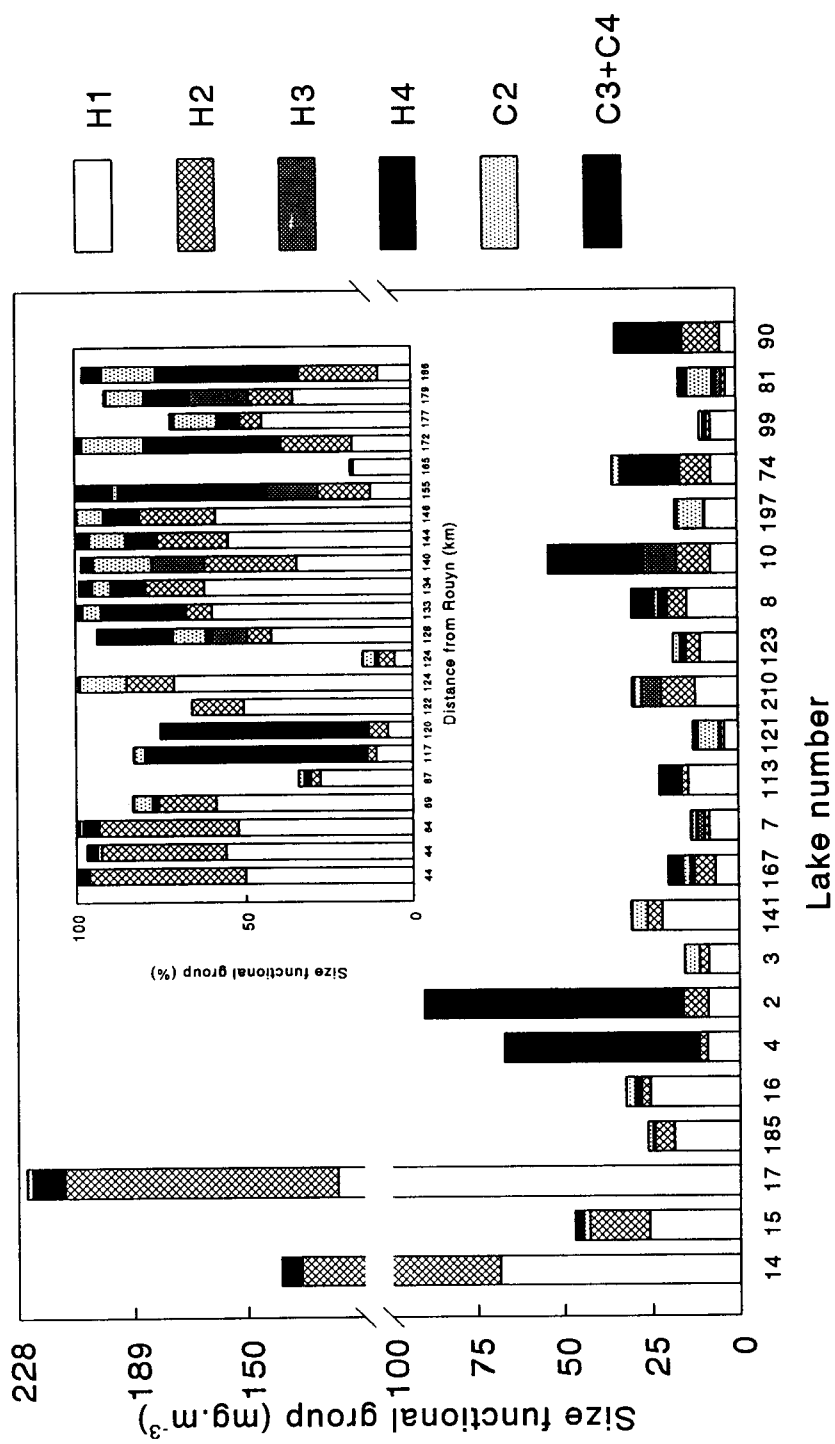


Fig. 9. Size-functional classification of zooplanktonic organisms (*Chaoborus* excluded) among the study lakes, ordered on distance from Rouyn.

munities, strongly suggesting that non-stratification/higher heat budgets or cyprinid planktivory in lake 15 conditioned these lake communities. Lakes 10, 74, 81 and 90 had a more equal representation of the six functional groups. These lakes had low numbers of *Chaoborus* and large differences in fish biomass (Figure 9). Lakes 74 and 90 had 13 and 31 times more fish biomass than lake 10, yet these differences could not be discerned from the size-functional feeding spectrum. Common factors associated with these four lakes were their relatively long renewal times and high epilimnetic to total lake volume ratios. Lakes where the relative biomass of *Chaoborus* exceeded 27% (99, 167, 197) had a pronounced reduction of larger prey size classes. In lake 197, most of the biomass was concentrated in the h1 class.

The study lakes revealed strong discontinuities with respect to morphometry/stratification, pH and/or distance from Rouyn and *Chaoborus* abundance. Although the impact of *Chaoborus* predation on zooplankton has been studied in fishless lakes (Pope *et al.*, 1973; Von Ende, 1979; Yan *et al.*, 1982) and enclosures (Neill and Peacock, 1980), large reductions in zooplankton species, under natural conditions, as seen in many of our lakes, are less well documented. *Chaoborus* success in our low-pH lakes (<5.6) is probably due to reduced fish predation. However, a reduction in the zooplankton size spectrum was even observed in the large, less acidic *Chaoborus*-dominated lakes with relatively higher fish biomasses (lakes 99 and 197); thus, large depressions of crustacean planktonic biomass during *Chaoborus* emergence may be more general than previously thought.

The predominance and acid tolerance among the small herbivorous zooplankters *B.longirostris*, *D.minutus* and *D.brachyurum* in acidic metal-contaminated lakes is now well established (Sprules, 1975a,b; Roff and Kwiatkowski, 1977; Yan and Strus, 1980). In the case of *B.longirostris*, it appears that this is due to greater tolerance to low pH (Havens and Heath, 1989), rather than to changes in phytoplankton species composition or size.

With respect to zooplankton species distribution, pH and morphometry, our results are similar to those of Sprules (1975a) who studied the distribution and species associations in 47 acidified lakes of the La Cloche Mountains. The major determinant of the species assemblages was pH, with lake area and depth playing a minor role. *Mesocyclops edax*, *D.minutus*, *H.gibberum*, *Bosmina*, *C.bicuspidatus thomasi* and *Diaphanosoma leuchtenbergianum* occurred throughout the pH range (3.8–7.0), whereas *E.lacustris*, *L.kindtii*, *Tropocyclops prasinus mexicanus*, *Diaptomus oregonensis* and *D.galeata mendotae* were never or rarely found below a pH of 5.0. A third group of species, including *Polyphemus pediculus*, *Daphnia catawba* and *D.pulicaria*, were primarily found in lakes with pH <6.

The simplified communities with very high diaptomid biomass in the small weakly stratified lakes (14, 15, 16, 17) was not only due to their greater pH tolerance, but may also be the result of the higher heat budgets or restricted available niches in these systems. In a comparative study of two ELA lakes, Schindler and Noven (1971) attributed the higher observed biomass of *D.minutus* in lake 132 to the warmer waters relative to lake 122.

The widespread distribution and abundance of *D.minutus*, the observation that it does not respond to variations in fish predatory pressure and that it is not replaced by a larger copepod in lakes where fish predation is low, as seen in European lakes (Eriksson *et al.*, 1980), led Pope *et al.* (1989) to conclude that this calanoid was not an important component of fish nutrition. This view is supported by our own results; for our study lakes with a pH > 5.6, adult *D.minutus* were well correlated to the biomass of other large species, *L.kindtii* (0.77\*\*), *E.lacustris* (0.70\*) and total mass of *Daphnia* (0.82\*\*), indicating that size-selective fish predation may not be as significant in these oligotrophic lakes.

The distribution of *H.gibberum* in lakes within 120 km of Rouyn merits further investigation. Lakes 2, 3 and 4 were morphometrically comparable and had similar levels of *Chaoborus* abundance; however, lake 3, with a pH of 4.9, lacked *H.gibberum*. Since losses to predation by *Chaoborus* are known to be minimal for *H.gibberum* (Tessier, 1986), competitive release from other more acid-vulnerable cladocera could explain its success in lakes 2 and 4. Sensitivity to trace metals may have limited the abundance of *H.gibberum* in lakes closer (14–17, 185) to Rouyn. Lawrence and Holoka (1987) determined that *H.gibberum* was more sensitive to cadmium additions than *B.longirostris* in ELA lake 223 enclosures. Cumulative lake sediment Cu and Pb concentrations were 50% and 23% higher, respectively, in lake 16 compared to lake 4 (Carignan, 1989). Assuming conservatively that 75% of the atmospherically derived Cu and Pb is retained by the lake sediment (cf. Dillon *et al.*, 1988), this implies an ~2-fold difference in trace metal loading in the two lakes; thus, sensitivity to trace metals could have limited the biomass of *H.gibberum* in lake 16. Analogously, both *B.longirostris* and *D.leuchtenbergianum* were dominant in the metal-contaminated lakes near Sudbury, while *H.gibberum* only dominated the more remote acidic La Cloche Mountain lakes (Yan and Strus, 1980), suggesting that its success may have been limited by trace metal contaminants.

*Bosmina longirostris*, an indicator of maximal predation according to Zaret (1980), was found not only in lakes where fish biomass was high, but coexisting with other large cladocera, possibly due to differential resource partitioning (Demott and Kerfoot, 1982).

In our non-acid lakes, there was evidence for a trophic cascading (Carpenter *et al.*, 1985) as piscivore-dominated lakes with low *Chaoborus* biomass had abundant large *Daphnia* and/or *H.gibberum* (lakes 10, 81, 90, 99, 113 and 210). Similarly, Pope *et al.* (1989) found large *D.pulex* and *D.catawba* across a range of non-acid lakes. These included fishless lakes, those with inefficient planktivorous predators (lake trout and suckers) as well as cyprinid-dominated communities. They also report that *H.gibberum* was often abundant in the planktivorous perch or cyprinid-dominated lakes, a result confirmed in our study (0.582\*). Large daphnids were also abundant in brook trout- or perch-dominated Adirondack lakes, whereas large crustaceans were uncommon in golden shiner-dominated lakes (Siegfried *et al.*, 1988).

In contrast, the distribution of *L.kindtii* was related to the level of total and piscivore fish biomass; had a coarser mesh net been employed to minimize avoidance, clearer relationships would no doubt have emerged from our study.

However, the distribution of *L.kindtii* did not affect zooplankton size distribution. An analysis of lakes 8, 10 and 74–99 represents a 30 times difference in fish biomass, yet reveals no consistent pattern in size distribution (Figure 9).

A 'broad' size structure across the functional classes is apparent only in lakes that have relatively low flushing rates (lakes 8, 10, 74, 81 and 90). Thus, the oligotrophic nature of our lakes may constrain the fish biomass, reducing the impact of predation on zooplankton community structure.

In summary, four conclusions may be drawn from this study. (i) As lakes acidified, changes in the microcrustacean zooplankton community probably occurred concurrently with modifications in the fish community; no linear combination of zooplankton species was more effective than pH and *Chaoborus* for discriminating among piscivorous and non-piscivorous lake types. (ii) Dominance by organisms comprising the h1 and h2 size–functional group characterizes small kettle-type, weakly or non-stratified lakes and these communities appear to be independent of strong predatory interactions. (iii) The abundance ranges of several species, such as *H.gibberum*, *D.longiremis*, *M.edax*, *C.bicuspidatus thomasi*, *E.lacustris*, *L.kindtii* and *D.minutus*, could be individually semiquantitatively related to specific lake characteristics such as lake depth or size, pH, or mean volume-weighted temperatures. (iv) Physiological intolerance to increasing acidity seemed to control the distribution of *Daphnia*. Large cladocerans (i.e. *L.kindtii*) appear to be related to the level of fish biomass, and future work involving more accurate quantitation may reveal more subtle differences related to differences in fish community structure.

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