CRUSTACEAN PLANKTON IN NORTHEASTERN ONTARIO LAKES SUBJECTED TO ACIDIC DEPOSITION

W. KELLER

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

and

J. ROGER PITBLADO

Geography Department, Laurentian University, Sudbury, Ontario, P3E 2C6 Canada

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Abstract. During the summer of 1981, crustacean plankton was sampled in 249 northeastern Ontario lakes, including a large proportion of acidic lakes. Species cluster analysis showed that a major species group containing *B. longirostris*, *D. minutus*, *H. gibberum*, and *M. edax* was common to most lakes. Two species subgroups most associated with more productive waters (*D. retrocurva*, *D. oregonensis*, *T. p. mexicanus*, and *Diaphanosoma* sp.) and less productive waters (*D. longiremis*, *C. scutifer*, *D. g. mendotae*, *C. b. thomasi*, *E. longispina*, and *E. lacustris*) in the study area were identified. Acidic lakes were characterized by reduced numbers of species related to declines in the importance of cyclopoids, Daphnidae, *L. kindtii* and *E. lacustris* and high relative abundance of *D. minutus*. Stepwise multiple linear regression of physico-chemical lake characteristics against percent composition of individual species failed to explain much of the variation in species proportions. However, variables related to lake thermal structure were most frequently the primary correlates with species proportions in near-neutral lakes while in acidic lakes the best statistical predictors of species percent composition were most often variables directly related to lake acidity.

1. Introduction

Although on a broad geographical scale glacial history may influence lentic zooplankton communities (Carter *et al.*, 1980; Roff *et al.*, 1981), regional studies in Ontario (Carter, 1971; Patalas, 1971; Sprules, 1975, 1977) have demonstrated general relationships between lake chemistry and/or morphometry and crustacean species assemblages.

H^+ has long been recognized as a factor influencing the structure and diversity of crustacean plankton communities (Lowndes, 1952). Restricted crustacean faunas have been found in naturally acidic freshwater bodies (Fryer, 1980) as well as in manmade impoundments acidified by acid inputs from coal mining activity (Janicki and DeCosta, 1979). Reductions in zooplankton community diversity in lakes acidified due to acidic precipitation have been identified in Norway (Leivestad *et al.*, 1976), Sweden (Almer *et al.*, 1974), the USA (Confer *et al.*, 1983) and Ontario (Sprules, 1975; Roff and Kwiatkowski, 1977).

For decades, aquatic environments in the Sudbury, Ontario area have been subjected to atmospheric inputs of contaminants associated with large-scale, local smelting activity. Investigations in the greater Sudbury area (Beamish and Harvey, 1972; Conroy *et al.*, 1978) have documented a large zone of acidified lakes extending northeast-southwest of Sudbury. Many Sudbury area lakes also exhibit elevations in trace metal concentra-

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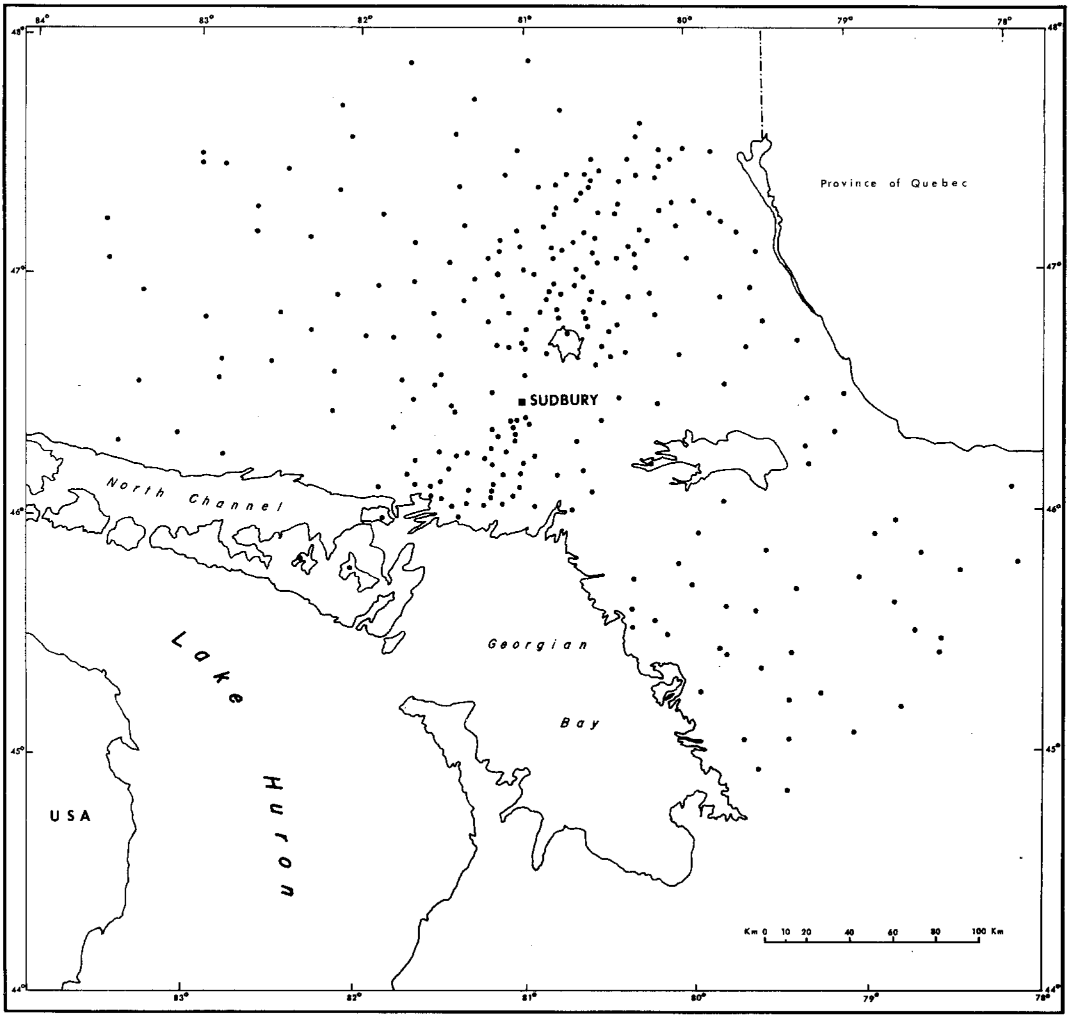

Fig. 1. Locations of the study lakes.

tions related to smelting activity (Cu, Ni) or to increased metal dissolution and mobilization from watersheds under acidic conditions (Al, Mn).

This paper examines associations between lake water quality and crustacean plankton communities in 249 lakes, including a large proportion of acidic lakes, within a 250 km radius of Sudbury (Figure 1).

2. The Study Lakes

Although predominantly on the Precambrian Shield, the lakes studied vary in chemistry, morphometry and surficial geological setting, spanning a cross-section of lake types occurring in northeastern Ontario. Pitblado *et al.* (1980) have divided northeastern

Ontario lakes into 7 groups based on principal components and hierarchical cluster analyses of 23 limnological variables. The lake groups derived are briefly described below, and a summary of group averages for physico-chemical characteristics is provided in Table I.

TABLE I

Average values of physico-chemical variables for lake groups defined by water chemistry

	Lake Group (*n*)						
	1(23)	2(49)	3(59)	4(22)	5(32)	6(57)	7(8)
Area (ha)[a]	3974	656	786	496	273	1391	2281
Depth (m)[b]	11	14	28	18	21	21	13
pH	6.6	6.5	6.6	6.9	4.7	5.9	7.9
Conductivity (μS cm^{-1})	55	41	42	66	50	45	210
Alkalinity (mg L^{-1} as $CaCO_3$)[c]	9.03	5.37	5.71	13.71	− 1.31	2.03	73.88
Calcium (mg L^{-1})	5.0	3.7	3.8	6.8	3.4	4.0	20.6
Magnesium (mg L^{-1})	1.64	1.02	1.10	1.87	0.98	1.14	6.77
Sodium (mg L^{-1})	1.7	1.3	1.1	1.2	1.9	1.1	5.2
Potassium (mg L^{-1})	0.67	0.50	0.43	0.54	0.43	0.43	0.77
Sulphate (mg L^{-1})	11.1	8.9	9.4	12.0	13.5	12.8	15.9
Silica (mg L^{-1})	0.90	1.31	1.06	1.32	0.90	0.92	0.97
Chloride (mg L^{-1})	1.88	1.25	0.91	0.90	3.00	1.02	9.52
Total Nitrogen (μg L^{-1})	508	356	242	303	215	200	273
Total Phosphorus (μg L^{-1})	19	10	6	10	5	5	9
Total Zinc (μg L^{-1})	5	3	3	3	18	8	2
Total Copper (μg L^{-1})	4	1	1	3	27	3	4
Total Nickel (μg L^{-1})	15	3	2	9	61	15	23
Total Iron (μg L^{-1})	153	134	45	87	95	62	45
Total Aluminum (μg L^{-1})	60	53	31	62	310	60	44
Total Manganese (μg L^{-1})	52	37	18	23	185	60	9
Color (Hazen)	34.2	31.4	14.3	21.2	10.6	7.7	6.1
Secchi disc (m)	3.1	3.7	6.8	4.6	10.6	7.1	7.4
Epilimnion thickness (m)	3.3	3.8	5.1	4.3	5.0	4.6	4.4
Hypolimnion thickness (m)	2.6	4.9	15.9	7.9	8.0	9.0	3.2
Deep-water temperature (°C)[d]	12.9	11.0	7.7	9.2	11.8	9.8	11.3

[a] Excluding 5 very large lakes with $A_0 > 10000$ ha.

[b] Depth at sampling station.

[c] Total inflection point alkalinity.

[d] Temperature at the top of the hypolimnion or 1 m above the lake bottom in shallow lakes.

2.1. GROUP 1

The lakes in this group are near-neutral and are typified by high concentrations of N and P and low Secchi disc transparency in comparison to the other lake groups. Concentrations of trace metals related to smelting activity (Cu, Ni) are elevated in the lakes closest to Sudbury.

2.2. GROUPS 2 AND 3

Lake groups 2 and 3 include the characteristic highly dilute, near-neutral lakes of the Precambrian Shield. Differentiation between the groups is based primarily on nutrient status with Group 3 lakes exhibiting generally lower nutrient concentrations and higher transparency than Group 2 lakes. Concentrations of trace metals are low in both lake groups.

2.3. GROUPS 4, 5, AND 6

These groups encompass a related set of clear, nutrient-poor lakes which show impacts (ranging from severe to slight) associated with emissions from the Sudbury smelting industry. Group 4 lakes show slightly elevated concentrations of SO_4 and trace metals indicating a slight impact by Sudbury emissions. These lakes are inherently more buffered and more productive than lakes in groups 5 and 6 reflecting high assimilation capacity for acidic inputs. Group 6 lakes are very clear, poorly buffered and slightly acidic. Trace metal concentrations related to smelter emissions (Cu, Ni) are often elevated. Group 5 contains the lakes which have been most strongly influenced by Sudbury emissions. They are typically extremely clear and highly acidic with elevated concentrations of trace metals related to watershed inputs (Al, Mn). Concentrations of Cu and Ni are very high in the lakes closest to Sudbury due to smelter emissions.

2.4. GROUP 7

These lakes show atypically high (for the study area) ionic strength related to occurrence of calcareous bedrock/overburden or inputs of urban runoff and exhibit wide variation in trophic state and trace metal concentrations.

3. Methods

3.1. DATA COLLECTION

Each lake was sampled once at a central location during the period June 15th to August 14th, 1981. Sampling visits were scheduled such that lakes within a given geographical portion of the study area were sampled at different times throughout the study. Crustacean plankton samples were collected as single vertical net (12.5 cm diameter; 76 μm mesh) hauls from 1 m above bottom to surface in each lake. Two hundred and six lakes were sampled with a flow-meter-equipped net, allowing calculation of filtration efficiency. The remaining lakes (n = 43) were sampled with a non-metered net. Samples were immediately preserved with 5% buffered formalin. Identification and enumeration procedures followed those outlined in Yan and Strus (1980). Water samples were collected as water column composites by the tygon tube method (Ministry of the Environment (MOE) 1979). Nutrient samples were collected through the euphotic zone estimated as twice the Secchi disc transparency plus 1 m. Samples for other chemical analyses were taken to the lower limit of the metalimnion, defined as the depth below the region of greatest temperature change at which the observed temperature decrease was less than or equal to 0.5 °C m^{-1}. Points of inflection of lake temperature profiles and respective temperatures were measured with a YSI Model 43TD telethermometer.

Samples were placed in sample-rinsed containers (250 mL polystyrene for nutrients; 500 mL acid washed polyethylene for trace metals – HNO_3 preserved; and 500 mL polystyrene for pH and major ion analyses) for transportation to the laboratory. Conductivity, pH and alkalinity (total inflection point) determinations were completed at the Sudbury MOE laboratory on the day following collection (after overnight refrigeration). Other analyses were carried out at the MOE Laboratories in Toronto following procedures outlined in MOE (1981).

3.2. STATISTICAL ANALYSIS

The data array consisted of 35 physico-chemical variables and 39 zooplankton species for each of the 249 study lakes. Statistical analyses were done at Laurentian University using the SPSS package of computer routines (Nie *et al.*, 1975; Hull and Nie, 1981) and a number of FORTRAN programs written by JRP.

The relative abundance of species in a lake formed the major part of the zooplankton portion of the data array. The number of individuals of a particular species in a sample was expressed as a percentage of the total number of individuals (excluding nauplii) with calanoid and cyclopoid copepodids (only identified to suborder) apportioned according to the relative abundance of their adult forms in the respective groups of Copepoda. Absolute zooplankton densities were computed only for the 206 lakes sampled by metered hauls.

Examination of the zooplankton data set for any biases introduced by the sampling format (i.e. single samples over a 2 mo period) indicated that the data did accurately reflect changes in community composition across the range of lake types. Comparison of the present data with data for 187 of the lakes which were sampled more frequently (2 to 7 times) during 1974–76 (Keller, 1981) showed similar lake group averages for species occurrence and percent composition. Linear regression analyses of species richness, density and percent composition against sampling date did not show any significant correlations, and inspection of the scattergrams did not reveal any non-linear relationships between attributes of the zooplankton communities and time.

As indicated previously, in an earlier paper (Pitblado *et al.*, 1980), 187 lakes of the Sudbury area were classified into seven groups by employing 23 physico-chemical variables reduced to four principal components: Nutrient status, Buffering Status, Atmospheric Deposition Status and Sodium-Chloride Status. Based on statistics derived from that study, the current 249 lakes were similarly classified using the assignment procedure of the SPSS multiple discriminant analysis routine. The only departure from this approach was our overriding assignment of all lakes with pH < 5.0 to Group 5, and lakes with pH between 5.0 and 5.5 to Group 6. This step, which had little effect on the integrity of the previous classification procedures, was undertaken to ensure that the influence of pH (considered a major variable potentially influencing biotic systems) was held relatively constant.

In order to examine relationships between species relative abundance and physico-chemical variables, forward stepwise multiple regression analyses were undertaken. The independent variables were initially chosen from those variables that had high relative loadings on the first three principal components and from additional variables not available for the earlier study but which potentially play important roles in influencing the distribution and abundance of zooplankton. The final list of independent variables was selected by keeping high intercorrelations to a minimum and thus reducing the chances of spurious multiple correlations being derived due to multicollinearity. The problem of bell-shaped or horseshoe-shaped distributions often common to this type of data (Austin and Noy-Meir, 1971; Roff *et al.*, 1981) was considered by inspecting the scattergrams of each of the independent variables with each of the zooplankton species, and by undertaking the multiple regression analysis using two sub-sets of data. The first sub-set included only lakes in Groups 5 and 6; the second included the lakes in Groups 1, 2, 3, and 4. Examination of the scattergrams indicated that species responses were essentially linear within these lake subsets.

Zooplankton community structure was determined using species presence/absence data in a hierarchical cluster analysis. This approach, using Euclidean distance squared as a measure of dissimilarity (Sokal and Sneath, 1963; Sneath and Sokal, 1973; Clifford and Stephenson, 1975), and the Ward's error clustering algorithm (Ward, 1963; Frenkel and Harrison, 1974; Mather, 1976), clearly differentiated the recurring patterns of the most common zooplankton species. The less common species were assigned to the major zooplankton communities using a computer program written to highlight the coexistence of those species with the major species clusters.

4. Results and Discussion

4.1. GENERAL SPECIES DISTRIBUTIONS

A total of 39 species (24 genera) of Crustacea, including 24 representatives of Cladocera and 15 species of Copepoda were collected from the plankton of the study lakes (Table II). Among the Copepoda, 8 calanoid and 7 cyclopoid forms were found.

Comparison of data from the present study with data from other synoptic surveys in eastern Canada (Rigler and Langford, 1967; Patalas, 1971; Brandlova *et al.*, 1972; MOE, 1973, 1975; Sprules, 1975; Pinel-Alloul *et al.*, 1979; Carter *et al.*, 1980; Joubert and Tousignant, 1981; and Jermolajev and Fraser, 1982) showed general similarity in species occurrence, with the species most common in our study generally occurring frequently in other extensive regional surveys. Of the 25 species present in $>5\%$ of our lakes, 19, 20, and 24 species respectively occurred in the ELA lakes of northwestern Ontario (Patalas, 1971), lakes in the arctic watershed of Ontario (MOE, 1973, 1975) and Quebec lakes south of the 52nd parallel (Joubert and Tousignant, 1981). Ten and

TABLE II

Relative occurrence of crustacean plankton species in 249 northeastern Ontario lakes

	% of lakes
Diaptomus minutus Lilljeborg	85
Bosmina longirostris (O. F. Müller)	84
Holopedium gibberum Zaddach	74
Cyclops bicuspidatus thomasi (S. A. Forbes)	64
Mesocyclops edax (S. A. Forbes)	64
Diaphanosoma sp.	61
Daphnia galeata mendotae Birge	56
Daphnia retrocurva S. A. Forbes	43
Cyclops scutifer Sars	41
Diaptomus oregonensis Lilljeborg	40
Daphnia longiremis Sars	38
Tropocyclops prasinus mexicanus Kiefer	35
Epischura lacustris S. A. Forbes	33
Eubosmina longispina (Leydig)	33
Eubosmina tubicen (Brehm)	21
Daphnia catawba Coker	19
Daphnia ambigua Scourfield	17
Daphnia pulex Leydig emend. Richard	14
Chydorus sphaericus (O. F. Müller)	13
Daphnia dubia Herrick	12
Leptodora kindtii (Focke)	10
Ceriodaphnia lacustris Birge	8
Cyclops vernalis (Fischer)	8
Polyphemus pediculus (Linné)	8
Senecella calanoides Juday	6
Sida crystallina (O. F. Müller)	4
Diaptomus sicilis S. A. Forbes	3
Limnocalanus macrurus Sars	2
Orthocyclops modestus (Herrick)	2
Ceriodaphnia pulchella Sars	1
Acroperus harpae Baird	<1
Alona quadrangularis (O. F. Müller)	<1
Diaptomus ashlandi Marsh	<1
Diaptomus sanguineus S. A. Forbes	<1
Eubosmina coregoni (Baird)	<1
Eucyclops agilis (Koch)	<1
Latona setifera (O. F. Müller)	<1
Ophryoxus gracilis Sars	<1
Simocephalus serrulatus (Koch)	<1

13 of these species are also present in the plankton of the Great Lakes (Superior and Huron, respectively) which adjoin the study area (Watson, 1974).

Examination of maps depicting species presence/absence in the study lakes showed no apparent geographical patterns in species distributions within our study area.

4.2. SPECIES RICHNESS AND DENSITY

Within individual lakes, the total number of crustacean species collected varied from 0 (1 lake only) to 17 with an overall average of 9.1 species per lake (Figure 2), identical

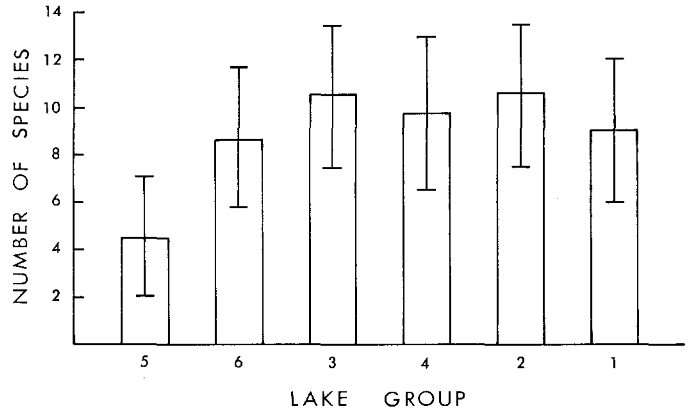

Fig. 2. Average and standard deviation of the number of crustacean plankton species in lake groups defined by water chemistry. Lake groups are arranged in order of generally increasing trophic status and pH. Group 7 lakes have been excluded because they showed widely varying trophic status.

to the average number of species per lake of 9.1 for single collections from 45 ELA lakes (Patalas, 1971). Species richness was much lower in acidic Group 5 lakes (average 4.5 species per lake) than in lakes within other groups (group averages of 8.5 to 10.5 species per lake) similar to the results of other investigations within the same portion of Ontario. Elimination of very scarce species ($<0.1\%$ of density in individual lakes) from our data set only slightly altered average species richness (4.3 species per lake in Group 5; 8.4 to 10.4 species per lake in other groups). Sprules (1975), based on single collections from 47 LaCloche Mountain lakes, reported 1 to 7 species in lakes with $pH < 5.0$ and 9 to 16 species in lakes with $pH > 5.0$. Yan and Strus (1980) reported averages of 2.9 to 3.9 species per collection from four highly acidic, metal-contaminated lakes near Sudbury while in the same study average species richness ranged from 7.0 to 14.6 species per collection in 6 near-neutral central Ontario lakes and one near-neutral lake near Sudbury.

Average crustacean density varied widely (Figure 3), but was greatest in the most nutrient rich Group 1 lakes (35 animals L^{-1}) and least in acidic Group 5 lakes (15 animals L^{-1}). Roff and Kwiatkowski (1977) have previously reported low crustacean densities in acidic lakes. Our average observed densities are similar to the range of ice free period averages reported by Yan and Strus (1980) for 6 near-neutral, oligotrophic lakes (18.2 to 45.5 animals L^{-1}).

4.3 SPECIES – LAKE TYPE ASSOCIATIONS

Figures 4 to 7 present the average frequency of occurrence and relative abundance when present of relatively common ($>5\%$ of the study lakes) species utilizing the lake groups as integrators of similar physico-chemical conditions. The groups are arranged in order of generally increasing trophic status and pH. Group 7 lakes have been excluded since they exhibited widely varying trophic status.

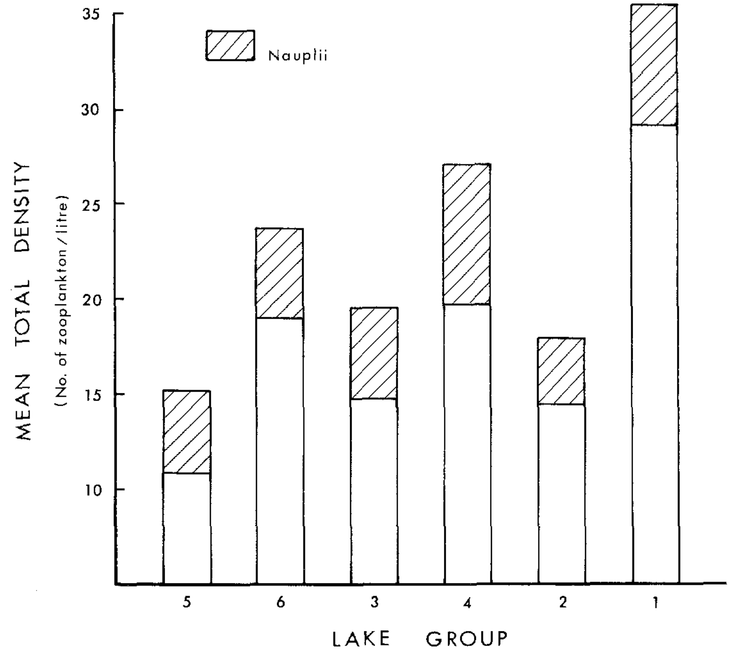

Fig. 3. Average crustacean density in lake groups defined by water chemistry.

4.3.1. *Cladocera*

Several authors (Almer *et al.*, 1974; Sprules, 1975; and others) have reported scarcity or absence of *Daphnia* in acidic lakes. Our data support these findings, but indicate variation in the environmental preferences of the species of Daphnidae collected (Figure 4). *D. catawba* and *D. ambigua* showed variation in importance between lake groups but demonstrated no obvious declines in acidic lakes (Group 5). Sprules (1975) indicated that *D. catawba* occurs primarily at low pH in LaCloche Mountain lakes and Carter (1971) has documented *D. ambigua* as the predominant cladoceran in four acidic (pH 4.0 to 5.0) ponds near Georgian Bay.

Other Daphnidae collected during our study showed markedly reduced importance in acidic lakes, considering both frequency of occurrence and relative abundance (Figure 4). Of these daphnids, *D. longiremis* was most common in near-neutral oligotrophic lakes (Groups 3 and 4) although the species reached highest relative abundance in the most productive lakes (Group 1). *D. g. mendotae* was consistently important in near-neutral lakes of all types but increased slightly in occurrence and relative abundance among Group 4 and 2 lakes. *D. retrocurva* was most prominent in the most productive lakes and showed generally increasing occurrence and relative abundance with increasing trophic status. *D. dubia* and *D. pulex* were most common in nutrient poor Group 3 lakes but varied widely in relative abundance among the lake groups. *C. lacustris* was conspicuously more important in the most productive lakes (Group 1).

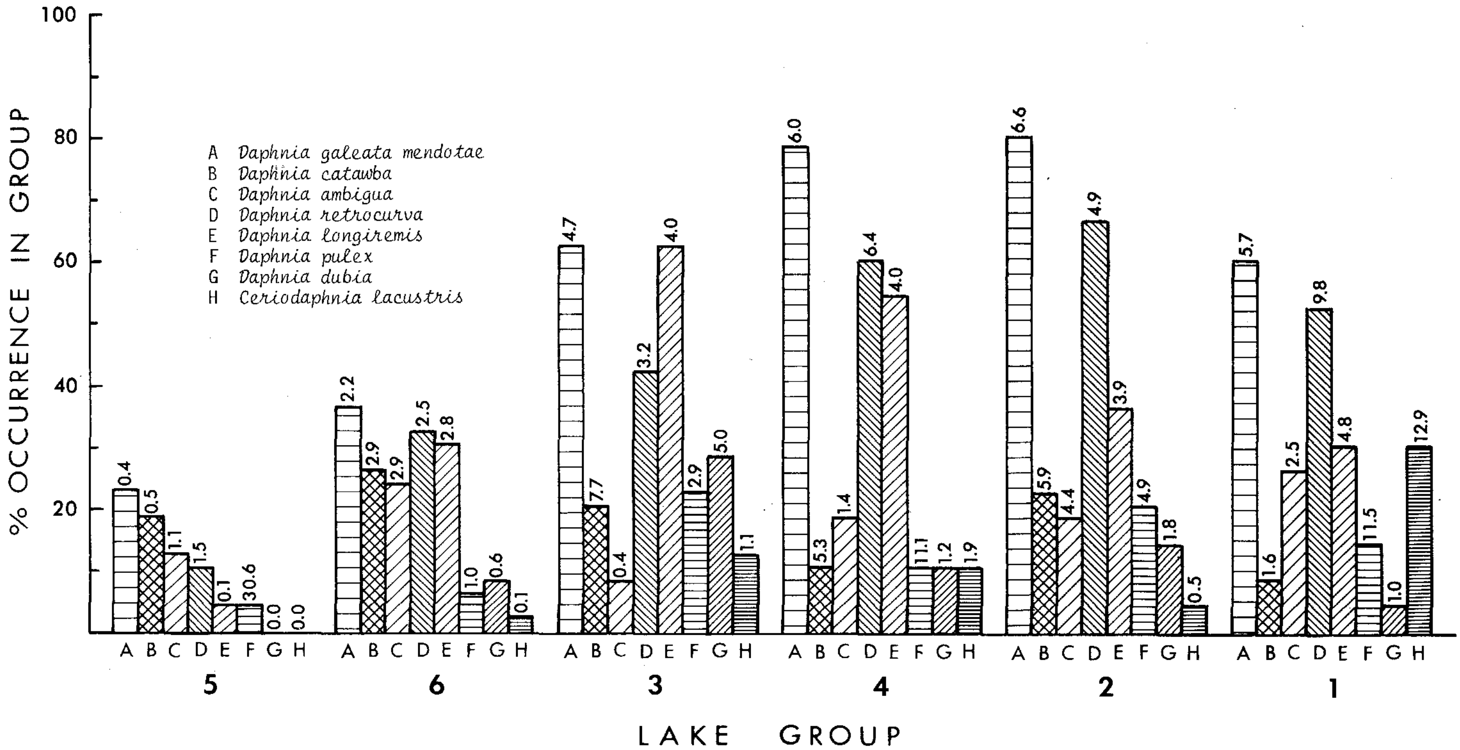

Fig. 4. Frequency of occurrence in lake groups (vertical bars) and average % contribution when present to crustacean density excluding nauplii (numbers above bars) of common Daphnidae (present in > 5% of the study lakes).

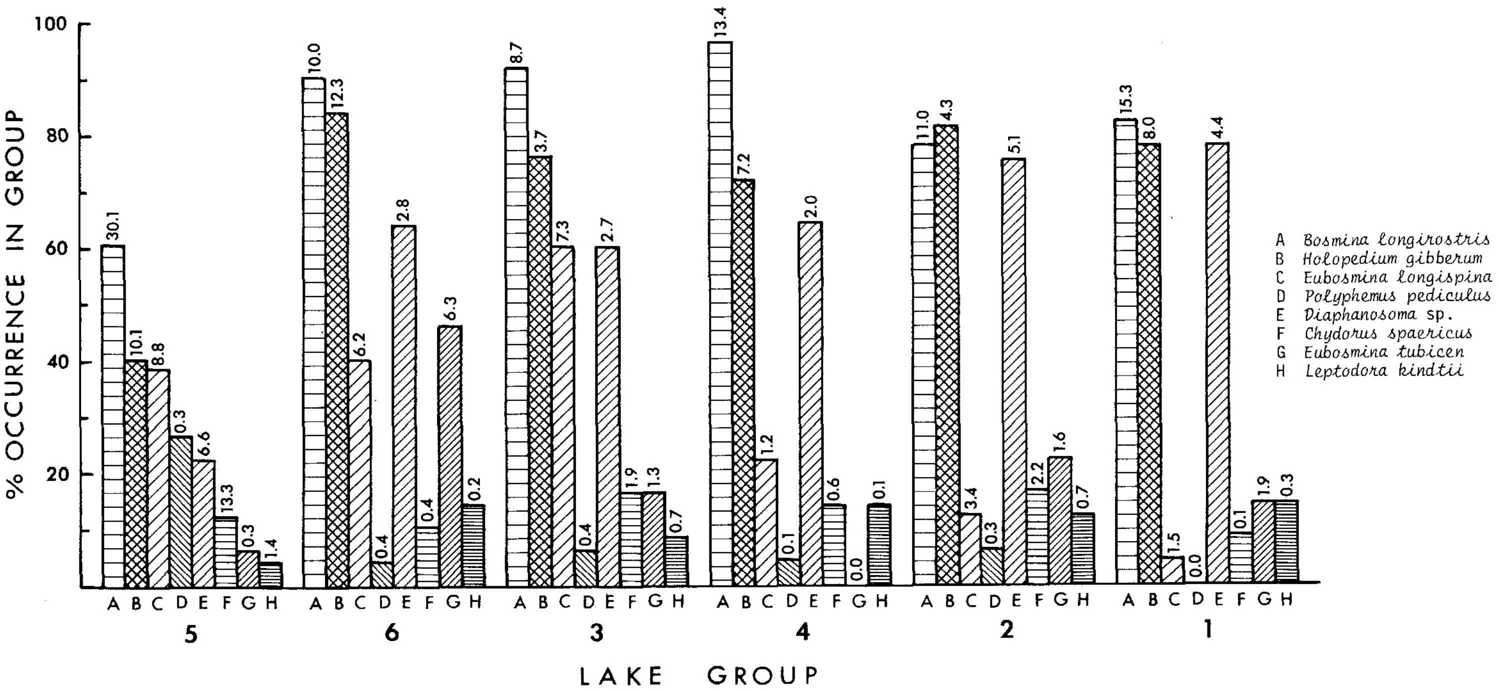

Fig. 5. Frequency of occurrence and average % contribution when present of common Cladocera (excluding Daphnidae).

B. longirostris, *H. gibberum*, and *Diaphanosoma* sp., the most common Cladocera in the study lakes (Table II), were important among all lake groups. Although frequency of occurrence of these species was somewhat reduced among acidic lakes (Group 5), when present, they contributed substantially to the communities (Figure 5). In the case of *B. longirostris* and *Diaphanosoma* sp. maximum relative abundances were reached in acidic lakes. Sprules (1975) has indicated that these species are distributed essentially without regard to pH in LaCloche Mountain lakes.

E. longispina was most common and abundant among highly oligotrophic lakes, including acidic lakes, and was much less prominent among more productive lakes (Groups 4, 2, and 1). *E. tubicen* was absent from Group 4 lakes and also from Group 7 lakes (not depicted in Figure 5) which exhibited the hardest waters of our study lakes (Table I) confirming the observation of Carter *et al.* (1980) that this species is restricted to very soft waters.

C. sphaericus and *P. pediculus* were present in lakes of all types (with the exception of Group 1 lakes which contained no *P. pediculus*) but showed increased importance among acidic lakes. *C. sphaericus* has previously been reported as important in acid, metal-contaminated lakes near Sudbury (Yan and Strus, 1980), and Sprules (1975) has indicated that *P. pediculus* occurs primarily at low pH in LaCloche Mountain lakes.

L. kindtii showed generally low abundance in our study lakes, similar to results obtained from surveys of ponds near Georgian Bay (Carter, 1971) and the ELA lakes of northwestern Ontario (Patalas, 1971). The particular scarcity of *L. kindtii* among our Group 5 lakes generally agrees with the data of Sprules (1975) which indicated absence from lakes with pH < 5.0.

4.3.2. *Calanoida*

D. minutus was the most common and abundant copepod in the study lakes (Figure 6). The importance of *D. minutus* was greatest in the most acidic, most oligotrophic Group 5 lakes where, when present, it comprised on average 74.3% of the crustacean density (excluding nauplii). Within other lake groups the average contribution of *D. minutus* to density ranged from 30.1 to 48.0%. *D. minutus* was less common in productive Group 1 lakes (47.8%) than in lakes of other groups (81.6 to 94.7%). *D. minutus* has been previously reported as very important in non-acidic (Schindler and Noven, 1971) and acidic (Sprules, 1975) oligotrophic Precambrian Shield lakes. Sprules (1975) has indicated that *D. minutus* is the only species which remains in some very acidic LaCloche Mountain lakes.

In contrast, *D. oregonensis* was rare in Group 5 lakes, and showed increasing occurrence and relative abundance with increasing trophic status. *D. oregonensis* is the predominant calanoid copepod in eutrophic Kawartha lakes, Ontario (Hitchin, 1976) and it has been shown to replace *D. minutus* after artificial fertilization (N and P) in a small, near-neutral Sudbury area lake (Yan and LaFrance, 1982). *E. lacustris* and *S. calanoides* were conspicuously absent from Group 5 lakes.

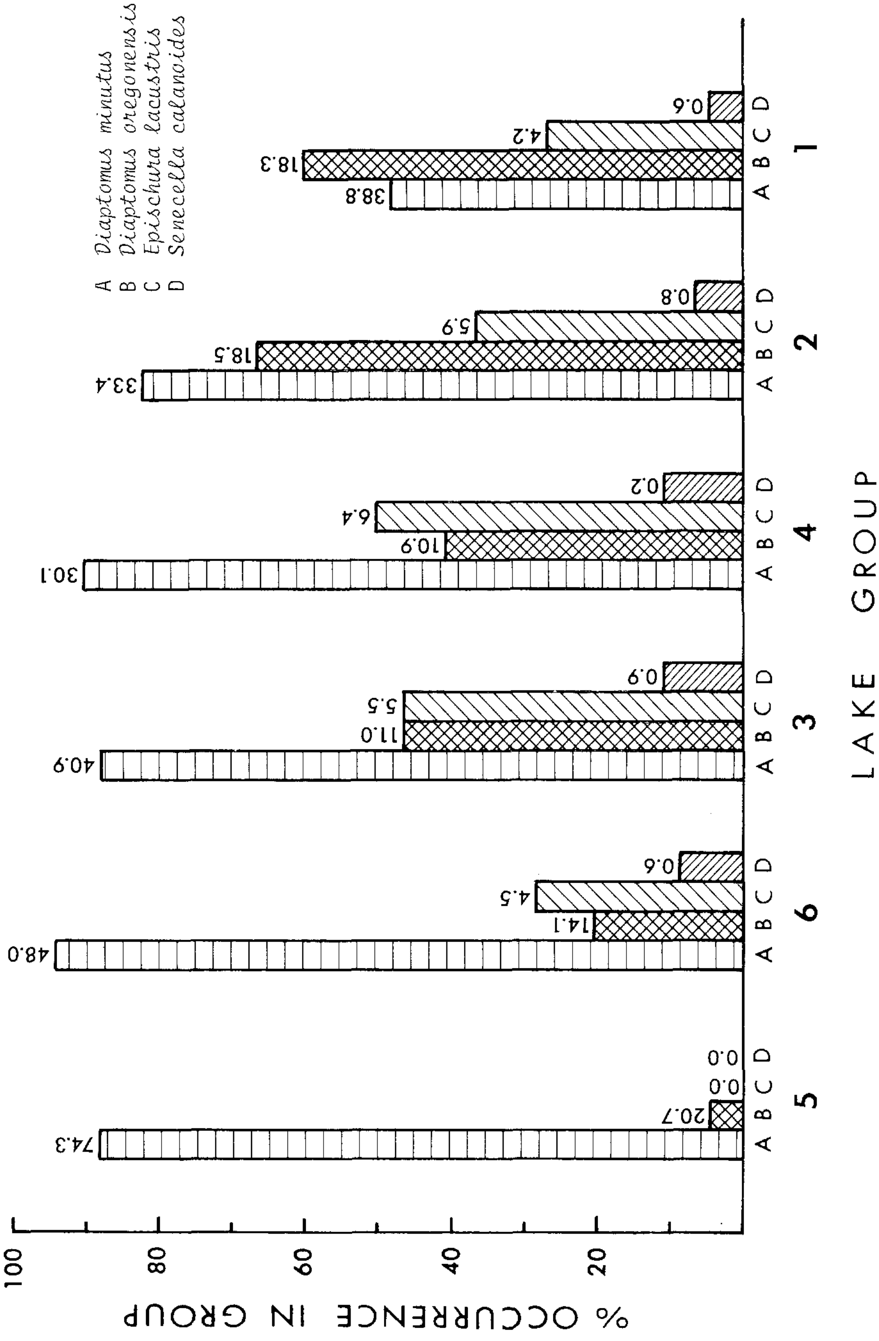

Fig. 6. Frequency of occurrence and average % contribution when present of common Calanoida.

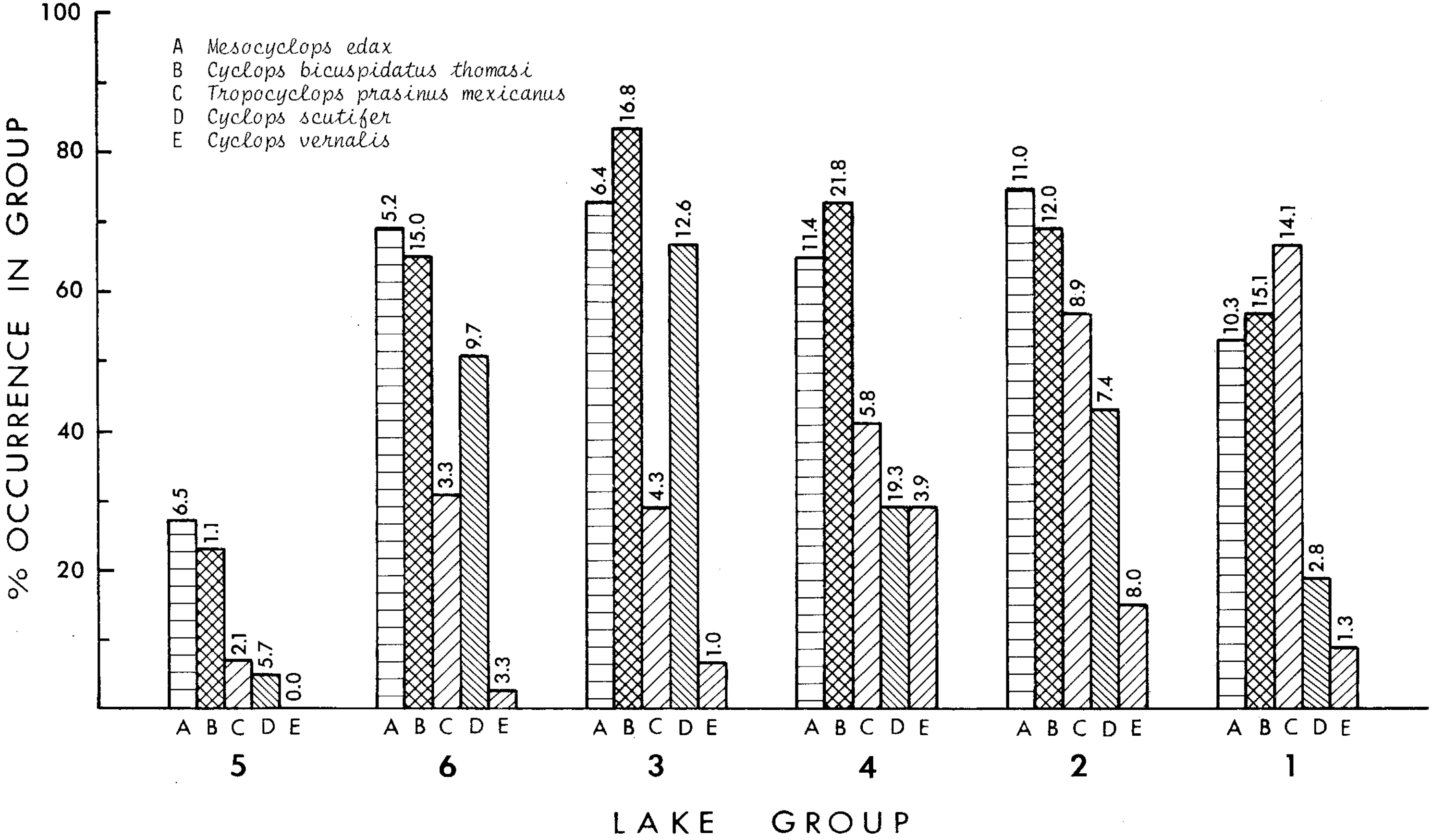

Fig. 7. Frequency of occurrence and average % contribution when present of common Cyclopoida.

4.3.3. *Cyclopoida*

Studies in Scandinavia (Nilssen, 1980), the U.S.A. (Confer *et al.*, 1983) and Ontario (Roff and Kwiatkowski, 1977) have reported a general scarcity of cyclopoids in acidic lakes, agreeing well with our data. Cyclopoids were much less common in Group 5 lakes than in lakes of other groups (Figure 7). Twenty-eight percent of Group 5 lakes had no cyclopoids in the collections (group average 0.9 cyclopoid species/lake) while within other lake groups only from 0 to 5.3% of the lakes contained no cyclopoids with group averages of 2.2 to 2.6 cyclopoid species/lake. *C. scutifer* was most prominent in oligotrophic, slightly acidic to near-neutral lakes (Groups 6 and 3) while *T. p. mexicanus* showed an apparent preference for more nutrient rich waters (Groups 2 and 1). Among near-neutral lakes *C. b. thomasi* and *M. edax* were important in all lake groups. *C. vernalis* occurred much less frequently and was not collected from Group 5 lakes, although previous sampling in the study area has shown the presence of *C. vernalis* in some of these acidic lakes (Keller, 1981).

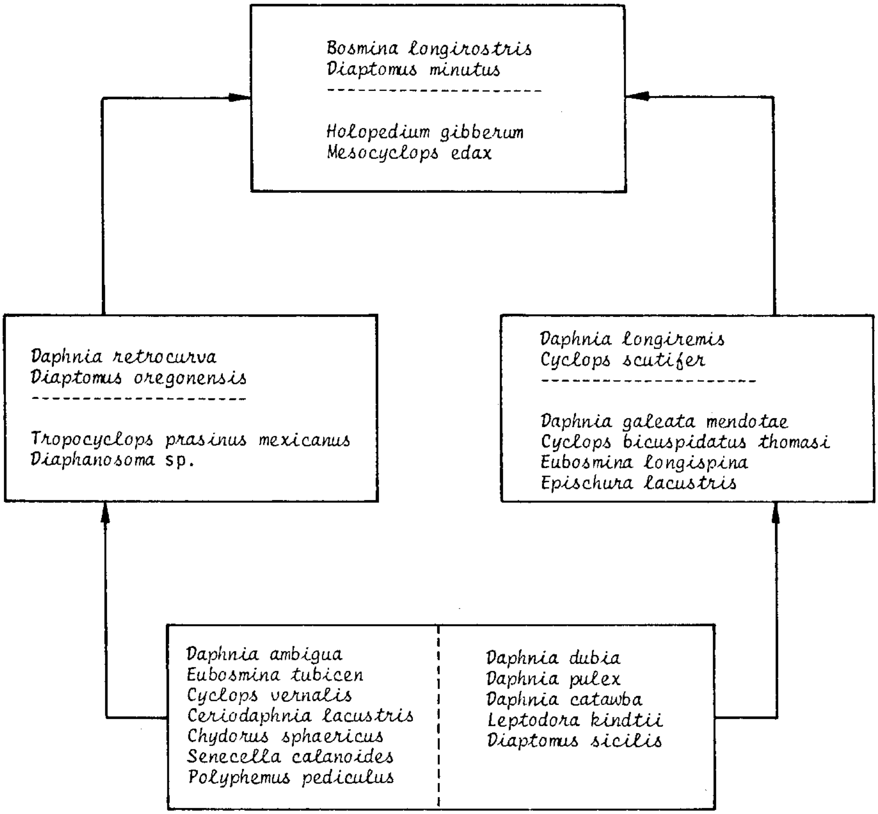

Fig. 8. Results of species cluster analysis.

4.4. INTERSPECIFIC ASSOCIATIONS

Cluster analysis (Figure 8) indicated that the study lakes were typified by a single major species group common to most lakes and containing *D. minutus*, *B. longirostris*, *H. gibberum*, and *M. edax*. These species were also present in the major recurrent group defined by Sprules (1975) for LaCloche Mountain lakes which in addition contained *Diaphanosoma* sp. and *C. b. thomasi*. In our analysis, the latter two species were assigned to different species subgroups (Figure 8). On the basis of the apparent environmental preferences of their constituent species, these subgroups may be generally categorized as typical of more productive waters (*D. retrocurva*, *D. oregonensis*, etc.), and less productive waters (*D. longiremis*, *C. scutifer*, etc.).

Other species shown in Figure 8 were too scarce to permit discrimination by cluster analysis. Based on the frequency of their co-occurrence with the major species in the subgroups, they have been divided into those species which appear most important in the communities of more productive and less productive lakes respectively. Often the division between these species was very indistinct.

4.5. GENERAL COMMUNITY STRUCTURE

If viewed from a functional standpoint, our acidic lakes exhibit basic differences in community structure in comparison to near-neutral lakes (Figure 9). The most conspicuous alterations include: a substantial reduction in the importance of Daphnidae and a concomitant increase in the relative abundance of smaller grazers (particularly *D. min-*

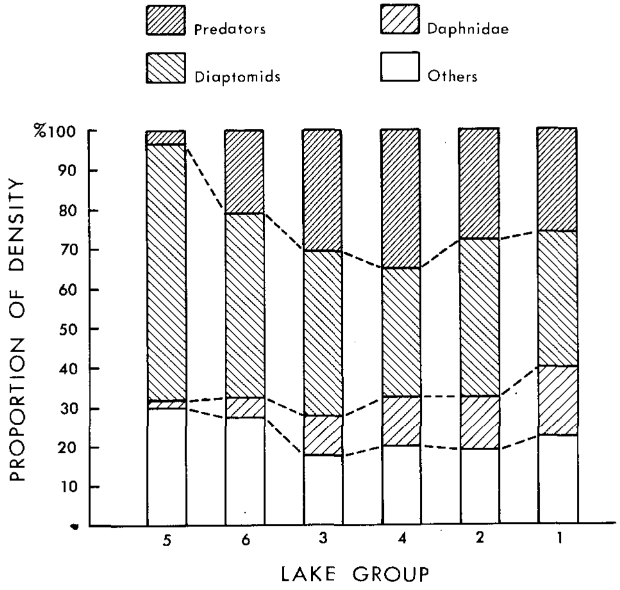

Fig. 9. Average % contribution to total density (excluding nauplii) by predators (Cyclopoida, *P. pediculus*, *L. kindtii*, and *E. lacustris*), Diaptomids, Daphnidae and other Crustacea in lake groups defined by water chemistry.

utus); and generally reduced abundance of crustacean predators (*L. kindtii*, *E. lacustris*, and cyclopoids).

The general trend toward increasing importance of smaller crustacean plankters in acidic lakes is apparent when communities are considered on the basis of average size class composition (Figure 10). It is noteworthy that this tendency occurs not only in general, but is manifested within genera. *D. minutus* increases in importance in acidic lakes while the larger *D. oregonensis* declines. Of the daphnids, the species which do not appear adversely affected in acidic lakes (*D. catawba*, and *D. ambigua*) are small representatives of the genus.

Although biomass was not measured in our study, the increased importance of smaller taxa (Figure 10) and the low density (Figure 3) in Group 5 lakes indicate reduced crustacean biomass under acidic conditions.

4.6 ENVIRONMENTAL INFLUENCES

The mechanisms of community alteration in acidic lakes are unclear, and may be diverse. The abrupt declines of some large species (i.e. most *Daphnia*, *S. calanoides*, and the predaceous *L. kindtii*, and *E. lacustris*) in acidic lakes imply direct toxicity by pH or a related variable, but other lake characteristics may be implicated. The increased importance of some cladoceran grazers (*B. longirostris*, *H. gibberum*, and *Diaphanosoma* sp.) in some acidic lakes suggests a response to reduced competition from *Daphnia*. It has been shown that *Daphnia* can depress *Bosmina* populations (DeMott and Kerfoot, 1982; Goulden *et al.*, 1982). As suggested by Sprules (1975) the increased importance

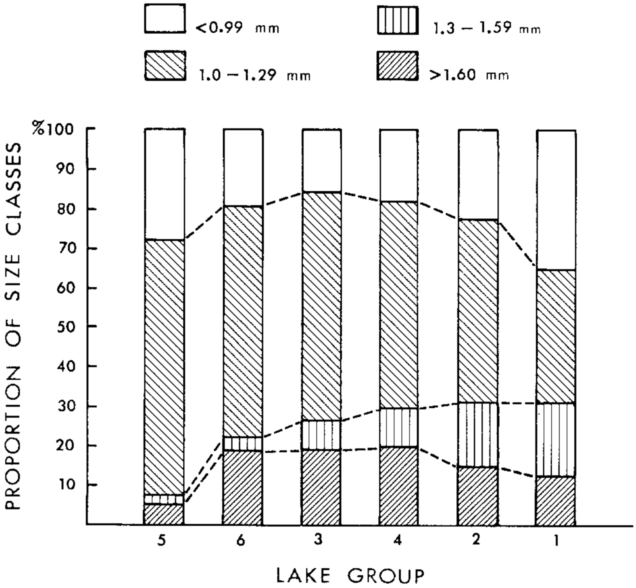

Fig. 10. Average % contribution to total density by size classes of crustacean plankton. The four size classes depicted are a condensation of the six categories reported by Roff *et al.* (1981). Assignment of species to categories followed Roff *et al.* (1981).

of *P. pediculus* in acidic lakes may reflect reduced competition from other predatory plankton. The reduction in importance of Cyclopoida in acidic lakes is confusing since cyclopoids generally seem tolerant of low pH (Lowndes, 1952) and some species common in our study area are at least occasionally important in highly acidic lakes (Janicki and De Costa, 1979; Yan and Strus, 1980). The generally very low productivity of our acidic study lakes may be implicated, since Neill and Peacock (1980) demonstrated high springtime mortality of juvenile *C. b. thomasi* at low food levels.

Eriksson *et al.* (1980) have suggested that with acidification and resultant elimination or reduction of fish predation the zooplankton grazing community shifts to dominance by larger species (particularly larger Calanoida) with a corresponding decrease in the importance of smaller Cladocera. These observations do not appear to hold true for our lakes in which the increased importance of Calanoida (*D. minutus*) is strongly associated with declines in the larger *Daphnia* species, and smaller Cladocera (notably *B. longirostris*) remain important. Further, although some large species such as *H. gibberum* may be important at low pH, a strong tendency toward dominance by smaller Crustacea (*D. minutus* and *B. longirostris*) remains evident even in the most acidic lakes which are completely devoid of fish populations.

Stepwise multiple linear regression analysis of selected limnological variables against the percent contribution of individual species failed to explain much of the variation in species proportions (Table III). Within near-neutral lakes (Groups 1, 2, 3, 4) on average only 11% of the variation in species proportions could be explained by the 'best' (based on order of occurrence in the regression equation) five or less predictive variables for each species. Considering the range of lakes over which the biological effects of acidification are manifested (Groups 5 and 6) five or fewer physico-chemical variables accounted for, on average, 25% of the variation in species proportions.

Although much of the variation in species proportions could not be explained on the basis of physico-chemical variables, examination of those variables apparently most important, based on regression analysis, is instructive. Within near-neutral lakes (Groups 1, 2, 3, 4) a characteristic related to lake thermal structure (epilimnion thickness, hypolimnion thickness or deep-water temperature) emerged as the best single predictor of species proportions for 9 out of 21 species. Although it has been shown that lake acidification may result in increased water clarity and attendant changes in thermal structure (Harvey *et al.*, 1981; Yan, 1983), among Group 5 and 6 lakes only 4 species were best correlated with a thermal characteristic, while for 9 species, including most of the species exhibiting substantial declines in acidic lakes, pH or the closely related alkalinity appeared as the primary correlates with percent composition. Lake pH also emerged as the single best correlate with total number of species ($r = 0.71$; $P < 0.01$) in lake Groups 5 and 6.

Considering other variables, in near-neutral lakes species proportions were in some cases best correlated with Secchi disc transparency (4 species), nutrient (N or P) concentrations (2 species), Cu (1 species), and lake depth (1 species). In Group 5 and 6 lakes, best correlations were found with Secchi disc transparency (2 species), nutrient concentrations (3 species), Cu (1 species), and depth (1 species).

TABLE III

Results of stepwise multiple linear regressions of limnological variables against % contribution of common crustacean plankton species to total density (excluding nauplii)

Species[a]	Lake Groups	Variables[b, c, d]	Multiple r[e]	Species[a]	Lake Groups	Variables[b, c, d]	Multiple r[c]
D. minutus	1, 2, 3, 4	SD, pH$^-$, Ao, TIA$^-$, TN$^-$	0.34***	*T. p. mexicanus*	1, 2, 3, 4	DT, TP, pH, SD$^-$, Cu	0.43***
	5, 6	SD, Cu$^-$, DT, pH$^-$, TP$^-$	0.62***		5, 6	DT, pH, TP, ET, TN$^-$	0.40**
B. longirostris	1, 2, 3, 4	Cu, SD$^-$, pH, TP, ET$^-$	0.40***	*E. lacustris*	1, 2, 3, 4	DT$^-$, pH, TN$^-$	0.20*
	5, 6	DE$^-$, TN$^-$, Cu, TP, pH$^-$	0.41**		5, 6	TIA, Al$^-$, SD$^-$, Cu$^-$, TN	0.70***
H. gibberum	1, 2, 3, 4	DT, ET$^-$, TN, Cu, TP	0.39***	*E. longispina*	1, 2, 3, 4	SD, DE, TIA$^-$, Ao, TN$^-$	0.49***
	5, 6	ET$^-$, HT$^-$, DT$^-$, TIA$^-$, pH	0.43**		5, 6	TN$^-$, DE, HT, TP$^-$, Al	0.49***
C. b. thomasi	1, 2, 3, 4	DT$^-$, pH, Al, DE, SD	0.43***	*D. catawba*	1, 2, 3, 4	pH$^-$, DE$^-$, SD, HT$^-$, TIA$^-$	0.45***
	5, 6	pH, DT$^-$, TN, ET, SD$^-$	0.63***		5, 6	–	–
M. edax	1, 2, 3, 4	pH$^-$, HT$^-$, TN$^-$, TP, ET	0.35***	*D. ambigua*	1, 2, 3, 4	–	–
	5, 6	pH, TN, SD$^-$, DT$^-$, Ao	0.41**		5, 6	TN, DT$^-$, DE$^-$, TIA$^-$, HT$^-$	0.38**
Diaphanosoma sp.	1, 2, 3, 4	SD$^-$, ET$^-$, Ao$^-$, Cu$^-$, pH$^-$	0.27*	*D. pulex*	1, 2, 3, 4	DT, pH, ET$^-$, Cu$^-$	0.24*
	5, 6	DT, Al$^-$, Cu, pH$^-$, TN	0.47***		5, 6	–	–
D. g. mendotae	1, 2, 3, 4	pH, TP, Ao, Cu$^-$, SD$^-$	0.27*	*C. sphaericus*	1, 2, 3, 4	pH, DT, TP$^-$, SD$^-$, ET	0.32**
	5, 6	TIA, pH, TN, DT$^-$, HT$^-$	0.44***		5, 6	Cu, Al, pH$^-$, TIA$^-$, ET	0.94**
D. retrocurva	1, 2, 3, 4	DE$^-$, TP, SD$^-$, TN, DT	0.34***	*D. dubia*	1, 2, 3, 4	TN$^-$, pH, TIA$^-$, ET, SD	0.36***
	5, 6	TP, pH, DT, TN$^-$, ET$^-$	0.40**		5, 6	pH, TP$^-$, Ao, Cu$^-$, SD$^-$	0.37**
C. scutifer	1, 2, 3, 4	SD, Ao, ET, HT, TIA	0.48***	*L. kindtii*	1, 2, 3, 4	DT, ET	0.18*
	5, 6	HT, SD$^-$, TN$^-$, ET$^-$, Cu$^-$	0.60***		5, 6	Ao, HT$^-$, TP$^-$, Al$^-$, ET	0.50***
D. oregonensis	1, 2, 3, 4	ET$^-$, TN, Cu$^-$, pH$^-$, Ao$^-$	0.28**	*C. lacustris*	1, 2, 3, 4	TP, Cu$^-$, TN, pH, Ao$^-$	0.26*
	5, 6	TIA, TN, Ao$^-$, pH, DT$^-$	0.42***		5, 6	TIA, pH, HT$^-$, SD$^-$, Cu$^-$	0.56***
D. longiremis	1, 2, 3, 4	DT$^-$, DE, ET$^-$, pH, Al	0.26*	*P. pediculus*	1, 2, 3, 4	–	–
	5, 6	pH, ET, DT$^-$, TIA, SD$^-$	0.56***		5, 6	SD, ET$^-$, DT, Al, pH$^-$	0.42***
S. calanoides	1, 2, 3, 4	HT, pH, DT$^-$, DE, ET	0.34***				
	5, 6	TIA, Ao$^-$, TN, HT	0.33*				

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[a] Only species present in >5% of the study lakes included; *E. tubicen* and *C. vernalis* are excluded since meaningful statistics could not be generated for these species.

[b] pH = pH; TIA = alkalinity; Al = Al; Cu = Cu; TN = total nitrogen; TP = total phosphorus; SD = Secchi disc; DE = bottom depth; HT = hypolimnion thickness; ET = epilimnion thickness; Ao = lake area; DT = deep-water temperature.

[c] Minus sign indicates variables which exhibited a negative relationship.

[d] Where fewer than five variables are listed additional variables could not be added and retain significance at $P < 0.1$; where no variables are listed no relationships were significant at $P < 0.1$.

[e] Levels of significance; *** = $P < 0.01$; ** = $P < 0.05$; * = $P < 0.1$.

5. Summary

Crustacean plankton assemblages in northeastern Ontario lakes largely reflect general water quality, particularly characteristics associated with lake trophic status and degree of acidification. The results of stepwise multiple linear regression analyses of species proportions against limnological characteristics suggest that of the individual physicochemical variables considered, characteristics related to thermal structure may be very important in near-neutral lakes while actual lake acidity may be a primary control in acidified lakes.

Overall, the lakes are characterized by a major group of very common species (*B. longirostris*, *D. minutus*, *H. gibberum*, and *M. edax*) and two species subgroups which can be differentiated into species prominent in more productive lakes and species which are more important in less productive lakes. Among acidic lakes, which are common in the study area, crustacean plankton communities showed low density and reduced numbers of species related to reduced importance of larger grazers (Daphnidae) and predators (Cyclopoida, *L. kindtii* and *E. lacustris*).

Our synoptically collected data shed little light on the actual mechanisms of community alteration; however, it is hoped that the information and discussion provided herein will provide a framework for more detailed consideration of the influences of acidification on crustacean plankton in Precambrian Shield lakes, and underscore the need for more temporally rigorous, quantitative study.

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References

Almer, B., Dickson, W., Ekstrom, C., Hornstrom, E., and Miller, U.: 1974, *Ambio.* **3**, 30.

Austin, M. P. and Noy-Meir, I.: 1971, *J. Ecol.* **59**, 763.

Beamish, R. J. and Harvey, H. H.: 1972, *J. Fish. Res. Board Can.* **29**, 1131.

Brandlova, J., Brandl, Z., and Fernando, C. H.: 1972, *Can. J. Zool.* **50**, 1373.

Carter, J. C. H.: 1971, *Arch. Hydrobiol.* **68**, 204.

Carter, J. C. H., Dadswell, M. J., Roff, J. C., and Sprules, W. G.: 1980, *Can. J. Zool.* **58**, 1355.

Clifford, H. T. and Stephenson, W.: 1975, *An Introduction to Numerical Classification*, Academic Press, New York.

Confer, J. L., Kaaret, T., and Likens, G. E.: 1983, *Can. J. Fish. Aquat. Sci.* **40**, 36.

Conroy, N. I., Hawley, K., and Keller, W.: 1978, *Extensive Monitoring of Lakes in the Greater Sudbury Area, 1974–76*, Ontario Ministry of the Environment, Tech. Rep. 40 p. plus appendices.

DeMott, W. R. and Kerfoot, W. C.: 1982, *Ecology* **63**, 1949.

Eriksson, M. O. G., Henrikson, L., Nilsson, B. I., Nyman, G., Oscarson, H. G., Stenson, A. E., and Larsson, K.: 1980, *Ambio* **9**, 248.

Frenkel, R. E. and Harrison, C. M.: 1974, *J. of Biogeography* **1**, 27.

Fryer, G.: 1980, *Freshwater Biology* **10**, 41.

Goulden, C. E., Henry, L. L., and Tessier, A. J.: 1982, *Ecology* **63**, 1780.

Harvey, H. H., Pierce, R. C., Dillon, P. J., Kramer, J. R., and Whelpdale, D. M.: 1981, *Acidification in the Canadian Aquatic Environment*, Publication NRCC No. 18475 of the Environmental Secretariat, National Research Council of Canada.

Hitchin, G.: 1976, 'The Zooplankton of the Kawartha Lakes, 1972', in *The Kawartha Lakes Water Management Study – Water Quality Assessment (1972–76)*, Ontario Ministry of the Environment and Ontario Ministry of Natural Resources, Tech. Rep. pp. 47–68.

Hull, C. H. and Nie, N. H.: 1981, *SPSS Update 7–9*, McGraw-Hill, New York.

Janicki, A. and DeCosta, J.: 1979, *Arch. Hydrobiol.* **85**, 465.

Jermolajev, E. and Fraser, J. M.: 1982, *Zooplankton in brook trout lakes of Algonquin Park, Ontario*, Ont. Fish. Tech. Rep. Ser. No. 3. 9 p.

Joubert, G. and Tousignant, L.: 1981, *The Effect of pH on the Distribution of Crustacean Zooplankton in 158 Quebec Lakes*, Manuscript rep., Ministère de l'Environnement du Québec. 24 p.

Keller, W.: 1981, *Planktonic Crustacea in Lakes of the Greater Sudbury Area*, Ontario Ministry of the Environment, Tech. Rep. 33 p. plus appendices.

Leivestad, H., Hendrey, G., Muniz, I. P., and Snekvik, E.: 1976, in F. W. Braekke (ed.), *Impact of Acid Precipitation on Forest and Freshwater Ecosystems in Norway*, Research Rep. 6/76, SNSF Project, Oslo, Norway, pp. 87–111.

Lowndes, A. G.: 1952, *Ann. Mag. Nat. Hist.* **5**, 58.

Mather, P. M.: 1976, *Computational Methods of Multivariate Analysis in Physical Geography*, Wiley, New York.

MOE (Ministry of the Environment): 1973, *Data for Northern Ontario Water Resources Studies 1971*, Bull. 1–4, Ontario Ministry of the Environment, Toronto, Ontario.

MOE (Ministry of the Environment): 1975, *Data for Northern Ontario Water Resources Studies 1972–73*, Bull. 1–5, Ontario Ministry of the Environment, Toronto, Ontario.

MOE (Ministry of the Environment): 1979, *Determination of the Susceptibility to Acidification of Poorly Buffered Surface Waters*, Ontario Ministry of the Environment, Tech. Rep. 21 p.

MOE (Ministry of the Environment): 1981, *Outlines of Analytical Methods*, Ontario Ministry of the Environment, Tech. Rep. 246 p. plus appendices.

Neill, W. E. and Peacock, A.: 1980, in W. C. Kerfoot (ed.), *Evolution and Ecology of Zooplankton Communities*, Univ. Press of New England, New Hampshire, pp. 715–724.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K., and Bent, D. H.: 1975, *SPSS: Statistical Package for the Social Sciences*, McGraw-Hill, New York.

Nilssen, J. P.: 1980, *Int. Revue ges. Hydrobiol.* **65**, 177.

Patalas, K.: 1971, *J. Fish Res. Board Can.* **28**, 231.

Pinel-Alloul, B., Legendre, P., and Magnin, E.: 1979, *Can. J. Zool.* **57**, 1693.

Pitblado, J. R., Keller, W., and Conroy, N. I.: 1980, *J. Great Lakes Res.* **6**, 247.

Rigler, F. H. and Langford, R. R.: 1967, *Can. J. Zool.* **45**, 81.

Roff, J. C. and Kwiatkowski, R. E.: 1977, *Can. J. Zool.* **55**, 899.

Roff, J. C., Sprules, W. G., Carter, J. C. H., and Dadswell, M. J.: 1981, *Can. J. Fish. Aquat. Sci.* **38**, 1428.

Schindler, D. W. and Noven, B.: 1971, *J. Fish. Res. Board Can.* **28**, 245.

Sneath, P. H. A. and Sokal, R. R.: 1973, *Numerical Taxonomy: The Principles and Practice of Numerical Classification*, Freeman, San Francisco.

Sokal, R. R. and Sneath, P. H. A.: 1963, *Principles of Numerical Taxonomy*, Freeman, San Francisco.

Sprules, W. G.: 1975, *J. Fish. Res. Board Can.* **32**, 389.

Sprules, W. G.: 1977, *J. Fish. Res. Board Can.* **34**, 962.

Ward, J. H.: 1963, *J. Amer. Statist. Assoc.* **58**, 236.

Watson, N. H. F.: 1974, *J. Fish. Res. Board Can.* **31**, 783.

Yan, N. D. and Strus, R.: 1980, *Can. J. Fish. Aquat. Sci.* **37**, 2282.

Yan, N. D. and Lafrance, C.: 1982, 'Experimental Fertilization of Lakes near Sudbury, Ontario', in *Studies of Lakes and Watersheds near Sudbury, Ontario*, Ontario Ministry of the Environment, Tech. Rep. (SES 009/82).

Yan, N. D.: 1983, *Can. J. Fish. Aquat. Sci.* **40**, 621.