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COMPARATIVE PATTERNS OF PLANKTON COMMUNITIES UNDER DIFFERENT REGIMES OF pH IN NOVA SCOTIA, CANADA

by

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Submitted in partial fulfillment of the

requirements for the Degree of

Doctor of Philosophy

at

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DEDICATION

To my parents, who always encouraged my curiosity as a child and supported my education as a student; and to Lyn, whose caring and understanding helped to get me through it all.

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ABSTRACT

A field program was conducted on three lakes in Kejimkujik National Park, Nova Scotia to study plankton-water chemistry relationships in a region of potential acid precipitation stress. Comparisons were made among lakes and between years. The three study sites represent two different types of lakes. Kejimkujik Lake (pH 4.8) and Pebbleloggitch Lake (pH 4.5) are both high-colored, dystrophic acidic lakes. Beaverskin Lake is a clear, oligotrophic lake which is not as acidic (pH 5.4).

The phytoplankton of Kejimkujik Lake was dominated by diatoms, Pebbleloggitch Lake was dominated by chlorophytes and chrysophytes, and Beaverskin Lake was dominated by cyanophytes. Kejimkujik Lake had the highest algal cell volume per liter, and Pebbleloggitch Lake the lowest.

Rotifer populations composed the majority of the zooplankton communities, while the crustacean zooplankton were dominated by the acid-tolerant copepod Diaptomus minutus. Kejimkujik Lake had the lowest and Pebbleloggitch Lake the highest zooplankton biomass per M^3, which may result from abundant detrital food resources in Pebbleloggitch Lake.

Multiple regression analysis of water chemistry variables with plankton species produced many significant effects, but failed to show clear patterns. Cause and effect relationships in aquatic ecosystems are poorly delineated by such techniques. A qualitative technique, loop analysis, was used to characterise and compare the structure of the planktonic foodwebs.

Large enclosures or limnocorrals were used in Beaverskin Lake to test the hypothesis that short-term pH alterations produce changes in plankton species abundance and composition. Results indicated that for many plankton groups, liming is more stressful than additional acidification.

A biogeographic study of twenty lakes in Nova Scotia showed that many acidic lakes retain diverse and abundant plankton communities. Stepwise multiple regression identified those factors best able to explain planktonic variances. Acidity was more likely to affect planktonic diversity than abundance. Effects of pH level on plankton communities were partially obscured by the compensating effects of phosphorus level.

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I am very grateful to the many individuals who provided assistance and encouragement during this study. Dr. Patricia Lane has provided invaluable discussion, guidance and motivation throughout the study. Dr. Joseph Kerekes of the Canadian Wildlife Service provided extensive logistical support and advice, and permitted use of his physical and chemical data on the study lakes. Mr. Stephen Beauchamp and Mr. Robert Tordon assisted in the field sampling and in collection of water chemistry data. Mr. John Wright wrote many of the computer programs used, and assisted in data analysis. Ms. Kathy Cook assisted in organization and management of the field program in 1980. Mr. Terrance Collins provided graphics services; and Mr. Ram Raju helped with taxonomy and sample processing. Professor D. G. Frey of Indiana University kindly identified several zooplankton species. The Canadian Wildlife Service, Environment Canada, provided financial support in the form of research contracts OSC80-00057, OSC81-00129, OSC81-00210, OSC82-00113, and OSC83-00190 to Dr. P. Lane, Dalhousie University, and also provided extensive support services.

CHAPTER 1.

INTRODUCTION -- ACID DEPOSITION AND LAKE PLANKTON COMMUNITIES

Substantial portions of the eastern United States, Canada, and northern Europe are being affected by acid deposition (Cogbill and Likens, 1974; Scheider et al., 1979; Wright and Snekvik, 1978; Bangay and Riordan, 1983; Loucks and Glass, 1984; Havas et al., 1984). There has been a ten-fold increase in rainfall acidity over the last few decades (Last et al., 1980). Sulfur and nitrogen oxides are emitted into the air as a result of fossil fuel combustion with sulfuric acid accounting for about 65-70% of the total acidity. Once acid deposits (wet and dry) reach the ground, the extent of effects on lakes is largely dependent upon bedrock geology in the catchment area. Lakes in locations situated over bedrock which provides little buffering capacity, such as Nova Scotia, are very prone to acidification.

Acid deposition causes multiple stresses on lakes which interact complexly within aquatic communities. Henriksen (1980) has determined three general stages of lake acidification:

1. The first stage is characterized by decreased alkalinity, but the bicarbonate buffer system is maintained, and pH levels stay above 5.5 - 6.0.

2. The bicarbonate buffer system is lost during longer periods of stress and severe pH fluctuations occur.

3. The final stage is characterized by chronically depressed pH levels (below 4.7) and an elevation in toxic metal concentrations, especially aluminum.

The most noticeable effects of lake acidification have been documented for fish populations. Symptoms of acid stress in fish include physical deformities, reproductive inhibition, decreased growth, and subsequently a depletion of fish stocks (Fromm, 1980; Harvey, 1980; Schofield, 1976; Muniz

and Leivestad, 1980). Lake trout (Salvelinus namaycush), brook trout (Salvelinus fontinalis), smallmouth bass (Micropterus dolomieui), and walleye (Stizostedion vitreum) are highly susceptible to acid rain (Keller et al., 1980). Atlantic salmon have declined in Nova Scotia recently in rivers below pH values of 5.0, and have disappeared in rivers below pH 4.7 (Watt et al., 1983). Shifts in species composition of fish communities with changes in pH have been documented for lakes in both North America and Europe (Rahel and Magnuson, 1983; Muniz et al., 1984; Somers and Harvey, 1984). Tolerant fish species such as yellow perch (Perca flavescens) become abundant in acidified lakes. Undoubtedly, these changes in fish stocks result in lake-wide alterations in predation patterns which subsequently affect plankton community structure (Fryer, 1980; Eriksen et al., 1980; De Costa, 1975; Lane et al., 1982).

Likewise, lake acidification directly affects much of the foodweb which supports fish production. Zooplankton communities in acidified lakes become less complex with fewer species coexisting as acidity increases. Some groups, such as the daphnilds, are intolerant of increasing acidity and disappear at a pH of approximately 5.0. (Raddum et al., 1980). Abundances of cyclopoid copepods also decrease in acid-stressed lakes (Raddum et al., 1980). Indirect effects of lake acidification on zooplankton, apart from direct effects of increased acidity, include changes in thermal regime, changes in food abundance or quality, increased metal concentrations, and shifts in predation and competition patterns (Malley et al., 1982). Phytoplankton communities exhibit a decrease in diversity (Kwiatkowski and Roff, 1976). As primary production decreases, transparency increases. A strong positive correlation between phaeophytin/chlorophyll ratios and secchi-disc depth has been established in acidified lakes (Raddum et al., 1980). Species shifts and changes in

abundance and productivity of primary producers have been noted, but consistent trends with pH are difficult to delineate (Conway and Hendry, 1982). Green algae and pyrrophytes tend to dominate in acidic lakes, while blue-greens increase at higher pH (Brezonik et al., 1984), but many exceptions to the general trends have been noted (U.S. EPA, 1983). Generally, there is a decrease in pelagic production per unit volume and a concurrent increase in acid-tolerant benthic macrophytes such as Sphagnum and Utricularia. To summarize, acid deposition causes increased acidity in lakes, leading to dramatic shifts in communities of aquatic organisms. The overall change is towards a more oligotrophic system, but an unnatural one which exhibits reduced diversity as compared to naturally-occurring, undisturbed oligotrophic lakes.

To date, there have been few detailed evaluations of whole lake response to acid deposition. The difficulty is to reconcile the direct effects of increasing acidity on the different groups of aquatic organisms with indirect effects related to the substantial shifts in the overall community foodweb, including effects of water chemistry on nutrient availability, changes in primary producers and their herbivores, changes in invertebrate predators, and changes in the fish community. Alterations of composition or abundance at each of these trophic levels may affect other components of the food web through direct interactions, indirect interactions by means of intervening variables along pathways of effect in the food web, or by means of changes in overall community feedback (Lane, 1985).

Management strategies to counteract the effects of lake and stream acidification most often center on some form of liming, whether applied directly to a lake or to tributary streams in the catchment area. The

intent of such efforts has been to reverse both the decline in pH and the declines in productivity and diversity which accompany lake acidification. There is, however, some evidence that increased nutrient supply may partly counteract the process of oligotrophication which seems to occur at reduced pHs (Kerekes et al., 1984). It is possible that some combination of liming and fertilization may be the best management stategy for restoration of acidified lake communities. Without a comprehensive understanding of the structure and function of lake communities, community responses to perturbations such as acidification or the effects of remedial management manipulations will remain difficult to predict.

Few studies concerning the effects of changes in pH on overall plankton community foodwebs have been conducted, and the results are often contradictory (Conway and Hendry, 1982). The work described here attempts to answer the following questions for lakes in Nova Scotia, an area subject to both natural sources of acidity (humic bog drainage) and anthropogenic acid deposition. These questions are important for the understanding of lake systems perturbed by pH shifts, and for design of management strategies:

1) What are the relationships between lake plankton communities and pH, together with associated water chemistry parameters, and what differences in plankton community structure can be found by comparing lakes of different pH levels? (Addressed in Chapter 2).
2) How do plankton community diversity and abundance respond to short-term (less than one year) shifts in pH, such as the depressions encountered during spring snow melt or the elevations resulting from lake liming? (Addressed in Chapter 3).
3) How does nutrient availability, which interacts with changes in pH, affect community responses? (Addressed in Chapter 3).

4) What are the larger-scale (biogeographical) patterns of lake plankton community composition and abundance in relation to pH and the range of other physical and chemical characteristics of lakes in Nova Scotia, and what may be concluded from such patterns concerning long-term adaptation of plankton communities to a range of pH levels? (Addressed in Chapter 4).

Answers to these basic questions have been sought here using several methodologies. Three study lakes were first selected in Kejimkujik National Park for intensive sampling in order to provide base-line data for lake characterizations, and to address question 1: Does increased acidity result both in reduced planktonic species diversity and in reduced productivity? This can be tested by examining adjacent lakes, which are currently at different pH levels, for differences in their plankton communities.

To address questions 2 and 3, one of the study lakes (Beaverskin Lake), with moderate pH but reduced buffering capacity, was selected for in situ experimental manipulations of pH and nutrient concentrations.

Finally, a biogeographical survey of twenty lakes in Nova Scotia, representing a broad range of pH and other limnological variables, was conducted in order to answer question 4.

The significance of this study will be to help clarify the patterns and mechanisms of lake plankton community responses to pH and related water chemistry parameters through the use of statistical analyses of water chemistry-plankton relationships, experimental manipulations, community foodweb modelling, and examination of plankton biogeographical patterns in relation to pH. Comprehensive baseline data will also be established for the study lakes for use in comparisons with future data to assess historical trends.

CHAPTER 2.

CHARACTERIZATION AND COMPARISON OF THREE, ACID-STRESSED LAKES

The purpose of this part of the study is to provide comparative information on the pelagic foodwebs of acidic lakes that are located in a vulnerable area in relation to anticipated stresses from acid precipitation. This information will address the first question posed in the introduction:

1) What are the relationships between lake plankton communities and pH, together with associated water chemistry parameters, and what differences in plankton community structure can be found comparing lakes of different pH levels?

The study lakes in Kejimkujik National Park are particularly interesting because they possess some of the lowest known calcium concentrations in the world (Kerekes, 1980a). The mean annual precipitation to this region has a pH value of 4.64 (wet deposition = 22 kg $SO_4^{=}$/ha. yr). The lakes show signs of acid stress: clear-water Beaverskin Lake has lost almost all of its bicarbonate alkalinity and can be considered to be at stage number two of Henriksen's (1980) model, while coloured Kejimkujik and Pebbleloggitch lakes which receive additional acidity from organic soils have depressed pH values year-round.

Plankton communities of the three lakes will be compared by statistical means to assess relationships with water chemistry, and by means of community food web analysis and modelling to compare structure and functioning of key trophic relationships in each lake.

The work described here was undertaken as a part of the Kejimkujik Calibrated Lake Catchments Program. The Program was initiated as an outgrowth of a joint Canadian Wildlife Service-Parks Canada investigation of the limnology of lakes of the Park. The Canadian Forestry Service had

also cooperated with Parks Canada in completing a biophysical survey of the Park which provided a valuable addition to the background information available for a watershed study. Because of the location in the highly sensitive region of Nova Scotia, the existence of extensive background information and the prospect of long term assurance of site control under Parks Canada, the decision was made to commit the major maritimes Long Range Transport of Atmospheric Pollutants (LRTAP) study to the Kejimkujik Park site (Kerekes, 1977). A variety of hydrological, chemical and biological studies have been conducted and reported on (Kerekes, 1982, 1983). The present study constitutes the planktonic component of the overall research effort.

A. Methods

1. Study Sites

Three study lakes (Pebbleloggitch, Beaverskin and Kejimkujik) were selected to represent a range of limnological factors in Kejimkujik National Park, Nova Scotia (Figures 1, 2, 3). Several morphometric and chemical parameters are summarized in Table 1. Pebbleloggitch and Beaverskin Lakes are small headwaters whereas Kejimkujik Lake is a larger, deeper lake. All of the lakes have silt bottoms and Beaverskin Lake in addition has a dense benthic growth of Sphagnum spp. Pebbleloggitch and Kejimkujik Lakes are highly colored, dystrophic lakes with low pH values. These two lakes are influenced by humic organic soils in their drainage basins, and are more acidic than would be predicted on the basis of precipitation chemistry alone (Kerekes et al., 1982). They both have poor macrophyte development because of poor light penetration in their highly colored waters. Beaverskin Lake is a clear, oligotrophic lake which is not as acidic as the other two and has good littoral macrophyte growth. Kejimkujik and Pebbleloggitch Lakes exhibit similar conductance values; calcium and magnesium concentrations are nearly identical in Beaverskin and Pebbleloggitch Lakes but higher in Kejimkujik Lake (Table 1). The ratios of anions/cations, however, are most similar for Pebbleloggitch and Beaverskin Lakes. Primary production and the carbon measures (DIC, TOC, DOC) are lowest in Beaverskin Lake (Beauchamp, 1983). All of the lakes may be nitrogen-limited at particular times of the year; nitrate plus nitrite concentrations are near the limits of detection. Except for soluble reactive phosphorus (Table 1), Beaverskin Lake exhibits the lowest phosphorus and nitrogen concentrations of the three lakes.

For several years, basic limnological data have been collected on several lakes in Kejimkujik National Park by Environment Canada (Canadian

Figure 1. Morphometric Map of Pebbleloggitch Lake, showing sampling station. Contour lines are water depths in meters. After Kerekes (1975 a).


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300
Meters

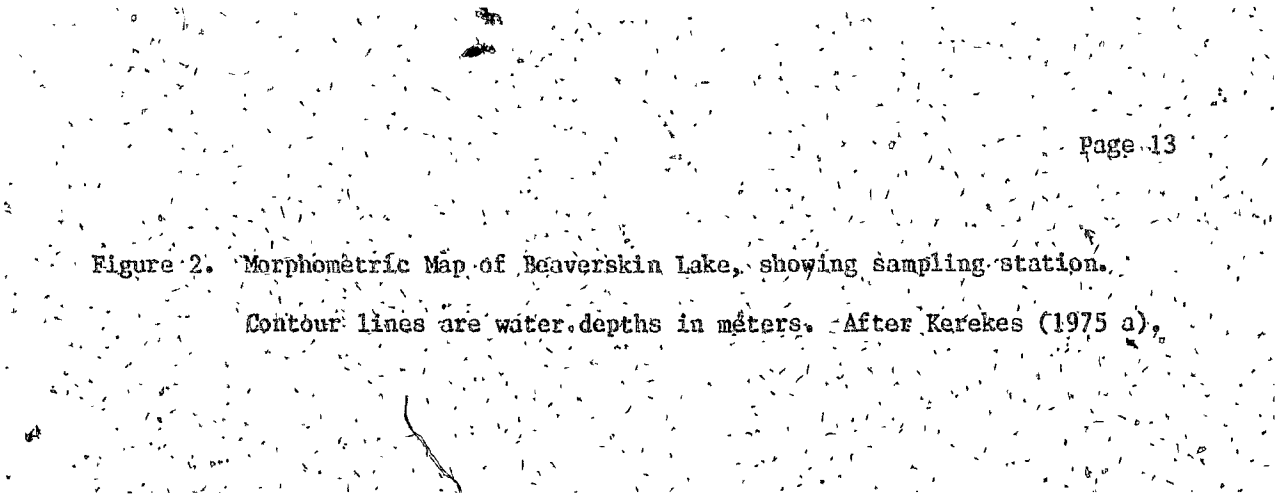
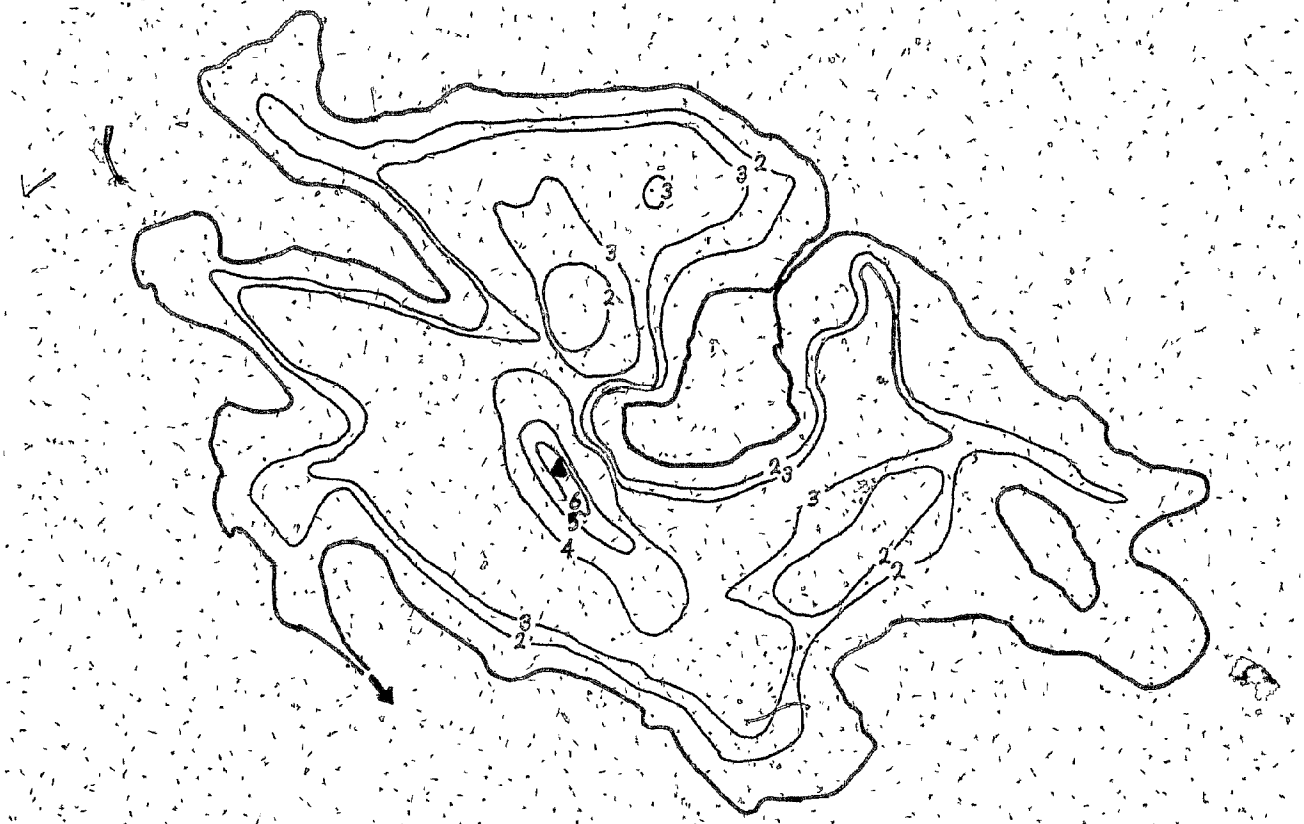


Figure 2. Morphometric Map of Beaverskin Lake, showing sampling station. Contour lines are water depths in meters. After Kerekes (1975 a).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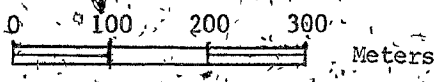
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Figure 3. Map of Kejimkujik Lake, showing sampling station.
After Kerekes (1975 a).

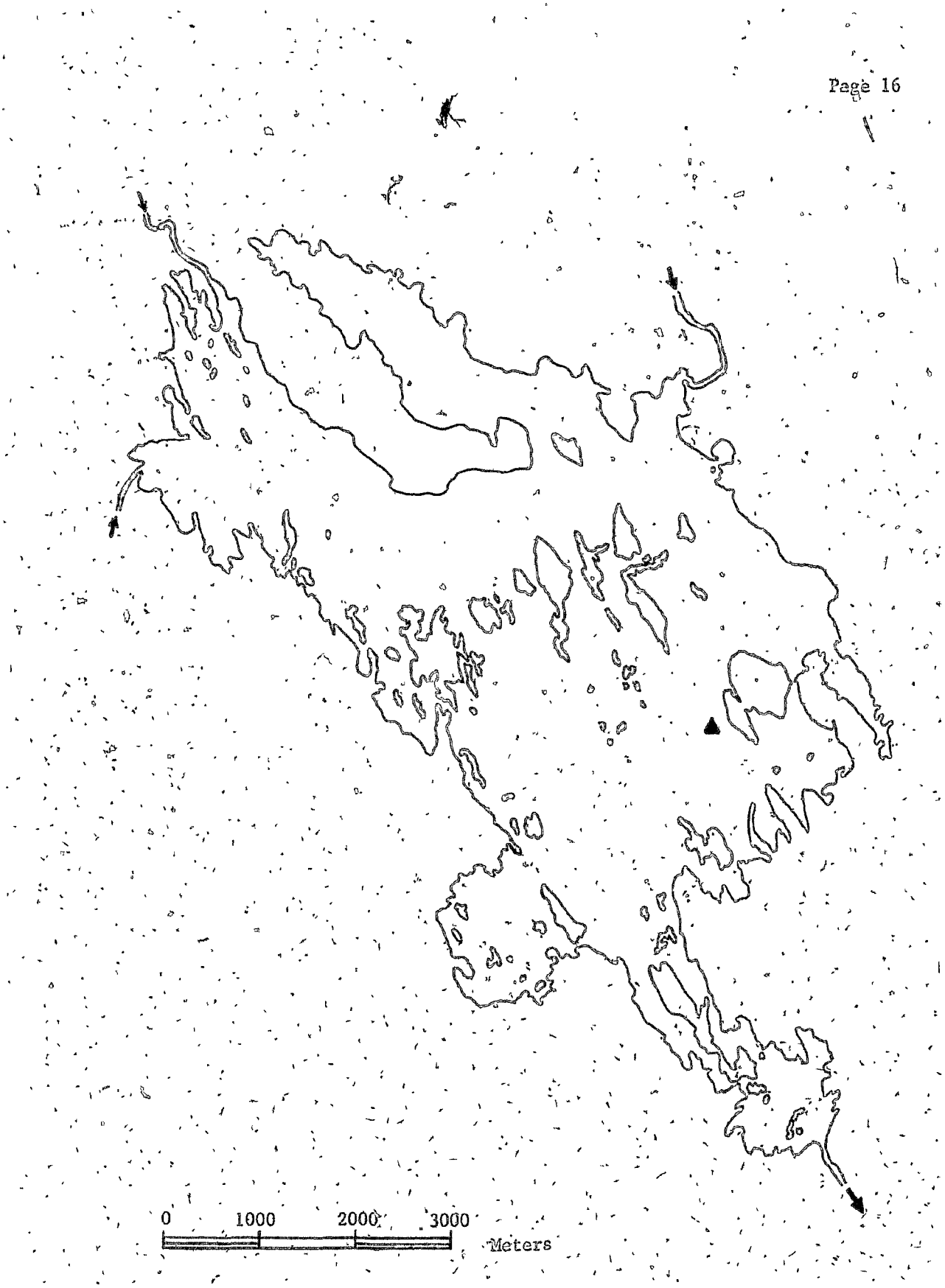
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Table 1. Physical and chemical data for three lakes in Kejimkujik Park, Nova Scotia. A. General Characteristics, B. Morphometry, C. Basic Physical - Chemical Measures, D. Cations and Anions, E. Algal Pigments and Carbon, and F. Nutrients. (After Kerekes, 1980 a,b; Stewart, Freedman and Dale, 1980).

	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
A.	Headwater	Headwater	Downstream
	Highly colored	Clear	Highly colored
	Dystrophic		Dystrophic
	Silt bottom	Silt bottom with peaty organics	Silt bottom
	Poor macrophyte development	Good macrophyte development	Poor macrophyte development
		Lowest planktonic primary production	

Table 1. Continued.

	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
B.			
Surface Area (km^2)	0.334	0.395	24.35
Drainage (km^2)	1.6	1.0	682.0
Maximum Depth (m)	2.5	6.25	19.2
Mean Depth (m)	1.4	2.2	4.4
Retention Time (yr)	0.3	0.91	0.16
C.			
Temp (^oC)	20.0	21.2	19.2
pH	4.49	5.38	4.80
Acidity (mg $CaCO_3$ eq./L)			
Titration to pH 5.6	2.29	0.02	0.91
Titration to pH 8.3	7.24	1.89	0.53
Conductance (umhos/cm)	40.9	25.8	34.0
Dissolved O_2 (mg/L)	8.08	7.83	7.59
% O_2 saturation	92.8	91.7	85.8
Turbidity (N.T.U.)	0.77	0.31	0.53
Color (Hazen units)	80.0	1.25	55.0

Table 1. Continued.

	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
D.			
u-equivalents/l			
Ca^{++}	16.5	16.0	33.9
Mg^{++}	23.8	27.9	38.6
Na^{+}	124.4	124.0	135.7
K^{+}	7.2	6.1	6.1
Fe^{II}	4.8	1.1	5.9
H^{+}	32.6	4.2	15.8
NH_4^{+}	0.5	0.3	0.3
Cations	209.8	179.6	236.4
$SO_4^{=}$	88.2*	57.0	81.1*
Cl^{-}	123.0	124.0	127.8
$NO_3^{=}$	0.6	0.6	0.6
Anions	211.8	181.6	209.5
Total Ions	421.6	361.2	446.6
Anions/Cations	1.01	1.02	0.89

* overestimate due to color interference of the methyl-thymol blue method

Table 1. Continued.

	Pebblelöggitch Lake	Beaverskin Lake	Kejimkujik Lake
E.			
Chlorophyll a (mg/m^3)	1.6	0.67	1.8
Phaeophytin (mg/m^3)	2.7	0.9	2.1
Dissolved inorganic C(mg/L)	0.46	0.34	0.50
Total organic C(mg/L)	16.5	4.2	10.3
Dissolved organic C(mg/L)	11.9	3.6	8.4
F.			
Total phosphorus (mg/m^3)	13.6	5.4	9.1
Total dissolved phosphorus (mg/m^3)	10.5	3.3	5.2
Soluble reactive phosphorus (mg/m^3)	2.2	1.1	1.0
Total nitrogen (mg/L)	0.32	0.20	0.76
Ammonia (mg/L)	0.09	0.05	0.09
Nitrate + nitrite (mg/L)	0.01	0.01	0.01

Table 1. Continued.

	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
N/P Ratios:			
Total nitrogen/ Total phosphorus	23.5	37.0	83.5
Ammonia + Nitrate + Nitrite/Soluble reactive phosphorus	45.5	54.5	100.0

Data are given as mean values over all depths and 8 dates from June 9 to Sept. 23, 1981.

Wildlife Service). Physical parameters (including the annual thermal cycle), water chemistry parameters, primary production and chlorophyll concentrations of the three study lakes have been measured (Drysdale and Timmons, 1980; Kerekes, 1975, 1980 a, b). Precipitation patterns, lake chemistry, and acid loading were given by Kerekes et al. (1982).

II. Physical and Chemical Measurements

Physical and chemical measurements and water sampling were done on the same day or within approximately two days of the plankton sampling. For Beaverskin Lake, data were not available for the last three dates. Details of water chemistry sampling procedures, techniques, and basic data interpretation may be found in Beauchamp and Kerekes (1981). Water chemistry is discussed here only as it relates to the plankton communities.

III. Phytoplankton

Phytoplankton were sampled with a two-liter van Dorn bottle; 350 ml of lake water were collected and preserved with 150 ml of Transeau's preservative (6 parts water: 3 parts 100 percent ethanol: 1 part 40 percent formaldehyde). Samples were taken bi-monthly on Kejimkujik Lake and monthly on Beaverskin and Pebbleloggitch Lakes from June 4, 1980 to October 29, 1980. Each lake was sampled approximately three times per month from June 1, 1981 to September 27, 1981. The Kejimkujik Lake samples were taken at two-meter intervals from the surface to 14 m. Samples from Beaverskin Lake and Pebbleloggitch Lake were taken at one meter intervals (0 to 5, and 0 to 1 m respectively). All samples were taken between 1100 and 1800 hr.

The samples were counted using the Utermohl sedimentation technique with a Zeiss inverted microscope and magnification of 256X. 25-ml sub-

samples were settled and at least two transects of each settling chamber were enumerated. Phytoplankton were counted as number of cells for each species and recorded as number of cells per liter (no large colonial forms were encountered). Species lists and taxonomic references used may be found in Appendix A. A discussion of the statistics of sub-sample counting may be found in Appendix B.

For the common species, 20 individuals were measured for three linear dimensions (length, width, height) and cell volumes were determined. Effective spherical diameters (ESD) were calculated for each species' volume by approximating their shapes to the nearest geometrical figures. Species were divided into three size categories base on their ESD values (1 = 0-9.9 microns, 2 = 10-39.9 microns, 3 = >40 microns). If ESD values were not available, size classes were estimated.

Phytoplankton species were assigned to functional groups based first on large taxonomic groupings: Chlorophyta (greens), Chrysophyta (diatoms and non-diatoms separately), Cryptophyta, Xanthophyta, Cyanophyta (bluegreens), Euglenophyta and Pyrrophyta; on the three size categories of cell volumes given above and third, based on a taxonomic-size combination.

IV. Zooplankton

Zooplankton samples were collected bi-monthly on Kejimkujik Lake and monthly on Beaverskin and Pebbleloggitch Lakes from June 4, 1980 to October 29, 1980. Replicate samples were taken with a 32 l Schindler-Patalas plankton trap. The trap was fitted with a 35 micron mesh net which retained most of the rotifers (Likens and Gilbert, 1970). Sampling dates and depths corresponded to those for phytoplankton. To prevent distortion of their carapaces after collection, the animals were placed in club soda (saturated CO_2 solution) and then preserved in a solution of 4 percent

formaldehyde with 40 g/l sucrose (Haney and Hall, 1973). In 1980, a second zooplankton sampling technique, the Clarke-Bumpus metered net, was used in Kejimkujik Lake for comparative purposes. Comparisons were made of abundance estimates (numbers per m^3) of individual species and zooplankton groups derived from the two methods. Results of the comparisons (Appendix C) indicated superior performance in sampling accuracy for smaller animals by the Schindler-Patalas trap, which had a smaller mesh size. It was subsequently used for all zooplankton sampling.

For enumeration, Wild dissecting microscopes were used at a magnification of 50-60X. Two or three sub-samples were counted and the total volume of the sample determined. Epischura nordenskioldi were counted in four categories: 1) adult females, 2) adult males, 3) copepodite stages CI-III, and 4) CIV-V. Diaptomus minutus and D. oregonensis were enumerated as adult females and males. As it was difficult to distinguish the immatures stages of these two species, copepodites CI-III and CIV-V were combined for both. Tropocyclops sp. and Mesocyclops edax were counted in three categories: adult females, adult males, and immatures. The nauplii of all copepods were not identified and were combined into one category.

After the zooplankton were enumerated, the raw values were converted to organisms per m^3. Zooplankton species were assigned to seven functional groups based on large taxonomic and developmental categories: cladocerans, calanoid copepods, cyclopoid copepods, copepodites, nauplii, rotifers, and macrozooplankton. Total zooplankton biomass units (mg/m^3) per dominant species were calculated by multiplying species densities times mean body weights determined from literature values.

V. Data Analysis

Several calculations were made for water quality data. Percent oxygen saturation was calculated as a function of dissolved oxygen and temperature (Collins and Wright, 1981):

```
% Oxygen saturation = 41.9 * (10.0**(1.202*DO/((DO-15.71*LOG(TMP/12.15+1.0)
                                -4.89)+22.62))-1.0)
```

where DO = Dissolved Oxygen(ppm), TMP = Temperature, and ** indicates an exponent. (Note: * represents multiplication.)

Water chemistry variables required transformation for normality to satisfy the assumptions of multiple regression analysis. Transformations of the form:

$X' = \ln(x/\text{median} + 1) * Q$ where $Q = \max/\ln(\max/\text{median} + 1)$

were employed. See Appendix D for details of data transformation methods.

For correlation and regression analysis of water quality data for Beaverskin Lake, fewer dates were used than for the other two lakes because of missing values.

The Dalhousie University CDC Cyber 170-720 computer was used for all data processing. A special correlation program with summary format was written in Fortran IV. The data breakdown, basic statistics and multiple regression calculations were obtained from the SPSS 8.0 data package. Some of the formats of the final data tables were produced by the report generator facility of SPSS. Sokal and Rohlf (1969) was used for statistical interpretation.

B. RESULTS

I. Kejimkujik Lake

Most of the algal species in Kejimkujik Lake were greens or diatoms (Table 2), with a strong dominance of diatoms in 1981 (Table 3). Similar numbers of species were noted in this lake in both years. No blue-greens were found in 1981. Abundances of all groups increased from 1980 to 1981 with the exception of the blue-greens. In both years, the dominant phytoplankton species in this lake was the diatom Asterionella formosa (Figure 4).

The cladocerans showed the highest diversity of the zooplankton groups in Kejimkujik Lake in both years (Table 4). Numerically, the dominant zooplankton group was the copepods, followed by rotifers (Table 5). Abundances were higher in all zooplankton groups, except copepodites, in 1981 as compared with 1980. The dominant species in 1980 was the calanoid copepod Diaptomus spp., while in 1981 it was the rotifer Keratella cochlearis (Figure 5).

II. Beaverskin Lake

The most diverse phytoplankton group in Beaverskin Lake in both years was the green algae (Table 2). A higher total number of algal species was found in 1981 than in 1980. Cyanophytes accounted for the majority of the total phytoplankton abundance in both years (Table 3). Total abundance was much higher in 1981 than 1980 primarily as a result of an increase in blue-greens. Green algae and euglenoids decreased in abundance from 1980 to 1981.

The phytoplankton community of Beaverskin Lake is strongly dominated numerically by a single species, the blue-green Agmenellum thermale (Figure 4). This is a colonial species which forms plates of small spherical

Table 2. Summary of phytoplankton species diversity (species number) and dominant species in functional groups for three lakes in 1980 and 1981. If only one species is given, it dominated in both years.

	1980		1981	
Pebbleloggitch Lake				
Blue-greens	0		0	
Greens	5	Oocystis lacustris	14	Sphaerocystis schroeteri
Diatoms	7	Asterionella formosa	13	
Miscell.	6	Mallomonas caudata	6	
Beaverskin Lake				
Blue-greens	4	Agmenellum thermale	4	
Greens	10	Sphaerocystis schroeteri	20	
Diatoms	3	Navicula sp.	6	
Miscell.	4	Trachelomonas sp.	5	Dinobryon bavaricum
Kejimkujik Lake				
Blue-greens	2	Agmenellum thermale	0	
Greens	15	Sphaerocystis schroeteri	17	
Diatoms	12	Asterionella formosa	11	
Miscell.	6	Chlorochromonas minuta	8	

Table 3. Comparison of absolute (cells/l) and relative % phytoplankton abundances by functional group for lake and year.

1980	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
1. Diatoms	44,200 (21.2)	6,460 (0.1)	194,000 (61.9)
2. Greens	21,300 (10.2)	384,000 (5.2)	43,500 (13.9)
3. Bluegreens	- -	6,640,000 (90.6)	11,000 (3.5)
4. Chrysophyceans	99,100 (47.5)	109,000 (1.5)	32,000 (10.2)
5. Cryptophyceans	5,030 (2.4)	- -	3,440 (1.1)
6. Xanthophyceans	38,800 (18.6)	- -	29,900 (1.1)
7. Euglenoids	- -	190,000 (2.6)	- -
8. Unknowns	- -	- -	- -
TOTAL	208,000	7,330,000	314,000

1981			
1. Diatoms	7,620 (13.5)	12,400 (0.1)	4,200,000 (91.6)
2. Greens	298,000 (52.6)	113,000 (0.5)	230,000 (5.0)
3. Bluegreens	- -	22,700,000 (97.7)	- -
4. Chrysophyceans	100,000 (17.1)	305,000 (1.3)	53,000 (1.2)
5. Cryptophyceans	3,490 (0.6)	- -	3,930 (0.1)
6. Xanthophyceans	91,800 (16.2)	29,000 (0.1)	98,700 (2.2)
7. Euglenoids	- -	1,240 (0.01)	- -
8. Unknowns	- -	71,800 (0.3)	- -
TOTAL	500,000	23,200,000	4,590,000

Figure 4. Comparison of relative mean phytoplankton abundances by functional group and individual species, for lake and year. Species with an asterisk are not numbered in the diagram, because their relative abundance values were less than 1%.

SPECIES CODES

Functional Group		
(1) Diatoms	1	Asterionella formosa
	2	Tabellaria fenestrata
	3	Tabellaria flocculosa
	4	Navicula sp.
	*5	Frustulia rhomboides
	*6	Synedra ulna
	*7	Hantzschia sp.
	8	Rhizosolenia eriensis
(2) Greens	9	Selenastrum minutum
	*10	Ulothrix variabilis
	11	Gloeocystis gigas
	12	Sphaerocystis shroeteri
	*13	Chlamydomonas sp.
	14	Quadrigula lacustris
	*15	Mougeotia sp.
	16	Schroederia setigera
	*17	Closterium parvulum
	18	Tetradesmus wisconsinensis
	19	Oocystis lacustris
(3) Bluegreens	20	Agmenellum thermale
	21	Chroococcus dispersus
	*22	Dactylococcopsis acicularis
	*23	Anabaena sp.
(4) Chrysophyceans	24	Mallomonas caudata
	25	Mallomonas urnaformis
	26	Mallomonas akrokomos
	27	Dinobryon bavaricum
(5) Cryptophyceans	28	Cryptomonas ovata
(6) Xanthophyceans	29	Chlorochromonas minuta
Euglenoids	30	Trachelomonas sp.

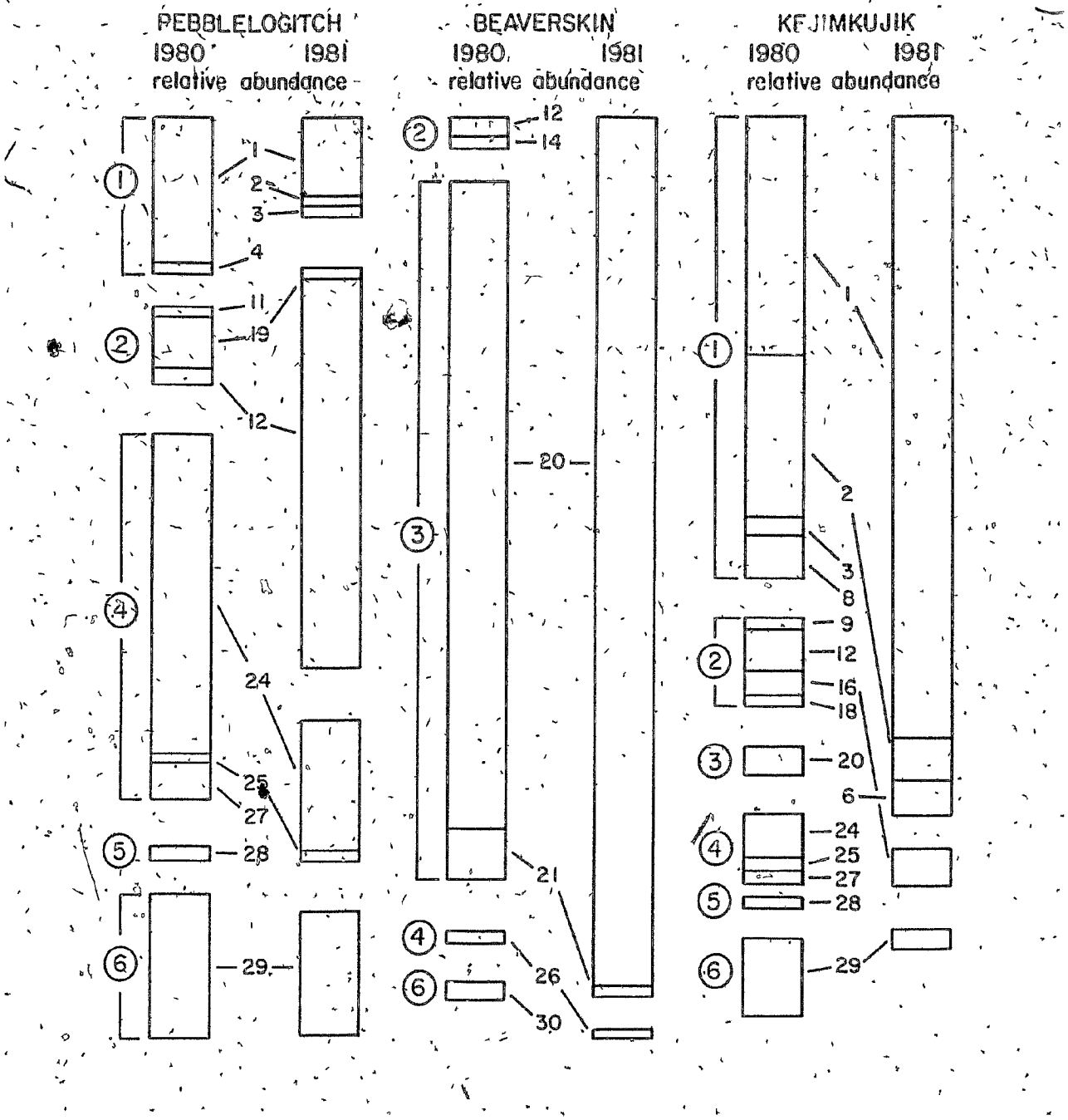

PEBBLELOGITCH
1980 1981
relative abundance
BEAVERSKIN
1980 1981
relative abundance
KEJIMKUJIK
1980 1981
relative abundance

Table 4. Summary of zooplankton species diversity (species number) and dominants in functional groups for three lakes in 1980 and 1981. If only one species is given, it dominated in both years.

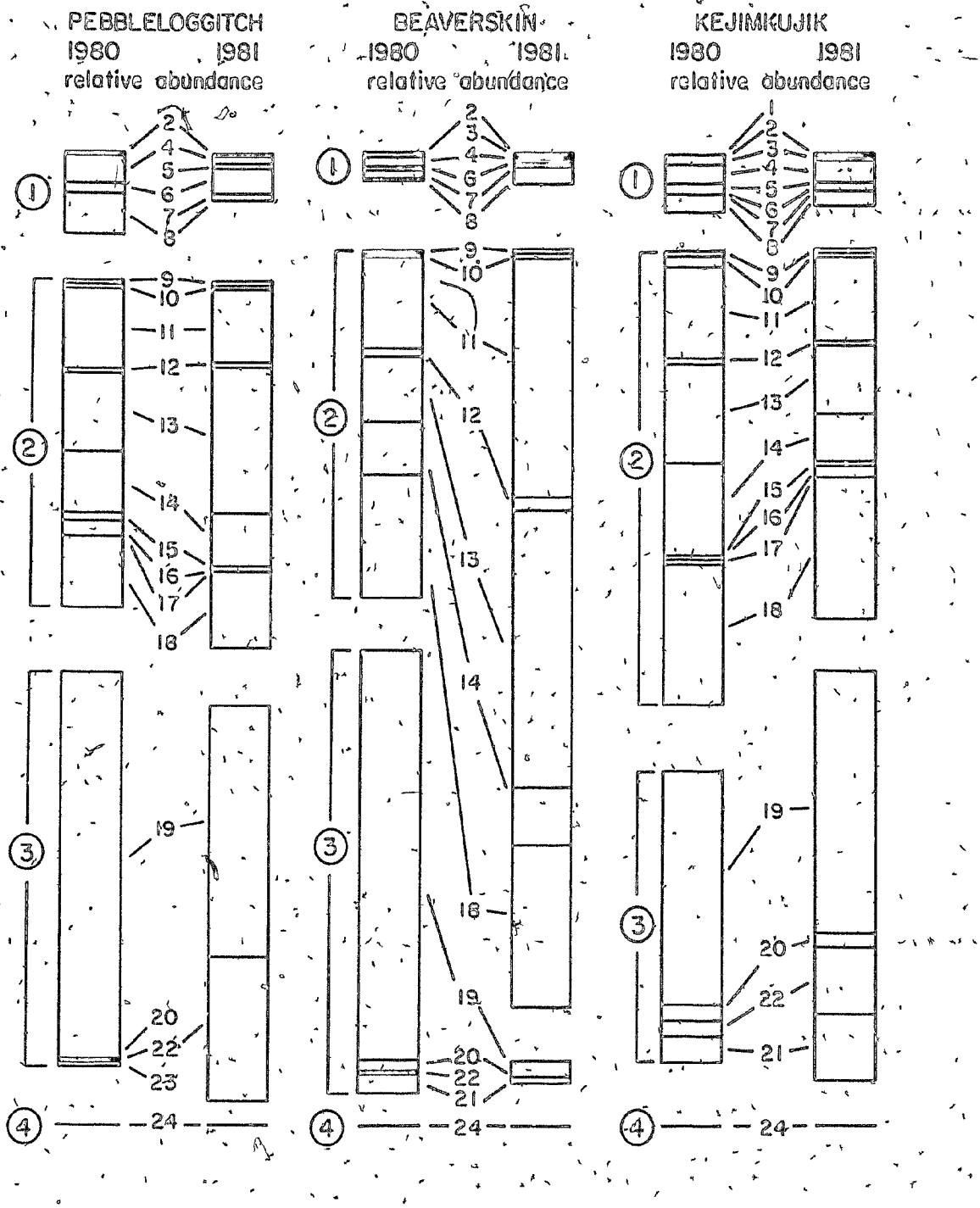
	1980		1981	
Pebbleloggitch Lake				
Cladocerans	5	*Diaphanosoma birgei*	5	*Holopedium gibberum*
Calanoid copepods	3	*Diaptomus minutus*	3	
Cyclopoid copepods	2	*Mesocyclops edax*	1	
Rotifers	7	*Keratella cochlearis*	2	
Macrozooplankton	1	*Chironomus* sp.	1	Water mite
Beaverskin Lake				
Cladocerans	5	*Eubosmina longispina*	6	*Diaphanosoma birgei*
Calanoid copepods	3	*Diaptomus minutus*	3	
Cyclopoid copepods	1	*Mesocyclops edax*	2	
Rotifers	6	*Keratella cochlearis*	2	
Macrozooplankton	0		0	
Kejimkujik Lake				
Cladocerans	13	*Eubosmina longispina*	7	
Calanoid copepods	3	*Diaptomus minutus*	3	
Cyclopoid copepods	2	*Mesocyclops edax*	2	
Rotifers	7	*Keratella cochlearis*	5	
Macrozooplankton	4	*Chaoborus punctipennis*	2	

Table 5. Comparison of absolute (organisms/m^3) and relative (%) zooplankton abundance by functional group for lake and year.

	Pebbleloggfitch 1980	Beaverskin 1980	Kajimkujik 1980
1. Cladocerans	17,000 (10.9)	3,790 (2.7)	5,290 (7.8)
2. Copepod nauplii	13,800 (8.8)	20,000 (14.4)	11,700 (17.3)
3. Copepodites	30,000 (19.1)	21,100 (15.1)	17,800 (26.4)
4. Copepod adults	19,900 (12.7)	17,500 (12.5)	8,630 (35.7)
5. Rotifers	76,300 (48.6)	77,000 (55.2)	24,100 (35.7)
TOTAL	157,000	139,000	67,500
	1981	1981	1981
1. Cladocerans	14,600 (5.1)	3,650 (3.4)	6,390 (5.9)
2. Copepod nauplii	26,200 (9.2)	21,200 (19.7)	19,000 (17.5)
3. Copepodites	75,700 (26.4)	46,300 (43.0)	17,700 (16.3)
4. Copepod adults	29,700 (10.4)	33,500 (31.1)	12,400 (11.4)
5. Rotifers	140,000 (48.9)	3,170 (2.9)	53,000 (48.8)
TOTAL	280,000	108,000	108,000

Figure 5. Comparison of relative mean zooplankton abundances by functional group and individual species, for lake and year.

Functional Group	SPECIES CODES	
(1) Cladocerans	1	Daphnia ambigua
	2	Daphnia catawba
	3	Bosmina longirostris
	4	Eubosmina longispina
	5	Eubosmina tubicen
	6	Holopedium gibberum
	7	Leptodora kindtii
	8	Diaphanosoma birgei
(2) Copepods	9	Epischura nordenskioldi (male & female adults)
	10	Epischura nordenskioldi (CI-CV)
	11	Diaptomus minutus (male & female adults)
	12	Diaptomus oregonensis (male & female adults)
	13	Diaptomus spp. (CIV-CV)
	14	Diaptomus spp. (CI-CIII)
	15	Mesocyclops edax (male & female adults)
	16	Mesocyclops edax copepodites
	17	Tropocyclops sp. (males, females, CI-CV)
	18	Copepod nauplii and copepodites
(3) Rotifers	19	Keratella cochlearis
	20	Kellicottia bostoniensis
	21	Polyarthra vulgaris
	22	Conochilis unicornis
	23	Ploesoma hudsoni
(4) Macrozooplankton	24	Chaoborus punctipennis
		Water mite


PEBBLELOGGITCH
1980 1981
relative abundance
BEAVERSKIN
1980 1981
relative abundance
KEJIMKUJIK
1980 1981
relative abundance
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
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23
24

cells (2 microns diameter). The high abundances of this species are misleading because of its small size. While it comprised over 90 per cent of the total phytoplankton abundance, it accounted for less than 1 per cent of the total algal cell volume in Beaverskin Lake.

The largest number of zooplankton species was found in the rotifer group in 1980 in Beaverskin Lake, while in 1981 the most diverse group was the cladocerans (Table 4). Rotifers made up more than 55 per cent of the total zooplankton abundance in 1980, but were reduced to less than 3 per cent in 1981 (Table 5). Cladocerans showed little change in abundance, while copepods increased from 1980 to 1981. The dominant zooplankton species in Beaverskin Lake in 1980 was the rotifer Keratella cochlearis, but this species was much reduced in 1981 and was replaced in the dominance order by the calanoid copepod Diaptomus minutus (Figure 5).

III. Pebbleloggitch Lake

The majority of phytoplankton species in Pebbleloggitch Lake belonged to the green algae and diatom groups in both years (Table 2). This lake had no cyanophyte species present. More algal species were found in 1981 than in 1980. The most abundant phytoplankton groups were the diatoms and other chrysophytes in 1980, while green algae composed over 50 per cent of the community in 1981 (Table 3). Total algal abundance decreased in Pebbleloggitch Lake from 1980 to 1981. The phytoplankton species composition of Pebbleloggitch Lake was uniform, with no one species strongly dominant. The most abundant algal species in 1980 was the chrysophyte Mallomonas caudata, while in 1981 the most abundant species was the chlorophyte Sphaerocystis schroeteri (Figure 4).

In 1980, the rotifers had the highest number of species of the zooplankton groups in Pebbleloggitch Lake, while in 1981 the cladoceran

group was the most diverse (Table 4). Although the number of rotifer species found in this lake decreased from 1980 to 1981, this group comprised almost half of the total zooplankton abundance in both years (Table 5). Abundances increased from 1980 to 1981 in all groups except the cladocerans. Species composition of the zooplankton was similar in the two years. The dominant species in 1980 was the rotifer Keratella cochlearis (Figure 5), while in 1981 the most abundant species was the calanoid copepod Diaptomus minutus.

C. Discussion

I. Comparison of the three lakes

Of the three study lakes, the phytoplankton communities of Pebbleloggitch and Kejimkujik Lakes were most alike. Both of these highly colored lakes were dominated by green algae and diatoms. Sphaerocystis schroeteri was a dominant green alga and Asterionella formosa the dominant diatom in each. Similar species successions through the course of both sampling seasons were also noted. An early bloom of diatoms was succeeded by green algae, followed by a second diatom bloom. A time-lag difference, however, was noted in the succession patterns of the two lakes. Because Pebbleloggitch Lake is only 2m deep, it warms more quickly in the spring than Kejimkujik Lake. Hence, the bloom of small green algae and Chlorochromonas which normally occurs during June in Pebbleloggitch Lake happens in late August in Kejimkujik Lake.

The phytoplankton community of Beaverskin Lake was quite distinctive in comparison with the other two lakes. It had an abundant blue-green component dominated by Agmenellum thermale. All of the algal groups, with the exception of diatoms, were more numerous in this than in the other two lakes. The seasonal succession pattern in Beaverskin Lake was from greens to blue-greens and back to greens.

Beaverskin and Kejimkujik Lakes were both strongly dominated by a single algal species (Agmenellum thermale and Asterionella formosa respectively), whereas Pebbleloggitch Lake had a more uniform pattern of relative abundance amongst its algal species.

N/P ratios were lowest in Pebbleloggitch Lake and highest in Kejimkujik Lake (Table 1), with Beaverskin Lake intermediate. The total nitrogen/total phosphorus ratio reflects the total nutrient pool, while the

ammonia + nitrate + nitrite/soluble reactive phosphorus ratio reflects the biologically-available nutrients. The dominance of diatoms in Kejimkujik Lake appears to be related to its higher N/P ratio (compared to the other lakes) which may confer a selective advantage on diatoms over greens in nitrogen utilization. Hutchinson (1967) also reported that diatoms (notably Asterionella spp.) flourished at high nitrogen levels, whereas green algae preferred low N/P ratios. Beaverskin Lake had a reduced diatom diversity, perhaps related to its low N/P ratio compared with the other two lakes. The increase in taxonomic diversity in Pebbleloggitch Lake, along with the dominance of greens, suggests that N/P ratios in this lake may be favorable for all functional groups of phytoplankton, although greens would appear to have an advantage.

In summary, a higher N/P ratio in Kejimkujik Lake favoured dominance by diatoms, whereas a lower N/P ratio in Pebbleloggitch Lake was more favorable to greens. Although Beaverskin Lake, with an intermediate N/P ratio, initially appeared to be dominated by blue-greens, greens and chrysophytes became more important when relative abundance was calculated in the absence of A. thermale, which contributed little cell volume.

When mean algal densities over depth for each sampling date for each lake were compared, Beaverskin Lake had the highest standing crops over the year, and Pebbleloggitch Lake showed the lowest algal abundances (Table 3). Kejimkujik Lake exhibited peaks in mean cell density in early June (1.3×10^7 cells/liter) and late September (1.1×10^7), and had the highest densities among the study lakes during this time. Beaverskin Lake exhibited the highest densities in mid-summer (1.0×10^7 cells/liter on July 30), whereas Pebbleloggitch Lake had a density peak in mid-August.

Kwiatkowski and Roff (1976) studied lakes in the Sudbury, Ontario region falling within a pH range similar to that of the present study lakes. While species diversities noted in this study were similar to those found by Kwiatkowski and Roff (1976), species composition was not. In the present study, a dominant blue-green component was found in the least acidic study lake (Beaverskin), while no blue-greens were noted in the most acidic Lake (Pebbleloggitch). In contrast, Kwiatkowski and Roff (1976) noted increased dominance of blue-greens at the lowest pH values. They also noted a trend toward increasing dominance by greens at higher pH values, while in the present study our most acidic lake was dominated by greens in 1981.

The phytoplankton diversities found here are lower than reported by Yan (1979) for Clearwater Lake in Ontario, a more acidic lake (pH 4.2) than Pebbleloggitch Lake (pH 4.5). Yan (1979) suggests greater sampling frequency and acid tolerance in Clearwater Lake species to explain the higher algal diversity observed compared with Kwiatkowski and Roff (1976). The present sampling regime, however, was similar to Yan's, and two of the study lakes (Pebbleloggitch and Kejimkujik) receive naturally acidic bog drainage (Kerekes et al., 1982) which has for some time contributed to the acidity of these two lakes. Yan (1979) and Yan and Stokes (1978) reported Peridinium spp. as dominant species in acid lakes in Ontario; however, this genus is rare in the present study lakes.

The three lakes exhibited similar species composition in their zooplankton communities in both number and dominant species per functional group (Table 4). Cladocerans and macro-zooplankton constituted minor groups in all three lakes whereas copepods and rotifers were the most abundant groups. Generally, the latter two groups were similar in terms of relative abundances for all lakes and both years except in Beaverskin Lake

in 1981 when rotifers were rare and copepods very abundant. Thus, the three zooplankton communities were more similar in 1980 than 1981. The dominant cladoceran species changed from one year to the next except in Kejimkujik Lake (Table 4).

The dominant copepod (Diaptomus minutus) and cladocerans (Eubosmina longispina and Holopedium gibberum) in the study lakes have been found to be dominant in other acid environments (Confer et al. 1983, Hendry et al. 1982). Kejimkujik Lake exhibited the most diverse cladoceran and macrozooplankton groups, which is probably related to its larger size and greater physical heterogeneity.

The overall dominance of Diatomus minutus in all lakes in both years agrees with Sprules (1975) who demonstrated this species' wide tolerance in acid-stressed lakes in Ontario. D. minutus exhibited a similar developmental sequence in all lakes and for both years. Some differences were noted in the rotifer communities in 1981 as compared with 1980: Keratella cochlearis was much reduced in Beaverskin Lake and Conochilus unicornis was absent. Different successional patterns were noted: K. cochlearis was replaced by C. unicornis in Pebbleloggitch Lake in late summer of 1981, which did not happen in 1980. K. cochlearis did not show the consistent increase over the season in Kejimkujik Lake in 1981 which it did in 1980.

The zooplankton communities of the three study lakes have maintained high diversities in spite of the relatively high acidities encountered. The zooplankton diversities were identical in Beaverskin Lake (pH 5.4) and Pebbleloggitch Lake (pH 4.5), the extremes of pH for the study lakes. The zooplankton communities of Kejimkujik Lake (pH 4.8) and Pebbleloggitch Lake had much higher diversities (9 or more crustacean zooplankton species) than

recently acidified lakes of comparable pH in the La Cloche region of Ontario (Sprules 1975), which typically had fewer than six species below a pH of 5.0. Confer et al. (1983) also noted that reduced zooplankton diversities in Adirondack Mountain lakes occurred below pH 5.0, again in contrast to the present study lakes. Roff and Kwiatkowski (1977), however, found crustacean and rotifer zooplankton diversities comparable to those of the present study in lakes of comparable pH in the Sudbury region in Ontario. Sampling intensities in the Roff and Kwiatkowski (1977) study and the present study were greater than that used by Confer et al. (1983) or Sprules (1975), which may explain the contrast in diversities.

While dominant species and the number of species in each of the functional groups were similar in these lakes, their densities were not. Pebbleloggitch Lake had the highest zooplankton abundances per volume and lowest on an areal basis. This is partially because of the greater mean depths of Kejimkujik Lake (4.4m) and Beaverskin Lake (2.2m) compared with Pebbleloggitch Lake (1.4m). The high mean zooplankton abundances per unit volume noted in Pebbleloggitch Lake may be partially sustained by detrital resources since this brown-water lake is shallow and subject to turbulent mixing.

Mean cladoceran densities (number/m^3) were similar in both years for all lakes (Table 5). Beaverskin and Pebbleloggitch Lakes had increased numbers of copepodites and adult copepods, while Kejimkujik Lake and Pebbleloggitch Lake had more nauplii in 1981 than 1980. Rotifers approximately doubled in Kejimkujik and Pebbleloggitch Lakes but declined drastically in Beaverskin Lake, whereas macro-zooplankton remained constant from 1980 to 1981. Total zooplankton densities increased substantially in 1981 compared with 1980 in Kejimkujik and Pebbleloggitch Lakes, but values were slightly reduced in Beaverskin Lake.

The zooplankton increase from 1980 to 1981 in Kejimkujik and Pebbleloggitch Lakes was paralleled by increased mean total algal abundance in these two lakes (Table 3). Kejimkujik Lake was dominated by diatoms and Pebbleloggitch Lake by greens in 1981, which are both appropriate food sources for zooplankton. In Beaverskin Lake, total phytoplankton also increased in 1981 mostly because of a large increase in the blue-green Agmenellum thermale. Since this alga is potentially toxic to grazing zooplankton (Arnold, 1971), it is not surprising to observe a decrease in overall zooplankton density in Beaverskin Lake in 1981 as compared with 1980.

In both 1980 and 1981, a gradient of zooplankton biomass was observed beginning with the lowest levels in Kejimkujik Lake, to the highest in Pebbleloggitch Lake (Table 6). This gradient ranged over a two-fold change in biomass. As with the biomass-abundance example of Agmenellum thermale above, comparisons should only be made in relation to definite reference points. This biomass gradient is based on per m^3 values. If the biomass values were related to surface area, the gradient would probably be reversed. These zooplankton biomass values are compared with several other production values for the three lakes and two study years in Table 6. In Pebbleloggitch Lake, total organic carbon, dissolved organic carbon, total phytoplankton density and volume, chlorophyll concentration and zooplankton biomass increased from 1980 to 1981. In Beaverskin Lake, total phytoplankton density and volume, chlorophyll concentration and zooplankton biomass increased from 1980 to 1981, whereas total organic carbon and dissolved organic carbon decreased. In the largest lake, Kejimkujik, total organic carbon, total phytoplankton density and volume, chlorophyll concentration and zooplankton biomass increased. Dissolved organic carbon

Table 6. A comparison of some production-related measures for the three lakes and two years. Carbon and chlorophyll values are annual means; plankton values are means over the summer sampling periods.

	Pebbleloggitch Lake		Beaverskin Lake		Kajimkujik Lake	
Variable	1980	1981	1980	1981	1980	1981
Total Organic Carbon (mg/l)	13.2	19.0	8.3	7.0	13.1	14.0
Dissolved Organic Carbon (mg/l)	11.5	13.8	6.8	5.8	10.9	10.9
Total Phytoplankton Volume (u^3/l)	3.70×10^7	71.7×10^7	82.3×10^8	216.5×10^8	55.9×10^7	570.4×10^7
Total Phytoplankton Density (#/l)	2.1×10^5	5.0×10^5	73.3×10^5	232.0×10^5	3.1×10^5	45.9×10^5
Chlorophyll (mg/m^3)	1.5	2.8	1.4	1.6	1.3	2.9
Zooplankton biomass (mg/m^3)	243.0	421.0	151.0	257.0	123.0	133.0

remained at the same level over the two years. In comparing the three lakes, Pebbleloggitch had the highest and Kejimkujik Lake the second highest levels of total and dissolved organic carbon. Total phytoplankton volume and density were lowest in Pebbleloggitch Lake in comparison with the other two lakes. There was a general trend of decreasing total phytoplankton cell volume with decreasing pH (Table 6). The highest zooplankton biomass was found in Pebbleloggitch Lake, which is the most acidic (Table 6). The zooplankton population in this lake is likely dependant on detritus and associated bacteria as a food source, which is supported by the high total organic carbon levels, and low phytoplankton abundances and cell volumes.

II. Plankton--Water Chemistry Relationships

Multiple regression analysis is often used in ecological research to define emirically-derived relationships between a dependant variable and a set of independant predictor variables. Those predictor variables which contribute significantly to a reduction in the unexplained variance of the dependant variable may be identified, and the overall significance of the multiple regression determined. Examples of the use of multiple regression in ecology are numerous. Brylinsky and Mann (1973) determined that on a wide geographical basis, solar energy input was a better predictor of lake productivity than nutrient concentration, but within narrower ranges of latitude nutrient variables are more important. Hameedi (1976) examined factors influencing marine primary productivity, comparing estuarine and coastal environments. Jones (1977) determined that a significant portion of the variance in numbers of bacteria could be explained by physical and biological variables (Jones, 1978). Mountford (1980) used multiple regression to study predation on marine zooplankton by ctenophores. Mathur and Robbins (1980) used the technique to predict the effects of thermal discharge to a freshwater impoundment on zooplankton production. Boswell et al. (1980) studied relationships between physiochemical parameters and ATP concentrations to aid in assessment of reservoir plankton dynamics. Wyngaard et al. (1982) studied freshwater copepod population dynamics, using multiple regressions to delineate relationships between copepod birth rates and prey populations.

A limitation of the technique is that regression relationships do not constitute strong evidence of causal relationships, limiting the scope of interpretation of results. Assumptions which must be satisfied include normality of the variables (requiring transformation if necessary) and lack

of strong correlations between predictor variables.

Table 7 summarized significant results from the multiple regression analyses of water chemistry variables (predictors) and plankton species (dependant variables) in 1980 and 1981. The statistical model design was linear stepwise multiple regression, in which the significance of each predictor variable is determined as it is added to the regression equation, and the overall significance of the regression is determined. Significance ($p < .05$) for a water chemistry variable in a partfoular lake is indicated by the initial letter of that lake name (see key for Table 7). Species having significant overall multiple regressions are noted in the "overall" column. An asterisk denotes significance in both years. Multiple regression results were unavailable for Pebbleloggitch Lake in 1980 because of insufficient chemical data. Pairwise Pearson correlation coefficients were also calculated between water chemistry and plankton variables.

Relationships between species and water chemistry variables for the three study lakes were inconsistent and clear patterns were difficult to delineate. The most discernable ones were those involving pH. In acidic Pebbleloggitch Lake, all significant correlations of pH with both zooplankton and phytoplankton species were positive, suggesting that pH has an adverse effect and that Pebbleloggitch Lake has a critical pH level for planktonic organisms. Correlations with pH, however, were not as consistent for the other two lakes. Usually, significant correlations of pH with phytoplankton for Beaverskin and Kejimkujik Lakes were negative, except for that with Schroederia setigera, which had a positive correlation with pH in Kejimkujik Lake. Correlations of pH with zooplankton for Beaverskin and Kejimkujik Lakes also varied greatly, although there appeared to be negative correlations with rotifers for both lakes.

Table 7. Summary of significant variables from multiple regression analyses for three lakes.

A. Phytoplankton B. Zooplankton

A. Phytoplankton

	Species	Over all	Multiple regression component variable													
			TMP	DO	O2S	PH	TRB	A56	A80	CHL	PHA	DIC	TOC	DOC	TP	TDP	SRP	TN	NH4	NO3
A.	Phytoplankton																			
B04	Agmenellum thermale	Bk	B									k	b	b	B	B	B	k		B
B05	Chroococcus dispersus	B	B	B		b									B	B	B	B		B
D03	Asterionella formosa	k	k				P					k								
D04	Tabellaria fenestrata	k	Pb		P		P								P		BK			B
D05	Tabellaria flocculosa	k										k								
D08	Eunotia pectinalis																			
D09	Eunotia arcus	P	P	P				P		K					P		K			
D11	Synedra ulna	PK	PK	K	PK	K	P	P			P			P	P	P	K	P		
D13	Navicula sp.	K	K	K	K	K	K		K	K			PK	K	K	K	K	K		
D15	Frustulia rhomboides							B												
G03	Arthrodesmus octocorne																			
G06	Chlamydomonas sp.																			
G07	Mougeotia sp.																		k	
G08	Selenastrum minutum	K																		

Table 7 A. Continued

	Species	Over all	Multiple regression component variable														
			THP	DO	O2S	PH	TRB	A56	A83	CHL	PHA	DIC	TOC	DOC	TP	TDP	SRP	TN	NH4	NO3
G09	Closterium parvulum																			
G22	Schroederia setigera	K	K		K	K	K								k			K	k	
G23	Gloeocystis gigas																			
G27	Oocystis lacustris	PB			P	P	P	P			PB	P	B	P			P	P		
G36	Sphaerocystis schroeteri	BK	B	BK			K				K						K			
G42	Elakatothrix gelatinosa	K																		
C01	Dinobryon bavaricum	BK	BK				K				K	BK	K						B	
C03	Dinobryon Divergens	K	K	K	K	K												K		
C05	Mallomonas caudata	BK	BK	BK			K	K	B		K	B	B	k			B	B		B
C06	Mallomonas urnaformis	K	K	K													K			
R01	Cryptomonas ovata																			
X02	Chlorochromonas minutus	B*	B				B										B		B	
U01	Unknown (large)	B	B	B								B					B		B	

Key: P = significant in Pebbleloggitch Lake, 1981
B = significant in Beaverskin Lake, 1981
b = significant in Beaverskin Lake, 1980
K = significant in Kejimkujik Lake, 1981
k = significant in Kejimkujik Lake, 1980
* = significant in both years

Table 7. Continued

B. Zooplankton

	Species	Over all	Multiple regression component variables															
			TMP	DO	O2S	PH	TRB	A56	A83	CHL	PHA	DIC	TOC	DOC	TP	TDP	SRP	TN	NH4	NO3
02	Daphnia catawba	B*	*	b			b			K	b	BK						b		
03	Bosmina longirostris																			
04	Eubosmina longispina	*			k	k				B					B	B		k		
05	Eubosmina tubicen	k		k			P	k												
06	Holopedium gibberum	*	k	b		k					k		k		k			k		
07	Leptodora kindtii	k		k						k			k		k					
08	Diaphanosoma leuchentenbergianum	B*	*	kB			B			B	B	Bk	k		k		B		b	
16	Epischura nordenskioldi adult	b*			b	*				bk										
18	Epischura nordenskioldi copepodites(CIV-CV)	Bk	B				k							k	B					
19	Epischura nordenskioldi copepodites(CI-CIII)	Bk	B	B			k			B				k	B				B	
20	Diaptomus minutus adult	PB*	k	k		bk	k	P	k	k	B	Bk	P	k				k	b		
22	Diaptomus oregonensis adult	bk	b				b			k		bk						k		
24	Diaptomus spp. copepodites (CIV-CV)	**	B			b	*	B		*k		bk	B					k		
25	Diaptomus spp. copepodites (CI-CIII)	b*		k		b	b			bk		k								

Table 7 B. Continued

	Species	Over all	Multiple regression component variable														
			TMP	DO	O2S	PH	TRB	A56	A83	CHL	PHA	DIC	TOC	DOC	TP	TDP	SRP	TH	NH4	NO3
26	Mesocylops edax adult	b																		
28	Mesocylops edax copepodites (CI-CV)	k				P	Pk									Bk	k		k	
32	Copepod nauplii																			
35	Keratella cochlearis	**		k			k													
36	Kellicottia bostonensis	*		k			k					k	k	k		k				
37	Conochilus sp.	k																		
38	Polyarthra vulgaris																			

Key: P = significant in Pebbleloggitch Lake, 1981
B = significant in Beaverskin Lake, 1981
b = significant in Beaverskin Lake, 1980
K = significant in Kejimkujik Lake, 1981
k = significant in Kejimkujik Lake, 1980
* = significant in both years

Table 7. Continued

Key to Variable Codes:

1. Physical/Chemical -

TMP - Temperature (^{o}C)

DO - Dissolved oxygen (mg/l)

O2S - Oxygen saturation (%)

PH - pH

TRB - Turbidity (N.T.U.)

A56 - Mineral acidity (mg/l)

A83 - Total acidity (mg/l)

CHL - Chlorophyll a (mg/m^3)

PHA - Phaeophytin (mg/m^3)

DIC - Dissolved inorganic carbon (mg/l)

TOC - Total organic carbon (mg/l)

DOC - Dissolved organic carbon (mg/l)

TP - Total phosphorus (mg/m^3)

TDP - Total dissolved phosphorus (mg/m^3)

SRP - Soluble reactive phosphorus (mg/m^3)

TN - Total nitrogen (mg/l)

NH4 - Ammonia (mg/l)

NO3 - Nitrate + nitrite (mg/l)

When the multiple regression analysis results were compared among lakes (Table 7), temperature and total phosphorus explained more of the plankton variance than other variables in Beaverskin Lake, while total turbidity and total organic carbon were the two most significant predictor variables for Pebbleloggitch Lake. For zooplankton, Leptodora kindtii and immature Mesocyclops edax were the species which had the largest portions of their variances explained by the water chemistry variables in Kejimkujik Lake. Diaphanosoma birgei and Epischura nordenskioldi (CI-III) were the species with the largest proportions of explained variance in Beaverskin Lake, as were Diaptomus minutus (adult females) and immature Mesocyclops edax in Pebbleloggitch Lake.

The phytoplankton species which were best explained by the water chemistry variables in Pebbleloggitch, Beaverskin, and Kejimkujik Lakes respectively were Oocystis lacustris, Mallomonas caudata and Navicula sp. Oocystis lacustris had significant interactions with total nitrogen, total phosphorus, and total dissolved phosphorus. M. caudata had significant interactions with nitrate, total phosphorus, and soluble reactive phosphorus, and Navicula sp. had significant interactions with total phosphorus, total dissolved phosphorus, and soluble reactive phosphorus. While these species were not abundant in their respective lakes, they did serve as indicators of nutrient conditions.

Many of the major zooplankton species in Kejimkujik Lake had significant amounts of their variation explained by the overall water chemistry data in both years. Eubosmina longispina, Holopedium gibberum, Diaphanosoma birgei, adult female Epischura nordenskioldi and Diaptomus minutus, Keratella cochlearis and Kellicotia bostoniensis had significant overall multiple regressions in both years. Beaverskin Lake had fewer consistent results between years, with only Daphnia catawba, Diaptomus spp.

copepodites and Keratella cochlearis showing significant overall regressions in both years. Algal species results were quite inconsistent in the two years. Only Chlorochromonas minuta in Kejimkujik Lake was significant overall in both years.

Individual factors which explained significant portions of the plankton species variances were not the same in the two years, which suggests that the plankton responded to the physical-chemical environment in different ways. Different biological interactions in the two years, which are not considered in multiple regression analyses, may contribute to the observed differences in response patterns.

Species showing significant interactions with the greatest number of water chemistry variables were also not consistent within a lake between years. In 1980, in Beaverskin Lake, the zooplankton and phytoplankton species which were significantly related to water chemistry variables were Daphnia catawba and Agmenellum thermale, while in 1981 they were Diaphanosoma birgei and Mallomonas caudata. In Kejimkujik Lake in 1980 the species most related to the water chemistry variables were Diaptomus minutus (females) and Mallomonas caudata while in 1981 they were Leptodora kindtii and Navicula sp. Results were unavailable for Pebbleloggitch Lake in 1980, but in 1981 the species whose variations were best explained by the water chemistry data were Diaptomus minutus (females) and Oocystis lacustris.

Factors accounting for the greatest portion of plankton species variance in 1980 were temperature, dissolved oxygen and chlorophyll in Kejimkijik Lake; and pH, dissolved oxygen and turbidity in Beaverskin Lake. In 1981, the important factors were total phosphorus and pH in Kejimkujik Lake, total phosphorus and temperature in Beaverskin Lake; and total

phosphorus, total organic carbon and turbidity in Pebbleloggitch Lake. There was some degree of consistency between lakes in that dissolved oxygen was an important factor in all lakes in 1980 and total phosphorus was important in all lakes in 1981. There was, however, no consistency within a lake between years in water chemistry variables contributing significance to the multiple regressions.

A qualitative foodweb modelling technique, loop analysis, was used to provide additional information on structure and causal relationships of the foodwebs of the three lakes. The models were derived from the field data for the three lakes for 1981 by Dr. P. A. Lane, and are used here with her permission. See Appendix E for details on methodology and construction of models, and resulting model diagrams. Comparisons will be made between the model results and the multiple regression results for 1981 only (significant results for the 1981 regressions are indicated in Table 7 by capitalized lake name initials - see Table 7 key).

The resulting community network diagrams (Appendix E, Figures E.2, E.3, E.4) are essentially three-layered systems, with three major nutrient variables and three major phytoplankton variables. Each of the main phytoplankton groups has one or more herbivores, and each diagram has several higher carnivore groups. In each model, a sub-structure comprising detritus, rotifer groups and carnivores connects to the rest of the diagram through an algal variable.

Analysis of these models can help to clarify the causal relationships underlying some of the statistical patterns noted in the multiple regression analyses. Many of the variables used for the regressions do not appear explicitly in the foodweb models; however, the nutrient variables do appear, along with a detrital variable which may be represented by the particulate organic carbon variable and which is likely related to

turbidity.

The loop model for Kejimkujik Lake (Appendix E, Fig. 2) shows that algal group 3 depends on the nutrient variable NP, which is a nitrogen-phosphate complex. The only member of A3 which has a significant regression with a nutrient variable is Eunotia arcus, which was significant with total dissolved phosphorus. Algal variable A2 depends on silica and phosphorus, and several members of A2 had total phosphorus as a significant regression component variable. Several members of A1 also had significant regression components involving either total phosphorus or total dissolved phosphorus, while the model demonstrates that A1 depends directly on phosphorus in the P and NP nutrient variables. For the Kejimkujik Lake zooplankton, Daphnia catawba had a significant regression with chlorophyll. This herbivore (Z7) depends on A1 in the model, and in turn is eaten by Z12, which is Leptodora kindtii. L. kindtii is a relatively rare predator in Kejimkujik Lake, and so predation pressure on D. catawba is likely moderate. This helps explain why this herbivore showed the significant relationship with chlorophyll, since its predator is probably not sufficiently numerous to absorb increases in the herbivore population.

The model for Beaverskin Lake (Appendix E, Fig. 3) differs from the other two lake models in the inclusion of the NH (ammonia) variable, and its special relationship to the blue-green algal variable A. Blue-greens are known to be nitrogen-fixers, and the component species of A (Agmenellum thermale and Chroococcus dispersus) showed significant regression components with both the nitrogen and phosphorus variables. The blue-greens are not grazed upon by any herbivores in the model, and so their relationships to the nutrient variables are not obscured by relationships to higher trophic levels. For zooplankton, Eubosmina longispina and

Diaphanosoma birgei, members of Z8 and Z7 respectively, had chlorophyll as a significant predictor in their multiple regressions. These grazers depend on the algal species in model variable A2, and Z7 also eats A1.

The Pebbleloggitch Lake foodweb model (Appendix E , Fig. 4) is similar to that for Beaverskin Lake, except that it has no blue-green algal component, and the detritus variable assumes greater importance as a food source. In the models for the other lakes, detritus served as food for the rotifer variables only, while in the Pebbleloggitch Lake model, zooplankton nauplii and Diaptomus spp. copepodites depend on D for food. This reinforces the evidence presented earlier that detritus is of greater nutritional importance in this lake than in the other two. Many of the significant interactions between algal species and the regression variables involve total organic carbon, turbidity, oxygen and temperature. It seems that physical factors in this lake are more impotant influences on the phytoplankton than are the nutrient variables.

In all of the models, variable Z9 (Epischura nordenskioldi) is a satellite variable for A3. This means that Z9 is not involved in feedback loops with any variables other than A3, and thus it buffers A3 against any changes. A3 is therefore not expected to show significant relationships with any of the other loop variables. The multiple regressions showed only one significant relationship between an A3 species and a nutrient variable (Eunotia arcus and TDP in Kejimkujik Lake).

The models all show that in these planktonic foodwebs, variables Z6 (Diaptomus spp.), Z10 (Mesocyclops edax), and Z12 (Leptodora kindtii) are the top carnivorous species.

CHAPTER 3.

ENCLOSURE EXPERIMENTS

Experimental work was undertaken *in situ* in order to answer the following questions:

How do plankton community diversity and abundance respond to short-term shifts in pH, such as the depressions encountered during spring snow melt or the elevations resulting from lake liming?

How does nutrient availability, which interacts with changes in pH, affect community responses?

Two years of experimental work were conducted in 1981 (Year I) and 1982 (Year II) to address these questions. The first years work consisted of a preliminary experiment using enclosures, or limnocorrals, to test the effects of acidification and liming on the zooplankton community. The second years work used larger experimental enclosures to examine the effects of acidification, liming and nutrient enrichment on both the phytoplankton and zooplankton communities.

The null hypotheses to be tested in these experiments are:

1) There are no significant differences in mean abundances of the plankton groups among experimental treatments.

2) There are no significant differences in mean abundances of the plankton groups among sampling dates.

3) There are no significant differences in mean abundances of the plankton groups among sampling depths.

4) There are no significant interactions among the above three factors.

Analysis of variance will be used to partition variance in the data among the above factors and to test for significant effects of each.

In addition to plankton abundances, zooplankton egg ratios were measured. The egg ratio (average number of eggs per female of a zooplankton species) has been found to be a sensitive measure of sub-lethal

stress resulting from exposure to various toxic materials in both laboratory and field mesocosm systems (Reeve et al., 1977; Berdugo et al., 1977; Moraitu-Apostolopoulu, 1979; Urech, 1979). Egg production also is regulated by available food supply (Checkley, 1980), and reflects physiological state in relation to stress from toxicants in doses below those causing mortality (Sullivan and Pilson, 1983).

Zooplankton egg ratio values are often used to calculate zooplankton production rates in cases where it is possible to distinguish between cohorts. No attempt will be made to calculate production rates from the present data. Egg ratio values are used here as a measure of stress to compare species response over time between the treatments applied. Decreasing egg ratio for a particular species is considered to reflect increasing physiological stress, either as a direct effect of changing pH, or through changes in associated water chemistry variables or food supply at different pH levels.

The National Research Council of Canada (NRCC, 1981) reported that, "Atmosphere transport plays a key role in the acidification phenomenon in Eastern Canada. . . . Maritime tropical air masses which push slowly northward from the Gulf of Mexico and accumulate pollutants from the heavily industrialized regions which they transverse, contribute a major portion of the acidic precipitation . . . . which falls in Eastern Canada." The geographical relationship of the northeastern United States and the experimental location, Beaverskin Lake (Kejimkujik National Park), is represented in Fig. 6. Beaverskin Lake is a small (41.8 ha surface area), relatively shallow (2.19 m mean depth), clear oligotrophic lake. It was chosen for experimental work because of its intermediate size and depth (making it suitable for limnocorral installation), relatively high pH (5.4)

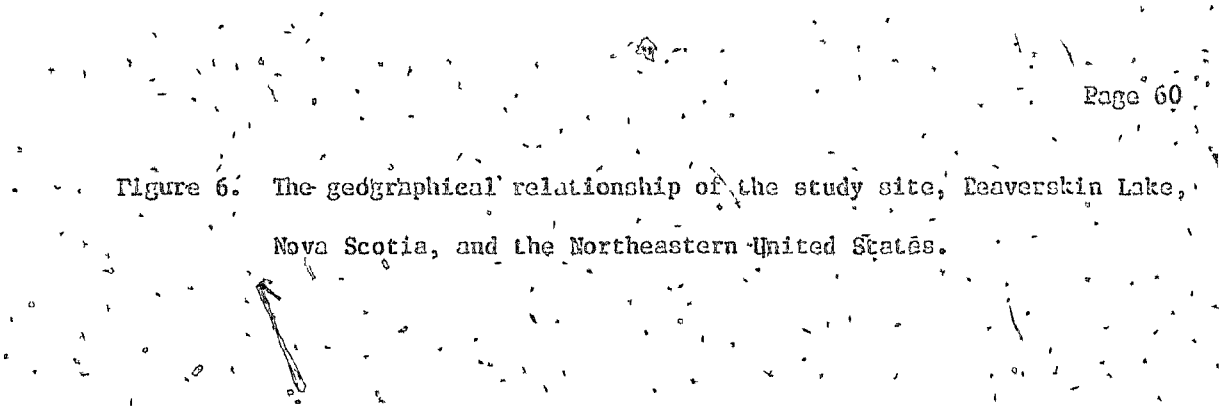
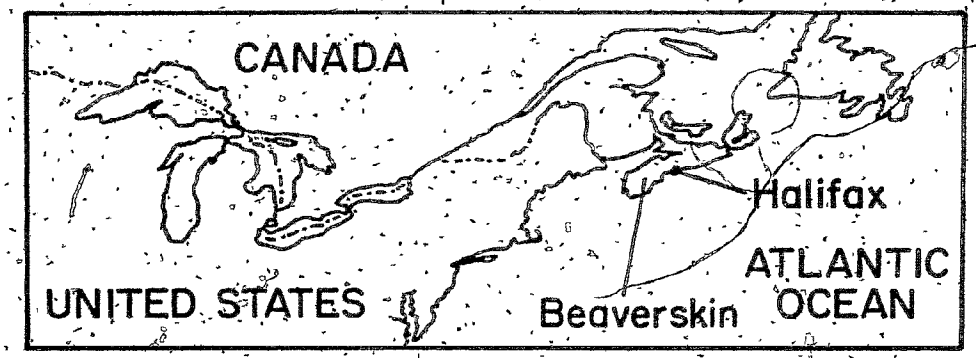


Figure 6. The geographical relationship of the study site, Beaverskin Lake, Nova Scotia, and the Northeastern United States.


CANADA
Halifax
ATLANTIC
OCEAN
UNITED STATES
Beaverskin

compared with the other study lakes, and its location away from the heavily used areas of the Park.

A. Methods

I. Enclosure Design

a. Year I

Nine enclosures of 6-mil translucent polyethylene were installed in Beaverskin Lake, in about 5 meters of water near the deep station. The enclosures were tubular, 1 meter in diameter, anchored in the sediments and supported at the surface by styrofoam floats. Galvanized steel rings at the surface and sediment kept the tubes expanded, and cement weights were used for solid anchoring. The tubes were open both to the sediments and the air. Installation was completed in one day to insure that each tube enclosed a similar, representative water column and plankton community.

Three of the limnocorrals were left untreated as controls (pH 5.4), three were gradually acidified to pH 4.9 by addition of very dilute sulfuric acid (100:1 H_2O:H_2SO_4), and three were treated with powdered lime ($CaCO_3$) in order to raise pH to about 6.8.

b. Year II

Eight translucent plastic enclosures, two meters in diameter, were supported by a wooden raft buoyed up by styrofoam floats (Figure 7 a.). The raft was anchored near the deep station (5.0 meters). The lower ends of the enclosures were embedded in and open to the sediments while the upper ends were exposed to the atmosphere (Figure 7 b). Ten-mil polyethylene bags were suspended by a clamp and chain system that allowed lowering and raising of the enclosures to compensate for water level fluctuations (Fig. 7 c).

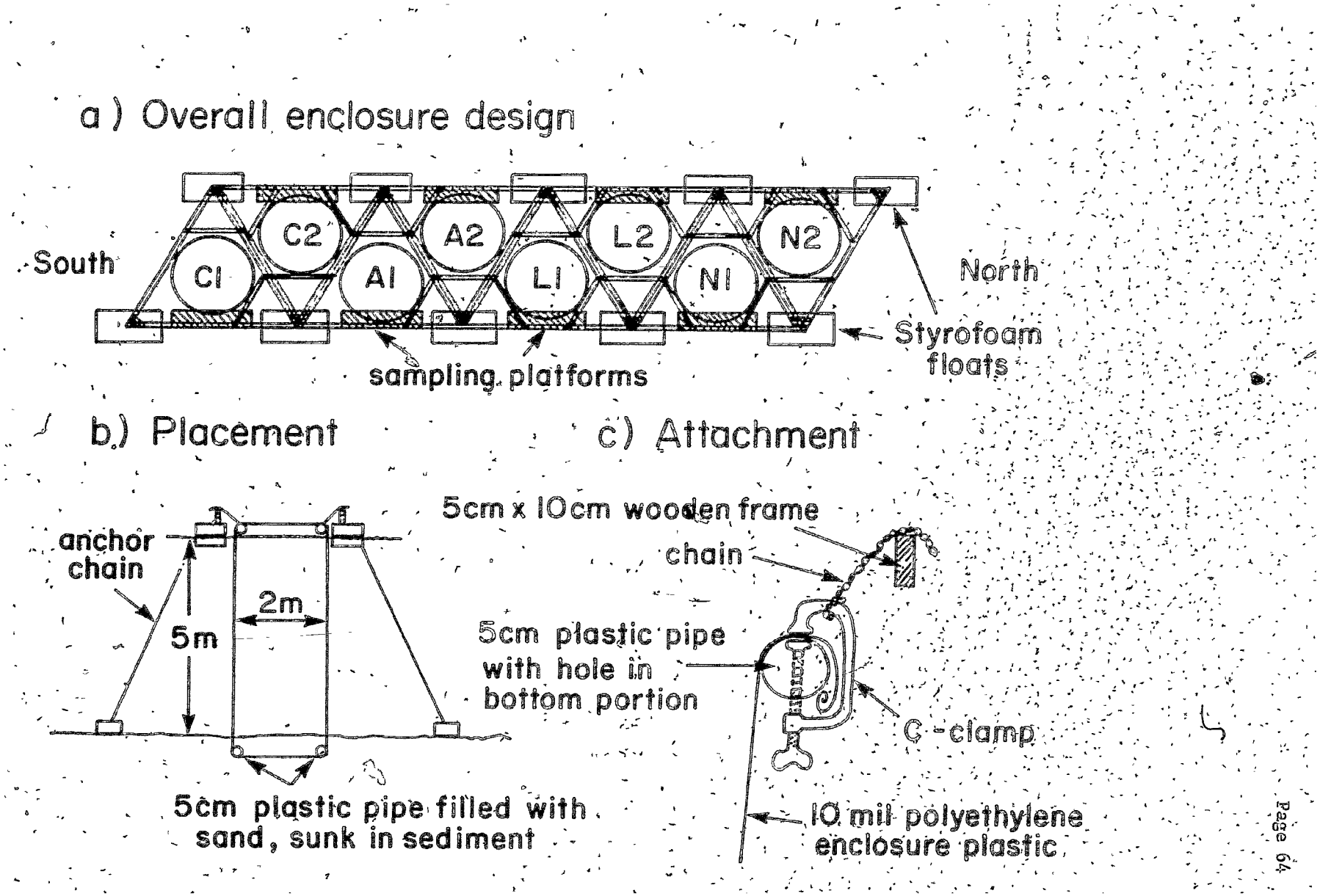
Two enclosures were left untreated and served as controls. Two each

Figure 7. The overall design of the experimental enclosures, Beaverskin Lake:

a) overall enclosure design,

b) placement, and

c) attachment.


a) Overall enclosure design
South
C1
C2
A1
A2
L1
L2
N1
N2
North
Styrofoam floats
sampling platforms
b) Placement
anchor chain
2m
5m
5cm plastic pipe filled with sand, sunk in sediment
c) Attachment
5cm x 10cm wooden frame
chain
5cm plastic pipe with hole in bottom portion
C - clamp
10 mil polyethylene enclosure plastic

of the remaining six enclosures served as replicates for the three experimental treatments. Ten grams of $CaCO_3$ suspended in one litre of SuperQ distilled water were added to the limed enclosures, one liter of 0.15% H_2SO_4 to the acidified enclosures, and a solution of 94 mg P as H_3PO_4 and 2355 mg N as NH_4Cl to the nutrient enriched enclosures (these amounts were calculated to be equal to ambient N and P amounts in the enclosures, with the same N:P ratio as ambient lake water). All additions were mixed at the surface in each of the respective enclosures on the following dates: August 12, 18, 27; September 1, 10, 16, 26; and October 1, 6, 11, 16, except for September 16, 26 and October 1, which were omitted from the nutrient addition schedule. There were no treatments from the date of installation, July 15, until August 12 thus allowing for a conditioning period prior to experimental manipulation.

II. Sampling

a. Year I

During the course of the experiment (August 10 - September 25), zooplankton were sampled approximately every ten days in each enclosure and in the lake. Samples were taken with a 32 liter Schindler-Patalas plankton trap at 2-meter intervals. Temperature and oxygen were measured in situ at 1-meter intervals with a YSI Model 54 oxygen meter. pH was determined in the field laboratory with a Radiometer TM29 pH meter. Water samples were collected with a 5-litre Van Dorn bottle near the surface of each enclosure for chemical analysis. All samples were preserved and analysed using previously described methods (section 2.1).

Egg ratios were calculated for zooplankton species from samples taken with net tows made with a 30 cm. conical net of 70 micron mesh size. The net was towed vertically from a depth of 4 meters to the surface in each enclosure on each sampling date. The net was used in order to take a larger sample size to ensure that sufficient numbers of ovigerous females were captured to give reliable egg ratio estimates. Sub-samples of sufficient volume were counted to yield at least 30 ovigerous females for each of the major zooplankton species.

b. Year II

The enclosures were installed July 8, and expanded to full volume July 15 with a gas-powered water pump. The eight enclosures and lake were sampled at depths of 0, 2, and 4 meters on seven dates: July 23, August 7 and 22, September 6 and 21, and October 6 and 21. Temperature, oxygen and pH were determined in the field as for Year I. Chlorophyll a samples were processed using a Millipore-90% acetone extraction and subsequently measured on a Turner fluorometer. Total and soluble reactive phosphorus,

and general analysis (total alkalinity, total acidity, color, turbidity, and conductivity) were measured by the Canadian Wildlife Service methods (Kerekes 1973). Ammonia was measured colorimetrically (Strickland et al. 1968), with the method modified for use with small volumes. Silicate, nitrate, and nitrite samples were frozen and later analyzed with a Technicon Autoanalyser II (Strickland et al. 1968).

Plankton were sampled concurrently with samples for water chemistry (Collins and Lane, 1984) in the enclosures and in Beaverskin Lake at 0, 2, and 4 meters. Phytoplankton and zooplankton were sampled and preserved using previously described methods (Chapter 2. A).

Phytoplankton were enumerated using the Utermohl sedimentation technique, while crustacean zooplankton and rotifers were identified and counted by dissecting microscope in replicate sub-samples of sufficient volume to include several hundred individuals. Plankton abundances are reported as numbers per liter for phytoplankton, and numbers per cubic meter for zooplankton. Egg ratios were calculated as described for year I. For all data, treatment replicates have been combined and mean values calculated.

III. Statistical Methods.

Data transformations for normality were done on the 1982 Beaverskin Lake enclosure data using the procedures outlined for the 1980-81 field data. (See Appendix D for details.)

To test the hypothesis that the treatments applied to the enclosures had significant effects on the abundances of plankton variables, ANOVAs were performed for both the 1981 and 1982 Beaverskin Lake enclosure experiments. The experiment was a nested design with repeated measurements (samples) made on each experimental unit (enclosure); therefore enclosure replicate is nested within enclosure treatment and the repeated measures MANOVA algorithm of SPSS was used for significance tests. The repeated measures procedure for a nested ANOVA design takes into account that the enclosures remain consistent over date; that is, that samples from a particular enclosure represent repeated measurements from that enclosure over time, and that the variance is partitioned accordingly. Separate ANOVAs were run for each of the nutrient and plankton taxonomic group variables. In each case, the hypothesis tested was that mean abundances of the variable in question were significantly affected by the experimental factors: treatment, depth, and date. The null hypotheses for these tests were as previously stated (Hypotheses #1-4).

B. Results

I. Year I - pH and Zooplankton

The enclosures had little apparent physical effect on the interior water columns. Temperature and oxygen profiles within the tubes were similar to those in Beaverskin Lake (Table 8), indicating that vertical mixing of the water columns was not impeded. Oxygen concentrations in all tubes were slightly lower than in the lake. pH values in the control enclosures remained similar to those in the lake throughout the experiment, while pH's in the limed enclosures quickly rose to near neutrality, and pH's in the acidified columns dropped more gradually to below 5 (Fig.8). Alkalinity, which was measured on two dates, was low or zero in the acidified treatments, slightly higher (around 0.5 mg/l as $CaCO_3$) in the controls, and higher with liming (5.5 mg/l as $CaCO_3$).

Standing Stocks-

The dominant zooplankton species in the enclosures were the calanoid copepod Diaptomus minutus and its immature stages, and the cladocerans Diaphanosoma birgei and Eubosmina tubicen.

Total copepod densities (numbers per m^3) as mean values taken between treatment replicates were lower in all enclosures than in the lake (Fig. 9). This was true from the beginning of the experiment, perhaps through avoidance of the enclosures by the relatively mobile copepods during the installation procedure. A gradual decrease in populations was noted over the course of the experiment in all tubes, and to a lesser extent in the lake. Within the tubes, acidification and liming both produced a steeper decline in copepod populations than in the controls. Numbers recovered to some extent in the acidified containers, remaining higher than the controls

Table 8. Physical / Chemical data for Beaverskin Lake enclosures, 1981.
(Alkalinity measured for two dates only).

	ENCLOSURE			
	B	C	A	L
AUGUST 8				
Temperature	21.9	21.8	21.8	21.8
Oxygen	9.6	8.8	9.2	9.1
pH	5.6	5.7	5.8	5.8
AUGUST 21				
Temperature	21.6	21.6	21.4	21.5
Oxygen	7.7	7.4	7.5	7.3
pH	5.3	5.4	5.2	6.5
Alkalinity	-	0.56	0.0	5.5
SEPTEMBER 11				
Temperature	19.0	19.0	19.0	19.0
Oxygen	8.4	8.2	8.0	8.2
pH	5.4	5.6	4.9	6.9
SEPTEMBER 26				
Temperature	16.0	16.0	16.0	16.0
Oxygen	9.6	9.3	8.9	9.4
pH	5.3	5.6	5.0	6.7
Alkalinity	-	0.44	0.2	5.5

Key : B - Beaverskin Lake C - Control enclosures
A - Acidified enclosures L - Limed enclosures

Figure 8. Mean pH values in enclosure experiments, 1981.

Key:

———— Beaverskin Lake

— — Control Enclosures

— — — — Acidified Enclosures

- - - - - - Limed Enclosures

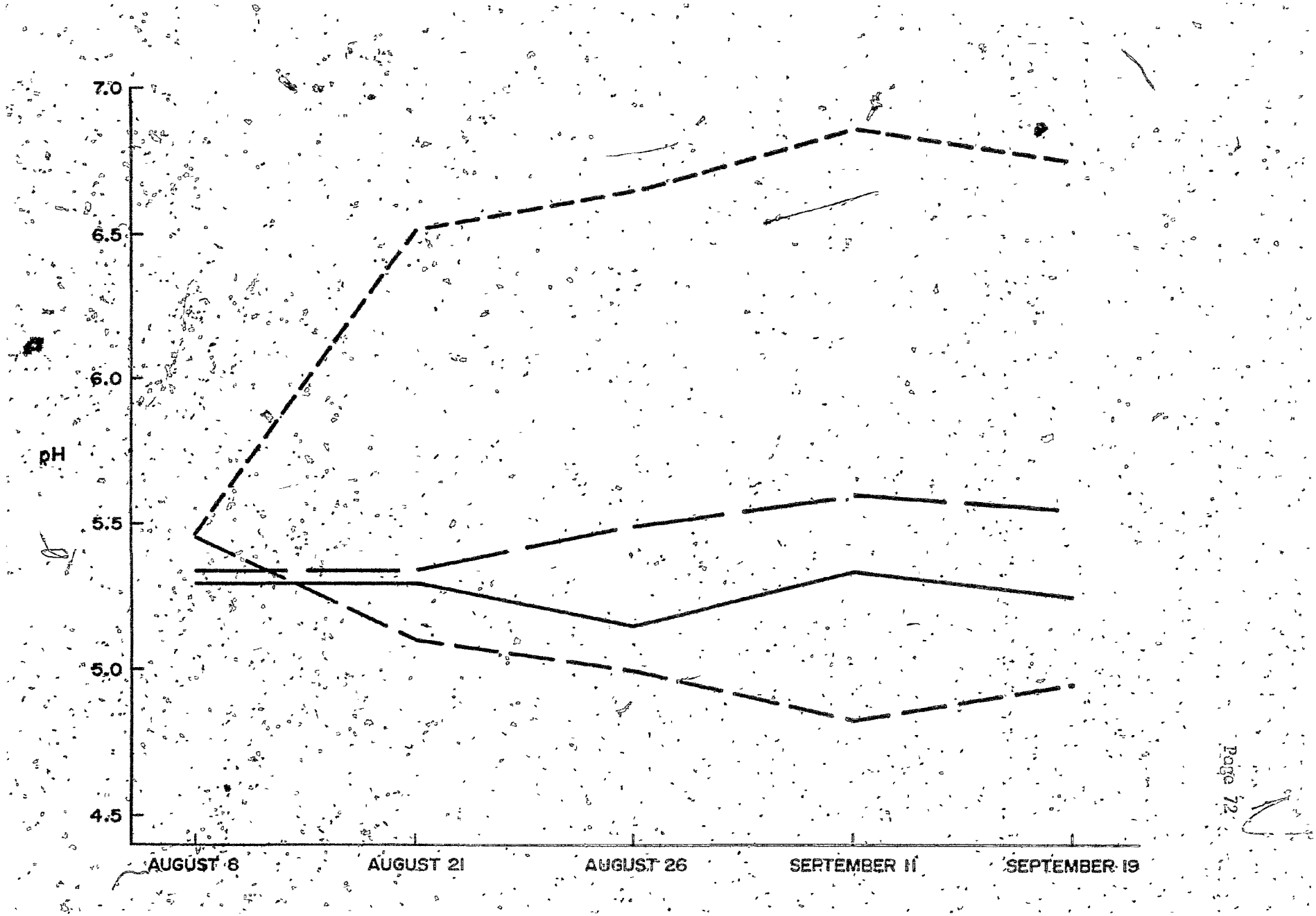

7.0
6.5
6.0
pH
5.5
5.0
4.5
AUGUST 8
AUGUST 21
AUGUST 26
SEPTEMBER 11
SEPTEMBER 19

Figure 9. Mean densities of copepods (nos./m^3) in Beaverskin Lake enclosure experiments, 1981.

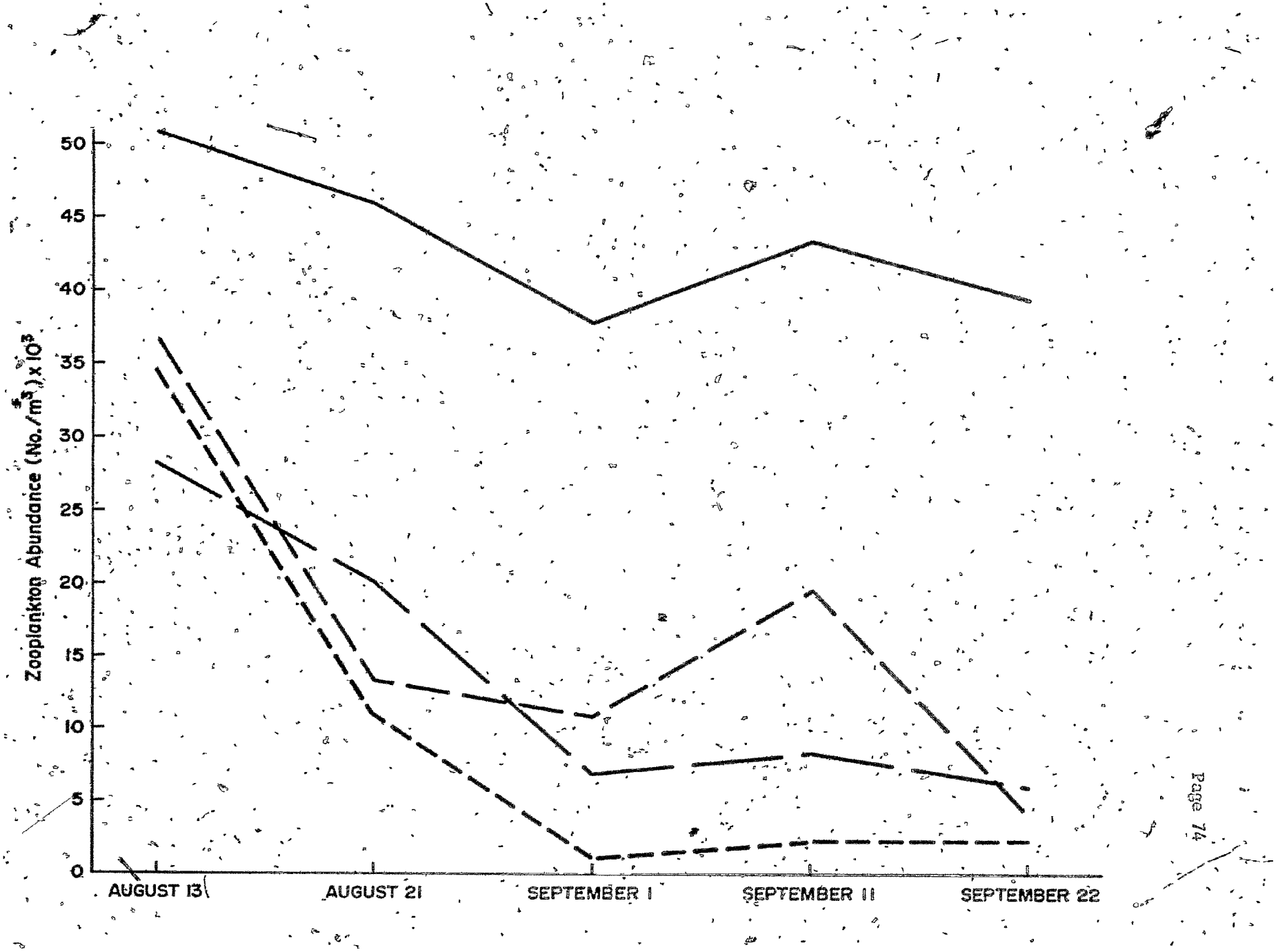
Key:

———— Beaverskin Lake

—— —— Control Enclosures

—— — —— Acidified Enclosures

– – – – – Limed Enclosures


Zooplankton Abundance (No./m³) x 10³
50
45
40
35
30
25
20
15
10
5
0
AUGUST 13
AUGUST 21
SEPTEMBER 1
SEPTEMBER 11
SEPTEMBER 22

throughout most of September. Populations of copepods in the limed enclosures remained consistently lower than any others.

Cladoceran numbers tended to be higher in the enclosures than in the lake, with the exception of one date (September 11) (Fig. 10). Within the experimental containers, a pattern similar to that for copepods was noted. Populations of cladocerans in the acidified enclosures were slightly higher than those in the controls over the last half of the experimental period, while numbers in the limed enclosures were consistently lower than in the other containers.

Egg Ratios-

Egg ratio values are presented, along with species densities, as average number of eggs per female for both copepods and cladocerans (Table 9).

Eubosmina tubicen had decreasing egg ratio values over the experiment in both the control and acidified enclosures. In the limed enclosures populations first declined, then later recovered. In the open lake, this species had high egg ratios on the first two dates, was absent on the third date and recovered slightly on the last date.

Diaphanosoma birgei showed declines in both numbers and egg ratio values through the experiment in the limed and acidified environments. In the controls and the lake, numbers first increased, followed by declines in numbers and egg ratio values.

With liming, the dominant zooplankton species Diaptomus minutus declined at first and then showed some recovery in numbers and egg ratio values by the end of the experiment. With acidification, there was a steady decline in population abundance. Egg ratio values increased at first, but then declined on the last two dates. In the controls, D.

Figure 10. Mean densities of cladocerans (nos./m^3) in Beaverskin Lake enclosure experiments, 1981.

Key:

——————— Beaverskin Lake

——— ——— Control Enclosures

——— — ——— Acidified Enclosures

— — — — — Limed Enclosures

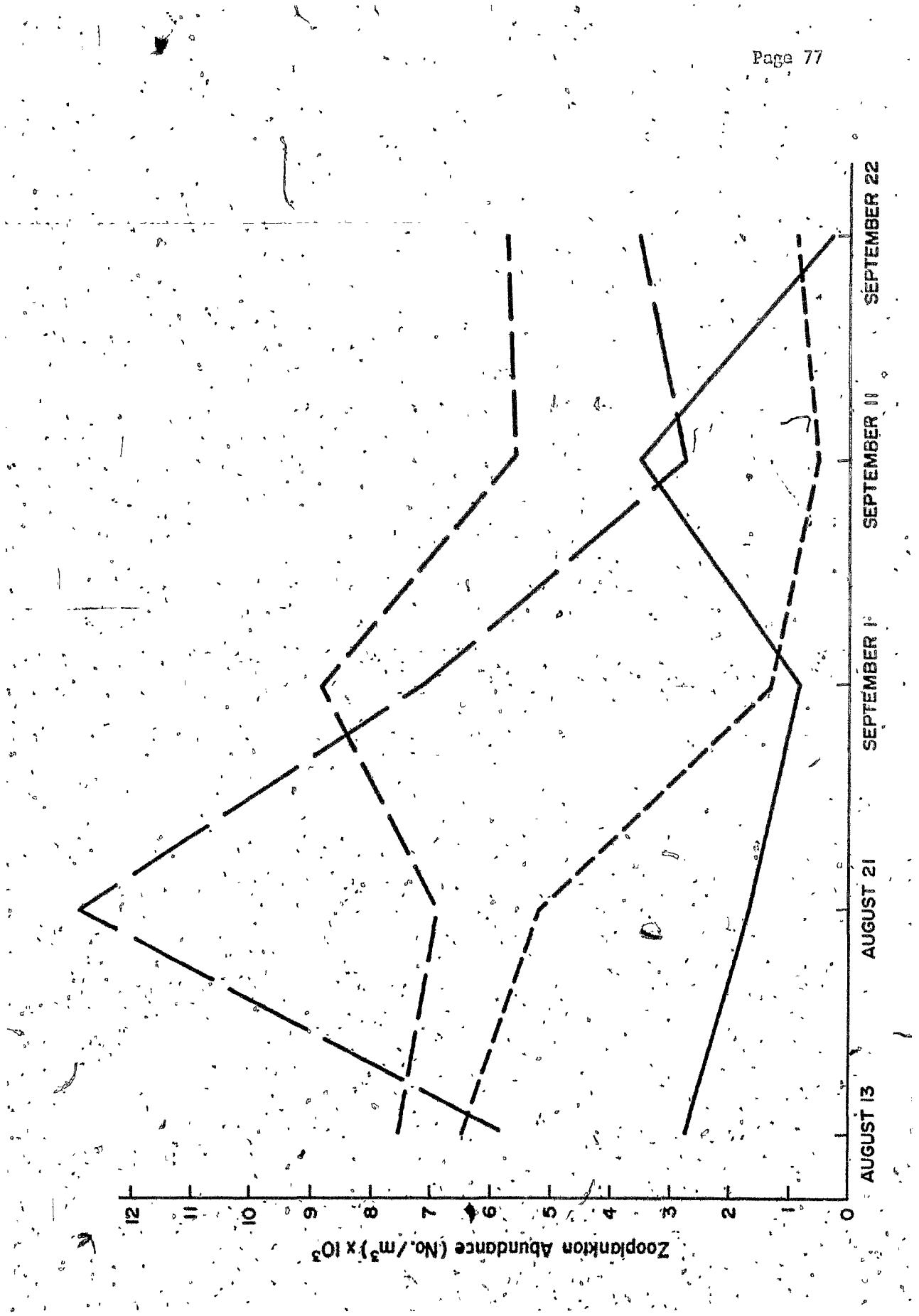

Zooplankton Abundance (No./m³) x 10³
0
1
2
3
4
5
6
7
8
9
10
11
12
AUGUST 13
AUGUST 21
SEPTEMBER 1
SEPTEMBER 11
SEPTEMBER 22

Table 9. Zooplankton population and egg ratio data for experimental enclosures. Number per liter (average number of eggs per female). (a) August 9, 1981.

SPECIES	ENCLOSURE B	C	A	L
Eubosmina tubicen	0.98 (0.88)	4.29 (0.43)	1.65 (0.54)	1.28 (0.84)
Diaphanosoma birgei	0.84 (0.33)	2.17 (0.28)	4.13 (0.28)	3.93 (0.56)
Epischura nordenskioldi males	0	0	0.01	0
Epischura nordenskioldi females	0	0.05 (0.0)	0.06 (0.0)	0
Diaptomus minutus males	6.7	3.13	1.44	2.06
Diaptomus minutus females	5.9 (0.4)	4.67 (0.06)	3.57 (0.02)	3.3 (0.05)
Diaptomus oregonensis males	0.56	0.34	0	0.10
Diaptomus oregonensis females	0.28 (0.0)	0.10 (0.0)	0.21 (0.0)	0.10 (0.0)
Diaptomus spp. CIV-V	22.0	10.4	14.1	13.9
Diaptomus spp. CI-III	7.3	9.93	9.03	10.4
Mesocyclops edax males	0.14	0	0	0
Mesocyclops edax females	0	0.10 (0.0)	0.06 (0.0)	0.10 (0.0)
Copepod nauplii	8.0	5.93	9.8	6.33
Holopedium gibberum	0	0	0	0.05 (1.0)

Key: B = Beaverskin Lake, A = Acidified enclosures
C = Control enclosures, L = Limed Enclosures

Table 9. (b) August 26, 1981.

SPECIES	ENCLOSURE B	C.	A	L
Daphnia catawba	0.31 (0.05)	0	0	0
Eubosmina tubicen	0.77 (1.60)	10.1 (0.25)	4.30 (0.10)	0.02 (0.0)
Diaphanosoma birgei	2.30 (0.07)	4.20 (0.46)	3.0 (0.13)	2.23 (0.28)
Epischura nordenskioldi males	0	0	0	0
Epischura nordenskioldi females	0	0.10 (0.0)	0	0
Diaptomus minutus males	2.0	0.36	0.08	0.01
Diaptomus minutus females	6.1 (0.8)	1.19 (0.26)	0.82 (0.70)	0.28 (0.0)
Diaptomus oregonensis males	0	0	0	0
Diaptomus oregonensis females	0.15 (0.0)	0	0	0.03 (0.0)
Diaptomus spp. CIV-V	30.4	6.57	4.73	4.13
Diaptomus spp. CI-III	9.5	2.67	2.24	0.84
Mesocyclops edax males	0	0	0	0
Mesocyclops edax females	0	0.15 (3.0)	0.03 (0.0)	0.03 (0.0)
Copepod nauplii	3.7	0.31	0.84	0.30
Holopedium gibberum	0	0.11 (0.06)	0.05 (0.17)	0.02 (0.0)

Key: B = Beaverskin Lake A = Acidified enclosures

C = Control enclosures L = Limed enclosures

Table 9. (c) September 15, 1981.

SPECIES	ENCLOSURE B	C	A	L
Eubosmina tubicen	0	0.36 (0.05)	4.38 (0.26)	0.14 (0.08)
Diaphanosoma birgei	0.46 (0.67)	0.79 (0.15)	2.39 (0.14)	0.27 (0.13)
Diaptomus minutus males	0.31	0.03	0.08	0.02
Diaptomus minutus females	1.1 (0.71)	0.19 (0.0)	0.69 (0.21)	0.15 (0.06)
Diaptomus oregonensis males	0	0	0	0
Diaptomus oregonensis females	0.46 (0.0)	0.03 (0.11)	0	0
Diaptomus spp. CIV-V	18.7	1.28	3.37	0.59
Diaptomus spp. CI-III	3.4	0.23	0.43	0.08
Mesocyclops edax males	0	0	0	0
Mesocyclops edax females	0	0.04 (0.0)	0.02 (6.67)	0.01 (2.0)
Tropocyclops prasinus males	0	0	0	0
Tropocyclops prasinus females	0	0.01 (0.0)	0	0.03 (3.33)
Copepod nauplii	0	0	0.27	0.05
Holopedium gibberum	0	0.05 (0.22)	0.02 (0.33)	0
Polyphemus pediculus	0	0	0.05 (0.0)	0
Camptocercus rectirostris	0	0	0.08 (0.29)	0
Chydorus sp.	0	0	0.20 (0.08)	0.01 (0.0)

Key: B = Beaverskin Lake A = Acidified enclosures
C = Control enclosures L = Limed enclosures

Table 9. (d) September 26, 1981.

SPECIES	ENCLOSURE B	C	A	L
Daphnia catawba	0	.05 (0.0)	0	0
Eubosmina tubicen	0.77 (0.20)	0.7 (0.19)	0.55 (0.21)	0.48 (0.45)
Diaphanosoma birgei	0.31 (0.0)	0.5 (0.27)	1.76 (0.12)	0.3 (0.5)
Epischura nordenskioldi males	0	0	0	.05
Epischura nordenskioldi females	0	0	0	0
Diaptomus minutus males	1.8	0.61	0.1	0.28
Diaptomus minutus females	2.3 (0.27)	1.72 (0.12)	0.65 (0.05)	0.67 (0.18)
Diaptomus oregonensis males	0	0	0	0.18
Diaptomus oregonensis females	0	0	0	0
Diaptomus spp. CIV-V	24.3	13.9	4.2	5.78
Diaptomus spp. CI-III	0.31	0.38	0.16	0.09
Mesocyclops edax males	0	0.08	0	0
Mesocyclops edax females	0	0.33 (0.5)	0.08 (2.67)	0.26 (0.0)
Mesocyclops edax immatures	0	0.51	0	0
Tropocyclops prasinus males	0	0	0	0.01
Tropocyclops prasinus females	0	0	0	0.12 (0.0)
Tropocyclops prasinus immatures	0	0	0	0.05

Key: B = Beaverskin Lake
C = Control enclosures
A = Acidified enclosures
L = Limed enclosures

Table 9. (d) (continued) September 26, 1981.

SPECIES	ENCLOSURE B	C	A	L
Copepod nauplii	0.77	0.53	0.15	0.21
Polyphemus pediculus	0	0.10 (0.0)	0.05 (0.0)	0
Chydorus sp.	0	0.39 (0.02)	0.43 (0.04)	0
Eurycercus sp.	0	0.10 (0.17)	0	0
Ophryoxus gracilis	0	0.03 (1.67)	0.2 (0.04)	0
Holopedium gibberum	0	0.08 (0.04)	0	0

Key: B = Beaverskin Lake; C = Control enclosures; A = Acidified enclosures; L = Limed enclosures

minutus first declined, and later recovered to some extent. A similar pattern was seen in the open lake.

Mesocyclops edax was virtually never seen in the lake samples, but did occur in the enclosures in low numbers. It showed the highest egg ratios on most dates in the acidified environments.

Holopedium gibberum did not occur in the lake samples, and was rare in the controls. With liming, it showed a rapid decline to zero, while in the acidified tubes it appeared only on the second and third dates.

Toward the end of the experiment (the last two dates), many species of Cladocera appeared in the control and acidified enclosures. These species (Polyphemus, Chydorus, Camptocercus, Eurycercus, Ophryoxus spp.) do not normally occur in the open lake water column, and were not seen in the controls.

Epischura nordenskioldi and Tropocyclops prasinus were rare and sporadic in their occurrences in the samples.

c. ANOVA Results

Analysis of variance was used to test for differences in mean abundances of the plankton between treatments.

For the 1981 enclosure experiment, the factors treatment and date were tested for the variables copepods and cladocerans. The null hypothesis (Hypotheses 1-4) in each case is that there is no difference in mean abundance of the variable over the different levels of the factor tested. The alternate hypothesis is that the abundances are significantly different for different factor levels. A rejection level of $p = 0.05$ was used in all cases. The probability level p represents the probability that differences in mean values of a variable compared between different levels of a factor are the result of random variation alone rather than the effects of that factor.

For copepod mean abundances, the null hypothesis was accepted ($p > .05$) for the factor treatment (Hypothesis 1), and was rejected ($p < .05$) for the factor date (Hypothesis 2) (Table 10), showing that copepod abundance was the same among treatments, but changed significantly over time. These changes over time reflect the natural seasonal changes in copepod population levels. The interaction term between treatment and date (Hypothesis 4) had a very low probability ($p = 0.054$) but was not quite significant. This indicates some likelihood that the changes in copepod abundance over time were not the same for each of the treatments, although the treatments did not by themselves have a significant effect. Similar results were found for the cladocerans. Treatment was not significant, date was significant, and the interaction term had a low but non-significant probability.

Table 10: ANOVA Results, Beaverskin Lake enclosure experiment, 1981.

F = F statistic for ANOVA

p = significance level for F

VARIABLE - Copepods

FACTOR	F	p
Treatment	1.37	0.325
Date	37.6	0.000
Treatment x Date	2.31	0.054

VARIABLE - Cladocerans

FACTOR	F	p
Treatment	2.46	0.166
Date	5.85	0.002
Treatment x Date	2.09	0.078

II. Year LI -- pH, Nutrients and Planktonic Food Webs

a. Water Chemistry

The variations of pH in the eight enclosures and in Beaverskin Lake are represented in Fig. 11. The close agreement of pH values during the pre-treatment period demonstrated that initial conditions were similar in all experimental enclosures prior to initiation of the experiment. The pH in Beaverskin Lake and the control enclosures remained similar throughout the experiment. In the limed (L) enclosure replicates, the pH in L-1 showed a gradual increase but in L-2 pH exhibited an unexplained lag and then a sharp increase between September 21 and October 6. The pH in the nutrient-enriched enclosures decreased as a result of an increased H^+ ion concentration with each addition of H_3PO_4. When nutrient additions were stopped (Sept. 21), a rapid return to control pH was observed without a subsequent decrease when nutrient additions were resumed (Oct. 6). Also, a small upward trend in pH was observed in the acidification enclosures on the last two sampling dates.

Table 11 is a summary of the most pertinent physical and chemical data collected in the experiment. For enclosures, all values are reported as the mean of treatment replicates. Neither the lake nor the enclosures were thermally stratified during the experimental period. The temperature profiles in the enclosures and in the lake were identical on each date, and mean values per date ranged from 23°C at the start of the experiment to 10°C at the end. A sharp decrease of 6°C was observed between September 21 and October 6. Silicate was measured but values were near or below the limits of detection. Oxygen profiles were similar to each other, and levels were always close to saturation values. Soluble reactive phosphorus values for most observations were near or below the limit of detection.

Figure 11. Mean pH in Beaverskin Lake enclosure experiments, 1982.

Key:

0 0 0 0 Beaverskin Lake

———— Control Enclosures

- - - - - - Acidified Enclosures

. . . . . Limed Enclosures

—.—.—.— Nutrient Enclosures

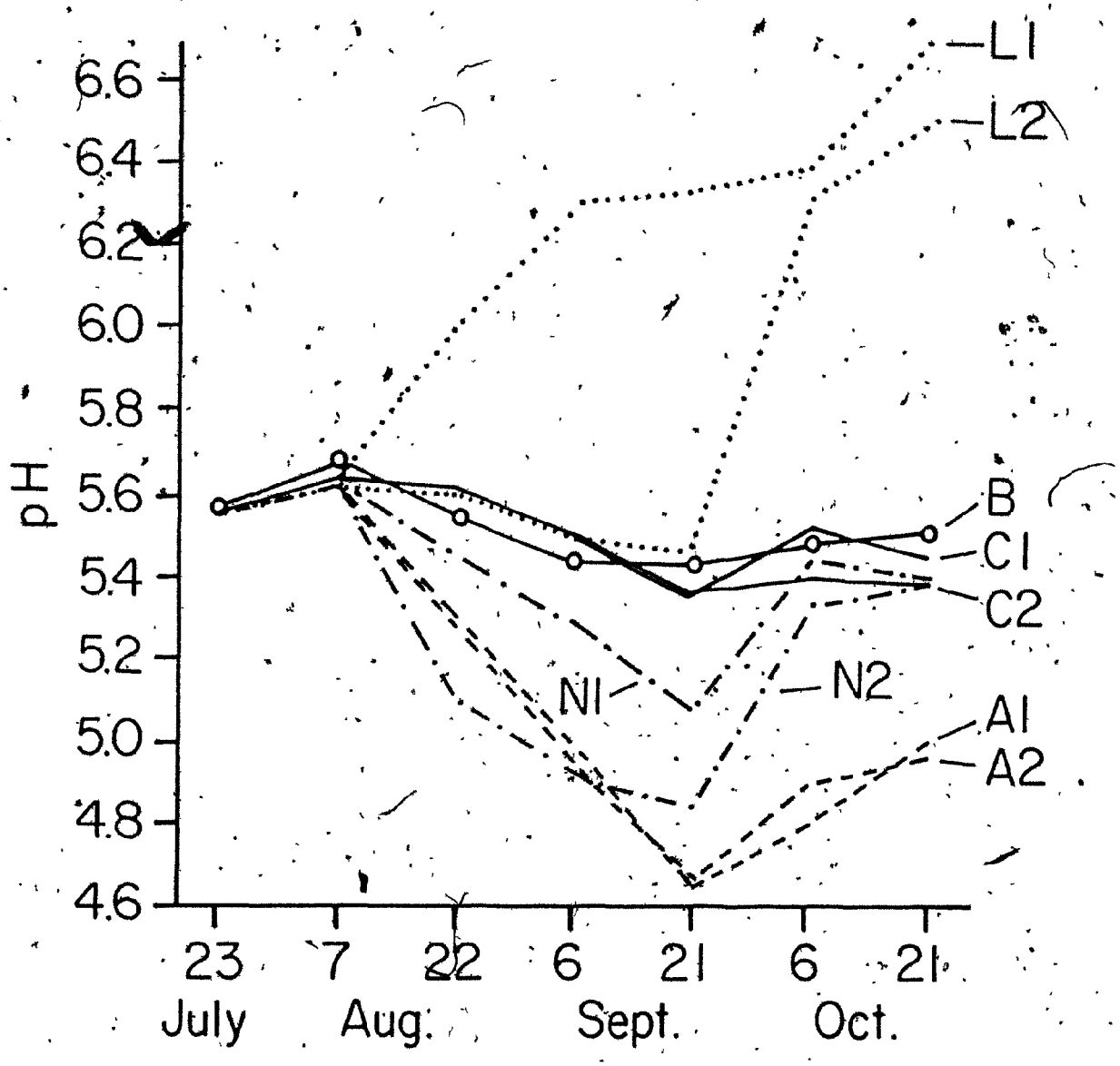

pH
6.6
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
23
7
22
6
21
6
21
July
Aug.
Sept.
Oct.
L1
L2
B
C1
C2
N1
N2
A1
A2

Table 11. Physical/Chemical Data for Beaverskin Lake Enclosures, 1982.

Enclosure/ Date	pH	Temp °C	Oxygen ppm	Chl. a	Nitrate + Nitrite	Ammonia	Total Phosphorus	Soluble Reactive Phosphorus	N/P Ratio
					($mg \cdot m^{-3}$)				
BEAVERSKIN									
820723	5.56	23.0	7.86	.97	5.24	32.3	3.62	.970	52.6
820807	5.66	21.0	7.78	.43	2.18	2.89	5.01	.500	10.6
820822	5.55	18.5	8.48	.95	4.34	3.17	1.11	.795	9.97
820906	5.47	19.0	8.70	1.2	1.49	7.99	2.08	.695	14.6
820921	5.43	18.0	8.58	.79	4.52	1.00	2.03	.500	11.0
821006	5.49	12.0	10.3	1.7	2.48	1.00	1.02	.500	6.96
821021	5.51	10.0	10.9	1.4	4.45	11.0	2.03	.965	16.8
CONTROL									
820723	5.56	23.0	7.37	.95	6.28	30.0	3.49	2.47	20.3
820807	5.63	21.0	7.25	1.1	1.40	13.2	1.29	.552	24.5
820822	5.59	18.4	8.31	1.7	5.30	4.81	2.42	.940	10.8
820906	5.46	19.0	8.53	1.5	4.01	9.10	1.70	.815	16.1
820921	5.33	18.0	8.60	1.7	6.91	1.00	1.04	.500	15.8
821006	5.45	12.0	10.1	2.2	2.52	1.00	.880	.500	7.04
821021	5.44	10.0	11.0	1.6	2.74	8.90	.791	.500	23.3

Table 11. Continued.

Enclosure/ Date	pH	Temp °C	Oxygen ppm	Chl. a	Nitrate + Nitrite	Ammonia	Total Phosphorus	Soluble Reactive Phosphorus	N/P Ratio
				($mg \cdot m^{-3}$)					
NUTRIENT									
820723	5.55	23.0	7.50	1.1	4.52	31.3	3409	1.70	24.7
820807	5.64	21.0	7.51	.92	1.40	2.10	3.77	.500	5.60
820822	5.29	18.5	8.64	4.6	5.01	20.5	2.74	2.30	18.5
820906	5.14	19.0	8.64	2.8	18.3	84.6	2.25	.562	190
820921	4.96	18.0	8.56	1.7	22.3	21.0	1.23	.500	86.5
821006	5.39	12.0	10.3	1.8	5.62	1.0	1.02	.500	13.2
821021	5.39	10.0	11.0	1.8	6.24	44.8	1.98	.570	92.8
LIMING									
820723	5.53	23.0	7.58	.91	4.34	32.9	3.13	2.26	18.5
820807	5.61	21.0	7.53	1.1	1.40	6.95	1.23	.517	16.3
820822	5.81	18.4	8.28	1.2	4.34	3.69	1.39	1.31	6.46
820906	5.89	19.0	8.45	.47	1.67	6.19	1.87	.617	13.5
820921	5.90	18.0	8.55	1.1	4.94	1.00	1.02	.500	11.9
821006	6.35	12.0	9.75	2.4	1.45	1.00	.904	.500	4.91
821021	6.59	10.0	10.5	1.9	3.83	5.89	.886	.500	19.44
ACIDITY									
820723	5.50	23.0	7.47	1.4	4.43	31.4	3.49	1.30	30.2
820807	5.63	21.0	7.50	1.0	1.40	10.4	1.25	.897	19.1
820822	5.30	18.5	8.33	1.2	4.52	4.96	2.54	1.55	8.68
820906	4.98	19.0	8.69	0.81	1.69	6.87	1.78	.825	10.3
820921	4.62	18.0	8.63	1.0	4.67	1.00	1.33	.500	11.3
821006	4.86	12.0	10.0	1.7	1.40	1.00	.888	.500	4.80
821021	5.01	10.0	11.0	1.2	1.73	7.71	.841	.500	18.9

Vertical profiles of nutrient and chlorophyll *a* concentrations for selected dates are represented in Fig. 12. Concentrations were quite uniform over depth. On September 6, five days after an addition of nutrients, an increase in nitrate + nitrite was observed in the enriched enclosures, but phosphorus was quickly utilized and remained low. Chlorophyll *a* concentration increased substantially between Aug. 7 and Aug. 22, during which time nutrient additions began. The nutrient and chlorophyll *a* concentrations in Beaverskin Lake and the controls remained very low. By September 21, nitrogen remained high in the nutrient enclosures, but chlorophyll *a* decreased to control levels, possibly because of phosphorus limitation. N/P ratios on these two dates were 190 and 86.5 respectively in the nutrient-enriched enclosures.

b. Phytoplankton

Data compiled for all algal species together (Fig. 13) showed one major (August 22) and one minor (October 6) peak in abundance for all treatments and the lake. Comparing treatments, there were differences in magnitudes of total algal abundance. The nutrient-enriched enclosures exhibited the highest populations, while acidification reduced algal abundances. Numbers in the limed enclosures followed a pattern similar to that of the controls and the lake community.

The cyanophytes, or blue-green algae, were by far the most abundant algal group (Table 12), and so their pattern among treatments was similar to that for the total algal community. A major peak occurred on Aug. 22, and a smaller one on Oct. 6 (Fig. 14). Highest abundances were generally found in the enriched enclosures and lowest numbers in the acidified ones. The control and limed populations showed patterns similar to each other throughout the experiment, while numbers of cyanophytes in the lake were

Figure 12. Vertical profiles of chlorophyll *a*, nitrate + nitrite, and soluble reactive phosphorus (all mg./l.) in Beaverskin Lake enclosure experiment, 1982.

Key:

——— Beaverskin Lake

. . . Control Enclosures

– – – Nutrient Enclosures

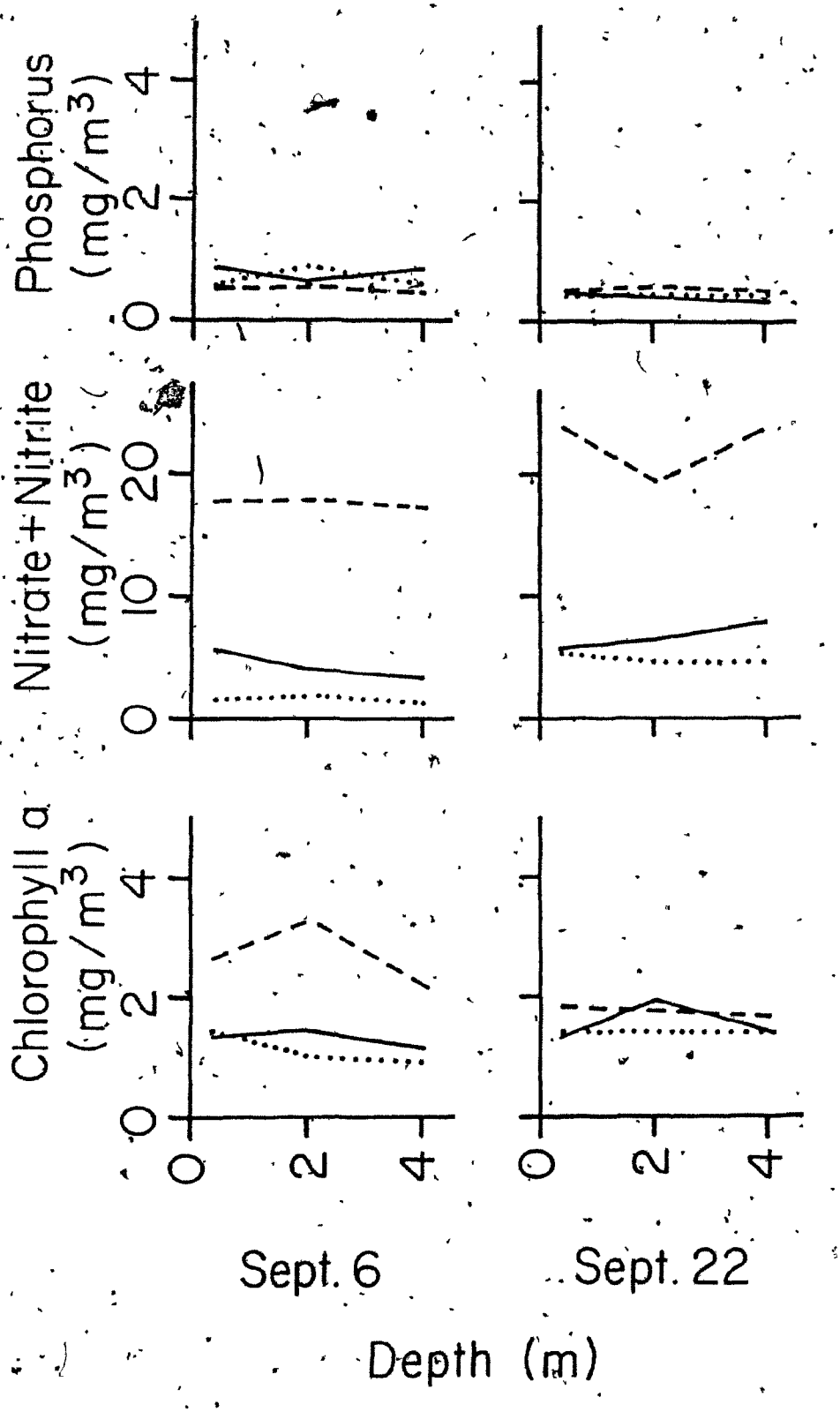
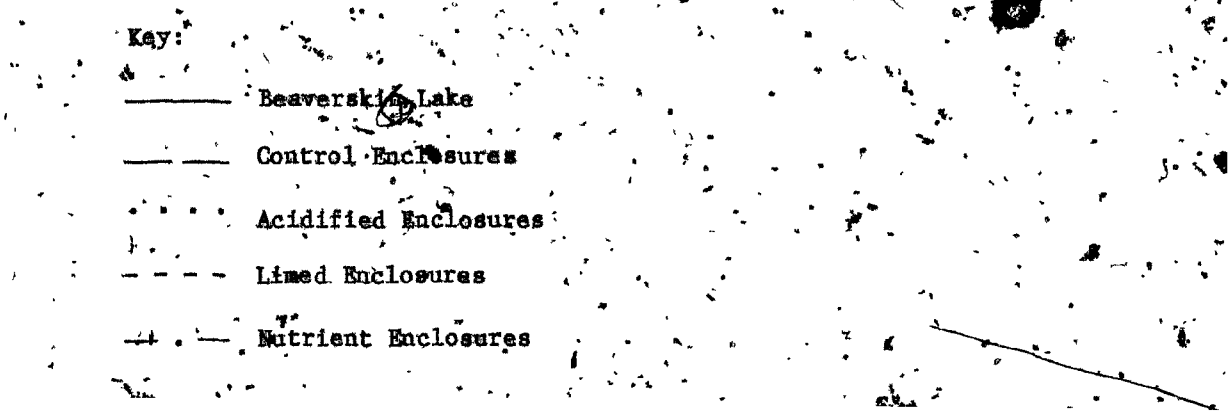

Phosphorus (mg/m3)
0
2
4
Nitrate+Nitrite (mg/m3)
0
10
20
Chlorophyll a (mg/m3)
0
2
4
0
2
4
Sept. 6
Sept. 22
Depth (m)

Figure 13. Total algal abundance (nos./liter) in Beaverskin Lake enclosures, 1982.



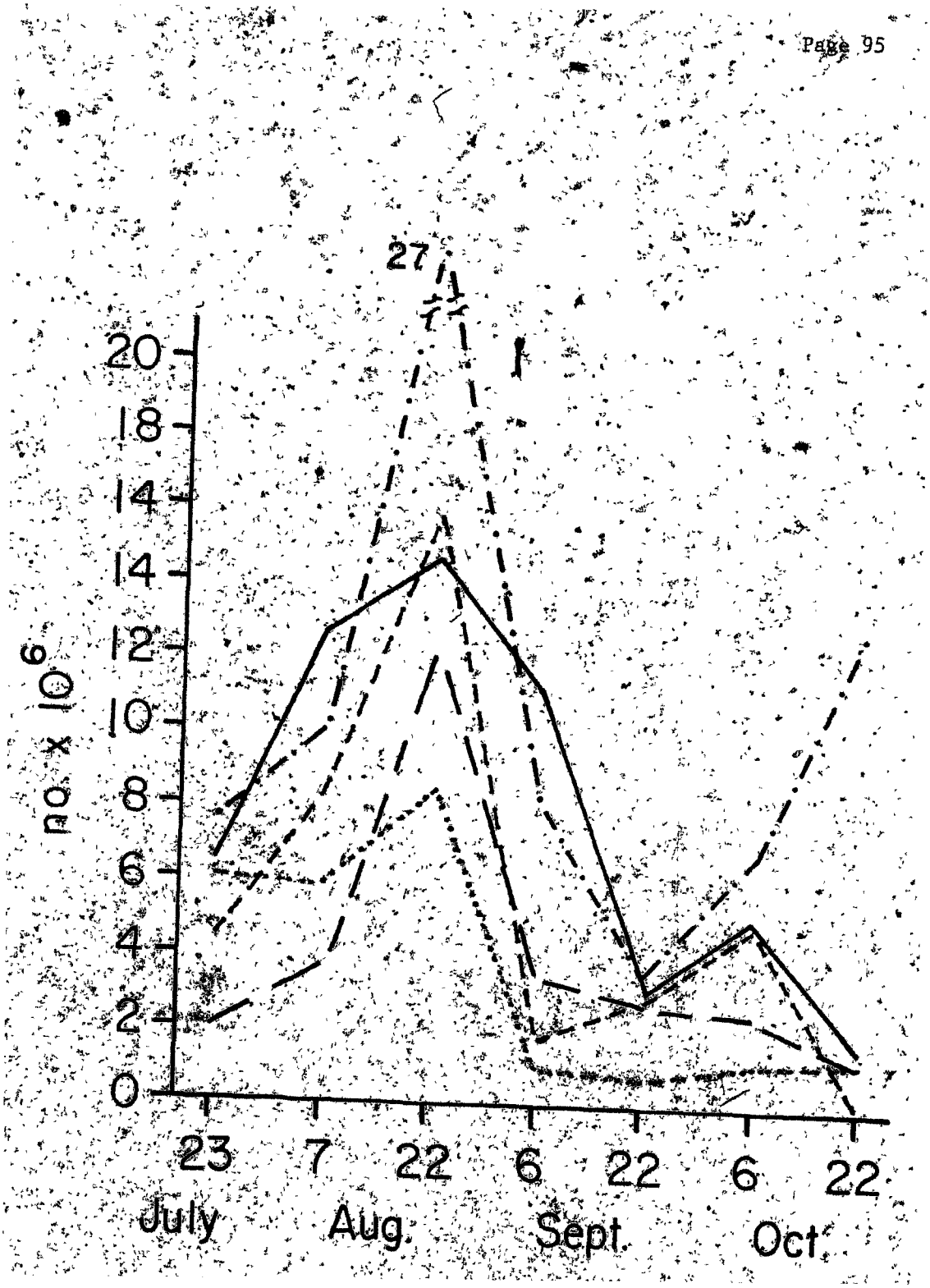

27
20
18
14
14
12
10
8
6
4
2
0
no. x 10⁶
23
7
22
6
22
6
22
July
Aug.
Sept.
Oct.

Table 12. Plankton functional group abundances for Beaverskin Lake enclosures, 1982. (Nos. per Liter- phytoplankton, nos. per M^3- zooplankton).

TREATMENT	DATE	GREENS	DIATOMS	BLUEGREENS	CHRYSOPHYTES
ACIDIFIED	820723	126000.	19000.	6630000.	4370.
	820807	9940.	7550.	5990000.	9150.
	820822	78800.	8750.	9120000.	25400.
	820906	22600.	25000.	1150000.	7950.
	820921	61700.	99900.	450000.	3180.
	821006	129000.	327000.	608000.	27000.
	821021	80900.	14300.	1130000.	42500.
	MEAN	72800.	71800.	3580000.	17100.
BEAVERSKIN	820723	87500.	7160.	6130000.	5560.
	820807	18300.	3180.	11400000.	21400.
	820822	259000.	18300.	13600000.	10300.
	820906	18300.	2380.	11300000.	9540.
	820921	67700.	4770.	2920000.	23800.
	821006	38900.	3970.	4140000.	36600.
	821021	35000.	2380.	1400000.	62000.
	MEAN	75000.	6020.	7290000.	24200.

Table 12. Continued.

TREATMENT	DATE	GREENS	DIATOMS	BLUEGREENS	CHRYSOPHYTES
CONTROL	820723	66000.	4370.	2070000.	2380.
	820807	48500.	11100.	3680000.	14700.
	820822	148000.	16300.	12600000.	15900.
	820906	57600.	15900.	3650000.	107000.
	820921	72200.	149000.	2110000.	32000.
	821006	48900.	73000.	2630000.	17900.
	821021	144000.	117000.	814000.	31800.
	MEAN	83700.	55300.	3940000.	31800.
LIMED	820723	15100.	15500.	4320000.	57800.
	820807	121000.	13500.	8590000.	8750.
	820822	100000.	9940.	17200000.	33400.
	820906	86300.	18300.	2000000.	61300.
	820921	45300.	20600.	2200000.	15100.
	821006	35000.	33400.	4300000.	59900.
	821021	28200.	33600.	93500.	25400.
	MEAN	61700.	20700.	5530000.	37400.
NUTRIENT	820723	9940.	5170.	6530000.	7550.
	820807	34600.	17500.	9740000.	9150.
	820822	265000.	38800.	27300000.	17900.
	820906	153000.	146000.	8540000.	14100.
	820921	89600.	83700.	3020000.	24300.
	821006	40900.	18300.	7160000.	52500.
	821021	67200.	15500.	1200000.	65200.
	MEAN	94400.	46400.	9070000.	27200.

Table 12. Continued.

TREATMENT	DATE	XANTHOPHYTES	UNIDENTIFIED
ACIDIFIED	820723	2780.	36200.
	820807	14700.	7160.
	820822	23400.	17500.
	820906	47700.	6760.
	820921	44800.	1190.
	821006	19000.	17100.
	821021	30200.	27400.
	MEAN	26100.	16100.
BEAVERSKIN	820723	1590.	30200.
	820807	7950.	18300.
	820822	10300.	30200.
	820906	18300.	31000.
	820921	9540.	55400.
	821006	93900.	86200.
	821021	23800.	38100.
	MEAN	23600.	41300.

Table 12. Continued.

TREATMENT	DATE	XANTHOPHYTES	UNIDENTIFIED
CONTROL	820723	4370.	33800.
	820807	19800.	6760.
	820822	95300.	19400.
	820906	85200.	10300.
	820921	72800.	1590.
	821006	30200.	10700.
	821021	30600.	7950.
	MEAN	48300.	12900.
LIMED	820723	4770.	30200.
	820807	7550.	11100.
	820822	13500.	32600.
	820906	24600.	20200.
	820921	76600.	20600.
	821006	79400.	71700.
	821021	15900.	16700.
	MEAN	31700.	29000.
NUTRIENT	820723	2380.	48100.
	820807	11900.	8750.
	820822	505000.	15500.
	820906	489000.	10700.
	820921	149000.	16700.
	821006	99800.	58100.
	821021	34200.	42100.
	MEAN	184000.	28600.

Table 12. Continued

TREATMENT	DATE	CLADOCERANS	CALANOID COPEPODS	CYCLOPOID COPEPODS	ROTIFERS
ACIDIFIED	820723	2310.	13500.	201.	704.
	820807	3570.	8100.	150.	7190.
	820822	18200.	14000.	1710.	6740.
	820906	29700.	15500.	528.	13600.
	820921	11300.	9910.	603.	6640.
	821006	6260.	5690.	729.	8750.
	821021	4560.	9300.	352.	48300.
	MEAN	10800.	10800.	610.	13100.
BEAVERSKIN	820723	12800.	86200.	905.	3720.
	820807	20300.	43800.	1610.	1200.
	820822	5430.	62300.	0	2210.
	820906	2450.	61100.	211.	1900.
	820921	4260.	50100.	0	12600.
	821006	603.	31100.	402.	23500.
	821021	2210.	46000.	2810.	57900.
	MEAN	6880.	54400.	849.	14700.

Table 12. Continued

TREATMENT	DATE	CLADOCERANS	CALANOID COPEPODS	CYCLOPOID COPEPODS	ROTIFERS
CONTROL	820723	4520.	51300.	502.	352.
	820807	2740.	4250.	368.	2620.
	820822	13000.	28900.	5640.	26300.
	820906	20200.	2160.	6330.	11900.
	820921	32500.	1110.	6120.	854.
	821006	21900.	1150.	4520.	13400.
	821021	6010.	4940.	1110.	24000.
	MEAN	14400.	13400.	3510.	11300.
LIMED	820723	8950.	29000.	0	8750.
	820807	2460.	13600.	402.	4780.
	820822	12660.	38000.	402.	1300.
	820906	8600.	23800.	201.	10100.
	820921	9660.	14800.	150.	2560.
	821006	2050.	6960.	150.	27700.
	821021	5280.	7390.	150.	15800.
	MEAN	7100.	19100.	208.	10100.
NUTRIENT	820723	9660.	31900.	301.	4720.
	820807	1550.	5130.	201.	2560.
	820822	8650.	11600.	1710.	9250.
	820906	12900.	6640.	2310.	17400.
	820921	15000.	8350.	3110.	15600.
	821006	1810.	6790.	150.	18600.
	821021	1250.	20700.	100.	91100.
	MEAN	7280.	13000.	1120.	22700.

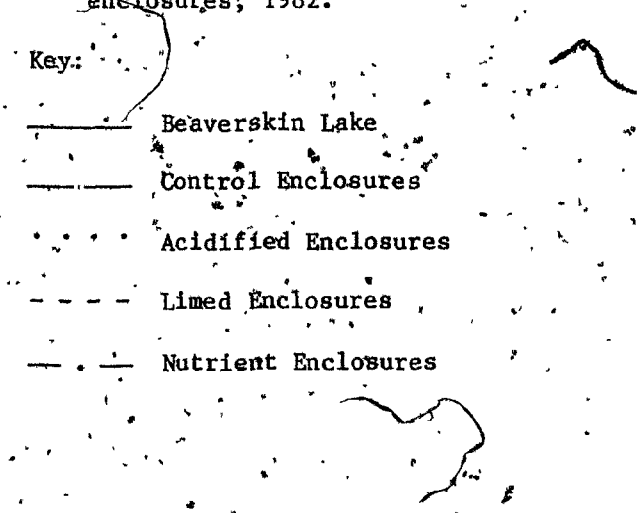
Table 12. Continued

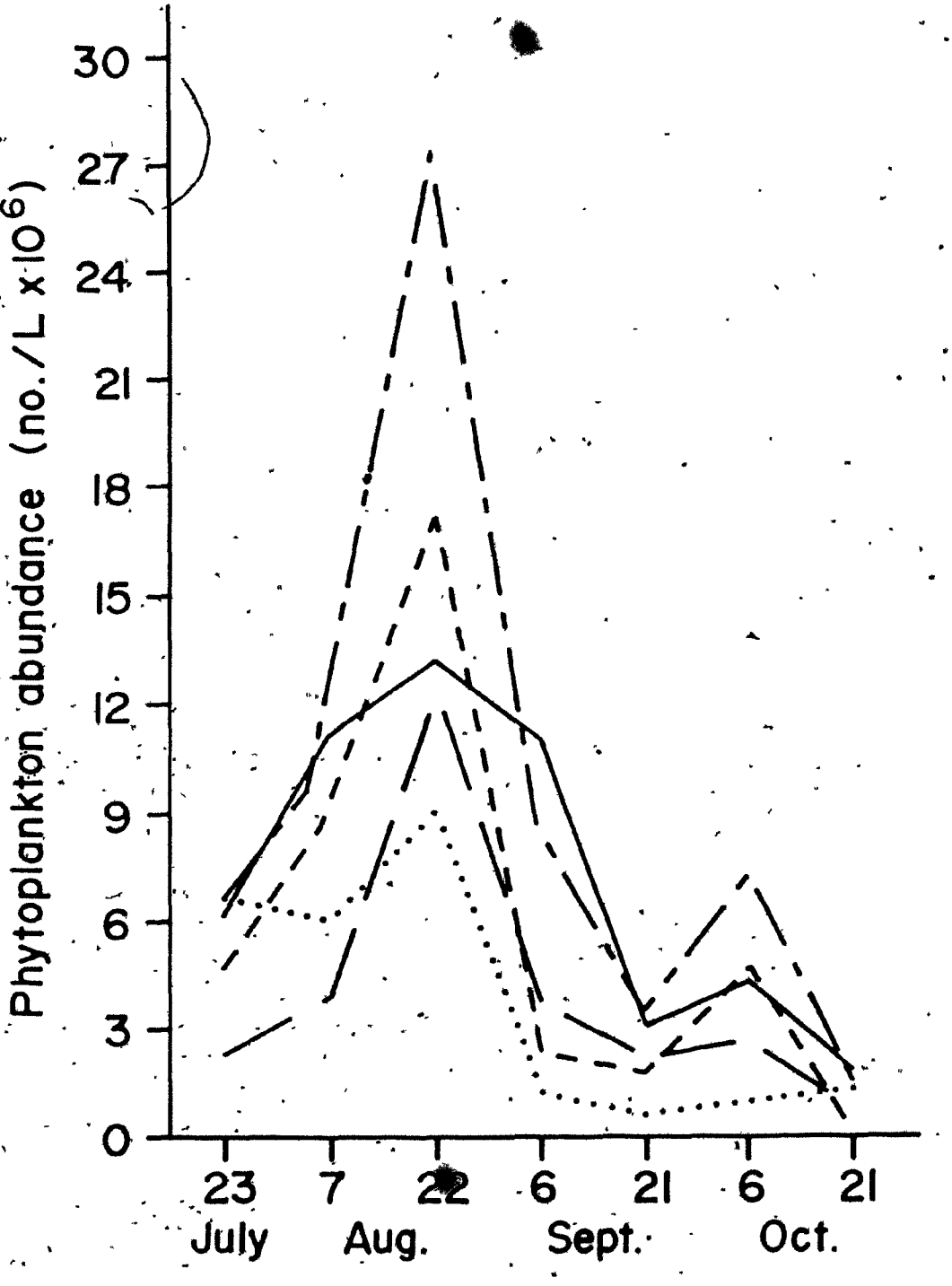
TREATMENT	DATE	INSECT LARVAE	COPEPOD NAUPLII	ARACHNIDS
ACIDIFIED	820723	0	42200.	0
	820807	0	4370.	0
	820822	0	8150.	0
	820906	0	4120.	0
	820921	0	4170.	0
	821006	0	5350.	0
	821021	0	13000.	0
	MEAN	0	11600.	0
BEAVERSKIN	820723	0	58500.	0
	820807	0	2810.	0
	820822	0	4420.	0
	820906	0	6080.	0
	820921	0	4580.	0
	821006	0	5230.	603.
	821021	0	14000.	0
	MEAN	0	13600.	86.

Table 12. Continued.

TREATMENT	DATE	INSECT LARVAE	COPEPOD NAUPLII	ARACHNIDS
CONTROL	820723	0	34400.	0
	820807	50.	1760.	0
	820822	0	13000.	0
	820906	5.	4520.	0
	820921	50.	2080.	0
	821006	0	2960.	0
	821021	0	1670.	0
	MEAN	15.	8640.	0
LIMED	820723	0	70200.	0
	820807	0	2510.	0
	820822	0	5830.	0
	820906	0	6640.	0
	820921	0	5780.	0
	821006	0	5560.	0
	821021	0	4370.	0
	MEAN	0	14400.	0
NUTRIENT	820723	0	49000.	0
	820807	0	2910.	0
	820822	0	5930.	0
	820906	0	8800.	0
	820921	0	5630.	0
	821006	0	4620.	0
	821021	0	10200.	0
	MEAN	0	12400.	0

Figure 14. Cyanophyte abundance (nos./liter) in Beaverskin Lake enclosures, 1982.




Phytoplankton abundance (no./L x10⁶)
30
27
24
21
18
15
12
9
6
3
0
23
July
7
22
Aug.
6
Sept.
21
6
Oct.
21

generally slightly higher than in these enclosures. Cyanophyte populations at the end of the experiment were similar in all locations.

The dominant cyanophyte species was Agmenellum thermale (Appendix F), a very small (2 micron diameter) colonial species which forms small mats of cells. This species was most abundant in the enriched enclosures, and least numerous with acidification. The other relatively abundant cyanophyte, Chroococcus dispersus, was also numerous with nutrient addition, however, the lowest mean levels for this species were noted in the controls. This species was not reduced by acidification in the same way as Agmenellum thermale.

Levels of chlorophytes, or green algae, were very similar in the enriched enclosures and in Beaverskin Lake (Table 12), showing a single peak on Aug. 22. Populations in the acidified and limed tubes were variable over the experimental period, but a trend emerged of increasing numbers in the acidified enclosures and decreasing numbers in the limed enclosures over time (Fig.15). Numbers of chlorophytes in the controls were more variable, with two abundance peaks occurring on Aug. 22 and Oct. 21.

The dominant chlorophyte, Schroederia setigera, showed its highest mean abundances over the course of the experiment in Beaverskin Lake, although variation was quite high, and this species was not present on all dates (Appendix F). Lowest mean abundance for this species was seen in the enriched environments. The pattern for S. setigera differs from the overall pattern for chlorophytes. The other dominant chlorophytes, Ulothrix variabilis and Gloeocystis maior were most abundant in the enriched tubes, and showed their second highest levels in the controls. Mougeotia sp., a filamentous chlorophyte, showed relatively high abundances only in the acidified enclosures; apparently it was enhanced by the decrease in pH. It

Figure 15. Chlorophyte abundance (nos./liter) in Beaverskin Lake enclosures, 1982.

Key:

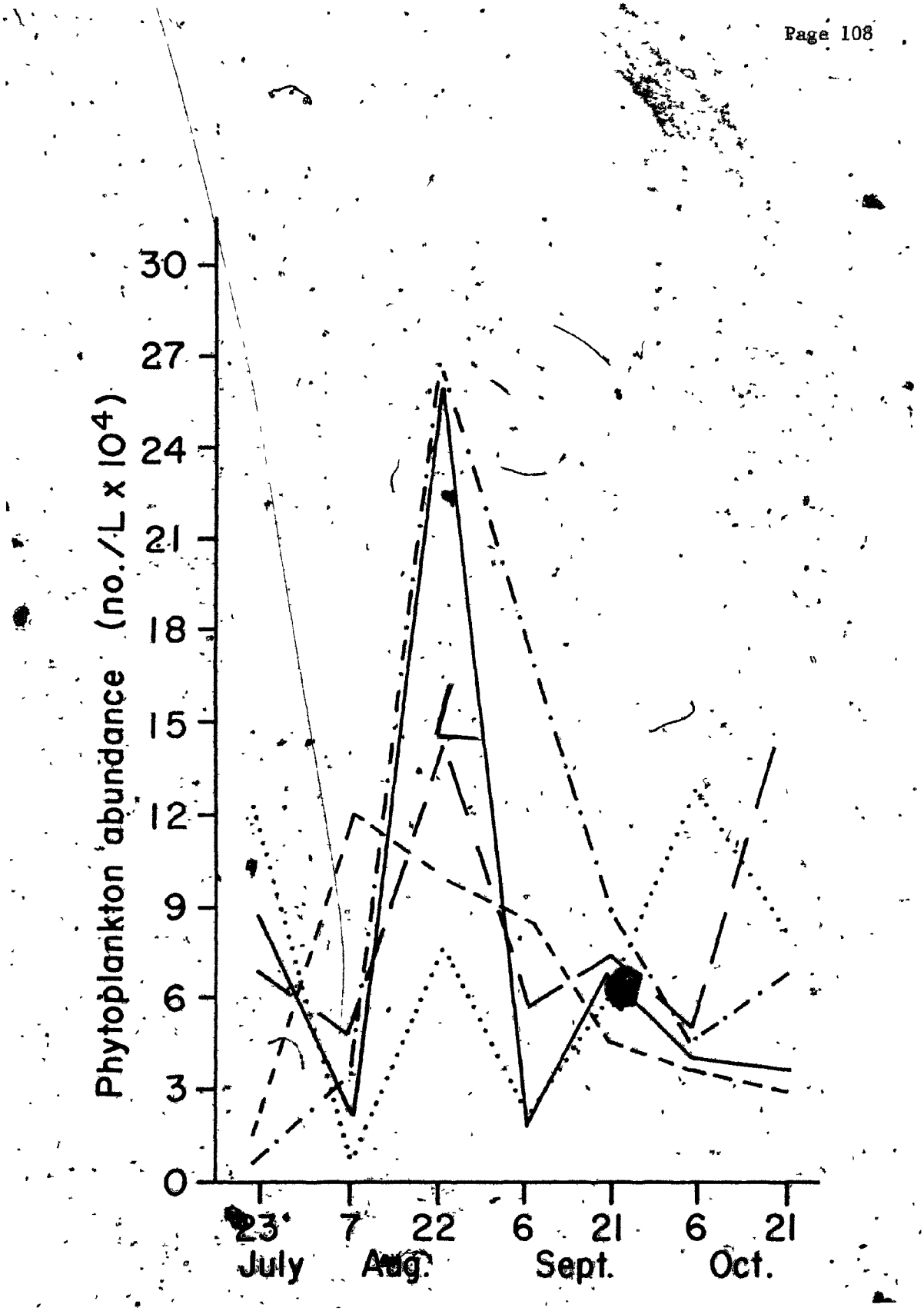
——— Beaverskin Lake

— — Control Enclosures

. . . . Acidified Enclosures

- - - - Limed Enclosures

— . — Nutrient Enclosures


Phytoplankton abundance (no./L x 10⁴)
30
27
24
21
18
15
12
9
6
3
0
23
July
7
Aug.
22
6
Sept.
21
6
Oct.
21

was a minor constituent of the Chlorophyta in the other environments.

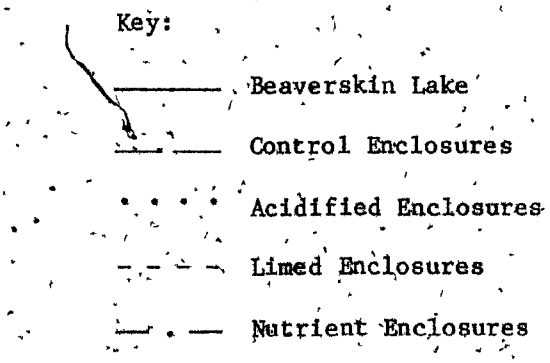
The chrysophytes have been divided into two groups - the diatoms, and other non-diatom chrysophytes (Table 12). Populations of diatoms were very low in Beaverskin Lake throughout the experiment, with no evident peaks (Fig. 16). Diatoms did exhibit blooms in the enclosures, however, with the exception of the limed ones. The highest levels occurred in the acidified enclosures, on Oct. 6, while peaks of intermediate size occurred in the control and enriched enclosures on Sept. 21 and Sept. 6 respectively. By the end of the experiment; populations of diatoms returned to low levels similar to those in the lake, with the exception of the control populations, which remained relatively abundant.

Two of the dominant diatom species were Tabellaria fenestrata and T. flocculosa (Appendix F). Both these species were less abundant in the lake than in any enclosures; however, these congeneric species responded to the treatments in markedly different fashions. T. fenestrata was more than ten times as abundant in the acidified environments as in any others, while T. flocculosa was most numerous with enrichment. Synedra pulchella, the other dominant diatom, did best in the controls, and was also abundant in the acidified tubes.

The non-diatom chrysophyte species were not abundant in any of the tubes, nor in the lake (Table 12). Population patterns during the experimental period were similar in all locations, with peaks occurring in the controls and limed enclosures on Sept. 6 (Fig. 17). Numbers tended to increase in all environments toward the end of the experiment.

Dinobryon bavaricum and Mallomonas caudata were the most abundant non-diatom chrysophyte species (Appendix F). Highest levels of D. bavaricum occurred in the control and limed enclosures, while M. caudata was most abundant in the enriched and limed environments.

Figure 16. Diatom abundance (nos./liter) in Beaverskin Lake enclosures, 1982.



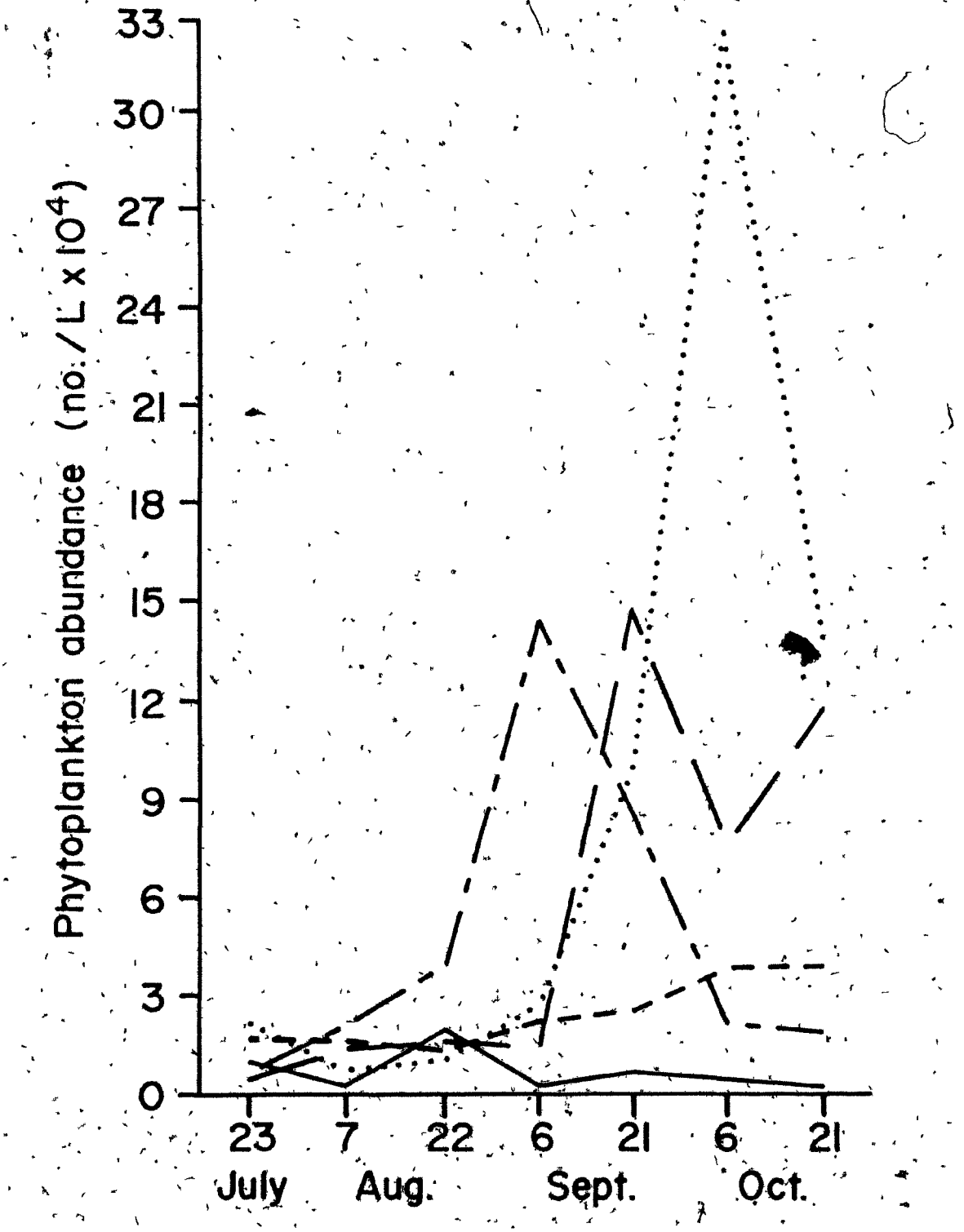

Phytoplankton abundance (no./L x 10⁴)
33
30
27
24
21
18
15
12
9
6
3
0
23
7
22
6
21
6
21
July
Aug.
Sept.
Oct.

Figure 17. Non-diatom chrysophyte abundance (nos./liter) in Beaverskin Lake enclosures, 1982.

Key:

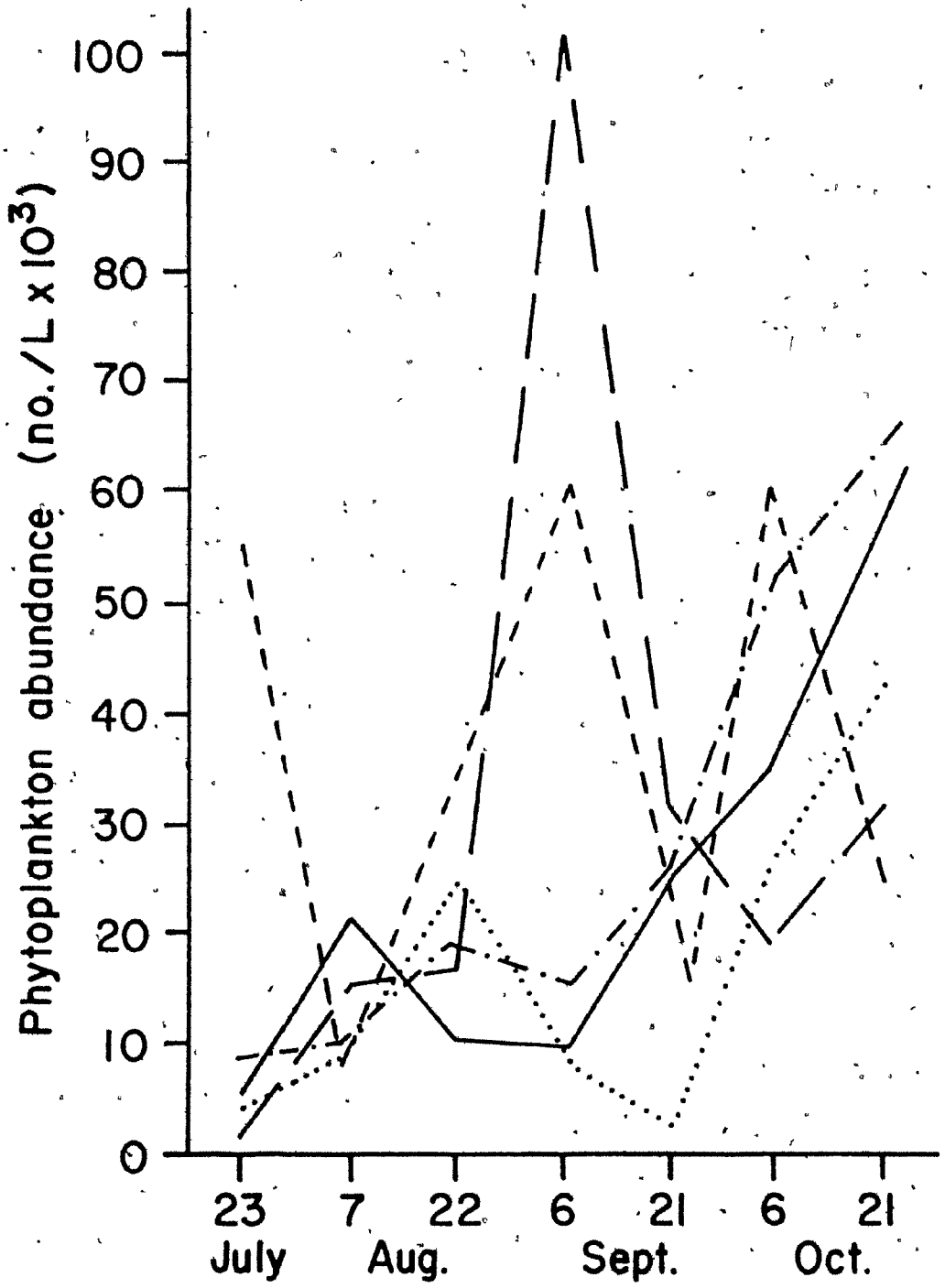
———— Beaverskin Lake

—— —— Control Enclosures

. . . . Acidified Enclosures

- - - - Limed Enclosures

— . — Nutrient Enclosures


Phytoplankton abundance (no./L x 10³)
100
90
80
70
60
50
40
30
20
10
0
23
July
7
22
Aug.
6
21
Sept.
6
21
Oct.

Xanthophytes, the yellow-green algae, showed one extremely high bloom in the enriched enclosures on Aug. 22 and Sept. 6 (Table 12), with minor peaks occurring in late August in the controls and early October in the lake and in the limed enclosures (Fig. 18).

The dominant xanthophyte, Chlorochromonas minuta, was very abundant in the enriched enclosures, although its numbers began to decline towards the end of the experimental period (Appendix F). Numbers in these enclosures were between five and nine times higher than in the other environments.

c. Zooplankton

1. Standing Stocks

Total rotifer densities were higher in the enriched enclosures than in the others, with a sharp increase in abundance at the end of the experimental period (Fig. 19). Rotifer densities showed a tendency to increase over time in the other environments as well, but not to such high levels. Rotifer populations were similar to each other in all other environments, with slightly higher levels occurring in the control enclosures (Table 12).

The dominant rotifer species in all environments was Conochilus unicornis (Appendix F). This species accounted for the majority of the dramatic increase in rotifer numbers in the enriched tubes at the end of October. The other abundant rotifer, Keratella cochlearis, also tended to increase in all environments toward the end of the experiment, especially in the enriched tubes and in the lake. A third rotifer species, Ploesoma hudsonii, was relatively abundant in the enriched enclosures in early September, at about the mid-point of the experiment. This species was only a minor component of the rotifer communities in the other tubes.

Figure 18. Xanthophyte abundance (nos./liter) in Beaverskin Lake enclosures, 1982.

Key:

———— Beaverskin Lake

— — — Control Enclosures

• • • • Acidified Enclosures

- - - - Limed Enclosures

— . — Nutrient Enclosures

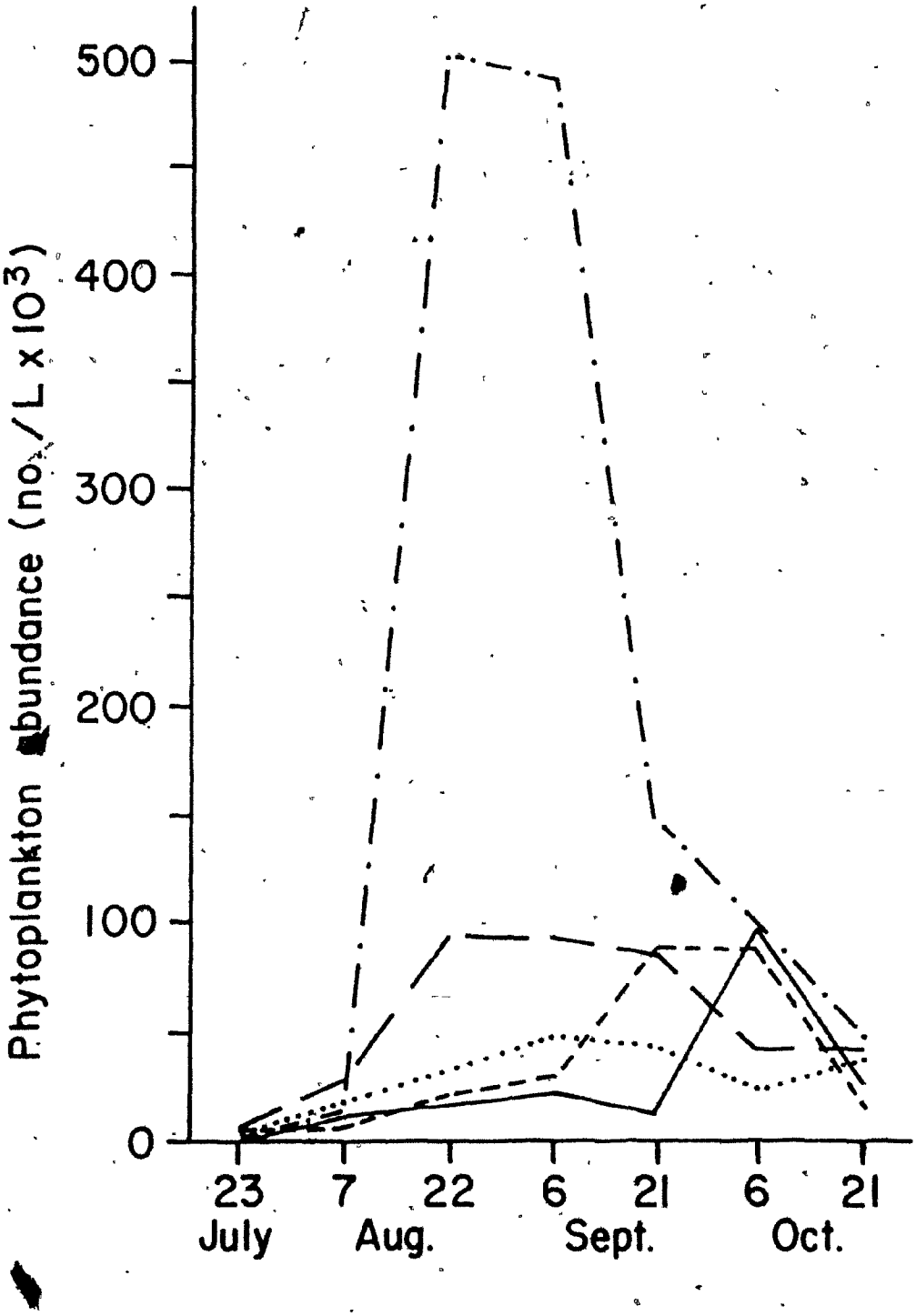

Phytoplankton abundance (no./L x 10³)
500
400
300
200
100
0
23 July
7
22 Aug.
6
21 Sept.
6
21 Oct.

Figure 19. Rotifer abundance (nos./meter^3) in Beaverskin Lake enclosures, 1982.

Key:

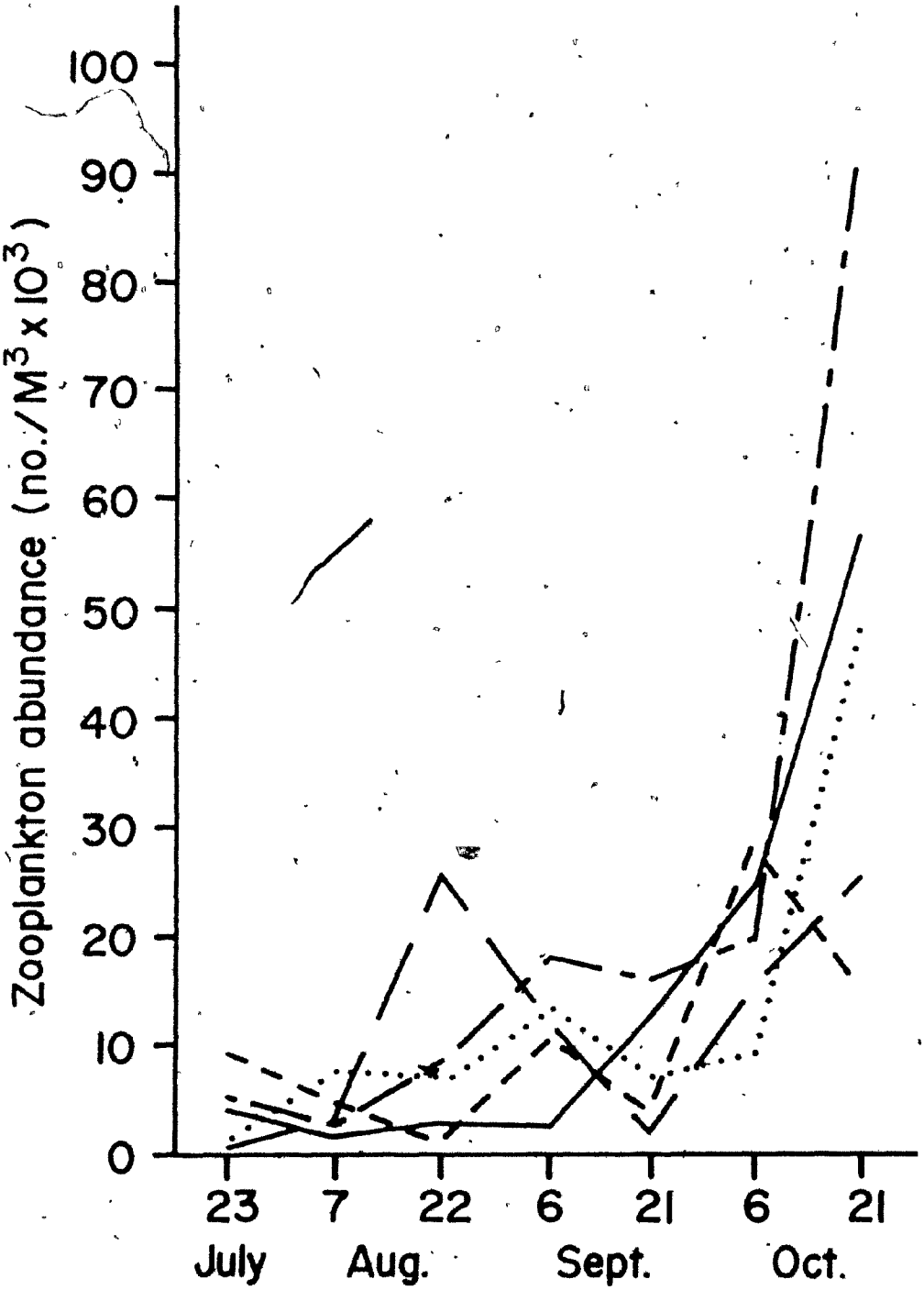
———— Beaverskin Lake

—— —— Control Enclosures

• • • • Acidified Enclosures

– – – – Limed Enclosures

— ·.— Nutrient Enclosures


Zooplankton abundance (no./M³ x 10³)
100
90
80
70
60
50
40
30
20
10
0
23
7
22
6
21
6
21
July
Aug.
Sept.
Oct.

Total cladoceran populations peaked at different times during the experiments in the various environments (Table 12). Following an early peak, numbers in the lake declined to levels below those in the enclosures. Numbers peaked in mid- and late September respectively in the acidified and control tubes, and to a lesser extent in the enriched tubes. Comparing within the enclosures, cladoceran numbers were lower on most dates in the limed enclosures than in the others (Fig. 20). Populations in all environments at the end of the experiment were similar to each other.

The dominant cladoceran species were Eubosmina tubicen and Chydorus sp. (Appendix F). E. tubicen exhibited its highest levels in the acidified and limed tubes, being apparently able to tolerate both extremes of pH. Its lowest abundances occurred in the controls. In contrast, Chydorus sp. was most abundant in the controls, with intermediate levels in the enriched enclosures and lowest numbers in Beaverskin Lake.

Calanoid copepods were less abundant in all enclosures than in the lake (Table 12, Fig. 21). Within the enclosures, numbers were higher on most dates in the limed set, although an increase was noted at the end of the experiment in the enriched treatment.

The dominant calanoid, Diaptomus minutus, was least numerous in the acidified environments, and most numerous in the limed enclosures (except that numbers were highest overall in the lake) (Appendix F). Although this is an acid tolerant species, these results suggest that it benefits from increased pH.

Cyclopoid copepods were much less abundant than calanoids (Table 12). Numbers were highest in the control enclosures, and were also relatively high in the enriched set during the middle of the experiment (Fig. 22). Comparing within the enclosures, liming resulted in reduced populations of cyclopoids on most dates. Numbers were lowest on two dates in the open

Figure 20. Cladoceran abundance (nos./meter^3) in Beaverskin Lake enclosures, 1982.

Key:

——— Beaverskin Lake

— — Control Enclosures

. . . . Acidified Enclosures

- - - - Limed Enclosures

— . — Nutrient Enclosures

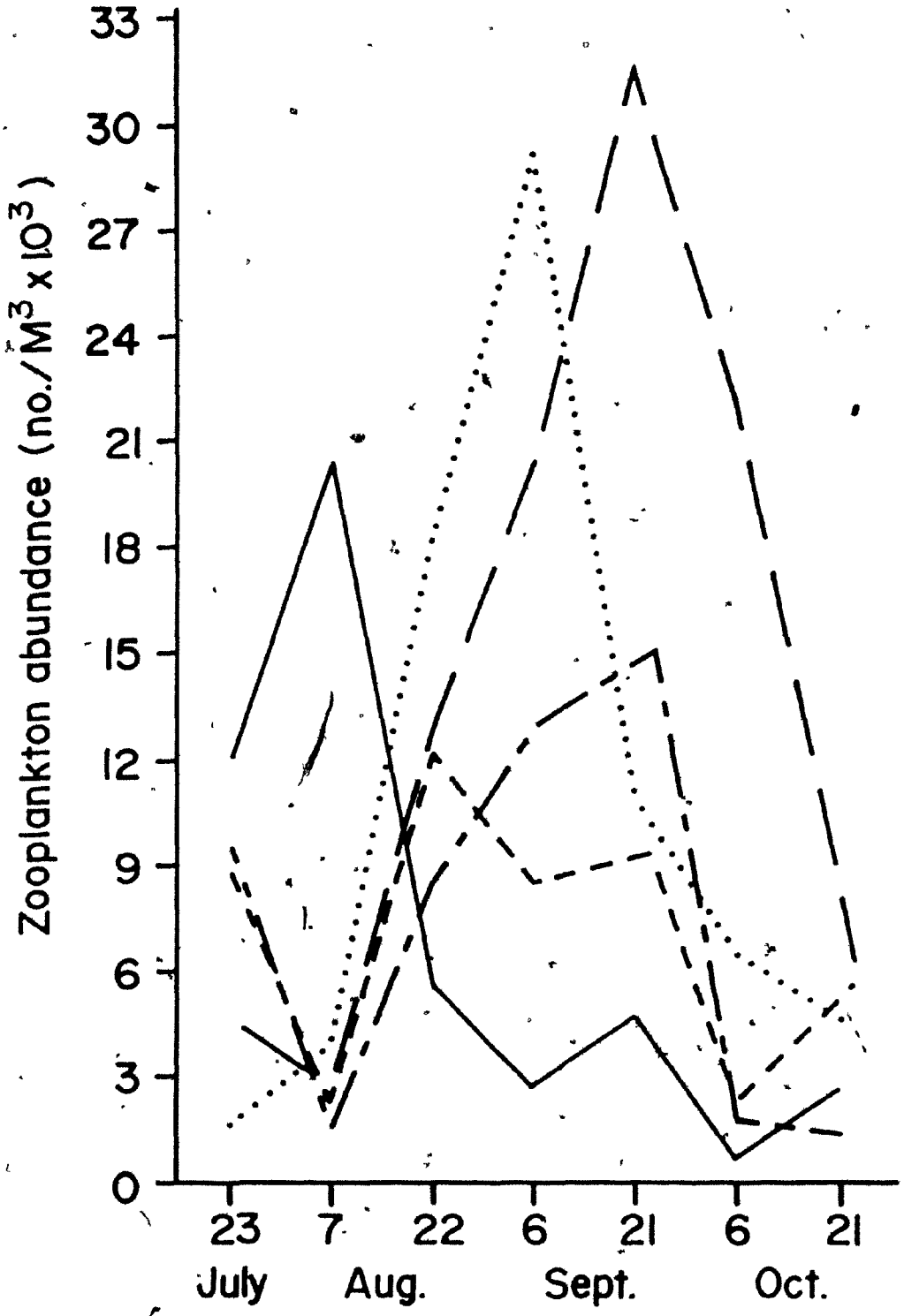

Zooplankton abundance (no./M³ x 10³)
33
30
27
24
21
18
15
12
9
6
3
0
23
7
22
6
21
6
21
July
Aug.
Sept.
Oct.

Figure 21. Calanoid copepod abundance (nos./meter^3) in Beaverskin Lake enclosures, 1982.

Key:

——— Beaverskin Lake

—— —— Control Enclosures

• • • • Acidified Enclosures

- - - - Limed Enclosures

— . — Nutrient Enclosures

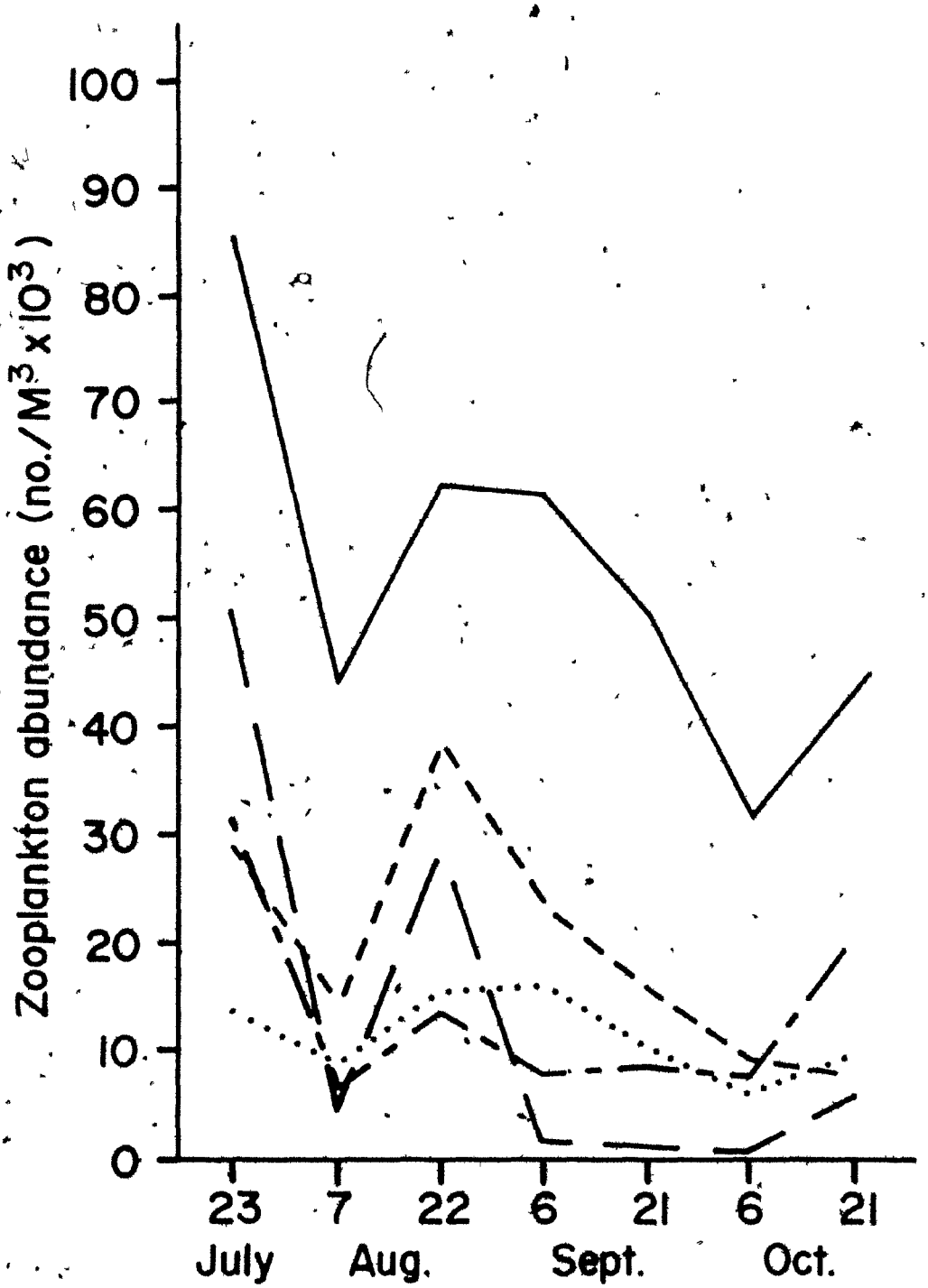

Zooplankton abundance (no./M³ x 10³)
100
90
80
70
60
50
40
30
20
10
0
23
July
7
Aug.
22
6
Sept.
21
6
Oct.
21

Figure 22. Cyclopoid copepod abundance (nos./meter^3) in Beaverskin Lake enclosures, 1982.

Key:

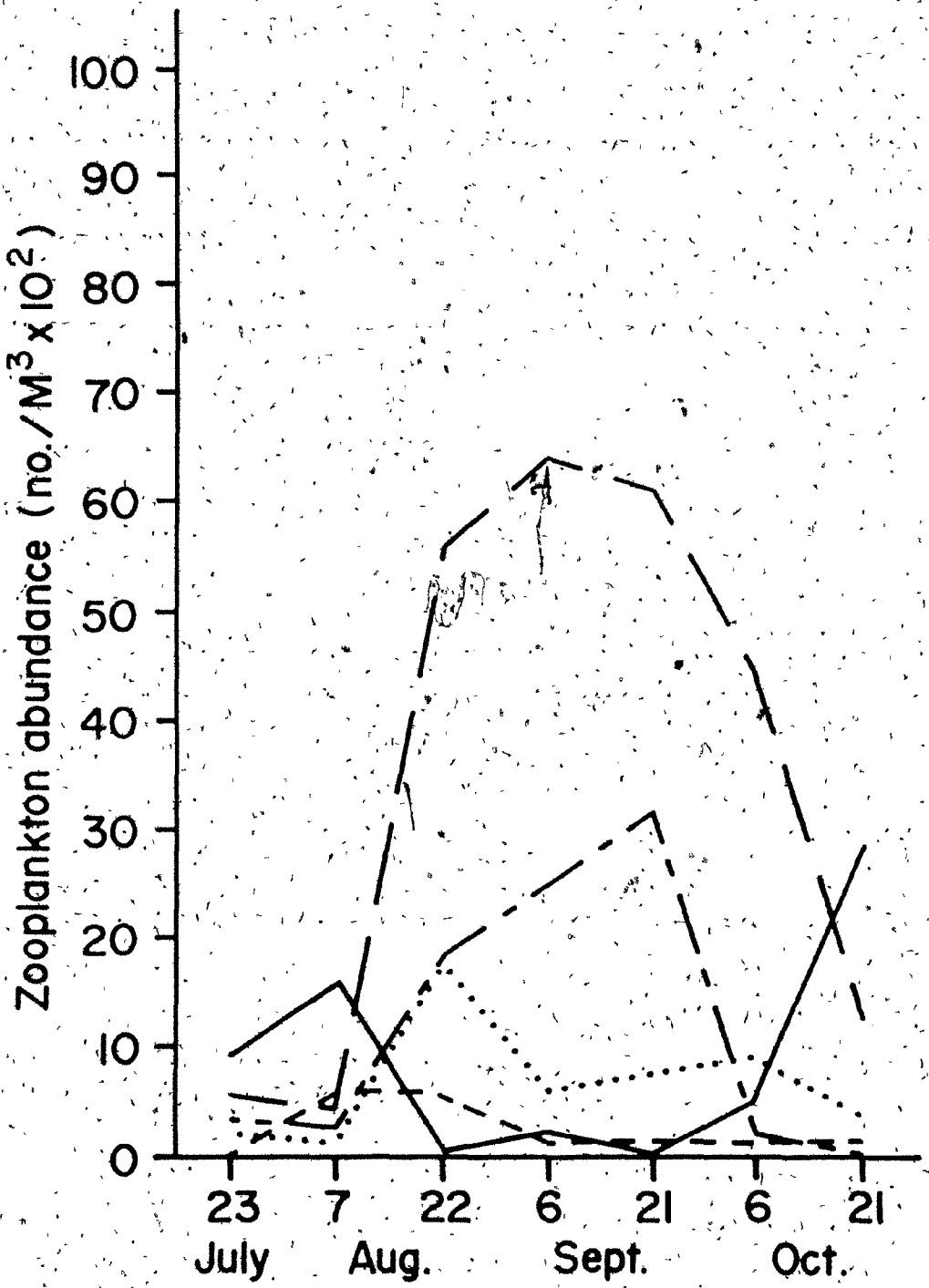
——— Beaverskin Lake

— — Control Enclosures

. . . . Acidified Enclosures

– – – – Limed Enclosures

— . — Nutrient Enclosures


Zooplankton abundance (no./M³ x 10²)
100
90
80
70
60
50
40
30
20
10
0
23
July
7
Aug.
22
6
Sept.
21
6
Oct.
21

lake.

Numbers of nauplii, the first life-cycle stage for copepods, were remarkably similar in all enclosures on all dates (Fig. 23). Abundances started very high in all environments at the initiation of the experiment (Appendix F), and rapidly declined to lower levels which remained relatively constant in all treatments and in the lake for the rest of the experiment.

2. Egg Ratios -

As for Year I, egg ratio values are presented as average number of eggs per female for each species (Appendix F).

Chydorus sp. was quite rare in the pelagic samples from Beaverskin Lake, but was more common in the enclosures. It was most abundant in the controls, where its egg ratio values at first declined and later recovered somewhat.

Eubosmina tubicen showed the highest population levels in the acidified enclosures, but had its highest egg ratio values in the nutrient enriched tubes. Lowest populations and ratios occurred in the lake and the controls. Ratios were variable in all environments but tended to be highest toward the end of the experiment.

Diaphanosoma birgei tended to decline in both population and egg ratio values through the experiment in all environments. Only in the limed enclosures were any eggs seen by the end of the experiment.

Daphnia catawba was more abundant in year 2 than in the first year's experiment. Its largest populations occurred in Beaverskin Lake, but the largest egg ratio values were seen in the nutrient enriched enclosures.

Holopedium gibberum was rare or absent in all environments in year 2, in contrast to year 1.

Figure 23. Copepod nauplii abundance (nos./meter^3) in Beaverskin Lake enclosures, 1982.

Key:

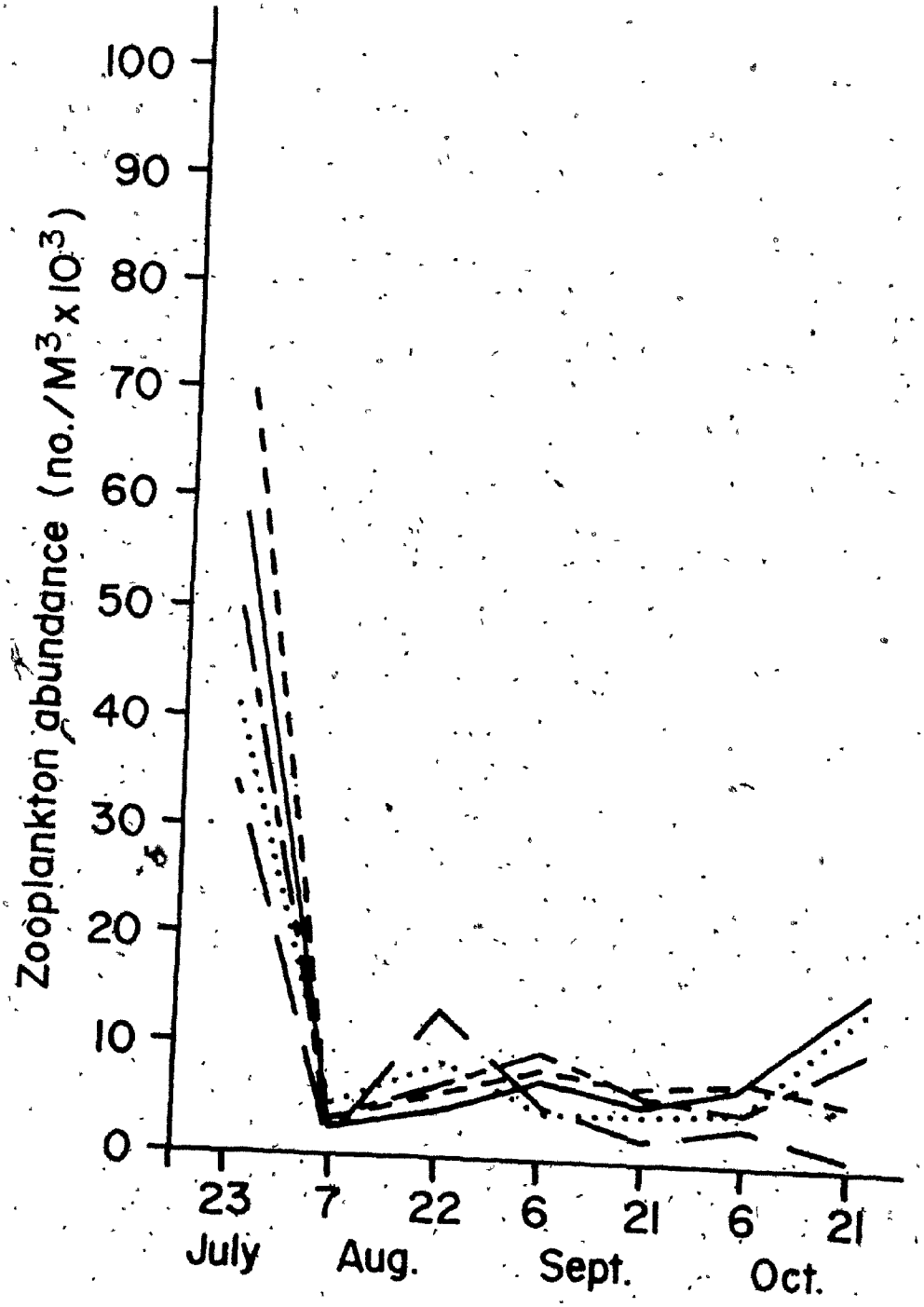
——— Beaverskin Lake

— — Control Enclosures

. . . . Acidified Enclosures

- - - - Limed Enclosures

—●— Nutrient Enclosures


Zooplankton abundance (no./M³ x 10³)
100
90
80
70
60
50
40
30
20
10
0
23
July
7
Aug.
22
6
Sept.
21
6
Oct.
21

As in year 1, a number of cladoceran species which do not normally occur in the open water were found in the enclosures. As in the previous year, these species occurred most often in the acidified enclosures. Many of them also appeared in the enriched enclosures.

The dominant copepod, Diaptomus minutus, was least abundant and showed its lowest egg ratio values (zero on many dates) in the control enclosures as compared with the other environments. In the acidified enclosures, egg ratio values for D. minutus at first increased and later declined. The population showed a peak which lagged behind the egg ratio peak. D. minutus egg ratio values in the limed enclosures showed a peak later in the experiment. Ratios for D. minutus in the lake and in the enriched enclosures were low, but relatively constant throughout the experiment.

Epischura nordenskioldi was rare and quite sporadic in the enclosures and the lake, and no eggs were noted.

Cyclopoid copepods were most abundant in the control enclosures, and rare elsewhere. Mesocyclops edax had high egg ratio values in the controls on many dates, but had disappeared by the end of the experiment.

d. ANOVA Results, 1982.

For the 1982 enclosure experiment, significance tests were done for the following factors: treatment, depth, date, and the possible interaction terms. The null hypotheses (1-4) were the same as previously described. The dependant variables examined included pH, chlorophyll a, and the major zooplankton and phytoplankton taxonomic groups. Preliminary ANOVA investigations suggested that for many variables, the lake was significantly different from the enclosures. For this reason, in order to obtain a more sensitive test for differences between enclosure treatments, the open lake samples are not included in the following ANOVAs.

For pH, the factors treatment and date (Hypotheses 1 and 2) were both significant ($p < .05$), as might be expected (Table 13), which confirms that pH was significantly altered by the additions of acid and lime to the different enclosures, and that the pH varied significantly over time. The interaction between treatment and date (Hypothesis 4) was also highly significant.

Chlorophyll a levels were not significantly different among treatments (Hypothesis 1), but did change significantly over time (Hypothesis 2). Depth was also a significant factor (Hypothesis 3), indicating that chlorophyll a was not homogeneously distributed in the enclosures even though no thermal stratification occurred. None of the interaction terms among factors (Hypothesis 4) were significant.

All the algal variables (chlorophytes, diatoms, non-diatom chrysophytes, xanthophytes and cyanophytes) showed significant responses to the date factor (Hypothesis 2); that is, their abundances changed significantly over time. None of the other factors was significant for the algal groups with these two exceptions: the non-diatom chrysophytes showed a significant interaction between treatment and depth, and the cyanophytes responded significantly to the treatments (Hypothesis 1). The cyanophytes were the only algal group to be significantly affected by the experimental manipulations imposed.

Among the zooplankton groups, a common pattern emerged of significant responses to the factors depth, date, and the interaction between depth and date (Hypotheses 2-4). These results suggest a combination of population changes over time, along with behavioural preferences for certain depths in the enclosures. None of the zooplankton groups was significantly affected by the treatments (Hypothesis 1), although for copepod nauplii the interaction for treatment, date and depth was significant (Hypothesis 4).

Table 13. ANOVA Results, Beaverskin Lake enclosure experiment, 1982.

F = F statistic for ANOVA

p = significance level for F

VARIABLE -	pH		Chlorophyll a	
FACTOR	F	p	F	p
Treatment	14.05	0.014	1.15	0.431
Depth	3.88	0.066	5.37	0.033
Treatment x Depth	0.63	0.703	2.67	0.100
Date	7.44	0.000	4.27	0.005
Treatment x Date	7.17	0.000	1.97	0.171
Date x Depth	0.98	0.477	1.46	0.171
Treatment x Date x Depth	1.38	0.149	0.95	0.556

VARIABLE -	Chlorophytes		Diatoms	
FACTOR	F	p	F	p
Treatment	1.16	0.427	0.30	0.825
Depth	0.35	0.713	0.07	0.930
Treatment x Depth	0.19	0.917	0.45	0.830
Date	4.69	0.003	5.51	0.001
Treatment x Date	1.72	0.106	1.58	0.147
Date x Depth	1.03	0.439	0.84	0.611
Treatment x Date x Depth	1.34	0.171	1.15	0.318

Table 13. (continued)

VARIABLE -	Non-diatom chrysophytes		Xanthophytes	
FACTOR	F	p	F	p
Treatment	1.44	0.355	1.15	0.431
Depth	0.63	0.559	3.12	0.100
Treatment x Depth	4.20	0.033	3.14	0.069
Date	3.09	0.022	4.12	0.006
Treatment x Date	0.81	0.674	0.67	0.811
Date x Depth	0.63	0.806	1.23	0.293
Treatment x Date x Depth	1.07	0.410	0.84	0.704

VARIABLE -	Cyanophytes		Cladocerans	
FACTOR	F	p	F	p
Treatment	15.6	0.011	0.54	0.678
Depth	3.43	0.084	29.4	0.000
Treatment x Depth	0.40	0.859	0.92	0.525
Date	16.1	0.060	7.96	0.000
Treatment x Date	0.89	0.596	1.19	0.343
Date x Depth	1.89	0.060	4.13	0.000
Treatment x Date x Depth	1.06	0.424	0.78	0.783

Table 13. (continued)

VARIABLE -	Calanoid copepods		Cyclopoid copepods	
FACTOR	F	p	F	p
Treatment	1.22	0.412	3.77	0.116
Depth	6.90	0.018	20.7	0.001
Treatment x Depth	2.09	0.166	1.24	0.378
Date	4.71	0.003	7.44	0.000
Treatment x Date	0.97	0.514	1.27	0.286
Date x Depth	6.10	0.000	2.45	0.014
Treatment x Date x Depth	0.92	0.595	1.21	0.262

VARIABLE -	Copepod nauplii		Rotifers	
FACTOR	F	p	F	p
Treatment	1.98	0.259	0.54	0.682
Depth	11.9	0.004	4.37	0.052
Treatment x Depth	0.80	0.594	0.72	0.647
Date	47.3	0.000	7.63	0.000
Treatment x Date	1.62	0.133	1.47	0.185
Date x Depth	8.57	0.000	2.44	0.014
Treatment x Date x Depth	2.03	0.011	0.78	0.785

C. Discussion

I. Year I

While preliminary in nature, consisting of a feasibility study for the larger scale investigations in 1982, the 1981 enclosure experiments in Beaverskin Lake suggest some interesting conclusions.

The copepod data showed that populations were lower in the limed enclosures, suggesting that of the two treatments applied, liming represented the greater stress to the copepods.

Some of the cladoceran species which occurred in the enclosures were littoral/benthic species not normally seen in the pelagic zone, suggesting that these individuals were using the enclosure walls as substrates and were at least occasionally getting from this habitat into the upper water column. The presence of these cladocerans would help to explain the higher numbers in the containers as compared with the open water of the lake. The Cladocera showed the same overall pattern of decline in the limed enclosures as did the copepods.

While the zooplankton were relatively unaffected by the additional acidification imposed, they were apparently adversely affected by a degree of liming sufficient to restore a near neutral pH value. Liming of acid lakes is becoming common management strategy both in North America and in Europe, usually with the goal of restoring conditions conducive to regeneration of fish stocks in acidified lakes and river systems (Rosseland and Skogheim, 1984; White et al., 1984; Schrieber and Rago, 1984). Fish populations are, of course, ultimately dependant on either primary production or, in the case of colored, humic lakes, on detritus as the food source for the lake ecosystem. The zooplankton constitute one of the most

important pathways for energy flow from primary producers to the higher trophic levels. If liming should prove detrimental to the zooplankton, then little would be gained by creating conditions in which fish may reproduce, if their food source is substantially reduced by the management technique which creates those conditions. The study lakes in Kejimkujik National Park have been acidic a long time because of the influence of acid bog drainage (Kejimkujik and Pebbleloggitch Lakes), combined with their poor buffering capacity (particularly Beaverskin Lake). This process has likely been accentuated by the relatively recent increase in acid deposition. The Kejimkujik Park study lakes all have fairly diverse and abundant phytoplankton and zooplankton assemblages, indicating that these communities can to some extent adapt over time to at least some degree of acidity. When this occurs, as in Beaverskin Lake, liming can apparently act as a detrimental stress to the zooplankton community, at least on a short-term basis. The results from the acidified enclosures in 1981 suggest that, having previously adapted over time to acidic conditions, the zooplankton of Beaverskin Lake were tolerant of a moderate degree of increased acidification.

II. Year II

In 1982, larger enclosures were used to test for plankton community responses to alterations of pH and nutrient availability. An overall goal was to elucidate causal pathways at the food web level. pH was manipulated and subsequent physical and chemical effects were examined. Similar nutrient trends over time were observed in the controls, limed, and acidified enclosures. A trend of uniformity at the nutrient level does not necessarily imply that the other trophic levels indirectly tied to the perturbation will be as consistent. The nutrient-enriched enclosures clearly showed increases in nitrogen, phosphorus, and chlorophyll a.

High N/P ratios (nitrate + nitrite + ammonia/soluble reactive phosphorus) suggest that phosphorus limitation was occurring in the lake and most enclosures. Even in the nutrient-enriched enclosures, after the addition of both nitrogen and phosphorus, higher N/P ratios occurred, suggesting rapid utilization of phosphorus. In all enclosures, but to a lesser extent in the nutrient enriched ones, total phosphorus decreased as the experiment proceeded. This decrease was either a result of export to the sediments or of nutrient uptake by the periphyton growing on the enclosure walls. In Beaverskin Lake, natural nutrient recycling seemed to prevent a similar pattern of nutrient depletion. Chlorophyll a values were variable, with the highest values in the nutrient-enriched enclosures.

Schindler and Wagemann (1980) reviewed the sources of buffering available in a fresh water system other than dissolved bicarbonate. Apparently some type of "auxiliary buffering" was acting on the acidified enclosures. A possible explanation could have been disturbance of the sediments during sampling, which may have released bicarbonate into the water column. Another plausible explanation might be a biological enclosure

effect. At low alkalinities the amount of free CO_2 would be low (Beaverskin < 1.0 mg $CaCO_3$/l); however, as pH decreased, the free CO_2 would increase. Towards the end of the experiment the periphyton on the walls of the enclosures increased markedly, particularly in the enriched containers, and CO_2 taken up during photosynthesis of these plants would not be readily returned to the water column. This lowering of CO_2 concentration would result in an increase in pH values. This could explain the observed rise in pH in the nutrient-enriched enclosures after additions had been stopped, and the prevention of pH decreases even when the addition of H_3PO_4 was resumed. In the case of the acidified enclosures, although H_2SO_4 was still being added towards the end of the experiment, removal of CO_2 by the periphyton on the walls of these tubes may have pushed the pH upwards slightly. Apparently more acid would be required to counter some of these non-bicarbonate types of buffering.

Although the analysis of variance showed few statistically significant responses of the algal and zooplankton groups to the treatments, some interesting patterns did emerge. The only significant response was shown by the blue-green algae, which increased with nutrient enrichment and decreased with acidification. The green algae and diatoms both increased with acidification and decreased with liming. The xanthophytes bloomed with nutrient addition.

Acidification has often been reported to lead to a dominance of the phytoplankton by Pyrrophyta (dinoflagellates) (Almer et al., 1978; Yan and Stokes, 1978; Stokes, 1980; Hendry, 1980). The most common genus reported in such studies has been Peridinium. Pyrrophytes are quite rare in Beaverskin Lake, and their frequency or abundance did not increase in the acidified enclosures. Green algae have been reported as dominant in some acid lakes (Crisman et al., 1980), which is in accordance with the increase

noted in Chlorophyta in the acidified enclosures of Beaverskin Lake. A similar pattern was also noted during the experimental acidification of Lake 223 (Schindler and Turner, 1982), when chrysophyceans were gradually replaced in importance by chlorophytes. Dominance by blue-greens in acidic conditions has been reported in acid humic lakes by Hultberg and Andersson (1982). In the Kejimkujik Park study lakes, blue-greens were rare in the humic lakes (Kejimkujik and Pebbleloggitch), and were found to decrease with acidification in the Beaverskin Lake enclosures. Hendry et al. (1982) noted reductions in cyanophyte diversity in acid lakes in New York state. Many previous studies (Conroy et al., 1976; Kwiatkowski and Roff, 1976; Hultberg and Andersson, 1982; Charles, 1982) have noted reductions in diatom diversity or abundance at reduced pH. In the present experimental study, however, diatoms were found to increase with acidification and decrease with liming.

Contradictory observations concerning the effects of lake acidity on plankton communities are common, and causal relationships in aquatic ecosystems are often poorly understood (U.S. Environmental Protection Agency, 1983). In an effort to delineate causal pathways and examine changes in community structure in the experimental enclosures, loop analysis was used to construct foodweb models for each of the experimental treatments and Beaverskin Lake (Appendix E, Figure 5).

The models all have in common three nutrient and four algal variables (Appendix E, Figure 5). Algal variable 3 is rarely used as a food resource by the zooplankton. The bluegreen algae are grazed on by one zooplankton group, and are the only algae which utilize the ammonia (NH) nutrient variable. Detritus and the rotifer variables form a sub-system appended to the rest of the community. Three zooplankton variables act as top

carnivores in these systems, and are always self-damped.

The community core network for the acidified environments had the fewest links, the lowest connectance, and was the least stable system (Lane and Blouin, 1984). The acidified network had the lowest degree of similarity to the Beaverskin Lake network of any of the experimental systems.

Liming altered the nature of many of the interactions between the nutrient and algal variables. The links from the NP variable to the algae are all one-way. NP has no positive effect on any algal variable, meaning that changes in NP will not affect the phytoplankton directly. Links to the detritus variable D have been increased, suggesting that detritus assumes greater importance in the limed systems, perhaps as a result of reductions in the algal community.

Nutrient enrichment results in two-way flows between most nutrient and algal variables, meaning that changes in nutrients can be passed along to higher trophic levels. Nutrient enrichment in the enclosures produced increases in the cyanophytes and xanthophytes at the phytoplankton level. In both cases, the increase took the form of a large bloom followed by a decline. The loop model for the enriched community shows that the blue-greens are linked directly to NH, ammonia, the nutrient on which they primarily depend in the model. The blue-green bloom is coincident with a sharp peak in ammonia concentration in late August, following initiation of nutrient additions, illustrating the direct effect of the NH-BG relationship.

For the zooplankton, acidification did not cause any major changes in any of the taxonomic groups. This confirms the findings of the Year I enclosure studies, that the zooplankton of Beaverskin Lake are apparently adapted to the present levels of acidity and able to tolerate the degree of

additional acid stress imposed.

In many instances, the dominant zooplankton species of Beaverskin Lake and the enclosures have been reported elsewhere as acid-tolerant and common in acidic conditions. Keratella cochlearis, the dominant rotifer, has been found in acid lakes in Sweden (Almer et al., 1978; Hulberg and Andersson, 1982). Bosminids are common in acid conditions, including the dominant cladoceran in the enclosures, Eubosmina tubicen (Roff and Kwiatkowski, 1977). Daphniids, which are rare in all three Kejimkujik Park study lakes, are commonly found to be less tolerant of acidic conditions than other cladocerans (Sprules, 1975).

The most abundant calanoid copepod in the Beaverskin Lake enclosures, Diaptomus minutus, and the most abundant cyclopoid copepod, Mesocyclops edax, have both been noted as acid tolerant in Ontario lakes (Roff and Kwiatkowski, 1977) and in the northeastern U.S. (Confer et al., 1983).

Liming of the enclosures resulted in reduction of the rotifers and cyclopoid copepods, and lack of abundance peaks in the cladocera which were noted in other enclosures. Only the calanoid copepods increased with liming, although not by a great amount and not on all dates. Apparently liming represented a greater stress to many of the zooplankters than did additional acidification. Reduction of zooplankton by liming has been previously reported for lakes of low pH (4.2-4.5) (Shieder and Dillon, 1976; Dillon et al., 1979), although liming of a lake of more intermediate pH (5.7) resulted in little change in the zooplankton (Yan et al., 1977). Increases in zooplankton populations are often reported following liming in Sweden (Eriksson et al., 1983; Hasselrot and Hultberg, 1984).

Nutrient enrichment resulted indirectly in abundance peaks in most zooplankton groups - for cyclopoid copepods in the middle of the

experiment, and for calanoid copepods and rotifers at the end of the experiment. Lack of a positive effect on cladocerans may result from the fact that cladocerans are subject to predation by the copepods. Thus, increases in nutrients are passed along the foodweb to higher trophic levels with only the higher predators evidently showing population increases. Effects on intermediate trophic levels would presumably be expressed in terms of increased growth and turnover rates. The rotifer groups are preyed upon in the model only by immature Epischura nordenskioldi, which were quite rare in the enclosures. Predation pressure was presumably light, allowing rotifer populations to increase. Increases in rotifers following nutrient additions to enclosures in an acid lake were also noted by DeCosta et al. (1983). They found greatly increased populations of Keratella toward the end of a two month enclosure fertilization experiment, a result quite similar to the pattern noted here for rotifers. In addition, they noted increases in the cladocerans (Bosmina and Diaphanosoma), which were not seen in the present study.

In summary, acidification seemed to affect aspects of community structure, as seen in the loop analysis models, but did not produce widespread changes in plankton populations. Liming resulted in reductions in many plankton groups and an increased importance of detritus in community trophic relationships. Nutrient enrichment led to increases in cyanophytes and the carnivorous zooplankton groups of the upper trophic levels.

CHAPTER 4.

BIOGEOGRAPHY OF LAKE PLANKTON IN RELATION TO pH AND WATER CHEMISTRY

To provide a more general approach to the question of plankton community patterns in relation to pH and associated water chemistry variables, larger numbers of lakes representing a broad range of acidity levels must be examined. This has not previously been done in Nova Scotia, which has lakes ranging from naturally acidic which have been subject to humic bog drainage for some time, to lakes which retain buffering capacity and near-neutral pH. This biogeographic study will address the following general question:

> What are the larger-scale (biogeographical) patterns of lake plankton community composition and abundance in relation to pH and the range of other physical and chemical characteristics of lakes in Nova Scotia, and what may be concluded from such spatial patterns concerning long-term adaptation of plankton communities to a range of pH levels?

Specific questions to be answered will be: What are the physical and chemical factors which are most influential in determining the composition of lake plankton communities?; what are the patterns of distribution of the major plankton groups in relation to pH and water chemistry?; and how does plankton community composition compare between a variety of lakes?. Answers to these questions may be found by use of simple graphical and regression techniques to relate plankton species numbers and abundances to pH, and use of more complex multivariate techniques such as multiple regression and cluster analysis to relate plankton community composition to a larger set of physical-chemical variables and to compare community similarity among a set of lakes.

A. Methods

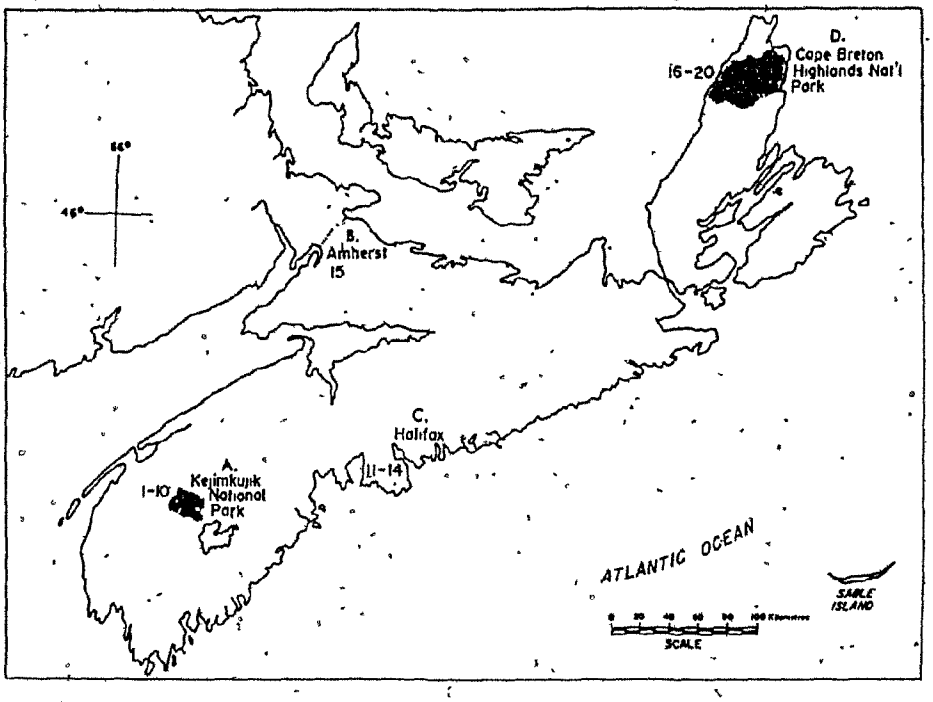
1. Study Lakes

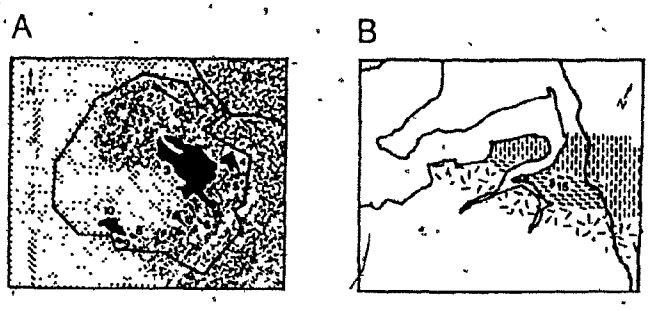
On the basis of previously available physical and chemical data, twenty lakes were selected from across Nova Scotia to provide a range of pH conditions for study. Ten lakes were located in Kejimkujik National Park, including the three original study lakes; five were located in Cape Breton Highlands National Park; four were located in the Halifax-Sackville area; and one was situated near Amherst (Fig. 24). The lakes range in depth from 2 to 30 meters, and in pH value from around 3.5 to 7.6 (Table 14). Most lakes were sampled five times (at approximately six week intervals) from May-November 1983, four lakes were sampled on four occasions (those in the Halifax-Sackville area), and one lake (Layton's Lake, Amherst) was sampled twice. Additional morphometric and chemical data for these lakes may be found in Kerekes (1975 a,b; 1983), Kerekes et al. (1981, 1984), Howell and Kerekes (1982), Clifford (1984), and MAPC (1972). Lake numbers (1-20) assigned in Fig. 24 are used in subsequent tables and figures for identification purposes.

The lakes of Kejimkujik National Park are located in the Southern Upland Interior geological region of Nova Scotia (Roland, 1982). Figures 24 (A,B,C,D) show the relationships of lake basins to underlying bedrock. Kejimkujik, Grafton and McGinty Lakes lie on a sandstone-shale conglomerate bedrock originating in the late Devonian/early Carboniferous period (370 million years ago). Big Dam East and Big Dam West Lakes occur north of Kejimkujik Lake on a border between the above bedrock and a shale-limestone area originating 500 million years ago in the Cambrian period. The other Kejimkujik Park lakes (Pebbleloggitch, Beaverskin, Peskawa, Mountain and Puzzle) are on or near the border of a Carboniferous-Devonian era (350-400 million year old) granite/diorite bedrock and a Cambrian era (500 million

Figure 24. Twenty study lakes for plankton biogeography, Nova Scotia, 1983. Basin locations and bedrock geology are indicated.

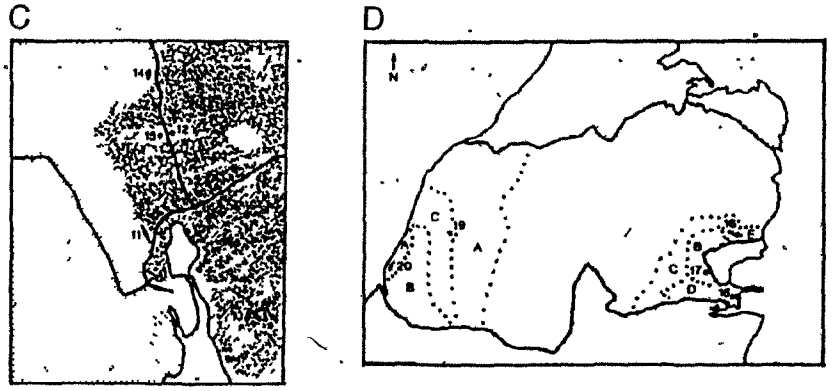
Kejimkujik National Park: (A)	Latitude	Longitude
1. Big Dam East Lake	44°27′	65°16′
2. Big Dam West Lake	44°27′	65°17′
3. Kejimkujik Lake	44°23′	65°15′
4. Grafton Lake	44°23′	65°11′
5. McGinty Lake	44°22′	65°10′
6. Puzzle Lake	44°19′	65°14′
7. Mountain Lake	44°20′	65°16′
8. Beaverskin Lake	44°18	65°20′
9. Pebbleloggitch Lake	44°18′	65°21′
10. Peskawa Lake	44°19′	65°22′
Halifax-Sackville Area: (C)		
11. Kearney Lake	44°42′	63°42′
12. Little Springfield Lake	44°48′	63°45′
13. Drain Lake	44°48′	63°45′
14. Lacey Mill Lake	44°51′	63°49′
Amherst Area: (B)		
15. Layton's Lake	45°48′	65°15′
Cape Breton Highlands National Park: (D)		
16. Freshwater Lake	46°39′	60°24′
17. Cann's Lake	46°40	60°26′
18. Warren Lake	46°43′	60°24′
19. French Lake	46°44′	60°52′
20. Presqu'ile Lake	46°41′	60°57′





KEY : Bedrock Type

- Granitic
- Goldenville Slate/Greywacke
- Halifax Slate/Schist
- Pictou Sandstone
- Windsor Sandstone/Limestone
- Riversdale Sandstone



A - Gneiss/Scist.
B - Granitic
C - Metamorphic Slate
D - Dioritic
E - Windsor Sandstone/Limestone

Table 14. Physical and chemical data for 20 biogeographic study lakes. (Mean values over dates and depths).

Lake	pH	Alk	TP	SRP	TN	TDN	DOC	SI
1) Big Dam East	5.2	0.7	12.8	0.2	.128	.010	3.4	1.44
2) Big Dam West	5.0	0.3	14.6	1.0	.162	.010	11.	1.96
8) Beaverskin	5.4	0.3	26.2	11.	.100	.010	2.0	0.36
17) Canns	6.2	2.2	8.84	0.7	.161	.010	3.7	1.10
13) Drain	4.2	0.0	38.5	1.3	.280	.030	1.5	1.45
19) French	5.5	1.1	9.97	0.8	.156	.018	5.9	0.89
16) Freshwater	6.8	12.	8.06	0.4	.110	.022	2.4	1.62
4) Grafton	5.9	1.3	16.5	1.3	.102	.012	4.2	0.78
11) Kearney	6.1	1.3	16.4	1.0	.214	.127	3.3	2.55
3) Kejimkujik	5.0	0.3	14.0	1.3	.077	.013	6.5	2.18
14) Lacey Mill	4.6	0.0	15.5	0.0	.078	.010	2.7	1.33
15) Laytons	7.5	38.	45.7	24.	.335	.200	4.7	0.85
5) McGinty	6.2	3.4	21.4	0.7	.175	.010	7.9	2.32
7) Mountain	4.9	0.1	14.8	1.0	.101	.011	2.9	1.16
9) Pebbleloggitch	4.4	0.0	25.4	0.4	.146	.010	9.6	1.56
10) Peskawa	4.8	0.1	22.9	5.1	.116	.012	6.3	2.20
20) Presqu'ile	7.6	52.	14.7	0.6	.161	.010	3.3	1.84
6) Puzzle	5.2	0.0	16.1	0.6	.106	.010	3.2	0.32
12) Ltl.Springfield	3.5	0.0	10.4	0.4	.100	.037	1.7	1.90
18) Warren	5.7	1.6	9.09	0.1	.133	.015	7.7	2.94

Table 14. Continued.

Lake	Al	z_{max}	$\bar{z}$	Area	Temp	Color
1) Big Dam East	.094	4.2	2.32	45.5	16.9	7.00
2) Big Dam West	.268	9.5	2.47	105.	16.1	108.
8) Beaverskin	.033	6.3	2.19	39.5	16.5	4.00
17) Canns	.106	9.2	2.00	10.4	13.5	6.67
13) Drain	.843	3.0	0.61	16.3	13.8	10.8
19) French	.140	2.0	1.04	7.0	10.8	43.3
16) Freshwater	.023	16.	6.50	42.2	12.4	4.33
4) Grafton	.067	9.0	2.8	270.	16.2	30.7
11) Kearney	.125	26.	9.17	63.9	9.9	5.42
3) Kejimkujik	.162	19.	4.35	24400	15.9	80.3
14) Lacey Mill	.346	5.4	1.5	16.0	12.5	3.75
15) Laytons	.102	11.	2.1	11.3	13.8	6.25
5) McGinty	.090	4.0	1.39	4.4	15.1	79.0
7) Mountain	.082	14.	4.26	136.	14.6	9.50
9) Pebbleloggitch	.212	2.5	1.42	33.4	16.2	118.
10) Peskawa	.218	9.0	3.16	388.	15.5	64.0
20) Presqu'ile	.027	3.0	2.10	4.4	13.8	5.0
6) Puzzle	.044	6.1	2.7	33.7	16.5	17.0
12) Ltl.Springfield	3.62	7.0	4.0	13.7	13.4	3.75
18) Warren	.233	31.	15.9	89.8	9.6	74.7

Table 14. Continued.

Key:

pH - pH (units)

Alk - Alkalinity (mg/l)

TP - Total Phosphorus (mg/m^3)

SRP - Soluble Reactive Phosphorus (mg/m^3)

TN - Total Nitrogen (mg/l)

TDN - Total Dissolved Nitrogen (mg/l)

DOC - Dissolved Organic Carbon (mg/l)

SI - Silica (mg/l)

Al - Aluminum (mg/l)

z_{max} - Maximum Depth (m)

$\bar{z}$ - Mean Depth (m)

Area - Surface Area (hectares)

Temp - Temperature (^oC)

Color - Color (Hazen Units)

year old) shale-limestone bedrock southwest of Kejimkujik Lake. The lakes of the Halifax area (Kearney, Little Springfield, Drain and Lacey Mill) are situated in the Southern Upland Coastal geological region on a border zone between sandstone-shale conglomerate bedrock (Devonian/Carboniferous, 370 million years old) and shale-limestone bedrock (Cambrian, 500 million years old). Cape Breton National Park is in the Northern Plateau geological region of Nova Scotia. Freshwater, Cann's and Warren Lakes are located on Carboniferous era (350 million year old) granite/diorite bedrock; Freshwater Lake is on the coast, while Cann's and Warren Lakes are at higher altitudes on the plateau. French Lake is near the maximum altitude area of the plateau, in an area of gneiss/schist bedrock of the Helikian period (900 million years old). Presqu'ile Lake is a coastal lake on an early Carboniferous (360 million year old) sandstone-shale conglomerate bedrock. Layton's Lake, near Amherst in northern Nova Scotia, is in a sandstone-shale-coal formation of the late Carboniferous period (300 million years old). Thus, a variety of bedrock types is represented in the drainage basins of the study lakes, providing a range of basic water chemistry and buffering capacity characteristics. Those lakes which are naturally acidic tend to lie on poorly drained bedrock with poor buffering capacity (granitic, dioritic, shale). Poor drainage and lack of buffering promote the formation of peat bogs, whose accumulation of organic acids provide acid drainage to adjacent lake basins. Those lakes in areas of sandstone-limestone bedrock receive runoff of higher pH and retain carbonate buffering capacity.

II. Sampling Methods

a. Physical and Chemical Factors

Many of the lakes are shallow and are well-mixed throughout most of the year. Hence, water samples for chemical analysis were taken at the surface (0.5-1.0 meters) in spring and fall for shallow, unstratified lakes. Deeper lakes were sampled at three depths (surface, intermediate depth, and near-bottom) on all dates. For those shallow lakes which did not stratify in the summer months, water sampling continued at the surface only.

Temperature and oxygen were measured in situ at three depths on each sampling trip as previously described (Section 3.A.II). One liter of water was collected at each depth sampled for nutrient and general analysis, and 500 ml. for metals analysis, using a 2-liter Van Dorn bottle. Between 200-500 ml. replicate samples from the surface were filtered on .45 micron Millepore filters for chlorophyll a and phaeophytin analysis (these samples were not taken on the first sampling date in May). General analysis (pH, conductivity, turbidity, color), chlorophyll and phaeophytin analyses were performed using standard CWS methods. Major ions and metals were analysed by the Canada Center for Inland Waters laboratory in Moncton, New Brunswick.

b. Phytoplankton and Zooplankton

Phytoplankton and zooplankton were sampled at three depths in all lakes on all dates using a water bottle and Schindler-Patalas trap, respectively, as previously described (Section 2.A). All sampling was conducted at the deep station of each lake. Replicate sub-samples were examined for phytoplankton and zooplankton enumeration using methods previously described (Section 2.A).

III. Statistical Analyses

In order to answer the questions posed concerning patterns of relationship between plankton variables and physical-chemical factors, pairwise correlations, regressions, multiple and stepwise multiple regressions were conducted on the various physical-chemical variables and plankton taxonomic groups, over the twenty lakes. All data were log-transformed for normality as previously described. The statistical package MINITAB was used for these analyses. MINITAB screens data for multiple regressions and automatically rejects predictor variables which are strongly correlated, or which do not vary sufficiently to be useful as predictors. The coefficient of determination, R^2, is also presented for each regression. R^2 is the proportion of unexplained variation in the dependent variable accounted for by the regression. A random variable has a mean and an associated variance produced by departure of each of the values from the mean, and all of this variance is initially unexplained. In linear regression, a line representing the regression equation is produced. For least squares regression, the equation selected minimizes the sum of the squares of the departures of the data points from the regression line. Thus, there is a residual variance produced by the departure of each of the values from the regression line, and this variance will be less than the variance about the mean of the dependent variable (unless the slope of the equation is zero). Thus, the unexplained variance in the dependent variable has been reduced (or explained) by some factor (R^2) as a result of performing the regression analysis. R^2 is equal to the correlation between the observed and predicted values of the dependent variable. The situation is analagous for multiple regression except that more than one predictor variable enters the regression equation. For

multiple regressions, R^2 should be adjusted for degrees of freedom of the regression, since the addition of predictor variables can increase R^2 even if the added variables are of no real predictive value.

Cluster analysis of the twenty lakes was conducted on the basis of taxonomic group sums, using the BMDP statistical package. Clustering was done using standardised data, with Euclidean distance and single-linkage amalgamation. Separate cluster dendrograms were generated using phytoplankton and zooplankton data.

Data plots were generated using the MINITAB package. T-tests of differences between means were also done using MINITAB.

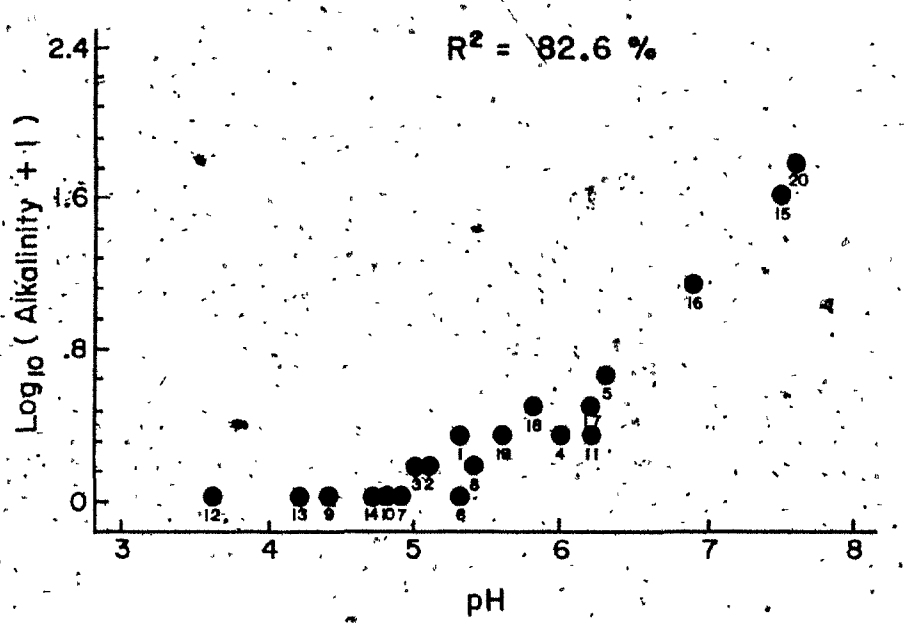
B. Results

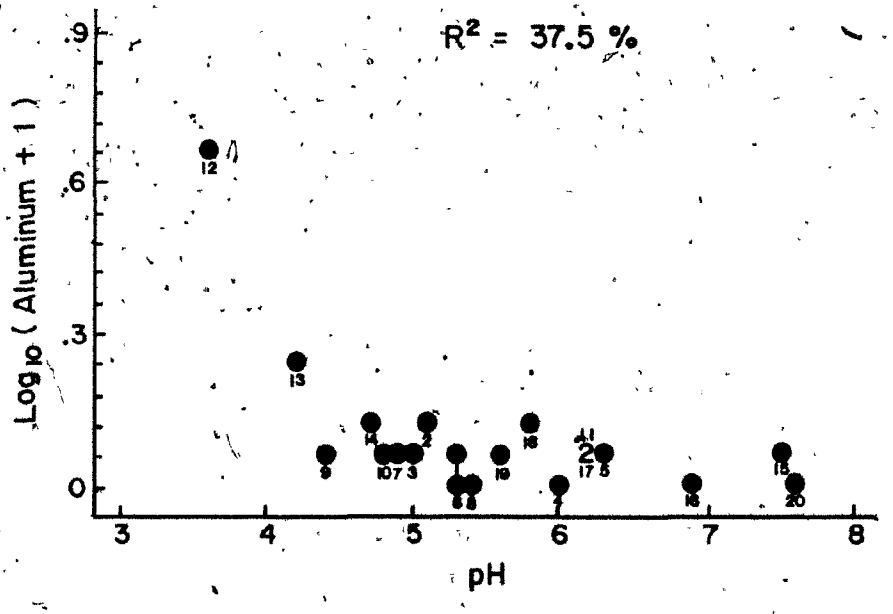
I. Lake Chemistry

The selected lakes represented a broad range of the limnological conditions found in Nova Scotia. The lakes of Kejimkujik National Park (Fig. 24, 1-10) were representative of the many types of inland waters of Nova Scotia, ranging from highly colored, acid humic waters to clear lakes of higher pH (Table 14). All Kejimkujik Park lakes were relatively undisturbed. The lakes of the Halifax-Sackville area (Fig. 24, 11-14) have been subject to varying degrees and types of watershed development, and showed extremes of pH, ranging from highly acidic Little Springfield Lake (pH 3.6) to Kearney Lake (pH 6.2). Little Springfield Lake has been influenced by construction in its drainage basin, exposing pyrite type bedrock and leading to highly acidic drainage and extremely high aluminum concentrations (3.6 ppm). The Little Springfield Lake outflow leads directly to Drain Lake, which receives an input of raw sewage effluent from a nearby trailer park. Drain Lake had higher pH values (mean=4.2), much higher phosphorus and nitrogen levels than Little Springfield Lake, and a lower concentration of aluminum. Layton's Lake, near Amherst (Fig.24, 15), is a meromictic, alkaline lake with high nutrient levels. This coastal lake was strongly influenced by historical fluxes of seawater from the Bay of Fundy. The lakes of Cape Breton Highlands National Park (Fig. 24, 16-20) ranged from coastal, near-neutral Freshwater and Presqu'ile Lakes to more acidic lakes at higher altitudes in the highlands. The twenty lakes as a group ranged in depth from 2 to 31 meters, and in area from 4.4 to 24,400 hectares, with corresponding variations in complexity of basin morphometry.

Alkalinity and aluminum both showed strongly curvilinear relationships to pH (Fig. 25 a,b). The transformed ($Log_{10}(x+1)$) data are plotted here

Figure 25. Log_{10} of a) Alkalinity and b) Aluminum versus pH.


R² = 82.6 %
Log₁₀ (Alkalinity + 1)
2.4
1.6
.8
0
3
4
5
6
7
8
pH


R² = 37.5 %
Log₁₀ (Aluminum + 1)
.9
.6
.3
0
3
4
5
6
7
8
pH

against pH. It is clear that highest alkalinities occurred at pH 6.0 or greater (as would be expected), while the highest aluminum concentrations were found below pH 5.0.

II. Lake Plankton-Water Chemistry Relationships

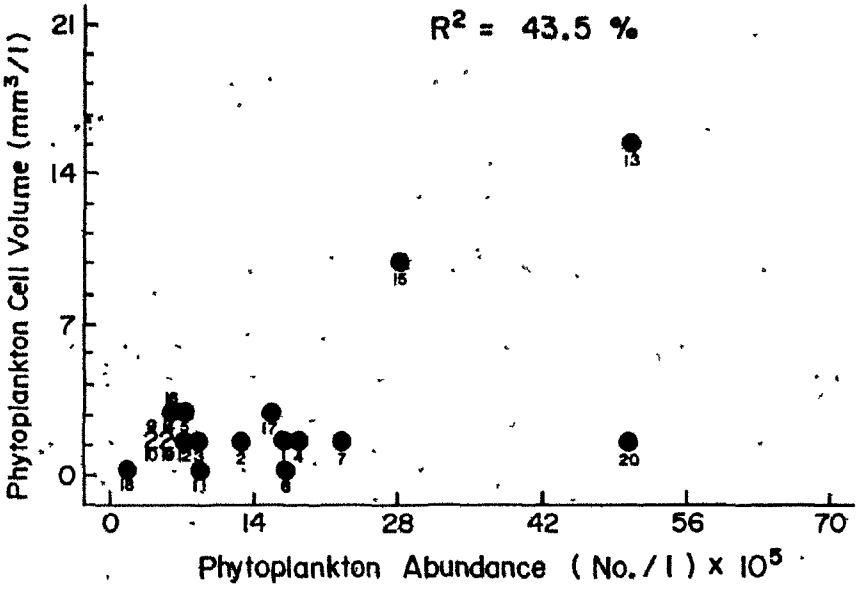
Highest total zooplankton numbers were noted in Layton's Lake, while highest algal populations were found in Beaverskin Lake (consisting mainly of the small cyanophyte (Agmenellum thermale) noted previously for this lake), (Table 15). Total cell volume for Beaverskin Lake was moderate compared with the overall data set, while Drain Lake and Layton's Lake had very high algal cell volumes. Layton's Lake was therefore highly productive in terms of the standing crop of the phytoplankton community. Drain Lake did not exhibit high zooplankton numbers, suggesting either that much of the algal biomass was in species unsuitable as food sources, or that conditions of low pH and high aluminum restricted zooplankton populations in this lake. The high algal cell volumes of Drain and Layton's Lakes were reflected by high chlorophyll a and phaeophytin levels. Relatively high cell volume and photosynthetic pigment values were also noted for Presqu'ile and McGinty Lakes. Both of these lakes had high pH levels. Thus, Drain Lake was an anomaly with abundant, productive phytoplankton at very low pH value.

Phytoplankton cell volume and chlorophyll a levels were both positively related to phytoplankton abundance, although the relationships were not strong (Fig. 26 a,b). These plots exclude Beaverskin Lake, whose unique population of extremely abundant, small cyanophytes made this lake an extreme outlier in these relationships. Between-lake differences in algal species composition partially obscured the cell volume-abundance relationship. The relationship was somewhat stronger for chloropyll a and algal abundance (R^2=0.54). The relationship of chlorophyll a to phytoplankton cell volume was quite strong (Fig. 27 a, R^2=0.84). This suggests that a unit of phytoplankton cell volume contains a predictable amount of chlorophyll a, because the cell volume was able to explain 84% of

Table 15. Total zooplankton (no./m^3) and algal (no./l) abundances, algal cell volume (mm^3/l), chlorophyll *a* and phaeophytin (mg/l).

Lake	Zooplankton	Algae	Cell Vol.	Chlor.a	Phaeo.
1) Big Dam East	74500	1630000	1.55	0.77	0.89
2) Big Dam West	103000	1200000	1.50	1.39	2.18
8) Beaverskin	215000	27400000	1.30	1.01	0.93
17) Canns	117000	1490000	2.13	0.60	0.92
13) Drain	133000	5060000	15.5	10.3	9.36
19) French	96600	589000	1.48	0.46	1.03
16) Freshwater	155000	624000	2.13	1.11	0.95
4) Grafton	84600	1830000	1.08	1.19	2.21
11) Kearney	21200	849000	0.21	0.39	0.52
3) Kejimkujik	86000	774000	1.64	1.00	1.77
14) Lacey Mill	72900	543000	0.70	0.23	0.29
15) Laytons	1540000	2810000	10.1	3.09	10.2
5) McGinty	290000	768000	3.31	2.46	5.19
7) Mountain	53700	2180000	0.81	0.55	0.68
9) Pebbleloggitch	198000	364000	0.74	1.27	2.01
10) Peskawa	100000	396000	0.74	0.80	0.90
20) Presqu'ile	335000	5080000	1.87	2.76	2.75
6) Puzzle	117000	1730000	0.55	0.92	1.54
12) Ltl.Springfield	26000	665000	0.85	0.49	0.71
18) Warren	36100	160000	0.20	0.85	1.14

Figure 26. a) Phytoplankton cell volume (mm^3/l) and b) Chlorophyll *a* (mg/l) versus phytoplankton abundance (no./l).


R² = 43.5 %
Phytoplankton Cell Volume (mm³/l)
21
14
7
0
0
14
28
42
56
70
Phytoplankton Abundance (No./l) x 10⁵

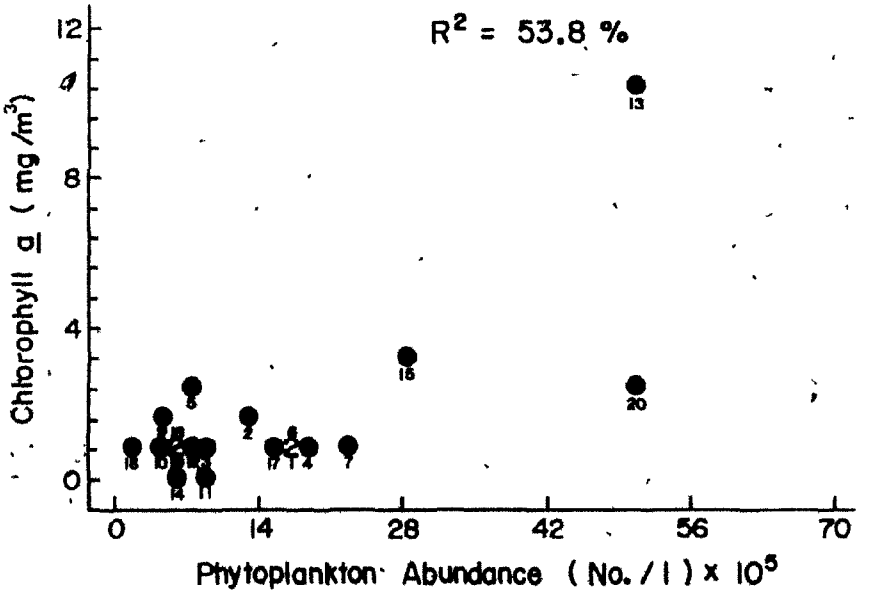
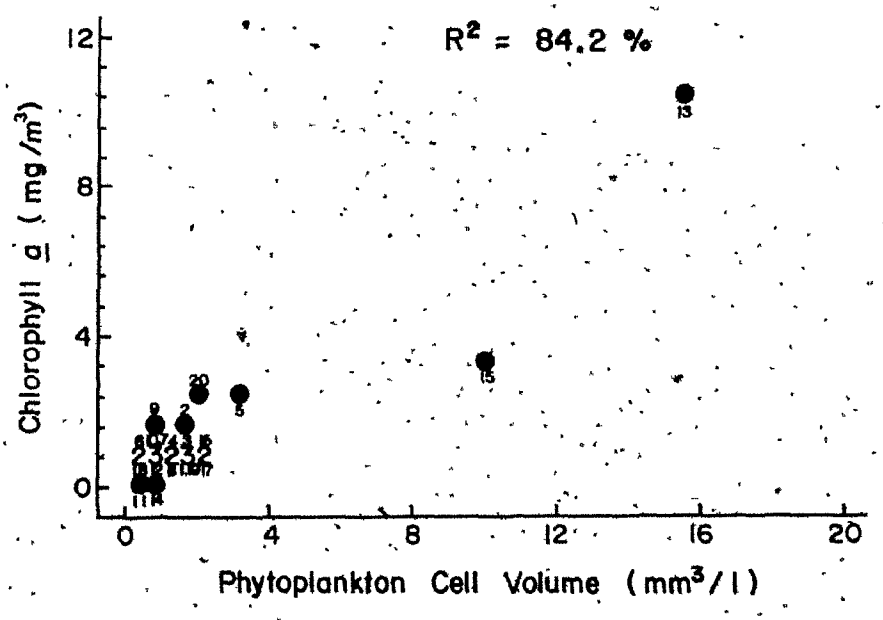
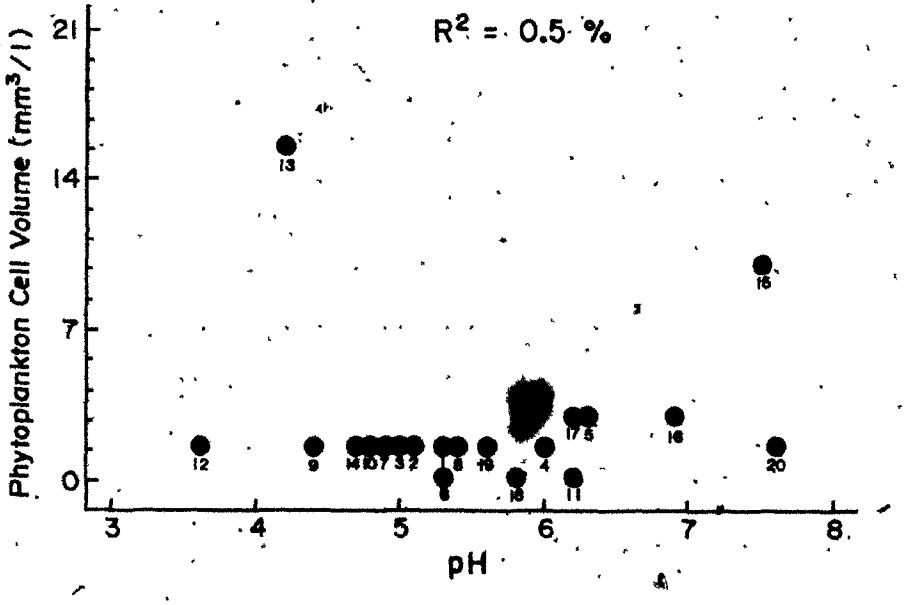

R² = 53.8 %
Chlorophyll a (mg/m³)
12
8
4
0
0
14
28
42
56
70
Phytoplankton Abundance (No./l) x 10⁵

Figure 27. a) Chlorophyll a (mg/l) versus phytoplankton cell volume (mm^3/l) and b) phytoplankton cell volume (mm^3/l) versus pH.


R² = 84.2 %
Chlorophyll a (mg/m³)
Phytoplankton Cell Volume (mm³/l)
0
4
8
12
16
20


R² = 0.5 %
Phytoplankton Cell Volume (mm³/l)
pH
0
7
14
21
3
4
5
6
7
8

the variation in the chlorophyll data. Phytoplankton cell volume, however, showed no relationship at all to pH (Fig. 27 b, $R^2 = 0.005$). A knowledge of pH would be of little value in predicting algal cell volume in a given lake.

Phytoplankton species numbers ranged from 17 (Kearney Lake) to 43 (Big Dam East Lake) (Table 16). The low species numbers in Kearney Lake were reflected in low abundances in most algal groups. Low algal diversity in Layton's Lake was not accompanied by low abundances in any group, although the true diversity may have been higher than shown, since this lake was sampled less frequently than the others. Lakes of very low pH such as Drain, Mountain, Pebbleloggitch and Peskawa Lakes still retained fairly high algal diversities and abundances. An extreme case was Little Springfield Lake, which at pH 3.6 still retained 26 species of phytoplankton, although abundances were fairly low in all categories. Lowest algal species numbers appeared in near-neutral lakes (Kearney and Layton's Lakes), although some exceptions were noted (Presqu'ile and Freshwater Lakes).

Plankton Community Composition and pH-

Occurrances of each species in the 20 lakes are indicated by appropriate lake numbers in Appendix A.

The most frequently occurring phytoplankton species in the overall data set were the diatoms Tabellaria flocculosa (19 lakes), Fragilaria crotonensis (15 lakes), and Navicula spp. (20 lakes); the chlorophytes Gloeocystis maior (16 lakes) and Sphaerocystis schroeteri (20 lakes); the chrysophytes Dinobryon bavaricum (19 lakes) and Mallomonas caudata (19 lakes); the xanthophyte Chlorochromonas minuta (20 lakes); and the cyanophyte Agmenellum thermale (16 lakes).

Table 16. Algal taxonomic group abundances (nos./l) and diversity (number of species). (Others - includes non-diatom chrysophytes, euglenophytes, xanthophytes, and pyrrophytes).

Lake	No. Spp.	Greens	Diatoms	Bluegreens	Others
1) Big Dam East	(43)	393000 (17)	157000 (12)	748000 (5)	336000 (9)
2) Big Dam West	(42)	361000 (12)	362000 (15)	421000 (6)	58900 (9)
8) Beaverskin	(26)	346000 (9)	14300 (7)	26700000 (2)	386000 (8)
17) Canns	(34)	84800 (8)	19300 (13)	502000 (5)	885000 (8)
13) Drain	(23)	1610000 (9)	76200 (8)	0 (0)	3370000 (6)
19) French	(40)	166000 (17)	245000 (12)	25900 (4)	153000 (7)
16) Freshwater	(24)	179000 (7)	350000 (7)	61800 (3)	33200 (7)
4) Grafton	(35)	404000 (13)	773000 (13)	567000 (3)	88300 (6)
11) Kearney	(17)	56600 (3)	8150 (7)	778000 (2)	6560 (5)
3) Kejimkujik	(23)	96700 (8)	576000 (7)	37100 (2)	64100 (6)
14) Lacey Mill	(28)	300000 (12)	44900 (8)	172000 (2)	26500 (6)
15) Laytons	(18)	918000 (8)	1700000 (4)	74400 (2)	117000 (4)
5) McGinty	(28)	231000 (8)	88100 (8)	243000 (4)	206000 (8)
7) Mountain	(31)	120000 (7)	292000 (14)	1640000 (4)	126000 (6)
9) Pebbleloggitch	(27)	97900 (8)	128000 (9)	24800 (3)	113000 (7)
10) Peskawa	(25)	40300 (7)	168000 (9)	12900 (3)	175000 (6)
20) Presqu'ile	(31)	2720000 (11)	2200000 (11)	52700 (1)	110000 (8)
6) Puzzle	(25)	318000 (5)	17000 (10)	1340000 (4)	54400 (6)
12) Ltl.Springfield	(26)	313000 (7)	83300 (10)	231000 (4)	37300 (5)
18) Warren	(33)	41000 (9)	20700 (10)	49600 (7)	48300 (7)

The most frequently occurring zooplankton species in the overall data set were the cladocerans Eubosmina tubicen (17 lakes), Bosmina longirostris (19 lakes), and Holopedium gibberum (17 lakes); the calanoid copepod Diaptomus minutus (19 lakes); the cyclopoid copepod Mesocyclops edax (19 lakes); and the rotifer Keratella cochlearis (20 lakes). These frequent phytoplankton and zooplankton species seem to be characteristic of Nova Scotia lakes in general.

The majority of the algal species were ubiquitous, occurring across the range of pH. Many were most numerous in the mid-range of pH (5.0-6.5), with reduced abundances at extreme pH values. Certain species showed strong preferences in terms of their occurrance for high or low pH. A group of species consisting of the blue-greens Dactylococcopsis acicularis, Spiculina major, Aphanocapsa pulchra, Calothrix abscendeus, the chrysophyte Chrysosphaerella longispina, the diatoms Synedra ulna and Pinnularia braunii, the greens Selenastrum minutum and Groenbladia neglecta, and the pyrrophyte Peridinium limbatum occurred only in lakes with pH values above 5.0. This group is evidently intolerant of very acidic conditions. A second group of species consisting of the blue-greens Anabaena flos-aquae and Anabaena variabilis, the diatom Nitzschia dissipata, and the greens Staurastrum connatum and Crucigenia tetrapedia occurred only in lakes of pH less than 6.0. This group shows a preference for acidic conditions.

Among the zooplankton, the rotifers Euchlanis sp., Filinia longista and Gastropus sp., and the cyclopoid copepod Tropocyclops prasinus were found only above pH 5.5, while the rotifer Trichocerca elongata only occurred below pH 6.0. Most of the other zooplankton were present across a broad range of pH values, except the calanoid copepod Diaptomus oregonensis, which only occurred in lakes of intermediate pH (5.0-6.0). This is in contrast to its congener D. minutus, which occurred in all lakes

but the most acidic one. The cyclopoid copepod Mesocyclops edax and the cladoceran Scapholeberis kingi were both found to occur only at the more extreme pH values, below 5.0 or above 6.5.

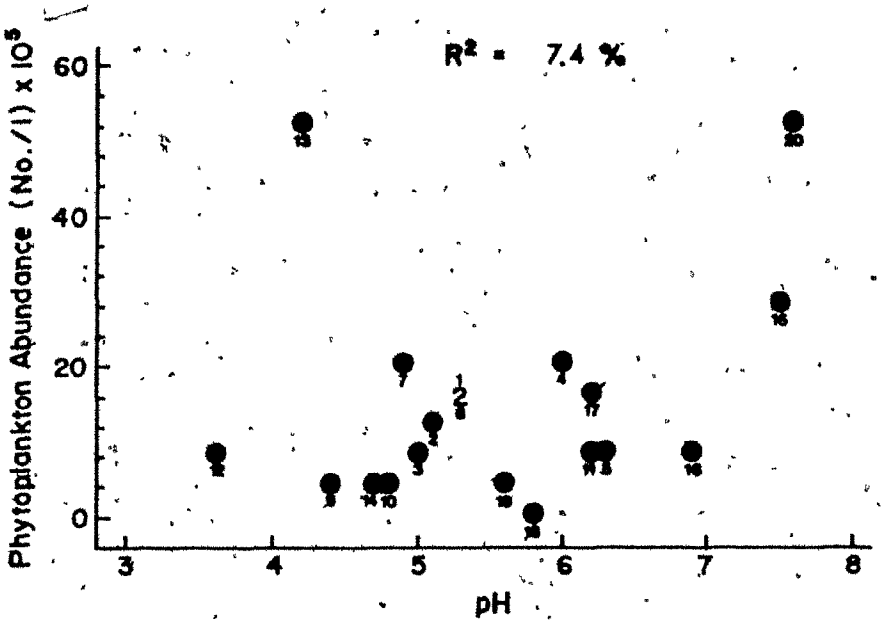
Plots of phytoplankton abundance and species number versus pH showed little relationship (Fig. 28 a,b). R^2 was very low in both cases, with no patterns evident. The plot of algal abundance versus pH again excludes Beaverskin Lake because of its anomalously high algal numbers.

None of the phytoplankton sub-groups showed any relationship between species number and pH. There was some indication for diatoms of a relationship between abundance and pH, with highest populations above pH 7, although considerable variation in abundance existed below this pH level.

Most lakes had between 14 and 20 zooplankton species, with less variation in diversity among lakes than for the phytoplankton (Table 17). Little Springfield Lake was notable for very few species in any of the groups, and low abundances of all forms except rotifers. Presqu'ile Lake also had low numbers of species in all groups, although it did have large populations of the primarily herbivorous groups - cladocerans and rotifers. Layton's Lake showed extremely abundant cladocerans and cyclopoid copepods. Drain Lake, near the other extreme of pH, also had abundant cyclopoids, and the highest levels of copepod nauplii. Evidently, the majority of nauplii in Drain Lake do not survive to adulthood.

Plots of zooplankton abundance and species number showed very weak relationships (Fig. 29 a,b), although an interesting pattern did emerge for zooplankton species numbers. There was some indication of a curvilinear relationship, with lowest species numbers occurring below pH value 5 or above pH value 7. Highest species numbers occurred between pH values 5 and 7, although variation was fairly high within this range.

Figure 28. a) Phytoplankton abundance (no./l) and b) Number of phytoplankton species versus pH.


R² = 7.4 %
Phytoplankton Abundance (No./l) x 10⁵
60
40
20
0
3
4
5
6
7
8
pH

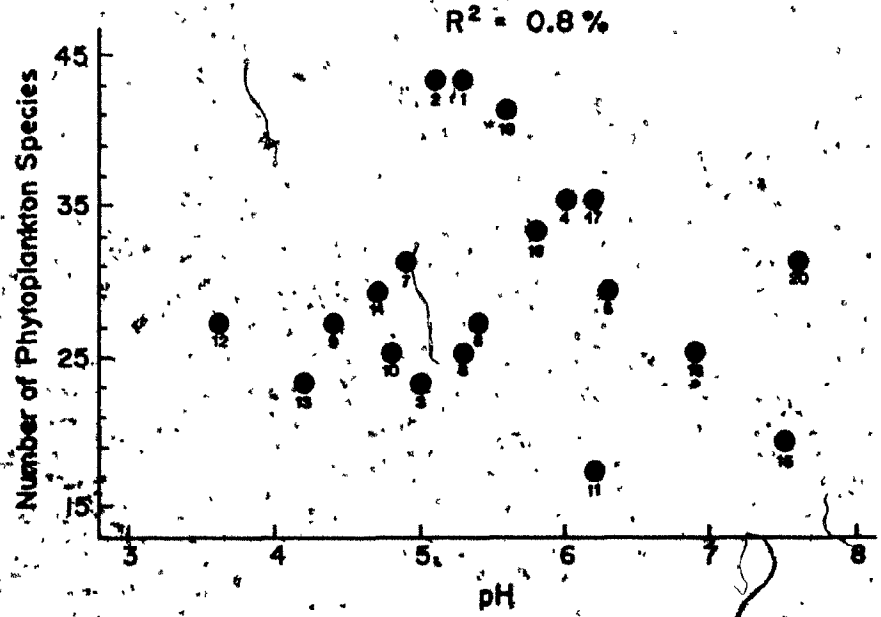
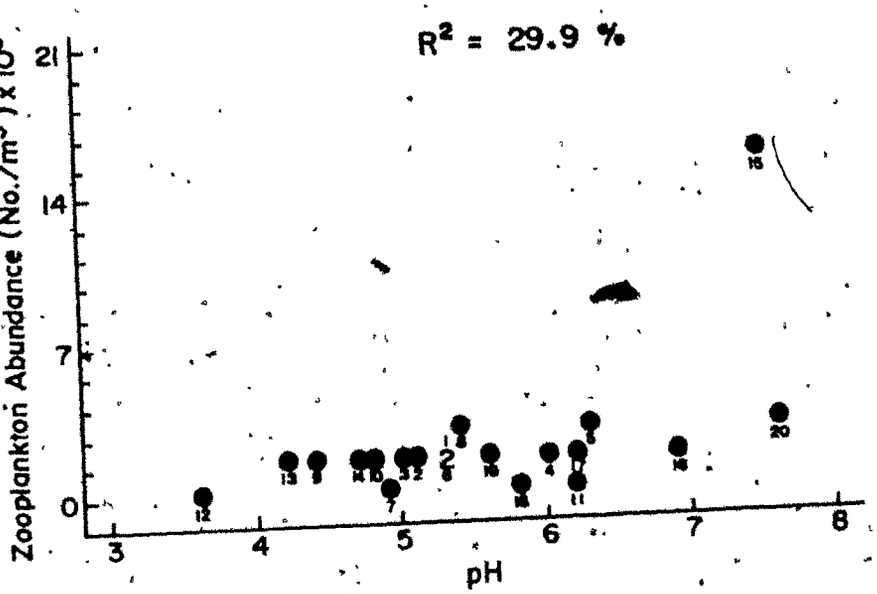
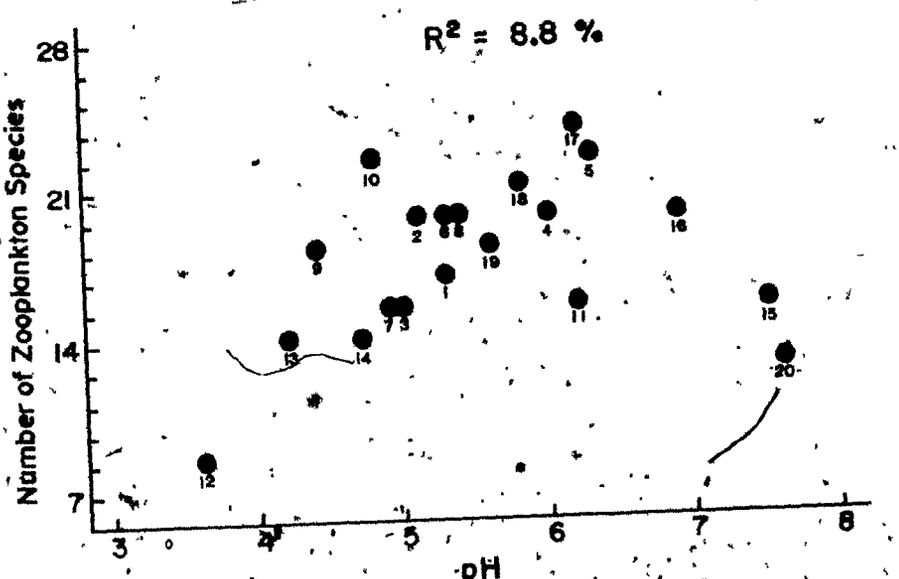

R² = 0.8 %
Number of Phytoplankton Species
45
35
25
15
3
4
5
6
7
8
pH

Table 17. Zooplankton taxonomic group abundances (nos./l) and diversity (number of species).

Lake	No. Spp.	Cladocera	Calanoid Copepods	Cyclopoid Copepods	CI-CV	Nauplii	Rotifers
1) Big Dam East	(17)	7170(7)	5330(3)	1290(3)	12700	29700	18300(4)
2) Big Dam West	(19)	9510(7)	7100(4)	1630(3)	11700	18400	54800(5)
8) Beaverskin	(19)	4500(6)	10900(6)	125(1)	30800	13500	155000(6)
17) Canns	(24)	7830(9)	4150(3)	1820(3)	10200	36700	56700(9)
13) Drain	(14)	8470(5)	78(1)	9590(3)	52	87100	27700(5)
19) French	(18)	10500(9)	9870(4)	21(1)	12000	6390	57800(4)
16) Freshwater	(19)	5950(7)	2480(4)	354(1)	2890	29900	113000(7)
4) Grafton	(20)	8670(7)	7380(5)	3920(3)	19500	16100	29100(5)
11) Kearney	(16)	3730(6)	3620(4)	335(2)	4320	4710	4490(4)
3) Kejimkujik	(16)	3460(6)	10600(4)	480(3)	28100	12900	30300(3)
14) Lacey Mill	(14)	6570(6)	3840(3)	39(1)	4840	2300	55300(4)
15) Laytons	(16)	1360000(5)	9270(2)	36800(4)	7610	57500	71100(5)
5) McGinty	(22)	13200(7)	11900(5)	13200(4)	11600	36300	203000(6)
7) Mountain	(15)	4930(5)	7800(3)	1000(3)	8450	18500	13100(4)
9) Pebbleloggitcch	(18)	21800(6)	10100(4)	2480(3)	32000	20600	112000(5)
10) Peskawa	(22)	8170(7)	6370(4)	1720(3)	36000	13200	34500(8)
20) Presqu'ile	(13)	69200(4)	781(2)	292(2)	2240	19900	222000(5)
6) Puzzle	(20)	6170(10)	16500(4)	573(3)	27800	17100	48500(3)
12) Ltl.Springfield	(8)	2020(4)	0(0)	645(3)	0	471	22900(2)
18) Warren	(21)	2290(6)	2090(3)	646(3)	1910	15700	13500(9)

Figure 29. a) Zooplankton abundance (no./m^3) and b) Number of zooplankton species versus pH.


R² = 29.9 %
Zooplankton Abundance (No./m³) x 10⁵
21
14
7
0
3
4
5
6
7
8
pH

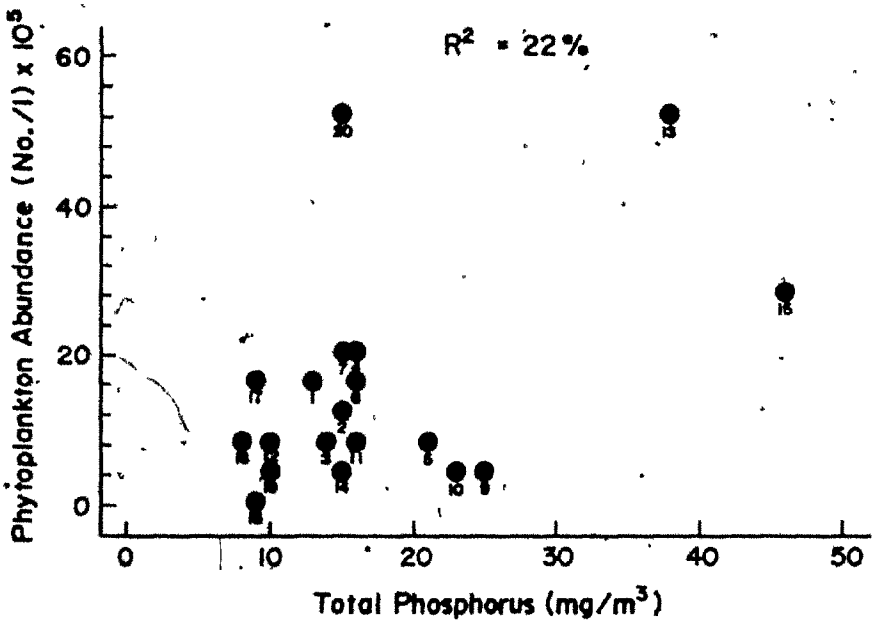

R² = 8.8 %
Number of Zooplankton Species
28
21
14
7
3
4
5
6
7
8
pH

Two of the zooplankton taxonomic categories showed patterns similar to the one described above. Both cladocerans and calanoid copepods had low species numbers at the extremes of pH value, and highest diversities between pH 5 and 7. Rotifers did show a weak tendency for greater abundances at higher pH, but variation was also high.

Some evidence was noted of a relationship between zooplankton abundance and algal cell volume, presumably reflecting trophic relationships between primary producers and consumers. Drain Lake, with highest cell volume but moderate zooplankton abundance, was an exception to the pattern.

Relationships of plankton abundances with pH are partly obscured by the effects of phosphorus on plankton abundance. There is a moderately strong relationship of phytoplankton abundance with total phosphorus (Fig. 30 a., R^2= 0.22), and a stronger relationship of phytoplankton cell volume with TP (Fig. 30 b., R^2= 0.58). There is also a relationship between chlorophyll level and TP (Fig. 31 a., R^2= 0.42). The present data set falls somewhat below the OECD chlorophyll/TP relationship, as was noted for humic lakes by Kerekes (1983). One of the lakes with very high TP levels, Drain Lake, has very high phytoplankton abundance and cell volume in spite of its low pH values. Several of the lakes with low TP and low algal standing crops values had high pH (Canns, Freshwater and Warren Lakes). Thus, the relationship of algal abundance to pH is partly confounded by the effects of the TP/algal biomass relationship. Zooplankton abundance is also related to TP (Fig. 31 b., R^2= 0.50). Layton's Lake has a strong effect on the relationships of plankton to TP, having high levels of both phosphorus and plankton abundances. This lake is also alkaline (pH = 7.55). The effects of the phosphorus are likely more important in determining the productivity of Layton's Lake than is the high pH.

Figure 30. a) Phytoplankton abundance (no./l) and b) Phytoplankton cell volume versus total phosphorus (mg/m^3).


R^2 = 22%
Phytoplankton Abundance (No./l) x 10^5
60
40
20
0
0
10
20
30
40
50
Total Phosphorus (mg/m^3)

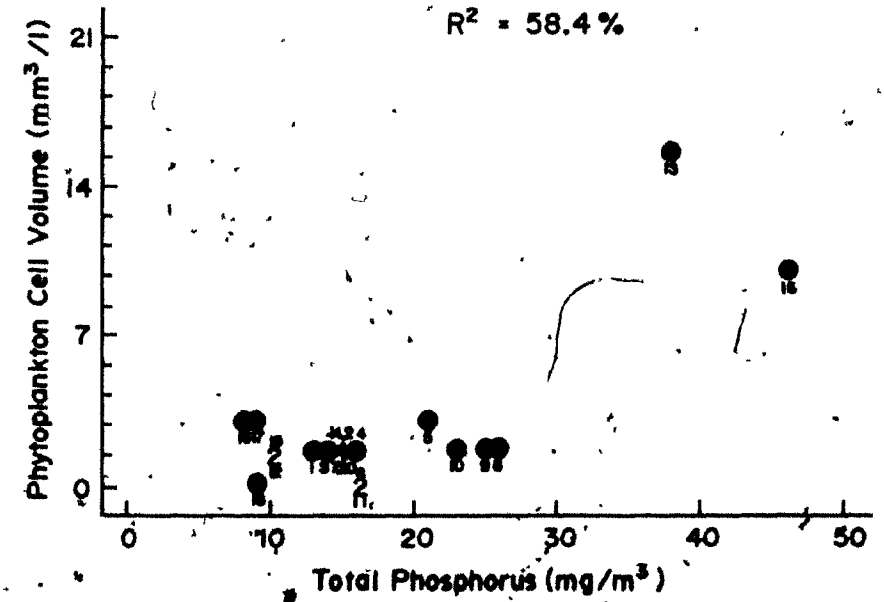
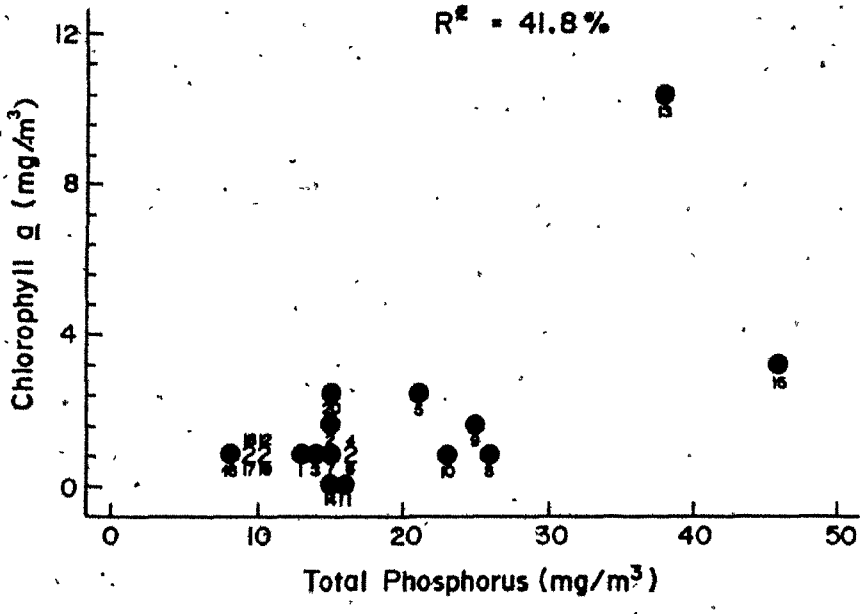
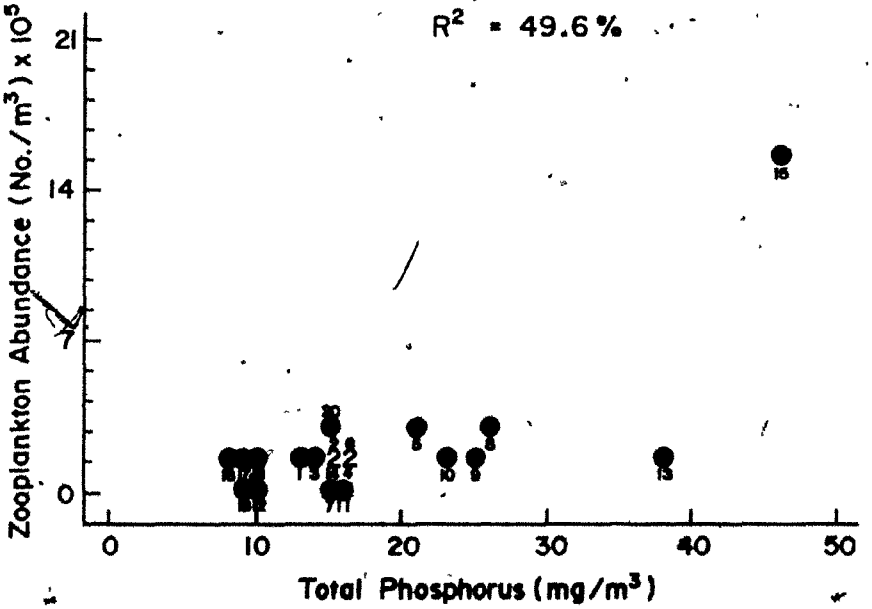

R^2 = 58.4%
Phytoplankton Cell Volume (mm^3/l)
21
14
7
0
0
10
20
30
40
50
Total Phosphorus (mg/m^3)

Figure 31. a) Chlorophyll a and b) Zooplankton abundance versus Total phosphorus (mg/m^3).


R² = 41.8%
Chlorophyll a (mg/m³)
Total Phosphorus (mg/m³)
0
4
8
12
0
10
20
30
40
50


R² = 49.6%
Zooplankton Abundance (No./m³) x 10⁵
Total Phosphorus (mg/m³)
0
7
14
21
0
10
20
30
40
50

Stepwise multiple regression was employed to determine the best predictor variables for the plankton group data from among the physical-chemical variables measured. The results, with R^2 and R^2 adjusted for degrees of freedom, are shown in Table 18. Predictive capacity of the physical-chemical data was quite good for most of the plankton group abundances, and for overall species numbers. No single physical or chemical variable was important to all of the phytoplankton, or all of the zooplankton variables.

Dendrograms were derived on the basis of phytoplankton communities (Fig. 32), and zooplankton communities (Fig. 33). Clustering of the lakes on the basis of these two criteria produced different results, as might be expected from the plankton data presented earlier (Tables 16 and 17). Amalgamation distances between lakes as a whole were smaller for the phytoplankton than the zooplankton, meaning that phytoplankton communities were more similar across the twenty lakes than were the zooplankton communities.

The phytoplankton communities (Fig. 30) formed four main lake groups:

- French, Peskawa, Pebbleloggitch and McGinty Lakes;
- Freshwater, Kejimkujik, Grafton and Big Dam West Lakes;
- Little Springfield and Lacey Mill Lakes;
- Big Dam East and Warren Lakes.

These twelve lakes formed a large group at an amalgamation distance of 1.1, with the additional lakes joining that cluster at progressively higher levels. Presqu'ile and Layton's Lakes formed a pair at a distance of 1.4, while Beaverskin Lake and Drain Lake were extreme outliers from the rest.

The zooplankton communities (Fig. 31) formed three main lake groups:

- Kejimkujik, Puzzle, Peskawa, Grafton and Big Dam West Lakes;
- Big Dam East, Mountain and Canns Lakes;

Table 18. Stepwise multiple regression results for plankton groups versus water chemistry.

Plankton Variable	Best Predictor Variables	R^2	Adjusted R^2
Phytoplankton –			
Greens	Alkalinity, pH, SRP, Z_{max}, DOC	78.1 %	70.3 % ***
Blue-greens	SRP, TDN, DOC, Alkalinity	53.7 %	41.4 % *
Diatoms	Alkalinity, Area, Temperature	91.4 %	89.7 % ***
Others	DOC, Color, Z, Temperature	30.9 %	12.5 % NS
Total Phytoplankton	SRP, TDN, DOC	54.5 %	46.0 % **
Number of Species	TDN, DOC, Color, pH	76.6 %	70.3 % ***
Zooplankton –			
Cladocera	SRP, TDN, Alk., Phaeo., Chl. *a*	95.5 %	93.9 % ***
Calanoid copepods	Temp., Al, Chl. *a*, Phaeo., Alk.	67.5 %	55.8 % **
Cyclopoid copepods	Phaeo., Chl. *a*, Phytoplankton Cell Volume	98.2 %	97.8 % ***
Rotifers	TDN, Z_{max}, pH, SI, SRP	69.8 %	59.0 % **
Total Zooplankton	SRP, Alk., Phaeo., Chl. *a*, Phytoplankton Cell Volume	98.6 %	98.1 % ***
Number of species	Al, Alk., pH, Color, Z_{max}	76.5 %	68.0 % **

Refer to Table 14 for Key for variable abbreviations and units.

* Significant at p=0.05

** Significant at p=0.01

*** Significant at p=0.001

NS Not significant

Figure 32. Cluster dendrogram of lakes based on phytoplankton communities.

	Lake Name	Abbreviation
1)	Big Dam East Lake	BDEA
2)	Big Dam West Lake	BDWE
3)	Kejimkujik Lake	KEJI
4)	Grafton Lake	GRAF
5)	McGinty Lake	MCGI
6)	Puzzle Lake	PUZZ
7)	Mountain Lake	MOUN
8)	Beaverskin Lake	BEAV
9)	Pebbleloggitch Lake	PEBB
10)	Peskawa Lake	PESK
11)	Kearney Lake	KEAR
12)	Little Springfield Lake	SPRG
13)	Drain Lake	DRAI
14)	Lacey Mill Lake	LACE
15)	Layton's Lake	LAYT
16)	Freshwater Lake	FRWA
17)	Cann's Lake	CANN
18)	Warren Lake	WARR
19)	French Lake	FREN
20)	Presqu'ile Lake	PRES

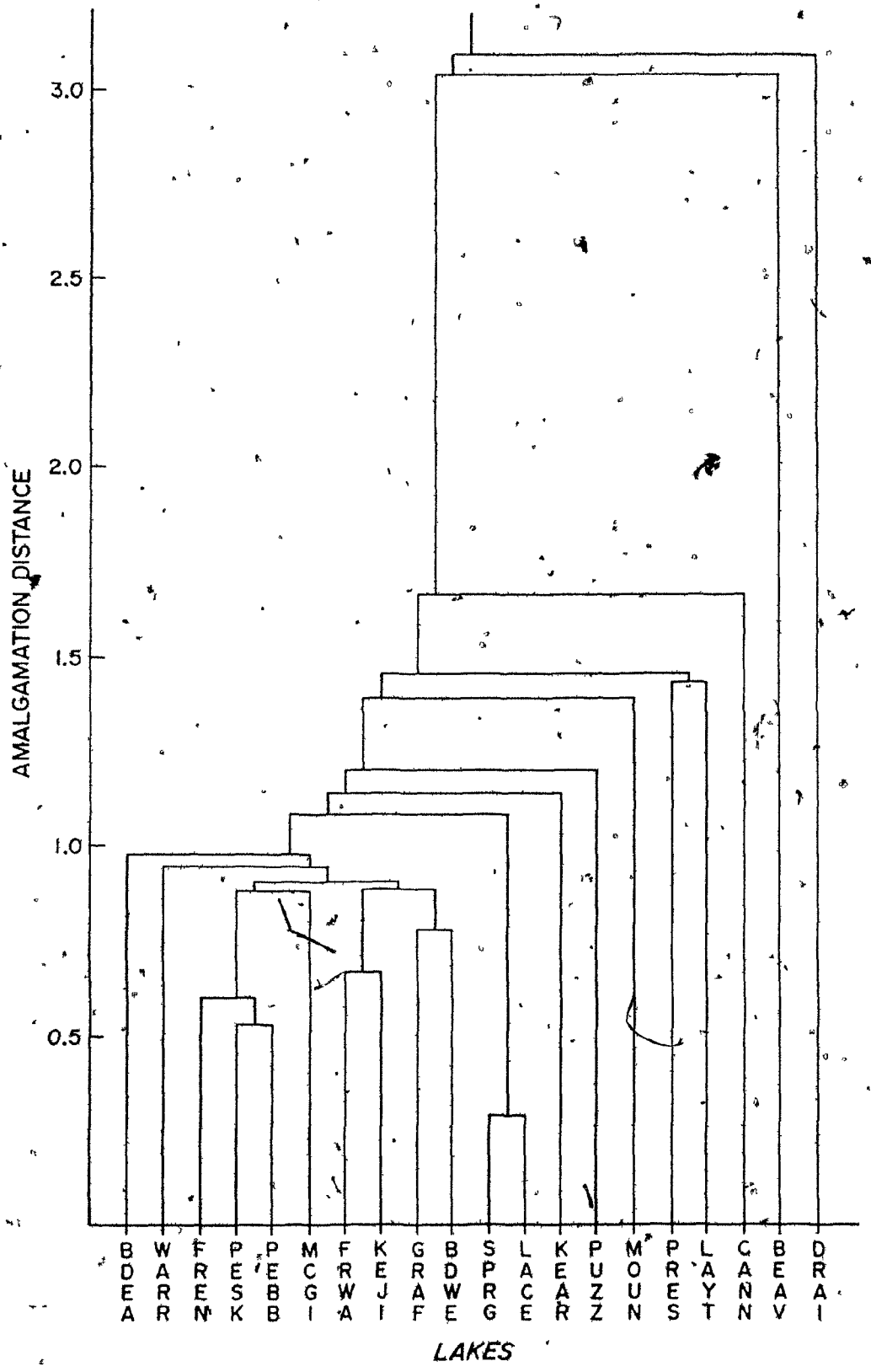
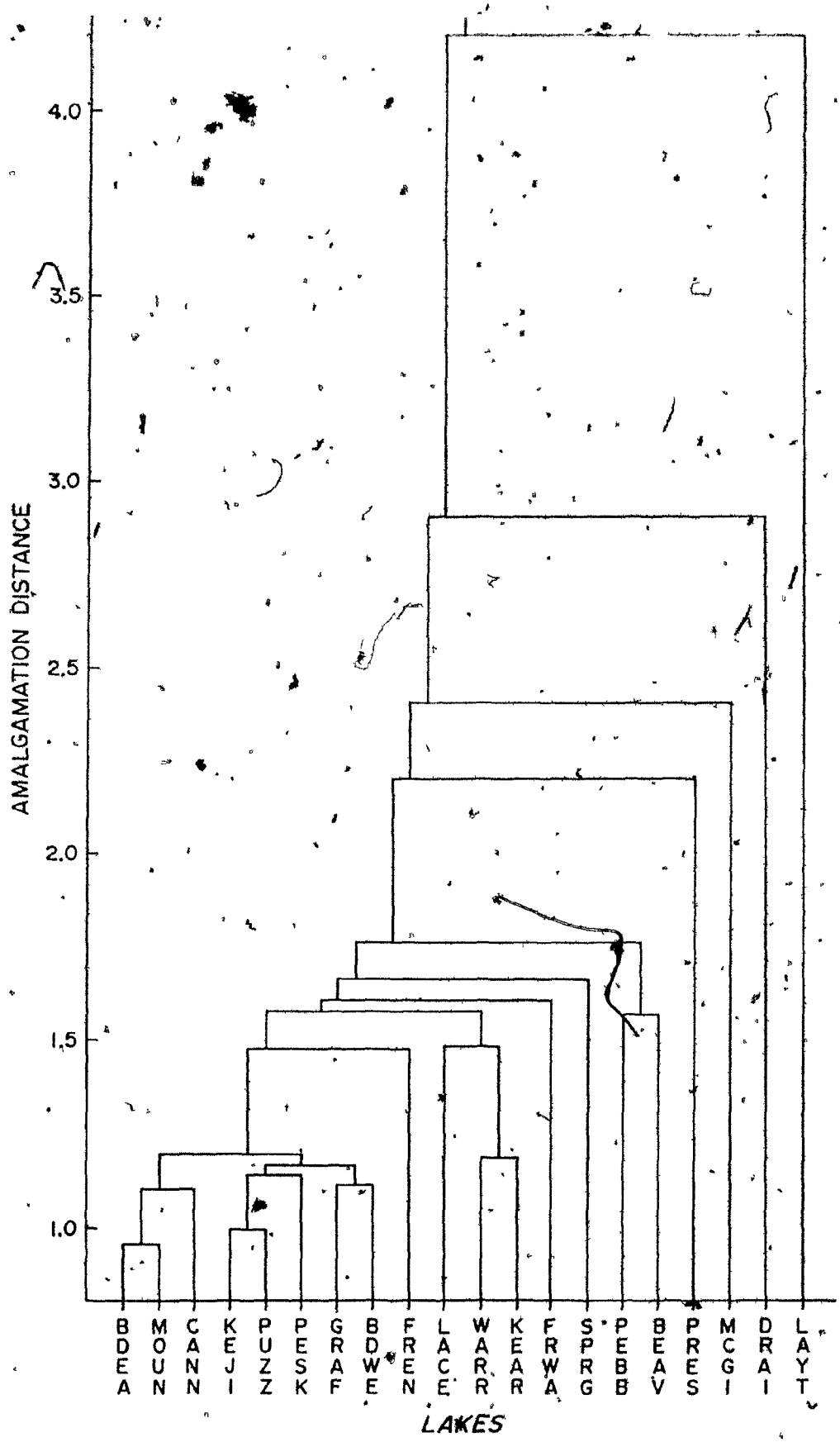

AMALGAMATION DISTANCE
3.0
2.5
2.0
1.5
1.0
0.5
BDEA
WARR
FREM
PESK
PEBB
MCGI
FRWA
KEJI
GRAF
BDWE
SPRG
LACE
KEAR
PUZZ
MOUN
PRES
LAYT
CANN
BEAV
DRAI
LAKES

Figure 33. Cluster dendrogram of lakes based on zooplankton communities.

	Lake Name	Abbreviation
1)	Big Dam East Lake	BDEA
2)	Big Dam West Lake	BDWE
3)	Kejimkujik Lake	KEJI
4)	Grafton Lake	GRAF
5)	McGinty Lake	MCGI
6)	Puzzle Lake	PUZZ
7)	Mountain Lake	MOUN
8)	Beaverskin Lake	BEAV
9)	Pebbleloggitch Lake	PEBB
10)	Peskawa Lake	PESK
11)	Kearney Lake	KEAR
12)	Little Springfield Lake	SPRG
13)	Drain Lake	DRAI
14)	Lacey Mill Lake	LACE
15)	Layton's Lake	LAYT
16)	Freshwater Lake	FRWA
17)	Cann's Lake	CANN
18)	Warren Lake	WARR
19)	French Lake	FREN
20)	Presqu'ile Lake	PRES


AMALGAMATION DISTANCE
4.0
3.5
3.0
2.5
2.0
1.5
1.0
BDEA
MOUN
CANN
KEJI
PUZZ
PESK
GRAF
BDWE
FREN
LACE
WARR
KEAR
FRWA
SPRG
PEBB
BEAV
PRES
MCGI
DRAI
LAYT
LAKES

- Lacey Mill, Warren and Kearney Lakes.

These eleven lakes, together with French Lake, formed a larger group at a distance of 1.6. Pebbleloggitch and Beaverskin Lakes formed a pair at a distance of 1.6, and joined the larger group along with Freshwater and Little Springfield Lakes at a distance of 1.8. Presqu'ile, McGinty, Drain and (especially) Layton's Lakes were outliers from the rest.

C. Discussion

The inverse relationship in the data set of alkalinity with pH is to be expected, since alkalinity (expressed in mg per liter as $CaCO_3$) is a measure of the compounds present which collectively shift pH to the alkaline end of the scale (Wetzel, 1975). The relationship of log (alkalinity) versus pH was essentially linear from pH 8 down to pH 5. Below pH 5, no alkalinity was measured.

The exponential increase in dissolved aluminum concentration with decreasing pH has been a common observation in previous studies (U.S. Environmental Protection Agency, 1983). The pattern may be partially obscured by the fact that levels of aluminum in many of the lakes were at or near the limits of detection, implying the possibility of larger relative error in these measurements. The pattern is nevertheless clear enough. Increased levels of aluminum and other metals in acidic waters are cause for concern in terms of both ecological effects of metal toxicity to aquatic organisms, and human health effects of metals in drinking water supplies and in fish ultilized as a food source.

The strong relationship between chlorophyll *a* and phytoplankton cell volume is of interest, since it offers a way to predict total cell volume from a simple measure of chlorophyll level. Estimation of a value of X, the predictor variable, from a measurement of Y, the dependent random variable, is straightforward from a linear regression, although calculation of the confidence limits associated with that estimate requires special methods (Sokal and Rohlf, 1969). Total algal cell volume is a better measure of primary producer biomass in a planktonic community than algal cell numbers (Wetzel, 1975), and so estimation of this variable from easily obtained chlorophyll measurements would provide valuable information on potential food resources in lake plankton communities. Phytoplankton

abundance does not accurately reflect biomass because of inter-species variation in cell size, nor does chlorophyll concentration correspond well with phytoplankton abundance (Fig. 26 b).

Total cell volume did not show any relationship with pH (Fig. 27 b). Conflicting observations have been obtained on the relationships of phytoplankton biomass and production with varying pH value. Kwiatkowski and Roff (1976), in a study of six Ontario lakes, found positive correlations of chlorophyll a with pH, and lowest primary productivity at lowest pH. Almer et al. (1978) noted highest algal biomass in the most acid conditions, and lowest biomass at intermediate pH, in a set of lakes from Sweden. During acidification of lake 223, Schindler and Turner (1982) observed increasing chlorophyll and algal biomass. There was some suggestion in the present data of higher cell volume (reflecting higher biomass) at high pH value (above 6.0), and one anomalous finding of high cell volume at low pH value (Drain Lake) (Fig. 27 b).

Many investigators have noted reductions in phytoplankton species numbers at lower pH levels, comparing among sets of lakes over a pH gradient. The same pattern has been found in Sweden (Almer et al., 1978), southern Norway (Leivestad et al., 1976; Raddum et al., 1980), the Sudbury region of Ontario (Yan, 1979; Stokes, 1980), the LaCloche Mountain region of Ontario (Kwiatkowski and Roff, 1976), the Adirondak region of New York (Hendry, 1980), and Florida (Crisman et al., 1980). In the present study, no relationship was found between algal species number and pH (Fig. 28 b). The six lakes with the highest number of species (>33) did occur in the intermediate range between pH 5.0 and pH 6.3, although many lakes in this range had much lower numbers. As was seen for species number, no clear pattern was noted for phytoplankton abundance with pH (Fig. 28 a).

In similar fashion to phytoplankton, many studies have noted fewer species of zooplankton in lakes of lower pH value across a range of lake pH values. This has been the case in Sweden (Almer et al., 1978; Hultberg and Andersson, 1982), Norway (Hendry and Wright, 1976; (Raddum et al., 1980), Ontario (Carter, 1971; Roff and Kwiatkowski, 1977; Sprules, 1975; Yan and Strus, 1980), the northeastern U.S. (Confer et al., 1983), and Great Britain (Fryer, 1980). Cladocerans have been noted as the most sensitive group (Raddum et al., 1980), particularly the daphnids (Sprules, 1975), although many cladocerans are fairly acid tolerant.

In the present study, zooplankton abundance was not related to pH except that the highest abundances occurred in one of the most alkaline lakes (Fig. 29 a). Species number showed no linear relation to pH values (Fig. 29 b), but the trend of lowest abundances at extreme pH's indicates long-term adaptation to moderate pH by most species. The trend below pH 6.0 is approximately linear with decreasing pH values.

The group of lakes at or below pH 5.0 (n=7) had an average of 14.7 zooplankton species, while the group of lakes between pH 5.1 and pH 6.5 (n=10) had an average of 18.6 species. Those lakes above pH 6.5 (n=3) had an average of 15.3 species. The acidic and medium range group means are significantly different (t-test, $p<.05$), but the alkaline group mean is not significantly different from either of the others. Thus, the present data conform in general to the previously reported results for biogeographic patterns of reduced zooplankton species richness at lower pH value mentioned above.

Species numbers found in a lake are influenced by sampling regime, as was suggested in Chapter 2, and many biogeographic surveys of lake plankton are based on single samples or multiple samples from a single date. The present study is based on multiple depths and dates from spring to late

fall, which increases the likelihood of encountering most or all pelagic species present in a given lake.

The stepwise multiple regressions for this data set showed some interesting results (Table 18). The diatoms were the phytoplankton group with the highest R^2. Alkalinity and physical factors explained almost 90% of the diatom variance. Alkalinity was also important in predicting levels of green and blue-green algae. These two groups also had soluble reactive phosphorus and dissolved organic carbon as important predictors. The miscellaneous phytoplankton group 'others' did not have a significant portion of its variance explained by any combination of predictor variables. This is perhaps because this group contains a number of unrelated species which may respond to their physical-chemical environments in different ways, obscuring any patterns. Total phytoplankton as a whole were well predicted by the dissolved nutrient variables (SRP, TDN, DOC), suggesting the overriding importance of trophic relationships with nutrients for phytoplankton as opposed to the influence of physical factors. Phytoplankton species number was well predicted by TDN, DOC, Color and pH.

The cladocera had a significant portion of their variance explained by a combination of nutrients, alkalinity and photosynthetic pigments. The copepods also had photosynthetic pigments as significant predictor variables, and in the case of calanoids, temperature, aluminum and alkalinity. Rotifers were significantly related to nutrients, maximum depth and pH. Total zooplankton were best explained by SRP, alkalinity, and measures reflecting phytoplankton productivity (photosynthetic pigments and cell volume).

The general patterns discerned suggest that the phytoplankton respond

more directly to the physical environment and the dissolved nutrient concentrations, while the zooplankton respond more to nutrient levels and those variables associated with algal production. Significant predictors for the zooplankton are often removed from them by two trophic levels. For example, the cladocera, largely herbivorous, have SRP and TDN as their most important predictors. The cyclopoid copepods, largely carnivorous, have phytoplankton measures as their best predictors. The rotifers respond to nutrients, depth and pH. Calanoid copepods were most strongly related to temperature, which may be a reflection of their seasonal life-history patterns.

The number of zooplankton species present is best predicted by aluminum, alkalinity and pH, water color and maximum depth.

It is interesting to note that while pH does not constitute one of the significant predictors of abundance for either phytoplankton or zooplankton, it is one of the important predictors of species richness of both zooplankton and phytoplankton.

Prediction and causality require careful interpretation in a complex system. While the predictor variables were usually able to explain highly significant proportions of the plankton variable variances, it is difficult to make definite conclusions concerning causality. In physics, a force acting on a mass causes acceleration, and the causality is clear and easily understood. In a carefully-conducted laboratory experiment, force and acceleration will be strongly related for a given mass, and force will predict acceleration to a high degree of precision. In ecology, it is more difficult to assign causal mechanisms. Alkalinity does not "cause" a certain population of green algae, even though alkalinity is the best predictor of chlorophyte abundance. Obviously many variables in an aquatic system intervene between these two in complex causal pathways. Some of

these intervening variables will be known and measured, others may be suspected but not measured, and still others may not be known.

Results of the cluster analyses were different for phytoplankton and zooplankton, although some similarities did appear. Kejimkujik, Grafton and Big Dam West Lakes were grouped closely in terms of both their phytoplankton and zooplankton communities. In terms of their physical and chemical data, these lakes do not stand out as a group from the overall set of lakes. Many of the physical-chemical measurements are similar for these three lakes, particularly calcium, color and DOC. Other lakes which are similar to these lakes in terms of physical-chemical factors, however, have different plankton communities.

Layton's, Presqu'ile and Drain Lakes were outliers in terms of both their zooplankton and phytoplankton communities. Layton's and Presqu'ile Lakes had phytoplankton communities more similar to each other than to the other lakes, and these were the only lakes above pH 7.0. Drain Lake was at the other end of the pH scale. Beaverskin Lake was an outlier in terms of it's phytoplankton community, which has been noted previously as being unusual in its dominance by a single cyanophyte species.

In general, the differences in the phytoplankton and zooplankton groupings are more striking than the similarities. This suggests that the phytoplankton and zooplankton do not respond in the same ways to their physical, chemical and biological environments, in that two lakes with similar phytoplankton communities are not more likely to have similar zooplankton communities, and vice-versa.

The lack of a strong effect of pH on the plankton communities of this data set suggests that lake plankton can adapt and continue to be productive over a broad range of pH. Changes in pH are more likely to

affect community species composition than total abundances or biomass.

An interesting example of the interacting effects of acidity and nutrient availability is provided by Little Springfield and Drain Lakes. Highly acidic Little Springfield Lake, with high aluminum levels and extremely clear water, supports moderate phytoplankton diversity and abundance. The outflow from this lake leads to Drain Lake. At one point along the outflow, an input of raw sewage is added which goes directly into Drain Lake. Addition of the sewage waste causes marked changes in the water chemistry and biology of Drain Lake as compared to Little Springfield Lake. Levels of total phosphorus, soluble reactive phosphorus and total nitrogen are two to three times higher in Drain Lake, pH is increased by 0.65 units, aluminum is substantially decreased and water color is increased.

Phytoplankton diversity is approximately equal in the two lakes, but phytoplankton abundance is 7 times greater in Drain Lake, cell volume is 18.5 times greater and chlorophyll a is 21 times greater. Zooplankton diversity is increased from 8 to 14 species, and zooplankton abundance is 2.9 times greater in Drain Lake. The major increase in the phytoplankton occurs in the chlorophyte and miscellaneous categories, while increases in the zooplankton are mostly in the copepod group. Increased photosynthetic activity in Drain Lake may be partly responsible for the increase in pH, and reductions in aluminum may result from reduction in solubility at higher pH combined with increased complexing of aluminum with organic material and transport to the sediments. Drain Lake has been found to have high productivity and a diverse biota, including several macrophyte species which do not normally occur at such low pH (Kerekes et al., 1984). Drain Lake also supports abundant benthic invertebrates, ducks and muskrats, and limited amphibian and fish populations. These findings are unusual for an

extremely acidic lake, and suggest that nutrient enrichment may help to overcome the negative effects of low pH values on productivity and diversity such as often occur in acidified lakes (Kerekes et al., 1984). Yan et al. (1982) observed that enrichment of an acidic lake in Ontario (pH 4.6) resulted in a phytoplankton bloom and subsequent increases in herbivore and invertebrate carnivore (Chaoborus) populations. Resilience of this community to nutrient addition was reduced compared with a second fertilized, non-acidic lake. Two years after fertilization, herbivorous populations had been severely reduced by invertebrate predation. This was attributed to a lack of vertebrate predators to control the invertebrate populations. Drain Lake, on the other hand, supports a fairly diverse predator community, which may help to stabilize the foodweb so that the benefits of fertilization appear at every level. Structure of a lake foodweb is therefore important in considerations of nutrient enrichment as a management tool to supplement liming of acid lakes.

APPENDIX A

Species Lists and Taxonomic References for Zooplankton and Phytoplankton.

Table A.1. List of zooplankton species found in Kejimkujik and Pebbleloggitch Lakes (1980, 1981) and Beaverskin Lake (1980, 1981, 1982). Numbers with each species refer to those of the twenty study lakes in which they occurred. Based on Edmondson (1959).

Table A.2. List of taxonomic references used in zooplankton species identifications.

Table A.3. List of phytoplankton species found in Kejimkujik and Pebbleloggitch Lakes (1980, 1981) and Beaverskin Lake (1980, 1981, 1982). Numbers with each species refer to those of the twenty study lakes in which they occurred. Based on Smith (1950).

Table A.4. List of taxonomic references used in phytoplankton species identifications.

Table A.1.

Phylum Arthropoda

Class Crustacea

Order Copepoda

Suborder Calanoida

Family Temoridae

Epischura nordenskioldi Lillj.
1,2,3,4,5,6,7,8,9,10,11,14,16,17,18

Family Diaptomidae

Diaptomus minutus Lillj.
1,2,3,4,5,6,7,8,9,10,11,13,14,15,16,17,18,19,20

Diaptomus oregonensis Lillj.
2,4,5,6,8,19

Suborder Cyclopoida

Family Cyclopidae

Mesocyclops edax Forbes
1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,20

Tropocyclops sp.
1,2,4,5,6,15,18

Tropocyclops prasinus Fischer
1,2,4,5,6,15,18

Suborder Harpacticoida

Family Metidae

Metis jousseaumei Richard
19

Order Cladocera

Suborder Haplopoda

Family Leptodoridae

Leptodora kindtii Focke
3,6

Suborder Eucladocera

Superfamily Polyphemoidea

Family Polyphemidae

Polyphemus pediculus L.
3,6,10,16,17,19

Superfamily Sidoidea

Family Sididae

Diaphanosoma brachyurum Lieven
3,9
Diaphanosoma birgei Fischer
1,2,3,4,5,6,7,8,9,10,12,14,15,17,19
Latonopsis sp.
9
Latona setifera (O.F.M.)
9

Family Holopediidae

Holopedium gibberum Zaddach
1,2,3,4,5,6,7,8,9,10,11,13,14,16,17,18,19

Superfamily Chydoroidea

Family Daphniidae

Daphnia ambigua Scourfield
3,4,11,16,17
Daphnia catawba Coker
1,2,3,4,5,6,7,8,9,10,11,15,17,18,19
Scapholeberis sp.
1,12,13,14,15,16,20
Ceriodaphnia sp.
3
Ceriodaphnia affinis Lilljeborg
13

Family Bosminidae

Bosmina longirostris (O.F.M.)
1,2,3,4,5,6,7,8,9,10,11,12,13,14,16,17,18,19,20
Eubosmina longispina (Leydig)
1,2,3,4,5,6,8,9,14,17,18,19,20
Eubosmina tubicen (Brehm)
1,2,3,4,5,6,8,9,10,11,14,15,16,17,18,19,20

Family Chydoridae

Alonella excisa (Fischer)
9
Alonella pulchella Herride
9
Acroperus sp.
9
Alona intermedia Sars
9
Alona affinis (Leydig)
9
Alona rustica Scott
9
Alona guttata Sars
9

Chydorus cf. brevilabris Frey
6,8,9,10,15,19
Chydorus bicornutus Doolittle
9
Chydorus piger Sars
9
Chydorus linguilabris Frey
9
Chydorus latus Sars
7,9,11,12,13,16,18
Camptocercus cf. rectirostris Schoedler
9
Eurycercus sp.
9

Family Macrothricidae

Ophryoxus gracilis Sars
9

Class Insecta

Order Diptera

Suborder Nematocera

Family Culicidae

Subfamily Chaoborinae

Chaoborus punctipennis Say
3

Family Chironomidae

Chironomus sp.
3

Class Arachnida

Order Acarina

Water mite
3,8

Phylum Rotifera

Class Monogononta

Order Plioma

Family Brachionidae

Subfamily Brachioninae

Kellicottia bostoniensis Rousselet
1,2,3,4,5,6,7,8,9,10,11,16,17,18,19,20

Keratella cochlearis Gosse
1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20
Keratella quadrata Carlin
14,15,16,17,18
Euchlanis sp.
3,5,20
Platyias polyacanthus Ahlstrom
11,13,18.
Lepadella patella Harring
3

Family Synchaetidae

Polyarthra vulgaris Carlin
1,3,4,5,7,8,9,10,11,15,16,17,18,20
Ploesoma hudsoni Imhof
3

Family Trichocercidae

Trichocerca elongata Gosse
8,10,18
Trichocerca multicrinis Jennings
2,5,10,14,17,19

Family Asplanchnidae

Asplanchna sp.
8,9,10,13,16,18

Family Gastropodidae

Gastropus sp.
15,16,18

Order Floscullariacae

Family Conochilidae

Conochilus unicornis Rousselet
1,2,4,6,7,8,9,10,13,16,17,19

Family Testudinellidae

Filinia longiseta Ehr.
15,20

Phylum Coelenterata

Class Hydrozoa

Order Hydroida

Family Hydridae

Hydra sp.
3

Table A.2.

Cladocera

Brooks, J.L. 1957. The systematics of North American Daphnia. Mem. Conn. Acad. Arts and Sci. 13:1-180.

Brooks, J.L. 1959. Cladocera p. 587-656. In. W.T. Edmondson (ed.) Fresh-water Biology. 2nd ed. John Wiley and Sons, Inc., New York.

Deevey, E.S. and G.B. Deevey. 1971. The American Species of Eubosmina Seligo (Crustacea, Cladocera). Limnol. Oceanogr. 16(2):201-218.

Copepoda

Czaika,, S.C. and A. Robertson. 1968. Identification of the copepodids of the Great Lakes species of Diaptomus (Calanoida, Copepoda). Proc. 11th Conf. Great Lakes Res. 39-60. International Assoc. Great Lakes Research.

Pennak, R.W. 1978. Copepoda p. 388-420. Freshwater Invertebrates of the United States. 2nd ed. John Wiley and Sons, Inc., New York.

Wilson, M.S. and H.C. Yeatman. 1959. Free living Copepoda. In: W.T. Edmondson (ed.) Freshwater Biology. 2nd ed. John Wiley and Sons, Inc., New York.

Diptera

Cook, Edwin F. 1956. The Neartic Chaoborinae (Diptera: Culicidae) U. of Minnesota Agricultural Experimental Station Tech. Bull. 218 102 pp.

Pennak, R.W. 1978. Diptera p. 666-709. Freshwater Invertebrates of the United States. 2nd ed. John Wiley and Sons, Inc., New York.

Rotifera

Ruttner-Kolisko, A. 1974. Plankton Rotifers, Biology and Taxonomy. E. Schweizerbart'sche Verlagsbuchandlung. Nagele u. Obermiller. Stuttgart. 146 pp.

Miscellaneous

Anonymous, 1972. Freshwater plankton. November 6-10, 1970. Kejimkujik National Park, Nova Scotia. Summary Report No. 46, C.O.I.C. Ref. No. 009F, 25 pp. Canadian Oceanographic Identification Centre, National Museum of Natural Sciences, Ottawa.

Anonymous, 1974. Special Zooplankton Report. July 23, 1974. Kejimkujik National Park, Nova Scotia. C.O.I.C. Reference Number 32F. Canadian Oceanographic Identification Centre, National Museum of Natural Sciences, Ottawa, Ontario. 10 pp.

Edmondson, W.T., (Ed.), 1959. Fresh-Water Biology. John Wiley and Sons. N.Y.

Table A.3.

Phylum Chlorophyta

Class Chlorophyceae

Order Volvocales

Family Chlamydomonadaceae

Chlamydomonas sp.
3

Family Volvocaceae

Eudorina elegans Ehr.
3

Order Tetrasporales

Family Palmellaceae

Sphaerocystis Schroeteri Chod.
1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20
Gloeocystis gigas (Kutz.) Lagerh.
3,7,19
Gloeocystis major Gerneck ex. Lemm.
1,2,4,5,6,7,9,10,11,12,13,14,16,17,18,20
Gloeocystis planktonica (W. and G.S. West) Lemm.
1,4,5,8,9,13,16

Family Coccomyxaceae

Elakatothrix gelatinosa Wille
1,2,4,5,6,8,10,11,12,13,16,17,18,19,20

Order Ulotrichales

Suborder Ulotrichineae

Family Ulotrichaceae

Ulothrix aequalis Kutz.
1,2,3,4,7,9,10,12,14,17,18,19
Ulothrix variabilis Kutz.
8,9,13,14,15
Geminella interrupta Turp.
8

Order Oedogoniales

Family Oedogoniaceae

Oedogonium sp.
3

Order Chlorococcales

Family Micractiniaceae

Golenkinia radiata (Chod.) Wille
3,8

Family Characiaceae

Schroederia setigera (Schroder) Lemm.
1,2,3,4,5,7,8,9,12,13,14,18

Family Oocystaceae

Chlorella vulgaris Beijerinck
3

Westella linearis G.M. Smith
3,19

Echinosphaerella limnetica G.M. Smith
3

Oocystis lacustris Chod.
2

Oocystis parva W. and G.S. West
1,2,3,4,5,6,7,8,9,10,14,15,16,17,18,19,20

Ankistrodesmus falcatus (Corda) Ralfs
2,5,12,19,20

Ankistrodesmus braunii (Nag.) Collins
3

Selenastrum minutum (Nag.) Collins
1,5,18,20

Kirchneriella lunaris (Kirchner) Mobius
8

Quadrigula lacustris (Chod.) G.M. Smith
3

Tetraedron minimum (A. Braun) Hansgirg
3,1

Family Scenedesmaceae

Scenedesmus bijuga (Trup.) Lagerh.
1,12,15,19,20

Scenedesmus quadricauda (Turp.) Brebisson
2

Tetradesmus smithii Prescott
3

Tetradesmus wisconsinensis G.M. Smith
3

Crucigenia tetrapedia (Kirchner) W. and G.S. West
1,2

Actinastrum sp.
3

Order Zygnematales

Family Zygnemataceae

Mougeotia sp.
8

Spirogrya sp.

Family Mesotaeniaceae

Gonatozygon brebisonii DeBary
1,8

Family Desmidiaceae

Closterium leibleinii Kutz.
19
Closterium parvulum Nag.
1,3,4,7,8,9,13,15,17,19,20
Euastrum insurale Roy
4
Staurastrum connatum (Lund.) Roy and Biaa.
8,13,14
Staurastrum gracile Ralfs
4
Staurastrum lacustris G.M. Smith
8
Staurastrum paradoxum Meyen
2,4,10,14,15,16,19,20
Arthrodesmus octocorne Ehr.
3,4,14,19,20
Spondylosium planum (Wolle) W. and G.S. West
2,14,16,17,18,19

Phylum Euglenophyta

Class Euglenophyceae

Order Euglenales

Family Euglenaceae

Trachelomonas sp.
15

Phylum Chrysophyta

Class Xanthophyceae

Order Hecterochloridales

Family Chloromoebaceae

Chlorochromonas minuta Lewis
1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20

Class Chrysophyceae

Order Chrysomonadales

Family Mallomonadaceae

Mallomonas akrokomos Ruttner
1,2,3,4,5,7,8,9,10,16,17,18,19,20
Mallomonas caudata Iwanoff
1,2,3,4,5,6,7,8,9,10,11,12,13,14,16,17,18,19,20
Mallomonas producta (Zacharias) Iwanoff
3
Mallomonas urnaformis Prescott
3

Family Ochromonadaceae

Dinobryon bavaricum Imhof
1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19
Dinobryon divergens Imhof
8,9
Dinobryon pediforme (Lemm.) Steinecke
1,2,3,5,7,8,9,13,14,17,19,20

Class Bacillariophyceae

Order Centrales

Suborder Coscinodiscineae

Family Coscinodiscaceae

Melosira granulata (Ehr.) Ralfs
19
Cyclotella meneghiniana Kutz.
7,10,15,16,19

Suborder Rhizosolenineae

Family Rhizosoleniaceae

Rhizosolenia eriensis H.L. Smith
1,2,3,6,8,9,11,12,14,17

Order Pennales

Suborder Fragilarineae

Family Tabellariaceae

Tabellaria fenestrata (Lyngb.) Kutz.
1,2,3,4,5,7,8,9,10,11,12,13,14,17,18,19,20
Tabellaria flocculosa (Roth) Kutz.
1,2,3,4,5,6,7,8,9,10,11,12,13,14,16,17,18,19,20

Family Fragilariaceae

Fragilaria capucina Desmazieres
3
Fragilaria crotonensis Kitton
1,2,3,4,5,6,7,8,9,10,12,13,14,17,18
Asterionella formosa Hass.
7,10,15,16,17,19,20
Synedra pulchella Kutz.
1,2,3,4,5,6,7,9,10,12,15,16,17,18,19
Synedra ulna (Nitz.) Ehr.
20

Family Eunotiaceae

Eunotia arcus Ehr.
2,4,5,6,7,10,11,12,16,17,18,19,20
Eunotia bidentula W. Smith
2
Eunotia lunaris (Ehr.) Grun.
3
Eunotia pectinalis (Kutz.) Rabenhorst
1,2,4,6,8,9,13,14,17,18,20

Suborder Achnanthineae

Family Achnanthaceae

Cocconeis placentula Ehr.
3

Suborder Naviculineae

Family Naviculaceae

Navicula sp.
1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20
Pinnularia major Kutz.
3
Pinnularia braunii (Grun.) Cleve
1,2,4,6,17,19
Diploneis sp.
3
Frustulia rhomboides (Ehr.) DeToni
3
Gyrosigma sp.
1,2,4,5,6,7,12,16,17,18,19,20

Family Gomphonemataceae

Gomphonema olivaceum (Lyngb.) Kutz.
1,4,5,6,7,9,11,12,13,14,17,18,20

Family Cymbellaceae

Cymbella caespitosa (Kutz.) Schutt
3

Suborder Surirellineae

Family Nitzschiaceae

Nitzschia dissipata (Kutz.) Grunow
13,14
Nitzschia palea (Kutz.) W. Smith
3,4,8,9,18
Hantzschia sp.

Family Surirellaceae

Surirella linearis W. Smith
1,4,7,10,13,19

Phylum Pyrrophyta

Class Dinophyceae

Order Peridiniales

Family Peridiniaceae

Peridinium limbatum (Stokes) Lemm.
1,2,16,19,20

Class Cryptophyceae

Order Cryptomonadales

Family Cryptomonadaceae

Cryptomonas ovata Ehr.
1,2,3,4,5,6,7,8,9,10,11,13,14,15,16,17,18,19,20

Phylum Cyanophyta

Class Myxophyceae

Order Chroococcales

Family Chroococcaceae

Chroococcus dispersus (Keissl.) Lemm.
8
Chroococcus limneticus Lemm.
1,2,4,6,7,10,15,16,18,19
Polycystis (=Microcystis) aeruginosa Kutz.
8
Rhabdoderma irregulare (Naumann) Geitler
2,5,6,7,11,12,15,16,18,20
Rhabdoderma lineare Schmidle and Lauterborn
8

Dactylococcopsis acicularis Lemm.
8,16,19
Aphanothece sp.
8
Agmenellum (=Merismopedia) thermale (Kutz.) Drouet and Daily
1,2,3,4,5,6,7,8,9,10,11,12,14,17,18,19,20
Coelosphaerium naegelianum Ungr.
8

Order Oscillatoriales

Suborder Oscillatorineae

Family Oscillatoriaceae

Phormidium sp.
3,8,9,12,17

Suborder Nostochineae

Family Nostocaceae

Anabaena flos-aquae (Lyngb.) Brebisson
1,12
Nostoc sp.
1,2,4,5,6,9,18,19
Aphanizomenon flos-aquae (L.) Ralfs
3,8

Table A.4.

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APPENDIX B

Statistics of Sub-Sampling

For a randomly distributed planktonic species where p, the probability of encountering an individual at a random point in space, is very small, the distribution of individuals in repeated samples will be characterized by the Poisson distribution, in which $\sigma^2=\mu$, that is , the variance equals the mean. Departure from this random distribution is common in plankton samples (Cassie, 1971), with overdispersion the most common situation, in which $\sigma^2>\mu$. In this case, in a set of samples, the relationship between the means and variances of the various sets will be: $\sigma^2_i=\mu_i+c\mu^2_i$, where c is a constant characteristic of the population, and i refers to the ith set. The right hand consists of the Poisson variance μ, arising from random variation, and the over-dispersion variance $c\mu^2$. For plankton populations, c is often between 0.1 to 0.2 (Cassie, 1971). For rare species (mean < 1), $c\mu^2$ is small and the distribution will be approximately Poisson. For larger means, the coefficient of variation decreases as the number of individuals counted increases, up to a limiting value which depends on c. To examine the statistics of sub-sampling, the common species Gloeocystis maior was chosen from Big Dam West Lake for examination. Table B.1 shows statistics associated with counts from replicate sub-samples. The mean value of c for all dates and depths was found to be 0.174, indicating a moderate degree of over-dispersion. In such a case, the optimum number of individuals to count per sub-sample would be 10-30 per species, for a coefficient of variation between .48-.55 (Cassie, 1971). Counting of additional individuals would yield little improvement in the coefficients of variation. Venrick (1978) has shown that for a total of about 100 individuals of a species counted in 4 sub-samples, the relative error of the mean will be approximately 30%.

Table B.1. Cell counts in replicate sub-samples for Gloeocystis maior in Big Dam West Lake. $\bar{x}$= mean, s= variance, cv= coefficient of variation, c= coefficient of dispersion.

Date	Depth (meters)		
	0	3	6
830524	28 11 50 27	47 24 37 22	17 2 9 28
	$\bar{x}$=29, s=16, cv=.55 c=.27	$\bar{x}$=32.5, s=11.7, cv=.36 c=.10	$\bar{x}$=14, s=11.2, cv=.8 c=.57
830709	9 11 15 3	21 22 16 14	8 4 13 4
	$\bar{x}$=9.5, s=5, cv=.53 c=.17	$\bar{x}$=18.3, s=3.9, cv=.21 c=0	$\bar{x}$=7.3, s=4.3, cv=.59 c=.21
830817	33 8 23 20	24 15 16 7	17 24 8 29
	$\bar{x}$=21, s=10.3, cv=.49 c=.19	$\bar{x}$=15.5, s=7, cv=.45 c=.14	$\bar{x}$=19.5, s=9.1, cv=.47 c=.17
830923	25 15 17 6	7 16 18 20	12 12 15 18
	$\bar{x}$=15.8, s=7.8, cv=.49 c=.18	$\bar{x}$=15.3, s=5.7, cv=.37 c=.07	$\bar{x}$=14.3, s=2.9, cv=.20 c=0
831104	6 10 7 19	4 4 7 8	32 8 16 12
	$\bar{x}$=10.5, s=5.9, cv=.56 c=.22	$\bar{x}$=5.8, s=2.1, cv=.36 c=0	$\bar{x}$=17, s=10.5, cv=.62 c=.32

APPENDIX C.

Comparison of Two Zooplankton Sampling Methods in Kejimkujik Lake (Schindler-Patalas plankton trap and Clarke-Bumpus net).

Table C.1. Comparison of total densities (no./m^3) and relative abundances (%) for zooplankton by species in Kejimkujik Lake collected with the plankton trap and the Clarke-Bumpus sampler.

Table C.2. Comparison of total densities (no./m^3) and relative abundances (%) for zooplankton by functional group in Kejimkujik Lake collected with the plankton trap and the Clarke-Bumpus sampler.

Comparison of the two sampling methods.

a) By Species (Table C.1.)

Only those environments in which both sampling methods were used simultaneously are included in this comparison.

The results show:

1. For most taxonomic categories, the plankton trap captured higher numbers of organisms. Exceptions included: Diaphanosoma birgei, Daphnia ambigua, and copepod males (excluding Diaptomus oregonensis).
2. For most of the larger organisms, the values for the two methods were similar.
3. For most of the small organisms, the Schindler-Patalas plankton trap was the more effective sampling device. Nauplii, rotifers and small copepodites are poorly collected with a Clarke-Bumpus sampler, and the Clarke-Bumpus sampler missed Eubosmina longispina as the dominant cladoceran and Keratella cochlearis as the dominant rotifer, likely because of their small size.
4. The plankton trap captured approximately three times more animals in total than the Clarke-Bumpus.

b. By Functional Group (Table C.2.)

1. Cladocerans were collected in similar numbers by the two methods.
2. Nauplii and rotifers were not trapped efficiently by the Clarke-Bumpus.
3. Only 50% of the macrozooplankton were collected with the Clarke-Bumpus as compared to the plankton trap.

Table C.1.

SPECIES	Abundance / Column Percent	PLANKTON TRAP	CLARKE-BUMPUS
Daphnia ambigua		0	33
		0	.0
Daphnia catawba		59200	42800
		1.8	3.6
Bosmina longirostris		4430	1160
		.1	.1
Eubosmina longispina		76400	65900
		2.3	5.5
Eubosmina tubicen		32800	20300
		1.0	1.7
Holopedium gibberum		5070	4890
		.1	.4
Leptodora kindtii		1270	1010
		.0	.1
Diaphanosoma birgei		87200	91000
		2.6	7.6
Diaphanosoma brachyurum		259	212
		.0	.0
Eurycercus sp.		178	0
		.0	0
Camptocercus cf. rectirostris		74	0
		.0	0
Alona rectangula		37	0
		.0	0
Epischura nordenskioldi (female)		7930	6160
		.2	.5
Epischura nordenskioldi (male)		5560	6790
		.2	.6

Table C.1. (continued)

Epischura nordenskioldi (CIV-CV)	17000	5930
	.5	.5
Epischura nordenskioldi (CI-CIII)	79600	22500
	2.4	1.9
Diaptomus minutus (female)	240000	189000
	7.1	15.8
Diaptomus minutus (male)	162000	165000
	4.8	13.8
Diaptomus oregonensis (female)	7620	5630
	.2	.5
Diaptomus oregonensis (male)	3900	2760
	.1	.2
Diaptomus spp. (CIV-CV)	440000	347000
	13.0	29.1
Diaptomus spp. (CI-CIII)	454000	193000
	13.4	16.1
Mesocyclops edax (female)	7120	5500
	.2	.5
Mesocyclops edax (male)	3190	4920
	.1	.4
Mesocyclops edax (immature)	13500	6970
	.4	.6
Tropocyclops sp. (male)	77	191
	.0	.0
Tropocyclops sp. (immature)	1040	1040
	.0	.1
Copepod Nauplii	496000	3190
	14.7	.3
Keratella cochlearis	1030000	337
	30.4	.0
Kellicotia bostoniensis	37100	877
	1.1	.1

Table C.1. (continued)

Chonochilus sp.	1320	363
	.0	.0
Polyarthra vulgaris	106000	12
	3.1	.0
Ploesoma hudsoni	74	45
	.0	.0
Trichocera elongata	321	0
	.0	0
Euchlanis sp.	758	0
	.0	0
Chaoborus punctipennis	127	126
	.0	.0
Chironomidae sp.	37	9
	.0	.0
Water mite	125	13
	.0	.0

Table C.2.

SPECIES (Abundance / Column Percent)	PLANKTON TRAP	CLARKE-BUMPUS	ROW TOTAL
Cladocerans	267000	227000	494000
	7.9	19.0	10.8
Calanoid copepods	1420000	945000	2360000
	41.9	79.0	51.6
Cyclopoid copepods	25000	18600	43600
	.7	1.6	1.0
Copepod nauplii	496000	3190	499000
	14.7	.3	10.9
Rotifers	1180000	1630	1180000
	34.8	.1	25.7
Macro-zooplankton	289	148	437
	.0	.0	.0
Column total	3390000	1200000	4580000
	73.9	26.1	100.0

Appendix D. Data Transformations

General experience has shown that many water chemistry parameters and population counts or densities are not normally distributed but rather are skewed to the right, giving a preponderance of smaller numbers. For water chemistry this applies most generally to concentrations either in mass/volume units or as proportions -parts per million. Some variables may be left-skewed. This can happen when there is a clear maximum value, such as for percent saturation of oxygen.

Most statistical procedures require that the data be normally distributed and will be biased when used on a skewed variable. The accepted procedure in such a case is to apply a non-linear function to all the values so that the relative difference between the larger and smaller values changes. If done properly, the distribution of values around the mean becomes more symmetric. This is called transforming the variable. It should be noted that linear functions can also be used to transform data but these only affect the scale and range of the variable and not its distribution.

For right-skewed data, the log function is most often used as a transformation. However, there is a practical problem in applying this function to a variable which has zero values, as the log of zero is infinitely negative and causes an error on most computers and calculators. "Ratio-scale" variables (that is, any variable where it makes sense to say that one value is twice as large as another) are all relative to zero, regardless of the scale of the variable. This distinction is lost when taking logs, and so a linear transform was used to change each variable to a consistent scale and range beginning at one. The median is used to scale the variable, as it is the measure of central tendency least sensitive to

extreme values. Thus the transform formula becomes:

$$X' = \text{LOG}\ (\ X/\text{MEDIAN} + 1\ )$$

This will transform zero to zero and the median value to log(2) and so on. If it is desired to keep the same scale in the transformed variable, then the above could be multiplied by the median/log(2). It makes no difference which base logs are used of course, since they are all proportional.

By this method the relationship between the untransformed variables and zero is kept, although only approximately, in the transformed values, and it is kept consistently for variables of different scale. If the variable range was changed without re-scaling, as in $X' = \log(X+1)$, then the ratio between untransformed values could change quite drastically depending on the scale of the variable.

Thus, for the Kejimkujik Park water quality data for 1980 and 1981, the following transformation for normality was employed:

$$X' = \ln(x/\text{median} + 1)*Q \quad \text{where } Q = \text{max}/\ln(\text{max}/\text{median} + 1)$$

The factor Q multiplies the transformed value into the same range of values, thus, $x' = x$ when x = maximum value. Note: one parameter, dissolved oxygen, was skewed to the left so a slight variation of this equation was used.

Percentages were usually skewed to the left between 0 and 100 and the following arcsin transformation was applied:

$$x' = \text{arcsin}(x/100)/(PI/2)*100$$

Since the software package (SPSS) used in data analysis only has an arctan function, the following identities were used:

$$\text{arccos}(x) = \text{arctan}\ (\ 1/x^2 - 1)$$

$$\text{arcsin}(x) = \text{arctan}\ (1/\ 1/x^2 - 1)$$

$$\text{arcsin}(x) + \text{arccos}\ (x) = \ /2$$

The following formulae were used for the water quality data:

Percent oxygen saturation (arcsin transformation)

$$\%\ O_2' = [\text{Atan}\ (\ 1.0/\text{SQRT}(1.0/((\%O_2/105)^{**}2) - 1.0))] / (3.1415/2)*100$$

Dissolved Oxygen (ln transformation)

$$DO' = 9.25 - 3.5 * \ln((9.25-DO) / (9.25-7.9) + 1)$$

Turbidity (ln transformation)

$$TRB' = \ln(\ TRB/0.4+1.0\ ) * 0.798$$

Mineral acidity (ln transformation)

$$MA' = \ln(\ \text{Min. acid.}/0.34+1.0\ ) * 1.313$$

Total acidity (ln transformation)

$$TA' = \ln(\ \text{Tot. acid.}/3.9+1.0\ ) * 7.17$$

Chlorophyll (ln transformation)

$$Chl.' = \ln(\ Chl./0.72+1.0\ ) * 2.25$$

Phaeophytin (ln transformation)

$$Pha.' = \ln(\ Pha./1.3+1.0\ ) * 3.63$$

Dissolved inorganic carbon (ln transformation)

$$DIC' = \ln(\ DIC/0.37+1.0\ ) * 0.941$$

Total organic carbon (ln transformation)

$$TOC' = \ln(\ TOC/8.4+1.0\ ) * 17.78$$

Dissolved organic carbon (ln transformation)

$$DOC' = \ln(\ DOC/7.2+1.0\ ) * 14.37$$

Total phosphorus (ln transformation)

$$TP' = \ln(\ TP/8.6+1.0\ ) * 15.22$$

Total dissolved phosphorus (ln transformation)

$$TDP' = \ln(\ TDP/4.25+1.0\ ) * 10.56$$

Soluble reactive phosphorus (ln transformation)

$$SRP' = \ln(\ SRP/0.25+1.0\ ) * 2.693$$

Total nitrogen (ln transformation)

$TN' = \ln(TN/0.156+1.0) * 0.499$

Ammonia (ln transformation)

$NH_4' = \ln(NH_4/0.047+1.0) * 0.1356$

Nitrate (ln transformation)

$NO_3' = \ln(NO_3/0.009+1.0) * 0.014$

Data transformations for normality were done on the 1982 Beaverskin Lake enclosure data using the procedures outlined for the 1980-81 field data. The data were first examined for skewness. A simple measure of skewness is the mean minus the median, divided by the standard deviation (Spiegel, 1961). This quantity is positive for right-skewness, negative for left-skewness, and zero for a symmetric (normally distributed) variable. Basic statistics and skewness measures were generated for the untransformed water quality variables in order to examine their distributions (Table D.1). As a guide, a variable with a value for the simple skew statistic outside the range (-.2,.2) has a fairly skewed distribution; that is, when the difference between the mean and median is 20% or more of the standard deviation.

Given these results, only temperature and pH were not right-skewed. Temperature was actually skewed left, but it is typically normal and is seldom transformed. (The skewness may be a result of an uneven effect from the date factor).

Conductivity, acidity, and a few of the concentrations were only slightly right-skewed but since other variables of the same type are more skewed, this is probably an anomaly of the data selection and it will be safer to transform.

Table D.1. Descriptive statistics and skewness for untransformed 1982 water quality data, Beaverskin Lake enclosure experiment.

CODE	FREQ	MIN	MAX	MEAN	STDEV	MEDIAN	SKEW
1) TEMP.	189	10.00	23.00	17.37	4.36	18.16	+.181
2) OXYGEN	189	7.20	11.20	8.79	1.18	8.51	-.237
3) pH	189	4.50	6.70	5.48	.41	5.50	+.049
4) CHLOR.A	189	.29	7.87	1.48	1.01	1.24	-.238
5) ACIDITY	189	1.45	3.38	2.27	.43	2.26	-.028
6) CONDUCT.	189	19.00	28.00	22.13	1.80	22.02	-.061
7) COLOR	189	5.00	10.00	5.32	1.22	5.03	-.238
8) TURBID.	189	.18	.88	.44	.14	.42	-.143
9) SILICA	189	28.00	81.20	29.36	6.86	28.28	-.157
10) NITRATE	189	1.40	36.40	4.50	5.78	3.97	-.092
11) NITRITE	189	.60	3.22	.63	.20	.62	-.025

Thus oxygen, chlorophyll and nutrient concentrations as well as color, acidity and conductivity were log transformed as follows:

O_2' = LOG(O_2/8.514 + 1) * 8.514/LOG(2)

Chlor.a' = LOG(Chlor.a/1.244 + 1) * 1.244/LOG(2)

Acidity' = LOG(Acid./2.258 + 1) * 2.258/LOG(2)

Conductivity' = LOG(Cond./22.02 + 1) * 22.02/LOG(2)

Color' = LOG(Color/5.027 + 1) * 5.027/LOG(2)

Turbidity' = LOG(Turb./.422 + 1) * .422/LOG(2)

Silica' = LOG(Silica/28.28 + 1) * 28.28/LOG(2)

Nitrate' = LOG(Nitrate/3.97 + 1) * 3.97/LOG(2)

Nitrite' = LOG(Nitrite/.615 + 1) * .615/LOG(2)

Where X' indicates the transformed variable.

Plankton population counts are highly right-skewed most of the time. For population group sums and other population variables where most of the values are non-zero, it is strongly advisable to use the median formula, rather than a simple log(x+1) transformation. (The consequences of not doing so are possibly "over-shooting" and having transformed variables which are left-skewed.)

Thus the plankton population variables were transformed as follows:

Greens' = LOG (Greens/28495 + 1) * 28495/LOG(2)

Diatoms' = LOG (Diatoms/14199 + 1) * 14199/LOG(2)

Blue-greens' = LOG(Blue-gr./3514120 + 1) * 3514120/LOG(2)

Chrysophytes' = LOG(Chrysoph./13708 + 1) * 13708/LOG(2)

Xanthophytes' = LOG(Xanthoph./23180 + 1) * 23180/LOG(2)

Unidentified' = LOG(Unident./18446 + 1) * 18446/LOG(2)

Cladocerans' = LOG(Cladocerans/4231 + 1) * 4231/LOG(2)

Calanoids' = LOG(Calanoids/8448 + 1) * 8448/LOG(2)

Cyclopoids' = LOG(Cyclopoids/228 + 1) * 228/LOG(2)

Rotifers' = LOG(Rotifers/5954 + 1) * 5954/LOG(2)

Insect larvae' = LOG(Larvae/2 + 1) * 2/LOG(2)

Copepod nauplii' = LOG(Nauplii/5217 + 1) * 5217/LOG(2)

Arachnids' = LOG(Arachnids/6 + 1) * 6/LOG(2)

Again, the multiplication factor on the right is merely to scale the transformed values back to a range similar to that of the untransformed.

APPENDIX E LOOP ANALYSIS

(Adapted from Lane and Blouin, 1985)

1. Introduction

Loop analysis is a qualitative network technique that uses signed diagraphs to represent sets of interaction variables. It represents a marked contrast to the more well-known computer simulations of system analysis which utilize masses of data to construct quantitative models. Loop analysis involves integration of feedback pathways in ecosystems which permit calculation of changes in basic production measures (standing crops and turnover rates) as well as identification of crucial entry points of ecological stresses into foodwebs. Lane and Levins (1977) have studied hypothetical freshwater plankton communities undergoing nutrient enrichment using this methodology. Briand and McCauley (1978) conducted lake manipulation studies and tested loop analysis predictions with their results. Lane (1982) and Lane and Morison (1981) have applied qualitative analysis to marine field communities in the field and laboratory. Loop anaylsis has not previously been used for an acid precipitation study.

Whole system understanding is urgently needed. Thousands of potential feedback pathways exist in acid-stressed lakes and indirect effects can swamp direct ones (Lane and Levins, 1977). Not only is better understanding needed to assess this stress, but also to insure that management strategies won't boomerang in unforeseen ways.

2. Methods

The three lakes modelled in this study are Pebbleloggitch, Beaverskin and Kejimkujik Lakes in Kejimkujik National Park, Nova Scotia. Their limnology (Kerekes et al., 1982), and descriptions of their plankton communities and the data collection plan for this study (Blouin et al.,

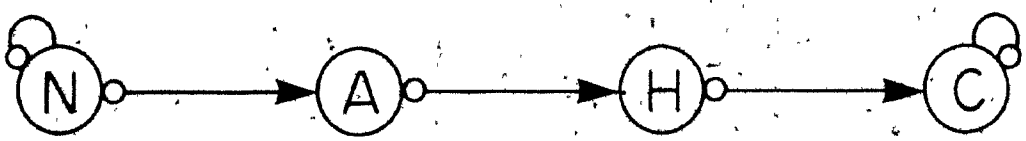
1983) have been given previously. Only the 1981 data are modelled here because nutrient values were not available for 1980. The mathematical formalism of loop analysis is also detailed elsewhere (Levins, 1973, 1975; Lane, 1982; Lane and Morison, 1981). In this study, the analysis consisted of fitting loop models to correlation matrices derived from field data (Blouin et al., 1983). Because loop models predict directed changes (+, - or 0 values) for each variable in the model, correlation signs for pairs of variables can also be predicted. The following example illustrates how this can be done.

Figure E.1 represents a four variable aquatic ecosystem. The large circles enclose the variables (N, A, H and C). The arrowheads indicate a positive effect on the variable the arrowhead touches and the circleheads indicate a negative effect on the variable they touch. The signs (+ and -) represent the qualitative effects of one variable on the rate of change of the second variable. (Thus, the signs are the qualitative values of the partial derivatives of the functions of each variable's rate of change evaluated at equilibrium). For example, herbivores (H) consume algae (A) causing an increase (positive) in H and a decrease (negative) in A.

The following definitions and rules summarize loop analysis as it is used here:

1. A loop of length k is a simple, closed path from a variable to itself through k steps which visits each variable on the loop only once. The value of a loop is the product of the α_{ij} of its links, and the sign is the sign of that product. Alpha (α_{ij}) is the interaction coefficient representing the effect of variable j on variable i. A loop of length 0 is by convention positive and has the value +1. Feedback is defined as the effect of a variable on itself by way of intervening variables.

Figure E.1. Loop diagram of a four variable aquatic ecosystem arranged as a single food chain. Nutrient (N) and carnivore (C) variables are self-damped whereas algal (A) and herbivore (H) variables are not. A circlehead indicates a negative effect on the adjacent variable. N-A, A-H and H-C interactions represent predator-prey relationships. For example, carnivores (C) are increased by feeding on herbivores (H); herbivores are decreased through carnivore predation.


N
A
H
C

2. Mathematically, the feedback at level k, (F_k), in a system of n variables is defined by $F_k = (-1)^{m+1} L(m,k)$. Feedback at level k is summed over all sets of products of m disjunct loops that total k elements. Disjunct loops have no variables in common (L = loops).

3. Loops of length 0 have a value of +1 and $F_0 = -1$. This is an algebraic convenience.

4. A path $P_{ij}^{(k)}$ is a product of (k-1) alpha values from X_j to X_i involving k variables, none of which are visited more than once. $P_{ii} = 1$.

5. The complement of a path is the set of variables not on the path.

6. Let C_h be any of s parameters of the system $dX_i/dt = f(X_1, X_2, X_3, \ldots, X_n; C_1, C_2, C_3, \ldots C_s)$. Then, the effect of a change in C_h on the equilibrium level of any variable (X_j) in the system is:

$$\partial X_j / \partial C_h = \Sigma \left(\partial f_i / \partial C_h \right) \times P_{ji}^{(k)} \times F_{n-k} \left[\text{Comp } P_{ji}^{(k)} \right] / F_n ,$$

that is, if C_h is a positive input to X_i, then its effect on X_j will have the sign of the sum of the products of each path from X_i to X_j, each multiplied by the feedback of its complement, and all divided by the feedback of the whole.

In Figure E.1, the path from nutrient to carnivore is positive, whereas the path from carnivore to nutrient is negative. There are three loops of length two representing predator-prey interactions and two self-damped loops (length one). There are no loops of higher length (level), that is, involving more than two variables. Table E.1 gives the qualitative predictions of changes in standing crops for four parameter inputs: an

Table 1. A. Predictions of directed changes in standing crops for variables in Figure 1, and

B. Predicted correlation signs between pairs of variables responding to increases in N and C.

A. Directed Changes

Increase in:	N	A	H	C	Variable
N	+	+	+	+	
A	−	+	+	+	
H	+	−	+	+	
C	−	+	−	+	

B. Correlation Values

Variable pair	Increase in: N	C
N-A	+	−
N-H	+	+
N-C	+	−
A-H	+	−
A-C	+	+
H-C	+	−

increase in nutrient (N), algae (A), herbivore (H), and carnivore (C) shown in the left-hand margin. The changes are read across each row. For example, an increase in A, perhaps reflecting a better environment for algae (more optimal temperature or light regime), results in a decrease in N and increases in A, H and C.

These directed changes can also be used to predict correlations between changes in pairs of variables (Table E.1). For example, if N is increased then there will be positive correlations between the changes in standing crops of all variable pairs. If C is increased, only N-H and A-C pairs will be positively correlated and all other pairs will exhibit negative correlation. Both directed changes in standing crops and the resultant correlation values generated by loop analysis can be tested with either field or laboratory data sets.

Figures E.2, E.3, and E.4 show the models for the three study lakes. These models were derived by fitting predicted correlation values from model predictions to observed correlation patterns from the 1981 field data.

Figure E.5 shows composite or core models for the experimental enclosures in Beaverskin Lake in 1982. A core model is a compilation of individual models. Each individual model is derived by fitting predicted variable changes from the model to observed changes in field data from one sampling date to the next. The core models represent those interactions which are most important in a particular environment. Solid links are those which appeared in more than 50% of the individual models, while dotted links are those which appeared in between 33%-50% of the individual models.

Figure E.2. Loop diagram of the plankton community of Kejimkujik Lake. Parameter input is a positive input to variable NP (nitrogen-phosphate complex). Symbols associated with loop variables are explained in Table E.2.

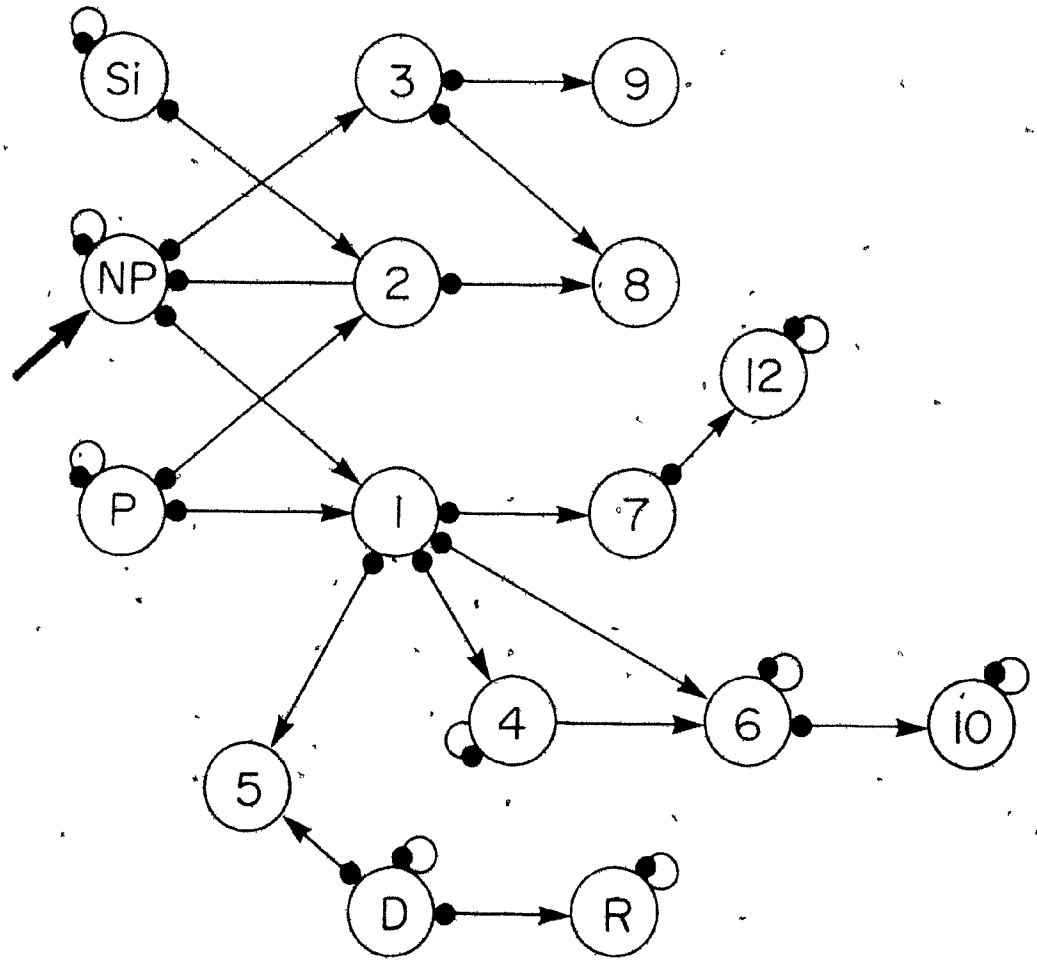

Si
3
9
NP
2
8
12
P
1
7
4
6
10
5
D
R

Figure E.3. Loop diagram of the plankton community of Beaverskin Lake. Parameter input is a positive input to variable NP (nitrogen-phosphate complex). Symbols associated with loop variables are explained in Table E.2.

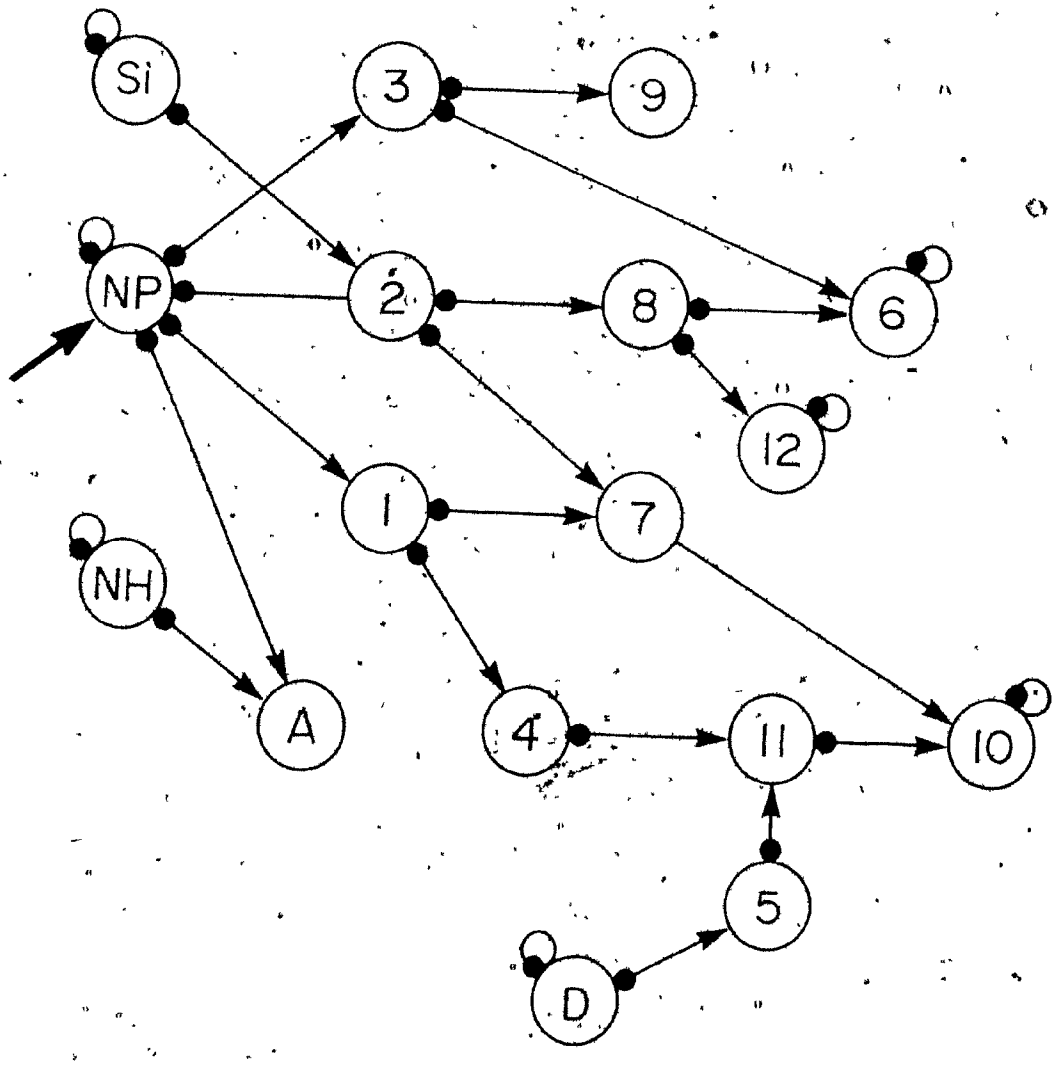

Si
3
9
NP
2
8
6
12
1
7
NH
A
4
11
10
5
D

Figure E.4. Loop diagram of the plankton community of Pebbleloggitch Lake. Parameter input is a positive input to variable N (nitrogen complex). Symbols associated with loop variables are explained in Table E.2.

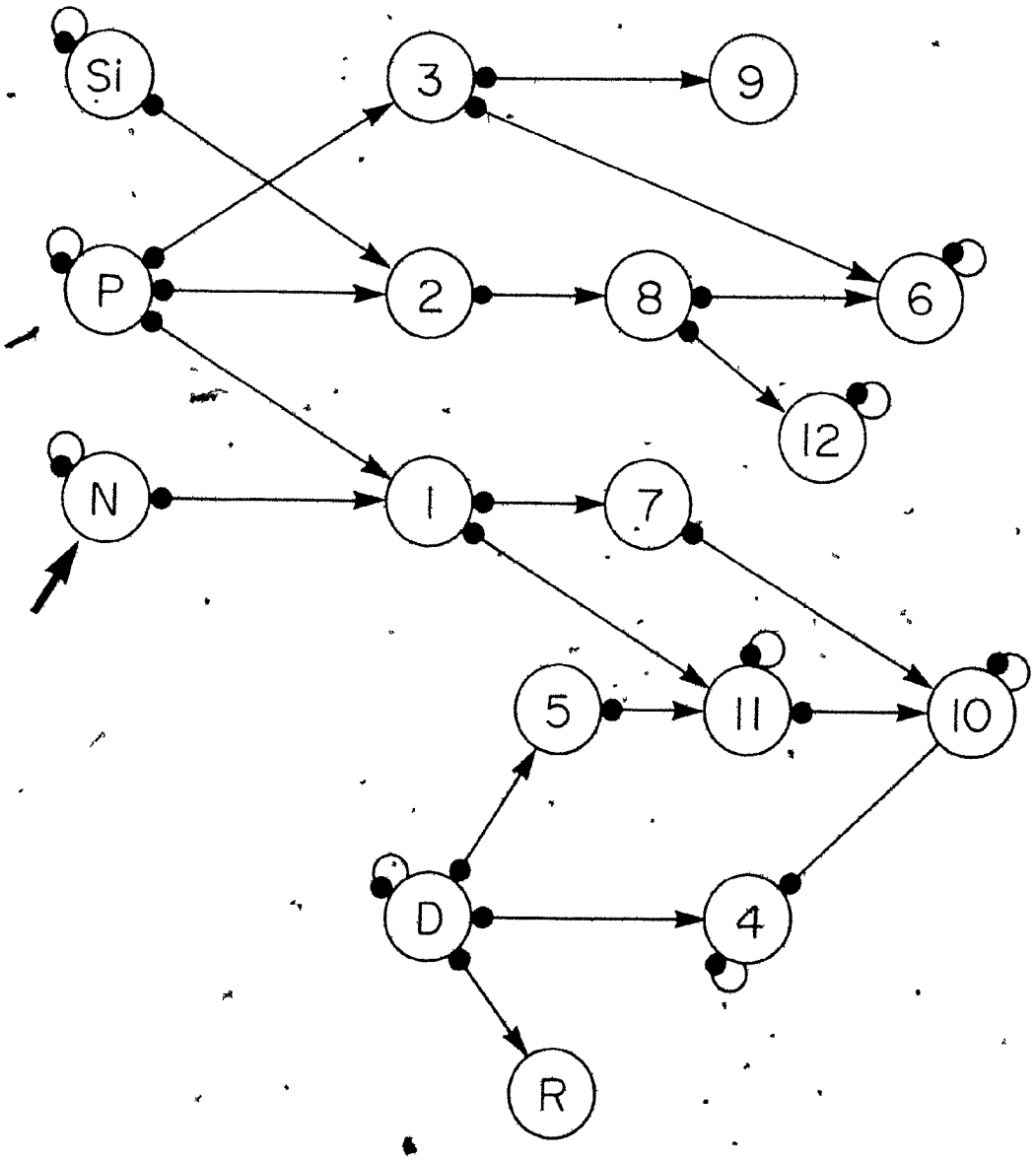

Si
3
9
P
2
8
6
12
N
1
7
5
11
10
D
4
R

Figure E.5. Loop diagrams for Beaverskin Lake enclosures, 1982. Symbols associated with loop variables are explained in Table E.2.

a) Control enclosures,

b) Nutrient enriched enclosures,

c) Acidified enclosures,

d) Limed enclosures,

e) Beaverskin Lake,

f) Summary core of all models.

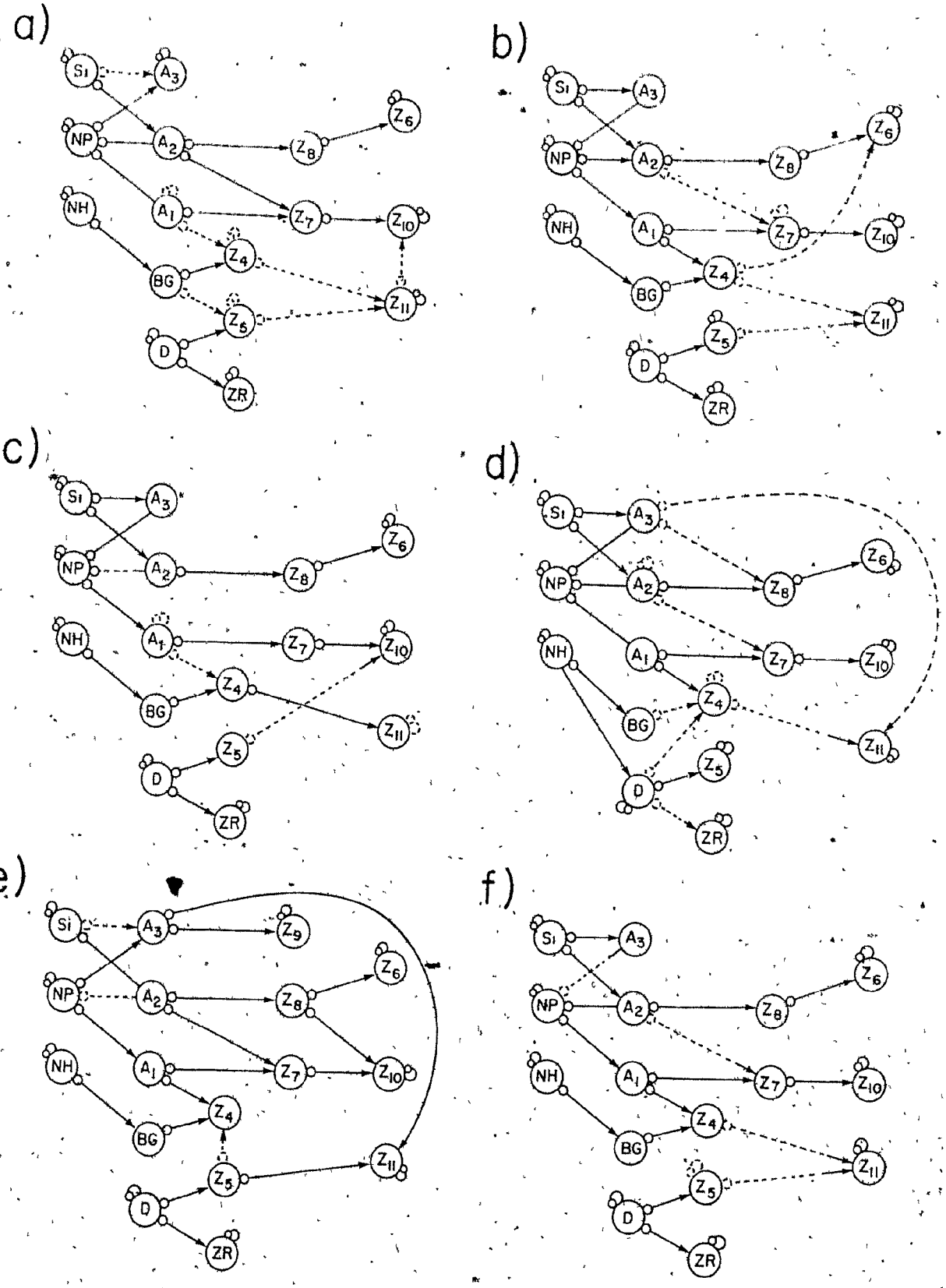

a)
b)
c)
d)
e)
f)
SI
NP
NH
BG
D
ZR
A3
A2
A1
Z4
Z5
Z6
Z7
Z8
Z9
Z10
Z11

Table 2. Key to variables used in the loop diagrams of individual lakes.

X indicates that the category does not apply.

Variable	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
I. Nutrients			
[redacted]	silica	silica	silica
P	phosphorus	phosphorus	phosphorus
NP	X	soluable reactive, total dissolved and total phosphorus. total nitrogen nitrate	soluable reactive, total dissolved and total phosphorus. total nitrogen nitrate
N	nitrogen.	nitrogen	nitrogen
NH	ammonia	ammonia	ammonia
D	detritus	detritus	detritus

Table 2. Continued

Variable	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
II. Phytoplankton			
A_1	Chlorochromonas minuta	Closterium parvulum	Sphaerocystis schroeteri
	Gloeocystis gigas	Sphaerocystis schroeteri	Schroederia setigera
	Cryptomonas ovata	Chlorochromonas minuta	Oocystis lacustris
	Oocystis lacustris	Navicula sp.	Sphaerocystis schroeteri
	Sphaerocystis schroeteri		Synedra ulna
	Eunotia arcus		Dinobryon divergens
	Frustulia rhomboides		Mallomonas caudata
	Mallomonas caudata		Mallomonas urnaformis
	Mallomonas urnaformis		

Table 2. Continued.

Variable	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
A_2	Asterionella formosa	Tabellaria fenestrata	Gloeocystis gigas
	Eunotia pectinalis	Mougeotia sp.	Asterionella formosa
	Synedra ulna	Oocystis lacustris	Tabellaria fenestrata
	Navicula sp.	Elakatothrix gelatinosa	Navicula sp.
	Tabellaria fenestrata	Dinobryon bavaricum	Eunotia pectinalis
	Closterium parvulum	Mallomonas caudata	Frustulia rhomboides
	Schroederia setigera	Chroococcus dispersus	Chlorochromonas minuta
			Cryptomonas ovata
A_3	Arthrodesmus octocorne	Selenastrum minutum	Arthrodesmus octocorne
	Mougeotia sp.	Asterionella formosa	Mougeotia sp.
	Selenastrum minutum	Synedra ulna	Closterium parvulum
	Dinobryon bavaricum		Elakatothrix gelatinosa
	Dinobryon divergens		Eunotia arcus
A	X	Agmenellum thermale	X

Table 2. Continued.

Variable	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
III. Zooplankton			
4	Nauplii	Nauplii	Nauplii
	Diaptomus spp. (CI-III)		Diaptomus spp. (CI-III)
R	X	X	Kellicottia bostoniensis
5	Keratella cochlearis	Keratella cochlearis	Keratella cochlearis
6	Diaptomus minutus adults	Diaptomus minutus adults	Diaptomus minutus adults
		D. oregonensis adults	D. oregonensis adults
		D. spp. (CIV-V)	
7	Daphnia catawba	Daphnia catawba	Daphnia catawba
		Diaphanosoma birgei	Diaphanosoma birgei

Table 2. Continued.

Variable	Pebbleloggitch Lake	Beaverskin Lake	Kejimkujik Lake
8	Eubosmina longispina	Bosmina longirostris	Bosmina longirostris
	Holopedium gibberum	Eubosmina longispina	Eubosmina tubicen
	Diaphanosoma birgei	Holopedium gibberum	Holopedium gibberum
9	Epischura nordenskioldi	Epischura nordenskioldi	Epischura nordenskioldi
10	Mesocyclops edax	Mesocyclops edax	Mesocyclops edax
11	Diaptomus spp. (CIV-V)	Diaptomus spp. (CI-III)	X
	Diaptomus oregonensis adults	Epischura nordenskioldi copepodites (CI-V)	
12	Leptodora kindtii	Leptodora kindtii	Leptodora kindtii

Appendix E. Plankton species data, Beaverskin Lake enclosure experiments, 1982.

Table El. A. Phytoplankton species abundances for Beaverskin Lake enclosures, 1982. (Numbers per Liter).

Table El. B. Zooplankton species abundances and egg ratio data for Beaverskin Lake enclosures, 1982. (Numbers per M^3, average number of eggs per female).

Appendix E

Table E1. A. Phytoplankton species abundances for Beaverskin Lake enclosures, 1982. (Numbers per Liter).

TREATMENT	DATE	Agmenellum thermale	Chroococcus dispersus	Anabaena flos-aquae	Aphanizomenon flos-aquae
ACIDIFIED					
	820723	5380000.	1240000.	0	0
	820807	5580000.	414000.	0	0
	820822	8790000.	328000.	0	0
	820906	1120000.	33300.	0	0
	820921	343000.	97000.	0	9940.
	821006	560000.	48500.	0	0
	821021	1070000.	53800.	0	0
BEAVERSKIN					
	820723	4680000.	1450000.	0	0
	820807	11000000.	366000.	0	0
	820822	13400000.	161000.	15100.	0
	820906	11100000.	150000.	0	0
	820921	2840000.	75400.	0	0
	821006	3960000.	183000.	0	0
	821021	1290000.	107000.	0	0
CONTROL					
	820723	1690000.	377000.	0	0
	820807	3290000.	382000.	0	0
	820822	12400000.	194000.	5560.	0
	820906	3530000.	119000.	0	0
	820921	1960000.	123000.	0	28200.
	821006	2520000.	113000.	0	0
	821021	719000.	86200.	7550.	1190.
LIMED					
	820723	3400000.	916000.	0	0
	820807	8120000.	463000.	0	0
	820822	16900000.	317000.	0	0
	820906	1870000.	122000.	0	3970.
	820921	2090000.	113000.	0	1190.
	821006	4130000.	167000.	0	0
	821021	54200.	39300.	0	0
NUTRIENT					
	820723	5210000.	1320000.	0	0
	820807	9160000.	587000.	0	0
	820822	26800000.	447000.	1590.	0
	820906	8360000.	174000.	4770.	0
	820921	2880000.	140000.	0	0
	821006	7000000.	156000.	0	0
	821021	1140000.	59200.	0	0

Table E1. A. Continued.

TREATMENT	DATE	Asterionella formosa	Tabellaria fenestrata	Tabellaria flocculosa	Eunotia arcus
ACIDIFIED					
	820723	397.	1980.	0	0
	820807	0	0	0	0
	820822	0	0	0	0
	820906	0	0	9940.	0
	820921	0	10300.	35000.	0
	821006	397.	296000.	10700.	0
	821021	0	1190.	1190.	0
BEAVERSKIN					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	795.	0
	820906	0	0	0	0
	820921	0	1590.	0	0
	821006	0	795.	0	0
	821021	0	0	0	0
CONTROL					
	820723	0	0	0	0
	820807	0	397.	0	0
	820822	1590.	0	397.	0
	820906	0	2780.	2380.	0
	820921	397.	1190.	62000.	0
	821006	0	7160.	36200.	0
	821021	1190.	2780.	15900.	0
LIMED					
	820723	397.	0	795.	0
	820807	0	397.	0	0
	820822	397.	397.	0	0
	820906	0	397.	4370.	0
	820921	0	1190.	14300.	0
	821006	0	1190.	25400.	0
	821021	0	4770.	18300.	0
NUTRIENT					
	820723	397.	397.	397.	0
	820807	0	397.	0	397.
	820822	0	795.	10300.	0
	820906	0	6760.	122000.	0
	820921	0	9150.	67800.	0
	821006	795.	2780.	9540.	0
	821021	795.	795.	9540.	0

Table E1. A. Continued.

TREATMENT	DATE	Synedra pulchella	Navicula Sp.	Cyclotella menenghiana	Pinnularia major
ACIDIFIED					
	820723	5960.	10300.	397.	0
	820807	0	7550.	0	0
	820822	2780.	5960.	0	0
	820906	13100.	1980.	0	0
	820921	43400.	11100.	0	0
	821006	16300.	3580.	0	0
	821021	11100.	795.	0	0
BEAVERSKIN					
	820723	3180.	3180.	0	795.
	820807	795.	2380.	0	0
	820822	14300.	2380.	0	795.
	820906	0	2380.	0	0
	820921	0	2380.	0	795.
	821006	0	3180.	0	0
	821021	0	2380.	0	0
CONTROL					
	820723	0	4370.	0	0
	820807	7950.	2780.	0	0
	820822	9540.	4770.	0	0
	820906	5960.	4770.	0	0
	820921	75800.	9940.	0	0
	821006	21300.	8350.	0	0
	821021	79300.	18100.	0	0
LIMED					
	820723	8750.	5560.	0	0
	820807	10700.	2380.	0	0
	820822	7950.	1190.	0	0
	820906	7950.	5560.	0	0
	820921	1980.	3180.	0	0
	821006	2780.	3970.	0	0
	821021	3580.	6980.	0	0
NUTRIENT					
	820723	1190.	2380.	397.	0
	820807	2380.	14300.	0	0
	820822	22100.	5560.	0	0
	820906	14300.	2380.	0	0
	820921	4770.	1980.	0	0
	821006	3580.	1590.	0	0
	821021	3970.	397.	0	0

Table E1. A. Continued.

TREATMENT	DATE	Arthrodesmus octocorne	Tetradesmus wisconsinensis	Mougeotia Sp.	Selenastrum minutum
ACIDIFIED					
	820723	0	0	0	0
	820807	0	0	0	1590.
	820822	0	0	397.	1590.
	820906	0	0	9150.	1590.
	820921	397.	0	11900.	795.
	821006	0	0	73400.	2380.
	821021	0	0	2380.	2380.
BEAVERSKIN					
	820723	0	0	0	2380.
	820807	0	0	0	3970.
	820822	0	0	0	2380.
	820906	0	0	4770.	2380.
	820921	0	0	0	2380.
	821006	0	0	0	3970.
	821021	0	0	795.	6360.
CONTROL					
	820723	0	0	0	1980.
	820807	0	0	0	3580.
	820822	1190.	0	1190.	5560.
	820906	0	0	1980.	6360.
	820921	397.	0	3970.	0
	821006	0	0	8350.	1980.
	821021	0	795.	5170.	1980.
LIMED					
	820723	0	0	0	0
	820807	0	0	0	5960.
	820822	0	0	397.	1980.
	820906	0	0	397.	795.
	820921	0	0	2780.	4370.
	821006	0	0	1190.	1590.
	821021	0	0	0	2380.
NUTRIENT					
	820723	0	0	3580.	795.
	820807	0	0	0	3580.
	820822	2780.	0	1190.	2380.
	820906	397.	0	8350.	795.
	820921	397.	0	17500.	397.
	821006	0	0	1190.	5170.
	821021	0	0	4370.	8360.

Table E1. A. Continued.

TREATMENT	DATE	Closterium parvulum	Spondilosium planum	Staurastrum paradoxum	Staurastrum connatum
ACIDIFIED					
	820723	0	5170.	0	0
	820807	397.	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	0	0
BEAVERSKIN					
	820723	795.	0	0	0
	820807	795.	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	0	0
CONTROL					
	820723	397.	0	0	0
	820807	795.	0	0	397.
	820822	397.	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	0	0
LIMED					
	820723	0	7550.	0	0
	820807	0	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	0	0
NUTRIENT					
	820723	397.	0	0	0
	820807	795.	0	0	0
	820822	0	10700.	397.	795.
	820906	0	0	0	0
	820921	0	6360.	0	0
	821006	0	0	0	0
	821021	0	0	0	0
	821021	0	0	0	0

Table El. A. Continued.

TREATMENT	DATE	Kirchneriella lunaris	Ulothrix variabilis	Schroederia setigera	Gloeocystis maior
ACIDIFIED					
	820723	0	0	109000.	7950.
	820807	0	0	0	2780.
	820822	0	16700.	19800.	37500.
	820906	0	4370.	0	5170.
	820921	0	4370.	22600.	19500.
	821006	0	6360.	37700.	5170.
	821021	0	1590.	62600.	1190.
BEAVERSKIN					
	820723	0	0	77900.	2380.
	820807	0	0	0	3180.
	820822	0	0	247000.	795.
	820906	0	0	0	795.
	820921	0	0	21500.	3970.
	821006	0	2380.	0	1590.
	821021	0	0	0	2380.
CONTROL					
	820723	0	0	54100.	9150.
	820807	0	0	33800.	3580.
	820822	0	1590.	65000.	67000.
	820906	0	1590.	0	46000.
	820921	0	33400.	16100.	8350.
	821006	0	27000.	0	8750.
	821021	0	35400.	91600.	3970.
LIMED					
	820723	0	0	397.	3580.
	820807	0	0	105000.	3180.
	820822	0	12300.	75100.	2380.
	820906	0	10700.	59600.	6360.
	820921	0	13500.	7950.	10300.
	821006	0	5960.	8750.	7550.
	821021	397.	4370.	8350.	7160.
NUTRIENT					
	820723	0	0	0	2380.
	820807	0	0	25400.	1980.
	820822	0	130000.	26900.	82800.
	820906	0	45900.	61600.	30100.
	820921	0	6360.	10300.	23900.
	821006	397.	2380.	15900.	4370.
	821021	1190.	4370.	37300.	2780.

Table E1. A. Continued.

TREATMENT	DATE	Oocystis parva	Oocystis lacustris	Scenedesmus bijuga	Quadrigula lacustris
ACIDIFIED					
	820723	0	397.	3180.	0
	820807	0	397.	0	0
	820822	0	0	0	0
	820906	1590.	397.	0	0
	820921	0	1190.	0	0
	821006	397.	0	1590.	0
	821021	3580.	4370.	0	1590.
BEAVERSKIN					
	820723	0	0	0	0
	820807	3970.	795.	0	0
	820822	795.	0	3180.	0
	820906	1590.	2380.	0	0
	820921	0	2380.	0	0
	821006	0	795.	0	0
	821021	7160.	9540.	0	5560.
CONTROL					
	820723	0	0	0	0
	820807	397.	0	0	0
	820822	0	0.	0	0
	820906	795.	397.	0	0
	820921	1980.	795.	4770.	0
	821006	397.	795.	0	0
	821021	1980.	1190.	0	0
LIMED					
	820723	0	1590.	0	0
	820807	795.	795.	1590.	0
	820822	1590.	795.	0	0
	820906	0	397.	0	0
	820921	1590.	0	0	0
	821006	1190.	2380.	1590.	0
	821021	397.	397.	1590.	1590.
NUTRIENT					
	820723	0	397.	0	0
	820807	1190.	0	0	0
	820822	0	0	0	0
	820906	1190.	1190.	0	0
	820921	0	397.	1190.	0
	821006	1590.	5170.	0	0
	821021	1590.	795.	1590.	2780.

Table E1. A. Continued.

TREATMENT	DATE	Gonatozygon brebisonii	Sphaerocystis schroeteri	Tetraedron minimum	Euastrum insulare
ACIDIFIED					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	397.	0
	820906	0	0	397.	0
	820921	0	0	0	795.
	821006	0	0	0	0
	821021	0	0	397.	0
BEAVERSKIN					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	1590.	0
	820906	0	0		0
	820921	795.	0	0	0
	821006	0	0	0	0
	821021	0	0	0	0
CONTROL					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	0	397.
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	397.	397.
LIMED					
	820723	0	397.	0	0
	820807	0	0	0	0
	820822	0	0	0	0
	820906	0	0	397.	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	397.	397.
NUTRIENT					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	0	397.
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	397.	0
	821021	0	0	0	0

Table E1. A. - Continued.

TREATMENT	DATE	*Elakatothrix gelatinosa*
ACIDIFIED		
	820723	0
	820807	3580.
	820822	2380.
	820906	0
	820921	0
	821006	795.
	821021	795.
BEAVERSKIN		
	820723	795.
	820807	1590.
	820822	1590.
	820906	3970.
	820921	2380.
	821006	2380.
	821021	3180.
CONTROL		
	820723	397.
	820807	3580.
	820822	4770.
	820906	0
	820921	1190.
	821006	795.
	821021	1190.
LIMED		
	820723	397.
	820807	3580.
	820822	3970.
	820906	1980.
	820921	3970.
	821006	3180.
	821021	795.
NUTRIENT		
	820723	2380.
	820807	1190.
	820822	5170.
	820906	397.
	820921	0
	821006	3970.
	821021	3180.

Table El. A. Continued.

TREATMENT	DATE	Dinobryon bavaricum	Dinobryon divergens	Mallomonas caudata	Mallomonas akrokomos
ACIDIFIED					
	820723	0	1190.	3180.	0
	820807	3180.	397.	5560.	0
	820822	15100.	3180.	7160.	0
	820906	2780.	3180.	1980.	0
	820921	0	1190.	1980.	0
	821006	16300.	0	10700.	0
	821021	17500.	397.	24600.	0
BEAVERSKIN					
	820723	0	0	5560.	0
	820807	0	0	21400.	0
	820822	0	0	10300.	0
	820906	1590.	0	7950.	0
	820921	7160.	795.	15900.	0
	821006	3970.	12700.	19800.	0
	821021	33400.	0	28600.	0
CONTROL					
	820723	0	0	2380.	0
	820807	7550.	0	7160.	0
	820822	8750.	397.	6760.	0
	820906	101000.	1190.	5560.	0
	820921	26100.	4370.	1590.	0
	821006	8350.	1980.	7550.	0
	821021	17100.	0	14700.	0
LIMED					
	820723	0	0	57800.	0
	820807	1190.	0	7550.	0
	820822	13900.	0	19400.	0
	820906	56200.	397.	4770.	0
	820921	6360.	0	8750.	0
	821006	31600.	795.	27400.	0
	821021	17900.	0	7550.	0
NUTRIENT					
	820723	0	0	7550.	0
	820807	795.	0	7950.	397.
	820822	397.	0	17500.	0
	820906	397.	0	13700.	0
	820921	0	0	24300.	0
	821006	12700.	397.	39300.	0
	821021	27800.	1190.	36200.	0

Table E1. A. Continued.

TREATMENT	DATE	Peridinium limbatum	Cryptomonas ovata	Chlorochromonas minuta	Unknown
ACIDIFIED					
	820723	0	0	2780.	36200.
	820807	0	1590.	13100.	7160.
	820822	0	795.	22600.	17500.
	820906	0	1980.	44500.	6760.
	820921	0	397.	44400.	1190.
	821006	0	1980.	17100.	17100.
	821021	0	795.	29400.	27400.
BEAVERSKIN					
	820723	0	0	1590.	30200.
	820807	0	0	7950.	18300.
	820822	0	1590.	8750.	30200.
	820906	0	1590.	16700.	31000.
	820921	0	0	9540.	55400.
	821006	0	1590.	92300.	86200.
	821021	0	0	23800.	38100.
CONTROL					
	820723	0	397.	3970.	33800.
	820807	0	0	19800.	6760.
	820822	0	1980.	93300.	19400.
	820906	0	2380.	82800.	10300.
	820921	0	0	72800.	1590.
	821006	0	1190.	29000.	10700.
	821021	0	795.	29800.	7950.
LIMED					
	820723	0	1190.	3580.	30200.
	820807	0	1190.	6360.	11100.
	820822	0	1190.	12300.	32600.
	820906	0	1590.	23000.	20200.
	820921	397.	397.	75800.	20600.
	821006	0	2380.	77100.	71700.
	821021	0	0	15900.	16700.
NUTRIENT					
	820723	0	0	2380.	48100.
	820807	0	1980.	9940.	8750.
	820822	0	6360.	498000.	15500.
	820906	0	0	489000.	10700.
	820921	0	397.	149000.	16700.
	821006	0	5560.	94300.	58100.
	821021	0	397.	33800.	42100.

Table El. A. Continued.

TREATMENT	DATE	Bambusina brebissonii	Micrasterias arcuata	Euastrum intermedium	Cosmarium Sp.
ACIDIFIED					
	820723	0	397.	0	0
	820807	1190.	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	1190.	0	0	0
	821021	0	0	0	0
BEAVERSKIN					
	820723	3180.	0	0	0
	820807	3970.	0	0	0
	820822	795.	0	0	795.
	820906	1590.	0	0	795.
	820921	34200.	0	0	0
	821006	27800.	0	0	0
	821021	0	0	0	0
CONTROL					
	820723	0	0	0	0
	820807	1980.	0	397.	0
	820822	0	0	0	795.
	820906	0	0	0	397.
	820921	795.	0	0	397.
	821006	397.	0	0	397.
	821021	397.	0	0	0
LIMED					
	820723	1190.	0	0	0
	820807	397.	0	0	0
	820822	2380.	0	0	0
	820906	5560.	0	0	0
	820921	397.	0	0	397.
	821006	1590.	0	0	0
	821021	0	0	0	0
NUTRIENT					
	820723	0	0	0	0
	820807	397.	0	0	0
	820822	1190.	0	0	795.
	820906	1980.	0	0	1190.
	820921	22600.	0	0	0
	821006	397.	0	0	0
	821021	795.	0	0	0

Table El. A. Continued.

TREATMENT	DATE	Peridinium inconspicuum
ACIDIFIED		
	820723	0
	820807	0
	820822	0
	820906	1190.
	820921	0
	821006	0
	821021	0
BEAVERSKIN		
	820723	0
	820807	0
	820822	0
	820906	0
	820921	0
	821006	0
	821021	0
CONTROL		
	820723	0
	820807	0
	820822	0
	820906	0
	820921	0
	821006	0
	821021	0
LIMED		
	820723	0
	820807	0
	820822	0
	820906	0
	820921	0
	821006	0
	821021	0
NUTRIENT		
	820723	0
	820807	0
	820822	0
	820906	0
	820921	0
	821006	0
	821021	0

Table E1. B. Zooplankton species abundances and egg ratio data for Beaverskin Lake enclosures, 1982. (Numbers per M^3, average number of eggs per female).

TREATMENT	DATE	Chydorus Sp.	Daphnia catawba	Bosmina longirostris	Eubosmina longispina
ACIDIFIED					
	820723	0	251.	0	0
	820807	0	150.	0	0
	820822	3720.	0	0	0
	820906	3900.	0	0	0
	820921	5180.	100.	50.	0
	821006	986.	0	0	0
	821021	100.	110.	0	0
BEAVERSKIN					
	820723	402.	1200.	0	0
	820807	402.	0	0	0
	820822	0	402.	0	603.
	820906	0	412.	0	0
	820921	0	1080.	0	1260.
	821006	0	201.	0	0
	821021	0	0	0	201.
CONTROL					
	820723	100.	100.	0	452.
	820807	788.	0	0	0
	820822	5870.	0	0	0
	820906	18600.	50.	0	50.
	820921	29900.	0	0	0
	821006	19500.	33.	0	0
	821021	3680.	100.	0	0
LIMED					
	820723	0	805.	0	0
	820807	100.	0	0	0
	820822	402.	0	0	0
	820906	895.	0	0	0
	820921	553.	100.	0	0
	821006	724.	0	0	0
	821021	1910.	0	0	0
NUTRIENT					
	820723	0	503.	0	0
	820807	0	100.	0	0
	820822	2110.	100.	0	0
	820906	8350.	201.	0	0
	820921	9250.	100.	0	0
	821006	603.	0	0	0
	821021	251.	100.	0	0

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Table El. B. Continued.

TREATMENT	DATE	Eubosmina tubicen	Holopedium gibberum	Leptodora kindti	Diaphanosoma leuchtenbergianum
ACIDIFIED					
	820723	1400.	201.	0	452.
	820807	2610.	0	0	654.
	820822	12000.	100.	0	1500.
	820906	24400.	0	0	1100.
	820921	3620.	0	0	1100.
	821006	5050.	0	0	0
	821021	4040.	0	0	50.
BEAVERSKIN					
	820723	4420.	0	0	6640.
	820807	16900.	0	0	2810.
	820822	402.	0	0	3820.
	820906	412.	0	211.	1410.
	820921	1240.	0	0	664.
	821006	201.	0	0	201.
	821021	1810.	0	0	201.
CONTROL					
	820723	2610.	201.	0	1050.
	820807	167.	0	0	1600.
	820822	2950.	0	110.	2780.
	820906	603.	0	0	50.
	820921	160.	0	0	100.
	821006	50.	0	0	335.
	821021	523.	0	0	134.
LIMED					
	820723	6230.	100.	0	1810.
	820807	301.	100.	0	1860.
	820822	9560.	0	0	2310.
	820906	6730.	0	0	805.
	820921	8600.	0	0	201.
	821006	1170.	0	0	100.
	821021	2960.	0	0	352.
NUTRIENT					
	820723	4620.	0	0	4420.
	820807	150.	201.	0	1100.
	820822	2610.	0	0	2510.
	820906	805.	0	0	603.
	820921	301.	0	0	1610.
	821006	1000.	0	0	0
	821021	603.	0	0	201.

Table E1. B. Continued.

TREATMENT	DATE	Scapholeberis kingii	Chironomidae	Eurycercus lamellatus	Camptocercus rectirostris
ACIDIFIED					
	820723	0	0	0	0
	820807	150.	0	0	0
	820822	0	0	0	503.
	820906	0	0	0	259.
	820921	0	0	301.	352.
	821006	55.	0	0	50.
	821021	0	0	0	261.
BEAVERSKIN					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	0	0
CONTROL					
	820723	0	0	0	0
	820807	50.	50.	0	83.
	820822	0	110.	110.	1060.
	820906	0	100.	50.	704.
	820921	0	50.	1550.	703.
	821006	0	150.	1280.	600.
	821021	0	0	345.	1220.
LIMED					
	820723	0	0	0	0
	820807	100.	0	0	0
	820822	301.	0	0	0
	820906	171.	0	0	0
	820921	0	0	0	201.
	821006	0	0	0	50.
	821021	0	0	0	50.
NUTRIENT					
	820723	0	0	0	100.
	820807	0	0	0	0
	820822	905.	0	0	301.
	820906	0	0	201.	2760.
	820921	0	0	1610.	2210.
	821006	0	0	100.	100.
	821021	0	0	0	100.

Table E1. B. Continued.

TREATMENT	DATE	Polyphemus pediculus	Ophryoxus gracilis
ACIDIFIED			
	820723	0	0
	820807	0	0
	820822	301.	0
	820906	0	0
	820921	603.	0
	821006	55.	60.
	821021	0	0
BEAVERSKIN			
	820723	201.	0
	820807	201.	0
	820822	201.	0
	820906	0	0
	820921	0	0
	821006	0	0
	821021	0	0
CONTROL			
	820723	0	0
	820807	0	0
	820822	0	0
	820906	0	0
	820921	0	0
	821006	0	0
	821021	0	0
LIMED			
	820723	0	0
	820807	0	0
	820822	100.	0
	820906	0	0
	820921	0	0
	821006	0	0
	821021	0	0
NUTRIENT			
	820723	0	0
	820807	0	0
	820822	100.	0
	820906	0	0
	820921	0	0
	821006	0	0
	821021	0	0

Table E1. B. Continued.

TREATMENT	DATE	Epischura nordenskioldi [Females]	Epischura nordenskioldi [Males]	Epischura nordenskioldi [C4-C5]	Epischura nordenskioldi [C1-C3]
ACIDIFIED					
	820723	0	0	0	201.
	820807	0	0	0	100.
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	100.	50.	0	0
	821021	221.	0	0	0
BEAVERSKIN					
	820723	0	0	100.	0
	820807	0	0	201.	201.
	820822	201.	0	402.	0
	820906	0	0	201.	0
	820921	0	0	0	0
	821006	402.	201.	0	0
	821021	0	0	0	0
CONTROL					
	820723	0	0	0	0
	820807	0	0	0	33.
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	0	0
	821021	0	0	0	0
LIMED					
	820723	0	0	0	0
	820807	50.	0	0	50.
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	50.	0	0	0
	821021	0	0	0	0
NUTRIENT					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	100.	0	0	0
	821006	0	50.	0	0
	821021	201.	201.	0	0

Table E1. B. Continued.

TREATMENT	DATE	Diaptomus minutus [Female]	Diaptomus minutus [Male]	Diaptomus oregonensis [Female]	Diaptomus oregonensis [Male]
ACIDIFIED					
	820723	805.	150.	0	0
	820807	956.	553.	201.	100.
	820822	3920.	1200.	503.	0
	820906	5070.	875.	110.	0
	820921	4020.	553.	100.	100.
	821006	2270.	719.	50.	0
	821021	2040.	2020.	110.	0
BEAVERSKIN					
	820723	25300.	28900.	503.	805.
	820807	9450.	2810.	0	0
	820822	13800.	11800.	603.	1400.
	820906	12300.	9730.	4310.	2250.
	820921	19400.	7920.	1730.	664.
	821006	8850.	6230.	603.	603.
	821021	9450.	11800.	402.	201.
CONTROL					
	820723	6130.	3920.	100.	0
	820807	318.	167.	67.	0
	820822	3930.	3210.	100.	201.
	820906	502.	201.	0	0
	820921	402.	150.	50.	0
	821006	150.	67.	0	0
	821021	1640.	301.	0	0
LIMED					
	820723	5430.	3520.	0	0
	820807	2960.	1050.	0	100.
	820822	12200.	6230.	201.	0
	820906	7450.	4160.	301.	0
	820921	6590.	2660.	503.	100.
	821006	3420.	764.	0	0
	821021	3370.	603.	0	0
NUTRIENT					
	820723	8250.	6230.	201.	0
	820807	1250.	251.	0	0
	820822	3520.	1910.	0	100.
	820906	2760.	654.	150.	251.
	820921	4120.	2210.	0	0
	821006	2660.	754.	100.	50.
	821021	7790.	5680.	150.	100.

Table El. B. Continued.

TREATMENT	DATE	Diaptomus Spp.[C4-C5]	Diaptomus Spp.[C1-C3]	Mesocyclops edax [Fem.]	Mesocyclops edax [Male]
ACIDIFIED					
	820723	1760.	10600.	0	100.
	820807	1710.	4470.	0	0
	820822	3420.	5030.	805.	0
	820906	8270.	1240.	211.	0
	820921	4620.	503.	50.	100.
	821006	810.	1680.	100.	0
	821021	1630.	3280.	0	0
BEAVERSKIN					
	820723	8350.	22100.	402.	402.
	820807	8650.	22500.	805.	0
	820822	24500.	9450.	0	0
	820906	29700.	2510.	0	0
	820921	17200.	3090.	0	0
	821006	10800.	3420.	0	0
	821021	20900.	3220.	0	0
CONTROL					
	820723	2910.	38200.	0	0
	820807	1140.	2530.	150.	0
	820822	16400.	5040.	653.	422.
	820906	1150.	301.	1600.	200.
	820921	200.	311.	673.	452.
	821006	201.	737.	885.	518.
	821021	1200.	1780.	0	67.
LIMED					
	820723	503.	19600.	0	0
	820807	2310.	7140.	201.	100.
	820822	13500.	5730.	0	0
	820906	9830.	2090.	0	0
	820921	3370.	1610.	0	0
	821006	1380.	1330.	0	0
	821021	1610.	1810.	50.	0
NUTRIENT					
	820723	905.	16300.	0	0
	820807	1000.	2610.	0	0
	820822	4020.	21[illegible]	603.	0
	820906	1400.	140[illegible]	805.	100.
	820921	905.	1000.	1400.	603.
	821006	1350.	1810.	50.	0
	821021	3820.	2760.	0	0

Table E1. B. Continued.

TREATMENT	DATE	Mesocyclops edax [C1-C5]	Tropocyclops Sp. [Fem.]	Tropocyclops Sp. [Male]	Tropocyclops Sp. [C1-C5]
ACIDIFIED					
	820723	100.	0	0	0
	820807	150.	0	0	0
	820822	905.	0	0	0
	820906	216.	0	100.	0
	820921	251.	0	201.	0
	821006	311.	0	317.	0
	821021	0	0	352.	0
BEAVERSKIN					
	820723	100.	0	0	0
	820807	805.	0	0	0
	820822	0	0	0	0
	820906	211.	0	0	0
	820921	0	0	0	0
	821006	402.	0	0	0
	821021	0	0	2810.	0
CONTROL					
	820723	502.	0	0	0
	820807	217.	0	0	0
	820822	4060.	0	100.	402.
	820906	3820.	201.	100.	402.
	820921	4420.	0	100.	472.
	821006	2500.	0	382.	231.
	821021	536.	0	402.	105.
LIMED					
	820723	0	0	0	0
	820807	100.	0	0	0
	820822	402.	0	0	0
	820906	201.	0	0	0
	820921	150.	0	0	0
	821006	50.	0	100.	0
	821021	0	0	100.	0
NUTRIENT					
	820723	301.	0	0	0
	820807	201.	0	0	0
	820822	1100.	0	0	0
	820906	1400.	0	0	0
	820921	1100.	0	0	0
	821006	100.	0	0	0
	821021	100.	0	0	0

Table E1. B. Continued.

TREATMENT	DATE	Copepod Nauplii
ACIDIFIED		
	820723	42200.
	820807	4370.
	820822	8150.
	820906	4120.
	820921	4170.
	821006	5350.
	821021	13000.
BEAVERSKIN		
	820723	58500.
	820807	2810.
	820822	4420.
	820906	6080.
	820921	4580.
	821006	5230.
	821021	14000.
CONTROL		
	820723	34400.
	820807	1760.
	820822	13000.
	820906	4520.
	820921	2080.
	821006	2960.
	821021	1670.
LIMED		
	820723	70200.
	820807	2510.
	820822	5830.
	820906	6640.
	820921	5780.
	821006	5560.
	821021	4370.
NUTRIENT		
	820723	49000.
	820807	2910.
	820822	5930.
	820906	8800.
	820921	5630.
	821006	4620.
	821021	10200.

Table El. B. Continued.

TREATMENT	DATE	Keratella cochlearis	Chonochilus Sp.	Polyarthra vulgaris	Ploesoma hudsoni
ACIDIFIED					
	820723	603.	0	0	100.
	820807	301.	6790.	0	100.
	820822	5630.	0	0	1100.
	820906	10600.	1500.	0	1540.
	820921	6080.	0	0	553.
	821006	5950.	2410.	0	216.
	821021	12600.	35100.	0	402.
BEAVERSKIN					
	820723	3620.	0	0	100.
	820807	1200.	0	0	0
	820822	2010.	0	0	201.
	820906	1900.	0	0	0
	820921	3030.	9650.	0	0
	821006	5430.	18100.	0	0
	821021	24700.	33200.	0	0
CONTROL					
	820723	352.	0	0	0
	820807	33.	2510.	0	83.
	820822	7650.	17200.	0	1430.
	820906	3260.	7540.	0	854.
	820921	553.	0	0	201.
	821006	6960.	6030.	0	201.
	821021	15700.	7540.	0	167.
LIMED					
	820723	1200.	7540.	0	0.
	820807	251.	4520.	0	0
	820822	805.	0	0	402.
	820906	6660.	3010.	0	503.
	820921	1860.	0	0	301.
	821006	12800.	14400.	50.	100.
	821021	12200.	3010.	201.	50.
NUTRIENT					
	820723	201.	4520.	0	0
	820807	251.	2260.	0	0
	820822	503.	3010.	0	5730.
	820906	1300.	1500.	0	14400.
	820921	3010.	3010.	201.	402.
	821006	14200.	3770.	251.	50.
	821021	19900.	70100.	855.	0

Table El. B. Continued.

TREATMENT	DATE	Trichocerca elongata	Chaoborus Sp.	Water mite	Asplanchna Sp.
ACIDIFIED					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	50.	0	0	120.
	821021	100.	0	0	50.
BEAVERSKIN					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	0	0	0	0
	820906	0	0	0	0
	820921	0	0	0	0
	821006	0	0	603.	0
	821021	0	0	0	0
CONTROL					
	820723	0	0	0	0
	820807	0	50.	0	0
	820822	0	0	0	0
	820906	50.	5.	0	251.
	820921	50.	50.	0	50.
	821006	0	0	0	284.
	821021	0	0	0	536.
LIMED					
	820723	0	0	0	0
	820807	0	0	0	0
	820822	100.	0	0	0
	820906	0	0	0	0
	820921	0	0	0	402.
	821006	0	0	0	261.
	821021	0	0	0	301.
NUTRIENT					
	820723	0	0	0	0
	820807	0	0	0	50.
	820822	0	0	0	0
	820906	0	0	0	201.
	820921	0	0	0	9050.
	821006	0	0	0	301.
	821021	0	0	0	150.

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