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THE EFFECTS OF LAKE ACIDIFICATION ON ZOOPLANKTON COMMUNITY STRUCTURE AND PHYTOPLANKTON-ZOOPLANKTON INTERACTIONS: AN EXPERIMENTAL APPROACH

by

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ABSTRACT

The effects of lake acidification on zooplankton communities and phytoplankton-zooplankton interactions were investigated by means of two field experiments in Eunice Lake, an oligotrophic, low alkalinity lake in the Coastal Range Mountains of British Columbia. Both experiments were carried out *in situ* using eight polyolefin enclosures, each holding 28,000 liters of lakewater and plankton.

From July to October 1979, acidification with H_2SO_4 and enrichment with NH_4NO_3 and H_3PO_4 were applied to enclosures both as separate treatments and in combination. Acidification alone lowered the epilimnetic pH to 5.6, but did not affect zooplankton, phytoplankton, or transparency. Enrichment alone increased chlorophyll *a* concentrations, the biomass of edible algal cells and zooplankton biomass. When acidification and enrichment were combined, biotic processsing of NH_4NO_3 lowered the pH to 5.4, causing high mortality to the zooplankton community dominant, *Daphnia rosea*.

The decline of *Daphnia* allowed chlorophyll *a* concentrations to increase 6-9 fold. It also led to major changes in the species composition, size structure and amplitude of biomass fluctuations of the zooplankton community. Phytoplankton appeared much more affected by acid-induced changes to zooplankton grazing than by direct abiotic effects of acidification.

The 1979 experiment suggested that if lakes of pH 5.0 to 5.5 are enriched, the probability of nuisance algal blooms may be increased, particularly if the herbivorous community dominants are both large and acid-sensitive.

In May 1980, unenriched enclosures were acidified over a ten day period to pH 5.5, 5.0 or 4.5, and then maintained at constant pH for seven weeks. Though the acid tolerance of D. rosea was very similar in both years' experiments, the copepod Diaptomus tyrrelli was more sensitive to acidification in 1980 than in 1979, due to differences in either life history stage, temperature or food. High rates of acidification increased toxicity near incipient lethal levels in both D. rosea and Bosmina longirostris. Acidification to pH 5.5, 5.0 and 4.5 decreased mean zooplankton biomass by 20%, 63% and 74%. However, both chlorophyll a concentrations and rotifer biomass increased with the level of acidification, due to apparent releases from grazing and competition (respectively).

Both my 1979 enclosure experiment and whole-lake manipulations performed elsewhere suggested that acidic lakes might show increased fluctuation in zooplankton biomass over circumneutral lakes. Analyses of unpublished zooplankton data from Ontario acidic lakes support this suggestion.

In general, the direction of zooplankton community change is determined by the intersection of acidification episodes with the spatial and temporal distributions of acid-sensitive species, and the competitive relationships within the community at the time of acidification. Both species distributions and

competitive relationships are sensitive to seasonal changes in temperature and nutrients, to which zooplankton life histories have been finely tuned. Long-term acidification may create "holes" in the temporal organization of zooplankton communities, with no acid-tolerant species available with the appropriate life history and temperature response physiology to fill them.

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"Sometimes the light's all shining on me,
Other times I can barely see.
Lately it occurs to me,
What a long, strange trip it's been..."

Garcia et al. 1970.

I. EXPERIMENTAL ACIDIFICATION AND FERTILIZATION OF ENCLOSED PLANKTON SYSTEMS (SUMMER 1979)

1. INTRODUCTION

1.1 Historical and Theoretical Background

Since the middle of the 19th Century, man has known that acid precipitation derived from atmospheric emissions can damage both natural systems and man-made structures (Smith 1852, cited in Cowling 1980). However, the spatial extent and severity of potential ecological impacts of acid precipitation were first recognized only in 1968. In that year, the Swedish scientist Svante Oden presented results clearly pointing to the long range transport of emissions in northern Europe and the increasing acidity of both precipitation and aquatic systems in parts of Scandinavia (Oden 1968, cited in Cowling 1980). Oden hypothesized that such chemical changes could lead to widespread losses of fisheries. Since 1968, a large number of meteorologists, soil scientists, chemists, limnologists, biologists, and foresters, primarily in Scandinavia and North America, have conducted research to identify and understand acid precipitation phenomena. Their intensive and extensive scientific investigations have been paralleled by widespread and vocal public concern about the effects of acid precipitation.

My research concerns the impacts of lake acidification on zooplankton community structure, and phytoplankton - zooplankton interactions. With the plethora of comprehensive review articles and books available on aquatic effects of acid precipitation, a detailed literature review is not necessary here (see Braekke 1976, Gorham 1976, Yan 1978, Almer et

al. 1978, Overrein et al. 1980, NRCC 1981, Haines 1981). However, in order to set a clear context for my research, I shall present a brief overview of lake acidification.

Lake acidification can be traced back to short or long range transport (i.e. 0-2000 km) of gaseous emissions of sulfur and nitrogen oxides (Likens et al. 1979). These emissions may be deposited through direct diffusion of gases to soils and vegetation, or may undergo chemical transformations to sulfate and nitrate compounds that reach the ground either in particulate or liquid phase (Yan 1978). Oxidation of sulfur and nitrogen oxides generates free hydrogen ions which can potentially acidify "sensitive" soils, streams or lakes (NRCC 1981).

The prime indicator of a lake's sensitivity to acidification is its alkalinity. Alkalinity is defined as the total quantity of base (usually in equilibrium with bicarbonate or carbonate) that can be titrated with a strong acid (Hutchinson 1957; pg. 667).

The time scale of acidification of lakes is generally not known precisely due to the absence or unreliability of historical data. Although some publications document temporal changes to the chemistry and biology (mostly fisheries) of acidifying lakes and rivers (Beamish and Harvey 1972, Dickson 1975, Watt 1979, Farmer et al. 1980, Overrein et al. 1980), the vast majority of reports rely on spatial comparisons of waters of different acidity. A wealth of such spatial evidence has now accumulated in North America and Scandinavia. Of special

interest to plankton systems is the evidence showing that relative to oligotrophic lakes of pH greater than 6.0, lakes of pH less than 5.0 consistently contain:

- fewer species and much lower abundances of fish (reviewed in Overrein et al. 1980, NRCC 1981, Haines 1981);
- fewer numbers of zooplankton species and different community dominants (Almer et al. 1974, Sprules 1975a and 1975b, Hendrey and Wright 1976, Roff and Kwiatkowski 1977, Hobaek and Raddum 1980, Nilssen 1980a, Keller 1981);
- reduced total zooplankton biomass (Yan and Strus 1980);
- different zoobenthic community structure (in terms of both taxonomic and functional groups) and reduced species diversity (Roff and Kwiatkowski 1977, Mossberg and Nyberg 1979, Okland and Okland 1980);
- different taxonomic composition and reduced species diversity of the phytoplankton community (Almer et al. 1974, Hendrey and Wright 1976, Kwiatkowski and Roff 1976, Yan and Stokes 1978, Yan 1979), but similar algal biomass (NRCC 1981, Almer et al. 1978);
- increased Secchi depth transparencies (Almer et al. 1978, NRCC 1981); and
- increased concentrations of aluminum, manganese and other metals (Almer et al. 1978, Dickson 1980).

Comparisons of key variables across a gradient of lake acidities are not a new idea (see Skadowski 1926, Manujlova 1949). While such studies do provide an understanding of the overall patterns associated with lake acidification, they do not reveal the causal pathways by which acidification alters the chemistry and biology of lakes. Nilssen (1980b) has pointed out that many surveys of aquatic organisms in acid lakes neglect to consider the roles of competition, predation and other processes in shaping the direction of ecosystem change under acidification. Too often, it is implicitly assumed that pH and other abiotic parameters affect ecosystem components independently of biotic interactions. Roff and Kwiatkowski (1977) stressed the limitations of their synoptic surveys for observing biotic interactions. In reviewing the similarities between species diversity vs. pH curves for phytoplankton and zooplankton from six Ontario lakes, the authors concluded that it was not possible to choose between reduced food availability and the direct action of pH as possible causes for the reduction in zooplankton species diversity.

Fortunately, there is some experimental work available to supplement synoptic surveys and monitoring studies. Detailed studies of the effects of neutralization and/or fertilization of several Ontario acid lakes (Dillon et al. 1979, Yan and Lafrance 1981, Yan and Dillon 1981) have revealed the relative rates of recovery of different ecosystem components, and in particular the responses of plankton systems to large increases in both pH and nutrient content. Whole lake and enclosure experiments at

the Experimental Lakes Area (Schindler 1980, Schindler et al. 1980a and 1980b, Muller 1980, Malley et al. 1982) continue to yield valuable information concerning the physical, chemical and biological processes affected by lake acidification. Finally, laboratory and field toxicity studies (Skadowski 1926, Jacenko 1928, Ivanova 1969, Kring and O'Brien 1976, Havas 1980, Malley 1980, Walton et al. 1982) are essential to separate direct toxicity from indirect biotic effects.

In spite of the above research, many critical theoretical and applied questions remain unresolved. From a theoretical perspective, we can consider acidification as a relatively rapid selection of a new and smaller set of species, and then ask: Does the simplified, acidified system still retain various organizational properties of more diverse, circumneutral systems? Which properties are dominant in determining the direction of change in phytoplankton and zooplankton communities during lake acidification?

In the following paragraphs, I list several key properties of plankton systems and discuss their relevance to lake acidification. Neither the properties listed, nor the literature cited are intended as comprehensive summaries of current knowledge of plankton systems.

1) Interactions between physical/chemical conditions and planktonic organisms. Seasonal changes in solar radiation, lake temperatures and precipitation alter both the rate of growth of phytoplankton and zooplankton, and the spatial distribution of organisms and compounds within the lake. In acid lakes, the

distribution of hydrogen ions may be strongly affected by the thermal regime. Late winter inverse temperature stratification has been observed to prevent mixing of acid meltwaters, creating acidic suface layers in acid lakes (Henriksen and Wright 1977; Hultberg 1977; Jeffries et al. 1979). Summer stratification may restrict acid loadings to the epilimnion (Schindler et al. 1980a). During periods with strong pH gradients, do surface-oriented zooplankton species suffer significantly higher mortality than deep-dwelling species? Do vertical distributions shift during such periods?

The activities of phytoplankton and bacteria can in themselves affect lake alkalinity and pH (NRCC 1981). Can these activities change the pH sufficiently to alter the toxicity of lakewater to zooplankton?

Acidification may affect water transparency by chemical means, such as coprecipitation of aluminum and humic materials (Almer et al. 1978), or colour changes in dissolved material (Schindler 1980). However, it is well known that the transparency of oligotrophic lakes is also strongly affected by changes in algal biomass or chlorophyll a concentrations (Carlson 1977, Dillon and Rigler 1975). As lakes acidify, what are the relative importances of these abiotic and biotic factors?

2) The ability of the herbivorous zooplankton community to efficiently utilize the available particle spectrum (see Gliwicz and Hilbricht-Ilkowska 1972, Lynch 1977, Gliwicz 1977, Nilssen 1978). Current studies indicate that zooplankton communities in

Ontario acid lakes contain smaller-sized community dominants and lower total zooplankton biomass than circumneutral lakes (Sprules 1975a, Yan and Strus 1980, Sprules 1981). Do these changes reduce the ability of zooplankton to efficiently graze the entire size spectrum of available algae, as suggested by Yan and Strus (1980)?

3) The ability of phytoplankton assemblages to resist grazing by herbivorous zooplankton (see Porter 1977, McCauley and Briand 1977). Phytoplankton can escape herbivore grazing by blooming prior to the emergence of zooplankton from overwintering stages, or by morphological adaptations such as large cells, long filaments, durable cell walls or gelatinous sheaths which inhibit ingestion or digestion by zooplankton (Porter 1977). Do the phytoplankton assemblages of acid lakes still maintain the temporal, morphological, and chemical features that prevent overgrazing by zooplankton?

4) The level of nutrients and primary production (see Gliwicz 1969a and 1969b, Nilssen 1978). Grahn (1974) suggested that acidification may produce a self-accelerating "oligotrophication", whereby increasing lake acidity shifted the decomposer community from bacteria to fungi, creating nutrient shortages that constrained production at all higher trophic levels. Consistent with the oligotrophication hypothesis, Kwiatkowski and Roff (1976) found that acid lakes contained lower rates of total water column primary production than circumneutral lakes. However, more recent studies have found no evidence of reduced primary production in acid lakes (Almer et

al. 1978, Dillon et al. 1979, Schindler 1980). Does acidification cause reductions in zooplankton production through lower primary production?

5) The response of plankton systems to experimental fertilization. Increases in zooplankton production follow nutrient enrichment of oligotrophic lakes, at both circumneutral (Smith 1969, Lebrasseur et al. 1972, Neill and Peacock 1980) and acidic pH levels (Yan and Lafrance 1981). However, plankton systems in lakes of pH less than 4.5 may be less able to absorb continued nutrient enrichment than are circumneutral systems, due to imbalances in plant-herbivore or predator-prey interactions (Yan and Lafrance 1981). Do the plankton systems in lakes of intermediate pH (5.0 to 6.0) respond to increased nutrients in the same manner as those of circumneutral lakes, or are symptoms of altered ecosystem functioning already apparent?

6) The role of interspecific competition in determining zooplankton community structure (see Brooks and Dodson 1965, Neill 1974 and 1975a, Hall et al. 1976, Hrbacek 1978, Lynch 1978, Kerfoot and Demott 1980, Olenick 1982). Recent studies have revealed many complexities in competition between herbivorous zooplankton, including different sensitivities of age classes to resource changes (Neill 1975a) and temporal fluctuations in both resources and competitive abilities (Lynch 1978). Since acid stress can remove herbivorous community dominants, competitive relationships may be of great importance in determining species replacements. (See Nilssen (1980a) regarding competition in Norwegian acid lakes.) Does

acidification affect the outcome of competition between herbivores?

7) The effects of vertebrate and invertebrate predators on zooplankton community structure (see Hrbacek 1962, Brooks and Dodson 1965, Dodson 1970, Lynch 1977, Northcote et al. 1978, Lynch 1979, Neill and Peacock 1980, Zaret 1980, Neill 1981a). Over the last 20 years many studies have demonstrated that predators can effect the structure of zooplankton communities in circumneutral lakes. Does the importance and form of predation change with acidification? Ericksson et al. (1980) and Henrikson et al. (1980) used results from circumneutral lakes to speculate that loss of fish populations from Swedish acid lakes may increase the abundance of invertebrate predators (particularly Chaoborus larvae), causing a shift to larger sized herbivores. Erickson and co-workers further suggest that the predator-induced size shift could decrease nutrient cycling, contributing to the oligotrophication effects hypothesized by Grahn (1974). Nilssen (1980a) proposed that the invertebrate predator Heterocope saliens played a size-structuring role in the zooplankton communities of Norwegian acid lakes. To date, only Yan and Lafrance (1981) have demonstrated experimentally that invertebrate predation can have an important impact on crustacean zooplankton in acid lakes. However, their three year study occurred in an experimentally fertilized acid lake. Are invertebrate predators as important in unenriched acid lakes?

In addition to addressing the theoretical questions posed above, research on acid-stressed plankton systems has practical benefits for managers responsible for monitoring, protecting or restoring lakes that are sensitive to acid precipitation, zooplankton community structure integrates "unseen" episodic events, providing a valuable indicator of biotic change in lakes within the pH range 4.7-5.3. Such "transition lakes" (Henriksen 1980) are characterized by periods of severe pH fluctuations with deleterious biotic effects. In transition lakes, the spring pH commonly decreases 1 to 1.5 pH units within a one to two week period and then returns to above pH 6.0 (Jeffries et al. 1979). Chemical monitoring programs can easily miss such critical, episodic, abiotic events. A knowledge of plankton community changes induced by acidification can usefully supplement chemical indicators of lake status.

In many Scandinavian and a few Ontario lakes of pH > 5.0, neutralizing agents such as calcium carbonate and calcium hydroxide have been used to counteract alkalinity losses. Successful implementation of such actions not only requires knowledge of the capacity of water and sediments to chemically neutralize added base, but also demands an understanding of the sensitivity of plankton communities to sudden pH fluctuations, and the amount of biotic alkalinity generation by algae and bacteria.

If acidification induces food shortages for zooplankton in lakes of pH 5.0-6.0, then moderate nutrient enrichment might alleviate such conditions. Very little is known about either

the availability of food for zooplankton or the chemical and biological effects of fertilization, in this intermediate pH range.

In some acid lakes of pH < 4.5, scientists have combined lake neutralization and fertilization to restore nontoxic pH levels and increase zoobenthic and zooplankton production prior to the reintroduction of fish (Dillon et al. 1979). Occasionally, these manipulations have unintentionally caused near total elimination of the zooplankton community (Dillon et al. 1979, Yan and Lafrance 1981). What factors influence the ability of plankton systems to absorb neutralization and enrichment perturbations?

1.2 Research Objectives

My overall goals in this research were to improve upon existing methods for studying the effects of lake acidification on plankton systems, to address some of the foregoing theoretical questions, and to provide useful information for lake management. To achieve these goals, I formulated the following seven research objectives:

1. to evaluate the use of limnocorrals (large plastic enclosures floating in a lake) in simulating the effects of lake acidification on plankton systems;
2. to examine the abiotic and biotic controls on alkalinity, pH and transparency under experimental acidification and fertilization.
3. to determine the effects of experimental

acidification on zooplankton populations, community structure and biomass, in the absence of predation;

4. to determine whether experimental acidification can cause starvation in crustacean zooplankton by altering the availability of edible phytoplankton;
5. if (4) is true, to assess whether nutrient enrichment during experimental acidification can alleviate such starvation effects;
6. to compare the responses of acid-stressed and circumneutral plankton systems to experimental enrichment; and
7. to assess the relative importances of acid toxicity, competition and food supply in changing the species composition of experimentally acidified zooplankton communities.

Section I of this thesis describes a field experiment I conducted from mid-July to mid-October in 1979, targeted to the above research objectives. Questions stimulated by the results of the 1979 experiment were addressed in a second field experiment that ran from mid-May to mid-July, 1980 (Section II).

2. MATERIALS AND METHODS

2.1 Study Site

Enclosure experiments were performed in 1979 in Eunice Lake, a montane lake in the University of British Columbia (U.B.C.) Research Forest, located east of Vancouver near Haney, British Columbia (Figure 1). Table 1 summarizes some of Eunice Lake's physical and chemical properties, and its zooplankton community. The geology and soils of the surrounding area are described in Efford (1967) and Feller (1975 and 1977).. Briefly, the area is underlain by massive, igneous bedrock of horneblende diorite, with generally deep, permeable podzolic tills.

Eunice Lake is an appropriate location for acidification experiments. Its alkalinity, total dissolved solids and total phosphorus levels are all low (Table 1), and typical of lakes in both the Coastal Range of British Columbia and areas of Eastern Canada that are considered sensitive to acid precipitation (NRCC 1981, Dillon et al. 1978). Exports of anions and cations in a calibrated watershed within the University of British Columbia Research Forest (Feller 1975) are strikingly similar to calibrated watersheds in the Muskoka Haliburton Region of Ontario (NRCC 1981). Feller (1975, and unpublished data) has monitored the chemistry and volume of precipitation falling in the U.B.C. Research Forest on a weekly basis during the last decade. The annual average atmospheric deposition of H^+ is 45 ± 6.6 $meq \bullet m^{-2} \bullet yr^{-1}$ (SE; n = 8), and the mean pH of precipitation events is 4.7, compared to 67 $meq \bullet m^{-2} \bullet yr^{-1}$ and pH 4.2 in the

Figure 1. Location of study site. From Neill (1978)

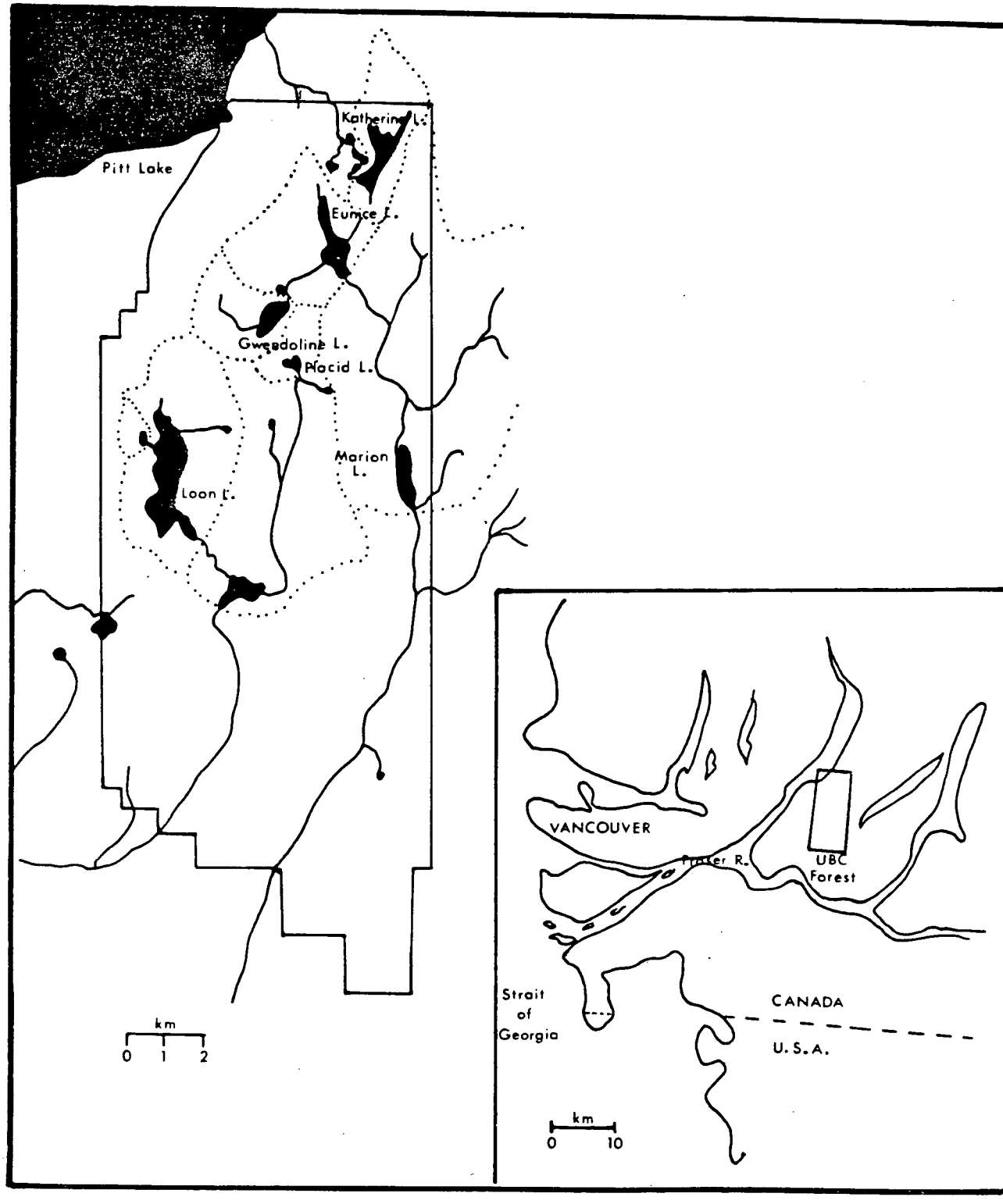

Katherine L.
Pitt Lake
Eunice L.
Gwendoline L.
Placid L.
Marion L.
Loon L.
km
0 1 2
VANCOUVER
Fraser R.
UBC Forest
Strait of Georgia
CANADA
U.S.A.
km
0 10

Table 1. Physical, chemical, and biological characteristics of Eunice Lake. Crustacean densities are maximum summer densities in limnetic zone, averaged over the entire water column. Adapted from Northcote and Clarotto (1975), Olenick (1982), and Neill (unpublished data).

Elevation (m)	480
Drainage area (ha)	191
Surface area (ha)	18.2
Maximum depth (m)	42
Mean depth (m)	15.8
Total dissolved solids ($mg \cdot l^{-1}$)	16
Mean pH	6.4
Mean alkalinity ($\mu eq \cdot l^{-1}$)*	90
Total phosphorus ($\mu g \cdot l^{-1}$)	5
Colour (Pt units)	10
Transparency (secchi disc; m)	6-10
Epilimnion depth, late summer (m)	4-6
Hypolimnion O_2 minimum (mg/l)	0.6
Crustacean density (#/100 l)	
Daphnia rosea	233
Holopedium gibberun	124
Diaphanosoma brachyurum	253
Polyphemus pediculus	13
Ceriodaphnia pulchella	rare
Bosmina longirostris	230
Diaptomus kenai	70
Diaptomus leptopus	0.5
Diaptomus tyrrelli	800
Cyclopoid copepods	27
Years zooplankton sampled 1967, 1969, 1971, 1972.	

* Total fixed end point (pH 4.5) alkalinity. Inflection point alkalinity is 70 $\mu eq \cdot l^{-1}$.

Muskoka-Haliburton Region of Ontario (NRCC 1981). Spring pH depressions are commonly observed in the Muskoka-Haliburton Area of Ontario (Jeffries et al. 1979) in lakes that are chemically quite similar to Eunice Lake. Measurements in Eunice Lake are insufficient to ascertain whether unusual alkalinity depressions occur seasonally, or whether acid deposition in the last decade has been sufficient to gradually erode lake alkalinities. The functional relationship between alkalinity and pH is called a titration curve. This nonlinear curve steepens considerably in the pH range of 5.0 to 6.0. Eunice Lake's mean pH has not changed since 1970 (Northcote and Clarotto 1975), which is expected since current pH and alkalinity levels are above the steep part of the lakewater's titration curve.

The Eunice Lake zooplankton community contains several species commonly found in Western North America (Carl 1940; Edmundson 1959; Anderson 1974), notably within high elevation, low alkalinity water bodies that are relatively sensitive to lake acidification. Since some of these lakes are experiencing alkalinity declines attributable to acid precipitation (Lewis 1982), an understanding of acidification effects on Eunice Lake zooplankton is of immediate and widespread relevance.

2.2 Experimental Methods

In late June 1979, eight limnocorrals were placed in Eunice Lake. These enclosures were used for experimental acidification and fertilization. This section describes all experimental and analytical methods used; the specific hypotheses tested are described in Section 2.3.

Limnocorral design and setup was very similar to that described by Neill (1978). The enclosures were constructed of translucent polyolefin fabric suspended from wood and polystyrene floats (Figure 2), and measured 2 m in diameter by 9 m deep. The top 66 cm of the cylinders were coated with a second layer of polyolefin, coloured orange to prevent ultraviolet degradation of the material; no degradation was apparent two years later. The bottom of the enclosures were sealed and not in contact with lake sediments, thereby eliminating a potential source of acid neutralizing bases, potentially toxic metals, zooplankton emerging from overwintering eggs, and phytoplankton developing from resting stages. This aspect of the design increased experimental control and physical stability of the enclosures, at the expense of some loss of chemical and biological realism.

After being anchored near the western shore of Eunice Lake (Figure 3), the enclosures were filled with lakewater from several depths, filtered through a 54 μm net to remove crustacean zooplankton, nauplii and most rotifers but permit grazable seston to pass. Zooplankton were collected with townets from several lake depths and placed in cool storage

Figure 2. Plan view of limnocorral design .

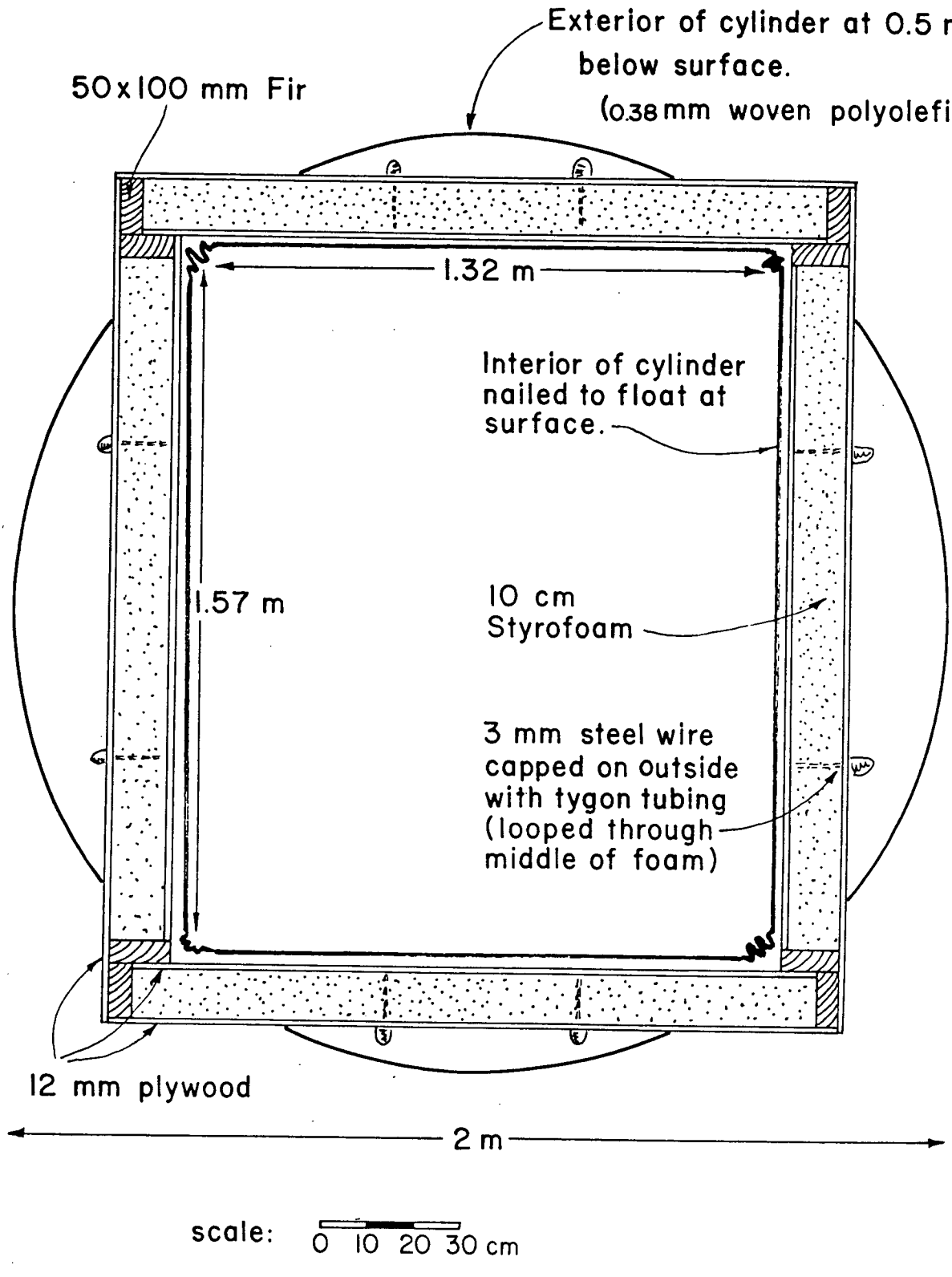
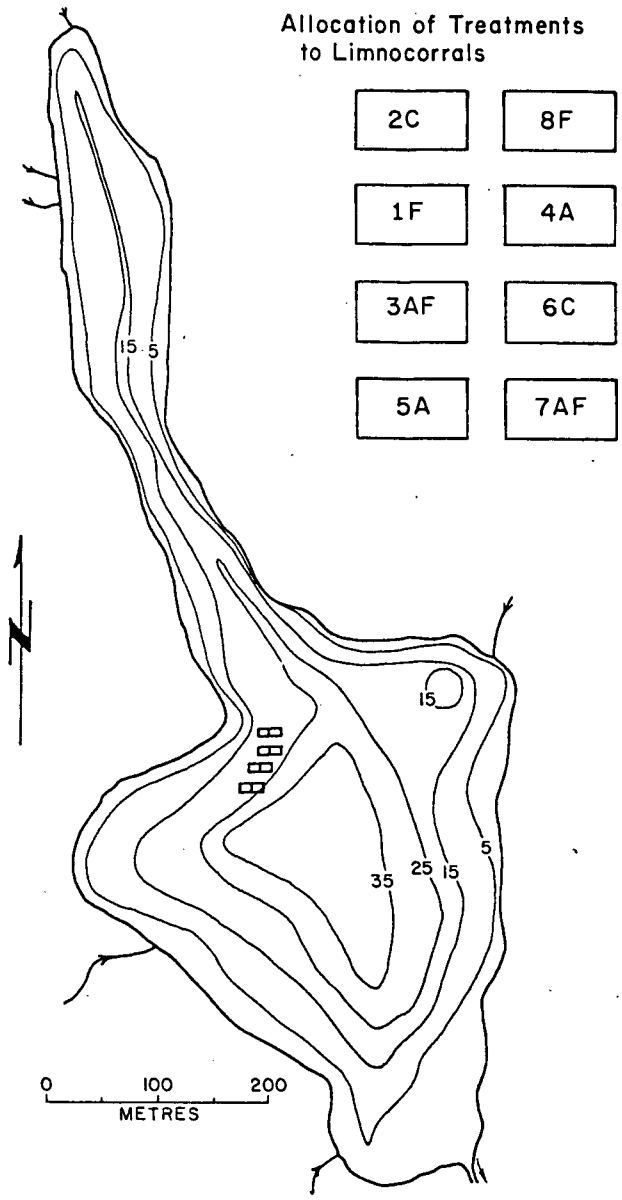

Exterior of cylinder at 0.5 m
below surface.
(0.38 mm woven polyolefin)
50 x 100 mm Fir
1.32 m
Interior of cylinder
nailed to float at
surface.
1.57 m
10 cm
Styrofoam
3 mm steel wire
capped on outside
with tygon tubing
(looped through
middle of foam)
12 mm plywood
2 m
scale:
0 10 20 30 cm

Figure 3. Location of limnocorrals in Eunice Lake. Depth contours from Hume (1978).


Allocation of Treatments
to Limnocorrals
2C
8F
1F
4A
3AF
6C
5A
7AF
15
5
15
35
25
15
5
0
100
200
METRES

containers along the shore. Lake densities and species composition of zooplankton were estimated from a pooled sample of 10 replicate hauls of a 54 μm Wisconsin net through the upper 10 m of water near the lake's deepest point. After making additions to the storage containers to remove biases in species composition, sufficient volumes of "plankton soup" were added from the storage containers to yield lake densities of zooplankton in the enclosures (21 animals•L^{-1}). In estimating lake densities, I assumed the Wisconsin net to be 35% efficient (W.E. Neill pers. comm.). Eunice Lake cutthroat trout were excluded from the cylinders.

Two replicates of three experimental treatments were randomly assigned to six of the enclosures; the other 2 served as controls (Table 2). Experimental acidifications with reagent-grade H_2SO_4 were performed on six occasions in treatments A (acidification) and AF (acidification plus fertilization), by adding acid to the surface and mixing with an oar. In total, approximately 62 μeq•L^{-1} of H^+ were added to the epilimnion of each acidified cylinder. Treatments F and AF received 10 μg•L^{-1} of P (as dissolved reagent grade H_3PO_4) and 150 μg•L^{-1} of N (as dissolved reagent grade NH_4NO_3) on four occasions, providing an N:P molecular ratio of approximately 33:1. (These concentrations are based on a 4 m deep epilimnion.)

I sampled water, phytoplankton, chlorophyll and zooplankton by means of a 9 m long, 2.5 cm diameter hose, connected to a battery operated bilge pump that delivered 34 L•min^{-1}. Both

Table 2. Experimental Treatments.

Treatment		Cylinder Numbers		Total Quantities of Chemicals Added to Epilimnion (top 4 m)
C:	control	2C	6C	no chemical additions
F:	fertilization	1F	8F	40 µg/L P and 600 µg/L N*
A:	acidification	4A	5A	62 µeq/L of H+**
AF:	acidification and fertilization	3AF	7AF	treatments A and F combined

* divided equally over four additions.

** divided unequally over six additions of sulfuric acid.

Eunice Lake and the enclosures were sampled weekly, and all samples were taken prior to any scheduled chemical additions.

2.2.1 Physical and Chemical measurements

Chemical samples (300 ml) were taken weekly, from depths of 1, 3, 5, and 7 m. I performed pH measurements and fixed end point alkalinity titrations (to pH 4.5 with 0.01 N sulfuric acid) within 4 to 24 hours of sampling, using a buffer-calibrated Fisher Accumet pH meter or Fisher Automatic Titrator. The two instruments did not differ in their measured alkalinity, and yielded standard errors within 1.5% of the mean. All measurements were performed on stirred 100 ml subsamples equilibrated to room temperature. In May 1980, Gran titrations (Stumm and Morgan 1970) were performed on 3 lakewater samples to determine the inflection point or bicarbonate alkalinity (Table 1).

To examine treatment x time x depth variations in both hydrogen ion concentrations and alkalinities, three-way analyses of variance (ANOVA) were performed on untransformed data using the program UBC GENLIN (Greig and Berring 1977). Mean pH was determined from mean [H+]. Since the standard errors of pH means are not symmetric, I computed a "mean standard error" to simplify presentation of results:

$$pSE = \frac{[pH(high) - pH(low)]}{2} \qquad (1)$$

where pSE = mean standard error of pH;

pH(high) = -log ([H+] - SE);
pH(low) = -log ([H+] + SE);
[H+] = mean hydrogen ion concentration; and
SE = standard error of [H+].

Secchi disc depths were measured weekly, to the nearest 0.25 m, and compared to chlorophyll concentrations using linear regression analysis. Water temperatures were recorded on each sampling date by pumping water from 1 m depth intervals over a thermometer accurate to ± 0.5° C. Depth-time isoclines of temperature, pH and alkalinity were produced using the subroutine CNTOUR, developed at the University of Alberta Computing Centre and adapted by Susan Mair of the UBC Computing Centre and myself to run at UBC.

2.2.2 Phytoplankton

(i) Methods Used

For phytoplankton analysis, a 300 ml water sample was obtained from a mixture containing 1000 ml of water pumped from each of four depths (1, 3, 5, and 7 m), and preserved in Lugol's solution. A 100 ml subsample was allowed to settle in a graduated cylinder for 24-36 h. The top 75 ml of the supernatant was then decanted and the remaining 25 ml left to settle in a counting chamber for a further 24 h. Using an inverted, phase-contrast microscope at 400X magnification, two or more microscope fields were examined until at least 200 cells greater than 2 μm had been counted. All cells were classified according to their shape (see Appendix A for categories), size

(two measurements for each shape) and type (single, colony or filamentous). As well as being measured, cells and colonies were classified according to their maximum dimension into one of seven size classes (< 2, 2-5, 5-9, 9-13, 13-18, 18-30 and > 30 μm) while filaments were assigned to a separate class. Where possible, taxonomic identification to genus was performed for the most common forms, using Prescott (1978), Smith (1951) and Stein (1975). A FORTRAN computer program (Appendix A) was used to compute total cell, colony, and filament volumes (and biomass) by size class, taxon and phylum. In converting algal volume to biomass, I assumed cells had a specific gravity of 1.0. The volume of Dinobryon colonies was computed as the sum of separate lorica volumes.

The proportion of total algal volume identified taxonomically varied with the treatment. In the lake, control and A cylinder samples, the percent of phytoplankton volume identified taxonomically averaged 87% and was never less than 70%. However, in enclosures 1F, 8F, and 3AF, an average of only 59.0% of the phytoplankton volume was identified. The observed proportion of phytoplankton volume in any phylum should therefore be regarded only as a rough minimum estimate of the true fraction.

For chlorophyll analyses, one liter water samples (containing 250 ml from each of 1, 3, 5 and 7 m depths) were gently filtered through glass fiber filters, using a field hand pump. The filters were immediately frozen and stored in the dark to be later analyzed on a Turner Model III Fluorometer for

chlorophyll *a* and phaeophytin *a* according to Strickland and Parsons (1968). The fluorometer was calibrated using a spectrophotometer and a 12-day old (early stationary phase) culture of the dinoflagellate *Prorocentrum minimum* Schiller, obtained from Northeast Pacific Culture Collection (NEPCC) and grown in artificial seawater medium.

Since phaeophytin *a* represents degraded or digested chlorophyll *a*, I used live chlorophyll *a* as an index of available food for zooplankton. To detect gross changes in the food quality and physiological state of the phytoplankton, I computed the ratios of live chlorophyll *a* concentrations to total algal biomass, and the ratios of live chlorophyll *a* to phaeophytin *a*.

Periphyton (on the sides and bottom of the enclosures) were not quantitatively sampled. However, visual observation confirmed that such algae were sparse in unfertilized cylinders, but significant in the fertilized ones.

Algal size class volumes, chlorophyll *a* concentrations and phaeophytin *a* concentrations were log-transformed and subjected to two way analyses of variance (treatment x time). Significance levels therefore refer to differences in geometric means. Mean values quoted are arithmetric means unless otherwise stated.

(ii) Precision of Algal Cell Volume and Chlorophyll Determinations

I used both chlorophyll a concentrations and total cell volume as estimators of algal biomass. Chlorophyll a concentrations reflect not only the biomass of algae in the water, but also the cell chlorophyll content, which is known to vary with light levels, nutrient supply, algal growth phase, species composition and pH (Daley and Brown 1973, Nicholls and Dillon 1978). Although total algal cell volumes are therefore generally considered more reliable measures of algal biomass than chlorophyll a concentrations, this is only assured if adequate numbers of cells are counted under the microscope to reduce subsampling error to a reasonable level. Unfortunately, the criterion I used to decide on the number of microscopic fields to be examined (sufficient to yield more than 200 cells in all size categories) resulted in very low numbers of cells and low precision in most size categories, as shown in columns 3 and 4 of Table 3. Comparing columns 5 with 6, and columns 7 and 8 with 9 and 10, illustrates that the observed mean 95% confidence limits on algal volumes in each size class are well predicted (for six of eight size classes) solely by Poisson frequency distribution confidence limits on the mean numbers of counted cells. That is, the observed within treatment variation in algal volumes appeared largely due to counting (subsampling) error, rather than real differences between replicates. The only exceptions to this pattern were the 2-5 μm and filament size classes, which showed greater than predicted within

Table 3. Variability in phytoplankton volume estimates due to low numbers of counted cells.

Size Class of Algae (µm)	(1) Mean Cell Volume ± 2 (SE) (μm^3)	(2) Total # Cells Measured in All Samples	(3) Mean # "Cells" Counted/ Sample[2]	(4) (5) Predicted 95% C.I.* on # Cells/Sample[3] As # Cells	As % of Mean # Cells/S.	(6) Observed 95% C.I. on Within Treatment Mean Algal Volume[4]	(7) (8) Predicted 95% C.I. on Total Counted Vol. In (μm^3)[5]	% of Total	(9) (10) Observed 95% C.I. on Total Counted Vol. In (μm^3)[6]	% of Total
< 2	0.268[1]	0	15	± 8.2	± 55%	± 57%	± 220	0.9%	± 263	± 1.0%
2-5	6.4± 1.3	21605	202	±27.9	± 14%	± 53%	± 179	0.7%	± 942	± 3.7%
5-9	150± 56	776	7.2	± 5.8	± 80%	± 94%	± 870	3.4%	± 892	± 3.5%
9-13	479± 210	277	2.6	± 3.8	±146%	± 128%	± 1820	7.1%	± 1293	± 5.0%
13-18	532± 192	2211	20.7	± 9.4	± 45%	± 67%	± 5001	19.6%	± 5162	±20.0%
18-30	2979±1226	234	2.2	± 3.6	±163%	± 146%	±10724	42.0%	±12707	±49.3%
> 30	1315± 315	504	4.7	± 5.0	±106%	± 101%	± 6575	25.8%	± 3936	±15.3%
Fil.	10± 6	3656	34.2	±12	± 35%	± 124%	± 118	0.4%	± 565	± 2.2%
Total		29263	288.6			± 55%	(25507)	100%	(25760)[7]	100%

[1] Volume assumed constant at 26.8 μm^3/100 cells in < 2 µm category. Cells in < 2 µm category counted in batches of 100. Mean # cells/sample is therefore approximately 1500, but items counted = 15.

[2] Based on 107 samples. Colonies are regarded as single "cells", except for Dinobryon sp. (See Methods.)

[3] Based on Poisson distribution (Ricker 1937); calculated as 0.5*(upper limit-lower limit).

[4] Computed as mean of $1.96(SE)/\bar{X}$ x 100, calculated for 47 cases (4 treatments x 12 dates - 1), where $\bar{X}$ = mean algal volume for date and treatment.

[5] Computed from (C.I. on # cells/sample) * (mean cell volume) (i.e. ignoring cell size variation).

[6] Mean C.I. computed from confidence intervals for each date and treatment's mean volumes.

[7] Actual C.I. for total algal volume is less than sum of C.I.'s for each size class, since "errors" cancel. Observed C.I. was ± 17911 μm^3 or 70% of sum of C.I.'s.

* Confidence interval

treatment variation, suggesting real differences between replicates in the volumes of these size classes.

Subsampling errors were volumetrically most significant in the 13-18, 18-30, and > 30 μm size classes, since small errors in estimating the numbers of large cells or colonies causes considerable errors in the estimated total algal volume. A single large colony of Chrysocapsa sp. for example, made up 50% of the counted phytoplankton volume in cylinder 3AF on July 26.

The observed mean 95% confidence limits on within-treatment total algal volume (expressed as a percentage of the mean) were ± 55%. This is much less than the mean of the confidence intervals for each size class, presumably since underestimates in some size classes cancelled overestimates in other size classes. The equivalently-calculated within-treatment 95% confidence interval for chlorophyll a plus phaeophytin a was ± 23%. In view of the subsampling errors on algal volume estimates, and the higher precision of chlorophyll a measurements, I relied primarily on the latter for examining changes over time. However, between treatment comparisons of arithmetic or geometric mean algal cell volumes averaged over 12 sampling dates still served to indicate major treatment effects, since the estimated grand means had confidence limits of approximately ± 16% (55 x sqrt(1/12)). Since the imprecision of my algal biomass estimates affected the ratios of chlorophyll to algal biomass, I discuss primarily the overall mean ratios, rather than the time series.

2.2.3 Zooplankton

Depth-integrated zooplankton samples were taken by pumping for 30 sec from eight depths: 0.5 m; 1.5 m; 2.5 m; 3.5 m; 4.5 m; 5.5 m; 6.5 m; and 7.5 m, with the pump outflow passing through a 54 μm mesh net. Depth-stratified samples (four 2 m strata) were taken instead of integrated samples on August 1 and September 6, 1979. The hose and bilge pump method of zooplankton sampling has been previously shown to produce excellent replicability with minimal sampling bias (Peacock 1981, Neill 1981a). Samples were preserved in a sucrose-formaldehyde mixture (Haney and Hall 1975), and enumerated by species, sex, stage of maturity, reproductive condition, and number of eggs, using Edmondson (1959) and Pennak (1978) for taxonomic identification. Using the subsampler described in Northcote and Clarotto (1975), successive sixths of the samples were enumerated until 200 individuals of each species were encountered. Loose copepod and cladoceran eggs were assigned proportionately to species based on the abundance of attached eggs.

I tested the overall precision of the zooplankton sampling and counting method by sampling cylinder 8F twice on October 5, 1979 and processing the two samples through two different field assistants (Table 4). Coefficients of variation in Table 4 therefore reflect variability due to four sources: inconsistency in field sampling technique; zooplankton patchiness in space and time; errors in subsampling; and identifier bias and error. Compared to similar studies of sampling error (Wiebe et al. 1968, Gibson and Grice 1977), the coefficients of variation

Table 4. Test of precision of zooplankton sampling method. Cylinder 8F was sampled twice on October 5, 1979 and the two samples counted by different individuals.

Species	No. Animals in Sample*		$\bar{X}$	S	$100 \cdot S/\bar{X}$** (%)
	Sample A	Sample B			
D. kenai	24	18	21	4.2	20.2
D. tyrrelli	164	146	155	12.7	8.2
Daphnia rosea	213	218	216	3.5	1.6
Bosmina longirostris	3072	2754	2913	224.9	7.7
Diaphanosoma brachyunum	18	37	28	13.4	48.9
Chydorus sphaericus	1470	1221	1346	55.7	13.1
Acroperus harpae	27	25	26	1.1	5.4
Loose Cladoceran eggs	38	16	27	15.6	57.6
Loose Copepod eggs	137	153	145	11.3	7.8

* 134 liters

** Coefficient of variation.

in Table 4 are relatively low.

Using 25X (and occasionally 50X) magnification, 20 adults and 20 juveniles of each species were measured from each treatment on four occasions: July 26, August 9, August 23, and September 13. Cladoceran measurements extended from the anterior tip of the carapace to its posterior, excluding all accessory structures such as helmets or caudal spines. Copepods were measured from the anterior tip of the cephalothorax to the posterior end of the urosome, not including setae.

These lengths were converted to juvenile and adult biomass estimates using length-weight regressions from Peacock (unpublished data), Dumont et al. 1975 and Bottrell et al. 1976; see Appendix B. The overall mean and variance of each species' lengths were computed for specific dates based on the proportions of juveniles and adults present. Separate one-way ANOVAs and Tukey multiple range tests were performed on untransformed zooplankton total biomasses for each date. Numbers of animals, total numbers of eggs and mean brood sizes were log-transformed and analyzed with 2-way ANOVA (treatment X time). Note that

$$\log(\text{brood size}) = \log(\text{eggs}) - \log(\text{ovigerous females}) \quad (2)$$

Therefore, if both log(eggs) and log(ovigerous females) are normally distributed, log(brood size) will also be normally distributed.

To compare the transient behaviour of acidified and circumneutral systems exposed to identical fertilizer additions, I plotted the simultaneous changes in total zooplankton biomass and live chlorophyll as phase plane trajectories. Zooplankton filtering rates were estimated by multiplying mean species densities by published filtering rates measured at similar temperatures but circumneutral pH (Haney 1973, Buckingham 1978).

2.2.4 Statistical Methods

> "As far as the laws of mathematics refer to reality, they are not certain; and as far as they are certain, they do not refer to reality."
>
> Einstein

Univariate analyses of variance (ANOVA) were used in three different ways in this study:

(i) one-way treatment comparisons of 5 treatments on specific dates, with Tukey multiple range tests;

(ii) two-way (treatment x time) comparisons of two treatments over all sampling dates; and

(iii) three-way (treatment x time x depth) comparisons of two treatments over all sampling dates.

One-way ANOVAs (across all treatments on a single sampling date) used the Tukey multiple range test to compare all pairs of treatment means. The Tukey test is a relatively conservative

test which accounts for the overall range in treatment means in assessing the significance of individual paired comparisons (Li 1964). The advantage of treatment x time comparisons is that overall treatment effects can be isolated from temporal fluctuations due to seasonal forces. Green and Hobson (1970) used 2-way ANOVAs in this manner to analyze the spatial and temporal structure of an intertidal community. The most important assumptions of ANOVA are that the within group errors are independent (of each other and of the group mean), normally distributed and homogeneous among groups (Glass et al. 1972, Green 1979). In all applications of ANOVA to the enclosures, the "groups" consisted of two limnocorrals exposed to the same treatment, and measured on a single day. Independence of within group errors from each other was assured since treatments were randomly assigned to enclosures, and enclosures receiving the same treatment could in no way physically affect one another. (Note that the independence assumption is violated if one included within the same group two measurements taken from the same enclosure on successive sampling dates).

Independence of within group errors from within group means was tested prior to each ANOVA by examining the linear regression (Taylor 1961, Green 1979):

$$\log S^2 = \log a + b \log X \qquad (3)$$

where S^2 = within group sample variance;

X = within group sample mean;

$\log a$ = regression intercept, and

b = regression slope.

When b was close to 0, no transformation was performed. In most cases, b was within the range 1.75 to 2, and the data therefore subjected to the logarithmic transformation Z = log (X), or if the data included zero values, Z = log(X+1) (Green 1979). This transformation also served to make the within group errors more normally distributed, although I did not test for normality statistically. Note that statistical tests on log-transformed data assess the significance of differences between geometric, not arithmetic means.

Homogeneity of residual variances was tested with Bartlett's test, using the computer program UBC GENLIN (Greig and Bjerring 1977); heterogeneous variances are noted in the Results section. Glass et al. (1972) showed that nonnormality and heterogeneity of variances affect the significance level of two-tailed statistical tests only slightly, provided that the study has a balanced design. All statistical tests between enclosures were balanced (2 replicates/group). ANOVAs between the control enclosures and the lake were unbalanced, since only one sample was obtained from Eunice Lake. These tests therefore examined the differences between the lake and the controls relative to the variation within the two control cylinders.

2.3 Experimental Design

The four treatments applied to the enclosures were intended to test a set of hypotheses concerning the effects of acidification, fertilization, and enclosure (Table 5). Although most of these hypotheses were presented in my research proposal (Marmorek 1979), other hypotheses evolved during the course of my field work and data analysis. I attempted to falsify each hypothesis by comparing key indicator variables, both between treatments and over time (Table 6).

The hypotheses listed in Table 5 require some elaboration. With respect to hypotheses 2(i) and 5(i), I was particularly interested in whether changes in zooplankton populations were primarily due to direct toxicity, changes in competition, altered food supply or a combination of these factors. Similarly, I was interested in whether phytoplankton community shifts were primarily due to abiotic conditions, or to changes in herbivore filtering (following from hypotheses 2(ii) and 5(ii)). In the absence of primary productivity and zooplankton grazing measurements, and without performing laboratory toxicity tests, it is not always possible to choose between these alternate explanations. However, I used careful examination of the variation in several indicators (both over time and between treatments) to suggest which mechanisms were more probable.

Before testing whether enrichment alleviates acid-induced shortages of phytoplankton food for zooplankton (hypothesis 4(ii)) it is necessary to show that:

1) such food shortages do occur with acidification

Table 5. Hypotheses tested by the 1979 experiment.

Null Hypothesis	Test
1. Enclosure of plankton systems and removal of cutthroat trout predation does not affect light transmission, pH, alkalinity, phytoplankton, or zooplankton.	Compare all indicators in control cylinders (C) and Eunice Lake (LK).
2. Gradual, experimental acidification of oligotrophic waters to pH 5.0:	
(i) does not affect zooplankton populations or community biomass;	Compare zooplankton performance in A and C relative to both pH distribution over depth and time, and phytoplankton biomass and size composition.
(ii) does not affect phytoplankton community biomass or size composition;	Compare phytoplankton indicators in A and C relative to both pH over time, and estimates of zooplankton grazing pressure.
(iii) does not affect the abiotic component of light extinction;	Compare secchi depth-chlorophyll *a* regression lines in A and C.
(iv) is not affected by biotic generation or consumption of alkalinity; and	Compare theoretical and observed alkalinity decreases in A.
(v) realistically simulates lake acidification.	Compare changes in key indicators with observations from multiple lake surveys and whole lake experiments.

Table 5 Continued ...

Null Hypothesis	Test
3. Moderate nutrient enrichment of circumneutral waters:	
(i) does not affect alkalinity, pH or transparency;	Compare alkalinity, pH and transparency in F and C.
(ii) does not affect zooplankton populations or community biomass; and	Compare indicators of zooplankton performance in F and C.
(iii) does not change the availability of phytoplankton food for zooplankton.	Compare phytoplankton indicators in F and C.
4. Moderate nutrient enrichment during experimental acidification to pH 5.0:	
(i) does not alter alkalinity, pH or transparency from the levels observed by acidification alone; and	Compare alkalinity, pH and transparency in AF and A.
(ii) does not alleviate acid-induced shortages of phytoplankton food for zooplankton.	Compare indicators of zooplankton performance in AF and A.
5. Gradual, experimental acidification of moderately enriched waters:	
(i) (ii) same as 2(i), 2(ii)	Perform comparisons listed for 2(i) and 2(ii), but for treatments F and AF.
(iii) does not alter the ability of plankton systems to absorb enrichment perturbations; and	Compare joint fluctuations of phytoplankton and zooplankton in F and AF.
(iv) does not alter transparency from the levels observed in non-acidified, moderately enriched waters.	Compare transparency in AF and F.

Table 6. Indicator variables monitored in the 1979 study, and their justification.

Variables	Monitored to Indicate
Physico-Chemical Conditions:	
• temperature	- thermocline; metabolic rates
• pH	- abiotic stress
• alkalinity	- degree of acification (acid balance·
	- biotic effects on alkalinity
• secchi depth	- abiotic and biotic effects on transparency
Phytoplankton:	
• chlorophyll *a*	- algal biomass
	- biotic effects on transparency
• pheophytin *a*	- chlorophyll degradation, including digestion by zooplankton
• algal cell counts	- size composition and edibility of phytoplankton
	- taxonomic composition
	- total algal biomass
Zooplankton:	
• species densities by age class	- overall effects of life histories and perturbations
• lengths	- growth effects (copepods)
	- age structure (cladocerans)
	- biomass

Table 6. Continued ...

Variables	Monitored to Indicate
Zooplankton (continued):	
• mean brood size, percent of ovigerous females, total egg production	- food availability - reproductive status of population - birth rates
• vertical distribution	- actual exposure to abiotic stress - overlap in species' spatial distribution

alone;

2) zooplankton in the A and AF enclosures are exposed to the same degree of acid stress (hypothesis 4(i)).

3. RESULTS

3.1 Physical and Chemical Conditions

3.1.1 Precipitation and Temperature

Daily precipitation during the experiment is shown in Figure 4. Since the experimental enclosures were isolated from watershed flushing and materials export, precipitation could have increased differences between the lake and the enclosures. During the first month of the experiment however, the complete absence of precipitation (Figure 4) reduced flushing and materials export to a minimum. This dry period, which resulted in a high forest fire risk on land and likely exacerbated nutrient shortages in the lake, was ended by 24 mm of rainfall during August 14-22, followed by 126.7 mm of rainfall during September 1 to 8. The last major storm events of the experiment occurred September 26-29, contributing 32.8 mm of rain.

Daily air temperature minima and maxima are shown in Figure 5, and lake water temperatures by depth-time isotherms in Figure 6. The dashed lines on Figure 6 outline the upper and lower boundaries of the thermocline, and were determined by estimating the plane of maximum decrease in temperature (Hutchinson 1957; pg. 428) from vertical depth profiles. Graphical determination of metalimnion thickness (Wetzel 1975; pg. 70) showed the upper metalimnetic boundary to be always within 0.5 m of the start of the thermocline, due to the sharp decrease in temperature there. The temperature change below the

Figure 4. Daily precipitation (1979) .

Figure 5. Daily variation in air temperature (1979) .

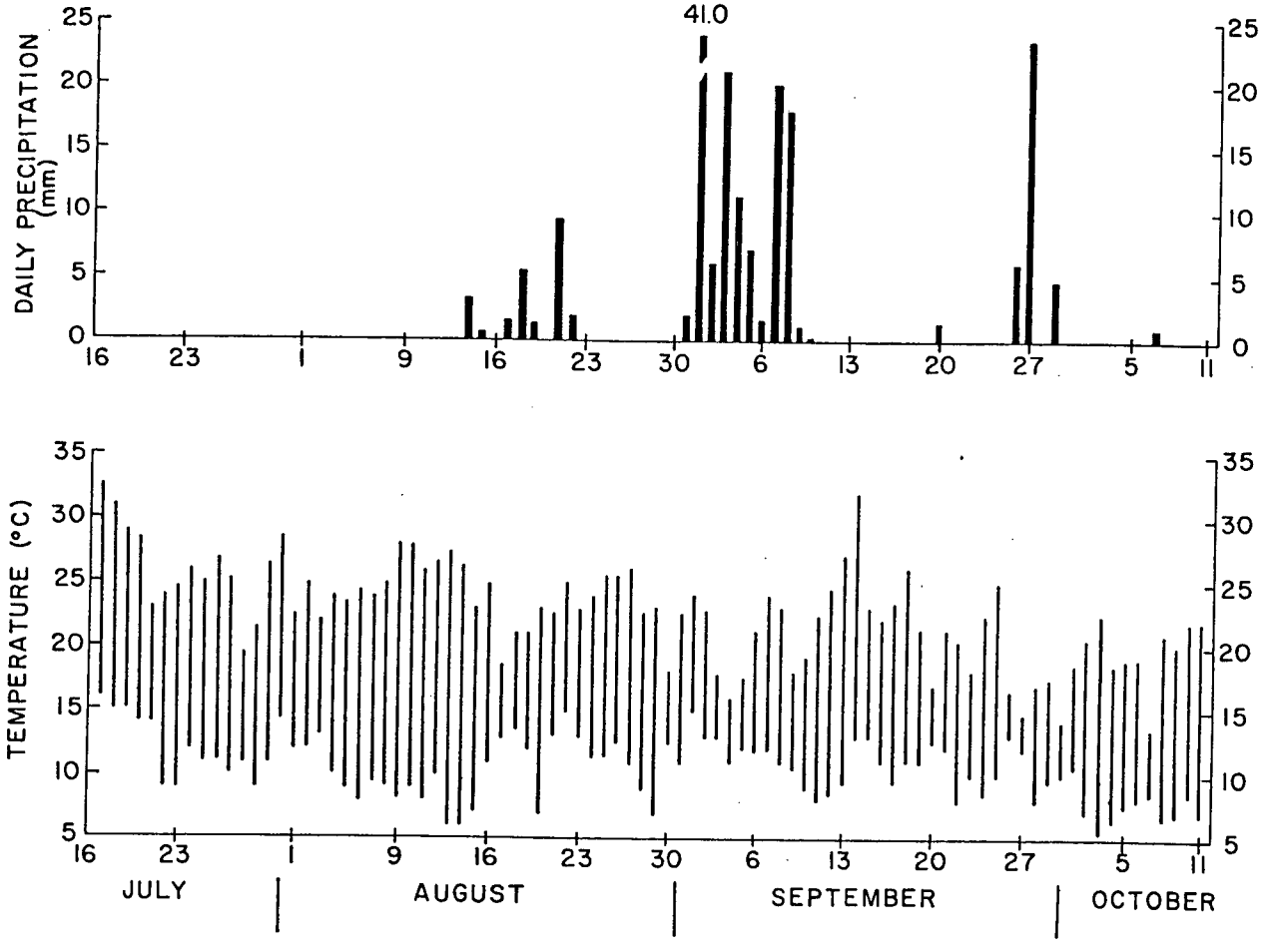
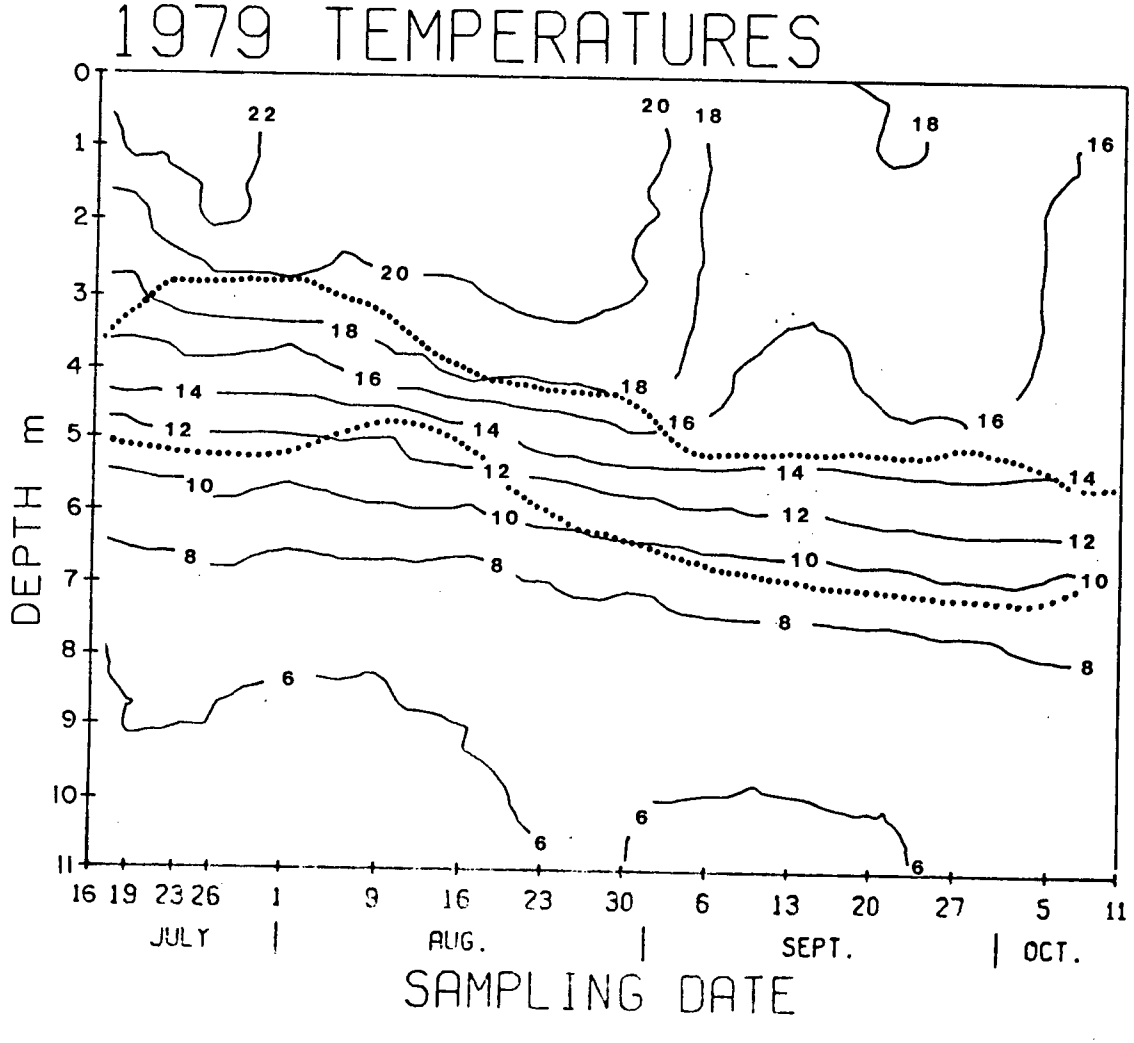

DAILY PRECIPITATION (mm)
41.0
25
20
15
10
5
0
16
23
1
9
16
23
30
6
13
20
27
5
11
TEMPERATURE (°C)
35
30
25
20
15
10
5
JULY
AUGUST
SEPTEMBER
OCTOBER

Figure 6. Eunice Lake water temperatures during 1979 . Dashed lines indicate upper and lower limits of metalimnion.


1979 TEMPERATURES
DEPTH m
0
1
2
3
4
5
6
7
8
9
10
11
22
20
18
18
16
20
18
16
18
16
16
14
12
14
14
14
12
12
12
10
10
10
10
8
8
8
8
6
6
6
6
16 19 23 26 1 9 16 23 30 6 13 20 27 5 11
JULY
AUG.
SEPT.
OCT.
SAMPLING DATE

thermocline was more gradual.

Figure 6 illustrates the gradual transfer of heat from the lake surface to lower depths, with the isotherms between 8°C and 14°C sinking at rates of 0.4-0.7 m/month over the course of the experiment. More significant however, are the changes in the strength and position of the thermocline. During the last two weeks of July, warm daytime temperatures heated the upper 2 m to above 22°C, and the thermocline remained at the 3 to 5 m depth interval. The stratification sharpened considerably during the first two weeks of August, with lower nighttime temperatures (Figure 5) likely responsible for cooling the upper 2 m. A very strong thermocline between 4 and 5 m had formed by the second week of August, but then became more gradual, stretching between 4 and 6 m by August 30. The series of major storms in the first week of September (Figure 4) cooled and mixed the upper 4 m, shifting the thermocline down to the 5-7 m stratum for the remainder of the experiment.

Following the storms in the first week of September, the thermal structure remained essentially stable until the end of the month, when another major storm cooled and mixed the top 4 m to a homogeneous temperature of 16°C.

3.1.2 Hydrogen Ion Concentration and Alkalinity

The pH and alkalinity over time and depth are illustrated in Figures 7 and 8 respectively, with mean values for each treatment in Table 7. Mean differences in composite alkalinity (1-7 m) between treatments are shown for each sample date in

Table 8. Appendix C details the results of three-way analyses of variance (treatment, time and depth) of cylinder alkalinites and H^+ concentrations; only a summary of these analyses is presented here.

(i) Enclosure Effects

Did enclosure affect alkalinity and pH levels? The enclosure of water significantly reduced mean epilimnetic (1-3 m) alkalinities (Table 7 and Appendix C). Epilimnetic alkalinities in Eunice Lake and the controls differed by more than 25 $\mu eq \bullet L^{-1}$ on August 1 and August 30 (Figure 8). Both the lake and the control cylinders showed a net decline in epilimnion alkalinity over August, though the lake showed greater temporal fluctuations (Figure 8 and Appendix C). Epilimnetic pH levels were lower in the controls than in Eunice Lake (Figure 7 and Table 7) but differences were small relative to the alkalinity gap. This is because water has a high buffering capacity at pH values close to 6.4, the approximate equivalence point of bicarbonate and carbonic acid (Stumm and Morgan 1970).

At 5-7 m, control cylinder mean alkalinities and pH levels were significantly higher than Eunice Lake measurements, and differed in depth gradients as well (Appendix C).

In summary, the controls showed smaller vertical gradients and temporal fluctuations in alkalinity than did Eunice Lake. Light limitation from limnocorral shading likely contributed to these enclosure effects (discussed in Section 4.1).

Figure 7. 1979 pH levels by depth and time, and timing of chemical additions. Values at 3 m (not shown for clarity) were always within 0.05 units of pH at 1 m. Bars show μeq of H^+ added to total cylinder volume from sulfuric acid; dots indicate timing of nutrient additions. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

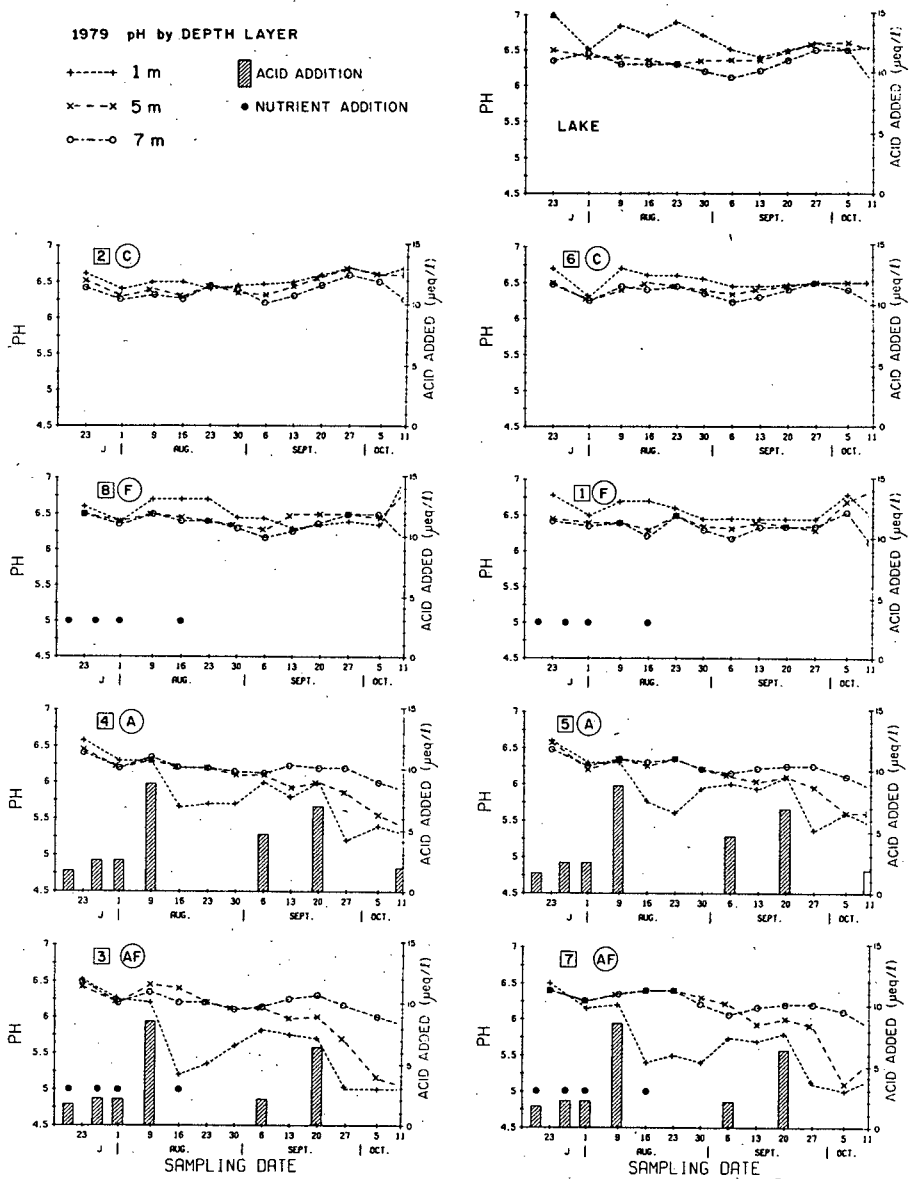

1979 pH by DEPTH LAYER
1 m
5 m
7 m
ACID ADDITION
NUTRIENT ADDITION
LAKE
2 C
6 C
8 F
1 F
4 A
5 A
3 AF
7 AF
PH
ACID ADDED (μeq/l)
J
AUG.
SEPT.
OCT.
SAMPLING DATE

Figure 8. Depth-time diagrams of alkalinity isopleths during 1979 . Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

1979 ALKALINITY ($\mu eq/\ell$)
BY DEPTH AND TIME

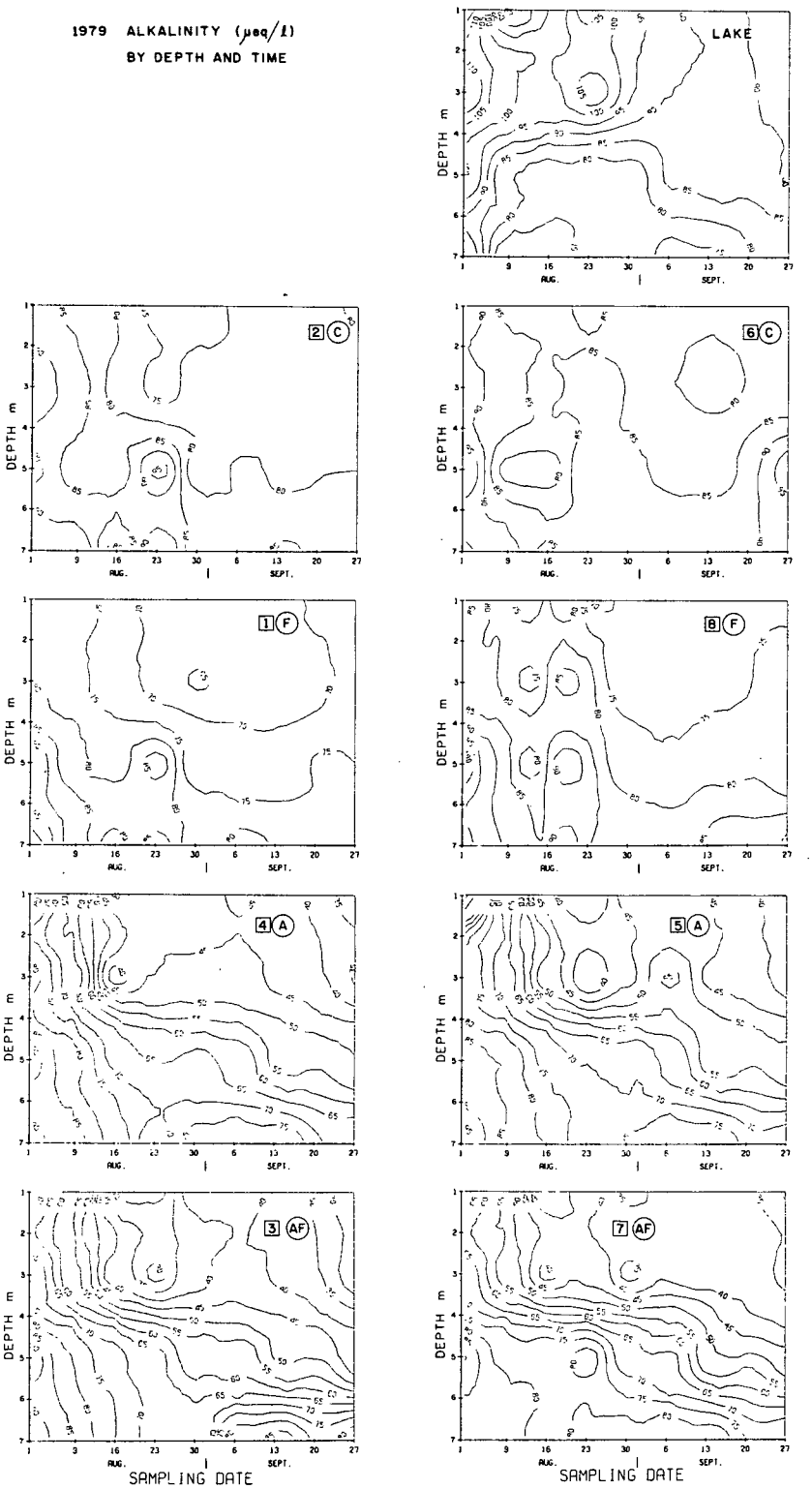


Table 7. Mean pH and alkalinity by treatment and depth stratum (mean ± s.e. (n)).

Treatment	pH			Alkalinity (μeq/l)		
	1-7 m	1-3 m	5-7 m	1-7 m	1-3 m	5-7 m
Lake	6.45 ± 0.03 (43)	6.61 ± 0.03 (21)	6.34 ± 0.03 (22)	89 ± 2.4 (31)	98 ± 2.9 (15)	81 ± 2.3 (16)
C	6.44 ± 0.01 (86)	6.51 ± 0.02 (43)	6.39 ± 0.02 (43)	84 ± 0.9 (61)	82 ± 1.1 (31)	87 ± 1.3 (30)
F	6.45 ± 0.02 (86)	6.52 ± 0.03 (43)	6.38 ± 0.02 (43)	79 ± 1.2 (63)	74 ± 1.2 (32)	84 ± 1.7 (31)
A	5.85 ± 0.04 (96)	5.72 ± 0.05 (48)	6.06 ± 0.05 (48)	62 ± 2.3 (63)	49 ± 2.6 (31)	74 ± 2.2 (32)
AF	5.60 ± 0.05 (96)	5.42 ± 0.06 (48)	5.91 ± 0.10 (48)	59 ± 2.7 (64)	43 ± 2.5 (32)	73 ± 2.9 (32)

Table 8. Differences between treatments in mean water column alkalinity (μeq/l) on each sampling date.

Column 1: Effect of enclosure.

Column 2: Cumulative amount of acid added to A enclosures as H_2SO_4.

Column 3: Observed effect of acidification.

Column 4: Amount of acid added to F enclosures as fertilizer.

Column 5: Observed effect of fertilization on circumneutral waters.

Column 6: Amount of acid added to AF enclosures as fertilizer.

Column 7: Observed effect of fertilization on acidifying waters.

Date	Change in Composite Alkalinity Due to Treatment (μeq/l)						
	Control Enclosures	Acidification in A Enclosures		Fertilization in F Enclosures		Fertilization in AF Enclosures	
	(1) $(\bar{C}-\overline{LK})$	(2) H^+ from H_2SO_4	(3) $(\bar{A}-\bar{C})$	(4) H^+ from H_3PO_4 and NH_4NO_3*	(5) $(\bar{F}-\bar{C})$	(6) H^+ from H_3PO_4 and NH_4NO_3	(7) $(\overline{AF}-\bar{A})$
July 16	-5	0	-4	0	3	0	1
Aug. 1	-14	-5	-7	-0.38	-3	-0.38	-6
9	+3	-8	-11	-0.57	-3	-0.56	-6
16	-5	-18	-22	-0.57	-4	-0.56	-3
23**	-6	-18	-33	-0.77	-3	-0.72	2
30	?	-18	-17	-0.77	-7	-0.72	-7
Sept. 6	-4	-18	-20	-0.77	-7	-0.72	-4
13	-3	-23	-26	-0.77	-8	-0.72	-2
27	-1	-31	-41	-0.77	-10	-0.72	-3

? Difference not calculable due to missing data.

* Calculated from dissociation constants for H_3PO_4 and NH_4NO_3 at 20°C in pure water, and mean epilimnetic pH for each treatment (Kester and Pytokowicz 1967, Thurston et al. 1974). About 98% of the H^+ comes from H_3PO_4 at the observed pH levels.

** Only two samples taken for 0-4 m and 4-8 m, rather than four samples.

(ii) Effect of H^+ ion Loading in Precipitation

A calculation of the total H^+ loading from precipitation during the course of the experiment is shown in Table 9. Even allowing for a 20% increase for evaporative concentration (Yan and Lafrance 1981), the precipitation could only have increased epilimnetic [H+] (maximally decreased alkalinity) within the enclosures by 0.247 $\mu eq \cdot L^{-1}$. Hence H^+ loading from the atmosphere during this experiment was negligible relative to the observed range of fluctuation in epilimnion alkalinity.

(iii) Effects of Experimental Acidification

The amount of sulfuric acid added to the A enclosures is shown by the bars on Figure 7, expressed as $\mu eq \cdot L^{-1}$ of H^+ averaged over the entire volume of the cylinder. Was the acidification of the A cylinders affected by biotic generation or consumption of alkalinity? This question can be answered by comparing the expected H^+ loading to treatment A (the second column of Table 8) with the observed difference in mean alkalinity between treatments C and A (the third column). The A enclosures showed composite alkalinities 4 $\mu eq \cdot L^{-1}$ less than the controls on July 16 prior to any acid additions. When this initial difference is deducted from subsequent (A-C) alkalinity differences the mean ratio of observed to expected alkalinity differences is 0.98 ± 0.11 (SE; n = 8). Hence, it appears that the added sulfuric acid was close to 100% efficient in removing alkalinity. The exceptionally large alkalinity difference on August 23 was due to an increase in the controls' mean

Table 9. Hydrogen ion[1] loading from precipitation during 1979 experiment.

Date of Collection	Total Rainfall[2] (m)	Mean pH of Rain	H^+ Loading/ Enclosures[3] (µeq)	Potential Increase in Epilimnetic (H^+)[4] (µeq/l)
Aug. 7-27	0.024	6.0	50	0.005
Aug. 27-Sept. 13	0.1267	5.1	2094	0.2
Sept. 18-29	0.0332	5.2	436	0.042
Total	0.1839		2580	0.247

[1] Source: Dr. Michael Feller, Department of Forestry, U.B.C. Precipitation Sampling Stations 6 km from Eunice Lake.

[2] From Figure 3.1.

[3] Calculated assuming surface area of enclosure = 2.08 m^2.

[4] Calculated assuming epilimnetic depth = 4 km and allowing 20% for evaporative concentration (Yan and Lafrance 1981).

alkalinity rather than a decrease in the A enclosures. In conclusion, net alkalinity changes due to biota were negligible, consistent with hypothesis 2(iv) on page 41.

The thermal regime clearly affected the vertical distribution of added H^+. When alkalinity contours in the A enclosures are compared with the controls (Figure 8), it is evident that although some acid was able to penetrate the sharp August thermocline at 5 m, bottom water alkalinities lagged behind surface concentrations by two to three weeks. Coincident with windmixing and weakening of the thermocline in the first half of September, alkalinities dropped in the 4-6 m zone. Alkalinity increases at the 7 m level during this period were presumably due to CO_2 production from microbial metabolism (to be discussed in Section 4.1).

Reductions in pH in the A treatments were largely restricted to the upper 4 m during August (Figure 7). Following a major acid addition on August 9 (10 $\mu eq \bullet L^{-1}$) the mean pH in the 1-3 m layer of the A enclosures dropped from 6.3 ± 0.00 to 5.72 ± 0.06. In the absence of acid additions between August 9 and September 6, the epilimnetic pH recovered, probably due to generation of alkalinity by photosynthetic NO_3^- uptake and mixing with less acid water at 5 m; by September 6, the vertical pH gradient between 1 and 5 m had disappeared. It was not until late September that the pH at 5 m dropped below 6.0.

(iv) Effects of Experimental Fertilization

Epilimnetic alkalinities were on average 8 $\mu eq \cdot L^{-1}$ lower in the F cylinders than in the controls (Table 7), a difference which was highly significant statistically (Appendix C). At 5-7 m, the mean difference in alkalinities was only 3 $\mu eq \cdot L^{-1}$, but still significant (Table 7; Appendix C).

Unlike the acidifed cylinders (treatment A), the fertilized cylinders were probably affected by biotic controls on alkalinity. Column 5 of Table 8 contains the mean observed alkalinity difference between the C and F treatments (F-C), calculated from 1-7 m composite alkalinities. Comparing column 5 to column 4 (the theoretical chemical contributions of H^+ from dissociation of H_3PO_4 and NH_4NO_3) it seems that biotic rather than abiotic processing of the added nutrients must have been responsible for the observed loss of alkalinity in the F cylinders. Preferential algal assimilation of NH_4^+ over NO_3^- and bacterial nitrification appear to be the two most likely causes of the alkalinity decrease (to be discussed in Section 4.1). Note that the loss of alkalinity in the F cylinders was insufficient to decrease the pH (Figure 7; Table 7). Observed $[H^+]$ differences between treatment F and the controls were not statistically significant (Appendix C). Therefore, part of null hypothesis 3(i) (page 41) was contradicted (that moderate nutrient enrichment of circumneutral waters does not affect alkalinity), and part was not contradicted (that pH is not affected).

(v) Effects of Experimental Acidification and Fertilization

During the week after the major acid addition on August 9, when the mean epilimnetic pH in the A enclosures dropped from 6.3 to 5.72, the AF enclosures showed a much larger decrease, from 6.24 ± 0.06 to 5.30 ± 0.10 (Figure 7). This had tremendous biological repercussions in AF (to be discussed).

Since the same amount of H_2SO_4 was added to the A and AF enclosures prior to August 16, and dissociative contributions of H^+ from NH_4NO_3 and H_3PO_4 were negligible (Table 8), the greater acidification of AF must have been due to biotic processing of the added nutrients. Such nutrient processing resulted in a highly significant difference in overall mean epilimnetic alkalinities between treatments A and AF (Table 7; Appendix C). Though the alkalinity difference between treatments A and AF was on average 2 $\mu eq \cdot L^{-1}$ less than the difference between C and F, nutrient-induced alkalinity losses resulted in a much greater supplementary pH decline in AF than F. This is because the concurrent H_2SO_4 additions to the AF treatments decreased the pH to a level (5.7) where the buffering capacity was theoretically about 53% of that available in the F treatment at pH 6.5 (Stumm and Morgan 1970). (Buffering capacity is the slope of the titration curve, or d (pH)/d (alkalinity) (Stumm and Morgan 1970).)

Differences in pH between treatments A and AF closely reflected the alkalinity differences. Over the course of the experiment, the mean epilimnetic pH was significantly lower in treatment AF (5.42 ± 0.06) than in treatment A (5.72 ± 0.05)

(Appendix C). Therefore, in contrast to null hypothesis 4(i) (page 41), moderate nutrient enrichment during experimental acidification to pH 5.0 did alter alkalinity and pH from the levels observed by acidification alone.

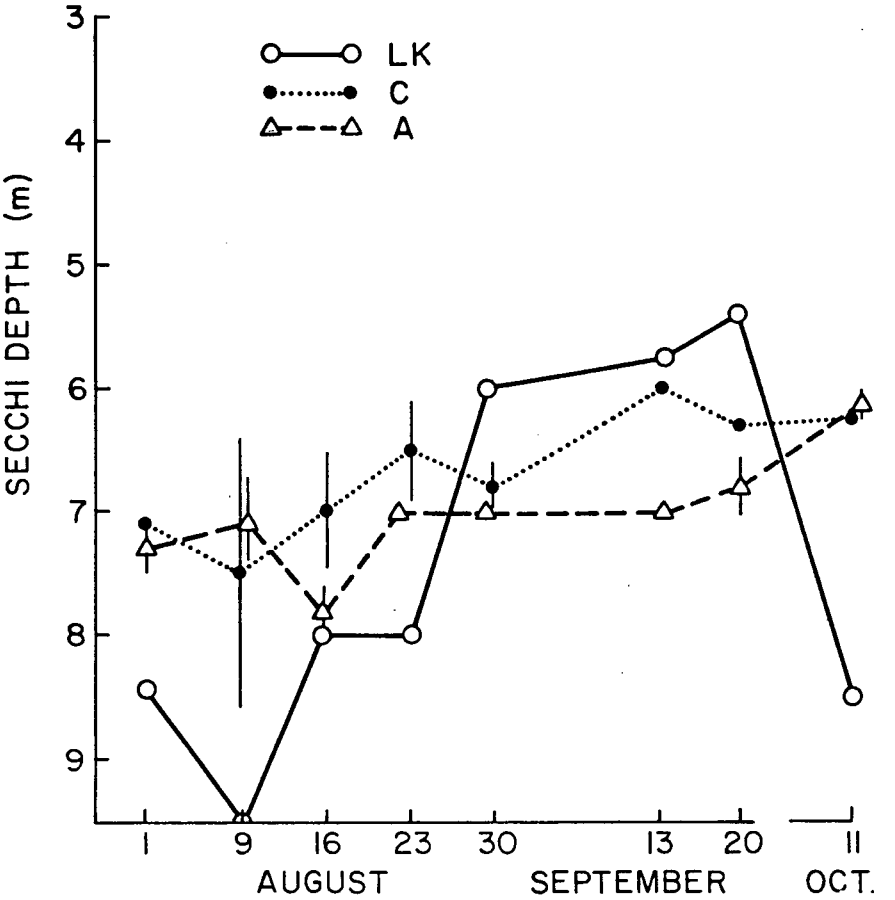
3.1.3. Transparency

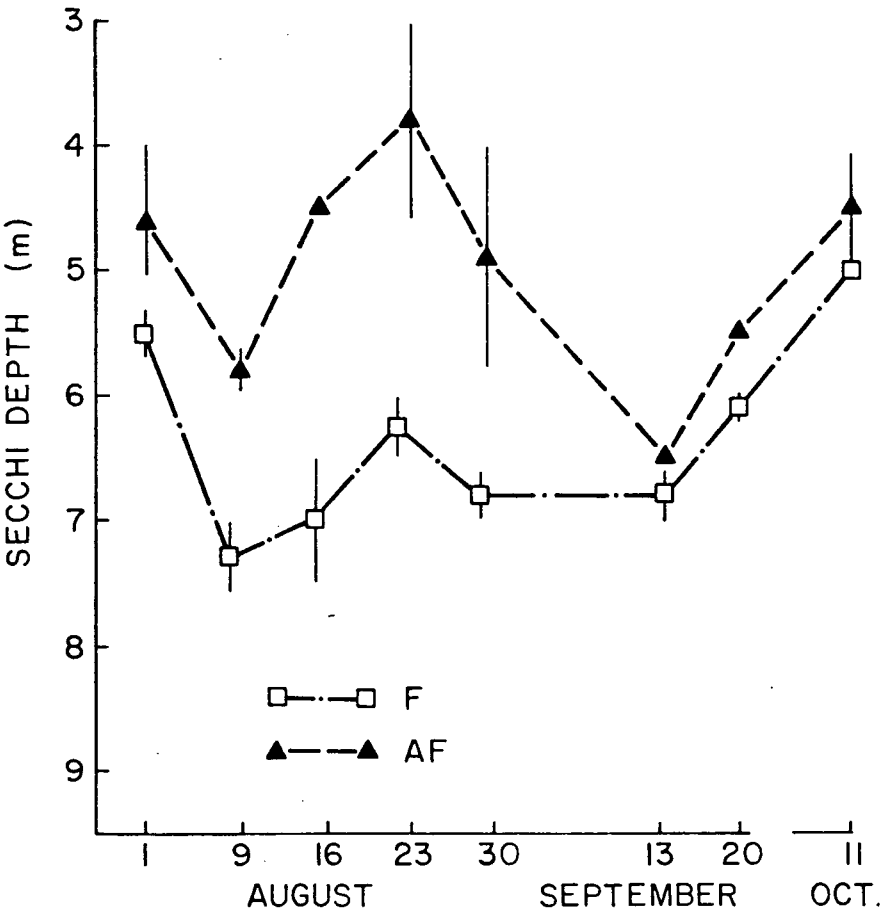
The null hypotheses concerning water transparency (page 41) focussed on the effects of enclosure, the effects of experimental acidification (particularly on the abiotic component of water transparency), and the effects of experimental fertilization (in both circumneutral and acidic waters). These questions were approached by both graphical comparison of Secchi depth changes over time (this section), and statistical comparisons of between treatment differences in Secchi depth vs. chlorophyll *a* nonlinear regressions (summarized in this section and detailed in Appendix D).

Relative to the lake, transparency was reduced in the controls during August and October, but slightly greater in September (Figure 9). Enclosure increased light extinction due to abiotic factors, most likely shading from the floats of the limnocorrals (Appendix D).

Did experimental acidification affect transparency? On September 13 and 20, Secchi depth in treatment A averaged 6.9 ± 0.13 m, compared to only 6.1 ± 0.07 m in the controls (Figure 9). This transparency difference occurred when the mean epilimnetic pH in the A cylinders was 5.92 ± 0.05 (versus 6.39 ± 0.03 in the controls), and the total chlorophyll *a*

Figure 9. Mean Secchi disc depths by treatment and time . Error bars show ± SE. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.


LK
C
A
SECCHI DEPTH (m)
3
4
5
6
7
8
9
1
9
16
23
30
13
20
11
AUGUST
SEPTEMBER
OCT.


F
AF
SECCHI DEPTH (m)
3
4
5
6
7
8
9
1
9
16
23
30
13
20
11
AUGUST
SEPTEMBER
OCT.

concentrations (chlorophyll plus phaeophytin) in A and C were similar (0.93 ± 0.14 and 0.89 ± 0.07 $\mu g \cdot L^{-1}$ respectively). Overall mean Secchi depths in treatment A (7.14 ± 0.23 m) were not significantly different from the controls (6.72 ± 0.35 m). Finally, regression analyses of Secchi disc depths versus total chlorophyll (Appendix D) did not show significant changes in light extinction with experimental acidification (treatment A). In conclusion, there is insufficient evidence to contradict hypothesis 2(iii) (page 41), that experimental acidification (at least to pH 5.5) does not affect the abiotic component of light extinction.

Secchi depths in treatment F were very similar to the controls for most of the experiment, but were significantly lower (particularly in 8F) during chlorophyll peaks on August 1 and September 27-October 5 (Figure 9; Figure 20, page 120). Between treatment differences on these dates were sufficient to reject part of null hypotheses 3(i): that nutrient enrichment of circumneutral waters does not affect transparency.

In the AF enclosures, Secchi depths tracked the large fluctuations in chlorophyll (Figure 20, page 120). During the period from August 9 to 23, when these cylinders showed six to sevenfold increases in total chlorophyll, mean Secchi depth decreased from 5.8 ± 0.2 m to 3.8 ± 0.8 m. These dramatic changes in chlorophyll and transparency were associated with major acid-induced decreases in total zooplankton biomass (Section 3.3.5). Due to the high chlorophyll levels, the fraction of subsurface light attenuated by chlorophyll was

significantly higher in treatment AF than in the other treatments (Appendix D). In conclusion, lower Secchi depths in treatment AF than treatment A contradict part of hypothesis 4(i) (page 41): that nutrient enrichment during acidification to pH 5.0 does not alter transparency from the levels observed by acidification alone. Null hypothesis 5 (iv) (that acidification of moderately enriched waters does not alter its transparency) was also contradicted, since Secchi depths were much lower in AF than F (Figure 9).

3.1.4 Summary of Physical and Chemical Results

1. A strong thermocline at 4-6 m persisted throughout the dry, warm months of July and August, before weakening with the storms and cool weather in September.
2. Enclosure of water reduced mean epilimnetic alkalinity by 16 $\mu eq \bullet L^{-1}$ and raised mean metalimnetic alkalinity by 6 $\mu eq \bullet L^{-}L$. However, mean pH levels changed by less than 0.1 units.
3. Biotic processes did not cause a net change in alkalinity in treatment A, since experimental additions of sulfuric acid to the A cylinders removed as much alkalinity as was expected from laboratory titration of lakewater.
4. Due to summer thermal stratification, pH levels at 5 m in A and AF remained above 6.0 until late September.

5. In both treatments F and AF, fertilization significantly reduced epilimnetic alkalinities, through biotic processing of nitrogen additions. The alkalinity loss did not affect pH levels in F, but reduced the epilimnetic pH in AF by 0.4 units relative to A.
6. Fertilization-induced alkalinity losses reduced the buffering capacity of AF cylinder waters, increasing the sensitivity of pH levels to subsequent acid additions.
7. Enclosure of water increased light extinction due to factors other than chlorophyll, probably limnocorral shading.
8. Experimental acidification did not affect the abiotic component of light extinction, but did increase transparencies slightly relative to the controls.
9. Fertilization decreased transparency in both treatments F and AF, but to a much greater extent in AF, where Secchi depths decreased 2 m between August 9 and 23.

3.2 Zooplankton

In this section, I describe the biomass fluctuation, species succession, and vertical distribution of the zooplankton communities within the experimental enclosures. The communities are compared both to one another and to Eunice Lake.

The zooplankton communities consisted almost exclusively of crustaceans within the subclasses Cladocera and Copepoda. The most important cladoceran species (in order of mean biomass across all treatments) were Daphnia rosea, Chydorus sphaericus, Holopedium gibberum, Bosmina longirostris, Diaphanosoma brachyurum, and Ceriodaphnia pulchella. The two other important species were calanoid copepods, Diaptomus tyrrelli and Diaptomus kenai, which together averaged 20% of the total zooplankton biomass across all samples. Other crustacean zooplankton species commonly identified in the samples were the cladocerans Polyphemus pediculus and Scapholeberis kingi, the calanoid copepod Diaptomus leptopus and the cyclopoid copepod Diacyclops thomasi, but these made negligible contributions to total zooplankton biomass. Rotifers were never abundant, with only Keratella sp. reaching densities as high as 2 per liter, and that on only one occasion. Larvae of the genus Chironomus were occasionally found in samples from cylinders receiving fertilizer additions, especially if the sampling hose accidentally brushed the side or bottom of the cylinder.

Since the results in this section are presented by treatment, rather than by species, a few comments are necessary to familiarize the reader with both the location of tables and

figures, and their interpretation. The calculated biomass of the eight major species listed above are shown for all cylinders in Figure 10, and expanded into a graph of percentage composition in Figure 11. Statistical analyses of total zooplankton biomass are summarized in Table 10, for each date across all treatments. Analyses of variance of the abundance, egg production and clutch sizes of the major species are shown for particular treatment comparisons (across all dates) in Table 11. Some of the numbers on which these analyses are based are shown graphically in Figures 12 to 17.

When examining the graphs of D. tyrrelli and D. kenai abundance and egg production (Figures 14 to 16), it is important to consider the life histories of these diaptomid copepods. Though not documented precisely, the life histories generally conform to the patterns described by Chapman and Green (unpublished data) and summarized by Olenick(1982). In Eunice Lake, D. tyrrelli nauplii emerge from resting eggs in April or May and reach adulthood by July or August. These adults produce subitaneous eggs, yielding a second generation with its peak of adults in September or October. The larger Diaptomus kenai hatch from eggs (likely both subitaneous and resting eggs) in December, reaching reproductive maturity by April. In May and June, these adults produce either subitaneous eggs (which mature into adults by August and September) or resting eggs (which only hatch in late August or September). The diaptomid copepod populations in all of the experimental cylinders appeared to conform to these generalized life history patterns. Copepod

nauplii densities (not identified to species but probably D. tyrrelli) declined to less than 10 per 100 L by mid-August (Figure 16). D. tyrrelli densities were highly variable, but showed a consistent transition from copepodites to adults over August, with very few copepodites present after September 13 (Figure 14). D. kenai also moved from the copepodite to adult stage during July and August; I found virtually no D. kenai copepodites after August 30. Loose calanoid eggs (not identified to species) showed highest abundance in late August and September, coincident with the sexual maturation of both diaptomids (Figure 16).

Cladocerans, unlike copepods, do not show distinctly separable cohorts, and reproduce asexually throughout spring and summer. Males and sexual ephippial eggs appear in the fall, usually coinciding with a decline in food conditions or temperature.

Although lengths of the animals did vary both between treatments and seasonally (see Appendix E) the effects of these variations on biomass were negligible relative to fluctuations in densities. I therefore make reference to statistical analyses of species abundance to explain variations in biomass.

3.2.1 Effects of Enclosure

Replication within the control cylinders was excellent (Figure 10). The major effects of enclosure (as determined by comparing the controls to the lake) were a rapid decline of Holopedium gibberum, changes in the seasonal dynamics of Daphnia

Figure 10. Cumulative biomass of major zooplankton species in 1979 experiment. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

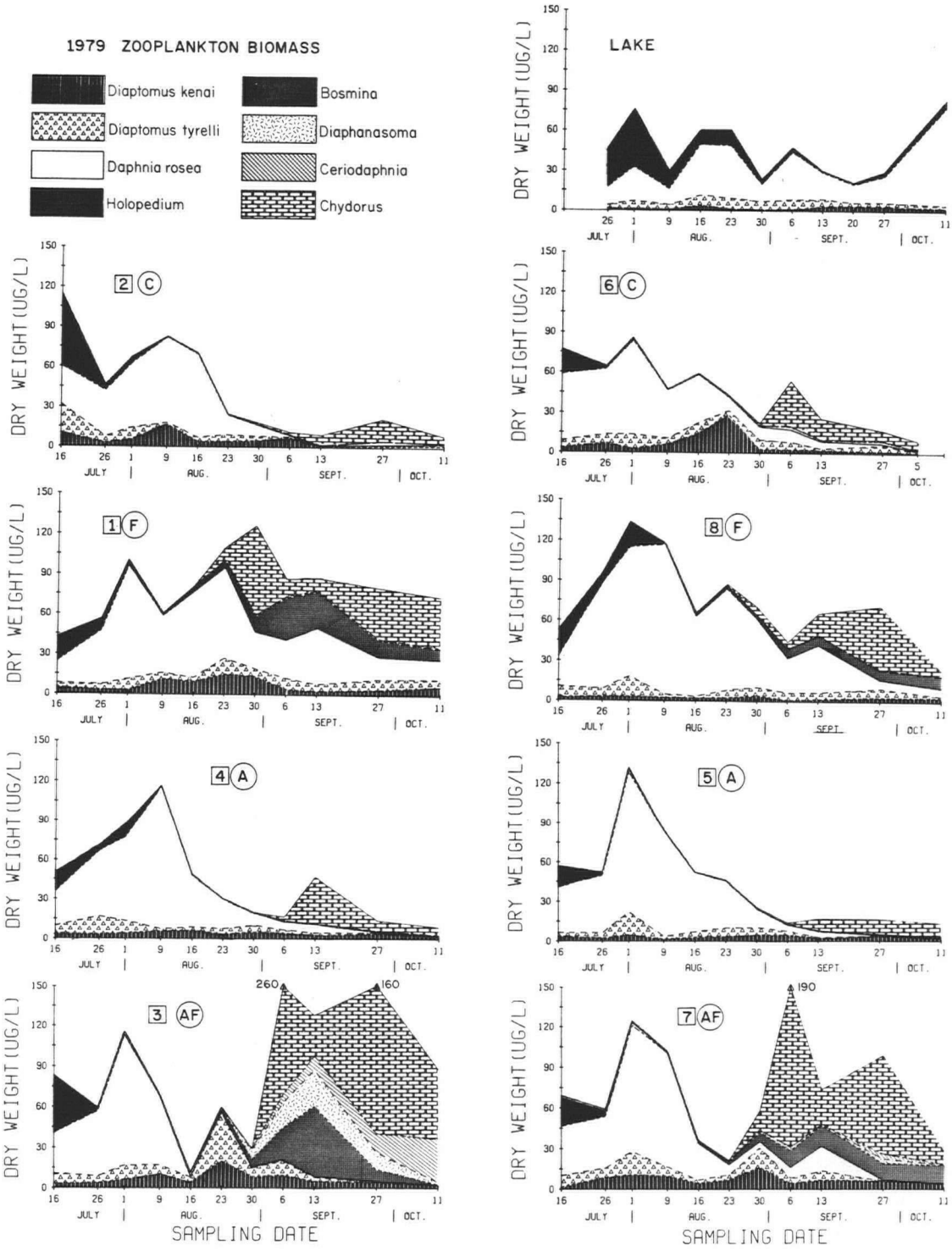

1979 ZOOPLANKTON BIOMASS
Diaptomus kenai
Diaptomus tyrelli
Daphnia rosea
Holopedium
Bosmina
Diaphanasoma
Ceriodaphnia
Chydorus
LAKE
2 C
6 C
1 F
8 F
4 A
5 A
3 AF
7 AF
DRY WEIGHT (UG/L)
JULY
AUG.
SEPT.
OCT.
260
160
190
SAMPLING DATE

Figure 11. Percent composition of total zooplankton biomass in 1979 experiment. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

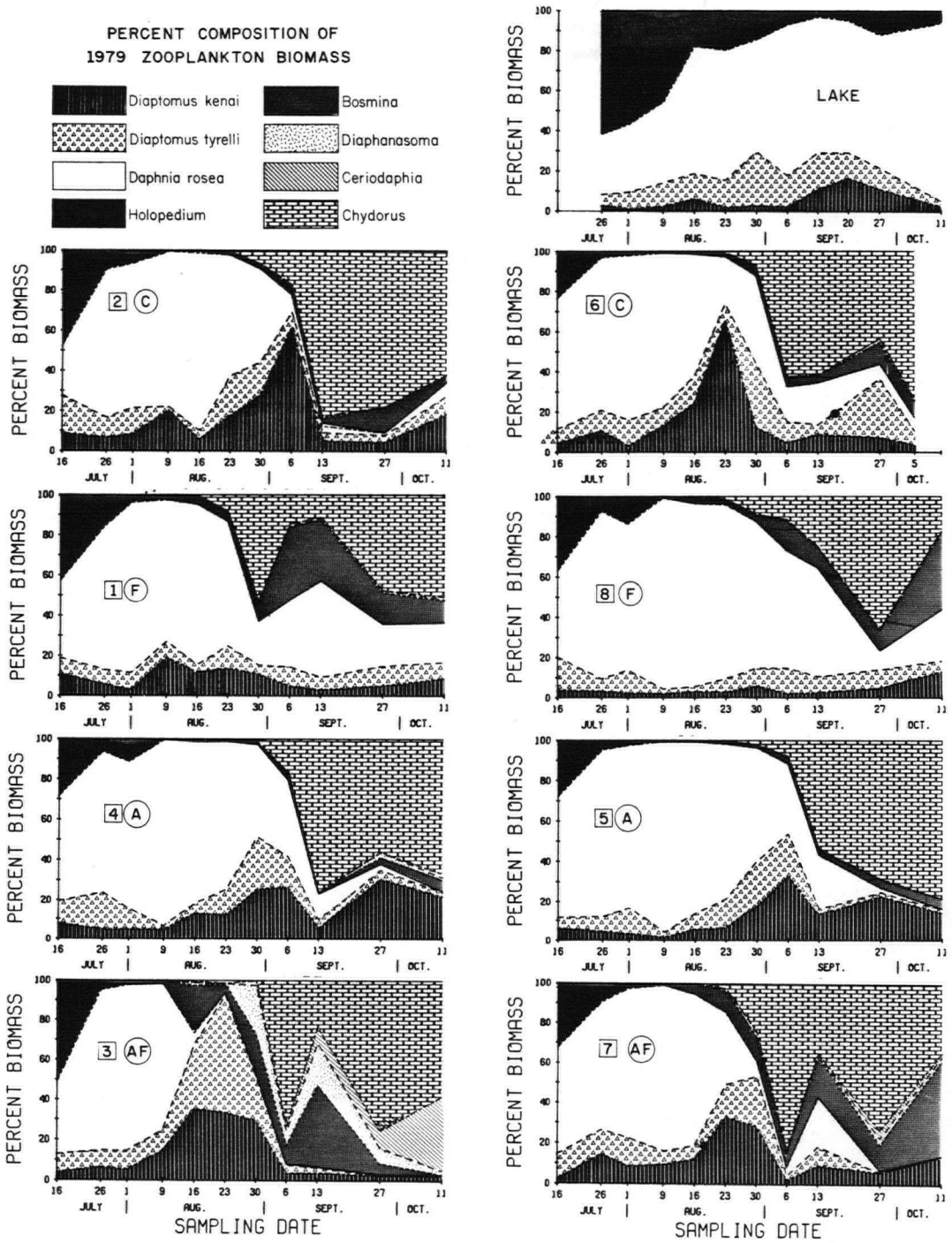

PERCENT COMPOSITION OF
1979 ZOOPLANKTON BIOMASS
Diaptomus kenai
Diaptomus tyrelli
Daphnia rosea
Holopedium
Bosmina
Diaphanasoma
Ceriodaphia
Chydorus
LAKE
2 C
6 C
1 F
8 F
4 A
5 A
3 AF
7 AF
PERCENT BIOMASS
JULY
AUG.
SEPT.
OCT.
SAMPLING DATE

Table 10. Mean zooplankton community biomass by treatment and date. Probability of no treatment effect in column labelled "P" obtained from analyses of variance on total biomass values (untransformed unless stated). Results of Tukey multiple range tests show treatments listed in ascending order of biomass from left to right. Underlining indicates homogeneous subsets i.e. treatments are not significantly different from one another at stated probability level.

Date	Zooplankton Community Biomass by Treatment ($\bar{X}\pm SE$) in µg/L					P	Tukey Significant Differences n = 2 replicates/treatment	
	C	F	A	AF	LK		α = 0.10	α = 0.05
July 16	96±19	49± 6	54± 3	76± 7	*	0.10	ns	ns
26	56± 9	76±20	61±10	59±0.3	47	0.67	ns	ns
Aug. 1	76± 9	117±17	109±22	120± 4	77	0.29	ns	ns
9	65±18	89±29	100±16	85±16	31	0.44	ns	ns
16	65± 5	73± 8	51± 2	24±12	61	0.06	AF•A•LK•C•F	ns
23	34± 9	99±11	38± 8	41±19	61	0.09	C•A•AF•LK•F	ns
30	20± 3	98±28	22± 3	43±14	24	0.10	C•A•LK•AF•F	ns
Sept. 6	33±21	66±21	15± 1.4	225±36	48	0.01	A•C•LK•F•AF	A•C•LK•F•AF
13	18± 8	76±11	32±15	101±27	30	0.09	C•LK•A•F•AF	ns
27	19± 3	76± 5	15± 1.2	132±33	30	0.03	same as α=0.05	A•C•LK•F•AF
Oct. 11	9±0.3	48±25	11± 2**	58±30	83	0.25[h]	ns	ns
All Dates (2-way ANOVA)	45± 6	79± 6	46± 7	87±13	49±6	$(10^{-5})^{H}$	C•A•LK•AF•F	C•A•LK•AF•F

* Sample destroyed.

** Sample from October 5 used for 6C since Oct. 11 sample lost.

h Variances heterogeneous at $p < 0.05$.

H Variances heterogenous at $p < 0.01$.

ns Differences not significant at stated α level.

Table 11. Two-way analyses of variance on log-transformed zooplankton species abundance, egg production, and brood size per ovigerous female. If $p < 0.05$, the treatment listed is the one that was significantly higher. See Materials and Methods for explanation of log transform applied to brood sizes. Number in brackets is probability of significant treatment effect ($F_{1,11}$ for C vs. LK; $F_{1,22}$ for all other comparisons). Most time effects ($F_{10,22}$) were significant at $p < 0.01$.

Species and Variable		Treatment Comparison				
		C vs. LK	C vs. A	C vs. F	F vs. AF	A vs. AF
D. kenai:	log (#)	ns(0.11)h	ns(0.54)H	ns(0.86)h	ns(0.058)	AF(0.0002)
	log(# eggs)	ns(0.11)	ns(0.7)	ns(0.96)	ns(0.38)	ns(0.2)
	log (brood size)	ns(0.36)	ns(0.94)	ns(0.79)	ns(0.46)	ns(0.2)
D. tyrrelli:	log (#)	ns(0.2)h	ns(0.06)	F(0.05)	F(0.006)IH	ns(0.9)
	log(# eggs)	ns(0.09)	ns(0.36)	F(0.002)i	ns(0.64)i	AF(10^{-5})h
	log(brood size)	ns(0.25)	ns(0.94)	ns(0.08)	ns(0.24)I	AF(0.01)
D. rosea:	log(#)	LK(0.001)IH	ns(0.68)	F(10^{-5})IH	F(10^{-5})IH	A(10^{-5})i
	log(# eggs)	LK(0.006)	ns(0.76)	F(10^{-5})	F(0.0009)H	AF(0.03)
	log(brood size)	ns(0.46)	ns(0.32)	F(0.014)	ns(0.19)	ns(0.07)h
B. longirostris:	log(#)	C(0.08)	C(0.05)	F(10^{-5})Ih	ns(0.84)	AF(10^{-5})IH
	log(# eggs)	C(0.0004)	C(0.02)	F(10^{-5})	AF(0.03)	AF(10^{-5})H
	log(brood size)	ns(0.10)	ns(0.20)	ns(0.07)	ns(0.08)	ns(0.14)
C. sphaericus:	log(#)	C(10^{-5})IH	ns(0.28)	F(0.02)	ns(0.83)	ns(0.06)
D. brachyurum:	log(#)	C(0.01)	ns(0.88)	F(0.0005)	AF(0.004)H	AF(10^{-5})iH
C. pulchella:	log(#)	C(10^{-5})IH	ns(0.10)H	F(0.02)H	AF(0.002)H	AF(10^{-5})IH
Calanoid eggs:	log(#)	C(0.01)	ns(0.57)H	ns(0.12)	AF(0.004)	AF(10^{-5})
Copepod nauplii:	log(#)	ns(0.13)	C(0.04)	ns(0.10)	ns(0.46)	AF(0.0036)

ns Not significant at $\alpha = 0.05$.
h Variances heterogeneous at $\alpha = 0.05$.
H Variances heterogeneous at $\alpha = 0.01$.
i Treatment * time interaction significant at $\alpha = 0.05$.
I Interaction significant at $\alpha = 0.01$.

Figure 12. Densities of Daphnia rosea by age class . Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

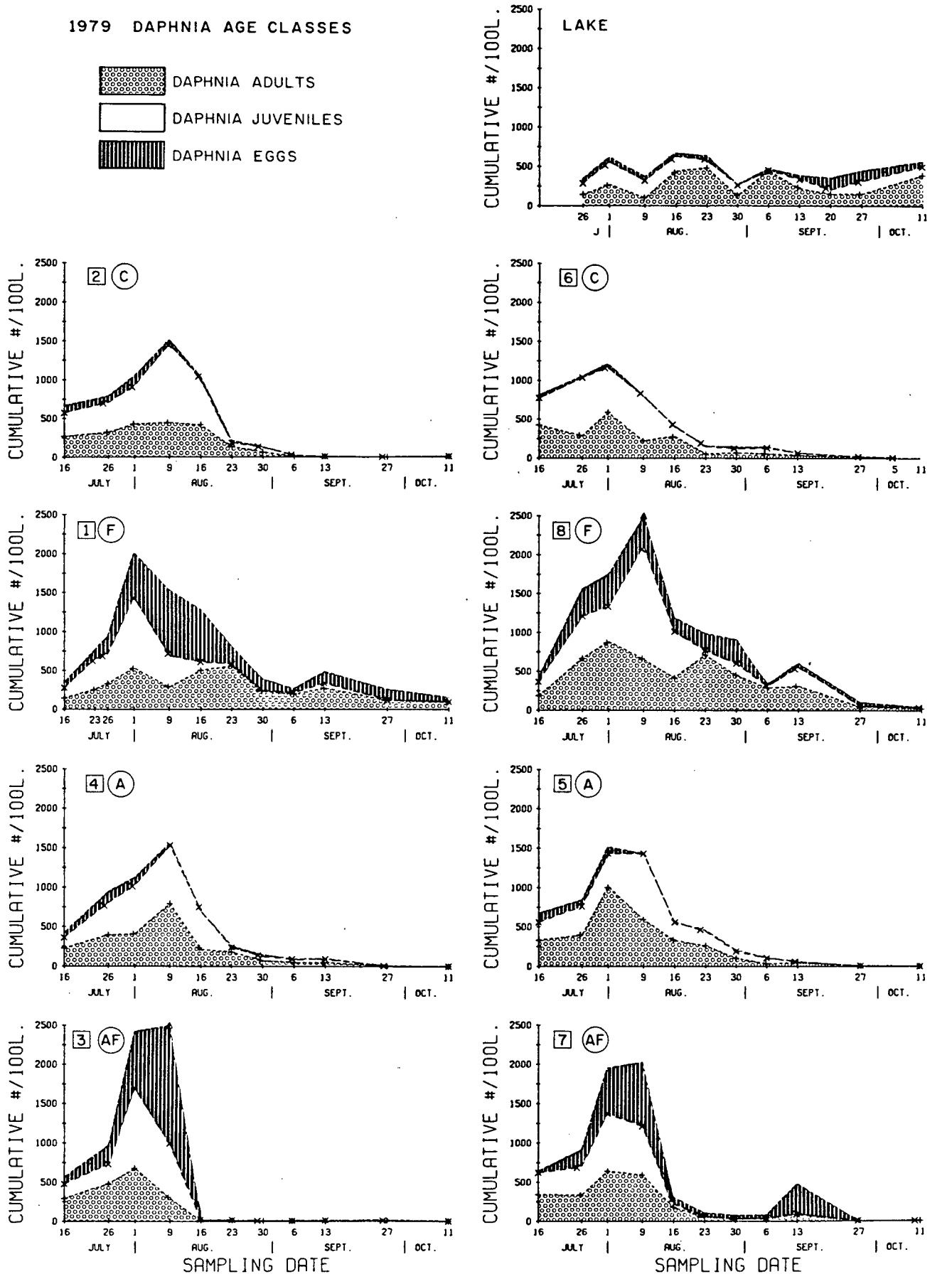

1979 DAPHNIA AGE CLASSES
DAPHNIA ADULTS
DAPHNIA JUVENILES
DAPHNIA EGGS
LAKE
2 C
6 C
1 F
8 F
4 A
5 A
3 AF
7 AF
CUMULATIVE #/100L.
0
500
1000
1500
2000
2500
16 26 1 9 16 23 30 6 13 27 11
16 23 26 1 9 16 23 30 6 13 27 11
26 1 9 16 23 30 6 13 20 27 11
JULY
AUG.
SEPT.
OCT.
J
SAMPLING DATE

Figure 13. Daphnia rosea reproduction: % ovigerous females and mean brood sizes. Number of ovigerous females indicated if less than ten. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

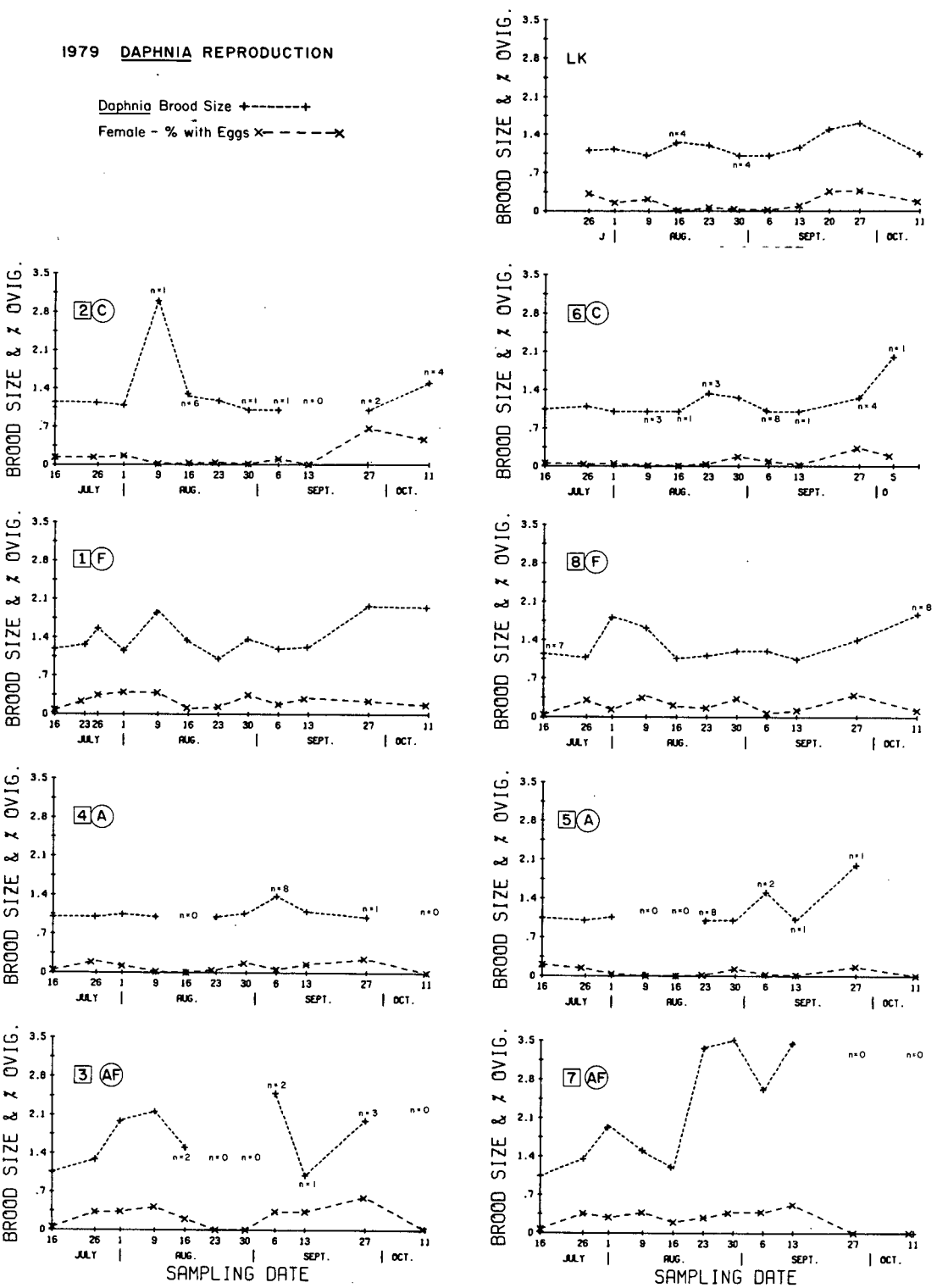

1979 DAPHNIA REPRODUCTION
Daphnia Brood Size +-------+
Female - % with Eggs x- - - - -x
LK
2 C
6 C
1 F
8 F
4 A
5 A
3 AF
7 AF
BROOD SIZE & % OVIG.
JULY
AUG.
SEPT.
OCT.
SAMPLING DATE

Figure 14. Densities of Diaptomus tyrrelli. Graphs show attached eggs only; loose eggs in Figure 16. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

1979 DIAPTOMUS TYRRELLI

+-------+ ADULTS

x - - - x COPEPODITES

– · – · – · – EGGS

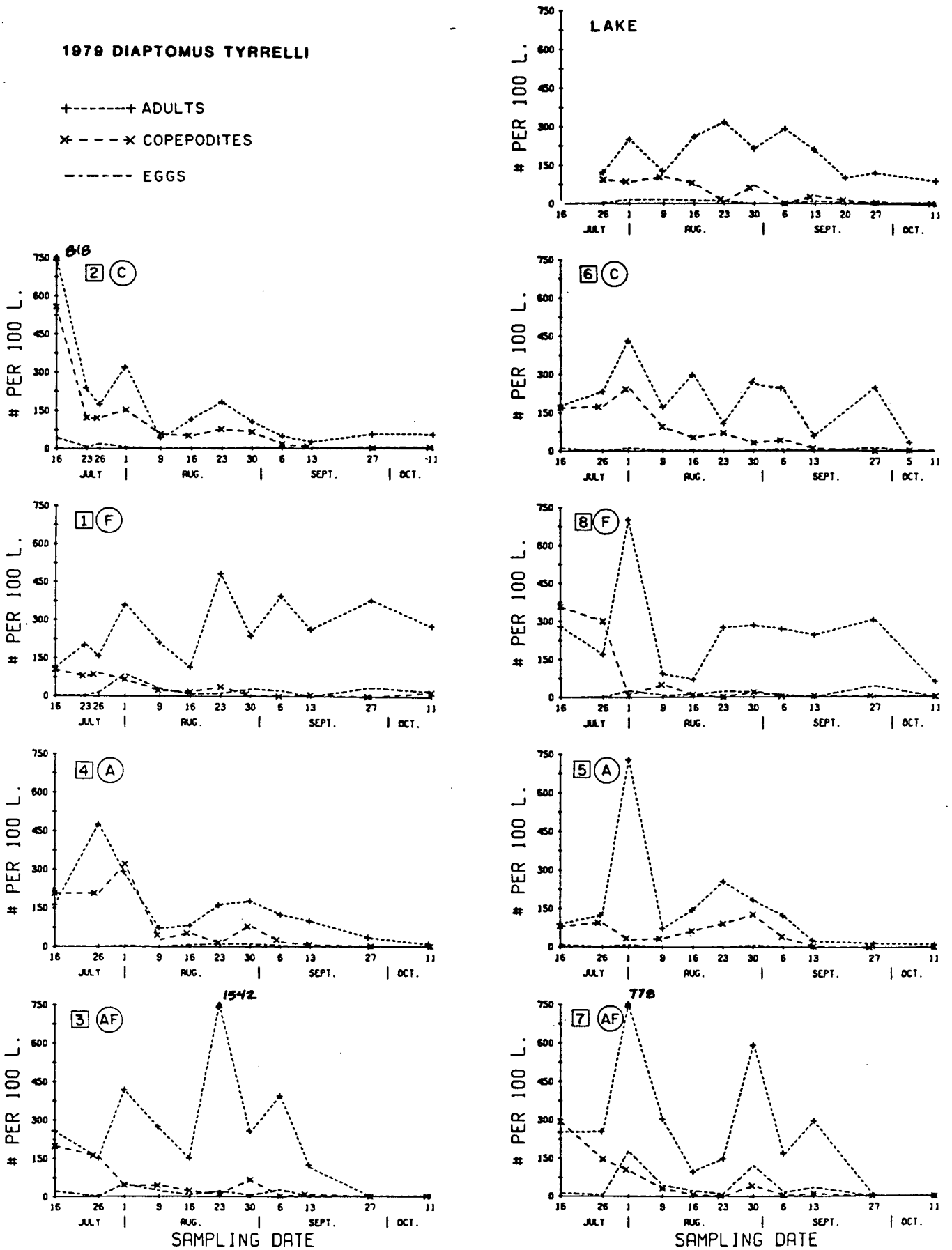


Figure 15. Densities of Diaptomus kenai. Graphs show attached eggs only; loose eggs in Figure 16. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

1979 DIAPTOMUS KENAI

+-------+ ADULTS

X- - - -X COPEPODITES

□-·-·-·-□ EGGS

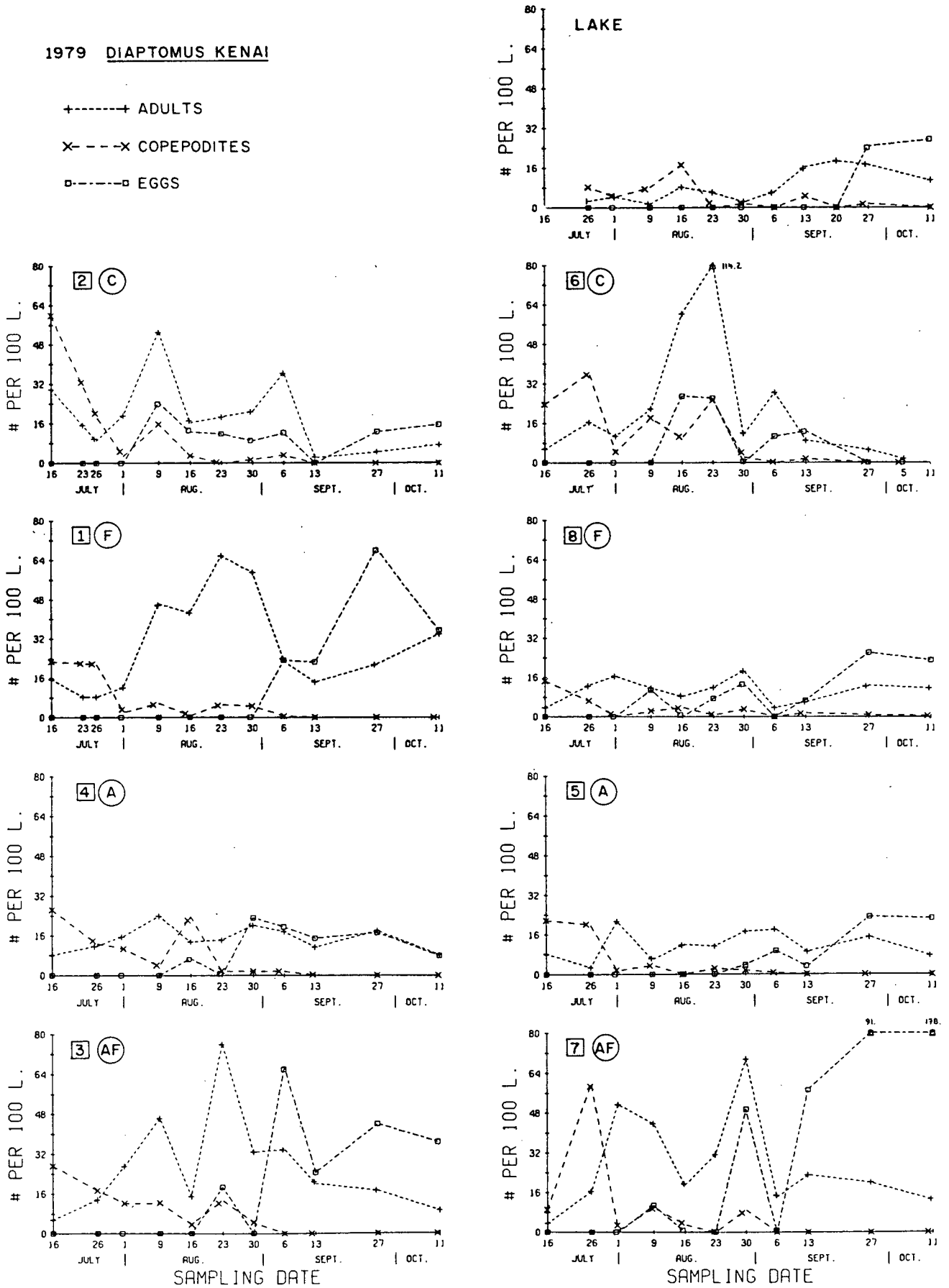


Figure 16. Densities of loose calanoid copepod eggs and nauplii. Note that logarithmic scale differs slightly between graphs. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

1979 COPEPOD EGGS / NAUPLII

+------+ LOOSE CALANOID EGGS

×- - -× COPEPOD NAUPLII

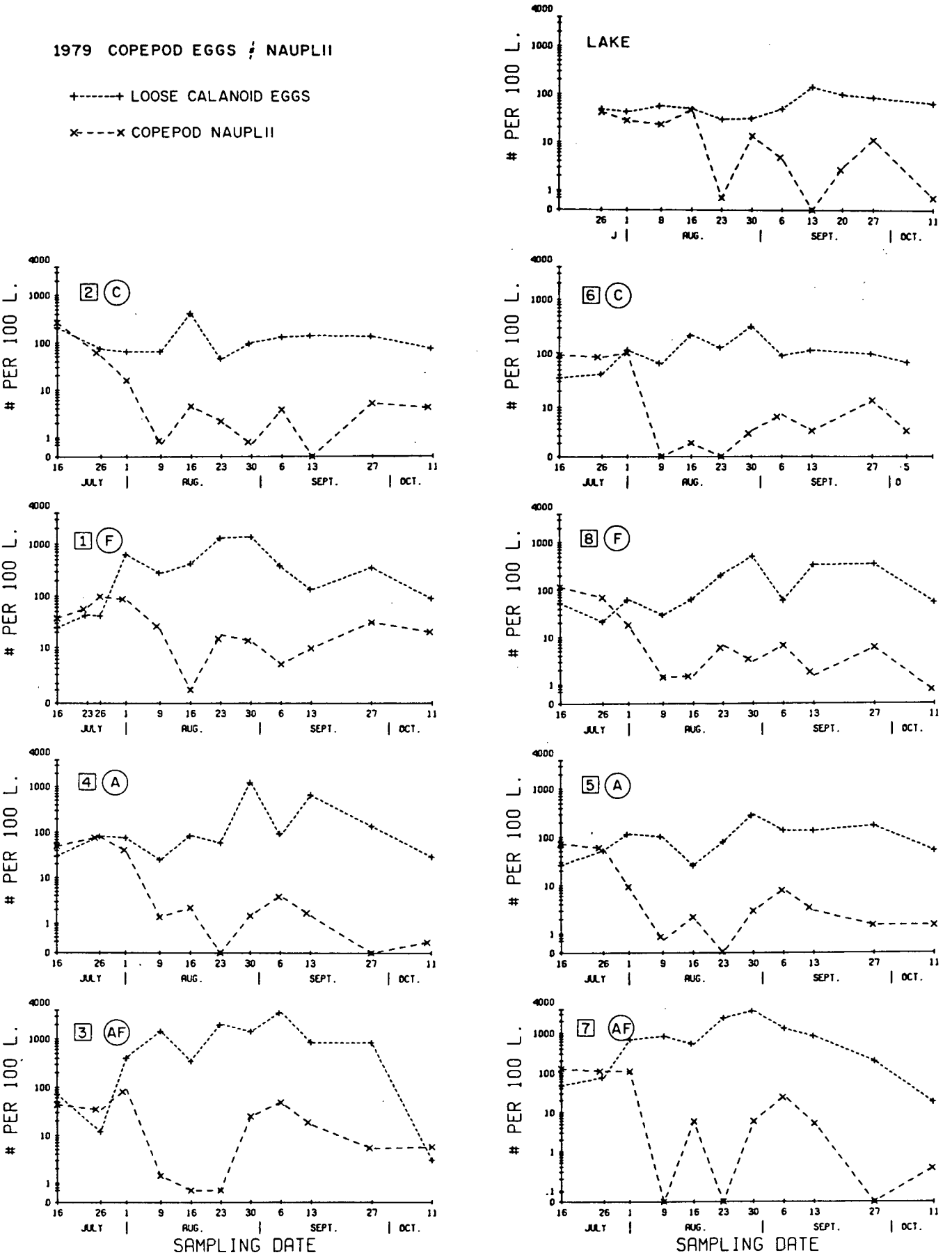


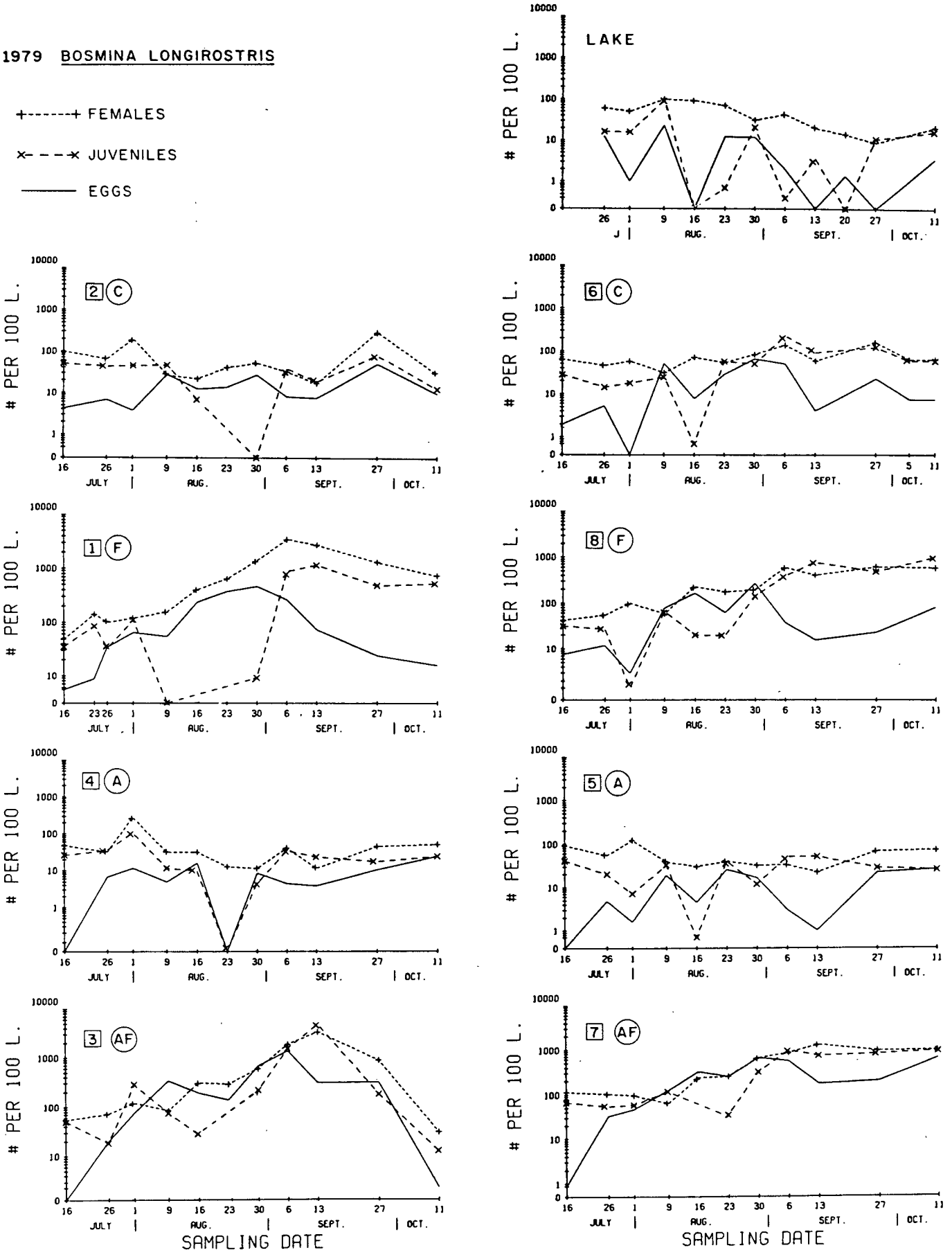
Figure 17. Densities of Bosmina longirostris. Note that logarithmic scale differs slightly between graphs. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

1979 BOSMINA LONGIROSTRIS

+------+ FEMALES

x- - -x JUVENILES

——— EGGS



rosea, replacement of Daphnia rosea by Chydorus sphaericus as community dominant, and an earlier "shutdown" of the zooplankton community. Enclosure also affected the lengths of some zooplankton species.

H. gibberum often has difficulties surviving in limnocorrals during warm-water conditions (W.E. Neill, pers. comm.; Buckingham 1978). The loss of H. gibberum (in all treatments) was not attributable to my 10 m enclosures being too shallow for this species to reach optimum depth, since stratified samples on August 1 showed H. gibberum concentrated in the upper 2 m of cylinders 1F, 8F, 4A, and 7AF (the only enclosures with sufficient numbers of animals to calculate a vertical distribution). Also, H. gibberum suffered a similar decline in another limnocorral experiment conducted in Eunice Lake in 1979, but with 15 m enclosures (R.J. Olenick, pers. comm.).

Since the lake was not sampled on July 16, I cannot be certain whether all of the species were properly stocked in the enclosures. However, the July 26 samples suggest that the replacement of H. gibberum by Daphnia rosea may have been partially due to initial underrepresentation of H. gibberum and overrepresentation of D. rosea (Figures 10, 11 and 12). (Note that the mean weight of adult H. gibberum used in biomass calculations was twice that of D. rosea). Peak biomass levels of D. rosea in the control cylinders (August 1 in 6C, August 9 in 2C) were about double the biomass of lake D. rosea on August 1. This was due either to initial overstocking of D. rosea, or an increase in resources caused by the collapse of H. gibberum,

or both factors. However, D. rosea could not maintain this biomass in the control cylinders, as evidenced by low egg densities on the peak dates and subsequent sharp decreases in abundance (Figure 12). In the lake, D. rosea densities oscillated with a period of about three weeks, the troughs of the oscillations occurring August 9, August 30, and September 20, with maximum densities on October 11 (Figure 12). There is a striking difference between the collapse of the control cylinder populations in September and the sharp recovery of the lake's population.

Statistical analysis confirmed that D. rosea populations in the controls behaved differently from the Eunice Lake population. When all counts of D. rosea made over the three month experiment are analyzed together, lake populations showed significantly higher geometric mean density and egg densities than the controls (Table 11). Mean brood sizes were not significantly different however (Table 11). As well as statistically significant differences in abundance (i.e. a treatment effect), the contrast in D. rosea temporal patterns between the lake and the controls produced a significant ($p < 0.01$) treatment x time interaction. This difference in temporal patterns may have been partially due to fish predation controlling the size of the lake population.

With the decline of D. rosea in the control cylinders at the end of August, the generally littoral cladoceran, Chydorus sphaericus, became dominant in terms of biomass (Figure 11). C. sphaericus densities were significantly higher in the control

cylinders than in the lake (Table 11).

When tested together with other treatments using a Tukey multiple range test, the arithmetic mean zooplankton biomass in the controls (45 ± 21 $\mu g \cdot L^{-1}$) was not significantly different from the lake (49 ± 15 $\mu g \cdot L^{-1}$) (Table 10). The most obvious difference between the lake and the controls was the longer persistence of the lake zooplankton community through the autumn. Between September 27 and October 11, the mean zooplankton biomass of the controls fell from 19 ± 3 to 9 ± 0.3 $\mu g \cdot L^{-1}$, while the lake biomass grew from 30 to 83 $\mu g \cdot L^{-1}$ (Figure 10).

Enclosure affected the lengths of the larger crustaceans, probably due to the removal of cutthroat trout size-selective predation. The mean lengths of adult and juvenile D. rosea were consistently lower in Eunice Lake than in the controls (Table 12 and Appendix E), which supports the view that size-selective fish predation affected Daphnia. On September 13, the mean length of D. kenai adults was considerably less in Eunice Lake (1.82 ± 0.070 (10)) than in the control cylinders (1.94 ± 0.024 (14)), though not significantly different ($p=0.08$). By contrast, the mean lengths of the smaller species Diaptomus tyrrelli and Bosmina longirostris did not differ significantly between Eunice Lake and the controls on any of the four dates examined. These observations are consistent with the results of Northcote et al. (1978), who found that cutthroat trout (added to Eunice Lake in 1974 and 1975) greatly preferred D. kenai and D. rosea to D. tyrrelli and B. longirostris. Interestingly,

Table 12. Lengths of *Daphnia rosea* in Eunice Lake and the controls, compared using Student t-tests on each date. Abbreviations: C=controls; LK=Eunice Lake; p=probability of significant inter-treatment difference (if less than 0.1); ns=no significant difference.

Date	Treatment	Mean Length of *Daphnia rosea* (mm)±SE (n) Juveniles	Adults
July 26	C	0.80 ± 0.027 (20)	1.32 ± 0.034 (20)
	LK	0.77 ± 0.057 (10)	1.24 ± 0.027 (10)
		ns	ns
Aug. 5	C	0.83 ± 0.024 (20)	1.31 ± 0.033 (20)
	LK	0.78 ± 0.053 (10)	1.21 ± 0.035 (10)
		ns	p=0.07
Aug. 23	C	0.95 ± 0.017 (20)	1.42 ± 0.038 (20)
	LK	0.82 ± 0.037 (10)	1.25 ± 0.035 (10)
		p=0.002	p=0.01
Sept. 13	C	0.97 ± 0.030 (13)	1.37 ± 0.038 (17)
	LK	0.81 ± 0.029 (10)	1.27 ± 0.040 (10)
		p=0.002	p=0.09

Northcote et al. attributed changes in the lengths of crustaceans primarily to increased competition between herbivores (following the elimination of Chaoborus predation) rather than to increased fish predation. By contrast, the length changes observed in my experiment suggest that fish predation did have a significant effect on Eunice Lake zooplankton. The difference between my results and those of Northcote et al. may be due to changes in the density of fish in Eunice Lake (higher in 1979 than 1976 (W.E. Neill, pers. comm.)).

Fish predation may have also affected the densities of D. rosea and D. kenai. As reported above, D. rosea densities were significantly higher in Eunice Lake than in the controls. Mean densities of D. kenai adults and juveniles were considerably higher in the control cylinders (0.22 ± 0.028 and 0.10 ± 0.03 L^{-1} respectively) than in Eunice Lake (0.08 ± 0.011 and 0.041 ± 0.016 L^{-1}) but statistically not significantly different ($p = 0.11$; Table 11).

3.2.2 Effects of Acidification

When comparisons were made between treatments A and C over the entire length of the experiment, there were no highly significant ($p < 0.01$) statistical differences in abundances, egg production or brood sizes of any of the major species (Table 11). Only Bosmina longirostris and copepod nauplii showed differences significant at $p < 0.05$. Though the controls showed significantly higher B. longirostris densities and egg

production ($p = 0.05$ and 0.02 respectively), the very low biomass of B. longirostris in both the controls and treatment A (Figure 11) makes this result of negligible importance at the community level. Similarly, the high variability and low densities of nauplii in both treatments C and A (Figure 16) diminishes the importance of the statistically significant ($p = 0.04$) difference in nauplii between these two treatments.

If acidification were to cause acute toxicity, one would expect to see mortality following the August 9 and September 20 acid additions, which generated the sharpest pH declines (Figure 12). The degree of exposure to such pH drops varied with the vertical distribution of the species, since only the upper 4 m were strongly acidified (See Section 3.2.5).

What happened after the August 9 acid addition? The major difference between treatments A and C during August 9 to 16 was the sharper drop in total zooplankton biomass and D. rosea densities in A (Figures 10 and 12). Since D. rosea abundances in A subsequently stabilized and were very similar to C (Figure 12), it seems unlikely that D. rosea mortality in A during August 9-16 was induced by the concurrent drop in mean pH from 6.3 to 5.7. The D. rosea populations in A and C were not exactly in phase. This leads me to believe that the observed differences between A and C on August 9 were due to my sampling schedule bracketing the peak abundances of D. rosea in the controls, but tracking the population in A.

After the September 20 acid dose, the abundances of D. rosea (Figure 12) were too low to clearly detect any increased mortality. Averaging together four acidification and four control cylinder samples taken after September 20 revealed lower densities of D. tyrrelli in A (0.19 ± 0.06 L^{-1}) than C (1.00 ± 0.50). The pH in the upper 4 m of the A cylinders averaged 5.36 during September 20 to October 11, the most acid conditions observed in this treatment. Although acid-induced mortality of D. tyrrelli is a possible explanation of the observed declines in A cylinders, the evidence is not compelling due to the relatively low densities of animals prior to the acidification.

Null hypothesis 2(i) (page 41) stated that gradual, experimental acidification of oligotrophic waters to pH 5.0 does not affect any zooplankton populations or community biomass. The treatment A cylinders did not reach pH 5.0 until the very end of the experiment, so that the null hypothesis was only tested definitively down to pH 5.6. It is impressive that at pH 5.6 (almost a tenfold increase in $[H^+]$) the zooplankton in treatment A cylinders appeared to be replicates of the controls; there were no differences in zooplankton populations or biomass.

Hypothesis 4(ii) (page 41) stated that nutrient enrichment during acidification does not alleviate acid-induced shortages of phytoplankton food. Since zooplankton in treatment A showed no evidence of increased food limitation (relative to the controls), this hypothesis became irrelevant to pH levels of 5.6 or higher.

3.2.3 Effects of Fertilization

The function of treatment F was first to test whether nutrient additions removed food shortages (particularly for the most acid-sensitive zooplankton species) and second, to serve as a control for the effects of acidification in the AF cylinders. Though fertilization had no apparent effect on *H. gibberum* or *D. kenai*, it significantly benefited *D. rosea*, *B. longirostris*, *D. tyrrelli*, *C. sphaericus*, and *D. brachyurum*. The two fertilization replicates were virtually identical, though *B. longirostris* was considerably more abundant in 1F than 8F.

Effects of fertilization on zooplankton biomass were most evident in the Cladocera. This was expected given their continuous recruitment and rapid rates of development. *D. rosea* and *B. longirostris* increased significantly over the controls in densities of both animals and eggs (Table 11). Mean brood sizes of *D. rosea* (Figure 13) and *B. longirostris* were also higher under fertilization (1.37 ± 0.07 and 1.12 ± 0.03 respectively) than in the controls (1.05 ± 0.13 and 0.90 ± 0.09) but these differences were statistically significant only for *D. rosea* (Table 11). *D. rosea* remained abundant for much longer in treatment F than in the controls, causing a highly significant treatment x time interaction term (Table 11). *C. sphaericus* appeared in the community one week earlier in treatment F than in C or A. Its biomass and densities were significantly greater in F than in treatment A or the controls (Figure 10 and Table 11).

Copepods respond to increases in food availability through more rapid growth and higher egg production, which after a time lag that is dependent on generation time and life history, shows up in increased abundance (see Smith 1969). Fertilization had several positive effects on D. tyrrelli. Relative to the controls, treatment F adults showed significantly higher attached egg production ($p = 0.002$; Table 11) and the geometric mean density of adults plus copepodites was also significantly higher ($p = 0.05$; Table 11). Over August 23 and 30 (i.e just after the nutrient additions) there were much higher mean densities of loose calanoid eggs in the F tubes (8.5±2.9 eggs$\bullet L^{-1}$ (SE;n=4)) than in the controls (1.5±0.6 eggs$\bullet L^{-1}$). When analyzed over the entire experiment however, the geometric mean densities of loose calanoid eggs in F were not significantly higher ($p = 0.09$; Table 11). Similarly, D. tyrrelli mean clutch sizes and percent ovigerous females were higher on August 23 and 30 in F (2.18 ± 0.12 eggs/female and 5.56 ± 1.58% ovigerous females) than in C (1.00 ± 0.35 eggs/female and 1.23 ± 0.44% respectively), but were not significantly different when compared over the whole season.

Since loose calanoid eggs were not identified to species, I cannot say definitively whether D. tyrrelli or D. kenai was responsible for late August increases in loose eggs. However, there was a significant increase in the total number of eggs carried by D. tyrrelli in F tubes (relative to the controls) and no such effect in D. kenai (C vs. F; Table 11). As these two diaptomid copepods did not appear to be differentially prone to

egg loss in sampling or laboratory handling, I suspect that D. tyrrelli contributed more to the large pool of loose calanoid eggs. In summary, D. tyrrelli appeared to benefit more from fertilization than did D. kenai.

Not surprisingly, the mean zooplankton biomass over all samples was significantly higher in the fertilized cylinders than in the controls (Table 10).

In conclusion, treatment F falsified null hypothesis 3(ii) (page 41), that moderate nutrient enrichment does not affect zooplankton populations or community biomass. However, enrichment did not shift the overall zooplankton community structure.

3.2.4 Effects of Combined Acidification and Fertilization

The AF treatment had in essence two "controls". Relative to treatment F, the AF cylinders showed the effects of acidification upon a nutrient enriched system. When compared to treatment A, AF illustrates the effects of enrichment of acidifying waters. I intended this latter comparison to reveal whether increased food resources benefitted acid-stressed zooplankton (page 13). However, the significantly lower pH levels in AF destroyed one of the necessary conditions for examining this question, namely, that the acid stress would be equivalent in both food limited (A) and food rich (AF) environments. Zooplankton would have more food in AF than in A, but would concurrently have to deal with greater acid stress. This represents an overly strong test of food limitation. After

performing the pH measurements on August 16, I considered increasing the acid additions to the A cylinders to produce similar pH levels to AF. However, due to the danger of overacidifying the A cylinders (which would weaken the test of food limitation), and my uncertainty at the time as to why pH differed in A and AF, I decided to continue to give the same amount of acid to the two treatments. I nevertheless was able to test the hypothesis of food limitation, by examining acid-stressed zooplankton populations in AF.

In the following pages, patterns of change in total zooplankton biomass and cladoceran composition are described first, followed by analyses of the responses of the two diaptomid copepods. The AF treatment produced the most interesting results of my experiment, and is therefore reported in considerably greater detail than the other treatments.

(i) Total Zooplankton Biomass and Response of Cladocera

Changes in community composition in AF centred on cladoceran species replacements, triggered largely by the loss of Daphnia rosea. From July 16 to August 9 zooplankton species composition and biomass were essentially identical in AF and F (Figure 10; Table 10). During this period, D. rosea populations in the AF and F cylinders had shown very similar behaviour, in terms of both densities of animals (Figure 12) and reproductive indicators (Figure 13). In treatment F, over the four samples from July 16 to August 9, the mean percentage of ovigerous females, mean brood size, and mean percentage of juveniles in

the population were (respectively) 25 ± 4.7% ovigerous, 1.41 ± 0.10 eggs per female and 52.5 ± 3.9% juveniles. In AF cylinders these statistics were very similar: 27 ± 4.9% ovigerous, 1.54 ± 0.16 eggs per female and 50.4 ± 4.1% juveniles respectively.

However, major pH drops between August 9 and 16 (Figure 7) were associated with massive mortality of D. rosea juveniles and adults in both AF tubes (Figure 12). It is interesting that D. rosea reductions were less severe in 7AF (81.7% between August 9 and 16) than in 3AF (98.4%). This variation in response of these two replicates was not likely due to differences in epilimnetic pH; the August 9 to 16 pH decline in 7AF (6.24 ± 0.05 to 5.34 ± 0.10) was very similar to that of 3AF (6.24 ± 0.05 to 5.29 ± 0.10). It is possible that D. rosea was distributed deeper in 7AF than 3AF on August 9 and therefore lost fewer individuals in the acid epilimnion. This hypothesis was suggested by my stratified samples from August 1, which showed 97% of the D. rosea juveniles and 93% of the adults above 4 m in 3AF, whereas in 7AF this stratum contained only 41% of the juveniles and 58% of the adults. It is not clear why the vertical distributions were different on August 1, nor whether the contrast in distributions of D. rosea was maintained until the acid additions of August 9.

Due to the collapse of D. rosea, the August 16 mean total zooplankton biomass in AF cylinders (24 ± 12 $\mu g \cdot L^{-1}$) was about one third that of the F cylinders (73 ± 8 $\mu g \cdot L^{-1}$), (Figure 10 and Table 10). Mean total zooplankton biomass in AF remained at 41-43% of that in F for August 23 and 30. D. rosea never

recovered in 3AF, but in 7AF adults persisted at low densities (0.50 ± 0.12 L^{-1}) from August 23 until September 13, during which time mean epilimnetic pH values varied from 5.5 ± 0.1 to 5.74 ± 0.01). D. rosea was absent however from samples taken in 7AF following the September 20 acidification, which reduced the mean epilimnetic pH from 5.77 ± 0.025 to 5.15 ± 0.05 (see Figures 7 and 12). These results suggest that a pH of 5.3 to 5.4 causes acute toxicity in D. rosea juveniles and adults.

How did the zooplankton community respond to the loss of D. rosea? Figure 14 shows an enormous increase in D. tyrrelli adults in cylinder 3AF between August 16 and 23 (from 2.8 L^{-1} to 23.4 L^{-1}) and a smaller but still substantial increase in 7AF on August 30. Since there were far too few copepodites to have generated such high numbers of adults, I believe these results are anomalous. The number of D. tyrrelli adults in treatment AF quickly dropped back down to "reasonable" levels, suggesting that the peaks on August 23 in 3AF and August 30 in 7AF were likely due to sampling errors. The sampling hose may have contacted dense "patches" of D. tyrrelli, or the animals may have suffered sublethal acid stress and been less able to escape capture.

With the exception of D. tyrrelli in these two samples, the major short term response to the loss of D. rosea was in the Cladocera, not the copepods. After a time lag of about three weeks, small, opportunistic cladocerans showed dramatic increases in densities, particularly in 3AF (Figure 10). The rapid growth of Chydorus sphaericus, and to a lesser extent

Bosmina longirostris and Diaphanosoma brachyurum, caused a 523% increase in treatment AF mean total zooplankton biomass in the week between August 30 and September 6 (Table 10); this is equivalent to 26.7% day^{-1} assuming exponential growth. Keen(1967) found that laboratory populations of C. sphaericus increased at 23.7% day^{-1} under high food conditions and temperatures of 25°C, and 15.7% day^{-1} at 15°C. Since the AF populations of C. sphaericus were mostly found at 5-7 m and temperatures of 8-14°C (Section 3.2.5), the observed rate of increase was exceptionally high. A shift in the distribution of C. sphaericus from the sides of the enclosures to the centre may have been partially responsible for the very large increase (See discussion in Section 4.4.1 (iv)).

In spite of these sharp biomass increases in AF tubes, overall geometric mean densities of B. longirostris were not significantly different between treatments AF and F (Figure 17 and Table 11). The same was true for C. sphaericus although mean densities during August 30 to October 11 were seven times higher in AF than F (75 ± 32 L^{-1} and 10.3 ± 2.5 L^{-1} respectively). Note that C. sphaericus fluctuations in both AF cylinders were out of phase with other small cladocerans during most of September (Figure 11). I did find significant differences between treatments AF and F in geometric mean densities of D. brachyurum and Ceriodaphnia pulchella. These two cladocerans were rare in both F cylinders, common in 7AF during September and abundant in 3AF on several sampling dates. (D. brachyurum reached peak densities of 21.3 L^{-1} on September

13 in 3AF.)

Cylinder 3AF showed higher total biomass than 7AF between September 6 and 27 (Figure 10). This difference was primarily due to higher populations of B. longirostris, D. brachyurum and C. pulchella in 3AF, though mean densities of Chydorus sphaericus during September tended to be higher in 3AF (91 ± 37 animals•L^{-1}) than in 7AF (47 ± 19 L^{-1}) as well. The varied response in the AF replicates may be indirectly due to differences in the August 9-16 D. rosea declines (to be discussed in Section 4.4).

In contrast to the relatively constant total zooplankton biomass of the F tubes, AF total zooplankton biomass showed a large amplitude 3 week fluctuation during September, with peaks on September 6 and 27 (Figure 10). By October 11, the total biomass in AF was again similar to F (58 ± 30 and 48 ± 25 $\mu g \cdot L^{-1}$ respectively). The arithmetic mean total biomass in AF over the whole experiment was not significantly different from F (Table 10), though the variability in AF (as measured by overall standard error) was twice that of the F cylinders.

Statistical tests on densities, egg production, and brood sizes generally confirmed the above patterns in cladoceran abundance and succession, but for D. rosea yielded some surprising results (Table 11). The density of adult plus juvenile D. rosea, and the total number of daphnid eggs, were significantly lower in AF than F, as would be expected. However, there was no significant difference in overall geometric mean brood sizes per ovigerous female between

treatments F and AF (1.37 ± 0.07 and 1.53 ± 0.24 eggs/female respectively).

Numbers of ovigerous D. rosea females counted in 3AF were too low to give reliable mean brood sizes after August 9 (see Figure 13). However, cylinder 7AF mean brood sizes between August 23 and September 13 were all based on more than 15 ovigerous females per sample (mean of 31 ± 9.3) and hence the sample sizes are sufficiently large to yield meaningful statistical comparisons. Comparing cylinder 7AF with treatment F cylinders between August 23 and September 13, I found the mean percentage of ovigerous females and mean brood sizes (uncorrected for body size) to be much higher in the acid-stressed population of cylinder 7AF (38.3 ± 4.8% and 3.28 ± 0.23 respectively) than in the two F cylinders (20.0 ± 3.7% and 1.16 ± 0.04).

Differences in brood sizes and percentages of ovigerous females between cylinder 7AF and treatment F were partially due to differences in the age structure of the populations. The mean percentage of juvenile D. rosea was much lower in 7AF (4.4 ± 1.6% juveniles) than in the F cylinders (14.6 ± 4.9%). Since the postnatal development time of D. rosea juveniles at 18-20°C, neutral pH and "high" seston concentration (1.0 mg•L^{-1}) is 6 to 7 days (Neill 1981b), more juveniles "should" have been seen in 7AF in late August and early September. Their absence suggests that following August 9, the "bottleneck" for D. rosea was survival through the embryo and/or neonate stages. The adult D. rosea in 7AF were able to produce eggs at a relatively high

rate (possibly assisted by a reduction in intraspecific competition) but at pH levels of 5.4 to 5.6 relatively few of these eggs developed into first instar juveniles. (The possible reasons for this are discussed in Section 4.4.1(i).) Through late August and September, the population age structure in 7AF became strongly weighted towards larger, older adults with ample brood pouches. This is evident from the significantly higher mean lengths of D. rosea adults on September 13 in treatment AF (1.79 ± 0.051 (n=17)) than in treatment F (1.46 ± 0.046 ,n=20); ($p<0.0001$ (t-test), see Appendix E). Scaling brood sizes according to body lengths (Hebert 1978) would likely yield similar brood sizes for treatments F and AF between August 23 and September 13.

D. rosea densities were significantly lower in AF than A, in spite of significantly greater mean egg densities in AF (Table 11). The toxicity effects caused by the lower pH in treatment AF apparently overwhelmed the benefits of increased food.

(ii) Response of Diaptomid Copepods

The copepod response to acidification and fertilization was divergent: Diaptomus tyrrelli appeared acid sensitive but Diaptomus kenai was acid tolerant. D. tyrrelli adults did not decline in AF after the August 9 acid solution, but declined rapidly to zero after the September 20 acidification (Figure 14)). By contrast, D. tyrrelli maintained their densities during September 13-27 in the F cylinders.

D. tyrrelli adults were therefore slightly less acid sensitive than D. rosea adults and juveniles. Even including the high peak (suspected sampling error) on August 23 in Bag 3AF, the geometric mean densities of D. tyrrelli were significantly higher in F than AF (Table 11). This result is due to the consistently low densities of D. tyrrelli in AF cylinders after September 13. Attached egg production by D. tyrrelli did not differ significantly between AF and F (Table 11).

Unlike D. tyrrelli, Diaptomus kenai showed no negative impacts from acidification in AF, and in some respects performed better there than in treatment F. D. kenai geometric mean densities were higher in AF than F, (0.30 ± 0.018 and 0.20 ± 0.019 L^{-1} respectively), although this difference was not significant ($p = 0.058$, Table 11). When analyzed over the whole experiment, geometric mean densities of attached D. kenai eggs also did not differ significantly between F and AF (Table 11). However, mean densities of attached D. kenai eggs were higher in AF than F after the collapse of Daphnia (i.e. from August 23 to October 11): 0.47 ± 0.14 eggs•L^{-1} in AF; and 0.19 ± 0.055 eggs•L^{-1} in F.

A clearer difference between AF and F is in the geometric mean number of loose copepod eggs, which were significantly higher in AF ($p = 0.004$; Table 11 and Figure 16). Although these loose eggs were not identified to species, the timing of calanoid copepod attached egg production suggests that (unlike in treatment F) many of the loose eggs could be due to D. kenai (Figures 14 and 15). I hypothesize that the acid-induced

elimination of D. rosea in treatment AF increased the availability of resources to D. kenai resulting in greater attached and loose egg production. Also, the mean length of D. kenai adults was significantly higher ($p=0.0012$, t-test) in treatment AF (2.06 ± 0.025, $n=20$) than in treatment F (1.91 ± 0.039, $n=17$) on September 13, suggesting improved growth in AF.

3.2.5 Vertical Distribution

Both copepods and cladocerans commonly show vertical migrations near sunset and sunrise (Wetzel 1975). My two daytime stratified samplings on August 1 and September 6) were taken between the hours of 10 a.m. and 5 p.m., and therefore represent only the daytime distribution. Nonetheless, these data give a preliminary indication of:

1. the mean temperatures at which eggs and juveniles of each species were developing;
2. the degree to which particular species were exposed to acid epilimnetic waters;
3. the spatial overlap in daytime distributions of different species, and
4. treatment effects on vertical distributions.

Vertical distributions of adult forms of selected species are shown in Figures 18 and 19. Neither the August 1 nor September 6 samplings revealed vertical migrations for any of the species when their vertical distributions were examined in a sequence corresponding to the time of sampling. Accurate

Figure 18. Vertical distributions of adult forms of zooplankton. Graphs show % of population at each of four strata: 0-2 m; 2-4 m; 4-6 m; and 6-8 m.; Vertical distributions omitted if fewer than 10 animals counted. Species abbreviations: KA = D. kenai adults; TA = D. tyrrelli adults; DA = D. rosea adults; DOF = D. rosea ovigerous females BA = B. longirostris adults; CHYA = C. sphaericus adults. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

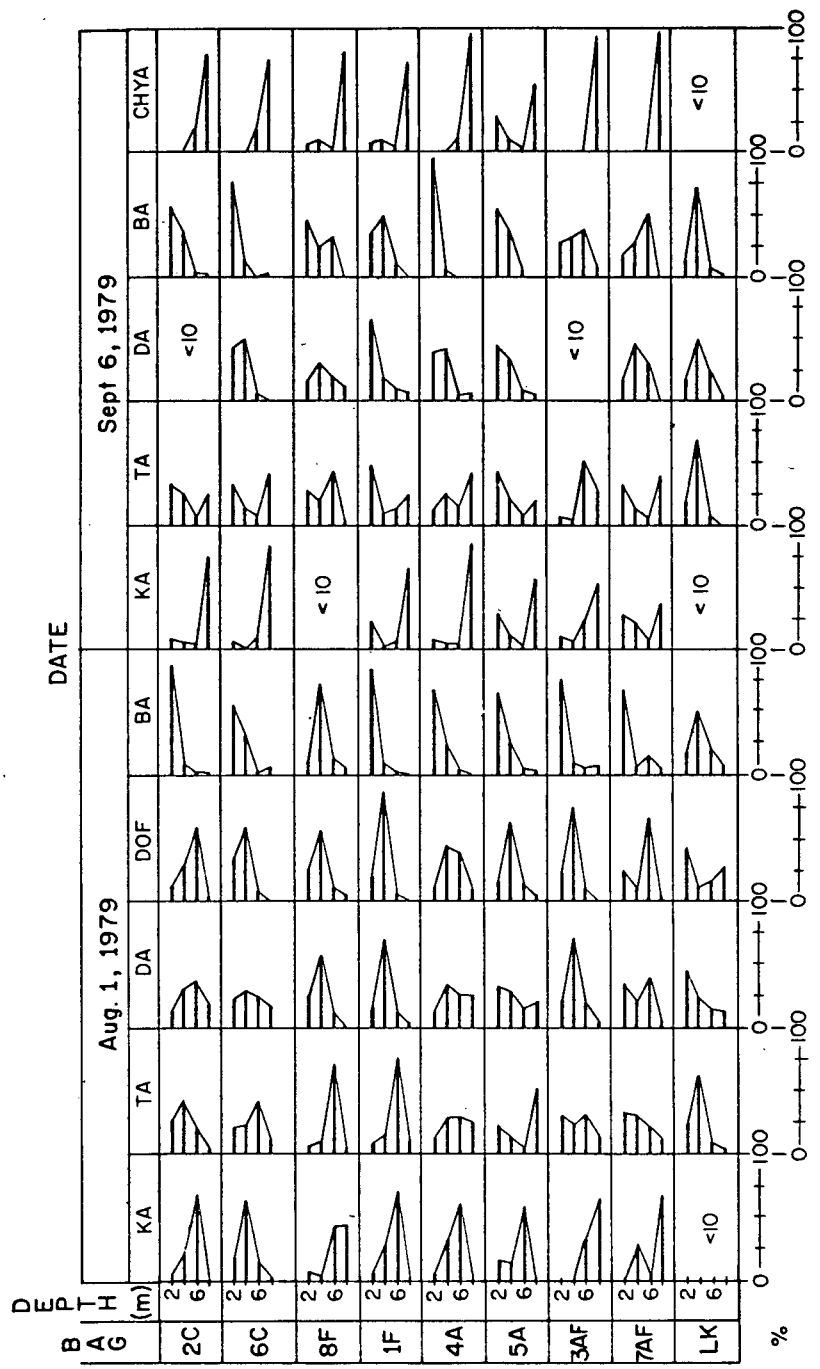

DATE
Aug. 1, 1979
Sept 6, 1979
BAG
DEPTH (m)
KA
TA
DA
DOF
BA
CHYA
2C
6C
8F
1F
4A
5A
3AF
7AF
LK
<10
%
0
100

Figure 19. Vertical distributions of immature forms of zooplankton, and Diaphanosoma brachyurum. Graphs show % of population at each of four strata: 0-2 m; 2-4 m; 4-6 m; and 6-8 m.; Vertical distributions omitted if fewer than 10 animals counted. Species abbreviations: TJ = D. tyrrelli juveniles; DJ = D. rosea juveniles; BJ = B. longirostris juveniles; CHJ=C. sphaericus juveniles; N = copepod nauplii; DIA = D. brachyurum adults and juveniles. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

DATE
Aug. 1, 1979
Sept. 6, 1979
BAG
DEPTH (m)
TJ
DJ
BJ
N
TJ
DJ
BJ
CHJ
N
DIA
2C
6C
8F
1F
4A
5A
3AF
7AF
LK
2
6
<10
%
0
100

assessment of time of day effects on vertical distributions would have required several 24-hour samplings of the enclosures in random order.

Some consistent trends in species' vertical distributions are seen in Figures 18 and 19. Diaptomus kenai adults were mostly in the cooler waters below 4 m and therefore shielded from the acid epilimnion. Insufficient numbers of D. kenai copepodites were counted to warrant graphs of their vertical distribution. Of the 15 vertical distributions of D. kenai adults in Figure 18, the greatest proportion of animals was at 6-8 m in ten cases, and at 4-6 m in four. The pattern of concentrating at lower depths is sharpened by the fact that in 12 of these 14 "deep peak" cases the proportions within the densest 2 m stratum were greater than 50%. Fedorenko (1975a, 1975b) found a distinct reverse vertical migration in Eunice Lake D. kenai (i.e. deeper at night), but this pattern may have changed with the elimination of Chaoborus in 1976. No clear differences in D. kenai distribution were evident between treatments.

Though most commonly found at 4-6 m, Diaptomus tyrrelli adults were much more equitably distributed through the water column than were D. kenai, B. longirostris, or C. sphaericus. Copepodites were on average 2 m higher in the water column, most commonly concentrated at 2-4 m. In general, variability in D. tyrrelli vertical distributions appeared as large within treatments as between. Significant fractions of the adult and juvenile populations in A and AF cylinders were found in the

epilimnion, and therefore susceptible to acid stress. Fedorenko (1975a, 1975b) observed no vertical migration in Diaptomus tyrrelli. Olenick (1982) determined the diurnal and nocturnal vertical distributions of enclosed Eunice Lake zooplankton on July 5-6 and September 18-19, 1979. On both dates, diurnal samples showed 50% of D. tyrrelli adults and 50% of the copepodites at 0-2m (percentages based on total numbers of animals in all enclosures). Nocturnal distributions were about 2m lower. It is not clear why the diurnal distribution of D. tyrrelli was somewhat higher in Olenick's enclosures than in mine.

Daphnia rosea females (both ovigerous and nonovigerous) were evenly distributed in a manner similar to D. tyrrelli adults, and were therefore also within the acidified zone. Juvenile D. rosea showed distributions strikingly similar to D. tyrrelli copepodites in 5 of the 12 cases where both species contained sufficient numbers to permit comparison; in only one of 12 cases (cylinder 4A on September 6) were the two species' juvenile forms distributed very differently. Replication within C, A, and F cylinders was good enough on August 1 to permit cautious comparisons between these treatments; adults and juveniles were equitably (and similarly) distributed in treatment A and the controls, but showed consistent clumping at 2-4 m in the F cylinders.

In Section 3.2.4(i), I noted that the relatively deep distribution of D. rosea adults and juveniles in cylinder 7AF on August 1 may have accounted for the better survival of D. rosea

in 7AF than 3AF. Olenick (unpublished data) observed day to night shifts in the vertical distribution of Eunice Lake D. rosea in only 8 of 21 stratified samples, and 6 of these 8 were downward shifts. Therefore, my daytime samples are probably reasonable estimators of maximum acid exposure.

Bosmina longirostris was the most surface-oriented species of the community and therefore experienced the greatest exposure to acid conditions. Clumping in the 0-2 m stratum was evident for adults in 11 of 18 samples, and for juveniles in 11 of 16 cases. In these cases, the proportions of animals at 0-2 m were relatively high, averaging 75 ± 3.1% (n = 22). B. longirostris was consistently segregated from Chydorus sphaericus, but these two species are often found together at night near the surface of the water (W.E. Neill, pers. comm.).

Chydorus sphaericus was not in sufficient abundance on August 1 to examine its vertical distribution. On September 6, both juveniles and adults were clumped at 6-8 m in all eight cylinder samples, with mean proportions of 83 ± 5% and 84 ± 4%. If those chydorids sampled at 6-8 m remained there consistently, they would never have been exposed to pH levels below 5.9. However, C. sphaericus has frequently been recorded as displaying an upward vertical migration after sunset (Meyers 1980, W.E. Neill pers. comm.), and therefore was likely exposed to the more acid zone.

The vertical distributions of more minor constituents of the plankton (Holopedium gibberum, copepod nauplii, and Diaphanosoma brachyurum) were also examined. In the five cases where

sufficient numbers were present to estimate the vertical distribution, most H. gibberum were in the 0-2 m stratum. Most copepod nauplii were found near the surface as well; 9 of the 11 graphs in Figure 19 show more than half the nauplii in the top 2 m. D. brachyurum only had sufficient numbers for analysis in treatment AF, where it was centered about the 2-4 m stratum.

3.3 Phytoplankton and Phytoplankton-Zooplankton Interactions

3.3.1 Effects of Enclosure

The phytoplankton of the control enclosures were compared to Eunice Lake to see if differences were apparent in either mean conditions or temporal patterns. Table 13 shows that mean chlorophyll and phaeophytin a levels in the controls were not significantly different from Eunice Lake. However, chlorophyll concentrations did not peak so sharply in the control cylinders as in the lake during September (Figure 20), perhaps due to greater nutrient replenishment in the lake following the storms of September 1 to 9 (Figure 4, page 47). These storms would have transported large quantities of nutrients from both Eunice and particularly Gwendoline Lakes' watersheds, since Gwendoline was experimentally fertilized in the summer of 1979 (C.J. Walters, pers. comm.).

Other phytoplankton indicators differed between the controls and Eunice Lake. Mean total algal biomass was higher ($p = 0.014$) in the lake (0.85 ± 0.11 mg$\bullet L^{-1}$) than in the controls (0.58 ± 0.08), with the bulk of this biomass difference contributed by the colonial green alga Gleocystis sp in the 13-18 μm size category (Tables 14 and 15, Figures 21, 22 and 23). These colonies formed between 52 and 90% of the total phytoplankton volume in the August and September lake samples (Appendix F). Prior to August 1, both Eunice Lake and control cylinder samples were dominated (volumetrically) by colonies of the chrysophyte Dinobryon, which were classified in the > 30μm

Table 13. Results of analyses of variance on chlorophyll measurements. (See Table 11 for abbreviations and degrees of freedom.)

Variable	Treatment Geometric Means ± SE (µg/l)				
	LK	C	F	A	AF
Chlorophyll *a*	0.39 ± 0.049	0.32 ± 0.036	0.51 ± 0.044	0.36 ± 0.031	1.39 ± 0.11
Pheophytin *a*	0.38 ± 0.030	0.41 ± 0.025	0.87 ± 0.056	0.42 ± 0.027	1.82 ± 0.10

Variable	Treatment Comparison				
	C vs. LK	C vs. A	C vs. F	F vs. AF	A vs. AF
Log (Chlorophyll *a*)	ns (0.13)	ns (0.31)	F (0.00002)	AF (10^{-5}) IH	AF (10^{-5}) IH
Log (Pheophytin *a*)	ns (0.23)	ns (0.81)	F (10^{-5}) IH	AF (10^{-5}) IH	AF (10^{-5}) IH

Figure 20. Live chlorophyll *a* and phaeophytin *a*. Note missing sample on August 9 in 7AF; estimated chlorophyll concentration (based on Secchi depth - chlorophyll regression equation in Table D1) is 0.5 $\mu g \cdot L^{-1}$. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization. Note also no samples taken between August 30 and September 13.

1979 CHLOROPHYLL A

LIVE CHLOROPHYLL a

PHAEOPHYTIN a

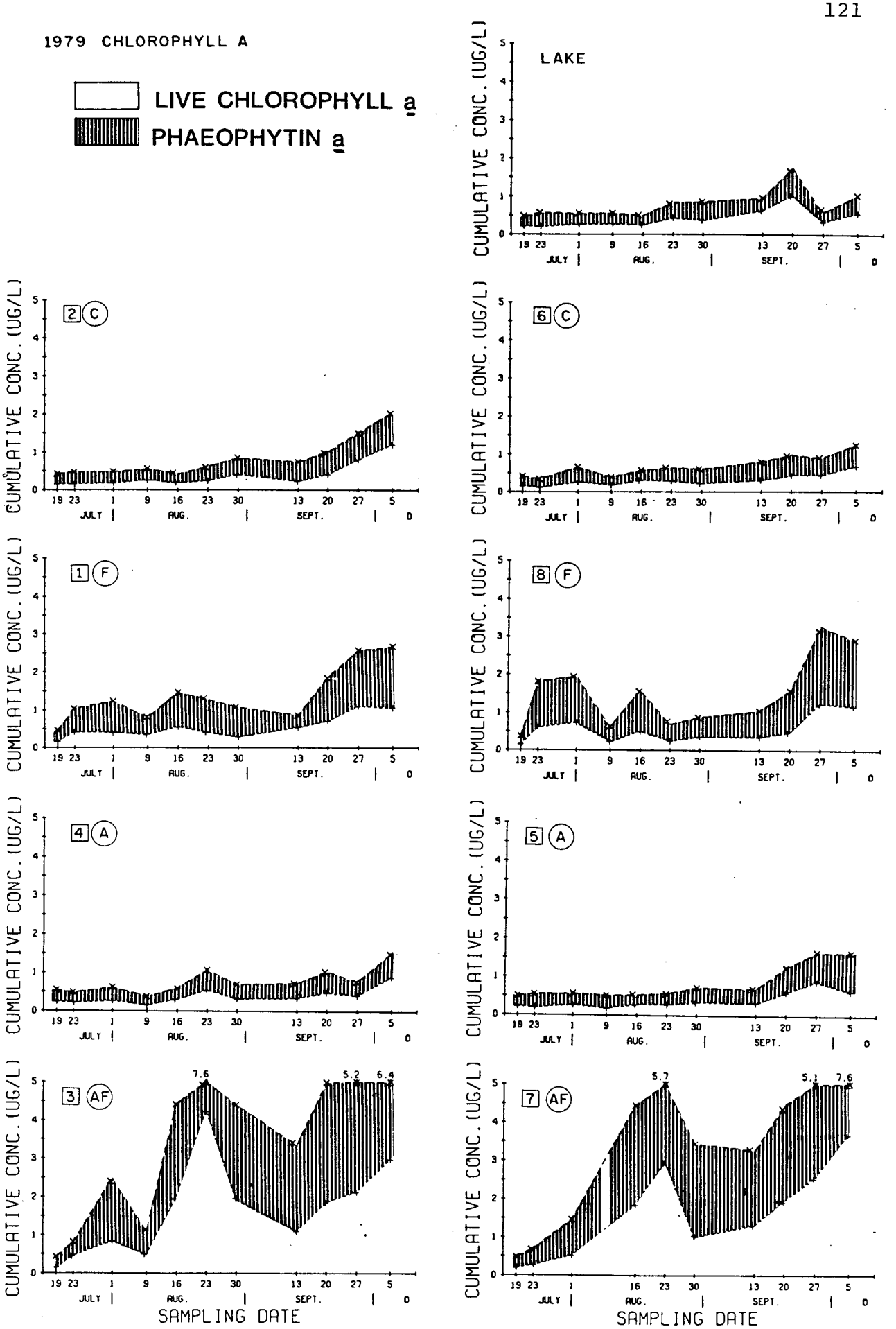


Table 14. Results of analyses of variance on algal volumes in particular size classes. See Table 11 for abbreviations and degrees of freedom.

Cell Size Class Used for Volume Comparisons	Treatment Comparison				
	C vs. LK	C vs. A	C vs. F	F vs. AF	A vs. AF
< 13 µm*	LK(0.03)IH	ns(0.19)	F (0.002)IH	ns(0.86)IH	AF(0.001)h
< 2 µm	ns(0.13)	ns(0.56)	C (0.037)H	AF(0.046)h	ns(0.49)
2-5 µm	C(0.027)	ns(0.54)	ns(0.67)	AF(0.013)h	AF(0.026)h
5-9 µm	LK(10^{-5})IH	ns(0.78)	F (0.0002)IH	ns(0.63)I	AF(0.004)h
9-13 µm	ns(0.19)	ns(0.17)	C (0.0036)IH	ns(0.17)IH	AF(0.025)Ih
13-18 µm	LK(0.0006)	ns(0.57)	C (10^{-4})IH	ns(0.85)	A (10^{-5})IH
18-30 µm	ns(0.12)H	ns(0.8)	ns(0.28)	AF(0.023)H	AF(0.009H
> 30 µm	ns(0.94)	ns(0.41)	C (10^{-5})IH	AF(0.028)Ih	A (0.003)I
Filaments	ns(0.92)	ns(0.52)H	ns(0.4)H	AF(0.019)h	AF(0.002)H
Total Algal Biomass	LK(0.014)	ns(0.55)	C (0.0005)	AF(0.005)ih	ns(0.60)h

* Accumulated from separate size categories.

Table 15. Mean percentage of algal volume in particular size classes, by treatment (± SE).

Cell Size Class Used for Proportion Comparisons	Treatment				
	LK	C	A	F	AF
< 5 µm*	3.4 ± 0.5	12.0 ± 2.4	10.5 ± 2.9	20.3 ± 3.3	15.0 ± 2.7
5-9 µm	4.3 ± 0.8	2.8 ± 0.6	2.7 ± 0.7	12.8 ± 2.4	4.9 ± 1.0
9-13 µm	2.2 ± 0.7	2.2 ± 0.6	2.7 ± 0.6	10.8 ± 2.4	6.3 ± 2.0
13-18 µm	57 ± 9.7	38 ± 6.1	38 ± 6.3	18.2 ± 2.9	11.8 ± 2.5
> 18 µm*	33 ± 9.2	45 ± 6.5	46 ± 6.2	36.2 ± 5.5	57.7 ± 5.2
Filaments	0.19 ± 0.1	0.4 ± 0.2	0.3 ± 0.2	1.8 ± 1.1	4.2 ± 1.3

* Accumulated from separate size categories.

Figure 21. Algal biomass by major size classes. See Figure 22 and Table 15 for detailed size breakdown. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

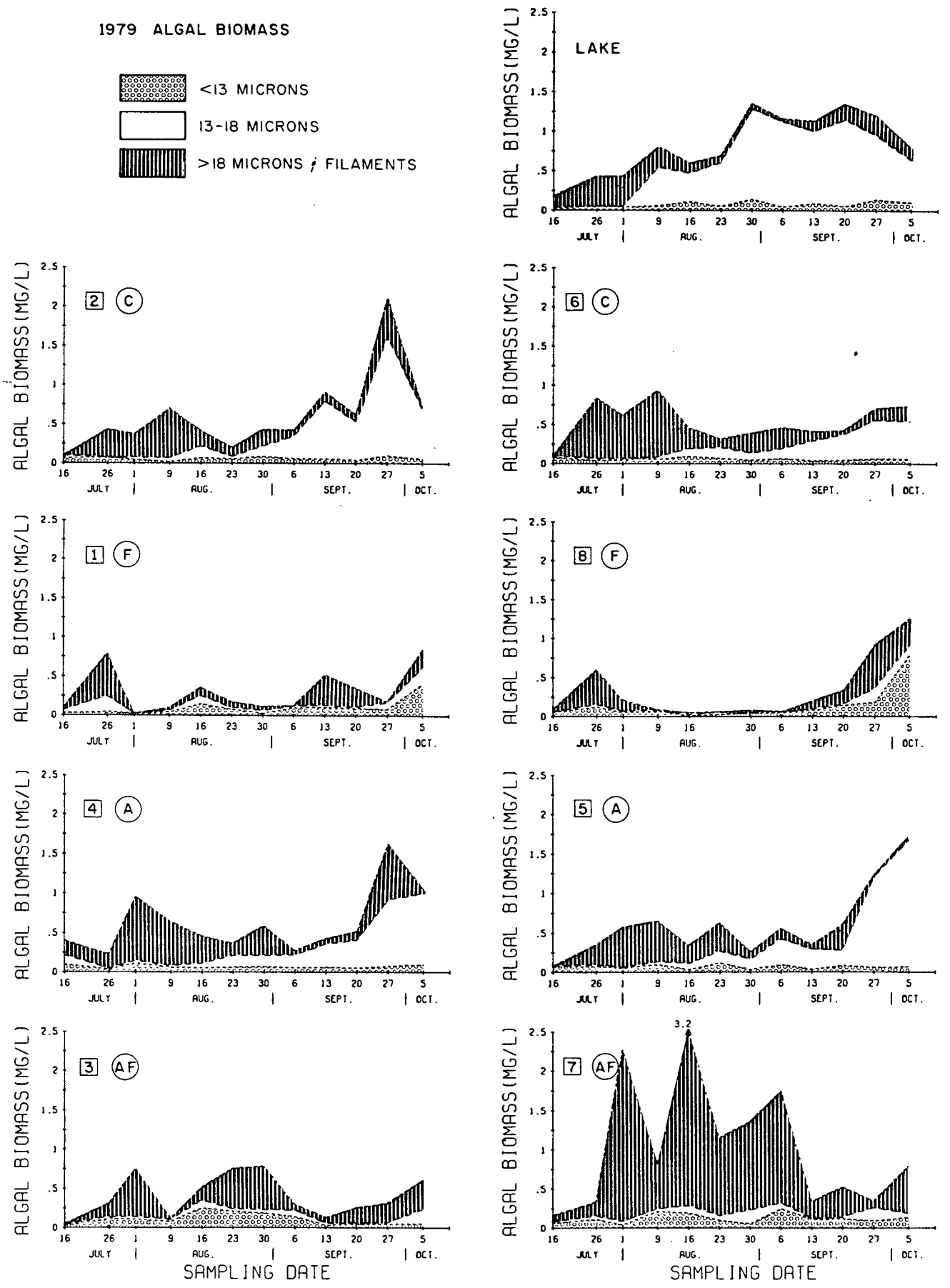

1979 ALGAL BIOMASS
<13 MICRONS
13-18 MICRONS
>18 MICRONS / FILAMENTS
LAKE
2 C
6 C
1 F
8 F
4 A
5 A
3 AF
7 AF
3.2
ALGAL BIOMASS (MG/L)
0 .5 1 1.5 2 2.5
16 26 1 9 16 23 30 6 13 20 27 5
JULY | AUG. | SEPT. | OCT.
SAMPLING DATE

Figure 22. Percent composition of algal biomass by detailed size classes. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

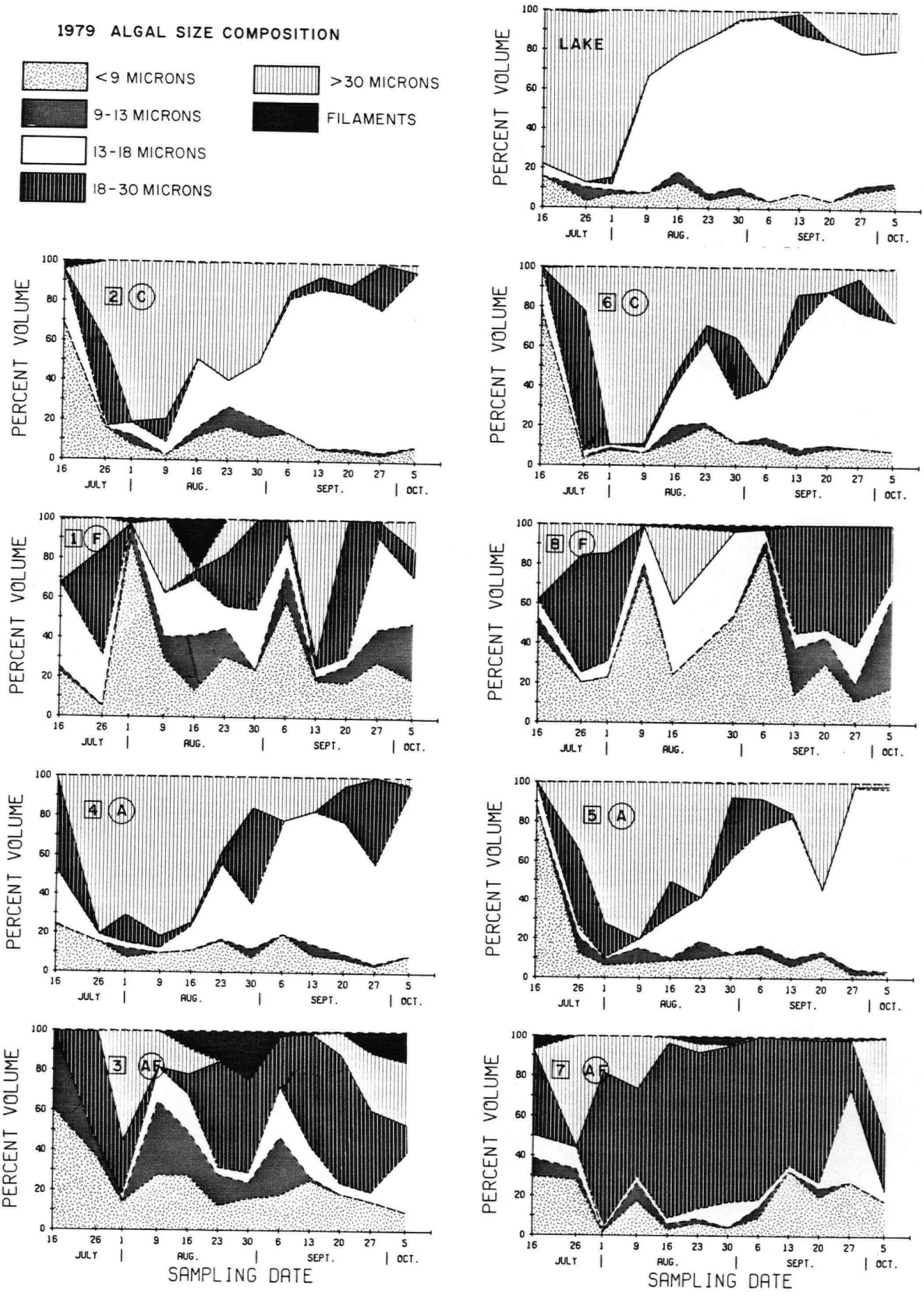
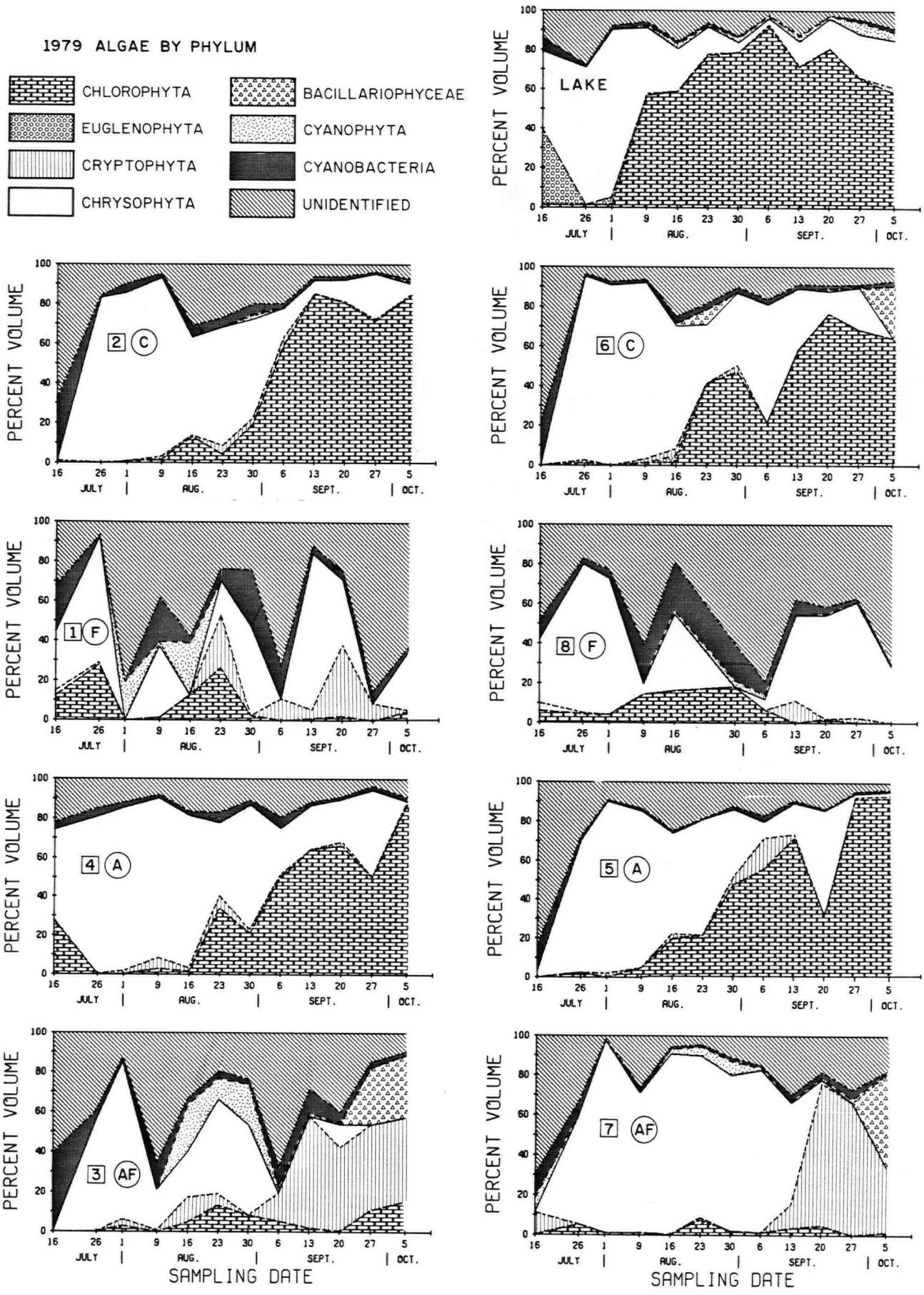

1979 ALGAL SIZE COMPOSITION
<9 MICRONS
9-13 MICRONS
13-18 MICRONS
18-30 MICRONS
>30 MICRONS
FILAMENTS
LAKE
2 C
6 C
1 F
8 F
4 A
5 A
3 AF
7 AF
PERCENT VOLUME
JULY
AUG.
SEPT.
OCT.
SAMPLING DATE

Figure 23. Phyletic composition of algal volume. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.


1979 ALGAE BY PHYLUM
CHLOROPHYTA
EUGLENOPHYTA
CRYPTOPHYTA
CHRYSOPHYTA
BACILLARIOPHYCEAE
CYANOPHYTA
CYANOBACTERIA
UNIDENTIFIED
LAKE
2 C
6 C
1 F
8 F
4 A
5 A
3 AF
7 AF
PERCENT VOLUME
0 20 40 60 80 100
16 26 1 9 16 23 30 6 13 20 27 5
JULY | AUG. | SEPT. | OCT.
SAMPLING DATE

size class due to their 45 μm long loricas. The shift in dominance from Dinobryon sp. to Gleocystis that occurred in Eunice Lake about August 1 also occurred in the control cylinders, but not until September 6 to 13 (Figure 23 and Appendix F). These differences in dominant taxa explain why the proportion of algal volume in size classes greater than 13 μm differed between the lake and the controls (Figure 22 and Table 15).

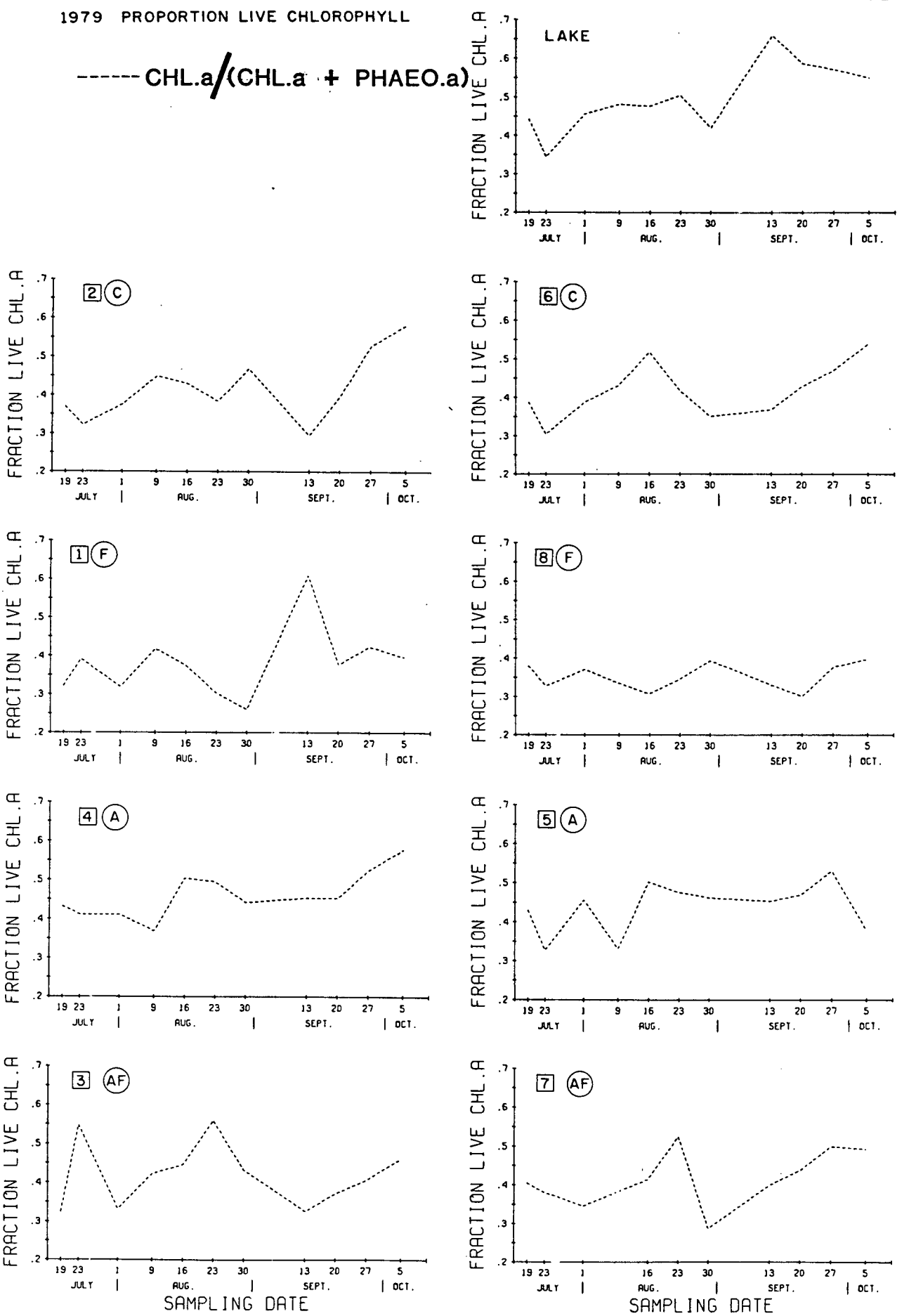
The mean volume in algal cells less than 13 μm in diameter was greater in the lake (0.076 ± 0.012 μm^3) than in the controls (0.060 ± 0.004), a difference significant at $p = 0.03$ (Table 14). I suspect that most cells of this size were capable of being ingested and digested by zooplankton (Burns 1968; Porter 1973, 1977). It is possible that cutthroat trout predation in Eunice Lake lessened the herbivorous grazing pressure on these small algal cells, or that lower light levels in the controls affected primary production.

It is difficult to assess inter-treatment differences in the proportion of live chlorophyll a or mean algal chlorophyll content, since these ratios are sensitive to variability in both the numerator and denominator. The proportion of live chlorophyll a (Figure 24) rose sharply in Eunice Lake between August 30 and September 13 (during the period of high precipitation) but did not increase in the controls. Examined over the whole experiment, the mean proportion of live chlorophyll a was higher in Eunice Lake (49.8 ± 2.6%) than in the controls (41.8 ± 1.6%). Mean algal chlorophyll content

Figure 24. Proportion of live chlorophyll a. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

1979 PROPORTION LIVE CHLOROPHYLL

------ CHL.a/(CHL.a + PHAEO.a)



(Figure 25) did not differ significantly between Eunice Lake (0.50 ± 0.062 μg chlorophyll • (mg algal biomass)$^{-1}$) and the control cylinders (0.68 ± 0.086).

Phase planes of the simultaneous changes in live chlorophyll a and zooplankton biomass (Figure 26) illustrate inter-treatment differences in plankton system behaviour. It should be stressed that chlorophyll a is an inaccurate index of edible algal biomass, and total zooplankton biomass represents a group of herbivores rather than a single herbivore. Nevertheless, the phase planes in Figure 26 illustrate the overall effect of plant-herbivore interactions, and seasonal changes in primary and secondary production. I did not graph phase planes of total zooplankton biomass vs total algal biomass due to poor estimation of algal biomass in the larger size classes (Section 2.2.2 (ii)).

Phase plane trajectories in the control cylinders diverged from the path shown in Eunice Lake. The control cylinders both showed an initial cycle in late July and early August, but then dwindled to low zooplankton densities by late September, despite relatively high chlorophyll a concentrations. By contrast, the lake managed to maintain total zooplankton biomass throughout September and October. I suspect that the October revival of Eunice Lake zooplankton biomass may have been caused by increases in primary production following the storms of early September, but do not have measurements to test this possibility.

Figure 25. Chlorophyll a per unit algal biomass. Computed by dividing live chlorophyll a by total algal biomass. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

1979 ALGAL CHLOROPHYLL CONTENT

------ CHL. A/ALGAL BIOMASS

● ALGAL BIOMASS INTERPOLATED (July 19 & 23)

○ CHLOROPHYLL A INTERPOLATED (July 26 & Sept. 6)

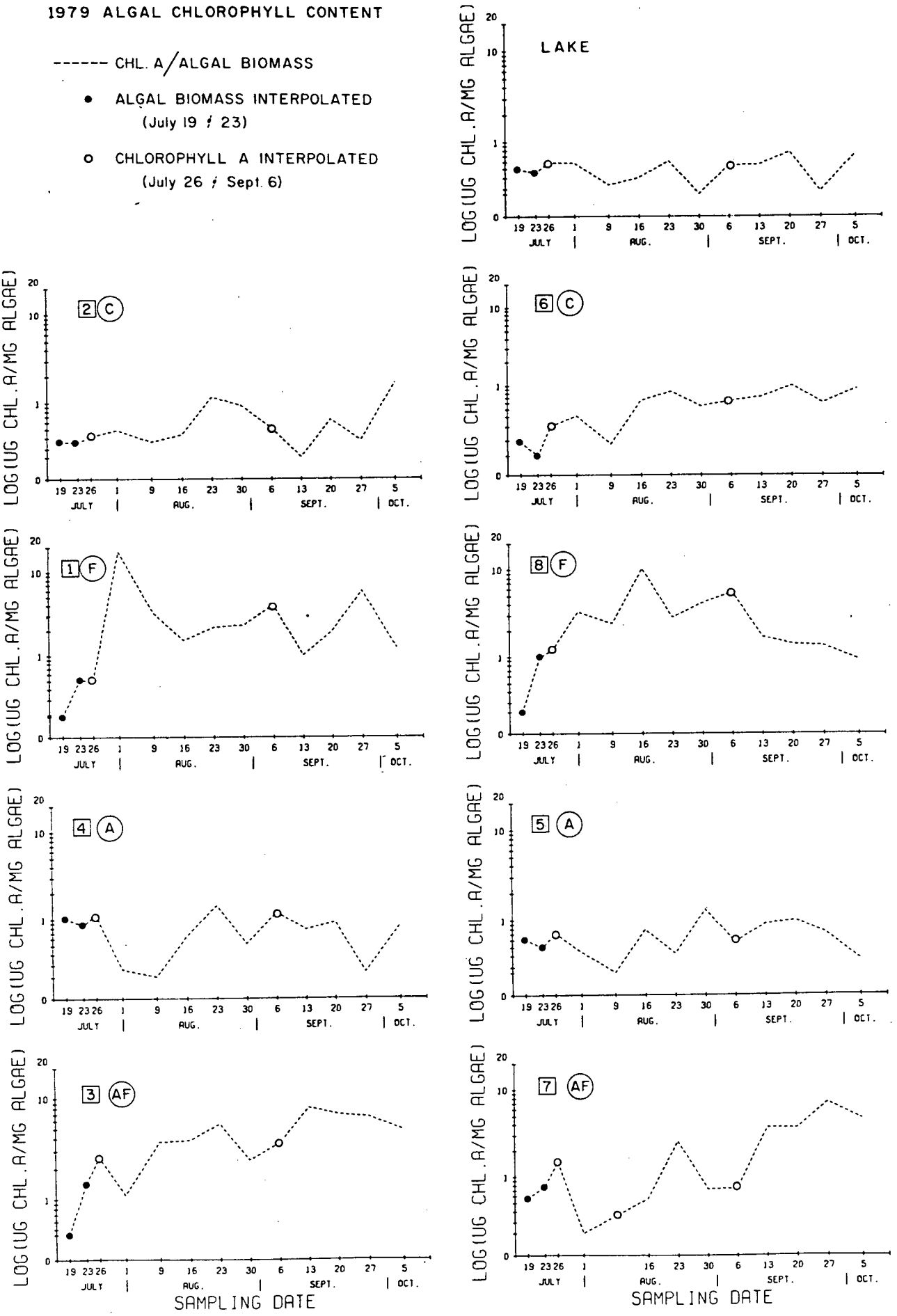
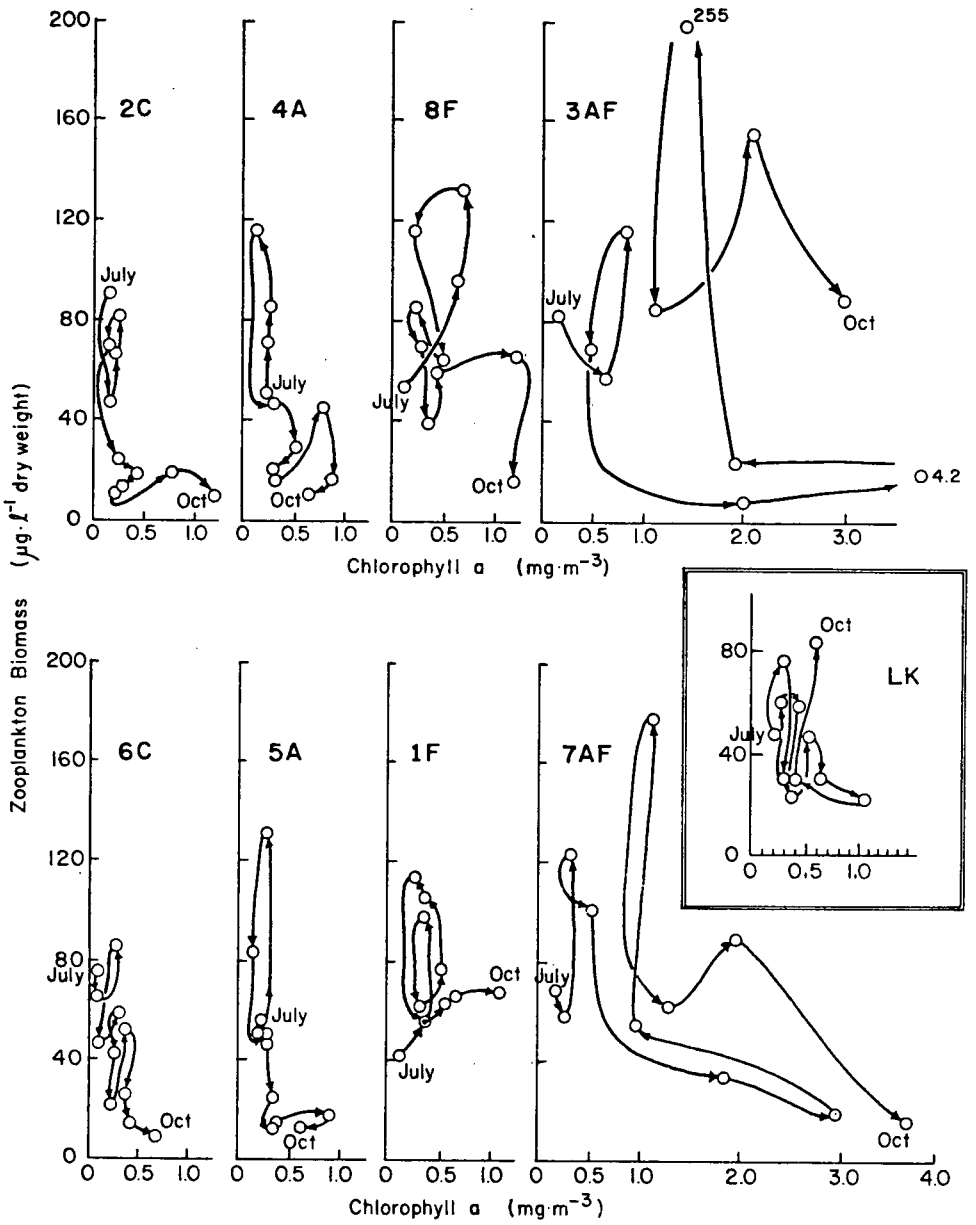


Figure 26. Phase plane trajectories through time of total zooplankton biomass and live chlorophyll *a* concentrations . Points describe values of these two variables on July 16 and 26; August 1, 9, 16, 23 and 30; September 6, 13, and 27; and October 11. The trajectory of enclosure 1F passes through the same point twice. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.


2C
4A
8F
3AF
6C
5A
1F
7AF
LK
July
Oct
255
4.2
Zooplankton Biomass (μg·l⁻¹ dry weight)
Chlorophyll a (mg·m⁻³)

3.3.2 Effects of Acidification

The behaviour of phytoplankton indicators in treatment A was remarkably similar to the controls. None of the phytoplankton characteristics shown in Figures 20 to 25 (and compared in Tables 13 to 15) differed significantly between the acidification cylinders and the controls. Other than demonstrating higher zooplankton biomass in early August, the A cylinder phase planes of total zooplankton biomass and chlorophyll (Figure 26) were qualitatively similar to the controls. In terms of available food for zooplankton, it is noteworthy that the volume of "small, mostly edible" algal cells (less than 13 μm in diameter) did not decrease in the A cylinders during the most acid period (August 9 to 30) when the mean epilimnetic pH was 5.72 ± 0.06. There were also no major shifts in other size classes of algae relative to the controls during August (Figure 22). Though it is possible that the taxonomic composition within particular size categories could have shifted to less palatable species, partial taxonomic identifications did not reveal any changes in major taxa (Appendix F).

Null hypothesis 2(ii) (page 41) stated that acidification to pH 5.0 does not affect phytoplankton community biomass and size composition. The results provide no evidence against this hypothesis, at least for acidification to pH 5.6. Most importantly, the abundance of small, mostly edible forms of algae did not change. This is consistent with the absence of any evidence of increased food limitation of zooplankton in

treatment A (Section 3.2.2).

3.3.3 Effects of Fertilization

Treatment F contained significantly higher chlorophyll *a* and phaeophytin *a* concentrations than the controls (Table 13). Wetzel (1975, page 353) list 0.3-3 $\mu g \cdot L^{-1}$ as a typical range of chlorophyll *a* concentrations (uncorrected for phaeophytin *a*) in oligotrophic lakes, and 2-15 $\mu g \cdot L^{-1}$ as typical for mesotrophic lakes. The observed range of pigment concentrations (Figure 20) suggests that fertilization shifted the cylinders trophic status from oligotrophic to oligo-mesotrophic.

Nutrient enrichment also resulted in larger amplitude phase plane trajectories (Figure 26). Rather than declining in total zooplankton biomass like the controls, the two F cylinder trajectories continued to circulate around centroids at approximately 80 $\mu g \cdot L^{-1}$ zooplankton and 0.4 $\mu g \cdot L^{-1}$ chlorophyll, until late September.

In late September, the phase plane trajectories in treatments C, A and F all showed increased chlorophyll *a* concentrations (Figure 26). These increases were apparently not the result of changes in algal chlorophyll content (Figure 25), but may have been due to cladocerans switching to investing energy in resting eggs rather than asexual eggs and new (algae-consuming) individuals.

The mean percentage of live chlorophyll (Figure 24) was lower in treatment F (36.6 ± 1.4%) than in treatment C (41.8 ± 1.6%), though cylinder 1F showed an anomalous peak of 60.9% on

September 13. Phaeophytin a may have generally been a larger fraction in the F cylinders because of greater zooplankton grazing, which leads to digestion of chlorophyll a and its conversion to phaeophytin a (Daley and Brown 1973).

The mean total algal biomass was significantly lower ($p = 0.0005$) in the F cylinders (0.33 ± 0.07 mg•L^{-1}) than in the controls, due to far less cell volume in the 13-18 μm and >30 μm size categories (Table 14 shows differences significant at $p < 0.0001$). However, the mean biomass of algal cells less than 13 μm (which I assume to be mostly edible) was significantly greater in the F cylinders (0.12 ± 0.035 mg•L^{-1}) than in the controls (0.060 ± 0.004). The percent of total algal biomass less than 13 μm averaged 43.9% in treatment F, but only 17% in the controls (Figure 22 and Table 15). Nutrient enrichment may have preferentially benefitted smaller cells, or may have simply allowed primary production to stay ahead of zooplankton herbivory.

Given the higher chlorophyll and lower total algal biomass in F than C, it is no surprise that the ratio of these variables, an estimate of algal chlorophyll content (Figure 22), was higher in F (3.7 ± 1.0 μg chlorophyll a • mg algae^{-1}) than in C (0.67 ± 0.09). Estimated algal chlorophyll contents (which are only approximate due to imprecise estimates of algal biomass) reached maxima of 17.5 μg chlorophyll a • mg algae^{-}L on August 1 in cylinder 1F and 10.3 on August 16 in 8F. By comparison, the mean icefree season algal chlorophyll content in 31 lakes in the Kawartha Lakes - Bay of Quinte region of Ontario

was about 3.07±0.67 μg chlorophyll *a* • mg algae^{-1} (computed from 28 points in Figure 4 of Nicholls and Dillon (1978)).

Since in the fertilized cylinders an average of only 56 ± 5% of the cell volume was identified taxonomically, comparisons of phyletic composition of the phytoplankton community in the C and F treatments are not worthwhile.

In summary, fertilization increased the algal chlorophyll content and abundance of small, mostly edible cells. Though I do not have data on primary production, there is good evidence (from phytoplankton size distributions, phaeophytin concentrations and zooplankton reproduction) of increased food availability to crustacean zooplankton. This result contradicts null hypothesis 3(iii) (page 41), which stated that fertilization alone does not affect the availability of phytoplankton food for zooplankton.

3.3.4 Effects of Acidification and Fertilization

(i) Joint Fluctuations in Chlorophyll, Phaeophytin and Total Zooplankton Biomass

When averaged over the whole experiment, both the mean and variance of algal pigment concentrations were much higher in AF cylinders (1.39 ± 0.11 μg•L^{-1} chlorophyll *a* and 1.82 ± 0.10 μg•L^{-1} phaeophytin *a*) than in F (0.51 ± 0.044 and 0.87 ± 0.056). Until August 9, chlorophyll and phaeophytin *a* concentrations were similar under the F and AF treatments (Figure 20). During August 9 to 23 (when *Daphnia rosea* densities rapidly declined),

phaeophytin-corrected chlorophyll concentrations increased 910% in cylinder 3AF, and approximately 580% in cylinder 7AF. (The August 9 chlorophyll concentration in 7AF is missing from Figure 20, but was likely close to 0.5 $\mu g \cdot L^{-1}$ based on the Secchi depth at that time (5.5 m) and the chlorophyll-Secchi depth regression equation in Appendix D).

Were the large increases in treatment AF chlorophyll concentrations the result of reduced zooplankton grazing, or did primary productivity in AF cylinders increase relative to the F cylinders? Without primary productivity measurements I cannot discriminate between these two possibilities. However, the fact that chlorophyll concentrations on August 23 were 2 $\mu g \cdot L^{-1}$ higher in 3AF than 7AF is consistent with the view that the chlorophyll increases were due primarily to the loss of D. rosea, since significantly lower densities of daphnids were present in 3AF than in 7AF during this period (Figure 12 and Section 3.2.4(i)).

The percent of live chlorophyll (Figure 24) increased sharply between August 16 and 23 in both AF cylinders, but not in the F enclosures. This difference may have been due to lower herbivore grazing in treatment AF, causing reduced conversion of chlorophyll to phaeophytin (Daley and Brown 1973). The decrease in percent phaeophytin a in treatment AF (increase in percent live chlorophyll) was probably not related to direct pH effects on the algae, since Daley (1973) found the reverse: decreased pH led to an increased rate of phaeophytin a formation from chlorophyll. Overall, the mean % live chlorophyll was lower in

F (36.6 ± 1.4%) than in AF (42.0 ± 1.7%).

Chlorophyll concentrations declined 2 $\mu g \cdot L^{-1}$ in both AF cylinders between August 23 and 30, with very little increase in total zooplankton biomass until the following week (Figure 26). These events created "L-shaped" phase plane trajectories in the AF cylinders that were analogous to the path seen in Eunice Lake in late September, but of much larger amplitude.

Changes in both herbivore grazing and primary production were likely responsible for the "L-shape" trajectories in AF. Increases in the food available to cladoceran zooplankton lead to greater feeding rates (Burns and Rigler 1967, Buckingham 1978), developmental rates (Weglenska 1971, Neill 1981b) and reproduction (Weglenska 1971). In treatment AF, high chlorophyll *a* concentrations on August 23 were followed by high densities of cladoceran eggs on August 30, with development of those eggs into adults in the following week (See Figure 17 (page 89) for *Bosmina longirostris*). (With abundant food and temperatures of 16-18°C *B. longirostris* and *Chydorus sphaericus* require only 5 to 6 days to reach reproductive maturity (Goulden et al. 1978, Weglenska 1971).) The grazing rates of *Bosmina* and *Chydorus* must have been high to have produced such dramatic increases in egg and animal densities between August 23 and September 6, and may have been entirely responsible for the August 23 to 30 declines in chlorophyll *a* concentrations. This suggestion is supported by the sharp decrease in *Chydorus* densities after September 6, which was very likely due to the population overshooting the available food supply. However,

nutrient limitation and/or self-shading (note the transparency decreases during August 9 to 23 in Figure 9) perhaps also contributed to the sudden decline in chlorophyll a.

The September 6 to 13 reductions in total zooplankton biomass (67% in 3AF and 66% in 7AF) may have allowed chlorophyll to increase significantly in the following week due to reduced herbivore grazing. Two uncertainties which weaken this explanation are the diet of Chydorus sphaericus (did it feed off both periphytic algae and phytoplankton?) and the absence of chlorophyll measurements on September 6.

(ii) Estimates of Algal Biomass by Cell Counts

Replication of algal biomass (estimated by cell volumes) appeared adequate in the AF cylinders in the < 13 μm and 13-18 μm size categories, but was very poor in the 18-30 μm size category (Figure 21). Table 16 shows that during the period from August 1 to September 13, the marked differences in total algal biomass between AF replicates were due almost entirely to differences in the abundance of one taxon only: large, spherical colonies of Chrysocapsa sp. Note that the sum of differences in total algal biomass between the two replicates over this six week period was only 0.1% apart from the sum of differences in Chrysocapsa biomass (Table 16). The low numbers of colonies counted (Table 16) suggest that the large within-treatment variation may have been due primarily to inadequate sub-sampling procedure as discussed in Section 2.2.2 (ii). These globular colonies (which measured on average 22 μm in diameter and 5600

Table 16. Differences in total algal biomass and biomass of *Chrysocapsa* colonies between cylinders 7AF and 3AF during the period August 1 to September 13, 1979.

Date		Cylinder								
		3AF			7AF			(7AF-3AF)		
		Total Algal Biomass ($mg \cdot L^{-1}$)	*Chrysocapsa* Colonies		Total Algal Biomass ($mg \cdot L^{-1}$)	*Chrysocapsa* colonies		Total Algal Biomass ($mg \cdot L^{-1}$)	*Chrysocapsa* colonies	
			Biomass ($mg \cdot L^{-1}$)	No. Colonies		Biomass ($mg \cdot L^{-1}$)	No. Colonies		Biomass ($mg \cdot L^{-1}$)	No. Colonies
August	1	0.75	0.18	1	2.28	1.78	10	1.52	1.60	9
	9	0.13	0.	0	0.82	0.36	2	0.69	0.36	2
	16	0.51	0.04	10*	3.25	2.85	16	2.74	2.80	*
	23	0.76	0.36	2	1.16	0.89	10	0.40	0.53	8
	30	0.79	0.36	2	1.37	1.07	9	0.58	0.71	7
September	6	0.31	0.	0	1.75	1.42	8	1.44	1.42	8
	13	0.14	0.	0	0.35	0.18	1	0.22	0.18	1
Biomass Totals		3.38	0.94		10.97	8.54		7.59	7.60	

(Numbers may not sum to totals due to rounding errors.)

* Smaller colonies 8μm in diameter. (All other colonies were 24μm in diameter.) The difference between 7AF and 3AF in No. Colonies is not shown due to this size difference.

μm^3 in volume) are mostly clear mucilage (Prescott 1978), so that they would not contribute much chlorophyll. This suggestion is consistent with observed chlorophyll concentrations, which were lower in 7AF than 3AF in spite of a much greater volume of Chrysocapsa in the former tube. Chrysocapsa also caused the ratio of chlorophyll to algal biomass (Figure 25) to be much lower in the 7AF (2.9 ± 0.85 μg chlorophyll mg algal biomass^{-1}) than in 3AF (4.8 ± 0.75).

Due to Chrysocapsa, the mean biomass in the 18-30 μm size class was greater in AF than F. Treatment AF also contained a greater mean biomass of filaments and cells of diameter above 30 μm (Table 14 and Appendix F). Although Chrysocapsa was more abundant in AF than F, it does not follow that acidification of nutrient-enriched waters facilitated the growth of Chrysocapsa; relatively large numbers of colonies were present in 7AF on August 1 when the epilimnetic pH was still 6.15. The concurrent sharp increases in total zooplankton biomass and Chrysocapsa colonies during the period from July 26 to August 1 indicates that the abundance of these large colonies were not reduced by intensive zooplankton grazing pressure. Consumption of smaller algal cells by Daphnia may have facilitated growth of Chrysocapsa through removal of competitors, as suggested by Lynch and Shapiro (1981) for Aphanizomenon.

Of particular interest was the biomass of small, mostly edible algal cells < 13 μm in treatment AF, relative to treatments F and A. Over the whole experiment, there was no significant difference between treatments AF and F in the mean

biomass less than 13 μm (0.12 ± 0.14 mg•L^{-1} in AF and 0.12 ± 0.035 in F; p=0.86). However, differences between F and AF in the algal biomass < 13 μm were apparent in the second half of the experiment, and are discussed in the next section in detail. Lastly, I found significantly greater mean volumes of algae less than 13 μm diameter in AF than A (p = 0.001; Table 14).

In addition to chlorophyll measurements and microscope cell counts, I obtained information on net plankton composition (larger than 54 μm) from zooplankton samples. Net plankton became very abundant in the zooplankton samples taken in AF cylinders after August 23. Common genera were Tabellaria spp., Oedogonium spp. and Mougeotia spp. Mougeotia was mostly distributed at 5-7 m, based on vertically stratified samples taken from the AF cylinders on September 6 and October 11. Although the above algal genera were also found in zooplankton samples from the F cylinders, their densities were considerably lower.

(iii) Effects of Loss of Daphnia on Herbivore Control of Phytoplankton and Phytoplankton Community Size Structure

In this section, I compare the herbivorous zooplankton communities in treatments F and AF in terms of their size structure and particle removal capabilities. The objective of this comparison is to determine whether acid-induced mortality of Daphnia substantively altered the apparent impact of herbivores on the phytoplankton community. Therefore, the analysis examines zooplankton and phytoplankton data before and

after the loss of D. rosea in AF.

Figure 27 shows the estimated filtering rates for each species in the F and AF treatments, both prior to Daphnia's decline (July 16 to August 9th) and following it (August 30 to October 11). The eight species have been graphed according to their mean sizes to reflect zooplankton community size structure. Estimated filtering rates were computed by multiplying mean species densities by published filtering rates measured at similar temperatures but circumneutral pH (Table 17). These filtering estimates are only approximate, since they assume that 1) the sizes of animals, seston concentration and size distribution, and food quality in Heart Lake (Haney 1973) were similar to those found in the F and AF cylinders; and 2) filtering rate change are negligible. I will comment on these two assumptions before discussing the estimated filtering rates.

Figure 27. Estimated filtering rates of zooplankton species present in treatments F and AF over two time periods; July 16 - August 9 (prior to collapse of D. rosea in AF); and August 30 - October 11 (when other cladocerans had replaced Daphnia rosea). Abbreviations used for treatments: F=fertilization only; AF=acidification and fertilization. Standard deviations applied to mean lengths to illustrate the range of animal sizes and implied particle handling capability. Average of 68 ± 20.0 (SD) animals per species measured in first time period and 32 ± 8.5 in second. Filtering rate standard errors based on n = 8 and n = 10 for first and second time periods respectively. Total filtering rates ("Total = ") are the sums of individual species ' mean rates. Large size of D. rosea in AF during August 30 - October 11 period explained in Section 3.2.4(i). Mean filtering rates per individual animal drawn from sources listed in Table 17.

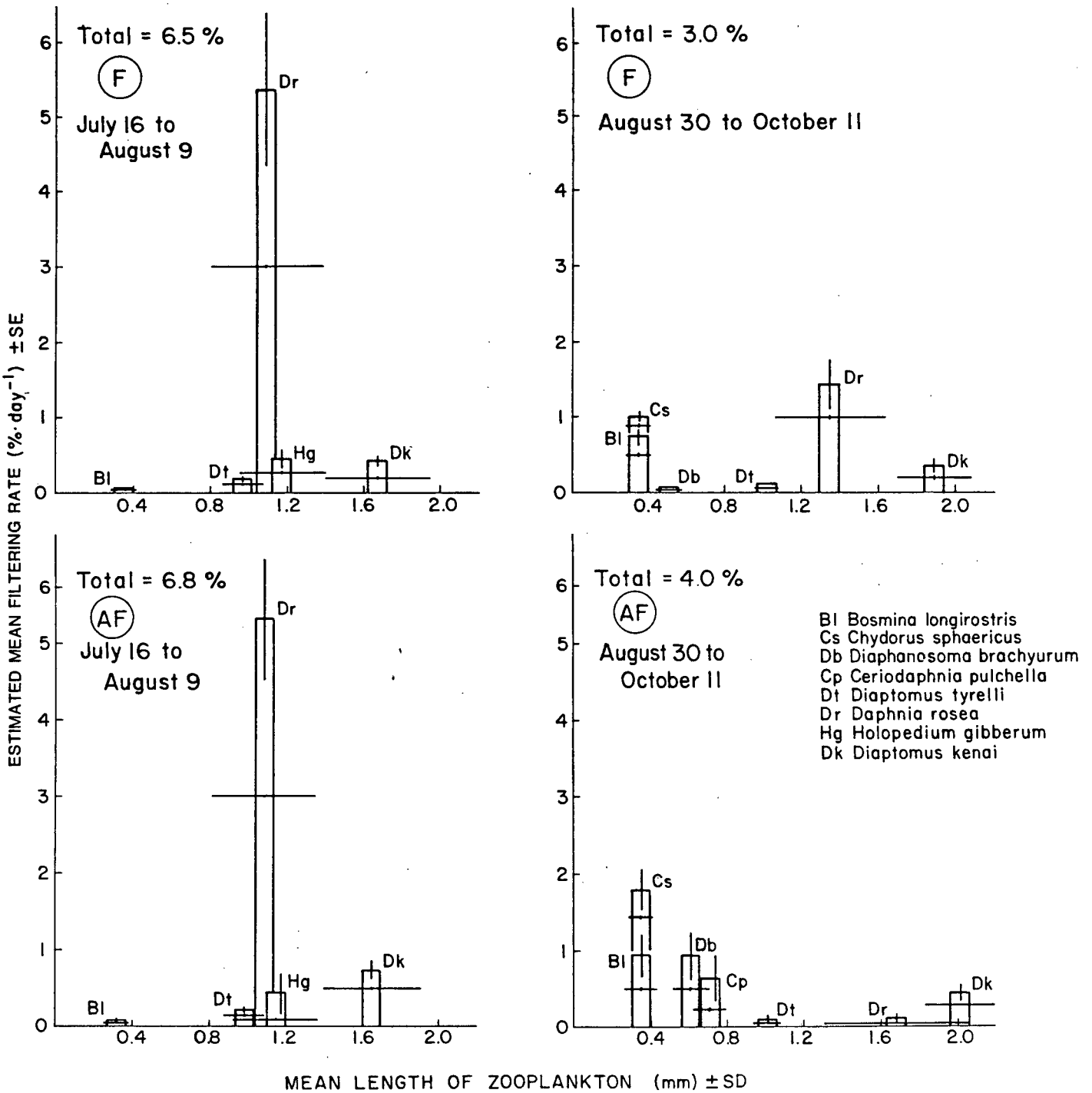

Total = 6.5 %
F
July 16 to August 9
Total = 3.0 %
F
August 30 to October 11
Total = 6.8 %
AF
July 16 to August 9
Total = 4.0 %
AF
August 30 to October 11
Bl Bosmina longirostris
Cs Chydorus sphaericus
Db Diaphanosoma brachyurum
Cp Ceriodaphnia pulchella
Dt Diaptomus tyrelli
Dr Daphnia rosea
Hg Holopedium gibberum
Dk Diaptomus kenai
ESTIMATED MEAN FILTERING RATE (%·day⁻¹) ±SE
MEAN LENGTH OF ZOOPLANKTON (mm) ±SD

Table 17. Assumed filtering rates for species in Figure 27.[1]

Species	Filtering Rate ml•ind^{-1}•day^{-1}	Reference
Daphnia rosea	5.5	Haney (1973)
Diaptomus kenai	16.6	Buckingham (1978) [2]
Diaptomus tyrrelli	0.48	Haney (1973) [3]
Holopedium gibberum	9.4	Haney (1973)
Bosmina longirostris	0.44	Haney (1973)
Diaphanosoma brachyurum	1.6	Haney (1973)
Ceriodaphnia pulchella	4.6	Haney (1973)
Chydorus sphaericus	0.18	Haney (1973)

[1] % filtered•day^{-1}=(ind•ml^{-1})x(ml•ind^{-1}•day^{-1})x100
[2] assuming a dry weight seston concentration of 5 mg•liter^{-1}, temperatures of 8-12°C and mean Diaptomus kenai biomass of 21.7 μg.
[3] measured for D. oregonensis

With respect to the first assumption, the lengths listed by Haney (1973; page 110) were generally greater than those shown in Figure 27, and mean seston levels in treatments AF and F were about 3-6 times lower than the levels found in Heart Lake (15 mg•liter^{-1}). (As seston was not measured in the enclosures, this estimate is based on mean phytoplankton concentrations and previous measurements of lake seston (Neill 1978).) Since lower food abundance requires higher filtering rates to obtain the same energy (Burns and Rigler 1967), Figure 27 likely underestimates the percent of enclosed water the animals would

have filtered per day.

Assumption 2) may be justifiable for acid-tolerant species, but this is by no means certain. Though in Haney's study, B. longirostris showed no reduction in filtering rate between circumneutral Heart Lake and Bog Lake (pH 4.5), sudden changes in pH may cause temporary decreases in maximal filtering rates (Ivanova 1969, Kring and O'Brien 1976). These considerations notwithstanding, the relative magnitudes of filtering shown in Figure 27 are likely reasonable.

Prior to the decline of D. rosea August 9 to 16, treatment AF filtering was very similar to treatment F (Figure 27). From July 16 to August 9, D. rosea provided on average about 80% of the total zooplankton filtering in treatments F and AF. It is not known what size classes of algae the daphnids actually consumed. However, I can estimate the maximum size particle ingested via the empirical relationship developed by Burns (1968):

$$Y = 22X + 4.87 \qquad (4)$$

where:

Y = diameter of largest plastic bead ingested (μm), with a 95% confidence interval of $\pm 9\mu$m; and

X = carapace length of a filter-feeding cladoceran (mm)

Substituting the mean length of D. rosea (1.1mm) into equation (4) leads to the suggestion that algal cells up to 29±9 μm in diameter could theoretically have been ingested by D. rosea.

From August 30 to October 11, treatment AF had a greater mean total filtering rate (4.0%) than F (3.0%); (Figure 27). However, this filtering was largely provided by small cladocerans, which were apparently not so effective as the F cylinder zooplankton at grazing chlorophyll down to low concentrations (Figure 26). I hypothesize that the loss of D. rosea in AF created an unbalanced size distribution of herbivores, greatly reducing the filtering of larger algae and therefore allowing chlorophyll concentrations to increase. Again using the empirical equation of Burns (1968), I estimate that during the period from August 30 to October 5, about 85% of the herbivorous filtering in the AF cylinders during the August 30 - October 5 period would have been by species consuming primarily algal cells less than 13μm in size. D. kenai was the only herbivore in AF large enough to filter large cells, but its numerical response was too slow to fill the gap left by D. rosea (at least within the time horizon of this experiment). D. kenai eggs produced in fall do not mature into copepodites until the following February (A. Chapman, unpublished data).

If the zooplankton community changes in AF decreased total herbivore filtering of the algae, but increased the filtering of smaller particles, one would expect greater total algal biomass in AF than F, but a smaller proportion of total algal biomass in cells ≤13μm in diameter. Phytoplankton data were generally consistent with these expectations. Table 18 lists the biomass of phytoplankton in forms with maximum dimension ≤13μm, and biomass of larger forms. Chrysocapsa colonies are not included

in Table 18, due to their inedible nature and their strong bias on estimated algal biomass (Section 3.3.4 (ii)).

Table 18. Mean algal biomass by major size classes in treatments F and AF, before and after the collapse of *Daphnia* in AF. Biomass of *Chrysocapsa* colonies not included - see text for explanation.

Time Period	Treatment	Algal Size Class[1]	Mean Biomass ± SE [mg/L]	% of Mean Total Biomass
July 16 to Aug. 9	F	≤13μm	0.05±0.01	37.9
		>13μm	0.09±0.04	62.1
		Total	0.14±0.04	100.
(n=8)	AF	≤13μm	0.10±0.02	32.5
		>13μm	0.20±0.07	67.5
		Total	0.30±0.07	100.
Aug. 30 to Oct. 5	F	≤13μm	0.18±0.06	59.1
		>13μm	0.12±0.04	40.9
		Total	0.30±0.08	100
(n=12)	AF	≤13μm	0.11±0.02	28.8
		>13μm	0.27±0.05	71.2
		Total	0.38±0.05	100

[1] based on maximum dimension of cell or colony. Filaments (included in >13μm size class) were <5% of the total biomass in AF, and <2% in F (Table 15 and Figure 22).

Prior to the collapse of *D. rosea* in the AF cylinders (July 16 to August 9) the percent of total algal biomass ≤13μm was similar in AF and F (Table 18) which is consistent with the similar filtering pattern these two treatments showed during this period (Figure 27). It is surprising that the mean total algal biomass was nearly twice as high in AF as in F during this

period, since mean chlorophyll a levels were similar (0.37 ± 0.07 $\mu g \cdot L^{-1}$ in F and 0.42 ± 0.08 $\mu g \cdot L^{-1}$ in AF). It is possible that sublethal pH levels in treatment AF lowered both the actual filtering rates of herbivores (as shown by Kring and O'Brien (1976) for Daphnia pulex) and also the chlorophyll content of algal cells. However, I have no data on actual filtering rates. After the collapse of Daphnia (August 30 to October 5), treatment AF contained less algal biomass in small cells than did treatment F, both quantitatively and as a percent of total algal biomass (Table 18).

These results, and the high chlorophyll a concentrations in AF after the loss of D. rosea, suggest that acidification-induced mortality of Daphnia: 1) reduced overall herbivore consumption of large particles; and 2) led to zooplankton community changes which increased grazing pressure on small particles.

Higher chlorophyll concentrations in treatment AF than F in September might have been partially due to greater primary production. Nutrient turnover may have been faster in AF during this month, since smaller herbivores have faster metabolic rates and higher P release rates per unit biomass (Peters and Rigler 1973, Lehman 1980a). Turnover rates may affect both the rate and quality of phytoplankton production (Lehman 1980b). Without measurements of particle size-segregated primary production and zooplankton grazing rates, I cannot quantitatively assess the importance of changes in primary production relative to changes in herbivore grazing.

The results in this long section are best summarized by referring back to the original null hypotheses in Table 5 (page 41).

Null hypothesis 4(ii) stated that nutrient enrichment during experimental acidification to pH 5.0 does not alleviate acid-induced shortages of phytoplankton food for zooplankton. Section 3.3.2 demonstrated that acidification alone (to pH 5.6) did not decrease the availability of phytoplankton food. Section 3.3.4 showed that fertilization during acidification increased the chlorophyll a concentrations and biomass of edible algae (≤13μm) over that in treatment A. However, the benefits of this increased food to acid-sensitive Daphnia rosea were overwhelmed by the toxicity of pH 5.4 water (Section 3.2.4 (i)).

Null hypothesis 5(ii) stated that gradual experimental acidification of moderately enriched waters does not affect phytoplankton biomass or size composition. The results from treatments F and AF contradict this hypothesis. After the collapse of D. rosea in treatment AF, mean chlorophyll a concentrations increased six fold, while in treatment F concentrations remained constant. The replacement of D. rosea by smaller herbivores in treatment AF greatly increased the estimated filtering rates of algal cells smaller than 13 μm, and decreased filtration of larger cells, apparently causing AF algal biomass to become dominated by larger cells. In treatment F (where D. rosea persisted), algal biomass was dominated by smaller cells.

Null hypothesis 5(iii) stated that gradual experimental acidification of moderately enriched waters does not affect the ability of plankton systems to absorb enrichment perturbations. The experiment did not proceed long enough to rigorously test this hypothesis. However, the results suggest that acidification may increase the amount of plankton system fluctuation following enrichment. During the six weeks following the collapse of Daphnia, treatment AF chlorophyll a concentrations increased six fold, then dropped sharply as Chydorus sphaericus, Bosmina longirostris, and Diaphanosoma brachyurum increased, and then again increased abruptly when these zooplankters collapsed. By contrast, treatment F chlorophyll a concentrations fluctuated relatively little during the same period.

4. DISCUSSION

> "In our endeavor to understand reality we are somewhat like a man trying to understand the mechanism of a closed watch. He sees the face and the moving hands, even hears its ticking, but has no way of opening the case. If he is ingenious, he may form some picture of a mechanism which could be responsible for all the things he observes, but he may never be quite sure his picture is the only one which could explain his observations."
>
> Einstein (1938; page 31)

This experiment attempted to simulate lake acidification within plastic enclosures over a period of three months, though acidification actually takes place in whole lakes (and their watersheds) over periods generally greater than ten years. There are three major ways in which the experimental setting and treatments could misrepresent lake acidification:

1) Enclosure effects: differences in biophysical conditions between the lake and the experimental enclosures;

2) Nature of the perturbation: differences between the physical and chemical conditions observed in acidifying lakes and the conditions produced by my

experimental treatments.

3) Response to perturbation: differences between lakes and enclosures in their responses to increased acid and/or nutrient loading, due to the limited size and duration of the enclosure experiment.

The first two issues are considered in Sections 4.1 and 4.2. I have addressed the third issue throughout Sections 4.3 to 4.5, by comparing the responses of particular ecosystem components in this experiment with those observed in acidic lakes.

4.1 Enclosure Effects

Differences between the control cylinders and the lake do not affect comparisons between cylinders. However, the value of this experiment as a simulation of lake acidification depends upon keeping the behaviour of the control cylinders from diverging too far from that of the lake. The major results relevant to the null hypotheses concerning enclosure effects are listed in Table 19.

Control enclosures showed significantly lower alkalinities and hydrogen ion concentrations than the lake at 1 and 3 m, which I hypothesize was primarily the result of light limitation on photosynthetic uptake of NO_3^-, a process that generates alkalinity (Brewer and Goldman 1976). Since mean alkalinities were 16 $\mu eq \cdot L^{-1}$ less in the controls than in Eunice Lake, algae in the controls would had to have taken up roughly 16 $\mu eq \cdot L^{-1}$

Table 19. Summary of 1979 results relevant to hypotheses on enclosure effects.

Null Hypotheses (from pg 41)	Major Results
Enclosure of plankton systems and removal of cutthroat trout predation does not affect:	
light transmission,	- falsified: increased light extinction by non-chlorophyll factors in controls (vs. lake)
pH,	- no evidence against hypothesis
alkalinity,	- falsified: epilimnetic alkalinity significantly reduced, metalimnetic alkalinity significantly increased
phytoplankton, and	- some evidence against hypothesis: controls had decreased biomass of algal cells < 13 μg and *Gleocystis*, and apparent decrease in primary production near end of experiment
zooplankton	- some evidence against hypothesis: controls showed collapse of *Holopedium gibberum* populations, altered dynamics of *Daphnia rosea*, appearance of *Chydorus sphaericus*, increased lengths of *Daphnia rosea* and *Diaptomus kenai*

less NO_3^- (0.99 mg•L^{-1}) than did Eunice Lake algae (See Section 4.3 for stoichiometric equations). Unfortunately I have no measurements of NO_3^- levels to test whether or not this condition prevailed. Neill (unpublished data) made photometer measurements in limnocorrals anchored in Gwendoline Lake, upstream of Eunice Lake. He found that light levels at 1m depth were 20% lower in the limnocorrals than in the lake, but that differences in light intensity decreased with depth and were negligible below 5 m (Neill, pers. comm.). Though my enclosures were 0.5 m larger in diameter than Neill's, they probably shaded the upper waters at least as much due to the UV-protective orange coating on the cylinder's top 0.7 m. Consistent with the hypothesis of limnocorral shading is the control cylinders' greater kw (extinction coefficient for factors other than chlorophyll). Light limitation is probably negligible in experiments with cylinders greater than 5 m in diameter. Muller (1980) found no difference in extinction coefficients of light intensity between control tubes and lake 223; his enclosures were 10 m in diameter and 2.5 m deep. At the other size extreme, Marshall and Mellinger (1980) found that light intensities in 8 liter translucent polyethylene carboys were equivalent to Lake Michigan light intensities 1.7 m deeper.

Though light limitation seems responsible for reduced epilimnetic alkalinity in the controls, two alternative hypotheses to explain this observation are:

1) nutrient limitation in the "limnetic zone" of the tubes, due to either periphyton growth on the sides

and isolation from watershed nutrient replenishment, and

2) loss of bicarbonate contributions from the watershed to maintain alkalinity.

Periphyton growth was not observed in the top 2 m of the control cylinders, and was probably not sufficient at 3 m to cause nutrient limitation. The extremely dry weather of July and August (Figure 4) makes it unlikely that watershed flushing of either nutrients or buffers were responsible for lower alkalinities during these months. These two alternate hypotheses therefore appear inadequate to explain lower epilimnetic alkalinities in the controls than in the lake.

One consequence of the difference in epilimnetic alkalinity between the controls and Eunice Lake is that the cylinders contained less photosynthetic buffering against acidification than in the lake. The epilimnetic pH reductions achieved by my acid additions to A cylinders were about 0.5 pH units more severe than would have occurred under equivalent H^+ loading to the lake. This is estimated from the pH drop caused by the last 16 $\mu eq \cdot L^{-1}$ decline in alkalinity in treatment A (16=the mean alkalinity difference between the controls and Eunice Lake).

The vertical distribution of pH and alkalinity is strongly affected by the utilization of CO_2 in the zone of primary production (trophogenic layer) and its liberation in the decomposition or tropholytic zone (Hutchinson 1957; pg. 685). Deep, oligotrophic lakes with orthograde oxygen curves frequently show the gradual decline in pH and alkalinity with

depth exhibited by Eunice Lake (ibid, pg. 685). Unlike the lake, the control cylinders showed increases in alkalinity and pH between 5 and 7 m. Since control tube oxygen measurements on August 1 (only date taken) showed concentrations of 9.5 $mg \cdot L^{-1}$ at 7 m, it seems unlikely that anaerobic conditions and denitrification could have generated the alkalinity. Alkalinity is increased by aerobic decomposition of organic nitrogen to NH_4^+ and OH^- (Brewer and Goldman 1976). However, if the NH_4^+ so generated were converted into NO_3^- by nitrifying bacteria, which commonly occurs above aerobic sediments (Keeney 1972), I would have seen a net decrease rather than an increase in alkalinity. Without nitrate and ammonia measurements in the cylinders and the lake, it is difficult to deduce the processes behind the observed alkalinity differences at 5-7 m.

The increase in densities of Chydorus sphaericus in the controls six weeks after the start of the experiment may have been assisted by the existence of the cylinder walls. C. sphaericus is a substrate-oriented, littoral cladoceran rarely found in the limnetic zone of Eunice Lake (Fryer 1968, Northcote and Clarotto 1975). Marshall and Mellinger (1980) noted very large increases in Chydorus sphaericus after three weeks in 8 liter enclosures (relative to Lake Michigan), but in experiments they performed in 150 m^3 enclosures in Lake 223, Chydorus sphaericus did not differ in abundance between the controls and the lake.

The rapid extinction of Holopedium gibberum in all limnocorrals was important, since this cladoceran is relatively acid tolerant. (Malley et al. (1982) found that densities of H. gibberum increased twentyfold as Lake 223 was acidified from pH 6.8 to 5.37.) However, since the biomass of H. gibberum in Eunice Lake declined to very low levels by the the end of August (Figure 10), enclosure effects were not solely responsible for the extinction of H. gibberum in the limnocorrals.

Mean densities of daphnids and their eggs were lower in the controls than in Eunice Lake, daphnid lengths were longer in the controls, and the control populations collapsed much sooner than the lake population. These differences were probably due primarily to lower primary production in the controls, and the removal of cutthroat trout predation (which would increase daphnid lengths and perhaps also cause overgrazing).

Differences between the controls and Eunice Lake in densities and lengths of Diaptomus kenai also suggest that size-selective predation was important in Eunice Lake. It would be valuable to repeat this experiment in larger limnocorrals with a few added fish.

Lastly, it should be stressed that within season extinctions of zooplankton in acidifying enclosures do not necessarily imply year-to-year extinctions in acidifying lakes. Different abiotic conditions in acidifying lakes may alter the level of physiological stress; the slower rate of change in abiotic conditions in lakes may allow some populations to become more acid tolerant; and resting eggs in less acid bottom waters (or

populations in unacidified upstream lakes) may allow acid-sensitive species to persist.

4.2 Evaluation of the Physical and Chemical Effects of the Experimental Acidification

Did the experimental acidification in this study properly simulate lake acidification? This section compares acid lakes to the acidified limnocorrals with respect to four properties: ionic content, effectiveness of acidification in removing alkalinity, rates of pH change, and transparency.

The acidification of watersheds and lakes is correlated with many chemical changes that were not simulated in this experiment. The chemistry of lakes with pH levels similar to the AF cylinders is nearly always characterized by increased concentrations of sulfate and aluminum and often shows elevated levels of calcium, manganese, magnesium, mercury, cadmium, zinc, and lead (Almer et al. 1978, Gjessing et al. 1978, Henriksen and Wright 1978, Hutchinson et al. 1978, Scheider et al. 1979, Galloway and Likens 1979, Driscoll et al. 1980, Dickson 1980). Mobilization of metals from watershed soils (Cronan and Schofield 1979) and lake sediments (Schindler et al. 1980b) were also not simulated. Also, only sulfuric acid was added to the enclosures, but not nitric acid, which contributes about a third of the acidity in precipitation in Norway (Braekke 1976) and the northeastern United States (Likens et al. 1979).

Extrapolations from my experiment to acidifying lakes require one to assume that increased $[H^+]$ and $[SO_4^{-2}]$ are the key ionic shifts affecting plankton community change in acid lakes. This assumption is not valid for highly metal-contaminated acid lakes (e.g. less than 20 km downwind of Sudbury, Ontario) where both zooplankton and phytoplankton communities have likely been altered by high copper and nickel concentrations (Hutchinson and Stokes 1975, Whitby et al. 1978, Yan and Miller 1981).

In acid lakes distant from emission sources, increased aluminum concentrations are the most frequently cited metal contamination (reviewed by NRCC 1981). Although I did not measure total aluminum concentrations, they could not have increased significantly with acidification in the absence of either watershed or sediment sources of metal.

It is not known whether aluminum concentrations in acidified lakes increase pH toxicity to zooplankton. Experimental studies have demonstrated that the concentration and species of aluminum greatly influences the survival of brown trout (Muniz and Leivestad 1980) and brook trout fry (Driscoll et al. 1980, Baker and Schofield 1980) at low pH. Low pH kills zooplankton primarily by loss of ion regulation leading to high rates of sodium loss (Potts and Fryer 1979, Havas 1980). Havas (1980) found that additions of 1 mg $Al \bullet L^{-1}$ to pond water did not change the mortality of *D. magna* at pH 4.5 (median survival time was 70 hours), but adding 5 mg Al/l reduced median survival to 10 hours. She also found that adding 20 mg $Al \bullet L^{-1}$ to pond water at

pH 4.5 reduced the median survival time of D. middendorffiana from 140 to 10 hours. Sublethal effects may however occur at much lower concentrations: Biesinger and Christensen (1972) found 16% impairment of reproduction in Daphnia magna at 0.32 mg $Al \cdot L^{-1}$. Mean aluminum concentrations in Ontario and Norwegian acid lakes of pH 4.5 are about 15 to 60 times lower than Havas' lethal concentrations, but are comparable to levels causing reproductive impairment in the laboratory (Table 20). In examining Table 20, it is important to recognize that spring melt episodes may generate aluminum concentrations significantly higher than the mean and increase toxicity (Driscoll et al. 1980). Malley et al. (1982) concluded that experimental acidification of Lake 223 to pH 5.37 did not elevate either heavy metals or aluminum to toxic levels, but their experiment did not acidify the watershed.

Therefore, there is not yet sufficient evidence to reject the assumption that sulfuric acid additions alone (without aluminum additions) adequately simulate the toxicity effects of acidification on zooplankton communities at pH levels above 5.0. At pH levels of 4.5 or lower, this assumption appears more tenuous.

The acidification treatment applied in this experiment was approximately 98% effective in depleting the enclosures' alkalinity. This contrasts with major spring melt H^+ loads to acidifying lakes in Norway (Henriksen and Wright 1977), Sweden (Hultberg 1977) and Ontario (Jeffries et al. 1979). Meltwater, although causing sharp pH declines in the near surface waters,

Table 20. Mean and standard deviation of aluminum concentrations in acidified and non-acidified lakes in Norway (Gjessing et al. 1976) and Ontario (NRCC 1981).

Location	No. Lakes	pH	Al (mg/l)
Norway			
Central	52	6.4 ± 0.64	0.028 ± 0.047
Coastal	20	5.4 ± 0.40	0.086 ± 0.066
Western	23	5.22 ± 0.17	0.055 ± 0.019
South-central and eastern	26	4.76 ± 0.33	0.208 ± 0.086
Ontario			
Muskoka-Haliburton	14	5.6 - 6.8	0.049
Sudbury	2	5.5	0.069
Sudbury	5	4.0 - 4.6	0.280 - 0.380

tends to be buoyed up by inverse stratification and moves across the top of the lake to the outlet only partially mixed. For example, in Norway's Lake Lantjern, 85-90% of the acid meltwater leaves the lake without depleting alkalinity (Henriksen and Wright 1977). Summer stratification can create important refuges from surface acid additions. The thermocline shielding of deeper waters evident in treatments A and AF was also observed by Schindler et al. (1980a) in the experimental acidification of Lake 223.

Had I used both nitric and sulfuric acid in the acidification treatments, I would have needed to add more H^+ to consume the same amount of alkalinity, since NO_3^- assimilation by algae generates alkalinity (See Section 4.3). Also, increased NO_3^- concentrations would probably have affected the species composition of the phytoplankton community, and perhaps the rate of primary production.

Under low oxygen conditions, bicarbonate generation from sulfate-reducing bacteria can greatly reduce the acidifying effect of summer additions of H_2SO_4 (Schindler et al. 1980a). In Lake 223 in 1977, such buffering increased the volume-weighted average alkalinity 11 $\mu eq \cdot L^{-1}$, and was largely responsible for the added H_2SO_4 being only 31% efficient at removing alkalinity (Schindler et al. 1980a). Fertilization of acidic Mountaintop Lake in Ontario (pH 4.62) also generated large increases in hypolimnetic alkalinity attributable to sulphate reduction (Yan and Lafrance 1981). Kelly et al. (1982) have shown that the hypolimnia of artificially eutrophied lakes

could potentially produce enough alkalinity to neutralize typical levels of acid deposition, though unenriched lakes could not. However, as water in the A enclosures was well oxygenated, there was no possibility for such buffering. Presumably with deeper cylinders extending into Eunice Lake's anoxic zone, I would also have encountered increases in hypolimnetic alkalinity generated by sulfate-reducers.

The important one unit pH change observed August 9 to 16 in the epilimnion of the AF enclosures, although coming in summer rather than spring, is within the observed range of spring pH depressions in the surface waters of lakes in Central Ontario (Jeffries et al. 1979). Therefore, though the overall rate of change in mean pH was much faster than has been observed in acidifying lakes (Dickson 1975), the simulated pH depressions were reasonable.

It is difficult to assess whether the experimental acidification in treatment A produced "reasonable" changes in transparency. First, published studies showing correlations between lake acidity and transparency do not reveal whether high transparency is present because of acidification, or existed previously (NRCC 1981). Second, the most thoroughly monitored case study at intermediate pH levels was the experiment acidification of Lake 223, which did not include acidification of the watershed.

Experimental acidification in treatment A caused: 1) a transient 0.8m increase in transparency; 2) no significant change in mean nonchlorophyll light extinction; and 3) a slight

increase in mean Secchi depths (7.14±0.23 m in treatment A at mean pH 5.85, versus 6.72±0.35 m in the controls at mean pH 6.44) (Section 3.13). These results can be compared to both multi-lake surveys and the Lake 223 results. In a survey of 209 lakes in the Sudbury Area, the 25 lakes with mean pH 5.5-6.0 had a mean Secchi depth of 5.80±0.42 m; 68 lakes with mean pH 6.5-7.0 had a mean Secchi depth of 4.80±0.22 m (NRCC 1981). Experimental acidification of Lake 223 from pH 6.79 to 6.08 during 1976-1977 was accompanied by a 0.8m increase in mean Secchi depths, with no concurrent decrease in algal biomass (Schindler et al. 1980a).

Almer et al. (1978) have shown that aluminum can rapidly precipitate humic materials at pH 5, and suggested that this mechanism may be partially responsible for the clarity of acid lakes. Lake 223 aluminum concentrations were far below the levels shown by Almer et al. to affect transparency (Schindler et al. 1980a); this was very likely also the case in the A cylinders. Schindler (1980) has hypothesized that increases in clarity at pH levels near 6 may be due to changes in the colour of dissolved materials. Since Lake 223 did not show changes in absorption of blue (425 nm) light (Schindler et al. 1980a), this hypothesis depends upon acid waters showing decreased absorption at longer wavelengths, a prediction which should be relatively easy to test.

4.3 Biotic Processing of Ammonium Nitrate Additions

Additions of fertilizer were responsible for statistically significant decreases in epilimnetic alkalinity in both the F and AF treatments; in the latter treatment, the alkalinity decrease was of great biological significance. I suggest that these decreases were due partially to preferential algal assimilation of NH_4^+ over NO_3^-, and partially to bacterial nitrification. These two possibilities are discussed separately below.

The stoichiometry of algal NH_4^+ assimilation first proposed by Redfield et al. (1963) and recently confirmed by Brewer and Goldman (1976) and Goldman and Brewer (1980), is as follows:

$$106CO_2+106H_2O+16NH_4^+ \rightarrow (CH_2O)_{106}+(NH_3)_{16}+16H^++106(O_2) \quad (5)$$

While each molecule of assimilated NH_4^+ depletes an equivalent quantity of alkalinity, the reverse occurs under nitrate assimilation:

$$106CO_2+138H_2O+16NO_3^- \rightarrow CH_2O)_{106}+(NH_3)_{16}+16OH^-+138(O_2) \quad (6)$$

Since NH_4NO_3 is balanced in alkalinity-increasing and depleting forms of nitrogen, the alkalinity decreases I observed in fertilizer treatments could only have been due to algal assimilation if NH_4^+ was assimilated preferentially. Most of the algal species studied to date show preferential assimilation of NH_4^+ over NO_3^- when both are present. (Pratt and Fong 1940;

Cramer and Myers 1948; Lui and Roels 1972; Brewer and Goldman 1976, Bates 1976; McCarthy et al. 1977; Eppley et al. 1979; Olson 1980). It is possible that the change in phytoplankton species composition induced by my experimental fertilization affected overall rates of NH_4^+ and NO_3^- assimilation.

The mechanism responsible for preferential NH_4^+ uptake is suppression of intracellular nitrate reduction (failure of induction of nitrate reductase) when ammonium is present in growing cells (Zink and Veliky 1977). McCarthy et al. (1977) showed that NH_4^+ concentrations greater than 0.5 to 1.0 μg-atom $N \bullet L^{-1}$ almost totally suppressed NO_3^- utilization by a wide variety of phytoplankton species. Since the epilimnion of my fertilized enclosures (F and AF) received approximately 5.4 μg-atom $N \bullet liter^{-1}$ as NH_4^+ during each of 4 nutrient additions (total of 21.6), it seems reasonable that NO_3^- uptake was temporarily suppressed.

Under the stoichiometry shown in equation (9), each of the four nutrient additions could have caused an alkalinity reduction of 5.4 $\mu eq \bullet L^{-1}$ assuming only NH_4^+ assimilation. To yield the 10 $\mu eq \bullet L^{-1}$ decrease in alkalinity observed in F entirely by algal nitrogen processing, the ratio of NH_4^+:NO_3^- algal assimilation would have to have been at least 1.9 (i.e. 21.6/[21.6-10]). Similarly, the 8 $\mu eq \bullet L^{-1}$ decrease in AF would have required an NH_4^+:NO_3^- assimilation ratio of 1.6. Pratt and Fong (1940) observed alkalinity decreases due to algal NH_4^+ uptake, but following the depletion of NH_4^+ in their cultures the pH rose rapidly, which they attributed to

absorption of nitrate ions. Given the very high N:P atomic ratio of my nutrient additions (33.2:1, with half of the nitrogen as NH_4^+) it is possible that NH_4^+ never did become depleted; without nutrient measurements I cannot tell.

Bacterial nitrification can also deplete alkalinity, by oxidizing ammonium to nitric acid via the following reactions (Weber and Stumm 1963):

$$2NH_4^+ + 3O_2 \rightarrow 2NO_2 + 4H^+ + 2H_2O \quad (7)$$

$$2NO_2 + O_2 \rightarrow 2NO_3^- \quad (8)$$

The reactions in equations (7) and (8) are performed by the bacteria Nitrosomonas and Nitrobacter respectively. Note that equation (7) potentially produces twice as much acidity as NH_4^+ assimilation by algae (Equation 8).

Was nitrification as important in treatment AF as in F? Bacterial nitrification of industrial watersheds has been responsible for the acidification of Lake Orta in Northern Italy to pH values near 4 (Gerletti and Provini 1978). Gerletti and Provini demonstrated experimentally that nitrification at 25°C proceeded considerably slower at pH 5 than at pH 7. In addition, natural Lake Orta densities of nitrifiers had to be augmented in order to produce measurable nitrification in less than two to three months. Their results suggest that less nitrification occurred in treatment AF than F.

In retrospect, it would have been possible to distinguish between algal assimilation and bacterial nitrification with a 24 hr series of NH_4^+, NO_3^- and NO_2^- measurements, since only nitrification would affect nighttime NO_3^- concentrations. Alternatively, I could have examined daytime alkalinity and nitrogen changes following urea additions, since algal assimilation of urea ($CO-(NH_2)_2$) does not produce acidity (Brewer and Goldman 1976), but bacterial oxidation of urea does (Hunt and Boyd 1981).

Biotic processing of nitrogen appears to have been important in this experiment - how important is it in low alkalinity lakes generally? There is good evidence that the acidity of oligotrophic, poorly buffered lakes is quite sensitive to the form of nitrogen available to algae. Experimental fertilization of low alkalinity Lake 227 with $NaNO_3$ caused the pH to increase from 6.5 to 10.2 (Schindler 1971 and 1973). Crosson Lake, an oligotophic acid lake in Ontario, showed a pH increase from 5.1 to 6.6 between May and August of 1978, which was attributed to algal NO_3^- assimilation (NRCC 1981). By contrast, fertilization of acidic Mountaintop Lake with NH_4NO_3 caused the epilimnetic pH to drop from 4.5 to 4.2 in the summer of 1977, and from 4.8 to 4.5 in 1978 (Yan and Lafrance 1981). Yan and Lafrance's analysis of NH_4^+ and NO_3^- concentrations in Mountaintop showed that algal preferential uptake of NH_4^+ over NO_3^- could explain the observed alkalinity decreases; nitrification was discounted due to the low pH. Their data indicate ratios of NH_4^+:NO_3^- assimilation of 1.6, 2.3 and 1.4 during 1976, 1977, and 1978 in

Mountaintop Lake (calculated over 2.5 to 3.5 month periods). These ratios compare reasonably well with the minimum theoretical assimilation ratios of 1.6 and 1.9 that I calculated were necessary for the alkalinity changes in AF and F (respectively) to be due entirely to algae.

Some coastal mountain lakes in British Columbia have been fertilized with NH_4NO_3 and ammonium phosphate to increase salmonid production (Shortreed et al. 1981), but no epilimnetic alkalinity decreases have been observed (K.S. Shortreed, pers. comm.). The enrichment was likely too small to affect alkalinity: nitrogen additions were only 30 to 40 mg $N \cdot m^{-2}$, as compared to 600 $mg \cdot m^{-2}$ in each of my nutrient additions.

Though in the AF cylinders, algal activities decreased pH beyond the lethal threshold for a dominant zooplankton species, the reverse may also occur. O'Brien and de Noyelles (1972) demonstrated that nutrient enrichment of small ponds (with triple superphosphate, ammonium nitrate and muriate of potash) led to an <u>increase</u> in pH from 9.9 to 11.0, causing massive mortality of <u>Ceriodaphnia reticulata</u> . Why did a pH increase occur after additions of NH_4NO_3? At the temperatures and pH levels in O'Brien and de Noyelle's experiment (about 21°C and pH 10), roughly 80% of the added NH_4^+ would have been converted to NH_3 (Thurston et al. 1974). I suggest that NH_4^+ levels may have been too low to inhibit nitrate reduction.

Since nitric acid contributes about one third of the H^+ in precipitation in Norway and the northeastern U.S., generation of alkalinity by nitrate assimilation could be an important natural

buffering mechanism for acid lakes. However, most of the nitrate deposited on watersheds is taken up by plants and soil, and never reaches the lake (Henriksen and Wright 1977, Dillon et al. 1980). It is possible that in lakes limited by phosphorus rather than nitrogen, continual nitrate loads from precipitation may eventually end up accumulating in the increasingly acid water. Though some acid lakes show high nitrate levels relative to circumneutral lakes (Gjessing et al. 1976), these are probably in basins with very low watershed to lake area ratios (i.e. low nitrate retention). I have not found evidence in the literature showing nitrate accumulations over time in acid lakes. This appears to be a topic worthy of further research, since Likens et al. (1979) have noted a recent increase in the ratio of nitric:sulfuric acid concentrations in precipitation.

4.4 Zooplankton Community Structure

The experimental tests of the original null hypotheses concerning zooplankton community structure are summarized in Table 21. The absence of measurable acidification effects on community structure in treatment A cylinders demonstrates that the community can tolerate pH 5.6, at least during the period from July to October. However, the null effect of treatment A means that a discussion of the mechanisms by which acidification alters zooplankton communities must focus on treatment AF, and use the other treatments for comparisons. Four major community changes occurred in the AF cylinders:

1) *D. rosea* declined precipitously August 9 to 16;

Table 21. Summary of 1979 results relevant to hypotheses on zooplankton communities.

Null Hypotheses (from pg 41)		Major Results
2(i)	Gradual experimental acidification of oligotrophic waters to pH 5.0 does not affect zooplankton populations or community biomass	- no evidence against hypothesis down to pH 5.6 (A vs. C) - too few animals and samples for adequate test at pH < 5.6
2(ii)	Moderate nutrient enrichment of circumneutral waters does not affect zooplankton populations or community biomass	- hypothesis falsified (F vs. C) - significant increases in densities and reproduction of all species except Diaptomus kenai and Holopedium gibberum - significant increases in biomass
5(i)	Gradual, experimental acidification of moderately enriched waters does not affect zooplankton populations or community biomass	- hypothesis falsified (AF vs. F) - mortality of Daphnia rosea at pH 5.4 led to significant changes in species composition and biomass

2) D. brachyurum, C. sphaericus, B. longirostris and C. pulchella replaced Daphnia;

3) D. tyrrelli disappeared after September 20; and

4) D. kenai showed improved reproduction (relative to F).

I consider each species separately in this discussion, and attempt to identify whether acid toxicity, competition, food supply, predation or some combination of these factors were responsible for its performance in treatment AF, relative to both other treatments and other studies. Where acid toxicity appears important, I attempt to identify the "critical pH" and the most acid-sensitive life history stages.

The effects of acidification on phytoplankton-zooplankton relationships are discussed in Section 4.5.

Comparisons of pH toxicity between studies must account for different methodologies and terminologies. Researchers studying acidification effects on zooplankton use the term "critical pH" differently depending on the scale of the investigation. Laboratory tests of acid stress have generally defined critical pH as the pH below which sharp decreases are seen in rates of survival (Havas 1980; Parent and Cheetham 1980), reproduction (Parent and Cheetham 1980) or intrinsic rate of population increase (Walton et al. 1981). Surveys of zooplankton communities across many lakes of different acidity have emphasized the mean lake pH at which significant changes are seen in species composition, particularly numbers of species, number of community dominants or species diversity indices (summarized in Table 22, which is discussed below).

Table 22. Summary of literature showing changes in numbers of crustacean zooplankton species across lakes of different pH.

Location	# Lakes Sampled	# Sampling Dates/Lake $\bar{X}$ ± SE	Method of Sampling	# of Crustacean Species in Lakes with Mean pH in Stated Range ($\bar{X}$/lake ± SE (# of Lakes))						Source
				4.0 - 4.4	4.5 - 4.9	5.0 - 5.4	5.5 - 5.9	6.0 - 6.4	6.5 - 6.9	
1. LaCloche Mts., Ontario	47	1	75 µmnet	3.9±0.7 (9)	3.0±0.5(13)	7.2±1.1(10)	11.3±2.0 (4)	10.3±1.1 (8)	11.0±1(2)	Sprules (1975)
2. Greater Sudbury Area, Ontario[2,3]	187	5 ± 0.1	76 µmand 80 µmnets	5.3 (12)	6.6 (23)	9.3 (19)	10.1 (23)	10.9 (26)	11.7(32)	Keller (1981)
3. Sudbury and Muskota-Haliburton, Ontario	11	26 ± 5	34 L trap; 80µm net	3.4±0.1 (4)[1]	-	-	9.5±1.5 (2)[1]	11.7±1.2 (4)[1]	11.9 (1)[1]	Yan and Strus (1980)
4. S. Norway[3]	57	1	95µm net	2.5 (2)	2.7 (9)	3.3 (14)	3.7 (6)	3.9 (11)	4.2 (1)	Hendrey and Wright (1976)
5. S. Norway	27[5]	2.7 ± 0.2	90 µmnet	-	3.9±0.5 (7)	-	10.0±0.9 (5)	6 ±1.2 (5)	9.0 (1)	Hobaek and Raddum (1980)
6. S. Sweden[3,4]	84	1	75µm net	-	4 (14)	5 (17)	5 (8)	7 (13)	7 (12)	Almer et al. (1974)
7. Island of Rhum and Yorkshire, U.K.	74	1	?[6]	6.4±0.9(14)[6]	10.0±1.2(11)[6]	16.3±1.1 (4)[6]	13.3±2.2 (3)[6]	14.8±2.0 (9)[6]	15.6±1.7(9)[6]	Fryer (1980)

[1] Mean # species per sample, not per lake.

[2] Some overlap exists between lakes sampled in locations 1 and 2, and between locations 2 and 3.

[3] Standard error not computable from published material.

[4] Only 1 significant digit in mean no. of species interpretable from published material.

[5] Three humic acid lakes and 6 alpine lakes not included here.

[6] Includes littoral and limnetic habitats in tarns and ponds.

Each level of approach has its weaknesses. Regional surveys can easily miss critical episodic pH declines that affect zooplankton communities, and at best provide only correlative evidence for the processes responsible for between lake differences. However, acidification experiments in the laboratory or limnocorrals may not adequately simulate the conditions (or rate of change in conditions) present in acidifying lakes.

Since the life history traits of cladocerans and copepods differ fundamentally (Allen and Goulden 1980), I will discuss these two groups separately.

4.4.1 Cladocerans

(i) Daphnia rosea

The primary effect of acidification in the AF cylinders was the mortality of D. rosea, which occurred at a pH of 5.3 to 5.4. This mortality was undoubtedly associated with low pH rather than starvation or predation, since:

1) daphnid egg production, as well as phytoplankton cell sizes and chlorophyll concentrations all indicate that food was abundant;
2) the only potential predators in the AF cylinders were Diacyclops thomasi and Diaptomus kenai. D. thomasi is too small to prey on adult Daphnia (Peacock 1981), and in any case was far too rare (0.01 L^{-1}) to have any impact. D. kenai, labelled by Gerritsen (1980) as a predator, has

been found in the UBC Research Forest lakes to be primarily herbivorous, though it may consume rotifers or nauplii (W.E. Neill, E. Krause, and J. Bowerman, pers. comm.).

3) Subsequent experiments in 1980 with pH kept uniform over all depths (Section II) confirmed that Daphnia rosea shows similar acid sensitivity under conditions of lower nutrients and colder temperatures.

Reductions in the abundance of D. rosea during August 9 to 16 were less severe in cylinder 7AF than 3AF, in spite of identical pH regimes. In Section 3.2.4 (i), I hypothesized that this difference was due to between replicate differences in the proportions of the cylinder populations exposed to the most acid zone of the water column (0-4m). Though depth-stratified samples are not available from August 9 to test this hypothesis, it nevertheless seems reasonable. Within-treatment differences in the vertical distribution of D. rosea were present in treatment AF on August 1, and were also observed in other treatments (e.g. treatment F on September 6). Such differences may have been due to changes in sunlight during the day, since the enclosures were sampled (and acidified) sequentially rather than simultaneously.

Whatever the reason for its occurrence, the between-replicate difference in treatment AF on August 9 ultimately resulted in significant differences in zooplankton community composition one month later (to be discussed). The principle which emerges from these results is that random variation in the

vertical distribution of acid-sensitive organisms can greatly reduce (or increase) the impact of acid pulses to surface waters.

The results demonstrate clearly that starvation of D. rosea via acidification-induced changes in food supply is not likely. As phytoplankton community structure and biomass are unaffected by acidification to mean pH 5.7 (treatment A in this study, Yan et al. 1977), starvation effects would need to be manifested in the narrow band between pH 5.7 and 5.4. Weak buffering makes it virtually impossible for lakes with mean pH 5.4-5.7 to hold their pH above 5.4 over the entire icefree season (NRCC 1981, pg. 161). D. rosea would therefore probably be killed by acid toxicity before any decreases in food supply occurred. Malley et al. (1982) found that total edible phytoplankton (defined as less than 20μm in their study) actually increased when Lake 223 was experimentally acidified to pH 5.37, allowing a second daphnid to colonize the zooplankton community.

The mortality of D. rosea can be compared to published information on other Daphnia species, from multi-lake surveys, laboratory experiments and whole lake manipulations; unfortunately I have not found any published information regarding pH effects on D. rosea.

Multi-Lake Surveys

Interpretation of pH sensitivity from regional surveys is often confounded by large between lake variation in both abiotic and biotic factors. Also, extrapolation from one region to

another is risky, as illustrated by a study of 32 ponds near Georgian Bay, Ontario (Carter 1971). In this study, Diaptomus minutus occurred in many alkaline ponds but never in ponds of mean pH less than 5.2. Carter included D. minutus in a group of species that he suggested may have been excluded from acid ponds by unfavourable water chemistry. However, D. minutus is generally dominant in acid lakes with pH less than 5.0 in both the Sudbury Area of Ontario (Keller 1981) and the Adirondacks of New York State (J.L. Confer, pers. comm.).

Numerous researchers have remarked upon the apparent sensitivity of daphnids to acid conditions. Lake surveys in Ontario (Keller 1981, Sprules 1975a, Roff and Kwiatkowski 1977), Sweden (Almer et al. 1974) and Norway (Hobaek and Raddum 1980, Nillsen 1980a) have all found decreasing abundances of most daphnids below pH 6.0. However, significant drops in total numbers of crustacean species are not seen until pH 5.0: 20-60% fewer species are found in lakes of mean pH 4.5-4.9 than in lakes of pH 5.0-5.4 (Table 22). Actual numbers of species found within given pH ranges vary with the frequency and methods of sampling, number of lakes sampled, range of elevations and humic content, and other factors. The most consistent pattern is the sharp change at pH 5.0.

Laboratory Experiments

The major results of five studies of the toxicity of pH to Daphnia have been summarized in Table 23. Differences in experimental methods restrict comparisons between these studies;

Table 23. Summary of experimental studies of the pH tolerance of daphnids.

Species	Reference	Food Source	Water Temperature Source and Alkalinity[1]	Effects on Survival: Length of Test and (Age of Animals)	Effects on Survival: LC50[2]	Effects on Survival: LC0[2]	Effects on Reproduction	Other Effects/Comments
Daphnia pulex	Walton et al. (1982)	*Ankistrodesmus angustus*, grown in ASM-1 medium plus vitamins	- 18°C - pond - 5.6	12 hr (4 ± 1 d)	4.2	4.3	Reproductive maturity delayed below pH 5.0 (30-60% increase)	Intrinsic rate of population increase (r) decreased below pH 5.0
				21 day (< 1 d)	4.4	5.0	Brood size unaffected	Body length at day 21 reduced at pH 4.4
D. pulex	Davis and Ozburn (1969)	Yeast	- 22°C - aquarium - 70	32 hr	> 50% survival from pH 4.2 to 10.4		Parthenogenesis only between pH 7.0 - 8.7	Poor pH control Limited reproductive data
D. magna	Parent and Cheetham (1980)	Yeast	- 18-20°C - river - 11	24 hr (14 d)	4.2	4.5	Not measured	
				21 day (7 d)	5.4	6.0	No reproduction below pH 5.0	Survival of neonates not examined
				21 day (4 d)	5.8	7.0	No reproduction below pH 5.5	
D. magna	Havas (1980)	*Chlorella*, *Scenedesmus*, and yeast		14 hr	4.0	4.5	% ovigerous and brood size unaffected by pH	
				Under chronic exposure, neonate survival 20% at pH 5.5, 40% at 6.0, 100% at 8.0 (control)				
D. middendorffiana	Havas (1980)	Pond algae	- 12-18°C - pond - 95	15 hr variable	4.0	4.5	Not examined	Experiments performed in situ showed higher survival in controls, but same pattern

[1] Of water used in experiments, prior to acid additions (in mg/l as $CaCO_3$).

[2] LC0 = pH causing same mortality as controls (not necessarily 0%).
LC50 = pH causing 50% mortality.

nevertheless some general patterns emerge which are relevant to the observed behaviour of D. rosea populations in the AF cylinders.

All five acute tests in Table 23 found daphnid survival to be less sensitive to pH than were D. rosea populations in the AF cylinders. If I ignore differences between experimental settings and compare the chronic tests by Parent and Cheetham (1980) and Walton et al. (1982) with my limnocorral results, it suggests that D. rosea is more tolerant of chronic exposures than D. magna, and less tolerant than D. pulex. This conclusion is only tentative, given the contrasts between limnocorral and laboratory environments.

The only evidence of comparable daphnid sensitivity to acute exposures comes from Skadowski (1926) who performed experiments with Daphnia longispina. Anderson (1974) has observed that many historical records of D. longispina were probably D. rosea, so Skadowski's results are particularly relevant. He found that deleterious effects were strongly evident at pH levels of 5.3. Unfortunately, Skadowski described neither what these effects were, nor under what experimental conditions they were observed.

High neonate mortality (Havas 1980; Table 23) and delayed reproductive maturity (Walton et al. 1982, Table 23) are consistent with the observed shift in the age structure of the 7AF Daphnia population towards older individuals. However, the apparent neonate mortality in 7AF was not necessarily due only to acid stress. Neonate survival could also have been affected by competition with the dense populations of B. longirostris and

C. sphaericus, which probably grazed primarily on algal cells < 13μm (Section 3.3.5 (iii)); neonate daphnids would have been competing for these same cells. It is not clear that these cells were limiting in 7AF, but they were much less abundant in treatment AF than F during September and October (Table 18). Neill (1975a) and Lynch (1978) have shown how small cladocerans may create competitive bottlenecks for immature stages of larger herbivorous crustaceans.

The acid-stressed Daphnia population in 7AF had higher percentages of ovigerous females and higher brood sizes than did the F cylinder populations, which I suggest was due to decreased intraspecific competition in the adult stage. That is, daphnid adults had few competitors but the neonates competed with Chydorus and Bosmina. In contrast to treatment AF, Walton et al. (1982) and Havas (1980) found no change in brood sizes, and Parent and Cheetham (1980) found a decrease. In these laboratory studies, more than one animal was present per container, but food was frequently replenished, so that intraspecific competition would have been low in all treatments. This probably is why none of these studies observed increased brood sizes as some animals died. Walton et al. (1980) point out that reproduction may have been higher in their study than in that of Parent and Cheetham (1980) since Walton's animals were fed a more nutritious diet (Table 23). The great reductions in reproduction observed by Davis and Ozburn (1969) cannot be substantiated because of poor pH control and limited reproductive data. Their animals may also have produced few

eggs on a diet consisting only of yeast.

Walton et al. found delayed maturity in D. pulex at pH 5.0, but no decrease in survival until pH 4.4. If this pattern held for D. rosea in the field, I should have seen a decline in egg densities at sublethal pH levels in treatment A (about 0.3 pH units above lethality). However, this did not occur.

At pH 4.4, Walton et al. (1982) observed a decrease in the body length of 21 day old D. pulex. In my experiment mean body lengths of AF cylinder adult D. rosea increased relative to all other treatments. These two observations are not contradictory, since the mean length of adults in a field population with overlapping generations integrates both age structure and growth rate changes, whereas toxicity test measurements of uniform age animals reflect only the latter.

The filtering and feeding rates of many cladocerans reach a maximum in a narrow pH range (close to that of the body of water from which the animals were collected) and decrease at both higher and lower pH (Ivanova 1969, Ivanova and Klekowski 1972, Kring and O'Brien 1976). Feeding rates of D. rosea may consequently have been reduced, and possibly failed to acclimate. In any case, this did not inhibit egg production after August 16 (Figure 12). Under more limiting food conditions, reductions in feeding rate may be more critical, but they are still less important than direct toxicity (Section II).

One critical factor in extrapolating from the laboratory to the field is the actual amount of overlap in the spatial and temporal distributions of organisms and hydrogen ions.

Variations in the vertical distribution of Daphnia were likely responsible for differences between the AF replicates in Daphnia mortality August 9 to 16. Groterud (1972) found that Cyclops strenuus strenuus was entirely absent from surface waters of Lake Sandtjern only when the pH at 0-2 m was less than 5.0. This pattern probably resulted from mortality in the upper waters but the cyclopoids may also have avoided acid strata. Avoidance of low pH zones is well known in fish (Muniz and Leivestad 1980). However, the vertical distributions of crustaceans on August 1 and September 6 did not demonstrate any shifts in response to acidification of the epilimnion.

Whole Lake Manipulations

Useful information on the acid tolerance of daphnids may be gleaned from two whole lake manipulations in Ontario: the neutralization of Nelson Lake in the Sudbury area (Yan et al. 1977) and the acidification of Lake 223 in the Experimental Lakes Area (ELA) (Malley 1981). In 1975, the mean pH of Nelson Lake was raised from 5.7 to 6.4 with calcium hydroxide and calcium carbonate (Yan et al. 1977). Zooplankton community structure did not change significantly after neutralization, and still strongly resembled the nonacidic ELA lakes of northwestern Ontario sampled by Patalas (1971). However, it is intriguing that Daphnia longiremis was rare in Nelson Lake prior to neutralization but became dominant subsequently (Yan et al. 1977). (The term 'dominant' here means greater than 10% of the total crustacean density, excluding nauplii.) It is possible

that Nelson Lake D. longiremis were acid-stressed prior to neutralization since depth-integrated water samples in the spring of 1975 measured pH 5.4-5.5, and surface pH values were likely lower.

Acidification of Lake 223 from mean pH 6.8 to 5.6 (1976-1979) was associated with a steady decline in Daphnia galeata mendotae (Malley et al. 1981). However, with acidification to pH 5.25 in 1980, densities of D.galeata mendotae recovered, and a previously unrecorded daphnid, D. schoedleri, became twice as abundant as D. galeata mendotae (Malley et al. 1981). Comparing these results with my 1979 experiment suggests that D. rosea is more acid sensitive than either D. galeata mendotae or D. schoedleri, though the rate of acidification was much faster in my experiment than in Lake 223.

In conclusion, Daphnia rosea appears more acid sensitive than most other daphnids studied to date, either in laboratory or whole lake acidification studies. The 1979 experiment suggests that changes in intraspecific and interspecific competition during acidification may alter the reproduction and survival of daphnid populations from the patterns observed in laboratory toxicity studies. However, laboratory studies of chronic exposures with complete life table analyses (as performed by Walton et al. 1982) gave results generally similar to mine.

(ii) Diaphanosoma brachyurum

In general, D. brachyurum in Eunice Lake breaks diapause in July and reaches peak densities of 2-3•L^{-1} by early August (Northcote and Clarotto 1975, W.E. Neill and C.J. Walters unpublished data). The timing of the resource peak in the AF enclosures was therefore particularly advantageous to D. brachyurum and accelerated its rate of increase. Smith (1969) observed a doubling in mean densities of D. brachyurum after fertilizing Crecy Lake in 1959. Numbers of D. brachyurum also often increase in fertilized enclosures in Gwendoline Lake (W.E. Neill, pers. comm.). However, there is strong evidence suggesting that the acidification-induced removal of Daphnia rosea grazing was the most critical factor in permitting Diaphanosoma brachyurum to reach such high densities in 3AF.

First, in treatment F, which received the same amount of nutrients as AF, densities of D. brachyurum never exceeded 0.78 L^{-1} and averaged only 0.25±0.05 L^{-1}. Under the AF treatment, D. brachyurum densities reached a peak of 21.3 L^{-1} (in 3AF) and averaged 2.7±1.1 L^{-1}.

Second, D. brachyurum performed much better in 3AF than 7AF (Figure 10). This difference could not be due to direct pH effects on either D. brachyurum or its food sources, since the two AF replicates contained identical pH regimes. Reduced competition with D. rosea is a reasonable explanation for the superior performance of D. brachyurum in 3AF, since densities of D. rosea were much lower in 3AF than in 7AF (Figure 12). The two species may have similar depth preferences, since stratified

samples in AF enclosures on September 6 showed D. brachyurum at 2-4 m, the stratum in which D. rosea had previously been most abundant.

The above results suggest,. but do not prove, that Daphnia was the main competitor of Diaphanasoma in treatment F. Lowering the pH in AF may have also lowered the grazing rates of other potential competitors (e.g. D. tyrrelli). However, other evidence supports the suggestion that D. rosea and D. brachyurum compete. Neill (in prep.) found that removal of D. rosea from enclosures significantly increased densities of D. brachyurum; removal of Daphnia from nutrient-enriched enclosures increased Diaphanasoma still further. Therefore, the acidification of lakes to mean pH values in the range 5.0-5.5 may release Diaphanosoma from competition with Daphnia. The degree of competitive release obseved will depend on the acid tolerance and community dominance of the particular species of Daphnia, as well as the trophic status and predation regime of the lake.

Gliwicz (1977) proposed that high summer concentrations of net phytoplankton inhibited the feeding and egg production of two daphnids in eutrophic Mikolajskie Lake. Summer declines of these species (and others) were accompanied by increases in D. brachyurum, Chydorus sphaericus, and Ceriodaphnia quadrangula, which were attributed to their smaller carapace crevices that do not admit net plankton. Although net phytoplankton were abundant in zooplankton samples from the AF cylinders in late August, daphnid brood sizes concurrently increased (data available for 7AF only). Net phytoplankton

interference with daphnid filtration was therefore not responsible for the increase in D. brachyurum, C. sphaericus, and C. pulchella observed in 7AF.

The tolerance of D. brachyurum to pH 5.2 is supported by both experimental studies and regional surveys. D. brachyurum remained abundant during the acidification of Lake 223 to pH 5.25 (Malley et al. 1981). Nillsen (1980a) reported that in southern Norway D. brachyurum was generally dominant in lakes of pH 5.0-5.5, common at 4.8-5.0 and scarce at lower pH values. Interestingly, he named D. brachyurum, Holopedium gibberum and Bosmina longispina as a group of filter feeders that frequently occupied the niche of Daphnia spp. after their disappearance. Hobaek and Raddum (1980), also working in Southern Norway, found D. brachyurum to be generally common or dominant in clear lakes of pH 4.9-6.3, and also in humic lakes of pH 4.47-6.48.

D. leuchtenbergianum, which may only be another variety of D. brachyurum (Carter et al. 1980), also appears in many acid lakes. In the Sudbury area of Ontario, it was present in 11 of 17 lakes of pH 4.5-5.0 and dominant in five (Keller 1981), Sprules' data (1975a) showed a similar pattern in a survey partially overlapping Keller's. Anderson (1977) found D. leuchtenbergianum codominant with B. longirostris in a Virginia brown water lake of pH 4.5. In acidic, metal-contaminated Cheat Lake however, D. leuchtenbergianum was abundant only in less acid backwaters of mean pH 5.5 and relatively scarce in the main lake, with mean pH 4.5-5.0 (Janicki and DeCosta 1979).

The above studies suggest that humic lakes, clear acid lakes and acid metal-contaminated lakes constitute a gradient of increasing toxicity for Diaphanosoma. Studies by Hobaek and Raddum (1980) and Yan and Strus (1980) show that zooplankton species diversity decreases along this gradient. Therefore, metal chelation by humic materials (Almer et al. 1978) may be as important to acid-stressed zooplankton as it is to fish (Baker and Schofield 1980; Haines 1981).

(iii) Bosmina longirostris

Brooks and Dodson (1965), Goulden et al. (1978), Lynch (1978) and many others have examined the question of whether bosminids and daphnids compete. Unlike Diaphanosoma brachyurum, the abundance of Bosmina longirostris appeared more closely associated with fertilization than with the loss of Daphnia rosea. Mean densities of B. longirostris were not significantly different between F and AF, though much higher in these two fertilized treatments than in A and C (Table 11). Elimination of D. rosea may however have helped to raise B. longirostris egg production in the AF enclosures to significantly higher levels than in F (Table 11 and Figure 17). Also, near total elimination of D. rosea in 3AF was associated with 3 X higher peak densities of B. longirostris than in 7AF, where D. rosea persisted. Both Olenick (1982) and Neill (in prep.) found that spring removal of D. rosea from enclosures resulted in greater increases in B. longirostris than Diaphanosoma brachyurum. Differences in our results may have been due to the later

removal of D. rosea in my experiment.

The improved performance of B. longirostris with fertilization is not an isolated case. Increases in B. longirostris are commonly observed following fertilization of both enclosed and whole lake zooplankton communities in Gwendoline Lake (W.E. Neill, C.J. Walters, pers. comm.). Why does fertilization benefit B. longirostris over other species? Increases in planktivorous fish, cited as possible causes by Brooks (1969) and McNaught (1975) are inapplicable to both my results and those from Gwendoline Lake, since both environments were fishless when fertilized.

Goulden et al. (1978) performed laboratory studies of the intrinsic rates of natural increase of various daphnids and B. longirostris. They predicted that Bosmina could only dominate over Daphnia at low food densities, when the latter's fecundity would drop low enough to give Bosmina a higher reproductive rate. The results of my experiment were the exact converse: Bosmina performed worse (relative to Daphnia) at low food densities (A and C) than at high (F and AF). Demott (1982) demonstrated in the laboratory that at low concentrations of the alga Chlamydomonas, the ingestion rates (per unit biomass) of B. longirostris are 1.6-4.8 times higher than D. rosea; at high algal cell concentrations however, feeding efficiencies of the two species are similar. Demott's study also suggests that B. longirostris should outperform D. rosea at low food densities, the converse of what I found.

The two laboratory studies discussed above used much less diverse size spectra of food resources than are present in nature. B. longirostris may have benefitted by fertilizer-induced increases in the quantity of small algal cells and bacteria. Substituting the overall mean length of B. longirostris (0.36 mm) into equation (4; page 152), suggests a maximum ingested particle size of 12.8 μm. The mean algal biomass < 13 μm was significantly greater in F than in C, and significantly greater in AF than in A (Table 13, Figures 21 and 22). Production of particles < 13 μm likely increased even more than biomass, as phytoplankton growth rates tend to vary inversely with cell size (Kalff 1972, Parsons and Takahashi 1973, Gutelmacher 1975, Redfield 1980). This increase in abundance of small particles may have particularly benefitted Bosmina juveniles, which have low energy reserves relative to both bosminid adults and daphnid juveniles and adults (Goulden and Hornig 1980).

Differences in particle size preferences may permit the coexistence of Daphnia and Bosmina. Kerfoot and Demott (1980) found that although D. pulex competitively excluded B. longirostris in beakers when both were fed Chlamydomonas, the two species were able to coexist in field enclosures. Experimental enrichments with algae and bacteria strongly suggested that Bosmina may use small bacterial particles in preference to some phytoplankton species (Kerfoot and DeMott 1980). However, not all environments rich in nutrients contain the diversity of resources necessary to allow coexistence of

Daphnia and Bosmina. In a series of competition experiments in enclosures within eutrophic Pleasant Pond, Lynch (1978) found that Bosmina was consistently out-competed by Daphnia.

The geographic distribution of Bosmina suggests that it is tolerant to both eutrophication and acidification. In North America, B. longirostris frequently attains extreme dominance in both eutrophic (Gannon and Stemberger 1978, Brooks 1969) and acidified lakes (Yan and Strus 1980, DeCosta and Janicki 1978, Keller 1981). It is also very common, though generally less dominant, in circumneutral mesotrophic and oligotrophic lakes (Carter et al. 1980, Patalas 1971, Patalas and Salki 1973). In Scandinavia, B. longirostris is sometimes associated with eutrophication (Pejler, 1975), but in acid lakes B. coregoni (Almer 1974), B. longispina Leydig (Hobaek and Raddum 1980) or Eubosmina longispina (Nilssen 1976, Hendrey and Wright 1976) are the dominant bosminids. (Hobaek and Raddum (1980) suggest that Swedish reports of B. coregoni were likely B. longispina).

Both nutrient-enriched and acidic conditions were present in the 1979 experiment. During September and October (when B. longirostris was abundant) F enclosures could be classified as oligo-mesotrophic and the AF enclosures mesotrophic, based on mean chlorophyll concentrations of 2.04 ± 0.31 and 5.35 ± 0.53 $\mu g \cdot L^{-1}$ respectively (Wetzel 1975). Exposure of Bosmina to pH 5.0-5.5 in AF caused no apparent physiological disturbance, and actually increased reproduction relative to F.

(iv) Chydorus sphaericus

During the first week of September AF Chydorus numbers increased at 26.7% day^{-1}, which exceeds the rate of 23.7% found by Keen (1967) in a well-fed laboratory culture of the same species, at higher temperatures. It is possible that: 1) treatment AF provided for higher rates of chydorid production due to periphyton growth on the sides of the enclosures; and 2) a large part of the observed increase in Chydorus was due to a shift in their distribution from the sides and bottom of the enclosures towards the middle, rather than due to increased reproduction and survival. These two issues are addressed in sequence.

Both during the 1979 experiment and subsequently when the cylinders were removed and scrubbed clean, it was apparent that the AF cylinders contained much greater quantities of periphyton than the other treatments. Muller (1980), Hendrey (1976), and Hall et al. (1980) all observed increased periphyton growth with increased [H+]. Their similar results were attributed to different causes: Muller (1980) interpreted his data as evidence for algal species preferences for high [H+]; Hendrey (1976) and Hall et al. (1980) concluded that reduced grazing by invertebrates and microheterotrophs were responsible. Several investigators (Laake 1976, Hendrey 1976, Muller 1980) report large biomasses of Mougeotia sp. and Tabellaria sp. as periphyton at pH 4.0-6.0. Both of these genera were abundant (annoyingly so) in my zooplankton samples from the AF enclosures. The trunk limb claws of C. sphaericus are well-

adapted for scraping periphyton and bacteria from the sides of containers and floating filaments (Fryer 1968). These resources are generally unavailable to other zooplankton (Kerfoot and Demott 1980).

The appearance of C. sphaericus in the pelagic zone during blue green and green algal blooms has been attributed to the value of filaments as limnetic substrates (reviewed by Fryer 1968) and to the changes in light quality and intensity associated with algal blooms (Hutchinson 1967). Though blue green filaments did increase after the collapse of Daphnia (Figures 22 and 23; Appendix F), the increase in green filaments was much more noticeable. These green filaments and the changes in light quality associated with the 2 m decrease in sechhi depth (August 9 to 23) may have drawn chydorids from the sides of the enclosures to the middle.

Did the loss of Daphnia from the AF enclosures benefit C. sphaericus? Peacock (1981) found that fertilization of limnocorrals in Gwendoline Lake increased both blue green algae and the densities of C. sphaericus. However, she reported still larger C. sphaericus increases if D. rosea was removed from the cylinders by predation from Chaoborus spp., and concluded that C. sphaericus is constrained by competition with Daphnia. An alternate explanation is that removal of Daphnia allowed blue green filaments to grow large enough to increase the limnetic habitat of Chydorus. Kerfoot and Demott (1980) observed habitat partitioning by D. pulex and C. sphaericus in both beaker and limnocorral environments, and concluded that they did not

compete. Allen and Goulden (1980) point out that the intrinsic rate of increase of C. sphaericus may be too low to allow it to compete successfully with more productive limnetic species. Direct competition between Daphnia and Chydorus in treatment AF seems unlikely due to their dependency on different resources. However, the loss of Daphnia probably did benefit Chydorus indirectly by increasing the abundance of filaments and large algal cells, providing useful substrate for Chydorus.

Jacenko (1928), cited in Ivanova (1969) and briefly discussed by Skadowski (1926), found that under temperatures of 22-24°C and total darkness, C. sphaericus reproduced successfully between pH 5 and 9. Surprisingly, maximum rates of reproduction occurred at the extreme ends of the pH range. Multi-lake surveys (Yan and Struss 1980, Keller 1981) indicate that C. sphaericus is quite acid tolerant, but rarely dominant. However, when two Ontario acid lakes were neutralized and fertilized, C. sphaericus replaced B. longirostris and formed up to 97% of the mean total zooplankton biomass (Yan and Lafrance 1981). This suggests that although C. sphaericus may be as acid tolerant as B. longirostris, it requires very high levels of food (or substrates) to gain dominance in the pelagic zone. (Yan and Lafrance also noted that peak abundances of C. sphaericus were not consistently correlated with blooms of blue green algae.) Both my fertilized cylinders (Figure 11) and those of Peacock (1981) consistently showed negative correlations between B. longirostris and C. sphaericus, suggestive of possible competition. Although their daytime

distributions show strong segregation (Section 3.2.5), at night B. longirostris and C. sphaericus are often found together in the epilimnion (W.E. Neill, pers. comm.).

(v) Ceriodaphnia pulchella

This species is generally rare in Eunice Lake (Northcote and Clarotto 1975), and its appearance in the AF cylinders in September may have been delayed due to very low initial densities. I was unable to find any records of C. pulchella in acidic environments, unlike its congener C. quadrangula which is tolerant of conditions below pH 5.0 (Carter 1971, Hobaek and Raddum 1980, Lowndes 1952).

The appearance of Ceriodaphnia in the AF cylinders (particularly 3AF) may have been related to both the loss of Daphnia and shifts in the resource spectrum to smaller particles. Like D. brachyurum, Ceriodaphnia was much less abundant in treatment F than AF (Table 11). In a series of experiments by Lynch (1977), Daphnia pulex did occasionally competitively exclude Ceriodaphnia reticulata, but the reverse occurred more frequently. Also, C.quadrangula outcompeted Daphnia magna in a study by Neill (1975b). In Neill's study, the efficiency of C. quadrangula at grazing small particles (3-6 μm) was shown to be a key competitive ability. Therefore the significantly higher mean biomass of 2-5 μm particles in the AF enclosures (as compared to F) may have been advantageous to Ceriodaphnia (Table 14, page 122). Since there was a one month time lag between the disappearance of Daphnia in the AF

cylinders and the appearance of Ceriodaphnia, a shift in the resource spectrum seems the more probable proximal cause for the increase in densities of Ceriodaphnia. Declines in Bosmina and Diaphanosoma may also have assisted Ceriodaphnia.

4.4.2 Copepods

Diaptomus tyrrelli and Diaptomus kenai were affected very differently by my experimental treatments. Fertilization significantly increased D. tyrrelli egg production, adult lengths, and mean densities (Section 3.2.4 (ii)) but did not affect D. kenai. Acidification and fertilization to pH 5.15 caused high mortality of D. tyrrelli, but resulted in increased egg production and growth in D. kenai.

I propose that in 1979 D. tyrrelli eventually succumbed to acid stress, but that the congener D. kenai benefitted by the loss of Daphnia. Longer experiments are necessary to reveal whether D. kenai recruitment is as acid resistant as adult survival.

In the most acid lakes of the Sudbury area and the Adirondack Mountains, the small diaptomid Diaptomus minutus is usually dominant, or codominant with Bosmina longirostris (Keller 1981, J.L. Confer pers. comm.). Similarly, in southern Norway the most acid lakes are frequently dominated by the small calanoid copepod Eudiaptomus gracilis and Bosmina longirostris (Hoboek and Raddum 1980). The high acid sensitivity of D. tyrrelli (which is about the same length as D. minutus) and the acid tolerance of the much larger D. kenai highlight the

variability in zooplankton acid tolerance within both phyletic families and size classes.

It is surprising that the cyclopoid copepod Diacyclops thomasi did not increase in treatments F and AF, since Neill and Peacock (1980) found that fertilization significantly increased the survival of juvenile stages of Diacyclops thomasi. Initial densities may have been too low. Also, the timing of my nutrient additions may have been too late in the season for Diacyclops thomasi, which changes from herbivorous to carnivorous feeding by August (McQueen 1969, Peacock 1981).

4.5 Phytoplankton and Phytoplankton-Zooplankton Interactions

The experimental tests of the original null hypotheses concerning phytoplankton and phytoplankton-zooplankton interactions are summarized in Table 24. The absence of any changes in phytoplankton with acidification to pH 5.6 suggests that in acidifying lakes, highly acid-sensitive species such as D. rosea will be affected by acid toxicity before they experience alterations in their food supply (Section 4.4.1 (i)). In treatment A, the pH did not drop below 5.6 for long enough to test whether pH levels of 5.0-5.6 affect the availability of phytoplankton food for more acid-tolerant species.

Increases in the availability of phytoplankton food with fertilization (in both the F and AF treatments) were expected on the basis of previous studies in both circumneutral and acidic oligotrophic lakes (Nelson and Edmundson 1955, Smith 1969, Schindler and Fee 1974, Yan et al. 1981). The 1979 results

Table 24. Summary of 1979 results relevant to hypotheses on phytoplankton and phytoplankton-zooplankton interactions.

Null Hypotheses (from pg 41)		Major Results
2(ii)	Gradual, experimental acidification of oligotrophic waters to pH 5.0 does not affect photoplankton community biomass and size composition	- no evidence against hypothesis to pH 5.6 (A vs. C) - too few samples for adequate test at pH < 5.6
3(iii)	Moderate nutrient enrichment of circumneutral waters does not change the availability of phytoplankton food for zooplankton	- hypothesis falsified (F vs. C) - treatment F showed significantly higher chlorophyll a and pheophytin a concentrations, greater biomass of edible algal cells · < 13 µg, and longer sustained production of zooplankton
4(ii)	Moderate nutrient enrichment during experimental acidification to pH 5.0 does not alleviate acid-induced shortages of phytoplankton food for zooplankton	- no evidence of acid-induced food shortages (see 2(ii) above) - relative to treatment A, treatment AF showed significantly higher chlorophyll a and pheophytin a concentrations, greater biomass of edible algal cells, and longer sustained production of zooplankton - benefits of increased food to *Daphnia rosea* overwhelmed by increased acid toxicity

Table 24. Continued.....

Null Hypotheses (from pg 41)		Major Results
5	Gradual, experimental acidification of moderately enriched waters:	
(ii)	does not affect phytoplankton community biomass and size composition; and	- hypothesis falsified (AF vs. F) - AF showed significantly higher chlorophyll *a* concentrations after the collapse of *Daphnia rosea* and a shift in phytoplankton community size structure to larger cells
(iii)	does not alter the ability of plankton systems to absorb enrichment perturbations	- some evidence against hypothesis - collapse of *D. rosea* in AF allowed large algal cells to increase - much greater fluctuations in phase plane trajectories

confirm that pH levels of 5.4-5.7 do not constrain the overall ability of the phytoplankton community to capitalize on periodic pulses of nutrients.

In the AF cylinders, the major indirect effects of acidification began as a result of changes in the zooplankton community, not because of changes to the phytoplankton. Acid-induced mortality of D. rosea reduced the herbivorous consumption of large algal cells, shifted the size structure of the phytoplankton community to larger cells, and greatly increased the amplitude of fluctuations in zooplankton biomass and chlorophyll a concentrations. How do these changes in phytoplankton-zooplankton interactions compare with previous studies in acidic lakes?

The most complete analysis of acid-stressed phytoplankton zooplankton interactions is that of Yan and Strus (1980), who analyzed six years of phytoplankton and zooplankton data from acidic (pH 4.3), metal-contaminated Clearwater Lake. Like treatment AF, the zooplankton biomass of Clearwater Lake was dominated by cladocerans, with Bosmina longirostris forming 79-95% of mean biomass during the icefree season. Since about 50% of the phytoplankton biomass in Clearwater Lake consisted of dinoflagellates (particularly Peridinium inconspicuum) that were too large to be grazed by B. longirostris, the authors hypothesized that approximately half the phytoplankton biomass was unavailable as a food source to the zooplankton community. A somewhat similar situation prevailed in treatment AF after the collapse of D. rosea. About 85% of the herbivorous filtering

was by zooplankton species consuming only algal cells less than 13 μm in size, whereas 71.2% of the total algal biomass was in cells larger than 13 μm (Table 18, Section 3.3.5 (iii)).

However, Clearwater Lake and treatment AF differed considerably in other respects. The Clearwater Lake zooplankton community was estimated to filter only 0.22-0.75% day^{-1} of the lake's volume (5-18 times less than the zooplankton community of a nearly circumneutral, oliogotrophic lake). By contrast, treatment AF zooplankton filtered approximately 4% day^{-1} of the cylinder volume. Treatment AF could support a much higher biomass of zooplankton, due to higher nutrient levels, only one tenth the $[H^+]$, and no Cu or Ni contamination. Because of the low filtering rate of the Clearwater Lake zooplankton community, Yan and Strus also hypothesized that changes in the structure of the phytoplankton community were not attributable to zooplankton grazing. In the AF cylinders however, the biomass of small cladocerans grew high enough to significantly reduce the chlorophyll *a* concentrations and the abundance of smaller particles (Section 3.3.4 (iii)).

The most common community dominants in North American acid lakes of pH<5.0 are *B. longirostris* and *Diaptomus minutus*, both small crustaceans (Sprules 1975a; Keller 1981; J.L. Confer pers. comm.). If enriched, such lakes would presumably display increases in the biomass of large algae that exceed those observed when nutrients are added to circumneutral lakes with larger herbivores. In transition lakes (pH 4.7 to 5.3), the ability of plankton systems to deal with enrichment

perturbations may be reduced, particularly if these perturbations occur during episodic pH depressions and the herbivorous community dominants are both large and acid sensitive.

The effects of enrichment of acidic (pH 4.2) Mountaintop Lake (Yan et al. 1981; Yan and Lafrance 1981) support the contention that fertilization of acidic waters increases the impact of herbivores on phytoplankton, and of invertebrate predators on zooplankton. In 1971, fertilization of Mountaintop Lake took place in the absence of invertebrate predators, and led to such rapid increases in B. longirostris and D. minutus that algal biomass was reduced to almost zero, and B. longirostris crashed. It is at first surprising that no large algae were able to escape the grazing of these small herbivores. However, the phytoplankton species diversity of Mountaintop Lake was already low, relative to circumneutral lakes, prior to fertilization (N.D. Yan, pers. comm.). After enrichment, algal diversity decreased still further, with the community entirely dominated by a few small cryptomonads that were heavily grazed (Yan and Lafrance 1981). Fertilization of Labelle Lake, which at pH 6.0 was the control for the Mountaintop Lake experiment, caused effects similar to my treatment F, with increases in the biomasses of both phytoplankton and zooplankton. The absence of zooplankton overgrazing in Labelle Lake was attributed to cyclopoid predation (Yan and Lafrance 1981), but blooms of filamentous Oscillatoria may also have been contributory.

Dickman and Efford (1972) demonstrated how nutrient enrichment of enclosed phytoplankton in circumneutral Marion Lake was generally followed by sharp decreases in algal species diversity. In the highly simplified phytoplankton communities of lakes with pH < 5.0, such decreases may lead to large crashes of zooplankton due to overgrazing. Analogous events may occur at the herbivore-invertebrate predator level. Continued fertilization of Mountaintop in 1977 and 1978, when predatory Chaoborus larvae were abundant, led to the virtual extinction of all herbivorous zooplankton and enormous increases in phytoplankton biomass. The uniformly small size of the crustacean zooplankton probably made the community considerably more vulnerable to Chaoborus predation.

Although potential herbivore grazing impacts on algae have been considered in detail, abiotic factors, especially pH, light, and nutrients, almost certainly also affected phytoplankton community composition. Ideally, the experiment would have monitored nutrients and primary production, or included an AF treatment with all herbivores removed, to separate out abiotic effects on phytoplankton community size structure. Taxonomic description of the phytoplankton within the AF cylinders was incomplete (Figure 23 and Appendix F), but was sufficient to suggest that the effects of acidification differed from those observed elsewhere. In Ontario and Sweden, dinoflagellates are a small percentage of total algal biomass in circumneutral lakes, but become dominant in lakes with pH < 5.0 (Yan 1979, Yan and Stokes 1978, Hornstrom et al. 1973 (cited by

Yan and Stokes 1978)). In the Adirondacks some lakes around pH 5.0 maintain Chrysophyceae as community dominants, (the normally dominant phylum in circumneutral, oligotrophic lakes) but dinoflagellates still form about 20% of the community biomass during the icefree months (Hendrey et al. 1980). Based on these data, and evidence that dinoflagellates (particularly Peridinium inconspicuum) are favoured by short term, rapid depressions in pH (Yan and Stokes 1978), I expected to see an increase in dinoflagellates within the AF cylinders. However, no Dinophyceae were observed in the AF samples, and either Chrysophyceae or (later) Cryptophyceae appeared dominant (Figure 23). Differences in dominant phyla between the above described acid lakes and the AF cylinders could be due to the latter's higher pH (particularly below 4m), lower transparency and/or higher total N and total P. Of these three factors, nutrient concentrations seem the least likely to have excluded dinoflagellates: in Ontario acid lakes the proportion of total algal biomass contributed by dinoflagellates is negatively correlated with [H+] ($r^2 = 0.50$), but uncorrelated with total P (Yan 1979). Also, Peridinium inconspicuum became dominant during the third year of fertilization of Mountaintop Lake (Yan and Lafrance 1981), demonstrating that this alga can maintain its dominance under low and high nutrient levels in acid lakes.

II. EXPERIMENTAL ACIDIFICATION OF ENCLOSED ZOOPLANKTON COMMUNITIES (SPRING 1980)

1. INTRODUCTION

To date, the effects of lake acidification on zooplankton communities have been studied primarily through multi-lake surveys, monitoring studies, or laboratory toxicity experiments (reviewed in Section I). With the exception of the Lake 223 experiment in the Experimental Lakes Area (Malley et al. 1981), there are no published studies demonstrating the responses of an entire zooplankton community to experimental acidification.

In the summer of 1979, I conducted a three month limnocorral experiment in Eunice Lake to examine the effects on plankton systems of three experimental manipulations: 1) acidification, 2) fertilization and 3) both acidification and fertilization (Section I). The results of the experiment stimulated several questions concerning the responses of zooplankton to acidification, at both community and population levels of organization:

1) The 1979 experiment was conducted in midsummer. Would the zooplankton community respond similarly to experimental acidification in spring, when temperatures are lower, food resources are generally higher quality (Neill 1981b), and different zooplankton species and life history stages are present?

2) In 1979, the mean epilimnetic pH remained at or above 5.6 in the unfertilized enclosures, and did not affect zooplankton performance. What are the effects on unenriched plankton systems of higher levels of

acidification, specifically to pH 5.5, 5.0 and 4.5?

3) Major mortality of the dominant herbivore, Daphnia rosea, occurred in 1979 in acidified, nutrient-enriched enclosures when the pH dropped in one day from 6.2 to 5.3. Does the rate of pH change affect the toxicity of different pH levels to particular zooplankton populations? This question is especially pertinent to spring acidification experiments. In many areas of Eastern North America and Scandinavia, low alkalinity lakes show severe episodic spring pH depressions, as hydrogen ions stored in the snowpack are released (Jeffries et al. 1979, Hultberg 1977).

4) In 1979, surface additions of sulfuric acid failed to penetrate the midsummer thermocline. Though this created a strong pH gradient with depth, a common feature of acidifying lakes (Schindler et al. 1980, Henriksen and Wright 1977), it also created chemical refugia for deep-dwelling species or subpopulations. This lowered the value of the experiment as a toxicity test. Would the apparent pH tolerances of the various species (and the consequent community shifts) be different if the pH were uniform over all depths?

In the spring of 1980, I conducted a two month limnocorral experiment in Eunice Lake to address the above four questions, and to compare zooplankton communities and populations in experimentally acidified enclosures with those of acidified

lakes. As in 1979, I intended to use such comparisons to speculate on the relative importance of toxicity, competition, predation and food supply in determining the direction of zooplankton community change under experimental acidification.

2. MATERIALS AND METHODS

2.1 Experimental Design and Execution

The experiment was designed to expose enclosed zooplankton communities to low, medium or high rates of acidification (to pH 5.5, 5.0 or 4.5) over a period of 10 days, and then hold the pH constant for four weeks (Figure 28). Between treatment comparisons during the two week acidification phase were used to estimate incipient lethal pH levels and assess whether the rate of pH change affected zooplankton mortality rates at specific pH levels (Figure 28). During the constant pH phase, between treatment comparisons indicated the overall direction of change in zooplankton community biomass and structure at each pH level.

The study area, limnocorral design, and procedures used to fill and sample the enclosures are described in Section I. In May 1980, the eight enclosures used in 1979 were drained, scrubbed to remove epiplastic algae (periphyton) from the walls, and refilled with Eunice Lake zooplankton at lake densities. The low (L), medium (M) and high (H) acidification treatments were randomly assigned to six of the eight enclosures; the other two served as controls (C). Table 25 shows the correspondence between 1979 and 1980 treatments. I compared replicate 6C with 8C, and 3L with 7L to assess whether heavy periphyton growth under the acidification and fertilization treatment in 1979 had any residual impact in 1980.

Figure 28. Design of 1980 experiment. Lines show intended pH change under each treatment. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate. Open circles illustrate examples of between-treatment comparisons to evaluate effects of rate of pH change on toxicity (i.e. treatments L, M, and H reach pH 5.5 after 10, 7, and 5 days respectively). Closed circles are examples of between-treatment comparisons during constant pH phase. Triangles show sampling intensity.

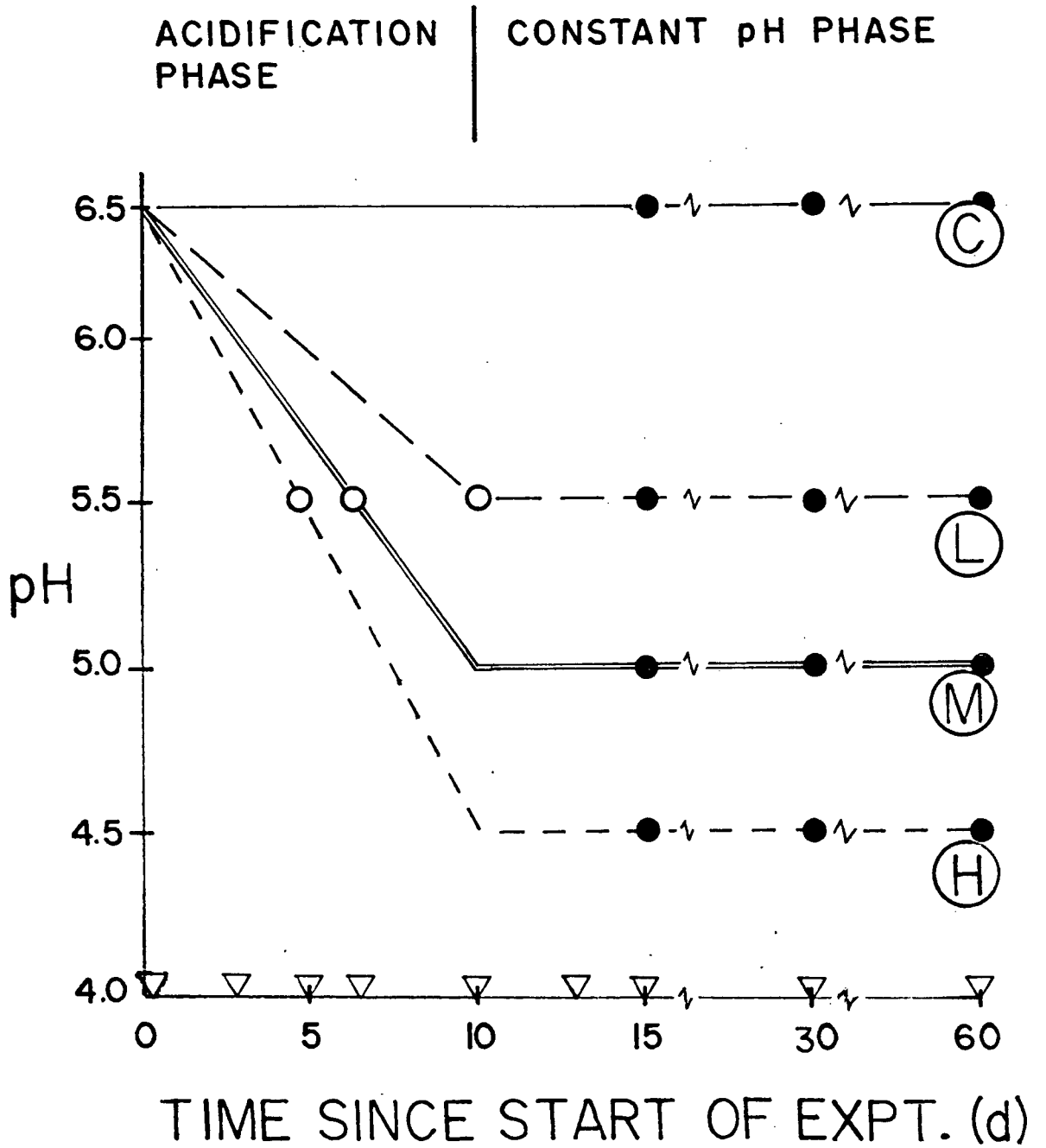

ACIDIFICATION PHASE
CONSTANT pH PHASE
6.5
6.0
5.5
5.0
4.5
4.0
pH
C
L
M
H
0
5
10
15
30
60
TIME SINCE START OF EXPT. (d)

Table 25. Correspondence between 1979 and 1980 experimental treatments. The enclosures were numbered differently in 1979 and 1980. Treatments were randomly assigned to enclosures in both years. Abbreviations:

C = controls
A = acidification only
F = fertilization only
AF = acidification and fertilization
L = low acidification
M = medium acidification
H = high acidification

1979		1980	
#	Treatment	Treatment	#
3	AF	C	6
5	A	C	8
4	A	L	3
7	AF	L	7
2	C	M	2
6	C	M	5
8	F	H	1
1	F	H	4

During the acidification phase of the experiment (May 13 to 23) I used a titration curve developed from lakewater samples and daily depth-stratified pH measurements to compute the appropriate amount of 1M H_2SO_4 (or 1M NaOH) to add to each enclosure. Chemicals were added daily to each of four depth strata (0-2 m, 2-4 m, 4-6 m, and 6-8 m) using a bilge pump and hose. Each acid or base dose was first diluted with 9 L of water pumped from the appropriate depth stratum. This procedure was designed to maintain vertically homogeneous pH levels without disrupting natural temperature gradients. All acid additions were performed subsequent to zooplankton sampling. I obtained water samples for pH measurements 1-4 h after acid additions (to allow time for physical mixing and chemical equilibration) and measured pH levels in the laboratory within 6 h of sampling, according to the procedures described in Section I.

Chlorophyll a was measured on July 19 only. Sampling and flourometric analysis followed the procedures described in Section I, except that I filtered an additional 500 ml through a 12 μm nucleopore filter. By subtracting the chlorophyll concentration yielded by the 12μm filtration from the concentration estimated with glass fiber filters, I roughly estimated the chlorophyll a present in algal cells small enough to be grazed by all crustaceans in the zooplankton community (See Section I Discussion). In retrospect, a 2-stage filtration of one water sample would have yielded better precision than two separate filtrations.

Zooplankton samples were obtained at 2-3 day intervals during the first 17 days of the experiment, then weekly for three weeks, and then once a month later. With the exception of depth-stratified samples obtained on June 19 (four 2 m strata), all samples were depth-integrated. Samples were preserved and enumerated according to the procedures described in Section I.

Following the procedures outlined in Section I, I measured 20 adults and 20 juveniles of each species from each treatment on three occasions: May 13, June 5, and July 16. These lengths were converted to estimates of mean adult and juvenile weights (see Appendix A) that were used to estimate the total biomass of each species on each date. Mean weights from May 13 were used for all May samples, and mean weights from June 5 for all June samples.

2.2 Statistical and Simulation Analyses

To determine the statistical significance of inter-treatment differences on each sampling date, the total zooplankton biomass and numbers of animals and eggs of each species were analyzed with 1-way ANOVA and Duncan multiple range tests. Analyses were performed on untransformed data unless Bartlett's test indicated heterogeneous within group variances, in which case data were log transformed. I used 1-way ANOVA instead of 2-way treatment by time ANOVA due to the varying duration of sampling intervals, and the contrasting conditions during the two phases of the experiment (i.e. acidification vs. constant pH).

Since Daphnia rosea commonly forms 70% of the herbivorous grazing pressure in Eunice Lake, and is also acid sensitive (Section I) I analyzed its mortality in the 1980 experiment in considerable detail. Daphnia mortality rates were estimated using both three-stage and two-stage models. The three-stage model is an unpublished computer program written by E. Guindon, based on the methods of Argentisi et al. (1974) and Seitz (1979). In the program, the population is represented by three stages: eggs, juveniles, and adults, each with its own rates of recruitment and mortality. The two-stage model, based on Paloheimo (1974), considers only eggs and "animals" (i.e. it does not differentiate between adults and juveniles). Both models are described in Appendix G, which includes a listing of the computer program used for the three stage model.

To roughly estimate the incipient lethal pH in each treatment, I graphed mean estimated mortality rates against the pH range experienced by each population during each sampling interval. This graphical method is merely a means of illustrating statistics compiled from field data, and not a rigorous toxicity test curve. The experiment violated two key assumptions of toxicity tests (Brown 1978):

1) that subjects chosen to be tested at each dose level have been randomly selected; and
2) that experimental conditions are the same for each dose.

The first assumption is violated by the declining pH levels within each treatment, since the subpopulation that survives to pH 5.0 is likely more acid tolerant than the starting population. The second assumption is violated because temperatures, food and the densities of competitors may change with time and treatment.

Also, since the pH changed daily during the acidification phase of the experiment, lethal effects which took longer than 24 h to occur may appear associated with a later, lower pH; this would lead to an underestimate of pH sensitivity.

For species other than Daphnia, I estimated the lethal pH range as simply that existing at the time of major declines or extinctions. As mentioned above, this method will tend to underestimate pH sensitivity.

3. RESULTS

3.1 Temperature and pH Measurements

Cold, rainy weather during May and June 1980 maintained much lower water temperatures than in July and August 1979 (Figure 29). This was not only a seasonal effect, as mean temperatures on July 16 1980 (10.4°C over 0-8m, Figure 29) were considerably less than on the same date in 1979 (12.8°C, Figure 6, page 49). Rates of zooplankton development and phytoplankton growth are highly temperature dependent (Hebert 1978, Lund 1965) and therefore were likely significantly lower than in my 1979 experiment.

As in 1979, control cylinders showed less of a vertical pH gradient than did Eunice Lake (Figure 30), most likely due to limnocorral shading (Section I). The depth-stratified daily additions of acid successfully produced vertically homogeneous pH levels and the desired rates of pH change (Figure 30). In treatments L and M, the total amount of sulfuric acid added was 2.7% and 13.0% less (respectively) than the amount expected from lakewater titrations; treatment H required 1.8% more than expected (Table 26). Differences between expected and observed acid additions cannot be considered significant in treatments L and H. In treatment M however, biotic generation of alkalinity (e.g. algal nitrate assimilation) was apparently exceeded by H ions either generated within the enclosure (e.g. ammonium assimilation) or deposited in precipitation. It seems unlikely that differences in chemical buffering were responsible for

Figure 29. Eunice Lake water temperatures during 1980 .

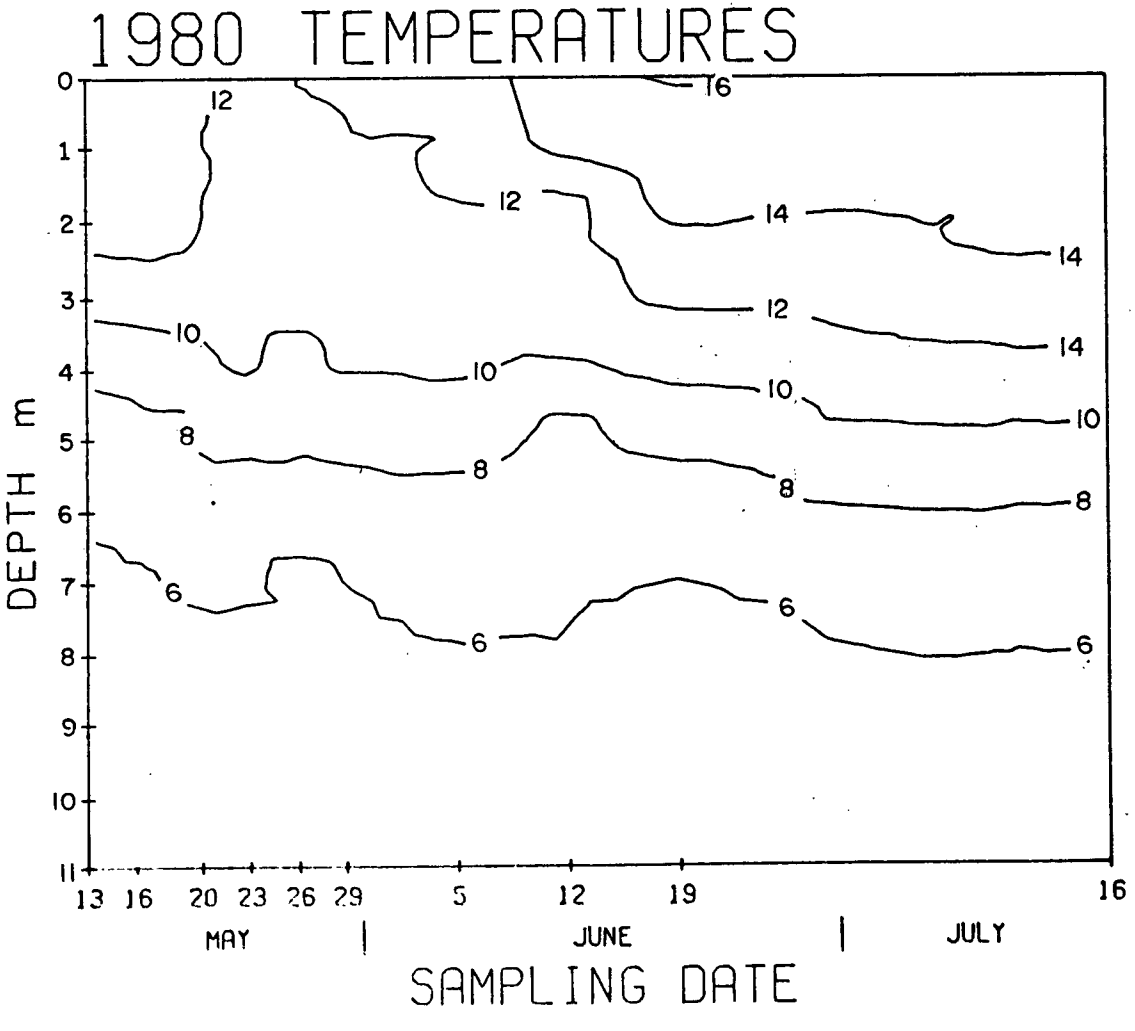

1980 TEMPERATURES
DEPTH m
0
1
2
3
4
5
6
7
8
9
10
11
12
16
14
12
14
12
14
10
10
10
10
8
8
8
8
6
6
6
6
13 16 20 23 26 29 5 12 19 16
MAY
JUNE
JULY
SAMPLING DATE

Figure 30. 1980 pH levels by depth and time. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

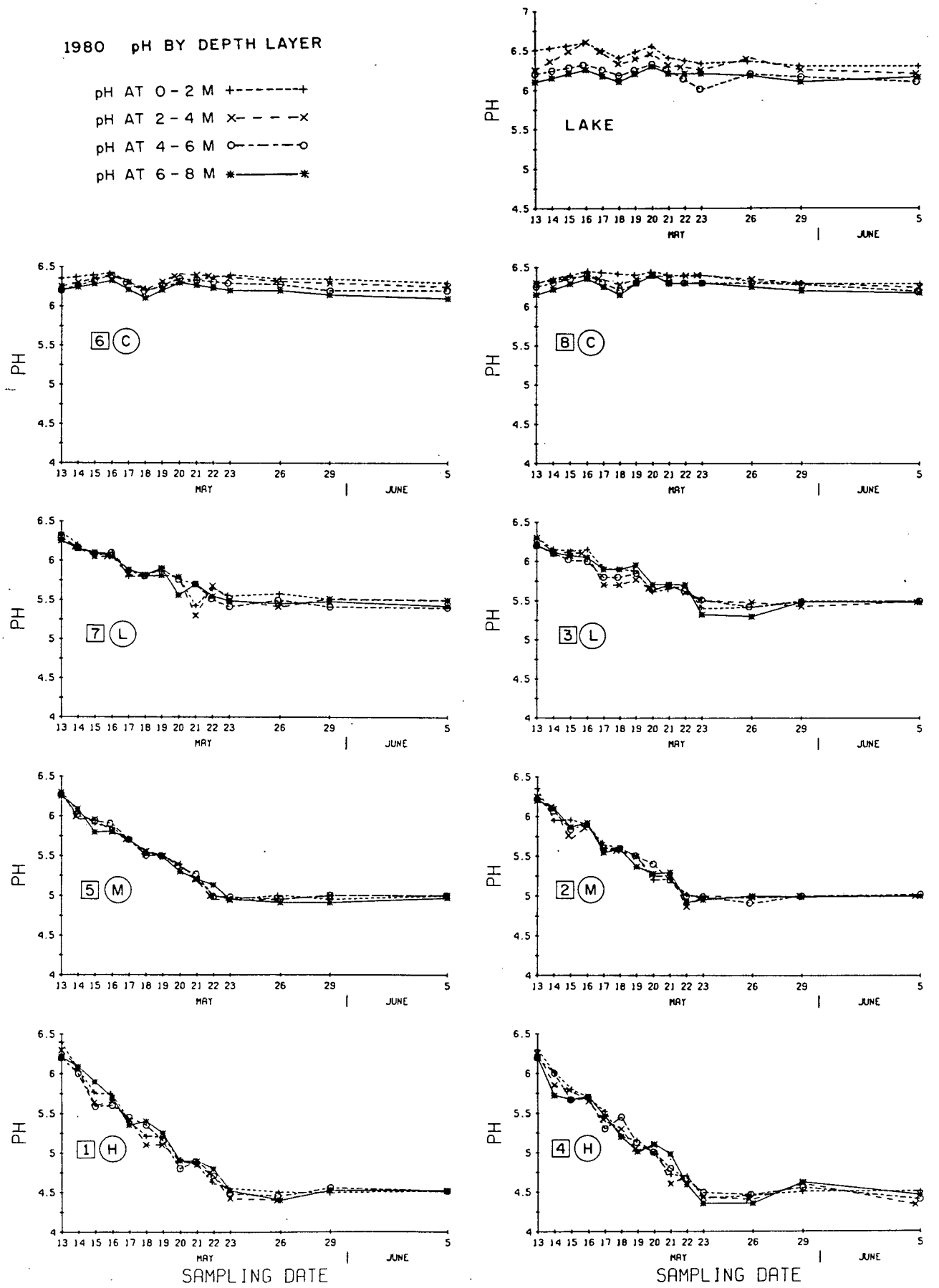

1980 pH BY DEPTH LAYER
pH AT 0 - 2 M
pH AT 2 - 4 M
pH AT 4 - 6 M
pH AT 6 - 8 M
LAKE
6 C
8 C
7 L
3 L
5 M
2 M
1 H
4 H
PH
MAY
JUNE
SAMPLING DATE

Table 26. Expected and observed amounts of sulfuric acid added to cylinders. Expected amount computed from lake water titrations and cylinder volume of 28.2 m^3.

Treatment	Expected Amount of H^+ Required for Acidifying Each Cylinder (meq)	Actual Amount of H^+ Added Over the Whole Experiment (meq) ($\bar{x}$ ± SE)
L (to pH 5.5)	803.7	782 ± 14
M (to pH 5.0)	1198.5	1043 ± 46
H (to pH 4.5)	1974.0	2009 ± 6

these gaps between expected and observed amounts of acid additions, since the limnocorrals were isolated from both watershed and sediment sources of potential buffers.

During the 6 week period from June 5 to July 16 I made only one acid addition, to cylinder 4H on June 5. Increases in mean pH levels of 0.09-0.14 pH units during this period suggest that biotic processes generated a small surplus of alkalinity (Table 27).

3.2 Overall Effects on the Plankton Community

3.2.1 Effects of Enclosure

Two types of potential enclosure effects were examined in 1980: 1) differences between control enclosures and Eunice Lake; and 2) effects of reusing limnocorrals subjected to acidification and fertilization in my 1979 experiment.

Relative to Eunice Lake, the control enclosures were initially stocked with too few Holopedium gibberum and too many Diaptomus kenai. On May 13 and 16, biomasses of H. gibberum and D. kenai averaged 1.7 ± 0.45 and 5.2 ± 0.60 $\mu g \cdot L^{-1}$ in the controls, but 5.2 ± 1.2 and 1.6 ± 0.015 $\mu g \cdot L^{-1}$ in Eunice Lake. H. gibberum dwindled to extinction in the controls, but became increasingly important in the lake. Differences in Holopedium biomass were largely responsible for much higher total zooplankton biomass in Eunice Lake than in the controls after June 12 (Figures 31 and 32). Fertilization of upstream Gwendoline Lake in 1979 likely contributed to the unusually high

Table 27. Mean pH levels June 5 to July 16. Standard errors computed with n = 8 according to method described in Section I.

Date	Treatment				
	Eunice Lake	Control	Low	Medium	High
June 5	6.18 ± 0.041	6.22 ± 0.025	5.47 ± 0.015	5.00 ± 0.005	4.46 ± 0.028
June 12	6.23 ± 0.050	6.32 ± 0.038	5.55 ± 0.029	5.09 ± 0.017	4.54 ± 0.013
June 19	6.25 ± 0.007	6.28 ± 0.044	5.55 ± 0.032	5.06 ± 0.016	4.51 ± 0.011
July 16	6.16 ± 0.08	6.35 ± 0.041	5.61 ± 0.037	5.14 ± 0.015	4.55 ± 0.015

Figure 31. 1980 total zooplankton biomass . Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

TOTAL ZOOPLANKTON BIOMASS (1980)

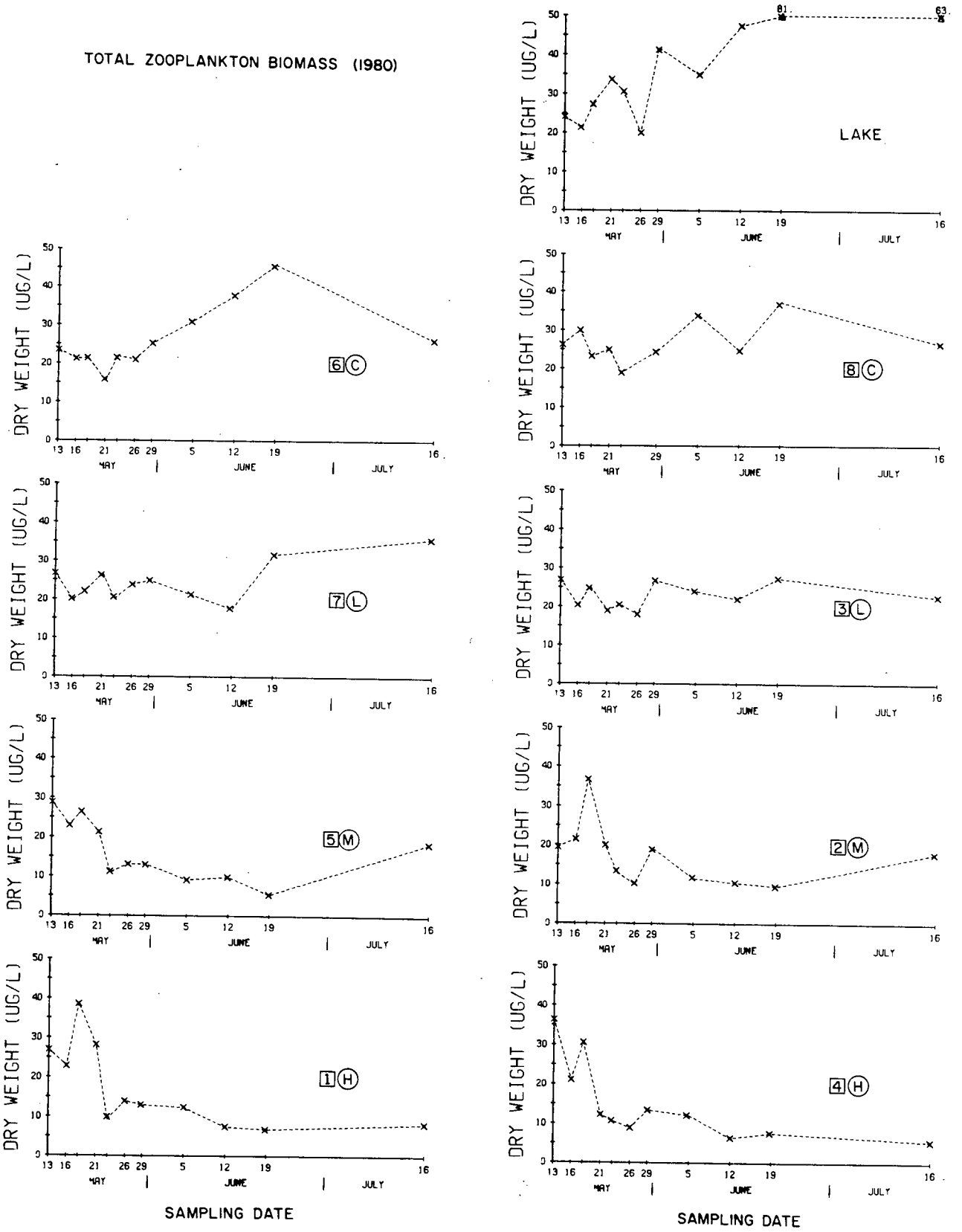
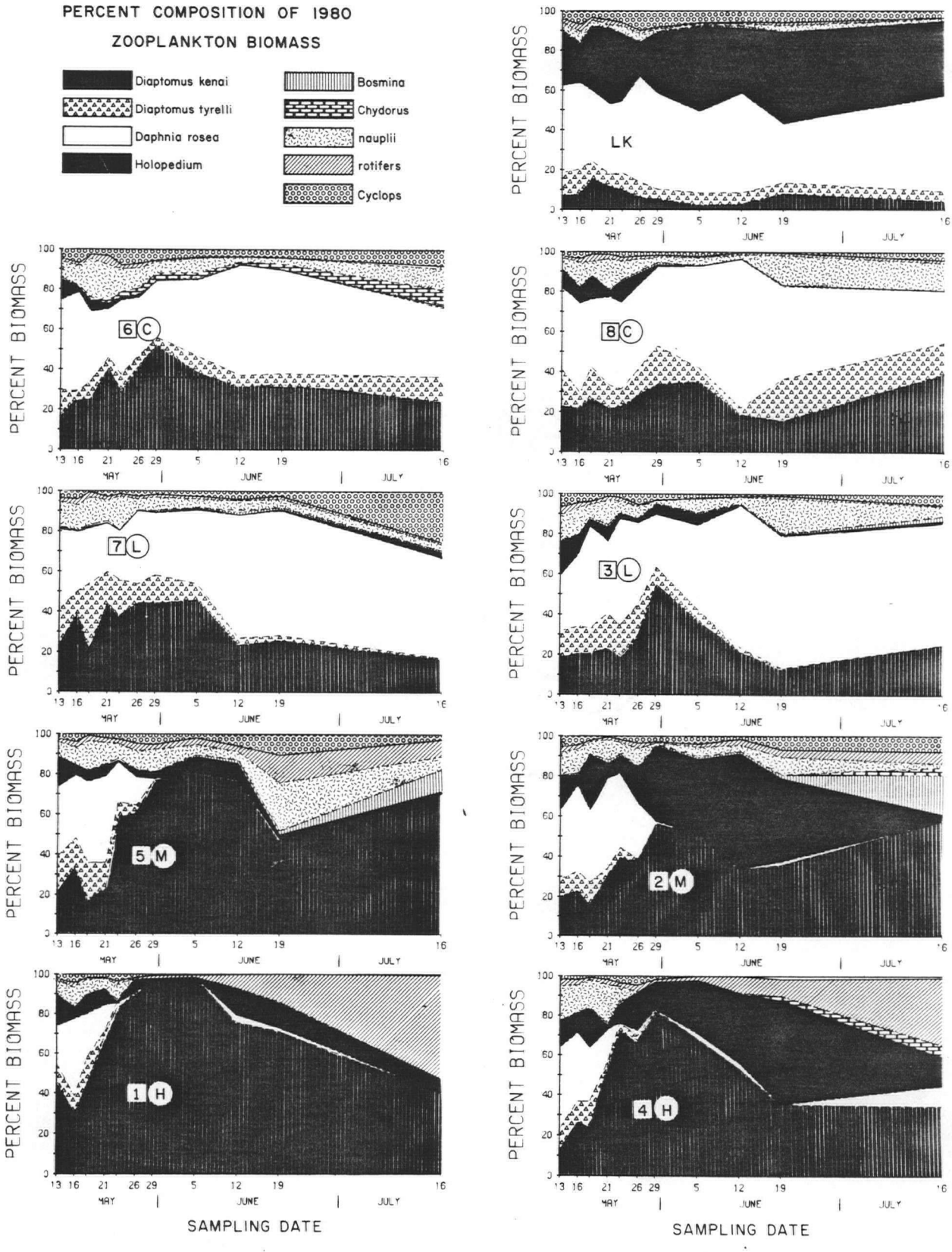


Figure 32. Percent composition of total zooplankton biomass in 1980 . Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.


PERCENT COMPOSITION OF 1980
ZOOPLANKTON BIOMASS
Diaptomus kenai
Diaptomus tyrelli
Daphnia rosea
Holopedium
Bosmina
Chydorus
nauplii
rotifers
Cyclops
PERCENT BIOMASS
LK
6 C
8 C
7 L
3 L
5 M
2 M
1 H
4 H
13 16 21 26 29 5 12 19 16
MAY
JUNE
JULY
SAMPLING DATE

total zooplankton biomass in Eunice Lake in 1980 and the improved performances of Holopedium and Diacyclops thomasi (C.J. Walters and W.E. Neill, unpublished data; Peacock 1981).

Initial biomasses of other species did not differ significantly between the controls and Eunice Lake (Figures 31 and 32). However, the enclosed Daphnia rosea populations initially contained far fewer eggs and a smaller percentage of ovigerous females than did the population in Eunice Lake (means in all cylinders on May 13: 0.33 ± 0.056 eggs /L and 13.0 ± 2.8% ovigerous females; in Eunice Lake: 1.50 eggs /L and 47.9% ovigerous). This was apparently due to errors in stocking the limnocorrals.

Due to the random assignment of treatments to cylinders, analyses of the effects of 1979 treatments on the performance of enclosed zooplankton communities in 1980 were only possible in the controls and in treatment L (Table 27). Both total zooplankton biomass and species composition were similar in the two control cylinders (Figures 31 and 32). However, cylinder 6C contained higher biomasses of Chydorus sphaericus and Diacyclops thomasi (Figure 32). Improved performances of these two species in 6C could have been due to a failure to remove all of the previous year's periphyton growth (under acidification and fertilization). C. sphaericus reached extremely high densities under acidification and fertilization in 1979 (Section I); D. thomasi, though rare in 1979, generally benefits from increased nutrients (Peacock 1981), which may have been released into 6C from decaying periphyton. Based on the differences

between the two control cylinders, I expected higher densities of C. sphaericus and D. thomasi in cylinder 7L than 3L, since only 7L was exposed to acidification and fertilization in 1979 (Table 27). D. thomasi biomass was higher in 7L (Figures 31 and 32), but no significant differences were apparent in C. sphaericus. In conclusion, carryover effects from 1979 may have affected two minor species in 1980, but had negligible impacts on overall zooplankton community structure and biomass.

3.2.2 Zooplankton Biomass and Community Composition

The initial stocking of the enclosures was generally consistent between cylinders. With the exception of high Diaptomus kenai biomass in cylinder 1 H and high Daphnia rosea biomass in 4H, all enclosures showed similar zooplankton community composition and total biomass on the first two sampling dates (Figures 31 and 32, Table 28). Overstocking of Diaptomus kenai may however have been responsible for the surprisingly high total zooplankton biomass in cylinder 1H on May 18 and 21.

Changes in total zooplankton biomass and community composition are most easily presented by moving through the three treatments along a gradient of increasing acidification. Acidification to pH 5.5 (treatment L) caused the gradual elimination of Diaptomus tyrrelli, but did not otherwise perturb community composition (Figure 32). Treatment L mean total zooplankton biomass differed significantly from the controls on June 5 (Table 28); this difference was due to the cumulative

Table 28. Mean zooplankton community biomass by treatment and date. Probability of overall treatment effect in column labelled "P" obtained from analyses of variance on total biomass values (untransformed unless stated). Results of Duncan multiple range tests show treatments listed in ascending order of biomass from left to right. Underlining indicates homogeneous subsets i.e. treatments are not significantly different from one another at stated probability level.

Date	Zooplankton Community Biomass by Treatment ($\bar{x}$ ± SE) in µg/L dry wt.				P	Duncan Significant Differences, n = 2 Replicates/Treatment	
	C	L	M	H		α = 0.05	α = 0.01
May 13	24.8 ± 1.4	26.8 ± 0.14	24.1 ± 4.7	31.6 ± 4.7	0.49	ns	ns
16	25.5 ± 4.4	20.0 ± 0.16	22.2 ± 0.76	22.0 ± 0.86	0.47	ns	ns
18	22.3 ± 0.94	23.6 ± 1.6	31.6 ± 5.1	34.6 ± 4.0	0.15	ns	ns
21	20.2 ± 4.8	22.8 ± 3.8	20.6 ± 1.0	20.2 ± 7.9	0.98	ns	ns
23	20.4 ± 1.5	20.3 ± 0.25	12.0 ± 1.0	9.9 ± 0.7	0.003	H M L C	H M L C
26	21.0 *	20.9 ± 2.8	11.6 ± 1.4	11.4 ± 2.4	0.13	ns	ns
29	24.8 ± 0.35	25.8 ± 0.98	16.1 ± 3.1	13.2 ± 0.29	0.01	H M C L	ns
June 5	32.5 ± 1.4	22.6 ± 1.3	10.4 ± 1.2	12.2 ± 0.13	0.0005	M H L C	M H L C
12	31.2 ± 6.5	19.8 ± 2.2	10.1 ± 0.27	6.9 ± 0.52	0.03	H M L C	ns
19	36.4 ± 7.0	29.6 ± 2.2	7.5 ± 2.0	7.2 ± 0.39	0.009	H M L C	H M L C
July 16**	26.3 ± 0.13	29.3 ± 6.6	18.4 ± 0.27	6.9 ± 1.4	0.008	H M C L	H M C L
All Dates	26.7 ± 5.1	23.8 ± 3.2	16.8 ± 5.4	16.0 ± 7.2			

* Sample destroyed

** Data log-transformed to remove heterogeneous variances

effect of lower biomasses of Daphnia rosea, Diaptomus kenai and Diaptomus tyrrelli in treatment L. In spite of the loss of D. tyrrelli from treatment L, total zooplankton biomass was not significantly different from the controls on subsequent sample dates (Table 28). This was because of high within-treatment variation in the controls on June 12 and 19, and higher mean biomass of D. rosea in treatment L than the controls on July 16 (15.8 ± 2.1 and 7.9 ± 1.1 $\mu g \cdot L^{-1}$ respectively).

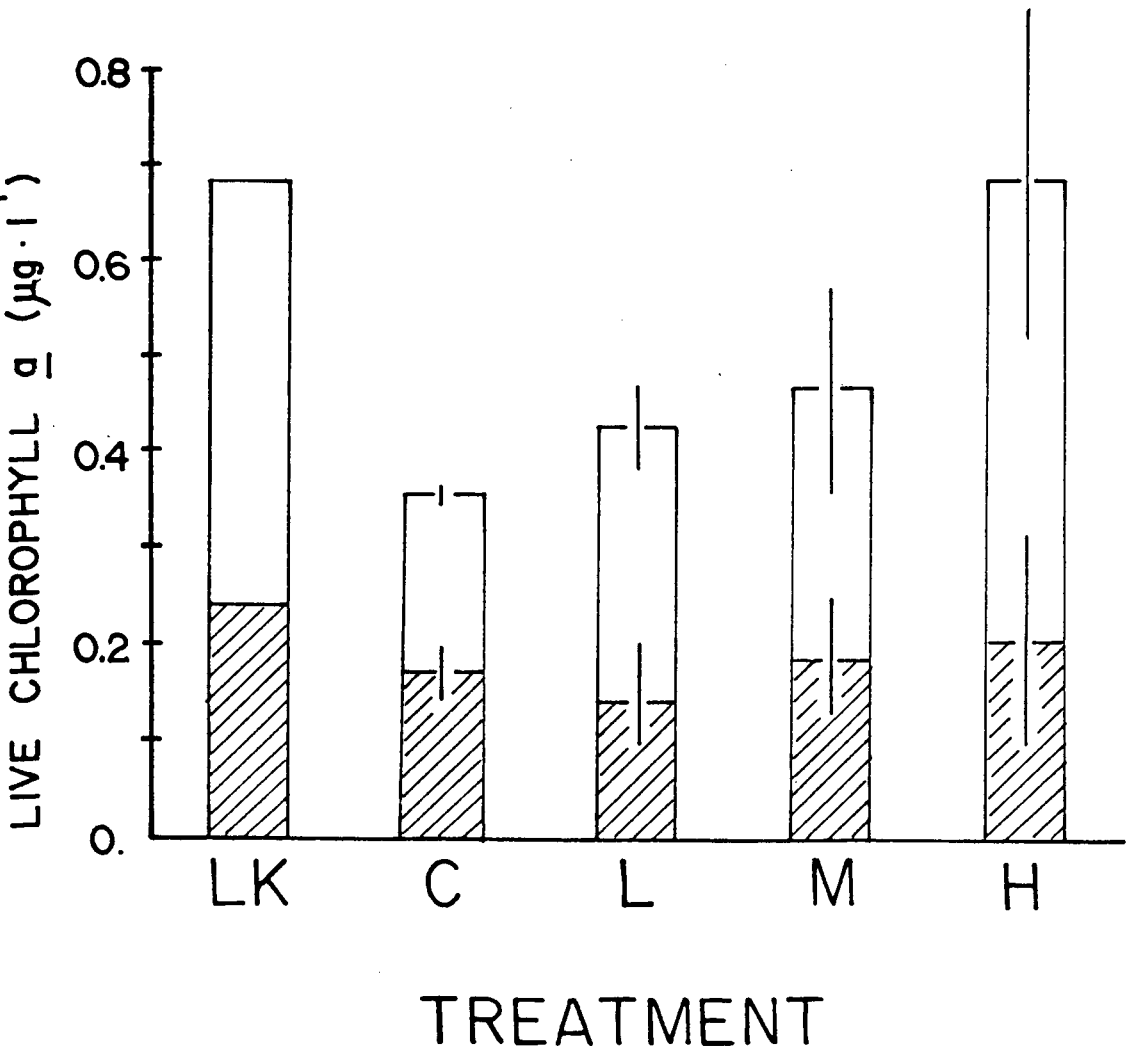
Acidification to pH 5.0 (treatment M) produced major changes in both total zooplankton biomass and community composition. By May 23, Daphnia rosea and Diaptomus tyrrelli had virtually disappeared from treatment M and total zooplankton biomass was significantly lower there than in treatment L (Table 28 and Figure 31). Though the loss of Diaptomus tyrrelli and Daphnia rosea from treatment M increased the relative importances of Holopedium gibberum, Diaptomus kenai and rotifers (Figure 32), these taxa did not replace the lost biomass (Figure 40). From May 23 to June 19, treatment M total zooplankton biomass was significantly lower than treatment L on 4 of 6 sampling dates, and significantly lower than the controls on 5 of these 6 dates (Table 28). However, between June 19 and July 16, increases in the biomasses of Diaptomus kenai and Bosmina longirostris caused mean total zooplankton biomass in treatment M to increase 250%, reaching about 75% of the level in treatment L. The increase in Bosmina was particularly striking; on July 16, Bosmina biomass was much higher in treatment M (2.75 ± 0.71 $\mu g \cdot L^{-1}$) than in treatment L (0.40 ± 0.12 $\mu g \cdot L^{-1}$).

The differences in mean total zooplankton biomass between pH 5.0 and 4.5 (treatments M and H) were relatively small. From May 23 to June 19, total zooplankton biomass remained relatively constant in treatments M and H, averaging 11.3 ± 0.95 $\mu g \cdot L^{-1}$ and 10.2 ± 0.79 $\mu g \cdot L^{-1}$ respectively; Duncan multiple range tests revealed no significant biomass differences during this period (Table 28). However, on July 16 total zooplankton biomass was significantly higher in treatment M than treatment H (Table 28). This was due to the absence of copepod nauplii from treatment H, and the higher biomasses of B. longirostris and Diaptomus kenai in treatment M (2.75 ± 0.71 and 11.6 ± 1.6 $\mu g \cdot L^{-1}$ respectively) than treatment H (0.01 ± 0.01 and 2.6 ± 0.71 $\mu g \cdot L^{-1}$). Biomass differences in these two species far outweighed (literally) the higher biomass of rotifers in treatment H (3.1 ± 1.2 $\mu g \cdot L^{-1}$) than treatment M (1.3 ± 0.27 $\mu g \cdot L^{-1}$).

3.2.3 Chlorophyll Concentrations

Mean concentrations of live chlorophyll a on July 19 did not differ significantly between treatments ($F(3,1) = 2.68$; $p > 0.1$). However, both mean chlorophyll a concentration and the proportion of chlorophyll in larger cells appeared to increase with the level of acidification (Figure 33). Cylinder 1H contained especially high chlorophyll a concentrations (0.88 $\mu g \cdot L^{-1}$ relative to the overall mean concentration of 0.49 $\mu g \cdot L^{-1}$).

Figure 33. Mean concentrations of live chlorophyll a on July 19, 1980 . Top of bar represents concentration on glass fiber filter (virtually all cells); shaded area is estimated concentration of cells not retained by a 12μm nucleopore filter. Error bars are ± SE. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.


LIVE CHLOROPHYLL a (µg·l⁻¹)
0.8
0.6
0.4
0.2
0.
LK
C
L
M
H
TREATMENT

Chlorophyll a concentrations were much higher in Eunice Lake than in the controls and treatment L (Figure 33). This was probably due to the high flow of nutrient-rich water from Gwendoline Lake into Eunice Lake, but not into the enclosures. Year to year comparisons of chlorophyll a concentrations in Eunice Lake confirm the downstream effects of the fertilization of Gwendoline Lake. On July 19 1980, concentrations were 0.68 $\mu g \cdot L^{-1}$, compared to mean concentrations of only 0.21 ± 0.01 in July of 1979 (Figure 20, page 120). Note that acidification to pH 4.5 (treatment H) resulted in chlorophyll a concentrations very similar to those in Eunice Lake (Figure 33). I suspect that removal of herbivores was the prime reason for the high chlorophyll a concentrations in treatment H.

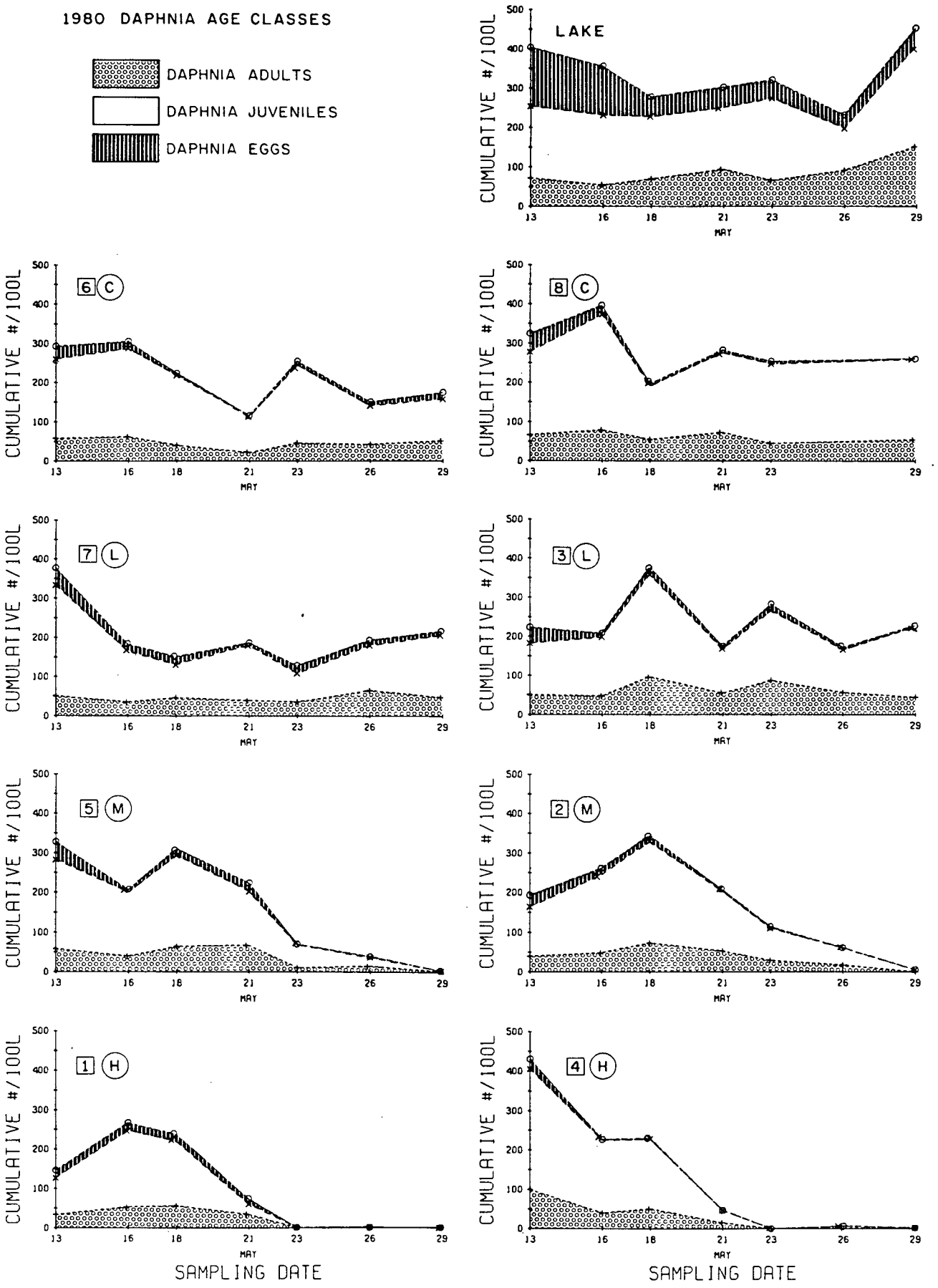
3.3 Performance of Particular Taxa under Acid Stress

3.3.1 Daphnia rosea

Enclosure clearly affected Daphnia rosea. Relative to the controls, the Eunice Lake population of D. rosea contained higher egg densities (Figure 34), animal densities (Figure 35), mean brood sizes (Table 29) and percentages of females with eggs (Table 30). This was in part the result of initial differences (i.e. stocking errors), but largely due to the effects of elevated nutrients in Eunice Lake (Section 3.2.1). A consequence of the low egg densities in all cylinders is that acidification generally caused less significant changes in egg densities than in animal densities.

Figure 34. Densities of Daphnia rosea by age class (May 13-29). Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

Figure 35. Densities of Daphnia rosea by age class (May 29-July 16). Densities not shown for treatments M and H since all samples contained less than 4 animals per 100 L.


1980 DAPHNIA AGE CLASSES
DAPHNIA ADULTS
DAPHNIA JUVENILES
DAPHNIA EGGS
LAKE
6 C
8 C
7 L
3 L
5 M
2 M
1 H
4 H
CUMULATIVE #/100L
0
100
200
300
400
500
13
16
18
21
23
26
29
MAY
SAMPLING DATE

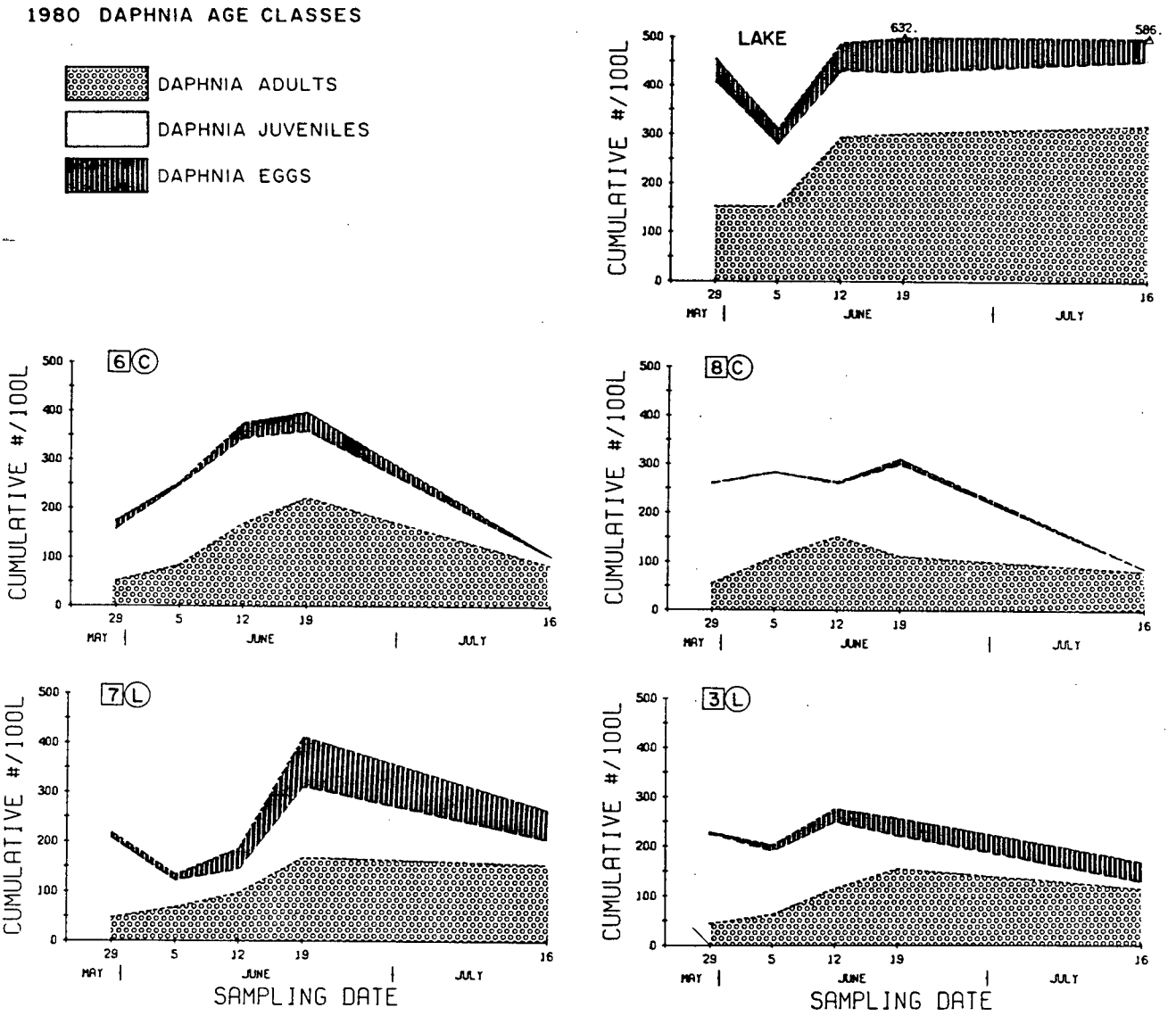

1980 DAPHNIA AGE CLASSES
DAPHNIA ADULTS
DAPHNIA JUVENILES
DAPHNIA EGGS
LAKE
632.
586.
6 C
8 C
7 L
3 L
CUMULATIVE #/100L
0
100
200
300
400
500
29
5
12
19
16
MAY
JUNE
JULY
SAMPLING DATE

Table 29. Daphnia rosea mean brood sizes ± SE.

Date	LK	C	L	M	H
May 13	3.00	1.69 ± 0.19+	1.42 ± 0.22	1.64 ± 0.24	1.67* +
16	2.70	1.45 ± 0.30+	1.17 ± 0.03	1.71 * +	1.1 ± 0.1+
18	1.43	1.0 ± 0.0+	1.17 ± 0.17	1.17 ± 0.17+	1.0 ± 0.0+
21	1.33	1.25 ± 0.25+	1.13 ± 0.13+	1.03 ± 0.03	1.1*
23	1.28	1.10 ± 0.10	1.07 ± 0.07+	1.33 * +	-
26	1.30	-	1.25 ± 0.25+	-	-
29	1.16	1.17 ± 0.17+	1.08 ± 0.08+	-	-
June 5	1.22	1.0 ± 0.0+	1.0 ± 0.0	-	-
12	1.02	1.0 ± 0.0+	1.08 ± 0.08	-	-
19	1.05	1.0 ± 0.0+	1.47 ± 0.41	-	-
July 16	1.09	-	1.08 ± 0.09	-	-

Table 30. Daphnia rosea mean % of females ovigerous ± SE.

Date	LK	C	L	M	H
May 13	47.9%	13.8 ± 4.2%	19.9 ± 5.1%	14.9 ± 2.1%	6.8%*
16	56.3%	9.2 ± 3.5%	24.5 ± 7.8%	16.3%*	13.5 ± 7.8%
18	11.3%	6.2 ± 2.1%	13.1 ± 1.5%	7.8 ± 6.0%	6.1 ± 3.9%
21	18.1%	4.2 ± 1.1%	10.5 ± 0.9%	10.5 ± 6.2%	22.2%*
23	36.2%	12.3 ± 0.2%	12.2 ± 9.6%	7.9%*	-
26	12.3%	-	4.4 ± 2.4%	-	-
29	18.4%	4.3 ± 2.2%	8.4 ± 5.9%	-	-
June 5	13.1%	3.2 ± 2.2%	9.4 ± 0.5%	-	-
12	15.3%	2.4 ± 0.2%	21.9 ± 6.3%	-	-
19	22.7%	3.9 ± 0.1%	13.3 ± 7.5%	-	-
July 16	24.6%	-	14.0 ± 1.7%	-	-

* Only 1 replicate with ovigerous females.
\+ $n < 5$ ovigerous females in either replicate.
\- $n < 2$ ovigerous females in both replicates.

Treatment L Daphnia populations showed no negative effects from acidification to pH 5.5. Mean brood sizes of daphnid females were similar in treatment L and the controls (Table 29), the mean percentages of ovigerous females were consistently higher in treatment L (Table 30), and densities of animals (juveniles plus adults) were not significantly different (Table 31). At the end of the experiment (July 16), treatment L actually contained significantly higher densities of daphnid eggs than did the controls (Table 31). On this date, animal densities were also higher in treatment L (1.66 ± 0.38 L^{-1}) than in the controls (0.97 ± 0.07 L^{-1}), but this difference was not statistically significant.

By May 29, treatment M (acidification to pH 5.0) had decreased D. rosea densities to levels significantly lower than treatment L and the controls (Table 31). As expected treatment H caused faster declines: densities were significantly lower in treatment H than in the other treatments on May 21, 23 and 26 (Table 31).

Analysis of D. rosea mortality rates using the three-stage model yielded extremely low (often negative!) estimates of juvenile mortality rates (Figure 36). An examination of why the model underestimated juvenile mortality rates is given in Appendix H. Estimated juvenile mortality rates increased with time (and acidity) in treatments M and H, but showed considerable within-treatment variation. Estimated adult mortality rates (Figure 37) also increased with levels of acidification, but were much higher than juvenile mortality

Table 31. Results of analyses of variance and Duncan multiple range tests of inter-treatment differences in densities of cladocerans, and cladoceran eggs. Holopedium and Chydorus eggs were too infrequent to merit analysis. Treatments are listed in ascending order of densities from left to right, with underlining to indicate homogeneous subsets not significantly different from one another at $\alpha = 0.05$, and n = 2 replicates/treatment. Probability of no treatment effect listed in brackets if less than 0.05; otherwise considered not significant (ns). Abbreviations: C = controls; L = low acidification (pH 5.5); M = moderate acidification (pH 5.0); H = high acidification (pH 4.5).

Date		Daphnia rosea		Holopedium	Bosmina longirostris		Chydorus sphaericus
		Adults & Juveniles	# Eggs	Adults & Juveniles	Adults & Juveniles	# Eggs	
May	13	ns	ns	ns	ns	ns	ns
	16	ns	ns	ns	ns	ns	ns
	18	ns	ns	ns	ns	ns	ns
	21	H L C M (0.045)	ns	ns	ns	ns	ns
	23	H M L C (0.0007)	H M C L (0.024)	ns	ns	ns	ns
	26*	H M C L (0.028)	ns	ns	H M L C (0.038)	ns	ns
	29	H M C L (0.0008)	ns	ns	H M C L (0.019)	ns	ns
June	5	M H L C (0.002)	H M C L (0.011)	ns	H M C L (0.025)	ns	ns
	12	M H L C (0.0009)	H M C L (0.018)	L C H M (0.022)	ns	H C M L (0.0007)	ns
	19	M H L C (0.002)	H M C L (0.003)	ns	H C M L (0.003)	H L C M (0.035)	ns
July	16	M H C L (0.004)	M C H L (0.0004)	ns	H C L M (0.017)	H C L M (0.043)	ns

* One observation missing (Bag 8C)

Figure 36. Instantaneous mortality rates of juvenile Daphnia rosea, as estimated from 3-stage model . Points on graph refer to mortality over preceding sampling interval. Mortality rates cannot be estimated if densities of eggs, juveniles or adults equalled zero. Occurrence of negative mortality rates discussed in Section 3.3.1 and Appendix H. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

JUVENILE DAPHNIA MORTALITY

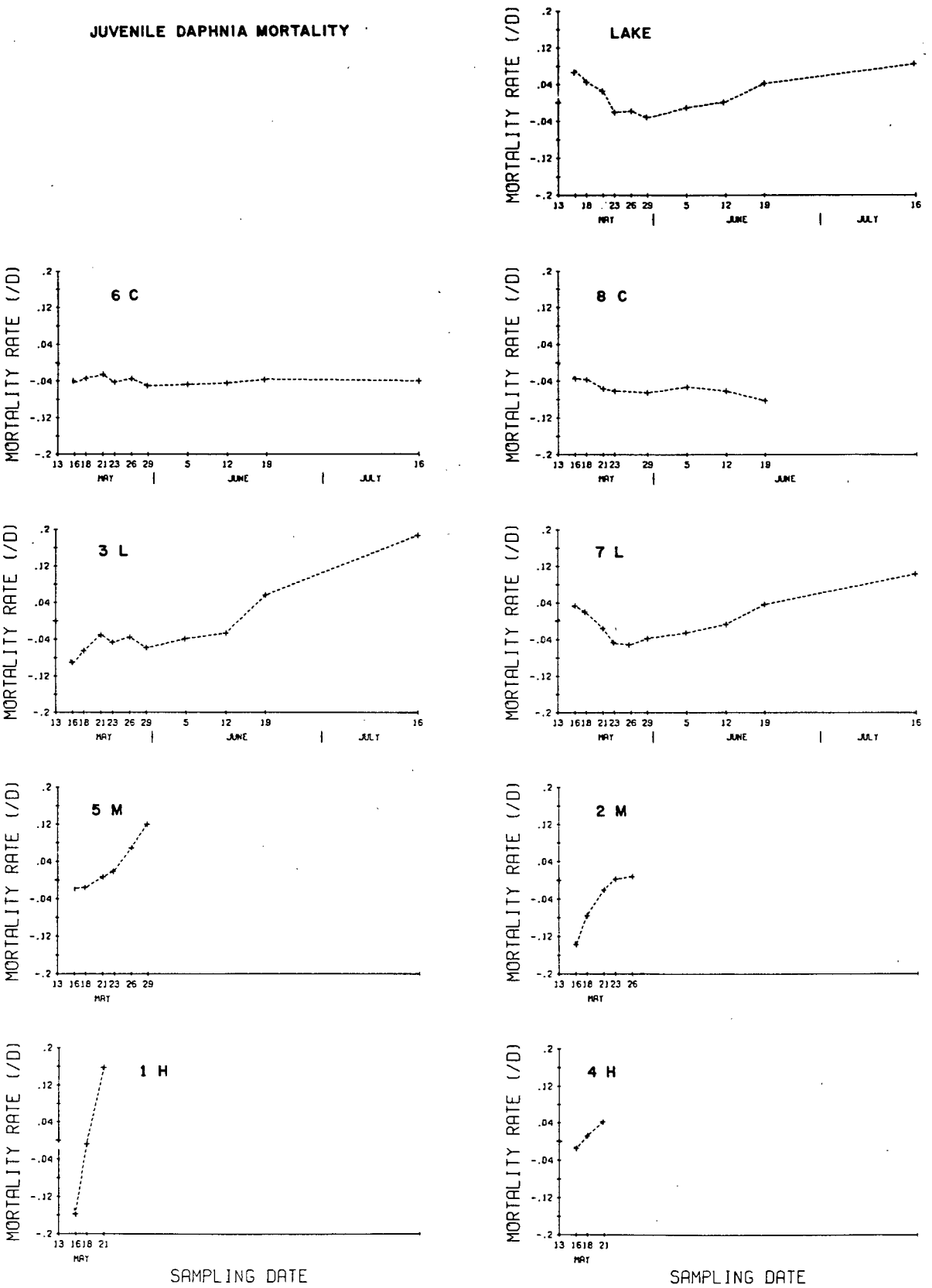
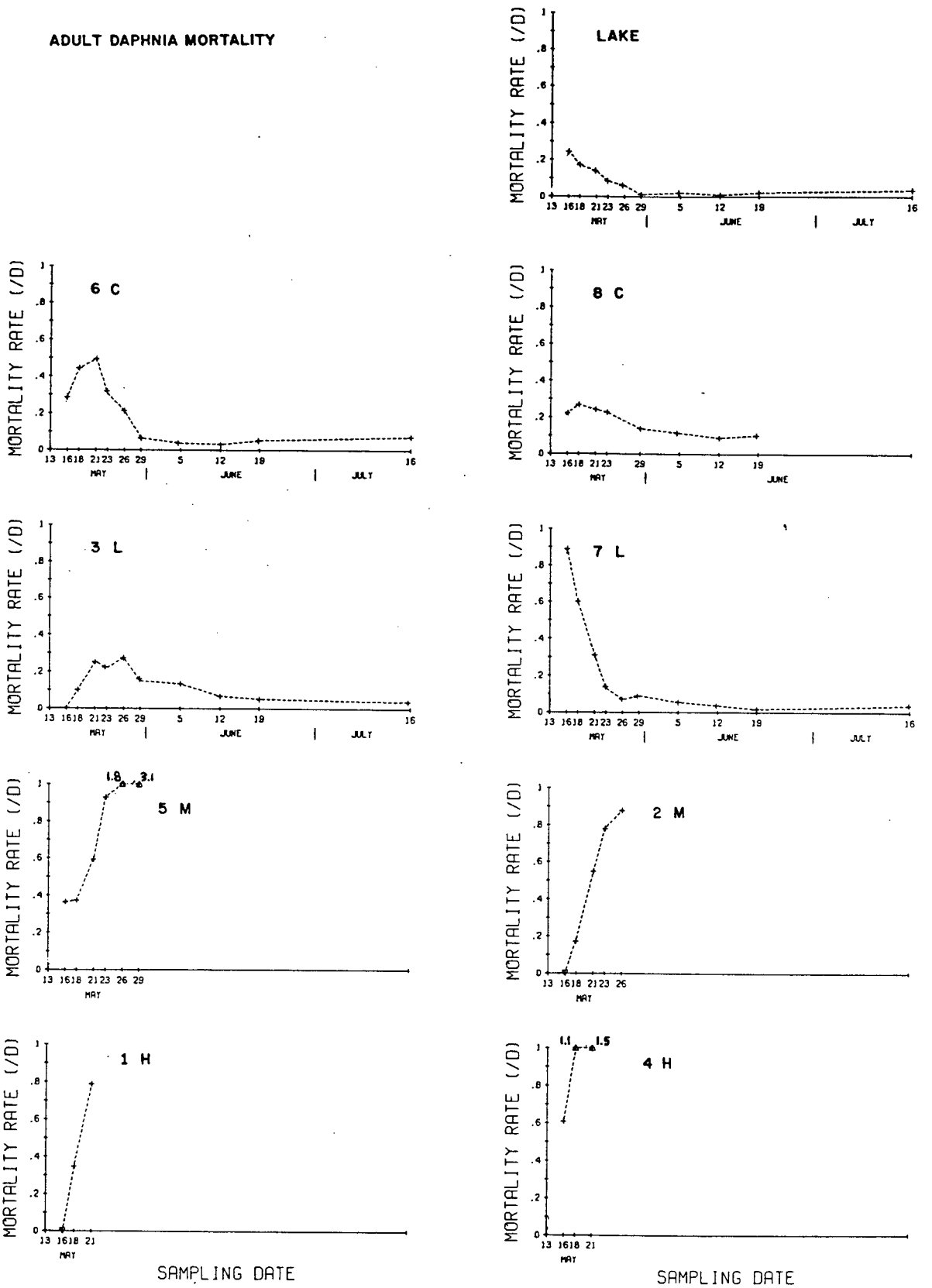


Figure 37. Instantaneous mortality rates of adult Daphnia rosea, as estimated from 3-stage model . Points on graph refer to mortality over preceding sampling interval. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

ADULT DAPHNIA MORTALITY



rates. Cylinder 7L showed very high estimated adult mortality between May 13 and May 18 (Figure 37). The reasons for this are not clear.

Did the rate of pH change (experimental treatment) affect estimated mortality rate at given pH levels? In view of the problems with juvenile mortality rate estimates in the three-stage model, I examined only adult mortality rates in addressing this question. (Results from the two-stage model are discussed below.) Mean estimated adult mortality rates exceeded 0.5 in treatment H with pH 5.68-5.40, but were consistently less than 0.2 (equivalent to the controls) in treatment L at pH 5.45 (Figure 38). This suggests that either: 1) mortality increased rapidly at pH 5.45-5.40 (independent of the rate of pH change); 2) the high rate of change of acidity in treatment H increased daphnid mortality at pH 5.4-5.5; or 3) food resources were more limiting to D. rosea in treatment H than in treatment L. Unfortunately, the range in observed pH levels and variation in estimated mortality rates make it impossible to choose between the first two suggestions. The third explanation seems unlikely on the basis of brood sizes, percentages of ovigerous females, and chlorophyll a concentrations (Tables 29 and 30, Figure 33 respectively).

The two-stage model produced total mortality rate estimates with lower means and variances than the adult mortality rates estimated by the three-stage model (Figure 39). As with the three-stage model (Figure 38), the two-stage model suggests an incipient lethal pH of 5.3-5.4, and greater mortality in

Figure 38. Mean mortality rates of adult Daphnia rosea versus pH exposure (using 3-stage model). Vertical bars show ± SE. Horizontal bars show pH range during sampling period. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

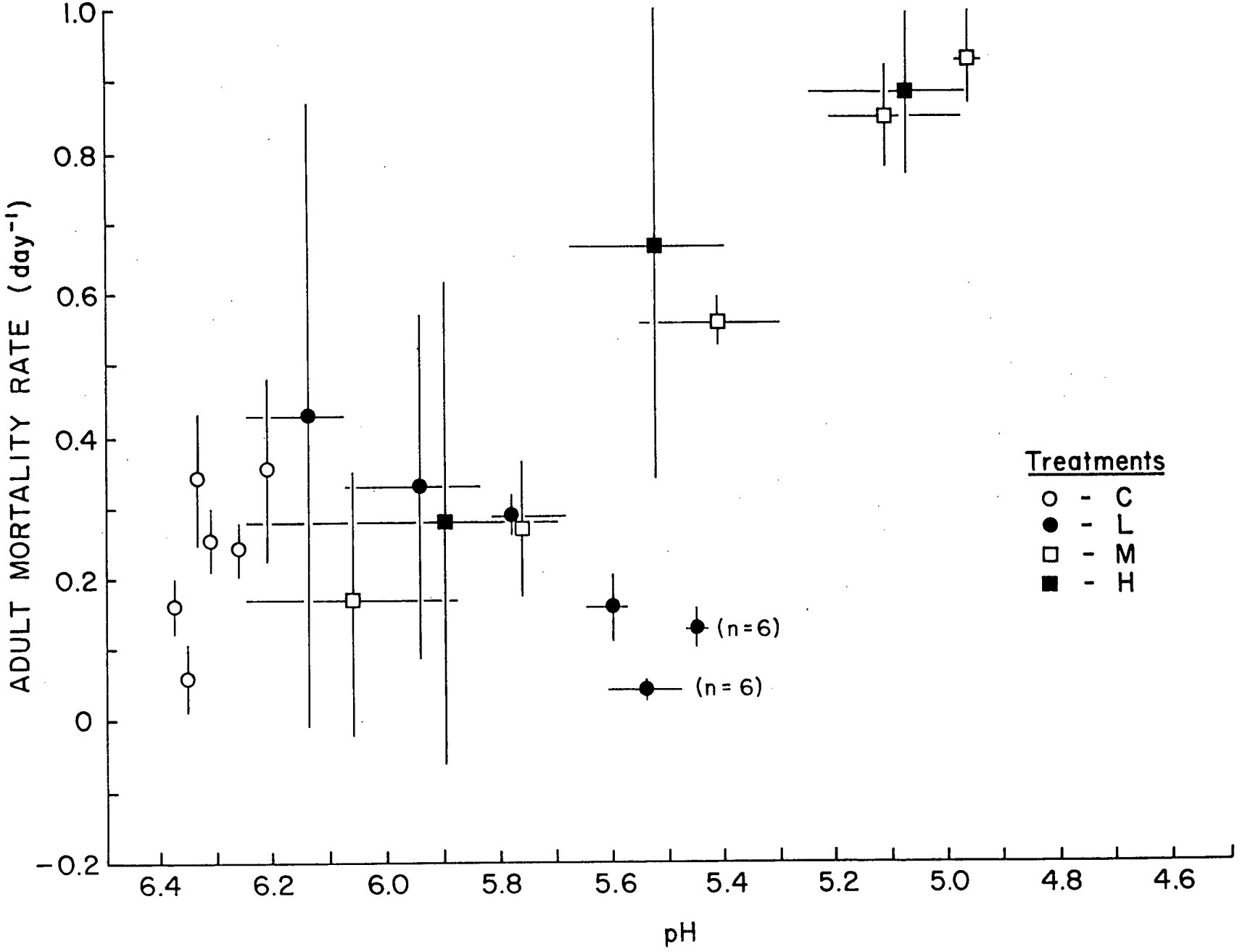
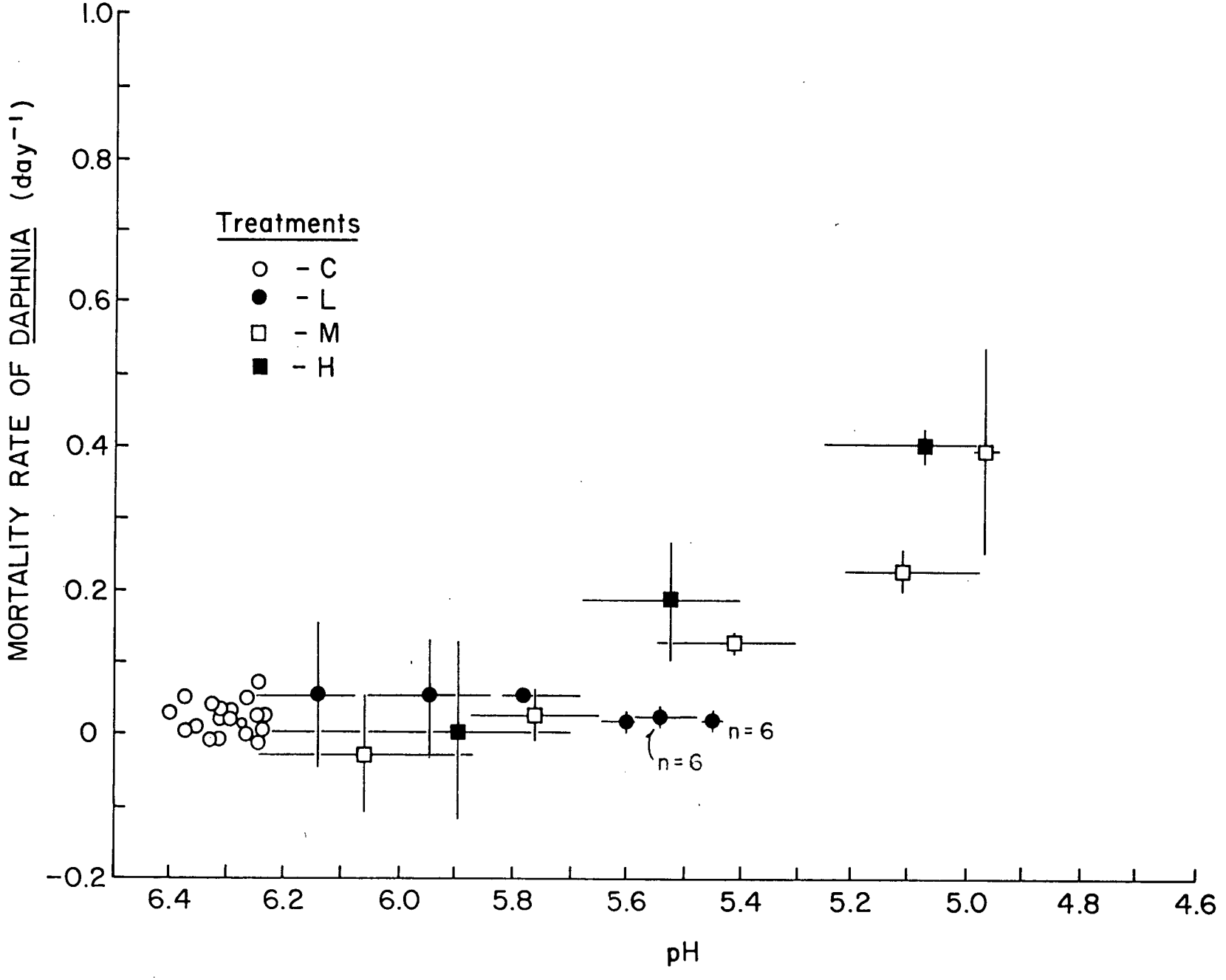

ADULT MORTALITY RATE (day⁻¹)
1.0
0.8
0.6
0.4
0.2
0
-0.2
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
pH
Treatments
○ - C
● - L
□ - M
■ - H
(n=6)
(n = 6)

Figure 39. Mean mortality rates of Daphnia rosea versus pH exposure (using 2-stage model). Vertical bars show ± SE. Horizontal bars show pH range during sampling period. Error bars and pH range not shown for controls due to lack of space. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.


MORTALITY RATE OF DAPHNIA (day⁻¹)
1.0
0.8
0.6
0.4
0.2
0
-0.2
Treatments
○ - C
● - L
□ - M
■ - H
n = 6
n = 6
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
pH

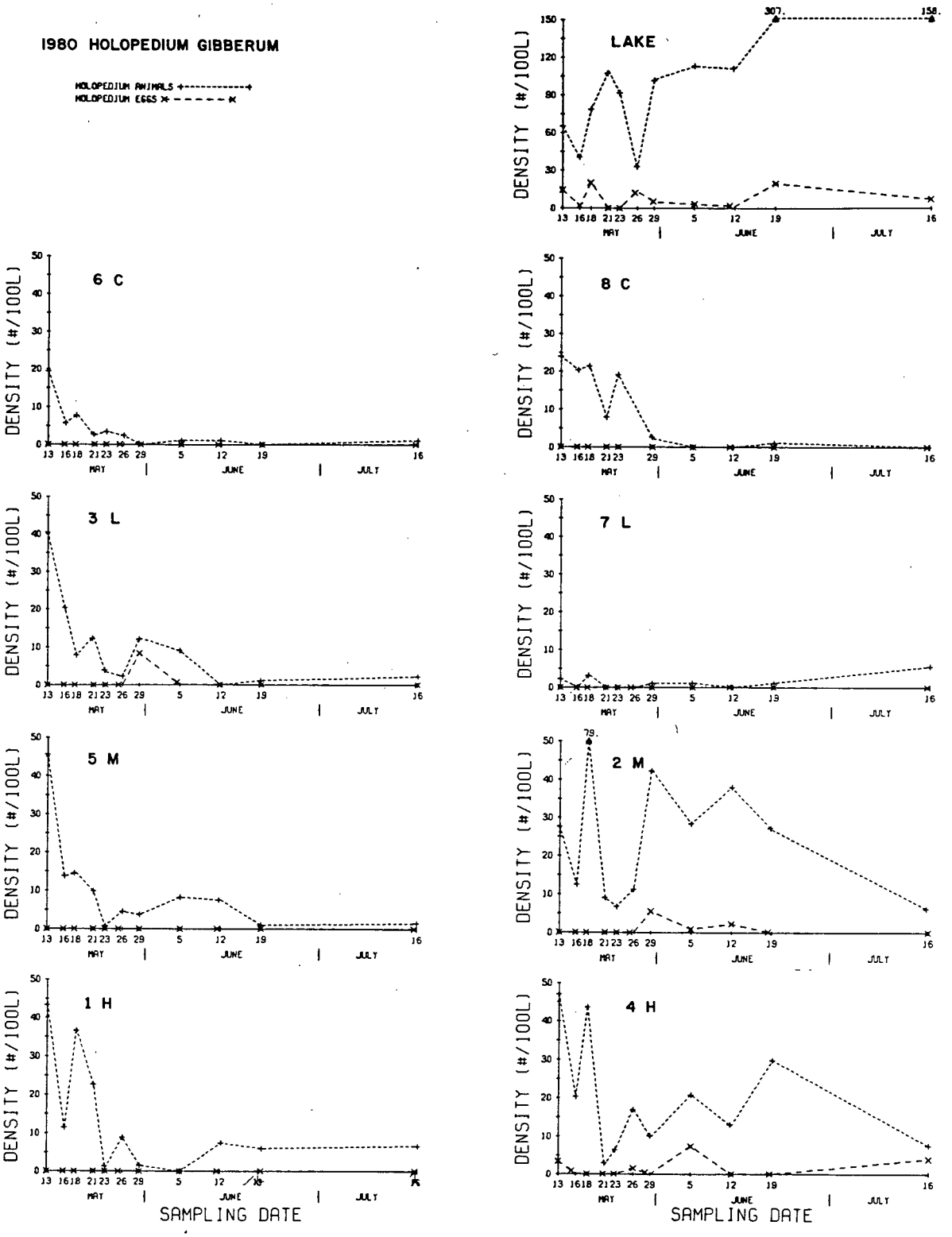
treatment H at pH 5.40-5.68 than in treatment L at pH 5.45 (Figure 39). Figure 39 provides no consistent evidence that pH 5.0-5.2 was more lethal under high rates of acidification than under medium rates. Though the estimated mean mortality rate in treatment H at pH 5.0-5.3 was higher than in treatment M at pH 5.0-5.2, Daphnia mortality in M at pH 4.9-5.0 was similar to that in H at pH 5.0-5.3.

3.3.2 Holopedium gibberum

Holopedium gibberum declined quickly to low densities in most of the enclosures but increased fivefold in Eunice Lake (Figure 40). Over all dates, mean densities of Holopedium (juveniles and adults) were much higher in Eunice Lake (1.09 ± 0.22 L^{-1}) than in the controls (0.067 ± 0.018 L^{-1}), treatment L (0.057 ± 0.020 L^{-1}), treatment M (0.18 ± 0.19 L^{-1}), or treatment H (0.17 ± 0.15 L^{-1}). Holopedium also declined after enclosure in 1979 (Section I). In 1980, differences between the lake and the controls were magnified by the fertilization of Eunice Lake.

Densities of Holopedium were relatively high in cylinders 2M and 4H, but the replicate cylinders (5M and 1H) behaved similarly to treatment L and the controls (Figure 40). Low starting densities and very few ovigerous females were the likely causes of the high within-treatment variation. In spite of this variation, mean densities of Holopedium on June 12 were significantly higher in treatments M and H than in treatment L and the controls (Table 31). Both the overall mean densities of Holopedium and the inter-treatment differences on June 12

Figure 40. Densities of Holopedium gibberum. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.


1980 HOLOPEDIUM GIBBERUM
HOLOPEDIUM ANIMALS
HOLOPEDIUM EGGS
LAKE
6 C
8 C
3 L
7 L
5 M
2 M
1 H
4 H
DENSITY (#/100L)
SAMPLING DATE
MAY
JUNE
JULY
13 16 18 21 23 26 29 5 12 19 16
307.
158.
79.

indicate that Holopedium was certainly not adversely affected by acidification to pH 5.0 and 4.5. Holopedium populations in cylinders 2M and 4H may actually have benefitted by the extinctions of Daphnia rosea and/or Diaptomus tyrrelli.

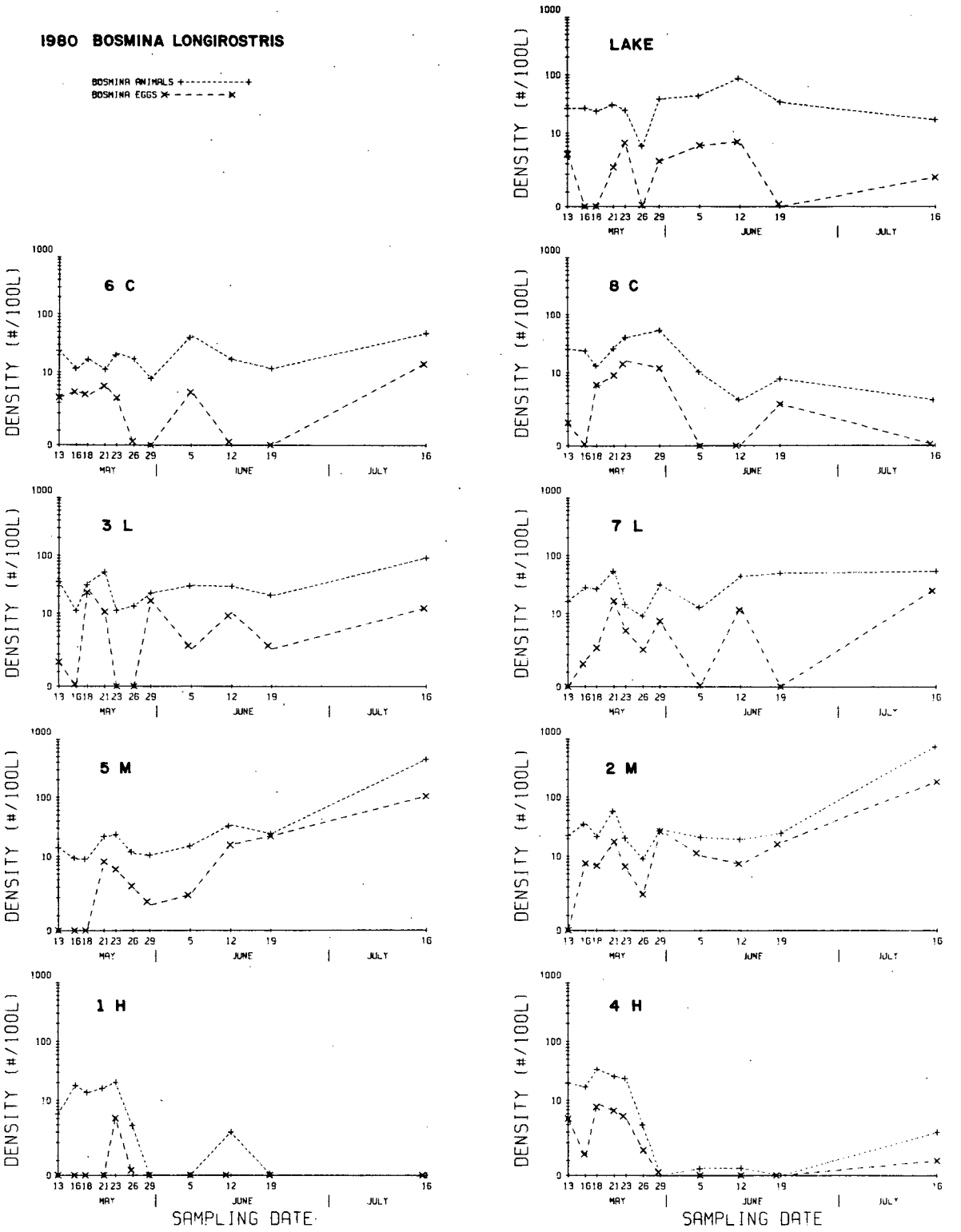
3.3.3 Bosmina longirostris

Acidification to pH 5.5 (treatment L) affected densities of B. longirostris eggs or animals on only two dates: egg densities were higher in treatment L than in the controls on June 12, and animal densities were higher in treatment L on June 19 (Figure 41 and Table 31).

In treatment M, Bosmina outperformed the controls, with significantly higher egg densities on June 12, June 19 and July 16, and 24 times higher animal densities on July 16 (602 ± 164 L^{-1} in M versus 25 ± 22 L^{-1} in the controls); see Figure 41 and Table 31. Animal densities in treatments M and L were not significantly different on any dates, and egg densities differed only on one date (Table 31).

Though exposure to pH 5.0 appeared to help Bosmina, rapid acidification to pH 4.5 was clearly detrimental. Between May 23 and 26, mean animal densities in treatment H dropped from 21.6 ± 1.5 to 3.7 ± 0 L^{-1}, coincident with a pH decline from 4.68 ± 0.023 to 4.42 ± 0.017. Bosmina densities in treatment H were significantly lower than in all other treatments on May 26, May 29, June 5 and June 12, and significantly lower than treatments L and M on July 16 (Table 31). Also, bosminid eggs were absent from 9 of 10 samples taken from treatment H after May 26, but

Figure 41. Densities of Bosmina longirostris. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.


1980 BOSMINA LONGIROSTRIS
BOSMINA ANIMALS +----------+
BOSMINA EGGS * - - - - - *
LAKE
6 C
8 C
3 L
7 L
5 M
2 M
1 H
4 H
DENSITY (#/100L)
1000
100
10
0
13 1618 2123 26 29 5 12 19 16
MAY | JUNE | JULY
SAMPLING DATE

more common in the other treatments (Figure 41).

3.3.4 Diaptomus kenai

As in my 1979 experiment (Section I), Diaptomus kenai was relatively acid tolerant. Copepodite, adult and total densities showed no significant treatment effects until June 19 (Table 32; Figure 42). Mean copepodite densities in treatments M and H dropped significantly below treatment L and the controls on June 19 and remained significantly lower than the controls on July 16 (Table 32).

If the relative declines in copepodite densities in treatments M and H were caused by increased mortality, densities of adult Diaptomus kenai in these two treatments should have been relatively low on July 16. However, treatment M adult densities were higher than all other treatments on July 16, providing no evidence for mortality. In contrast to treatment M, treatment H contained the lowest densities of adults on July 16 (significantly lower than treatment M), and the lowest densities of adults plus copepodites (significantly lower than all other treatments). Acidification to pH 4.5 may therefore have increased Diaptomus kenai mortality, but sampling in July was insufficient to demonstrate this conclusively.

Effects of acidification on D. kenai reproduction can only be assessed by examining densities of loose calanoid eggs, since ovigerous D. kenai females were too rare to merit statistical comparisons of numbers of attached eggs. Densities of loose calanoid eggs (Figure 43) were higher in May than June in all

Figure 42. Densities of Diaptomus kenai. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

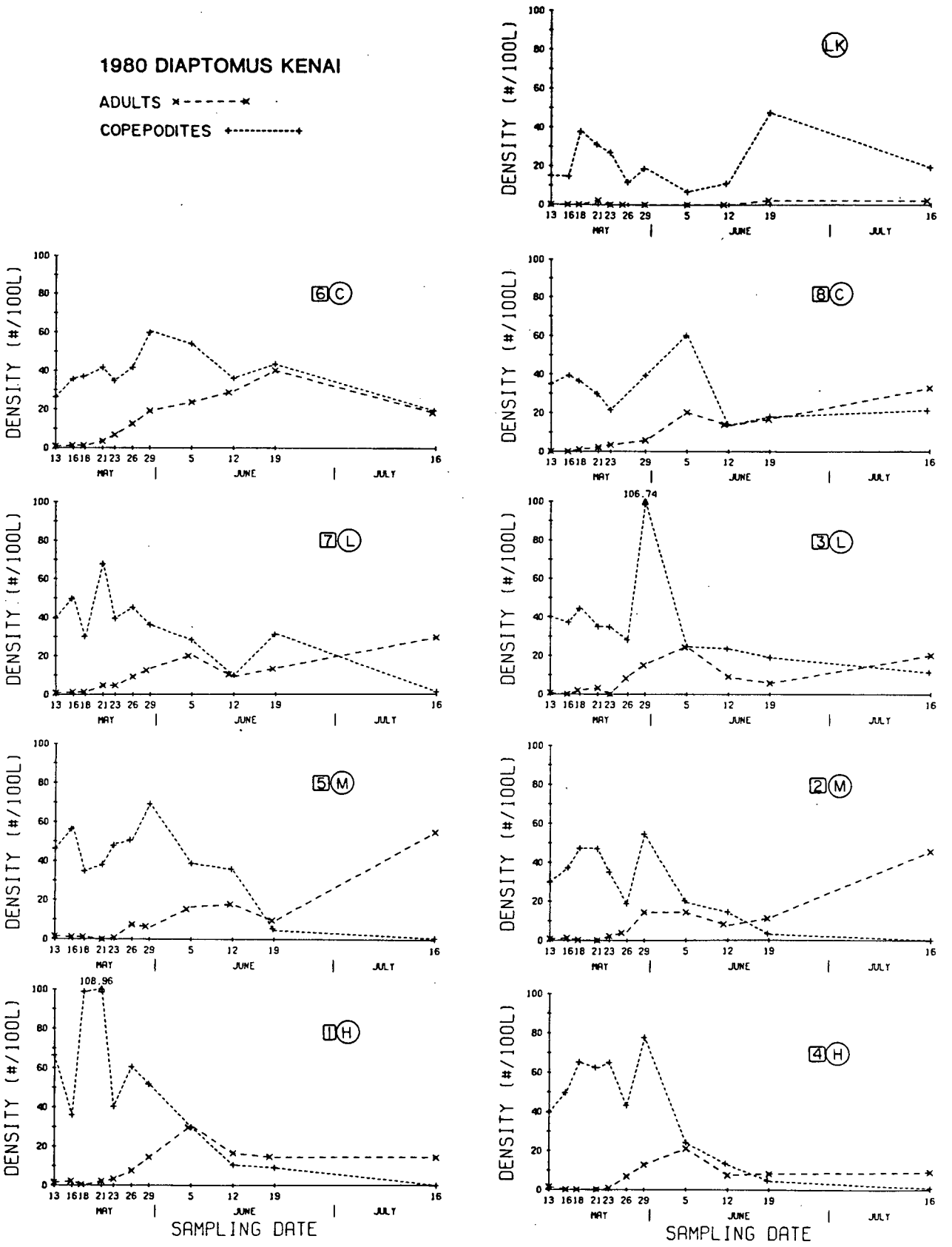

1980 DIAPTOMUS KENAI
ADULTS
COPEPODITES
DENSITY (#/100L)
LK
6C
8C
7L
3L
5M
2M
1H
4H
108.96
106.74
13 16 18 21 23 26 29 5 12 19 16
MAY
JUNE
JULY
SAMPLING DATE

Table 32. Results of analyses of variance and Duncan multiple range tests of inter-treatment differences in densities of diaptomid copepods and loose calanoid eggs. See Table 27 for explanation of symbols and abbreviations.

Date		*Diaptomus kenai*			*Diaptomus tyrrelli*			Loose Calanoid Eggs
		Copepodites	Adults	Total	Copepodites	Adults	Total	
May	13	ns	ns	ns	ns	ns	ns	ns
	16	ns	ns	ns	ns	ns	ns	ns
	18	ns	ns	ns	ns	ns	ns	ns
	21	ns	ns	ns	H M C L (0.044)	ns	H M C L (0.044)	ns
	23	ns	ns	ns	H M C L (0.018)	H M C L (0.005)	H M C L (0.017)	ns
	26	ns	ns	ns	ns	H M C L (0.005)	ns (0.058)	M H L C (0.002)
	29*	ns	ns	ns	H M L C (0.0001)	ns	M H L C (0.001)	H M L C (0.013)
June	5	ns	ns	ns	M H L C (0.0002)	H M C L (0.0002)	M H L C (0.0004)	ns
	12	ns	ns	ns	H M L C (0.0004)	H M L C (0.023)	H M L C (0.004)	ns
	19	M H L C (0.029)	ns	ns	H M L C (0.013)	H M L C (0.002)	H M L C (0.004)	ns
July	16	H M L C (0.039)	H C L M (0.035)	H L C M (0.006)	H M L C (0.00001)	H M L C (0.003)	H M L C (0.0007)	L H M C (0.033)

* one observation missing (Bag 8C)

cylinders, but showed the reverse pattern in Eunice Lake, presumably as a result of elevated nutrient levels in the lake. Egg densities were statistically significantly lower in treatments M and H during late May (Table 32), but it is not clear whether D. kenai or D. tyrrelli was responsible for these differences.

Analyses of variance showed that lengths of D. kenai adults and copepodites did not differ significantly between treatments on either May 13 or June 5. Growth of D. kenai was therefore not seriously affected by acidification.

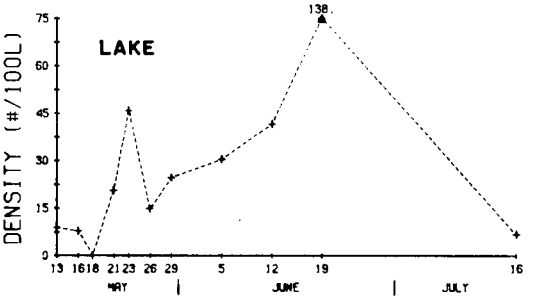
3.3.5 Diaptomus tyrrelli

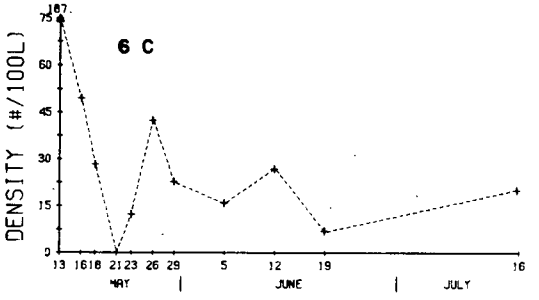
In 1980, Diaptomus tyrrelli was the most acid-sensitive crustacean of the Eunice Lake zooplankton community. Though maintaining starting densities in the controls, D. tyrrelli slowly declined at pH 5.5 in treatment L, and disappeared quickly in treatments M and H (Figure 44).

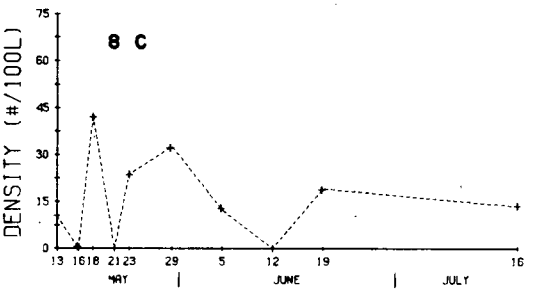
Densities of D. tyrrelli copepodites in treatment L began to drop below control cylinder levels on June 5, and were significantly lower by June 19 (Figure 44, Table 32). Treatment L also contained lower densities of adults than the controls on June 19 and July 16, though these differences were not statistically significant. These results strongly suggest that three week exposures to water of pH 5.5 were lethal to D. tyrrelli.

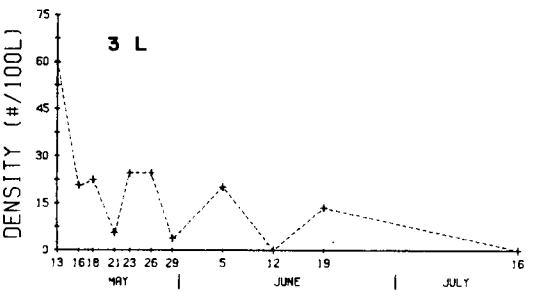
Figure 43. Densities of loose calanoid eggs. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

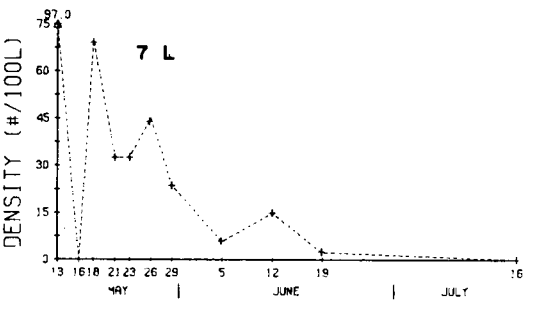
1980 LOOSE CALANOID EGGS

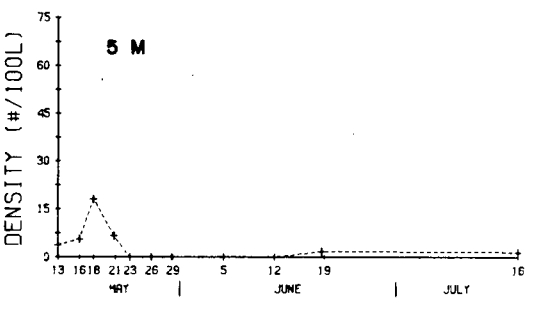


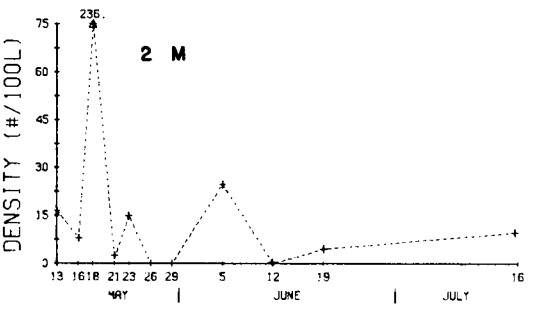


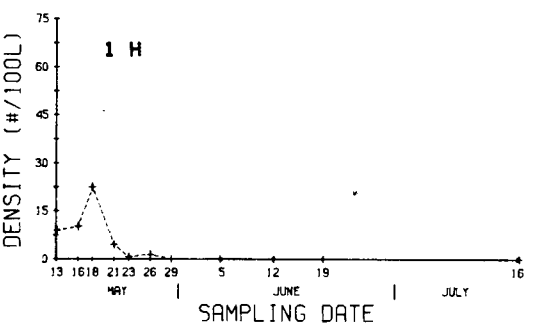












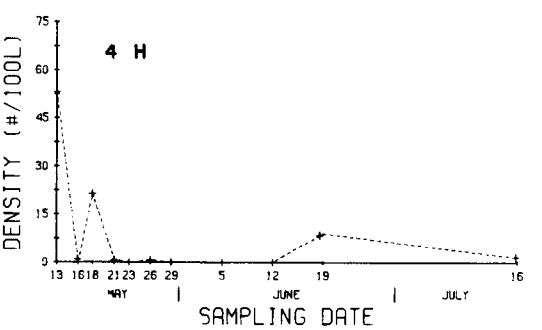
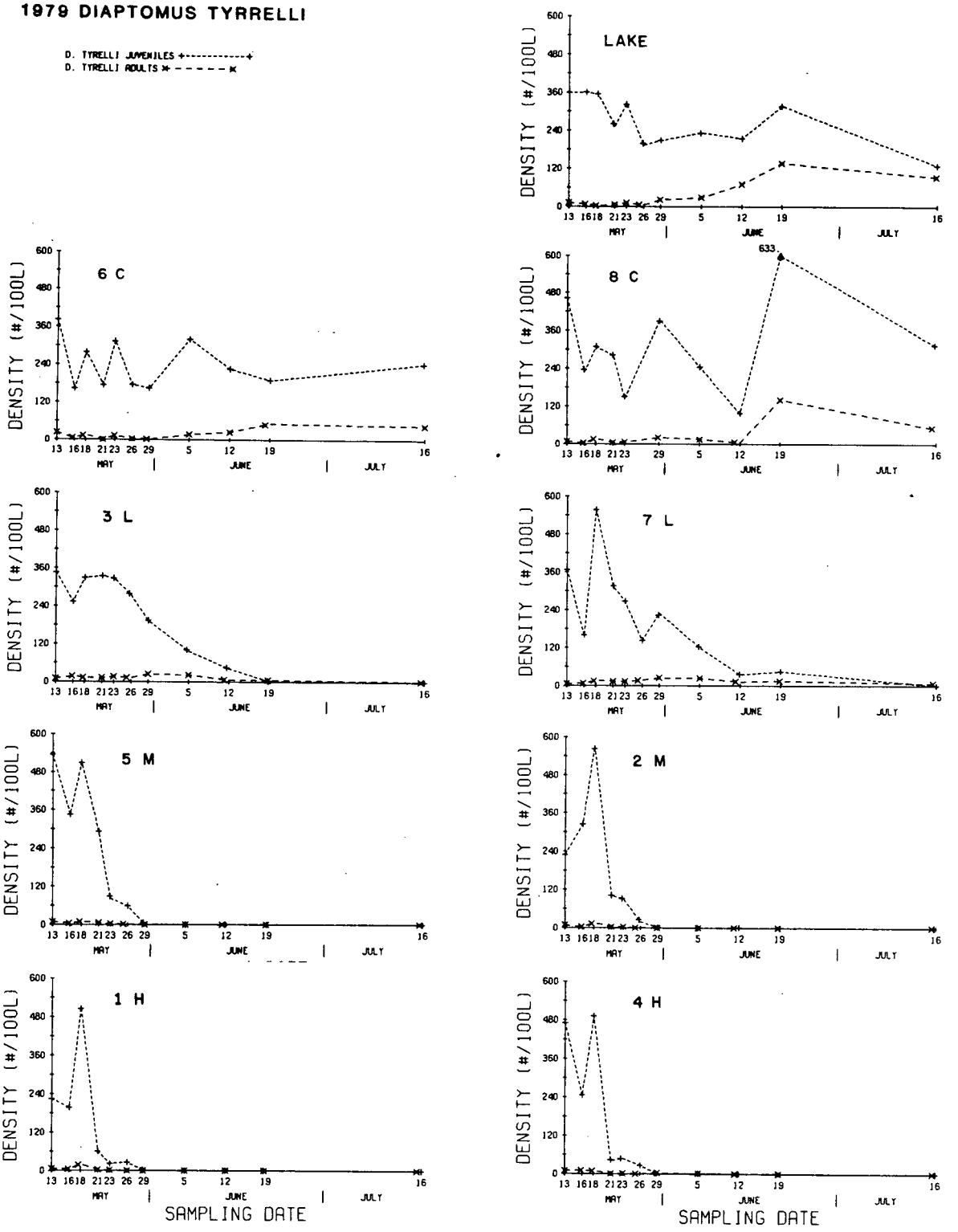


Figure 44. Densities of Diaptomus tyrrelli. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

1979 DIAPTOMUS TYRRELLI

D. TYRELLI JUVENILES +----------+
D. TYRELLI ADULTS * - - - - - *



It is highly unlikely that predation by Diacyclops thomasi contributed to the decline of D. tyrrelli in treatment L. First, evidence for cyclopoid predation on copepodites of D. tyrrelli is mixed: Anderson (1974) found such evidence but McQueen (1969) did not. Second, though densities of D. thomasi did not differ significantly between treatment L and the controls on any sampling dates, D. tyrrelli disappeared only in treatment L. One could argue that D. tyrrelli was less able to escape cyclopoid predation in treatment L due to sublethal effects of low pH on escape responses. However, if this were the case, one would expect D. tyrrelli to have declined faster in cylinder 7L than 3L, since D. thomasi was more abundant in 7L (Figure 45). Instead, declines were a little faster in 3L (Figure 44).

In treatments M and H, D. tyrrelli densities declined sharply between pH 5.3 and 5.0 (Table 33). Though the pH causing incipient mortality cannot be precisely determined, there is no evidence that the incipient lethal pH differed between treatments M and H.

All four cylinders receiving treatments M and H showed unexpectedly high densities of D. tyrrelli on May 18, at pH 5.3 to 5.6 (Table 33). In my 1979 experiment, D. tyrrelli densities also showed an unexplained enormous increase at mean epilimnetic pH 5.3 to 5.5 (Section I, 3.2.4 (ii)). It may be that the pH range 5.3-5.6 decreases the ability of D. tyrrelli to avoid capture by the sampling pump. If so, D. tyrrelli was undersampled at circumneutral pH levels. It would be worthwhile

Table 33. Major changes in Diaptomus tyrrelli copepodites in Treatments M and H.

Treatment	Cylinder	Date	Mean pH*	(Density of Copepodites in Cylinder)/(Mean Density of Copepodites in Controls)
M	2M	May 16	5.84 ± 0.05	1.65
		18	5.60 ± 0.02	1.94
		21	5.28 ± 0.04	0.44
		23	4.95 ± 0.03	0.39
	5M	May 16	5.90 ± 0.03	1.75
		18	5.70 ± 0.00	1.73
		21	5.35 ± 0.02	1.27
		23	5.01 ± 0.03	0.35
H	1H	May 16	5.69 ± 0.06	1.01
		18	5.40 ± 0.02	1.72
		21	4.88 ± 0.02	0.26
		23	4.70 ± 0.03	0.09
	4H	May 16	5.72 ± 0.03	1.24
		18	5.41 ± 0.04	1.67
		21	5.05 ± 0.03	0.17
		23	4.66 ± 0.02	0.21

* At time of sampling of zooplankton (i.e. prior to acid addition for each day).

to perform laboratory experiments to assess the effects of sublethal pH exposures on the escape responses of D. tyrrelli.

3.3.6 Diacyclops thomasi and copepod nauplii

The cyclopoid copepod D. thomasi becomes carnivorous by the fourth copepodite stage (C IV) and feeds primarily on its own nauplii and copepodites, as well as on diaptomid copepod nauplii (McQueen 1969, Peacock 1981). The life history of D. thomasi has been described for two lakes in the University of British Columbia Research Forest : Marion Lake (Mcqueen 1969) and Placid Lake (Peacock 1981). In both these lakes, carnivorous CIV stages are usually first present in April, moulting to adults which reproduce throughout May and June. Eggs and nauplii are found during May and June, developing into young copepodites by July, which either diapause or develop into carnivorous copepodites by August. The old generation of adults dies out by the end of June.

In processing samples from my 1980 experiment, I did not distinguish between calanoid and cyclopoid copepod nauplii, nor identify cyclopoid copepodite stages. Nevertheless, D. thomasi did appear to follow the expected life history. Peak densities of cyclopoid eggs were observed in May in all enclosures (Figure 45), coinciding with high copepod nauplii densities (Figure 46); re-examination of samples showed both calanoid and cyclopoid nauplii were present in May. Copepodite densities increased over June and July in Eunice Lake and all treatments except H, where acidification effects were evident (Figure 45).

Figure 45. Densities of Diacyclops thomasi. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

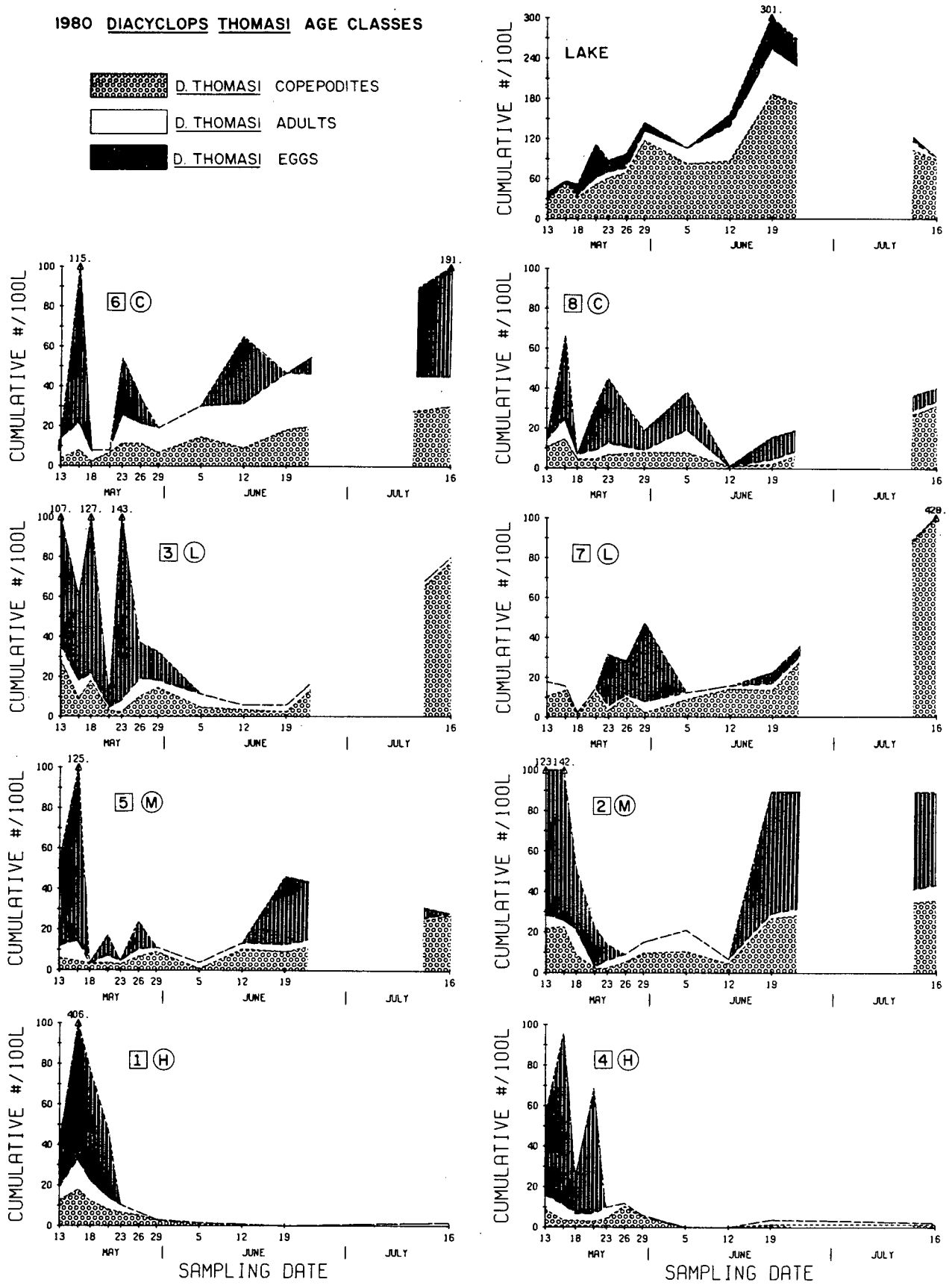
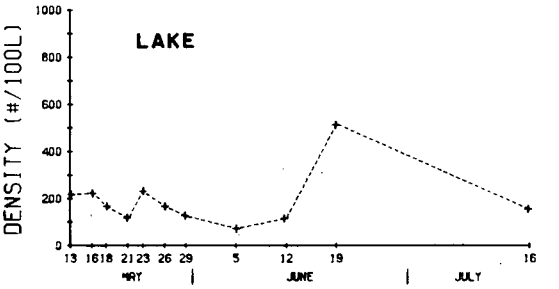
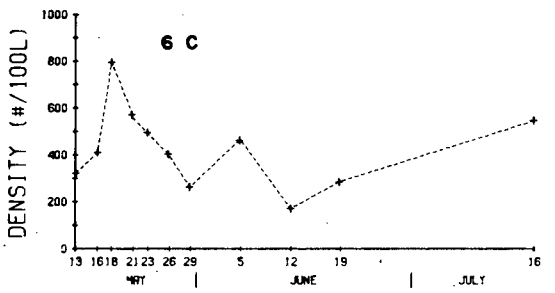
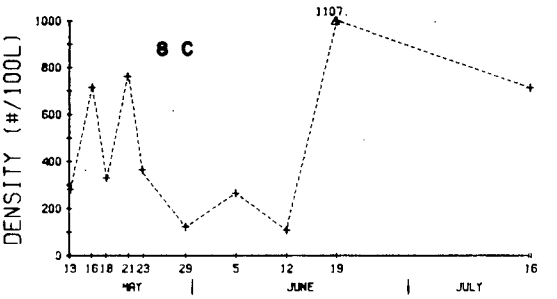

1980 DIACYCLOPS THOMASI AGE CLASSES
D. THOMASI COPEPODITES
D. THOMASI ADULTS
D. THOMASI EGGS
LAKE
6 C
8 C
3 L
7 L
5 M
2 M
1 H
4 H
CUMULATIVE #/100L
SAMPLING DATE
MAY
JUNE
JULY

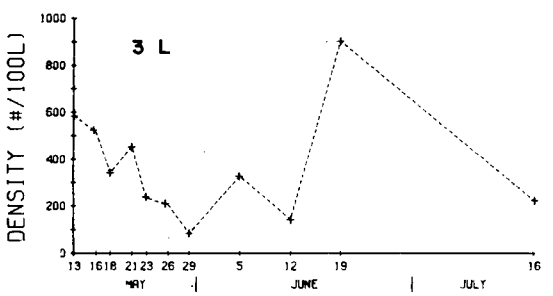
Figure 46. Densities of copepod nauplii. Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

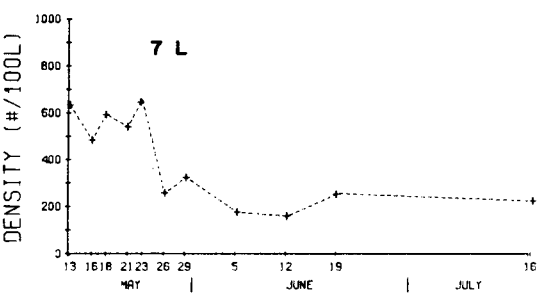
1980 COPEPOD NAUPLII

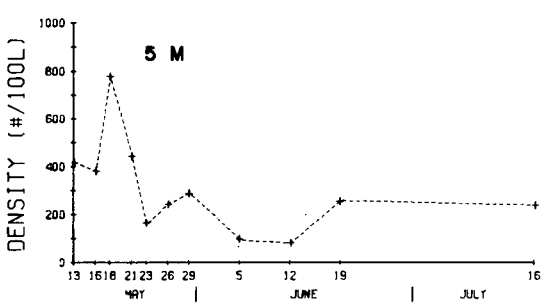


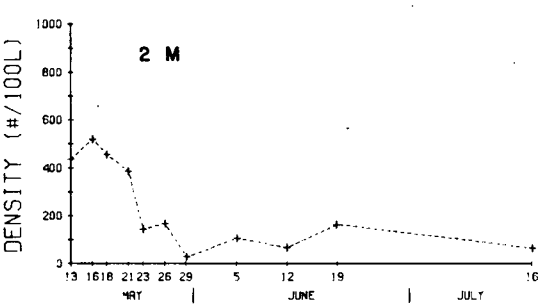


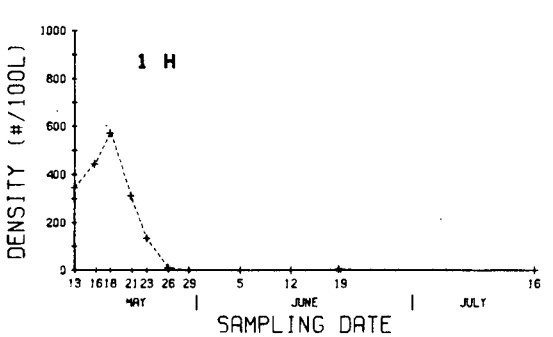


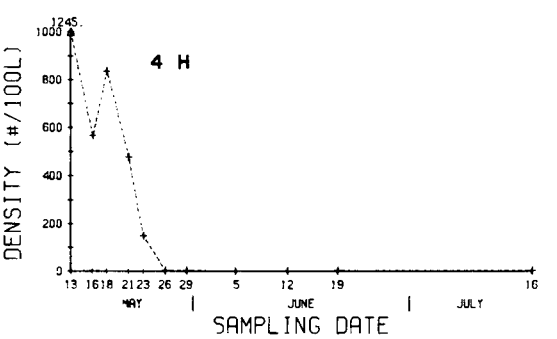












Acidification to pH 4.5 (treatment H) drastically reduced densities of cyclopoid eggs, copepodites and adults after May 29 (Figure 45; Table 34). Also, copepod nauplii were absent from treatment H from May 26 onwards, but significantly higher in the other treatments and Eunice Lake (Table 34). I reexamined the June 19 and July 16 samples to determine whether treatment H acidification had removed "potential" cyclopoid nauplii or calanoid nauplii; 98% of the nauplii in treatments C, L, M and Eunice Lake were cyclopoid. Therefore, it appears that all life history stages of D. thomasi (nauplii, copepodites and adults) were killed by water of pH 4.5.

3.3.7 Rotifers

I only enumerated four rotifer genera (Keratella, Kellicottia, Polyarthra, and Conochilus) since other forms were extremely rare.

Moderate and high levels of acidification greatly benefitted Keratella. By June 12, Keratella had reached significantly higher mean densities in treatment H (14.0 ± 0.6 L^{-1}) than in treatment M (7.0 ± 0.8 L^{-1}) which was in turn significantly higher than both treatment L (1.54 ± 0.28 L^{-1}) and the controls (1.74 ± 0.19 L^{-1}); see Figure 47 and Table 34. Keratella densities increased in all treatments between June 12 and July 16 (Figure 47), but remained significantly higher in treatments M and H (Table 34).

Table 34. Results of analyses of variance and Duncan multiple range tests of inter-treatment differences in densities of cyclopoid copepods, copepod nauplii and rotifers. See Table 27 for explanation of symbols and abbreviations.

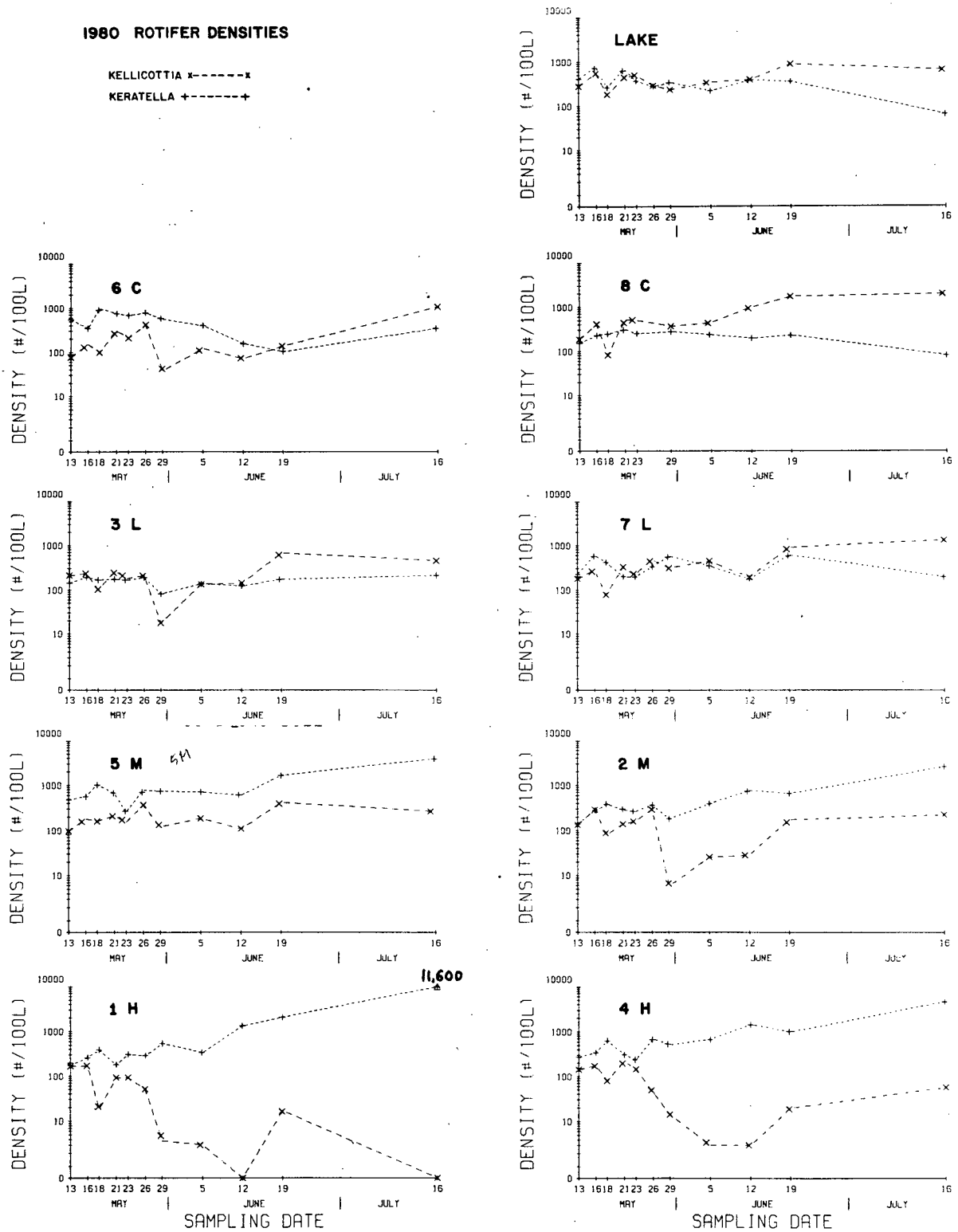
Date		*Diacyclops thomasi*		Copepod Nauplii***	ROTIFERS*		
		# Adults & Juveniles	Eggs		*Keratella*	*Kellicottia*	*Polyarthra*
May	13	ns	ns	ns	ns	ns	ns
	16	ns	ns	ns	ns	ns	ns
	18	ns	ns	ns	ns	ns	H M C L (0.037)
	21	ns	ns	ns	ns	ns	H L M C (0.019)
	23	ns	H M C L (0.037)	ns	ns	ns	ns
	26	ns	ns	H M L C (0.019)	ns	H L M C (0.026)	ns
	29**	ns	ns	H M L C (0.033)	ns	ns	ns
June	5	H M L C (0.05)	ns	H M L C (0.0001)	ns	H M L C (0.032)	ns
	12	ns	ns	H M C L (0.0002)	L C M H (0.0006)	H M L C (0.042)	M L H C (0.023)
	19	ns	ns	H M L C (0.006)	ns	ns	ns
July	16	H M C L (0.012)	ns	H M L C (0.002)	C L M H (0.007)	ns	ns

* *Conochilus* not listed. No significant treatment effects found.

** One missing observation (Bag 8C).

*** Both calanoid and cyclopoid. (June 19 and July 16 samples were 99% cyclopoid.)

Figure 47. Densities of Keratella and Kellicottia . Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.

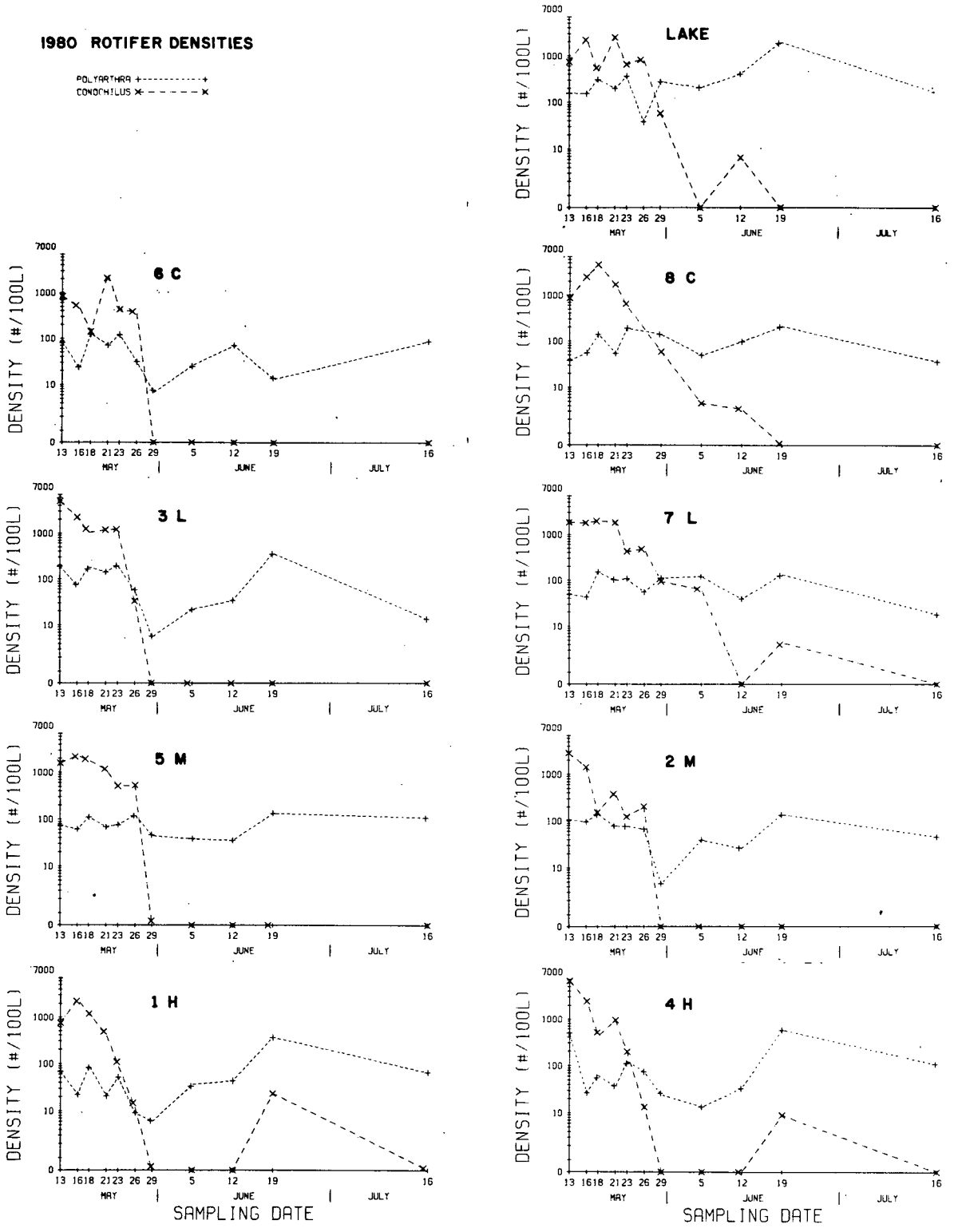

1980 ROTIFER DENSITIES
KELLICOTTIA x------x
KERATELLA +------+
LAKE
6 C
8 C
3 L
7 L
5 M
2 M
1 H
4 H
11,600
DENSITY (#/100L)
10000
1000
100
10
0
13 1618 2123 26 29 5 12 19 16
MAY | JUNE | JULY
SAMPLING DATE

I reexamined the June 12, June 19, and July 16 samples to determine which species of Keratella flourished under acidification; all samples were dominated by Keratella taurocephala. Vertically stratified samples taken June 19 revealed that in all treatments (and in Eunice Lake), the distribution of Keratella was strongly biased to the 0-2 m stratum (92.5% of the sampled Eunice Lake population was found at 0-2 m; 78.0 ± 1.7% in the controls; 87.6 ± 3.8% in L; 91.5 ± 0.26% in M; and 89.7 ± 6.5% in H). In those treatments where Daphnia rosea survived (treatment L and the controls), K. taurocephala showed a strong spatial overlap with Daphnia rosea on June 19: 42.9 ± 4.9% of daphnid juveniles and 32.5 ± 7.7% of the adults were found at 0-2 m.

In contrast to Keratella, Kellicottia appeared adversely affected by high acidification. On May 26, June 5 and June 12 densities of Kellicottia were significantly lower in treatment H than the other treatments (Table 34, Figure 47). However, since no significant inter-treatment differences remained at the end of the experiment, the populations in treatment H may have only experienced transient effects.

Neither Polyarthra nor Conochilus showed any sustained inter-treatment differences (Figure 48; Table 34). Conochilus, which generally forms large colonies in spring, was very rare after May 29 in all treatments.

Figure 48. Densities of Polyarthra and Conochilus . Abbreviations used for treatments: C=controls; L=low rate of acidification; M=medium rate; H=high rate.


1980 ROTIFER DENSITIES
POLYARTHRA
CONOCHILUS
LAKE
6 C
8 C
3 L
7 L
5 M
2 M
1 H
4 H
DENSITY (#/100L)
7000
1000
100
10
0
13 1618 2123 26 29 5 12 19 16
MAY
JUNE
JULY
SAMPLING DATE

4. DISCUSSION

This discussion is divided into two parts. Section 4.1 considers community-level responses of zooplankton to experimental acidification, and compares these responses to the results of both other studies (Section 4.1.1) and my 1979 experiment. Section 4.2 addresses questions of toxicity, competition and predation at a population-level, species by species.

4.1 Changes in Zooplankton Biomass and Community Structure

4.1.1 Comparisons with Other Studies

In the 1980 experiment, acidification to pH 5.0 and 4.5 caused significant reductions in total zooplankton biomass . Were the observed reductions a reasonable simulation of the expected responses of acidifying lakes? To date, there are no studies showing the sequence of changes in zooplankton biomass in an acidifying lake, and only one region with accurate measurements of zooplankton biomass in acidic and nonacidic lakes (Yan and Strus 1981, Yan and Greiling (in prep)). Table 35 lists some of the zooplankton biomass data of Yan and co-workers, together with my experimental results. Mean values in the limnocorrals were computed over 4 sampling dates in June and July, and therefore cannot be directly compared to the lake data, calculated over the entire ice-free season (April to November). However, the relative declines in zooplankton biomass under acidification can be compared, and are quite

Table 35. Comparison of total zooplankton biomass in 1980 limno-corrals and Ontario lakes. Limno-corral means based on samples taken June 5, 12, 19 and July 16; Ontario lake means are averaged over entire ice-free period. Ontario lake data obtained from Yan and Strus (1981), Yan and Greiling (in prep.) and N.D. Yan (unpublished data).

Location	Mean pH	TP ($\mu g \cdot L^{-1}$)	Mean Total Zooplankton Biomass ± SE (n) ($\mu g \cdot L^{-1}$)	Percent Total Biomass		
				Cladocera	Copepoda	Rotataria
1980 Treatments:						
Controls	6.28	~ 5	31.6 ± 2.3 (8)	49.0	50.2	0.8
L	5.54	~ 5	25.3 ± 2.1 (8)	57.6	41.5	0.9
M	5.07	~ 5	11.6 ± 1.6 (8)	26.1	68.8	5.1
H	4.51	~ 5	8.3 ± 0.9 (8)	22.1	63.9	14.0
$\frac{\text{Mean Biomass in Treatment H}}{\text{Mean Biomass in Controls}}$ = 0.26						
ONTARIO						
Non-Acid Lakes:						
Blue Chalk (1977)	6.53	7.7	45.3 (23)	35.8	63.6	0.6
Red Chalk (1977)	6.38	6.4	35.3 (25)	30.8	68.7	0.5
Jerry (1977)	6.35	9.7	32.7 (26)	20.8	78.2	1.0
Harp (1977)	6.34	8.2	40.4 (27)	44.0	55.2	0.8
MEAN	6.40	8.0	38.4	32.9	66.4	0.7
Acid Lakes:						
Clearwater (1976)	4.23	5.2	12.9 (21)	54.0	12.7	33.3
Clearwater (1977)	4.10	6.5	16.5 (15)	78.6	5.0	16.4
Clearwater (1978)	4.40	4.6	9.0 (7)	58.0	14.5	27.5
MEAN	4.24	5.4	12.8	63.5	10.7	25.7
$\frac{\text{Mean Biomass in Clearwater Lake}}{\text{Mean Biomass in Non-Acid Lakes}}$ = 0.33						

similar. Mean total zooplankton biomass in acidic Clearwater Lake is on average 33% of the biomass in circumneutral lakes of similar trophic status and the mean biomass in treatment H was 26% of the level in the controls. No data are available for Ontario lakes of pH 5.0-5.5 to compare with treatments M and L.

The relative contribution of rotifers to total zooplankton biomass was less than 1% in the controls, treatment L and Ontario nonacidic lakes, but increased exponentially with declining pH levels (Table 35). The proportion of rotifer-biomass may be higher in Clearwater Lake than in treatment H due to lower pH or to the longer period of acidification. Clearwater has been acidic for at least two decades (Yan and Strus 1980).

In Mirror Lake (New Hampshire), rotifers formed only 16.3% of the total zooplankton biomass , but accounted for 39.8% of zooplankton production (Makarewicz and Likens 1979). Rotifers constituted 14.0% of the total zooplankton biomass in treatment H during June and July (Table 34). Based on Mirror Lake, I expect that roughly one third of treatment H zooplankton production came from rotifers. As most algal cells consumed by rotifers are smaller than 12μm in diameter (Wetzel 1975), herbivore filtering of cells larger than 12μm may have been relatively weak in treatment H. This suggestion is supported by the relatively high concentrations of chlorophyll *a* in larger cell sizes in treatment H.

Rotifer biomass increases quantitatively as well as proportionately at low pH. Clearwater Lake rotifer biomass averaged 12.2 times the mean biomass in the nonacidic lakes, and treatment H rotifer biomass averaged 4.6 times levels in the controls. These results conflict with those of Roff and Kwiatkowski (1976), who reported greatly reduced densities of rotifers in lakes of pH 4.5. Yan and Greiling (in prep) point out: 1) that densities of the invertebrate predator Chaoborus were much higher in their acid lakes than in the ones studied by Roff and Kwiatkowski, and 2) that Chaoborus predation on crustaceans can remove competitive constraints on the performance of rotifers (shown experimentally by Neill, in press). In my 1980 experiment, these competitive constraints were removed directly through the acidification-induced extinction of D. rosea, rather than indirectly via Chaoborus predation (see discussion of Keratella at the end of Section 4.2).

Multi-lake surveys indicate that zooplankton communities generally show an increasing proportion of cladoceran and rotifer biomass with eutrophication (Gannon and Stemberger 1978). Relative to copepods, cladocerans and rotifers mature more rapidly, have a shorter generation time, and lay many more clutches of eggs (Allen and Goulden 1980), all of which are advantageous in productive waters, or those seasonally pulsed with nutrients (Allen 1976). The higher reproductive potential of cladocerans and rotifers would be expected to give them a relative advantage in short-term acidification experiments. At

most times of the year, resources made available by the removal of acid-sensitive herbivores could be more quickly transformed into cladoceran and rotifer biomass than into copepod biomass. In 1979, cladocerans quickly increased and dominated the biomass after the decline of Daphnia rosea in treatment AF. In 1980, the cladoceran Bosmina longirostris increased its densities following the decline of Daphnia rosea and Diaptomus tyrrelli in treatment M, and the rotifer Keratella taurocephala proved its opportunistic capabilities in both treatments M and H. However, the copepod Diaptomus kenai dominated the biomass of treatments M and H for most of the 1980 experiment (Figure 32, Table 35). This was not because D. kenai increased, but simply that it did not decrease while other species declined.

In acidic lakes, where acidification takes place over several decades, life history differences between rotifers, cladocerans and copepods do not obviously imply an advantage to any group. Indeed, the percentage of total biomass contributed by cladocerans is quite variable in acidic lakes. Some Ontario acid lakes, such as Clearwater, are dominated by the cladoceran Bosmina longirostris, while the copepod Diaptomus minutus is dominant in others (Yan and Strus 1981). Plankton in Scandinavian acid lakes are frequently dominated by the cladocerans Eubosmina coregoni or E. longispina, but about as often by the copepod Diaptomus gracilis (Hobaek and Raddum 1980). In treatment H, crustacean biomass was dominated primarily by the copepod Diaptomus kenai and secondarily by the cladoceran Holopedium gibberum. In conclusion, consistent

trends in crustacean zooplankton taxonomic composition (at the subclass level) are probably less likely with acidification than with eutrophication.

This conclusion follows logically from evolutionary considerations. Many temperate zone oligotrophic lakes slowly change towards eutrophy with sedimentation from their watersheds, remaining in trophic equilibria for long periods (G.E. Hutchinson 1969, 1973). Such conditions probably provide repeated opportunities for the natural selection of physiologies and life histories suited to eutrophic conditions, across many taxa.

Though oligotrophic lakes also commonly develop into dystrophic lakes with high concentrations of humic acids (Wetzel 1975), acidification via naturally generated sulfuric acids is an uncommon event, requiring such sources as sulphur springs (Yamamoto 1970), spontaneous burning of bituminous shales (T.C. Hutchinson et al. 1978), or volcanic gases (Wetzel 1975). Sulfur-driven acidification probably both occurs more sporadically in time and space, and proceeds more rapidly than eutrophication. Due to the nonlinear shape of lakes' titration curves, the mean pH of sensitive lakes can decline from 6 to below 5 within a few decades, crossing the lethal pH threshold for many zooplankton species. Surveys in acidified regions reveal a bimodal frequency distribution of lake pH, with few lakes at intermediate pH levels of 5 to 6 (T.C. Hutchinson et al. 1978, NRCC 1981, Driscoll and Bisogni 1983). I suspect that the adaptations demanded by acidic conditions

(e.g. maintenance of ionic balance) require major changes to the organism's physiology. The adaptations necessary for survival in eutrophic conditions (e.g. faster assimilation and utilization of pulses of resources) may require fewer generations to evolve.

Diaptomids may be common in acidic lakes simply because so many species exist in the Diaptomidae in circumneutral lakes, rather than due to a familial acid tolerance. Certainly, the diaptomids in my 1980 experiment demonstrated a very wide variance in acid-sensitivity: D. kenai tolerated pH 4.5 whereas D. tyrrelli was eliminated at pH 5.5. The frequency distribution of acid tolerances of other families (such as Daphniidae) is likely narrower (see Discussion in Section I).

Note that the most frequently dominant crustacean in Ontario acidic lakes (the relatively small Diaptomus minutus) is approximately the same size as acid-sensitive Diaptomus tyrrelli. I suspect that acid tolerance is uncorrelated with the size of crustacean species, but that the low species diversity in acidic lakes commonly produces a biased community size structure. The probability that two species are both relatively small (or large) is greater than the probability that ten species are all relatively small (or large). In treatment H, the two dominant crustaceans were relatively large (Diaptomus kenai and Holopedium gibberum). Small species dominate the crustacean communities of Ontario's acidic lakes (Sprules 1975), while Swedish acidic lakes are often dominated by large crustaceans (Erickson et al. 1980). Sprules (1980) speculated

that the Ontario pattern may have been caused by small zooplankton being more efficient at filtering bacteria and detritus. Erickson and co-workers maintained that the size structure of zooplankton communities in Swedish lakes was the result of intense invertebrate predation on small zooplankton. Neither Sprules nor Erickson provided experimental evidence for their 'biotic hypotheses'. Treatment H shows that large zooplankton may become dominant in the absence of invertebrate predators, simply as a result of greater acid tolerance. (The relative importance of invertebrate predation in acidic lakes is discussed in Section III).

Multi-lake surveys across pH gradients have consistently observed strong correlations between numbers of crustacean zooplankton species and lake pH (see Table 4.2, Section I). Surprisingly, this study and the acidification of Lake 223 (Malley et al. 1981) are the first field, experimental demonstrations that reductions in pH can in fact cause decreasing numbers of species. Though multi-lake surveys show significant declines in numbers of species only at pH < 5.0 Table 4.2, Section I), the Eunice Lake zooplankton community began to change markedly below pH 5.4. Clearly, a knowledge of the relative acid sensitivities of different crustaceans is an asset in interpreting the results of synoptic surveys. Due to replacement of acid-sensitive taxa by other species during the acidification period, reductions or extinctions of sensitive species will almost certainly occur prior to declines in overall numbers of species.

4.1.2 Comparisons with the 1979 experiment

The rates of loss and recovery of zooplankton biomass in the 1980 experimental treatments can be compared with my 1979 results to show the aggregate effects of variations in temperature, pH, nutrients, and life history. In August 1979, acidification to pH 5.3 (in nutrient-enriched cylinders) caused massive mortality of Daphnia rosea. Over the following two weeks, the mean total zooplankton biomass in acidified and fertilized enclosures was only 38% of the biomass in fertilized enclosures (Section I, Table 10). In 1980, during the first two weeks of exposure to pH 5.0 (May 23 to June 5), mean total zooplankton biomass in treatment M was 46% of the mean biomass in the controls. Initial biomass declines were likely higher in 1979 due to the greater dominance (% of total biomass) of acid-sensitive D. rosea. Huge increases in total zooplankton biomass occurred in 1979 (at about pH 5.5), with Diaphanosoma brachyurum, Chydorus sphaericus, and Bosmina longirostris replacing Daphnia; these recoveries occurred three weeks after the initial crashes. In 1980, recovery of zooplankton biomass was slow and incomplete at pH 5.0, and nonexistent at pH 4.5. On July 16, eight weeks after the initial collapses, mean zooplankton biomasses in treatments M and H were still 30% and 74% less (respectively) than levels in the controls.

Why did Diaphanosoma, Chydorus, and Bosmina not replace Daphnia biomass in treatment M in 1980 to the extent they did in 1979? Diaphanosoma usually breaks diapause in July, but probably because of cool temperatures in 1980, had still not

appeared in Eunice Lake by July 16 and was therefore not present in the enclosures either.

Chydorus and Bosmina, unlike Diaphanosoma, were both present in treatment M when Daphnia crashed. Production rates per unit biomass of these species may have been slightly inhibited by the lower pH in 1980 (5.0) than 1979 (5.0-5.5), but were likely more strongly constrained by the lower nutrient levels and temperatures in 1980. In my discussion of Chydorus in the 1979 experiment (Section I 4.4.1 (iv)) I concluded that its success at 5.0-5.5 was due primarily to abundant growth of periphyton and filamentous algae; a direct release from competition with Daphnia seemed less probable. The 1980 results show that under lower temperatures and nutrient levels, removal of Daphnia by acidification was insufficient to permit Chydorus to colonize the spring zooplankton community at pH 5.0. The 1980 Chydorus results are therefore consistent with my expectations from the 1979 experiment. However, to demonstrate that it was the absence of suitable substrate (and not life history constraints) which prevented Chydorus from colonizing treatment M, I would need to repeat the 1980 experiment during July to October. Bosmina also performs better with fertilization (Section I 4.4.1 (iii)) but unlike Chydorus, was able to slowly penetrate the zooplankton community in treatment M in 1980.

Acidification-induced losses of zooplankton biomass in 1979 were accompanied by 6-9 fold increases in chlorophyll a concentrations (Section I 3.3.5). Unfortunately, chlorophyll a was not monitored regularly in 1980. A single sampling at the

end of the experiment (July 19) did however show results consistent with my 1979 experimental results. Mean chlorophyll *a* concentrations increased with the level of acidification, particularly in treatment H among larger algal cells. Even though the crustaceans surviving at pH 4.5 were relatively large (*Diaptomus kenai* and *Holopedium gibberum*), their total filtering was apparently insufficient to crop the production of cells larger than 12 μm; *Keratella taurocephala* was probably primarily responsible for the absence of any increase in smaller algal cells. Though inter-treatment differences in chlorophyll *a* concentrations were not statistically significant, one would not expect as large an algal response to reduced herbivore grazing in the nutrient-poor enclosures of 1980 as in the nutrient-enriched enclosures of 1979.

4.2 Performance of Particular Taxa Under Acid Stress

Daphnia rosea displayed essentially identical acid sensitivity in the 1979 and 1980 experiments. In 1979, no effects on *Daphnia rosea* densities or reproductive indicators were evident at pH 5.6-5.7 (under acidification alone) but high mortality occurred at pH 5.3-5.4 (under acidification and fertilization). Results in 1980 were similar: daphnid densities and reproductive indicators were not reduced by pH 5.5 (treatment L), and estimated mortality rates increased sharply at pH 5.4 in treatments M and H (under both two-stage and three-stage rate estimation models). Thus, the seasonal timing of acidification episodes does not appear to alter their effects on

D. rosea.

In detailed laboratory studies, Walton et al. (1982) observed a significant increase in the time to first reproduction of Daphnia pulex at pH 5.0, but no decline in survival until pH 4.4. If Daphnia rosea also suffers delayed reproduction at sublethal pH levels, I should have observed gradual reduction in daphnid egg densities in treatment L, which at pH 5.5 was only 0.1-0.2 pH units above the lethal threshold. Instead, treatment L egg densities equalled or exceeded levels in the controls. The implications of this result are twofold. First, sublethal pH effects are either less important in D. rosea than D. pulex or less important in the field than the laboratory, or both. Second, acidification to pH 5.5 does not lower the availability or palatability of spring food resources for D. rosea; if it did, egg densities would have decreased. I found the same result for summer food resources in 1979 (Section I).

The 1980 experiment did not provide convincing evidence of age-specific acid sensitivity in Daphnia. This result was due to primarily to uncertainty in mortality rate estimation (See Section 3.3.1) and also to the absence of an extended period of intermediate level toxicity, where only the most acid-sensitive life history stage would be affected. Daphnia either did well (treatment L) or went extinct quickly (treatments M and H). In contrast to 1979, when neonate mortality was apparently very high (Section I 4.4.1(i)), the three-stage model indicated very low juvenile mortality in 1980. This difference in results may

have been due to methodological problems with the three-stage model (Appendix H). Accurate determination of demographic changes in acid-stressed field populations will require labour-intensive in situ measurements of egg and juvenile developmental rates, as well as frequent measurements of egg age distributions (Threlkeld 1979). Large enclosures would be required for such studies, so that the already declining acid-stressed populations can be adequately and frequently sampled without significantly diminishing their densities.

The experiment also did not provide a definitive answer to the question of whether the rate of pH change affects the sensitivity of Daphnia to different pH levels. At incipient lethal levels (pH 5.4) high rates of acidification caused greater mortality than low rates of acidification; at lethal exposures (pH 5.0-5.2) there were no consistent differences between mortality rates in treatments M and H. More precise answers to this question would be best pursued through laboratory experiments, due to the high level of experimental control and large numbers of replicates required. However, these field results provide a useful benchmark for evaluting whether laboratory tests are producing reasonable toxicity estimates.

Holopedium gibberum suffered enclosure effects in both 1979 and 1980. However, its improved performance in cylinders 2M and 4H implies that it can become increasingly important at pH 4.5-5.0. This is consistent with observations of increased Holopedium dominance in acidic lakes in both Ontario (Sprules

1975; Keller 1981) and Scandinavia (Hobaek and Raddum 1980).

The poor performance of Bosmina longirostris in treatment H was surprising, since this species commonly dominates acid lakes of pH < 4.5 (Yan and Strus 1980, DeCosta and Janicki 1978, Keller 1981). Acidification in treatment H may have been too rapid to permit physiological acclimation and/or parthenogenic reproduction by the more acid-tolerant individuals of the population. In acid lakes of mean pH < 4.5 where Bosmina is dominant, acidification has generally occurred over more than one decade. When such lakes passed through the 'transition zone' (pH 5.3 to 4.7) episodic pH declines may have served to select the most acid-tolerant clones of the population.

If acidic lakes are neutralized very rapidly, it is possible that high Bosmina mortality could occur due to either an inability to reacclimate to higher pH, or inadequate time to produce sufficient offspring tolerant of circumneutral conditions. In Ontario, the neutralization of Middle, Hannah and Lohi Lakes from pH 4.3-4.4 to pH 7.0-8.0 led to catastrophic declines in the abundance of Bosmina, which had previously been the community dominant (Scheider et al. 1976, Yan and Dillon 1981).

As mentioned in Section 4.1.2, the improved performance of Bosmina in treatment M near the end of the 1980 experiment may have been partially due to a release from competition with Daphnia. Experimental or predator-induced removal of Daphnia under circumneutral conditions sometimes causes an apparent competitive release of Bosmina (Brooks and Dodson 1965, Lynch

1979, Neill (in prep.)) and sometimes does not (Kerfoot and Demott 1980). Treatment M acidification not only removed Daphnia rosea and Diaptomus tyrrelli as potential competitors, it may also have lowered the competitive abilities of other crustaceans.

In 1979, Diaptomus kenai was unaffected by pH 5.3 but it was not clear whether this was due to its acid tolerance or to its concentration below the thermocline in circumneutral waters. The 1980 experiment confirmed that D. kenai populations perform normally at pH 5.0, though survival from copepodite to adult stages may have been reduced at pH 4.5.

Diaptomus tyrrelli was gradually eliminated by acidification to pH 5.5 (treatment L) in the spring of 1980, though in the summer of 1979 it had survived two weeks of exposure to pH 5.3-5.4. This difference may be due a change in acid sensitivity with life history stage. In May 1980 copepodites made up about 95% of the treatment L D. tyrrelli populations, whereas in August 1979 only 12% of the acid-stressed populations were copepodites. Molting between copepodite stages, and from copepodite to adult may have increased the sensitivity of D. tyrrelli to low pH. Lee and Buikema (1979) found that molting caused increased sensitivity of Daphnia pulex to chromate. They speculated that this was due to either rapid uptake of chromate as the body volume increased during molting, or to calcium deficiency of the new exoskeleton. Also, Malley (1980) found that decreased pH lowered the rate of calcium uptake by postmolt crayfish (Orconectes virilis) and decreased

their survival. Temperature and food differences between 1979 and 1980 may also have been important to D. tyrrelli, but there are no published studies showing the effects of these factors on the pH sensitivity of this species. Finally, the existence of a deepwater refuge from acid water may have been important to D. tyrrelli in 1979.

Diacyclops thomasi was much more abundant in 1980 than in 1979, most likely because of the fertilization of upstream Gwendoline Lake (C. Walters and W.E. Neill pers. comm.). The extinction of Diacyclops thomasi in treatment H is consistent with observations of this species in Ontario. Yan and Strus (1981) noted the relative scarcity of Diacyclops thomasi in Clearwater Lake (pH 4.3) compared to nonacidic lakes within the same zogeographic region. Sprules (1975) found that D. thomasi was dominant (> 10% numerically) in only one of 23 La Cloche Mt. Lakes of pH < 5.0. Similarly, Keller (1981) found that D. thomasi was dominant in none of 21 Sudbury Area lakes of pH < 5.0. In both Sprules' and Keller's surveys the frequency of D. thomasi dominance increased with lake pH. Finally, Roff and Kwiatkowski (1976) found great reductions in the seasonal abundance of D. thomasi in 2 Sudbury Area lakes of pH < 5.0, as compared to 4 lakes of pH ≥ 5.0.

Yan and Strus (1981) and DeCosta and Janicki (1978) have suggested that cyclopoid predation (by C. vernalis in Clearwater Lake, and by Mesocyclops edax in Cheat Lake (pH 4.5)) may be important controls on spring populations of Bosmina longirostris. The acid sensitivity of D. thomasi suggests that

it probably could not fulfill this role in Eunice Lake if the lake were to acidify to pH 4.5; cyclopoid predation would likely only become important if a more acid-tolerant cyclopoid colonized the lake.

The improved performance of Keratella taurocephala under moderate and high acidification was very likely due to a release from competition with D. rosea. This statement is supported by the strong overlap in the vertical distributions of K. taurocephala and D. rosea (Section 3.3.7) and by a series of competition experiments by Neill (in press) in nearby Gwendoline Lake. Neill found that removal of D. rosea increased densities of K. cochlearis 1 to 2.5 orders of magnitude, while a quadrupling of D. rosea densities decreased densities of K. cochlearis by 85%. Hutchinson (1967) noted that K. taurocephala is quite acid tolerant. Malley et al. (1982) found that experimental acidification of Lake 223 led to large increases in both K. taurocephala and K. cochlearis. Also, Yan and Greiling (in prep) have observed roughly 9 times higher mean densities of K. taurocephala in acidic Ontario lakes than in nonacidic lakes.

If acidification-induced removal of D. rosea benefitted Keratella taurocephala in June of 1980, why did this not occur when Daphnia collapsed in August of my 1979 experiment? It is possible that sensitivity to high temperatures or life history forces caused Keratella to peak early in 1979 and be scarce in July when the cylinders were stocked. No data are available to confirm this. Neill found that in 1976 and 1978 K. cochlearis

consistently declined by June or July, even if Daphnia had been removed from experimental enclosures; Yan (in prep) found relatively low densities of K. taurocephala during August in 4 of 4 lake-years of data. However, Schindler and Noven (1971) found that K. taurocephala was at maximum densities in August in Lakes 122 and 132. An alternative explanation for the absence of K. taurocephala in 1979 is that it was outcompeted by very high densities of Bosmina longirostris, Chydorus sphaericus and Diaphanosoma brachyurum. The major weakness of this explanation is that these three species increased in abundance three weeks after the crash of Daphnia; with its shorter generation time, Keratella should have been able to bloom sooner.

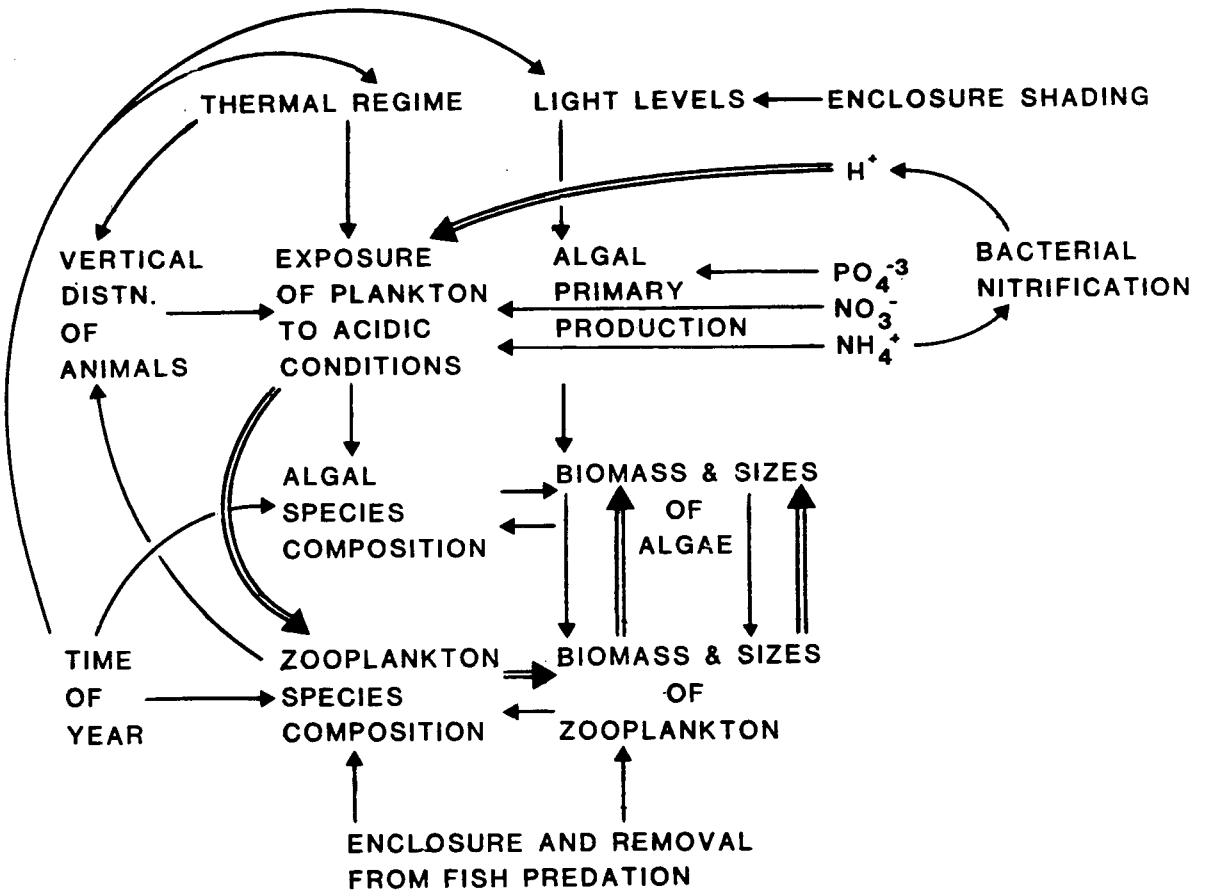
III SUMMARY AND CONCLUDING DISCUSSION

1. SUMMARY

My research consisted of two field experiments performed July to October 1979, and May to July 1980. These studies explored the effects of experimental acidification and fertilization on enclosed plankton communities, concentrating on the ecosystem components and interactions shown in Figure 49.

In both experiments, the direction of zooplankton community change depended primarily on the intersection of acidification episodes with the spatial and temporal distributions of acid-sensitive zooplankton species, and the competitive relationships within the community at the time of acidification. Underlying both species distributions and competitive relationships were seasonal changes in temperature and nutrients (Figure 49), since the life histories of the zooplankton species have been "tuned" to these factors over evolutionary time. (Within Eunice Lake and other lakes of the University of British Columbia Research Forest, the timing of the initial appearance and final decline of each species, and the peak densities attained within the season, are strongly affected by lake temperatures and nutrient levels (C.J. Walters and W.E. Neill, unpublished data).) Temperatures and nutrients also affected the distribution and concentration of $[H^+]$ in the water column, altering the animals' exposure to acidity (Figure 49). The primacy of these ecosystem interactions is evident from the major results of the study, which are summarized below.

Figure 49. Primary ecological interactions in the 1979 and 1980 field experiments . Arrows connecting boxes show ecosystem linkages (double lines for most important linkages). An arrow connecting two boxes through another box represents the means by which the 'independent' component at the arrow's origin influenced the 'dependent' component at the arrow's point.


THERMAL REGIME
LIGHT LEVELS
ENCLOSURE SHADING
H+
VERTICAL DISTN. OF ANIMALS
EXPOSURE OF PLANKTON TO ACIDIC CONDITIONS
ALGAL PRIMARY PRODUCTION
PO4-3
NO3-
NH4+
BACTERIAL NITRIFICATION
ALGAL SPECIES COMPOSITION
BIOMASS & SIZES OF ALGAE
TIME OF YEAR
ZOOPLANKTON SPECIES COMPOSITION
BIOMASS & SIZES OF ZOOPLANKTON
ENCLOSURE AND REMOVAL FROM FISH PREDATION

The three 1979 treatments were acidification, fertilization, and acidification plus fertilization. Summer thermal stratification largely confined acid additions to the epilimnion. Acidification alone lowered the epilimnetic pH to 5.6, but did not significantly alter transparency, phytoplankton or zooplankton relative to the controls. Fertilization alone significantly increased chlorophyll a concentrations and the biomass of edible algal cells, with concurrent significant increases in total zooplankton biomass . Algal assimilation and bacterial nitrification of the ammonium in NH_4NO_3 additions (Figure 49) caused a significant loss of alkalinity in fertilized enclosures but did not affect the pH.

However, when acidification and fertilization were combined, biotic processing of ammonium lowered the epilimnetic pH an additional 0.2 units (to 5.4), causing massive mortality of the zooplankton community dominant, D. rosea. This mortality was clearly due to acid-associated toxicity, and not starvation or predation.

The collapse of D. rosea precipitated major changes to both phytoplankton and zooplankton communities. Chlorophyll a concentrations increased 6-9 fold within two weeks, providing abundant resources for more acid-tolerant species to increase their densities (Bosmina longirostris, Diaphanosoma brachyurum, Chydorus sphaericus, and Ceriodaphnia pulchella). I concluded that C. sphaericus benefitted primarily from increases in filamentous algae and periphyton, whereas the other replacement species fed on small algal cells (<13 μm) released from daphnid

herbivory.

The above replacement species soon overshot their food resources, leading to a collapse of zooplankton biomass and a second large increase in chlorophyll *a* concentrations. Comparisons with fertilized enclosures demonstrated that the loss of *D. rosea* was associated with significant increases in both the amplitude of zooplankton biomass - chlorophyll *a* fluctuations and the biomass of algal cells larger than 13 μm. In Figure 49, I have emphasized the importance of this sequence of changes by having a double line leading from "exposure of plankton to acidic conditions", to "zooplankton species composition", and continuing on to "biomass and sizes of algae". The reverse pathway (acid-induced changes to phytoplankton species composition affecting zooplankton biomass and size composition) is deemed to be of lesser importance in Figure 49. This reflects the fact that the dominant influences on phytoplankton were via acid-induced changes to the zooplankton community, rather than to direct effects of acidification on phytoplankton.

In May 1980, I experimentally acidified all depths of the enclosures over a ten day period, and then maintained the pH at a constant level (5.5, 5.0 or 4.5) for seven weeks.

The 1980 experiment demonstrated that the acid tolerances of some zooplankton species vary seasonally, but others are unchanged. *Daphnia rosea* showed very similar acid sensitivity in 1979 and 1980 (collapsing at pH 5.4), but *Diaptomus tyrrelli* (which survived pH 5.3 in 1979) dwindled to extinction at pH 5.5

in 1980. I speculated that the acid sensitivity of D. tyrrelli copepodites was greater than that of D. tyrrelli adults, but changes in temperature and food conditions may also have affected this species' acid tolerance.

Modelling analyses of D. rosea mortality rates in 1980 suggested that the rate of acidification (as opposed to actual pH level) influenced toxicity near the incipient lethal pH level of 5.4. Rapid rates of acidification may also have worsened the effects of pH 4.5 on Bosmina longirostris, as this species survives in Ontario lakes of this acidity. However, it was difficult to precisely determine mortality rates in the 1980 experiment, due to uncertainty in developmental rates and the rapid mortality of acid-sensitive species.

Mean total zooplankton biomass declined nonlinearly with pH across the three acidification treatments. Declines at pH 5.5 were not significant, but at pH 5.0, rapid extinctions of D. rosea and D. tyrrelli caused a significant 63% decrease in zooplankton biomass relative to the controls. This decrease in biomass was partially restored by a significant increase in densities of Bosmina longirostris, but recovery was much slower than in 1979, presumably due to lower temperatures and nutrients. Two species which had replaced D. rosea in 1979 did not do so in 1980, due to either the absence of suitable substrate (in the case of C. sphaericus) or life history constraints (D. brachyurum). At pH 4.5, biomass declines were similar to pH 5.0, but no recovery occurred, as even relatively acid tolerant crustaceans were impaired by the acidity

(B. longirostris, Diaptomus kenai, and Diacyclops thomasi). The rotifer Keratella taurocephala proved extremely acid-tolerant however, reaching its highest biomass at pH 4.5. The pattern of change in crustacean and rotifer biomasses in the 1980 experiment was shown to be very similar to that observed in multi-lake surveys of Ontario acidic lakes.

Chlorophyll a concentrations were measured only once in 1980, but showed a pattern consistent with 1979 results and Figure 49: as treatment pH and zooplankton biomass decreased, chlorophyll a concentrations increased, primarily in algal cells larger than 12 μm.

2. CONCLUDING DISCUSSION

2.1 Temporal Fluctuations of Plankton Systems in Acidic Lakes

Results from both Mountaintop Lake (Yan and Lafrance 1981) and my 1979 experiment demonstrated that nutrient enrichment can potentially cause much greater plankton system fluctuations in acid lakes than in circumneutral ones (See Figure 26 on page 136). Are symptoms of increased fluctuation evident in the annual phytoplankton and zooplankton cycles of unenriched acid lakes? One simple measure of the degree of fluctuation of plankton systems would be the mean squared distance from the centroid of a phase plane to points on the trajectory. To make this measure comparable for lakes of different productivity, the distances should be expressed in relative units (i.e. the components divided by the mean biomasses of phytoplankton and zooplankton). Therefore, we have

$$D^2 = \frac{\sum_{i=1}^{n} \frac{[Pi-P]^2}{P^2} + \frac{[Zi-Z]^2}{Z^2}}{n} \qquad [7]$$

where:

D^2 = mean squared distance from centroid to trajectory;

n = number of samples taken per year;

Pi = phytoplankton biomass in sample i;

P = mean phytoplankton biomass;

Zi = zooplankton biomass in sample i; and

Z = mean zooplankton biomass.

If we replace n by (n-1) in the denominator of equation (1), it simplifies to

$$D^2 = [Sp/P]^2 + [Sz/Z]^2 \qquad [8]$$

where:

Sp = standard deviation of phytoplankton biomass; and

Sz = standard deviation of zooplankton biomass.

The right side of equation (14) is linearly proportional to the sum of the squared coefficients of variation of phytoplankton and zooplankton biomasses. In this form of the equation, the numbers of zooplankton and phytoplankton samples taken through the season may be unequal.

Based on the preceding results and discussion, I hypothesized that the coefficients of variation of phytoplankton and zooplankton biomasses (and hence D^2) would be greater in acid than in circumneutral lakes. To assist in testing these hypotheses, Mr. Norman Yan and Dr. Ken Nicholls of the Ontario Ministry of Environment very kindly provided 26 lake-years of zooplankton and phytoplankton biomass data.

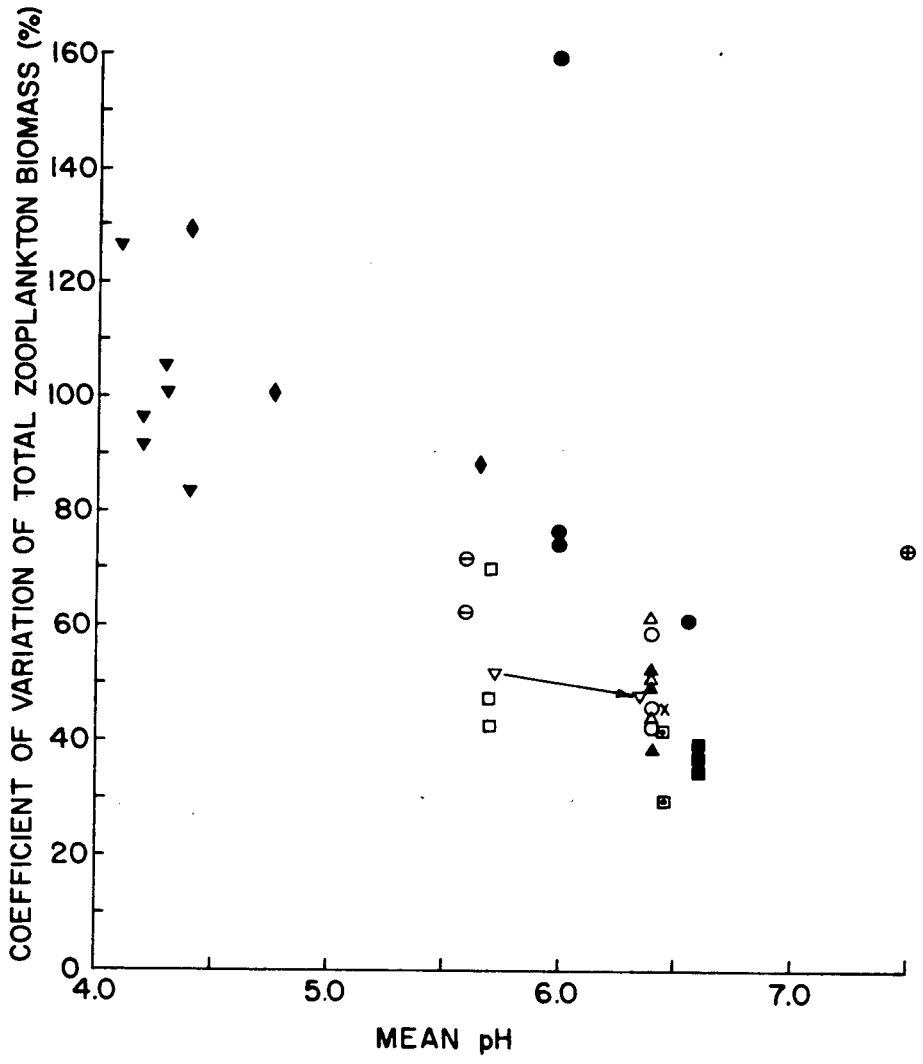
Detailed analysis of phytoplankton biomass coefficients of variation (and the effect of 'n' on the error associated with D^2) will appear elsewhere (Marmorek, Yan and Nicholls, in prep.). It is worth noting here only that the coefficients of variation of phytoplankton biomass were uncorrelated with pH. The Ontario zooplankton data were supplemented by data from acidic Cheat Lake (Decosta 1975; Decosta and Janicki 1978), circumneutral Lago Maggiore (Ravera 1969) and the F and AF cylinders from my 1979 experiment. Sampling in the 1980

experiment was not of sufficient duration or regularity to determine within-season fluctuations in zooplankton biomass. Annual coefficients of variation in total zooplankton biomass were computed from all samples taken between May 1 and November 30, and graphed against the mean pH of the water body (Figure 50). The pattern in Figure 50 is gratifyingly consistent with the hypothesis that the coefficient of variation in total zooplankton biomass increases in acid lakes. Some important comments on Figure 50:

1) data were available for only two lakes with pH less than 5.5 (Clearwater and Cheat). Both these lakes show extreme dominance by B. longirostris, which may affect the level of observed biomass fluctuations. Many North American acid lakes are dominated by the copepod Diaptomus minutus (Yan and Strus 1980), and Norwegian acid lakes often contain significant densities of the invertebrate predator Hetercope saliens (Nilssen 1980).
2) Dickie Lake likely shows greater variability in zooplankton biomass because it is both much shallower and more productive than the other Ontario lakes graphed (N.D. Yan, pers. comm.).

The coefficients of variation of total zooplankton biomass could vary inversely with pH because of "holes" in the temporal organization of the communities, with no acid-tolerant species available with the appropriate life history and temperature response physiology to fill them. Such holes would increase the

Figure 50. Coefficients of variation of May to November total zooplankton biomass for 33 lake-years of data and of July to October total zooplankton biomass for 4 limnocorrals and Eunice Lake. The three points for Cheat Lake represent different parts of the same reservoir in one year, and the arrow shows the neutralization of Nelson Lake. References are (1): N.D. Yan, unpublished data; (2-3): Decosta 1975, Decosta and Janicki 1978; (4): Ravera 1969.



Symbol	Lake	# Samples	Source
▼	Clearwater	9-24	(1)
□	Chub	23-24	(1)
▽	Nelson	8-9	(1)
●	Dickie	22-27	(1)
○	Harp	21-25	(1)
△	Jerry	16-24	(1)

Symbol	Lake	# Samples	Source
▲	Red Chalk	20-24	(1)
♦	Cheat	13-14	(2,3)
⊕	Maggiore	9	(4)
⊖	AF Cylinders	11	this study
⊞	F Cylinders	11	this study
x	Eunice	11	this study

variability in zooplankton biomass without causing sudden collapses of the entire community (as occurred in Mountaintop Lake with invertebrate predation or the absence of herbivore-resistant phytoplankton). More seasonal data is required for lakes of pH less than 5.5 before the pattern in Figure 50 can be confirmed; and more experiments are required to uncover the processes underlying such patterns.

Given the obvious pattern in Figure 50 one wonders why the coefficients of variation of phytoplankton biomass were not correlated with pH. Though phytoplankton species diversity is lower in acid than in circumneutral lakes, there are still thirty or more phytoplankton genera at pH 4.3 (N.D. Yan and K.H. Nicholls, unpublished data from Clearwater Lake), roughly ten times the number of zooplankton species in such lakes (Yan and Strus 1981). Temporal holes in the phytoplankton community may therefore be more easily filled than holes in the zooplankton community.

I would speculate that an extension of Figure 50 with more points at higher pH values, would reveal a roughly parabolic scatter of points. Lakes of higher pH are generally (though not always) more productive, and within-season variability in total zooplankton biomass would likely increase with trophic status. A more comprehensive approach would be to add to Figure 50 a third dimension of total phosphorus concentration. Lastly, since coefficients of variation of phytoplankton biomass will increase significantly with the amount of natural seasonal variation in light and temperature, lakes from regions with

large climatic differences should not be graphed together.

2.2 Relative Importance of Toxicity, Competition and Predation in Acidifying Lakes

The 1979 and 1980 experiments provide a useful perspective on community changes in acidifying lakes, provided that the necessary simplifications of the experiments (accelerated acidification schedule, elevated nutrient status, spatial limits, etc.) are firmly kept in mind.

The degree of change observed as lakes acidify into the "transition zone" (pH 4.7 to 5.3 according to Henriksen (1980)) must depend upon whether the dominant herbivores and predators (at pH > 5.3) are acid-sensitive. In the absence of acidification effects on food resources, loss of an acid-sensitive dominant herbivore should decrease competition among the remaining herbivorous species, since zooplankton biomass has been reduced below the current carrying capacity. By contrast, the decline or extinction of an acid-sensitive predator should cause zooplankton biomass to increase (unless the predator is replaced). The relative acid tolerances of predators and dominant herbivores will determine which of these two process occurs first.

The degree of dominance of acid-sensitive herbivores is obviously important. Removal of a low density herbivore through toxicity would liberate relatively few resources to its competitors whereas loss of a "superdominant", such as *Daphnia rosea* in Eunice Lake could cause major changes. In the four UBC

Research Forest lakes that have been studied in detail, D. rosea generally contributes more than 75% of the summertime grazing pressure on lake seston (Neill, unpublished data). In both 1979 and 1980, the acid-induced mortality of D. rosea at transition pH levels appeared to release several species from competition (treatment AF in 1979 and treatment M in 1980).

At a pH less than 4.7 (i.e. beyond the transition zone) the competitive relationships within the community are probably less important. Declines in total zooplankton biomass and increases in chlorophyll a at pH 4.5 (treatment H in 1980) suggest that food resources were probably not limiting. However, very few species were sufficiently acid-tolerant to convert this food into increased animal densities (only Keratella taurocephala). With negligible predation and reduced competition, acid tolerance was the overwhelming determinant of zooplankton community structure. For predation to be important in lakes of pH<4.7, the predator(s) would obviously have to be unusually acid tolerant (see next section).

Connell (1975,1980) has suggested that competition is most likely to occur in environments with an intermediate level of disturbance. At low levels of disturbance, predation and parasitism keep prey populations well below the environment's carrying capacity, and hence reduce competition. At high levels of disturbance, abiotic constraints lower the densities of prey populations directly, also reducing competition. The patterns observed in the 1979 and 1980 experiments seem consistent with Connell's ideas. Enclosure could be considered as an

intermediate disturbance, which by removal of fish predation probably increased competition between herbivores for food. However, as the level of disturbance increased (with experimental acidification) zooplankton biomass declined, and competition for food became progressively less important.

What do my experiments imply for the zooplankton communities of other zoogeographic regions? Sprules (1975) compared the crustacean zooplankton communities of 47 La Cloche Mt. lakes (33 of which showed pH < 5.5) with the communities of 45 non-acidic (pH > 5.6) lakes in the Experimental Lakes Area (ELA) studied by Patalas (1971). In spite of major differences in chemistry, both regions featured a single major recurrent group of six species, five of which were common to the two areas. Daphnids were not part of either region's recurrent group. The similarity in species composition between the two regions may be partially due to the absence of acid-sensitive daphnid dominants in La Cloche lakes prior to their acidification. Lakes in the La Cloche Mountain and Sudbury areas are within the same zoogeographic region as the Muskoka-Haliburton Region of Ontario, and the ELA, both of which have few lakes with daphnid dominants (Patalas 1971, Sprules 1975, Yan and Strus 1981).

The ratio of cladocerans to copepods tends to increase with lake trophic status (Gannon and Steinberger 1978). However, lake sensitivity to acidification tends to decrease with trophic status (NRCC 1981). Therefore, there may not be many lakes both sensitive to acidification and dominated by daphnids.

Nilssen (1980) stressed the importance of replacement of Daphnia spp. by other filter-feeders in acidified lakes of southern Norway. The species replacements that Nilssen report parallel my experimental observations much more closely than do the community shifts observed by Sprules (1975) in Ontario. However, some of the observed community shifts in Norwegian acid lakes may also have been due to invertebrate predation, particularly by Heterocope saliens (Nilssen 1980, but see Hobaek and Raddum 1980).

In general, there appears to be interregional consistency in zooplankton acid tolerance at the species level, and it seems reasonable to cautiously apply my results to other regions. At the level of family however, the pattern is less clear. Daphnids appear to be relatively acid-sensitive, and bosminids relatively acid-tolerant, but diaptomids show a wide range in sensitivity. Within the limited number of species examined in this study, acid tolerances appeared unrelated to either relative size or taxonomic subclass (i.e. Cladocera or Copepoda).

Would invertebrate predation be a significant factor if Eunice Lake were acidified to pH 5.0? A discussion of this question requires some historical background. In 1973, the dominant predators in Eunice Lake were Chaoborus larvae, with peak densities of Chaoborus trivittatus and C. americanus (third and fourth instars) of 2000 m^{-2} and 100 m^{-2} respectively (Northcote et al. 1978). Introduction of cutthroat trout (Salmo clarki) in 1974 and 1975 virtually eliminated C. americanus and

drastically reduced C. trivittatus (Northcote et al. 1978).

Although I was unable to find published information on the pH sensitivity of cutthroat trout, salmonids are generally relatively acid sensitive (Haines 1982; NRCC 1981; EIFAC 1969). Hence, acidification of Eunice Lake to pH 5.0 would likely greatly reduce the cutthroat trout population, as well as eliminating D. rosea and D. tyrrelli by direct toxicity.

Ericksson et al. (1980) have speculated on the importance of acid-induced fish kills in increasing Chaoborus predation pressure on crustacean zooplankton. C. americanus is tolerant of pH levels < 4.5 (Yan and LaFrance 1981) and could therefore theoretically increase if cutthroat trout were eliminated from Eunice Lake. I found no information on the acid tolerance of C. trivittatus. However, even assuming that both chaoborids returned to their 1973 densities, significant crustacean community shifts would be unlikely. Neill (1980) found that at densities of 2400 m^{-2}, fourth instar C. trivittatus only temporarily reduced abundances of D. brachyurum and B. longirostris, but had little longterm effect on any species. Although Neill and Peacock (1980) and Yan and Lafrance (1980) demonstrated decimation of crustaceans by Chaoborus, these effects required very high nutrient concentrations (at least 10 X normal levels). Peacock (1981) showed that cyclopoids, unlike Chaoborus, are not able to decimate their prey (even at very high nutrient levels).

In conclusion, I believe that acidification of Eunice Lake to pH 5.0 would not cause significant crustacean community shifts via increases in invertebrate predators. Rather, the likely course of events would be the gradual elimination of Daphnia rosea and Diaptomus tyrrelli by toxicity effects, and concurrent replacements by Bosmina longirostris, Diaphanosoma brachyurum, Holopedium gibberum, Diaptomus kenai, Keratella taurocephala, Chydorus sphaericus, and/or Ceriodaphnia pulchella. The community shift caused by the elimination of D. rosea would probably be less in Eunice Lake than that which occurred in treatment AF in 1979. First, cutthroat trout apparently reduced the dominance of D. rosea in both 1979 and 1980. Second, Eunice Lake is less productive than the AF cylinders were, and would not support so high a zooplankton biomass. These two factors must be weighed against the consideration that natural acidification would occur much more slowly, allowing other species opportunities to colonize the community.

Short-term experiments could reveal a great deal about the potential role of invertebrate predators in acid lakes. Experimental treatments could vary both the rate of acidification and the density of stocked Chaoborus, in a manner analogous to Neill (1980) and Peacock (1981).

2.3 Implications for Higher Trophic Levels and Lake Management

Do the effects of acidification on plankton systems have potential ramifications for higher trophic levels? As discussed above, potential biotic linkages in acidic lakes must be judged relative to the abiotic stresses that organisms experience independently. For example, the impacts of sudden decreases in zooplankton biomass on the most acid-sensitive planktivorous fish species are likely negligible relative to direct physiological stress on the fish from ambient chemical conditions. Changes in plankton system behaviour could however be significant for relatively acid-tolerant predators.

In Eunice Lake limnocorrals, *Daphnia rosea* suffered very high mortality at pH 5.3-5.4. As *Daphnia* is a preferred prey for many planktivorous fish (including the cutthroat trout of Eunice Lake) it is tempting to speculate that the loss of *Daphnia* could cause food shortages for any planktivorous fish species which are still present in lakes of pH 5.3-5.4. Though food shortages are certainly possible, there are at least three reasons which make them unlikely. Firstly, most daphnids appear more acid-tolerant than *Daphnia rosea* (Section I 4.4.1 (i)). Secondly, other crustacean species large enough to be seen by visually feeding planktivorous fish can at least partially replace lost *Daphnia* biomass in lakes of intermediate pH. In Eunice Lake, *Holopedium gibberum* and *Diaptomus kenai* are two such species. Thirdly, reductions in the abundance of acid sensitive fish species (expected below pH 5.5) would likely lower both inter and intraspecific competition for zooplankton.

There are to date no published experimental studies of fish-zooplankton interactions in acid lakes. However, data on the growth of yellow perch in acid lakes provides some insights on the potential for acidification-induced shortages of fish food. Yellow perch less than 140 mm in size often feed heavily on crustacean zooplankton (Tharatt 1959). Work by Ryan and Harvey (1980) indicates that yellow perch less than three years of age (less than 140 mm) were relatively well fed in acid lakes: in 39 La Cloche Mountain Lakes, mean lengths of young perch (age 1 to 3) were greatest in the most acid lakes, lower in transition lakes and lowest in circumneutral lakes. The reverse was true for the older, primarily piscivorous age classes of perch, which were apparently unable to find sufficient numbers of small fish (Ryan and Harvey 1980). These and other preliminary results (NRCC 1981) imply that acid-induced reductions in the abundance of zooplankton are unlikely to have major, long-term impacts on the fish populations of acid lakes.

It is difficult to generalize the interactions between zooplankton and invertebrate predators as lakes acidify. This difficulty is partially due to the wide range of observed acid tolerances of invertebrate predators. For example, Mysis relicta declined sharply in Lake 223 at pH 5.6-5.9 (Nero 1981), whereas Chaoborus americanus reached very high densities in Mountaintop Lake in spite of a mean lake pH of 4.2 (Yan and Lafrance 1981). Acidification-induced shifts in prey size distributions could benefit tolerant invertebrate predators in

the short-term, but may also produce unstable predator-prey associations, as observed in Mountaintop Lake.

In both Mountaintop Lake and treatment AF in 1979, zooplankton declines were followed by huge increases in algal biomass. Such blooms are considered a nuisance, and can potentially increase hypolimnetic oxygen deficits harmful to coldwater fish and other organisms. Most acidifying lakes are likely too nutrient-poor for their algae to be able to increase so dramatically following the removal of herbivorous grazing. However, in lakes which are potentially susceptible to both acidification and anthropogenic nutrient enrichment (e.g. lakes with extensive cottage development) relatively small nutrient loads may trigger large algal blooms if acidification removes the herbivorous community dominant.

Relative to phytoplankton, zooplankton are slow to recolonize formerly acid lakes which have been neutralized (Dillon et al. 1979). Fertilization of such partially rehabilitated lakes has been previously attempted in order to increase zooplankton and zoobenthic biomass prior to restocking fish (Yan and Lafrance 1981). If the zooplankton community of such lakes is still impoverished, large algal blooms, hypolimnetic deoxygenation and coldwater fish kills could potentially occur.

The zooplankton species' acid tolerances in the 1979 and 1980 experiments can be of use to scientists responsible for managing lakes in regions that are geologically sensitive to acidification, provided that some of the same species are

present and historical records of their abundances are available. The two most acid-sensitive species in Eunice Lake (Daphnia rosea and Diaptomus tyrrelli) are common throughout western North America (Edmundson 1959). D. tyrrelli is more common at high elevations than low. Within areas sensitive to acid precipitation, higher elevation lakes are generally less well buffered and exposed to higher rates of acid loading (Cronan and Schofield 1979, Lewis 1982). I speculate that some of these lakes may be losing (or have already lost) their populations of D. tyrrelli.

In conclusion, I believe that acidification experiments using enclosed plankton communities can reasonably simulate the changes occurring in acidifying lakes, and provide explanations of the mechanisms by which such changes occur. Such knowledge is of relevance to ecologists interested in the factors which underly community organization and function, and to lake managers faced with the difficult tasks of assessing the risk or alleviating the damage from acid precipitation.

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APPENDIX A: COMPUTER PROGRAM USED TO CALCULATE ALGAL CELL VOLUMES

```
C ================================================================
C =                                                              =
C =     PROGRAM TO COMPUTE ALGAL CELL VOLUMES AND TOTAL ALGAL    =
C =          BIOMASS BY BAG, DATE, GENERA AND SIZE CLASS.        =
C =                                                              =
C ================================================================

C  BY DAVID MARMOREK .  THIS PROGRAM EXAMINES THE FILES PHYTO1 AND
C PHYTO2 FOR CONSISTENCY AND CALCULATES PHYTOPLANKTON VOLUMES
C BY SIZE CLASS AND TAXON FOR A GIVEN BAG AND DATE.
C THE PROGRAM IS FIRST RUN WITH TWO DUMMY SUBROUTINES (CRUNCH AND
C OUTPUT, STORED IN PCHECK.DUMMY) TO CLEANSE THE DATA FILES OF
C CODING SINS.  THEN THE PROGRAM IS RUN WITH THE REAL CRUNCH AND
C OUTPUT SUBROUTINES, STORED IN PCHECK.CRUNCH OR PCHEK.RESIZE.
C PCHEK.CRUNCH KEEPS CELLS IN THE CATEGORIES BY WHICH THEY WERE CODED.
C PCHEK.RESIZE GETS RID OF THE "COLONY" CATEGORY AND ALLOCATES COLONIES
C TO ONE OF THE FOLLOWING SIZE CATEGORIES: <2,2-5,5-9,9-13,13-18,18-30
C OR >30 MICRONS. CELLS IN THE >18 MICRON CATEGORY ARE SPLIT INTO
C 18-30 AND >30 MICRONS.
C UNIT 1=PHYTO1; #CELLS, #SHAPES, AND #FIELDS
C UNIT 2=PHYTO2; GENERA, SHAPES AND DIMENSIONS
C UNIT 3=PCHEK.DATA; VARIOUS CONSTANTS TO BE READ INTO THIS PROGRAM.
C.....................................................................
C
C                      VARIABLES USED IN PROGRAM
C
C CONFAC - # OF MICRONS/MICROMETER UNIT
C NTAXA  - # OF TAXONOMIC CATEGORIES IDENTIFIED (DIMENSION OF GVOL
C          MUST BE GREATER THAN OR EQUAL TO NTAXA)
C          OUTPUT SUBROUTINE FORMAT STATEMENT MUST BE CHANGED IF
C          NTAXA IS CHANGED.
C NUNK   - IS TAXON ID NO. USED FOR "UNKNOWN" (E.G. 999)
C TINYV  - IS VOLUME TO BE ASSUMED FOR ALL CELLS < 2 MICRONS DIAM.
C FPC    - # MICROSCOPE FIELDS/COUNTING CHAMBER CYLINDER (E.G. AT
C          400X WITH 22.25MM. CYLINDER FPC=6181.4)
C ICHECK - A FLAG. TO CHECK PHYTO1 AND PHYTO2 FOR
C          CONSISTENCY SET ICHECK=1 IN PCHEK.DATA. TO SKIP
C          CHECKING, SET ICHECK=0.
C DATE   - 6 DIGITS (YYMMDD)
C BAG    - # OF BAG OR SAMPLING LOCATION
C IYEAR  - YEAR (2 DIGITS)
C VOLSET - VOLUME OF WATER SETTLED INTO COUNTING CHAMBER (ML.)
C FIELDS - # OF MICROSCOPE FIELDS COUNTED.
C NCELL(8) - # OF CELLS COUNTED WITHIN EACH OF 8 SIZE CLASSES:
C            1. <1 MICROMETER UNIT       5. 7-10
C            2. 1-3                      6. >10
C            3. 3-5                      7. COLONIES (>3 CELLS)
C            4. 5-7                      8. FILAMENTS
C CAT(8)    - 3 CHARACTER CODES SPECIFYING ABOVE SIZE CLASSES
C NSHAPE(8) - # OF DIFFERENT CELL SHAPES IN EACH OF 8 SIZE CLASSES
C SHAPE(10)- ID NUMBERS OF SHAPES (E.G. 1=SPHERE, 2=ELLIPSOID ETC.)
C             WITHIN EACH SIZE CLASS (MAX. OF 5 TAXA/SHAPES)
C             THE FUNCTION VOLUME (IN PCHEK.CRUNCH) MUST BE ALTERED
C             IF SHAPES OTHER THAN THOSE LISTED HAVE BEEN RECORDED.
C TAXON(10)  - TAXA FOUND WITHIN ONE SIZE CLASS (MAX 10)
C MCELL(10)  - # CELLS OF GIVEN SHAPE AND TAXON WITHIN A SIZE CLASS
C DIM1(10)   - FIRST DIMENSION OF THE CELL (IN MICROMETER UNITS)
C DIM2(10)   - SECOND DIMENSION OF THE CELL
C NS        - CURRENT COUNTER OF SIZE CLASS
C GVOL(50)  - VOLUME OF DIFFERENT TAXA (INITIALLY AS CUBIC MICRONS;
```

```
C       THEN CONVERTED TO MG/L)
C GPCNT(50) - GVOL AS A PERCENTAGE OF TVOL
C SVOL(8)   - VOLUME WITHIN EACH SIZE CLASS (UNITS LIKE GVOL)
C SPCNT(8)  - SVOL AS A PERCENTAGE OF TVOL
C TVOL      - TOTAL PHYTOPLANKTON VOLUME FOR A PARTICULAR DATE
C              AND BAG) THAT WAS ACTUALLY COUNTED FROM FIELDS SEEN.
C              (IN CUBIC MICRONS)
C ETVOL     -  TVOL IN MG/L, ACCOUNTING FOR VOLSET AND FIELDS
C CVOL      - VOLUME OF PHYTOPLANKTON OF ONE TAXON AND SIZE CLASS
C AVGCV(8)  - AVERAGE CELL VOLUME WITHIN A SIZE CATEGORY
C.....................................................................
$CONTINUE WITH PCHEK.C RETURN
      LOGICAL ERROR,FATAL
      INTEGER ICAT(8),LIST(1),OLDATE/0/
      REAL*8 CVMEAN(8),CVSD(8)
      DATA ICAT/' <1','1-3','3-5','5-7','710','>10','COL','FIL'/
      DATA LIST(1)/'*'/
      DO 3 I=1,8
      SVOL(I)=0.D0
      SVOL2(I)=0.D0
      CAT(I)=ICAT(I)
      SUMCV(I)=0.D0
      SUMCV2(I)=0.D0
      NCV(I)=0
3     CONTINUE
      LINES=60
      FATAL=.FALSE.
      NERRS=0
C
C...IF ICHECK>0 SKIP ERROR CHECKING
      READ(3,LIST)CONFAC,NTAXA,NUNK,TINYV,FPC,ICHECK,PLUGOL
5     READ(1,10,END=999)IYEAR,DATE,BAG,VOLSET,(NCELL(I),I=1,8),
     1                  (NSHAPE(I),I=1,8),FIELDS
10    FORMAT(I2,I4,I1,F3.0,8I4,8I2,2X,F1.0)
      ERROR=.FALSE.
C
C....SET TOTAL AND TAXON VOLUMES TO ZERO BEFORE LOOPING
C....THROUGH SIZE CLASSES.  SIZE CLASS VOLUME IS SET TO
C....ZERO AT EACH ITERATION.
      TVOL=0.D0
      DO 15 I=1,NTAXA
15    GVOL(I)=0.
      DO 18 I=1,8
      SVOL(I)=0.D0
      SVOL2(I)=0.0D0
18    CONTINUE
C
C...LOOP THROUGH SIZE CATEGORIES CHECKING FOR ERRORS
      DO 100 NS=1,8
      IF(NS.EQ.1)GO TO 70
      IF(NSHAPE(NS).EQ.0)GO TO 100
      LAST=NSHAPE(NS)
      READ(2,20)DATE2,BAG2,SIZE,(TAXON(I),SHAPE(I),DIM1(I),DIM2(I),
     1          MCELL(I),I=1,5)
20    FORMAT(2X,I4,I1,A3,5(I3,I2,2F2.0,I3))
      IF(LAST.GT.5)READ(2,25)(TAXON(I),SHAPE(I),DIM1(I),DIM2(I),
     1                        MCELL(I),I=6,LAST)
25    FORMAT(10X,5(I3,I2,2F2.0,I3))
      IF(ICHECK.GT.0)GO TO 70
      IF(DATE2.EQ.DATE)GO TO 30
```

```
      WRITE(4,801)DATE,DATE2
      FATAL=.TRUE.
      GO TO 900
30    IF(NS.NE.2.OR.BAG.EQ.BAG2)GO TO 40
      WRITE(4,802)BAG,BAG2
      FATAL=.TRUE.
      GO TO 900
40    IF(SIZE.EQ.CAT(NS))GO TO 50
      WRITE(4,803)SIZE,CAT(NS)
      FATAL=.TRUE.
      GO TO 900
C
C...CHECK THAT #CELLS MATCH IN PHYTO1 AND PHYTO2
C...CHECK THAT DIMENSIONS HAVE NOT BEEN OMITTED. SHAPES 1,8 AND 9
C...ONLY REQUIRE ONE DIMENSION.
50    TCELLS=0
      DO 60 I=1,LAST
      IF(DIM1(I).NE.0.D0)GO TO 53
      ERROR=.TRUE.
      WRITE(4,807)CAT(NS),I
      NERRS=NERRS+1
53    IF(SHAPE(I).EQ.1.OR.SHAPE(I).EQ.8.OR.SHAPE(I).EQ.9)GO TO 56
      IF(DIM2(I).NE.0.D0)GO TO 56
      ERROR=.TRUE.
      WRITE(4,807)CAT(NS),I
      NERRS=NERRS+1
56    TCELLS=TCELLS+MCELL(I)
60    CONTINUE
      IF(TCELLS.EQ.NCELL(NS))GO TO 70
C
C...ALLOW TOTAL # CELLS IN COLONIES TO BE > THAN #COLONIES
      IF(NS.EQ.7.AND.TCELLS.GT.NCELL(NS))GO TO 70
      WRITE(4,805)TCELLS,NCELL(NS),CAT(NS)
      ERROR=.TRUE.
      NERRS=NERRS+1
C...CALCULATE VOLUME OF PHYTOPLANKTON IN EACH SIZE CLASS
70    CALL CRUNCH
100   CONTINUE
C...CALCULATE TOTAL VOLUME IDENTIFIED IN CUBIC MICRONS
C...AND MEAN CELL VOLUME WITHIN SIZE CATEGORY.
C...FOR COLONIES, THIS IS MEAN COLONY VOLUME.
      TVOL=0.
      DO 120 NS=1,8
      TVOL=TVOL+SVOL(NS)
      AVGCV(NS)=0.
      IF(NCELL(NS).EQ.0)GO TO 120
C     AVGCV(NS)=SVOL(NS)/DFLOAT(NCELL(NS))
      IF(BAG.NE.9)GO TO 120
C NEXT STATEMENTS BYPASSED UNDER RESIZE CALCULATION
C     SUMCV(NS)=SUMCV(NS)+SVOL(NS)
C     SUMCV2(NS)=SUMCV2(NS)+SVOL2(NS)
C     NCV(NS)=NCV(NS)+NCELL(NS)
120   CONTINUE
C
C...FORMATS FOR ERROR STATEMENTS.....................................
801   FORMAT(' DATE',I5,' DOES NOT MATCH',I5)
802   FORMAT(' BAG',I2,' DOES NOT MATCH',I2)
803   FORMAT(' SIZE',A5,' DOES NOT MATCH',A5)
805   FORMAT(' # OF CELLS MISMATCH:',I5,' AND',I5,' IN SIZE',A5)
806   FORMAT(' ERROR OCCURRED ON',I5,' FOR BAG',I2/)
```

```
807   FORMAT(' MISSING DIMENSIONS IN CATEGORY',A5,'; TAXON',I2)
      IF(.NOT.ERROR.AND..NOT.FATAL)GO TO 950
900   WRITE(4,806)DATE,BAG
      IF(FATAL)STOP
      IF(NERRS.GT.15)STOP
950   CALL OUTPUT(OLDATE)
      OLDATE=DATE
      GO TO 5
C
C CALCULATE AND OUTPUT MEAN CELL VOLUMES IN EACH SIZE CATEGORY
999   WRITE(4,1000)
1000  FORMAT(' SIZE   MEAN VOLUME',T23,'STD. DEV',T36,'# CELLS OR COL.')
      DO 1020 NS=2,8
      XN=DFLOAT(NCV(NS))
      IF(XN.LE.0)GO TO 1020
      CVMEAN(NS)=SUMCV(NS)/XN
      CVSD(NS)=DSQRT((SUMCV2(NS)-SUMCV(NS)**2/NCV(NS))/(XN-1.))
      WRITE(4,1010)ICAT(NS),CVMEAN(NS),CVSD(NS),NCV(NS)
1010  FORMAT(A5,2F15.2,I7)
1020  CONTINUE
      STOP
      END
      SUBROUTINE JULIA(IDATE,IMONTH,IDAY,JDAY)
      INTEGER IMATCH(12,2)/716,726,801,809,816,823,830,906,913,
     1 920,927,1005,196,206,212,220,227,234,241,248,255,262,269,277/
C
C SEPARATE MONTH AND DAY AND CALCULATE JULIAN DATE
      IMONTH=IDATE/100
      IDAY=IDATE-IMONTH*100
      DO 5 I=1,12
      IF(IMATCH(I,1).NE.IDATE)GO TO 5
      JDAY=IMATCH(I,2)
      GO TO 10
5     CONTINUE
      WRITE(5,8) IDATE
8     FORMAT(I6,' NOT LISTED IN JULIA''S DRAWERS')
      STOP
10    RETURN
      END
C
C ***************************************************************************
      FUNCTION VOLUME(ISHAPE,D1,D2)
C...THIS FUNCTION CALCULATES THE VOLUME OF A GEOMETRICAL SHAPE
C...BASED ON 2 MEASUREMENTS OF ITS DIMENSIONS. ISHAPE SPECIFIES THE
C...TYPE OF GEOMETRICAL FIGURE:
C
C  ISHAPE                GEOMETRICAL FIGURE
C      1    SPHERE
C      2    ELLIPSOID (EQUAL MINOR AXES)
C      3    ELLIPSOID (2ND MINOR AXIS=.5*1ST)
C      4    CYLINDER
C      5    CRESCENT
C      6    CONE
C      7    PEAR OR TEARDROP
C      8    TETRAHEDRON
C      9    CUBE
C      10   FILAMENT
C      11   FUSIFORM OR SPINDLE SHAPE
C      12   RECTANGULAR PLATE (THICKNESS=.25*LENGTH)
C      13   ELLIPTIC PLATE (THICKNESS=0.033*MINOR AXIS)
```

```
C      14  RECTANGULAR PLATE (THICKNESS=.5*WIDTH)
C      15  S-SHAPED TAPERING FILAMENT
C      16  CAPSULE
C      17  PIE-SLICE (EQUILATERAL TRIANGULAR PLATE)
C      18  HEMI-ELLIPSOID
C      19  ELLIPTIC PLATE (THICKNESS=WIDTH)
C      20  HEMI-ELLIPTIC PLATE (THICKNESS=.5*WIDTH)
C      21  RECTANGULAR PLATE (THICKNESS=0.16667*LENGTH)
C      22  RECTANGULAR PLATE (THICKNESS=WIDTH)
C
C FORMULAE HAVE BEEN CODED FOR MAXIMUM CLARITY
C RATHER THAN MAXIMUM COMPUTING EFFICIENCY
C STATEMENT #(ISHAPE*10) HAS FORMULA FOR ISHAPE.
      REAL*8 PI,D1,D2,THETA,ONE333,TWO,THREE,FOUR,Z3,SIX
      DATA FOUR/4.0D0/,THREE/3.0D0/,Z33/0.0333333333333/
      DATA PI/3.14159265/,ONE333/1.3333333333/,TWO/2.0D0/
      DATA SIX/6.0D0/
      GO TO(10,20,30,40,50,60,70,80,90,100,110,120,130,140,150,
     1      160,170,180,190,200,210,220),ISHAPE
C
C...SPHERE. D1=DIAMETER
10    VOLUME=ONE333*PI*(D1/TWO)**3
      RETURN
C
C ELLIPSOID WITH EQUAL MINOR AXES. D1=MAJOR; D2=MINOR
20    VOLUME=ONE333*PI*D1/TWO*(D2/TWO)**2
      RETURN
C
C...ELLIPSOID WITH THICKNESS=HALF MINOR AXIS (D2)
30    VOLUME=ONE333*PI*D1/TWO*D2/TWO*D2/FOUR
      RETURN
C
C...RIGHT CIRCULAR CYLINDER. D1=HEIGHT; D2=DIAMETER
40    VOLUME=PI*D1*(D2/TWO)**2
      RETURN
C
C CRESCENT. D1=TIP TO TIP LENGTH (DIAMETER)
C           D2=WIDTH AT CENTRE (ARC LENGTH)
C CALCULATE ANGLE SUBTENDED IN RADIANS.  ASSUME THICKNESS IS ONE
C HALF OF ARC LENGTH.
50    THETA=TWO*D2/D1
      VOLUME=D1**2/TWO*THETA*D2/TWO
      RETURN
C
C...CONE. D1=HEIGHT; D2=DIAMETER
60    VOLUME=PI/THREE*D2**2/FOUR*D1
      RETURN
C
C...PEAR SHAPE. D1=LONG AXIS; D2=SHORT. TREATED AS ELLIPSOID WITH
C...ALL AXES REDUCED 10%.
70    VOLUME=ONE333*PI*0.729D0*D1/TWO*(D2/TWO)**2
      RETURN
C
C...TETRAHEDRON. D1=LENGTH OF EACH EDGE
80    VOLUME=0.11785*D1**3
      RETURN
C
C...CUBE. D1=LENGTH OF EACH EDGE
90    VOLUME=D1**3
      RETURN
```

```
C
C FILAMENT. D1=LENGTH D2=WIDTH=THICKNESS
100   VOLUME=D1*D2**2
      RETURN
C
C FUSIFORM. D1=LENGTH; D2=WIDTH AT CENTRE. TREAT AS 2 CONES.
110   VOLUME=PI/THREE*D1*D2**2
      RETURN
C
C RECTANGULAR PLATE. D1=LENGTH; D2=WIDTH. THICKNESS=D1/4
120   VOLUME=D1**2/FOUR*D2
      RETURN
C
C ELLIPTIC PLATE. D1=MAJOR AXIS; D2=MINOR AXIS; THICKNESS=.033*D2
130   VOLUME=PI*D1/TWO*D2/TWO*D2*0.033
      RETURN
C
C RECTANGULAR PLATE. THICKNESS=D2/2
140   VOLUME=D1*D2**2/TWO
      RETURN
C
C...S-SHAPED. D1=HEIGHT; D2=THICKNESS AT MIDPOINT
C...ASSUME TRUE LENGTH=1.57*HEIGHT
C...ASSUME AVG. THICKNESS=0.5*D2
150   VOLUME=1.57*D1*0.25*D2**2
      RETURN
C
C...CAPSULE. D1=LENGTH; D2=WIDTH
C...ASSUME CYLINDER OF HEIGHT=(D1-D2) CAPPED BY HEMISPHERES OF
C...RADIUS D2/2.
160   VOLUME=PI*(D1-D2)*(D2/TWO)**2 + ONE333*PI*(D2/TWO)**3
      RETURN
C
C...EQUILATERAL PIE SLICE. D1=LENGTH OF SIDE; D2=THICKNESS
170   VOLUME=0.43301*D1**2*D2
      RETURN
C
C...HEMIELLIPSOID. D1=MAJOR AXIS; D2=MINOR AXIS/2
180   VOLUME=(ONE333*PI*D1/TWO *D2**2)/TWO
      RETURN
C
C...ELLIPTIC PLATE. THICKNESS=D2
190   VOLUME=PI*D1/TWO*D2/TWO*D2
      RETURN
C
C...HEMI-ELLIPTIC PLATE. THICKNESS=D2/2
200   VOLUME=(PI*D1/TWO*D2)/TWO *D2/TWO
      RETURN
C
C...RECTANGULAR PLATE. THICKNESS=D2/6
210   VOLUME=D1*D2*D2/SIX
      RETURN
C
C...RECTANGULAR PLATE. THICKNESS=D2
220   VOLUME=D1*D2*D2
      RETURN
      END
```

APPENDIX B: LENGTH-WEIGHT REGRESSIONS USED FOR CALCULATION OF ZOOPLANKTON BIOMASS (1979 AND 1980)

Table B1. Length-weight regressions used for calculation of zooplankton biomass,and mean zooplankter weights. Rotifer biomass only considered in 1980.

Species	Length-Weight [1] Regression Used		1979 Expt. Mean Wt.(μg) [2]		1980 Expt. Mean Wt.(μg) [2]		Source of Regression or Mean Weight
	a	b	Juveniles	Adults	Juveniles	Adults	
Diaptomus kenai	3.15	2.98	9.50	22.55	12.27	25.23	Neill & Peacock [3]
Diaptomus tyrrelli	1.89	3.07	1.06	2.16	0.83	2.48	Neill & Peacock [3]
Daphnia rosea	4.36	2.55	3.13	10.51	2.43	9.07	Neill & Peacock [3]
Holopedium gibberum	24.3	1.44	10.14	19.42	7.66	16.77	Walters [3]
Bosmina longirostris	0.322	1.45	0.47	0.82	0.49	0.80	Neill & Peacock [3]
Chydorus sphaericus	89.43	3.93	0.49	2.34	0.50	2.05	Dumont et al. (1975)
Diaphanosoma brachyurum	3.76	2.11	0.64	1.12	-	-	Dumont et al. (1975)
Ceriodaphnia pulchella	10.24	2.26	2.16	5.21	-	-	Dumont et al. (1975)
Polyphemus pediculus	6.93	2.15	2.66		2.06		Dumont et al. (1975)
Diacyclops thomasi	6.25	2.17	2.86		4.00		Peacock (1981)
Keratella taurocephala					0.037		Bottrell et al. (1976)
Kelicottia sp.					0.017		Bottrell et al. (1976)
Polyarthra sp.					0.043		Bottrell et al. (1976)
Conochilus sp.					0.015		Bottrell et al. (1976)

[1] log(Weight) = log a + b log(Length). No regression used for rotifers, just mean weights.

[2] averaged over all treatments and dates.

[3] unpublished data

APPENDIX C: THREE-WAY ANALYSES OF VARIANCE OF ALKALINITY AND H^+ CONCENTRATIONS (1979)

The analyses are presented separately for the 1-3 m and 5-7 m strata, since this breakdown divides epilimnetic and metalimnetic processes. Note that the use of H+ ion concentrations (rather than pH) in statistical analyses ensures correct calculation of mean pH, but tends to generate highly significant differences in $[H^+]$ even when pH differences are clearly negligible.

Figure C1. Results of 3-way analyses of variance comparing $[H^+]$ and alkalinity in the controls with Eunice Lake. Vertices of triangles represent three effects tested: E = experimental treatment; T = time; D = depth. Probability levels for independent effects listed at each vertex, and illustrated by circles around effect abbreviation: dashed circle for $p < 0.05$; single circle for $p < 0.01$; and double circle for $p < 0.001$. Probability levels for two-way interactions listed along sides of triangle (e.g. probability of (experimental treatment) x (time) interaction in Figure 3.6 (a) is 0.14), with extra lines and arrows for significant interactions. Probability level for three-way interaction listed in centre of triangle. Overall mean pH and alkalinity levels (for the whole experiment) are listed for each depth stratum. Abbreviations used for treatments: C = controls; LK = Eunice Lake.

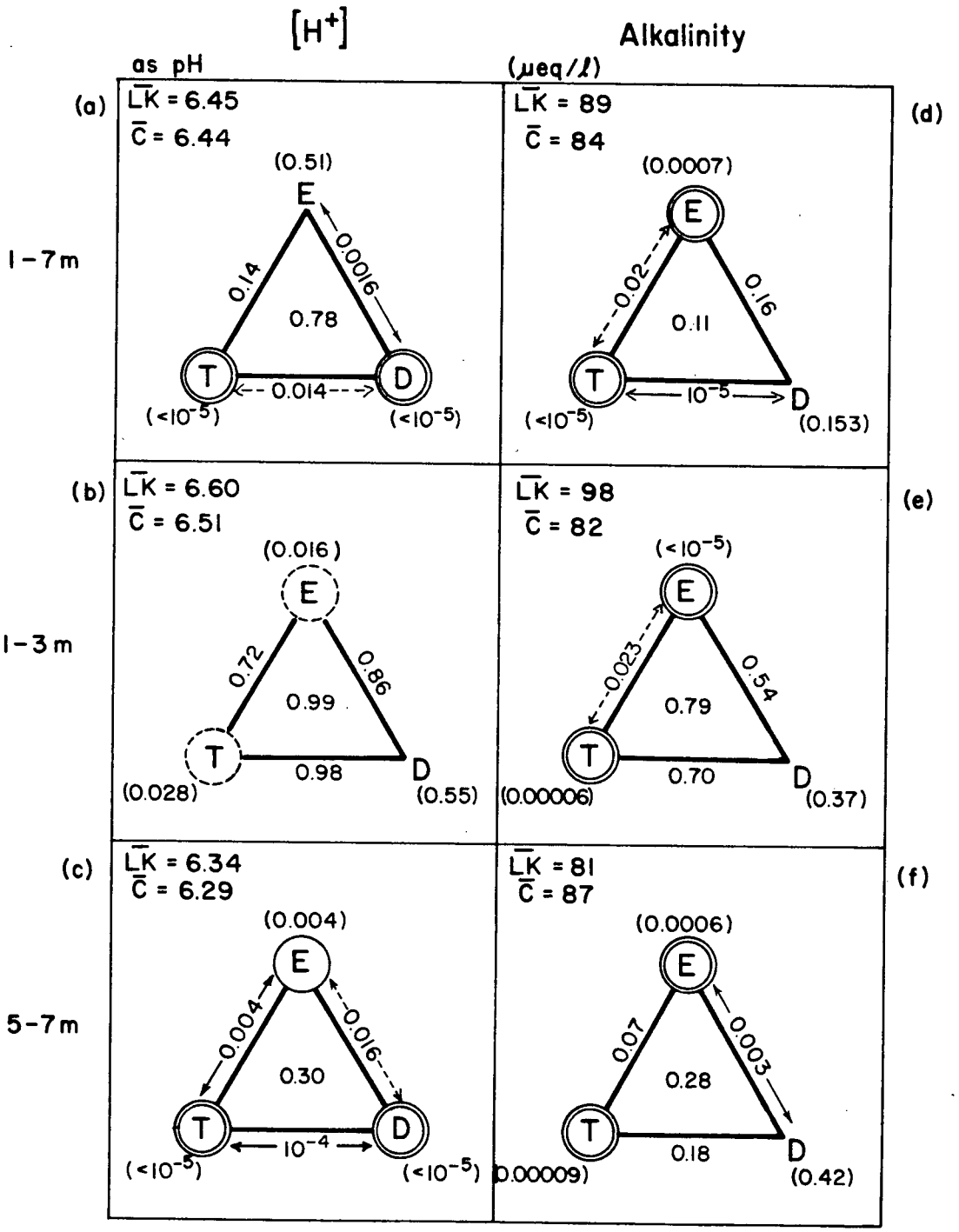

[H+]
as pH
Alkalinity
(μeq/l)
(a)
LK = 6.45
C = 6.44
(0.51)
E
0.0016
0.14
0.78
T
D
0.014
(<10-5)
(<10-5)
(d)
LK = 89
C = 84
(0.0007)
E
0.02
0.16
0.11
T
D
10-5
(<10-5)
(0.153)
1-7m
(b)
LK = 6.60
C = 6.51
(0.016)
E
0.72
0.86
0.99
T
D
0.98
(0.028)
(0.55)
(e)
LK = 98
C = 82
(<10-5)
E
0.023
0.54
0.79
T
D
0.70
(0.00006)
(0.37)
1-3m
(c)
LK = 6.34
C = 6.29
(0.004)
E
0.004
0.016
0.30
T
D
10-4
(<10-5)
(<10-5)
(f)
LK = 81
C = 87
(0.0006)
E
0.07
0.003
0.28
T
D
0.18
(0.00009)
(0.42)
5-7m

Figure C2. Results of 3-way analyses of variance comparing $[H^+]$ and alkalinity in the controls with treatment F . Symbols used to represent statistical effects and their significance are described in Figure C1. Mean pH and alkalinity levels listed for each depth stratum. Abbreviations used for treatments: C = controls; F = fertilization only.

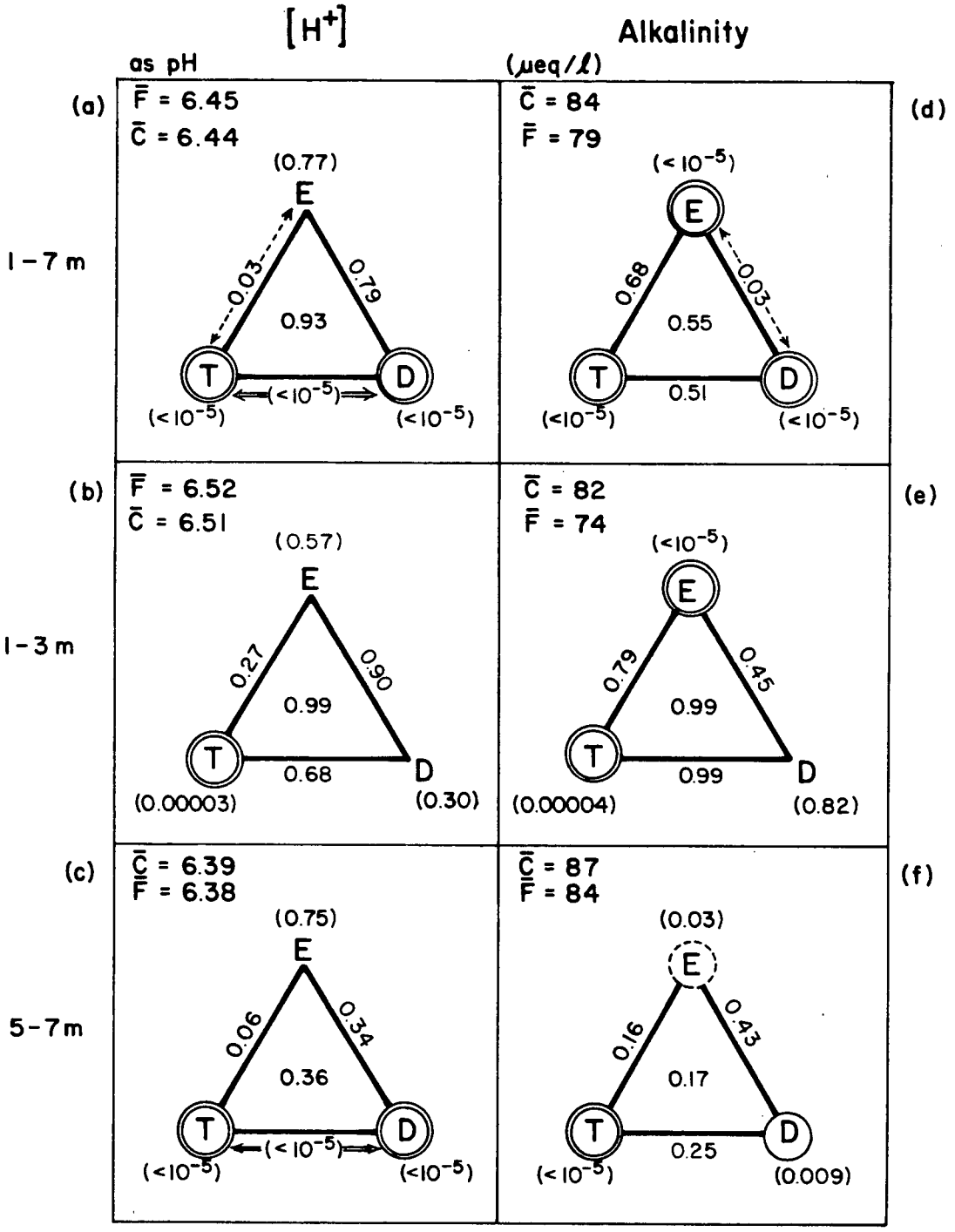
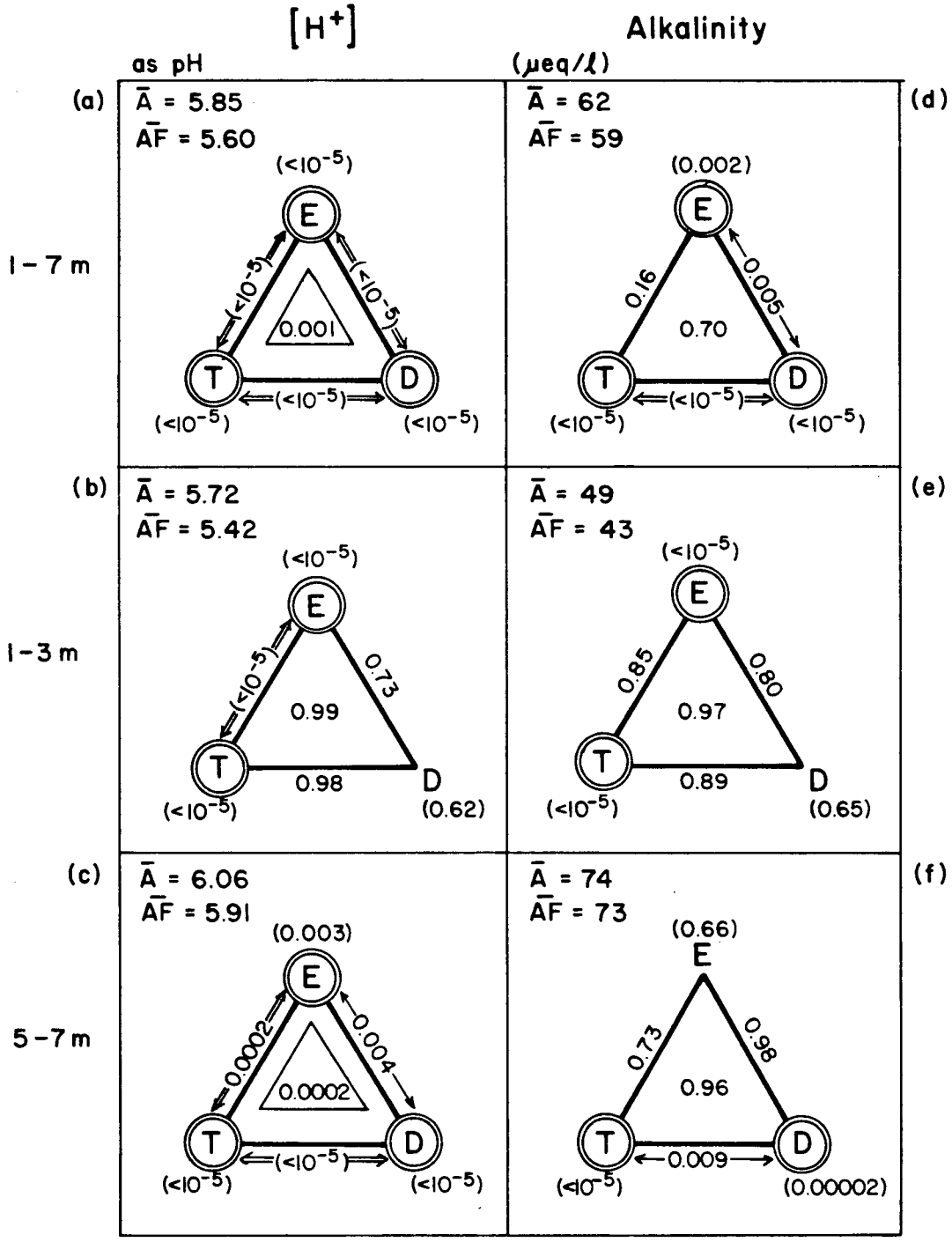

[H+]
as pH
Alkalinity
(μeq/ℓ)
(a)
F̄ = 6.45
C̄ = 6.44
(0.77)
E
0.03
0.79
0.93
T
D
(<10⁻⁵)
(<10⁻⁵)
(<10⁻⁵)
(d)
C̄ = 84
F̄ = 79
(<10⁻⁵)
E
0.68
0.03
0.55
T
D
0.51
(<10⁻⁵)
(<10⁻⁵)
1-7 m
(b)
F̄ = 6.52
C̄ = 6.51
(0.57)
E
0.27
0.90
0.99
T
D
0.68
(0.00003)
(0.30)
(e)
C̄ = 82
F̄ = 74
(<10⁻⁵)
E
0.79
0.45
0.99
T
D
0.99
(0.00004)
(0.82)
1-3 m
(c)
C̄ = 6.39
F̄ = 6.38
(0.75)
E
0.06
0.34
0.36
T
D
(<10⁻⁵)
(<10⁻⁵)
(<10⁻⁵)
(f)
C̄ = 87
F̄ = 84
(0.03)
E
0.16
0.43
0.17
T
D
0.25
(<10⁻⁵)
(0.009)
5-7m

Figure C3. Results of 3-way analyses of variance comparing $[H^+]$ and alkalinity in treatments A and AF . Symbols used to represent statistical effects and their significance are described in Figure C1. Mean pH and alkalinity levels listed for each depth stratum. Abbreviations used for treatments: A = acidification only; AF = acidification and fertilization.


[H+]
as pH
Alkalinity
(μeq/ℓ)
(a)
Ā = 5.85
ĀF = 5.60
(<10-5)
E
(<10-5)
(<10-5)
0.001
T
D
(<10-5)
(<10-5)
(<10-5)
(d)
Ā = 62
ĀF = 59
(0.002)
E
0.16
0.005
0.70
T
D
(<10-5)
(<10-5)
(<10-5)
1-7 m
(b)
Ā = 5.72
ĀF = 5.42
(<10-5)
E
(<10-5)
0.73
0.99
T
0.98
D
(<10-5)
(0.62)
(e)
Ā = 49
ĀF = 43
(<10-5)
E
0.85
0.80
0.97
T
0.89
D
(<10-5)
(0.65)
1-3 m
(c)
Ā = 6.06
ĀF = 5.91
(0.003)
E
0.0002
0.004
0.0002
T
D
(<10-5)
(<10-5)
(<10-5)
(f)
Ā = 74
ĀF = 73
(0.66)
E
0.73
0.98
0.96
T
0.009
D
(<10-5)
(0.00002)
5-7 m

APPENDIX D: REGRESSION ANALYSES OF SECCHI DEPTH-CHLOROPHYLL A RELATIONSHIPS (1979)

In order to analyze the likelihood of acidification causing changes in light extinction from non-biological matter, it is necessary to separate the different components of light extinction. Light intensity in the water column can be represented most simply by:

$$Iz = Io\, e^{-kz} \qquad \text{(Hutchinson 1957; pg. 383)} \qquad (D1)$$

where Iz = light intensity at depth z,
Io = light intensity at the lake surface,
z = depth, and
k = total light extinction or attenuation coefficient.

The total extinction coefficient was originally partitioned by Aberg and Rodhe (1942) into three additive coefficients (for water itself, suspended particles, and dissolved compounds). I chose to follow Megard et al., (1980) and consider only two functional attenuations, that due to total chlorophyll concentrations (kc), and the extinction due to factors other than chlorophyll (kw). Equation (D1) then becomes:

$$Iz = Io\, e^{-[kw + (kc)\, C]\, Z} \qquad (D2)$$

or,

$$\frac{1}{Z} = \frac{kw}{\ln(Io/Iz)} + \frac{(kc)C}{\ln(Io/Iz)} \qquad (D3)$$

Where C = chlorophyll a concentration uncorrected for phaeophytin a.

Equation (D3) was used to calculate regression lines to predict the inverse of the Secchi depth based on total chlorophyll a levels (i.e. chlorophyll a plus phaeophytin a). Note that ln(Io/Iz) can be assumed to be roughly constant over all measurements (Idso and Gilbert 1974). Regressions performed separately for each treatment, and for all the data pooled, are shown in Table D1. Treatment effects on the attenuation of light per unit chlorophyll should be reflected in slope changes, since the slope is proportional to kc. Changes in attenuation due to other factors should shift the intercept, which is proportional to kw. One can use the intercept to slope ratio (kw/kc) to calculate "f", the fraction of subsurface light attenuated by chlorophyll (Bannister 1974; Megard et al. 1980):

$$f = \frac{C}{(kw/kc) + C} \qquad (D4)$$

Values of f based on the mean total chlorophyll (f* in Table D1) suggest that in all treatments and in Eunice Lake the attenuation by non-chlorophyll factors far exceeded that by chlorophyll. The higher f* value in AF cylinders would be expected given their elevated chlorophyll levels, but the marked differences in f* and (kw/kc) between the lake and all other treatments require an alternative explanation. I propose that shading by the UV-protective coating and wooden float of each limnocorral formed a significant fraction of kw (extinction due

Table D1. Linear regressions of inverse secchi depth (1/Z) and total chlorophyll a (C), for each treatment. f* is the fraction of subsurface light attenuated by chlorophyll. R^2 is the coefficient of determination, k_c the extinction due to chlorophyll, k_w the extinction due to factors other than chlorophyll, I_o the surface light intensity, and I_Z the light intensity at the secchi-depth.

Treatment	n	$\bar{Z}$ (m)	$\bar{C}$ (mg/m)	$a = \frac{k_w}{\ln(I_o/I_Z)}$	$b = \frac{k_c}{\ln(I_o/I_Z)}$	R^2	$\frac{kw}{kc}$	$f^* = \frac{\bar{C}}{(k_w/k_c) + \bar{C}}$
C	14	6.7	0.67	0.131 ± 0.030*	0.030 ± 0.043**	0.16	4.4	0.13±0.009
F	14	6.6	1.22	0.123 ± 0.022	0.024 ± 0.017	0.44	5.1	0.19±0.014
A	14	7.1	0.72	0.128 ± 0.011	0.017 ± 0.015	0.35	7.5	0.09±0.007
AF	13	5.1	3.93	0.137 ± 0.062	0.018 ± 0.015	0.40	7.6	0.34±0.027
LK	7	7.3	0.86	0.093 ± 0.047	0.057 ± 0.050	0.63	1.6	0.35±0.026
All pooled	62	6.5	1.51	0.130 ± 0.008	0.019 ± 0.004	0.66	6.7	0.18±0.031

** 95% confidence intervals assuming e_i; ~ N (0, σ^2).

to factors other than algae). This suggestion is discussed in Section I, 4.1.

Since both the Secchi depth and chlorophyll values in these regressions are autocorrelated, the residuals do not have the independence necessary for confidence interval calculation (Draper and Smith 1969; pg. 58). Assuming that the residuals' departures from statistical independence were negligible, I calculated hypothetical 95% confidence intervals for the slopes and intercepts of the regression lines. The hypothetical confidence intervals for each treatment's y intercept overlap, which suggests that background attenuation of light is not significantly different among treatments. In particular, there is no evidence of a significant change in non-chlorophyll attenuation among the controls and the A cylinders. Also, the overlap in slope confidence intervals implies that chlorophyll-caused attenuation does not differ significantly between treatments.

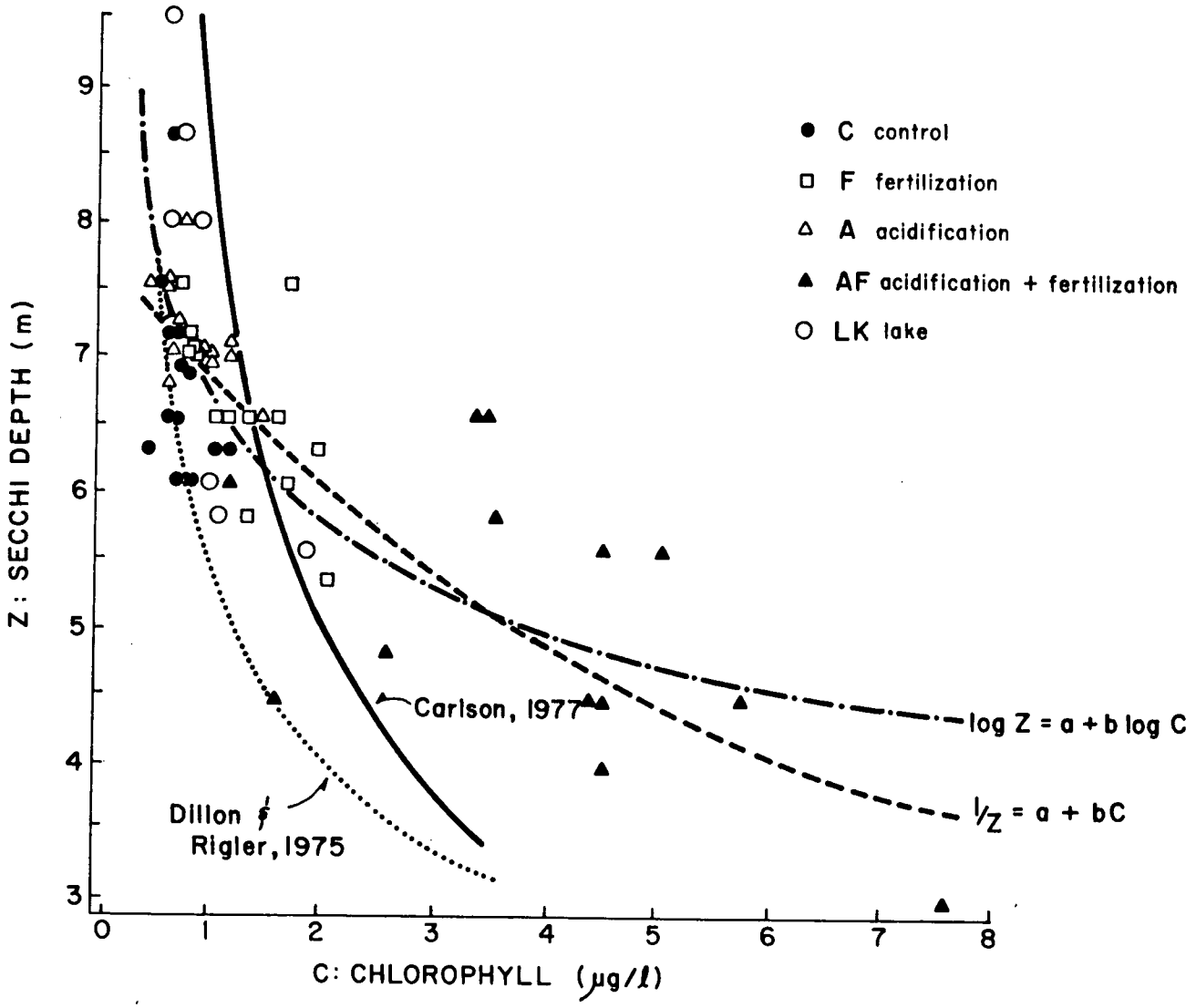
When all the data were pooled and fitted to equation (D3), (see Figure D1 and the last row of Table D1), the calculated regression line predicted considerably greater transparencies at chlorophyll levels above 2 $\mu g \cdot L^{-1}$ than do two other regression equations in the literature (Carlson 1977; Dillon and Rigler 1975). The reasons for this difference are not clear.

I also fitted my data to the exponential model employed by Dillon and Rigler (1975):

$$\log Z = a + b \log [chl]. \qquad (D5)$$

Use of this equation did not improve the overall data fit (R^2)

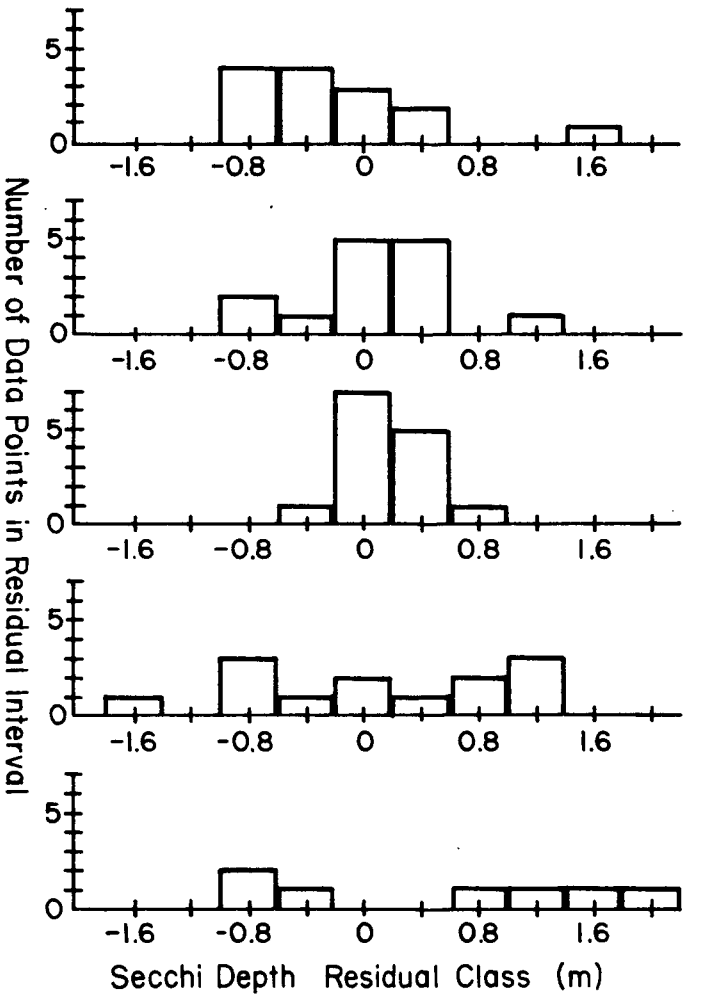
Figure D1. Non-linear regressions of Secchi disc depth vs. total chlorophyll a, with data pooled from all treatments. Dashed lines show two regression equations fitted to limnocorral data. Solid line and dotted line show two previously published regression equations for circumneutral lakes.


Z: SECCHI DEPTH (m)
C: CHLOROPHYLL (µg/l)
C control
F fertilization
A acidification
AF acidification + fertilization
LK lake
Carlson, 1977
Dillon & Rigler, 1975
log Z = a + b log C
1/Z = a + bC

nor appreciably change predicted Secchi depths above 2 $\mu g \cdot L^{-1}$ chlorophyll, but was more suited to the data at higher Secchi depths.

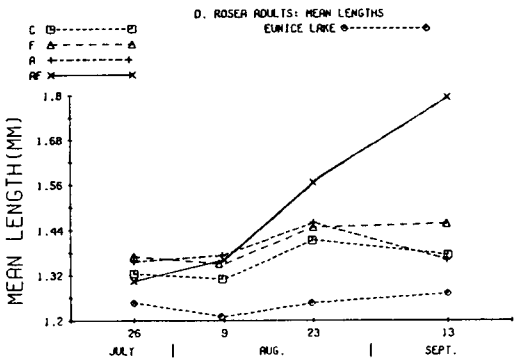
If transparency was increased because of my experimental acidification, one would expect residuals calculated from the pooled data regression line (observed Secchi depths minus predicted) to be greater for treatment A than for the controls. This expectation is confirmed by Figure D2, since the mean residual from the treatment A points was significantly higher ($p=0.018$; one-tailed t-test) than the mean calculated for the controls. However, these differences in residuals are not large enough to be compelling evidence when one considers the poor precision of Secchi discs in measuring transparency. Also, the lake data points may have pulled the regression away from the controls. Photometer measurements of light extinction coefficients are necessary in order to rigorously test the effects of acidification on transparency.

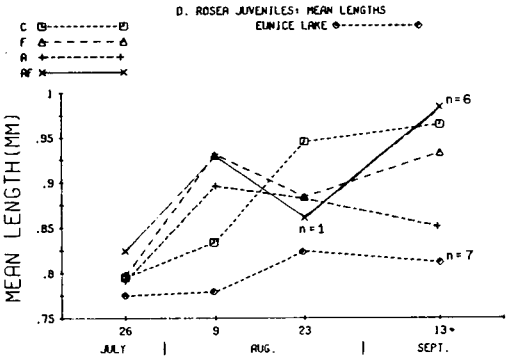
Figure D2. Distribution of residual Secchi depths from Secchi depth - chlorophyll regression on pooled data on pooled data. Residuals computed as observed Secchi depth minus Secchi depth predicted by pooled data regression equation (Table D1). Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

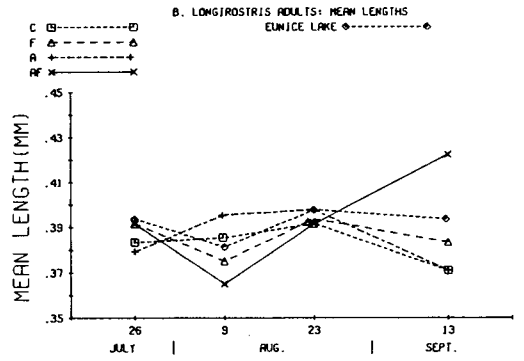
Treatment	Mean Residual (m) ± SE (n)	Distribution of Secchi Depth Residuals
C	-0.27 ±0.18 (14)	
F	0.09 ±0.13 (14)	
A	0.20 ±0.08 (14)	
AF	0.09 ±0.27 (13)	
LK	0.51 ±0.49 (7)	

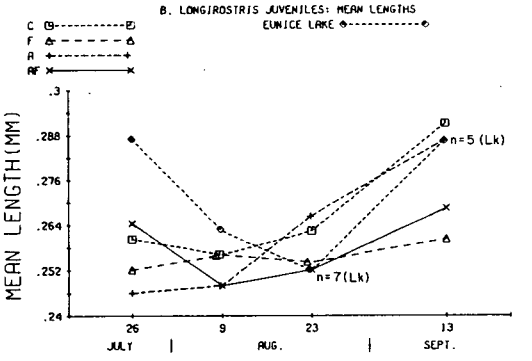
APPENDIX E: ZOOPLANKTON LENGTHS (1979)

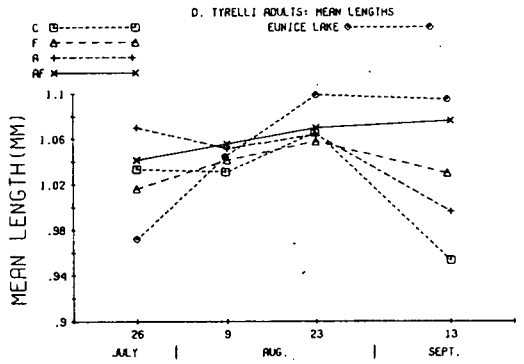
Figure E1. Mean lengths of zooplankton by treatment and time (1979) . Note that scales differ between graphs. Number of animals measured noted if less than 10. Abbreviations used for treatments: C=controls; F=fertilization only; A=acidification only; AF=acidification and fertilization.

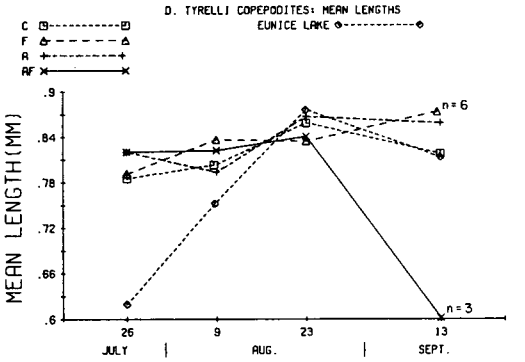

D. ROSEA ADULTS: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
1.8
1.68
1.56
1.44
1.32
1.2
26
9
23
13
JULY
AUG.
SEPT.

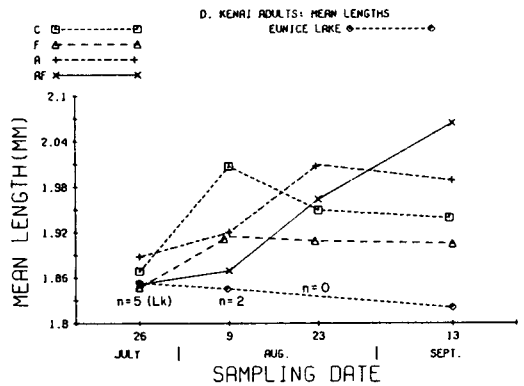

D. ROSEA JUVENILES: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
1
.95
.9
.85
.8
.75
n=6
n=1
n=7
26
9
23
13
JULY
AUG.
SEPT.

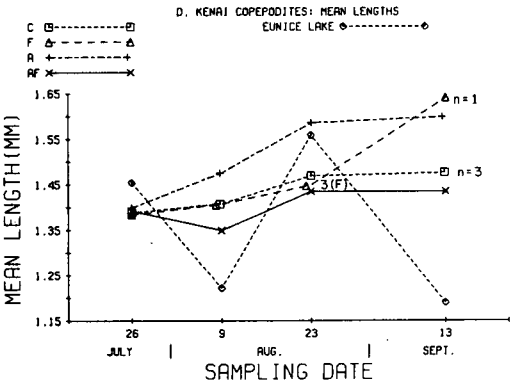

B. LONGIROSTRIS ADULTS: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
.45
.43
.41
.39
.37
.35
26
9
23
13
JULY
AUG.
SEPT.


B. LONGIROSTRIS JUVENILES: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
.3
.288
.276
.264
.252
.24
n=5 (Lk)
n=7(Lk)
26
9
23
13
JULY
AUG.
SEPT.


D. TYRELLI ADULTS: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
1.1
1.06
1.02
.98
.94
.9
26
9
23
13
JULY
AUG.
SEPT.


D. TYRELLI COPEPODITES: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
.9
.84
.78
.72
.66
.6
n=6
n=3
26
9
23
13
JULY
AUG.
SEPT.


D. KENAI ADULTS: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
2.1
2.04
1.98
1.92
1.86
1.8
n=5 (Lk)
n=2
n=0
26
9
23
13
JULY
AUG.
SEPT.
SAMPLING DATE


D. KENAI COPEPODITES: MEAN LENGTHS
EUNICE LAKE
C
F
A
AF
MEAN LENGTH(MM)
1.65
1.55
1.45
1.35
1.25
1.15
n=1
n=3
3(F)
26
9
23
13
JULY
AUG.
SEPT.
SAMPLING DATE

APPENDIX F: PHYTOPLANKTON VOLUMES BY TAXA FOR EACH CYLINDER AND SAMPLING DATE (1979)

1979-CYLINDER 1F : ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->													
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.0126	0.2209	0.0	0.0013	0.0466	0.0470	0.0030	0.0	0.0052	0.0082	0.0	0.0420	0.0322	0.0623
CHLAMYDOMONAS	0.0	0.0	0.0	0.0	0.0206	0.0	0.0030	0.0	0.0011	0.0	0.0	0.0	0.0021	0.0059
GLOEOCYSTIS	0.0	0.1762	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0420	0.0182	0.0512
ANKISTRODESMUS	0.0021	0.0398	0.0	0.0013	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0036	0.0114
OOCYSTIS	0.0105	0.0	0.0	0.0	0.0	0.0088	0.0	0.0	0.0	0.0	0.0	0.0	0.0016	0.0038
SCENEDESMUS	0.0	0.0049	0.0	0.0	0.0049	0.0123	0.0	0.0	0.0041	0.0082	0.0	0.0	0.0029	0.0041
UNIDENT. DESMID	0.0	0.0	0.0	0.0	0.0	0.0259	0.0	0.0	0.0	0.0	0.0	0.0	0.0022	0.0075
UNIDENT. CHLOROPHYTE	0.0	0.0	0.0	0.0	0.0211	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0018	0.0061
CRYPTOPHYTA	0.0026	0.0089	0.0	0.0	0.0	0.0471	0.0	0.0147	0.0235	0.1285	0.0164	0.0065	0.0207	0.0366
CYPTOMONAS	0.0	0.0	0.0	0.0	0.0	0.0471	0.0	0.0091	0.0235	0.1285	0.0154	0.0	0.0186	0.0375
UNIDENT. CRYPTOPHYTE	0.0026	0.0089	0.0	0.0	0.0	0.0	0.0	0.0056	0.0	0.0	0.0010	0.0065	0.0020	0.0032
CHRYSOPHYTA	0.0303	0.5011	0.0	0.0371	0.0	0.0309	0.0548	0.0	0.4146	0.1186	0.0	0.2484	0.1196	0.1740
CHRYSOCAPSA	0.0	0.4270	0.0	0.0	0.0	0.0	0.0548	0.0	0.0	0.1186	0.0	0.1186	0.0599	0.1245
DINOBRYON	0.0303	0.0741	0.0	0.0371	0.0	0.0309	0.0	0.0	0.3707	0.0	0.0	0.1236	0.0556	0.1063
UNIDENT. CHRYSOPHYTE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0439	0.0	0.0	0.0062	0.0042	0.0126
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0020	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0002	0.0006
UNIDENT. DIATOM	0.0	0.0	0.0	0.0020	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0002	0.0006
CYANOPHYTA	0.0002	0.0003	0.0044	0.0006	0.0940	0.0001	0.0003	0.0004	0.0	0.0	0.0	0.0003	0.0084	0.0270
MERISMOPEDIA	0.0	0.0	0.0038	0.0002	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0003	0.0011
RAPHIDIOPSIS	0.0002	0.0003	0.0006	0.0004	0.0004	0.0001	0.0003	0.0004	0.0	0.0	0.0	0.0003	0.0002	0.0002
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0936	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0078	0.0270
CYANOBACTERIA	0.0236	0.0065	0.0	0.0230	0.0117	0.0108	0.0347	0.0213	0.0205	0.0157	0.0112	0.0199	0.0166	0.0092
CYANOBACTERIA	0.0236	0.0065	0.0	0.0230	0.0117	0.0108	0.0347	0.0213	0.0205	0.0157	0.0112	0.0199	0.0166	0.0092
UNKNOWN	0.0328	0.0536	0.0183	0.0397	0.2092	0.0415	0.0291	0.0966	0.0625	0.0879	0.1571	0.5407	0.1141	0.1459
CYST	0.0	0.0	0.0	0.0	0.0989	0.0	0.0	0.0	0.0086	0.0	0.0	0.0	0.0090	0.0284
COCCOID	0.0111	0.0173	0.0069	0.0144	0.0054	0.0264	0.0054	0.0416	0.0305	0.0320	0.0387	0.0277	0.0214	0.0130
FUSIFORM	0.0	0.0	0.0	0.0	0.0	0.0060	0.0	0.0165	0.0	0.0	0.0008	0.0	0.0019	0.0049
NOT IDENTIFIED	0.0217	0.0363	0.0114	0.0253	0.1049	0.0091	0.0237	0.0385	0.0234	0.0559	0.1176	0.5130	0.0817	0.1402
TOTAL VOLUME	0.1020	0.7913	0.0226	0.1036	0.3614	0.1774	0.1218	0.1329	0.5264	0.3589	0.1848	0.8576	0.3117	0.2783

1979-CYLINDER 2C : ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->													
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.0	0.0	0.0026	0.0114	0.0547	0.0088	0.0839	0.2517	0.7786	0.5068	1.5176	0.6073	0.3186	0.4662
CHLAMYDOMONAS	0.0	0.0	0.0	0.0	0.0044	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0004	0.0013
GLOEOCYSTIS	0.0	0.0	0.0	0.0	0.0503	0.0	0.0839	0.2517	0.7132	0.4719	1.5102	0.5978	0.3066	0.4587
ANKISTRODESMUS	0.0	0.0	0.0026	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0037	0.0029	0.0008	0.0014
OOCYSTIS	0.0	0.0	0.0	0.0114	0.0	0.0088	0.0	0.0	0.0654	0.0349	0.0037	0.0066	0.0109	0.0198
CRYPTOPHYTA	0.0010	0.0	0.0	0.0104	0.0033	0.0091	0.0130	0.0175	0.0	0.0037	0.0173	0.0	0.0063	0.0069
CYPTOMONAS	0.0	0.0	0.0	0.0	0.0	0.0086	0.0086	0.0148	0.0	0.0	0.0173	0.0	0.0041	0.0065
UNIDENT. CRYPTOPHYTE	0.0010	0.0	0.0	0.0104	0.0033	0.0005	0.0044	0.0027	0.0	0.0037	0.0	0.0	0.0022	0.0031
CHRYSOPHYTA	0.0	0.3632	0.3185	0.6313	0.2088	0.1236	0.2176	0.0618	0.0618	0.0695	0.4864	0.0417	0.2153	0.1983
CHRYSOCAPSA	0.0	0.1779	0.0	0.0712	0.0	0.0	0.0	0.0	0.0	0.0	0.4744	0.0	0.0603	0.1408
DINOBRYON	0.0	0.1853	0.3185	0.5601	0.2088	0.1236	0.2176	0.0618	0.0618	0.0695	0.0	0.0232	0.1525	0.1623
MALLOMONAS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0120	0.0185	0.0025	0.0061
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0	0.0	0.0	0.0088	0.0	0.0	0.0	0.0	0.0027	0.0010	0.0026
UNIDENT. DIATOM	0.0	0.0	0.0	0.0	0.0	0.0	0.0088	0.0	0.0	0.0	0.0	0.0027	0.0010	0.0026
CYANOPHYTA	0.0	0.0	0.0	0.0	0.0	0.0	0.0021	0.0022	0.0021	0.0016	0.0042	0.0036	0.0013	0.0015
MERISMOPEDIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0021	0.0	0.0021	0.0016	0.0042	0.0016	0.0010	0.0014
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0022	0.0	0.0	0.0	0.0020	0.0003	0.0008
CYANOBACTERIA	0.0307	0.0044	0.0169	0.0129	0.0236	0.0098	0.0230	0.0078	0.0157	0.0096	0.0146	0.0103	0.0149	0.0076
CYANOBACTERIA	0.0307	0.0044	0.0169	0.0129	0.0236	0.0098	0.0230	0.0078	0.0157	0.0096	0.0146	0.0103	0.0149	0.0076
UNKNOWN	0.0668	0.0693	0.0371	0.0348	0.1305	0.0556	0.0868	0.0845	0.0566	0.0386	0.0810	0.0539	0.0663	0.0271
CYST	0.0	0.0066	0.0	0.0	0.0	0.0148	0.0323	0.0	0.0088	0.0111	0.0234	0.0	0.0081	0.0107
COCCOID	0.0492	0.0420	0.0224	0.0063	0.0277	0.0259	0.0237	0.0257	0.0282	0.0216	0.0297	0.0189	0.0268	0.0108
NOT IDENTIFIED	0.0176	0.0207	0.0147	0.0285	0.1028	0.0149	0.0308	0.0588	0.0196	0.0059	0.0279	0.0350	0.0314	0.0262
TOTAL VOLUME	0.0986	0.4370	0.3751	0.7007	0.4210	0.2069	0.4352	0.4255	0.9147	0.6298	2.1212	0.7194	0.6238	0.5226

1979-CYLINDER 3AF: ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->													
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.0	0.0	0.0214	0.0	0.0239	0.1015	0.0661	0.0164	0.0026	0.0011	0.0354	0.0944	0.0302	0.0371
CHLAMYDOMONAS	0.0	0.0	0.0021	0.0	0.0	0.0093	0.0	0.0	0.0026	0.0011	0.0	0.0	0.0013	0.0027
ANKISTRODESMUS	0.0	0.0	0.0	0.0	0.0034	0.0039	0.0	0.0	0.0	0.0	0.0	0.0	0.0006	0.0014
OOCYSTIS	0.0	0.0	0.0132	0.0	0.0	0.0099	0.0	0.0	0.0	0.0	0.0	0.0	0.0019	0.0046
SCENEDESMUS	0.0	0.0	0.0061	0.0	0.0205	0.0430	0.0307	0.0164	0.0	0.0	0.0	0.0	0.0097	0.0147
MOUGEOTIA	0.0	0.0	0.0	0.0	0.0	0.0354	0.0354	0.0	0.0	0.0	0.0354	0.0	0.0088	0.0160
UNIDENT. CHLOROPHYTE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0944	0.0079	0.0273
CRYPTOPHYTA	0.0	0.0	0.0262	0.0009	0.0649	0.0445	0.0	0.0437	0.0757	0.1124	0.1389	0.2576	0.0637	0.0763
CYPTOMONAS	0.0	0.0	0.0241	0.0	0.0519	0.0445	0.0	0.0437	0.0757	0.1124	0.1389	0.2576	0.0624	0.0765
UNIDENT. CRYPTOPHYTE	0.0	0.0	0.0021	0.0009	0.0130	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0013	0.0037
CHRYSOPHYTA	0.0	0.1779	0.5949	0.0258	0.1167	0.3558	0.3558	0.0	0.0	0.0309	0.0	0.0	0.1381	0.1966
CHRYSOCAPSA	0.0	0.1779	0.1779	0.0	0.0439	0.3558	0.3558	0.0	0.0	0.0	0.0	0.0	0.0926	0.1400
DINOBRYON	0.0	0.0	0.4170	0.0258	0.0662	0.0	0.0	0.0	0.0	0.0309	0.0	0.0	0.0450	0.1189
UNIDENT. CHRYSOPHYTE	0.0	0.0	0.0	0.0	0.0066	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0005	0.0019
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0927	0.1902	0.0236	0.0589
TABELLARIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0927	0.1853	0.0232	0.0576
UNIDENT. DIATOM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0049	0.0004	0.0014
CYANOPHYTA	0.0003	0.0	0.0006	0.0	0.1200	0.0803	0.1575	0.0073	0.0017	0.0016	0.0002	0.0004	0.0308	0.0559
MERISMOPEDIA	0.0	0.0	0.0	0.0	0.0021	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0002	0.0006
RAPHIDIOPSIS	0.0003	0.0	0.0006	0.0	0.0017	0.0016	0.0100	0.0034	0.0017	0.0003	0.0002	0.0004	0.0017	0.0028
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.1162	0.0787	0.1475	0.0039	0.0	0.0013	0.0	0.0	0.0290	0.0534
CYANOBACTERIA	0.0196	0.0147	0.0152	0.0172	0.0166	0.0279	0.0205	0.0323	0.0166	0.0147	0.0089	0.0118	0.0180	0.0065
CYANOBACTERIA	0.0196	0.0147	0.0152	0.0172	0.0166	0.0279	0.0205	0.0323	0.0166	0.0147	0.0089	0.0118	0.0180	0.0065
UNKNOWN	0.0307	0.1250	0.0965	0.0822	0.1713	0.1485	0.1864	0.2066	0.0385	0.1071	0.0482	0.0587	0.1083	0.0599
CYST	0.0	0.0	0.0129	0.0353	0.0	0.1059	0.0482	0.0706	0.0	0.0086	0.0064	0.0	0.0240	0.0346
COCCOID	0.0254	0.0885	0.0632	0.0170	0.0324	0.0373	0.0410	0.0240	0.0269	0.0251	0.0271	0.0369	0.0371	0.0200
FUSIFORM	0.0	0.0	0.0	0.0157	0.0037	0.0	0.0470	0.1038	0.0044	0.0	0.0	0.0	0.0145	0.0312
NOT IDENTIFIED	0.0053	0.0365	0.0204	0.0142	0.1352	0.0053	0.0502	0.0082	0.0072	0.0734	0.0147	0.0218	0.0327	0.0383
TOTAL VOLUME	0.0506	0.3177	0.7547	0.1262	0.5135	0.7585	0.7863	0.3064	0.1352	0.2677	0.3242	0.6130	0.4128	0.2639

1979-CYLINDER 4A : ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->													
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.1131	0.0	0.0	0.0188	0.0066	0.1259	0.1259	0.1413	0.2794	0.3461	0.8180	0.9224	0.2415	0.3138
CHLAMYDOMONAS	0.0	0.0	0.0	0.0065	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0005	0.0019
GLOEOCYSTIS	0.0839	0.0	0.0	0.0	0.0	0.1259	0.1259	0.1259	0.2769	0.3461	0.8180	0.8810	0.2320	0.3091
ANKISTRODESMUS	0.0034	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0060	0.0008	0.0019
OOCYSTIS	0.0176	0.0	0.0	0.0	0.0066	0.0	0.0	0.0154	0.0	0.0	0.0	0.0	0.0033	0.0065
SCENEDESMUS	0.0082	0.0	0.0	0.0123	0.0	0.0	0.0	0.0	0.0025	0.0	0.0	0.0	0.0019	0.0041
MOUGEOTIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0354	0.0029	0.0102
CRYPTOPHYTA	0.0	0.0005	0.0173	0.0370	0.0084	0.0241	0.0115	0.0044	0.0	0.0101	0.0077	0.0154	0.0114	0.0110
CYPTOMONAS	0.0	0.0	0.0173	0.0370	0.0084	0.0241	0.0104	0.0	0.0	0.0071	0.0	0.0154	0.0100	0.0118
UNIDENT. CRYPTOPHYTE	0.0	0.0005	0.0	0.0	0.0	0.0	0.0011	0.0044	0.0	0.0030	0.0077	0.0	0.0014	0.0024
CHRYSOPHYTA	0.1884	0.1853	0.8020	0.5251	0.3639	0.1390	0.3787	0.0653	0.0963	0.1122	0.7117	0.0	0.2973	0.2621
CHRYSOCAPSA	0.1884	0.0	0.1186	0.0	0.0	0.0	0.2847	0.0	0.0	0.0890	0.7117	0.0	0.1160	0.2097
DINOBRYON	0.0	0.1853	0.6834	0.5251	0.3491	0.1390	0.0940	0.0653	0.0741	0.0232	0.0	0.0	0.1782	0.2249
MALLOMONAS	0.0	0.0	0.0	0.0	0.0148	0.0	0.0	0.0	0.0222	0.0	0.0	0.0	0.0031	0.0074
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0011	0.0	0.0097	0.0	0.0009	0.0028
CYMBELLA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0011	0.0	0.0	0.0	0.0001	0.0003
UNIDENT. DIATOM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0097	0.0	0.0008	0.0028
CYANOPHYTA	0.0	0.0001	0.0	0.0	0.0	0.0	0.0050	0.0	0.0009	0.0	0.0	0.0	0.0005	0.0014
MERISMOPEDIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0050	0.0	0.0	0.0	0.0	0.0	0.0004	0.0014
RAPHIDIOPSIS	0.0	0.0001	0.0	0.0	0.0	0.0	0.0	0.0	0.0001	0.0	0.0	0.0	0.0000	0.0000
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0008	0.0	0.0	0.0	0.0001	0.0002
CYANOBACTERIA	0.0150	0.0095	0.0250	0.0100	0.0096	0.0200	0.0094	0.0160	0.0059	0.0059	0.0235	0.0201	0.0142	0.0067
CYANOBACTERIA	0.0150	0.0095	0.0250	0.0100	0.0096	0.0200	0.0094	0.0160	0.0059	0.0059	0.0235	0.0201	0.0142	0.0067
UNKNOWN	0.0890	0.0341	0.1150	0.0523	0.0771	0.0627	0.0639	0.0545	0.0501	0.0478	0.0586	0.0971	0.0668	0.0234
CYST	0.0	0.0	0.0445	0.0	0.0	0.0	0.0141	0.0	0.0089	0.0111	0.0	0.0	0.0065	0.0130
COCCOID	0.0308	0.0210	0.0286	0.0279	0.0228	0.0470	0.0271	0.0305	0.0133	0.0218	0.0488	0.0470	0.0305	0.0114
NOT IDENTIFIED	0.0582	0.0131	0.0419	0.0244	0.0543	0.0157	0.0227	0.0240	0.0279	0.0149	0.0098	0.0501	0.0297	0.0170
TOTAL VOLUME	0.4055	0.2296	0.9592	0.6431	0.4655	0.3716	0.5944	0.2815	0.4336	0.5220	1.6293	1.0550	0.6325	0.4006

1979-CYLINDER 5A : ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->													
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.0	0.0088	0.0	0.0338	0.0695	0.1391	0.1259	0.3146	0.2539	0.1956	1.1327	1.5941	0.3223	0.5064
CHLAMYDOMONAS	0.0	0.0	0.0	0.0220	0.0	0.0	0.0	0.0	0.0022	0.0	0.0	0.0	0.0020	0.0063
GLOEOCYSTIS	0.0	0.0	0.0	0.0	0.0629	0.1259	0.1259	0.3146	0.2517	0.1888	1.1327	1.5941	0.3164	0.5096
ANKISTRODESMUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0068	0.0	0.0	0.0006	0.0020
OOCYSTIS	0.0	0.0088	0.0	0.0077	0.0066	0.0132	0.0	0.0	0.0	0.0	0.0	0.0	0.0030	0.0047
SCENEDESMUS	0.0	0.0	0.0	0.0041	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0003	0.0012
CRYPTOPHYTA	0.0	0.0	0.0120	0.0	0.0087	0.0	0.0108	0.0870	0.0067	0.0	0.0084	0.0219	0.0130	0.0243
CYPTOMONAS	0.0	0.0	0.0120	0.0	0.0071	0.0	0.0096	0.0	0.0067	0.0	0.0084	0.0219	0.0055	0.0069
UNIDENT. CRYPTOPHYTE	0.0	0.0	0.0	0.0	0.0016	0.0	0.0012	0.0870	0.0	0.0	0.0	0.0	0.0075	0.0250
CHRYSOPHYTA	0.0027	0.2422	0.5080	0.5251	0.1777	0.3767	0.0897	0.0463	0.0556	0.3255	0.0232	0.0340	0.2006	0.1917
CHRYSOCAPSA	0.0	0.1186	0.0890	0.0	0.0	0.0	0.0712	0.0	0.0	0.0	0.0	0.0	0.0232	0.0433
DINOBRYON	0.0027	0.1236	0.4190	0.5251	0.1777	0.3707	0.0185	0.0463	0.0556	0.3255	0.0232	0.0309	0.1766	0.1845
UNIDENT. CHRYSOPHYTE	0.0	0.0	0.0	0.0	0.0	0.0060	0.0	0.0	0.0	0.0	0.0	0.0031	0.0008	0.0019
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0014	0.0	0.0	0.0001	0.0004
UNIDENT. DIATOM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0014	0.0	0.0	0.0001	0.0004
CYANOPHYTA	0.0002	0.0	0.0	0.0	0.0	0.0	0.0016	0.0	0.0013	0.0002	0.0048	0.0045	0.0010	0.0018
MERISMOPEDIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0013	0.0	0.0016	0.0	0.0002	0.0006
RAPHIDIOPSIS	0.0002	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0002	0.0	0.0001	0.0000	0.0001
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0	0.0	0.0016	0.0	0.0	0.0	0.0032	0.0044	0.0008	0.0015
CYANOBACTERIA	0.0103	0.0081	0.0037	0.0078	0.0044	0.0044	0.0023	0.0169	0.0035	0.0030	0.0074	0.0137	0.0071	0.0046
CYANOBACTERIA	0.0103	0.0081	0.0037	0.0078	0.0044	0.0044	0.0023	0.0169	0.0035	0.0030	0.0074	0.0137	0.0071	0.0046
UNKNOWN	0.0696	0.0963	0.0530	0.0885	0.0846	0.1136	0.0314	0.0937	0.0316	0.0814	0.0564	0.0611	0.0718	0.0258
CYST	0.0066	0.0148	0.0177	0.0445	0.0	0.0353	0.0026	0.0222	0.0141	0.0	0.0	0.0148	0.0144	0.0143
COCCOID	0.0461	0.0306	0.0243	0.0327	0.0207	0.0381	0.0161	0.0511	0.0118	0.0371	0.0182	0.0383	0.0304	0.0123
FUSIFORM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0004	0.0	0.0	0.0	0.0000	0.0001
NOT IDENTIFIED	0.0169	0.0509	0.0110	0.0113	0.0639	0.0402	0.0127	0.0204	0.0053	0.0443	0.0382	0.0080	0.0269	0.0196
TOTAL VOLUME	0.0828	0.3554	0.5766	0.6551	0.3449	0.6337	0.2617	0.5586	0.3527	0.6070	1.2328	1.7294	0.6159	0.4520

1979-CYLINDER 6C : ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->													
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.0	0.0107	0.0	0.0132	0.0074	0.1328	0.1858	0.1004	0.2413	0.3226	0.4854	0.4724	0.1643	0.1808
CHLAMYDOMONAS	0.0	0.0107	0.0	0.0	0.0074	0.0069	0.0142	0.0077	0.0	0.0	0.0	0.0062	0.0044	0.0051
GLOEOCYSTIS	0.0	0.0	0.0	0.0	0.0	0.1259	0.0629	0.0839	0.2265	0.2832	0.4615	0.4405	0.1404	0.1729
ANKISTRODESMUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0034	0.0044	0.0	0.0006	0.0015
OOCYSTIS	0.0	0.0	0.0	0.0132	0.0	0.0	0.1087	0.0088	0.0148	0.0360	0.0154	0.0257	0.0185	0.0307
SCENEDESMUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0041	0.0	0.0003	0.0012
EUGLENOPHYTA	0.0	0.0	0.0	0.0	0.0154	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0013	0.0044
UNIDENT. EUGLENOID	0.0	0.0	0.0	0.0	0.0154	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0013	0.0044
CRYPTOPHYTA	0.0	0.0105	0.0	0.0167	0.0163	0.0	0.0123	0.0	0.0	0.0	0.0	0.0	0.0046	0.0070
CYPTOMONAS	0.0	0.0086	0.0	0.0167	0.0103	0.0	0.0111	0.0	0.0	0.0	0.0	0.0	0.0039	0.0060
UNIDENT. CRYPTOPHYTE	0.0	0.0019	0.0	0.0	0.0060	0.0	0.0012	0.0	0.0	0.0	0.0	0.0	0.0008	0.0018
CHRYSOPHYTA	0.0	0.7784	0.5638	0.8340	0.2863	0.0960	0.1431	0.2780	0.1287	0.0477	0.1495	0.0	0.2755	0.2922
CHRYSOCAPSA	0.0	0.5931	0.0	0.0	0.0	0.0	0.0	0.0	0.0712	0.0	0.1186	0.0	0.0652	0.1705
DINOBRYON	0.0	0.1853	0.5638	0.8340	0.2471	0.0927	0.1390	0.2780	0.0556	0.0477	0.0309	0.0	0.2062	0.2541
MALLOMONAS	0.0	0.0	0.0	0.0	0.0367	0.0	0.0041	0.0	0.0	0.0	0.0	0.0	0.0034	0.0106
UNIDENT. CHRYSOPHYTE	0.0	0.0	0.0	0.0	0.0025	0.0033	0.0	0.0	0.0019	0.0	0.0	0.0	0.0006	0.0012
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0	0.0065	0.0241	0.0	0.0	0.0	0.0042	0.0	0.1937	0.0190	0.0554
TABELLARIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1853	0.0154	0.0535
UNIDENT. DIATOM	0.0	0.0	0.0	0.0	0.0065	0.0241	0.0	0.0	0.0	0.0042	0.0	0.0084	0.0036	0.0071
CYANOPHYTA	0.0	0.0	0.0	0.0002	0.0	0.0	0.0	0.0	0.0001	0.0	0.0013	0.0	0.0001	0.0004
RAPHIDIOPSIS	0.0	0.0	0.0	0.0002	0.0	0.0	0.0	0.0	0.0001	0.0	0.0	0.0	0.0000	0.0001
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0013	0.0	0.0001	0.0004
CYANOBACTERIA	0.0213	0.0098	0.0103	0.0149	0.0153	0.0099	0.0110	0.0127	0.0094	0.0081	0.0099	0.0192	0.0126	0.0042
CYANOBACTERIA	0.0213	0.0098	0.0103	0.0149	0.0153	0.0099	0.0110	0.0127	0.0094	0.0081	0.0099	0.0192	0.0126	0.0042
UNKNOWN	0.0775	0.0307	0.0476	0.0595	0.1160	0.0594	0.0406	0.0766	0.0363	0.0396	0.0635	0.0519	0.0583	0.0236
CYST	0.0129	0.0	0.0	0.0	0.0088	0.0	0.0	0.0	0.0141	0.0064	0.0086	0.0	0.0042	0.0056
COCCOID	0.0513	0.0236	0.0368	0.0439	0.0206	0.0461	0.0189	0.0332	0.0149	0.0213	0.0254	0.0412	0.0314	0.0122
NOT IDENTIFIED	0.0133	0.0071	0.0108	0.0156	0.0866	0.0133	0.0217	0.0434	0.0073	0.0119	0.0295	0.0107	0.0226	0.0227
TOTAL VOLUME	0.0988	0.8400	0.6216	0.9384	0.4632	0.3222	0.3929	0.4677	0.4158	0.4222	0.7096	0.7372	0.5358	0.2387

1979-CYLINDER 7AF: ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->												
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN STD.DEV.
CHLOROPHYTA	0.0	0.0179	0.0230	0.0088	0.0061	0.0875	0.0273	0.0222	0.0123	0.0256	0.0	0.0107	0.0201 0.0232
CHLAMYDOMONAS	0.0	0.0	0.0037	0.0	0.0	0.0253	0.0	0.0	0.0	0.0	0.0	0.0	0.0024 0.0073
GLOEOCYSTIS	0.0	0.0	0.0	0.0	0.0	0.0315	0.0	0.0	0.0	0.0	0.0	0.0	0.0026 0.0091
ANKISTRODESMUS	0.0	0.0047	0.0	0.0	0.0	0.0026	0.0103	0.0	0.0	0.0045	0.0	0.0107	0.0027 0.0040
OOCYSTIS	0.0	0.0132	0.0132	0.0088	0.0	0.0066	0.0088	0.0099	0.0	0.0	0.0	0.0	0.0050 0.0056
SCENEDESMUS	0.0	0.0	0.0061	0.0	0.0061	0.0215	0.0082	0.0123	0.0123	0.0	0.0	0.0	0.0055 0.0070
UNIDENT. CHLOROPHYTE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0211	0.0	0.0	0.0018 0.0061
EUGLENOPHYTA	0.0	0.0	0.0	0.0	0.0	0.0142	0.0	0.0	0.0	0.0	0.0	0.0	0.0012 0.0041
UNIDENT. EUGLENOID	0.0	0.0	0.0	0.0	0.0	0.0142	0.0	0.0	0.0	0.0	0.0	0.0	0.0012 0.0041
CRYPTOPHYTA	0.0185	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0428	0.3781	0.2332	0.2595	0.0777 0.1330
CYPTOMONAS	0.0185	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0428	0.3781	0.2332	0.2595	0.0777 0.1330
CHRYSOPHYTA	0.0	0.1853	2.1962	0.5720	2.9394	0.9359	1.0675	1.4233	0.1779	0.0093	0.0	0.0	0.7922 0.9708
CHRYSOCAPSA	0.0	0.0	1.7792	0.3558	2.8467	0.8896	1.0675	1.4233	0.1779	0.0	0.0	0.0	0.7117 0.9198
DINOBRYON	0.0	0.1853	0.4170	0.2162	0.0927	0.0463	0.0	0.0	0.0	0.0	0.0	0.0	0.0798 0.1312
UNIDENT. CHRYSOPHYTE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0093	0.0	0.0	0.0008 0.0027
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0015	0.0	0.0	0.0	0.3707	0.0310 0.1070
TABELLARIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3707	0.0309 0.1070
UNIDENT. DIATOM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0015	0.0	0.0	0.0	0.0	0.0001 0.0004
CYANOPHYTA	0.0118	0.0	0.0004	0.0003	0.0798	0.0542	0.0928	0.0156	0.0020	0.0042	0.0059	0.0039	0.0226 0.0334
MERISMOPEDIA	0.0	0.0	0.0	0.0	0.0031	0.0079	0.0	0.0	0.0	0.0	0.0	0.0	0.0009 0.0024
RAPHIDIOPSIS	0.0118	0.0	0.0004	0.0003	0.0004	0.0011	0.0052	0.0010	0.0020	0.0042	0.0059	0.0039	0.0030 0.0035
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0763	0.0452	0.0876	0.0146	0.0	0.0	0.0	0.0	0.0186 0.0324
CYANOBACTERIA	0.0197	0.0239	0.0161	0.0196	0.0396	0.0125	0.0264	0.0223	0.0121	0.0161	0.0176	0.0069	0.0194 0.0084
CYANOBACTERIA	0.0197	0.0239	0.0161	0.0196	0.0396	0.0125	0.0264	0.0223	0.0121	0.0161	0.0176	0.0069	0.0194 0.0084
UNKNOWN	0.1157	0.1130	0.0434	0.2172	0.1841	0.0523	0.1528	0.2641	0.1046	0.0968	0.0957	0.1397	0.1316 0.0647
CYST	0.0192	0.0	0.0	0.0792	0.1404	0.0193	0.0	0.0066	0.0	0.0	0.0	0.0	0.0221 0.0436
COCCOID	0.0316	0.0710	0.0215	0.1247	0.0383	0.0192	0.0350	0.0342	0.0529	0.0488	0.0815	0.1071	0.0555 0.0339
FUSIFORM	0.0	0.0	0.0	0.0	0.0	0.0049	0.0033	0.0568	0.0023	0.0	0.0	0.0	0.0056 0.0162
NOT IDENTIFIED	0.0649	0.0420	0.0219	0.0133	0.0054	0.0089	0.1145	0.1665	0.0494	0.0480	0.0142	0.0326	0.0485 0.0480
TOTAL VOLUME	0.1657	0.3403	2.2792	0.8178	3.2492	1.1564	1.3669	1.7491	0.3517	0.5301	0.3525	0.7914	1.0959 0.9329

1979-CYLINDER 8F : ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->												
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.0058	0.0255	0.0088	0.0127	0.0078	0.0154	0.0041	0.0	0.0068	0.0	0.0	0.0079	0.0077
CHLAMYDOMONAS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0068	0.0	0.0	0.0006	0.0021
ANKISTRODESMUS	0.0058	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0005	0.0017
OOCYSTIS	0.0	0.0132	0.0088	0.0	0.0053	0.0	0.0	0.0	0.0	0.0	0.0	0.0025	0.0046
SCENEDESMUS	0.0	0.0123	0.0	0.0061	0.0025	0.0154	0.0041	0.0	0.0	0.0	0.0	0.0037	0.0055
UNIDENT. CHLOROPHYTE	0.0	0.0	0.0	0.0066	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0006	0.0020
CRYPTOPHYTA	0.0038	0.0041	0.0	0.0	0.0	0.0	0.0	0.0232	0.0	0.0249	0.0	0.0051	0.0095
CYPTOMONAS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0232	0.0	0.0241	0.0	0.0043	0.0096
UNIDENT. CRYPTOPHYTE	0.0038	0.0041	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0008	0.0	0.0008	0.0016
CHRYSOPHYTA	0.0309	0.4505	0.1495	0.0046	0.0185	0.0	0.0034	0.0890	0.1779	0.5344	0.3595	0.1653	0.1951
CHRYSOCAPSA	0.0	0.3558	0.1186	0.0	0.0	0.0	0.0	0.0890	0.1779	0.5338	0.3558	0.1483	0.1871
DINOBRYON	0.0309	0.0947	0.0309	0.0	0.0185	0.0	0.0034	0.0	0.0	0.0	0.0037	0.0166	0.0287
UNIDENT. CHRYSOPHYTE	0.0	0.0	0.0	0.0046	0.0	0.0	0.0	0.0	0.0	0.0006	0.0	0.0005	0.0014
CYANOPHYTA	0.0003	0.0	0.0005	0.0008	0.0008	0.0027	0.0013	0.0001	0.0033	0.0	0.0	0.0009	0.0011
MERISMOPEDIA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0031	0.0	0.0	0.0003	0.0009
RAPHIDIOPSIS	0.0003	0.0	0.0005	0.0008	0.0	0.0007	0.0	0.0001	0.0002	0.0	0.0	0.0002	0.0003
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0008	0.0020	0.0013	0.0	0.0	0.0	0.0	0.0004	0.0007
CYANOBACTERIA	0.0088	0.0179	0.0088	0.0162	0.0117	0.0155	0.0043	0.0162	0.0117	0.0194	0.0098	0.0128	0.0046
CYANOBACTERIA	0.0088	0.0179	0.0088	0.0162	0.0117	0.0155	0.0043	0.0162	0.0117	0.0194	0.0098	0.0128	0.0046
UNKNOWN	0.0467	0.1026	0.0498	0.0537	0.0092	0.0509	0.0499	0.0784	0.1407	0.3394	0.8915	0.1648	0.2570
CYST	0.0	0.0066	0.0	0.0	0.0	0.0041	0.0	0.0111	0.0	0.0	0.0	0.0020	0.0037
COCCOID	0.0320	0.0844	0.0357	0.0387	0.0031	0.0165	0.0297	0.0149	0.0326	0.0406	0.0172	0.0314	0.0211
FUSIFORM	0.0	0.0	0.0	0.0070	0.0	0.0056	0.0044	0.0	0.0272	0.0014	0.0	0.0041	0.0081
NOT IDENTIFIED	0.0147	0.0116	0.0141	0.0080	0.0061	0.0247	0.0158	0.0524	0.0809	0.2974	0.8743	0.1273	0.2618
TOTAL VOLUME	0.0963	0.6006	0.2175	0.0880	0.0480	0.0844	0.0630	0.2069	0.3404	0.9180	1.2608	0.3567	0.4037

1979-EUNICE LAKE: ------ PHYTOPLANKTON VOLUMES BY TAXA (MG/L WET WEIGHT)

TAXONOMIC CATEGORY	SAMPLING DATE---------->													
	JULY16	JULY26	AUG. 1	AUG. 9	AUG.16	AUG.23	AUG.30	SEPT 6	SEPT13	SEPT20	SEPT27	OCT. 5	MEAN	STD.DEV.
CHLOROPHYTA	0.0025	0.0053	0.0071	0.4603	0.3524	0.5365	1.0676	1.0682	0.8098	1.0910	0.7898	0.4615	0.5543	0.4156
CHLAMYDOMONAS	0.0	0.0	0.0	0.0051	0.0	0.0	0.0	0.0	0.0	0.0028	0.0	0.0	0.0007	0.0016
GLOEOCYSTIS	0.0	0.0	0.0	0.4195	0.3524	0.5034	1.0571	1.0571	0.7971	1.0697	0.7866	0.4615	0.5420	0.4128
OOCYSTIS	0.0	0.0053	0.0071	0.0357	0.0	0.0316	0.0105	0.0053	0.0	0.0185	0.0032	0.0	0.0098	0.0124
SCENEDESMUS	0.0025	0.0	0.0	0.0	0.0	0.0	0.0	0.0025	0.0041	0.0	0.0	0.0	0.0008	0.0014
UNIDENT. DESMID	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0033	0.0	0.0	0.0	0.0	0.0003	0.0010
UNIDENT. CHLOROPHYTE	0.0	0.0	0.0	0.0	0.0	0.0015	0.0	0.0	0.0086	0.0	0.0	0.0	0.0008	0.0025
EUGLENOPHYTA	0.0712	0.0	0.0154	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0072	0.0206
UNIDENT. EUGLENOID	0.0712	0.0	0.0154	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0072	0.0206
CRYPTOPHYTA	0.0	0.0	0.0	0.0062	0.0003	0.0046	0.0	0.0119	0.0062	0.0012	0.0041	0.0222	0.0047	0.0066
CYPTOMONAS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0041	0.0222	0.0022	0.0064
UNIDENT. CRYPTOPHYTE	0.0	0.0	0.0	0.0062	0.0003	0.0046	0.0	0.0119	0.0062	0.0012	0.0	0.0	0.0025	0.0039
CHRYSOPHYTA	0.0741	0.3048	0.3726	0.2703	0.1297	0.0953	0.0680	0.0371	0.1432	0.2085	0.2678	0.1880	0.1799	0.1064
CHRYSOCAPSA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1186	0.0	0.0	0.0	0.0099	0.0342
DINOBRYON	0.0741	0.3048	0.3726	0.2703	0.1297	0.0927	0.0556	0.0371	0.0202	0.2085	0.2548	0.1544	0.1646	0.1159
MALLOMONAS	0.0	0.0	0.0	0.0	0.0	0.0	0.0124	0.0	0.0	0.0	0.0130	0.0336	0.0049	0.0103
UNIDENT. CHRYSOPHYTE	0.0	0.0	0.0	0.0	0.0	0.0026	0.0	0.0	0.0044	0.0	0.0	0.0	0.0006	0.0014
BACILLARIOPHYCEAE	0.0	0.0	0.0	0.0	0.0003	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0000	0.0001
UNIDENT. DIATOM	0.0	0.0	0.0	0.0	0.0003	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0000	0.0001
CYANOPHYTA	0.0	0.0001	0.0	0.0079	0.0151	0.0041	0.0327	0.0138	0.0273	0.0173	0.0724	0.0336	0.0187	0.0209
MERISMOPEDIA	0.0	0.0	0.0	0.0079	0.0151	0.0025	0.0327	0.0138	0.0252	0.0173	0.0724	0.0336	0.0184	0.0209
RAPHIDIOPSIS	0.0	0.0001	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0000	0.0000
CYANOPHYTE FILAMENTS	0.0	0.0	0.0	0.0	0.0	0.0016	0.0	0.0	0.0021	0.0	0.0	0.0	0.0003	0.0007
CYANOBACTERIA	0.0122	0.0047	0.0079	0.0159	0.0067	0.0106	0.0126	0.0059	0.0089	0.0037	0.0176	0.0139	0.0100	0.0045
CYANOBACTERIA	0.0122	0.0047	0.0079	0.0159	0.0067	0.0106	0.0126	0.0059	0.0089	0.0037	0.0176	0.0139	0.0100	0.0045
UNKNOWN	0.0264	0.1225	0.0345	0.0471	0.0949	0.0435	0.1755	0.0270	0.1419	0.0325	0.0531	0.0719	0.0726	0.0500
CYST	0.0	0.0267	0.0140	0.0	0.0	0.0089	0.0	0.0	0.0	0.0	0.0177	0.0234	0.0076	0.0103
COCCOID	0.0078	0.0086	0.0058	0.0345	0.0136	0.0129	0.1609	0.0185	0.0275	0.0242	0.0250	0.0323	0.0310	0.0420
NOT IDENTIFIED	0.0186	0.0872	0.0147	0.0126	0.0813	0.0217	0.0146	0.0085	0.1144	0.0083	0.0104	0.0162	0.0340	0.0373
TOTAL VOLUME	0.1864	0.4373	0.4375	0.8076	0.5995	0.6947	1.3564	1.1638	1.1372	1.3541	1.2048	0.7911	0.8475	0.3920

APPENDIX G: METHODS OF ESTIMATING DAPHNIA MORTALITY RATES (1980)

Daphnia mortality rates were estimated using both three-stage and two-stage models. The three-stage model is an unpublished computer program written by E. Guindon, based on the methods of Argentisi et al. (1974) and Seitz (1979). In the program, the population is represented by three stages: eggs, juveniles, and adults, each with its own rates of recruitment and mortality. The population demography is described by the following system of differential equations (Argentisi et al. 1974):

$$dE/dt = R_0 - R_1 - (me)\ E \qquad (G1)$$

$$dJ/dt = R_1 - R_2 - (mj)\ J \qquad (G2)$$

$$dA/dt = R_2 - (ma)\ A \qquad (G3)$$

where R_0 = the fecundity rate (# eggs produced);

R_1 = the birth rate (# eggs hatched);

R_2 = the maturation rate (# juveniles matured); and

me, mj, ma = the mortality rate of eggs, juveniles and adults respectively.

E, J, A = the numbers of eggs, juveniles and adults.

The above differential equations are solved as difference equations, using the collocation method on smoothed data (three date running averages). Each field sampling interval is divided into subintervals of duration 0.1 day. The densities of eggs, juveniles and adults are interpolated exponentially for each subinterval, and parameter values computed so as to satisfy the difference equations. The mean values of parameters over

all subintervals are considered as parameter estimates for the field sampling interval. Key assumptions of this analysis are that:

1) egg mortality rates equal adult mortality rates;
2) egg development times decrease exponentially with temperature, according to the data of Hall (1964) for Daphnia galeata, but are unaffected by pH;
3) juvenile development times decrease exponentially with temperature, according to laboratory studies by Neill (1981) and Guindon (unpublished data), but are also unaffected by pH; and
4) the fraction of eggs hatching per day, and the fraction of juveniles maturing per day are affected by the intrinsic growth rates of other compartments (e.g. the fraction of eggs hatching depends on the intrinsic growth rate of adults.)

The two-stage model, based on Paloheimo (1974), considers only eggs and "animals" (i.e. it does not differentiate between adults and juveniles). The animals' mortality rate is calculated as the difference between the instantaneous birth rate and the intrinsic rate of population increase. The instantaneous birth rate (or egg hatching rate) is given by:

$$b = \ln[(E/N) + 1]/D \qquad (G4)$$

where:

b = instantaneous birth rate;

E = the total number of eggs;

N = the total number of animals (juveniles plus adults);

D = the egg development time.

The intrinsic rate of population increase, r, is computed from two sequential samples, according to:

$$r = (\ln N_2 - \ln N_1)/(t_2 - t_1) \qquad (G5)$$

where: N_2 = the total number of animals counted at time t_2; and

N_1 = the total number of animals counted at time t_1.

APPENDIX H: SENSITIVITY ANALYSIS OF THREE STAGE MODEL FOR ESTIMATING DAPHNIA MORTALITY RATES (1980)

The three stage model frequently estimated negative mortality rates for juvenile Daphnia rosea. This indicates either erroneous assumptions in computation or errors in sampling and enumeration. In simulation tests to estimate known parameter values, Seitz (1979) found that his three-stage model overestimated hatching rates by 104.4% and maturation rates by 185%. Seitz attributed these errors to the deviation of stages from exponential growth, and the compounding of errors induced by using the intrinsic rates of growth of both juveniles and adults in the calculation of hatching and maturation rates.

In his simulation tests, Seitz used "true" values for developmental rates, and assumed zero sampling error. To partially assess the effect of errors in assumed development rates and/or sampling, I reran the three-stage model for cylinder 3L assuming:

1) an 8°C decrease in the temperature at which juveniles developed (so as to greatly increase juvenile developmental time);
2) an 8°C increase in the temperature at which eggs developed (to increase rate of egg hatching); and
3) a 50% increase in egg density.

4-7) all combinations of conditions 1), 2), and 3).

Table H1 shows that estimated juvenile mortality rates were consistently positive only when all the above radical changes were applied in combination. It seems highly unlikely that

Table H1. Sensitivity analysis of estimated mortality rates of juvenile Daphnia rosea in cylinder 3L. T_j = temperature of juveniles; T_e = temperature of eggs; E = egg density.

Sampling Interval	JUVENILE MORTALITY RATES (estimated) Assumed Conditions							
	T_j T_e E	T_j-8	T_e+8	E*1.5	T_j-8 T_e+8	T_j-8 E*1.5	T_e+8 E*1.5	T_j-8 T_e+8 E*1.5
May 13-16	-0.094*	-0.063	-0.077	-0.072	-0.033	-0.041	-0.026	0.004
May 16-18	-0.065	-0.022	-0.054	-0.051	-0.003	-0.009	-0.022	0.021
May 18-21	-0.030	0.007	-0.022	-0.020	0.021	0.017	0.001	0.038
May 21-23	-0.047	-0.014	-0.039	-0.040	-0.001	-0.007	-0.021	0.012
May 23-26	-0.035	-0.005	-0.029	-0.029	0.007	0.001	-0.012	0.019
May 26-29	-0.058	-0.018	-0.052	-0.054	-0.006	-0.014	-0.037	0.004
May 29-June 5	-0.039	0.002	-0.029	-0.033	0.020	0.007	-0.007	0.034
June 5-12	-0.026	0.015	-0.005	-0.015	0.052	0.026	0.041	0.083
June 12-19	0.056	0.099	0.131	0.107	0.230	0.150	0.304	0.346
June 19-July 16	0.188	0.238	0.356	0.310	0.532	0.361	0.752	0.802

* These are the estimated mortality rates shown in Figure 45 for cylinder 3L.

assumed developmental rates and estimated egg densities were both so far in error. Rather, I suspect that more fundamental errors (such as those described by Seitz) are inherent in the three stage model.