To the Graduate Council:

I am submitting herewith a thesis written by William L. Doolittle entitled "Qualitative Differences in Lake Biota Due to Fish Predation." I recommend that it be accepted in partial fulfillment of the requirements for the degrees of Master of Science, with a major in Ecology.

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Thesis
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QUALITATIVE DIFFERENCES IN LAKE BIOTA DUE TO FISH PREDATION

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

William L. Doolittle

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ABSTRACT

Two lakes in northern Minnesota, Arco and Deming, were compared for differences in their plankton communities. Phytoplankton in Deming Lake outnumbered phytoplankton in Arco Lake by an order of magnitude. On the other hand, zooplankton in Arco Lake had significantly greater length than zooplankton in Deming Lake. Experiments were conducted to determine the cause of these differences. Although diets of fish, insects, and zooplankton vary spatially and temporally, large herbivorous zooplankton, existing in the absence of vertebrate predator pressure, appear responsible for the lower algal numbers in the fish-free lake.

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I. INTRODUCTION

Approaches to restoring culturally eutrophied lakes have traditionally been aimed at the base of aquatic trophic systems. Shapiro, Lamarra, and Lynch (unpublished manuscript, 1975) note that 99% of the efforts to restore eutrophied lakes have been aimed at eliminating nutrient inputs. Although sometimes successful, these tactics are often very expensive ($130 million in Lake Washington, Edmondson, 1969); in other instances, complete elimination of nutrient inputs from diffuse sources is unfeasible.

Shapiro, et al (1975) propose attacking the problem of eutrophication at the opposite end of the trophic system. Termed biomanipulation, the process would involve stocking of piscivores to reduce planktivore populations through predation; the resulting reduction of predator pressure on zooplankton would allow zooplankton numbers and sizes to increase, inducing heavier grazing pressure on algal populations. Considering the reciprocal relationships of ecosystem trophic components, and assuming a 10% trophic efficiency between each trophic level, the authors note that a 1 kilogram stock of piscivores could potentially control 1 metric ton of algae through the piscivore--planktivore--zooplankton--phytoplankton interaction. If this interaction proves effective, the top carnivore level would be a very convenient control point. This process might also be effective in the face of nutrient influx.

Studies of several types of interactions support the theory of biomanipulation. Many authors have studied the effect of introducing planktivores into previously fish-free lacustrine systems: Brooks and Dodson (1965), Straškraba (1965), Grygierek et al (1966), Rief and Tappa (1966), Rozmajzlova-Rehackova (1966), Galbraith (1967), Wells (1970), Anderson (1972), Hurlbert et al (1972), Warshaw (1972), and Archibald (1975). In each study, the abundance and modal size of zooplankton decreased following introduction of planktivores; all authors note the elimination of the largest zooplankton species. These observations led Brooks and Dodson (1965) to formulate the size-efficiency hypothesis:

> 1) Planktonic herbivores all compete for the fine particulate matter (1 to 15 microns) of the open waters;
> 2) Larger zooplankters do so more efficiently and can also take larger particles;
> 3) Therefore, when predation is of low intensity, the small planktonic herbivores will be competitively eliminated by large forms (dominance of large Cladocera and calanoid copepods).
> 4) But when predation is intense, size-dependent predation will eliminate the large forms, allowing the small zooplankters (rotifers, small Cladocera), that escape predation, to become the dominants.
> 5) When predation is of moderate intensity, it will, by falling more heavily upon the larger species, keep the population of these more effective herbivores sufficiently low so that slightly smaller competitors are not eliminated.
> Thus, the antagonistic demands of competition and predation are considered to determine the body size of dominant herbivorous zooplankton.

Zooplankton size is important for the reduction of algal standing crop because the diameter of particles ingested is proportional to the body length, and the filtering

rate of zooplankton is proportional to the square, or even the cube, of the body length (Burns, 1968, 1969).

Another type of interaction studied by Hrbáček et al (1961, 1965) adds support to the theory. Fish poisoning in several back waters resulted in increased transparency and diminution of algal abundance. Despite a decrease in overall numbers of zooplankton, larger species appeared, and were thought to be responsible for the decrease in algal abundance.

Zaret and Paine (1973) studied a situation pertinent to the theory. A piscivore was accidentally introduced into a tropical lake, Lake Gatun, and it almost eliminated zooplanktivores while outcompeting other secondary carnivores. The resulting increase in zooplankton populations was expected to reduce the standing crop of phytoplankton, but no measurements were taken.

One well-documented encumbrance to the application of grazing pressure to control eutrophication is the non-edibility of certain algae (Arnold, 1971, Schindler, 1971, Porter, 1973). These findings determined that zooplankton could not digest the mucopolysaccharide sheaths of blue-green algae (Cyanophyceae). While some species can be ingested, they may pass through the gut undigested, or break apart, releasing nutrients and enhancing primary production (Gliwicz, 1975, Weers and Zaret, 1975, Porter, 1976).

Shapiro (1973) has determined that blue-green algae outcompete green algae for carbon dioxide with rising pH, due to greater efficiency of carbon dioxide uptake. In a

series of experiments, he has found that manipulation of the pH with additions of either carbon dioxide or hypochlorite will allow a shift in dominance from blue-greens to greens. In lakes, this shift could be induced by artificial circulation, which would lower the pH, and also bring dissolved oxygen to greater depths and reduce epilimnetic temperatures. Furthermore, dilution of zooplankton through the water column would reduce contacts with planktivores, and reduction of epilimnetic temperatures would probably increase the metabolic efficiency of zooplankton. The temperature for optimal size of Daphnia pulex is approximately 20°C; at higher temperatures, a greater proportion of the diet is required for maintenance (Lynch, unpublished data).

This thesis constitutes a pilot study describing some aspects of the biomanipulation theory in a natural setting. The study concentrates on responses of phytoplankton and zooplankton communities to planktivore pressure and responses in the absence of planktivore pressure.

II. METHODS

Two adjacent lakes in northern Minnesota were chosen for study during summer 1976. Arco and Deming Lakes lie in a natural setting within Lake Itasca State Park (Fig. 1). These two lakes have similar morphometries (Table 1) and water chemistries (Hooper, 1948, and Baker, 1973), but fish are absent from Arco while four species of planktivores inhabit Deming: Pimephales promelas (fathead minnow), Chrosomus eos (northern redbelly dace), Culea inconstans (brook stickleback), and Etheostoma nigrum (Johnny darter).

Both lakes are meromictic; they have incomplete vernal and autumnal overturns. The lower, anoxic, saline monimolimnions do not mix, while the upper mixolimnions behave as fully circulating lakes. Norway and white pine forests rise above steep basin walls, sheltering the lakes from winds. High relative depths (maximum depth expressed as a percentage of the surface area) add to the stability of the lake waters (Table 1); most lakes have relative depths of less than 2% (Wetzel, 1975).

Changes in certain physiochemical parameters throughout the summer season were monitored weekly. They were:

temperature	measured by	Hydrolab thermister
dissolved oxygen	measured by	azide modification of Winkler method
pH	measured by	Beckman pH meter
alkalinity	measured by	acidimetric method (Golterman and Clymo, 1969)
conductivity	measured by	Industrial Instruments conductivity bridge
transparency	measured by	Secchi disk

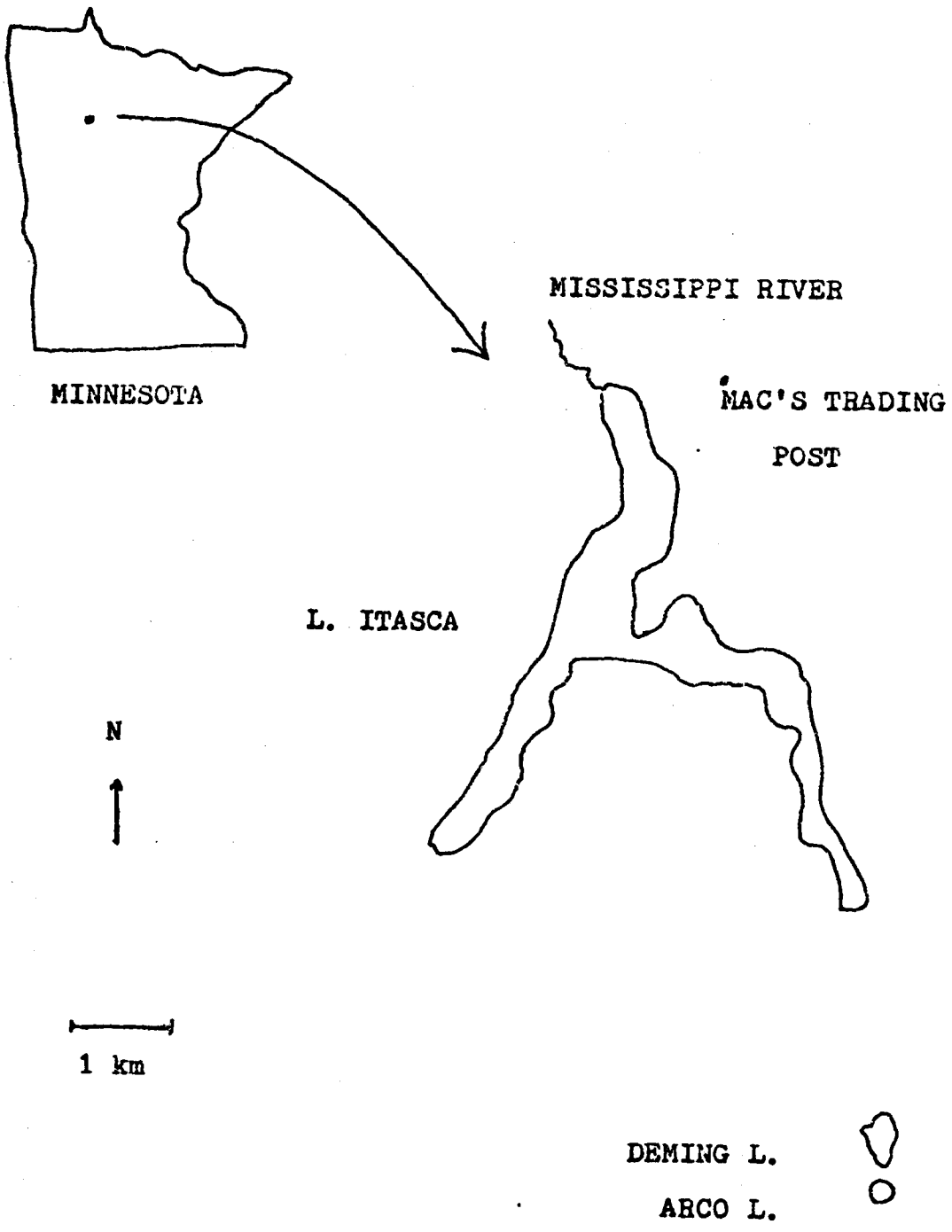


Figure 1. The Location of Deming and Arco Lakes in Northern Minnesota's Lake Itasca State Park

Table 1. Lake Morphometries of Deming and Arco Lakes, Minnesota, Compared to Lake Itasca, Minnesota

Parameter	Deming Lake	Arco Lake	Lake Itasca
Area (ha)	3.62	1.39	436
Volume ($m^3 \times 10^4$)	17.3	6.0	2290
Maximum Depth (m)	17.0	10.2	14
Average Depth (m)	4.78	4.32	5.2
Relative Depth (%)	7.92	7.65	2.85

Water samples were collected from 0 to 8 meters depth with a van Dorn or a Kemmerer sampler: 8 meters depth entered well into the monimolimnions of both lakes.

Biotic parameters monitored included biomass and species composition of the phytoplankton and biomass, species composition, and lengths of zooplankton. Biomass samples were collected with two plankton nets of 35 and 64 micron mesh; the two size categories were used for comparison of size ranges of plankton. Three vertical net hauls were taken at each lake for measurements of biomass. The plant and animal fractions were separated by density differences; relative to water, phytoplankton have a density of 1.200 and zooplankton 1.190. A sucrose solution was mixed to a density of 1.195. Each sample was added to the sucrose solution, and centrifuged. The plants passed through the solution, while the animals remained above its dense interface. Fractions were removed by pipetting and filtered through Millipore filtering apparatus holding filters of .8 or 10 micron pore size. The filters were then oven-dried for 12 hours at 30°C. Weighing was performed on a Mettler analytical balance.

Zooplankton species composition was determined from a fourth net haul, which was subsampled and counted using a Sedgewick-Rafter cell on a compound microscope. Measurement of zooplankton size was determined with an ocular micrometer. Samples for determination of phytoplankton species composition were collected from 0 to 8 meters using an integrated

sampler (Vollenweider, 1969). Counts were performed on an inverted microscope.

Species diversity was calculated using Simpson's index of diversity:

$$D = 1 - \sum_{i=1}^{S} (p_i^2)$$

where D = Simpson's index of diversity, S = the number of species in the sample, and p_1 = the proportion of individuals of species 1 in the community.

Several experiments were conducted in an effort to observe responses of plankton communities to manipulations. Field experiments were conducted in plexiglass columns inserted in the limnetic region of Deming Lake, and in 1 gallon jugs suspended in Deming Lake. Two-liter flasks were used for experiments in the laboratory. The experimental lake columns were developed by Klemer (1973), and have dimensions of 5.5 meters length and 25 centimeters diameter. A styrofoam collar was attached to the top end of the column for flotation, and the column was suspended from a cable stretched across the lake. The bottom end extended into the anoxic monimolimnion, and was screened with 1 millimeter mesh screen. Extension into the monimolimnion prevented migration of the plankton population in or out of the column, and the screen prevented entrance or exit of fish and insect larvae. Details of these experiments are given later in the paper.

III. RESULTS AND DISCUSSION

Physiochemical Parameters

Both lakes typically undergo severe summer temperature stratification, with thermoclines occurring between 3 to 5 meters depth (Fig. 2). Dissolved oxygen profiles for both lakes were positive heterograde curves (Fig. 3), due to stratification of species of Oscillatoria at approximately 4 meters in Deming and at approximately 5 meters in Arco (Klemer, 1973). Below these algal layers the lakes become anoxic. Secchi disk readings ranged from 1.8 to 2.3 meters in Deming and from 3.5 to 6.3 meters in Arco; in both lakes, the shallowest readings occurred in mid June and the deepest in mid to late July (Fig. 4).

Alkalinity increased with depth in Arco, and showed a positive heterograde curve in Deming (Fig. 5). In Deming, pH levels often declined from about 8 units in the mixolimnion to 6 units in the monimolimnion, while in Arco, the decline was from about 7.5 units to 6.5 units (Fig. 6). Conductivities generally increased in the monimolimnions of both lakes (Fig. 7). The effects of intensely stratified algae on the pH, alkalinity, and conductivity profiles can be seen in figures 5-7.

Seasonal monitoring of the two lakes shows their physiochemical parameters to be very similar, compared to Lake Itasca. Certain parameters, particularly pH, alkalinity, and conductivity (Figs. 5-7, and Baker, 1973), reinforce the

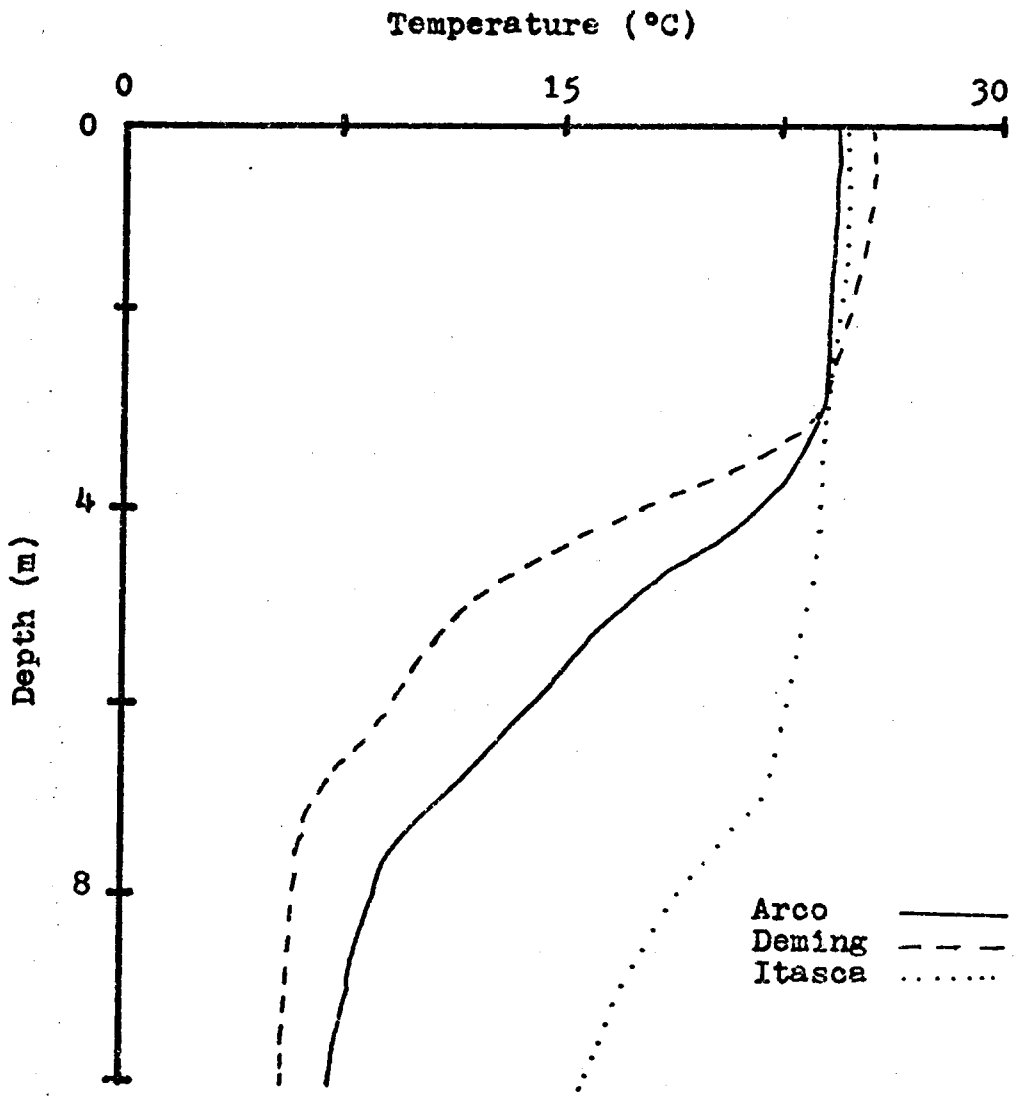


Figure 2. Typical Temperature Profiles in Arco and Deming Lakes, 23 July 1976, Compared to Lake Itasca, 24 July 1976 (Pittinger, 1977)

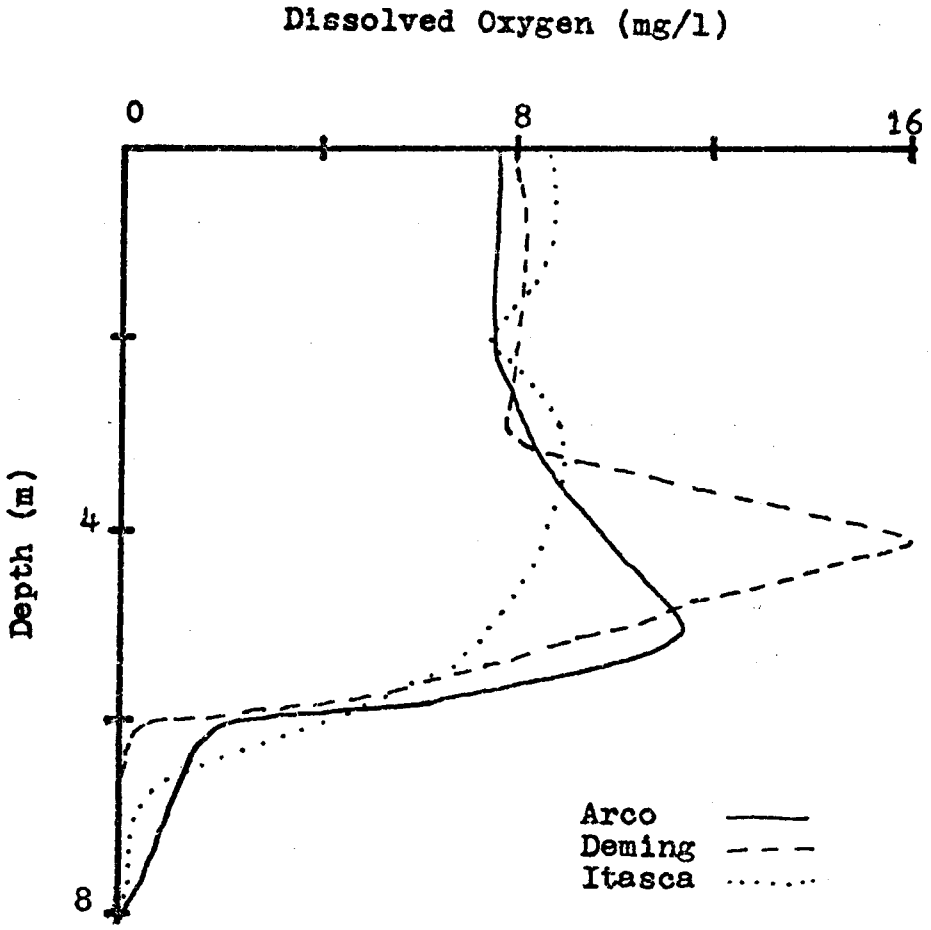


Figure 3. Typical Dissolved Oxygen Profiles in Arco and Deming Lakes, 23 July 1976, Compared to Lake Itasca, 24 July 1976 (Pittinger, 1977)

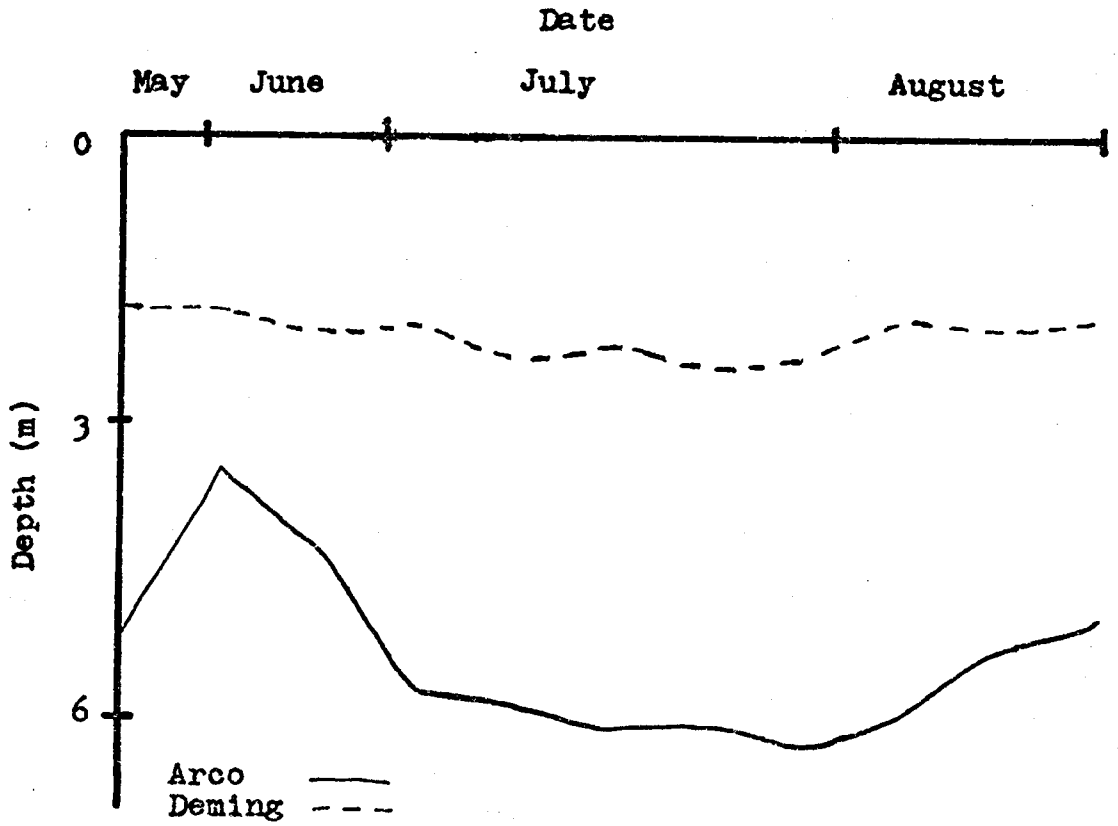


Figure 4. Secchi Disk Readings in Arco and Deming Lakes, Summer 1976

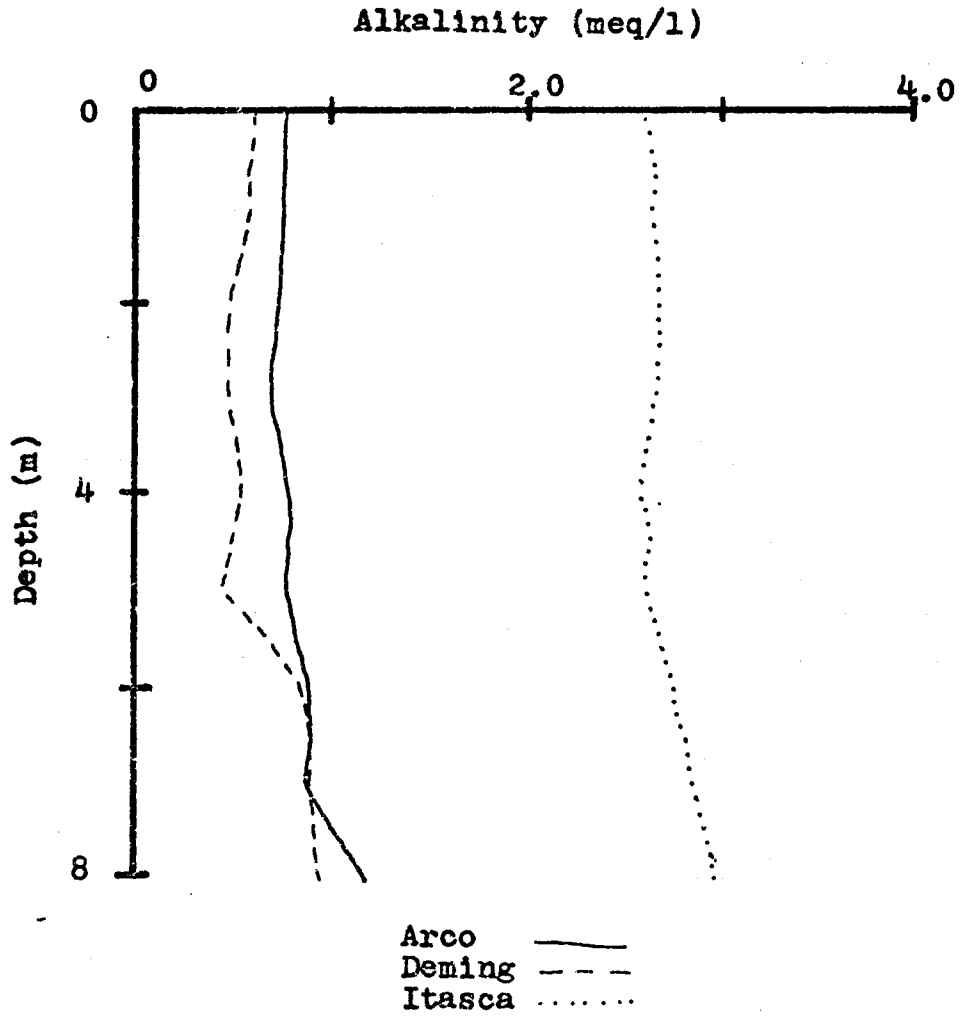


Figure 5. Typical Alkalinity Profiles in Arco and Deming Lakes, 23 July 1976, Compared to Lake Itasca, 24 July 1976 (Pittinger, 1977)

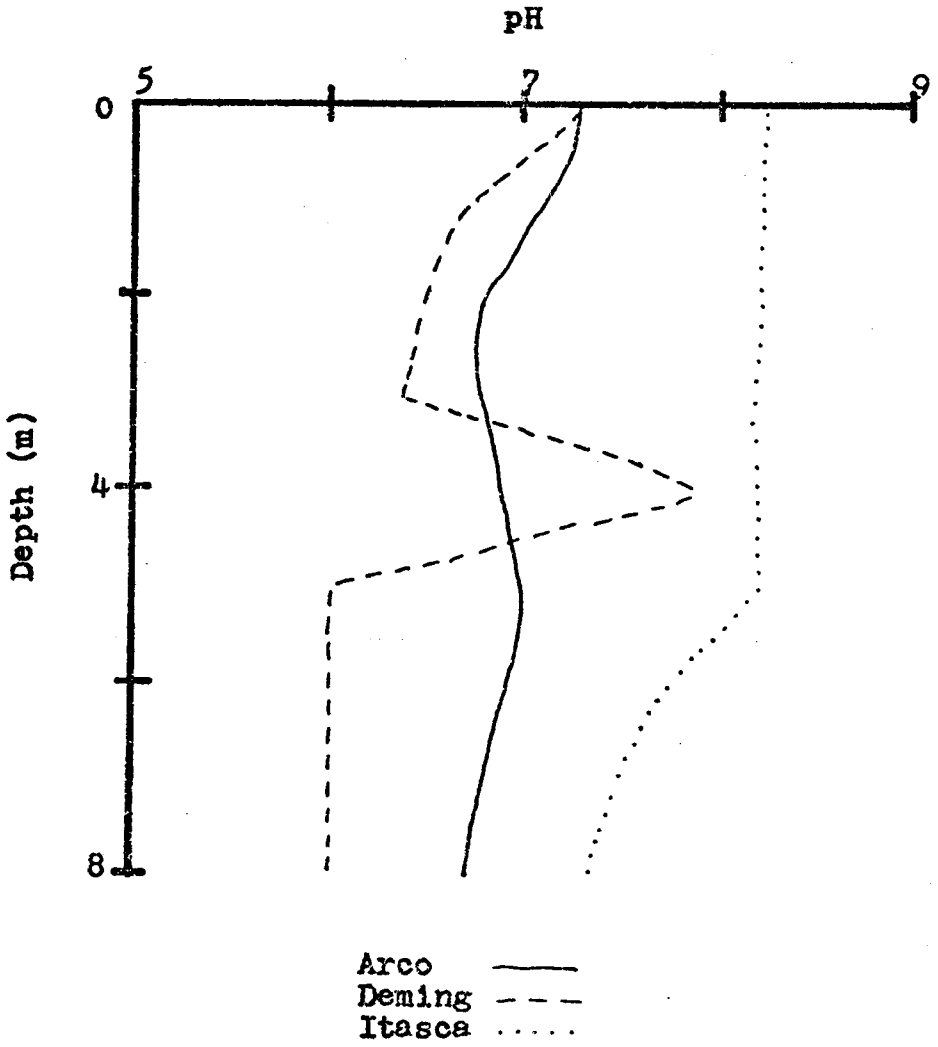


Figure 6. Typical pH Profiles in Arco and Deming Lakes, 23 July 1976, Compared to Lake Itasca, 24 July 1976 (Pittinger, 1977). On This Date, a Sharp Increase at 4 Meters Was Probably Due to Photosynthetic Activity.

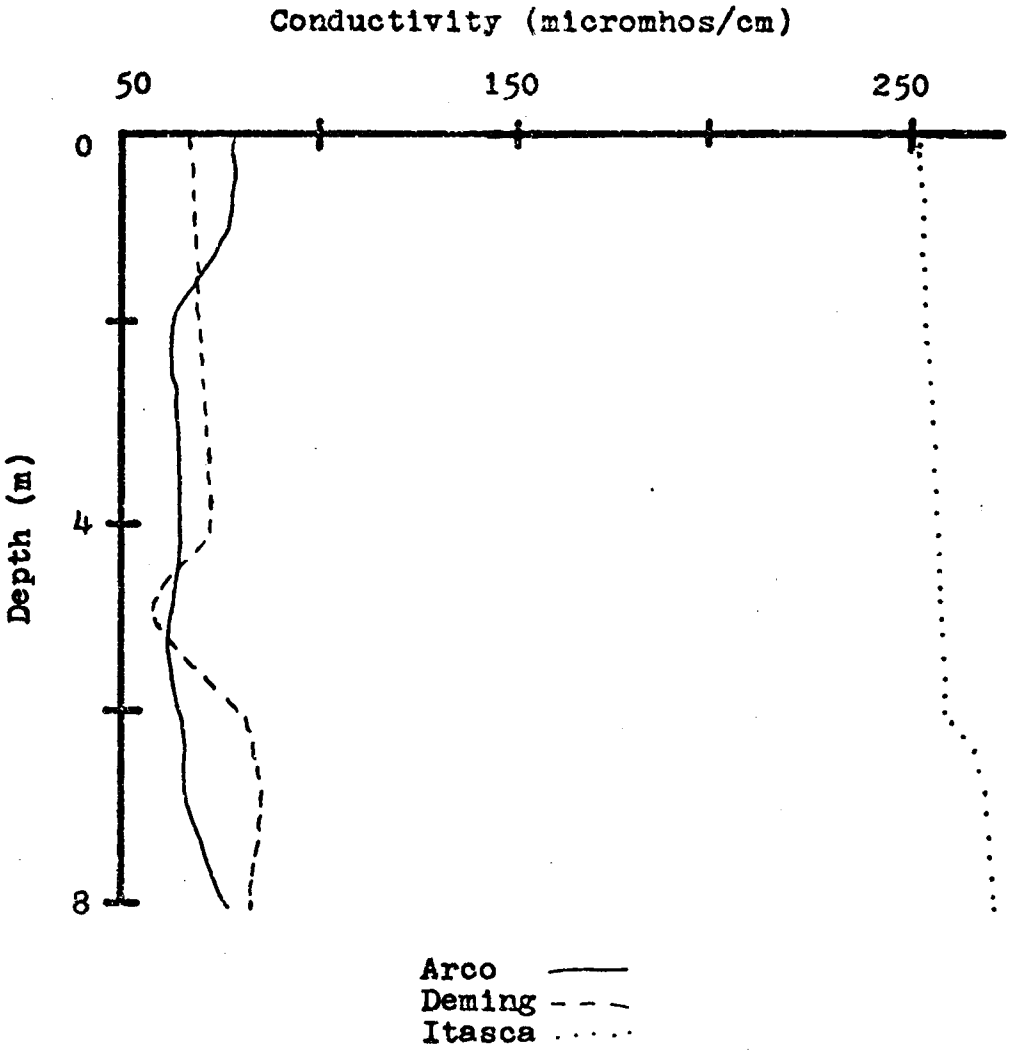


Figure 7. Typical Conductivity Profiles in Arco and Deming Lakes, 23 July 1976, Compared to Lake Itasca, 24 July 1976 (Pittinger, 1977)

description of the lakes as meromictic. The only striking difference between the lakes is the much greater Secchi disk transparency in Arco (Fig. 4).

Phytoplankton

Phytoplankton biomass estimates from 35 and 64 micron net hauls showed no consistency in comparison of magnitude or trend in either lake. Therefore, estimates from the two sizes were added to give a total estimate (Fig. 8). The changes in total biomass follow similar patterns in both lakes although Arco seemed to have a greater phytoplankton biomass throughout the summer.

Four groups of algae dominated the phytoplankton in each lake. In Arco, Arthrospira sp., Cryptomonas erosa, other Cryptomonads, and Oscillatoria sp. comprised the dominants through the summer. In Deming, Oscillatoria redekei, Anabena cylindrica, Lyngbya limnetica, and Oscillatoria agardhii comprised the dominants. Cyanophyceae clearly dominate the phytoplankton of both lakes.

Arco phytoplankton consistently exhibited greater species diversity than Deming, although diversity of both groups followed a similar pattern through the summer (Fig. 9). In early summer, during a general increase in biomass, the diversity also increased. However, during another general increase in biomass during late summer, the species diversity decreased.

Although the phytoplankton biomass estimates in Arco are

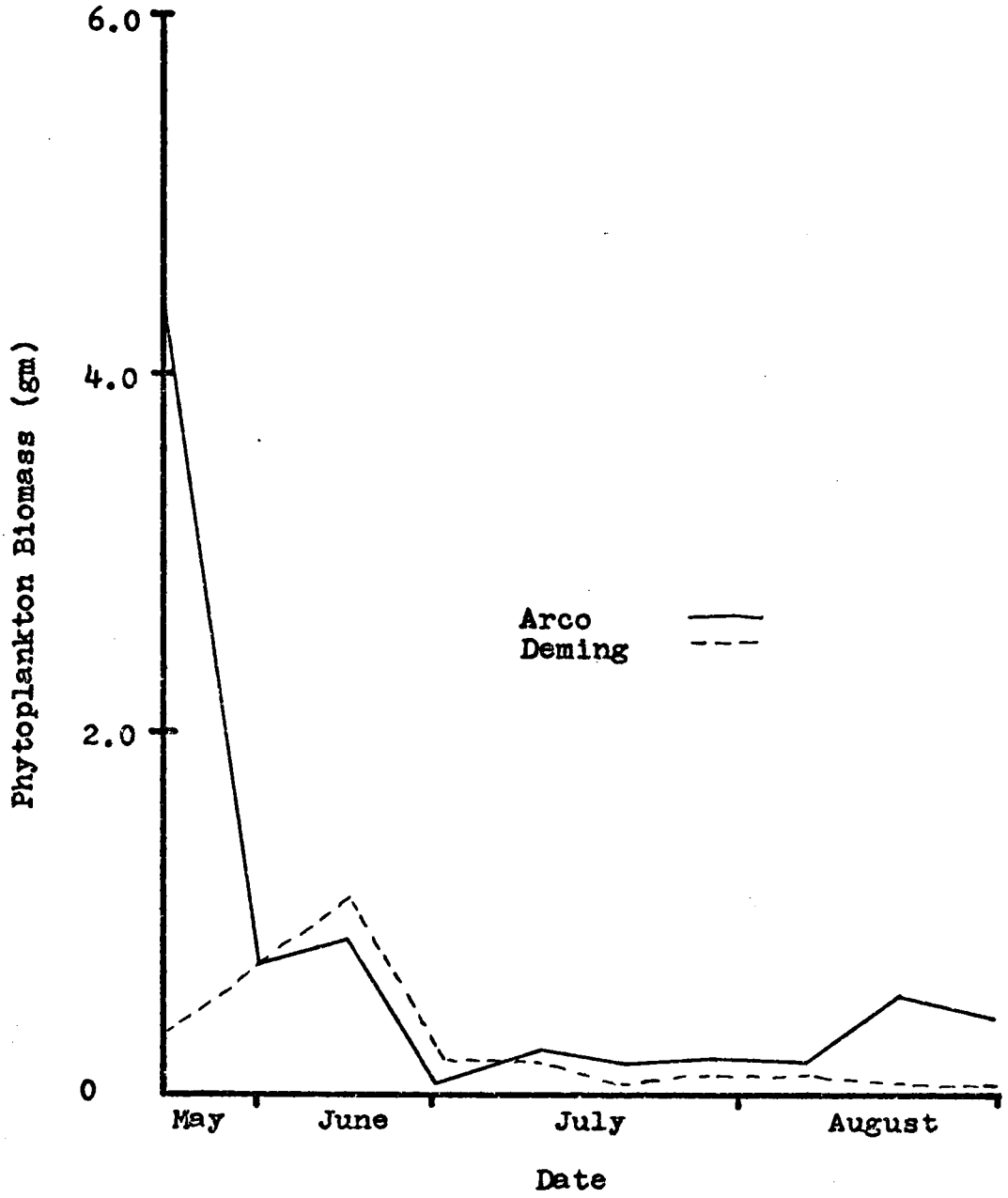


Figure 8. Phytoplankton Biomass of Combined Net Hauls in Arco and Deming Lakes, Summer 1976

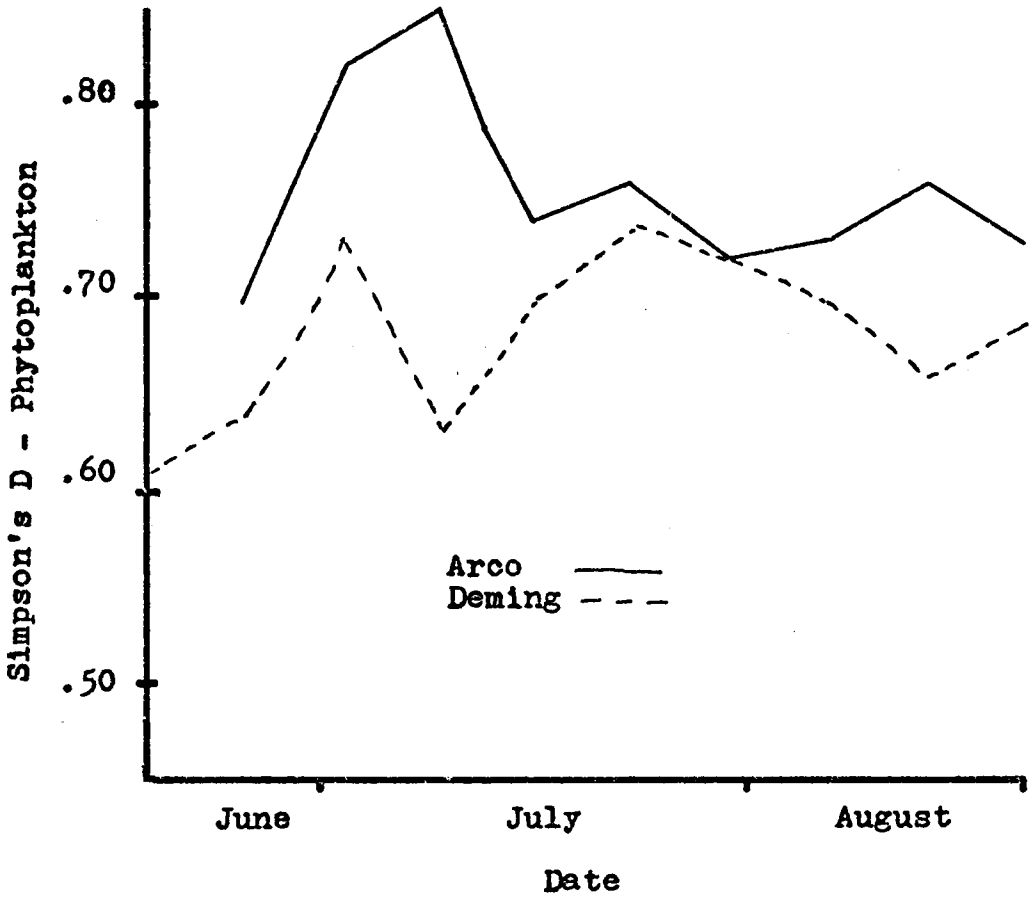


Figure 9. Phytoplankton Species Diversity in Arco and Deming Lakes, Summer 1976

usually greater than in Deming, total numbers of algal colonies in Deming exceed those in Arco by a factor of ten (Fig. 10). I am not sure of the explanation for this, but Deming also has more species that are large and filamentous. It is possible that the larger algae in Deming clog the nets faster than Arco phytoplankton, and as the net pores clog, the filtering process is hindered. Considering the differences in phytoplankton numbers and in Secchi disk readings, it seems unlikely that Arco would have more algae.

In terms of the biomanipulation theory, the lake with the lesser predator pressure on the zooplankton should have heavier grazing and thus, less algae. Certainly, Arco has fewer phytoplankton numbers (Fig. 10), and greater transparency (Fig. 4, p. 13).

Zooplankton

Biomass estimates for zooplankton from 35 and 64 micron net hauls also show no consistency in magnitude or tendency. Again, the two sizes were combined to give a total estimate. Total estimates show Arco to have greater zooplankton biomass than Deming (Fig. 11). As with the phytoplankton, the changes in total zooplankton biomass show similar patterns in both lakes through the middle of the summer. The high points in the Arco biomass curve are probably due to high numbers of Daphnia pulex and Chaoborus larvae in May, and to Chaoborus larvae in August. The Chaoborus larvae attain their greatest size at these times, prior to emergence.

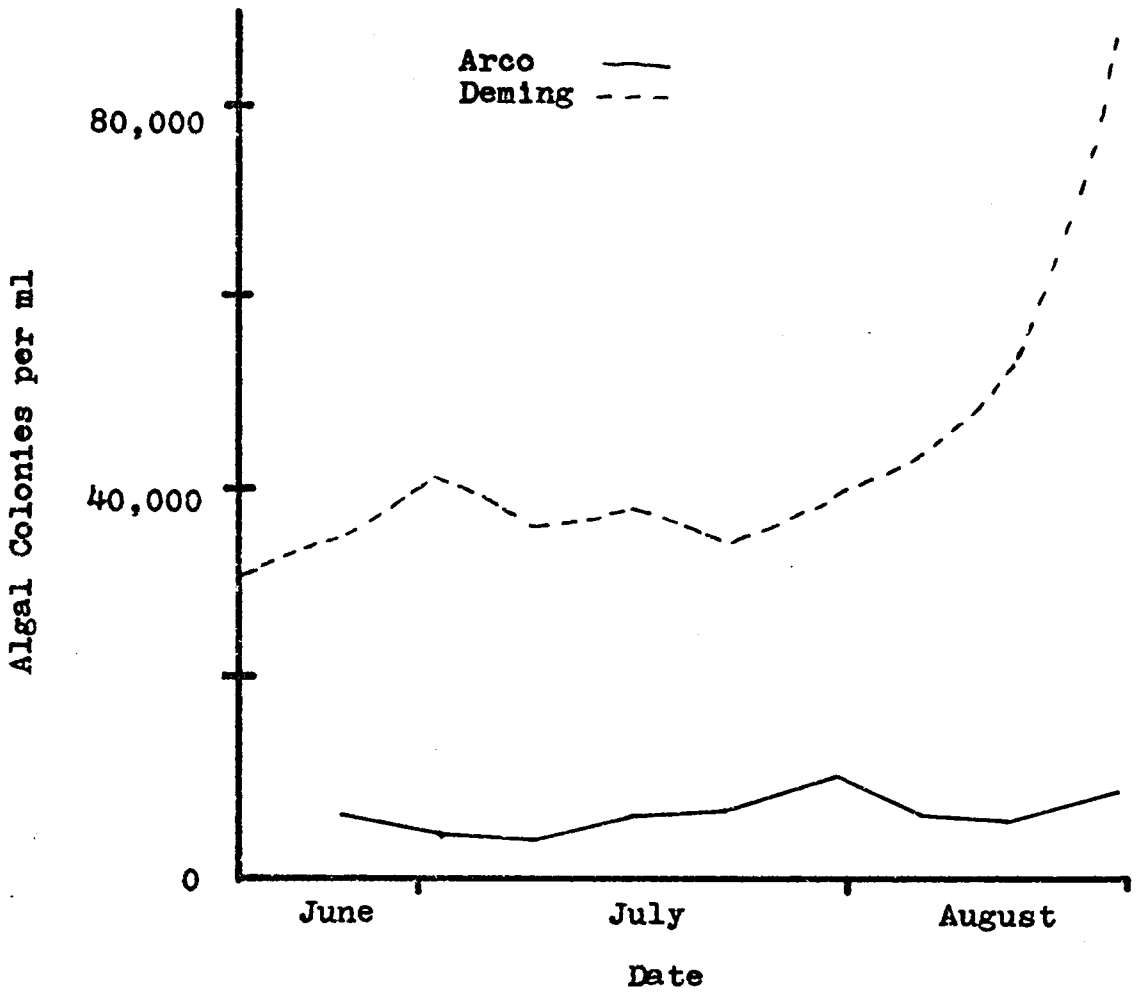


Figure 10. Algal Colonies per Milliliter in Arco and Deming Lakes, Summer 1976

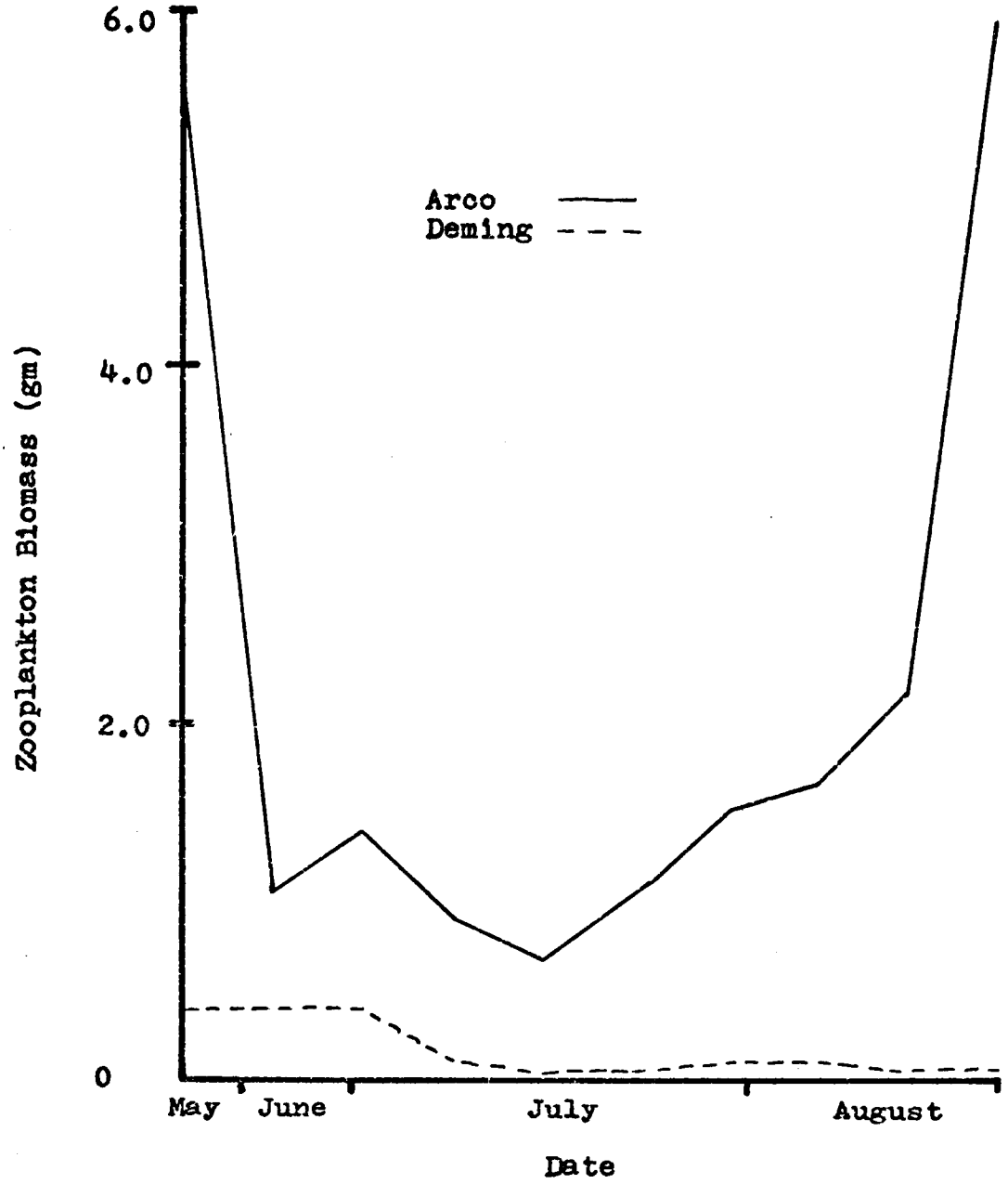


Figure 11. Zooplankton Biomass of Combined Net Hauls in Arco and Deming Lakes, Summer 1976

Rotifers and copepods dominated the zooplankton of both lakes. Kellicottia longispina, Keratella cochlearis, Cyclops varicans, and copepod nauplii dominated the zooplankton numbers in Arco. In Deming, Keratella cochlearis, copepod nauplii, Polyarthra sp., and Cyclops varicans were the most numerous species.

Deming zooplankton exhibited greater species diversity through the entire summer (Fig. 12). As with phytoplankton diversity, zooplankton diversity in both lakes was high in early summer when the biomass was high. In late summer, the diversity declined as the biomass showed a general increase.

To compare the zooplankton sizes in the lakes, an index for weighting the lengths by per cent species composition was utilized. Average lengths for each species were multiplied by the per cent composition; the products were added for the rotifer, copepod, and cladoceran groups, and the sums were divided by the per cent composition of each group. These weighted average lengths represent the composition of zooplankton sizes as predators would encounter them.

Weighted average lengths for each category of zooplankton in Arco were, with few exceptions, greater than in Deming (Table 2). Application of the Wilcoxon rank sum test to this data shows a significant difference of zooplankton lengths in the two lakes at the 99.5% confidence level. Average weighted lengths for each date were also greater for all zooplankton groups in Arco (Table 2). The average zooplankton length in Arco reaches a peak in midsummer, when invertebrate predation

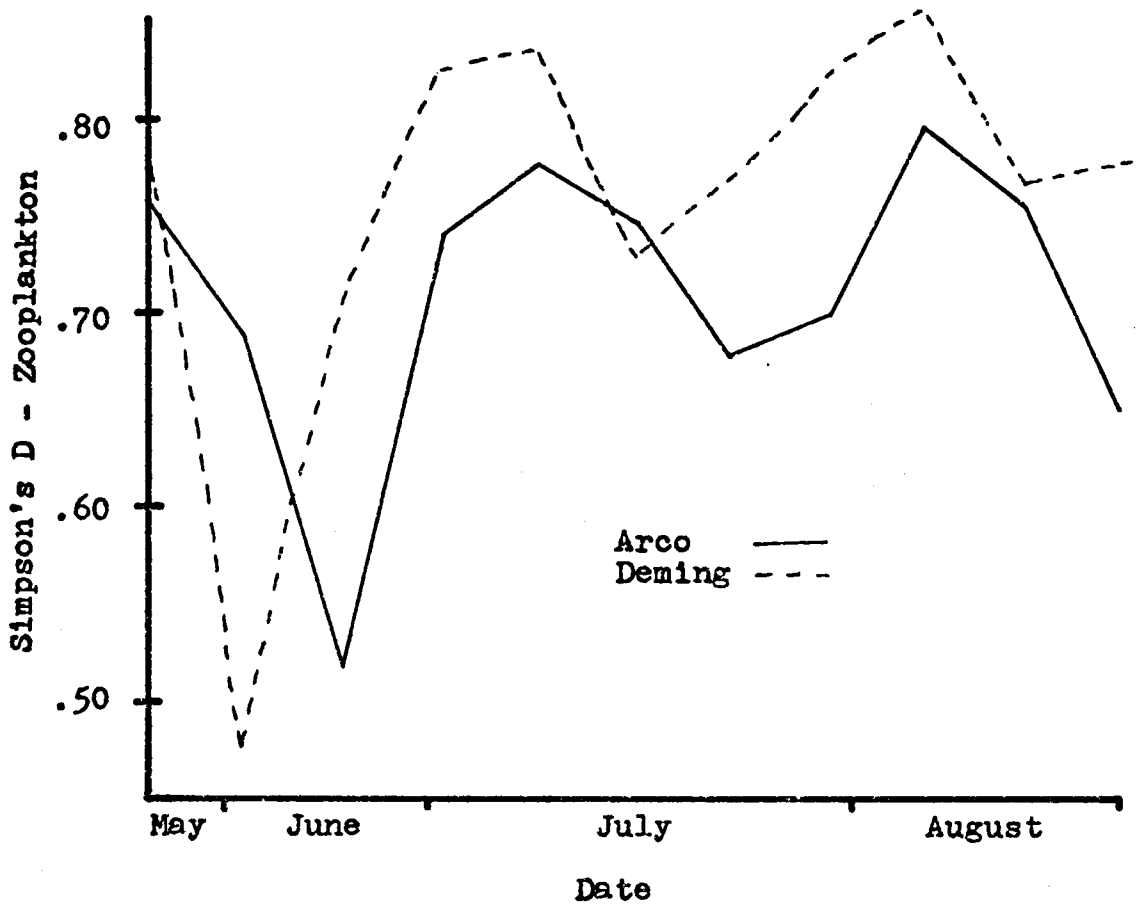


Figure 12. Zooplankton Species Diversity in Arco and Deming Lakes, Summer 1976

Table 2. Weighted Average Zooplankton Group Lengths (mm) in Arco and Deming Lakes, Summer 1976

	Date						
Group	21-5	25-6	9-7	30-7	13-8	20-8	Average
Rotifers							
Arco	.332	.648	.557	.546	.370	.275	.455
Deming	.152	.167	.178	.224	.220	.239	.222
Copepods							
Arco	---	2.010	.799	.646	.540	.573	.910
Deming	.632	.773	.725	.578	.565	.433	.618
Cladocerans							
Arco	1.093	1.568	1.567	.683	.901	1.682	1.249
Deming	---	.991	---	.891	.848	.401	.783
Zooplankton Length ($\bar{x}$)							
Arco	.472	.690	.723	.570	.449	.383	.548
Deming	.345	.241	.237	.328	.391	.335	.313

by insect larvae is presumably lower than in early or late summer (immediatly prior to emergence).

Zooplankton sizes were grouped in .250 mm intervals and graphed by relative abundance for the summer (Figs. 13 and 14). The smallest size interval (.250 mm) is the most abundant in Deming, while larger size intervals are more abundant in Arco. Neither of the two largest intervals (.750-1.000 mm and >1.000 mm) were present in Deming for the entire summer.

Because the zooplankton biomass samples were collected in the same net haul as the phytoplankton samples, the zooplankton biomass estimates are subject to the same suspected error as the phytoplankton biomass estimates. It is not possible to speculate on the true relative weights.

Although the relative numbers of zooplankton may be suspect, another factor may be more important. Shapiro et al note that the size of the zooplankton may exert a greater influence on grazing rate because of the greater filtering rates associated with larger zooplankton. As mentioned, sizes of zooplankton, particularly weighted average sizes, are greater in Arco, where vertebrate predator pressure is nonexistent. This is in accordance with the size-selective predation and biomanipulation theories, which state that zooplankton sizes should be larger where vertebrate predator pressure is less intense. So, in this respect, biotic conditions in the lakes correlate well with the theory.

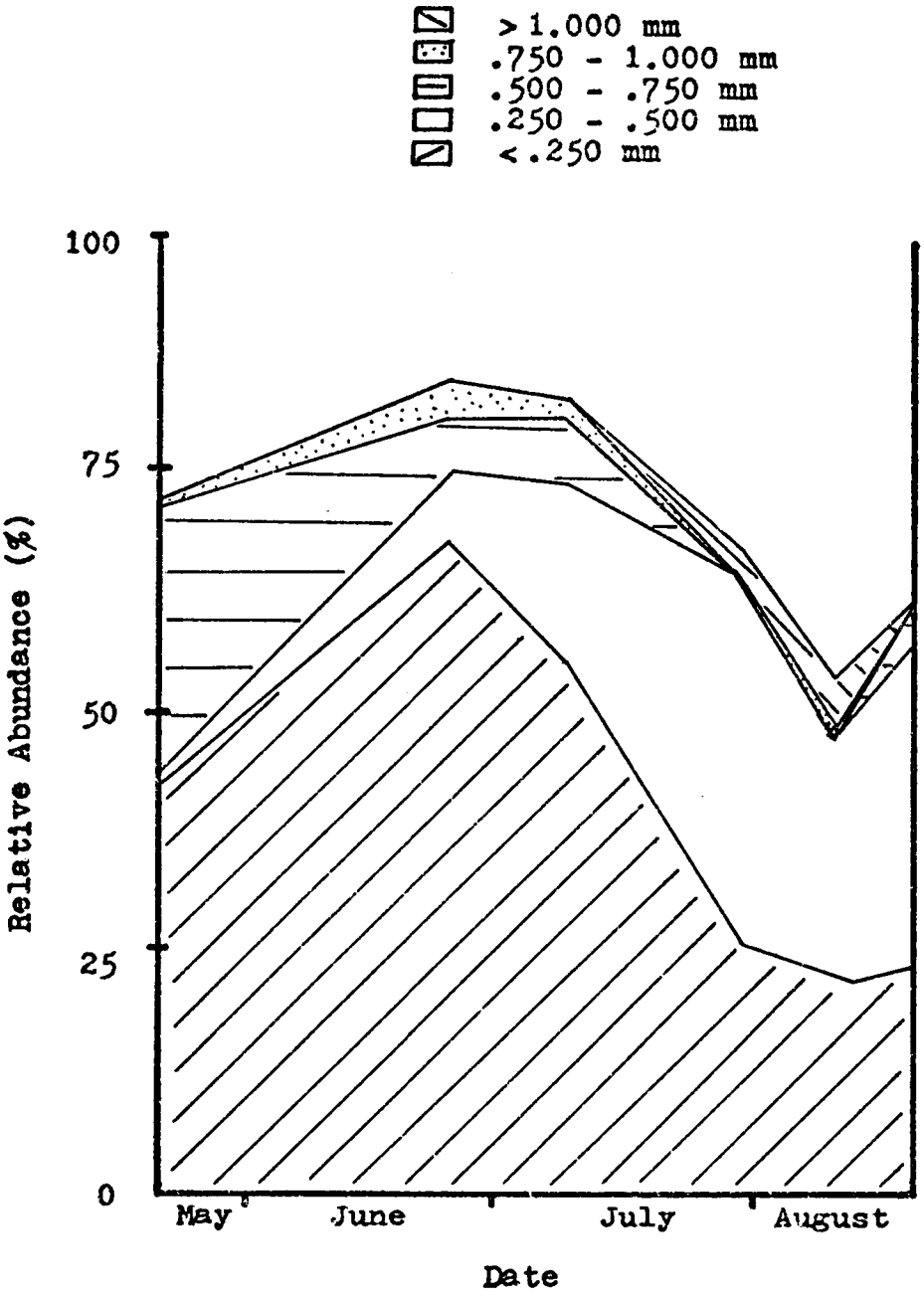


Figure 13. Relative Abundance of Deming Zooplankton Size Classes, Summer 1976

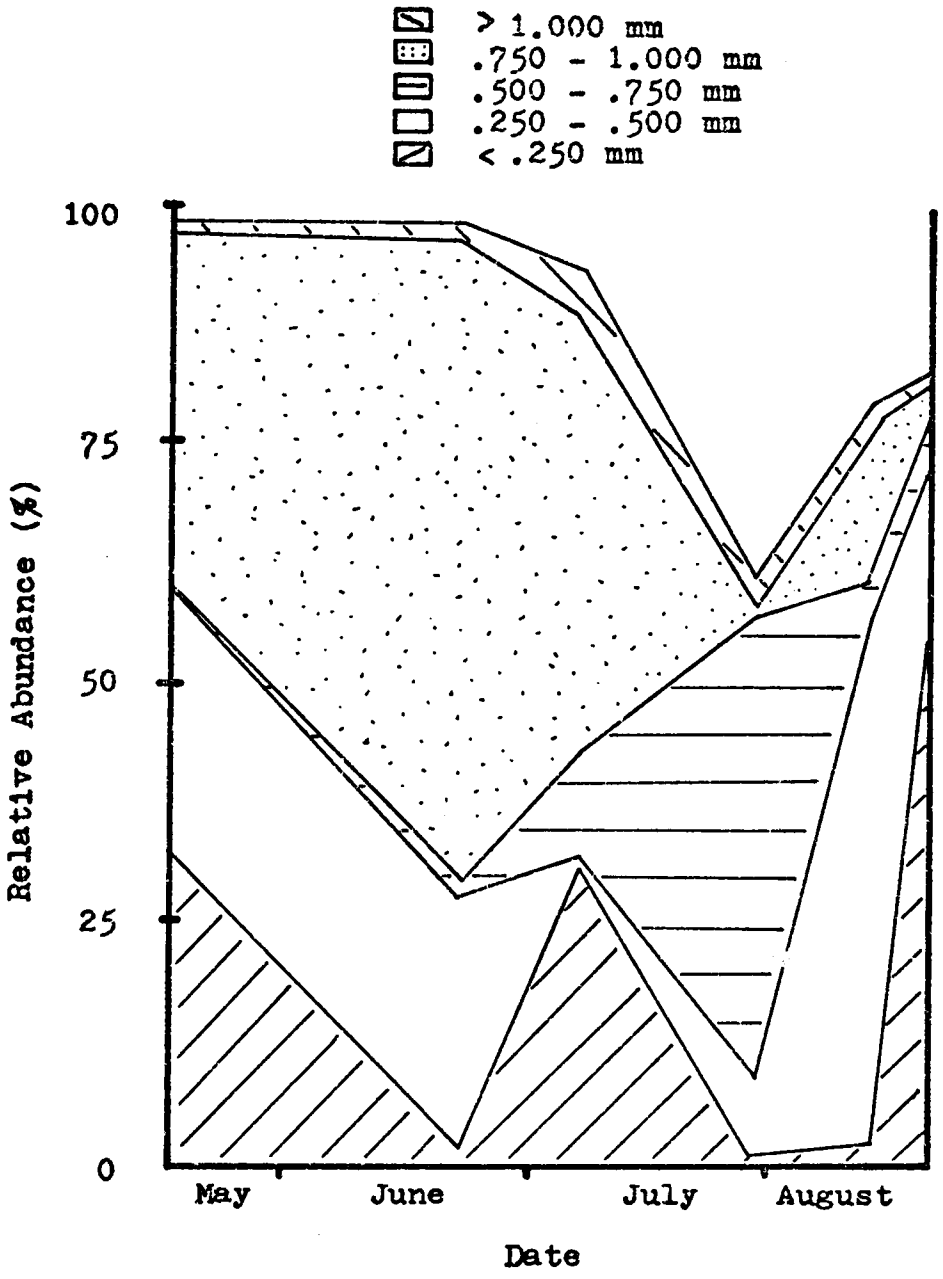


Figure 14. Relative Abundance of Arco Zooplankton Size Classes, Summer 1976

IV. EXPERIMENTS

Four experiments, designed to explore the interrelationships among trophic levels, were conducted during summer 1976. Experiment 1 was an observation of the grazing abilities of the larger zooplankton of Arco Lake on the phytoplankton of Deming Lake. The experimental and control columns contained Deming phytoplankton and any zooplankton passing through the 1 mm screen; these organisms were introduced as the column was inserted into the lake waters. In addition, the experimental column was stocked with zooplankton from Arco Lake. A 153 micron net was drawn thrice vertically through Arco and the zooplankton collected were placed into the experimental column. The smaller zooplankton passed through this size mesh, so the total effect of stocking was less than a three-fold increase of zooplankton. Fluorometer readings were taken initially and at the conclusion of the experiment to determine changes in algal standing crop; these samples were pumped from specific depths with a discrete-level sampler (Klemer, 1973). Changes in phytoplankton species composition were checked from these samples, while changes in zooplankton species composition were checked from a 64 micron net haul. The experiment ran for five days.

There was a significant reduction in algal biomass at 5 meters depth, as indicated by the fluorometer readings (Table 3). Concentrations of Oscillatoria redekei colonies were significantly reduced (Table 4). Three other algal

Table 3. Results of Experiment 1: Changes in Deming Phytoplankton Biomass Due to Arco Zooplankton Grazing. The Fluorometer Readings Shown in the Table are the Differences Between Initial and Final Conditions for the Lake, Control Column, and Experimental Column.

Depth (m)	Lake	Control	Experiment
1	-2.5	-2.5	-3.0
2	-2.0	-2.5	-2.5
3	-1.5	-3.0	-1.5
4	-1.0	-8.0	-9.0
5	-8.0	-8.0	-13.0

Table 4. Results of Experiment 1: Major Changes in Deming Phytoplankton Composition at Five Meters After Five Days

Species	Colonies/ml		%	
	Control	Experiment	Control	Experiment
Oscillatoria redekei	+2080	-4800	0	-10
Oscillatoria agardhii	+2480	-880	-3	0
Oscillatoria sp.	+1040	-1760	+2	-4
Anabena cylindrica	+1760	-1440	+1	-3

species experienced a reduction in numbers in the experimental column, while undergoing an increase in the control column. None of these species approached the change of Oscillatoria redekei. All species showing significant decreases were Cyanophyceae. Several Bacillariophyceae (Melosira sp., Synedra sp., Rhizosolenia sp.) and Chlorophyceae (Chlamydomonas sp. and Dimorphococcus sp.) also decreased in the experimental column while increasing in the control. However, these species represented less than 1% of the phytoplankton composition change.

Final species diversity (Simpson's D) at 5 meters depth was greater in the experimental column (.817) than in the control column (.779).

Experiment 2 was an attempt to determine the effect of exposing Arco zooplankton to vertebrate predator pressure. Columns were reinserted after the first experiment, enclosing the Deming plankton. Six fathead minnows (Pimephales promelas) were added to the experimental column. Algal standing crop was determined from fluorometer readings, algal composition from pumped samples, and zooplankton composition from a 64 micron net haul. Experiment 2 was equilibrated for two days to determine the effect of adding the planktivores to the column before the addition of the Arco zooplankton. Both columns were stocked with three 153 micron net hauls of Arco zooplankton.

This experiment produced no tenable results, because

the Daphnia pulex died in both columns after five days, presumably due to causes other than vertebrate predation. Observations in Arco Lake showed this particular week to be the beginning of the summer population crash exhibited by many zooplankton. However, the lack of decrease in fluorometer reading in the control column, which was equivalent to the experimental column in experiment 1, suggests that Daphnia pulex may have been largely responsible for the grazing effect in experiment 1.

The third experiment was a determination of the effect of the largest zooplankter from Arco, Daphnia pulex, on the densest concentration of phytoplankton in Deming Lake. Lake water and phytoplankton were pumped from 4.5 meters in Deming and placed in 2 one gallon jugs. A dozen Daphnia pulex were added to the experimental jug, and both jugs were resuspended at 4.5 meters from a mooring. Fluorometric readings were taken to determine changes in standing crop, and qualitative counts determined changes in species composition. The experiment was continued for three days.

The difference in fluorometer readings between experiment and control was 5 units, although the decrease in the experimental jug was only 1 unit from initial to final readings (Table 5). A greater decrease would have probably occurred if the nutrients from dead materials were lost by sedimentation, rather than retained in the jugs.

Because the experimental procedure was designed to produce equivalent initial conditions in the jugs, and

Table 5. Results of Experiment 3: Changes in Deming Phytoplankton Biomass Due to *Daphnia pulex* Grazing. The Fluorometer Readings Shown in the Table are the Differences Between the Control and Experiment Chambers.

Depth (m)	Control	Experiment
4.5	+4	-1

initial conditions were not checked, changes in the two jugs were measured against each other. Oscillatoria redekei again showed the greatest decrease in numbers, but Chlorophyceae accounted for the remaining significant changes in algae (Table 6). Species diversity was lower in the experimental jug (D=.746 to D=.794 in the control), as Cyanophyceae and Cryptophyceae increased their numerical dominance.

Experiment 4 was an observation of invertebrate predation by aquatic insect larvae on Arco zooplankton. Three 153 micron net hauls of Arco zooplankton were placed in each of three two-liter flasks in the laboratory. One flask served as the control, a second flask was stocked with about 20% of the Chaoborus larvae (phantom midge) found in one net haul, and a third flask was stocked with three Dytiscid larvae (predacious diving beetle). These experiments ran for three days, and were checked for changes in species composition as a means of determining the diet of the insect larvae.

Chaoborus larvae consumed mainly rotifers (Keratella cochlearis, Asplancha sp.) and Cladocera (Moina sp., Diaphanosoma brachyurum) (Table 7); Daphia pulex were not included in this experiment because the lake populations had declined to a very low level.

Dytiscid larvae also consumed mainly Cladocera (Moina sp., Diaphanosoma brachyurum) and a rotifer (Keratella cochlearis), and had been observed to attack and partially consume Chaoborus larvae (Table 8).

Table 6. Results of Experiment 3: Major Changes in Deming Phytoplankton Composition in the Experiment Chamber Compared to the Control Chamber

Species	Colonies/ml	%
Oscillatoria redekei	-440	-4
Arthrospira sp.	-400	-2
Chlamydomonas sp.	-320	-3

Table 7. Results of Experiment 4: Major Changes in Arco Zooplankton Composition Due to *Chaoborus* Predation

Species	Organisms/50 ml Control	Experiment	%
Moina sp.	16	1	-94
Diaphanosoma brachyurum	13	1	-92
Keratella cochlearis	219	96	-56
Kellicottia longispina	143	84	-41

Table 8. Results of Experiment 4: Major Changes in Arco Zooplankton Composition Due to Dytiscid Predation

Species	Organisms/50 ml Control	Experiment	%
Moina sp.	16	4	-75
Diaphanosoma brachyurum	13	8	-38
Keratella cochlearis	219	184	-16

Experiments 1 and 3 support the biomanipulation theory through the reduction of algal biomass by the large zooplankton existing under reduced vertebrate predator pressure. Apparent subsistence of Daphnia pulex on Oscillatoria redekei without stimulation of primary production contradicts the findings of Arnold (1971), Schindler (1971), Porter (1973, 1976), and Gliwicz (1975). For the most part, the Cyanophyceae used in their experiments were larger in size and had thicker mucopolysaccharide sheaths than Oscillatoria redekei. Zooplankton used in those experiments were also smaller in size, and thus probably had lower filtering capacities and rates. It is possible that each species of zooplankton has specific ingestive, assimilative, and digestive responses to each species of algae (Arnold, 1971, Schindler, 1971).

Experiment 4 indicates that invertebrate predation can significantly reduce smaller-sized zooplankton populations; the largest genera, Epischura and Diaptomus, were not reduced by insect predation. This is another factor which must be considered with vertebrate predation on zooplankton.

V. GENERAL DISCUSSION

Phytoplankton species diversity was generally greater under heavier grazing pressure. This is evident in comparison of the control and experimental columns in experiment 1, where the final diversity for the control was .779 and for the experiment .817. Arco Lake had consistently greater diversity values than Deming Lake (Fig. 9, p. 19). Hall et al (1970) have noted that grazing tends to increase floral diversity; Janzen (1970) has observed the same phenomenon with terrestrial flora.

Experiment 3 contradicts the above results, but for an explainable reason. The reduced volume of the experimental chamber (1 gallon) allowed grazing to reduce the edible algae to a point where the inedible algae were able to increase their numerical dominance, presumably due to a release from competition. This opposing response agrees with Harper's (1969) contentions; his experiments on terrestrial flora showed changes in diversity resulting from grazing to be dependent upon the edibility of the plants.

Looking at the broad categories of edibility (Table 9) as determined from experiments 1 and 3 and Porter (1973), the edible species in both lakes greatly outnumber the nonedible species in the early summer, but they decline through the summer as the nonedible species undergo a tremendous increase (Figs. 15, 16).

Allowing nonedible algae to increase their dominance as edible stocks are reduced will not perpetuate the grazers.

Table 9. Phytoplankton Species Edibility in Deming and Arco Lakes, Determined from Experiments 1 and 3, and from Porter (1973)

Species	Edible	Nonedible
Cyanophyceae		
Oscillatoria agardhii		x
Oscillatoria redekei	x	
Oscillatoria sp.		x
Arthrospira sp.		x
Lyngbya limnetica		x
Anabena cylindrica		x
Merismopedia sp.		x
Microcystis sp.		x
Gomphosphaeria sp.		x
Aphanocapsa sp.		x
Cryptophyceae		
Cryptomonas erosa	x	
Cryptomonads	x	
Euglenophyceae		
Euglena sp.	x	
Phacus sp.	x	
Chrysophyceae		
Synura sp.		x
Dinobryon sp.		x
Bacillariophyceae		
Melosira sp.	x	
Synedra sp.	x	
Rhizosolenia sp.	x	
Chlorophyceae		
Chlamydomonas sp.	x	
Schroederia sp.	x	
Ankistrodesmus sp.	x	
Selenastrum sp.	x	
Scenedesmus sp.	x	
Dimorphococcus sp.	x	
Chlorella sp.	x	
Chlorogonium sp.	x	
Closterium sp.	x	
Steurastrum sp.	x	
Crucigenia sp.	x	
Pyrrophyceae		
Peridinium sp.	x	

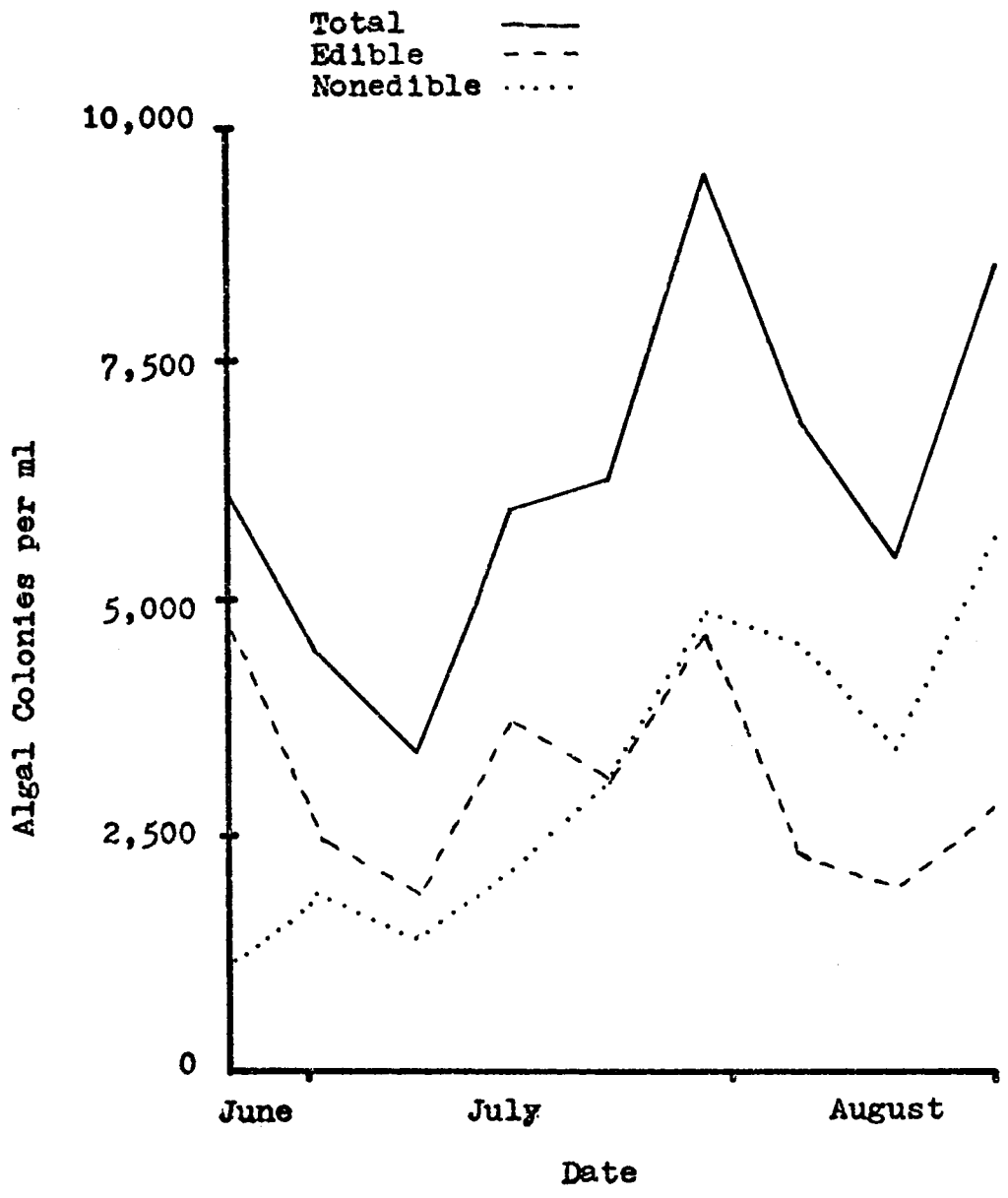


Figure 15. Edible and Nonedible Phytoplankton Colonies per Milliliter in Arco Lake, Summer 1976

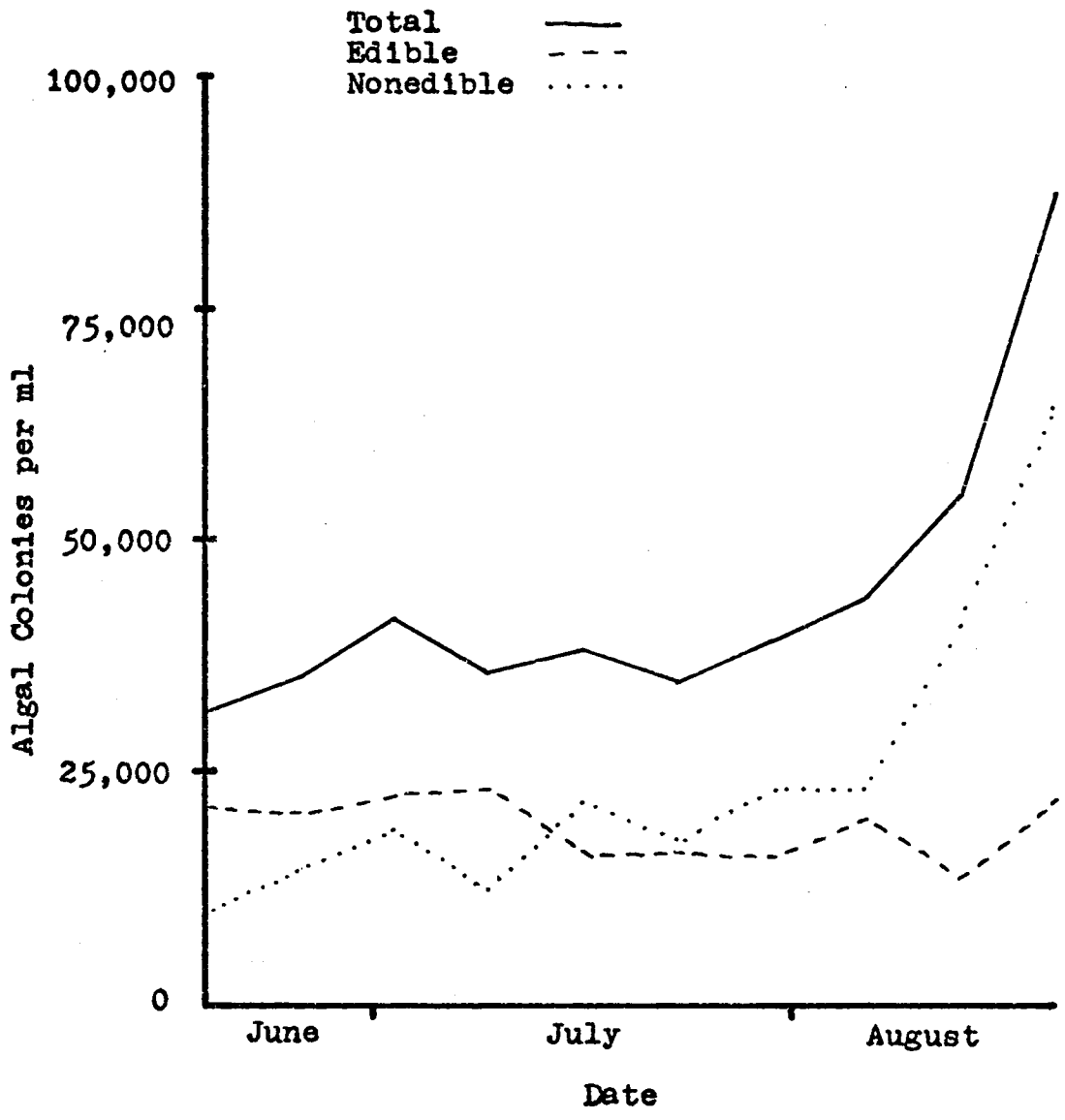


Figure 16. Edible and Nonedible Phytoplankton Colonies per Milliliter in Deming Lake, Summer 1976

Birth rates have been demonstrated to decline as suboptimal foods are selected (Arnold, 1971). The reduction of optimal foods in late summer coupled with increased vertebrate and invertebrate predation, as immature organisms develop, may form a complex of factors responsible for zooplankton population crashes. Perhaps artificial lake circulation would help correct this problem by allowing edible algae to increase over inedible algae and by decreasing the concentration of prey for the fish.

Predation increases diversity by reducing dominance (Paine, 1966, Hall et al, 1970), and zooplankton species diversity was found to be greater in Deming, where the vertebrate predation pressure was greater (Fig. 12, p. 24). Arco Lake, with less diversity, had two rotifer species which clearly dominated the zooplankton numbers.

These experiments accentuate the simplest type of food chain relationship envisioned for biomanipulation. A number of studies describe more complex interactions in the trophic system than Shapiro et al's piscivore--planktivore--zooplankton--phytoplankton system. Fedorenko (1975) and Johnson (1973) have investigated the zooplankton diet of aquatic insect larvae. Sprules (1972) cited salamander predation as a factor in the elimination of large zooplankton from certain ponds. Dodson (1974) has modified the size-efficiency hypothesis to include invertebrate predation on zooplankton. His experiments indicated that certain species of large zooplankton eliminated small zooplankton by predation.

Hall et al (1976) note that some large copepods (Epischura, Mesocyclops, Diaptomus, Cyclops) and Cladocera (Leptodora, Polyphemus) may be predacious, but some large Cladocera are primarily herbivorous (Daphnia, Diaphanosoma, Moina). Protozoa (Canter and Lund, 1968), crayfish (Flint and Goldman, 1975), and tadpoles (Dickman, 1968) may also exert significant grazing effects. Additionally, it is becoming clear that diet varies for all species, and diet for each species may change depending on the life cycle stage (McQueen, 1969, Dodson, 1975, Fedorenko, 1975). In this light, the concept of trophic levels loses meaning (Rigler, 1975).

Thus, trophic systems are more complex than chain-like interactions. Invertebrate predation pressure does occur on Arco zooplankton, mostly by aquatic insects and larvae (Chaoborus, Anisopterae, Dytiscidae, Trichoptera, Gyrinidae, Notonectidae, Belostomidae), leeches (Placobdella sp. and Haemopis sp.), and possibly zooplankton (Epischura, Diaptomus, Cyclops) (Barnes et al, 1976). But, judging from the zooplankton sizes in Arco Lake, invertebrate predation is not as intense as is vertebrate predation in Deming Lake.

Hall et al (1976) contrast vertebrate (fish) and invertebrate (insect) predation on zooplankton. Vertebrate predation is primarily visual, and vertebrates consume more than their own weight daily. Conversely, invertebrate predation is primarily tactile, and invertebrates consume less than their own weight daily. While large Daphnia are not too large for predation by certain aquatic insects, this

invertebrate predation falls more heavily on the smaller zooplankton. Again judging from results in Arco Lake, invertebrate predation may effect the population size of large zooplankton, but does not seem to eliminate them as vertebrate predation does.

Much of the evidence for the biomanipulation theory is derived from studies of population and community interactions. Some of these interactions appear contradictory to the theory, but the desired end result of biomanipulation is actually viewed from an ecosystem perspective. Community parameters in Arco Lake (i.e. lower algal numbers, greater zooplankton biomass, and larger zooplankton size) correlate well with those expected in the absence of vertebrate predation pressure, and presumably result from dynamics of the system. More importantly, the reduction of phytoplankton standing crop in experiments 1 and 3 (Table 3, p. 30, Table 5, p. 33) illustrate an effect from a cause. On the basis of the results in these interactions from this pilot study, the theory of biomanipulation appears plausible.

Applying biomanipulation to an entire lake for at least one season may encounter some problems. This study considered only the limnetic region, and neglected interactions between the littoral and limnetic regions. For example, would increased transparency (lower phytoplankton abundance) allow macrophytes to proliferate (Straškraba, 1965)? What would happen on a lake-wide basis for an entire season? How long would the effect of biomanipulation persist?

The ultimate test of biomanipulation is to determine its long-term effectiveness in the face of nutrient influx.

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APPENDICES

APPENDIX A. PHYSIOCHEMICAL PARAMETERS

Table A-1. Temperature Data (°C) in Deming Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	19.5	19.5	21.0	23.0	24.5	22.5	25.5	24.9	24.0	23.0	24.7
1	18.5	19.5	21.0	23.0	24.5	22.0	25.5	24.9	24.0	22.5	24.4
2	18.0	19.0	21.0	22.5	24.0	22.0	25.0	24.3	22.6	22.5	23.0
3	14.5	19.0	19.0	20.5	21.5	22.0	23.5	23.8	22.4	22.5	22.4
4	10.0	12.0	14.0	15.0	15.5	16.0	17.5	18.5	18.2	18.5	19.4
5	7.0	9.0	9.5	10.0	10.5	11.0	11.5	11.2	12.3	12.0	12.9
6	6.0	7.0	7.5	7.5	7.5	8.0	7.5	8.4	8.6	8.0	9.0
7	6.0	6.0	6.0	6.5	6.5	6.5	6.5	6.6	7.0	6.5	7.0
8	5.5	5.5	5.5	6.0	5.5	6.0	5.5	5.9	6.3	6.0	6.0
9	5.5	5.0	5.0	6.0	5.5	6.0	5.5	5.7	6.0	5.5	5.7
10	5.5	5.0	5.0	5.5	5.5	5.5	5.5	5.4	5.8	5.5	5.1

Table A-2. Temperature Data (°C) in Arco Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	18.5	21.5	22.0	24.5	26.7	23.3	24.4	24.0	22.2	23.0	24.5
1	17.0	21.3	22.0	23.0	25.0	23.3	24.2	23.9	22.2	23.0	24.0
2	16.0	20.0	22.0	22.5	24.7	23.0	24.1	23.8	22.2	23.0	23.3
3	15.0	19.8	21.0	22.0	24.1	22.8	24.0	23.7	22.2	23.3	22.7
4	12.5	16.0	17.5	19.0	20.0	20.6	21.5	22.5	22.1	22.5	22.3
5	9.0	12.5	14.0	14.5	15.1	15.7	16.9	17.6	17.5	18.0	18.9
6	8.0	10.5	11.5	12.0	12.6	12.4	13.9	13.8	13.4	14.0	14.6
7	7.0	8.5	8.5	10.0	9.5	9.8	10.5	10.7	10.2	11.0	11.3
8	6.5	7.0	7.5	8.0	8.3	7.8	8.5	8.8	8.0	8.5	8.6
9	6.0	6.5	7.0	7.0	7.5	7.0	7.6	8.0	7.0	7.5	8.0
10	--	6.0	6.5	7.0	7.1	6.8	7.2	7.7	6.7	7.0	7.8

Table A-3. Dissolved Oxygen Data (mg/l) in Deming Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	--	6.9	7.2	8.6	8.0	7.9	8.0	8.0	7.3	9.1	8.4
1	9.8	5.8	8.4	9.2	8.3	8.3	8.2	8.0	8.2	9.0	8.5
2	10.5	6.4	8.7	9.3	7.4	8.6	8.0	8.4	8.8	9.0	9.7
3	13.7	7.3	9.4	9.4	10.6	8.6	7.8	8.8	7.2	8.8	9.2
4	12.3	7.5	13.2	15.2	15.7	16.8	16.1	16.5	16.4	14.4	14.2
5	1.2	7.4	8.4	11.4	10.2	4.6	9.9	5.4	8.7	7.2	1.7
6	0	4.4	2.2	0.6	0	0.5	0.2	0	0.2	0	0
7	0	0.1	5.6	0	0	0	0	0	0	0	0
8	--	1.4	0	0	0	0	0	0	0	0	0.5

Table A-4. Dissolved Oxygen Data (mg/l) in Arco Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	--	7.0	6.4	7.4	7.5	7.4	7.7	6.4	7.4	7.6	7.4
1	8.7	8.2	7.3	7.8	7.6	7.4	7.6	7.0	7.6	7.6	7.8
2	--	7.9	6.6	7.8	7.6	7.6	7.6	7.0	7.4	6.9	8.2
3	9.9	8.2	7.1	7.8	7.5	7.6	8.4	6.9	7.4	7.5	8.2
4	12.9	12.1	11.4	11.7	9.8	10.1	9.8	8.9	7.4	7.1	7.3
5	12.8	10.0	10.1	11.1	12.1	10.8	11.5	11.4	9.2	9.2	8.4
6	10.2	3.1	5.4	1.3	3.6	2.0	1.8	2.2	1.6	3.1	1.9
7	--	0.3	8.2	0	0.3	0.8	0.7	0.3	0.4	0.3	0.6
8	0	0.1	7.9	0	0	0.2	0.1	0	0	0.2	0

Table A-5. Secchi Disk Transparencies (m) in Deming and Arco Lakes, Summer 1976

Date	Deming Lake	Arco Lake
21-5	1.75	5.00
18-6	1.77	3.45
25-6	2.00	4.30
2-7	1.95	5.75
9-7	2.28	5.90
16-7	2.11	6.12
23-7	2.40	6.10
30-7	2.25	6.30
6-8	1.90	6.00
13-8	2.00	5.33
20-8	1.83	5.00

Table A-6. Alkalinity Data (meq/l) in Deming Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	--	.57	.57	.55	.67	.60	.62	.72	.56	.62	.64
1	--	.58	.55	.57	.61	.66	.60	.59	.57	.63	.64
2	.55	.60	.58	.56	.66	.68	.58	.64	.56	.63	.70
3	.51	.60	.58	.61	.61	.68	.58	.58	.56	.63	.68
4	.59	.68	.63	.58	.65	.72	.62	.64	.58	.65	.69
5	.62	.74	.64	.67	.71	.65	.55	.50	.54	.56	.65
6	--	.84	.76	.77	.92	.85	.86	.62	.78	.91	.95
7	.83	1.01	.61	.89	.97	1.10	.90	.85	.82	.92	.92
8	--	.85	.96	.55	.94	1.10	.92	.88	.85	.92	.94

Table A-7. Alkalinity Data (meq/l) in Arco Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	--	.70	.64	.57	.62	.59	.76	.63	.66	.72	.72
1	.57	.64	.62	.61	.75	.62	.74	.66	.60	.67	.69
2	.56	.66	.61	.60	.70	.60	.73	.63	.63	.68	.72
3	.54	.65	.62	.64	.74	.61	.69	.66	.59	.71	.70
4	.61	.69	.62	.62	.86	.63	.78	.66	.63	.68	.70
5	.67	.74	.68	.68	.88	.71	.76	.71	.66	.74	.76
6	--	.83	.74	.71	.98	.70	.88	.76	.72	.86	.82
7	--	.89	.61	.76	1.02	.74	.88	.78	.74	.83	.85
8	--	--	.62	1.31	1.05	.99	1.17	1.05	.94	.92	1.18

Table A-8. pH Data (pH units) in Deming Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	--	8.2	8.4	7.6	8.2	7.6	7.3	7.1	7.6	7.1	6.9
1	--	8.3	8.5	7.1	7.1	8.1	6.7	7.2	7.7	7.1	6.8
2	8.2	8.3	7.5	7.3	6.8	8.2	6.5	7.3	7.7	7.2	6.9
3	8.6	8.4	7.2	7.0	7.2	8.2	6.4	7.5	7.7	7.1	6.8
4	7.4	8.5	7.3	7.6	7.6	8.6	7.9	8.6	8.2	7.2	6.8
5	6.3	7.3	7.1	6.6	6.6	7.7	6.0	8.0	7.9	7.2	6.9
6	--	6.8	6.5	6.4	6.4	7.3	6.0	7.4	7.4	7.2	6.8
7	6.3	6.4	7.2	6.3	6.4	6.8	6.0	7.2	7.3	7.0	6.8
8	--	6.4	6.5	7.0	6.4	6.8	6.0	7.0	7.4	7.0	6.5

Table A-9. pH Data (pH units) in Arco Lake, Summer 1976

	Date										
z	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
0m	--	6.8	7.0	7.1	7.2	7.3	7.3	7.3	7.2	7.5	7.1
1	6.9	7.1	6.9	6.6	7.2	6.7	7.1	6.3	6.9	7.5	7.1
2	6.6	7.2	6.8	6.7	7.2	6.5	6.8	6.2	7.0	7.6	7.3
3	6.6	7.4	7.0	6.7	7.2	6.5	6.8	6.3	7.2	7.5	7.5
4	6.9	7.2	7.1	6.7	7.1	6.5	6.9	6.3	7.1	7.8	8.0
5	6.9	7.1	7.0	6.4	7.2	6.5	7.0	6.2	7.2	7.7	7.4
6	--	6.9	6.8	6.3	7.1	6.4	6.9	6.1	7.2	7.3	7.0
7	--	6.8	7.0	6.2	7.0	6.4	6.8	6.3	7.2	7.1	6.8
8	--	6.6	6.9	6.2	6.9	6.3	6.7	6.1	7.1	7.0	6.6

Table A-10. Conductivity Data (micromhos/cm) in Deming Lake, Summer 1976

	Date									
z	21-5	18-6	25-6	2-7	9-7	23-7	30-7	6-8	13-8	20-8
0m	--	49	64	67	71	66	64	68	61	65
1	--	64	65	68	71	67	63	66	61	64
2	68	66	65	68	70	67	64	68	61	64
3	65	65	64	67	70	71	63	68	60	65
4	71	40	66	68	73	72	70	68	67	65
5	76	66	67	69	71	57	53	68	53	73
6	--	66	74	76	96	80	92	90	87	77
7	93	86	62	91	96	85	98	97	90	79
8	--	86	95	63	98	82	102	98	90	115

Table A-11. Conductivity Data (micromhos/cm) in Arco Lake, Summer 1976

	Date									
z	21-5	18-6	25-6	2-7	9-7	23-7	30-7	6-8	13-8	20-8
0m	72	74	66	72	75	81	64	63	62	65
1	74	73	66	72	74	76	64	63	63	65
2	70	72	66	71	73	62	61	65	63	66
3	89	72	67	70	72	63	69	65	61	64
4	75	71	68	72	71	65	66	64	62	67
5	85	75	74	75	74	61	72	73	67	61
6	85	81	80	80	80	64	77	78	72	86
7	94	83	67	82	82	66	77	80	74	98
8	101	100	67	130	99	76	116	108	79	97

APPENDIX B. PHYTOPLANKTON

Table A-12. Phytoplankton Biomass (gm) in Deming Lake, Summer 1976

Date	35 micron net	64 micron net	Total (35+64)
21-5	.1873	.1759	.3632
18-6	---	.1755	---
2-7	.4397	.6694	1.1091
9-7	.1345	.0962	.2307
16-7	.0557	.1345	.1902
23-7	.0331	.0276	.0607
30-7	.0640	.0631	.1271
6-8	.0781	.0515	.1296
13-8	.0289	.0538	.0827
20-8	.0229	.0377	.0606

Table A-13. Phytoplankton Biomass (gm) in Arco Lake, Summer 1976

Date	35 micron net	64 micron net	Total (35+64)
21-5	2.5016	1.9718	4.4734
25-6	.4409	.2974	.7383
2-7	.2481	.6312	.8793
9-7	.0175	.0512	.0687
16-7	.0721	.1729	.2450
23-7	.0727	.1178	.1905
30-7	.0907	.1229	.2136
6-8	.0506	.1208	.1714
13-8	.2688	.2889	.5577
20-8	.3324	.1155	.4479

List of Symbols for Tables A-14, A-15, A-16.

Cyanophyceae	
Oscillatoria agardhii	Os. a.
Oscillatoria redekei	Os. r.
Oscillatoria sp.	Os.
Arthrospira sp.	Arth.
Lyngbya limnetica	Ly. l.
Anabena cylindrica	An. c.
Merismopedia sp.	Mer.
Microcystis sp.	Mic.
Gomphosphaeria sp.	Gom.
Aphanocapsa sp.	Aph.
Cryptophyceae	
Cryptomonas erosa	Cr. e.
Cryptomonads	Cry.
Euglenophyceae	
Euglena sp.	Eug.
Phacus sp.	Pha.
Chrysophyceae	
Synura sp.	Syn.
Dinobryon sp.	Din.
Bacillariophyceae	
Melosira sp.	Mel.
Synedra sp.	Syd.
Rhizosolenia sp.	Rhi.
Chlorophyceae	
Chlamydomonas sp.	Chl.
Schroederia sp.	Sch.
Ankistrodesmus sp.	Ank.
Selenastrum sp.	Sel.
Scenedesmus sp.	Scen.
Dimorphococcus sp.	Dim.
Chlorella sp.	Cla.
Chlorogonium sp.	Clgn.
Closterium sp.	Clos.
Steurastrum sp.	Steu.
Crucigenia sp.	Cru.
Pyrrophyceae	
Peridinium sp.	Per.
Species Diversity	Sp. D.
Less than 1%	*

Table A-14. Deming Lake Phytoplankton Composition (colonies/ml), Summer 1976

Species	Date									
	19-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
Os. a.	3,680	2,760	5,360	3,480	4,240	3,640	2,120	1,640	1,600	3,520
Os. r.	18,960	19,440	19,160	20,680	14,320	14,200	13,520	17,720	11,800	19,520
Os.	760	2,320	2,600	1,000	760	2,200	1,440	1,560	1,440	6,880
Ly. l.	2,960	7,600	7,960	5,640	13,720	8,480	15,480	15,720	27,960	42,800
An. c.	2,240	1,520	2,320	1,920	2,800	3,280	3,840	3,760	9,560	10,160
Mic.	80	160	160	240	80	80	40	0	80	0
Mer.	0	40	0	0	0	40	0	40	40	0
Gom.	40	0	280	240	0	120	0	40	120	80
Aph.	0	0	0	0	0	40	40	40	40	160
Cr. e.	120	120	80	120	120	40	80	80	40	0
Cry.	600	200	680	1,400	880	1,200	1,040	1,160	920	800
Eug.	40	120	200	120	360	160	200	120	0	0
Syn.	360	0	280	80	160	80	280	360	360	720
Mel.	0	0	0	0	0	0	240	40	0	160
Syd.	360	280	560	400	240	160	240	720	520	640
Rhi.	0	0	0	0	0	160	240	80	0	0
Chl.	240	0	200	360	240	120	0	160	40	400
Sch.	0	0	160	120	120	120	160	0	0	0
Ank.	160	0	80	120	40	80	120	0	0	0
Scen.	0	0	0	0	0	0	0	0	0	160
Dim.	200	0	40	0	0	80	0	160	200	160
Clos.	0	0	960	0	0	0	0	0	0	0
Cla.	0	400	0	0	0	80	120	0	40	640
Clgn.	800	80	0	160	280	120	0	40	40	0
Per.	0	0	400	0	0	0	0	0	0	0

Table A-15. Deming Lake Phytoplankton Composition (%), Summer 1976

Species	Date 19-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
Os. a.	12	8	13	10	11	11	5	4	3	4
Os. r.	60	55	46	57	37	41	34	41	22	22
Os.	2	7	6	3	2	6	4	4	3	8
Ly. l.	9	22	19	16	36	25	39	36	51	49
An. c.	7	4	6	5	7	10	10	9	17	12
Mic.	*	*	*	*	*	*	*		*	
Mer.		*				*		*	*	
Gom.	*		*	*		*		*	*	*
Aph.						*	*	*	*	*
Cr. e.	*	*	*	*	*	*	*	*	*	
Cry.	2	*	2	4	2	3	3	3	2	*
Eug.	*	*	*	*	*	*	*	*		
Syn.	1		*	*	*	*	*	*	*	*
Mel.							*	*		*
Syd.	1	*	1	1	*	*	*	2	*	*
Rhi.						*	*	*		
Chl.	*		*	1	*	*		*	*	*
Sch.			*	*	*	*	*			
Ank.	*		*	*	*	*	*			
Scen.										*
Dim.	*		*			*		*	*	*
Clos.			2							
Cla.		1				*	*		*	*
Clgn.	3	*		*	*	*		*	*	
Per.			*							
Sp. D.	.610	.635	.726	.634	.700	.741	.716	.695	.659	.688

Table A-16. Arco Lake Phytoplankton Composition (colonies/ml and %), Summer 1976

Species	Date 25-6 No.	%	2-7 No.	%	9-7 No.	%	16-7 No.	%	23-7 No.	%	30-7 No.	%	6-8 No.	%	13-8 No.	%	20-8 No.	%
Os. r.			48	1	80	2	224	4			32	*			32	*	16	*
Os. a.							16	*	480	8	480	5	480	7	400	7	64	*
Os.	48	*	288	7	544	16	368	6	480	8	960	10	800	12	560	10	800	9
Arth.	640	11	1440	33	640	19	1600	27	2080	34	3312	38	3200	47	2400	44	4000	47
Ly. l.			32	*	160	5	64	1	16	*	16	*			48	*	240	3
An. c.	240	4	48	1	32	*	64	1	48	*			32	*			448	5
Gom.	16	*											32	*			32	*
Mer.			64	1	32	*	80	1			96	1			16	*	64	*
Aph.					32	*	16	*							16	*	16	*
Mic.	224	4																
Cr. e.	256	4	400	9	1008	30	2352	40	1936	31	3200	34	912	13	768	14	912	11
Cry.	3184	52	944	29	336	10	784	13	560	9	656	7	800	12	640	12	1280	18
Eug.	80	*	192	4	128	4	144	2	176	3	192	2	80	1	96	2	128	2
Din.																	64	*
Mel.			240	5	16	*			16	*					48	*	112	1
Syd.	64	1	128	3	16	*	16	*			96	1	128	2	64	1	112	1
Rhi.	64	1					16	*	16	*	32	*	32	*	48	*		
Chl.	96	2	160	4	160	5	48	*	112	2	128	1	144	2	64	1	176	2
Sch.	736	12	48	1	80	2	64	1	112	2	224	2	160	2	128	2		
Clgn.	336	5	224	5	48	1	32	*	160	3	96	1	64	*				
Clos.					16	*												
Steu.	48	*			16	*	48	*										
Cru.															80	1	16	*
Per.			96	2	32	*			16	*								
Sp. D.	.694		.819		.854		.744		.764		.721		.727		.756		.730	

APPENDIX C. ZOOPLANKTON

Table A-17. Zooplankton Biomass (gm) in Deming Lake, Summer 1976

Date	35 micron net	64 micron net	Total (35+64)
21-5	.1924	.2207	.4131
18-6	---	.2058	---
2-7	.1289	.2796	.4085
9-7	.0613	.0198	.0811
16-7	.0128	.0036	.0164
23-7	.0189	.0109	.0298
30-7	.0261	.0502	.0763
6-8	.0540	.0321	.0861
13-8	.0091	.0340	.0431
20-8	.0154	.0280	.0434

Table A-18. Zooplankton Biomass (gm) in Arco Lake, Summer 1976

Date	35 micron net	64 micron net	Total (35+64)
21-5	2.6254	3.0595	5.6849
25-6	.4722	.6393	1.1115
2-7	.5975	.8059	1.4034
9-7	.4011	.5077	.9088
16-7	.2143	.4522	.6665
23-7	.3962	.6478	1.0440
30-7	.6008	.9069	1.5077
6-8	.7535	.8858	1.6393
13-8	1.3710	.7842	2.1552
20-8	3.0348	2.9061	5.9404

Table A-19. Deming Lake Zooplankton Composition (%), Summer 1976

Species	Date										
	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
Cladocera											
Daphnia longispina			1	*	*			*	*	*	*
Copepoda											
Cyclops varicans	28	9	6	10	7	2	4	15	15	19	26
Diaptomus oregonesis		*	3	2	2	*	1	3	5	6	4
Nauplii & Copepodids	30	6	17	11	17	7	16	32	23	41	36
Rotifera											
Asplancha sp.						2	6	11	12	6	7
Brachionas quadridentata		*									
Conochilus sp.						*			2		
Filinia sp.				11	7	*	1				
Keratella cochlearis	26	71	49	14	12	27	5	6	10	12	8
Keratella quadrata	*	3	6	17	18	11	40	12	12	2	9
Polyarthra sp.	8		10	30	27	42	17	10	9		
Tetramastix opoliensis	7	9	9	5	3	5	1	5		1	1
Trichocerca sp.					6	2	9	4	7	7	6
Insecta											
Chaoborus sp.	*	*	*	*	*	*	1	3	6	6	2
Species Diversity	.790	.478	.713	.828	.836	.730	.769	.829	.861	.765	.778

* = less than 1%

Table A-20. Arco Lake Zooplankton Composition (%), Summer 1976

Species	Date										
	21-5	18-6	25-6	2-7	9-7	16-7	23-7	30-7	6-8	13-8	20-8
Cladocera											
Daphnia pulex	*	*	*	*	3	1	*	*	2	*	*
Diaphanosoma brachyurum	7	5	1	3	6	6	8	6	4	4	1
Moina sp.	10	7	2	2	3	2	*	1	1	1	*
Copepoda											
Cyclops varicans				3	4	4	2	9	16	14	14
Diaptomus oregonesis	*		1	2	8	5	2	1	2	3	1
Epischura sp.						2	*	2	1	*	*
Nauplii & Copepodids			2	2	2	1	4	5	16	17	11
Rotifera											
Asplancha sp.				4		*					1
Conochilus sp.						*					
Kellicottia longispina	20	10	66	42	34	41	49	48	22	12	5
Keratella cochlearis	27	15	20	25	29	26	26	22	30	41	56
Keratella quadrata	2	51									
Polyarthra sp.	33			11	2	3	3		1	2	2
Tetramastix opoliensis		10									
Trichocerca sp.			6	3	1	5	*				
Insecta											
Chaoborus sp.	*	*	2	2	9	4	2	5	6	6	7
Species Diversity	.763	.690	.519	.743	.778	.750	.681	.704	.804	.762	.646

* = less than 1%

Table A-21. Mean Lengths of Zooplankton (mm) in Deming Lake on Six Collecting Dates, Summer 1976

Species	Date 21-5	25-6	9-7	30-7	13-8	20-8	Average
Cladocera							
Daphnia longispina		.991		.891	.848	.401	.783
Copepoda							
Cyclops varicans	.627	.675	.675	.458	.412	.390	.540
Diaptomus oregonesis	.759	.970	.899	1.180	1.049	.709	.928
Rotifera							
Asplancha sp.	.416	.474	.493	.389	.417	.419	.435
Polyarthra sp.	.121	.137	.118	.116	.114	.113	.120
Keratella cochlearis	.152	.148	.142	.122	.127	.123	.136
Tetramastix opoliensis	.143	.190	.126	.132			.148
Keratella quadrata	.200	.285	.275	.258	.248	.223	.248
Trichocerca sp.			.203	.227	.218	.229	.219
Filinia sp.			.176	.158			.167
Insecta							
Chaoborus sp.	10	10	9	8	8	5	8.33

Table A-22. Mean Lengths of Zooplankton (mm) in Arco Lake on Six Collecting Dates, Summer 1976

Species	Date 21-5	25-6	9-7	30-7	13-8	20-8	Average
Cladocera							
Diaphanosoma brachyurum	.848	.714	.647	.414	.542	.743	.651
Moina sp.	.973	.990	.973	.875	.974	.804	.932
Daphnia pulex	4.0	3.0	4.0	2.108	2.264	3.5	3.145
Copepoda							
Diaptomus oregonesis			.868		.792	.948	.869
Cyclops varicans			.527	.268	.417	.473	.421
Epischura sp.		2.01	1.339	2.34	1.508	1.593	1.758
Rotifera							
Kellicottia longispina	.779	.796	.846	.682	.790	.658	.758
Keratella cochlearis	.253	.265	.247	.258	.259	.241	.254
Polyarthra sp.	.125	.153	.137		.122	.154	.138
Trichocerca sp.		.407	.669				.538
Asplancha sp.		.453	.464	.337		.485	.435
Insecta							
Chaoborus sp.	11	18.6	16		18	16	15.80

APPENDIX D. EXPERIMENTS

Table A-23. Results of Experiment 1: Arco Zooplankton Grazing on Deming Phytoplankton - Biomass (Initial/Final Fluorometer Units)

Depth	Lake	Control	Experiment
1m	11.5/ 9.0	11.5/ 9.0	12.0/ 9.0
2	12.0/10.0	11.5/ 9.0	11.5/ 9.0
3	11.5/10.0	13.0/10.0	12.5/11.0
4	23.0/22.0	31.0/25.0	36.0/26.0
5	41.0/33.0	39.0/31.0	35.0/22.0

Table A-24. Results of Experiment 1: Arco Zooplankton Grazing on Deming Phytoplankton - Species Composition at Five Meters Depth (colonies/ml)

Species	Control		Experiment	
	Initial	Final	Initial	Final
Oscillatoria agardhii	11,920	14,320	10,800	9,920
Oscillatoria redekei	5,440	7,520	8,640	3,840
Oscillatoria sp.	2,240	3,280	5,440	3,680
Lyngbya limnetica	9,600	17,680	8,240	11,280
Anabena cylindrica	3,440	5,200	5,040	3,600
Merismopedia sp.	160	240	240	---
Microcystis sp.	---	---	---	80
Gomphosphaeria sp.	240	---	80	80
Cryptomonads	1,040	640	800	480
Euglena sp.	320	320	320	80
Synura sp.	640	---	720	160
Melosira sp.	160	320	640	160
Synedra sp.	480	320	640	640
Rhizosolenia sp.	160	320	640	480
Chlamydomonas sp.	240	240	320	240
Schroederia sp.	320	---	---	---
Ankistrodesmus sp.	80	---	---	---
Scenedesmus sp.	160	160	160	320
Dimorphococcus sp.	80	80	240	---
Chlorella sp.	2,240	2,800	160	4,960
Species Diversity	.815	.779	.827	.817

Table A-25. Results of Experiment 2: Deming Planktivory on Arco Zooplankton - Biomass (Equilibration/Initial/Final Fluorometer Units)

Depth	Lake	Control	Experiment
1m	9/10/11	9/11/11	9/11/12
2	9/10/11	10/12/11	9/12/12
3	11/10/10	12/12/11	11/14/12
4	19/22/23	27/25/22	29/27/27
5	30/37/32	23/20/20	25/21/17

Table A-26. Results of Experiment 2: Deming Planktivory on Arco Zooplankton - Zooplankton Composition (10 ml subsample; initial-153 micron net, final-64 micron net)

Species	Control		Experiment	
	Initial	Final	Initial	Final
Daphnia pulex	6	--	4	--
Moina sp.	103	7	96	16
Diaphanosoma brachyurum	22	1	32	8
* *Cyclops varicans*	115	126	98	139
Epischura sp.	20	33	12	44
* *Diaptomus oregonesis*	18	44	28	45
Kellicottia longispina	62	--	113	--
* *Asplancha* sp.	9	37	4	57

* = species common to both lakes

Table A-27. Results of Experiment 3: Daphnia pulex Grazing on Deming Phytoplankton - Biomass (Fluorometer Units)

Parameter	Initial	Control	Experiment
Biomass	45	49	44
Dissolved Oxygen (mg/l)		11.4	10.3

Table A-28. Results of Experiment 3: Daphnia pulex Grazing on Deming Phytoplankton - Species Composition (colonies/ml)

Species	Control	Experiment
Oscillatoria agardhii	2640	6960
Oscillatoria redekei	1720	1280
Arthrospira sp.	480	80
Lyngbya limnetica	2840	2840
Anabena cylindrica	7160	11480
Gomphosphaeria sp.	200	200
Microcystis sp.	200	0
Cryptomonas erosa	1320	2200
Cryptomonads	40	40
Melosira sp.	120	40
Chlamydomonas sp.	880	560
Schroederia sp.	80	40
Ankistrodesmus sp.	160	440
Selenastrum sp.	40	0
Chlorella sp.	920	1560
Peridinium sp.	80	40
Species Diversity	.794	.746

Table A-29. Results of Experiment 4: Aquatic Insect Larvae Predation on Arco Zooplankton - Species Composition (animals/50 ml)

Species	Initial	Control	Chaoborus Predation	Dytiscid Predation
Moina sp.	30	16	1	4
Diaphanosoma brachyurum	138	13	1	8
Cyclops varicans	675	21	23	86
Diaptomus oregonesis	45	1	0	6
Epischura sp.	45	6	17	10
Keratella cochlearis	141	219	96	184
Kellicottia longispina	342	143	84	183
Asplancha sp.	93	1	0	0
Species Diversity	.736	.609	.691	.678

VITA

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