THOMAS DAVID SHAHADY. Jordan Lake Zooplankton: Potential
for Controlling Phytoplankton. (Under the direction of
DONALD E. FRANCISCO.)

Recently, some of the variance in primary productivity
observed in lakes has been associated with the variability
in piscivorous fish populations. This is because various
levels of zooplankton consumption by planktivorous fishes
result in varying grazing pressures on phytoplankton
assemblages. This study proceeds from the idea that in
Jordan Lake, zooplanktivory may have strong effects on the
composition and chlorophyll concentration of the
phytoplankton.

The investigation examines the ability of the
zooplankton community in a turbid, highly eutrophic
southeastern reservoir to control phytoplankton inside
enclosures that excluded all fish. The reservoir has a
large standing crop of gizzard and threadfin shad, black
crappie, bluegill and several other centrarchid and cyprinid
planktivores. Six experiments conducted using one meter
diameter enclosures between August and September 1986 and
May to June 1987 suggested that zooplankton were capable of
reducing phytoplankton biomass to very low levels
independent of nutrient concentrations when Daphnia spp. was
in the lake. The other dominant zooplankton, although
increasing in biomass in the absence of fish, did not reduce
phytoplankton biomass.

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INTRODUCTION

Traditionally, nutrients have been perceived as the
driving force of the trophic status of lakes and
reservoirs. However, more recently the higher trophic
levels of aquatic ecosystems have been shown to
dramatically alter biological trophic indicators in lakes
independent of nutrient inputs (Henrikson et al. 1980;
Leah et al. 1980; Lynch and Shapiro 1981; Shapiro et al.
1983; Shapiro and Wright 1984). Consequently, lake
management can be approached not only by controlling
nutrient inputs, but also by manipulating lake ecosystem
structure through the aquatic food web. Control of
nutrient inputs impacts food webs at the bottom, and these
perturbations move up through each trophic level.
Ecosystem structure manipulations impact food webs
primarily at the top, and these effects cascade down
through each trophic level. The effects of these
manipulations have been called "bottom up" and "top down"
(Kerfoot 1987).

High levels of phytoplankton biomass have been
recorded in Jordan Reservoir during its first three years
of existence (Weiss et al. 1984; Weiss et al. 1985; Weiss

et al. 1986). This excessive phytoplankton growth has been attributed to nutrient inputs and other abiotic factors. However, application of the Dillon-Rigler model (Dillon and Rigler 1974) to predict the chlorophyll a concentration in the lake as a function of TP has produced variable results (Weiss et al. 1985; Weiss et al. 1986). In two different years, chlorophyll a varied by as much as 5-fold for the same TP (total phosphorus) concentration, so TP could not have been the only important factor controlling phytoplankton growth.

Recently, this unexplained variability in lake productivity has been examined through food web interactions and their cascading effects on lake ecosystems (Carpenter et al. 1985; Carpenter and Kitchell 1987). The authors suggest that fluctuations in piscivory propagate through the food web causing changes in planktivory, herbivory and primary production. But, in eutrophic, turbid, warm monomictic reservoirs, the potential of "top down" control has not been examined.

Zooplankton and fish data in Jordan Reservoir are scarce. The relative changes in phytoplankton, zooplankton, and planktivorous and piscivorous fish have not been compared since lake was filled. This investigation is an initial attempt to address the possibility of phytoplankton control through food web dynamics, by examination of the relationship between

zooplankton and phytoplankton in the absence of fish predation. The results suggest that zooplankton can rapidly control phytoplankton independently of nutrient inputs, so long as planktivorous fish are absent.

TROPHIC STATUS OF JORDAN RESERVOIR

The topography of the land flooded by Jordan Lake and road causeways divide it into four basins and modify many water quality parameters (Figure 1). As a result, segment 2 of the lake exhibits mesotrophic conditions while segment 4 of the lake fits classification as hypereutrophic on the basis of chlorophyll a and algal taxonomic composition (Weiss et al. 1984; Weiss et al. 1985; Weiss et al. 1986). As a whole, Jordan Lake can be classified as eutrophic (Weiss and Kuenzler 1976).

The phytoplankton of all four segments of the lake has been dominated by diatoms, small green, and blue-green algae during the last few years (Weiss et al. 1984; Weiss et al. 1985; Weiss et al. 1986). During the first year after filling of the lake, a Prymnesiophycean, Chrysochromulina sp., was dominant throughout the lake (Weiss et al. 1984). In years 2 and 3, Chlorophyceae was dominant by density and Cyanophyceae and Bacillariophyceae were dominant by biovolume. Total phytoplankton biovolume decreased in year 2, partly because of a change to smaller
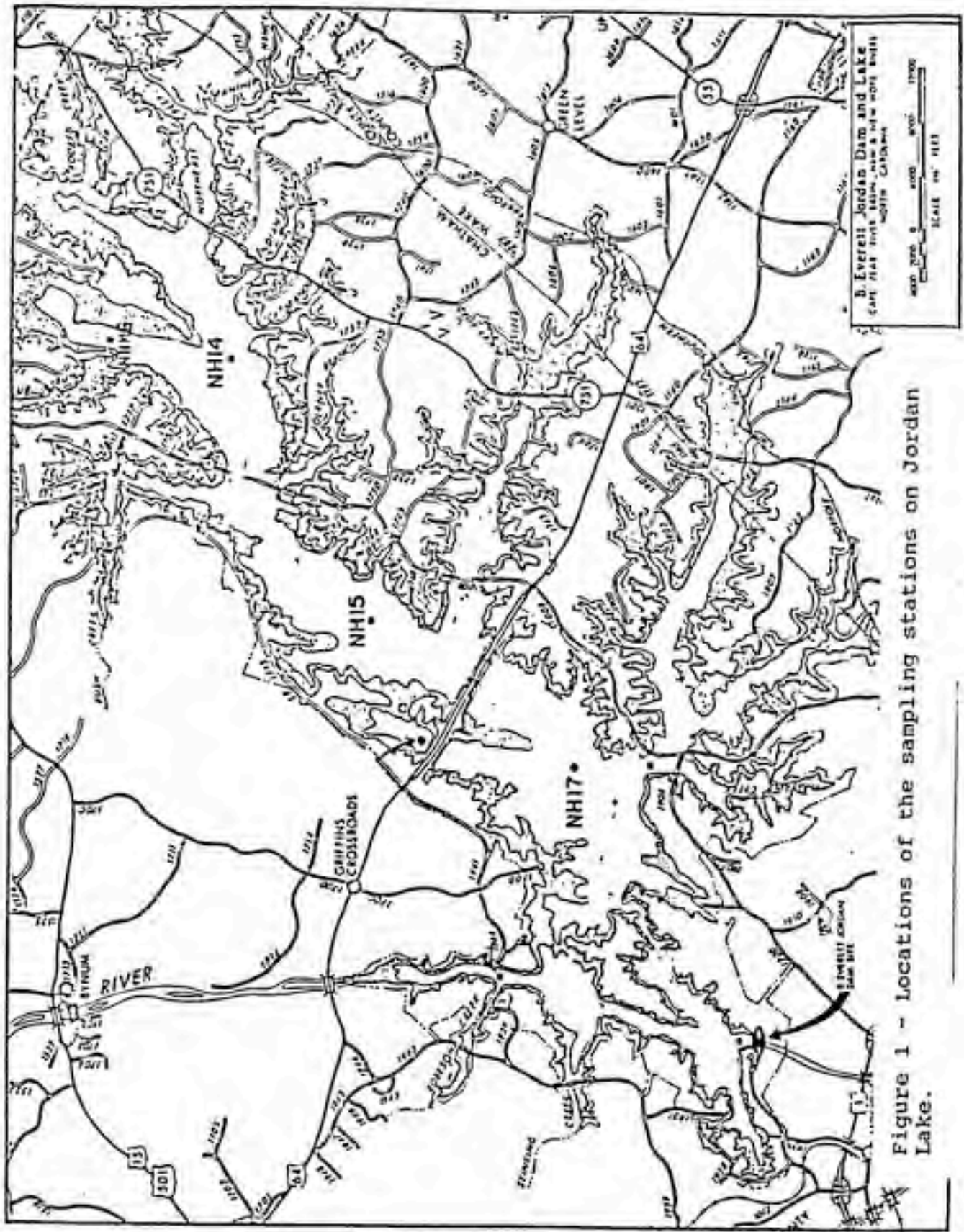
Figure 1 - Locations of the sampling stations on Jordan Lake.

forms, while density and biovolume decreased in year 3 (Weiss et al 1985; Weiss et al. 1986). Larger cells have consistently prevailed during the winter and spring, but smaller cells are prevalent during the summer and fall (Figure 2). Mean biovolume per cell decreased gradually, so that small-celled species were increasingly important.

The concentration of chlorophyll a in Jordan Reservoir has often exceeded the standard set by the North Carolina Environmental Management Commission (Weiss et al. 1984; Weiss et al. 1985; Weiss et al. 1986). As a result, the lake has been classified as nutrient sensitive by the North Carolina Environmental Management Commission and efforts are being made to control point source inputs of nutrients. As a supplement to controlling nutrients, reductions in algal biomass may also be achieved by increasing grazing rates on the small, presumably edible cells that dominate the Jordan Reservoir phytoplankton community.

THE PELAGIC FOOD CHAIN

The pelagic food chain can be separated conceptually into trophic levels as follows: algae-zooplankton-planktivorous fish-piscivorous fish. (Figure 3). Algae are the primary producers in the chain, and their densities can be regulated by nutrients that restrict

PHYTOPLANKTON SIZE
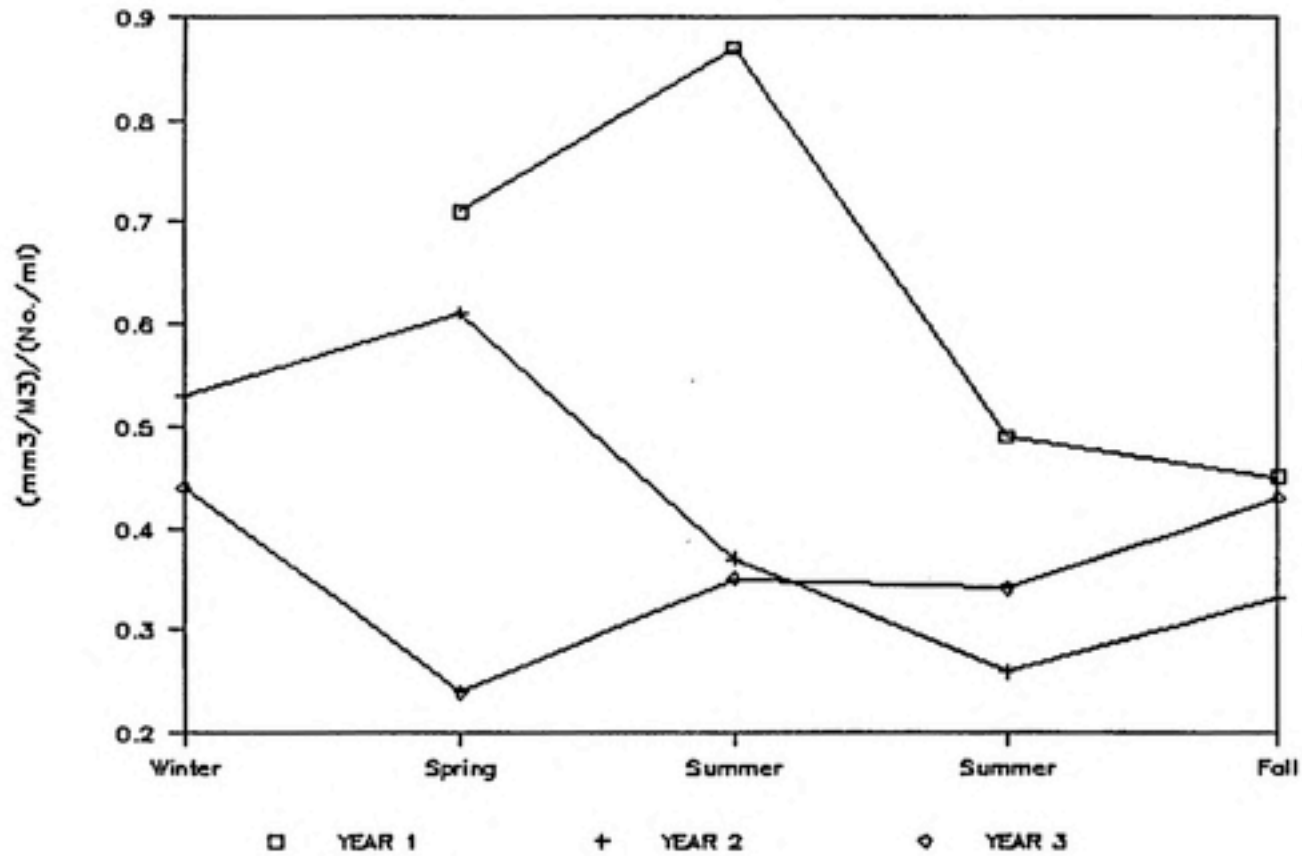
Figure 2 - Phytoplankton size through the first three years
of Jordan Lake. Phytoplankton size is estimated as
biovolume / density.

7

The Aquatic Food Chain
(Not to Scale)

Piscivorous
Fish

eat

Planktivorous
Fish

eat

Herbivores

eat

Algae

use

Nutrients

recycle

Benthivorous
Fish

Nutrients
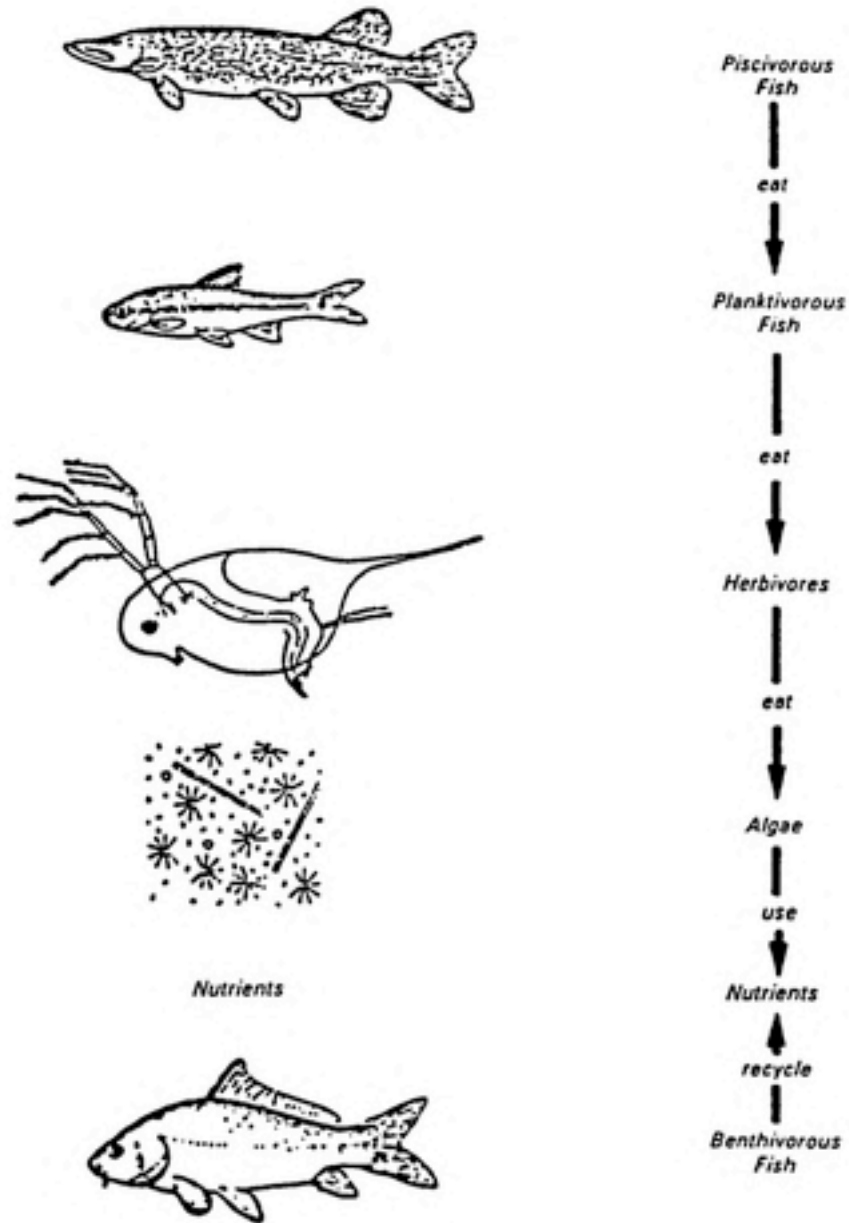
Figure 2.   The aquatic food chain (not to scale).

Figure 3 - Simplified version of aquatic food chain
structure (Shapiro et al. 1983).

rates of increase, and by zooplankton that restrict numbers by grazing (Sterner 1986). The amount and kinds of zooplankton which are grazing on a population of algae are often regulated by planktivorous fish predation (Lazzaro 1987). In turn, piscivorous fish may regulate the populations of planktivorous fish (Mills et al. 1987).

Thus, a food chain in a particular lake can be simplified into two types. One type has four distinctive trophic levels, with piscivorous fish at the top and small populations of planktivores. Zooplankton densities will be high, and their grazing pressure on algae will be intense. A second type of food chain has only three functional trophic levels due to the insignificance of piscivore predation. This food chain will be dominated by planktivorous fish, will have very low zooplankton densities, and consequently, very little grazing on algae. To manage lakes with this second type of food chain to achieve lower chlorophyll levels, piscivore populations might be stocked to reduce populations of planktivores. To explore the feasibility of this management strategy, the relationships between each set of trophic levels must be examined in greater detail.

ZOOPLANKTON FEEDING ON ALGAE

Zooplankton may be raptorial feeders, filter feeders, or both. Raptorial feeders attack the larger phytoplankton that cannot be consumed whole. The prey is consumed by ingesting portions at a time using the mouth parts. Cyclopoid copepods typically are raptorial feeders and actively seek out the larger particles (Reynolds 1984). In contrast, filter feeders ingest the prey whole by filtering them from the water column. Because the prey are ingested whole, the size of particle ingested is physically limited by factors related to the size of the zooplankton ingesting the particle (Burns 1968). As a zooplankter increases in size, larger particles can be ingested. Cladocerans are strictly filter feeders (Reynolds 1984; Hrbacek 1977). Calanoid copepods will filter feed on small particles and raptorial feed on large particles (Allan 1976). Thus, the types of zooplankton feeding can be distinguished between the classes of zooplankton.

The number of particles filtered per unit time is the filtering rate. Individual cladocerans are capable of filtering rates up to an order of magnitude higher than filter feeding calanoid copepods of a similar size (Peters and Downing 1984; Allan 1976). Due to this difference, cladocerans will be able to maintain greater grazing

intensity on algae than a similar population of calanoid copepods.

Filtering rates of zooplankton increase with zooplankton size (Peters and Downing 1984). For example, Reynolds (1984) determined that an 0.8 mm long Daphnia (cladoceran) is capable of filtering 7.6 ml per day while a 2.1 mm Daphnia in the same phytoplankton culture is capable of filtering 62.6 ml per day. Thus, phytoplankton densities can be reduced at a much greater rate when the mean size of Daphnia increases. Therefore, the type of zooplankton as well as the size of the individual zooplankton influence the filtration rate of zooplankton communities.

ALGAE-ZOOPLANKTON SIZE SPECIFIC RELATIONSHIPS

Size and type of algae are important for effective grazer control of algae. Filtration or ingestion rates differ among zooplankton types for different size ranges of algal cells. Calanoid copepods exhibit maximum ingestion rates for cells in the size of 82 um. Cladoceran maximum ingestion rates are for particles in the size of 5 um (Peters and Downing 1984). Each of these zooplankton types will also ingest a disproportionately high amount of size classes that are in the greatest abundance from a mixture of cells (Porter 1977). Thus,

zooplankton feeding will concentrate on the particles in the optimum size range as long as they are in abundance. If calanoid copepods have a sufficient supply of food in the 82 um size range they will continue to filter in this range. Likewise, cladocerans will concentrate their feeding efforts on phytoplankton in the 5 um range as long as they are abundant. In a lake with an abundance of small particles but with enough larger particles to satisfy the feeding of calanoids, the smaller particles will be neglected by the calanoids (McNaught 1975).

Another factor which determines the kinds of phytoplankton that are grazed is zooplankton size. Communities dominated by small zooplankton are less effective in reducing phytoplankton than by large zooplankton communities (Pace 1984; Vanni 1987a). This is due to the increases in the range of phytoplankton sizes that can be efficiently ingested as the zooplankton increases in length. Zooplankton communities dominated by small individuals are generally restricted to a very limited range of particle sizes and can effectively filter only a small portion of the total algal biomass. In summary, the type of zooplankton influences filtration rate and cell size preference. Zooplankton size influences filtration rate and the range of particles that can be selected.

According to the preference and the range of particles that are selected, zooplankton can be classified as specialist and generalist feeders. Specialist feeders actively seek out particles in the preferred range and are less efficient in grazing outside that particle range. Generalists are able to filter at high rates outside the preferred range of particles. Copepods are typically more specialized feeders (Porter 1977). They actively seek out the larger particles (Reynolds 1984 ; Allan 1976; Cushing 1976) and, therefore, may better suited for control of phytoplankton in waters that do not support dense populations of small algae. They do not seem to be effective where an abundance of small particles exists at high densities.

Cladocerans are generalist feeders (Allan 1976). They will feed on the preferred sizes as well as other sizes of algae. For example, copepods did not ingest filamentous green or chain forming diatoms, but Daphnia was able to break apart and ingest these colonial and filamentous algae (Hargrave and Green 1970). Cladocerans can effectively control small phytoplankton as well as large, chain-forming types. This makes them more effective than copepods for the control of algae typical in eutrophic waters.

EUTROPHY AND ZOOPLANKTON GRAZING

In eutrophic lakes, nutrient enrichment results in an increase of nannoplankton (< 50 um) biomass (Gannon and Stemberger 1978; Gilwicz 1975 Porter 1977; Reynolds 1984; Vanni 1987a). Without zooplankton grazing, the nannoplankton are dominant because they are superior competitors for available nutrients in relation to large algae (Gilwicz 1975; Porter 1977; McCauley and Briand 1979). However, with increased Daphnia grazing pressure, large algae increase to make up a greater proportion of the algal population (Gilwicz 1975; Lampert et al. 1986; Schoenberg and Carlson 1984). This would suggest that Daphnia are effective in removing algae typical of eutrophic lakes.

When large cells make up a greater proportion of phytoplankton community structure a favorable effect on the clarity of the water can result. A given amount of matter distributed as finer particles is more effective in light extinction than the same quantity in coarser conglomerates (Hutchinson 1967). As a result, secchi transparency is more sensitive to the number of particles scattering light than their total mass (Edmondson 1980). Therefore, secchi depth can be increased through a shift from small to large phytoplankton with no change in biomass (Henrikson et al. 1980).

In a study of the spring clear water phase, Lampert et al. (1986) observed that Daphnia grew exponentially and obtained highest biomass on the same day as greatest secchi depth. Copepod biomass remained the same throughout this period. At high Daphnia filtration rates, water can be cleared so rapidly that algae are unable to adapt to the improving light conditions and replace themselves by growth before most are removed (Reynolds 1984). Thus, Daphnia populations are capable of increasing water clarity where copepods have not been shown to do so (Sterner 1986). Therefore, blooms of algae in eutrophic lakes could be controlled by abundant populations of cladocerans, particularly Daphnia when fish predation is not a factor. However, the higher trophic levels of the food chain play an important role.

PLANKTIVOROUS FISH FEEDING ON ZOOPLANKTON

There are two general types of feeding behavior used by planktivorous fish. Pump filter feeding and particulate feeding. Pump filter feeding fish use rhythmic suctions of the mouth to capture prey items while swimming slowly or remaining quite stationary (Lazzaro 1987). Particulate feeders attack individual planktonic

prey items which they usually select from the water column (Lazzaro 1987).

Each type of feeding has a different effect on the structure of zooplankton communities. Pump filter feeders have higher feeding rates for the more easily captured types of zooplankton, but are not strongly selective on the basis of size alone (Drenner, et al. 1984). The resultant effect of pump filter feeding is a reduction in zooplankton biomass with little shift in zooplankton body size (Lazzaro 1987).

Particulate feeders are highly discriminatory, picking out larger prey because they are more visible (O'Brien 1979; Janssen 1976). Particulate feeding allows these fish to forage through a greater amount of water than pump filter feeders, but they do so selectively (Zaret 1980). Both particulate and pump filter feeding reduce the biomass of zooplankton; however, particulate feeding tends to selectively eliminate the largest zooplankton.

FACTORS AFFECTING PREY CAPTURE

Particulate feeders must see the prey to capture it. Therefore, any factor which enhances the visibility of the prey will enhance the capture rate. The reactive distance is a concept that defines the greatest distance at which a

fish can locate and will actively pursue the zooplankton prey (O'Brien 1979). A fish relies on reactive distance to choose the prey to be pursued and eaten. Several factors can influence the reactive distance of the fish and, hence, whether the prey will be located and eaten or not.

Reactive distance increases linearly with length of prey. The smaller the zooplankton, the less likely it will be located and eaten. In experiments to examine the effects of prey size, bluegill and crappie never bypassed a Daphnia over 1 mm in length (O'Brien 1979).

Zooplankton prey that move the least are least likely to be seen and eaten (Zaret 1980). Zooplankton typically have two types of swimming behavior. Copepods and some cladocerans swim in paddle-like thrusts that allow them to glide smoothly through the water. They remain motionless for a brief period and then swim again. Daphnia swim in a hopping fashion and continually remain in motion. This swimming behavior makes Daphnia very conspicuous to planktivorous fish. In addition, Daphnia have maximum, burst swimming speeds of up to 0.74 cm per second, while copepods can swim in bursts of 20 cm per second (Zaret 1980). The slower swimming speed and continuous swimming motion make Daphnia an easily detected and preferred prey item.

Transparency gives a strong advantage to zooplankton exposed to fish predation (Confer and Blades 1975). The more transparent the zooplankton, the shorter the reactive distance becomes to the planktivorous fish. Moina and Diaphanosoma can co-exist with fish partly because they are nearly transparent (Zaret 1980).

At high turbidity, reactive distance diminishes to low values and becomes almost independent of prey size (Vinyard and O'Brien 1976). Thus, particulate feeding planktivores detect fewer prey and are less size selective. The likelihood of larger and more conspicuous zooplankton such as Daphnia surviving increases at high turbidity due to reduction in the reactive distance.

THE EFFECT OF PLANKTIVOROUS FISH PREDATION ON ZOOPLANKTON COMMUNITIES

Intensive planktivorous fish predation results essentially in elimination of larger zooplankton (Brooks and Dodson 1965; Confer and Blades 1975; Henrikson et al. 1980; Zaret 1980). As a result, small zooplankton typically less than 1.5 mm in length, usually including Bosmina and small Daphnia, develop in lakes with many planktivores (O'Brien 1979).

For a given prey size, planktivorous fish show a preference for cladocerans (75%) over copepods (25%)

(Serrula et al. 1980; O'Brien 1979). In addition, when
Daphnia are no longer available, many fish switch to
benthic fauna and ignore copepods (Zaret 1980). This may
cause the elimination of _Daphnia_ and other large
cladocerans, and allow the enhancement the populations of
copepods. Fish reduce the number of invertebrate
predators as well. These invertebrate predators, such as
Chaoborus, choose copepods, nauplii and small cladocerans
over larger _Daphnia_ (Zaret 1980). The reduction of
invertebrate predators will further enhance small
cladoceran and copepod densities.

BIOMANIPULATION

In situations where management of nuisance algae by
reducing nutrients is impractical and/or unsuccessful,
increasing grazing rates of zooplankton on phytoplankton
may provide an alternate strategy for improving water
quality through a decrease in algal density (Schoenberg
and Carlson 1984). The phytoplankton in lakes where
nutrients are well above limiting levels should be much
more sensitive to changes in predators than to reductions
of nutrients (Lynch and Shapiro 1981; Vanni 1986a). Such
attempts to control phytoplankton biomass by manipulating
trophic levels in aquatic ecosystems while maintaining the
same nutrient inputs are included in the concept of

"biomanipulation". The feasibility of this "top down" approach has been explored through enclosure and whole lake experiments.

Shapiro et al. (1983) conducted a series of enclosure experiments in which bluegill sunfish were included and excluded. The results showed that large Daphnia galeata were eliminated in the presence of fish and survived when fish were excluded. When the large Daphnia galeata were not present, algal biomass increased to 16 fold over the biomass when Daphnia galeata was present. Anderson et al. (1978) found similar results in their enclosure experiments. Large Daphnia were again dominant until fish were introduced. Chlorophyll a rose to 440 ug/L inside the enclosure with fish, and fell to 20 ug/L in the enclosure without fish. In fish-free enclosures, there was a mixture of small blue greens, cryptomonads and diatoms. In enclosures with fish, Microcystis was dominant in the absence of large Daphnia. Schoenberg and Carlson (1984) found the above changes to be evident in their enclosures as well. In addition, they increased the biomass of the small cladoceran Bosmina to determine if it was capable of reducing and controlling algal density. They determined that Bosmina was not capable of controlling phytoplankton biomass. These enclosure experiments produced water quality improvements in the absence of planktivorous fish. No improvement in water

quality was detected when planktivores were present or zooplankton was dominated by small forms such as <u>Bosmina</u>.

Several investigators have observed improvements in water quality in small lakes after planktivorous fish were removed (Henrikson et al. 1980; Leah et al. 1980; Lynch and Shapiro 1981; Shapiro et al. 1983; Shapiro and Wright 1984). In every lake, Large <u>Daphnia</u> increased and as a result the grazing pressure on phytoplankton increased. The smaller size (< 50 um) phytoplankton were reduced due to the abundance of <u>Daphnia</u>. Transparency increased and the pH was lowered due to reduced consumption of CO_2 by phytoplankton.

STOCKING OF PISCIVOROUS FISH

If feeding activities of dense populations of planktivorous fish results in the reduction of zooplankton biomass and a resultant increase in algal biomass in Jordan Reservoir, a reduction in algal biomass should be achieved by a direct reduction in planktivores (Andersson et al. 1978). One way to reduce planktivorous fish and consequently the resultant improve water quality is to stock piscivorous fish. In Lake Michigan, the stocking of salmonine piscivores has reduced populations of the

planktivorous alewife (Scavia et al. 1986; Dorazio et al. 1987). The reduction in alewife has enabled large _Daphnia_ to become abundant along with a reduction in algal biomass and an increase in transparency.

If the Jordan Reservoir food chain can be influenced in the same way through the stocking of piscivores, the possible effects this may have are reflected in the following sequence of events.

1. INTRODUCTION OF PISCIVORES

2. REDUCTION OF PLANKTIVORES

3. INCREASE IN DAPHNIA BIOMASS

4. INCREASE GRAZING PRESSURE ON SMALL DOMINANT ALGAE

5. REDUCTION IN ALGAL BIOMASS

6. DECREASE IN PH

7. INCREASE IN SOLUBLE NUTRIENTS

OBJECTIVES OF STUDY

The present investigation is designed to: 1. Examine the Jordan Reservoir plankton community and establish any lake wide relationships and; 2. determine whether zooplankton when not suppressed by planktivorous fish predation, can change the composition and reduce the biomass of phytoplankton.

METHODS

STATIONS

The locations of stations sampled for monthly zooplankton and phytoplankton enumeration are shown in Figure 1. The two stations in Segment 4 are NHMG and NH14. NH15 is located in the middle of Segment 3 and NH17 is located in the middle of Segment 2. Station NH15 was not sampled on 5/13/86 and 6/4/86, nor was station NH14 sampled on 6/4/86.

FIELD DATA COLLECTION

1. PHYSICAL DATA

All physical, chemical and phytoplankton data were collected in conjunction with the monthly sampling of the B. Everett Jordan Lake Water Quality Study, Year V. Temperature, pH and dissolved oxygen were measured using a Hydrolab Surveyor II.

2. NUTRIENT DATA

Water for nutrient analysis was pumped from various depths using the Jabsco model 12460-0011 self-priming pump. The flow rate was 1.7 gal/min. All sample bottles used were acid-washed and rinsed prior to use in

the field. Polyethylene bottles (1L) were rinsed with sample water and then filled at the appropriate depth. Samples for total nutrient analysis were then transferred to acid-washed, 125 ml polyethylene bottles and preserved with three drops of concentrated sulfuric acid to bring the pH below 2. Samples for dissolved fractions were filtered in the field using a Schleicher and Schull pump syringe and Whatman GF-F filter. The Schleicher and Schull pump syringe and the Whatman GF-F filter were rinsed with distilled water between samples. One sample rinse discarded before collecting the final sample. All samples were transferred to ice and kept for transport to the laboratory.

3. ZOOPLANKTON STATION DATA

Zooplankton were collected by slowly drawing a 30 cm mouth diameter, 80 um mesh zooplankton net through the euphotic zone. The euphotic zone was determined to be the depth from the surface to one percent light penetration. Samples were immediately transferred to 30 ml sample bottles containing 3 ml of 37% formalin. Samples were mixed and stored on ice until returned to the lab.

4. PHYTOPLANKTON DATA

Lake survey phytoplankton species counts used in the report were provided by Dr. Peter Campbell. An integrated phytoplankton sample was taken by pulling a pumped sample hose slowly through the euphotic zone. One subsample was transferred to a polyethylene (0.5L) bottle for chlorophyll analysis and another was transferred to a 30 ml glass bottle and preserved with a neutral Lugol's solution. Lugol's solution was prepared by dissolving 60 grams potassium iodine and 40 grams iodine crystals in 1000 ml distilled water. Samples were stored on ice until return to the laboratory where they were stored in the dark until analysis.

ENCLOSURE DATA

All enclosure experiments were carried out in Segment 4 as close to NHMG as possible depending on the depth of the water. Enclosures were put in water 2.5 meters deep to allow 0.5 meters of the enclosure to remain out of the water to prevent splash over.

ENCLOSURES

Enclosure 1 was a clear, one piece fiberglass cylinder, 0.75 meters in diameter and 3.1 meters in length. Enclosure 2 was a two piece fiberglass cylinder,

0.75 meters in diameter and 2.7 meters in length. The bottoms of both enclosures were open and made of sheet aluminum to secure them in the sediments. The fiberglass was 1/8 inch thick and the enclosure was constructed by forming the fiberglass into a cylinder, riveting the top and middle to angle aluminum rings around the cylinder and securing the rings with 3 angle aluminum bars along each side. Each enclosure was anchored to an iron rod hammered into the sediments and extending out of the water above the top of the enclosure. The enclosure was fitted with cable rings allowing attachment to the iron rod.

Table 1 - Experimental design and sampling schedule

EXPERIMENT	START	SAMPLED	DAYS IN LAKE
1	8/7/86	8/15/86	8
2	8/25/86	9/2/86	8
3	9/2/86	9/10/86	8
4	5/11/87	5/19/87	8
		5/26/87	15
5	5/19/87	5/26/87	7
		6/3/87	15
		6/9/87	21
6	6/9/87	6/16/87	7

PHYSICAL AND CHEMICAL DATA COLLECTION PROCEDURES

Upon arrival at the enclosures, the boat was slowly positioned between the enclosures and the prevailing wind. Anchors on the bow and the stern were lowered and secured. The boat was maneuvered into position along side the enclosures by adjusting the scope on both anchor lines. Once the boat was secure, the enclosures were sampled. Secchi depth was immediately determined. Next, samples for nutrients and chlorophyll were taken by pumping water from the enclosures. Following sampling, the Hydrolab Surveyor II was lowered through the middle of the enclosure to obtain measurements. Each of the procedures were duplicated on the outside of the enclosures.

ZOOPLANKTON COLLECTION

After all other samples had been taken, zooplankton were collected in the enclosures with duplicate vertical hauls from 1.5 meters to the surface through the center of the enclosures. The samples were immediately transferred to glass bottles and preserved with formalin in the same manner as station zooplankton samples. Duplicate hauls were then made just outside the enclosures.

LABORATORY DATA ANALYSIS

1. ZOOPLANKTON

Zooplankton were enumerated by counting a subsample from each 30 ml bottle using two methods. The first method involved using a 10 ml pipette which had the tip removed. The opening of the pipette was 7 mm which was large enough not to impede any zooplankton from being sucked into the subsample. Zooplankton were shaken in the bottle to evenly distribute them. The pipette was quickly lowered into the bottle and a 1 ml subsample was taken. This subsample was dispensed into a gridded dish which contained a small amount of glycerin along the bottom and the entire contents were counted and lengths of all zooplankton were recorded to the nearest 0.05mm. Only the samples for experiments 1-3 were counted using this method. The second method was to obtain a subsample using the Folsom Plankton Sample Splitter. The entire sample was transferred to the splitter. A subsample was obtained by sequentially dividing the sample in half until a minimum of 100 organisms remained to count. This subsample was put into the gridded dish and enumerated.

A comparison of the pipette method with the plankton splitter revealed a 20 % overestimation by the pipette method. For enclosure experiments, this inconsistency

was the same for both the inside and outside samples and did not affect the comparisons.

Zooplankton were identified to genus and when possible, to species using the identification keys of Edmondson (1959) and Baker et al. (1984). Copepod nauplii and copepodites were identified as a single class. Zooplankton lengths were converted to biomass using the length-weight relationships derived in Bottrell, et al. (1976). The raw results from each haul are in Appendix # 1.

PHYTOPLANKTON DATA ANALYSIS

Only experiments 1 and 3 were enumerated for phytoplankton. This analysis was done by Dr. Peter H. Campbell inside and outside the enclosures using the same methodology as in Weiss et al. (1985).

NUTRIENT ANALYSIS

Total Kjeldahl nitrogen was analyzed using Kopp and McKee (1979), method no. 351.2. Total phosphorus was analyzed using Kopp and McKee (1979), method no. 365.4 These methods were slightly modified for determination by the Orion Scientific auto analyzer system.

MONTHLY SAMPLING

ZOOPLANKTON

Copepods accounted for most of the biomass on each sampling date in the lake (Figure 4). Biomass was as high as 110 ug/L and was consistently higher at stations NHMG and NH14. In comparison, cladocerans made up a small fraction of total zooplankton biomass (Figure 4). The highest cladoceran biomass was 7.5 ug/L at NHMG on 5/13/86, and values remained very low relative to copepod biomass throughout the entire sampling period. Thus, copepods made up most of the biomass of the zooplankton community.

Diaptomus pallidus

Diaptomus pallidus attained the largest biomass of any zooplankton species in Jordan Lake. During each sampling date, this calanoid copepod made up the majority of the zooplankton sampled. Diaptomus pallidus achieved a biomass as high as 90 ug/L at station NHMG (Figure 5). Biomass generally declined down the lake moving toward NH17.

CLADOCERANS
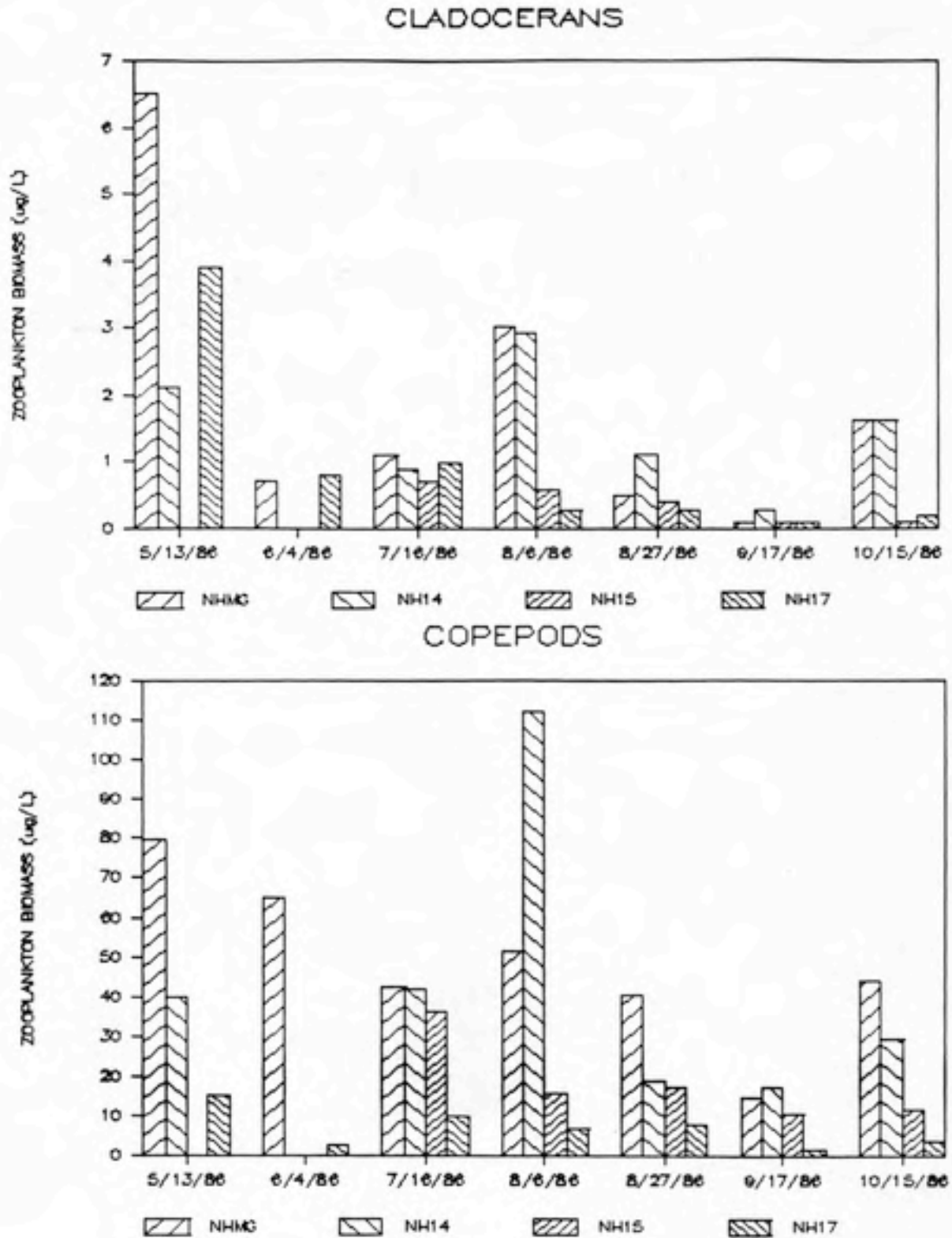
COPEPODS

Figure 4 - Biomass of cladocerans and copepods throughout the lake during the sampling period.
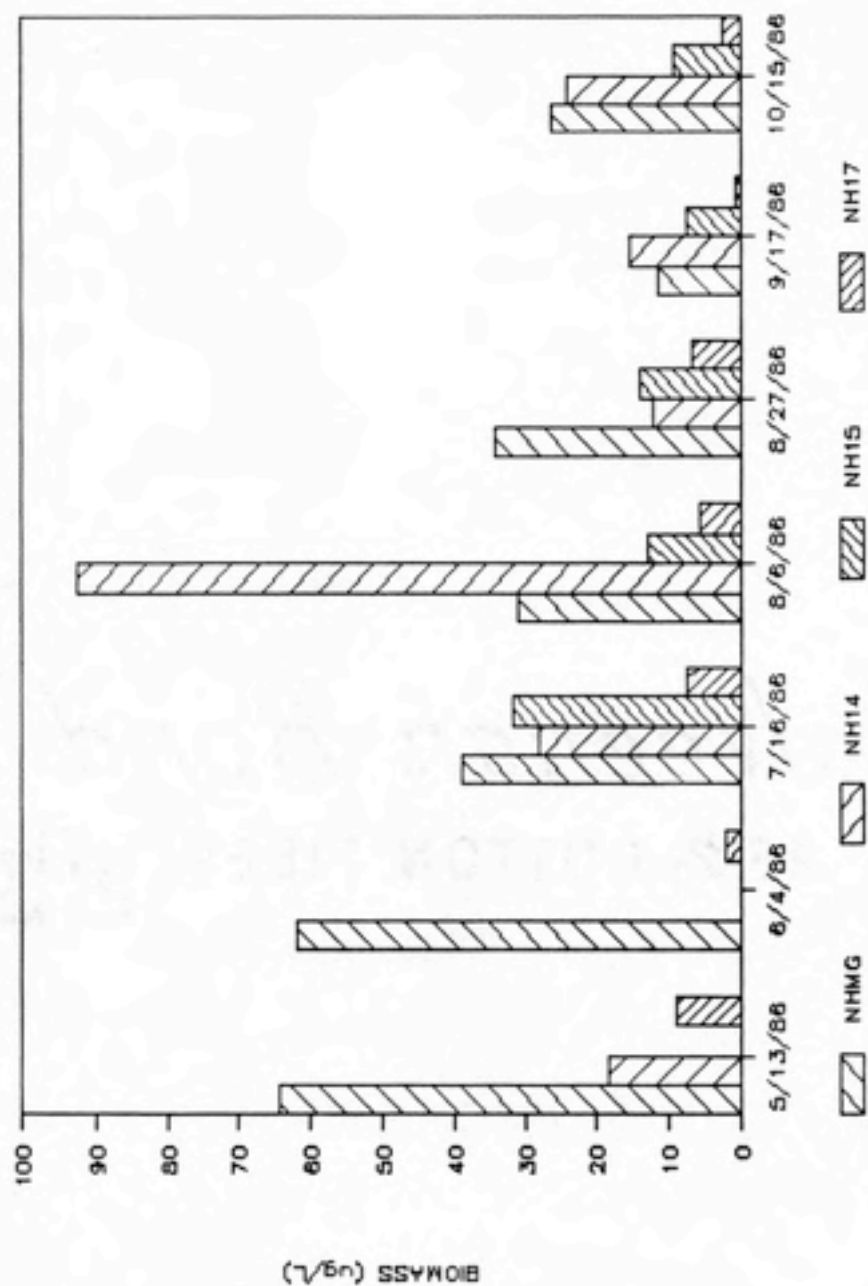
Figure 5 - Biomass of Diaptomus pallidus throughout the lake during the sampling period.

Cyclops vernalis

Cyclops vernalis had the second highest biomass of all zooplankton sampled (Figure 6). This cyclopoid copepod was more variable in biomass than D. pallidus. Biomass was greatest at stations NHMG and NH14 with a high of 14 ug/L at station NHMG. This peak biomass of 14 ug/L occurred during the months of May and October.

Mesocyclops edax

Mesocyclops edax had the third highest biomass found in the lake. Also a cyclopoid copepod, it did not appear in the samples until later in the sampling season (Figure 7). Biomass was relatively low, reaching a high of nearly 6 ug/L. Periods of high biomass were not restricted to stations NHMG and NH14 as in the previous two species of zooplankton. The appearance of Mesocyclops edax seemed to be associated with increasing temperature and increasing phytoplankton abundance.

Copepod Nauplii

Pulses in the biomass of nauplii were similar to pulses in biomass of adult copepods (Figures 4 and 8).

Daphnia spp.

Daphnia spp. did not attain a high biomass in the lake and almost completely disappeared from the

CYCLOPS VERNALIS
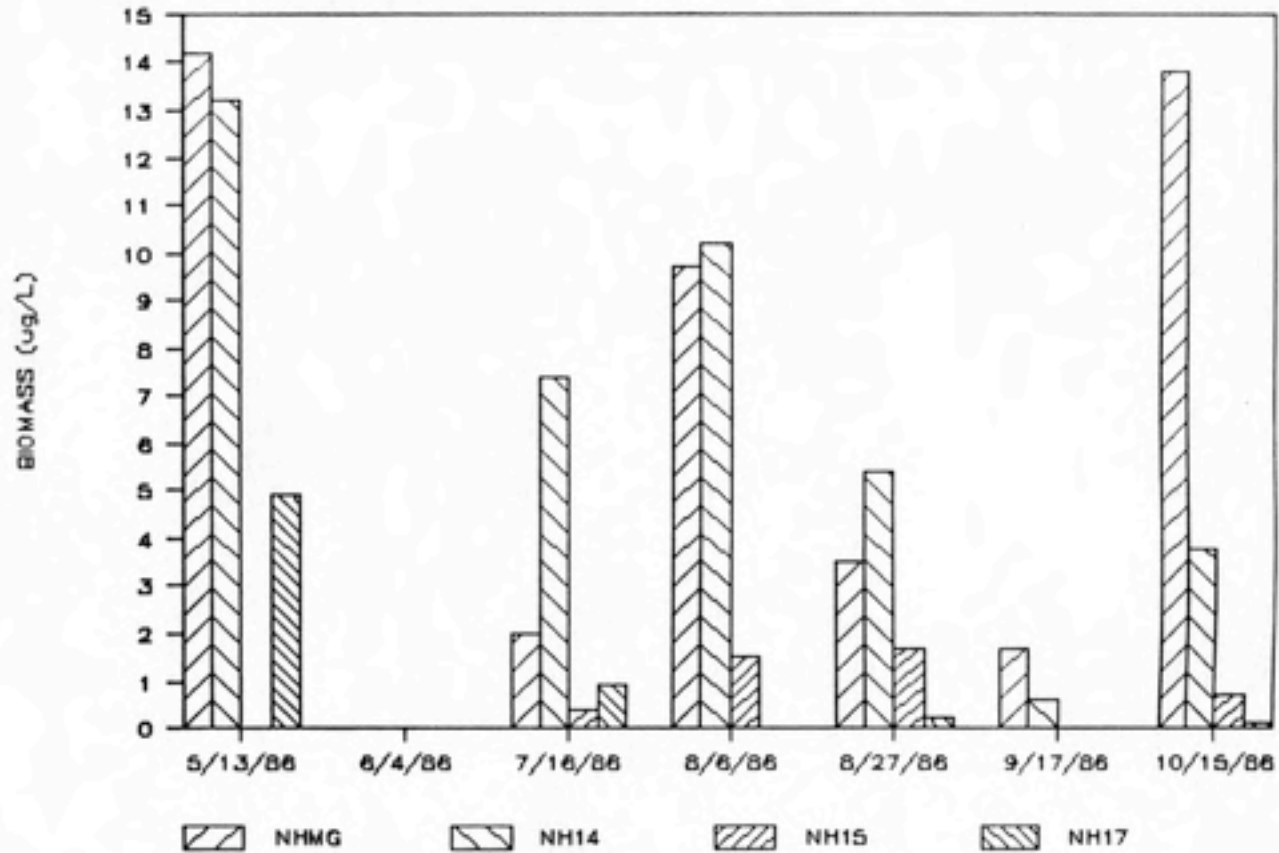
Figure 6 - Biomass of Cyclops vernalis throughout the lake
during the sampling period.
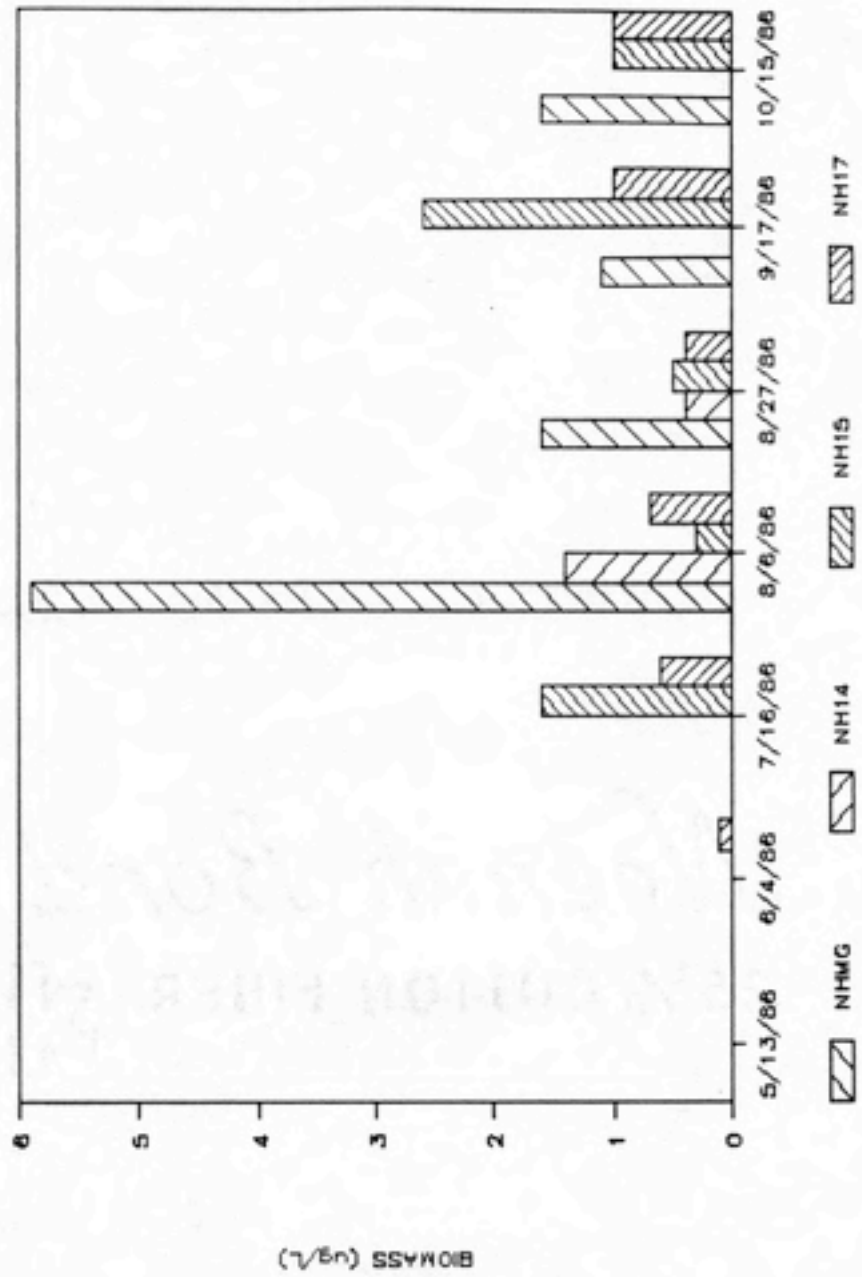
Figure 7 - Biomass of Mesocyclops edax throughout the lake during the sampling period.

COPEPOD NAUPLII
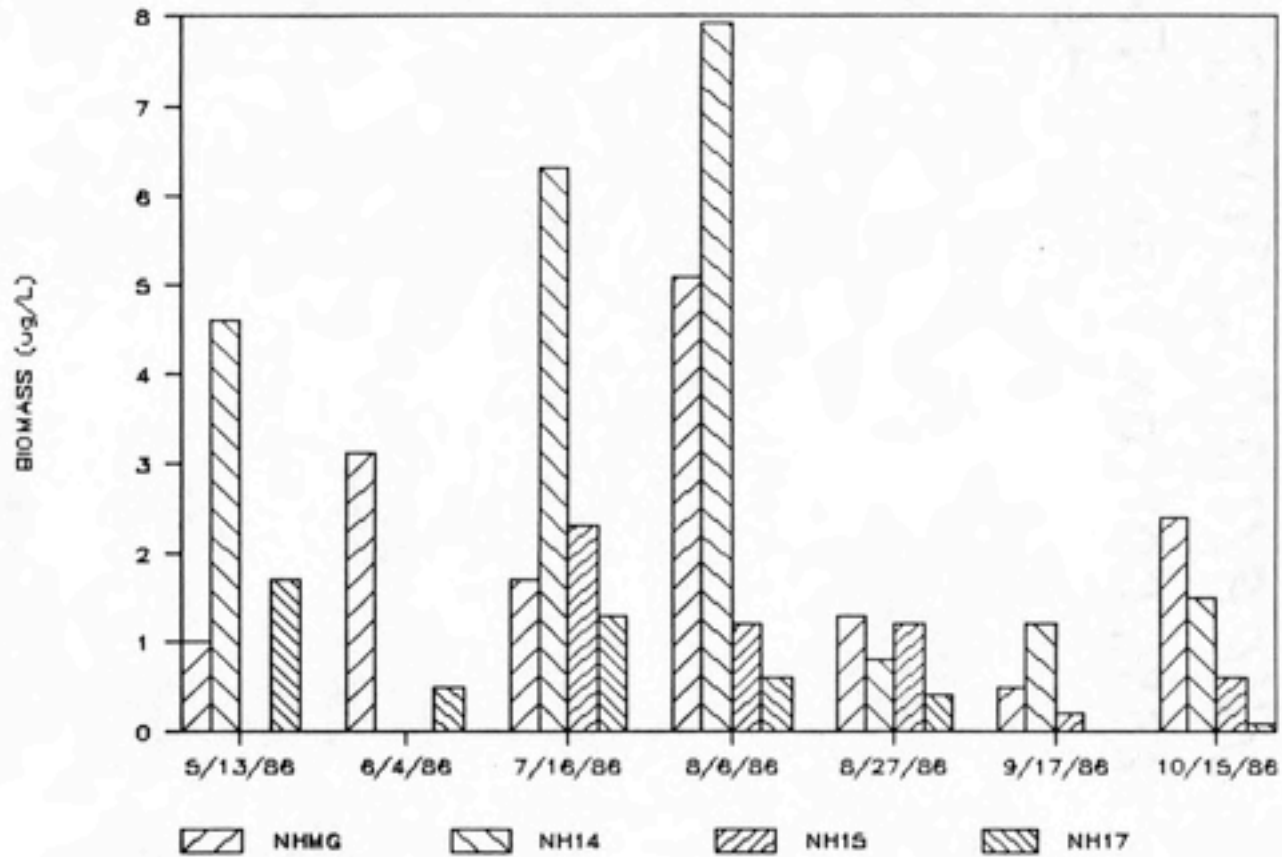
Figure 8 - Biomass of copepod nauplii throughout the lake during the sampling period.

samples after 5/13/86. The first sample date contained the highest biomass determined throughout the sampling period (Figure 9). This high of 6.5 ug/L was a small portion of the zooplankton community. Daphnia spp. was the only zooplankton to be present in the May sample and then abruptly decline in the lake.

Diaphanosoma sp.

Diaphanosoma sp. had the highest biomass of all cladocerans, and increased in biomass later in the sampling period. It attained a high of nearly 3 ug/L (Figure 10). Interestingly, Diaphanosoma sp. increased at about the same time Daphnia spp. declined (Figure 9).

Bosmina longirostris

Bosmina longirostris made up a very small portion of cladoceran biomass (Figure 11). An overlapping time sequence was observed among the three cladocerans. Daphnia spp. (Figure 9) was present in May, Bosmina longirostris (Figure 11) was present in May through August and Diaphanosoma sp. (Figure 10) was present from July to October.

DAPHNIA SPP.
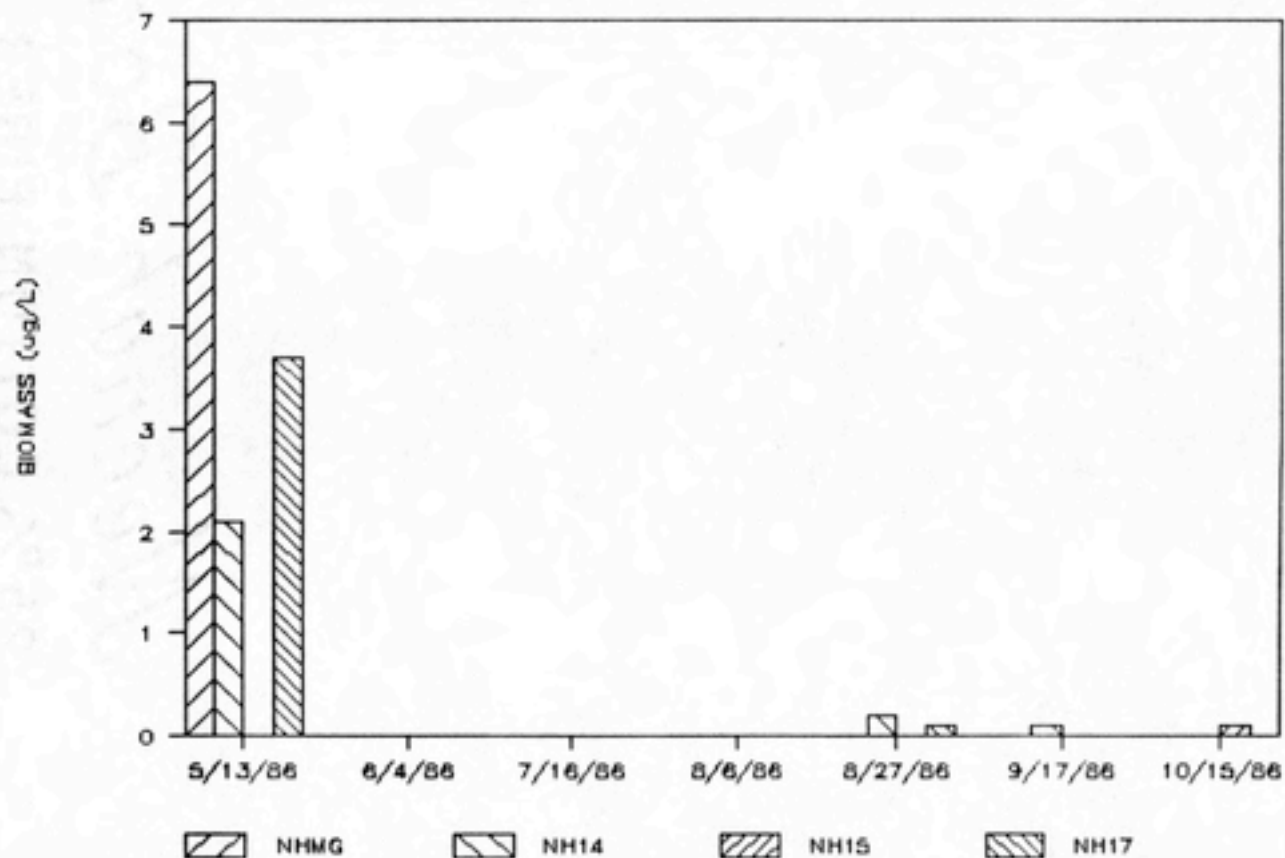
Figure 9 - Biomass of Daphnia spp. throughout the lake
during the sampling period.
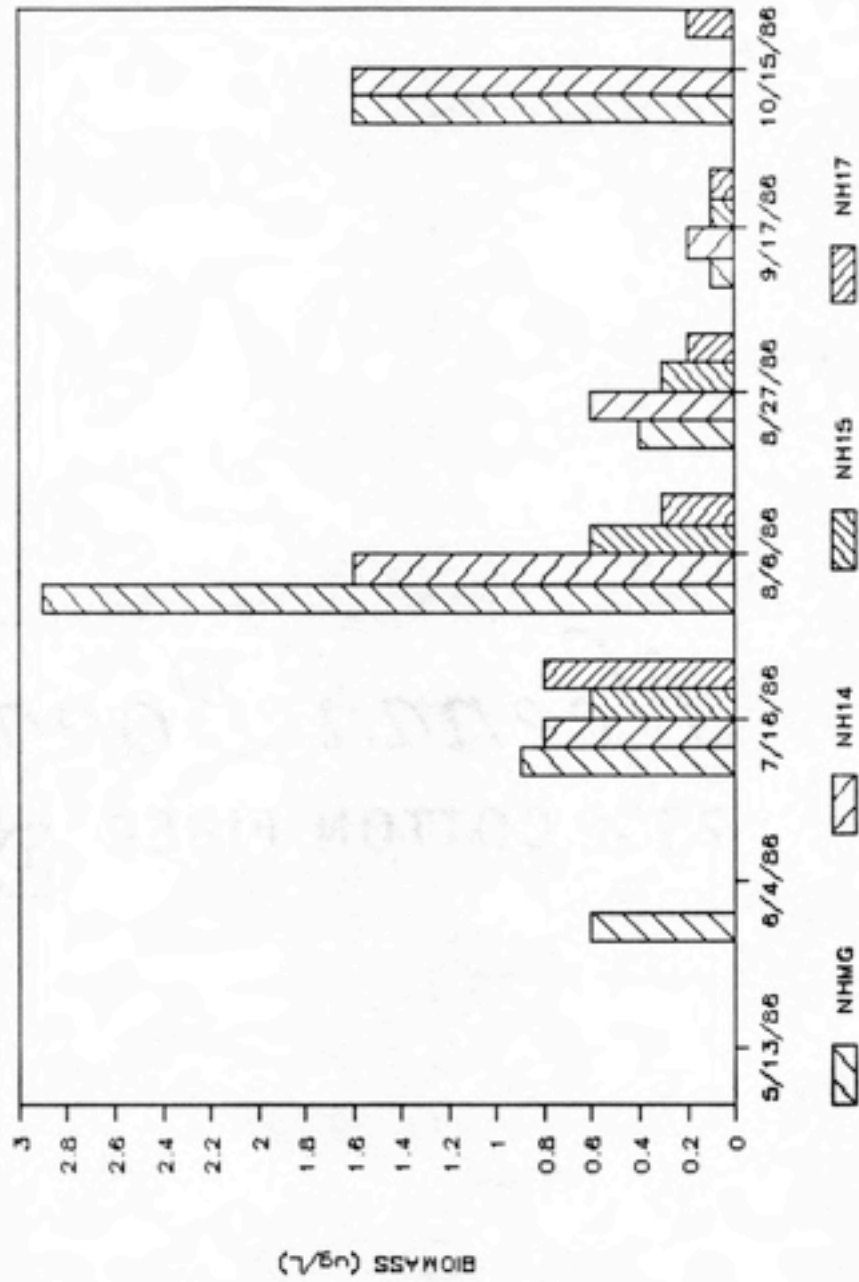
Figure 10 - Biomass of Diaphanosoma sp. throughout the lake during the sampling period.
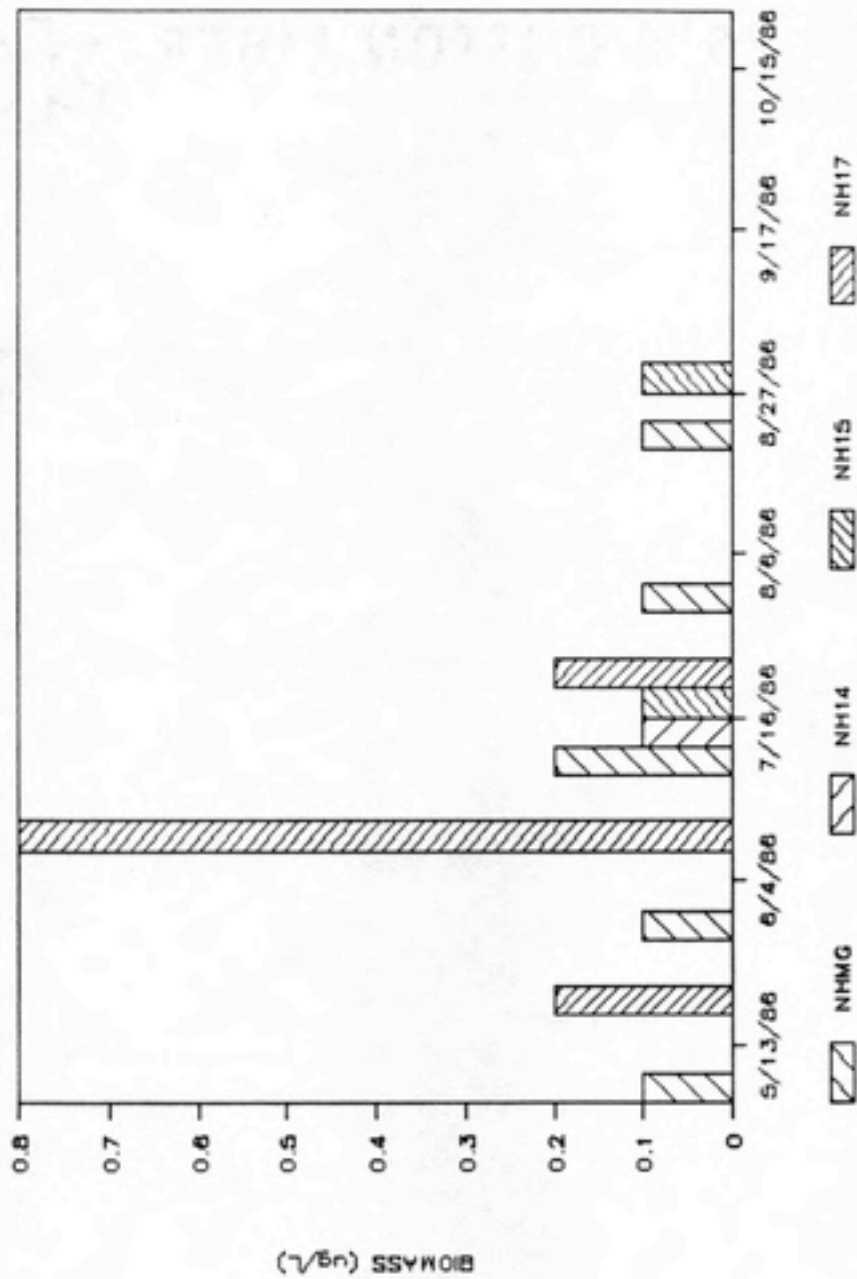
Figure 11 - Biomass of Bosmina longirostris throughout the lake during the sampling period.

Other zooplankton

Other zooplankton were found during the sampling period, but these were usually as isolated individuals, during a single sampling event or during the enclosure experiments. These zooplankton were as follows: Tropocyclops prasinus, Moina micrura, Chydorus sphaericus, Alona monacantha, Leydigia quadrangularis, Sida crystallina and Holopodium amazonicum.

PHYTOPLANKTON

Chlorophyll a

Chlorophyll a was lowest in May and June and increased during July and early August reaching a high of 157 ug/L at station NHMG (Figure 12). Chlorophyll a then declined during late August and September but increased on the final sampling date in October. Values were highest at NHMG and declined through the lake to NH17.

Phytoplankton size

Phytoplankton size was largest in May, and then declined to a smaller size throughout the remaining sampling period (Figure 13). Larger size of phytoplankton were present in the spring at lower chlorophyll a values

CHLOROPHYLL A
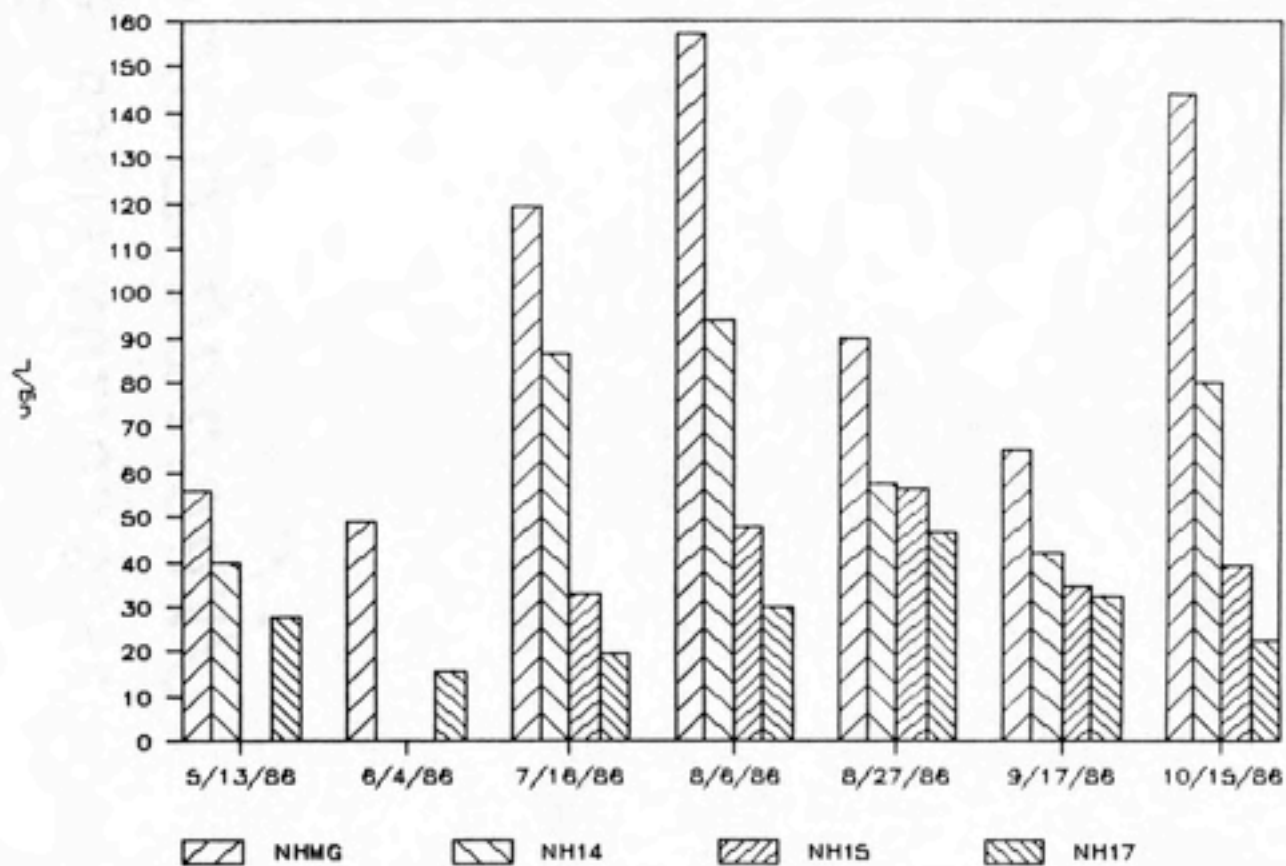
Figure 12 - Chlorophyll a throughout the lake during the sampling period.
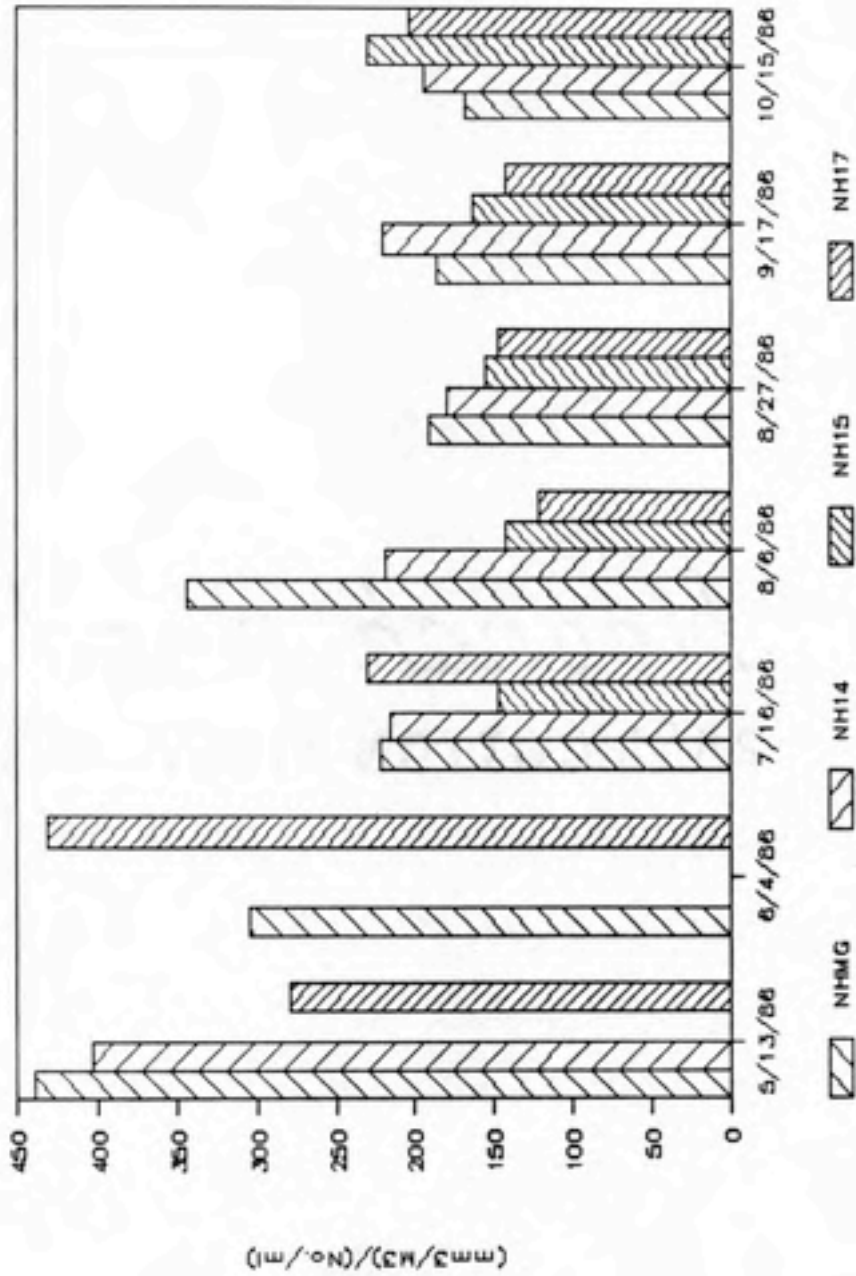
Figure 13 - Phytoplankton size (biovolume / density) throughout the lake during the sampling period.

while the small phytoplankton were associated with high chlorophyll <u>a</u> values (Figure 12).

Abundant Phytoplankton Classes

Bacillariophyceae attained the highest biovolume during the spring and fall (Figure 14). Cyanophyceae was the dominant phytoplankton class during the summer months (Figure 15). It was abundant in all segments of the lake throughout the sampling period and particularly NH15 in late August. The highest biovolumes for this class were attained at stations NHMG and NH14. Chlorophyceae was as abundant as the other phytoplankton at times throughout the sampling period. Greatest biovolume was at stations NHMG and NH14 (Figure 16). The lowest biovolumes were observed in late August. Euglenophyceae made up a smaller portion of total phytoplankton biovolume. Biovolume was higher at station NHMG and in most instances declined moving down lake to NH17 (Figure 17). Biovolume remained relatively consistent with the exception of August 6. Cryptophyceae made up a smaller portion of phytoplankton biomass as well. Its distribution and abundance was very similar to that of Euglenophyceae (Figure 17 and 18).
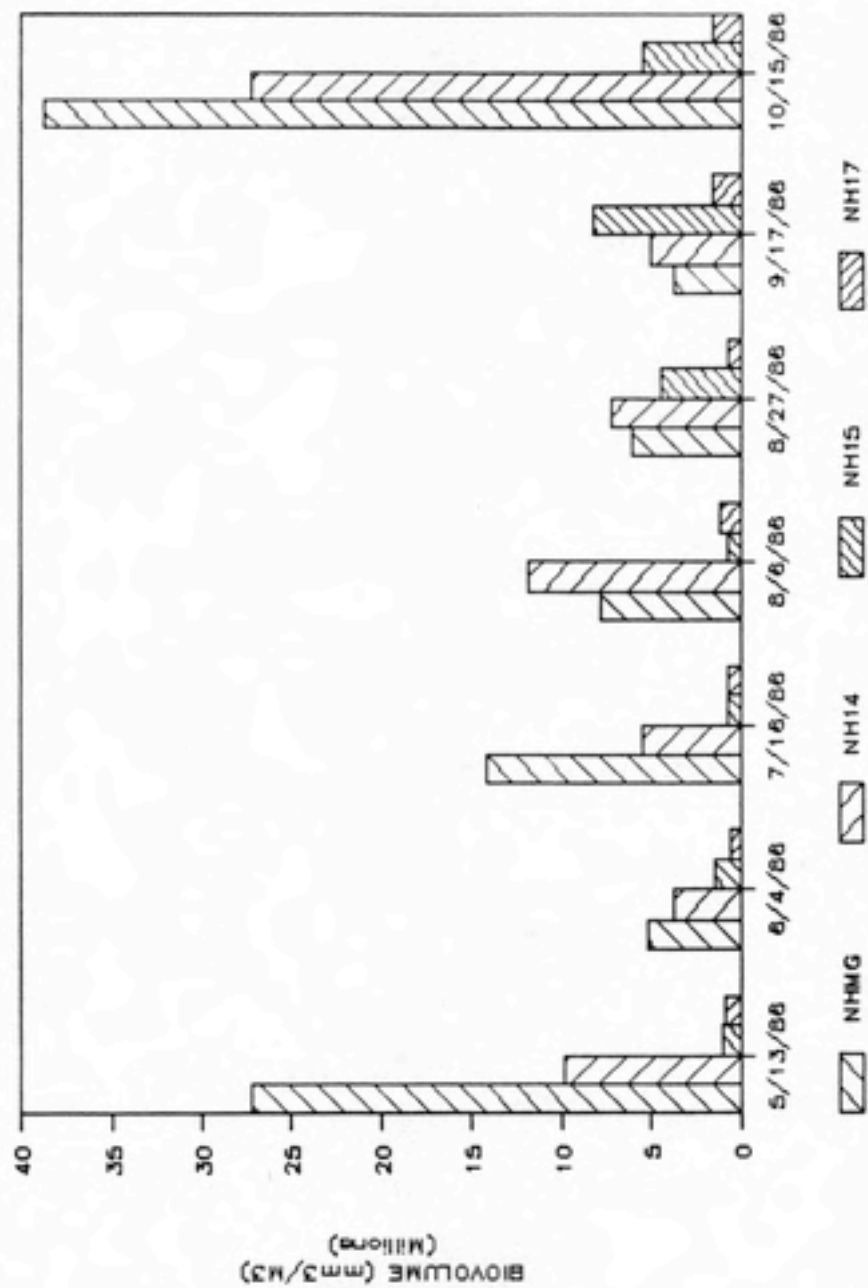
Figure 14 - Bacillariophyceae biovolume throughout the lake during the sampling period.
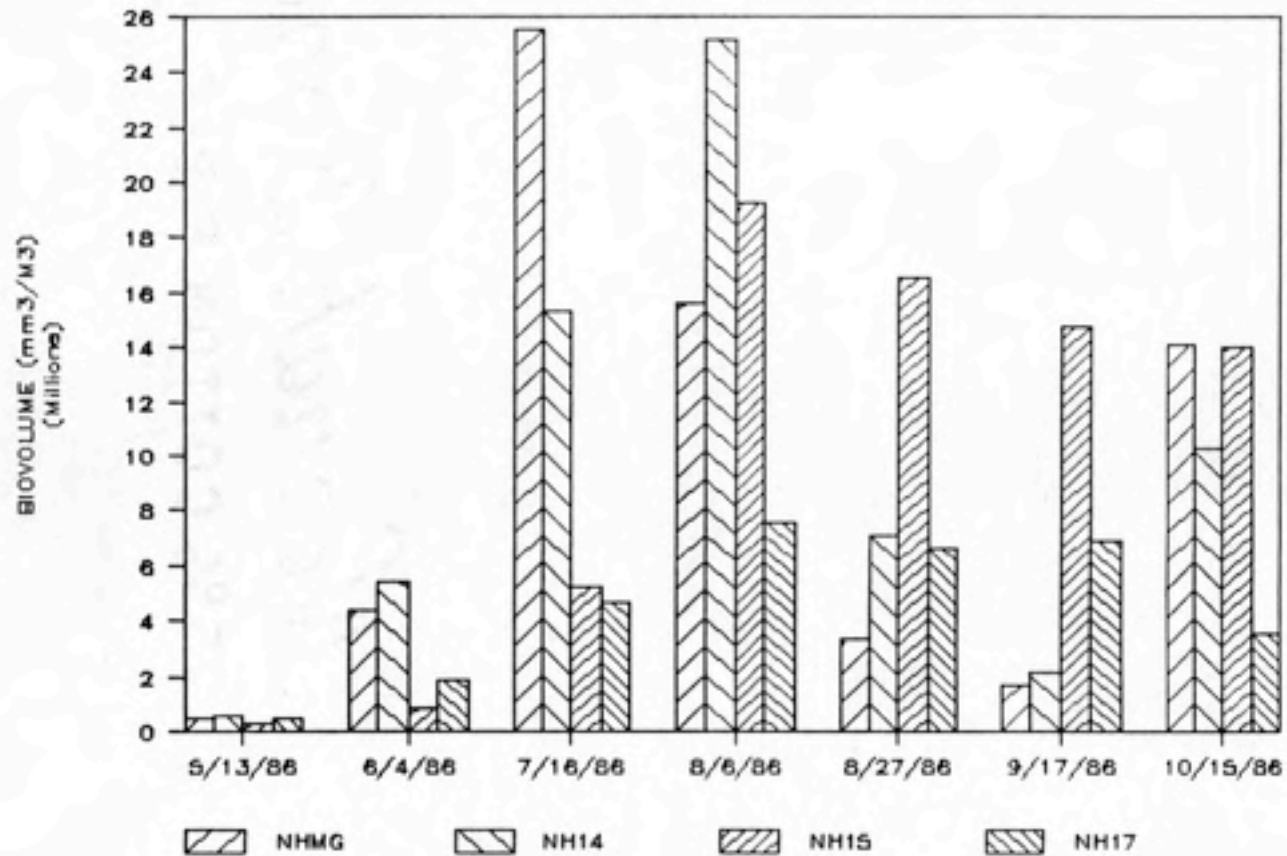
Figure 15 - Cyanophyceae biovolume throughout the lake during the sampling period.

CHLOROPHYCEAE (Greens)
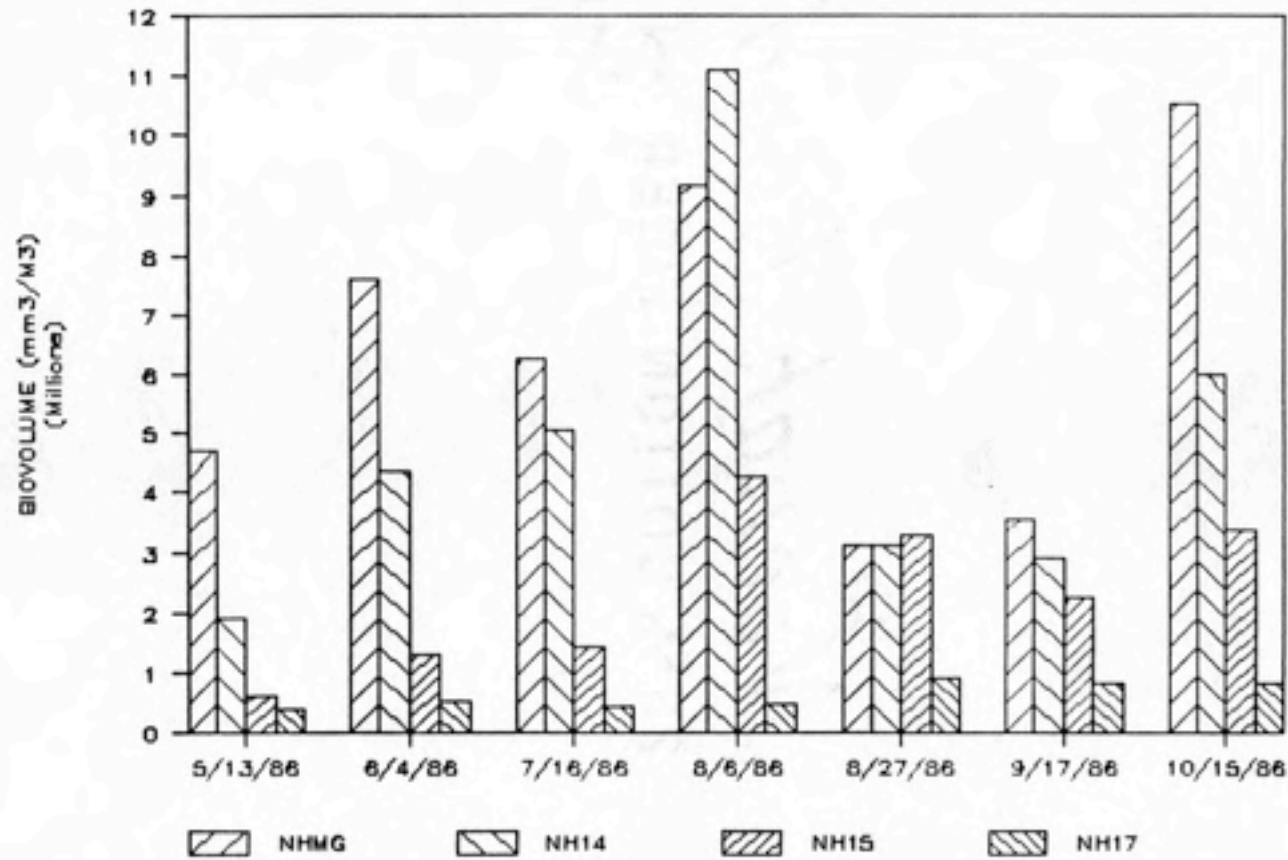
Figure 16 - Chlorophyceae biovolume throughout the lake during the sampling period.

EUGLENOPHYCEAE (Euglenoids)
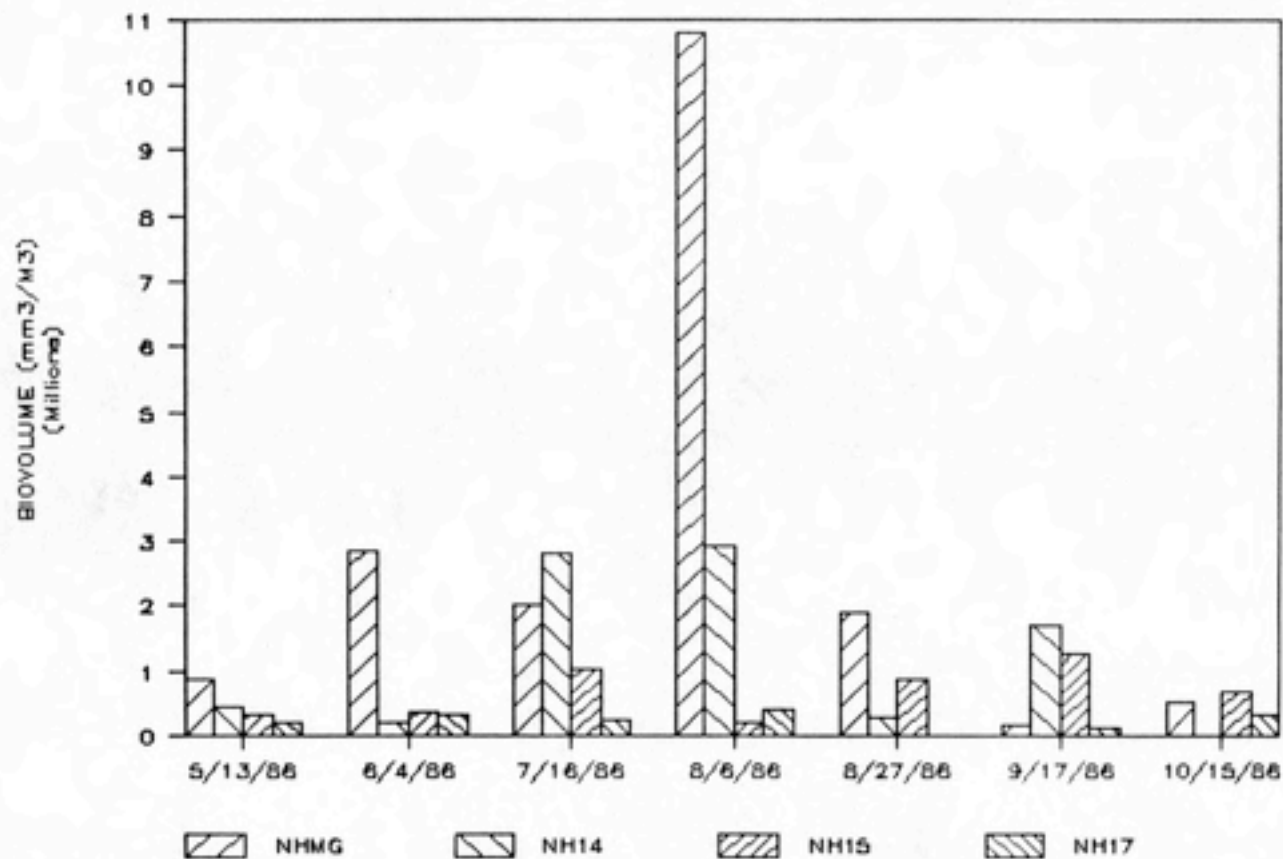
Figure 17 - Euglenophyceae biovolume throughout the lake during the sampling period.

CRYPTOPHYCEAE (Cryptomonads)
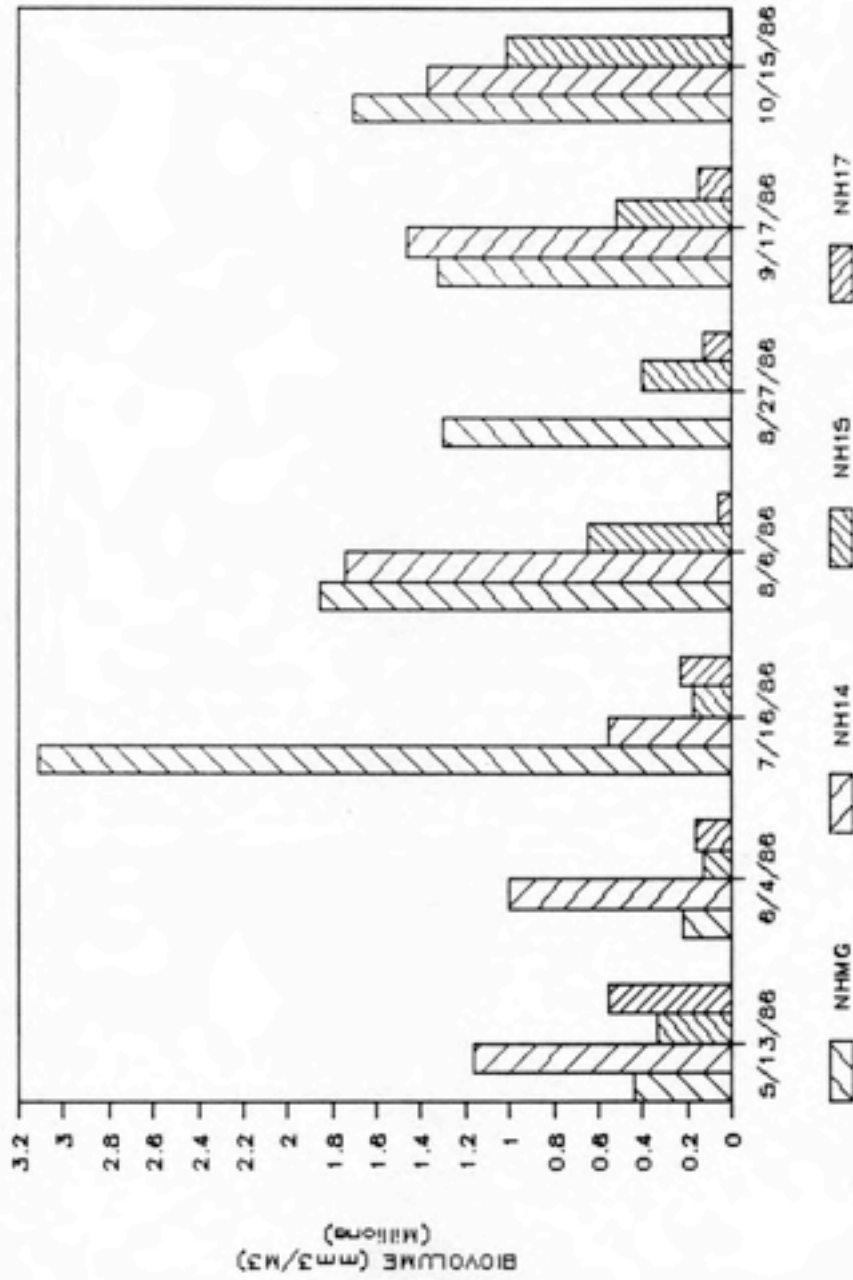
Figure 18 - Cryptophyceae biovolume throughout the lake
during the sampling period.

ENCLOSURE EXPERIMENTS

ZOOPLANKTON

Diaptomus pallidus

Diaptomus pallidus increased in biomass inside
the enclosures during the first week in all six of the
experiments (Figure 19). Biomass did not change markedly
outside the enclosures. By the end of the week biomass
levels inside the enclosures were many times greater than
densities outside the enclosures in the lake. The large
(> 1 mm) size classes of this copepod did not dominate
the growth inside the enclosures. Biomass of all size
classes increased inside the enclosures relative to
outside (Figure 20).

Cyclops vernalis

The biomass of Cyclops vernalis increased
inside the enclosures during the first week in all the
experiments (Figure 21). The greatest increase in biomass
inside the enclosures relative to the outside was during
experiments 1 and 5. During the remaining experiments,
there were smaller increases inside. Cyclops vernalis
inside the enclosure attained larger body sizes (Figures
22). In all of the experiments, individuals of length 1
mm and longer developed inside the enclosure while outside
the enclosures individuals longer than 1 mm did not occur

DIAPTOMUS PALLIDUS

Figure 19 - The changes in biomass of <u>Diaptomus</u> <u>pallidus</u> throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

Figure 20 - The length frequency of _Diaptomus pallidus_ in experiments 1 - 6. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled. All measurements are in mm.

CYCLOPS VERNALIS
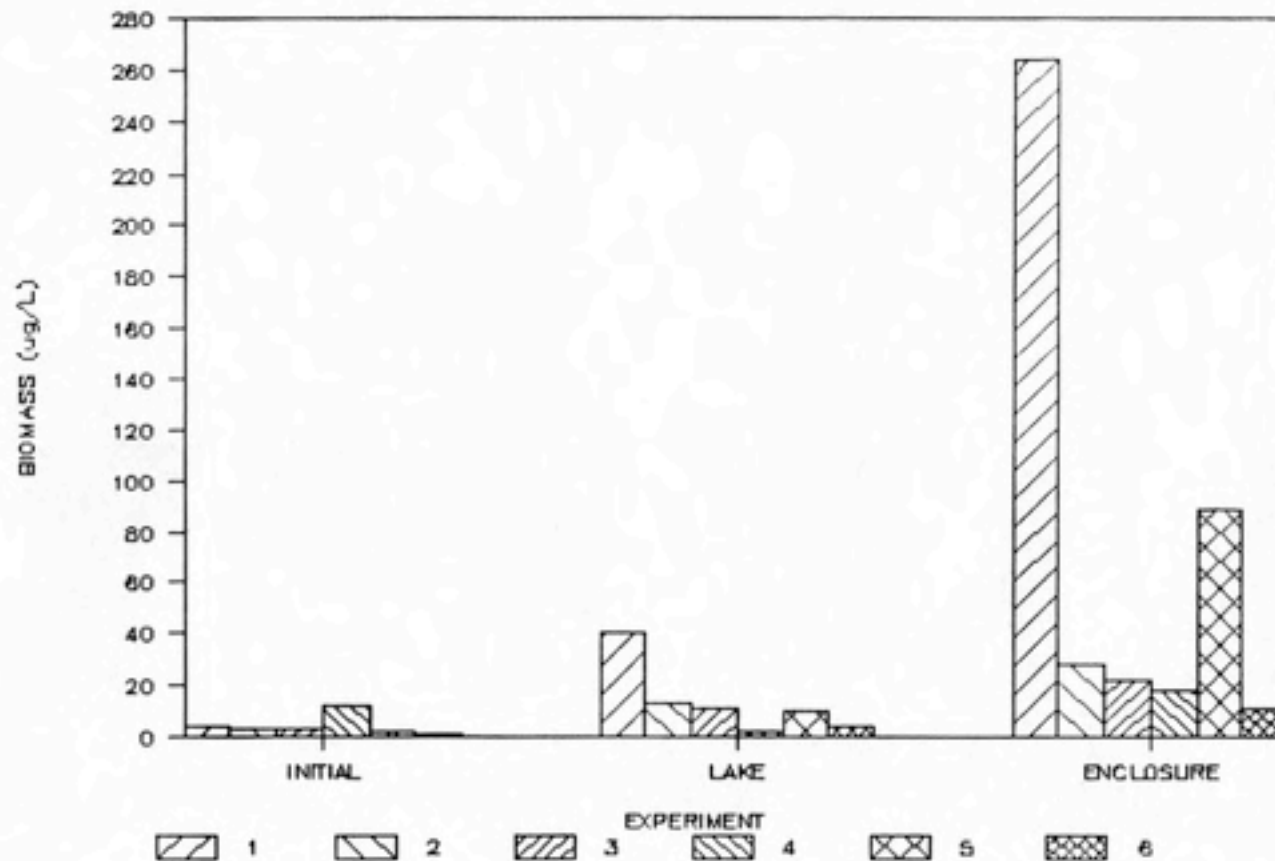
Figure 21 - The changes in biomass of Cyclops vernalis throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

Figure 22 - The length frequency of <u>Cyclops vernalis</u> in experiments 1 - 5. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled. All measurements are in mm.
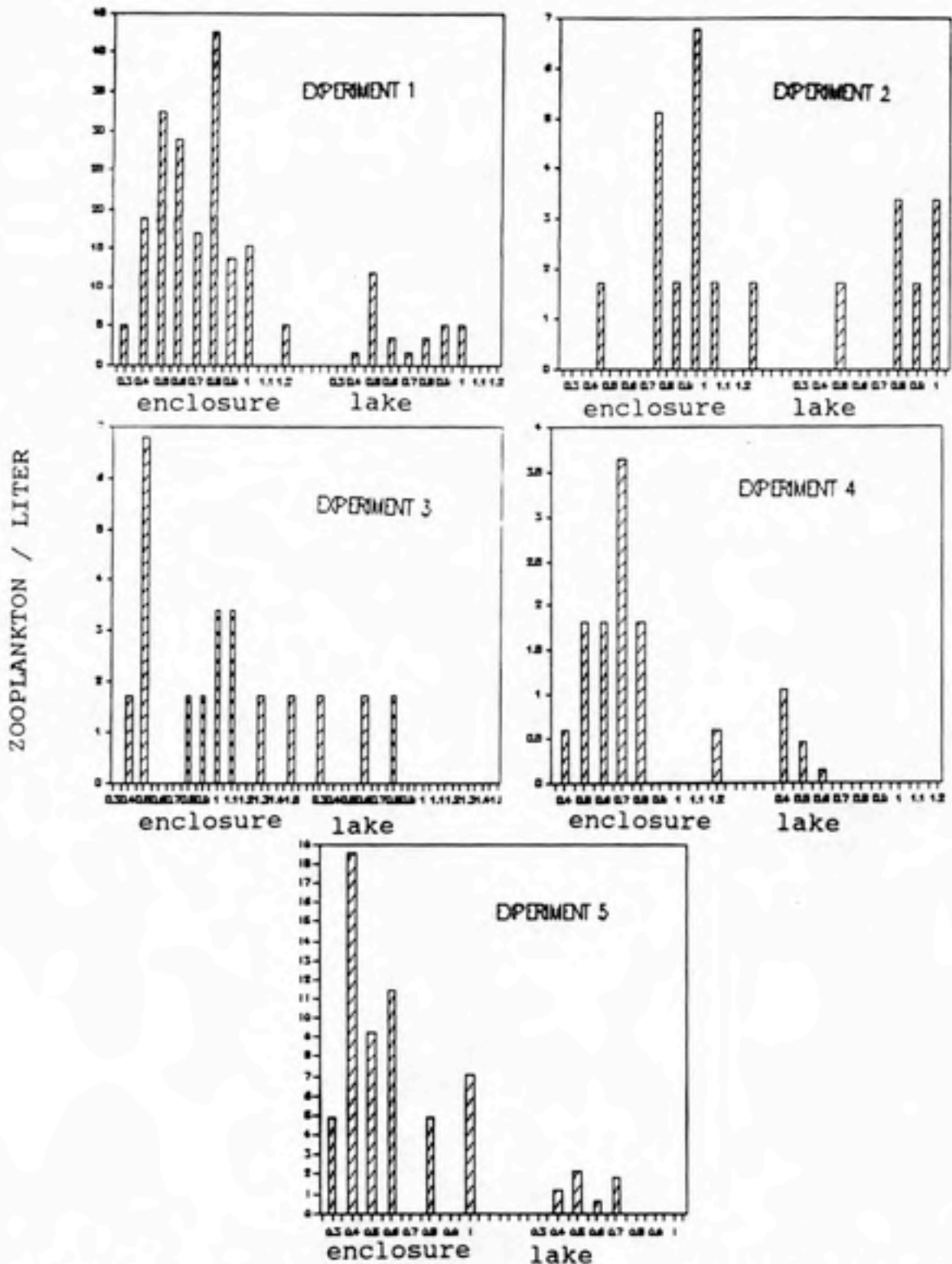
(Figure 22) The smaller size classes increased inside the enclosures as well.

Mesocyclops edax

Mesocyclops edax, although less abundant than the other copepods, increased in biomass during the first week of the experiments inside the enclosures (Figure 23). In experiments 1-3, Mesocyclops edax attained much higher biomass inside the enclosures than in experiments 4-6. This may be attributed to the higher biomass in the lake at the beginning of the first three experiments. Size frequency data were omitted because too few were collected outside the enclosure.

Copepod nauplii

Copepod naupliar biomass increased inside the enclosures during the first week in all of the experiments (Figure 24). The pattern of increase in biomass was very similar to that of the adult copepods in each experiment (Figure 19, Figure 21, Figure 23).

Daphnia spp.

If Daphnia spp. was present in measurable numbers at the beginning of each experiment during the first week, it increased in biomass inside the enclosures (Figure 25).

MESOCLYCOPS EDAX

Figure 23 - The changes in biomass of Mesocyclops edax throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

COPEPOD NAUPLII

Figure 24 - The changes in biomass of copepod nauplii
throughout each experiment. "INITIAL" = conditions at the
initiation of the experiment; "LAKE" = conditions outside
enclosures and "ENCLOSURE" = conditions inside enclosure.

DAPHNIA SPP.
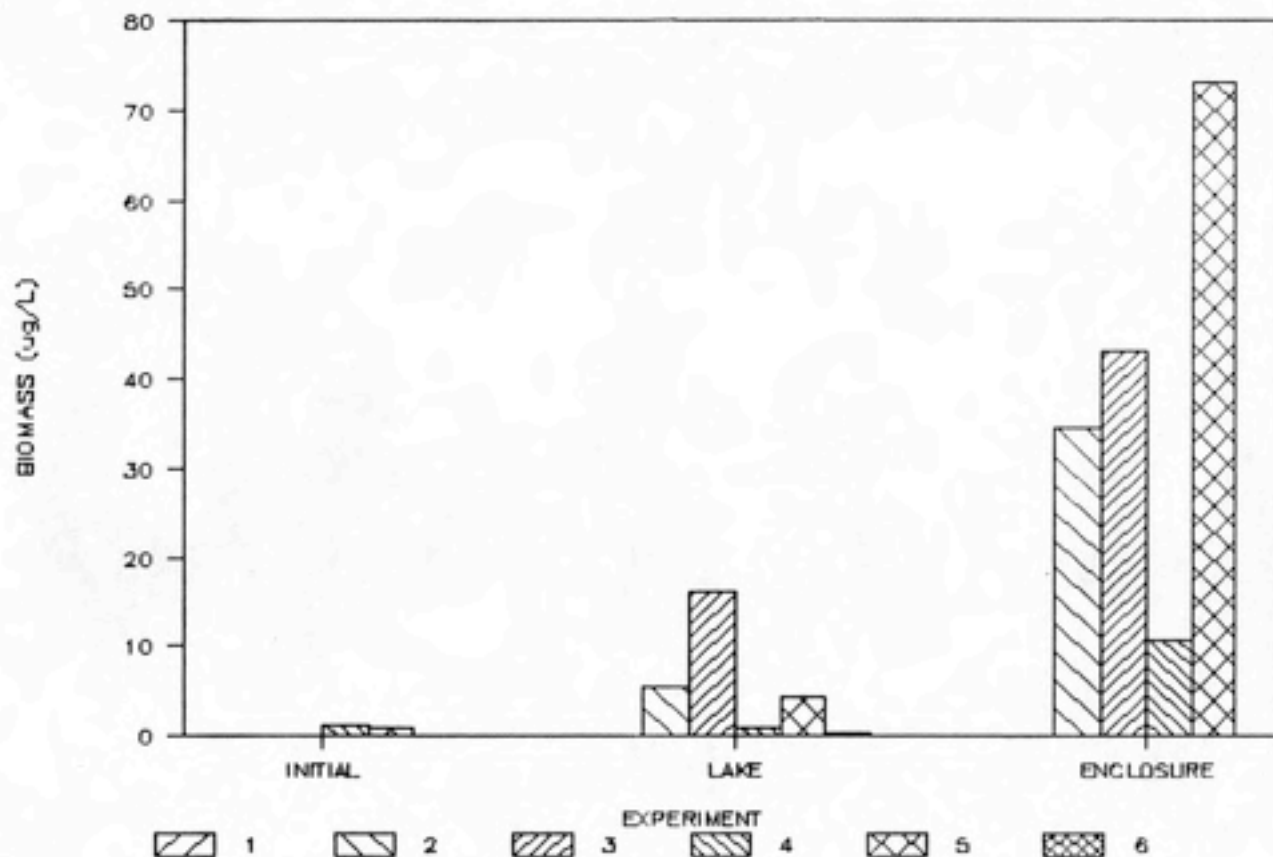
Figure 25 - The changes in biomass of <u>Daphnia</u> spp. throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

Individuals inside the enclosure generally did not achieve a larger size than those found outside the enclosure (Figures 26).

Diaphanosoma sp.

Diaphanosoma sp. biomass increased inside the enclosures in experiments 1-3 and experiment 6 during the first week (Figure 27). In experiments 4 and 5, Diaphanosoma sp. was not present outside the enclosures at the beginning of the experiments. In experiment 5, Diaphanosoma sp. appeared outside the enclosure during the course of the experiment but was not present inside the enclosure. When Diaphanosoma sp. was present inside the enclosures, its biomass increased to high levels relative to increases outside the enclosures. Densities of all size classes increased inside the enclosures (Figure 28).

Moina micrura

Moina micrura biomass followed a similar pattern to that of Diaphanosoma sp. inside and outside of the enclosures during the first week (Figures 27 and 29). It was not as abundant as Diaphanosoma sp., but it appeared at the same time and increased inside the enclosures during the same experiments.
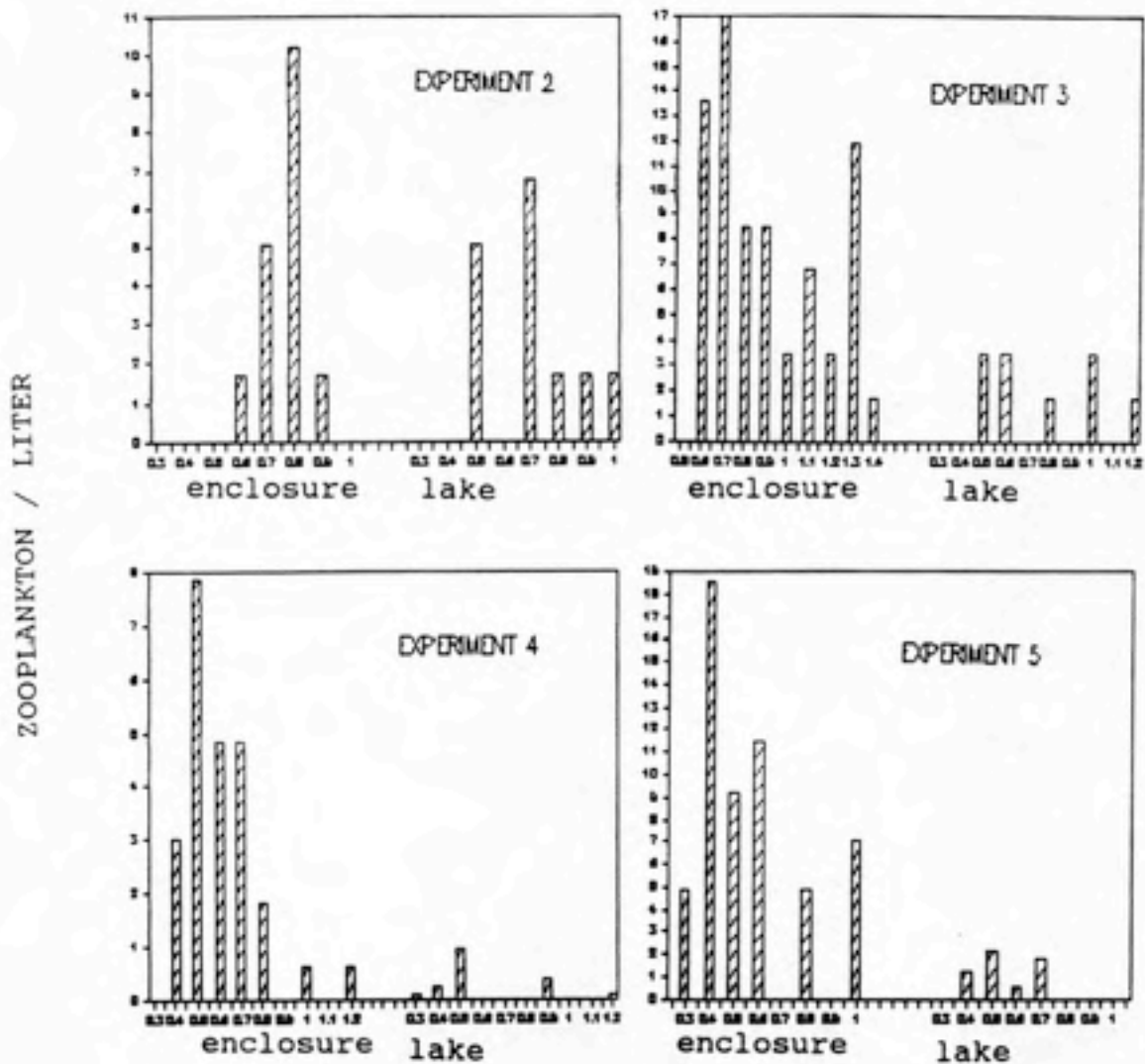
Figure 26 - The length frequency of _Daphnia_ spp. in experiments 2 - 5. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled. All measurements are in mm.
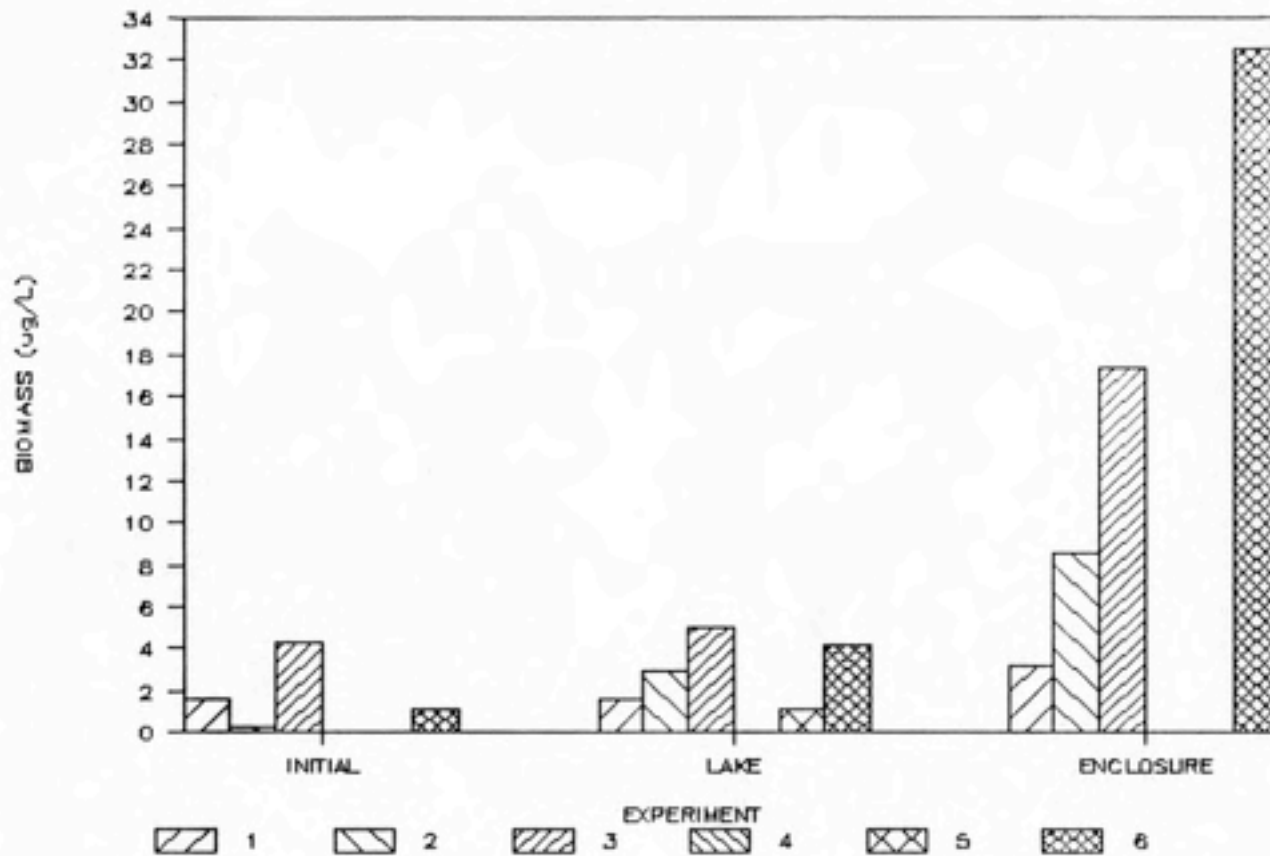
Figure 27 - The changes in biomass of Diaphanosoma sp. throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.
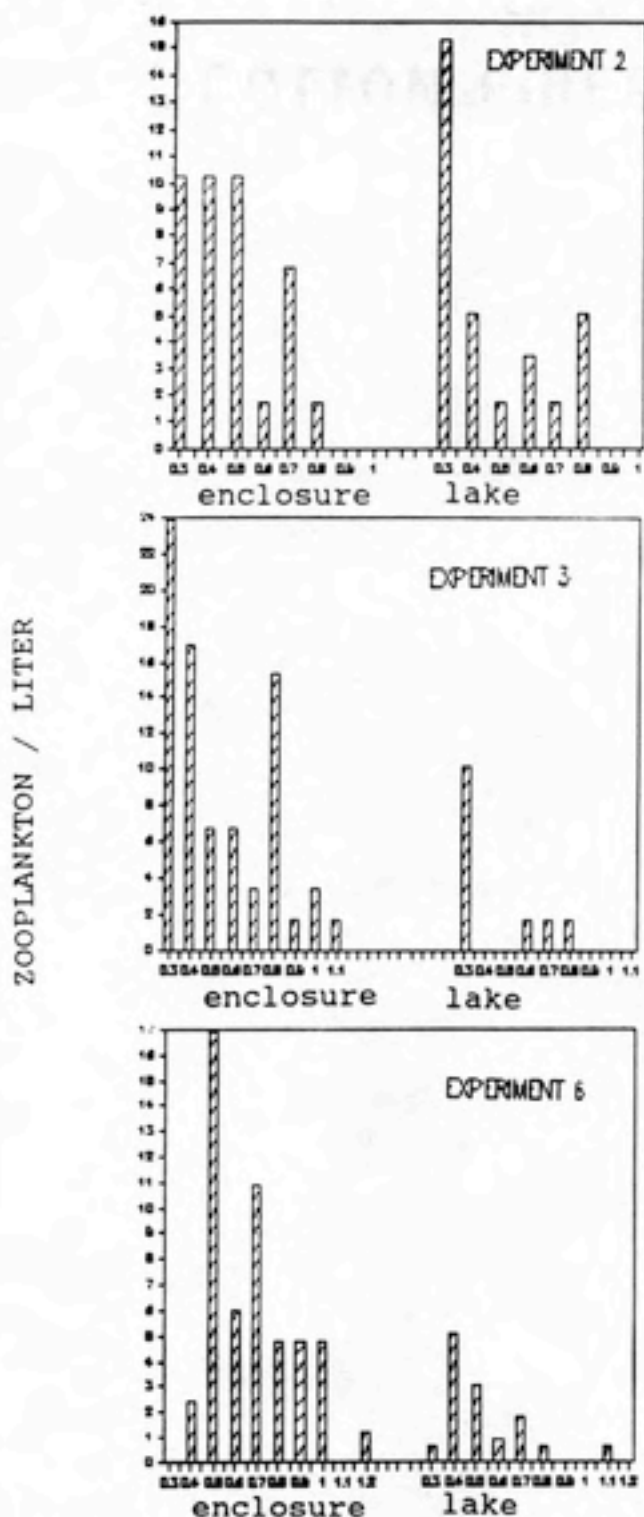
Figure 28 - The length frequency of <u>Diaphanosoma</u> sp. in experiments 2, 3, 5. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled. All measurements are in mm.

MOINA MICRURA
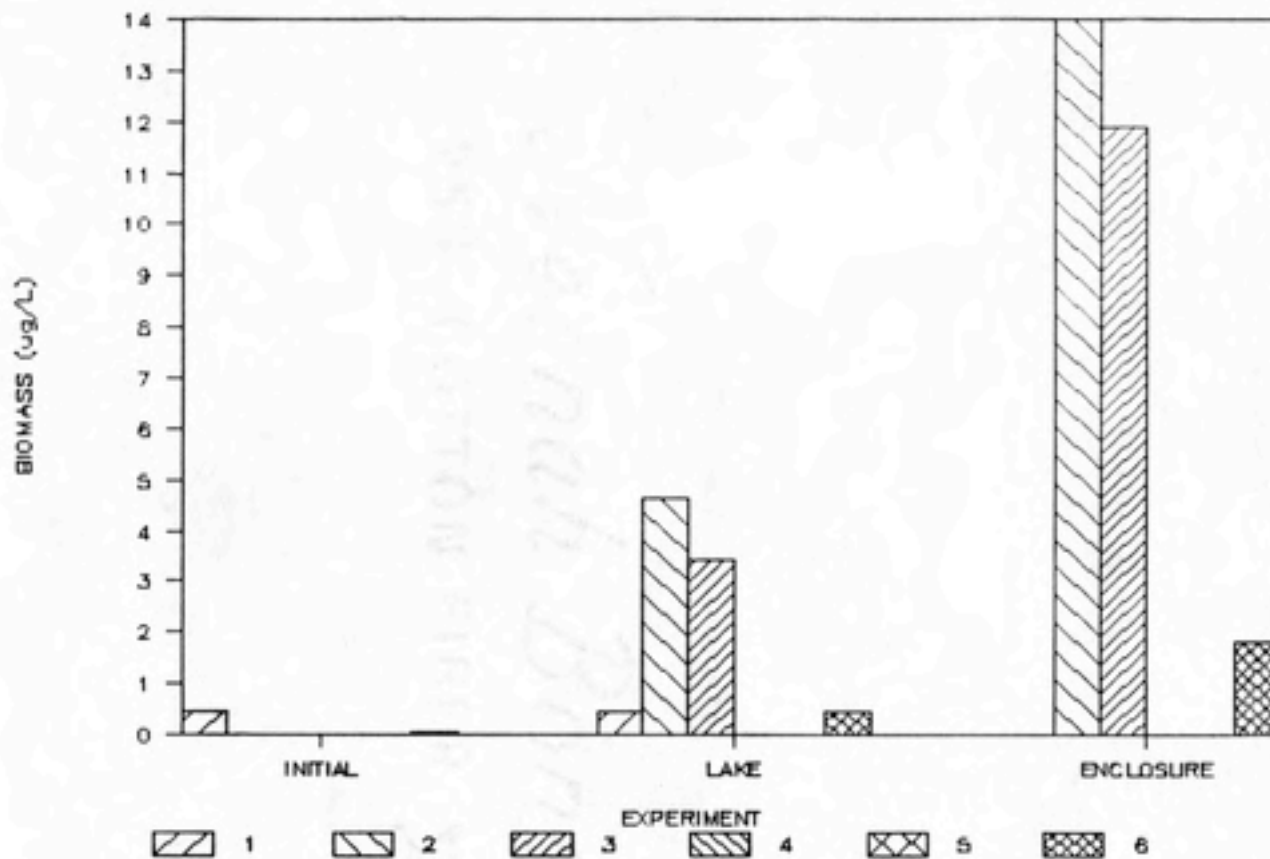
Figure 29 - The changes in biomass of <u>Moina</u> <u>micrura</u> throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

Bosmina longirostris

Bosmina longirostris was only present in experiments 4-6 (Figure 30). In these experiments, biomass increased inside the enclosure to relatively high amounts only in experiment 5. In experiments 4 and 6, biomass remained at the low levels both inside and outside of the enclosures.

PHYTOPLANKTON

Chlorophyll a

Inside the enclosures, chlorophyll a was reduced in four of the six experiments relative to concentrations outside the enclosures(Figure 31). In experiment 1, chlorophyll a increased outside the enclosure during the course of the experiments and remained at the same level inside the enclosure. In experiment 6, chlorophyll a increased inside and outside of the enclosure. In experiments 2-5, chlorophyll a levels remained similar during the experiments outside the enclosures while inside the enclosures levels were greatly reduced. In experiments 2 and 5, chlorophyll a fell to below 5 ug/L.

BOSMINA LONGIROSTRIS
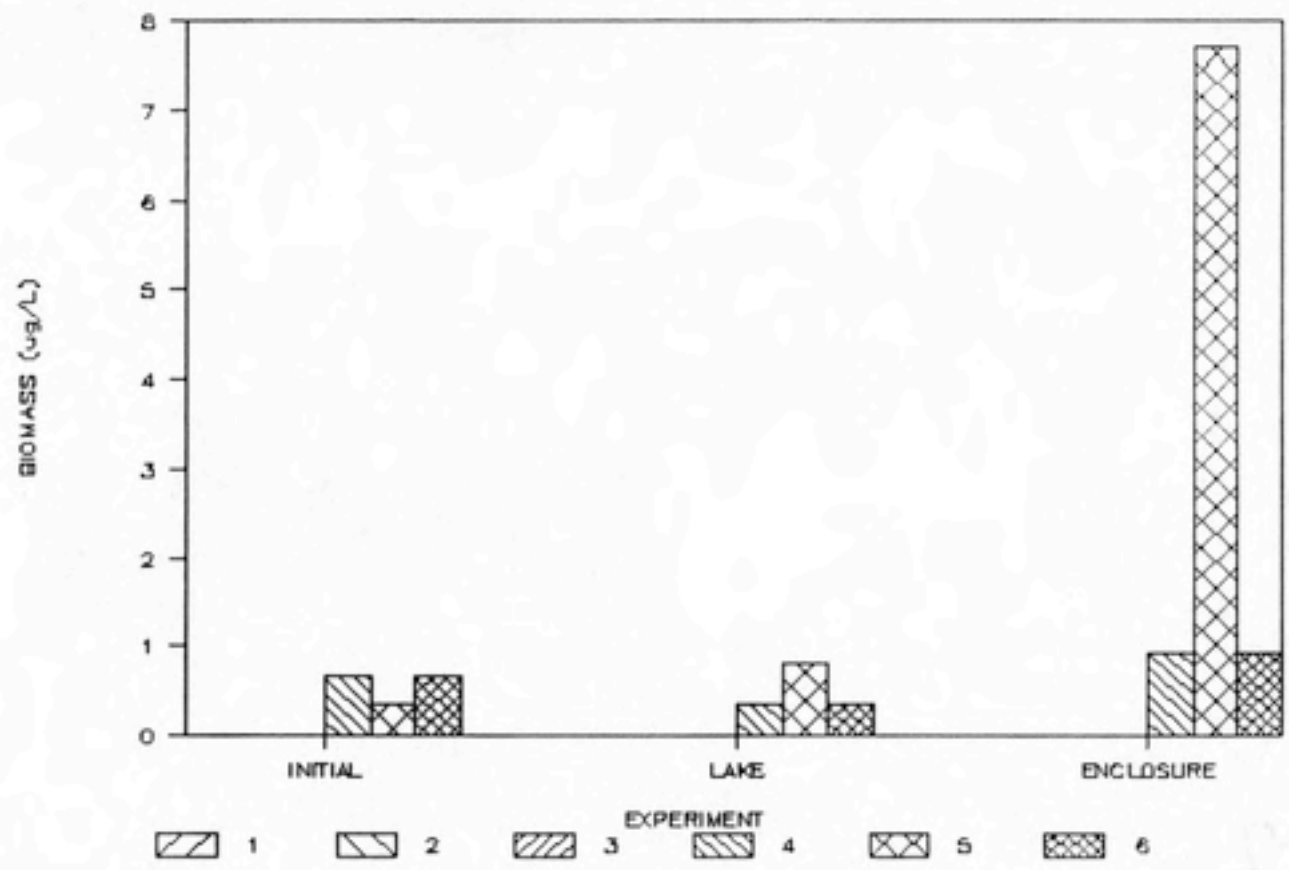
Figure 30 - The changes in biomass of <u>Bosmina longirostris</u> throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

CHLOROPHYLL A
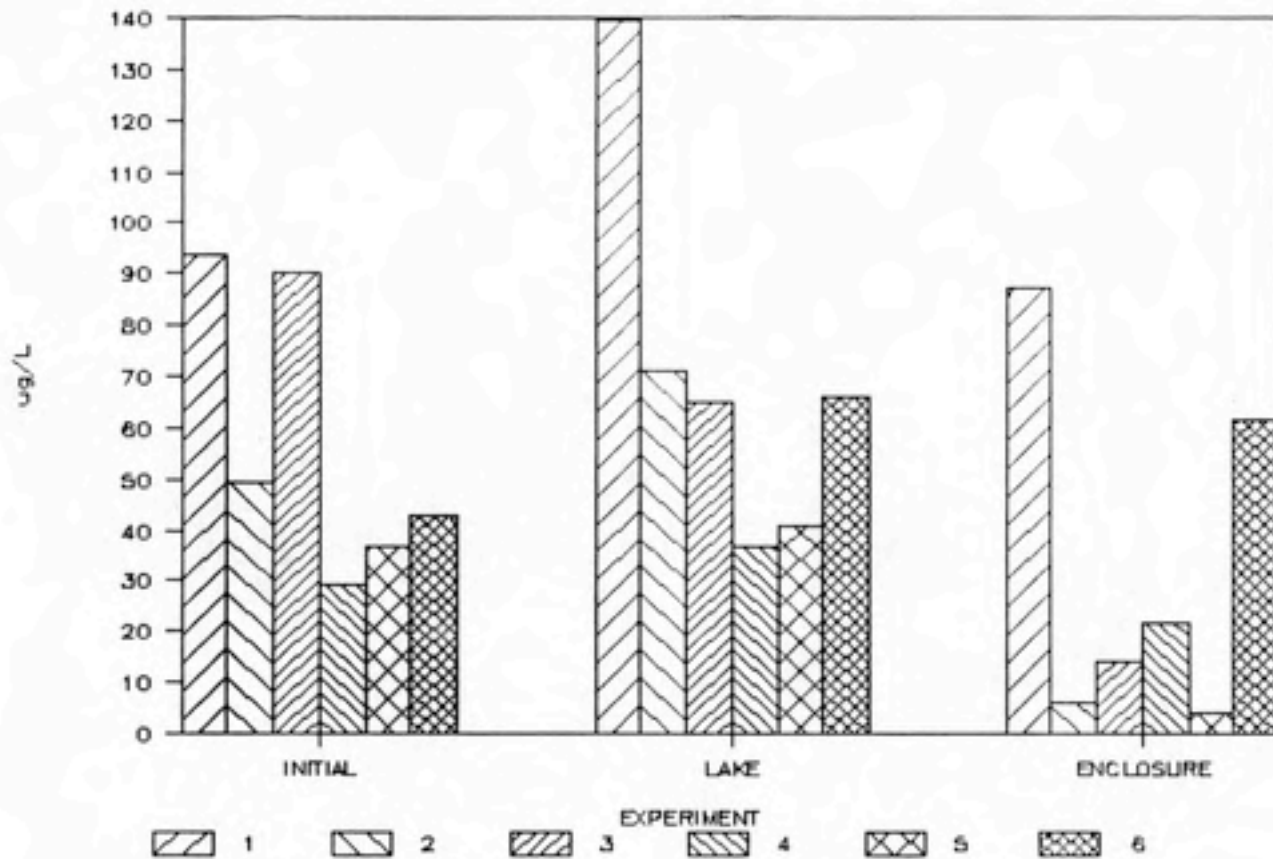
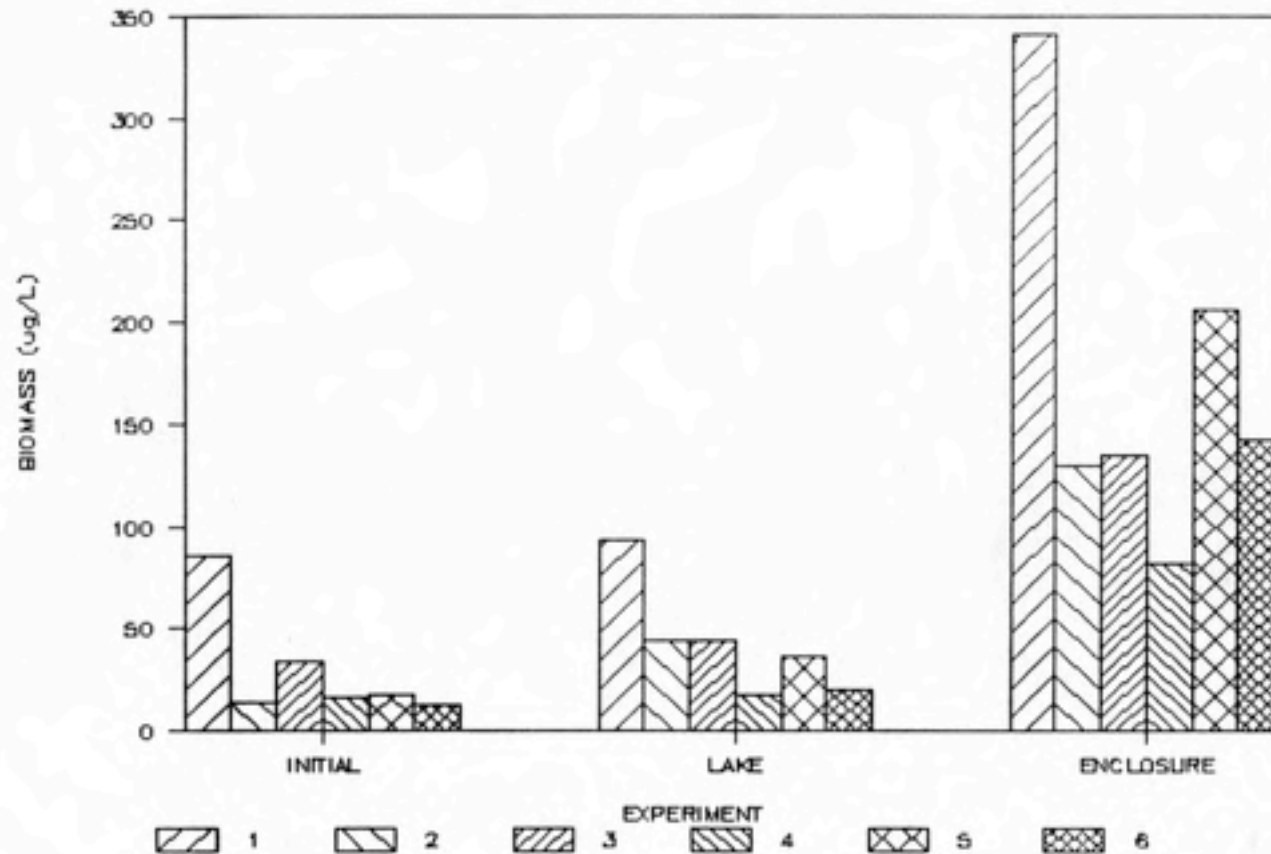**Figure 31** - The changes in chlorophyll <u>a</u> throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

Phytoplankton size

In experiment 1, phytoplankton size remained approximately the same both outside and inside the enclosure (Figure 32). In experiment 3, phytoplankton size became slightly smaller outside the enclosure and much larger inside the enclosure. From these experiments, the reduction in chlorophyll a (Figure 31) in experiment 3 can be associated with an increase in the size of phytoplankton. In the same way, the high chlorophyll a in experiment 1 can be associated with smaller phytoplankton cell size.

Phytoplankton composition and biovolume

Phytoplankton biovolume was little affected during experiment 1 (Figure 33). Cyanophyceae increased, Chlorophyceae and Bacillariophyceae remained very close to the same level, and Euglenophyceae and Chrysophyceae decreased by a small amount. Overall, phytoplankton biovolume was not reduced inside during experiment 1, but Bacillariophyceae increased substantially outside. In experiment 3, biovolumes of all classes of phytoplankton were considerably reduced inside the enclosure (Figure 34). Only Euglenophyceae, which are dominated by larger cells that may not be easily grazed by zooplankton, decreased more in biovolume outside the enclosure than inside during the experimental period. All other forms of

PHYTOPLANKTON SIZE (Biovolume/Density)
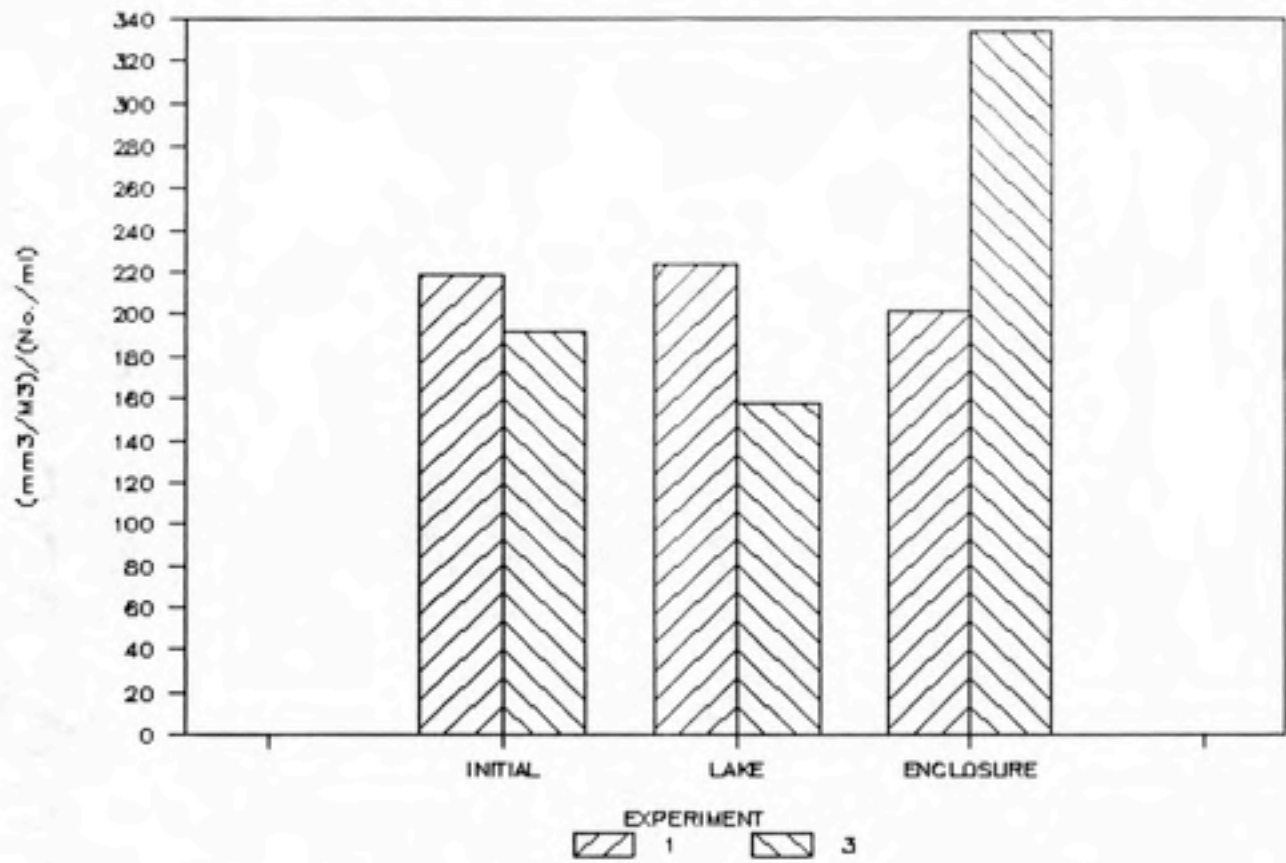
Figure 32 - The changes in phytoplankton size (biovolume / density) throughout experiments 1 and 3. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.
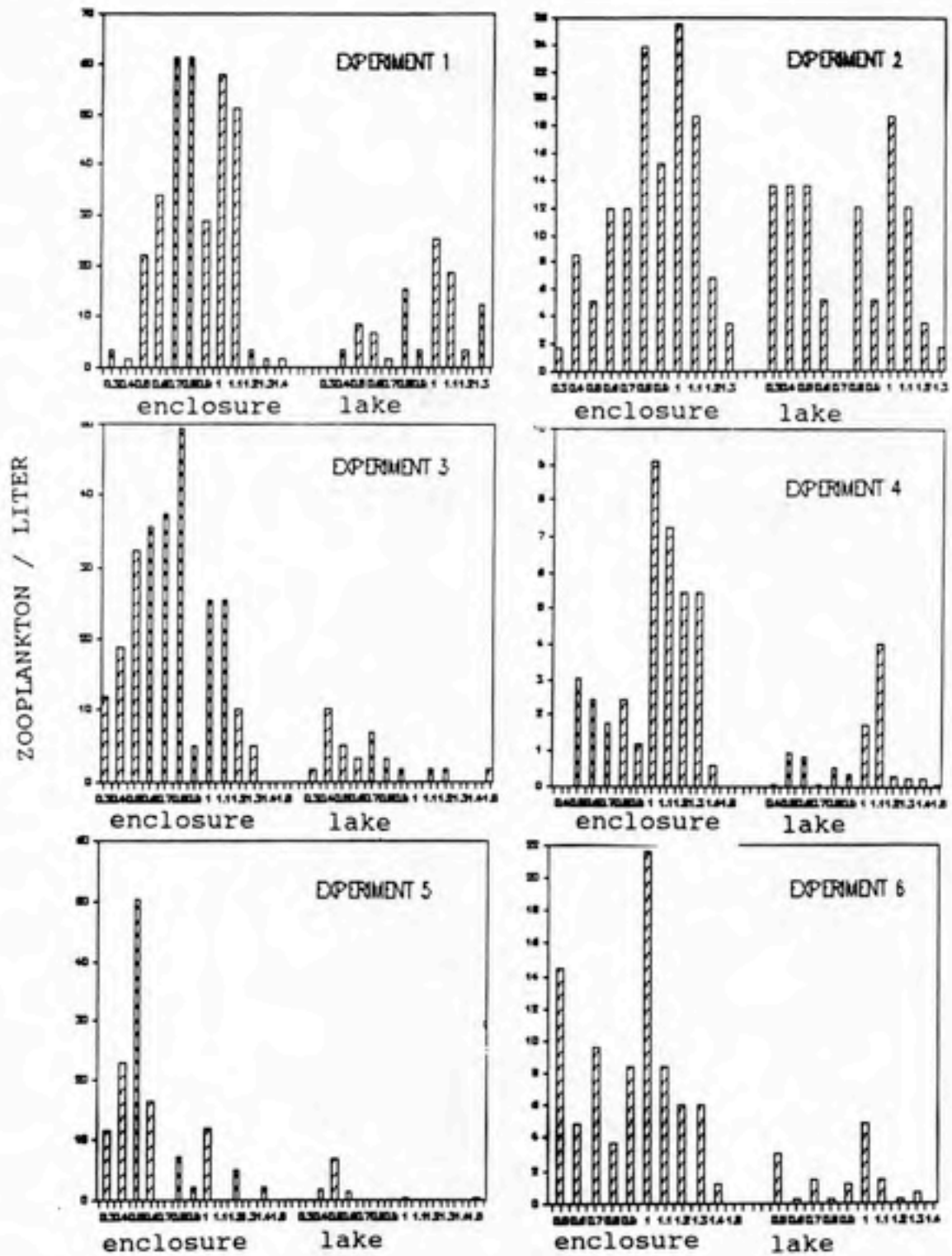
EXPERIMENT 1
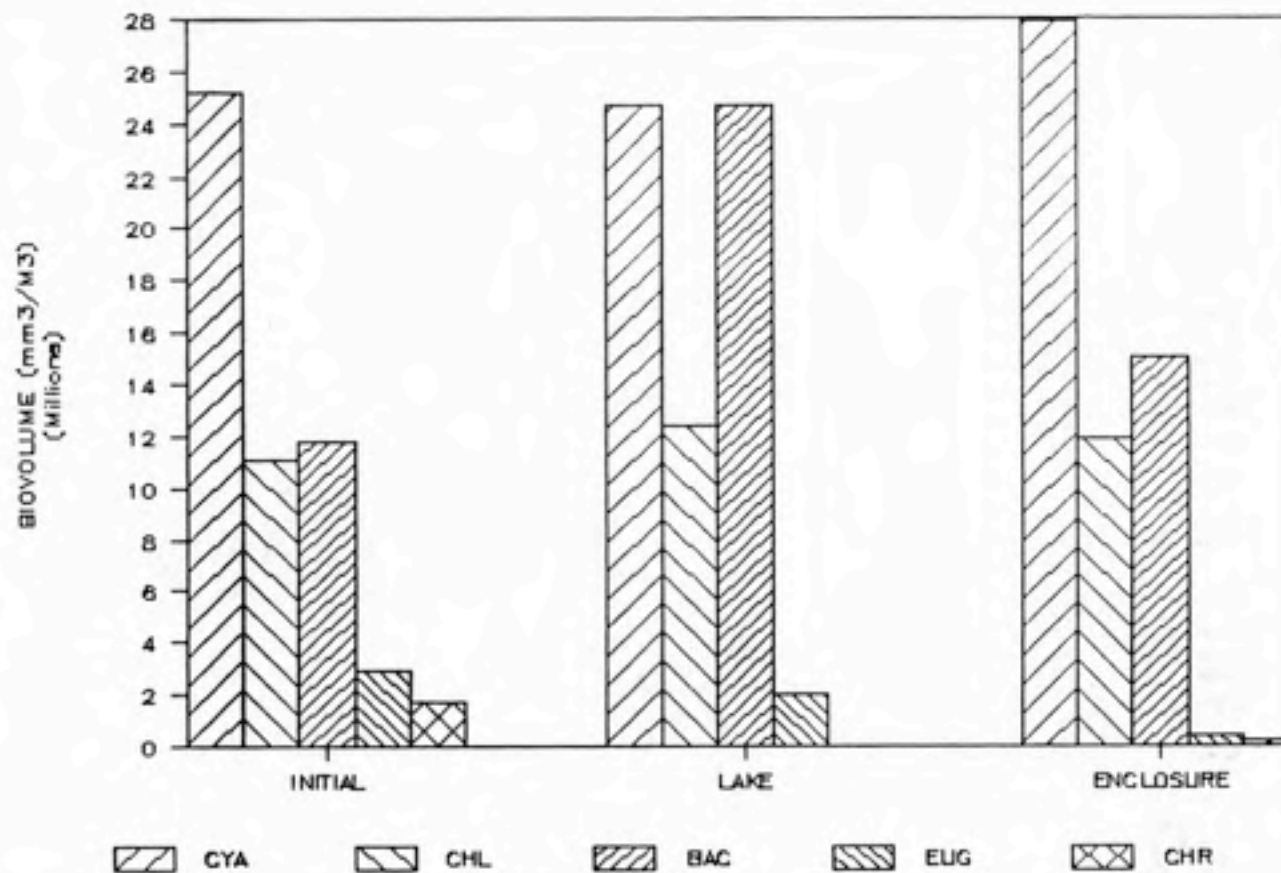
Figure 33 - Dominant classes of phytoplankton in experiment
1. "INITIAL" = conditions at the initiation of the
experiment; "LAKE" = conditions outside enclosures and
"ENCLOSURE" = conditions inside enclosure. (CYA) =
Cyanophyceae, (BAC) = Bacillariophyceae, (CHL) =
Chlorophyceae, (EUG)= Euglenophyceae, (CHR) = Cryptomonads.

EXPERIMENT 3
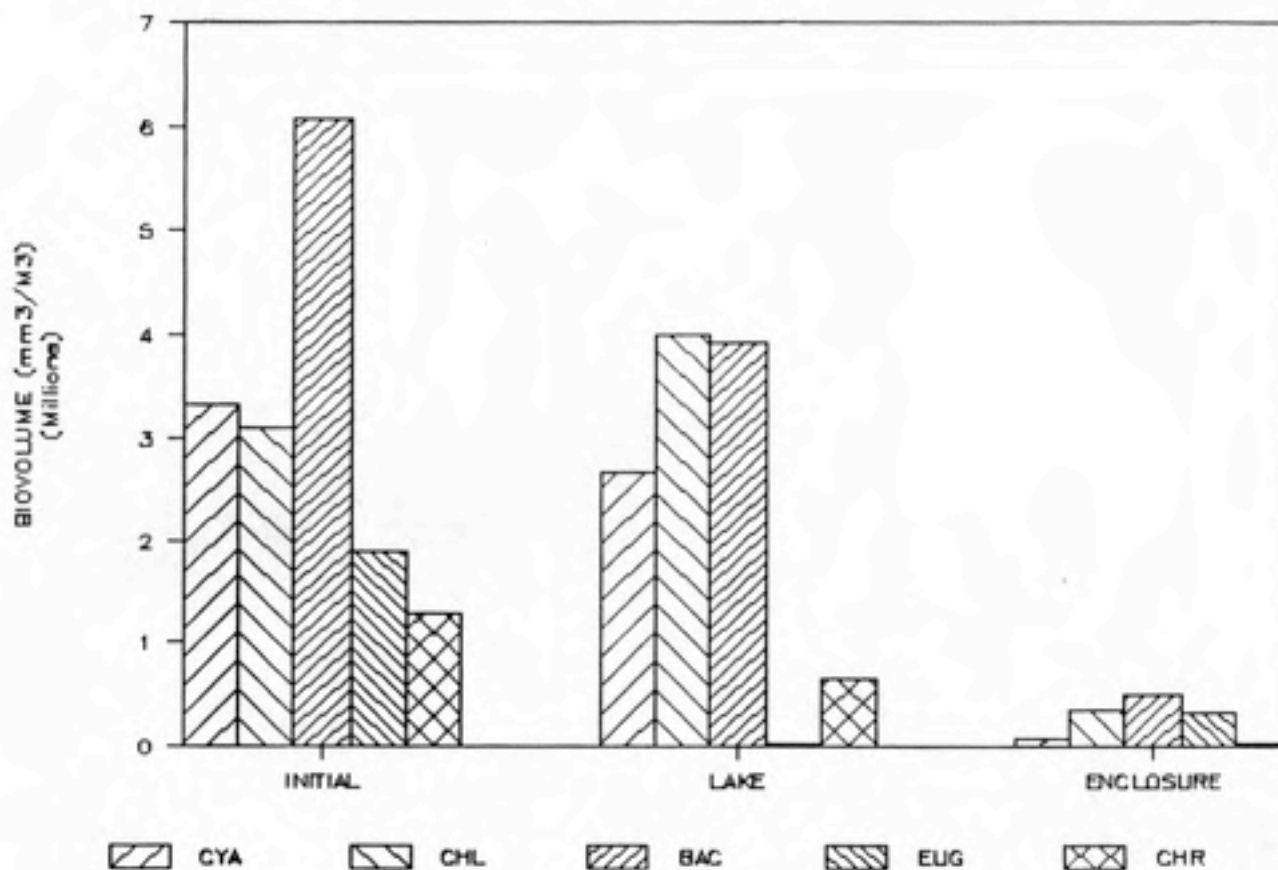
Figure 34 - Dominant classes of phytoplankton in experiment
3. "INITIAL" = conditions at the initiation of the
experiment; "LAKE" = conditions outside enclosures and
"ENCLOSURE" = conditions inside enclosure. (CYA) =
Cyanophyceae, (BAC) = Bacillariophyceae, (CHL) =
Chlorophyceae, (EUG)= Euglenophyceae, (CHR) = Cryptomonads.

phytoplankton, including Cyanophyceae, fell to lower levels inside the enclosure.

NUTRIENTS

Total Phosphorus and Total Kjeldahl Nitrogen

Total phosphorus remained very close to the same level throughout all of the experiments (Figure 35). In some experiments levels changed from the initial conditions to the final conditions, but these changes were just as great outside the enclosures as in. Total Kjeldahl nitrogen fluctuated considerably among the experiments (Figure 36), but concentrations outside the enclosure at the beginning were very close to concentrations inside and outside at the end of each experiment. Total Kjeldahl nitrogen as with total phosphorus did not differ inside and outside the enclosures.

Total Dissolved Phosphorus and Dissolved Kjeldahl Nitrogen

Total dissolved phosphorus concentrations were elevated inside the enclosures in experiments 2, 3, 5 and 6, but were very similar outside the enclosures (Figure 37). Experiments 2, 3 and 5 had greater increase while
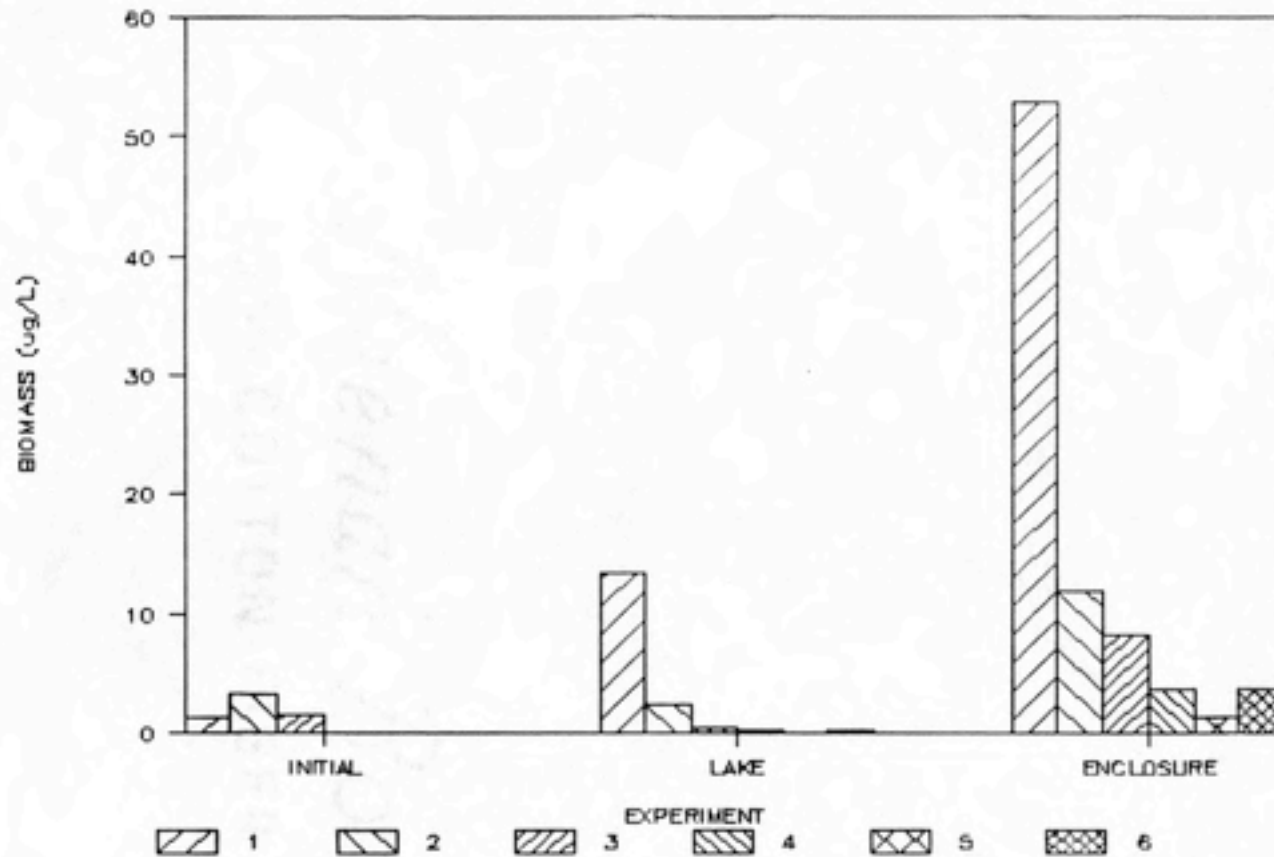
TOTAL PHOSPHORUS
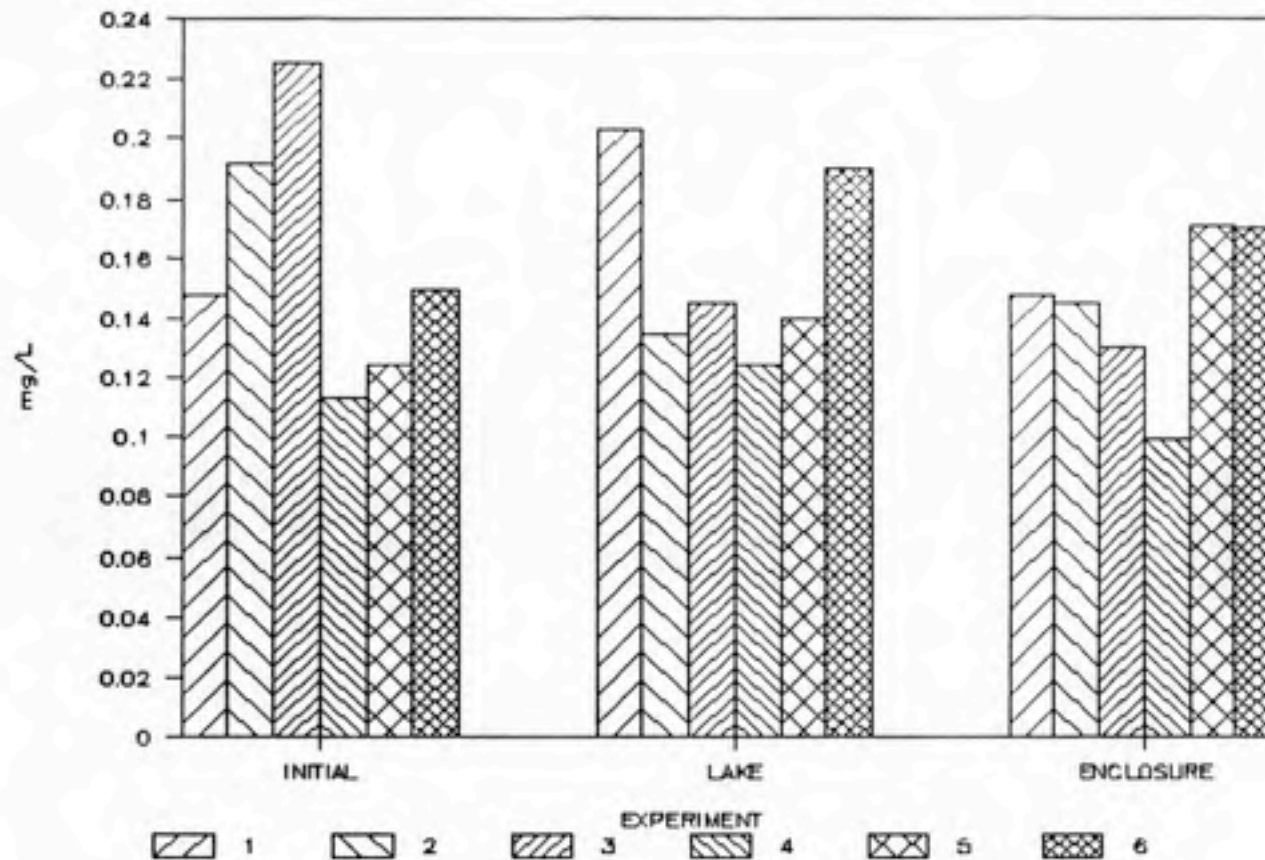
Figure 35 - The concentrations of total phosphorus throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.
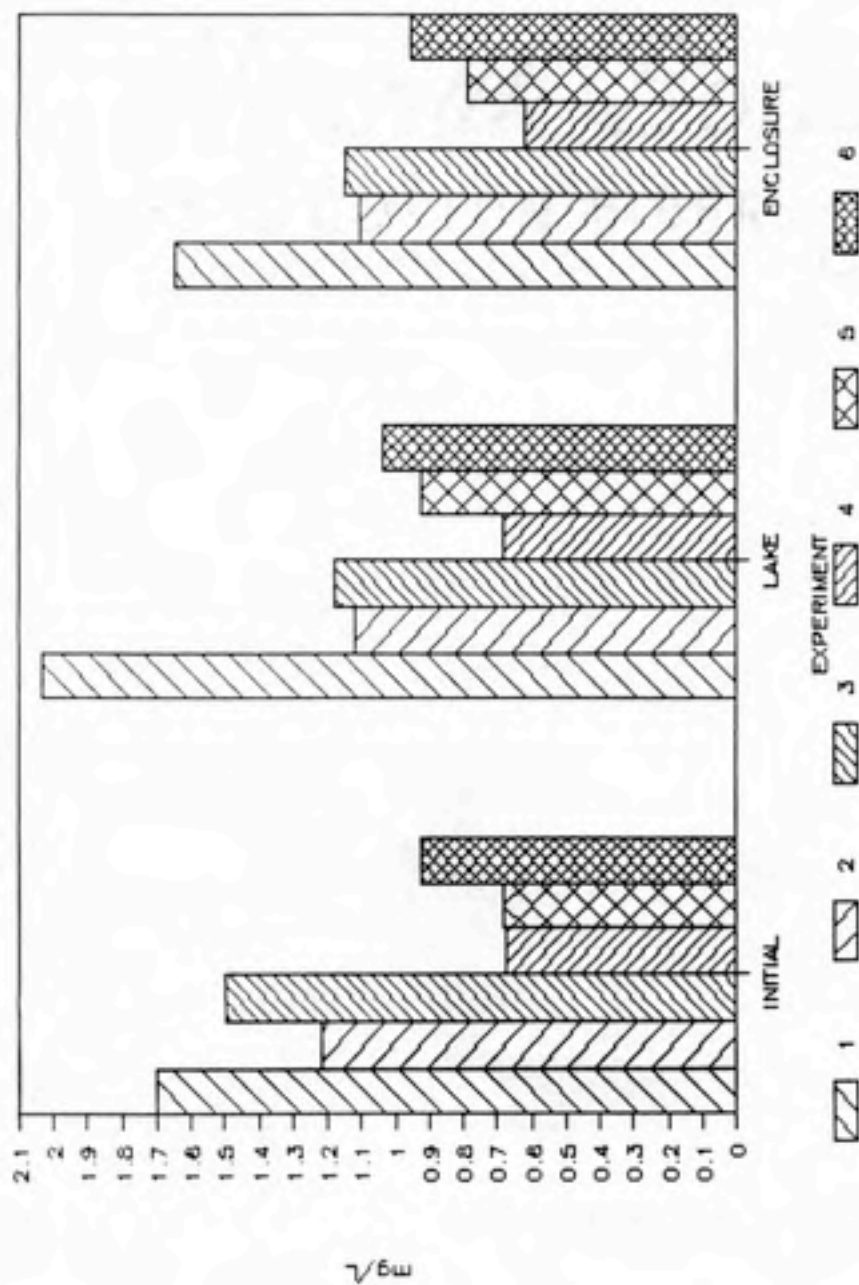
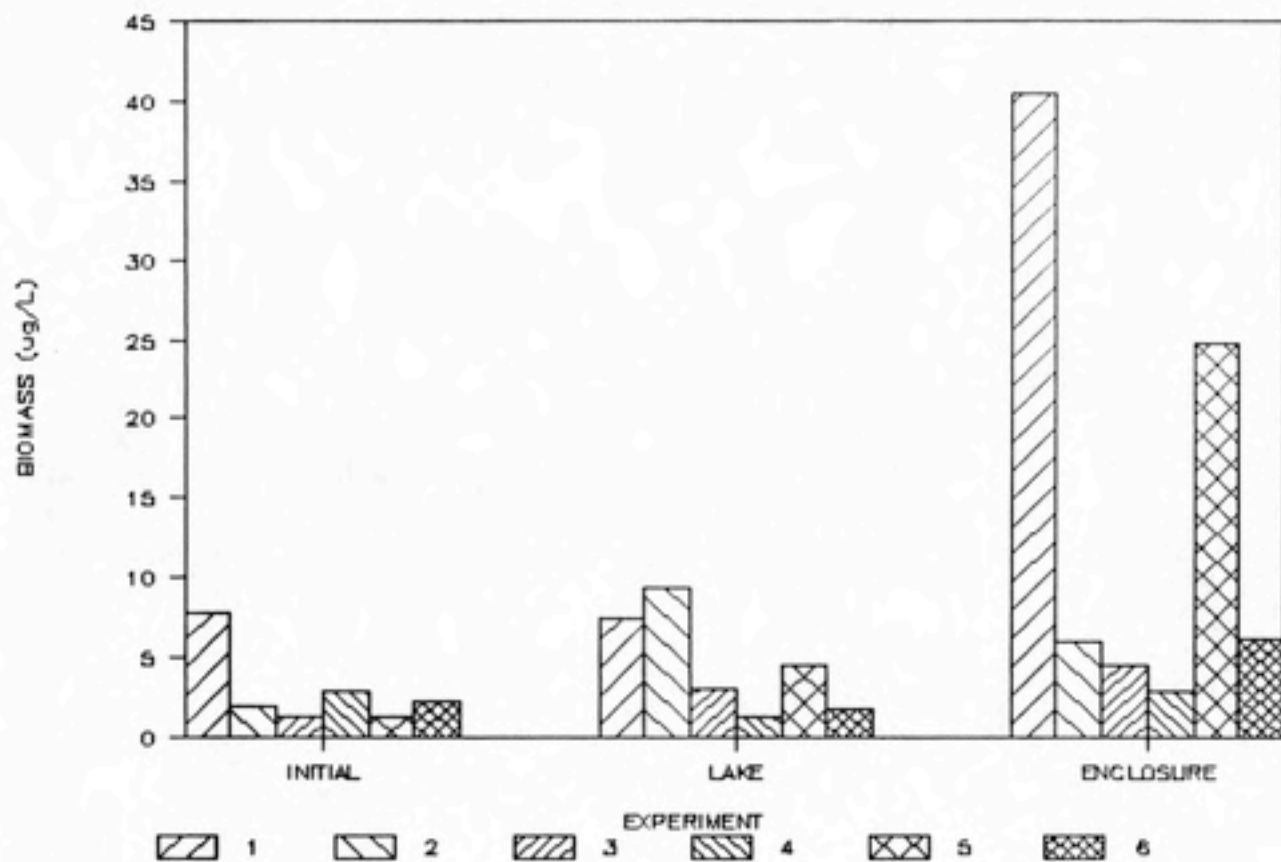Figure 36 - The concentrations of total kjeldahl nitrogen throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

TOTAL DISSOLVED PHOSPHORUS
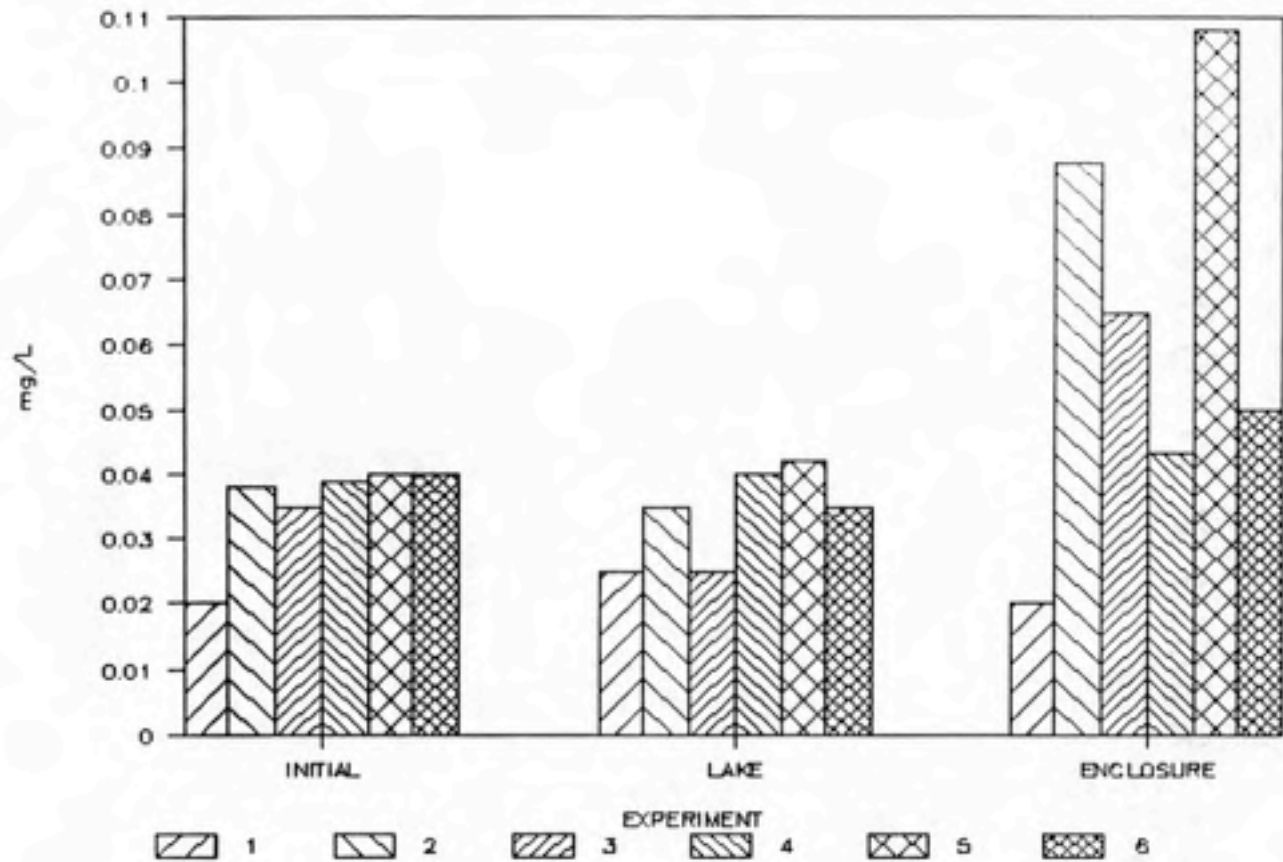
Figure 37 - The concentrations of total dissolved phosphorus throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

experiments 1 and 4 decreased or showed little change. Dissolved Kjeldahl nitrogen was elevated inside the enclosures in experiments 2, 3 and 5 (Figure 38). In experiments 1, 4 and 6, concentrations inside the enclosures remained similar to concentrations outside. Overall, dissolved nutrients increased in experiments with large reductions in phytoplankton biomass while total nutrients changed little.

PHYSICAL PARAMETERS

Dissolved Oxygen

Dissolved oxygen was generally lower inside the enclosures than outside (Figure 39). It was quite variable and dependent on time of day when measured. However, with less phytoplankton biovolume and chlorophyll a inside the enclosures, dissolved oxygen declined as well. In experiment 3, dissolved oxygen fell below 4 mg/L which could be considered undesirably low.

pH

pH remained at approximately the same level inside and outside the enclosure except in experiment 2 (Figure 40).

TOTAL DISSOLVED KJELDAHL NITROGEN
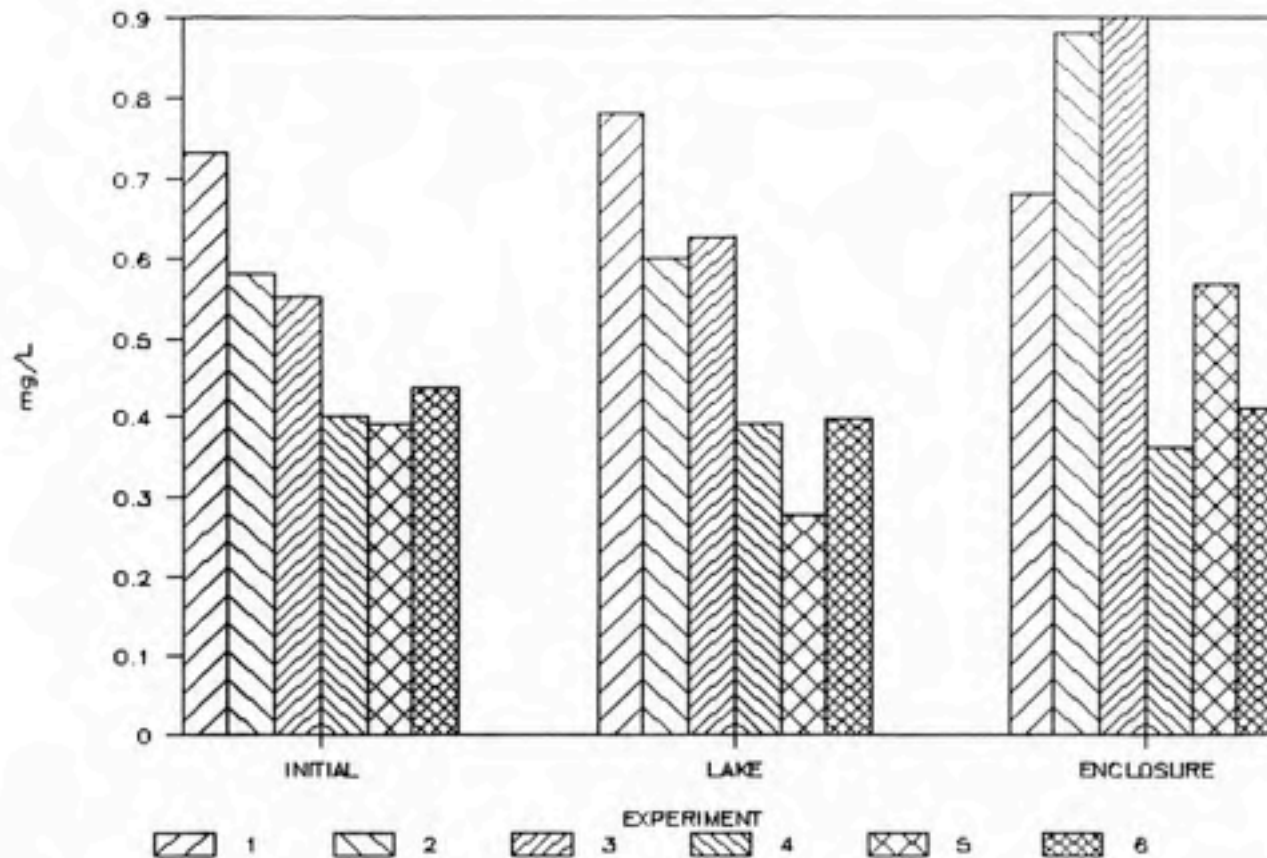
Figure 38 - The concentrations of total dissolved kjeldahl nitrogen throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure.

SURFACE DISSOLVED OXYGEN
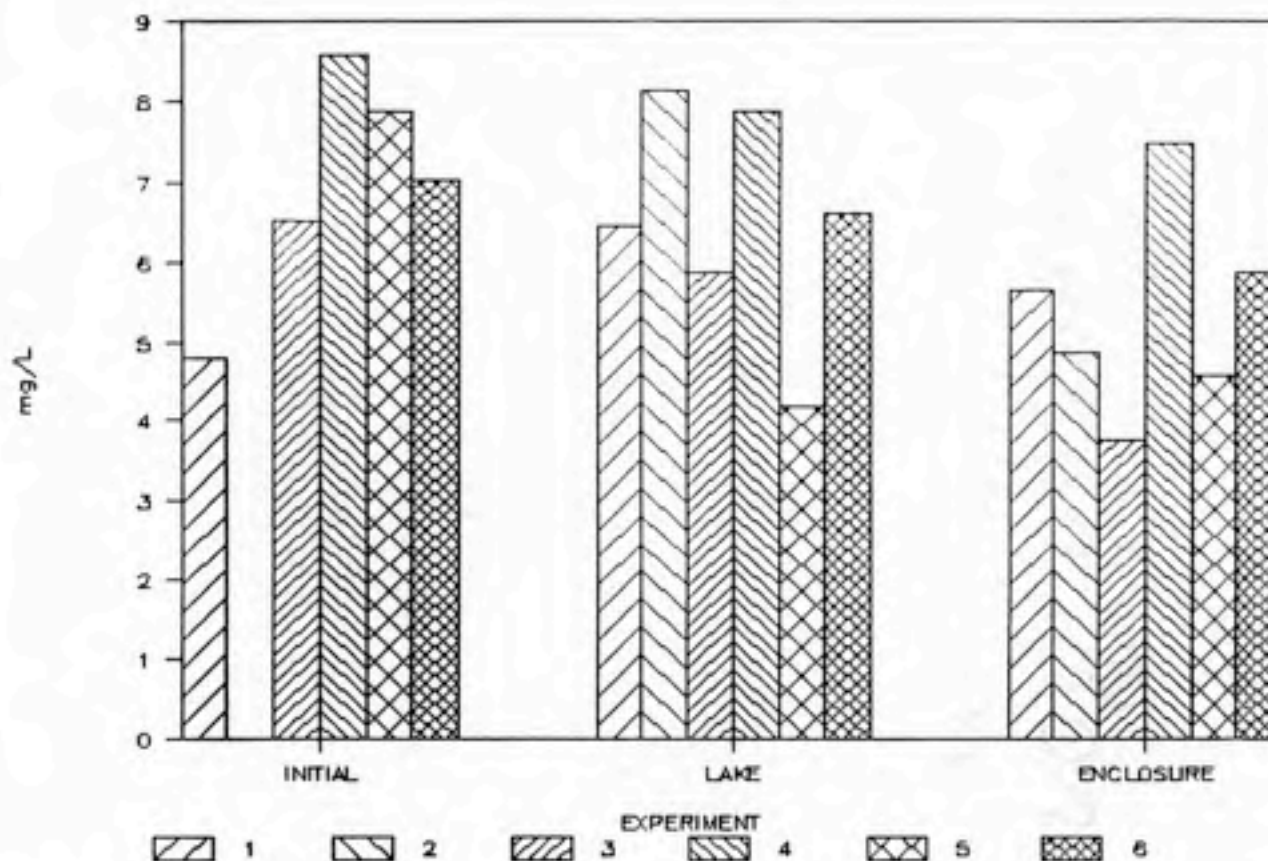
Figure 39 - The concentrations of dissolved oxygen at the surface throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure. Dissolved oxygen was not measured initially during experiment 2.
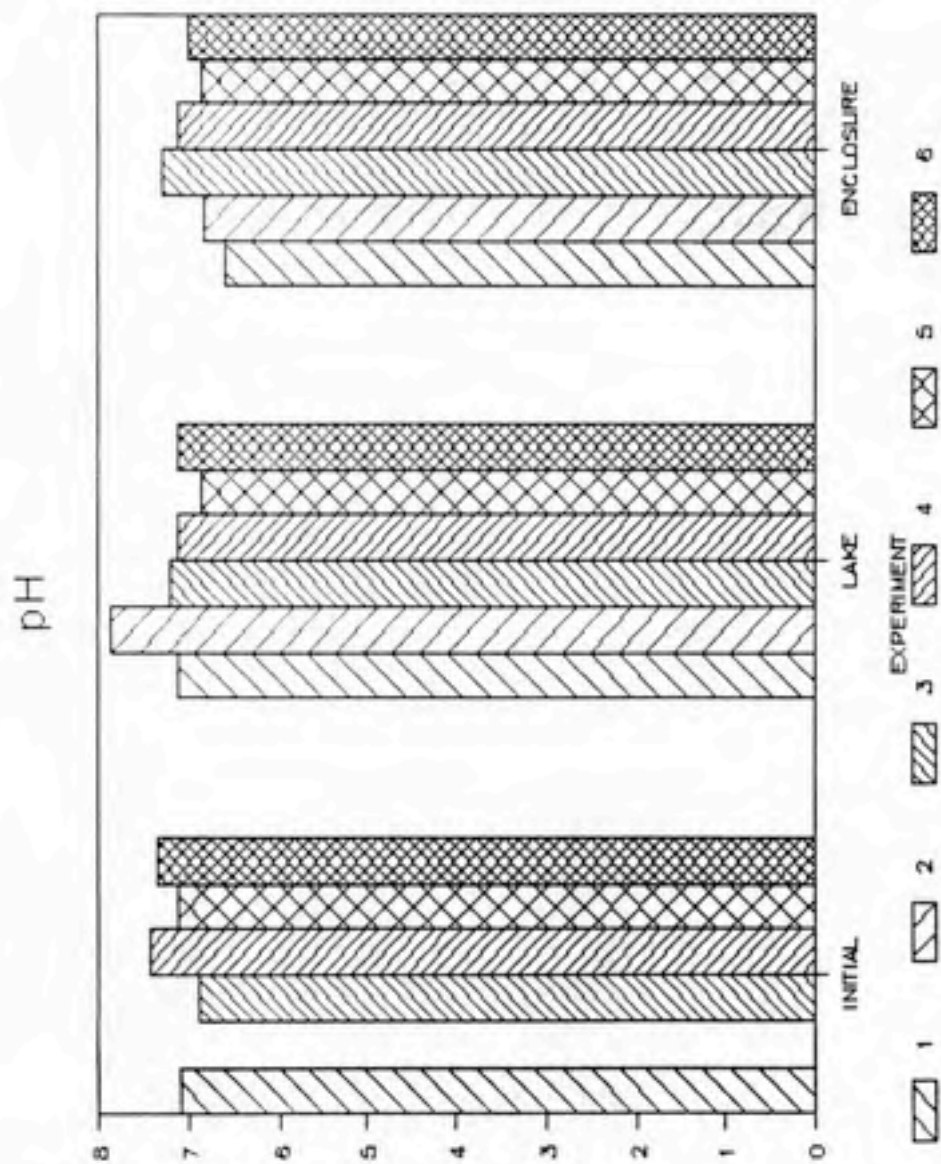
Figure 40 - pH throughout each experiment. "INITIAL" = conditions at the initiation of the experiment; "LAKE" = conditions outside enclosures and "ENCLOSURE" = conditions inside enclosure. pH was not measured initially during experiment 2.

Secchi Depth

Secchi depth was unchanged in experiments 2-3 but did change in experiments 1, 4, 5, 6 (Figure 41). Values outside the enclosures in experiments 2 and 3 were the same as values inside the enclosures. In experiments 1 and experiments 4-6, secchi depth increased inside the enclosures while staying relatively the same during the same period outside the enclosures. During experiment 5, secchi depth did increase outside as well as inside the enclosures.

EXTENDED EXPERIMENTS

Experiment 4 was extended for an additional week and experiment 5 for two additional weeks. These experiments were conducted to examine what additional changes would take place between the new zooplankton and phytoplankton communities.

Copepods

Copepod populations decreased substantially after a period of time in both experiments. In experiment 4, biomass which had doubled during the first week inside the enclosure, was reduced to levels equal to the outside populations by the second week (Figure 42). In experiment 5, biomass continued to increase throughout the second week to very high levels and then fell to levels equal to
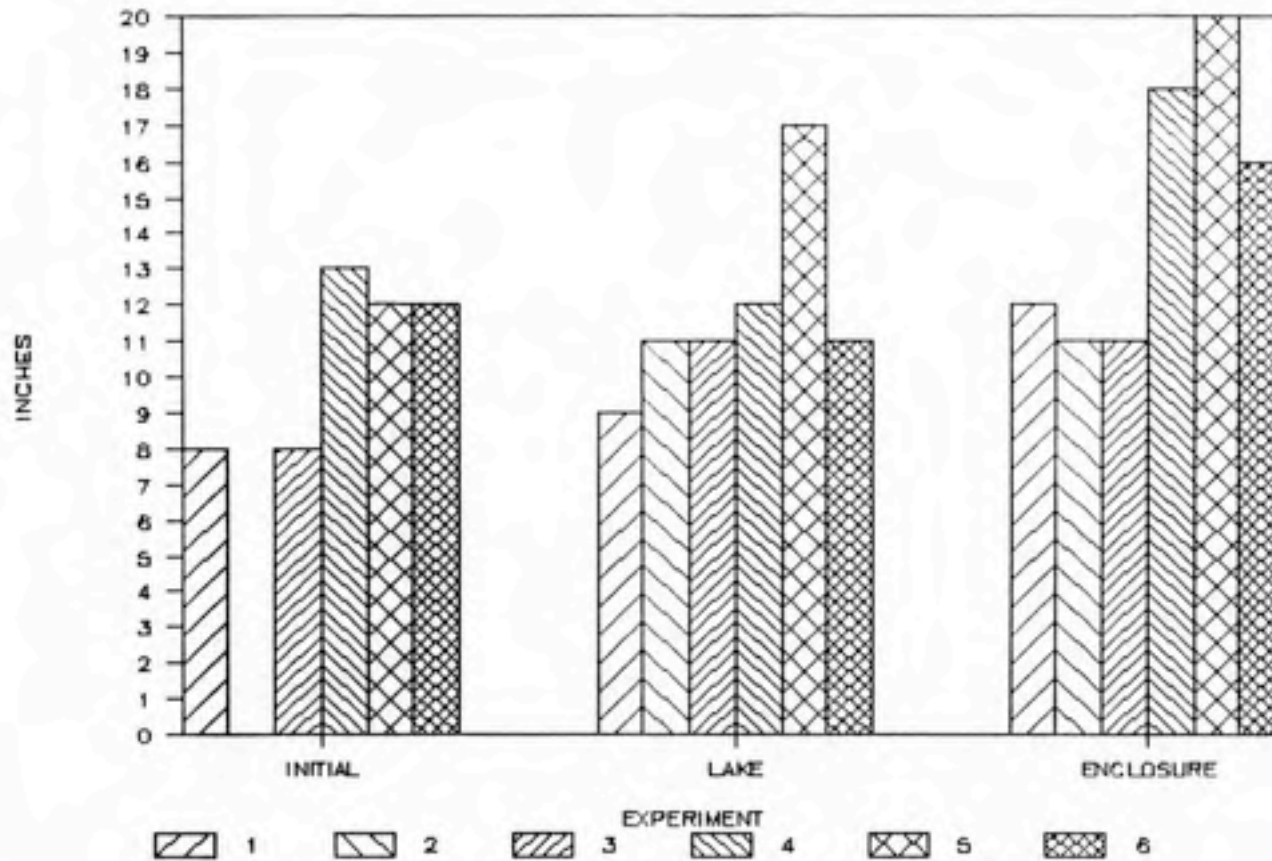
Figure 41 - Secchi depth throughout each experiment.
"INITIAL" = conditions at the initiation of the experiment;
"LAKE" = conditions outside enclosures and "ENCLOSURE" =
conditions inside enclosure. Secchi depth was not measured
initially during experiment 2.

COPEPODS
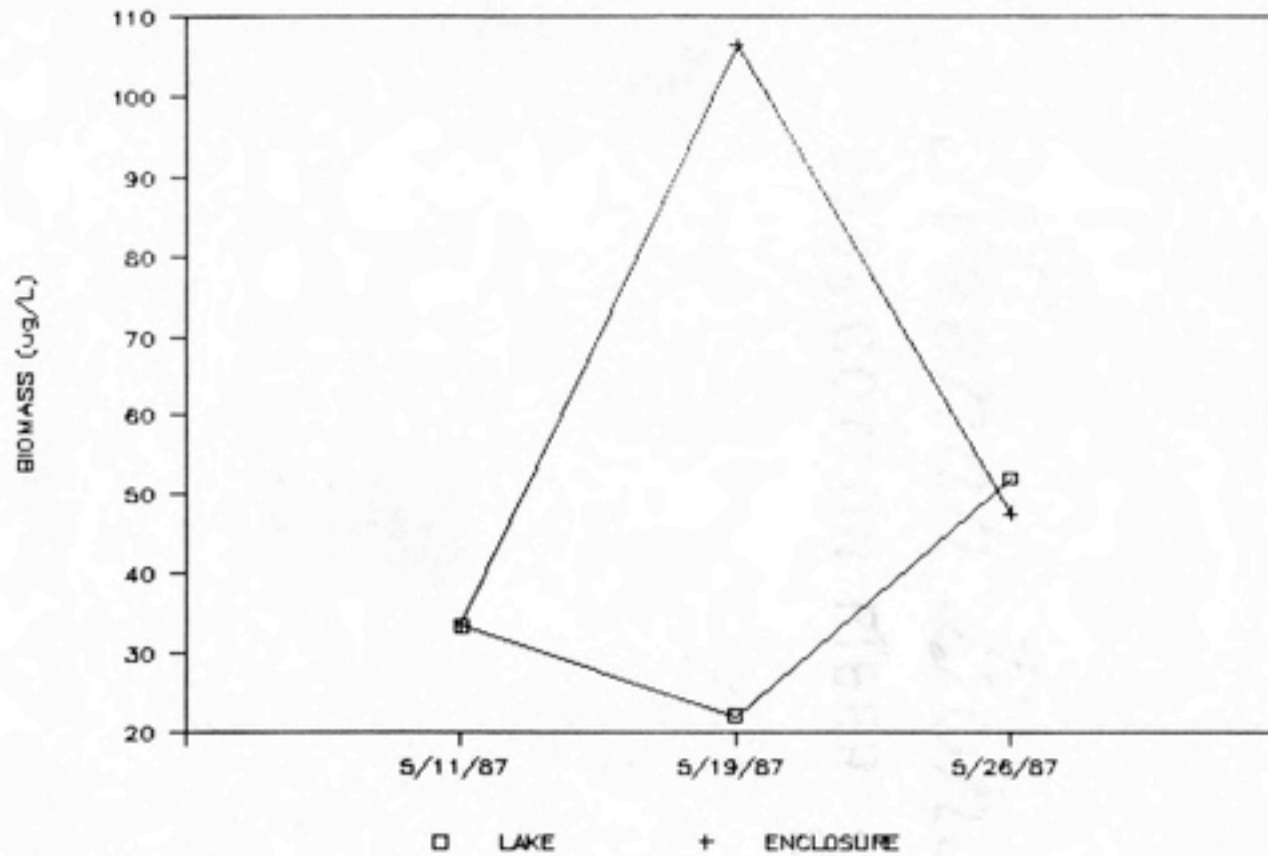
Figure 42 - Copepod biomass in the extended enclosure experiments. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled.

the outside after the third week (Figure 43). Copepod populations inside the enclosures were consistently reduced to levels equal to the outside after two to three weeks inside the enclosures.

After one week of experiment 4, copepods became very abundant in the large as well as the small size classes inside the enclosure (Figure 44). But during the second week, the large size classes were no longer present in the population and the population inside the enclosures resembled that of the outside . In experiment 5, the abundance of small copepods moved into the larger size classes after the second week (Figure 45). Total copepod biomass was much lower during the second week. During the third week, all of the size classes were reduced leaving a population inside the enclosure much smaller both in numbers and in biomass than the outside population.

Cladocerans

Cladocerans did not show consistent results between the two extended experiments. In experiment 4, cladocerans continued to increase in biomass throughout the second week (Figure 46). In experiment 5, cladoceran populations decreased to biomass levels equal to the outside after the second week and remained at that level into the third (Figure 47). One important difference between the two experiments was the number of cladocerans

COPEPODS
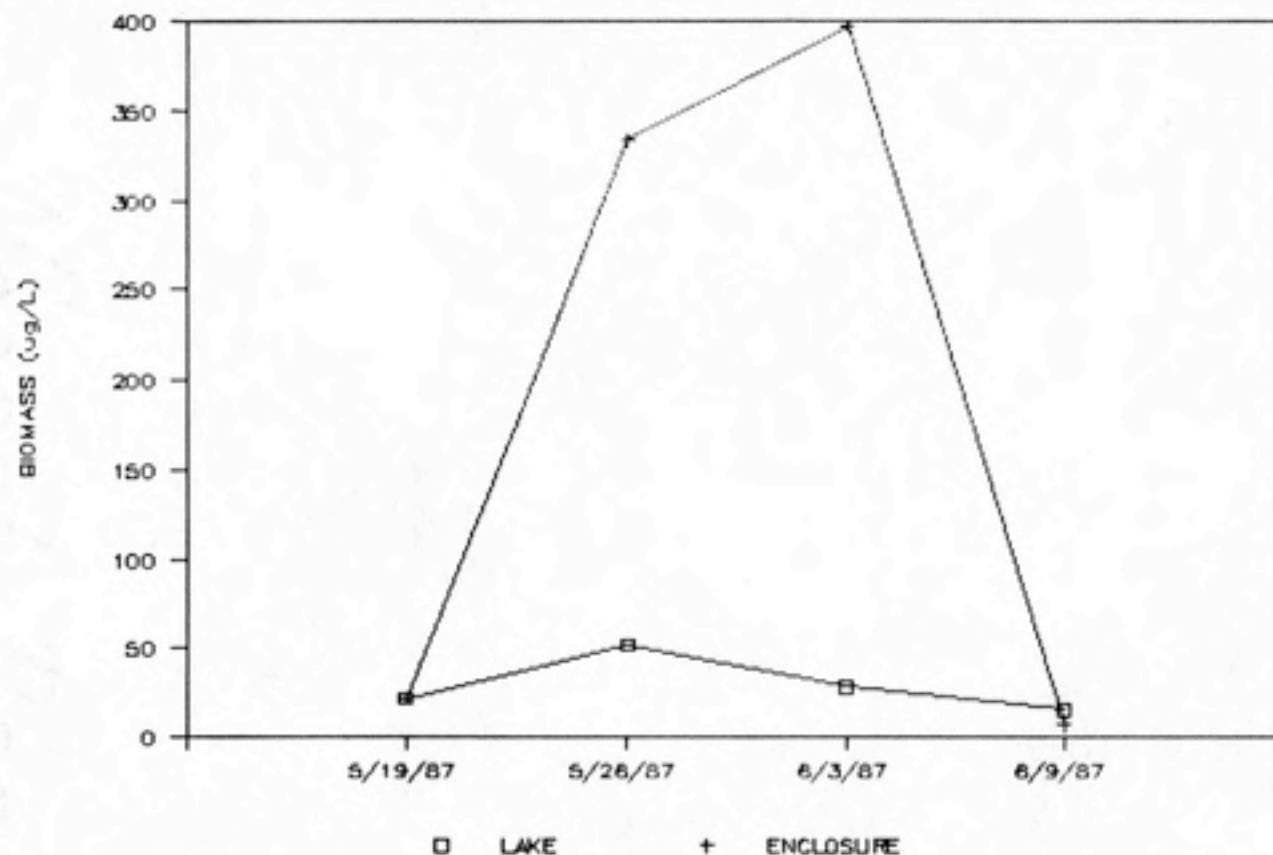
Figure 43 - Copepod biomass in the extended enclosure
experiments. "ENCLOSURE" refers to conditions inside and
"LAKE" refers to conditions outside the enclosure when it
was sampled.

Week 1

Week 2
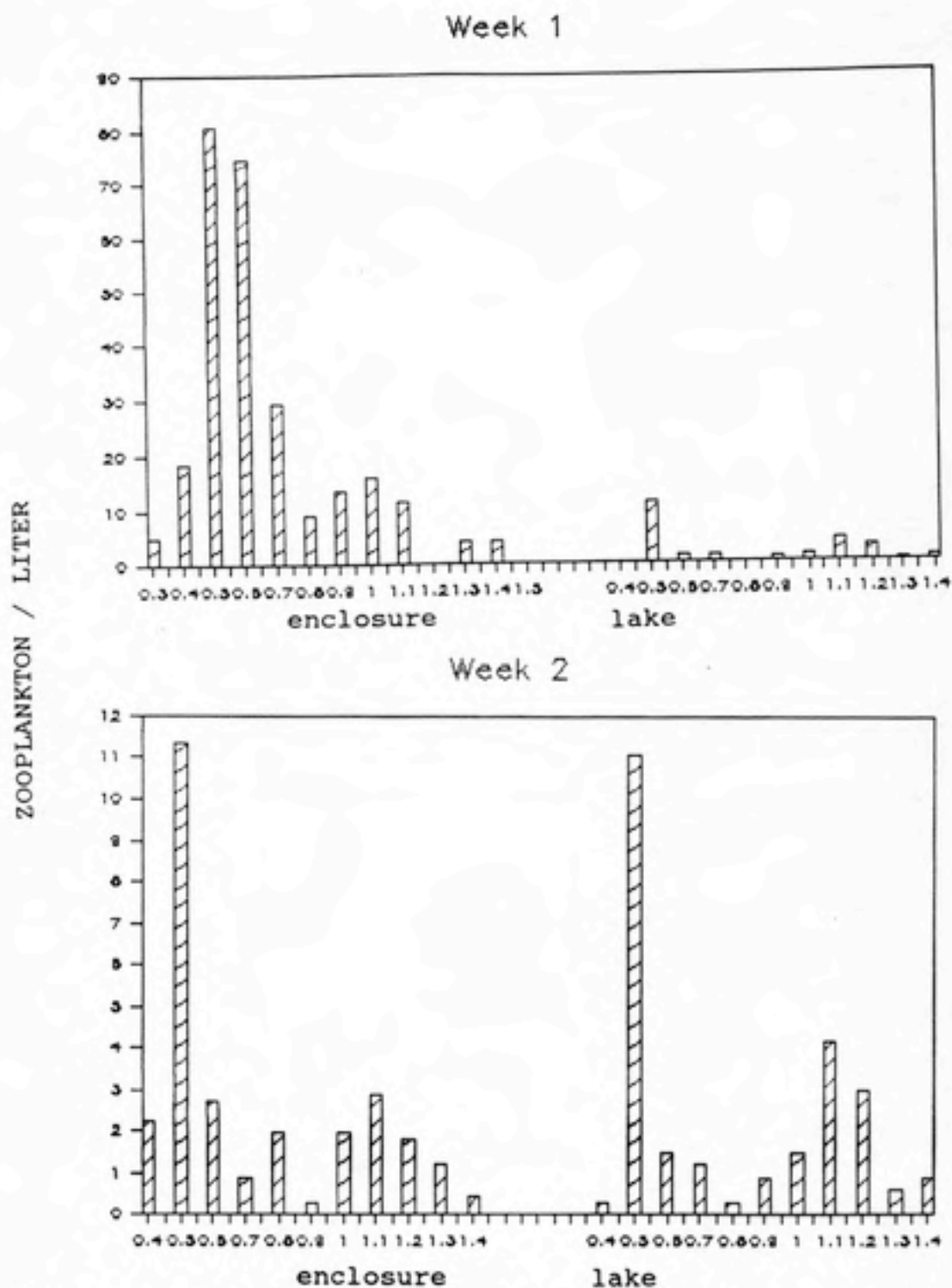
Figure 44 - The length frequency of copepods during each week in the extended enclosure experiment 4. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled. All measurements are in mm.
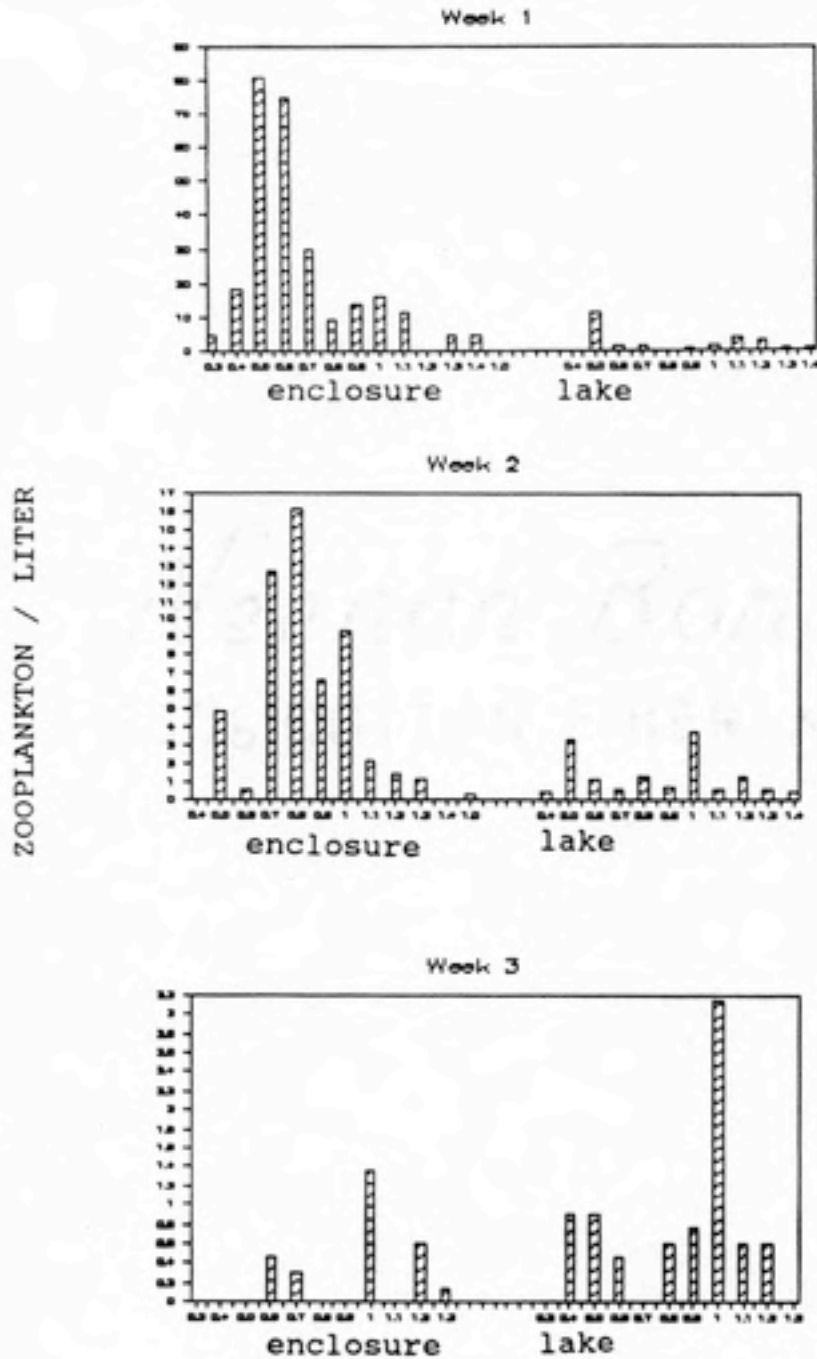
Figure 45 - The length frequency of copepods during each
week in the extended enclosure experiment 5. "ENCLOSURE"
refers to conditions inside and "LAKE" refers to conditions
outside the enclosure when it was sampled. All measurements
are in mm.
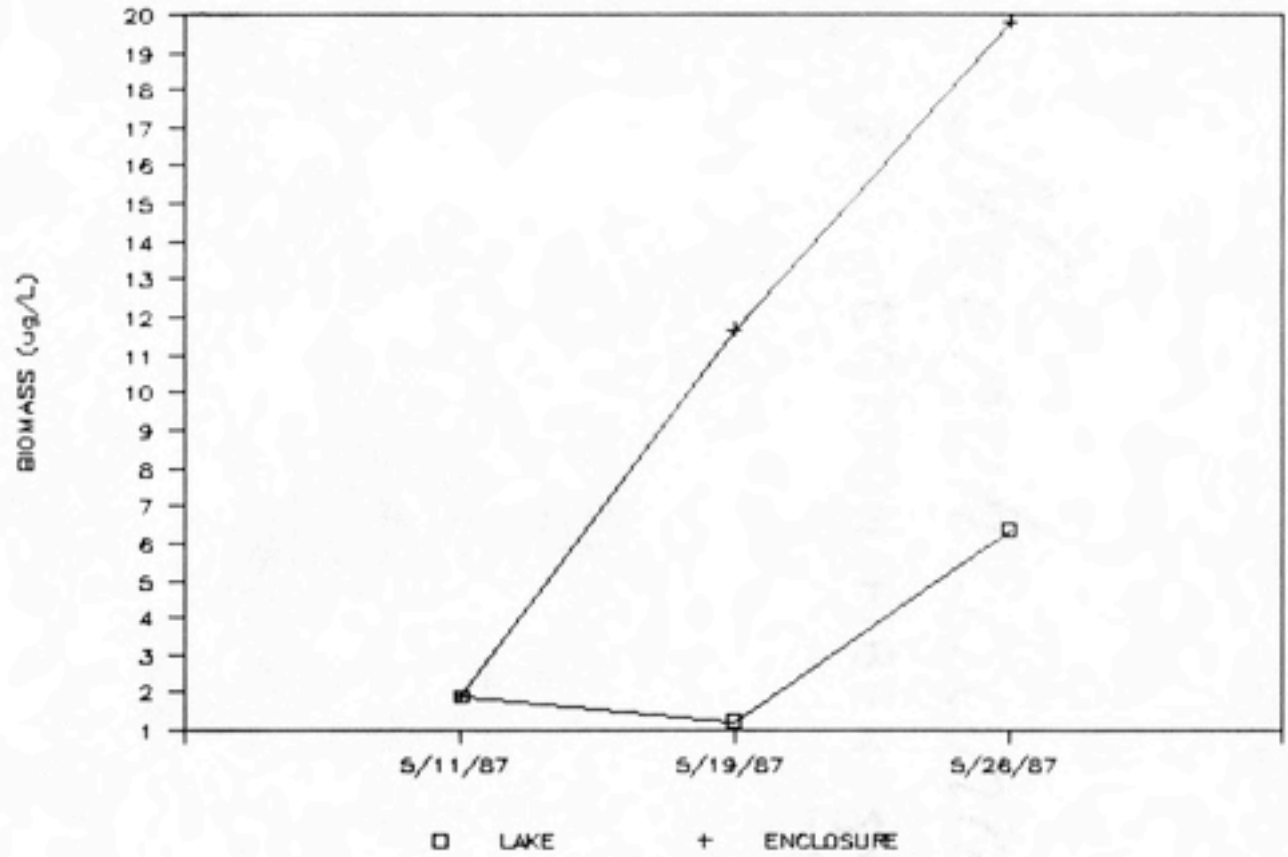
Figure 46 - Cladoceran biomass in the extended enclosure
experiments. "ENCLOSURE" refers to conditions inside and
"LAKE" refers to conditions outside the enclosure when it
was sampled.

CLADOCERANS
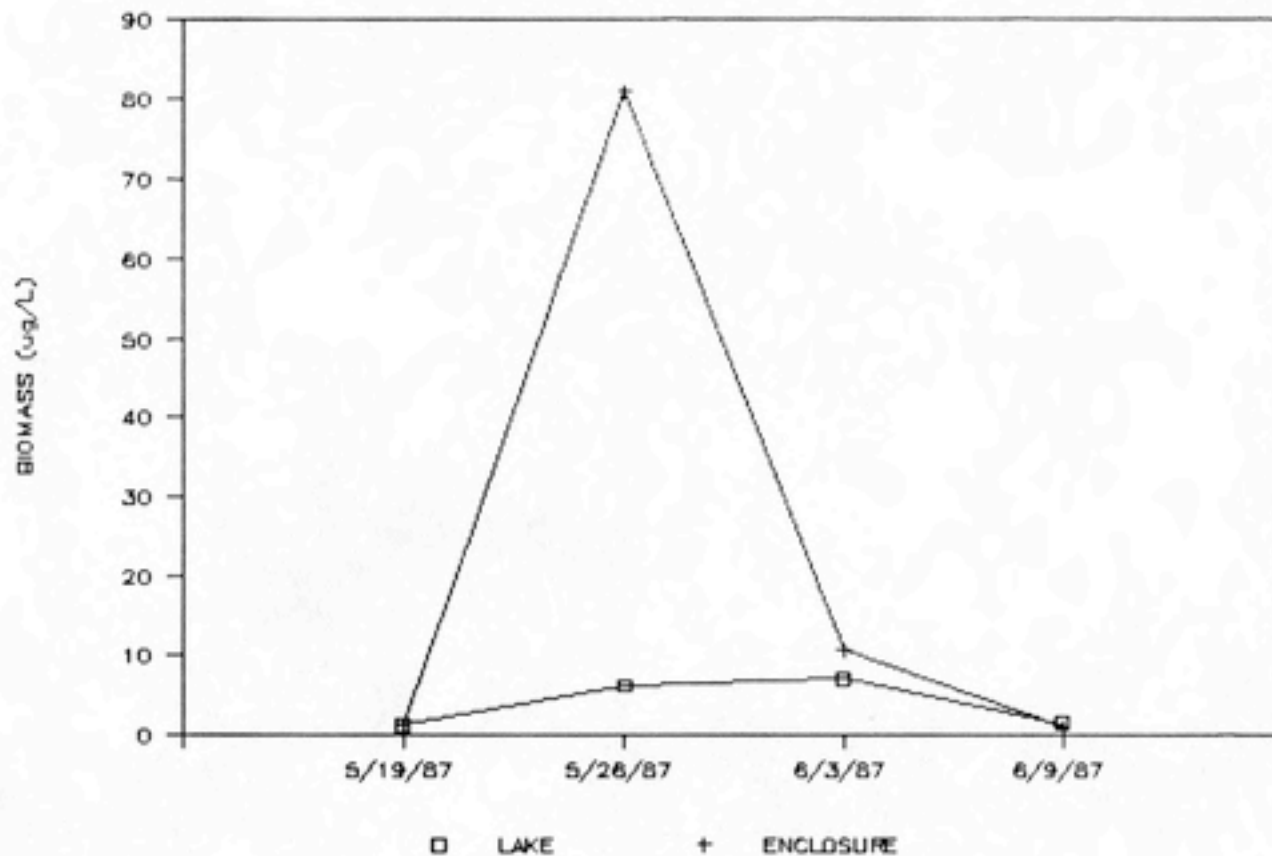
Figure 47 - Cladoceran biomass in the extended enclosure experiments. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled.

in experiment 4 as compared to experiment 5. Biomass in experiment 4 was only a fourth of that inside the enclosure in experiment 5.

Cladoceran size frequency distribution did not change during experiment 4. From week 1 to week 2, the larger individuals persisted while the smaller individuals declined (Figure 48). During week 2, the inside population was composed of both large and small individuals, while in the outside population only small individuals were abundant. Inside the enclosure during experiment 5, the abundance of individuals during the first week declined in the second week and disappeared at the third (Figure 49). The reduction of individuals was uniform across all size classes in both experiments. The outside population stayed relatively unchanged during the experiment.

Chlorophyll a

Chlorophyll a in the extended experiments continued to decline with time. In experiment 4, values continued to decrease inside the enclosures as values outside the enclosures continued to increase (Figure 50). In experiment 5, chlorophyll a declined very rapidly during the initial week, stayed at that level during the second week, and then began to increase during the third (Figure 51). In both experiments, chlorophyll a remained
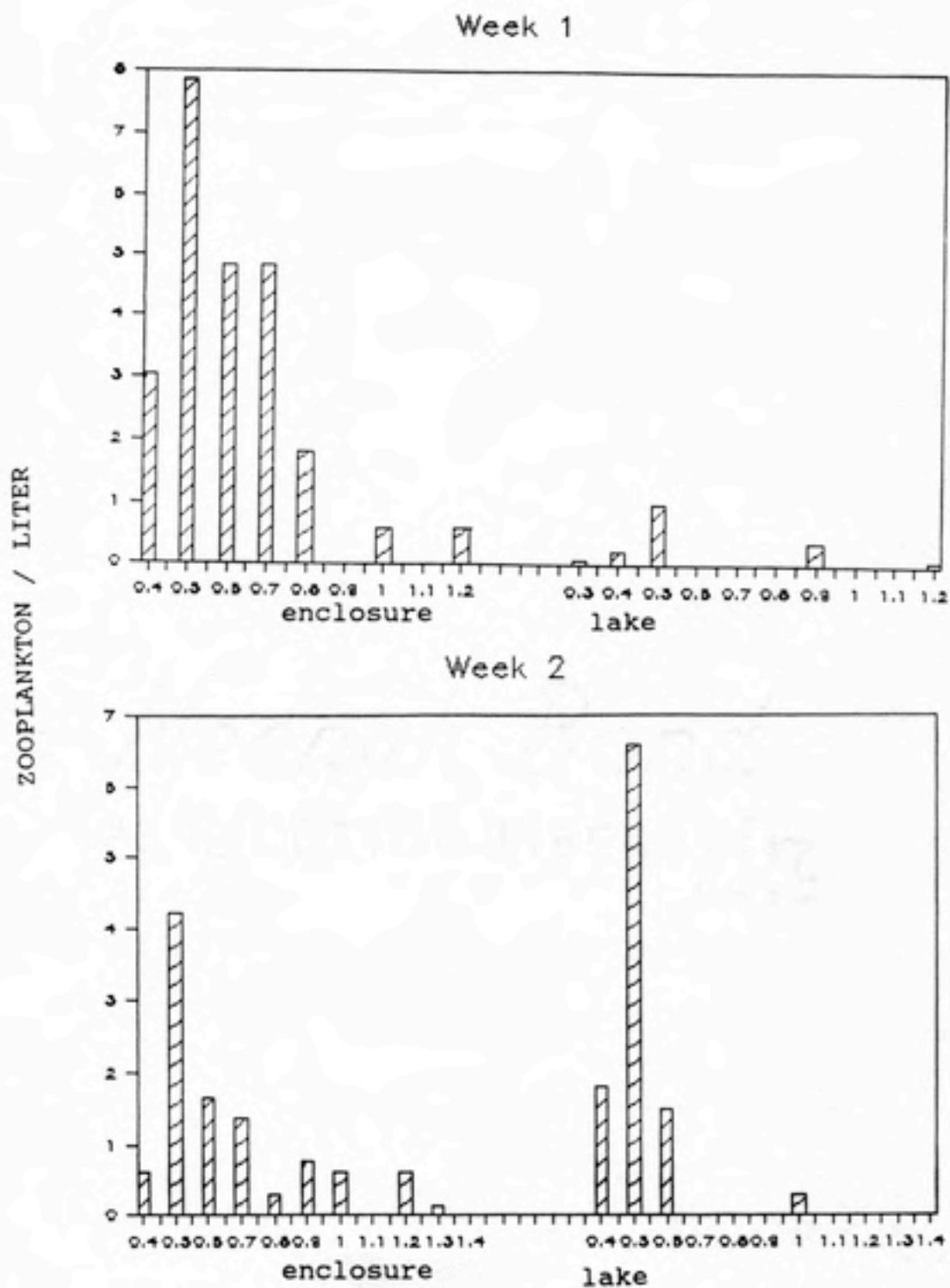
Figure 48 - The length frequency of cladocerans during each week in the extended enclosure experiment 4. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled. All measurements are in mm.
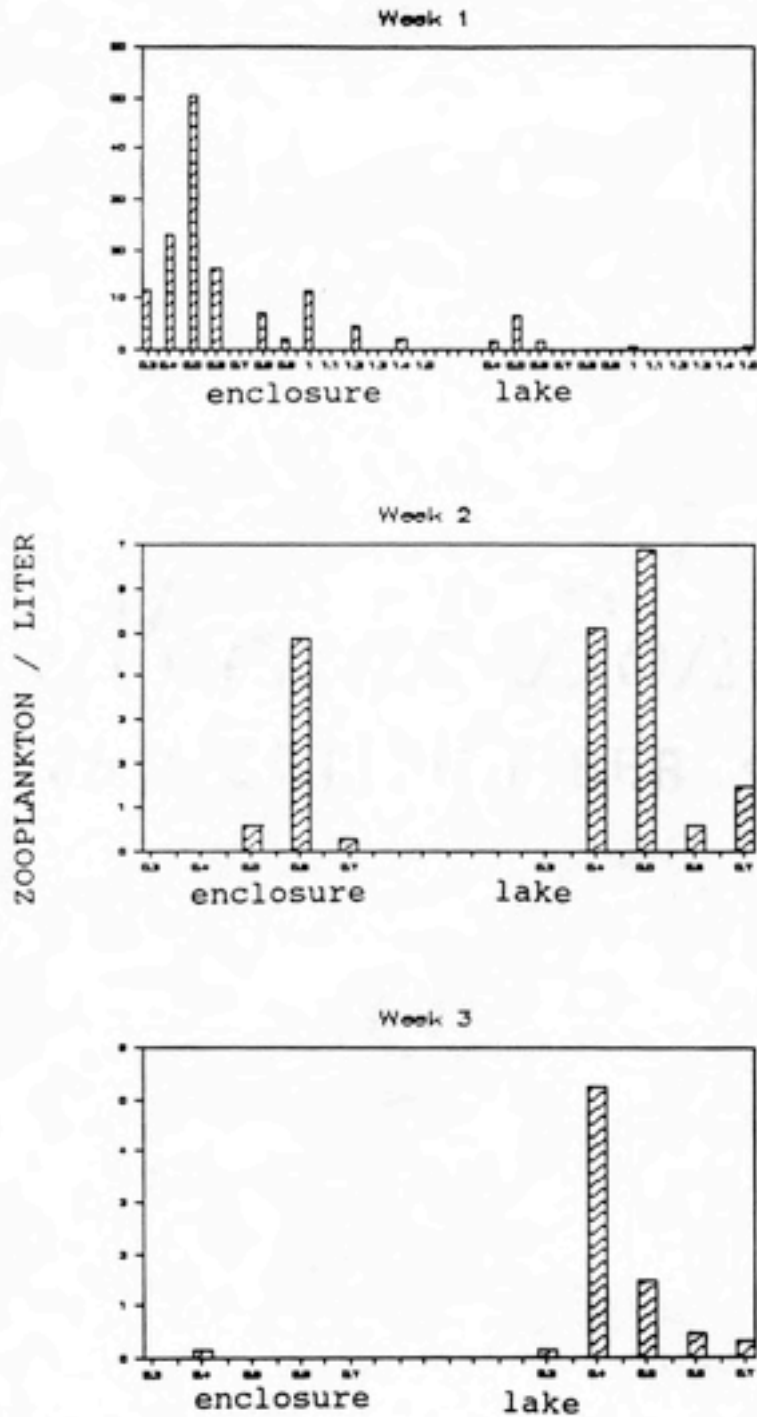
Figure 49 - The length frequency of cladocerans during each week in the extended enclosure experiment 5. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled. All measurements are in mm.

CHLOROPHYLL A
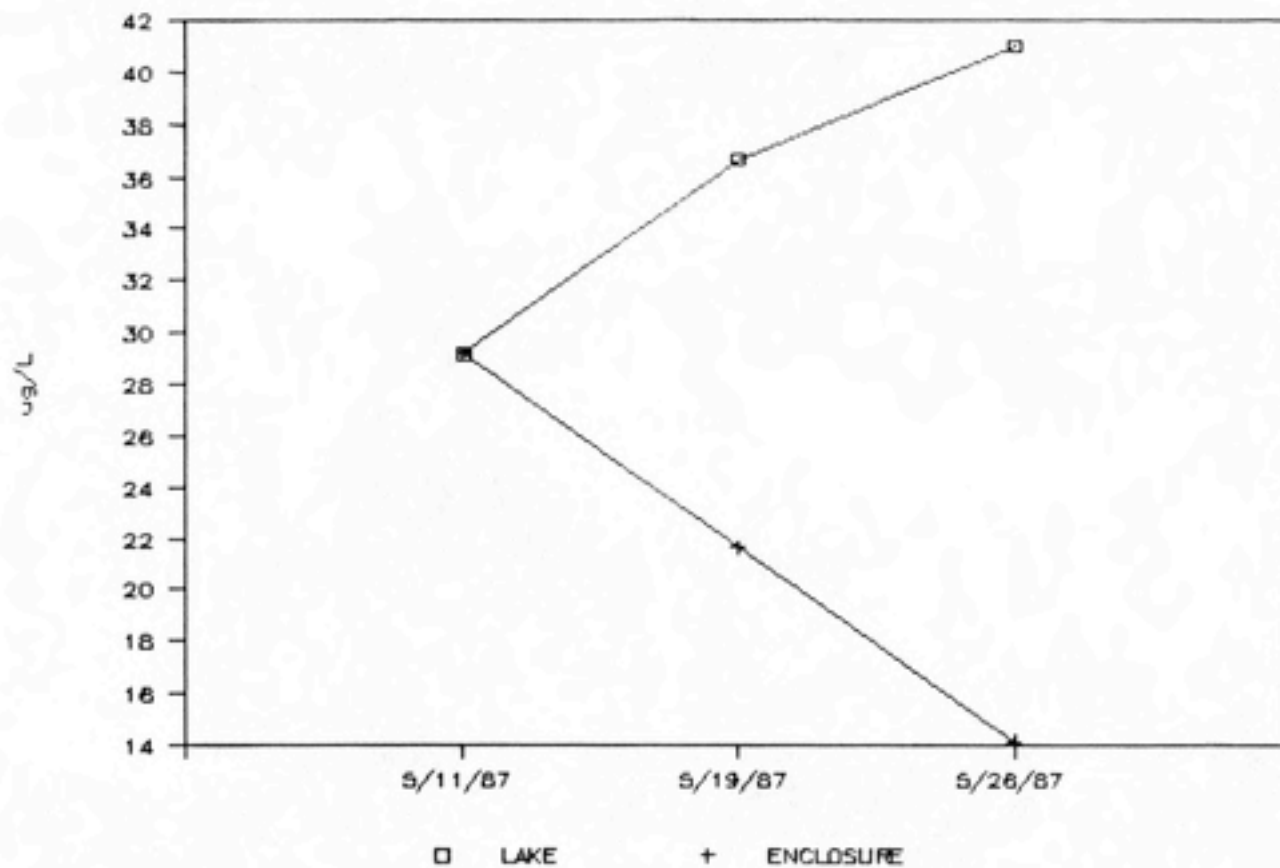
Figure 50 - Chlorophyll a in the extended enclosure
experiments. "ENCLOSURE" refers to conditions inside and
"LAKE" refers to conditions outside the enclosure when it
was sampled.

CHLOROPHYLL A
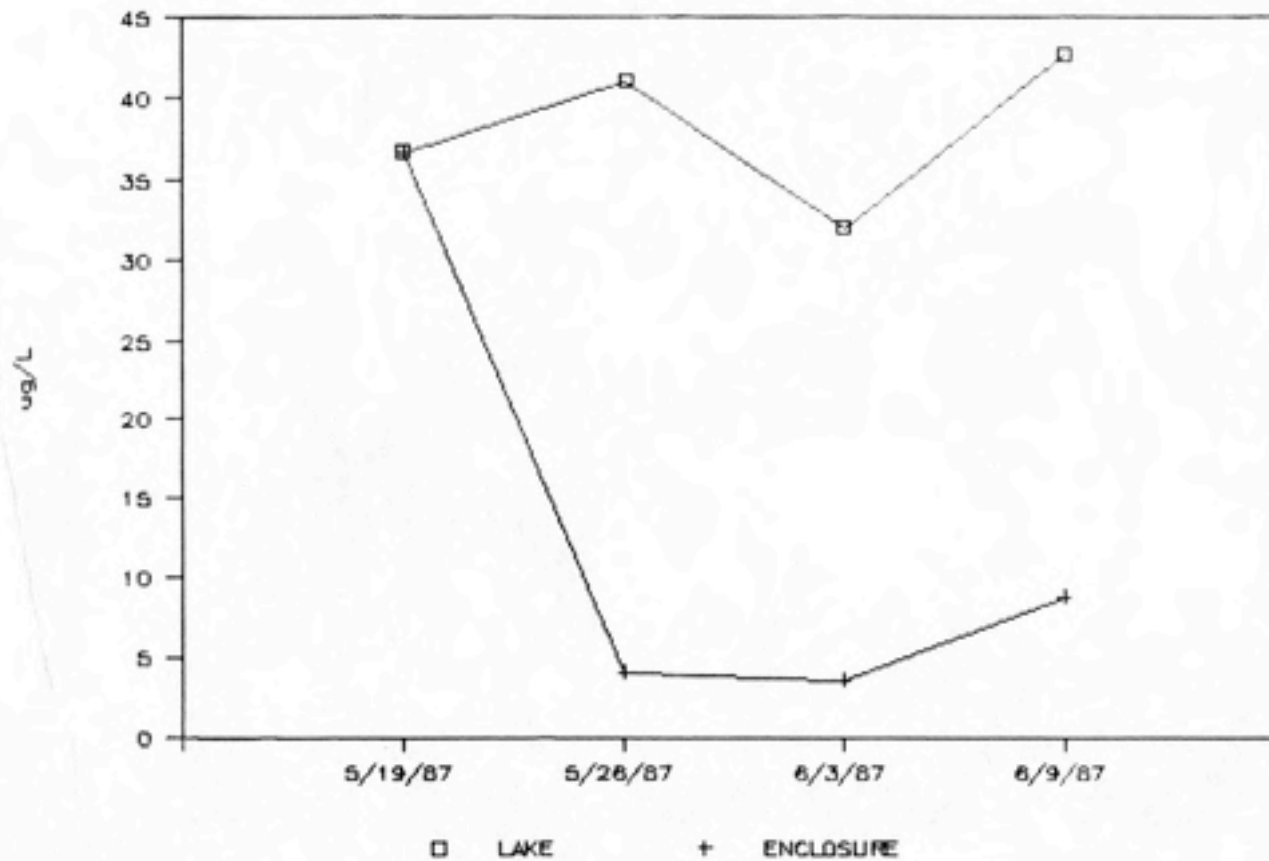
Figure 51 - Chlorophyll <u>a</u> in the extended enclosure experiments. "ENCLOSURE" refers to conditions inside and "LAKE" refers to conditions outside the enclosure when it was sampled.

considerably lower inside the enclosures relative to outside throughout the extended period of time.

DISCUSSION

JORDAN LAKE ZOOPLANKTON COMMUNITY

Small Body Size of the Zooplankton Community

A distinguishing feature of the Jordan Lake zooplankton community is that individuals have small body sizes. Predation has been shown to cause a smaller size in zooplankton (Gophen and Landau 1977; O'Brien 1979; Vanni 1987a). The small size of the Jordan Lake zooplankton is evident from the size frequency data for the dominant species of zooplankton in the lake (Figures 20, 22, 26, 28). In all of the zooplankton measured, the largest individuals never exceeded 1.5 mm. Vanni (1987 b) observed that zooplankton communities typical of fishless lakes had a mean individual body size of 2 mm. Therefore, the small size of the Jordan Lake zooplankton may be a response to heavy predation pressure.

Diaptomus pallidus (Figure 20) had a greater concentration of individuals over 1 mm outside the enclosures during the experiments than the other dominant zooplankton species (Figures 22, 26, and 28). Drenner et

al. (1982) observed that gizzard shad actually enhanced the populations of _Diaptomus pallidus_ in small pond experiments. The shift toward larger sizes in this species may be a response to gizzard shad predation.

The _Daphnia sp._ in Jordan Lake consisted primarily of _Daphnia parvula_. Stavn (1975) hypothesized that _Daphnia catawba_, which was the dominant species of _Daphnia_ in North Carolina watersheds in the early 1900's, was replaced by _Daphnia parvula_ and _Daphnia ambigua_ with the introduction of threadfin shad. Threadfin shad are particulate feeders that have the ability to selectively feed on large _Daphnia_ (Baker and Schmitz 1971). The smaller size of _Daphnia parvula_ and _Daphnia ambigua_ may have enabled these forms to coexist with this planktivore. Shapiro et al. (1983) observed a similar shift from the large _Daphnia pulex_ to the small _Daphnia parvula_ in enclosure experiments in Minnesota lakes. Vanni (1987a) demonstrated how fish prevent cladocerans from attaining large sizes. The dominance of _Daphnia parvula_ in Jordan Lake therefore is consistent with the presumption that zooplankton are controlled by planktivory. Predation seems to drive the _Daphnia_ population to extinction during the summer and fall season (Figure 9). Both patterns point to gizzard shad as important planktivores in the system.

Phytoplankton do not appear to be a factor in the summer decline in zooplankton abundance. Total zooplankton density decreased (Figure 4), while phytoplankton increased (Figures 14-18). Increases in algal biovolume should provide expanded resources for zooplankton and support increases in biomass. Instead, zooplankton biomass is observed to decrease. Moreover, Daphnia spp. disappears from the lake. Therefore, the summer and fall zooplankton communities would appear to be more likely a result of the increased planktivorous fish predation which intensifies in late May and early June.

PRESENT IMPACT OF THE ZOOPLANKTON COMMUNITY ON PHYTOPLANKTON

Zooplankton grazing can structure the phytoplankton community in several ways. Large size of the phytoplankton is advantageous against grazing. In many lakes it has been documented that the proportion of large algae increases with increased grazing (Gilwicz 1975; Lampert et al. 1986; Reynolds 1984). In Jordan Lake this pattern seems evident. A decline in mean size of phytoplankton in Jordan Lake follows the decline of Daphnia spp. (Figure 9). When Daphnia spp. is abundant in spring, the size of phytoplankton is larger on the

average (Figure 13). The mean size of phytoplankton was also larger in the spring for two out of the three previous years (Figure 1). If this is a trend, then Daphnia spp. may be a principle cause of larger cell sizes among the phytoplankton before Daphnia spp. are reduced by predation in summer.

Algae which coexist with abundant zooplankton have durable cell walls and gelatinous sheaths to protect them from physical damage during passage through the zooplankton gut (Porter 1977). In Jordan Lake, the phytoplankton community is dominated by small green algae, diatoms, and blue-greens which do not exhibit any of these traits (Weiss et al. 1984; Weiss et al. 1985; Weiss et al. 1986). The majority of phytoplankton are grazeable forms, with the exception of some blue-greens. This is to be expected given the low zooplankton biomass and dominance copepods (Figure 4).

ENCLOSURE EXPERIMENTS

Zooplankton

The enclosure experiments were designed to determine how the plankton community would change following the exclusion of planktivorous fish. When planktivore predation pressure is removed, the zooplankton community should increase in biomass, increase in size, and shift

toward a greater proportion of <u>Daphnia</u> in the community (Zaret 1980).

In all of the experiments, zooplankton biomass increased during the first week after excluding fish (Figure 19, Figure 21, Figure 23, Figure 24, Figure 25, Figure 27, Figure 29). The amount of increase varied between experiments, but all of the zooplankton present in the lake at the time of the experiments increased inside the enclosures. The increase in total biomass of zooplankton inside the enclosure supports the hypothesis that predation is the dominant factor controlling the biomass of zooplankton in the lake. Because all species of zooplankton increased inside the enclosures, it seems that copepods as well as cladocerans are being controlled by planktivores in this lake.

The size classes of zooplankton were affected inside the enclosures (Figures 20, 22, 26, 28). In several experiments a greater proportion of individuals 1 mm and over were present inside the enclosures as compared with out. However, the increase in abundance of all size classes of zooplankton inside the enclosures was more noticeable (Figures 20, 22, 26, 28). Because it is a pump filter-feeder, gizzard shad would suppress the small as well as the larger sizes of zooplankton (Drenner et al. 1982; Lazzaro 1987). Particulate feeding planktivores such as crappie tend to feed selectively on

the larger zooplankton first (Lazzaro 1987). Thus, if particulate feeders such as threadfin shad and crappie were having the greatest impact, the zooplankton inside the enclosures would be expected to shift to a larger size during the first week. Instead, all sizes increased in biomass. It can be concluded that gizzard shad have a greater impact than other planktivores in the lake.

PHYTOPLANKTON

The size and composition of phytoplankton inside the enclosures varied with the composition and biomass of zooplankton that developed in each experiment (Figures 32-34). This effect is illustrated by comparing experiments 1 and 3.

In experiment 1, the zooplankton community was dominated by copepods (Figure 19, Figure 21, Figure 23, Figure 24, Figure 25, Figure 27, Figure 29). The increase in zooplankton biomass that resulted inside the enclosure did not have a substantial effect on the phytoplankton community (Figures 32-34). This may be because most of the feeding was done by the less efficient copepods. The three dominant copepods, Diaptomus pallidus, Mesocyclops edax and Cyclops vernalis are omnivorous (Zaret 1980; Williamson and Butler 1986; Vanni 1987b). Williamson and Butler (1986) showed that

ingestion of rotifers by <u>Diaptomus</u> <u>pallidus</u> and
<u>Mesocyclops</u> <u>edax</u> increased with food concentration.
Clearance rates on rotifers was 5.5 to 6.2 times greater
than on algae at the same concentration. <u>Cyclops</u>
<u>vernalis</u> preys upon <u>Bosmina</u> sp. and other small
cladocerans (Zaret 1980). Therefore, increases in these
copepods might not directly reduce the phytoplankton
community and may indirectly enhance growth of small
phytoplankton by decreasing the herbivory of rotifers and
small cladocerans.

The resultant phytoplankton community of experiment
1 was dominated by smaller cells (Figure 32). The
dominant classes of phytoplankton present at the
initiation of the experiments were not reduced in
biovolume inside the enclosure (Figure 33). Blue-green
algae increased, chlorophyll <u>a</u> was only slightly reduced,
and phytoplankton size decreased inside the enclosure.
Essentially, the signs of eutrophy still persisted
inside the enclosure as well as out.

During experiment 3, <u>Daphnia</u> spp. appeared in the
lake (Figure 9). The sudden appearance may be attributed
to heavy rains during this period. The resultant
flooding of the lake would reduce visibility for
particulate-feeding planktivorous fish and therefore
especially enhance survival of <u>Daphnia</u> spp. (Vinyard and
O'Brien 1976). Inside the enclosure, zooplankton biomass

increased as in experiment 1, but the community composition had changed. <u>Daphnia</u> spp. now made up a significant portion of the zooplankton community. Phytoplankton size in experiment 3 increased inside the enclosure (Figure 32). All classes of phytoplankton were grazed down to very low levels (Figure 34). Blue-green algae were grazed as readily as other forms. Chlorophyll <u>a</u> was reduced to a low level relative to conditions outside the enclosure. The difference between experiment 1 and experiment 3 was the presence of <u>Daphnia</u> spp. Its presence had a substantial impact on phytoplankton.

By using chlorophyll <u>a</u> as an index for phytoplankton biomass, experiments 2, 4, 5, and 6 support this observation (Figure 31). In experiment 6, when <u>Daphnia</u> spp. was not in the lake, chlorophyll <u>a</u> inside and outside the enclosures was similar despite increases in the biomass of the other dominant zooplankton (Figure 19, Figure 21). When <u>Daphnia</u> spp. was in the lake during experiments 2, 4 and 5, it increased in biomass inside the enclosures and reduced chlorophyll <u>a</u> to extremely low levels relative to outside (Figure 25, Figure 32). Reduction in chlorophyll <u>a</u> inside the enclosures was a function of <u>Daphnia</u> spp. biomass (Figure 52).

This trend applied to the extended experiments as well. Chlorophyll <u>a</u> was initially reduced in and continued at very low levels in experiments 4 and 5

INSIDE ENCLOSURE
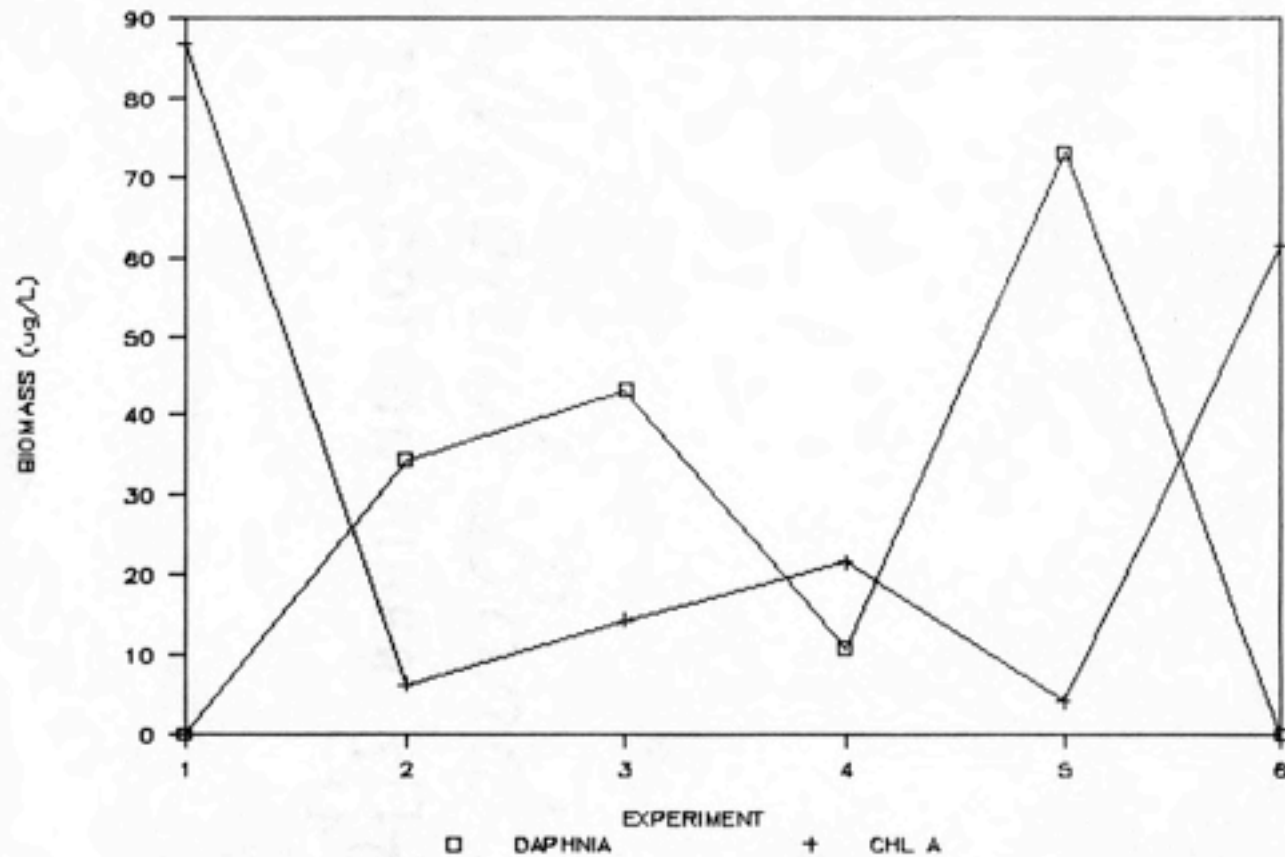
Figure 52 - Algal and _Daphnia_ spp. biomass inside the enclosure in experiments 1-6. (CHL A) = Chlorophyll _a_.

(Figures 50 and 51). In experiment 4, this continued decrease in chlorophyll a (Figure 50) paralleled a continued increase in cladocerans (Figure 46) and a decrease in copepods (Figure 42). During experiment 5, the very rapid decline of cladoceran biomass during the second and third weeks (Figure 48) may have been was the result of very low grazeable phytoplankton biomass as indicated by chlorophyll a (Figure 51). The increase in copepod biomass through the second week (Figure 44) seemed independent of the concentration of chlorophyll a (Figure 51). During the third week copepods declined, but in the second week they increased in biomass. Perhaps they were responding to increased prey densities. Reductions in algal biomass were best associated with changes in cladoceran biomass. Copepod reductions and increases were independent of changes in chlorophyll a .

WATER QUALITY PARAMETERS

Secchi depth increased inside the enclosures when sediment turbidity was not a factor (Figure 41). In experiments 2 and 3, sediment turbidity prevented a increase in transparency. Nevertheless, the increased turbidity from sediments did not prevent Daphnia spp. from reducing chlorophyll a inside the enclosures. In experiments 4 through 6 when inorganic turbidity was

(Figures 50 and 51). In experiment 4, this continued decrease in chlorophyll a (Figure 50) paralleled a continued increase in cladocerans (Figure 46) and a decrease in copepods (Figure 42). During experiment 5, the very rapid decline of cladoceran biomass during the second and third weeks (Figure 48) may have been was the result of very low grazeable phytoplankton biomass as indicated by chlorophyll a (Figure 51). The increase in copepod biomass through the second week (Figure 44) seemed independent of the concentration of chlorophyll a (Figure 51). During the third week copepods declined, but in the second week they increased in biomass. Perhaps they were responding to increased prey densities. Reductions in algal biomass were best associated with changes in cladoceran biomass. Copepod reductions and increases were independent of changes in chlorophyll a .

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lower, transparency increased with the reduction in chlorophyll a. Therefore, when sediment turbidity of the water was high, reduction in phytoplankton biomass did not produce an increase in transparency.

Dissolved oxygen levels were lower inside the enclosures (Figure 39). These lower values were associated with a decrease in algal biomass and were probably affected also by the reduction in wind mixing inside the enclosures. During experiment 3, dissolved oxygen dropped to very low levels. The very low values may also have been the result of an increase in respiration by bacteria, which were presumably decomposing zooplankton feces and killed cells. After these communities reached equilibrium, dissolved oxygen would be expected to return to levels near saturation due to reduced respiration and increased wind mixing.

If reductions in algal biomass cause lower photosynthesis rates, pH should decrease. In some of the experiments this took place while in others it did not (Figure 40). Reduction in pH has been shown to reduce the presence of blue-green algae (Shapiro 1973). However, as experiment 3 indicates (Figure 34), blue-greens were more likely reduced by grazing and not by the small reduction in pH.

Soluble nutrients increased inside the enclosures in all of the experiments (Figure 37 and 38). This increase

was apparently the result of release from phytoplankton biomass. Without phytoplankton to use the available nutrients, soluble levels increased inside the enclosures. Lehman (1980) observed an increase in soluble nutrients when chlorophyll a was reduced. He noted that in the presence of cladocerans, algal cells that were dividing rapidly were being cropped as fast or faster than they were being produced. In experiments 1-6, this would explain the inability of the phytoplankton to increase when soluble nutrients increased. As a result, grazing, not nutrients was the limiting factor for phytoplankton growth.

Total nutrients were very similar or only slightly lower inside the enclosures (Figures 35 and 36). The most promising aspect of the enclosure results is that reductions in algal biomass occurred under the same nutrient regime as that in the lake. The enclosures yielded a much lower chlorophyll a per unit TP, and this makes biomanipulation a possible management strategy for Jordan Lake.

MANAGEMENT IMPLICATIONS

The data indicate the importance of Daphnia spp. as part of the zooplankton community. The critical management question is the amount of Daphnia spp. biomass

needed for the control of phytoplankton. An increase in total zooplankton biomass (Figure 53), copepod biomass (Figure 54) and cladoceran biomass (Figure 55) did not always result in a reduction in chlorophyll $\underline{a}$. For biomass as high as 700 ug/L, chlorophyll $\underline{a}$ was not reduced to levels less than 40 ug/L. However, at $\underline{Daphnia}$ spp. biomass greater than 30 ug/L (Figure 56), chlorophyll a was reduced to very low levels. At biomass less than 20 ug/L, chlorophyll $\underline{a}$ responded to other limiting variables in the lake.

Management of the zooplankton community to control phytoplankton biomass should concentrate on two variables. The first is to keep $\underline{Daphnia}$ spp. in the lake throughout the year. Without $\underline{Daphnia}$ spp., increases in the other zooplankton will not control phytoplankton growth. The second is to sustain $\underline{Daphnia}$ spp. at a biomass of 30 ug/L or greater so that it may produce a desirable effect.

Predation by gizzard shad seemed to have the greatest impact on the zooplankton community in the lake. Reduction in the populations of this planktivore as well as other predators on $\underline{Daphnia}$ spp. may be a valuable tool for the enhancement of water quality.

TOTAL ZOOPLANKTON AND CHLOROPHYLL A
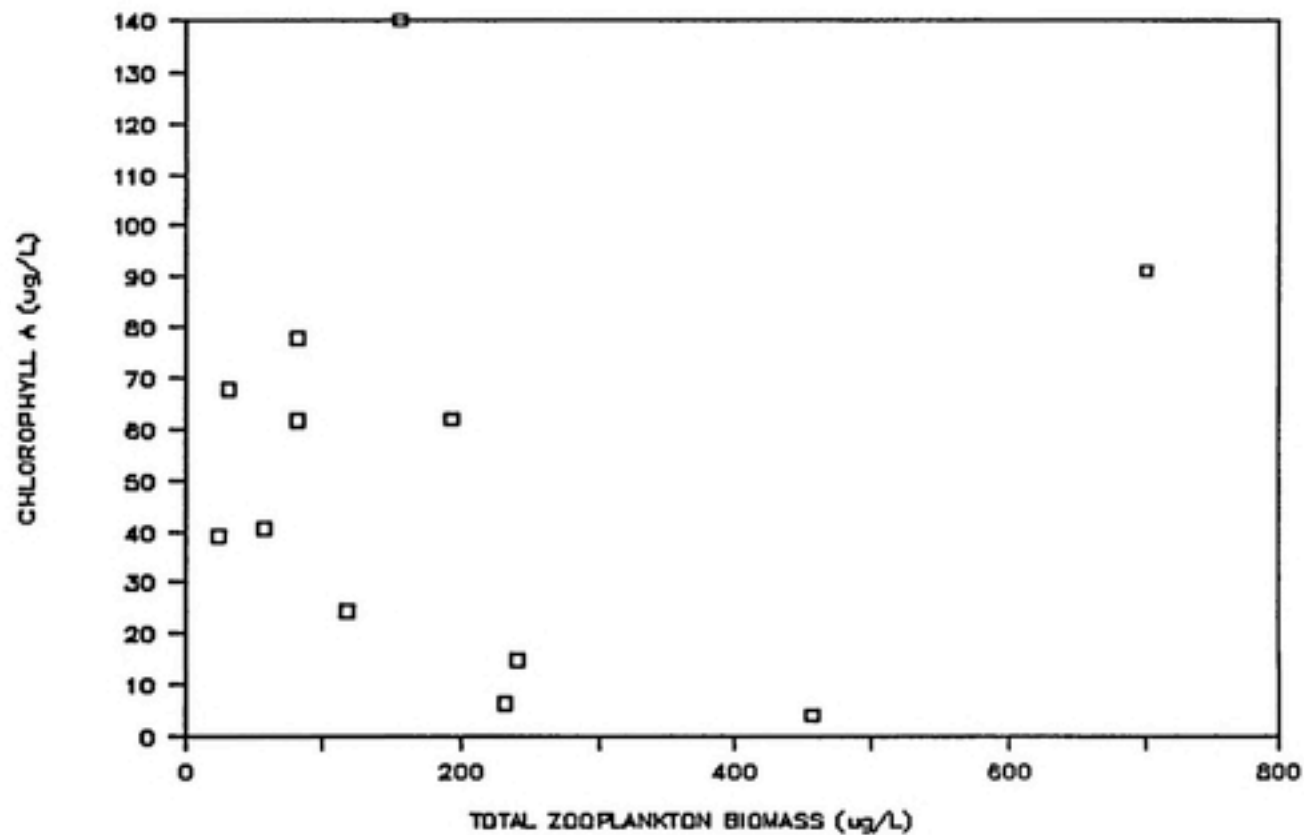
Figure 53 - Relationship between total zooplankton biomass and chlorophyll **a**.

TOTAL COPEPODS AND CHLOROPHYLL A
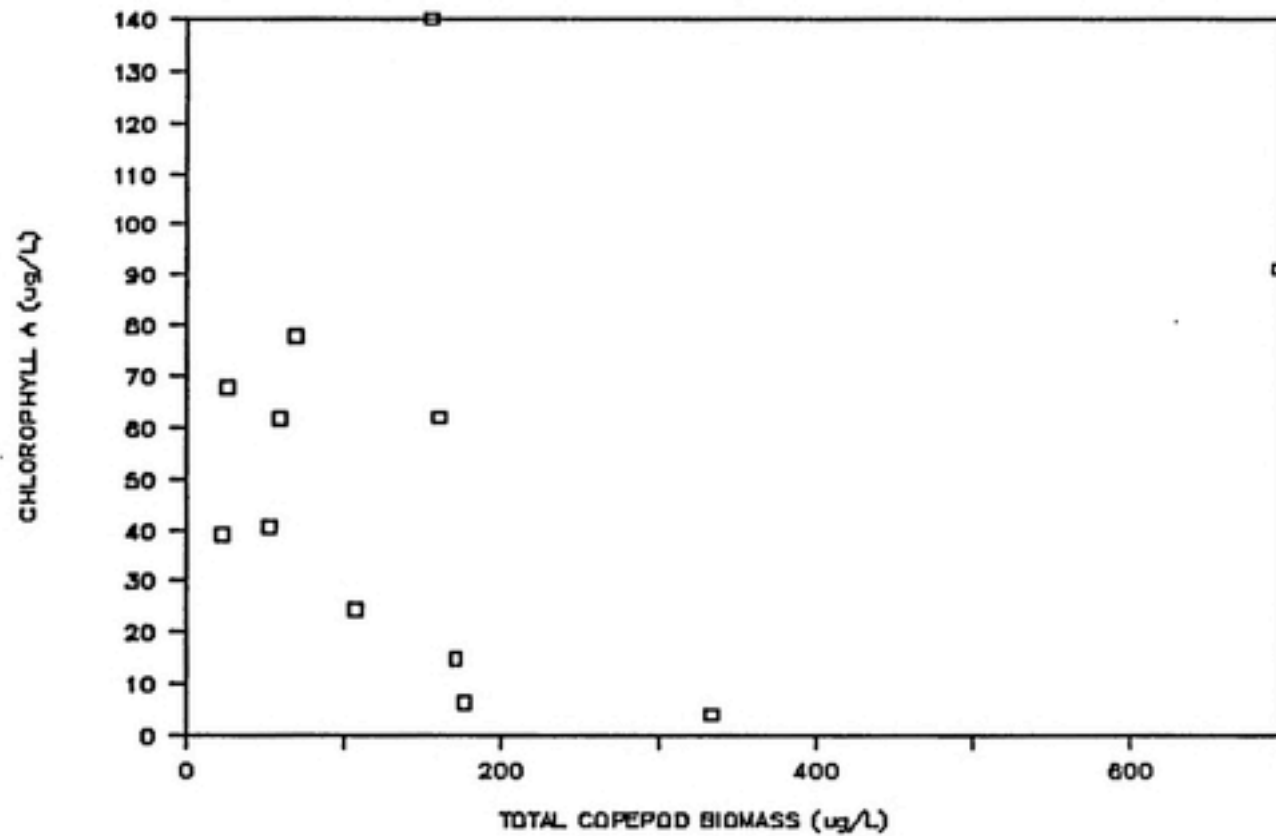
Figure 54 - Relationship between total copepod (exclusive of nauplii) biomass and chlorophyll a.

CLADOCERANS AND CHLOROPHYLL A
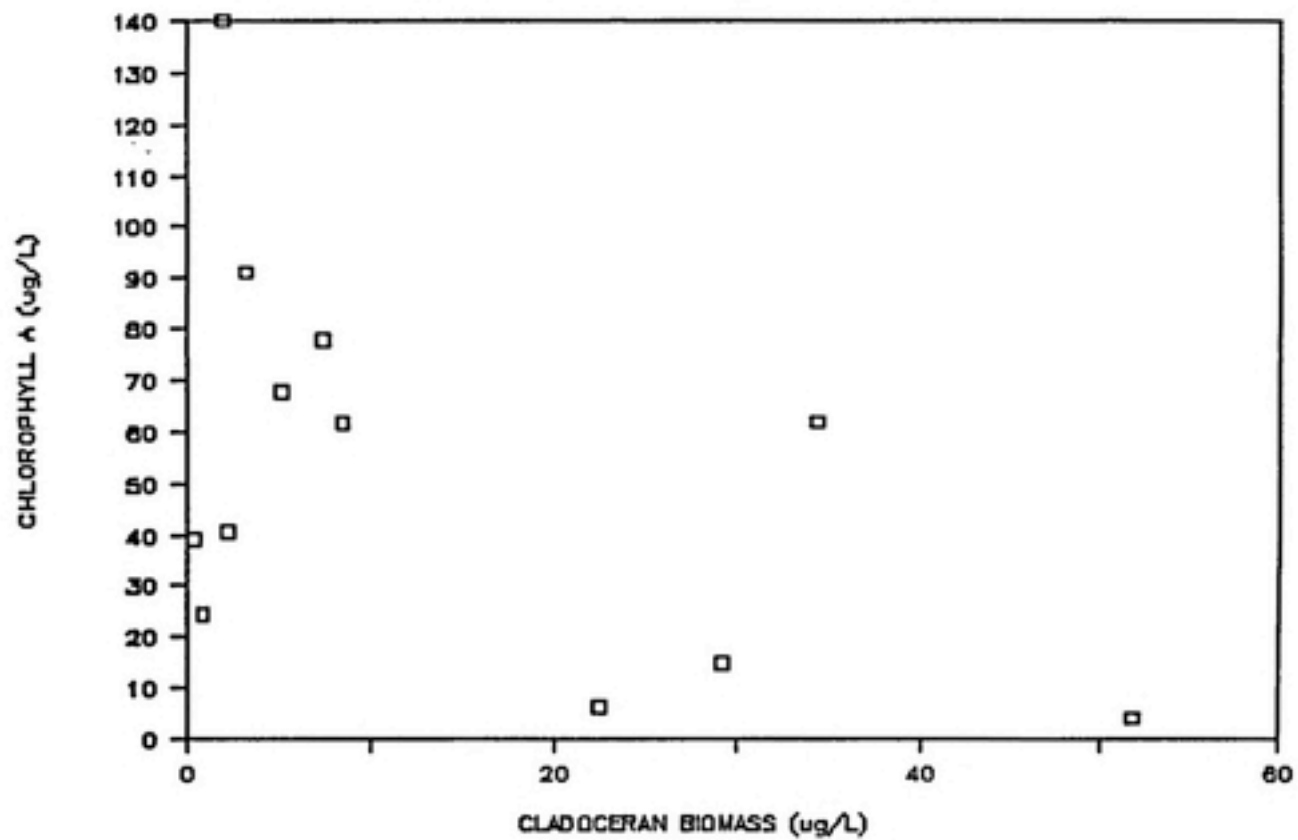
Figure 55 - Relationship between cladoceran (exclusive of Daphnia spp.) biomass and chlorophyll a.

DAPHNIA AND CHLOROPHYLL A
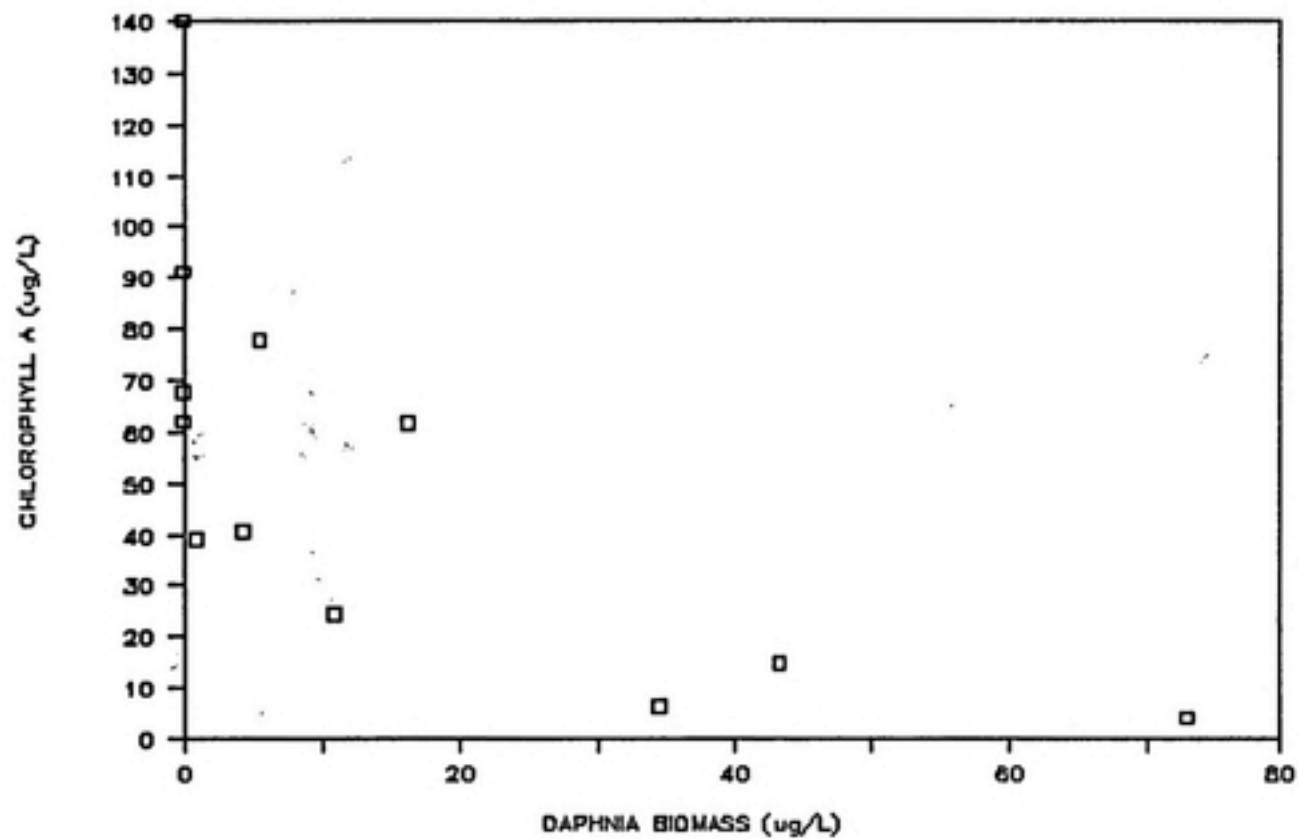
Figure 56 - Relationship between Daphnia spp. biomass and chlorophyll a.

LIMITATIONS OF THE STUDY

Due to technical problems and vandalism during the study, only one enclosure was in the water column at a time. Therefore, it was not possible to determine the variability due to chance within the experiments. However, the enclosure experiments were conducted over time which was very important in determining the role of Daphnia spp. in the entire process of improving water quality. Similar results were obtained at different times the experiment was conducted so long as Daphnia spp. was present. This study was performed to provide a initial framework for determining the relationships between the various trophic levels in the lake and the possible manipulation of the food web to improve water quality.

CONCLUSIONS

1. Zooplankton of Jordan Lake appear to be structured by planktivorous fish predation with gizzard shad probably the most important planktivore.

2. When planktivores were excluded from lake systems isolated by enclosures, the biomass of the zooplankton community increased and had the

potential to control phytoplankton biomass depending on the zooplankton community structure.

3. _Daphnia_ spp. at a biomass greater than 30 ug/L was strongly associated with and probably responsible for reductions in chlorophyll _a_ to very low levels in Jordan Lake.

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APPENDIX 1 - Zooplankton data for Experiments 1-6

TABLE 1A – Zooplankton of Experiment 1

Date: 8/15/86 Station: LAKE	Species / Liter			Biomass (ug/L)		
Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	127.4	236.9	182.1	5.2	9.8	7.5
D. pallidus	49.3	39.1	44.2	104.2	82.7	93.5
C. vernalis	16.1	21.2	18.7	34.6	45.4	40.0
M. edax	5.1	10.2	7.7	9.0	18.0	13.5
CLADOCERANS						
Diaphanosoma sp.	6.8	5.4	6.1	1.7	1.4	1.6
M. micrura	3.4	2.2	2.8	0.5	0.3	0.4
Daphnia sp.	0.0	0.0	0.0	0.0	0.0	0.0
ENCLOSURE						
COPEPODS						
Nauplii	467.1	1497.0	982.1	19.2	61.6	40.4
D. pallidus	327.8	535.5	431.7	259.2	423.4	341.3
C. vernalis	180.0	320.8	250.4	189.8	338.2	264.0
M. edax	54.4	52.6	53.5	53.7	52.0	52.8
CLADOCERANS						
Diaphanosoma sp.	8.5	17.8	13.2	2.1	4.4	3.3
M. micrura	0.0	0.0	0.0	0.0	0.0	0.0
Daphnia sp.	0.0	0.0	0.0	0.0	0.0	0.0

TABLE 2A – Zooplankton of Experiment 2

Date: 9/2/86
Station: LAKE

Species	Species / Liter			Biomass (ug/L)		
	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	307.2	150.3	228.8	12.6	6.2	9.4
D. pallidus	101.9	30.6	66.2	67.2	20.2	43.7
C. vernalis	10.2	11.9	11.0	12.5	14.6	13.5
M. edax	6.8	0.0	3.4	4.9	0.0	2.5
CLADOCERANS						
Diaphanosoma sp.	32.3	11.6	21.9	4.3	1.5	2.9
M. micrura	45.9	14.7	30.3	7.0	2.3	4.6
Daphnia sp.	17.0	0.9	8.9	10.5	0.5	5.5
ENCLOSURE						
COPEPODS						
Nauplii	97.7	196.2	146.9	4.0	8.1	6.0
D. pallidus	128.0	164.8	146.4	112.9	145.3	129.1
C. vernalis	18.5	22.9	20.7	25.1	31.1	28.1
M. edax	6.7	13.6	10.2	7.9	15.9	11.9
CLADOCERANS						
Diaphanosoma sp.	40.4	90.7	65.6	5.3	11.9	8.6
M. micrura	37.1	60.7	48.9	10.6	17.4	14.0
Daphnia sp.	18.5	29.7	24.1	26.5	42.5	34.5

TABLE 3A - Zooplankton of Experiment 3

Date: 9/10/86 Station: LAKE	Species / Liter			Biomass (ug/L)		
Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	63.7	88.3	76.0	2.6	3.6	3.1
D. pallidus	18.7	59.4	39.0	21.0	66.8	43.9
C. vernalis	2.6	9.3	5.9	4.6	16.8	10.7
M. edax	0.9	0.8	0.8	0.4	0.4	0.4
CLADOCERANS						
Diaphanosoma sp.	7.6	41.0	24.3	1.6	8.6	5.1
M. micrura	5.9	11.7	8.8	2.3	4.5	3.4
Daphnia sp.	6.8	21.2	14.0	7.8	24.4	16.1
ENCLOSURE						
COPEPODS						
Nauplii	134.1	89.1	111.6	5.5	3.7	4.6
D. pallidus	253.1	164.6	208.9	163.0	106.0	134.5
C. vernalis	23.8	10.2	17.0	31.2	13.4	22.3
M. edax	8.5	2.6	5.6	12.7	3.9	8.3
CLADOCERANS						
Diaphanosoma sp.	78.1	81.1	79.6	17.0	17.7	17.3
M. micrura	42.5	43.7	43.1	11.7	12.0	11.9
Daphnia sp.	78.1	31.4	54.8	61.7	24.8	43.3

TABLE 4A - Zooplankton of Experiment 4

Date: 5/19/87
Station: LAKE

Species	Species / Liter			Biomass (ug/L)		
	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	24.7	32.3	28.5	1.1	1.6	1.3
D. pallidus	7.9	11.2	9.5	15.2	21.4	18.3
C. vernalis	1.8	1.5	1.7	2.3	2.0	2.2
M. edax	0.0	0.2	0.1	0.0	0.1	0.1
T. prasinus	0.0	0.5	0.2	0.0	0.5	0.2
CLADOCERANS						
B. longirostris	4.2	4.5	4.4	0.4	0.3	0.3
Daphnia sp.	1.8	1.7	1.7	1.0	0.8	0.9
C. sphaericus	0.0	0.2	0.1	0.0	0.0	0.0
ENCLOSURE						
COPEPODS						
Nauplii	30.1	71.3	50.7	1.7	4.0	2.9
D. pallidus	25.4	50.7	38.1	49.3	113.8	81.6
C. vernalis	9.7	10.9	10.3	17.1	19.8	18.4
T. prasinus	2.4	3.6	3.0	2.8	4.4	3.6
CLADOCERANS						
B. longirostris	1.2	14.5	7.8	0.1	1.8	0.9
Daphnia sp.	12.1	35.0	23.6	5.2	16.3	10.8

TABLE 5A - Zooplankton of Experiment 4

Date: 5/26/87 Station: LAKE	Species / Liter			Biomass (ug/L)		
Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	141.9	64.6	103.3	6.2	3.0	4.6
D. pallidus	33.2	18.1	25.7	36.2	36.7	36.5
C. vernalis	4.8	7.2	6.0	7.1	12.4	9.8
T. prasinus	0.0	3.0	1.5	0.0	2.5	1.3
CLADOCERANS						
Diaphanosoma sp.	1.8	3.0	2.4	0.9	1.3	1.1
B. longirostris	17.5	3.0	10.3	1.5	0.1	0.8
Daphnia sp.	16.3	4.8	10.6	6.6	1.9	4.3
C. sphaericus	0.6	0.0	0.3	0.0	0.0	0.0
A. monacantha	0.6	0.6	0.6	0.0	0.1	0.1
L. quadrangularis	0.0	0.6	0.3	0.0	0.3	0.2
ENCLOSURE						
COPEPODS						
Nauplii	182.4	108.7	145.6	8.1	5.0	6.6
D. pallidus	27.8	13.6	20.7	37.8	20.9	29.4
C. vernalis	12.1	3.6	7.9	17.7	5.1	11.4
T. prasinus	0.0	0.9	0.5	0.0	0.7	0.4
CLADOCERANS						
Diaphanosoma sp.	2.4	1.5	2.0	0.5	0.3	0.4
B. longirostris	3.6	2.1	2.9	0.3	0.2	0.3
Daphnia sp.	13.3	4.5	8.9	9.7	2.7	6.2
S. crystallina	1.2	0.9	1.1	17.1	8.7	12.9
C. sphaericus	0.0	1.8	0.9	0.0	0.1	0.1

TABLE 6A - Zooplankton of Experiment 5

Date: 5/26/87 Station: ENCLOSURE	Species / Liter			Biomass (ug/L)		
Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean

COPEPODS

Nauplii	715.0	560.4	637.7	30.7	25.0	27.9
D. pallidus	260.9	183.6	222.3	288.3	123.8	206.1
C. vernalis	53.1	67.6	60.4	72.6	105.6	89.1
M. edax	4.8	0.0	2.4	2.8	0.0	1.4
T. prasinus	9.7	19.3	14.5	8.0	16.0	12.0

CLADOCERANS

A. monacantha	4.8	0.0	2.4	0.7	0.0	0.4
B. longirostris	77.3	19.3	48.3	8.3	7.1	7.7
Daphnia sp.	144.9	125.6	135.3	62.4	83.8	73.1
H. amazonicum	4.8	0.0	2.4	87.3	0.0	43.7

TABLE 7A - Zooplankton of Experiment 5

Date: 6/3/87
Station:ENCLOSURE

	Species / Liter			Biomass (ug/L)		
Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	163.7	125.6	144.7	6.7	5.2	6.0
D. pallidus	33.2	77.3	55.3	693.8	86.3	390.1
C. vernalis	0.6	0.0	0.3	0.9	0.0	0.5
T. prasinus	1.2	0.0	0.6	1.2	0.0	0.6
CLADOCERANS						
Diaphanosoma sp.	0.6	0.0	0.3	0.1	0.0	0.1
B. longirostris	15.1	106.3	60.7	0.9	15.4	8.2
Daphnia sp.	1.2	9.7	5.5	0.5	3.6	2.1
S. kingi	2.4	0.0	1.2	0.5	0.0	0.3
C. sphaericus	0.6	0.0	0.3	0.0	0.0	0.0

Station: LAKE

	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
Species						
COPEPODS						
Nauplii	152.8	129.8	141.3	6.5	5.8	6.2
D. pallidus	15.7	12.7	14.2	23.2	21.4	22.3
C. vernalis	0.0	0.3	0.2	0.0	0.4	0.2
CLADOCERANS						
Diaphanosoma sp.	14.5	12.7	13.6	3.6	2.1	2.9
B. longirostris	4.8	16.9	10.9	0.3	1.3	0.8
Daphnia sp.	0.6	0.3	0.5	0.1	0.1	0.1
M. micrura	0.6	0.9	0.8	0.1	0.2	0.2
H. amazonicum	0.0	0.3	0.2	0.0	0.6	0.3

TABLE 8A - Zooplankton of Experiment 5

Date: 6/9/87   Species / Liter   Biomass (ug/L)
Station: LAKE

Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	59.8	37.4	48.6	2.8	1.7	2.3
D. pallidus	8.5	7.9	8.2	14.6	10.1	12.4
C. vernalis	1.2	0.0	0.6	1.7	0.0	0.9
CLADOCERANS						
Diaphanosoma sp.	9.1	6.3	7.7	1.3	1.0	1.2
B. longirostris	4.2	1.8	3.0	0.2	0.2	0.2
M. micrura	0.6	0.0	0.3	0.1	0.0	0.1

Station: ENCLOSURE

Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	20.2	24.2	22.2	0.8	1.0	0.9
D. pallidus	4.2	1.5	2.9	8.1	3.0	5.6
C. vernalis	0.0	0.3	0.2	0.0	0.4	0.2
CLADOCERANS						
Diaphanosoma sp.	0.3	0.3	0.3	0.0	0.0	0.0
B. longirostris	3.9	4.5	4.2	0.1	0.2	0.2
H. amazonicum	0.3	0.0	0.2	1.0	0.0	0.5
A. monacantha	0.3	0.0	0.2	0.0	0.0	0.0
L. quadrangularis	0.6	0.0	0.3	0.3	0.0	0.2

TABLE 9A - Zooplankton of Experiment 6

Date: 6/16/87
Station: LAKE

Species	Species / Liter			Biomass (ug/L)		
	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	35.0	38.6	36.8	1.7	1.8	1.8
D. pallidus	10.9	15.7	13.3	14.2	26.6	20.4
C. vernalis	4.2	1.2	2.7	6.2	1.4	3.8
CLADOCERANS						
Diaphanosoma sp.	12.1	13.3	12.7	3.6	4.8	4.2
B. longirostris	2.4	0.6	1.5	0.3	0.1	0.2
M. micrura	1.8	2.4	2.1	0.6	0.3	0.5
Daphnia sp.	1.8	0.0	0.9	0.6	0.0	0.3

Station: ENCLOSURE

Species	First Haul	Second Haul	Mean	First Haul	Second Haul	Mean
COPEPODS						
Nauplii	147.3	130.5	138.9	6.4	6.0	6.2
D. pallidus	101.5	67.7	84.6	184.3	99.7	142.0
C. vernalis	16.9	0.0	8.5	21.7	0.0	10.9
CLADOCERANS						
Diaphanosoma sp.	74.9	29.0	52.0	44.0	21.1	32.6
B. longirostris	2.4	0.0	1.2	0.1	0.0	0.1
M. micrura	9.7	4.8	7.3	2.7	0.9	1.8

APPENDIX 2 - Top 5% of the Phytoplankton Species in

Experiments 1 and 3

Table 10A   Top 5% of Phytoplankton Species

Experiment 1	8/6/86 out	8/15/86 out	8/15/86 in
Species (top 5%)	cells/ml	cells/ml	cells/ml
Oscillatoria geminata	115000	118000	133000
Dactylococcopsis irreg.	21800	31100	32900
Chlorella sp.	14800	17000	17400
Cyclotella pseudostell.	0	0	0
Stephanodiscus minutus	12600	18800	10678
Melosira italica	5180	8140	1850
Euglena acus	0	0	0
Cryptomonas erosa	0	0	0
Lepocinclis salina	0	0	0

Experiment 3	9/2/86 out	9/10/86 out	9/10/86 in
Species (top 5%)	cells/ml	cells/ml	cells/ml
Oscillatoria geminata	15400	11500	315
Dactylococcopsis irreg.	7580	10500	185
Chlorella sp.	5550	7220	370
Cyclotella pseudostell.	21900	4630	241
Stephanodiscus minutus	0	0	0
Melosira italica	740	925	167
Euglena acus	185	0	0
Cryptomonas erosa	1295	925	19
Lepocinclis salina	19	0	0