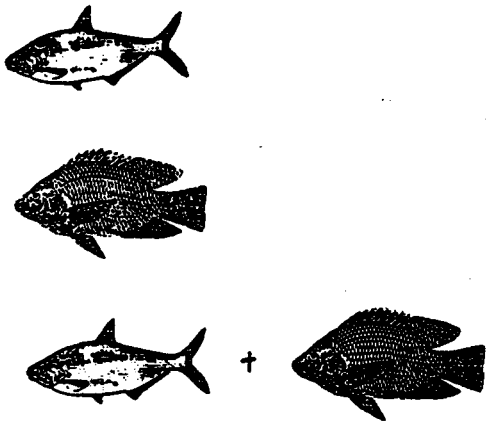
Special Publication SJ 88-SP1

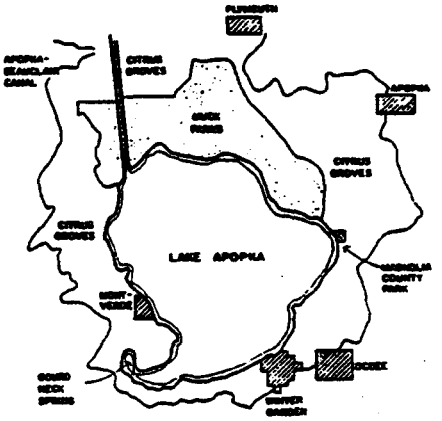
# LAKE APOPKA TROPHIC STRUCTURE MANIPULATION

by

Thomas L. Crisman
Principal Investigator

John R. Beaver
Graduate Assistant






Phase I Final Project Report

Submitted to

St. Johns River Water Management District

April 1988

TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

LIST OF FIGURES (cont.)

Page

# INTRODUCTION

The water quality of the Oklawaha Chain of Lakes in general and Lake Apopka in particular have concerned environmentalists, local and state agencies, and private citizens for at least the last twenty-five years (Lowe et al. 1986). Progressive eutrophication has eliminated many former users of the lake, especially recreation and sport fisheries. Since Lake Apopka is the largest and first lake in the Oklawaha Chain, any progress towards improving the water quality of this water system should logically begin with the headwaters as this is the worst damaged by cultural activities (Brezonik et al. 1978).

In 1985, the Florida Legislature funded studies aimed towards identification of feasible methods for restoring the lake (Chapter 85-148, Laws of Florida). Subsection 5 (4) of this law states that the St. Johns River Water Management District shall "examine techniques which may be used to modify the existing physical and biological characteristics of the lake". The research described in this report was performed under this directive.

Shapiro (1979) has suggested that the large amount of scatter in the chlorophyll a to total phosphorous relationship is likely due to variable intensity and effectiveness of zooplankton grazing. Since the quality and quantity of phytoplankton communities can be largely structured by zooplankton grazing, which are in turn often determined by fish predation, regulation of fish planktivory could become an effective and inexpensive means for restoration of lake water quality.

Shapiro and Wright (1984) tested this hypothesis in Round Lake, Minnesota by eliminating most planktivorous fish activity on zooplankton. Large decreases were seen in total phosphorous, total nitrogen and chlorophyll a and were accompanied by markedly increases in secchi depth transparency. Similar improvements have been noted in other trophic structure manipulation studies (Schoenberg and Carlson 1984, Good 1984).

The above examples of biomanipulation are from temperate lakes and it remains uncertain whether modification of fish zooplanktivory can achieve significant improvements in water quality in subtropical Florida lakes. In northern lakes, the principal zooplankton grazers are large cladocerans while the cladoceran assemblages of Florida lakes are dominated by small-bodied forms (Bays and Crisman 1983) which are less efficient algal grazers (Lynch and Shapiro 1981). Consequently, this mechanism may be less important in structuring the qualitative and quantitative characteristics of phytoplankton communities in Florida systems.

Despite the probable lack of significant zooplankton grazing in Florida lakes, the total grazing pressure on algal populations may be greater than temperate systems because of the presence of gizzard shad (Dorosoma cepedianum). Mesocosm studies indicate, however, that this clupeid is ineffective in cropping algal populations, and may in fact accelerate the growth of phytoplankton populations (Crisman and Kennedy 1982).

The potential mechanisms by which gizzard shad may increase lake trophic state include alteration of phytoplankton community

structure due to the inability of shad to digest some species of blue-green algae (e.g. Lyngbya contorta), increasing the proportion of cyanophyte species in the phytoplankton community through differential digestion (Crisman and Kennedy 1982).

Similarly, crustacean zooplankton poorly utilize both blue-green (Porter 1975) and gelatinous green algae (Porter 1973). Therefore, the biomass of herbivorous zooplankton does not increase proportionally to total phytoplankton biomass, which reduces grazing pressure on phytoplankton communities in highly productive lakes.

Zooplankton populations are directly reduced by shad grazing activities (Smith 1976) which allows algal production to increase.

An increase in the proportion of blue-green algae accelerates primary production rates in nitrogen-limited lakes via reducing the optimum N/P ratio (Smith 1982) which in turn increases nitrogen inputs through nitrogen fixation.

Finally, the submerged macrophyte beds used by centrachids for spawning are progessively eliminated or greatly reduced at higher trophic states due to shading by phytoplankton. These fish are likely the primary preators upon gizzard shad.

Assuming that the effects of shad grazing on trophic interactions described above are valid, then large-scale harvesting of gizzard shad should result in improvements in both water quality and game fish production. The rate of gross primary production would be lowered as well as a reduction in blue-green algae dominance. Zooplankton populations would increase, leading to an increase in sport fish production and

lower algal production. Reduction in phytoplankton populations would be accompanied by improved water clarity and an increased likliehood of macrophyte re-colonization of the lake bottom. Re-establishment of submerged macrophyte beds would greatly aid further assimilation of nutrient inputs into the lake, in addition to enhancing sportfish production.

Finally, large-scale harvesting of fish would directly remove substantial amounts of nutrients from the lake and thus lower the trophic state of the lake (EPA 1979a). Although the usual species removed in lake restoration is a macrophyte, large-scale fish harvesting appears to be better in some respects: 1) the alteration of trophic structure described above; 2) fish assimilate plankton and particulate matter unavailable to macrophytes; 3) fish move within a lake and this would remove nutrients from the entire system; 4) fish contain much higher concentrations of nutrients and less water when compared to macrophyte species. This situation is likely to make fish harvesting more cost effective than plant harvesting; 5) and finally, fish biomass can be marketed without extensive processing and may allow some financial return on the harvest expense (Ward et al. 1985).

This research project provides baseline data in order to evaluate the potential of extensive fish harvesting as a restoration technique for Lake Apopka as well as other eutrophic Florida lakes. Consequently, the research objectives are to 1) determine the effects of rough fish (gizzard shad and blue tilapia) predation on plankton community structure and plankton

primary productivity, 2) determine the rate at which rough fish could be harvested from Lake Apopka and its probable effects on water quality and the community structure of the fish population, 3) ascertain the relative nutrient exportation of this harvest to the total nutrient budget of Lake Apopka, and 4) evaluation of large-scale fish harvesting as a lake restoration technique for subtropical lakes.

Phase I of this research project addresses objective 1 and is described below.

## MATERIALS AND METHODS

Study Site - The study site selected for the enclosure experiment was at the north end of Lake Apopka (Fig. 1). This site was approximately 200 meters south of "Station A-2" described by Brezonik et al. (1978). These researchers determined that no statistically significant differences existed between areas of Lake Apopka in regard to their biological and chemical characteristics. The only exception to this situation was Gourd Neck Springs at the south end of the lake.

Consequently, almost any area of the lake selected for the enclosure studies should theoretically approximate plankton conditions of the lake. The site at the north end of the lake was originally chosen because of its close proximity to the University of Florida Agricultural Farms which was to be the location for boat launching. After several trips down the poorly graded access road, it was decided that Magnolia Park would be a better departure point. Construction however had already begun

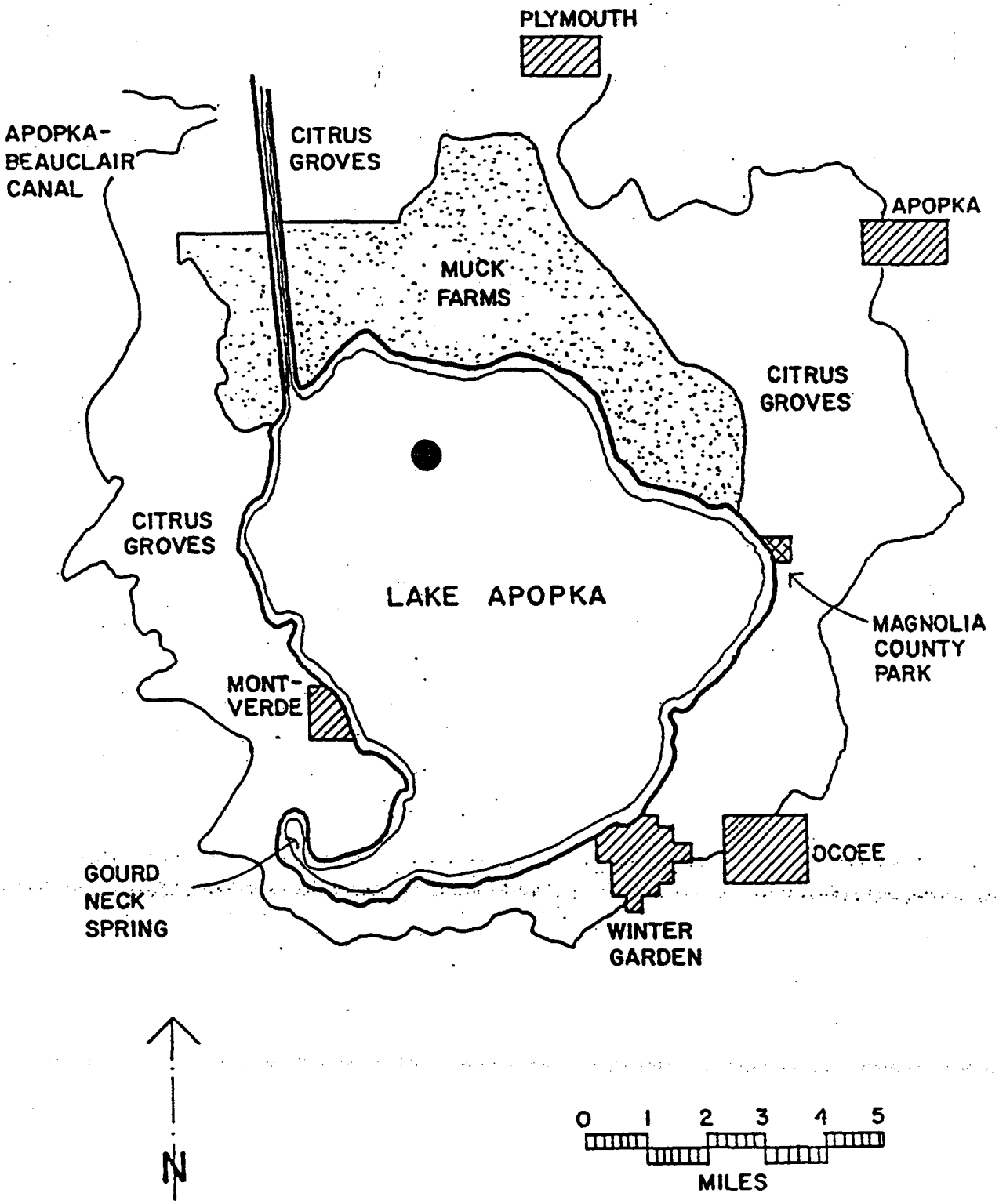



FIGURE 1. Location of the study site.

on the enclosure support structure, and so the original site was not changed.

Permitting - After several conversations with Mr. David Walker of SJRWMD and personnel from the Department of Environmental Regulation (Orlando), Dredge and Fill Permits, it was determined that a permit was necessary prior to construction. The permit application was submitted on 5 May and on 11 August the research project was added to an existing permit issued to SJRWMD.

Enclosures - The enclosures were approximately 10 $m^2$ in surface area and 2 m deep. These dimensions produced an approximate volume of 20 $m^3$.

The material used for bag construction was Scrimweave IUV 888 (Sto-Coat Products, Richland, Illinois), a material that is both structurally sound due to an internal nylon weave as well as being highly resistant to degradation by ultraviolet radiation. One large piece was cut for the sides and wrapped around in a circle and sewn upon itself. Likewise, a portion of material was cut for the bottom of the bags and sewn to the base of each side. Excess material on the top of the sides was folded over and sewn to form a hollow tube all around the top of the bag. All sewing operations were performed by a commercial upholsterer.

After all sewing and alteration of the bags to the prescibed dimensions, four styrofoam blocks (10´ x 1´ x 1´) were inserted into the collar for the purposes of flotation and to prevent excess intrusion of lake water through wave action. The addition of the styrofoam inserts squared off the tops of the enclosures.

The original design called for the bags to be anchored to a rigid wooden superstructure placed in the lake. This support strucuture was built by driving 14´ x 2´ x 4´ beams into the sediments approximately one meter, and followed by bolting and nailing horizontal 2´ x 4´ crossbeams to the vertical beams. This structure, which entailed aprroximately 10 days to build, was constructed twice during late July and August and each time was destroyed or heavily damaged by periodic, violent summer thunderstorms.

After the second demise of this wooden strucuture, it was decided that the basic design was not robust enough to withstand the weather conditions on Lake Apopka. Most of the damage inflicted upon the support structure seemed to be caused by the action of the enclosures filled with water and moving during wave action created by storms. It was therefore decided that the most practicable solution was to allow some movement during storm conditions. To accomplish this, each bag was then anchored to the sediments by tying a cinder block around each flotation collar with 1/2" nylon line. This modification generally held the bags in place unless severe winds and waves were encountered, in which case the enclosures may have drifted several meters.

Further structural stability was added to the bags by nailing 2´ x 4´ spanners atop the styrofoam floats. This square support was then bolted at the corners with steel L joints.

On September 20, 21, and 22 the bags were filled with fresh lake water by using a 3 1/2" gasoline-powered disphragm pump. Due to the early problems associated with the support structure,

some bags contained variable amounts of water prior to fish stocking. To remedy this problem, all bags were emptied before the above fill period.

Experimental Design and Fish Capture - The experimental design consisted of five treatments: 1) no fish (control), 2) gizzard shad, 3) blue tilapia, 4) gizzard shad and blue tilapia sampling was also performed at a lake station near the study site. All treatments were performed in triplicate except the lake station (Fig. 2).

Tilapia bags were stocked with two fish each and the average biomass per bag was 5.9 kg (Table 1). All of the tilapia captured were in a relatively narrow range of 270 to 400 mmm. The shad bags were stocked with two shad >220 mm and six shad <180 mm with a bag average of 3.6 kg. The combination bags were stocked with one tilapia each, one shad >220mm and six shad <180mm. The combination had a mean fish biomass of 4.0 kg.

Blue tilapia were collected from near Gourd Neck Springs utilizing an 8´ cast net on 23 and 24 September. After the fish were captured, they were taken to the enclosure site, weighed in a tared bucket and measured for lengths. Subsequent to these morphological determinations, the fish were placed in the appropriate bags. None of the captured tilapia died, nor was any sign of physiological stress evident during weighing.

Gizzard shad were comparatively easy to capture in Lake Apopka because of their prevalence, however they were substantially more difficult to keep alive. Problems were

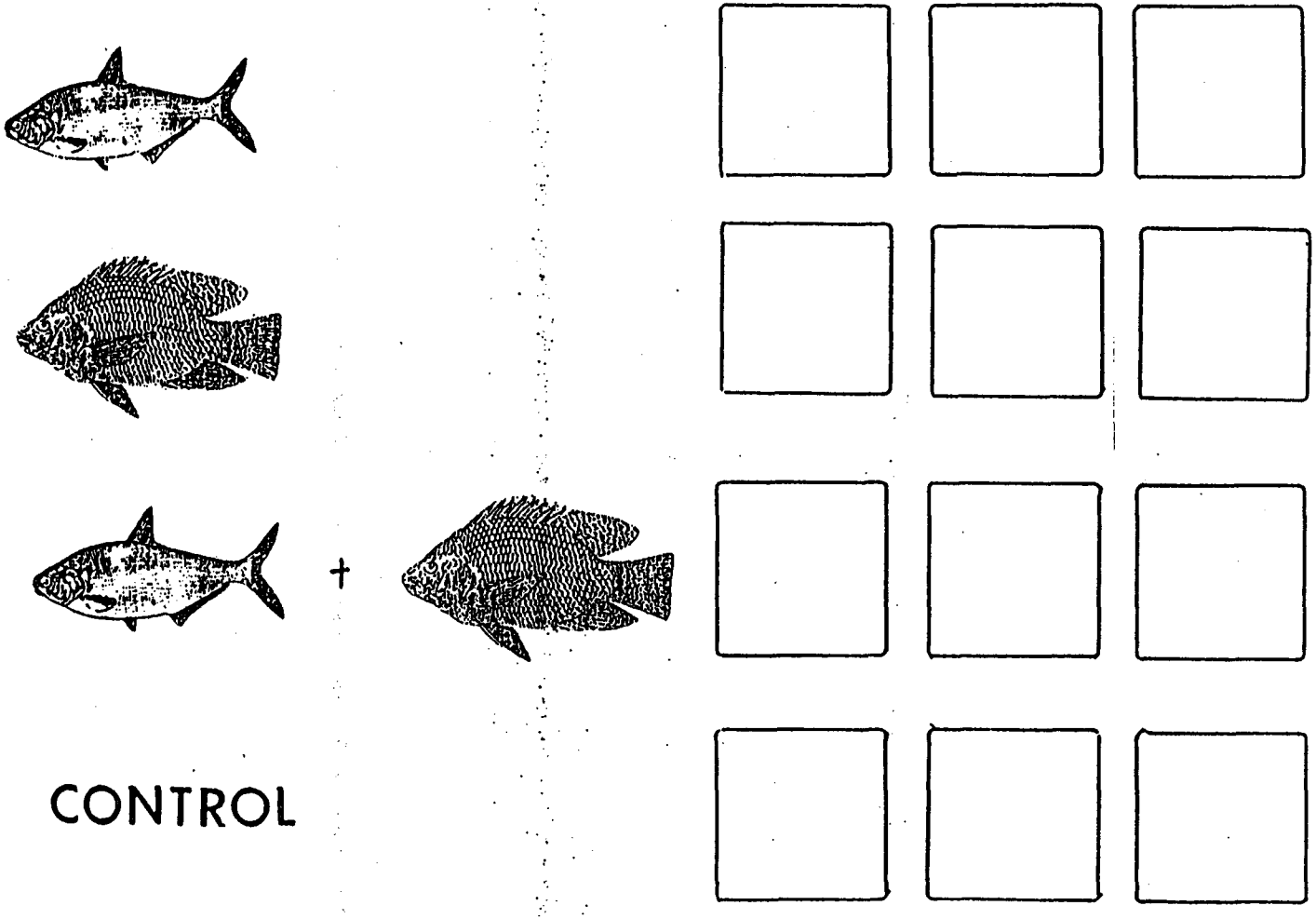



FIGURE 2. Experimental design for Lake Apopka biomanipulation investigation.

TABLE 1. Morphological characteristics (±SD) of the fish used in this study. I=Initial, F=Final.

| TREATMENT | Mean Length (cm) | Mean Biomass (kg)/bag |
|---|---|---|
| Tilapia | I=34 (5) F=35 (5) | I=1.22 (0.10) F=1.26 (0.13) |
| Shad | I=17 (7) F=not done | I=0.74 (0.03) F=not done |
| Combination -Tilapia | I=30 (2) F=31 (4) | I=0.41 (0.07) *F=0.44 (0.06) |
| -Shad | I=15 (4) F=not done | I=0.42 (0.02) F=not done |

* includes only 2 bags

encountered when fish were captured, whether by cast netting or electrofishing (with William Johnson, GFC), with high mortality prior to addition to the bags. On 22 and 23 September shad were captured from the north end of the lake and immediately taken to the study site, measured and weighed, and put into the appropriate bags.

Only the most hardy shad specimens were selected since as many 80% of them died prior to morphological characterization. The only attempts made during the course of the experiment to ascertain whether the fish were alive was visual observations on the surface of the bags. After a cold front passed through the area, all of the large shad (> 240 mm in length) stocked into the enclosures were found dead floating on the surface of the bags on 27 October. Data is reported only to 19 October in this report, and it is apparent that the shad likely died nearer 27 October due to the good condition of the corpses. This observation, however, confirmed that the shad were alive throughout the course of the experiment.

Plankton Collection - Plankton samples were collected from each bag and the lake on 24, 27, 30 September, 3, 6, 9, 12, 15, and 19 October. Throughout this report these dates will be referred to as Sampling Events (SE) 1 through 9.

Water samples were collected at 0.5 meter intervals from the surface to the bottom of the water column (exclusive of the sediments or bottom of the bags) and pooled aboard ship in a five gallon bucket.

From this composite, subsamples were withdrawn (and preserved) for bacteria (4.0% formalin), protozoa (2.5% mercuric chloride), phytoplankton (2.5% Lugol's solution), and zooplankton (10.0% Lugol's solution). Aliquots from all of the above samples with the exception of those for zooplankton were measured and added to 80 ml pill bottles. Zooplankton (rotfiers and crustaceans) were concentrated by passing 0.5 $l^{-1}$ of the composite through a #20 (mesh = 76-80 um) Wisconsin-style plankton net.

Samples for nitrogen and phosphorous forms, conductivity, pH, and chlorophyll were withdrawn and immediately iced. In addition to the above parameters, temperature and dissolved oxygen profiles were taken at 0.5 m intervals in each of the bags with a Model 54A YSI Dissolved Oxygen/Temperature meter, and secchi disk transparency was taken on each sampling event.

Productivity Studies - One each of the four treatments and the lake station were selected for productivity studies using continuous recording of dissolved oxygen in those bags.

A wooden box (approximately 3' x 3' x 2') was mounted on 14' x 2' x 4' wood stakes driven into the sediments. This structure housed five Model 8500X Nester dissolved oxygen meters attached to membraneless dissolved oxygen probes with 20' leads. This bank of meters was connected to a Model EL824 Omni data recorder. The probes were suspended over each respective bag with nylon filament line to a depth of 25 cm.

Dissolved oxygen readings were registered by the Omni

recorder at five minute intervals. The twelve hourly readings were averaged by the recorder and the value was stored in an attached data pack. The data pack was periodically removed and returned to the laboratory where the data was downloaded to a computer floppy disk. To ensure accuracy and to prevent the occurrence of any errors associated with meter malfunction, all probes were removed from the bags on sampling days, cleaned and recalibrated to the the air. In addition, individual probes and meters were occasionally rotated to different bags during the recalibration period.

The measurements of dissolved oxygen concentrations were the used to calculate gross primary productivity, net primary productivity and community respiration according to the methods of Odum and Hoskin (1958).

When the dissolved oxygen meters arrived from the vendor, one of them was found to be defective. This meter was repaired by the University of Florida's Digital Design Facility. It was not fixed however until several days after the fish incubations had begun, and as a result productivity calculations for the combination bag are based on eight less days than the other treatments.

On 12 October Hurrican Floyd threatened southern and central Florida. Although the storm largely skirted the penisula, the northern extremeties of the storm did cause substantial rains and sustained heavy winds (measured at 40 mph) at Lake Apopka. It was decided to remove the meters and recorder to prevent their

loss. Consequently, a gap exists in the productivity values between 12 October and 15 October.

Hurricane Floyd severely damage one each of the combination, control, and shad bags at this time. These bags were determined to have been punctured and were abandoned. All data in this study are based on the means for treatment groups, and thus the above treatment groups have two rather three points for a given parameter after SE 7.

## Laboratory Analysis

Bacteria - Bacteria densities were determined using the Acridine Orange (AO) modification of the epifluorescene direct count technique (Hobbie et al. 1977). Samples of 0.1 ml were counted and each count represented at least 10 random fields. If the total tally was less than 400 individuals after 10 fields, additional fields were counted until this minimum value was reached. Bacteria biomass was estimated by assuming that each cell had a volume of 1.5 $um^{-1}$ (Sorokin and Kadota 1972) and dry weight content of 50% (Bratbak and Dundas 1984).

Phytoplankton - Phytoplankton samples were counted by Greenville Hall (SJRWMD) but the precise methodology employed was not available at the time this report was written.

Ciliated Protozoa - Ciliated protozoa were enumerated using a modified version of the Utermohl sedimentation technique. An

appropriate volume (0.5 to 2.0 ml) was settled into an Utermohl chamber and the entire contents were enumerated at 400x. Ciliates were identified using Kahl (1930-1935), and abundances were converted to biomass by multiplying known volumes of taxa (Beaver and Crisman 1982, 1988; Beaver et al. 1988) times 0.279 pg dry weight/um$^3$ (Gates et al. 1982).

Zooplankton - Rotifer and crustacean analysis were performed on the concentrated sample taken from the composite. 1 ml aliquots were placed into a Sedgewick-Rafter chamber and counted at 200x. If the total tally was less than 150 individuals, an additional subsample was enumerated. Zooplanton identification followed the keys of Edmondson (1959), Ruttner-Kolisko (1974) and Deevey and Deevey (1971). Species abundances were converted to dry weight biomass using published values for individual taxa (Maslin 1969, Dumont et al. 1975).

Chlorophyll Analysis - Chlorophyll a analysis followed the trichromatic method (APHA 1982). Size fractionation of chlorophyll a was performed by slowly passing 15 to 25 ml of water at low vacuum through a 0.45 um glass fiber filter with a 41 um mesh nylon prefilter. Great care was taken to ensure that the prefilter did not clog. Those phytoplankton which passed through the mesh were operationally defined as nannoplankton. Net plankton chlorophyll was calculated by subtracting the value for nannoplankton from the chlorophyll value determined for water which was not passed through a prefilter. Each of these respective values was converted to dry weight biomass by multiplication by a factor of 67 (APHA 1982).

Nitrogen and Phosphorous Forms - Analyses of nitrogen and phosphorous forms followed accepted techniques (EPA 1979b), and were performed by the laboratory of Ramesh Reddy.

The techniques used for chemical analyses (and EPA Method Numbers) follow - nitrite (353.2), ammonia (351.2), total Kjeldahl nitrogen (351.2), soluble reactive phosphorous (365.2) and total phosphorous (365.4).

Conductivity and pH - Conductivity and pH concentrations were determined the morning after samples were taken. Measurements were taken at 25 $^{o}$C using an Orion Model 601A Ionalyzer and a YSI Model 33 Conductivity meter.

Statistical Analyses

ANOVAs were performed using Duncan's multiple range test (SAS 1985) and were deemed to be significant at $p < 0.05$.

All statistical analyses utilzed the Northeast Regional Data Center at the University of Florida. Although the lake data was not replicated, and some data is missing due to destruction of bags during the hurricane, ANOVAs were performed with this single and duplicate points. The authors recognize that this is not statistically valid but in the text will refer to differences in these situations as significant in order to emphasize general trends and to enhance clarity.

# RESULTS

## Chemical and Physical Parameters

### Temperature

Water temperature during the study declined from an inital value on SE 1 of 30.6 °C to a low of 19.5 °C on SE 8 (Fig. 3). The water column averaged 22.5 °C on the final day of the experiment, and the mean water temperature for the entire study was 24.1 °C.

### Secchi Disk Transparency

Secchi disk transparency varied little over the course of the experiment in the lake (Fig. 4) with values between 36cm and 26cm. The average value for the lake was 30cm. ANOVA indicated that no significant differences existed between treatments for any of the sampling events, although water transparency was consistently lower in the tilapia bags when contrasted with the lake. The overall averages by treatment were confined to a narrow range between 26cm and 30cm (Table 2).

### Hydrogen Ion Concentrations

pH values fluctuated little over the majority of the experiment period, however all treatments experienced slight declines after SE 6 (Fig. 5). During the first 6 days of the experiment pH values for all treatments averaged higher than the lake but then converged. Shad, combination, and control bags closely paralleled the lake in pH concentration after that time. The tilapia bags however exhibited a reduced pH compared to the

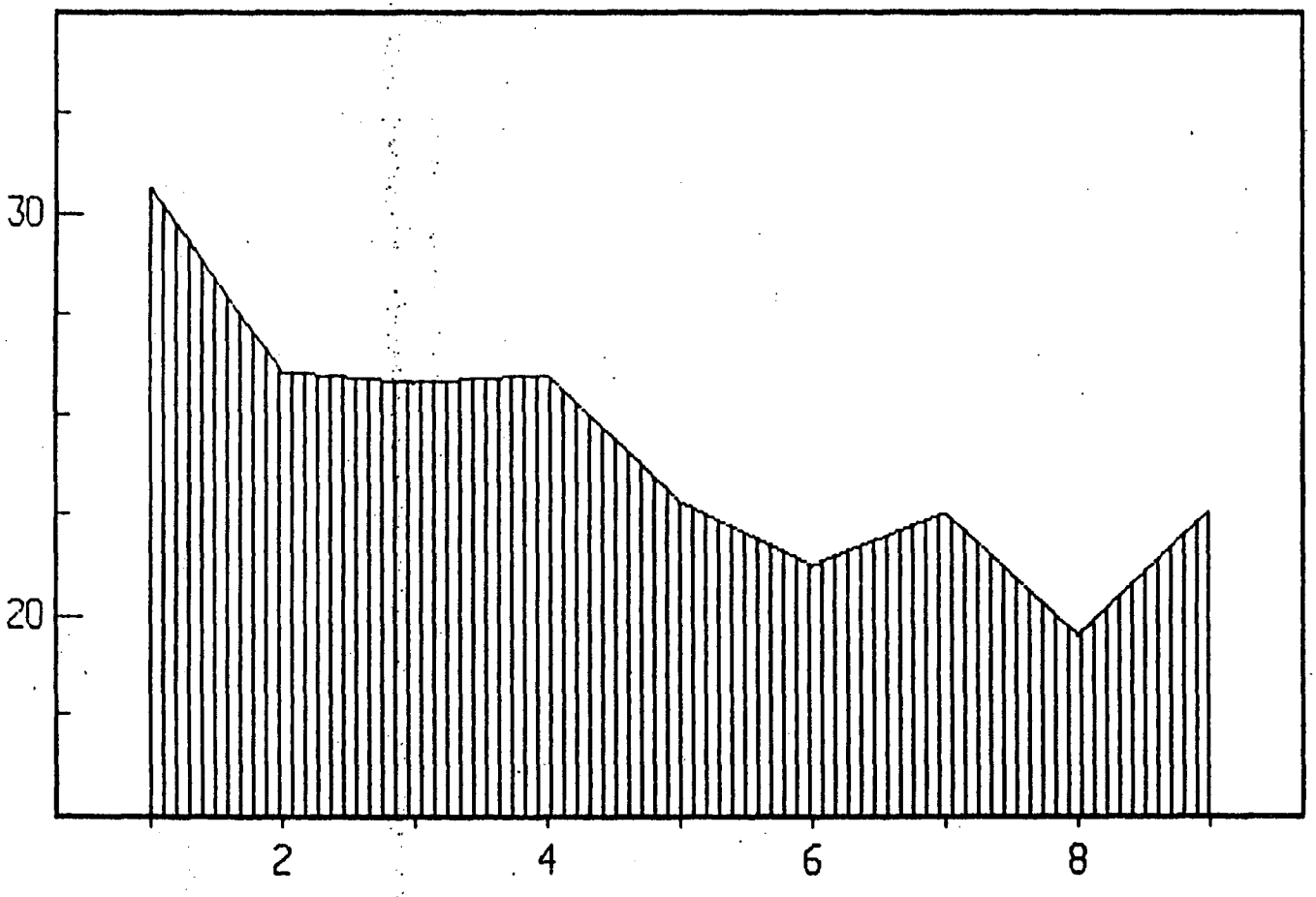



FIGURE 3. Changes in temperature ( °C) over the duration of the experiment.

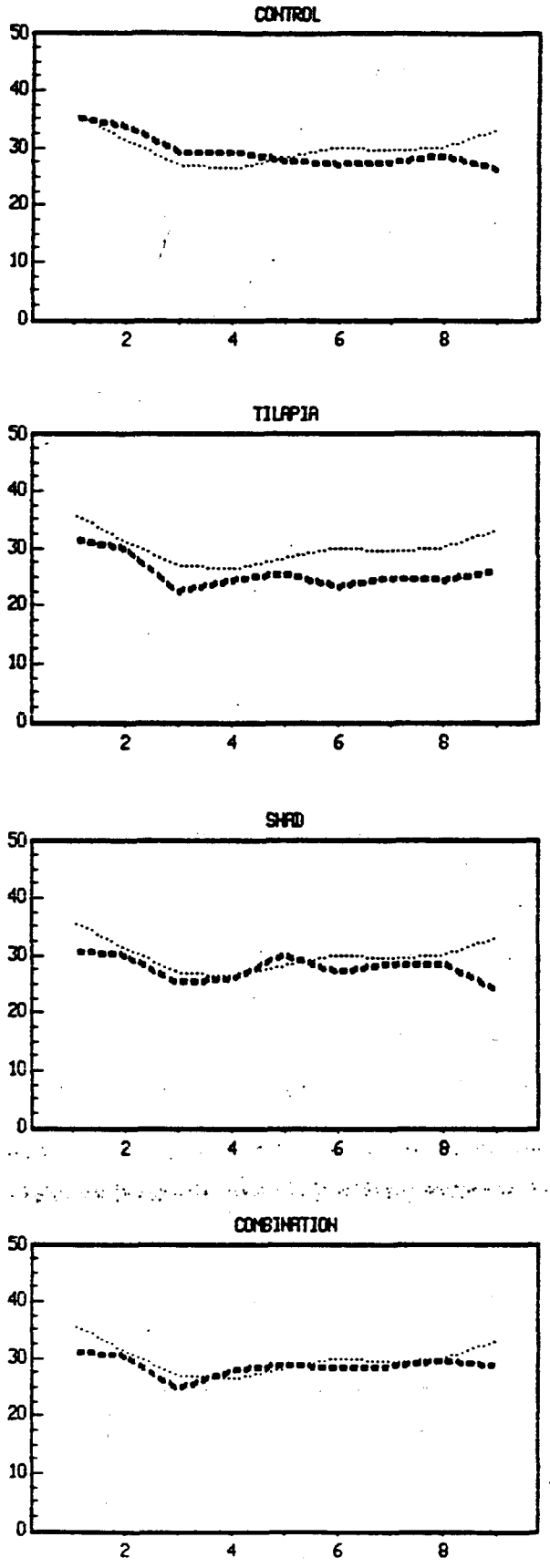



FIGURE 4. Changes in secchi disk transparency (cm) in the enclosures by sampling event. Dotted line represents lake values.

TABLE 2. Mean values (±SE) for chemical/physical parameters by treatment.

| | TREATMENT | | | | |
|---|---|---|---|---|---|
| | LAKE | CONTROL | TILAPIA | SHAD | COMBINATION |
| Secchi Disk | 30 (1) (n=9) | 29 (1) (n=25) | 26 (1) (n=27) | 28 (1) (n=25) | 28 (1) (n=25) |
| Conductivity | 319 (10) (n=9) | 313 (8) (n=25) | 311 (8) (n=27) | 307 (9) (n=25) | 312 (6) (n=25) |
| pH | 9.68 (.10) (n=9) | 9.81 (.07) (n=25) | 9.53 (.09) (n=27) | 9.79 (.07) (n=25) | 9.81 (.06) (n=25) |
| Nitrate | < 0.01 (0) (n=8) | < 0.01 (0) (n=25) | < 0.01 (0) (n=27) | < 0.01 (0) (n=24) | < 0.01 (0) (n=23) |
| Ammonia | 0.301 (.069) (n=8) | 0.192 (.014) (n=25) | 0.401 (.064) (n=27) | 0.240 (.025) (n=23) | 0.242 (.028) (n=23) |
| TKN | 7.19 (0.61) (n=8) | 5.53 (0.35) (n=25) | 6.98 (0.35) (n=27) | 6.22 (0.56) (n=24) | 5.51 (0.24) (n=23) |
| TN | 7.50 (0.59) (n=8) | 5.72 (0.36) (n=25) | 7.38 (0.38) (n=27) | 6.55 (0.59) (n=23) | 5.75 (0.26) (n=23) |
| SRP | 0.27 (0.20) (n=8) | 0.07 (0.03) (n=25) | 0.07 (0.01) (n=27) | 0.19 (0.09) (n=24) | 0.04 (0.01) (n=23) |
| TP | 0.50 (0.29) (n=8) | 0.27 (0.04) (n=25) | 0.32 (0.03) (n=27) | 0.49 (0.15) (n=24) | 0.28 (0.03) (n=23) |

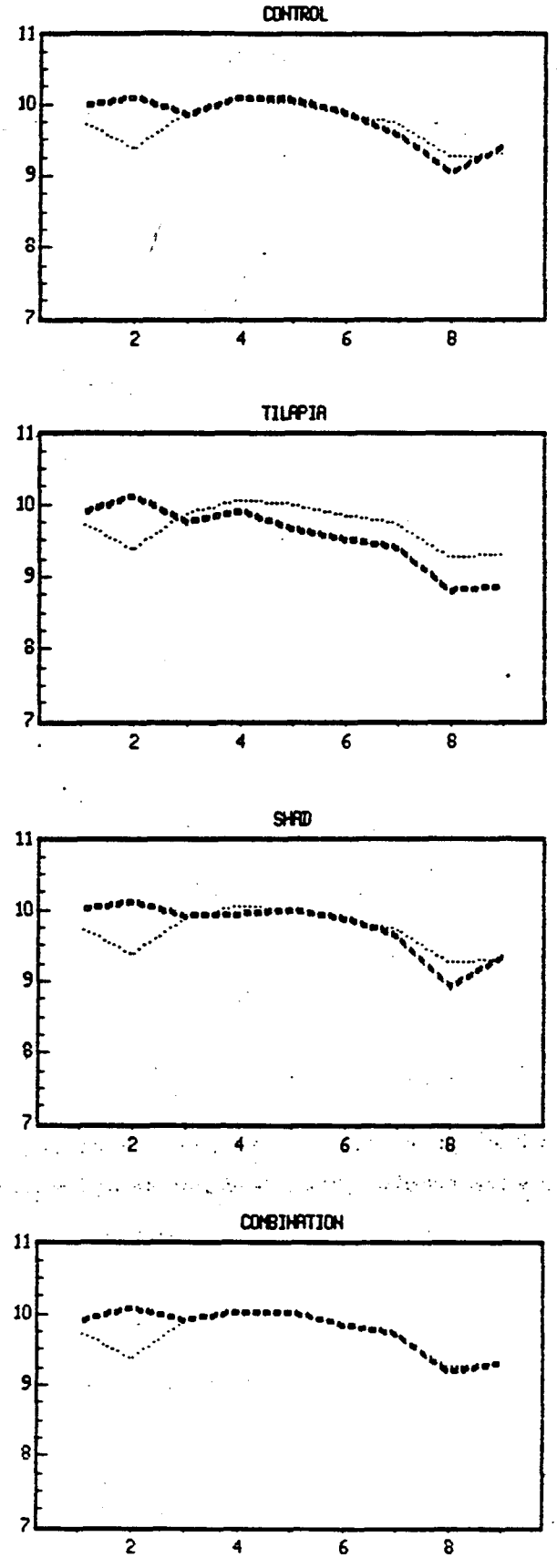



FIGURE 5. Changes in pH in the enclosures by sampling event. Dotted line represents lake values.

lake throughout the study after SE 3. ANOVA indicated that the pH in the tilapia bags was significantly lower than all treatments on SE 6 and 9, and was significantly lower from all treatments except the control on SE 7. The lake pH was significantly lower than all treatments on SE 2.

The mean pH by treatment over the entire study ranged from 9.53 for the tilapia bags to 9.81 for both the control and the combination treatments (Table 2).

Specific Conductance

Conductivity generally increased over the course of the experiment in all treatments (Fig. 6). Conductivity measurements for the lake were usually slightly higher than the mean for the bags. ANOVA indicated that no significant differences existed between bags until the final SE. At that time, the tilapia bags were statistically higher than the other treatments while the combination bags were significantly lower. The difference between tilapia and combination treatments, however, was only appproximately 10%. The fluctuations and trend for increased conductivty, respectively, are likely a reflection of periodic resuspension of sediments in the lake and settled plankton material in the bags due to meterological activity. Qualitative observations on the weather conditions indicated that the wind speed and storm activity progressively increased throughout the experiment. Since the bags were closed to the sediments, it is not unexpected that the conductivity in the lake would be higher due to the reservoir of sediment material.

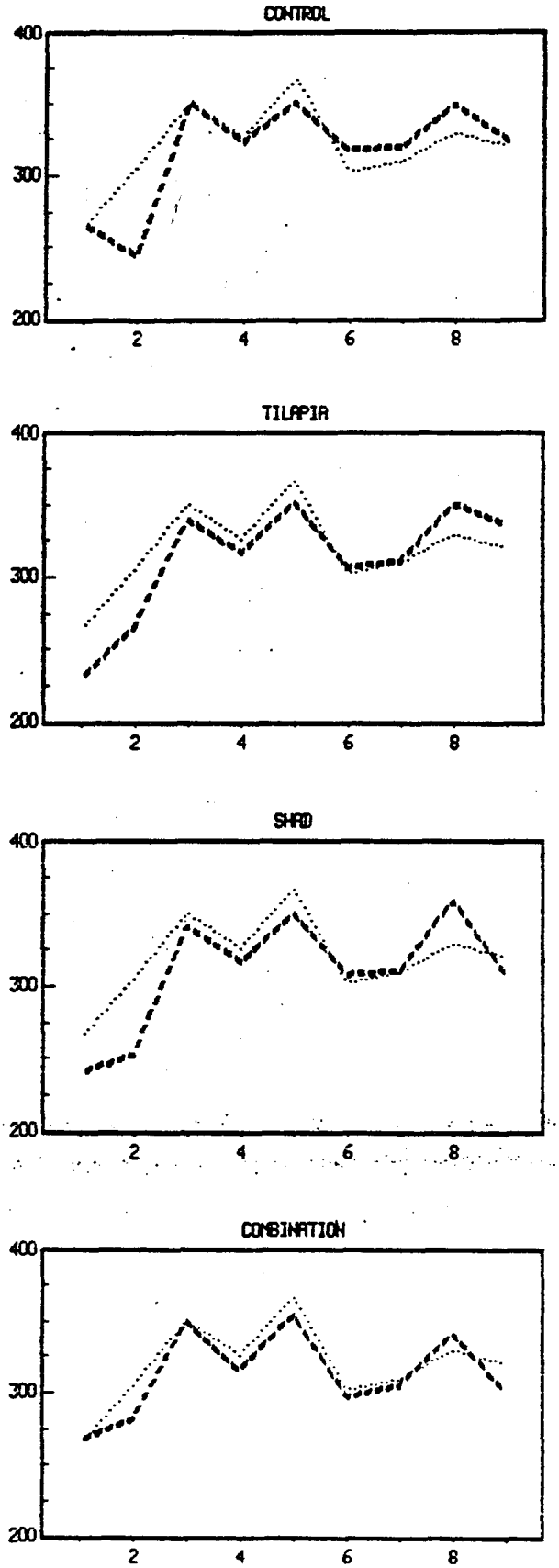



FIGURE 6. Changes in specific conductance (umhos cm$^{2}$) in the enclosures by sampling event. Dotted line represents lake values.

Similar to secchi disk transparency and pH, the mean for conductivity by treatment was within a narrow range of 307 umhos $cm^{-2}$ (shad) to 319 umhos $cm^{-2}$ (lake) (Table 2).

Ortho Phosphorous

Soluble reactive phosphorous (SRP) generally remained very low in the control, tilapia, and combination bags throughout the course of the experiment (Fig. 7). The lake experienced a peak in SRP (1.6 mg $l^{-1}$) on SE 2 and the shad bags frequently displayed elevated levels when contrasted with other treatments.

The only significant differences noted during the study were on SE 2 and 8 when the lake had higher SRP concentrations than the other treatments.

Total Phosphorous

The pattern in total phosphorous concentrations was analagous to that described for SRP. Control, tilapia and combination treatments exhibited relatively constant concentrations of total phosphorous (Fig. 8). The lake experienced a pronounced maxima on SE 2 while the shad bags displayed moderately elevated levels during the middle of the experiment.

The only significant difference in total phosphorus concentrations was on SE 2 when the lake was higher than all other treatments.

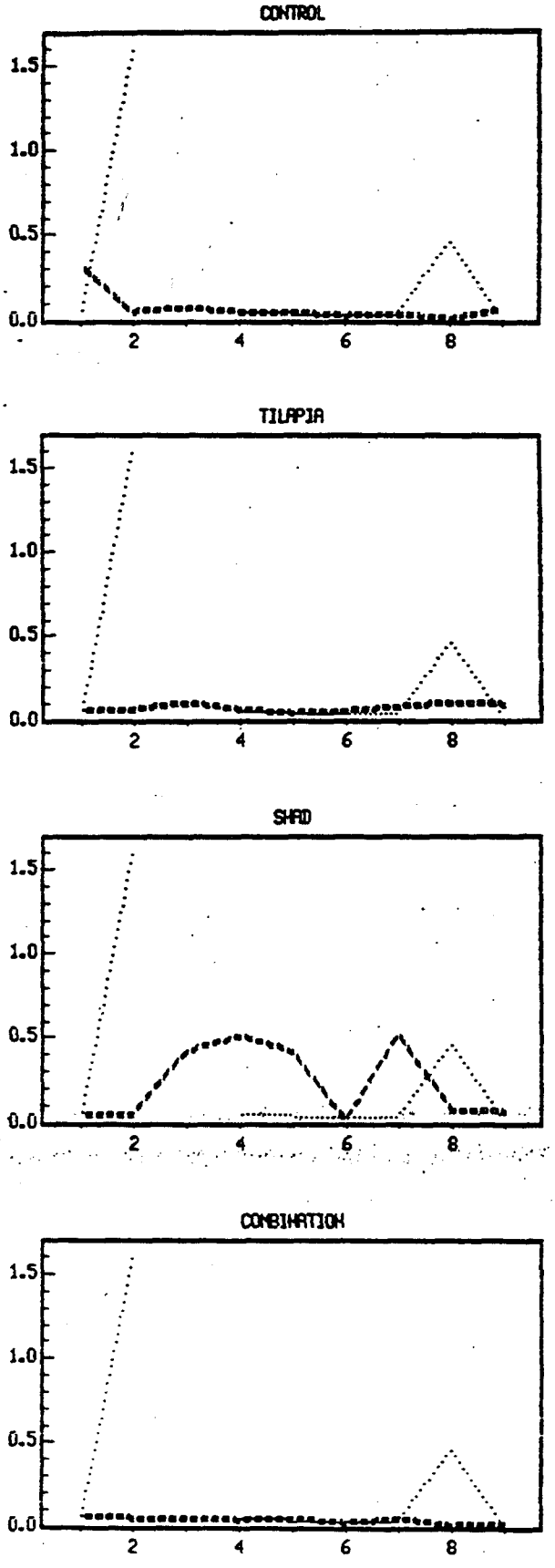



FIGURE 7. Changes in SRP (mg l$^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

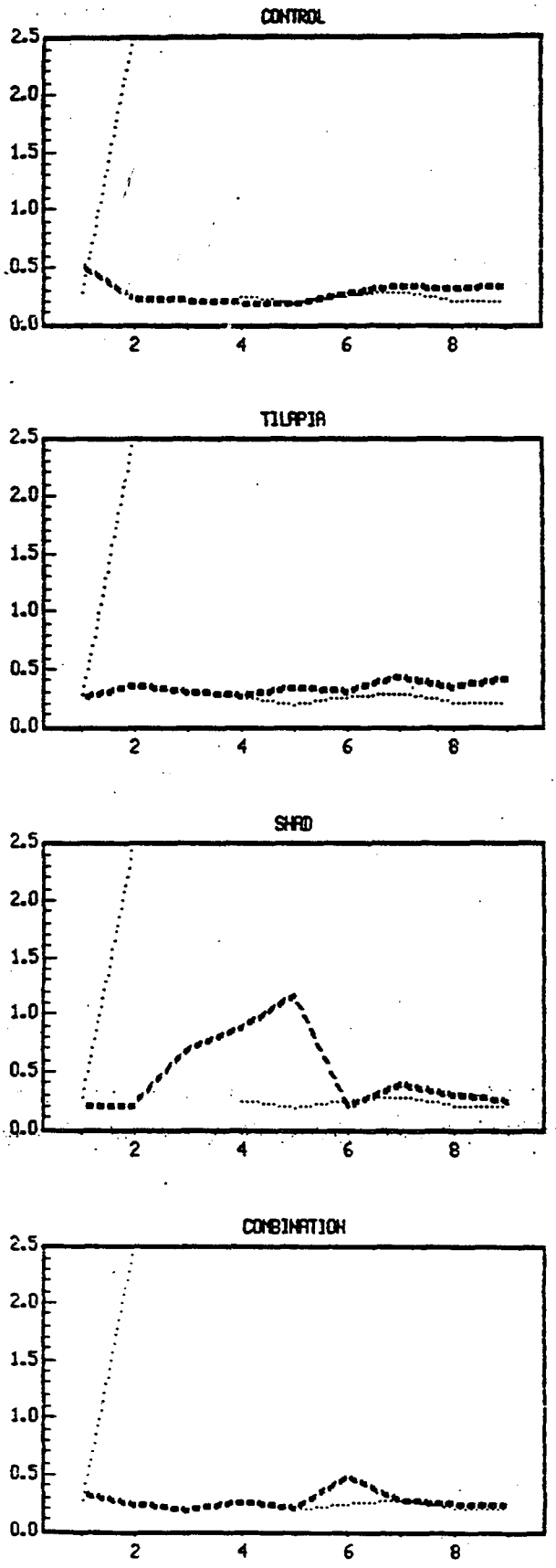



FIGURE 8. Changes in total phosphorous (mg $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

Nitrate

Nitrate nitrogen was always less than 0.01 mg $l^{-1}$ in all treatments.

Ammonia

Concentrations of ammonia exhibited little variation between treatments and were relatively constant throughout the study (Fig. 9). The tilapia treatment did however have a major surge of ammonia on the last sampling event.

The tilapia bags had a significantly higher concentration of ammonia on SE 5, 8, and 9 when compared to the control treatment, and was significantly higher than the shad bags on SE 3 and 8.

Total Kjeldahl Nitrogen

Patterns in total Kjeldahl nitrogen (TKN) were not evident, although there was a general tendency for this chemical component to increase in all treatments, including the lake, throughout the experiment (Fig. 10). TKN concentrations were usually higher in the tilapia treatments but were only significantly different from the shad and control bags on SE 3.

Total Nitrogen

The concentration of total nitrogen paralleled that described for TKN (Fig. 11). Values in the tilapia bags were usually higher than the other treatments, and were significantly different from the shad and control bags on SE 3. The estimate for total nitrogen for the lake station was significantly higher

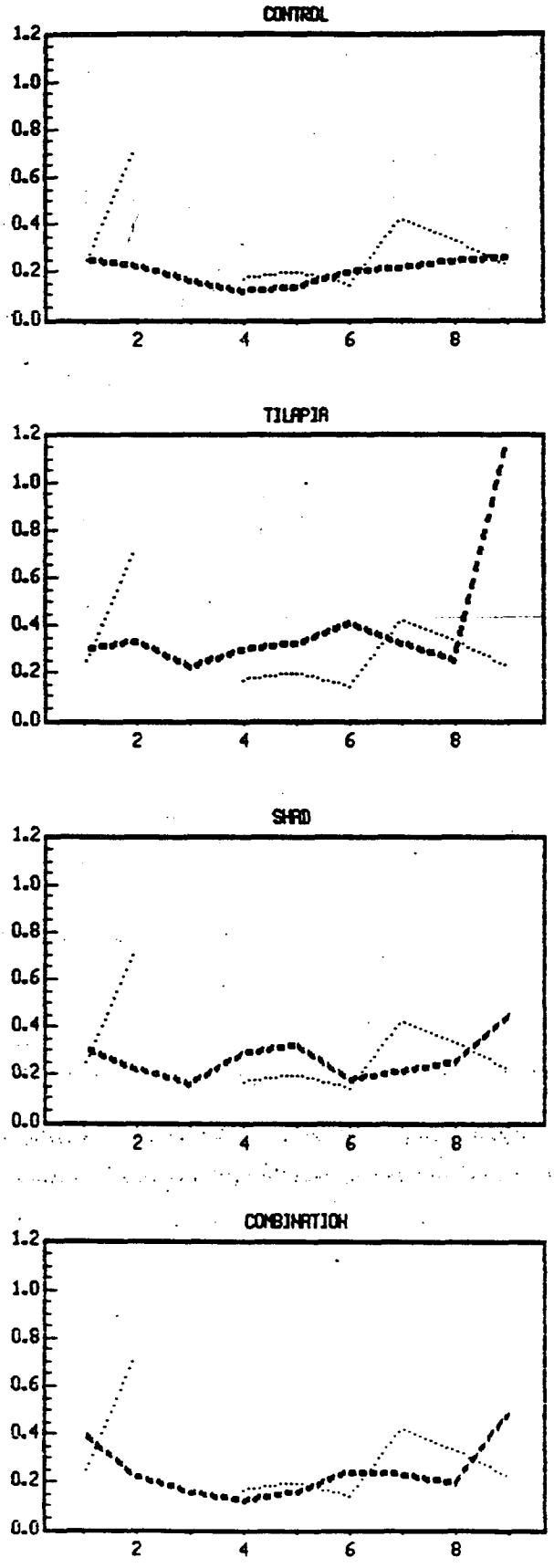



FIGURE 9. Changes in $NH_4^+$ (mg $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

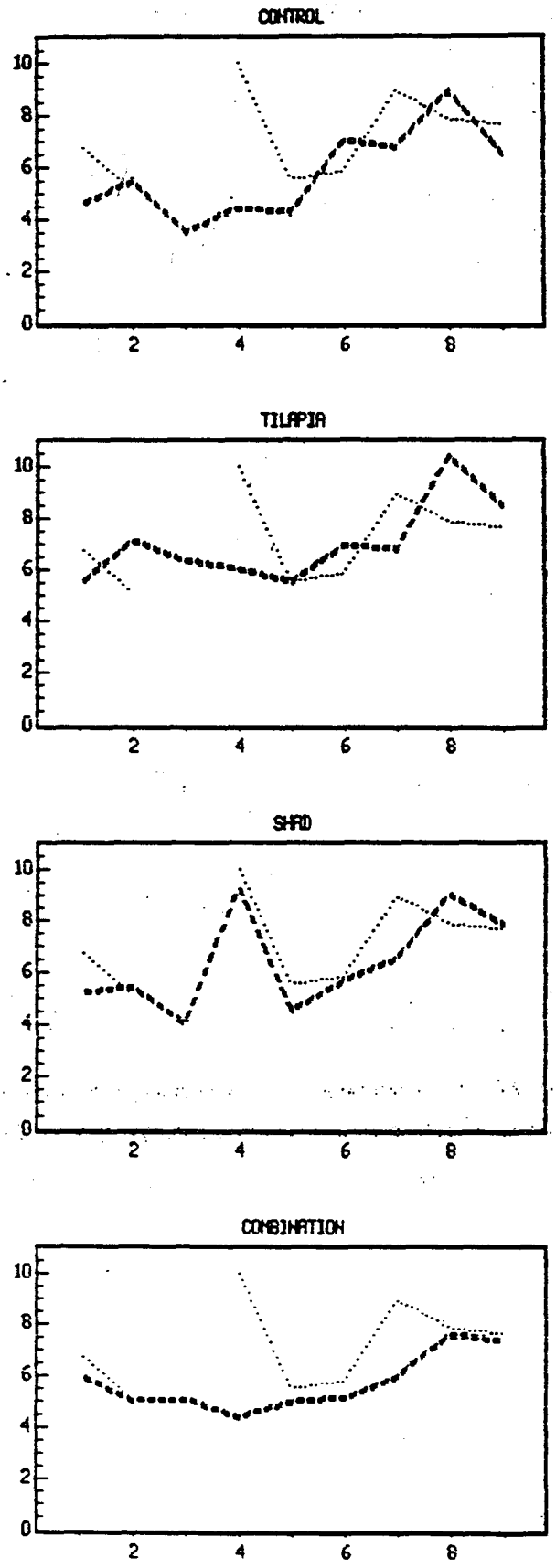



FIGURE 10. Changes in total Kjeldahl nitrogen (mg $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

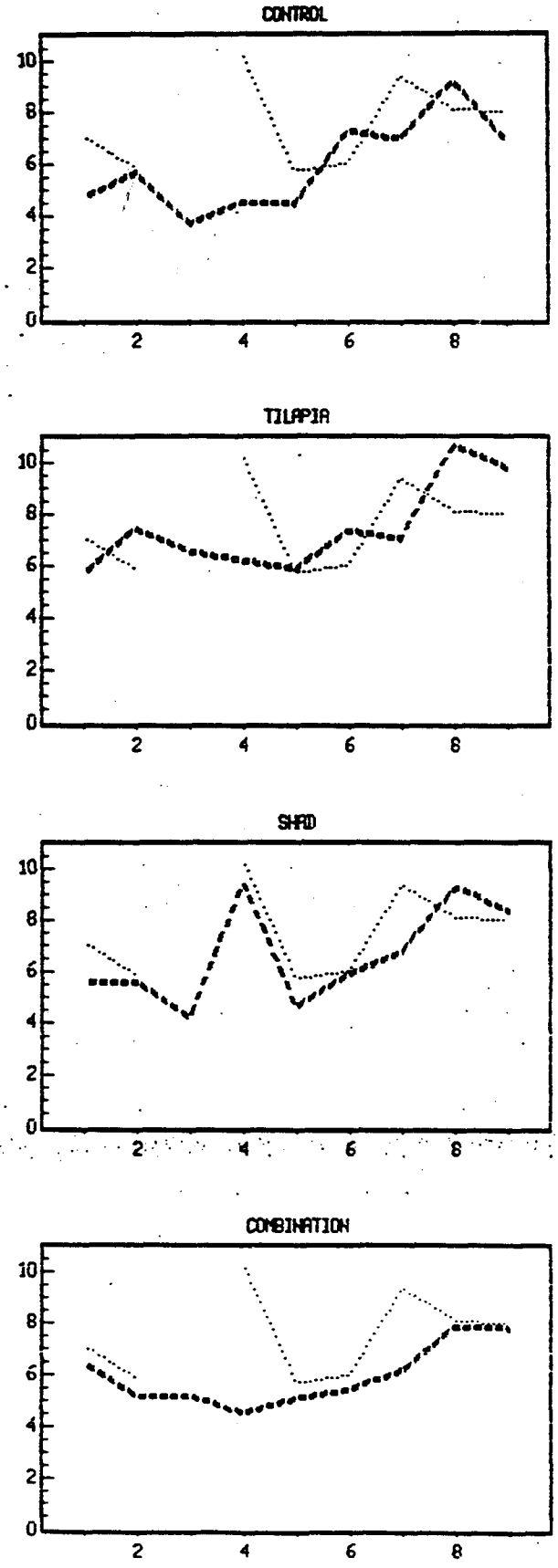



FIGURE 11. Changes in total nitrogen (mg $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

than all bag treatments on SE 7.

Ratio of Total Nitrogen to Phosphorous

The ratio of TN to TP was almost always greater than 20:1 in all treatments and the lake, indicating that through the duration of the experiment the mesocosms were functionally phosphorous limited.

Dissolved Oxygen

Dissolved oxygen will be discussed later in this report under the section on productivity.

## Biomass of Plankton Components

Total Plankton Biomass

Estimates of total plankton biomass were obtained by summing the values for each plankton component. This approximation contains measures for bacteria, phtytoplankton, protozoa, and zooplankton biomasses but does not include the fish component.

Total plankton biomass generally differed little on a temporal basis, although control and tilapia bags appeared to increase towards the end of the experiment (Fig. 12). ANOVA indicated that the tilapia bags had significantly higher measures of total plankton biomass compared to most treatments on SE 2, 3, 4, 5, and 8. Comparable estimates for the lake, shad, and control bags were usually lower when compared to the combination and tilapia bags but were statistically separated from the other treatments only on a few occasions.

On the average, the tilapia bags contained an estimated 32%

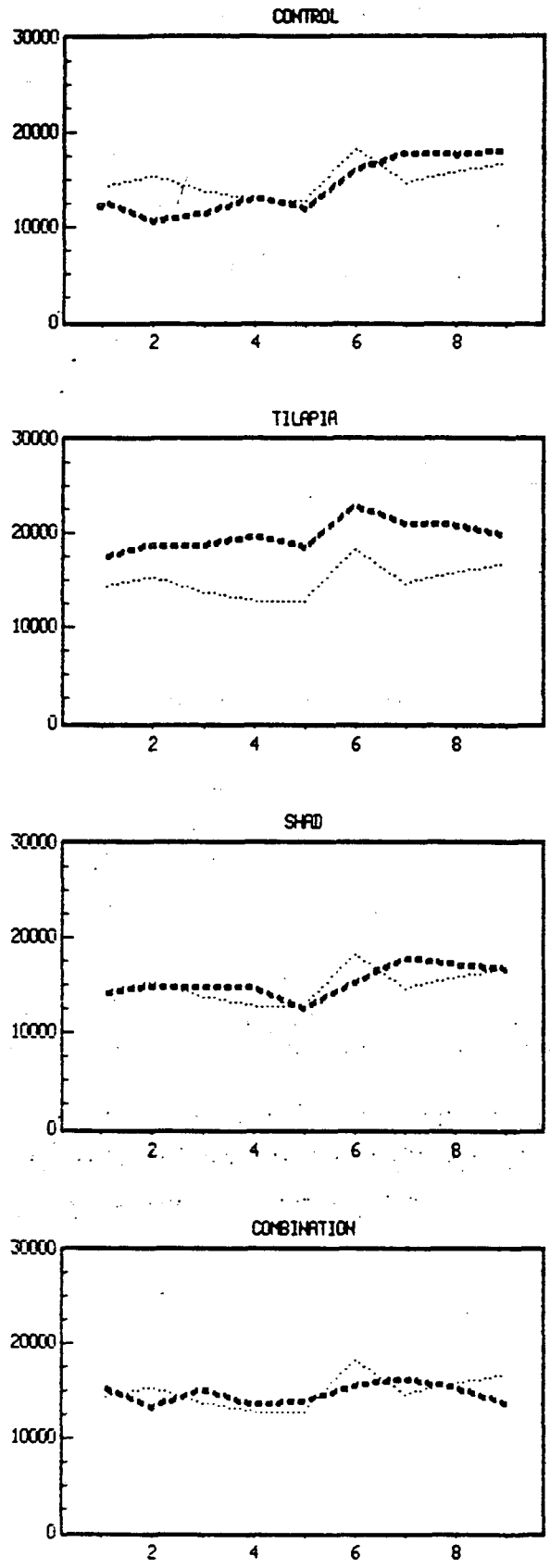



FIGURE 12. Changes in total plankton biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

more plankton biomass than the lake (Table 3).

Total Net Plankton Biomass

Total net plankton biomass was operationally obtained by summing biomass estimates of macrozooplankton, nauplii, rotifers, certain predatory ciliates, and the portion of phytoplankton which did not pass through a 41 um mesh net.

Throughout the duration of the experiment there was a general trend for all treatments to experience an increase in the amount of total net plankton biomass (Fig. 13). The values for the lake fluctuated more and were generally lower than that found in the bags. Total net plankton biomass was greatest in the shad and tilapia on most occasions after SE 2. Statistical separation of the treatments was variable with tilapia bags being significantly higher than the control bags on SE 2 and 4, greater than the combination bags on SE 2, 8, and 9, and more than the lake on SE 4 and 5. Although the values obtained for the shad bags were usually lower than the tilapia bags, the statisitical relationship was identical with the exception of SE when the shad bags were lower.

Tilapia bags had an average of 58% more net plankton biomass than the shad treatment and 81% greater than the lake and control bags (Table 3).

Total Nannoplankton Biomass

Nannoplankton biomass was operationally defined as those biotic components < 41um and included most ciliated protozoa, the

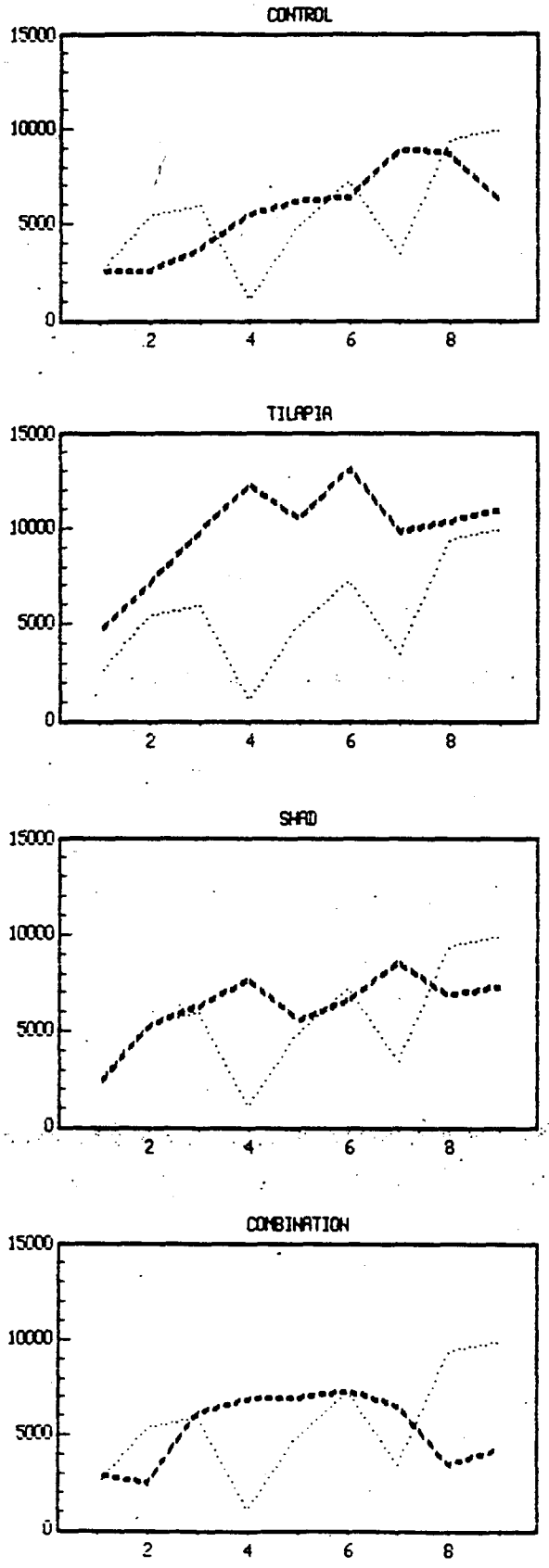



FIGURE 13. Changes in net plankton biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

TABLE 3. Means (±SE) for total, net and nannoplankton plankton biomass in the lake (n=9), control (n=25), tilapia (n=27), shad (n=25), and combination (n=25) treatments. Values in ug d.w./L.

| | TREATMENT | | | | |
|---|---|---|---|---|---|
| | LAKE | CONTROL | TILAPIA | SHAD | COMBINATION |
| Total Plankton | 14800 (600) | 14000 (600) | 19600 (700) | 15100 (500) | 14600 (400) |
| Net Plankton | 5400 (1000) | 5400 (600) | 9800 (700) | 6200 (500) | 5300 (500) |
| Nannoplankton | 9300 (700) | 8600 (400) | 9800 (400) | 8900 (400) | 9300 (400) |

chlorophyll fraction < 41um, and bacteria.

In contrast to the total net plankton biomass, total nannoplankton biomass exhibited little variation during the study (Fig. 14). However the percentage contribution of total nannoplankton biomass to total plankton biomass progressively decreased as the amount of total net plankton biomass rose. Total nannoplankton biomass moderately decreased from SE 1 and then rose slightly towards the end of the experiment in the bags. In the lake total nannoplankton biomass was frequently higher than all other treatments between SE 3 and 7. Little statistical patterns were evident from ANOVA with the tilapia bags being significantly higher than the control treatments on SE 2, the lake being higher than all treatments on SE 3, and the combination bags lower than all treatments except shad on SE 6. In addition, the lake was significantly lower than all treatments but the control on SE 8 and the control bags were significantly higher than the lake on the final sample and the combination bags were significantly lower than the lake on SE 6.

When expressed as an average for the study period, it is clear that little difference exists between treatments and the amount of nannoplankton biomass (Table 3).

Bacterial Concentrations

The biomass of bacteria in all treatments displayed minimal fluctuation during the course of the experiment (Fig. 15). Bacterial concentrations were highest on the initial sampling,

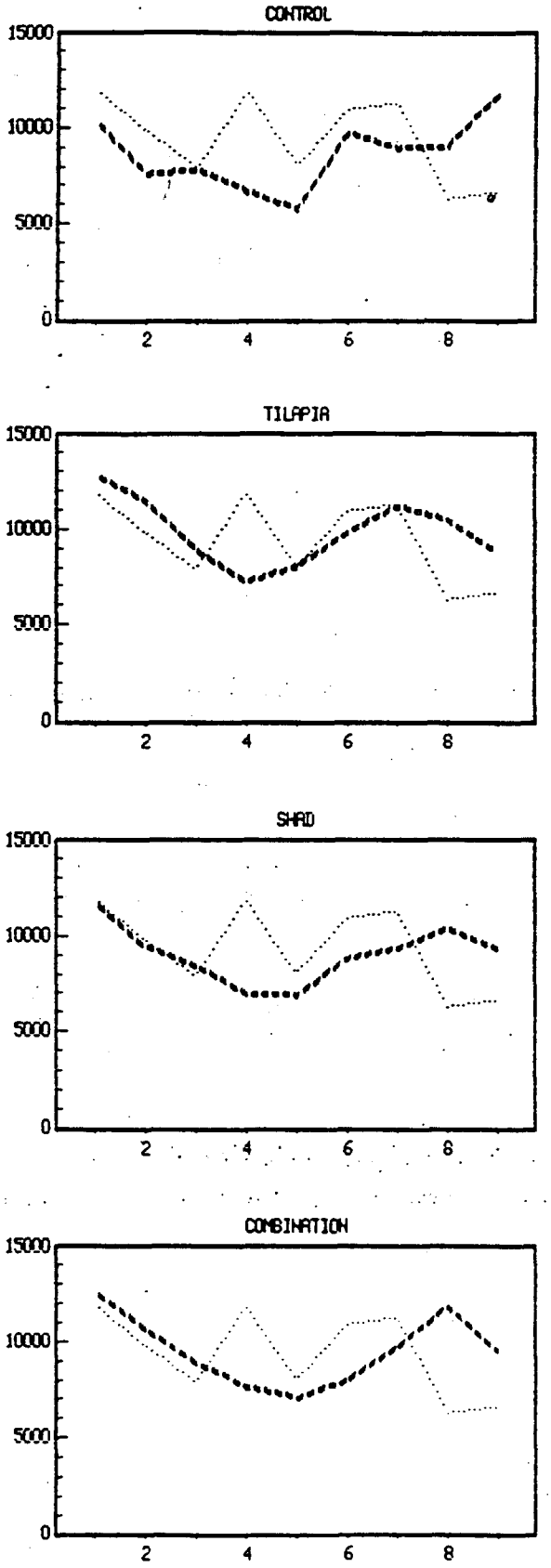



FIGURE 14. Changes in nannoplankton biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

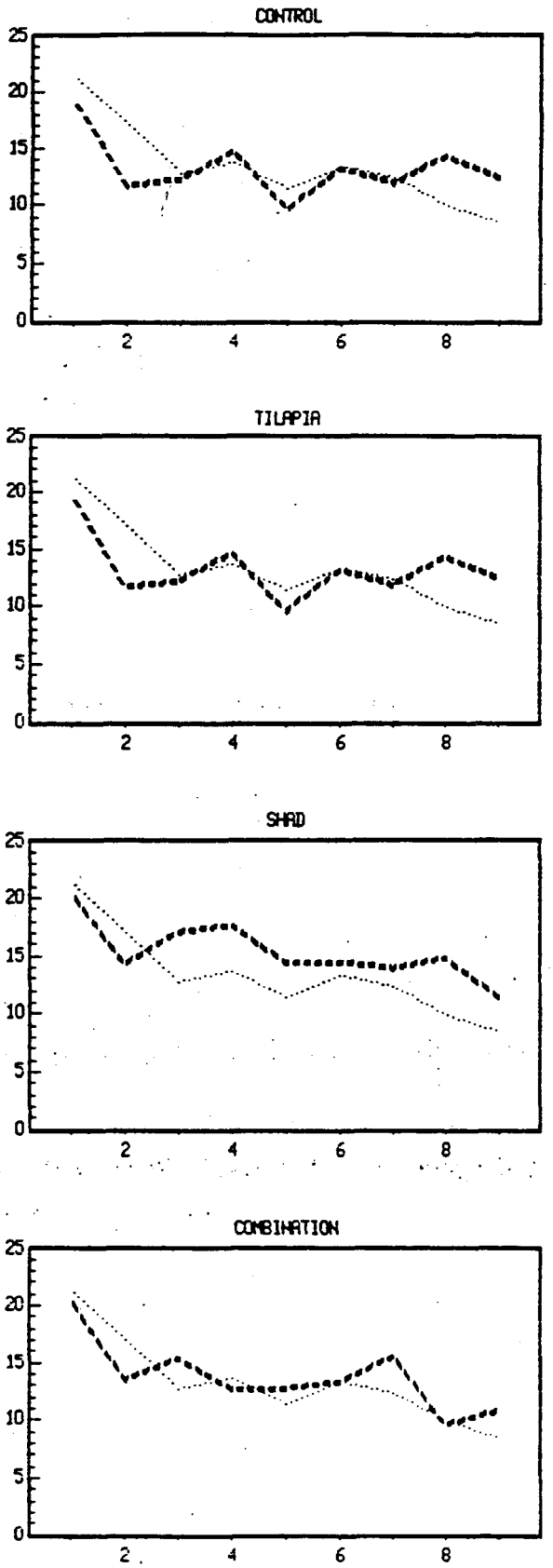



FIGURE 15. Changes in bacterial abundance ($10^6$ cells $ml^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

and then declined and stabilized. The only statistical differences between bags were on SE 5 when the control treatment was less than the tilapia bags. The shad and tilapia bags did appear to maintain slightly higher bacterial populations than the other treatments, both on a temporal and mean basis (Table 4).

Total Chlorophyll

Whole chlorophyll a values showed a progressive increase during the experiment (Fig. 16). The patterns for all bags and the lake appeared to be quite similar with a moderate pulse in chlorophyll concentrations occurring at SE 6. Values for total chlorophyll were generally higher in the tilapia bags. ANOVA indicated that tilapia bags had a significantly higher chlorophyll value than the control treatment on SE 2 and 4 and higher chlorophyll concentrations than shad bags on SE 6. The combination treatment was statistically lower than tilapia, lake, and shad on SE 2.

Lake, shad, and combination treatments all averaged approximately 160 mg $m^{-3}$ of chlorophyll a while the control and tilapia bags had means of 148 mg $m^{-3}$ and 190 mg $m^{-3}$, respectively Table 4).

Net Chlorophyll

There was a general tendency for net plankton chlorophyll a to increase from the initial sample (Fig. 17). All treatments displayed this pattern although the lake fluctuated more widely between sampling events. The tilapia treatments attained higher absolute net plankton chlorophyll concentrations than the other

TABLE 4. Mean values (±SE) for chlorophyll *a* fractions (mg/m$^3$) and bacteria densities (1,000,000 cells/ml) for the lake (n=9), control (n=25), tilapia (n=27), shad (n=25), and combination (n=25) treatments.

| | TREATMENT | | | | |
|---|---|---|---|---|---|
| | LAKE | CONTROL | TILAPIA | SHAD | COMBINATION |
| Total chlorophyll | 163 (9) | 148 (9) | 190 (6) | 161 (7) | 160 (5) |
| Net chlorophyll | 68 (14) | 63 (8) | 97 (7) | 78 (8) | 67 (7) |
| Nanno chlorophyll | 95 (9) | 85 (6) | 93 (6) | 83 (5) | 93 (6) |
| Bacteria | 13.36 (1.32) | 13.13 (0.72) | 16.78 (0.62) | 15.48 (0.81) | 14.07 (0.69) |

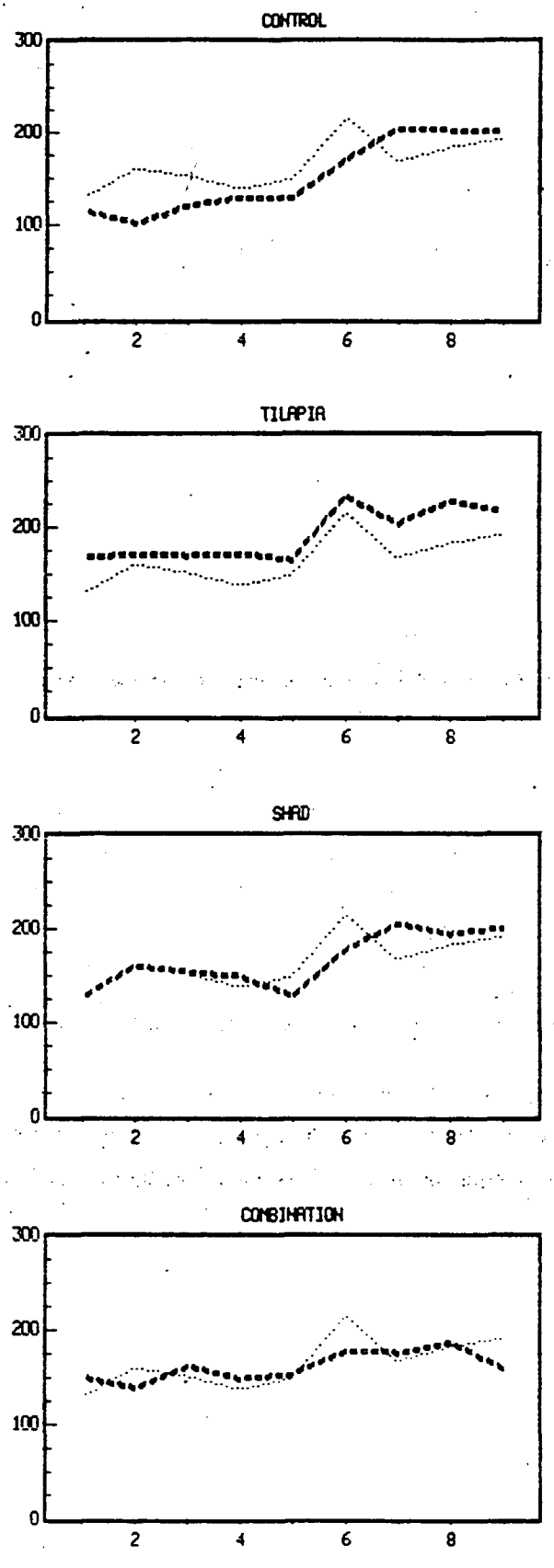



FIGURE 16. Changes in total chlorophyll *a* (ug $l^{-1}$) concentrations in the enclosures by sampling event. Dotted line represents lake values.

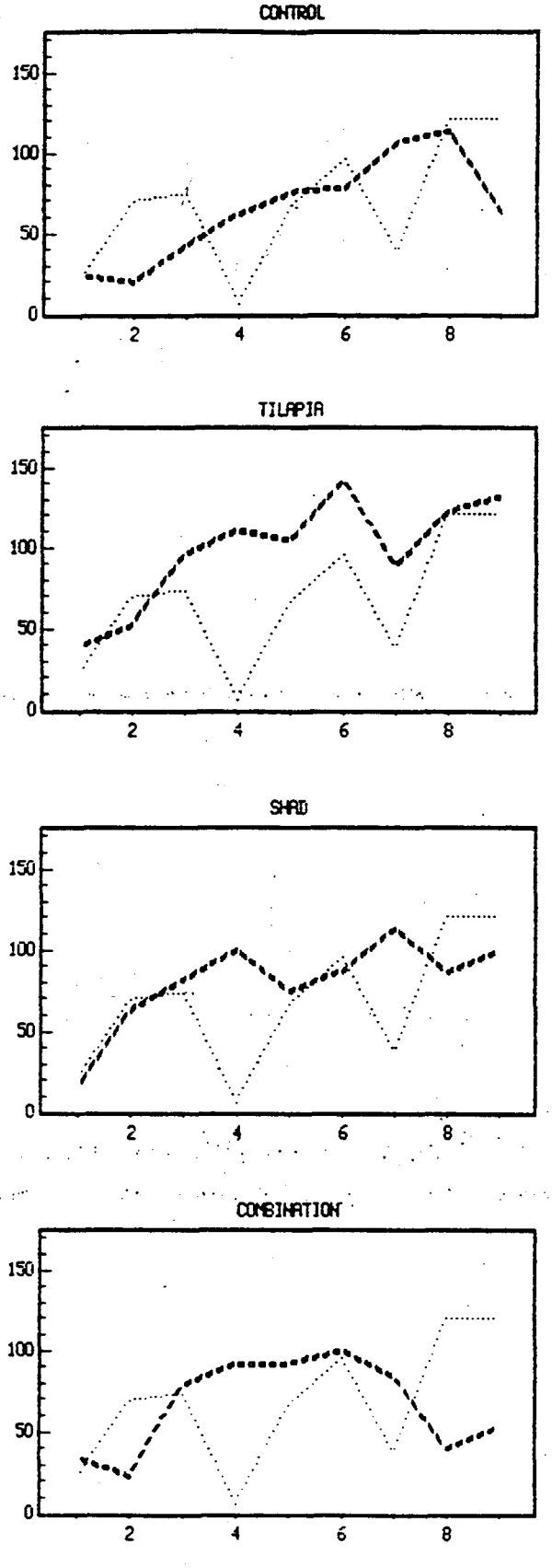



FIGURE 17. Changes in net plankton chlorophyll a (ug $l^{-1}$) concentrations in the enclosures by sampling event. Dotted line represents lake values.

treatments and also showed a more rapid increase. On SE 4 the concentration of net plankton chlorophyll a in the lake was significantly lower than all other treatments and tilapia values were significantly higher than concentrations in the control bags. Statistical separation was also detected on SE 8 and 9 with tilapia, lake, and control treatments being significantly higher than the combination bags on SE 8 while tilapia and lake values were significantly higher than those observed in the control and combination treatments.

Tilapia bags had an average of 24% greater net plankton chlorophyll a than the shad bags (Table 4).

Nannoplankton Chlorophyll

Nannoplankton chlorophyll a exhibited an opposite pattern to that described for net plankton chlorophyll (Fig. 18). All bag treatments experienced relatively rapid declines in the amount of nannoplankton chlorophyll a from SE 2 and then increased at SE 6. In contrast, the nannoplankton fraction in the lake appeared to fluctuate inverse to that seen in the bag treatments. ANOVA indicated that lake concentrations of nannoplankton chlorophyll a were significantly higher than the bag treatments on SE 4, and higher than shad and combination bags on SE 6. Nannoplankton chlorophyll concentrations in the lake precipitously declined after SE 7, and the values for the lake and control bags were significantly lower than the combination treatment at that time.

Expressed on an average by treatment basis, there was minimal difference between the lake and any bag grouping (Table 4).

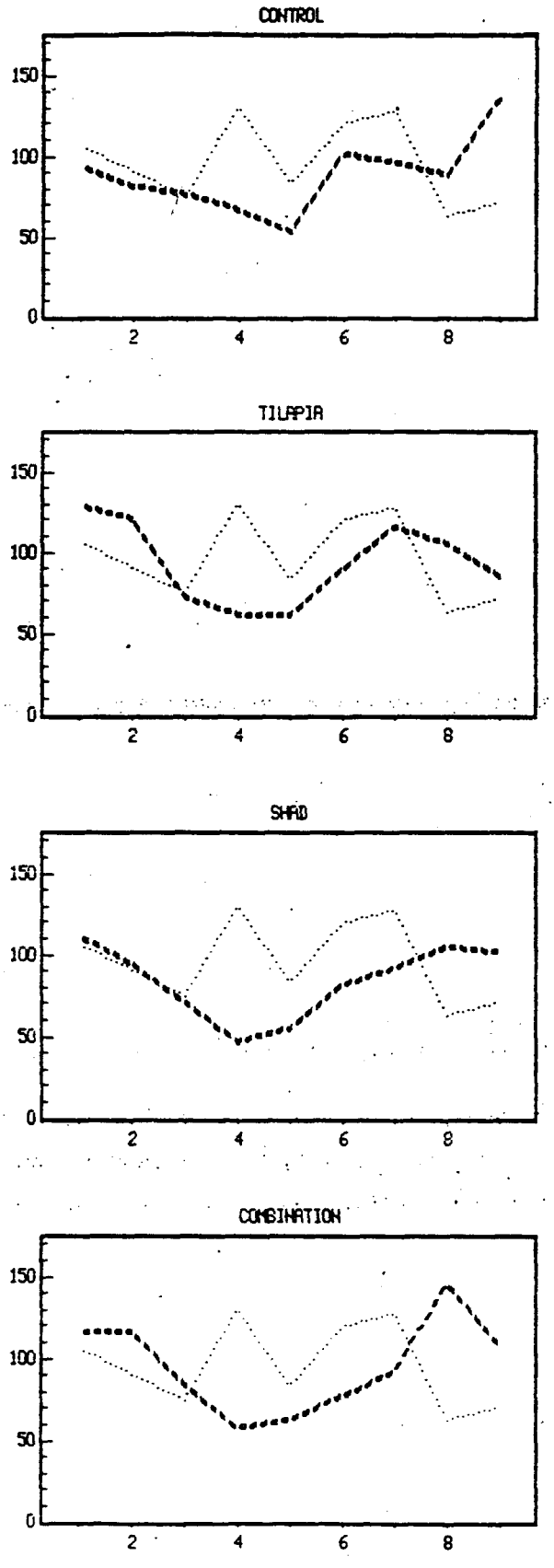



FIGURE 18. Changes in nannnoplankton chlorophyll a (ug $l^{-1}$) concentrations in the enclosures by sampling event. Dotted line represents lake values.

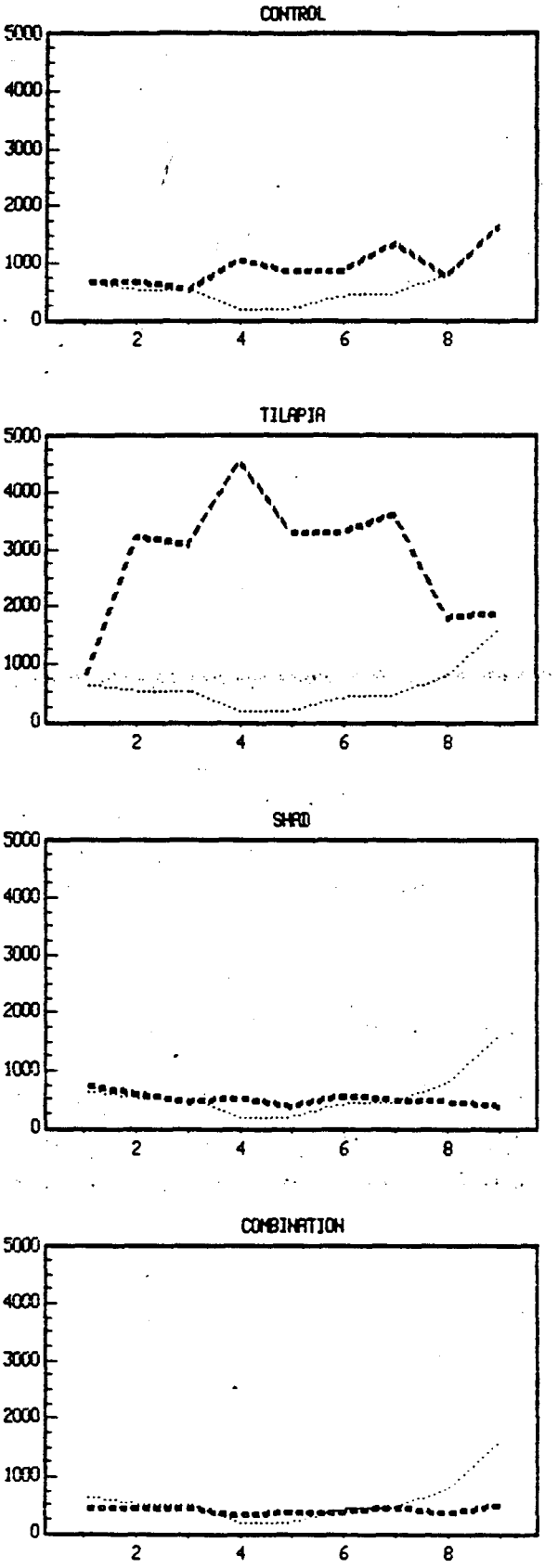



FIGURE 19. Changes in total zooplankton biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

TABLE 5. Means (±SE) for major zooplankton components for the lake (n=9), control (n=25), tilapia (n=27), shad (n=25), and combination (n=25) treatments. Values in ug d.w./L.

| | TREATMENT | | | | |
|---|---|---|---|---|---|
| | LAKE | CONTROL | TILAPIA | SHAD | COMBINATION |
| Total zooplankton | 1075 (128) | 1360 (144) | 3303 (416) | 1060 (64) | 901 (52) |
| Macrozooplankton | 570 (141) | 884 (146) | 2932 (420) | 503 (50) | 389 (41) |
| Microzooplankton | 505 (33) | 476 (25) | 371 (24) | 557 (34) | 512 (27) |
| Cladocerans | 293 (83) | 674 (144) | 2653 (427) | 283 (41) | 274 (40) |
| Calanoids | 242 (79) | 192 (49) | 252 (39) | 198 (45) | 105 (26) |
| Cyclopoids | 35 (17) | 18 (6) | 27 (11) | 22 (7) | 10 (4) |
| Nauplii | 87 (11) | 107 (11) | 105 (10) | 97 (18) | 93 (8) |
| Rotifers | 216 (28) | 252 (17) | 181 (16) | 247 (16) | 270 (18) |
| Total Ciliates | 202 (16) | 117 (13) | 85 (8) | 213 (26) | 149 (18) |
| Scuticociliates | 15 (3) | 15 (2) | 8 (1) | 21 (2) | 22 (3) |
| Oligotrichs | 75 (21) | 42 (6) | 38 (5) | 55 (5) | 48 (6) |
| Grazer protozoa | 147 (15) | 90 (11) | 76 (6) | 162 (21) | 115 (13) |

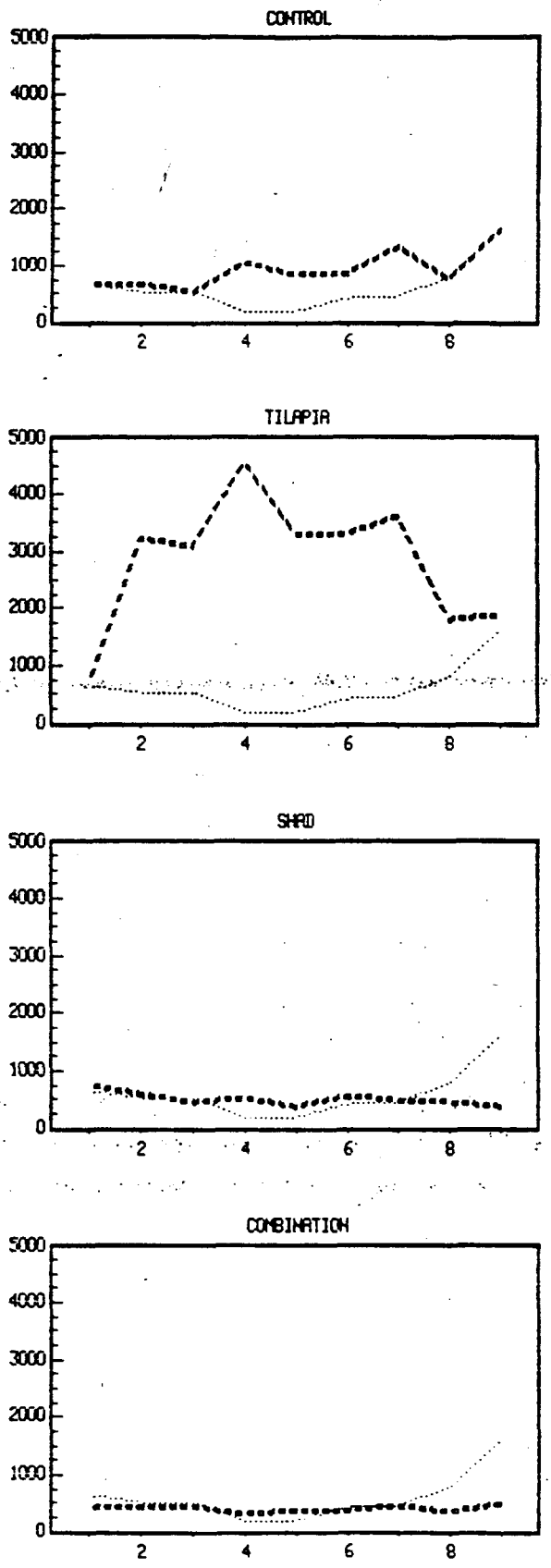



FIGURE 20. Changes in macrozooplankton biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

Total Zooplankton Biomass

Total zooplankton biomass displayed relatively little variation over the course of the study with the exception of the tilapia treatment (Fig. 19). The total zooplankton biomass in the tilapia bags increased very early in the experiment and maintained strikingly elevated levels compared to the other treatments until SE 8 and 9. Despite the apparent difference between the tilapia bags and the other treatments, ANOVA indicated that they were significantly higher than all other treatments only on SE 2, 3, 5. As will be discussed below, the major zooplankton component contributing to the elevated zooplankton populations in the tilapia bags was cladocerans.

With an overall mean of 3303 ug d.w. l-1, the total zooplankton biomass was 143% higher in the tilapia treatment than the control and 212% more than the shad bags (Table 5).

Macrozooplankton Biomass

The trend described above for total zooplankton biomass is essentially the same as that for macrozooplankton (Fig. 20). Tilapia bags contained much higher macrozooplankton biomass when compared to the other treatments. This is largely a reflection of the substantial contribution of cladocerans to macrozooplankton biomass (Table 5). The control treatment also demonstrated slightly higher macrozooplankton biomass compared to the lake, shad, and combination treatments. As observed in the total zooplankton biomass, the only statistical difference

demonstrated between treatments was between tilapia bags on SE 2, 3, and 5.

Microzooplanton Biomass

Microzooplankton biomass exhibited relatively little variation within or between treatments over the course of the experiment (Fig. 21). It does appear that the tilapia bags contained slightly less microzooplankton biomass than the other treatments. In 6 of the 9 sampling events, microzooplankton biomass in the tilapia bags averaged less than all other treatments . ANOVA indicated the only statistical difference occurred on SE 5 with the combination bags having significantly higher microzooplankton biomass than the mean for the tilapia treatment.

The averages by treatment ranged from 371 ug d.w. $l^{-1}$ to 557 ug d.w. $l^{-1}$, respectively, for tilapia and shad treatments (Table 5).

Cladoceran Biomass

The patterns described above for the differences between treatments in total zooplankton and macrozooplankton biomass was similar to that found for the temporal variation in cladoceran biomass (Fig. 22). Tilapia bags displayed trememdously higher cladoceran biomass and the control treatment had slightly more cladoceran biomass when contrasted with the remaining treatments. Despite the obvious difference between tilapia treatments and

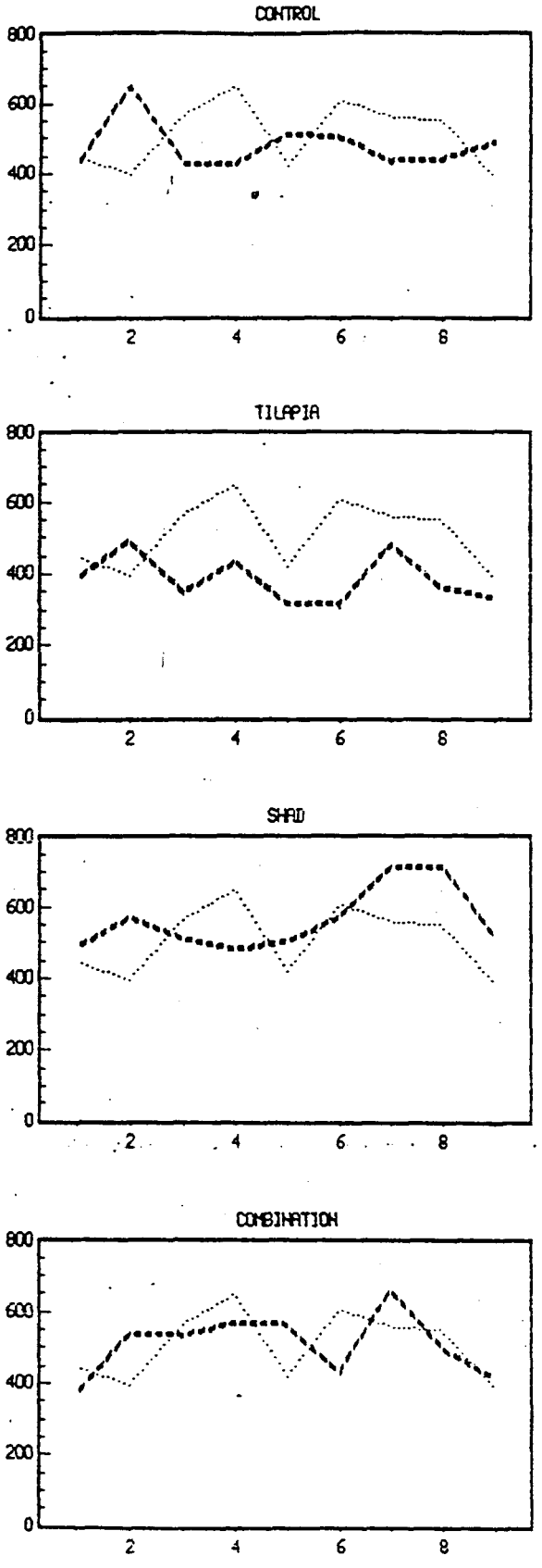



FIGURE 21. Changes in microzooplankton biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

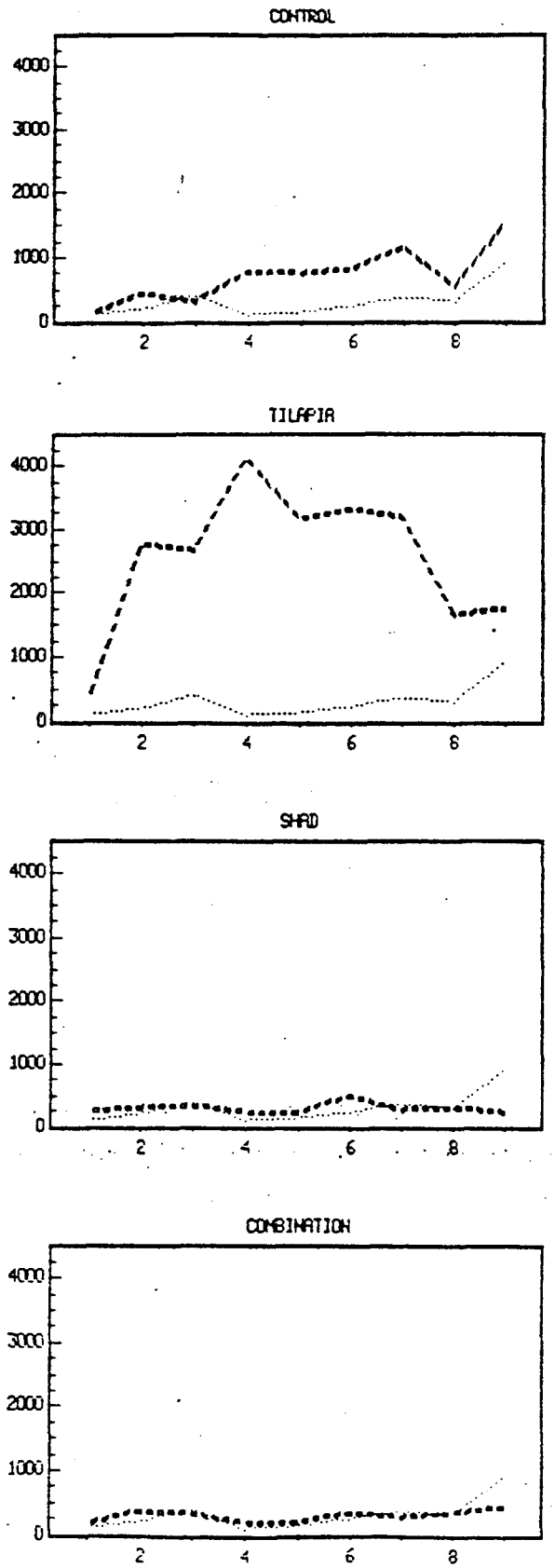



FIGURE 22. Changes in cladoceran biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

other bags, the only statistically significant difference was found on SE 5.

Tilapia bags had a mean cladoceran biomass 294% higher than the control treatment and an astounding 837% greater than the shad bags (Table 5).

All cladoceran species displayed elevated populations in the tilapia bags when compared to other treatments. However the cladoceran species distribution on a given sampling event did show wide variation within the tilapia bags. The species involved in these biomass surges were Eubosmina tubicen, Ceriodaphnia reticulata, Chydorus sphaericus, Daphnia ambigua, Diaphanasoma brachyrum, and Alona sp.

Calanoid Copepod Biomass

Calanoid copepod biomass showed declines early in the experiment period in all bag treatments except for tilapia which had a delayed decline and rapid return (Fig. 23). The calanoid biomass in the lake also declined early in the study but increased rapidly after SE 7. ANOVA indicated that lake values were significantly higher than all treatments on SE 6 and 9 while being significantly higher than combination bags on SE 8. The only calanoid copepod found during the study was Diaptomus dorsalis.

The overall averages for calanoid biomass were close with the exception of the combination treatment which had somewhat more depressed densities of this taxonomic group (Table 5).

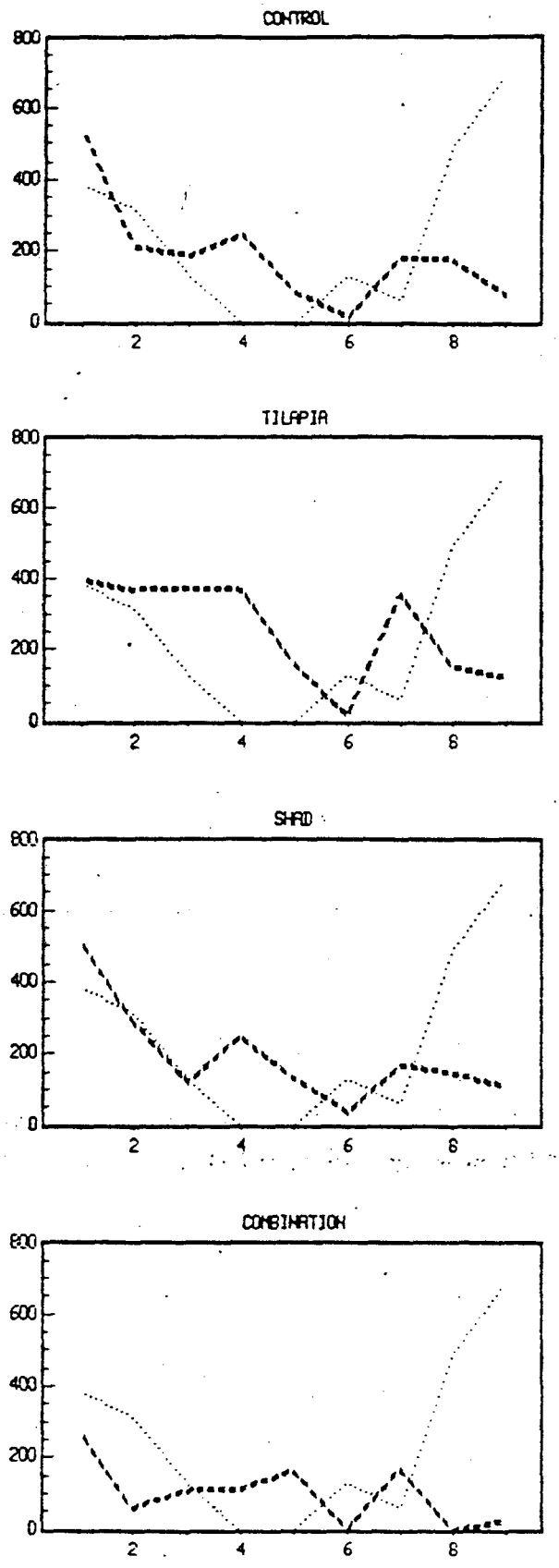



FIGURE 23. Changes in calanoid copepod biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

Cyclopoid Copepod Biomass

Cyclopoid copepods were relatively uncommon during this study, but Cyclops vernalis dominated the cyclopoid biomass at all times. There was comparatively little difference in the amount of cyclopoid biomass between treatments, however the lake experienced much higher cyclopoid biomass on SE 1 and moderately higher biomass during the middle of the experiment (Fig. 24). Other than SE 1 when cyclopoid biomass in the lake was higher than the bags, no significant differences were noted between treatments.

Nauplii Biomass

Patterns in nauplii biomass displayed considerable variation between and within treatments (Fig. 25). In general, the bag treatments experienced modest increases in nauplii abundance on SE 2 and then declined by SE 8. The shad bags showed a substantial nauplii peak on SE 8. Significant differences were noted on SE 2 when control, tilapia and shad bags were significantly higher than the lake, and on SE 6 when the shad treatment displayed significantly less nauplii biomass than the combination, control, and lake bags.

On the average, nauplii biomass varied little between treatments with all values found between 87 ug d.w. $l^{-1}$ (lake) and 107 ug d.w. $l^{-1}$ (control) (Table 5).

Rotifer Biomass

Rotifer biomass did not differ appreciably between bag

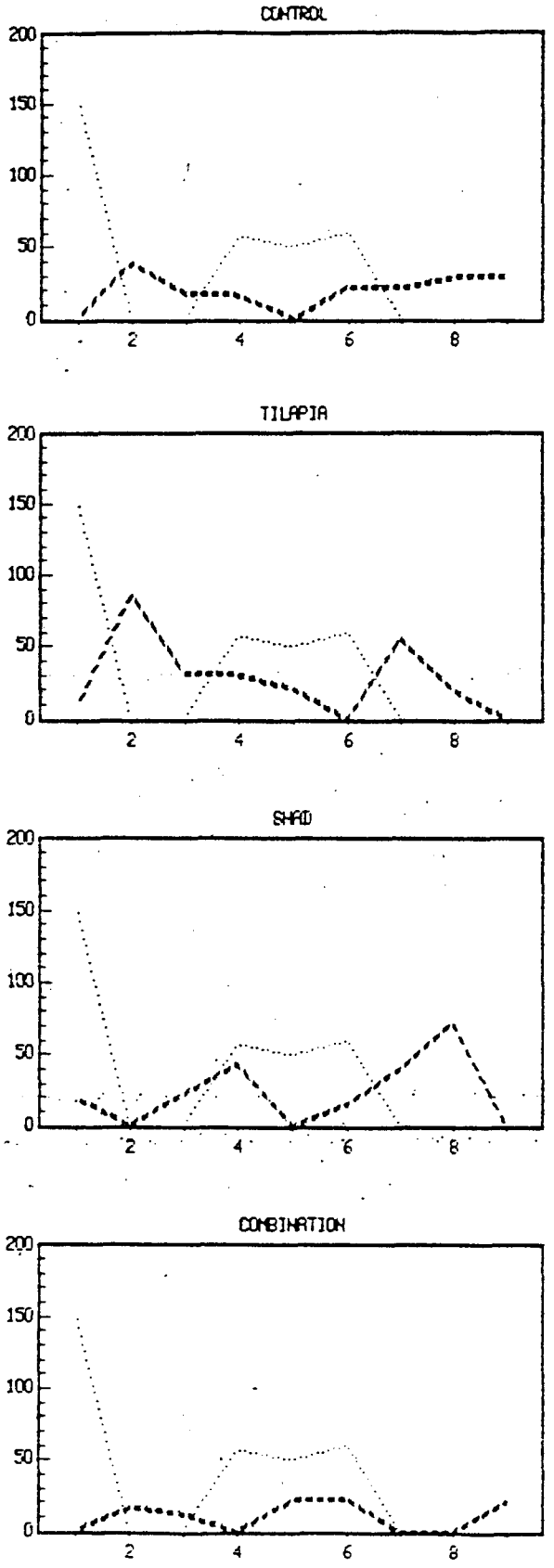



FIGURE 24. Changes in cyclopoid copepod biomass (ug d.w $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

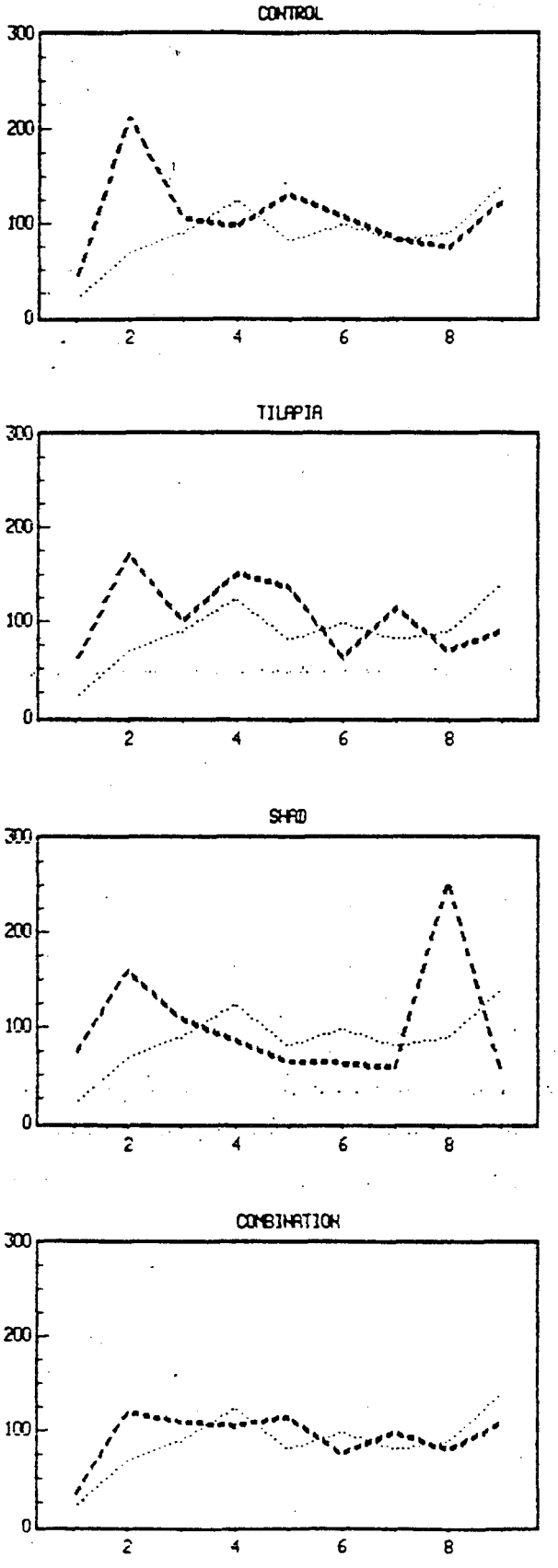



FIGURE 25. Changes in nauplii biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

treatments and usually ranged from 200 to 300 ug $l^{-1}$ (Fig. 26). Lake values oscillated more than the bag treatments and displayed two maxima on SE 3 and 7. ANOVA indicated that no significant differences existed between the treatments and the lake at any time. Rotifer communities of all bags were numerically dominated by Keratella cochlearis, and on a biomass basis Monostyla lunaris was the largest contributor to rotifer biomass.

Total Ciliate Biomass

Several differences were apparent between treatments and total ciliate biomass (Fig. 27). The total ciliate biomass found in the lake was much higher on SE 1 when compared to the bags. Control and tilapia bags had consistently lower total ciliate biomass when contrasted with values for the lake. Total ciliate biomass in the combination bags generally agreed with the values for the lake but the shad bags displayed an increase in total ciliate biomass relative to the lake from SE 5 to 7. Total ciliate biomass was significantly higher in the lake than all the bag treatments on SE 1 and from tilapia treatments on SE 2 and 4. The total ciliate biomass in the shad treatments were statisitically higher the tilapia and the control bags on SE 7.

Scuticociliate Ciliates

Scuticociliates displayed a general increase over most the experiment and decline towards the end (Fig. 28). Biomass

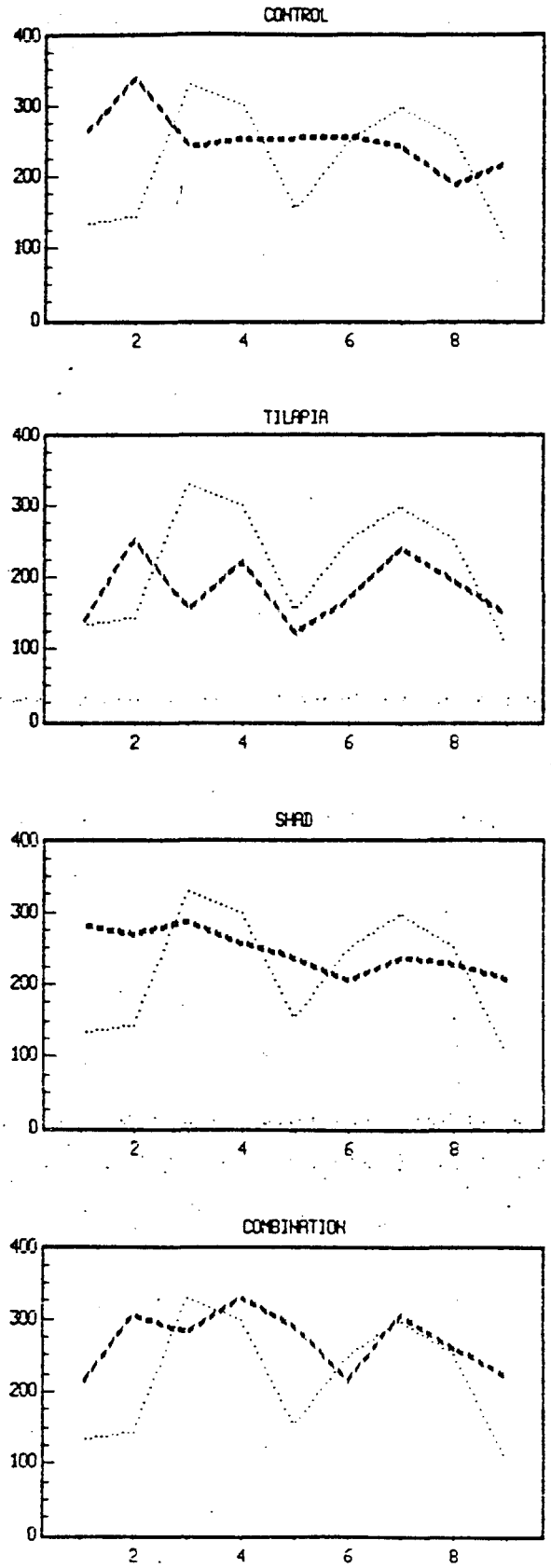



FIGURE 26. Changes in rotifer biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

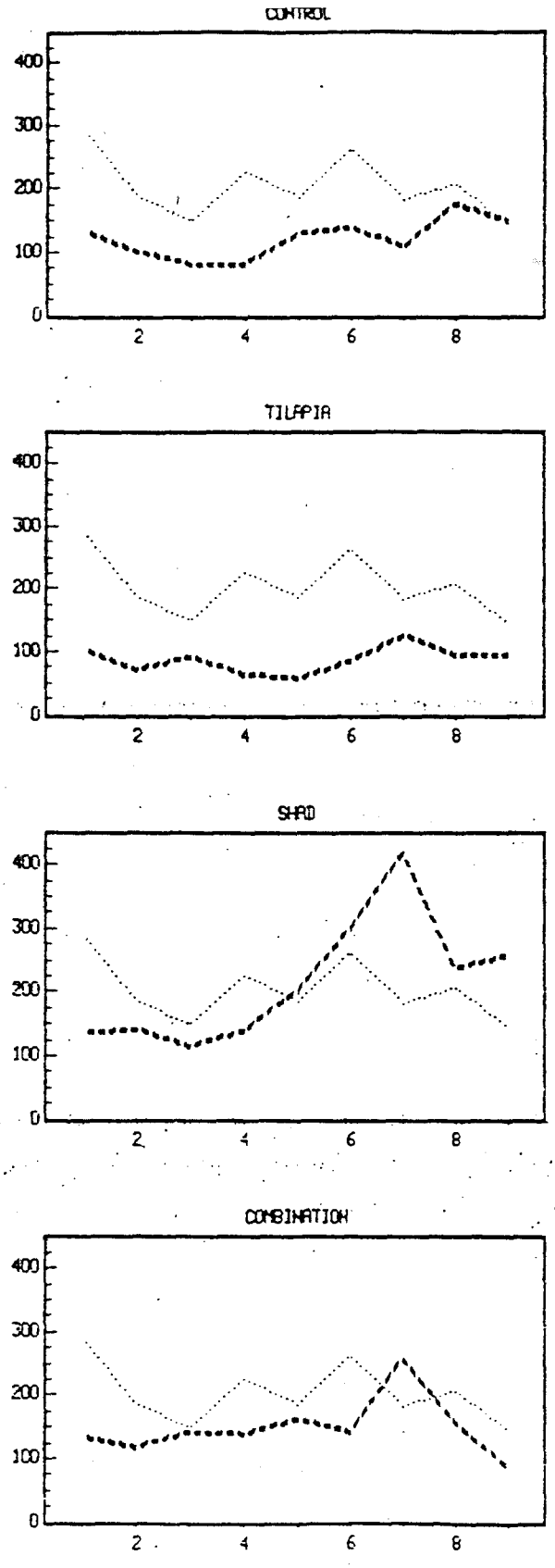



FIGURE 27. Changes in total ciliate biomass (ug d.w. l ) in the enclosures by sampling event. Dotted line represents lake values.

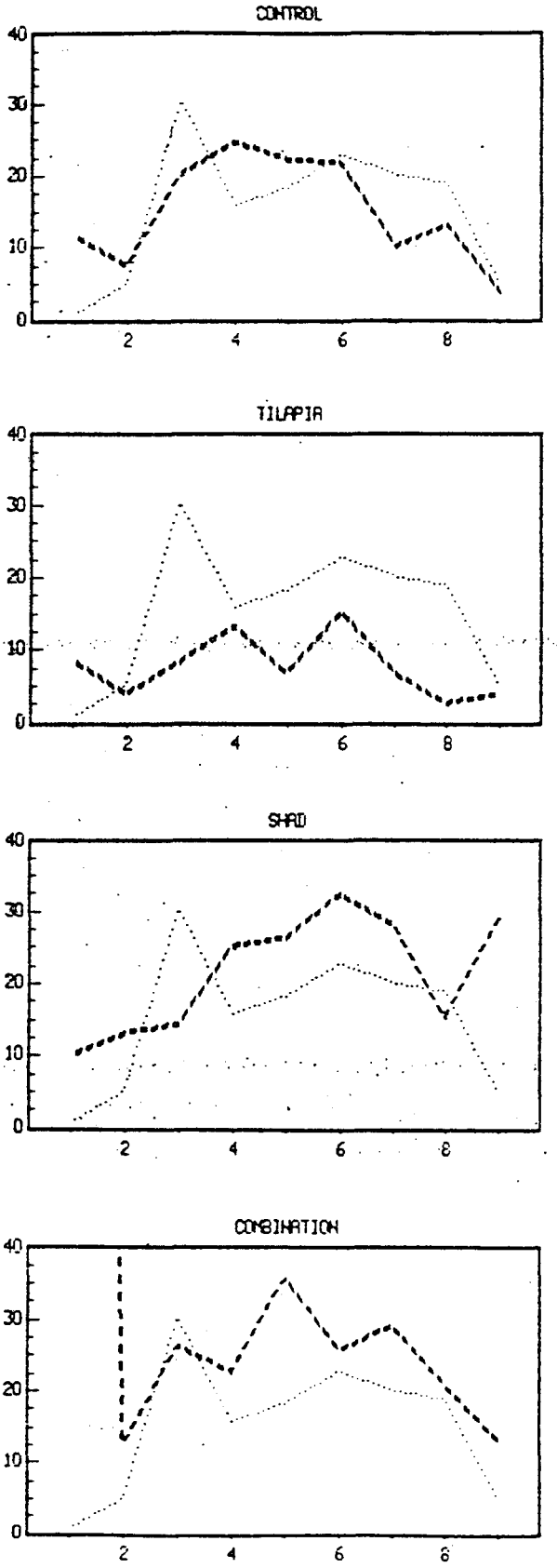



FIGURE 28. Changes in scuticociliate biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

estimates in the shad and combination bags were usually higher than the lake while the tilapia treatments were lower. Combination and shad bags had significantly higher scuticociliate biomass on SE 7 when compared to the control and tilapia treatments. On SE 8 the tilapia bags were significantly lower than the lake and control bags, and on SE 9 the scuticociliate biomass was significantly higher in the shad treatment when contrasted with all others. The dominant scuticociliate species found in the study was Cyclidium glaucoma which is ubiquitously distributed in Florida lakes (Beaver and Crisman 1988).

Oligotrich Ciliates

Oligotrich ciliates displayed little variation within or between treatments with the exception of the biomass estimates for the lake (Fig. 29). The estimates for oligotrich biomass in the lake showed a tendency to decline throughout most of the study, and ANOVA indicated that the lake was significantly higher than all the bag treatments on SE 1, 3, and 4 and greater than all treatments except shad on SE 2. On SE 6 the lake was significantly lower than the combination and shad treatments. The principal oligotrich in all treatments was Strobilidium humile, a relatively small bodied (< 25 um) species whose increased abundance is strongly related to trophic state in Florida lakes (Beaver and Crisman 1988).

Grazer Ciliates

Grazer ciliate biomass was determined by subtracting the biomass of predatory ciliates from total ciliate biomass. This

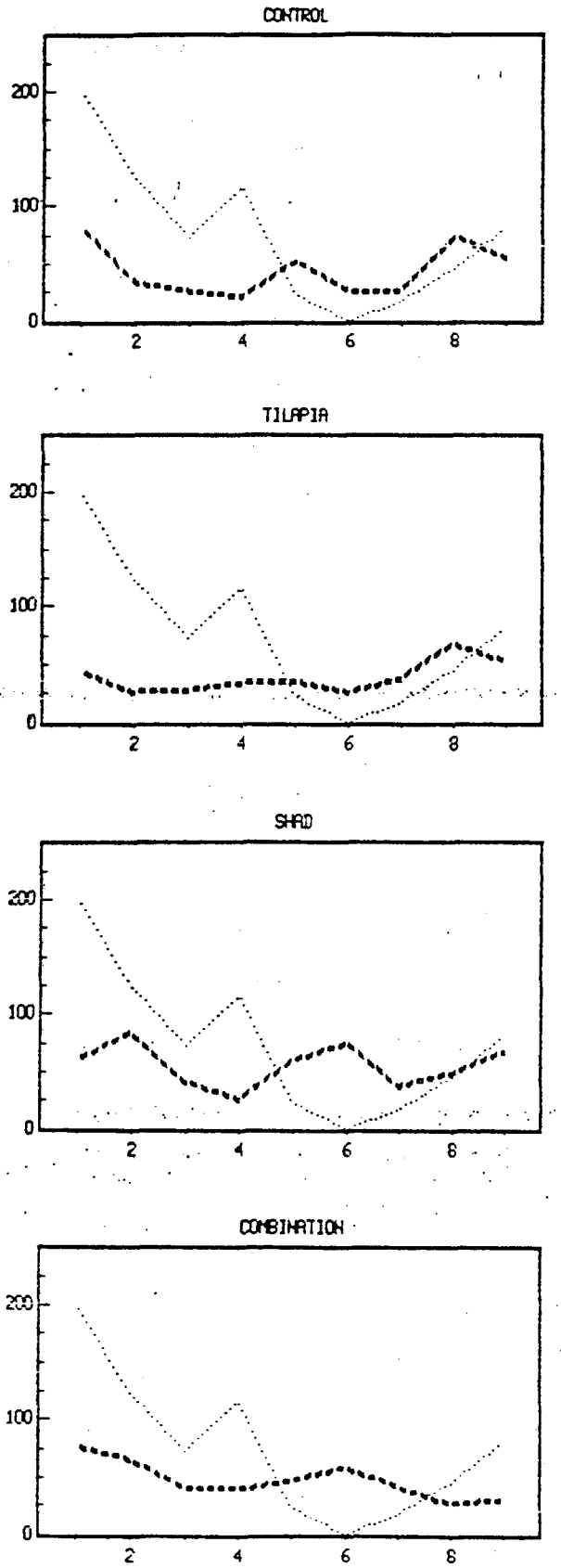



FIGURE 29. Changes in oligotrich biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

distinction was made due to the large difference in size between grazer and predator species, and thus more accurately reflects those protozoa involved in bacterial and nannnoplankton consumption. The principle predatory ciliate found during the study was Litonotus fasciola which has been characterized as an indicator of high productivity in Florida lakes (Beaver and Crisman 1988).

The most apparent trend in temporal changes in grazer ciliate biomass is the large maxima displayed by the shad treatments and the relatively low biomass encountered in tilapia and to a lesser extent the control bags (Fig. 30). As seen for oligotrich biomass, the lake exhibited a major maximum at the outset of the experiment. Significant differences were detected between the lake and all bags on SE 1 while the lake was significantly higher than the tilapia and control bags on SE 2. On SE 7 and 9 the shad treatment had significantly higher grazer ciliate biomass than the control and combination treatments, respectively.

Grazer protozoa averaged higher densities in the shad and tilapia bags when contrasted with the remaining treatments (Table 5).

Percentage Distribution of Macrozooplankton and Microzooplankton Biomass

Partitioning total zooplankton biomass into macrozooplankton (> 200um) and microzooplankton (<200 um) reveals that the tilapia treatment rapidly went to a macrozooplankton dominated system

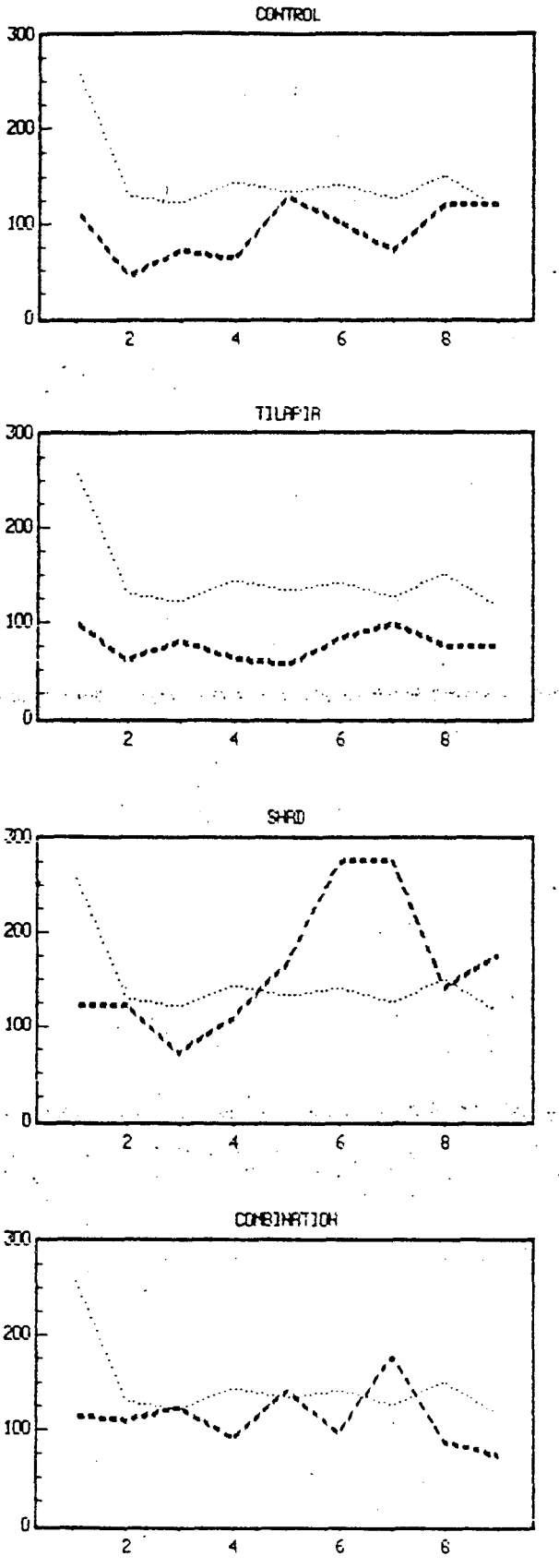



FIGURE 30. Changes in grazer ciliate biomass (ug d.w. $l^{-1}$) in the enclosures by sampling event. Dotted line represents lake values.

(Fig. 31). This shift to dominance by macrozooplankton was due to substantially elevated densities of all cladoceran species and persisted throughout the course of the study. After SE 1, the proportion of macrozooplankton in the tilapia bags was always > 75%.

The control bags exhibited a similar trend to the tilapia treatments, however the magnitude was less with the communities in those bags being composed of approximately equal portions of macrozooplankton and microzooplankton. From SE 7 to 9, however, the macrozooplankton proportion to increased to near 75%.

The percentage distribution of macrozooplanton to microzooplankton in the lake changed from an approximately equal partioning of biomass in the initial samples, to dominance by microzooplankton in the middle followed by an increase in the percentage of macrozooplankton at the end.

Shad treatments displayed little change over the course of the study with biomass being distributed roughly equally between the two major zooplankton size classes, although there was a trend towards a slightly greater percentage of microzoooplankton near the end of the experimental period.

The combination bags also did not change substantiallly during the study, however they did contain a lower percentage of macrozooplankton than either the shad or control treatments.

There is close agreement among lake, control, shad and combination treatments as to the mean percentage distribution of most major zooplankton taxonomic groups and size classifications.

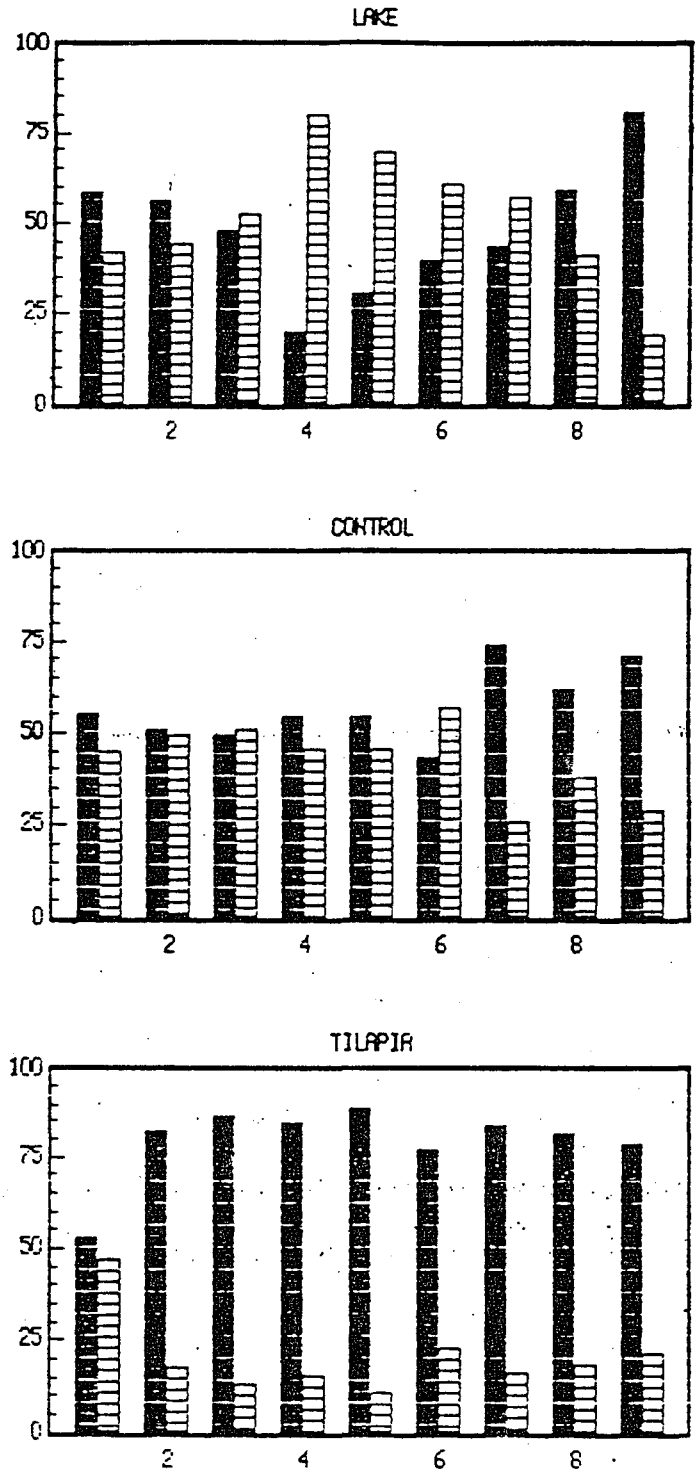



FIGURE 31. Changes in the percentage distribution of macrozooplankton (solid) and microzooplankton (open) in the enclosures by sampling event.

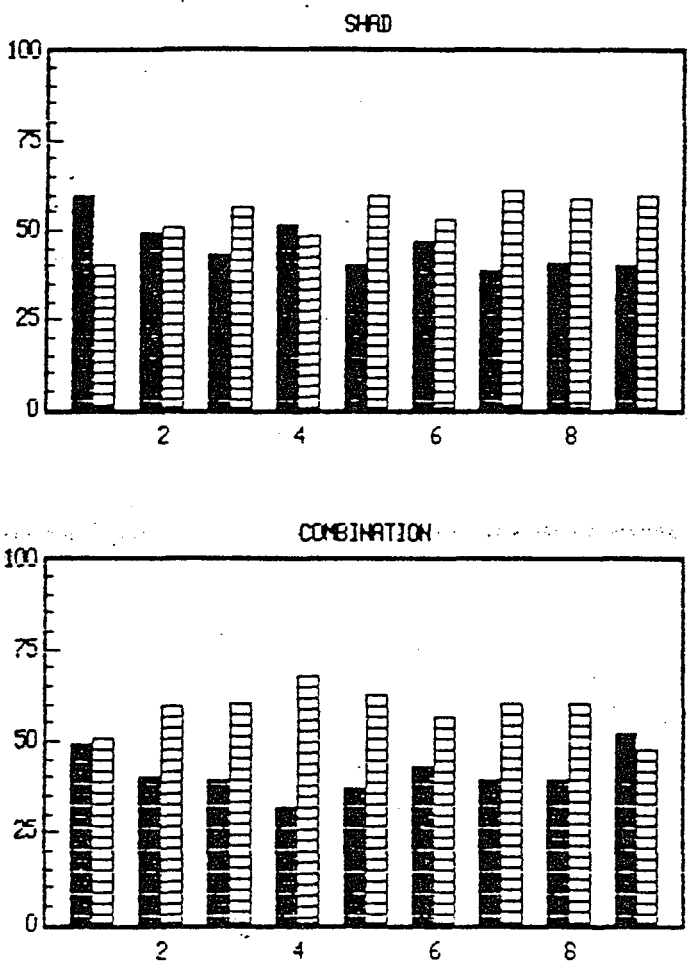



FIGURE 31. (continued).

TABLE 6. Mean percentage distribution (±SE) of major zooplankton components in the lake (n=9), control (n=25), tilapia (n=27), shad (n=25), and combination (n=25) treatments.

| | TREATMENT | | | | |
|---|---|---|---|---|---|
| | LAKE | CONTROL | TILAPIA | SHAD | COMBINATION |
| Macrozooplankton | 48.2 (5.9) | 56.5 (4.3) | 83.1 (2.5) | 46.0 (2.5) | 41.1 (3.1) |
| Microzooplankton | 51.8 (5.9) | 43.5 (4.3) | 16.9 (2.5) | 54.0 (2.5) | 58.9 (3.1) |
| Cladocerans | 24.9 (4.1) | 39.8 (5.0) | 70.9 (4.2) | 26.1 (2.8) | 28.8 (3.3) |
| Calanoids | 19.3 (5.4) | 15.4 (3.1) | 11.1 (2.2) | 17.7 (3.0) | 11.1 (2.6) |
| Cyclopoids | 4.0 (1.8) | 1.3 (0.5) | 1.1 (0.5) | 2.2 (0.7) | 1.1 (0.5) |
| Nauplii | 8.7 (1.3) | 9.4 (1.1) | 4.3 (0.6) | 9.1 (1.3) | 10.6 (0.9) |
| Rotifers | 22.3 (3.4) | 22.4 (2.3) | 8.4 (1.5) | 24.2 (1.6) | 30.3 (1.5) |
| Total ciliates | 20.9 (2.6) | 11.7 (2.1) | 4.2 (0.8) | 20.7 (2.4) | 18.0 (2.4) |

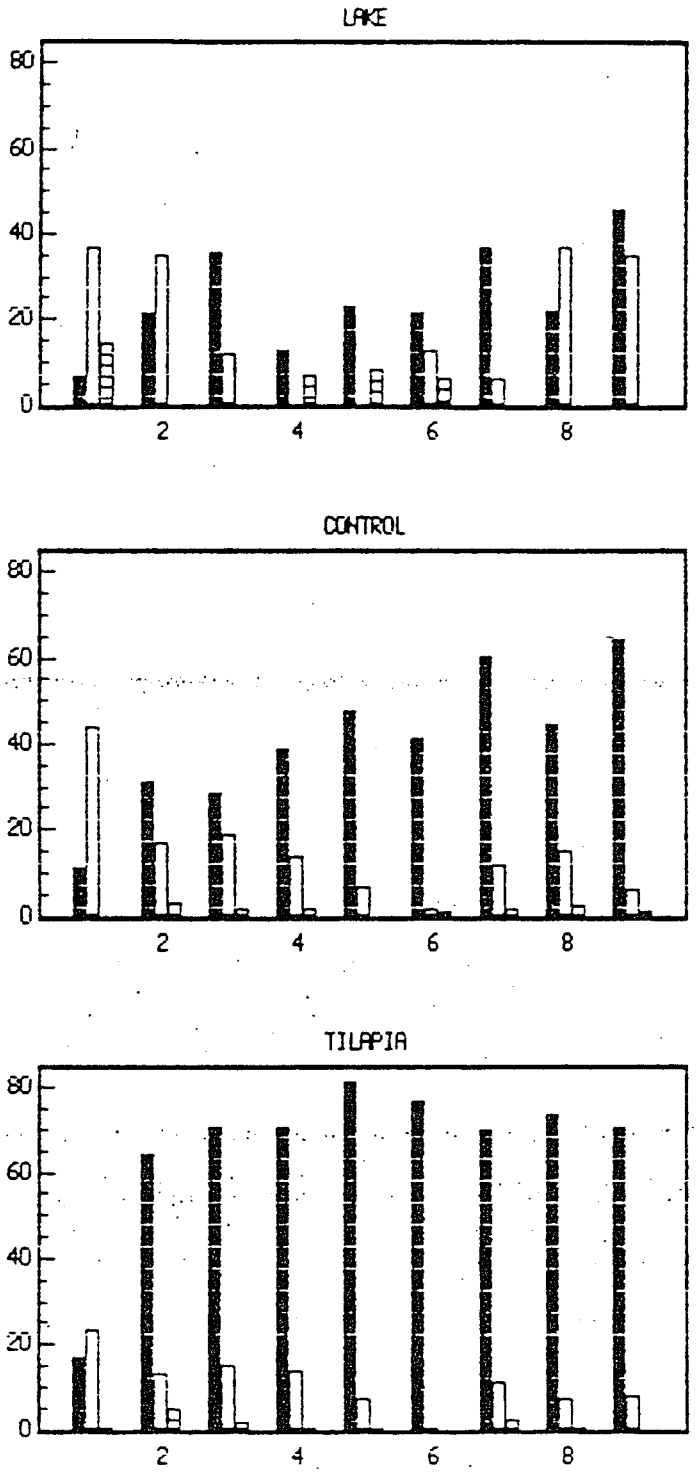



FIGURE 32. Changes in the percentage distribution of cladocerans (solid), calanoid (open) and cyclopoid copepods (striped) in the enclosures by sampling event.

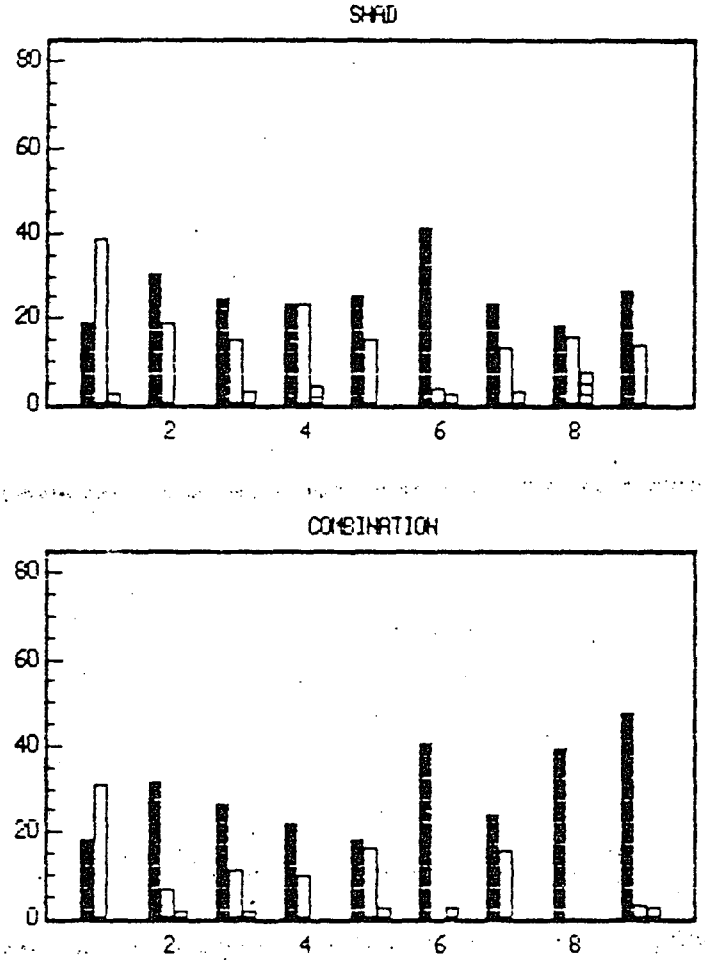



FIGURE 32. (continued).

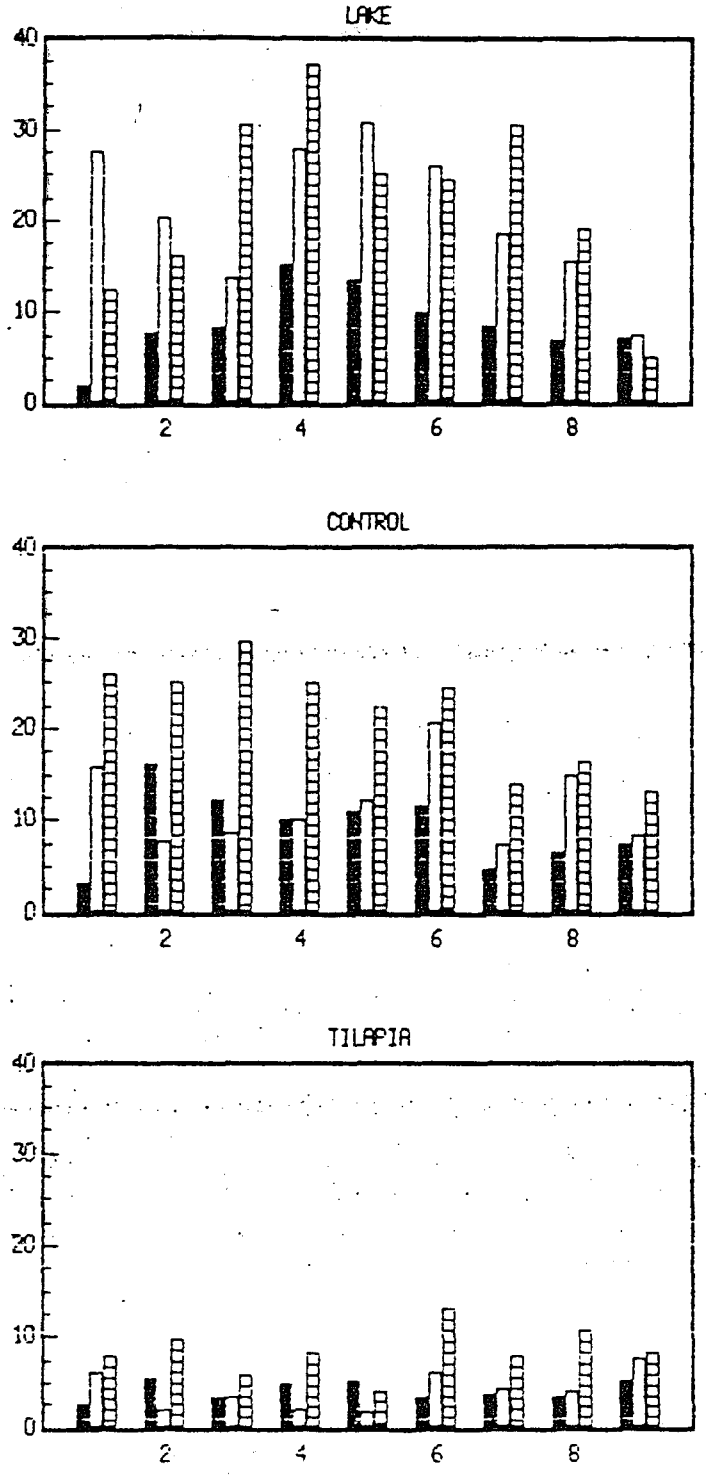



FIGURE 33. Changes in the percentage distribution of nauplii (solid), ciliates (open), and rotifers (striped) in the enclosures by sampling event.

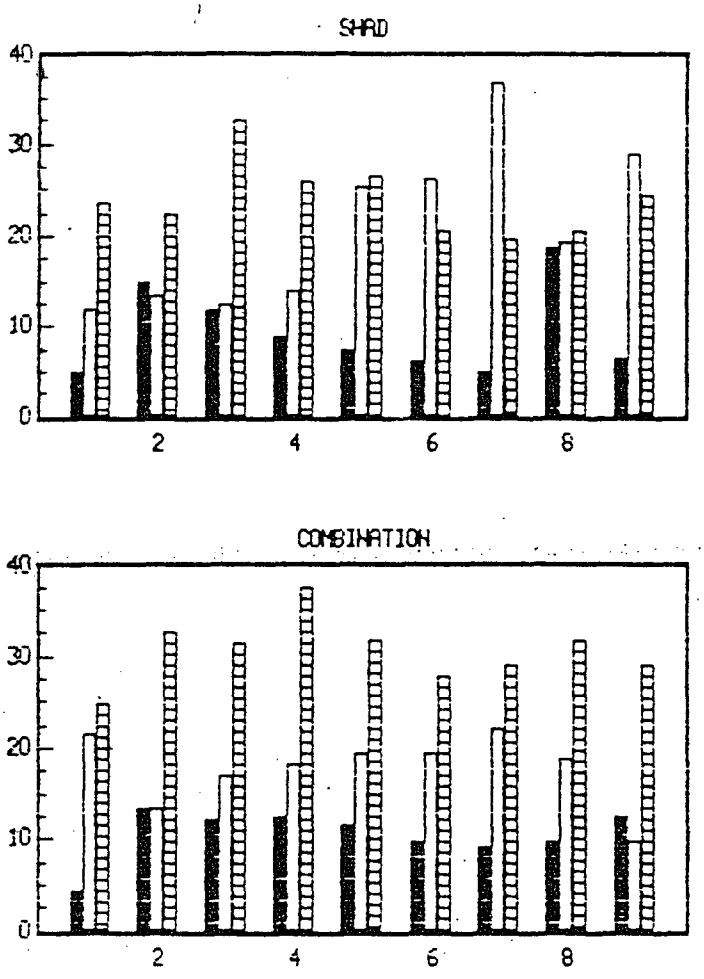



FIGURE 33. (continued).

The percentage distribution of the zooplankton components in the tilapia bags sharply contrasts with the other treatments due to the tremendous cladoceran populations found in those bags which shifted dominance to the macrozooplankton component (Table 6).

Percentage Distribution Within the Macrozooplankton

Partitioning the macrozooplankton communities of the treatments into percentages of cladocerans, calanoid copepods and cyclopoid copepods demonstrates that the control and tilapia bags were dominated by cladocerans during most of the study (Fig. 32). The dominance of cladocerans in the tilapia bags was much more pronounced than the control bags, although the control bags appeared to be approaching the level of the tilapia treatments when the study was terminated. Cladocerans also dominated the macrozooplankton biomass of the lake, combination and shad bags, but the magnitude was considerably reduced in comparison.

Calanoid copepods were important at the outset of the study, but declined to low levels for the remainder of the experiment except for the last two samples from the lake.

The percentage composition of cyclopoid copepods was negligible in all treatments for the duration of the study.

Percentage Distribution Within the Microzooplankton

The percentage distribution of microzooplankton biomass relative to total zooplankton biomass indicates that all microzooplankton components are relatively unimportant in the tilapia treatments (Fig. 33). The percentage contribution of all

microzooplankton compartments was frequently less than 10% of total zooplankton biomass in the tilapia bags.

In contrast to the tilapia treatments, all other bags displayed much higher proportions of the microzooplankton components, particularly rotifers and to a lesser degree ciliated protozoa. Nauplii biomass was on a percentage basis was a minor contributor to total zooplankton biomass.

## Productivity Studies

### Diurnal Patterns in Dissolved Oxygen Concentration

Patterns in diurnal change of dissolved oxygen content were essentially the same in the lake and bags, however the magnitudes and degrees of daily fluctuation differed between treatments. All bags and the lake displayed minimal oxygen concentrations around sunrise (6 a.m. - 8 a.m.) and maxima near sunset (5 p.m. - 7 p.m.). After the early morning minima, oxygen concentrations slowly increased throughout the morning and then rapidly increased during the afternoon. Timing of the maxima in dissolved oxygen concentrations varied on a daily basis due to the occasional presence of clouds in the late afternoon, however the timing was usually consistent between treatments on a given day.

On an average day, dissolved oxygen was lowest in the lake at 8 a.m. (mean = 8.47 mg $l^{-1}$) and reached the highest values at 5 p.m. (mean = 12.45 mg $l^{-1}$) (Fig. 34). The overall range of dissolved oxygen concentrations found in the lake during the study was 6.39 - 18.62 mg $l^{-1}$.

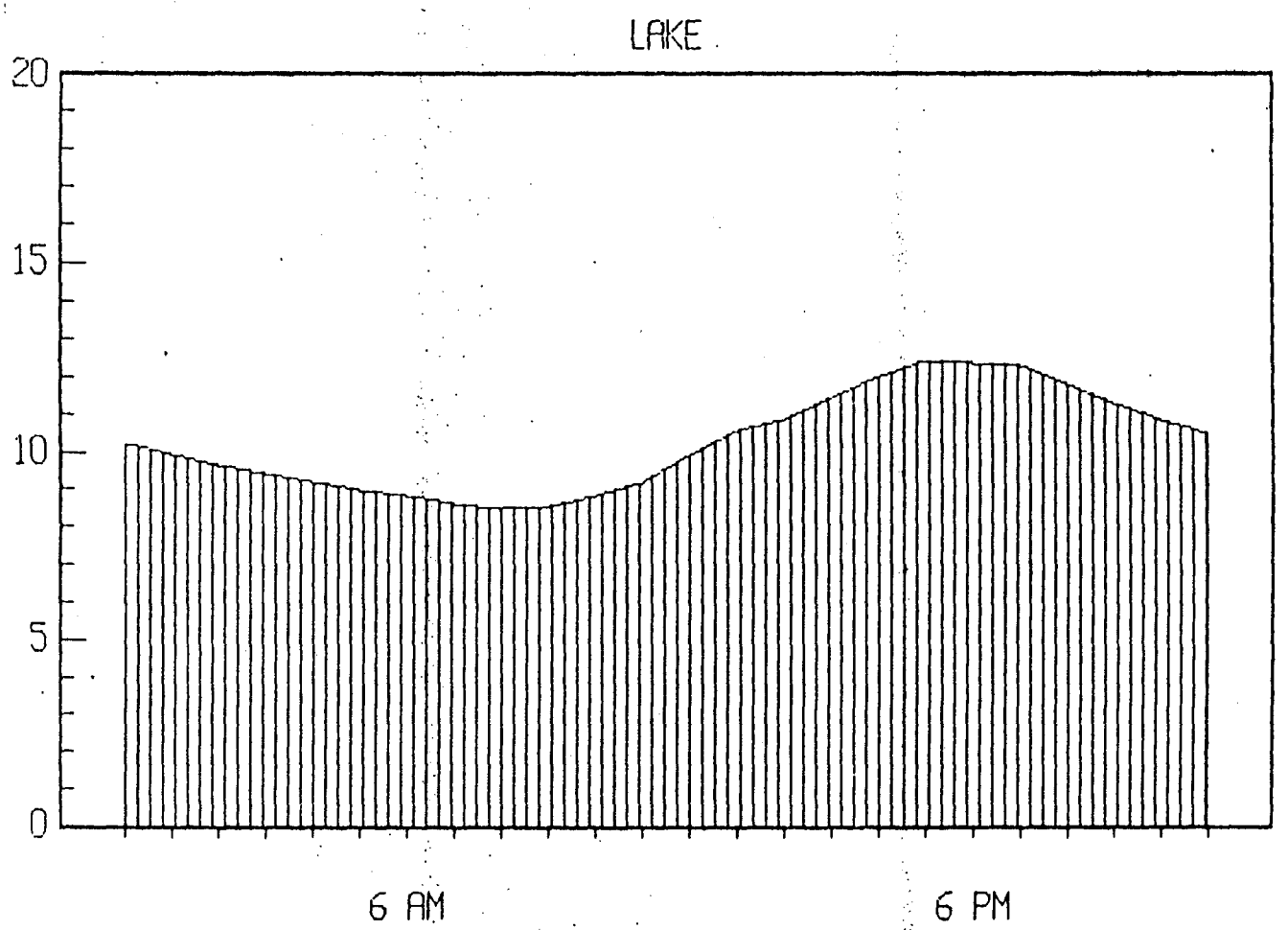



FIGURE 34. Mean hourly dissolved oxygen concentrations (mg $l^{-1}$) at the lake station.

The control bag strongly paralleled the lake but did achieve slighly higher values in the afternoon (Fig. 35). The minimum dissolved oxygen concentrations frequently were found at 8 a.m. (mean = 8.16 mg $l^{-1}$) and the maximum at 5 p.m. (mean = 13.34 mg $l^{-1}$). The lowest dissolved oxygen value recorded was 5.60 mg $l^{-1}$ and the highest was 22.72 mg $l^{-1}$.

The mean for dissolved oxygen concentration in the tilapia bag displayed the lowest average concentration for every hour of the generalized diurnal cycle (Fig. 36). Minimum values were noted at 8 a.m. (mean = 6.41 mg $l^{-1}$) and the maximum at 4 p.m. (mean = 10.75 mg $l^{-1}$). The lowest dissolved oxygen concentration found in the tilapia bag was 4.10 mg $l^{-1}$ and the highest value was 21.76 mg $l^{-1}$.

Dissolved oxygen readings were typically the highest in the shad treatment (Fig. 37). Peak values were usually recorded at 6 p.m. (mean = 16.67 mg $l^{-1}$) and the minima were seen at 8 a.m. (mean = 7.41 mg $l^{-1}$). This treatment had the widest range of dissolved oxygen concentrations with measurements ranging from an overall low of 2.94 mg $l^{-1}$ to a high of 27.37 mg $l^{-1}$. The dissolved oxygen curves for shad and tilapia showed remarkable agreement during nighttime hours but quickly departed near noon.

The diurnal curve for the combination treatment is roughly intermediate to that of the shad and tilapia bags and strongly resembles the pattern described for the lake (Fig. 38). Minimal concentrations were found at 8 a.m. (mean = 8.25 mg $l^{-1}$) and peaked at 4 p.m. (mean = 12.91). Dissolved oxygen ranged from 6.28 mg $l^{-1}$ to a maximum of 24.92 mg $l^{-1}$, but values were

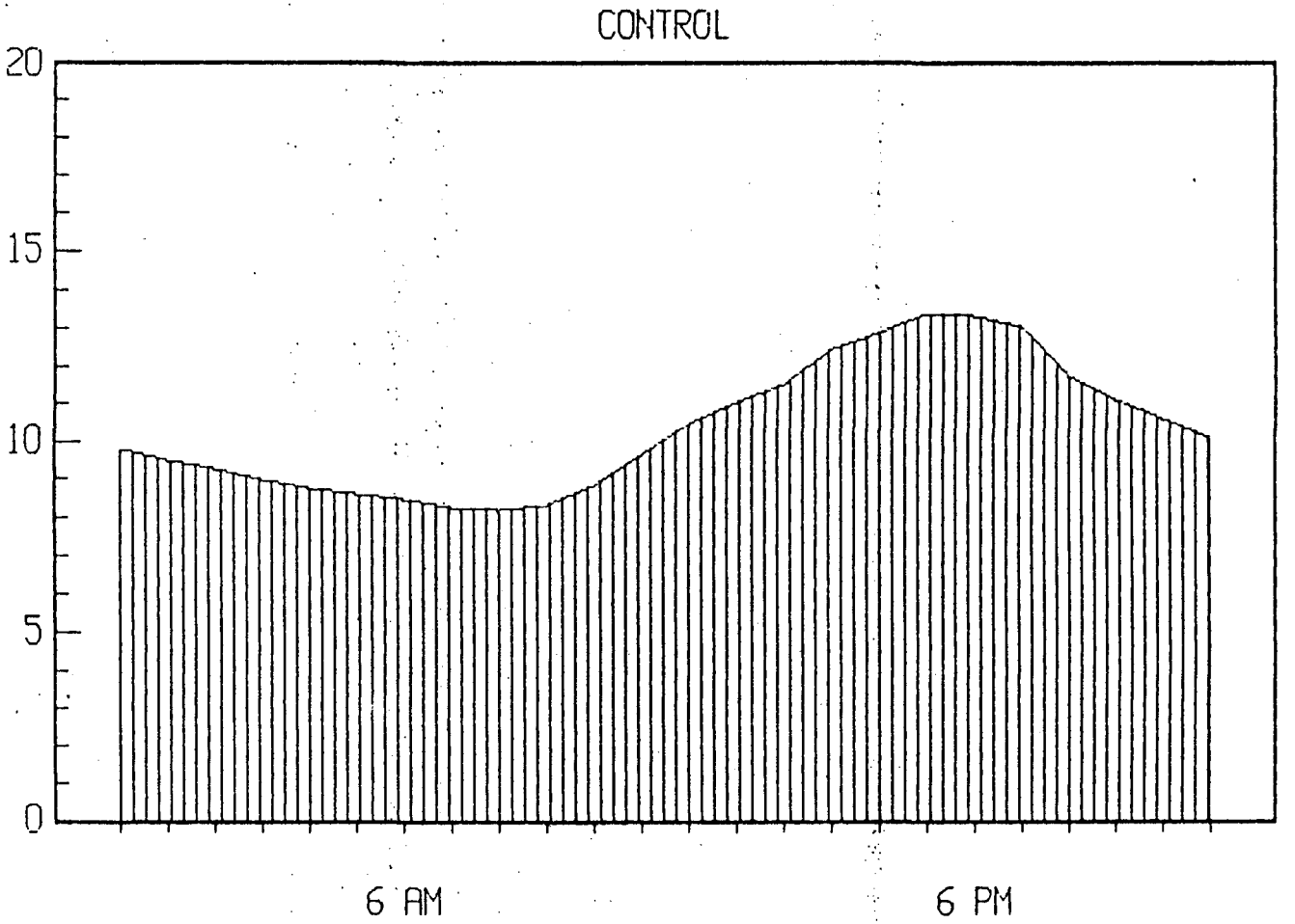



FIGURE 35. Mean hourly dissolved oxygen concentrations (mg $l^{-1}$) in the control bag.

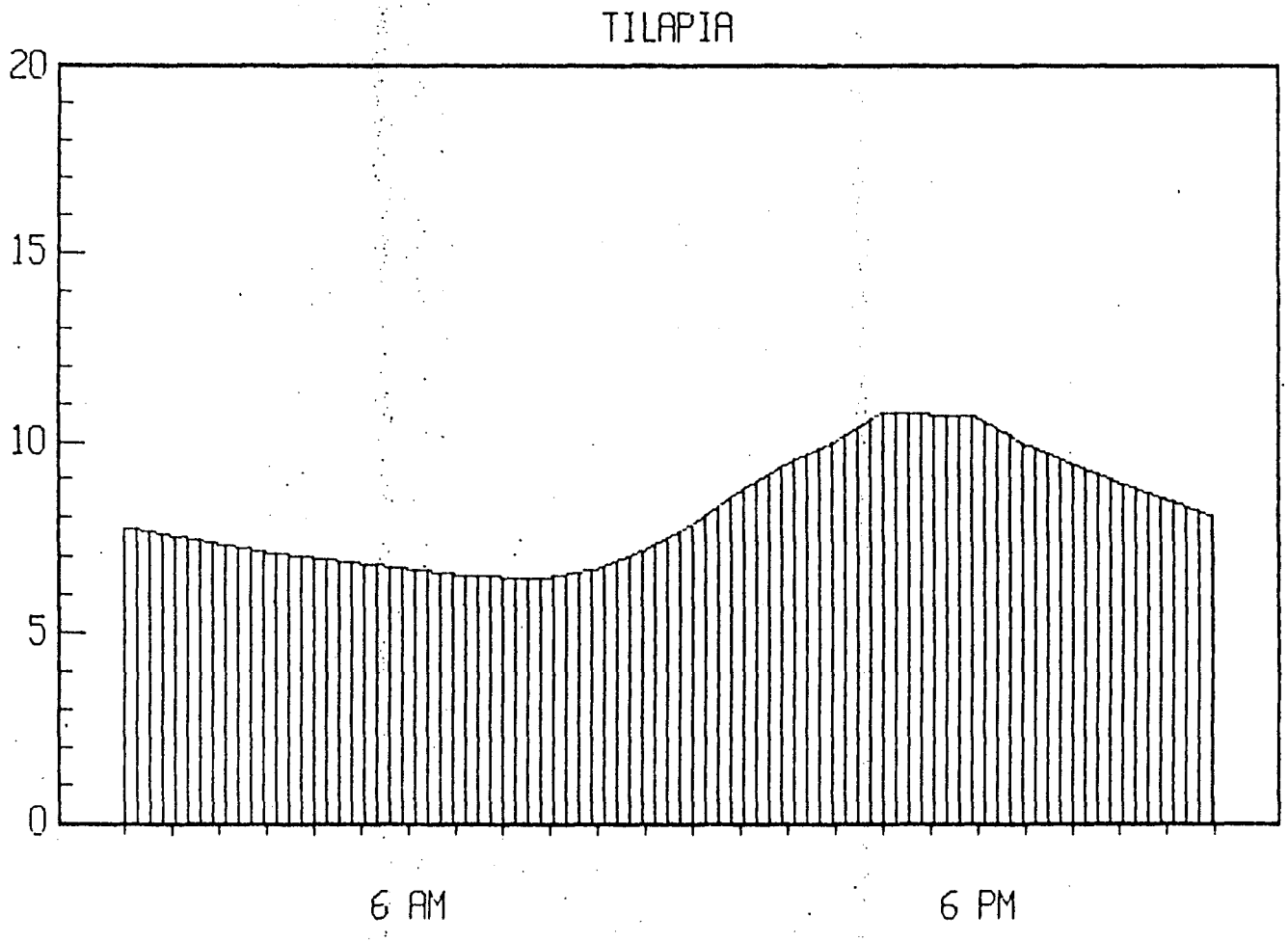



FIGURE 36. Mean hourly dissolved oxygen concentrations (mg $l^{-1}$) in the tilapia bag.

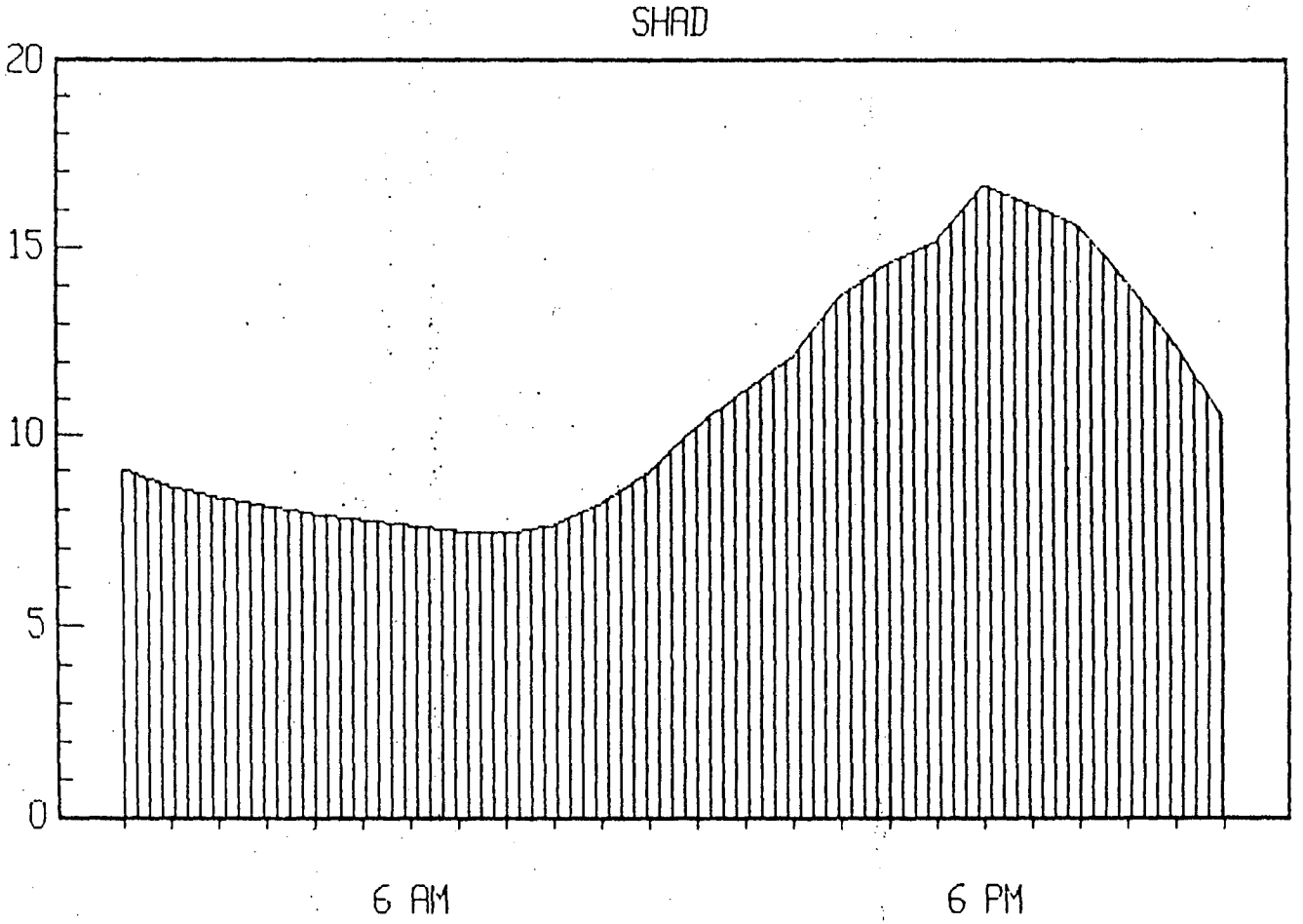



FIGURE 37. Mean hourly dissolved oxygen concentrations (mg $l^{-1}$) in the shad bag.

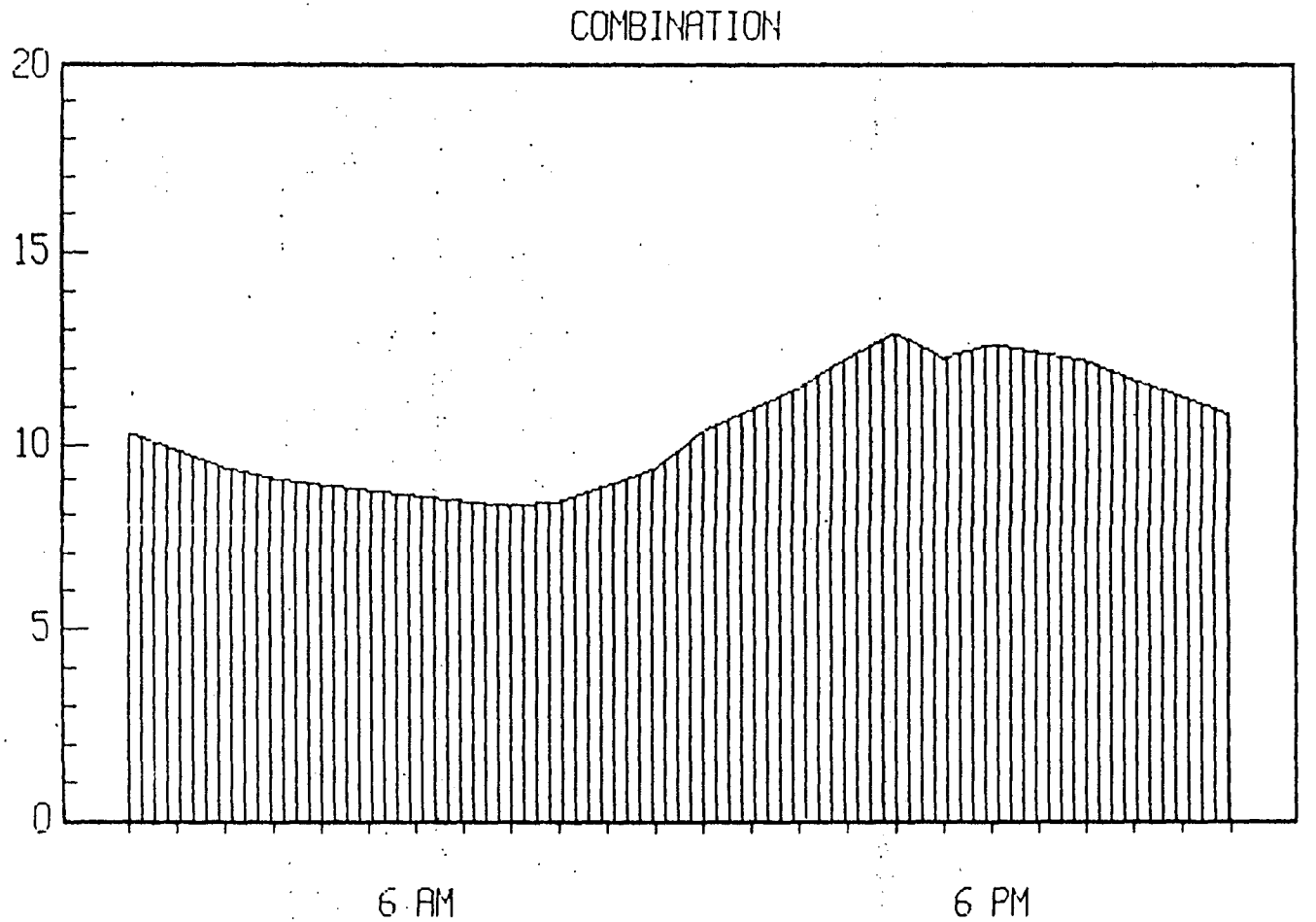



FIGURE 38. Mean hourly dissolved oxygen concentrations (mg $l^{-1}$) in the combination bag.

typically lower than this upper limit.

Variations in Daily Average Dissolved Oxygen

The daily mean oxygen concentrations were almost identical in the lake and control treatments (Figs. 39 and 40). The highest average oxygen concentrations attained were in the lake ( 13.32 mg $l^{-1}$ ) and control (14.77 mg $l^{-1}$ ) on 25 September. For the most of the remainder of the study oxygen fluctuated around 9-12 mg $l^{-1}$.

The tilapia bag dissolved oxygen mean was comparatively depressed which values typically averaging near 6-8 mg $l^{-1}$ (Fig. 41). The highest average dissolved oxygen was observed near the end of the experiment (14.42 mg $l^{-1}$). The lowest mean in the tilapia bag was on SE 3 (5.34 mg $l^{-1}$).

The shad treatment exhibited dramatically higher averages in dissolved oxygen concentration when compared to the other treatments, particularly during the first half of the study (Fig. 42). Four pronounced peaks ranging from 1-3 days were apparent. On 25 September the dissolved oxygen averaged 20.15 mg $l^{-1}$. The weather conditions on this day were extremely calm winds with high solar insolation.

Trends were not readily apparent in the combination bag because of the missing data, however the daily mean dissolved oxygen resembles that described for lake and control treatments (Fig. 43). A pronounced maxima in oxygen was noted on the last two days of the study period.

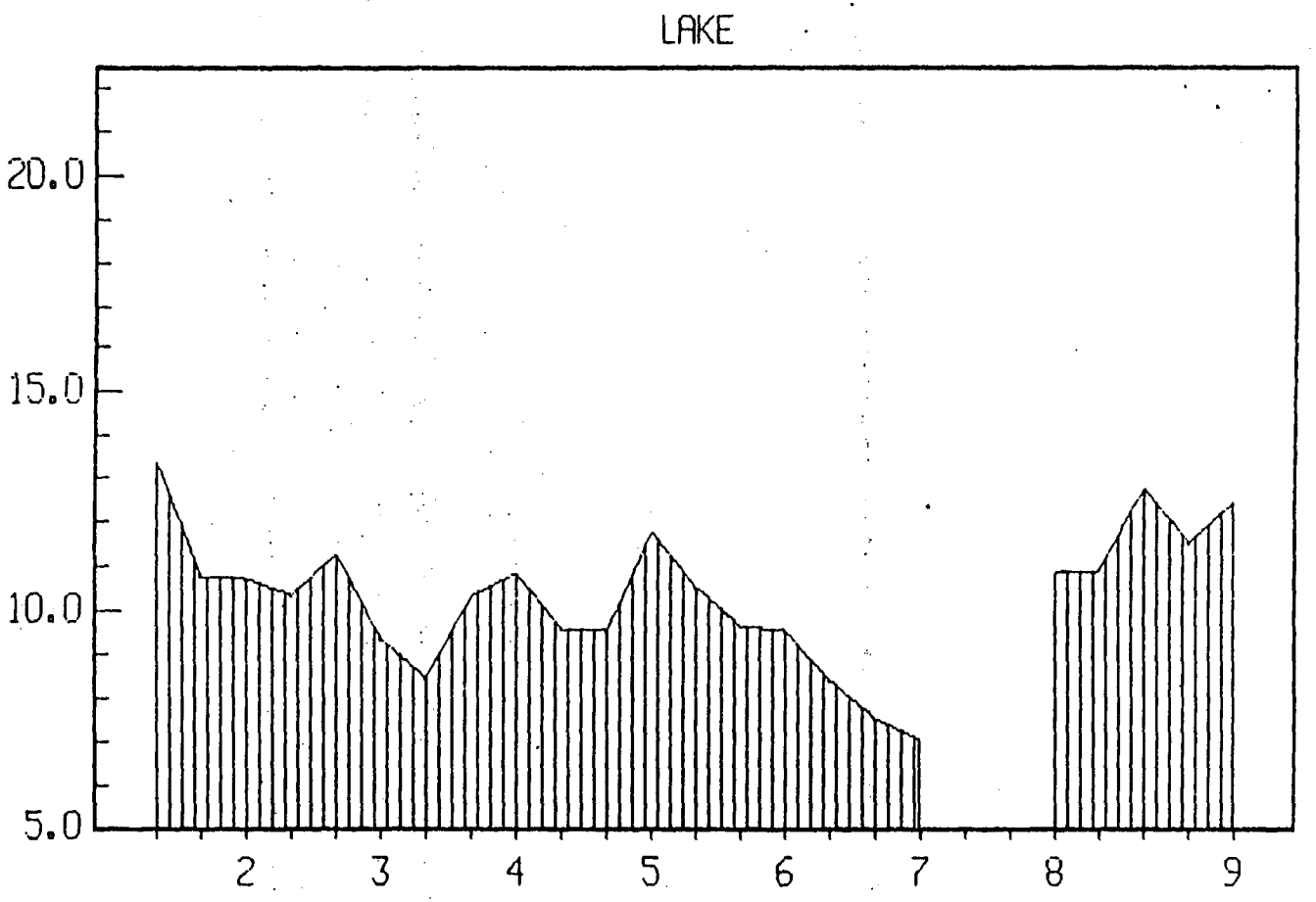



FIGURE 39. Daily average dissolved oxygen concentrations (mg $l^{-1}$) at the lake station.

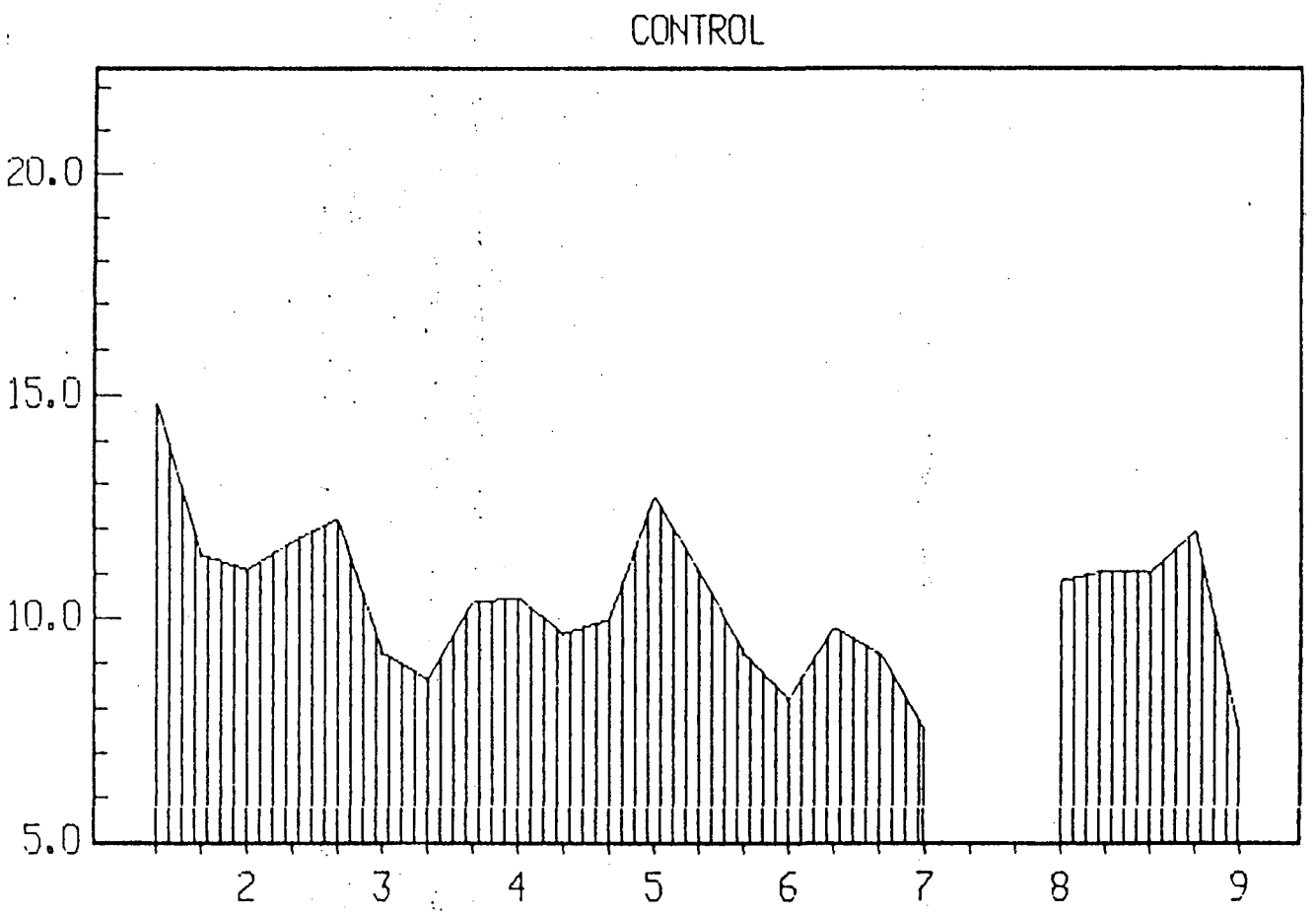



FIGURE 40. Daily average dissolved oxygen concentrations (mg $l^{-1}$) in the control bag.

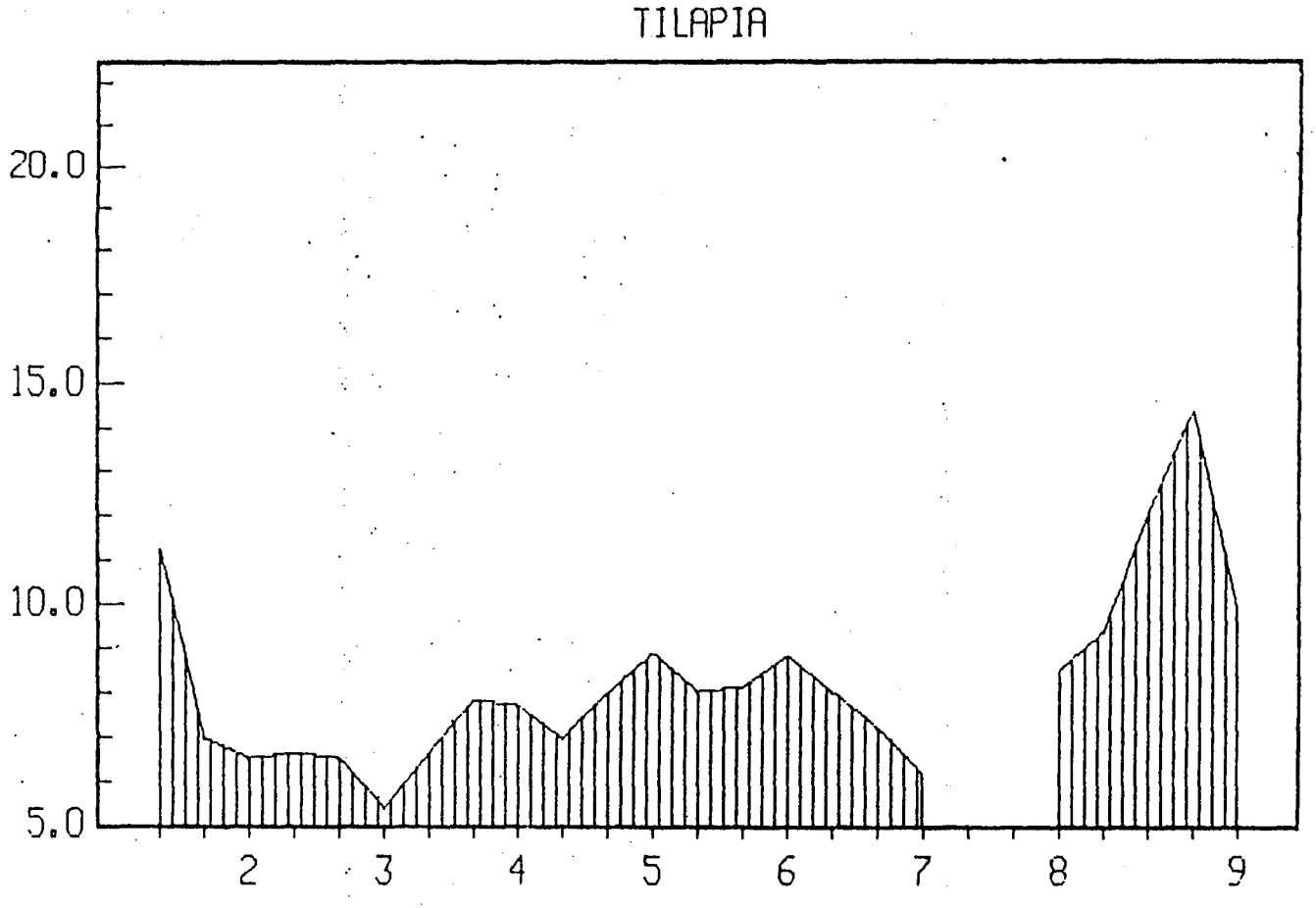



FIGURE 41. Daily average dissolved oxygen concentrations (mg $l^{-1}$) in the tilapia bag.

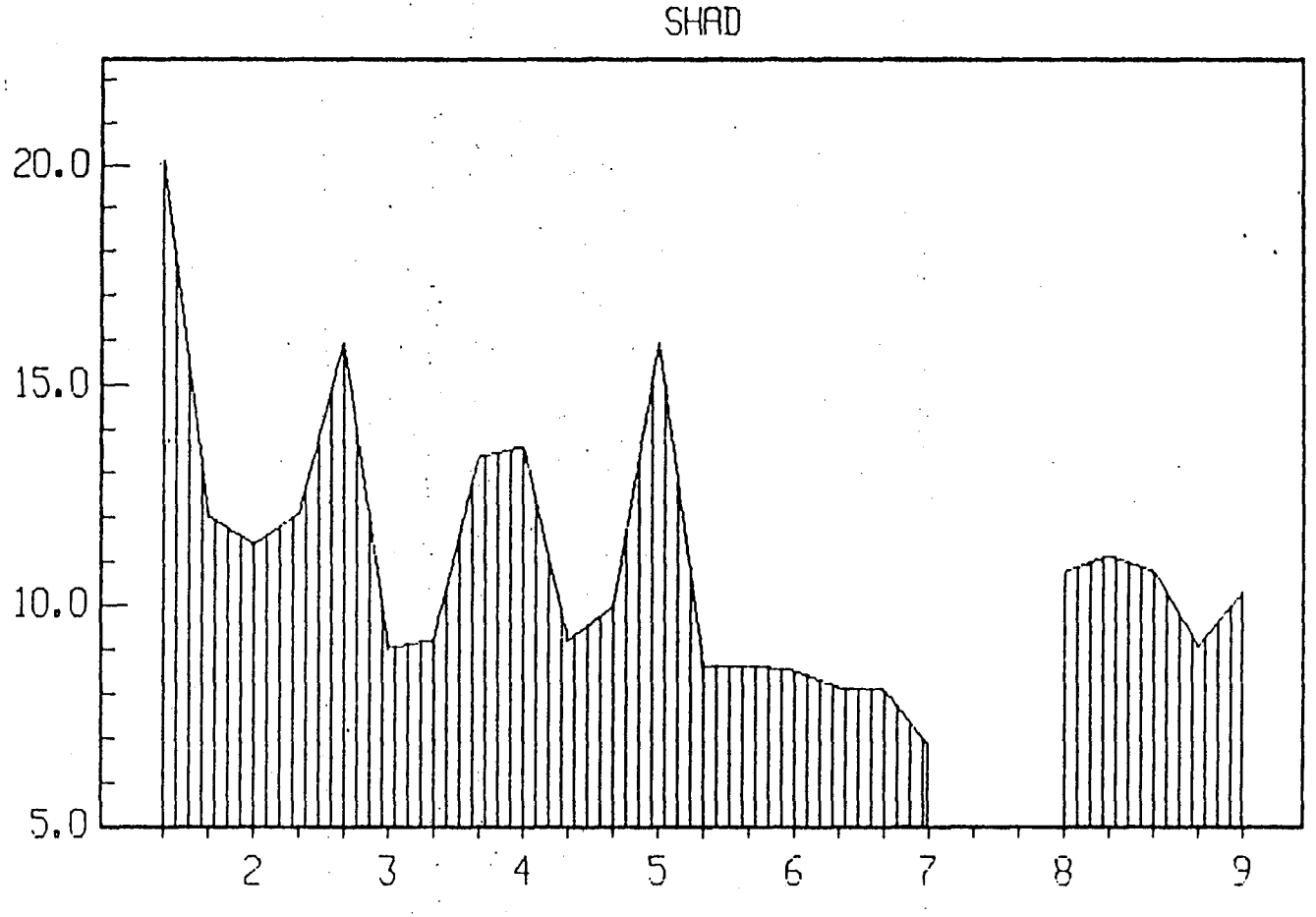



FIGURE 42. Daily average dissolved oxygen concentrations (mg $l^{-1}$) in the shad bag.

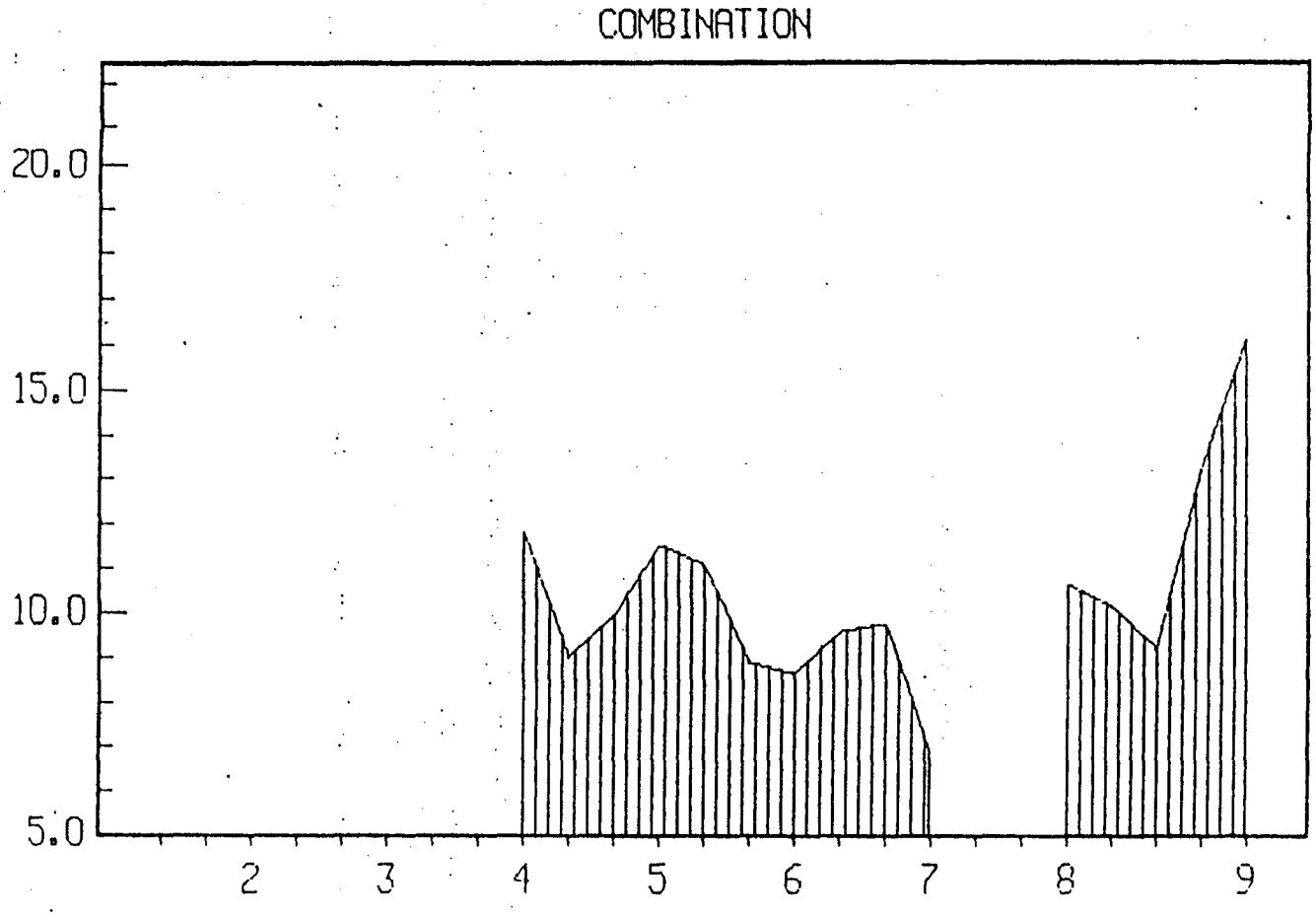



FIGURE 43. Daily average dissolved oxygen concentrations (mg $l^{-1}$) in the combination bag.

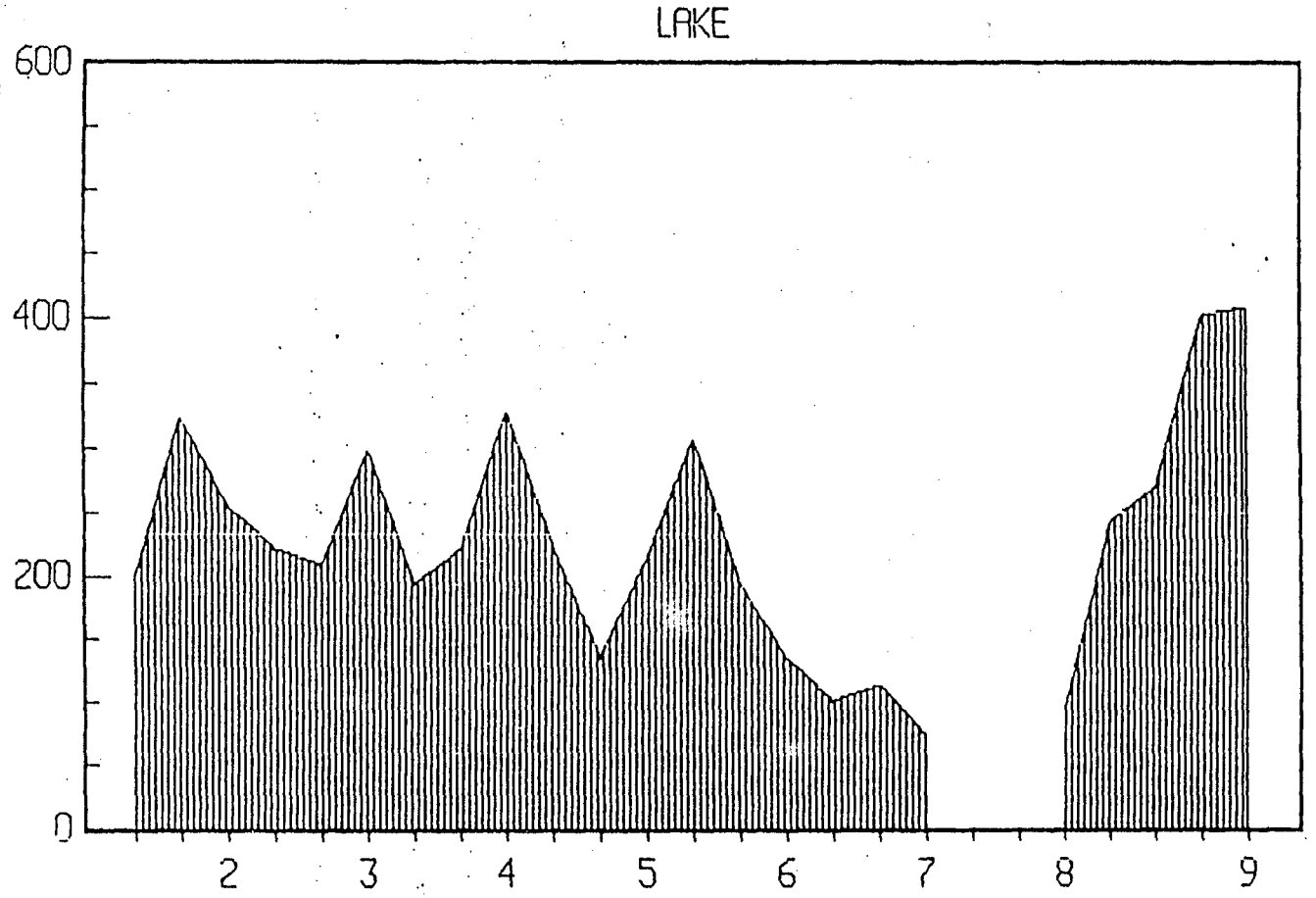



FIGURE 44. Gross primary productivity (mg C $m^{3}$ /hr) at the lake station.

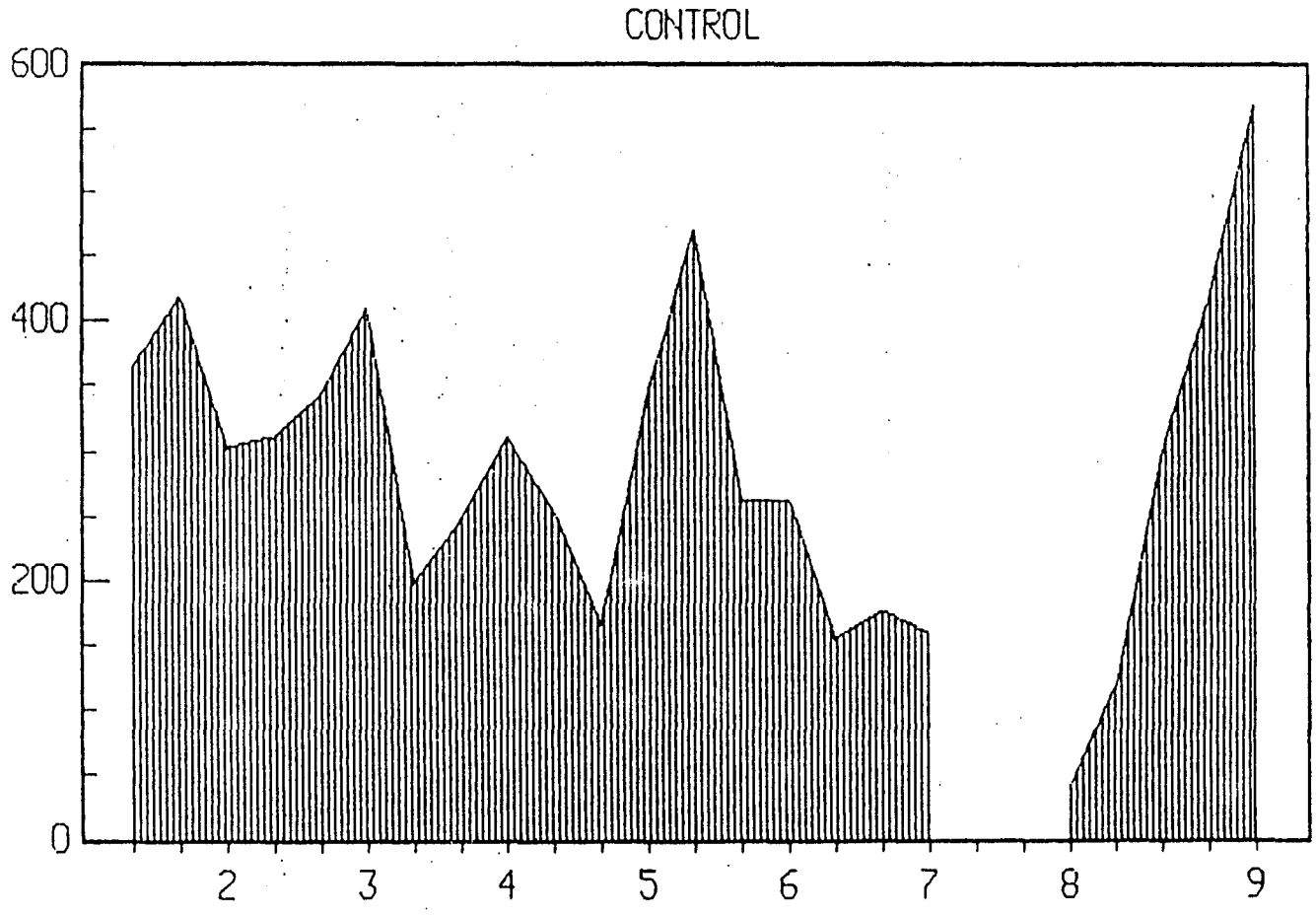



FIGURE 45. Gross primary productivity (mg C $m^{-3}$ /hr) in the control bag.

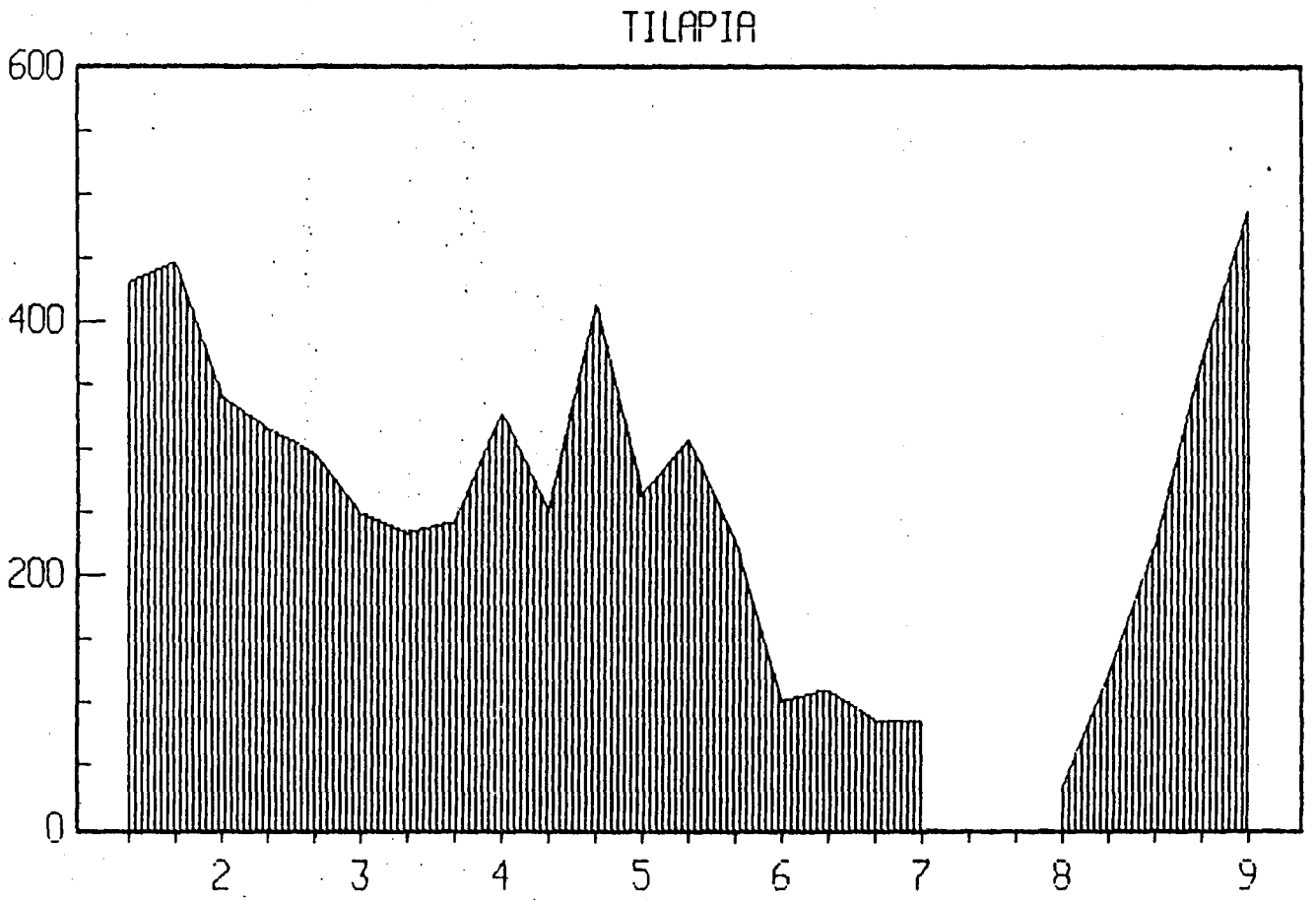



FIGURE 46. Gross primary productivity (mg C $m^3$ /hr) in the tilapia bag.

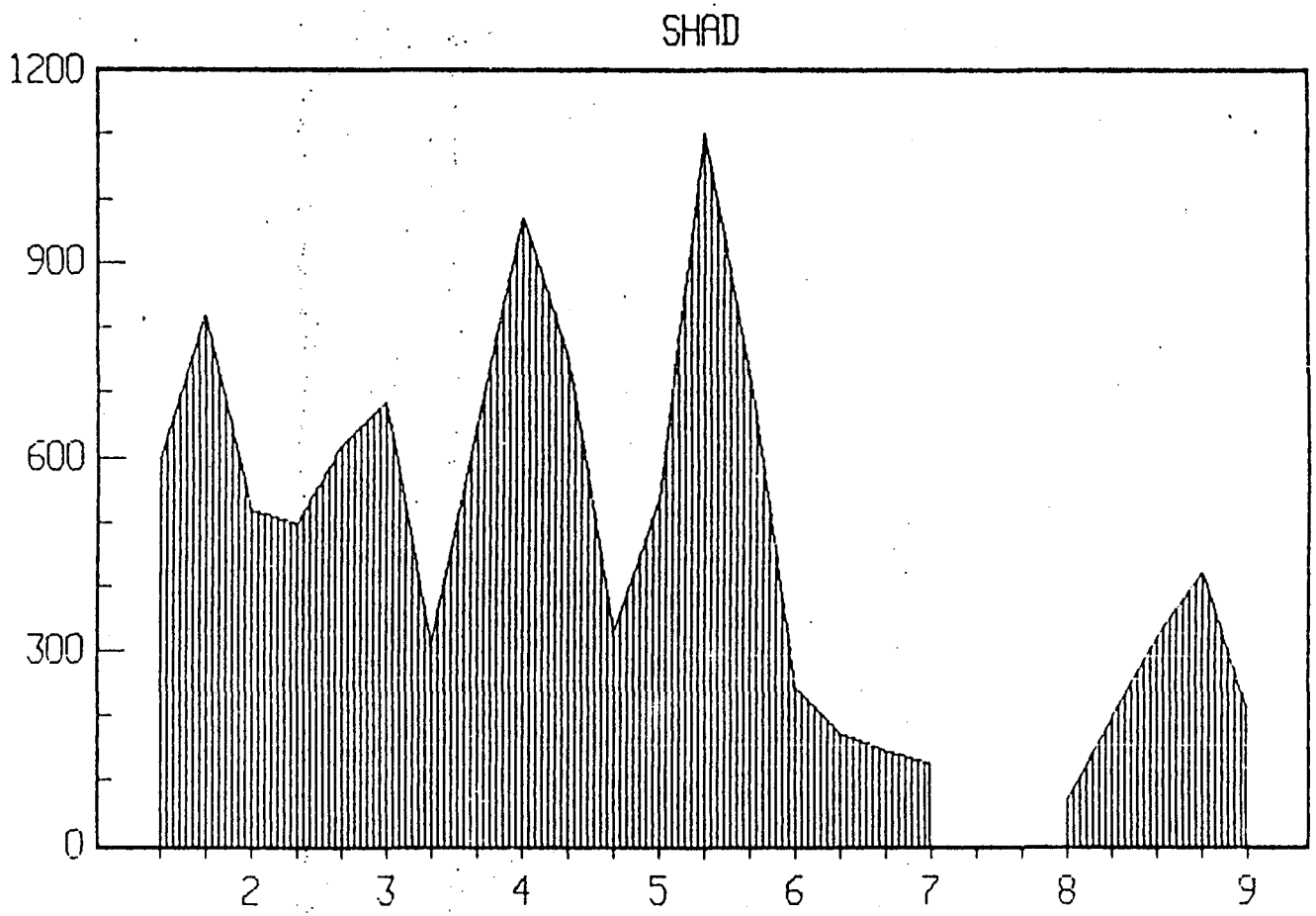



FIGURE 47. Gross primary productivity (mg C $m^{3}$ /hr) in the shad bag.

TABLE 7. Average productivity values (mg C cubic m/hr) (+ SE) for the lake (n=23), control (n=23), tilapia (n=23), shad (n=23), and combination (n=15) treatments. * denotes mean significantly different (ANOVA, $p < 0.05$) from other treatments.

| | TREATMENT | | | | |
|---|---|---|---|---|---|
| | LAKE | CONTROL | TILAPIA | SHAD | COMBINATION |
| Gross primary productivity | 224.0 (19.2) | 286.2 (25.9) | 258.4 (26.5) | * 477.4 (59.3) | 263.9 (26.0) |
| Net primary productivity | 74.1 (8.9) | 89.3 (10.8) | 78.9 (9.0) | * 153.2 (22.1) | 91.7 (14.0) |
| Respiration | 149.9 (14.7) | 196.9 (23.6) | 179.5 (21.6) | * 324.2 (45.6) | 172.2 (21.3) |
| GPP/Respiration | 1.56 (.09) | 1.58 (.09) | 1.53 (.08) | 1.56 (.07) | 1.64 (.14) |

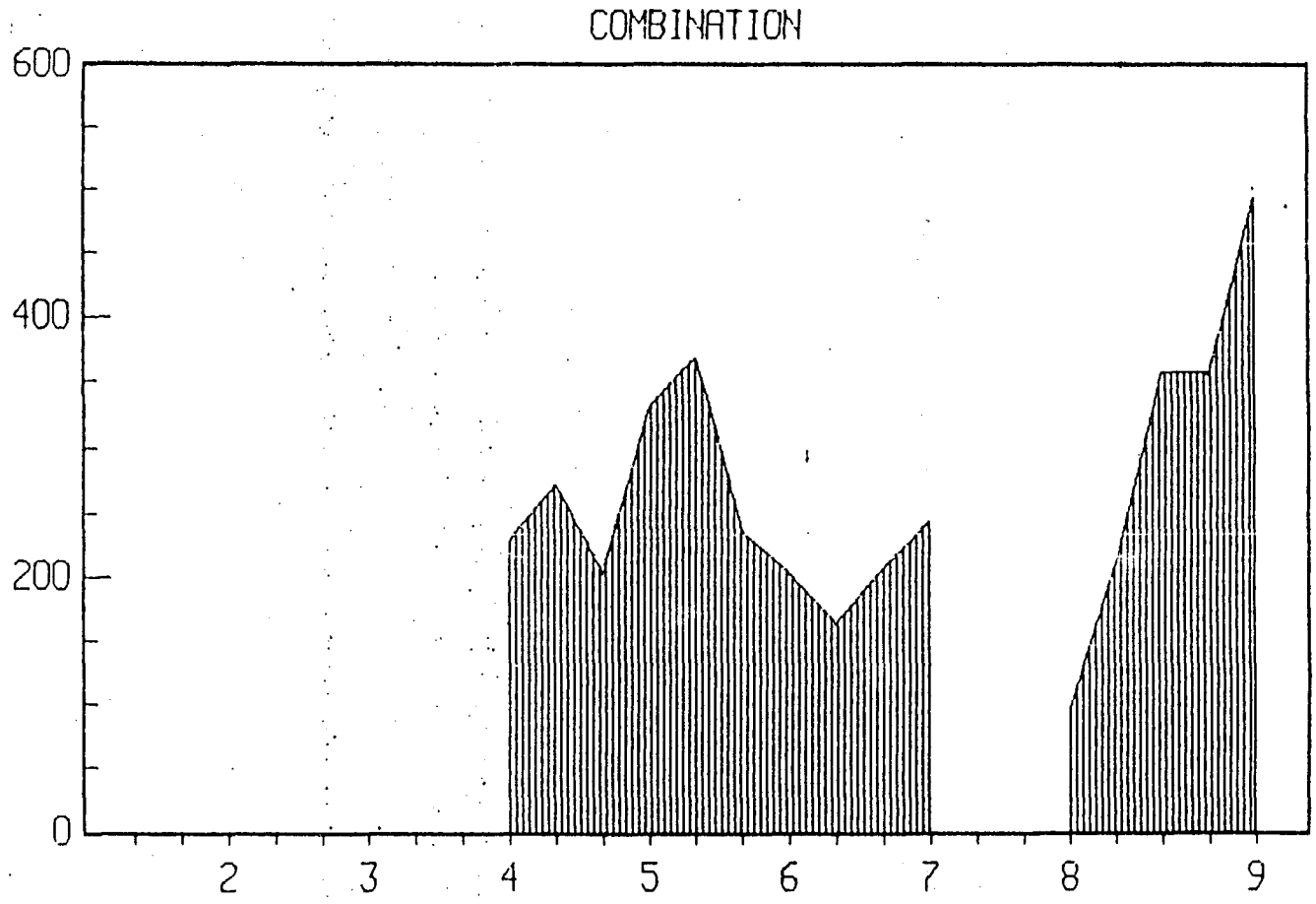



FIGURE 48. Gross primary productivity (mg C $m^{3}$ /hr) in the combination bag.

Gross Primary Production

Gross primary productivity at the lake station ranged from 72.4 mg C $m^3$ /hr on 12 October to 408.3 mg C $m^3$ on 19 October. (Fig. 44). The mean for the study period was 149.9 mg C $m^3$ /hr.

Gross primary productivity for the control treatment ranged from 40.2 mg C $m^3$ /hr on 15 October to 574.0 mg C $m^3$ /hr on 19 October (Fig. 45). The average for the study period was 286.2 mg C $m^3$ /hr.

In the tilapia bag, gross primary productivity ranged from a low of 31.8 mg C $m^3$ /hr on 15 October to a maximum of 488.3 mg C $m^3$ /hr on (Fig. 46). The average for the experiment was 258.4 mg C $m^3$ /hr. In general the tilapia treatment displayed less fluctuation on a day to day basis compared to control and lake treatments.

Gross primary productivity values for the shad bag were considerably higher than all bag treatments as well as the lake (Fig. 47). The range was 67.9 mg C $m^3$ /hr on 15 October to 1100.4 mg C $m^3$ /hr on 7 October. The average for the shad treatment, 477.4 mg C $m^3$ /hr, was significantly higher (ANOVA, $p < 0.05$) than all other bags and the lake (Table 7).

Although interpretation of the gross primary productivity data for the combination treatment is hampered by the missing values, the pattern resembles those in the lake and control treatments (Fig. 48). The range of gross primary productivity in the combination bag went from 94.6 mg C $m^3$ /hr on 15 October to 497.5 mg C $m^3$ /hr on 19 October, and the mean for the experiment

was 172.2 mg C $m^{3}$ /hr.

Community Respiration

Community respiration displayed the same general temporal variation within the treatments and the lake, however the magnitude varied depending upon the presence of fish.

The lake usually displayed the smallest values in community respiration with values always found between 75.3 mg C $m^{3}$ /hr and 285.3 mg C $m^{3}$ /hr (Fig. 49) The average daily respiration was 149.9 mg C $m^{3}$ /hr which was the lowest mean for all treatments.

The control bag displayed essentially the same timing in community respriation as the lake, but on days of high respiration the control treatment was typically greater (Fig. 50). The range of daily respiration ranged from 26.8 mg C $m^{3}$ /hr to 518.4 mg C $m^{3}$ /hr with an overall average of 196.9 mg C $m^{3}$ /hr which was second only to the lake.

In general, the tilapia treatment experienced more daily variation than the lake in community respiration (Fig. 51). The range of community respiration for the tilapia treatment was 20.9 mg c $m^{3}$ /hr to 423.1 mg C $m^{3}$ /hr with an experimental average of 179.5 mg C $m^{3}$ /hr.

The community respiration in the shad treatment was considerably higher than all other treatments although they corresponded to peaks of respiration in the other bags (Fig. 52). Values ranged from 45.3 mg C $m^{3}$ /hr to 644.3 mg $m^{3}$ /hr with an overall 324.2 mg C $m^{3}$ /hr which was significantly greater than the other four treatments (Table 7).

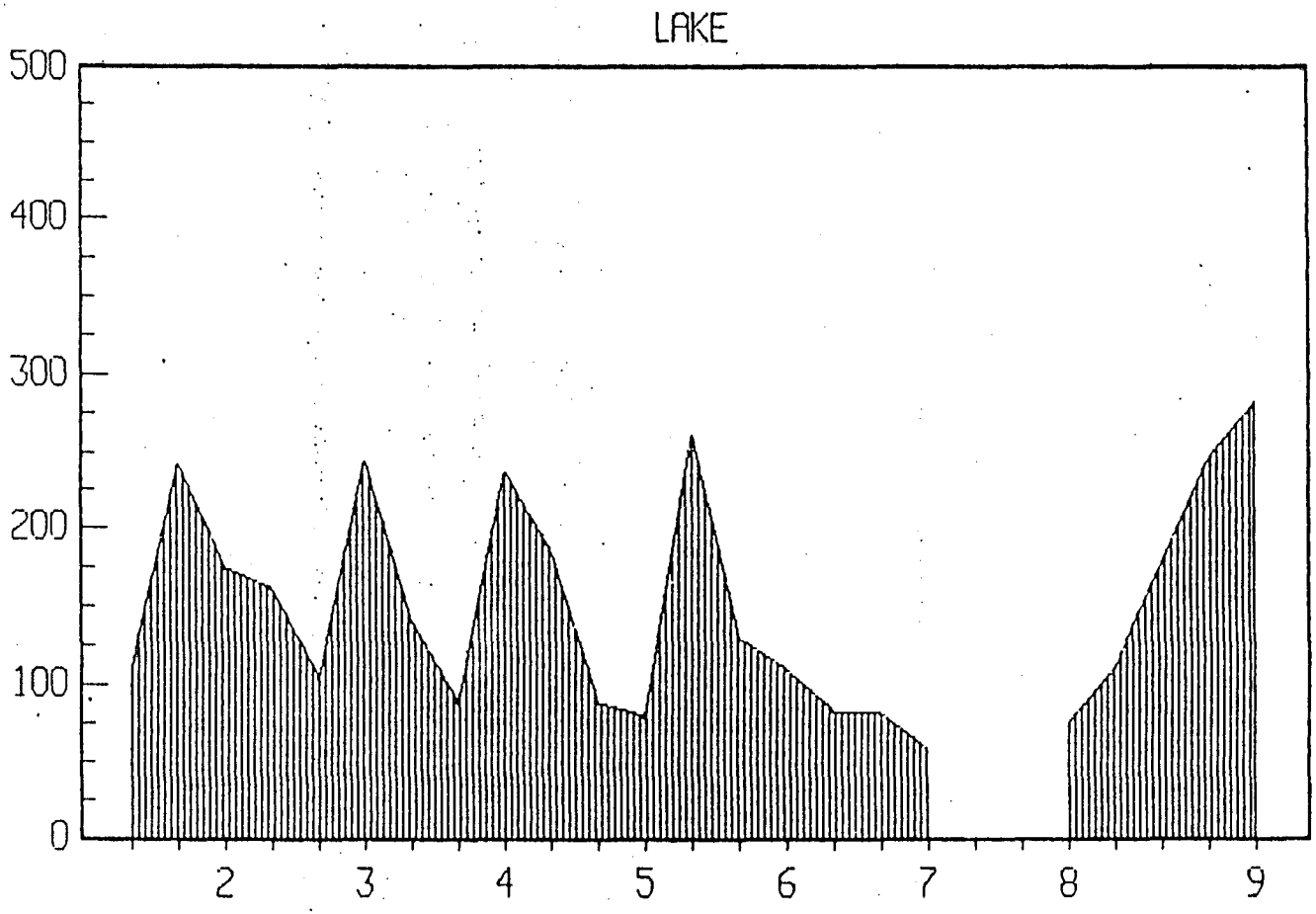



FIGURE 49. Community respiration (mg C $m^{3}$ /hr) at the lake station.

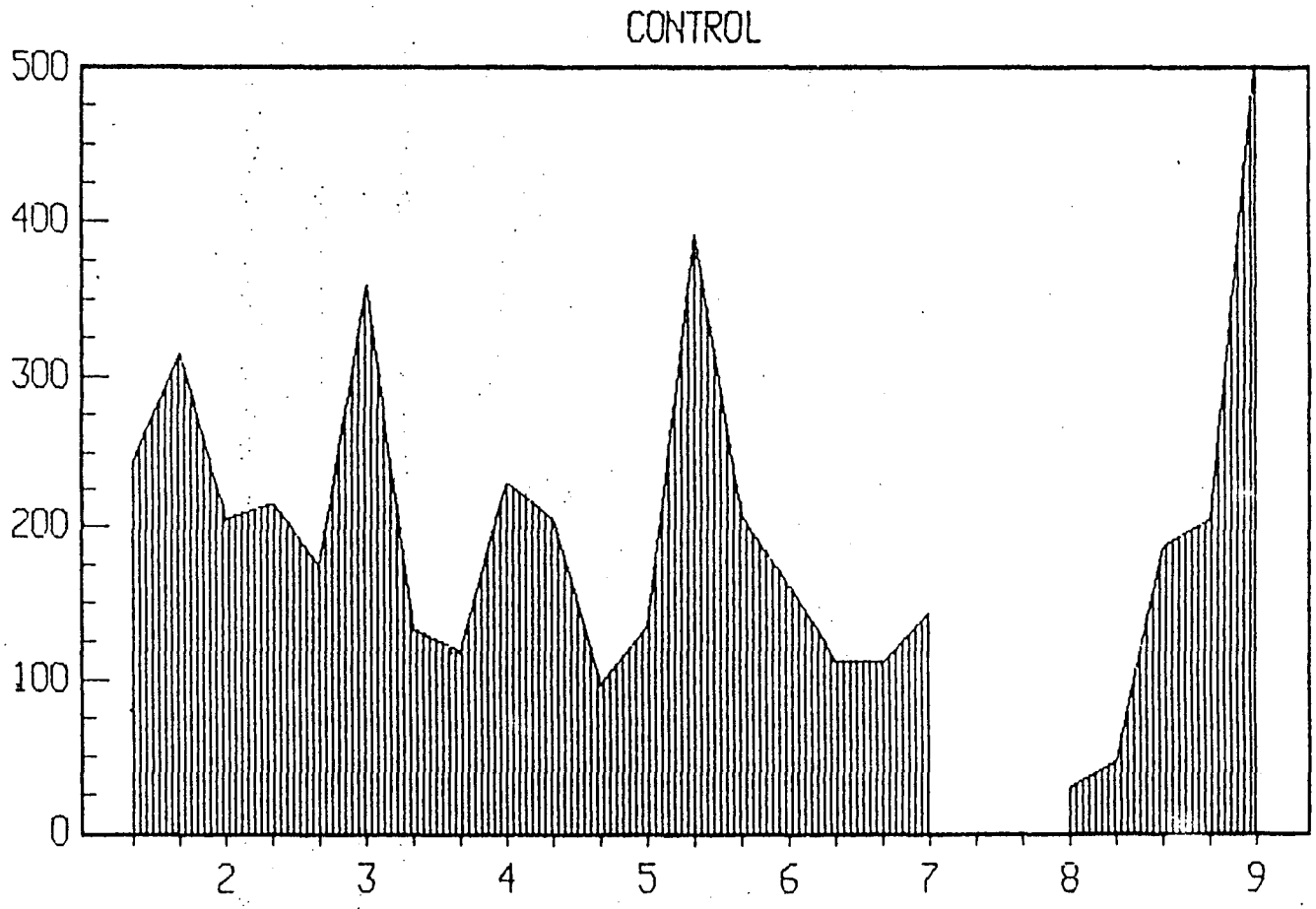



FIGURE 50. Community respiration (mg C $m^{-3}$ /hr) in the control bag.

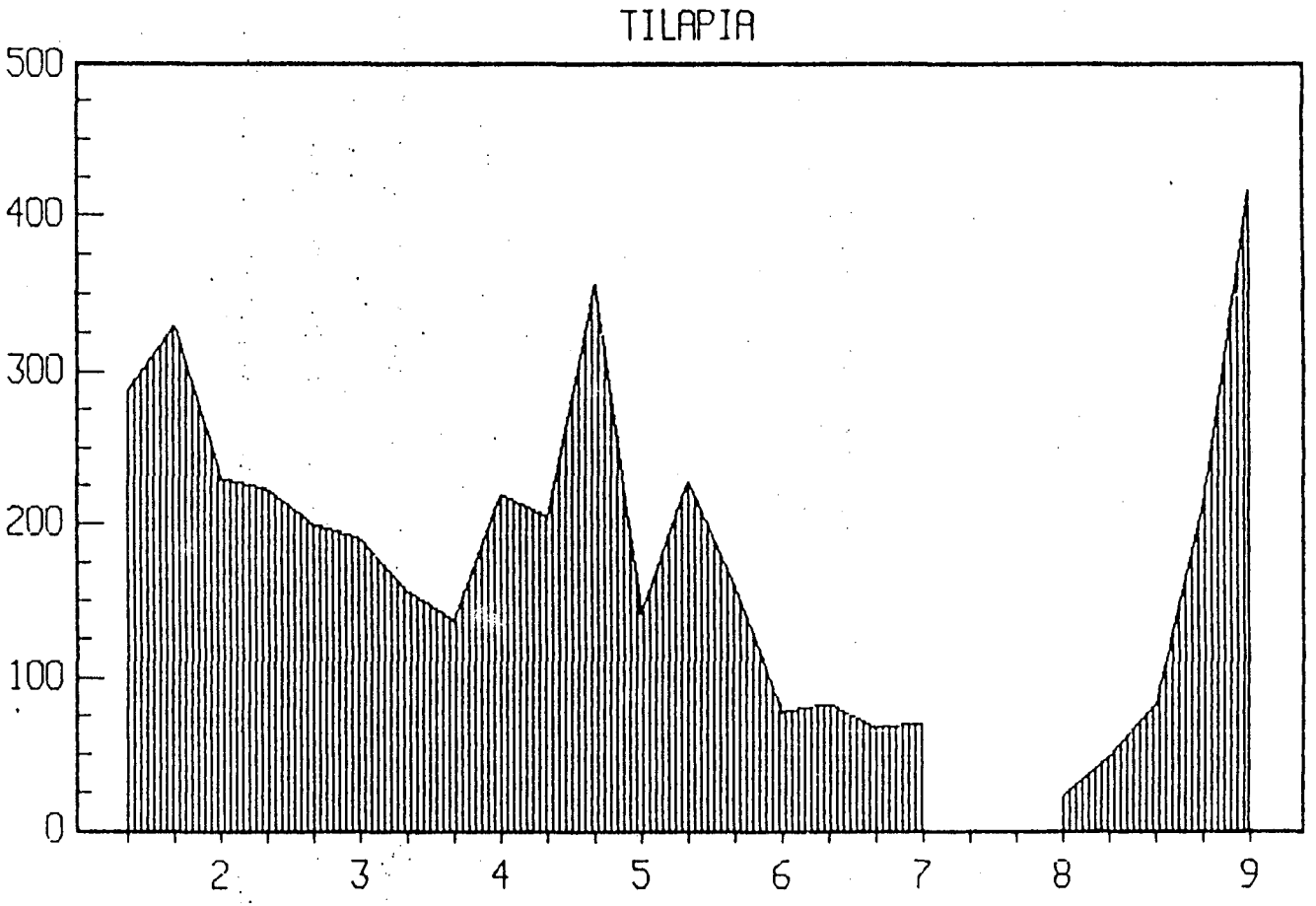



FIGURE 51. Community respiration (mg C $m^{-3}$ /hr) in the tilapia bag.

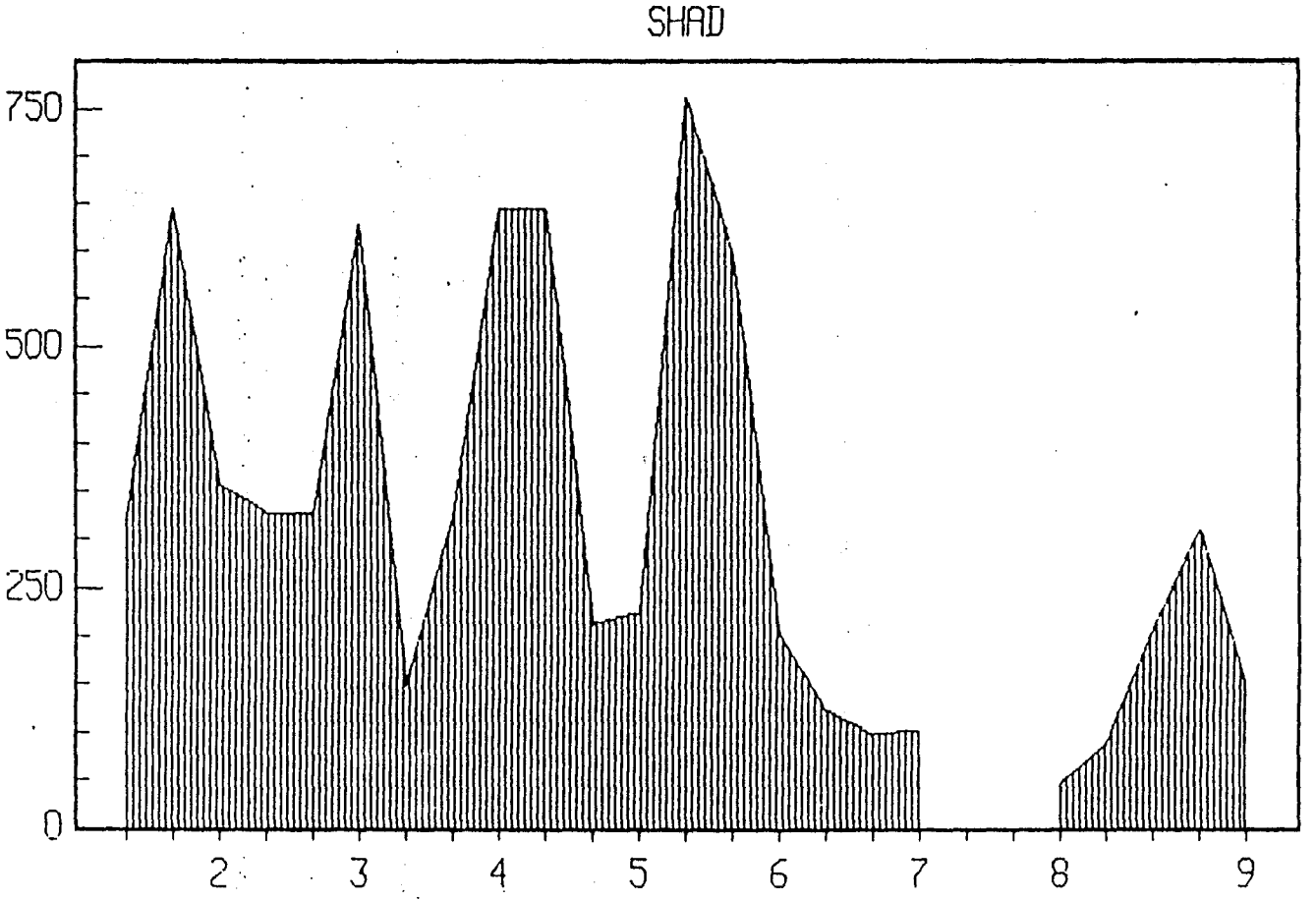



FIGURE 52. Community respiration (mg C $m^{3}$ /hr) in the shad bag.

Patterns in community respiration in the combination bag were less evident, but it appears that respiration fluctuated less than the other treatments (Fig. 53) Respiration ranged from 63.0 mg $m^3$ /hr to 362.3 mg C $m^3$ /hr with an average of 172.2 mg C $m^3$ /hr.

Net Primary Productivity

The patterns in net primary production strongly resemble those described for community respiration.

The lake displayed only small fluctuations in daily net primary productivity (Fig. 54). The mean for the lake was 74.1 mg C $m^3$ /hr and ranged from 16.1 mg $m^3$ /hr to 157.2 mg $m^3$ / hr. The maximum and mean above were lower than the comparable values from the other four treatments.

Net primary production in the control bag was somewhat higher than the lake (Fig. 55). The range for this treatment was 13.4 mg $m^3$ /hr to 211.2 mg C $m^3$ /hr with an overall mean of 89.3 mg C $m^3$ /hr.

The tilapia treatment had a considerable lack of variation on net primary producitivity on a day to day basis (Fig. 56). All values in net primary producitivity ranged from 10.9 mg C $m^3$ /hr to 160.0 mg C $m^3$ /hr with an average of 78.9 mg C $m^3$ /hr.

As previoulsy described for patterns in gross primary production and respiration, the shad treatment had significantly higher average of net primary productivity, 153.2 mg C $m^3$ /hr, when compared to the other treatments (Table 7). The range was between 22.0 mg C $m^3$ /hr to 339.1 mg C $m^3$ /hr with two large maxima

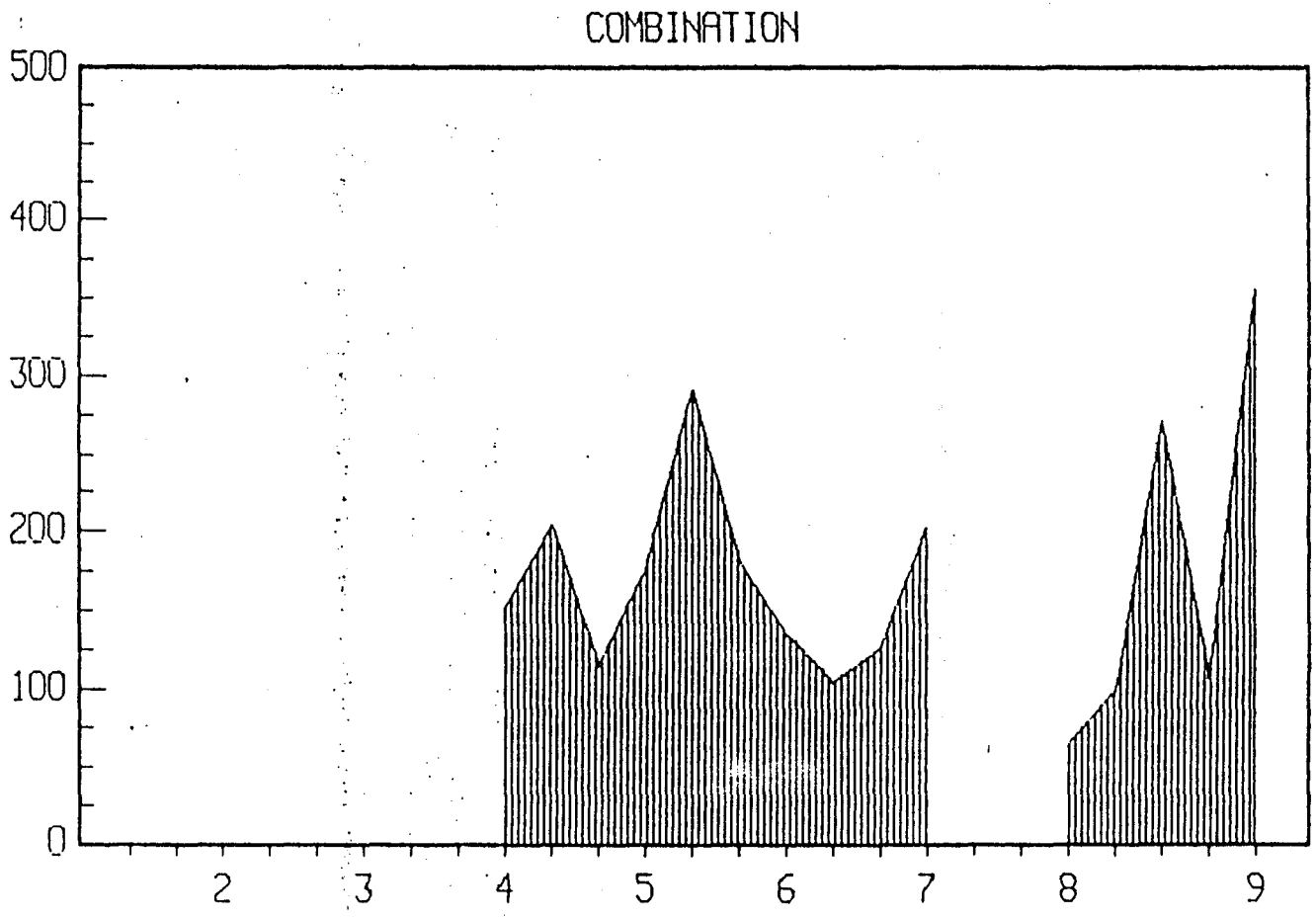



FIGURE 53. Community respiration (mg C $m^{-3}$ /hr) in the combination bag.

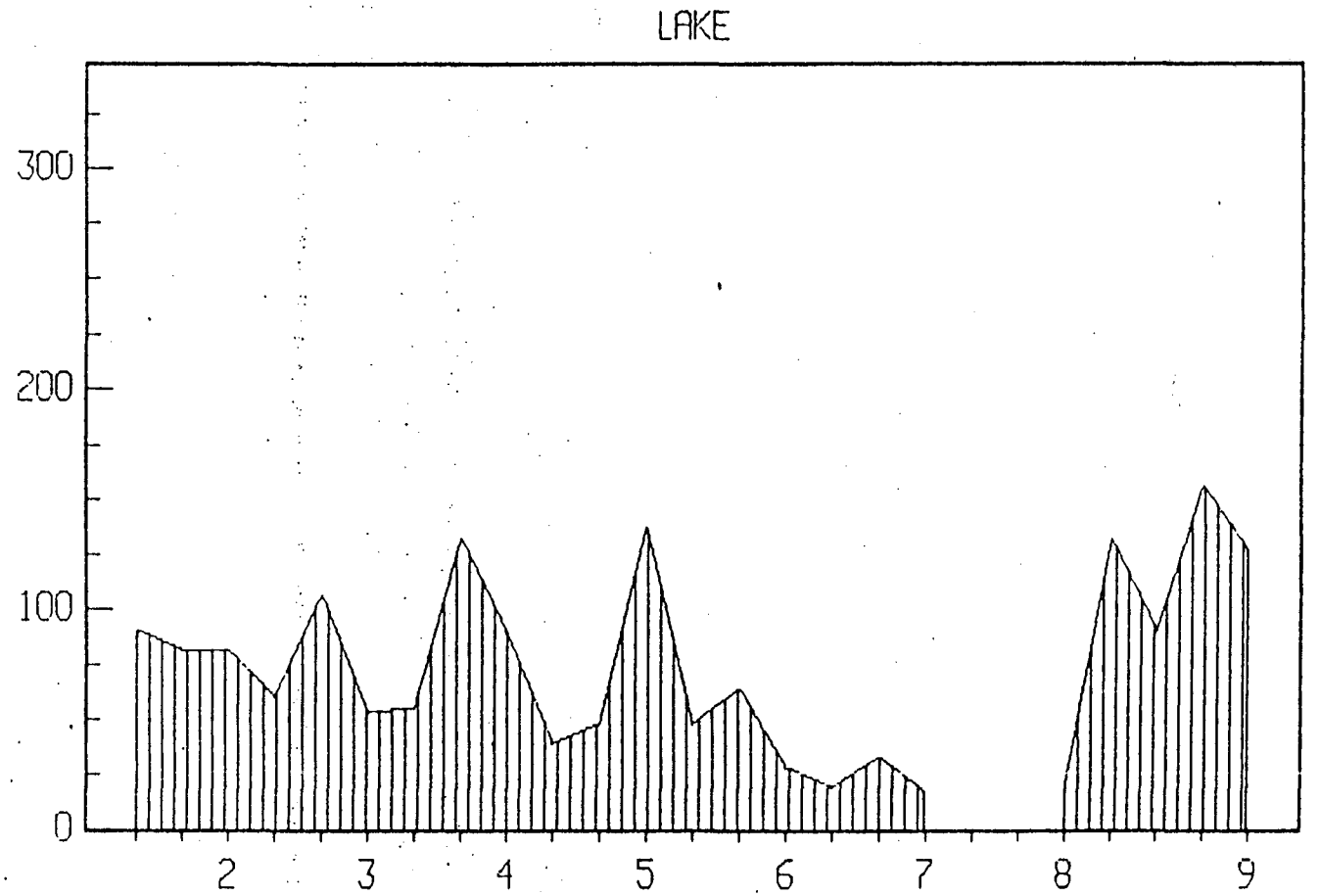



FIGURE 54. Net primary productivity (mg C $m^{3}$ /hr) at the lake station.

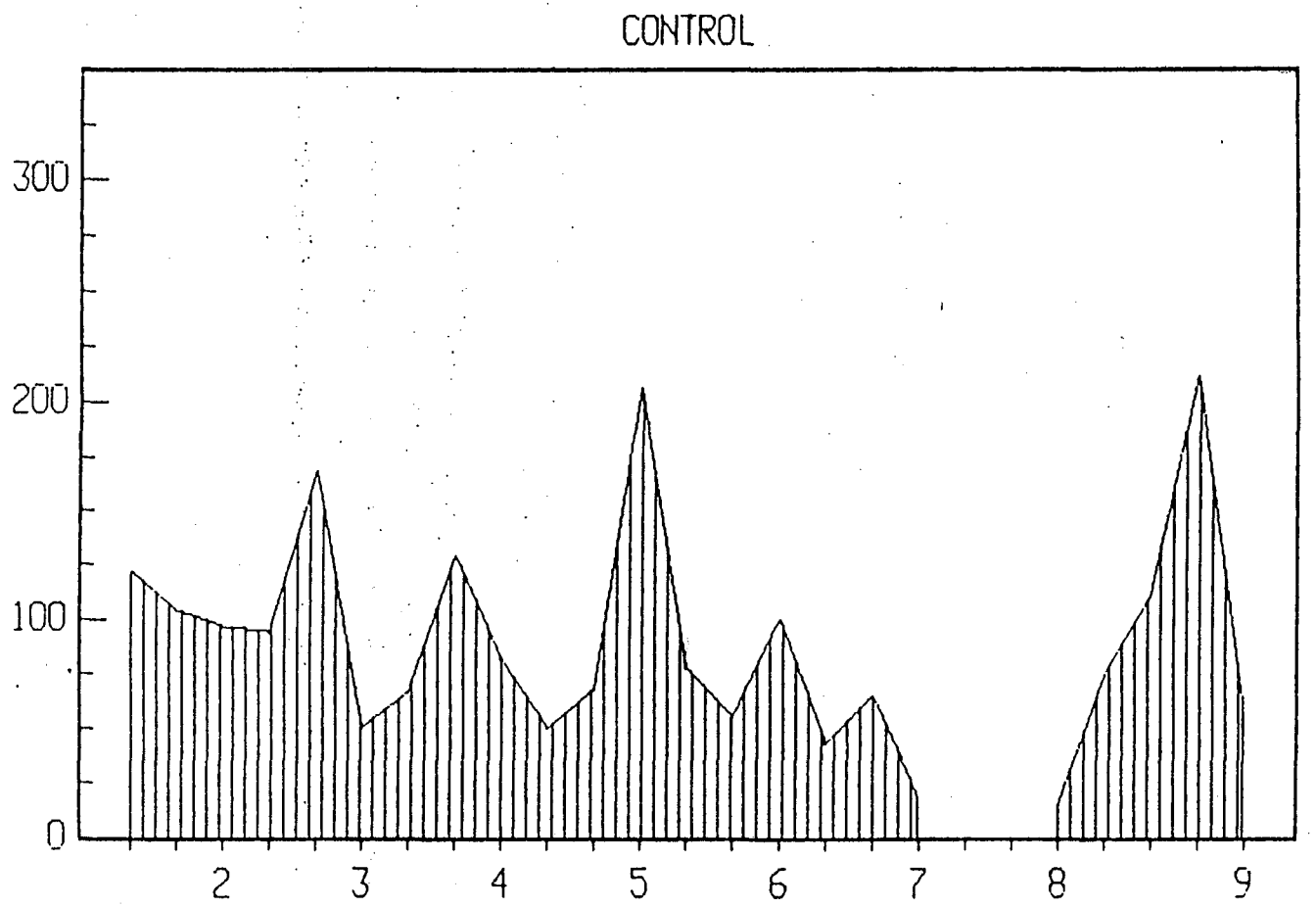



FIGURE 55. Net primary productivity (mg C $m^{-3}$ /hr) in the control bag.

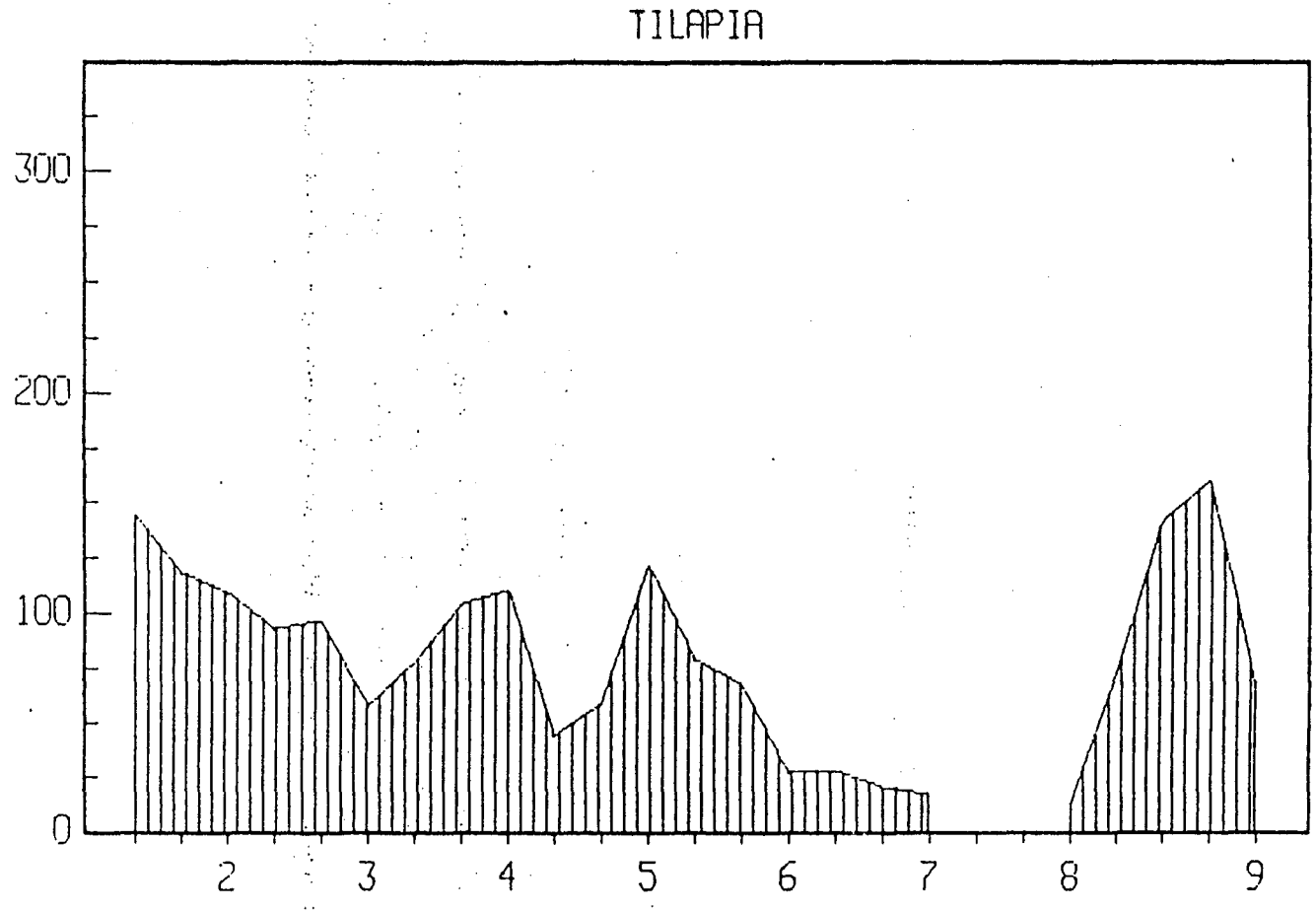



FIGURE 56. Net primary productivity (mg C $m^{3}$ /hr) in the tilapia bag.

in the middle of the study (Fig. 57).

Net primary production in the combination bag peaked during the last several days of the study (Fig. 58), and ranged from 31.6 mg C $m^3$ /hr to 246.7 mg C $m^3$ /hr. The mean for the period was 91.7 mg C $m^3$ /hr.

Ratio of Gross Primary Productivity to Community Respiration

The ratio of gross primary productivity to respiration closely tracked the gross primary productivity described previously. Maxima in the ratio were always associated with periods of elevated gross primary productivity.

The average ratio of each respective treatment were limited to between 1.53 (tilapia) and 1.64 (combination), and ANOVA indicated no statistical differences among treatments (Table 7).

## DISCUSSION

### Tilapia Feeding Ecology

Blue tilapia (Tilapia aurea), a fish native to Africa and the Middle East, was introduced into the United States as a means of controlling nuisance aquatic macrophytes (Courtenay and Robins 1973). After its original introduction the fish spread rapidly through the southeast, particularly Florida, but has been unsuccessful at controlling excessive macrophyte growth (Ware et al. 1975). There is some concern that the presence of blue tilapia reduces largemouth bass populations through competition for nesting sites or predation upon bass eggs (Noble et al. 1975).

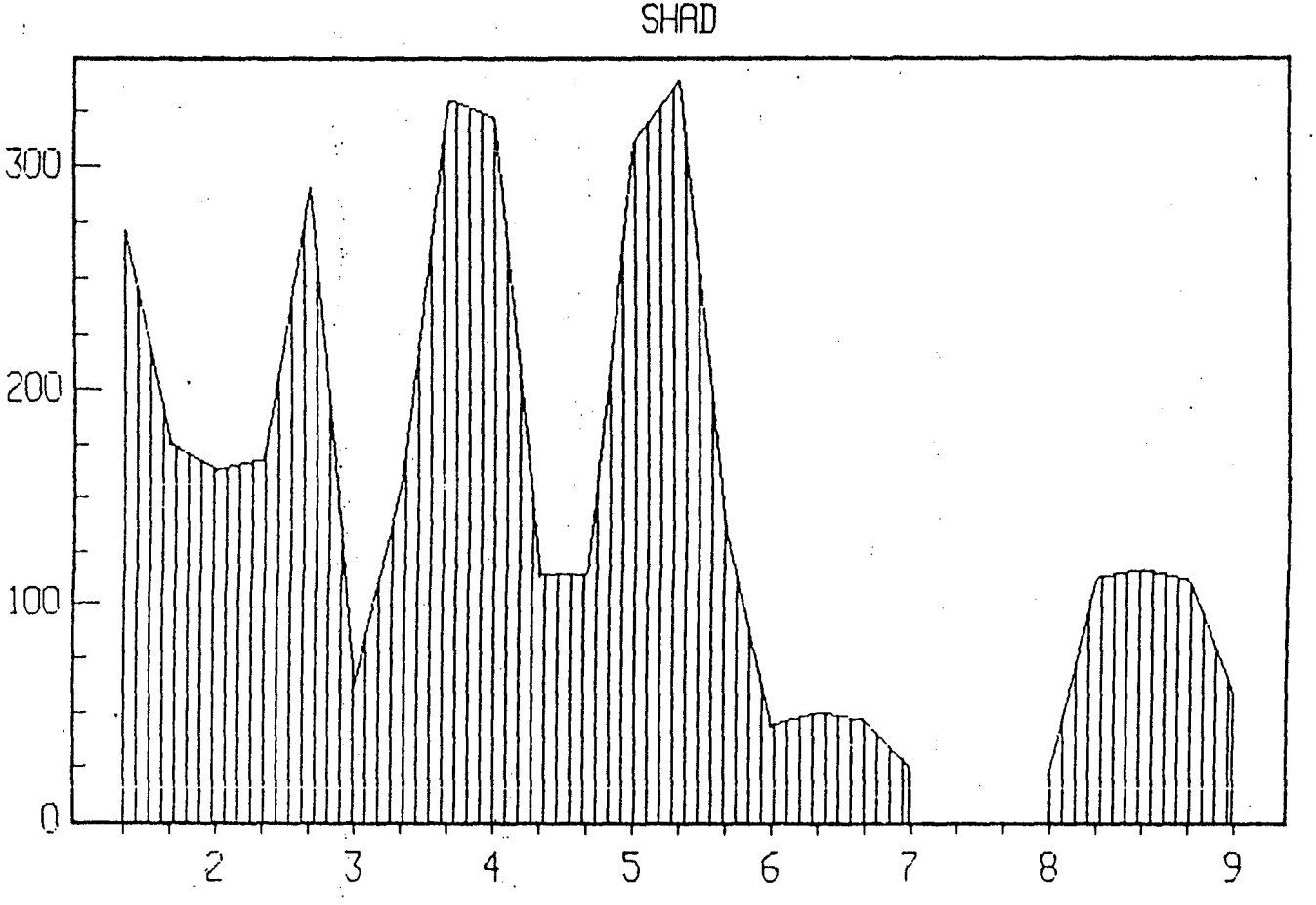



FIGURE 57. Net primary productivity (mg C $m^{3}$ /hr) in the shad bag.

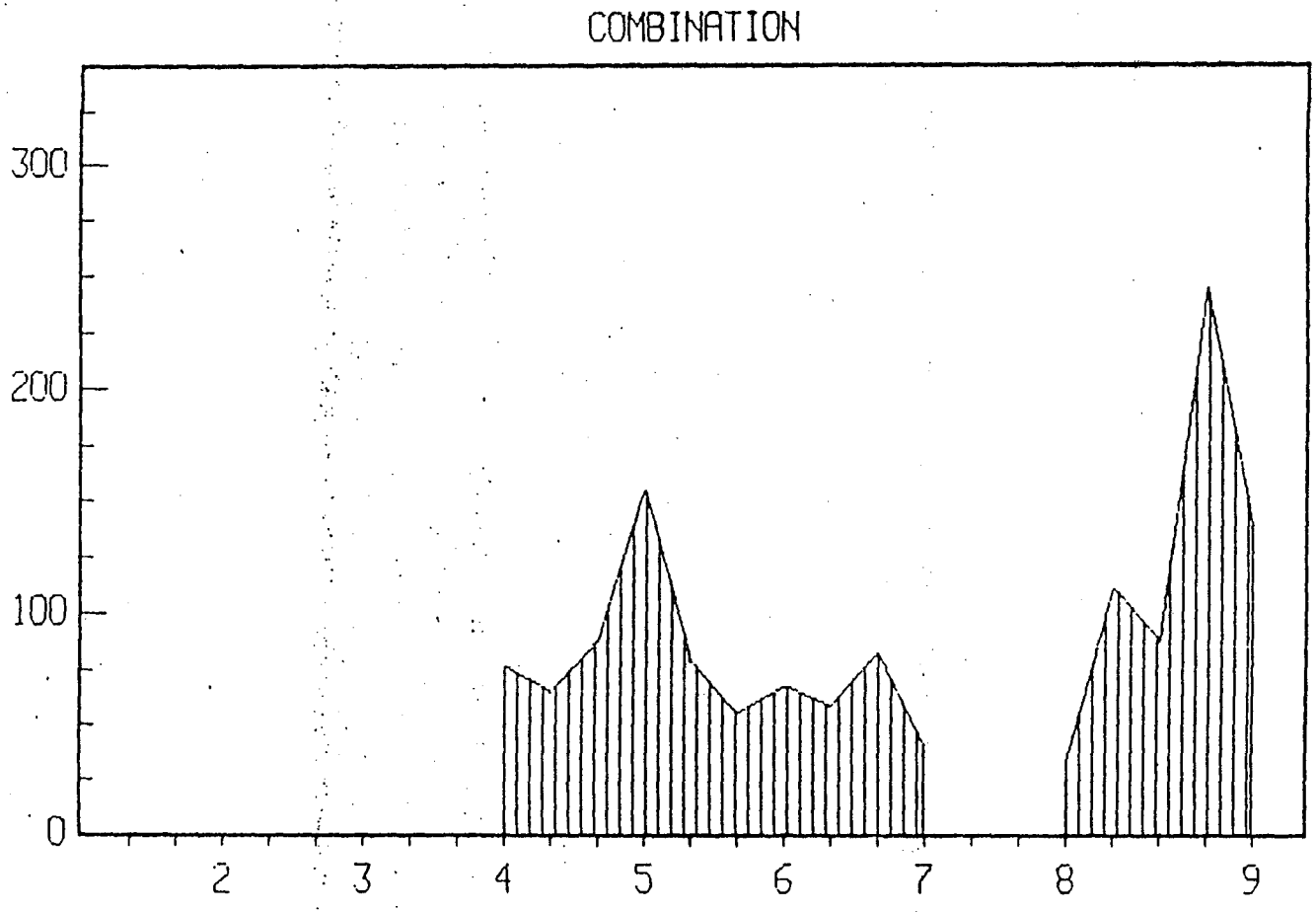



FIGURE 58. Net primary productivity (mg C $m^{3}$ /hr) in the combination bag.

Qualitative and quantitative measurements of the gut contents of blue tilapia in situ indicate that this species is an opportunistic omnivore, utilizing zooplankton (Spataru and Zorn 1978, Mallin 1986), phytoplankton (Hendricks and Noble 1980, Mallin 1986), and detritus (Hendricks and Noble 1980, Mallin 1986).

Laboratory analysis indicate that tilapia greater than 7.6 cm utilize a series of rapid suctions to draw prey into their buccal cavity. This mechanism is undirected and thus fish in this size range function as filter feeders. Tilapia smaller than 7.6 cm also function as filter-feeders, however they also feed as size selective predators on individual zooplankton species (Gophen et al. 1983).

Like shad, blue tilapia use gill rakers to strain particles from the water but also filter with small mucous-covered microbronchiosphines. These structures bear fine lateral spines and are located on the second to fourth gill arches, and are responsible for the effective small particle retention by cichlids (Fryer and Iles 1972).

Drenner et al. (1984a) demonstrated in pond studies that tilapia grazing significantly depressed the two large algas Uroglenopsis and Ceratium. In laboratory studies, blue tilapia efficiently consumed Oocystis and Navicula, but did not suppress their populations possibly due to the small size and high growth rates of the algae. The smallest phytoplankton taxa (Rhodomonas, Chrysochromulina, Chlamydomonas, Cyclotella) were enhanced in the presence of tilapia grazing activity. This enhancement was

ascribed to nutrient regeneration during gut passage and by fish excretion, as well as the accompanying compositional shifts in the herbivorous zooplankton community. Little information is available on the nutrient release and degree of algal digestion by blue tilapia, but Popma (1982) noted that some algal cells may remain viable following passage through the digestive tract of tilapia.

Drenner et al. (1984a) reported that grazing activities by blue tilapia also modify the composition of the zooplankton community. In the same ponds studies described above, the populations of Keratella were suppressed while copepodid and adult Diaptomus were enhanced. Gophen et al. (1983) reported that blue tilapia are selective feeders on Bosmina and Ceriodaphnia, taxa which have poor evasive capabilities when compared with more evasive zooplankters such as Mesocyclops.

Finally, Dickman and Nanne (1987) noted in Central American fish ponds that very high levels of tilapia (2.5 adults $m^{-2}$) suppressed zooplankton populations and increased the fraction of the bluegreen alga Microcystis aeruginosa.

## Feeding Ecology of Gizzard Shad

Drenner et al. (1986) have determined that feeding rates of gizzard shad increase with particle size. Spherical algae and zooplankton > 40 um are the most strongly suppressed plankton components in the presence of shad. The overall effect of shad grazing was to stimulate the phytoplankton community and to decrease secchi disk transparency. Shad primarily suppress most

cladocerans, and some rotifer and copepod species.

Gizzard shad are not site-selctive predators, but instead utilize a series of rapid suctions to draw water into the buccal cavity where prey items may be strained through the gill rakers (Drenner et al. 1978). The minimum and maximum particle sizes filtered by shad shifts upward with larger fish size, and therefore as the fish mature they become more dependent on zooplankton as this ingestion range increases. This shift in the range of filtered particles is probably related to increases in the spacing between gill rakers associated with growth (Mummert and Drenner 1986). Thus, there are similarities in the feeding mechanisms utilized by both species.

Shad do not effectively graze more evasive zooplankton such as Diaptomus (Drenner et al. 1978), particularly during the summer months, although other evasive herbivores may be simultaneously depressed (Drenner et al. 1982a). Many common algal taxa remain viable after gut passage through the digestive tract of shad, especially blue-greens (Velasquez 1939, Smith 1963, Crisman and Kennedy 1982).

It has been assumed that the enhancement of phytoplankton populations by shad grazing is an indirect effect caused by suppression of herbivorous zooplankton (Threlkeld 1987). Shad may also enhance phytoplankton populations directly by providing a larger quantity of highly assimilible nutrients from their digestive products (Crisman and Kennedy 1982). In addition, phytoplankton communities may be enhanced by nutrient release from dead shad, particularly in lakes where Dorosoma suffer large

population crashes (Adams et al. 1985).

Kutkuhn (1957) observed that the increase in the-young-of-the-year shad coincided with decreases in objectionable blue-green algae. Drenner et al. (1986) have suggested, however, that although shad may in fact efficiently graze some large algal species (e.g. Ceratium), they are not effective grazers in phytoplankton communities dominated by small nannoplankton or filamentous or colonial blue-greens (Drenner et al. 1982b, Drenner et al. 1984b). Consequently, young-of-the-year shad may exert some grazing pressure on undesirable algae during the spring, but the temporal positive effects of juvenile shad grazing on the phytoplankton community are more than offset by the indirect enhancement of phytoplankton communities as the fish mature.

## Biomanipulation of Fish Populations for Algal Control: The Temperate Experience

The hypothesis that planktivorous fish strongly influence the size distribution and taxonomic composition of limetic zooplankton communities has been well documented (Brooks and Dodson 1965, Stenson et al. 1978, Lynch 1979, Shapiro and Wright 1984). When zooplanktivorous fish are in high densities, small bodied herbivores and predatory copepods typically dominate the community. Conversely, large-bodied herbivores are the major component of the zooplankton population in the absence of zooplanktivores.

Grazing pressure by herbivorous zooplankton may strongly

influence the quality and quantity of the phytoplankton standing crop (Gliwizc 1977, Lynch and Shapiro 1981, Shapiro and Wright 1984). These large-bodied grazers preferentially feed upon small algae which approximate spheroids - cryptomonads, phytoflagellates, and some diatoms (Porter 1977), allowing net plankton to assume dominance despite their relatively slow generation time (Stenson et al. 1978). Included in this latter size group are problem algae such as colonial blue-greens which are less desirable food items for herbivorous zooplankton due to their poor palatability and larger size (Porter 1977).

Shapiro and Wright (1984) reported that reduction of fish populations by rotenone increased the average size of the zooplankton in Round Lake, Minnesota. Concurrent with this increase in zooplankton size, decreases were found in the mean epilimnetic chlorophyll a and total phosphorous concentrations.

Pace (1984) has demonstrated for a suite of north temperate lakes that increases in the mean size of zooplankton have a weak but statistically significant negative influence on the chlorophyll a to total phosphorous relationship. McQueen et al. (1986) and Edmondson and Litt (1982) similarly have underscored the significance of Daphnia > 1mm to an inverse relationship with algal standing crops. Finally, Threlkeld and Drenner (1987) have shown that zooplanktivory upon large cladocerans will have an immediate negative effect on phytoplankton populations while shad predation on small-bodied cladocerans is not likely to enhance algal communities. These studies provide indirect evidence that herbivorous zooplankton may exert some effect on phytoplankton

biomass. Zooplankton communities dominated by microzooplankton (rotifers, nauplii, ciliates) tend to have more chlorophyll a per unit phosphorous than those systems with larger proportions of macrozooplankton (Pace 1984).

Seasonal declines in zooplankton biomass and compositional shifts are frequently associated with blooms of cyanophytes such as Microcystis (Gliwicz 1977, Infante and Riehl 1984). Included among the mechanisms which likely contribute to these zooplankton declines are the production of toxins by the blue-greens (Lampert 1982), poor nutritional value (Holm and Shapiro 1984), and interference with filtration activities by colonial forms (Gliwicz 1977, Porter 1977). It has been suggested the inhibitory effects of Microcystis are less effective on small-bodied cladocerans when compared to larger daphnids (Lampert 1982), although at very high densities of Microcystis all sizes of cladocerans are suppressed (Fulton and Paerl 1987).

Copepods appear to be generally less inhibited by Microcystis because of their more refined selectivity in food (Fulton and Paerl 1987).

Population peaks of Microcystis frequently increase in subtropical lakes during the summer concurrent with calanoid copepods while cladoceran maxima occur in the spring and fall (Tuschall et al. 1979, Jarvis 1986). This juxtapositioning of algal species and cladoceran populations strongly suggests that an antagonistic relationship exists between the two groups. It

is therefore unlikely that small-bodied cladocerans can effectively control problem algae such as Microcystis.

The mechanism which excludes large-bodied cladocerans from subtropical and tropical lakes is likely the lack of severe environmental fluctuations more typical of northern climates. This stability, particularly in tropical regions, favors reduced phytoplankton diversity and domination by blue-greens. The absence of successional phenomena also favors small-bodied cladocerans which are more competitive when edible food sources are in poor supply (Foran 1986).

Biomanipulation as a Management Tool for Lake Apopka

It is clear from our enclosure experiments that filter-feeding by tilapia have an enhancing effect on the size distribution and taxonomic composition of the zooplankton communities in Florida lakes. Despite the elevated densities of several cladoceran species in the tilapia treatment, no discernible differences were evident in chlorophyll, nutrient concentrations or water clarity. This observation is consistent with the results of Crisman et al. (1986) which demonstrated that dramatically increasing the abundance of cladocerans in hypereutrophic Florida lakes only minimally impacts the composition and abundance of the phytoplankton community and does not lead to an observable improvement in water quality. The large increase in cladoceran biomass in the tilapia bags is in some disagreement with the studies cited earlier, but it must be underscored that our subtropical species assemblage differs from

the cladocerans used in these studies. In addition, since this fish as been characterized as an 'opportunistic omnivore' (Mallin 1986) its food preferences may be highly variable.

Likewise, it is equally apparent that the zooplankton grazing by gizzard shad is considerable when Dorosoma biomass is elevated four to five times that found in situ. This trend is in basic agreement with the known feeding ecology of Dorosoma with cladocerans being grazed by shad, particularly in comparison to the tilapia treatment. However the relationship between zooplankton populations and phytoplankton biomass is essentially identical to that seen in the tilapia treatment. Detailed algal data was unavailable at the time this report was prepared, but chlorophyll a fractionization strongly suggests that algal grazing in Florida lake by both tilapia and gizzard shad, whether through direct or indirect mechanisms, result in a phytoplankton community dominated by net plankton. This observation further supports the contention that small-bodied cladocerans are not capable of significantly cropping algal populations in hypereutrophic lakes since the size spectra of phytoplankton particles in both types of fish communities shifts towards larger particles ineffectively grazed by endemic cladocerans.

These results are in fundamental disagreement with the biomanipulation of Round Lake, Minnesota (Shapiro and Wright 1984), and indicate that zooplankton size structure and standing crop have only minimal influence on phytoplankton biomass in Florida lakes.

Although direct and indirect effects of tilapia and shad

grazing on the phytoplankton standing crop apparently are similar, the productivity data indicates that major differences existed between the rate of primary productivity and community respiration found in the two fish communities. Gizzard shad tended to accelerate the rate of community metabolism and primary productivity in comparison to tilapia. In addition, there is some evidence that the shad bags had comparatively higher rates of nutrient turnover. Although no apparent differences in phytoplankton standing crops between treatments were observed, it is important to note that the phytoplankton assemblage of Lake Apopka is likely light-limited due to the relatively small photic zone, and therefore the lack of significant differences in the amount of total algal biomass is not suprising. If gizzard shad function to increase productivity and re-mineralization in the plankton, it is probable that their effects on water quality and phytoplankton communities would be more deleterious in lakes of lower trophy and less light-limited than Apopka. Conversely, since it appears that tilapia retard nutrient flow and depress community metabolism in contrast to shad, lakes dominated by the former fish would be expected to have higher water quality and a smaller phytoplankton biomass at the same nutrient concentration provided light is not strongly limiting.

Considered from a theoretical viewpoint, bottom-up (producer controlled) and top-down (consumer controlled) forces structure the biomass and size distribution of each trophic compartment. McQueen et al. (1986) present convincing evidence that in eutrophic lakes top-down forces are strongest for

piscivore--zooplankton, less strong for planktivore--zooplankton, and are negligible for zooplankton--phytoplankton. Evidence from empirical studies (Post and McQueen 1987, Vanni 1987) indicates that only the bottom or the top of the food web responds strongly to alterations in food web organization, and with each succeeding 'trophic cascade' the response becomes more reduced.

According to the trophic cascade hypothesis, planktonic productivity is established by both biotic and abiotic factors (Carpenter et al. 1985). Potential system productivity is determined by abiotic mechanisms such as solar insolation, nutrient concentrations and degree of mixing. Realized productivity is regulated by the structure of the food web.

Evidence from empirical studies indicate that a one-to-one relationship exists between zooplankton biomass and primary productivity (Carpenter et al. 1985, Berquist and Carpenter 1986, Carpenter and Kitchell 1987), however they may positively or negatively correspond depending upon food web structure and the strength of trophic level interactions (e.g. the presence of grazer-adapted phytoplankters) (Carpenter et al. 1987).

Lakes with comparable nutrient supplies but differing food web hierarchies may have significant differences in primary productivity (Carpenter et al. 1985). Although this theory was developed from lakes in the north temperate zone is based on the 'traditional' piscivore--planktivore--zooplankton--phytoplankton food web, it nevertheless is applicable to the biomanipulation of Lake Apopka and other eutrophic Florida lakes. In this study, fish populations were manipulated such that plankton communities

with tilapia as the top planktivore experienced a 3x increase in the herbivorous zooplankton compared to shad and control communites. Despite this increase, no major differences occurred in total phytoplankton biomass. This is consistent with the trophic cascade hypothesis -- in productive lakes the largest response to food web alteration should be observed in the biomass at the next lower trophic level (zooplankton) and be considerably dampened at the next lowest trophic level (phytoplankton). However the substantial differences between treatments in nutrient re-mineralization and primary productivity suggests that alteration of food web structure by biomanipulation in Florida lakes will effect water quality, especially in those systems with moderate nutrient concentrations in comparison to Lake Apopka.

Finally, the wide fluctuations in dissolved oxygen content in the shad bag indicate that their grazing activities may cause higher fish mortality and a reduction in water quality. The elevated dissolved oxygen levels ($>20$ mg $l^{-1}$) reported here for the shad bag have been observed in Lake Apopka before, and have been related to gas embolisms in the circulatory systems of fish. This physiological phenomenon has been implicated with massive fish kills, including gamefish, and is coincident with supersaturation of dissolved oxygen in the water column. Subsequent to these fish kills, large phytoplankton blooms have been recorded in the lake and are believed to have been fueled by the large increase in nutrients associated with fish decomposition (Brezonik et al. 1978). At the other extreme, very low dissolved oxygen concentrations may also directly cause fish

mortality through asphyxiation.

The wider range of dissolved oxygen levels encountered in the shad bag is likely connnected with the highly assimilable and loose nature of the gizzard shad excreta. It may be hypothesized that during the day the dissolved oxygen values are maximal due to the photosynthetic activity of phytoplankton with a large amount of available nutrients, and conversely, the dissolved oxygen at night is greatly reduced because of the rapid respiration associated with decomposition of the loose excreta. Consequently, more degradable fish excretions should produce wider fluctuations in water column dissolved oxygen concentrations through increased rates of respiration and photosynthesis, respectively.

## CONCLUSIONS AND RECOMMENDATIONS

In view of the evidence presented in this report, it seems possible that biomanipulation of fish populations in Florida lakes can lead to a significant improvement in water quality. This statment, however, must be qualified in that our study was limited to one season, was conducted over a short temporal span and a complete analysis of the phytoplankton data relative to the zooplankton and chemistry has not been undertaken. A similar enclosure experiment performed during another season, preferably with replicate productivity data, would provide substantial evidence elucidating the nature of the filter-feeder -- zooplankton -- phytoplankton relationship for Florida systems.

Our experiment does provide evidence that the effects of

shad and tilapia on plankton community metabolism differed greatly. Although both filter-feeders possess similar grazing and digestive mechanisms, tilapia did not suppress the native cladoceran assemblage, and in fact enhanced their populations. The presence of shad caused wider fluctuations in daily dissolved oxygen concentrations, especially when compared to tilapia, which may stress or kill desirable game fish. There are also indications that the grazing activities of shad promote mineralization and accelerate phosphorous recycling as has been observed in other mesocosms (Crisman and Kennedy 1982, Drenner et al. 1986a).

The dramtically elevated primary productivity and community respiration of the shad bag, combined with the higher assimilable nutrient levels, suggests that in Florida systems which are not as nutrient enriched than Lake Apopka, biomanipulation can be a mitigating factor for cultural eutrophication if blue tilapia is allowed to replace gizzard shad.

Since the zooplankton communities of the tilapia treatment contained 2-4 times the biomass of herbivorous zooplankton than would be expected in a Florida lake of comparable trophy, it is difficult to consider modification of fish populations as a restoration technique in subtropical and tropical systems dominated by small-bodied cladoceran assemblages if it is assumed that the increased abundance of these herbivores will directly reduce phytoplankton standing crops through grazing pressure.

## REFERENCES

Adams, S.M., J.E. Breck and R.B. McLean. 1985. Cumulative stress-induced mortality of gizzard shad in a southeastern U.S. reservoir. Environ. Biol. Fishes 13: 103-112.

American Public Health Association. 1982. Standard methods, 15th edition, Public Health Association, Washington, DC.

Bays, J.S. and T.L. Crisman. 1983. Zooplankton and trophic state relationships in Florida lakes. Can. J. Fish. Aquat. Sci. 40: 1813-1819.

Beaver, J.R. and T.L. Crisman. 1982. The trophic response of ciliated protzoans in freshwater lakes. Limnol. Oceanogr. 27: 246-253.

Beaver, J.R. and T.L. Crisman. 1988. Analysis of the community structure of planktonic ciliated protozoa relative to trophic state in Florida lakes. Hydrobiologia: in press.

Beaver, J.R., T.L. Crisman and R.W. Bienert. 1988. Distribution of planktonic ciliates in highly coloured subtropical lakes: comparison with clearwater ciliate communities and the contribution of myxotrophic taxa to total autotrophic biomass. Freshwat. Biol. 20: in press.

Berquist, A.M. and S.R. Carpenter. 1986. Limnetic herbivory: effects on phytoplankton populations and primary production. Ecology 67: 1351-1360.

Bratbak, G. and I. Dundas. 1984. Bacterial dry matter content and biomass estimation. Appl. Environ. Micro. 48: 755-757.

Brezonik, P.L., C.D. Pollman, T.L. Crisman, J.N. Allinson and J.L. Fox. 1978. Limnological studies on Lake Apopka and the Oklawaha Chain of lakes: 1. Water quality in 1977. Report submitted to Florida Department of Environmental Regulation, 283 pp.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size and composition of plankton. Science 150: 28-35.

Carpenter, S.R., J.F. Kitchell and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

Carpenter, S.R. and J.F. Kitchell. 1987. The temporal scale of limnetic primary production. Am. Nat. 129: 417-433.

Carpenter, S.R., J.F. Kitchell, J.R. Hodgson, P.A. Cochran, J.J. Elser, D.M. Lodge, D. Kretchmer, X. He and C.N. von Ende. 1987. Regulation of lake primary productivity by food web structure. Ecology 68: 1863-1876.

Courtenay, W.R. and C.R. Robins. 1973. Exotic aquatic organisms in Florida with emphasis on fishes: a review and recommendations. Trans. Am. Fish Soc. 102: 1-12.

Crisman, T.L. and H.M. Kennedy. 1982. The role of gizzard shad (Dorosoma cepedianum) in eutrophic Florida lakes. Publication No. 64, Water Resources Research Center, University of Florida, Gainesville, FL, 83pp.

Crisman, T.L., J.A. Foran, J.R. Beaver, A.E. Keller, P.D. Sacco, R.W. Bienert, R.W. Ruble and J.S. Bays. 1986. Algal control through trophic-level interactions: investigations at Lakes Wauberg and Newnans, Florida. Report submitted to the Florida Department of Natural Resources, 178 pp.

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

Dickman, M. and H. Nanne. 1987. Impact of tilapia grazing on plankton composition in artifical ponds in Guanacaste Province, Costa Rica. J. Freshwat. Ecol. 4: 93-100.

Drenner, R.W., J.R. Strickler and W.J. O´Brien. 1978. Capture probability: the role fo zooplankter escape in the selctive feeding of planktivorous fish. J. Fish. Res. Bd. Can. 35: 1370-1373.

Drenner, R.W., F. deNoyelles and D. Kettle. 1982a. Selective impact of filter-feeding gizzard shad on zooplankton community structure. Limnol. Oceanogr. 27: 965-968.

Drenner, R.W., W.J. O´Brien and J.R. Mummert. 1982b. Filter-feeding rates of gizzard shad. Trans. Amer. Fish. Soc. 111: 210-215.

Drenner, R.W., S.B. Taylor, X. Lazzaro and D. Kettle. 1984a. Particle-grazing and plankton community impact of an omnivorous cichlid. Trans. Am. Fish. Soc. 113: 397-402.

Drenner, R.W., J.R. Mummert, F. deNoyelles and D. Kettle. 1984b. Selective particle ingestion by a filter-feeding fish and its impact on phytoplanton community structure. Limnol. Oceanogr. 29: 941-948.

Drenner, R.W., S.T. Threlkeld and M.D. McCracken. 1986. Experimental analysis of the direct and indirect effects of an omnivorous filter-feeding clupeid on plankton community structure. Can. J. Fish. Aquat. Sci. 43: 1935-1945.

Dumont, H.J., I. Vand deVelde and S. Dumont. 1975. The dry weight estimate of biomass in a selction of cladocera, copepods, and rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75-97.

Edmondson, W.T. (ed.). 1959. Freshwater biology, 2nd edition, Wiley Interscience, London.

Edmondson, W.T. and A. Litt. 1982. Daphnia in Lake Washington. Limnol. Oceanogr. 27: 272-293.

E.P.A. 1979a. Environmental impact statement - Lake Apopka Restoration Project, Lake and Orange Counties Florida. United States E.P.A., Region 4, Atlanta, GA, 445pp.

E.P.A. 1979b. Methods for chemical analysis of water and wastes. United States E.P.A, Cincinnati, OHIO, 298pp.

Foran, J. A. 1986. The relationship between temperature, competition and the potential for colonization of a subtropical pond by Daphnia magna. Hydrobiologia 134: 103-112.

Fryer, G. and T.D. Iles. 1972. The cichlid fishes of the great lakes of Africa. T.F.H. Publications, Neptune City, NJ.

Fulton, R.S. and H.W. Paerl. 1987. Toxic and inhibitory effects of the blue-green alga Microcystis aeruginosa on herbivorous zooplankton. J. Plank. Res. 9: 837-855.

Gates, M.A., A. Rogerson and J. Berger. 1982. Dry to wet weight biomass conversion constant for Tetrahymena elliotí (Ciliophora, Protozoa). Oecologia 55: 145-148.

Gliwicz, Z.M. 1977. Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake. Ekol. Pol. 25: 179-225.

Good, J.A. 1984. A biomanipulation experiment in Green Lake, Seattle, Washington. Arch. Hydrobiol. 102: 137-153.

Gophen, M., R.W. Drenner and G.L. Vinyard. 1983. Cichlid stocking and the decline of the Galilee Saint Peters Fish (Sarotherodon galilaeus) in Lake Kinneret, Israel. Can. J. Fish. Aquat. Sci. 40: 983-986.

Hendricks, M.K. and R.L. Noble. 1980. Feeding interactions of three planktivorous fishes in Trinidad Lake, Texas. Proc. Annu. Conf. SE Ass. Fish. Wildl. Agencies 33: 324-330.

Hobbie, J.E., R.J. Daley and S. Jasper. 1977. Use of nucleopore filters for counting bacteria by fluorescence microscopy. Appl. Environ. Micro. 33: 1225-1228.

Holm, N.P. and J.S. Shapiro. 1984. An examination of lipid reserves and the nutritional status of Daphnia pulex fed Aphanizomenon flos-aquae. Limnol. Oceanogr. 29: 1137-1140.

Infante, A. and W. Riehl. 1984. The effect of Cyanophyta upon zooplankton in a eutrophic tropical lake. Hydrobiologia 113: 293-298.

Jarvis, A.C. 1986. Zooplankton community grazing in a hypereutrophic lake (Hartbeespoort Dam, South Africa). J. Plank. Res. 8: 1065-1078.

Kahl. A. 1930-1935. Wimpertiere oder Ciliata (Infusoria). Tierwelt Deutschlands 26: 18, 21, 25, 30. 886 pp. Fischer.

Kutkuhn, J.H. 1957. Utilization of plankton by juvenile gizzard shad in a shallow prairie lake. Trans. Am. Fish Soc. 87: 80-103.

Lampert, W. 1982. Further studies on the inhibitory effect of the toxic blue-green Microcystis aeruginosa on the filtering rate of zooplankton. Arch. Hydrobiol. 95: 207-220.

Lowe. E., J. Adams, J. Bateman, C. Fall, D. Graetz, J. Hulbert, W. Ingram, A. Jenab, W. Johnson, P. Muller, L. Noll, R. Reddy, L. Snyder and V. Williams. 1986. Lake Apopka restoration progress report and recommendations. Report submitted to the 1987 Florida Legislature, 71 pp.

Lynch, M. 1979. Predation, competition and zooplankton community structure: an experimental study. Limnol. Oceaongr. 24: 253-272.

Lynch, M. and J. Shapiro. 1981. Predation, enrichment, and phytoplankton community strucutre. Limnol. Oceanogr. 26: 86-102.

McQueen, D.J., J.R. Post and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43: 1571-1581.

Mallin, M.A. 1986. The feeding ecology of the blue tilapia (T. aurea) in a North Carolina reservoir. pp. 323-326, in: Lake and reservoir management, Volume 2.

Maslin, P.E. 1969. Population dynamics and productivity of zooplankton in two sandhill lakes. Ph.D dissertation, University of Florida, Gainesville, FL.

Mummert, J.R. and R.W. Drenner. 1986. Effects of fish size on the filtering and selective particle ingestion of a filter-feeding clupeid. Trans. Amer. Fish. Soc. 115: 522-528.

Noble, R.L., R.D. Germany and C.R. Hall. 1975. Interactions of blue tilapia and largemouth bass in a power plant cooling reservoir. Proc. Annu. Conf. SE Game Fish. Comm. 29: 247-251.

Odum, H.T. and C.M. Hoskin. 1958. Comparative studies on the metabolism of marine waters. Publs. Inst. Mar. Sci. Univ. Texas 5: 15-46.

Pace, M.L. 1984. Zooplankton community structure, but not biomass, influences the phosphorous-chlorophyll a relationship. Can. J. Fish. Aquat. Sci. 41: 1089-1096.

Popma, T.J. 1982. Digestibility of selected feedstuffs and naturally occurring algae by Tilapia. Ph.D. dissertation, Auburn University, Auburn, AL.

Porter, K.G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244: 179-180.

Porter, K.G. 1975. Viable gut passage of gelatinous green algae ingested by Daphnia. Verh. Int. Verein. Limnol. 19: 2840-2850.

Porter, K.G. 1977. The plant-animal interface in freshwater ecosystems. Amer. Sci. 65: 159-170.

Post, J.R. and D.J. McQueen. 1987. The impact of planktivorous fish on the structure of a plankton community. Freshwat. Biol. 17: 79-89.

Ruttner-Kolisko, A. 1974. Plankton rotifers: biology and taxonomy. Die binnengewasser 26: 1-146.

SAS Institute, Inc. 1985. SAS user's guide: statistics. SAS Institute, Inc.

Schoenberg, S.A. and R.E. Carlson. 1984. Direct and indirect effects of zooplankton grazing on phytoplankton in a hypereutrophic lake. Oikos 42: 291-302.

Shapiro, J. 1979. The need for more biology in lake restoration, pp. 161-167, in: Lake restoration, United States E.P.A., Office of Water Planning and Standards, Washington, DC, 254 pp.

Shapiro, J. and D.I. Wright. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwat. Biol. 14: 371-383.

Smith, A. 1976. Some aspects of trophic relations of gizzard shad, Dorosoma cepedianum. Ph.D dissertation, Virginia Polytechnic Institute and State University, 88 pp.

Smith, V.H. 1982. The nitrogen and phosphorous dependence of algal biomass in lakes: an empirical and theoretical analysis. Limnol. Oceanogr. 27: 1101-1112.

Smith, W.L. 1963. Viable algal cells from the gut of the gizzard shad Dorosoma cepedianum (LeSeur). Proc. Okla. Acad. Sci. 43: 148-149.

Sorokin, Y.I. and H. Kadota. 1972. Microbial production and decomposition in fresh waters. IBP Handbook No. 23, Blackwell, Oxford.

Spataru, P. and M. Zorn. 1978. Food and feeding habits of Tilapia aurea (Steindachner) (Cichlidae) in Lake Kinneret (Israel). Aquaculture 13: 67-79.

Stenson, J.A.E., T. Bohlin, L. Henrikson, B.I. Nilsson, H.G. Nyman, H.G. Oscarson and P. Larsson. 1978. Effects of fish removal from a small lake. Verh. Internat. Verein. Limnol. 20: 794-801.

Threlkeld, S.T. 1987. Experimental evaluation of trophic-cascade and nutrient-mediated effects of planktivorous fish on plankton community structure. pp. 171-183, in: Predation: direct and indirect impacts on aquatic communities, University Press of New England, Hanover, NH.

Threlkeld, S.T. and R.W. Drenner. 1987. An experimental mesocosm study of residual and contemporary effects of an omnivorous, filter-feeding clupeid on plankton community structure. Limnol. Oceanogr. 32: 1331-1341.

Tuschall, J.R., T.L. Crisman, P.L. Brezonik and J.N. Allinson. 1979. Limnological studies on Lake Apopka and the Oklawaha Chain of Lakes 2. water quality in 1978. Report submitted to the Florida Department of Environmental Regulation, 114 pp.

Vanni, M.J. 1987. Effects of nutrients and zooplankton size on the structure of a phytoplankton community. Ecology 68: 624-635.

Velasquez, G.T. 1939. On the viability of alga obtained from the digestive tract of the gizzard shad, Dorosoma cepedianum (LeSeur). Am. Midl. Nat. 22: 376-412.

Ward, W.J., G.A. Perrot and D.G. Iredale. 1985. Fish waste as silage for use as an animal feed supplement. Can. Ind. Rep. Fish. Aquat. Sci. 158: 1-10.

Ware, F.J., R.D. Gasaway, R.A. Martz and T.F. Drda. 1975. Investigations of herbivorous fishes in Florida. pp. 79-84 in: Water quality management through biological control. Report No. ENV-07-75-1. Department of Environmental Engineering Sciences, University of Florida, Gainesville, FL.