THE ROLE OF ZOOPLANKTON - PHYTOPLANKTON COMMUNITY INTERACTIONS IN THE NUTRIENT DYNAMICS OF LAKE CHAPALA, MEXICO

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ABSTRACT

I investigated ammonia nitrogen (NH_3-N) regeneration and grazing by zooplankton and their effects on phytoplankton production and biomass. Two sets of experiments were conducted on samples from Lake Chapala, Mexico from September through December, 1983. One set of experiments was designed to measure zooplankton NH_3-N regeneration, and the other set was designed to measure the effects of zooplankton on phytoplankton production, biomass, and production efficiency (P/B).

Lake Chapala is a large, shallow, tropical lake with a wet season from late May to September, and a dry season the remainder of the year. I sampled four stations, representing major lake regions, five times each to provide water and organisms for 20 experimental series. Samples were returned to the laboratory for enclosure experiments incubated in a large heated outdoor tank for 3 to 5 days. Polyethylene enclosures retained and/or excluded zooplankton.

Six species of cladocerans were found in samples from Lake Chapala, with Ceriodaphnia pulchella as the

most abundant. Only two species of copepods occurred, but they were more abundant than the cladocerans. The most frequently encountered species was Diaptomus albuquerquensis at an average density of 31.48 per liter.

Zooplankton NH_3-N regeneration accounted for 14.5% of ambient NH_3-N concentration, for an average turnover time of 7.8 days. Regeneration provided an average of 33.0% of NH_3-N uptake by phytoplankton and 93.4% of the estimated nitrogen required for phytoplankton production.

Zooplankton NH_3-N regeneration significantly contributed to the NH_3-N pool but did not supply enough nitrogen to maintain phytoplankton production at all times during the study. Zooplankton NH_3-N regeneration was greatest in September when ambient nitrogen concentrations were highest.

The effect of zooplankton on phytoplankton production, biomass, and P/B ratio was less clear than the effect of zooplankton in NH_3-N regeneration. Few significant differences in phytoplankton production and biomass occurred between experimental and control enclosures. The effect of zooplankton on phytoplankton production and biomass seemed to change seasonally, as NH_3-N concentrations declined.

The presence of zooplankton improved phytoplankton production efficiency (P/B) in the middle part of the study. The relative change in phytoplankton P/B ratio between experimental and control enclosures increased from September to mid-October and declined thereafter.

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LITERATURE REVIEW

The role of nitrogen as a nutrient in aquatic ecosystems is both important and complex. Although a review of literature concerning the nitrogen cycle is not the objective here, it is important to provide some perspective of nitrogen as a dynamic nutrient, which not only enters and exits aquatic systems, but is subject to utilization and molecular change within such systems as well.

Nitrogen enters aquatic systems through rainfall, runoff, and fixation of molecular nitrogen by blue-green algae (Cyanobacteria) (Brezonik 1968, 1972; Dugdale 1976; Dugdale 1965). Nitrogen is lost (temporarily or permanently) to the sediments (Kimmel 1977; Rowe et al. 1977), through denitrification (Brezonik 1968, 1972; Clasby and Alexander 1970; Gersberg 1977), by volatilization (Murphy and Brownlee 1981a) and outflow.

Within aquatic ecosystems nitrogen can readily change molecular forms (Brezonik 1972; Dugdale 1976; Gersberg et al. 1980; Kimmel and Goldman 1977). These transformations result from biological processes (Alexander 1970; Goldman and Kimmel 1978; Kimmel 1981), and are subject to seasonal variations (Bostrom 1981;

Takahashi and Saijo 1981a; Takahashi et al. 1982; Vincent et al. 1984).

Knowledge of the role of zooplankton in the regeneration of NH_3-N and the contribution of regeneration to phytoplankton uptake are important to an increased understanding of the nitrogen cycle.

Phytoplankton uptake and zooplankton regeneration are also important links in grazer - producer interactions in aquatic ecosystems and will be discussed below.

Phytoplankton Uptake of Nitrogen

Phytoplankton production requires nutrient availability. Uptake of nitrogen as NO_3-N or NH_3-N is an important process in phytoplankton production (McCarthy 1981a, 1981b). Most studies of nitrogen uptake involve marine species (Eppley et al. 1979a; Gilbert et al. 1982a; Goldman and McCarthy 1978; Sharp et al. 1980), with relatively few freshwater studies (Axler 1979).

Phytoplankton uptake of nitrogen is an enzyme mediated rate process which transports NO_3-N or NH_3-N across the cell membrane following Michaelis-Menton uptake kinetics (Dugdale and Goering 1967; Eppley and Rogers 1970; Wheeler et al. 1982a).

Phytoplankton uptake rates are affected by many factors, in addition to substrate concentration. Nitrate uptake and phytoplankton production in Castle Lake, California were stimulated by additions of a micronutrient, molybdenum (Axler et al. 1980). Uptake rates in N-limited cultures appear to decrease with growth rate (Rhee 1978) but the capacity to assimilate NO_3-N and NH_3-N increases with increased N-limitation (Eppley and Renger 1974).

Eppley et al. (1969) found low nitrate reductase activity in the presence of NH_3-N. NH_3-N is the preferred form of nitrogen even when less abundant (Gilbert et al. 1982b; Takahashi and Saijo 1981b; Toetz 1981). McCarthy et al. (1977) found that very small amounts of NH_3-N (0.5 - 1.0 ug-atom N/l) is sufficient to suppress NO_3-N utilization.

Irradiance levels also affect phytoplankton uptake rates of NO_3-N (Bates 1976) and NH_3-N (Eppley et al. 1971). Eppley et al. (1979b) found that NH_3-N uptake rates varied with irradiance, Chlorophyll a concentration, and NH_3-N concentration. Uptake rate was slow in the dark and increased with light, but intense light suppressed NH_3-N uptake (Murphy 1980).

NH_3-N uptake rates vary with phytoplankton species and growth rate. Some species are able to

exploit NH_3-N even when available for short periods (Goldman and Gilbert 1982). Garside (1981) found nitrogen uptake varied seasonally, being higher in spring and summer, lower in fall and winter. Gilbert et al. (1982c) found higher rates of NH_3-N uptake in spring and summer also, which were influenced by species succession and correlated with temperature changes.

NH_3-N is recycled rapidly (McCarthy 1972; Takahashi and Ikeda 1975). NH_3-N uptake closely follows remineralization. Phytoplankton are able to utilize NH_3-N at the rate it is produced by heterotrophic processes (Gilbert 1982). Axler et al. (1982) reported a quasi steady-state of low NH_3-N concentration due to a balance between uptake and regeneration in Castle Lake, California.

Phytoplankton growth (and uptake) may be influenced by microscale patchiness. Phytoplankton growth may be near the physiological maximum even when nutrient concentrations are low (Goldman et al. 1979). Murphy and Brownlee (1981b) found blue-green alga uptake changed in response to large oscillations in NH_3-N concentration allowing the alga to optimize uptake.

Phytoplankton uptake rates may vary even though production is constant (Goldman et al. 1981a). NH_3-N uptake processes may be "uncoupled" from

growth processes (Goldman et al. 1981b; Horrigan and McCarthy 1982). Since growth and uptake can be uncoupled, the ability of phytoplankton to utilize nutrient patches is enhanced (McCarthy and Goldman 1979). Eppley (1981) states that balanced growth is not likely and that uptake can be quite variable geographically and by time of day.

Dugdale and Goering (1967) were the first to distinguish between production from new (NO_3-N) and regenerated (NH_3-N) forms of nitrogen. They estimated that probably 10% of daily nitrogen uptake by phytoplankton was supplied by zooplankton in the Sargasso Sea, near Bermuda, whereas Olson (1980) estimated that uptake between new and regenerated forms of nitrogen was approximately equal in the Arctic Sea.

Uptake of regenerated nitrogen (NH_3-N) may account for a sizeable fraction of total nitrogen uptake. Zooplankton regeneration therefore, may be important to phytoplankton production within aquatic ecosystems.

Zooplankton Regeneration of Nitrogen

Regeneration of nutrients by grazers is an important aspect of aquatic ecosystems (Johannes 1968). Though other grazers may add to regenerated NH_3-N

(Madeira et al. 1982; Smith and Whitledge 1982) zooplankton make the largest contribution.

Like phytoplankton uptake, zooplankton regeneration is a rate process. Regeneration rates are influenced by several factors including the method(s) used to measure them (Mullin et al. 1975). Most studies utilize some type of enclosure to compensate for phytoplankton uptake by removing phytoplankton (Ganf and Blazka 1974), saturating phytoplankton uptake (Lehman 1980a), or measuring nitrogen uptake concurrently with ^{15}N (Axler et al. 1981), though even more sophisticated methods have been utilized, such as measuring excretion from a single zooplanktor (Gardner and Scavia 1981).

Zooplankton regeneration changes seasonally and with changes in metabolism (Conover and Corner 1968). NH_3-N excretion rates increase as temperature (Ganf and Blazka 1974; Mayzaud and Dallot 1973) and respiration (Mayzaud 1973b) increase. Mayzaud (1973a) found nitrogen excretion rates increased in winter to approximately twice that of spring and that the primary excretion product was NH_3-N.

The feeding state of zooplankton also affects excretion rates. Starvation of zooplankton decreases NH_3-N regeneration rates (Mayzaud 1976; Takahashi and Ikeda 1975). Herbivores excrete less nitrogen than

carnivores (Blazka et al. 1982).

These seasonal and metabolic variations affect the significance of zooplankton regeneration in aquatic systems. Smith (1978) estimated that zooplankton regeneration accounted for up to 25% of nitrogen uptake by phytoplankton off the coast of Peru. Regeneration varied with the phytoplankton bloom, the dominant zooplanktor present and zooplankton biomass fluctuations. Zooplankton regeneration off the coast of northwest Africa may supply 44% of NH_3-N demand of phytoplankton and 25% of total nitrogen in the water column (Smith and Whitledge 1977). Zooplankton regeneration in Narragansett Bay contributed only 4.4% of nitrogen required by phytoplankton on an annual basis but supplied 186% of the nitrogen required during the post bloom period by the dominant diatom (Vargo 1979).

Lake George, Uganda is a large shallow tropical lake which is seasonally stable. Zooplankton regeneration in Lake George is believed to be sufficient to supply annual phytoplankton production needs (Ganf and Blazka 1974).

Grazer - Producer Interactions

Recycling of zooplankton regenerated nutrients is an important link between zooplankton grazers and phyto-

plankton production processes. Zooplankton grazing can adversely affect phytoplankton biomass and community structure (Berman and Richman 1974; Comita 1972; Gilwicz 1975; Porter 1977), but it can also be important in nutrient regeneration (Lampert 1978; Lehman 1978).

Porter (1976) found that some algal cells can survive passage through the gut of zooplankton and can absorb nutrients leading to enhanced production after being excreted. Grazers may be a rich localized source of nutrients utilized by producers.

Zooplankton regenerated nutrients may supply a sizable fraction of daily nitrogen and phosphorus for phytoplankton production. Regenerated nutrients are rapidly taken up, so pools of dissolved nutrients remain small while turnover rates are rapid (Lehman 1980b). Recycled nutrients are rapidly sequestered by algae and contribute substantially to growth rates of cells. If cycling fluxes are intense, less algal biomass is needed to maintain a given level of productivity (Gilwicz 1976; Lehman 1980a).

Redfield (1980) found a seasonal effect of zooplankton grazing on phytoplankton production in Castle Lake, California. Grazing increased Production:Biomass ratios through nutrient recycling in mid-season (summer) but shifted toward negative effects

later in the season (fall). Both NH_3-N assimilation by phytoplankton and phytoplankton production were correlated with zooplankton regeneration in the later half of summer (Axler et al. 1981). Zooplankton NH_3-N excretion can supply a large part of phytoplankton nitrogen demand at certain times of the year in Castle Lake. Nitrogen demand by phytoplankton and NH_3-N regeneration by zooplankton fluctuated seasonally in Lake Kinneret, Israel as well (Wynne and Gophen 1986). Zooplankton supplied a monthly average of only 17-20% of estimated nitrogen required, but values ranged from 4 to 37%. Zooplankton did stimulate algal growth as measured by cell counts and especially by Chlorophyll a concentration.

Fish grazing can affect phytoplankton production other than through nutrient regeneration and recycling. Cooper (1973) found enhanced primary productivity as a result of grazing by Notropis, unrelated to nutrient regeneration. If grazing pressure was not severe, grazing decreased standing crop but production was stimulated, a compensatory effect.

Zooplankton regeneration of NH_3-N may suppress nitrogen fixation of blue-green algae in Clear Lake, California (Roth and Horne 1981). NH_3-N regeneration from zooplankton grazing primarily on non blue-

green species may be sufficient to inhibit blue-green nitrogen fixation which leads to a summer succession to more edible forms of algae.

INTRODUCTION

This research determined the importance of zooplankton NH_3-N regeneration to phytoplankton uptake and utilization, and the overall effect of zooplankton grazing and nutrient regeneration on phytoplankton production and biomass. Grazing and nutrient regeneration are important interactions between grazers and producers in aquatic environments that affect production, community structure, biomass, and nutrient dynamics. While these interactions are important to the understanding of limnetic ecology, few appropriate investigations have been done in tropical lakes, and none in Mexico.

Nutrient recycling is an important interface between producers and grazers (Johannes 1968; Lehman 1980a). Primary production declines when nutrients become limiting or unavailable. When external inputs cease, nutrient availability declines as nutrients are transported out of the system, or deposited in the sediments. Zooplankton regeneration re-supplies nutrients to the aquatic system. If nutrients can be recycled before being lost, then higher production rates can be maintained over longer periods (Axler *et al*.

1981). Grazing herbivores are a significant factor in releasing and recycling nutrients and thereby increase phytoplankton production rates (Cooper 1973; Lehman 1980b; Porter 1976).

Zooplankton grazing alters phytoplankton community structure (Berman and Richman 1974; Porter 1977) and reduces phytoplankton biomass, but often without a proportionate decline in primary production (Lampert 1978; Comita 1972). Zooplankton grazing can improve production efficiency (P/B) of phytoplankton (Gliwicz 1976).

Redfield (1980) found that the effect of zooplankton on phytoplankton production changed seasonally in Castle Lake, California. Increased production correlated positively with increased zooplankton biomass in late July in this temperate subalpine lake. The effect of zooplankton on phytoplankton production gradually became less positive and by late September there was a significant negative correlation between zooplankton biomass and phytoplankton production.

The effect of zooplankton on phytoplankton production in seasonally stable tropical lakes may be more pronounced. Zooplankton regeneration in Lake George, Uganda is responsible for recycling nutrients at a rate which permits relatively high phytoplankton production

despite relatively low external nutrient input (Ganf and Blazka 1974). Lake George has a stable phytoplankton biomass, and like Lake Chapala, is a large shallow lake which does not stratify seasonally.

Not all tropical systems are as seasonally stable. For example, Lake Titicaca, Peru, is a large, deep, high-altitude lake which does stratify seasonally and has considerable seasonal variation in phytoplankton biomass, ambient NH_3-N concentration, and nitrogen uptake (Vincent et al. 1984). Nevertheless, nutrient regeneration by zooplankton in tropical systems may be as important as in temperate systems and potentially more so.

Several studies have been conducted on Lake Chapala, Mexico. Based on chemical data (Instituto de Ingeniería UNAM 1974) primary production was believed to be nitrogen limited. Species composition of phytoplankton and zooplankton communities (Ortiz et al. 1982) have been described and indicate variation in species abundances between wet and dry seasons. Despite these studies little is known of phytoplankton - zooplankton interactions within Lake Chapala.

The goal of my research was to determine the relationship between grazing and nutrient regeneration by zooplankton, and phytoplankton production processes

in Lake Chapala. To understand these interactions I asked three questions.

First, how much of the ambient concentration of NH_3-N is supplied by zooplankton regeneration?

Second, how much of the ambient concentration of NH_3-N is removed by phytoplankton uptake and is required to maintain phytoplankton production?

The answers for these two questions will indicate the importance of nutrient recycling in Lake Chapala. Zooplankton regenerated NH_3-N is important only if the ambient concentration is low and demand via phytoplankton uptake is high. Determining the amount of zooplankton regenerated NH_3-N relative to ambient concentration, phytoplankton uptake, and the amount of nitrogen required to maintain phytoplankton production is the first step in understanding grazer - producer interactions in the lake.

The next step is to determine the direct result of these nutrient dynamics and grazing effects on phytoplankton production processes.

Thus, the third question - is phytoplankton production, biomass, and/or (P/B) negatively affected, positively affected, or unchanged by zooplankton?

If nutrients are in short supply then zooplankton regeneration may improve phytoplankton production

efficiency (increase P/B). If on the other hand, demand for and utilization of regenerated nutrients is slight, zooplankton grazing may impact negatively phytoplankton production (decrease P/B).

The relative importance of nutrient regeneration and grazing probably changes with time in response to changing ambient NH_3-N concentration and other environmental factors such as light and temperature. It was unknown whether phytoplankton - zooplankton interactions in tropical Lake Chapala were relatively stable or changed seasonally.

I tested two hypotheses. First, zooplankton NH_3-N regeneration (and therefore recycling) in Lake Chapala is not significant. Second, zooplankton in Lake Chapala have no effect on phytoplankton production, biomass, and P/B. This study was conducted through the transition from the wet season to the dry season to determine if zooplankton - phytoplankton interactions change seasonally in Lake Chapala.

EXPERIMENTAL DESIGN

I conducted two sets of experiments to understand the interaction and relationship between phytoplankton production and zooplankton grazing in Lake Chapala. Each experiment used two groups of enclosured water samples. One group was treated by including zooplankton, either at ambient concentrations or at augmented concentrations. Control treatments had zooplankton removed.

I compared nutrient changes, phytoplankton production and biomass in enclosures with and without zooplankton. The effect of zooplankton on these variables was measured over time. Values reported for zooplankton regeneration, change in phytoplankton production, change in phytoplankton biomass, and change in phytoplankton P/B ratio are not simply changes from initial values, but rather are relative changes from initial values, between experimental and control groups.

Enclosures for the two sets of experiments were labeled PB, for production - biomass, and RG, for regeneration (Table 1). The PB set was used to evaluate changes in phytoplankton production, biomass, and P/B ratio, and to determine NH_3-N uptake by phyto-

Table 1. Experimental organization. Four enclosure treatments were used in each experimental series.

SETS	GROUPS	
	CONTROL	EXPERIMENTAL
PB	ambient NH_3-N no zooplankton	ambient NH_3-N with zooplankton
RG	spiked NH_3-N no zooplankton	spiked NH_3-N with zooplankton

plankton. The RG set was used to determine NH_3-N regeneration rates by zooplankton.

The basic assumption made in this experimental design was that changes in NH_3-N concentration result from increases from zooplankton regeneration and decreases from phytoplankton uptake (Lehman 1980). Stated mathematically:

$$\text{change in } [N] = (R * Z) - (U * P) \qquad (1)$$

where [N] is the NH_3-N concentration, R is the zooplankton regeneration rate, Z is the zooplankton biomass, U is the phytoplankton specific uptake rate, and P is the phytoplankton biomass. The quantity (R*Z) represents increases in [N] by zooplankton regeneration and the quantity (U*P) represents decreases in [N] by phytoplankton uptake.

Ammonia-Nitrogen Supplied by Regeneration

Additional assumptions are implied in determining regeneration in this approach. First, the rate of zooplankton regeneration is constant during incubation. As long as the food supply is ample (Mayzaud 1976, 1973a; Conover and Corner 1968; Corner et al. 1965) and the incubation temperature is relatively stable (Mayzaud 1973b; Mayzaud and Dallot 1973; Ganf and Blazka 1974)

excretion rates should be constant.

Second, zooplankton biomass remains relatively constant, that is, no mortality or natality. It is doubtful whether this assumption is strictly valid, even in a relatively short incubation of 3 to 5 days, but unless biomass changes are large, little effect should be realized.

In utilizing changes in NH_3-N concentration to determine zooplankton regeneration (Equation 1), one must account for the loss of nitrogen through phytoplankton uptake (U*P).

Specific uptake rates of NH_3-N are not constant. These rates vary with the phytoplankton species present (Goldman and Gilbert 1982; Eppley et al. 1971), their physiological state (Goldman and Gilbert 1982; Eppley 1981), environmental conditions such as light, temperature, or season (Garside 1981; Eppley et al. 1971, 1979b; Gilbert et al. 1982; Takahashi and Saijo 1981b) and NH_3-N concentration (McCarthy 1981a, 1981b; Dugdale 1976; Dugdale and Goering 1967; Murphy 1980). The factors which influence phytoplankton uptake are not of particular concern, because the interest is in determining uptake values and their relationship to the ambient concentration, zooplankton regeneration, and utilization of NH_3-N. Within an

experimental series none of these factors need be considered except concentration, which can be directly affected by zooplankton through regeneration.

Since phytoplankton uptake rates vary with concentration, following Michaelis-Menten uptake kinetics, zooplankton regeneration rates cannot be measured directly. However, regeneration can be measured as the relative change in concentration between experimental (with zooplankton) and control (without zooplankton) enclosures, after equalizing the phytoplankton uptake rates between the two. When NH_3-N concentrations are sufficiently high uptake becomes saturated and the specific NH_3-N uptake rates for experimental and control groups is equal.

It then becomes possible to measure zooplankton regeneration as follows:

From equation (1);

$$\text{relative change in [N]} = \frac{(\text{change in [N]} = (R*Z) - (U*P))_{exp.} - (\text{change in [N]} = (R*Z) - (U*P))_{con.}}{(R*Z)_{exp.} - (R*Z)_{con.}} \qquad (2)$$

This also assumes that not only is the specific uptake rate (U) equal between experimental and control groups,

but that phytoplankton biomass (P) remains equal as well.

Finally, if it can be assumed that regeneration (R*Z) in controls is zero because zooplankton are removed (Z=0) then equation 2 can be simplified to:

$$\text{rel. change in } [N] = (R*Z)_{exp.} \qquad (3)$$

where the regeneration rate (R) can be calculated if zooplankton biomass (Z) is known, and total regeneration (R*Z) can be obtained easily.

Ammonia-Nitrogen Removed by Uptake

Once the zooplankton regeneration rate for a given experimental series is determined, it can be used to find phytoplankton uptake. By applying equation 1 to experimental enclosures not spiked with NH_3-N (see Table 1), and measuring NH_3-N concentration changes, total NH_3-N uptake can be calculated. The input of NH_3-N from regeneration must be accounted for by applying the zooplankton regeneration rate for each experimental series and determining zooplankton biomass within each enclosure. The specific uptake rate can be determined after measuring phytoplankton biomass.

In measuring specific uptake rates it must be assumed that phytoplankton biomass remains relatively

stable. This condition is also difficult to satisfy strictly because phytoplankton populations can increase or decrease rapidly, but by taking measurements over a short time little change should occur.

The Effect on Production, Biomass, and P/B

The effect of zooplankton on phytoplankton production, biomass, and P/B ratio can be determined by measuring relative changes between experimental and control enclosures. For example, the change in P/B within each treatment is given by:

$$\text{change } (P/B) = (P/B)_{final} - (P/B)_{initial} \qquad (4)$$

Because I am interested in the effect zooplankton may have on the P/B ratio, the relative change between experimentals and controls is most useful and is given by:

$$\text{relative change in } (P/B) = \text{change } (P/B)_{exp.} - \text{change } (P/B)_{con.} \qquad (5)$$

If initial values for phytoplankton production, biomass, and therefore P/B in experimental and control enclosures are equal, then equation (5) can be

simplified to:

$$\text{relative change in } (P/B) = (P/B)_{\text{exp.(final)}} - (P/B)_{\text{con.(final)}}. \quad (6)$$

Relative changes in phytoplankton production and biomass are calculated similiarly.

STUDY AREA

Lake Chapala is a large, shallow, tropical lake in central Mexico (approximately 103 degrees W. longitude and 20 degrees N. latitude). It is located on the western edge of the central highlands (Mesa Central), approximately 40 km south of the city of Guadalajara, at an elevation of 1,524 m.

Lake Chapala has an area of 1,112 km^2, with a maximum length of 76.6 km and maximum width of 22.5 km (Subdirección de Estudios 1981a, 1981b). Mean lake volume is 7,962 x 10^6 m^3, with a mean depth of 7.2 m, and mean annual water temperature of 20 C.

Water inflow occurs with the rainy season which usually begins in May or June and lasts until September or October. Most of the input is via the Río Lerma (51%) with a drainage area of approximately 130,000 km^2. Direct rainfall accounts for another 27% of water input to the lake, the remaining 23% from other sources. Biggest losses are through evaporation (47%) and outflow through the Río Santiago (42%). Most of the nutrients transported into Lake Chapala through the Río Lerma are exported through the Río Santiago (Table 2).

Table 2. Import and export of organic matter, solids, and nutrients for Lake Chapala in 1978. Values are in metric tons per year. (Translated from Limón and Quijano 1982 as reported in Centro de Estudios Limnológicos 1978).

	Organic Matter	Total Solids	Total Nitrogen	Total Phosphates
Import from Rio Lerma	8,258	511,198	2,018	610
Export through Rio Santiago	5,305	424,794	1,785	452
Difference	2,953	86,404	233	158

Lake Chapala is frequently windy, generally well mixed, and does not stratify seasonally (Limón and Quijano 1982).

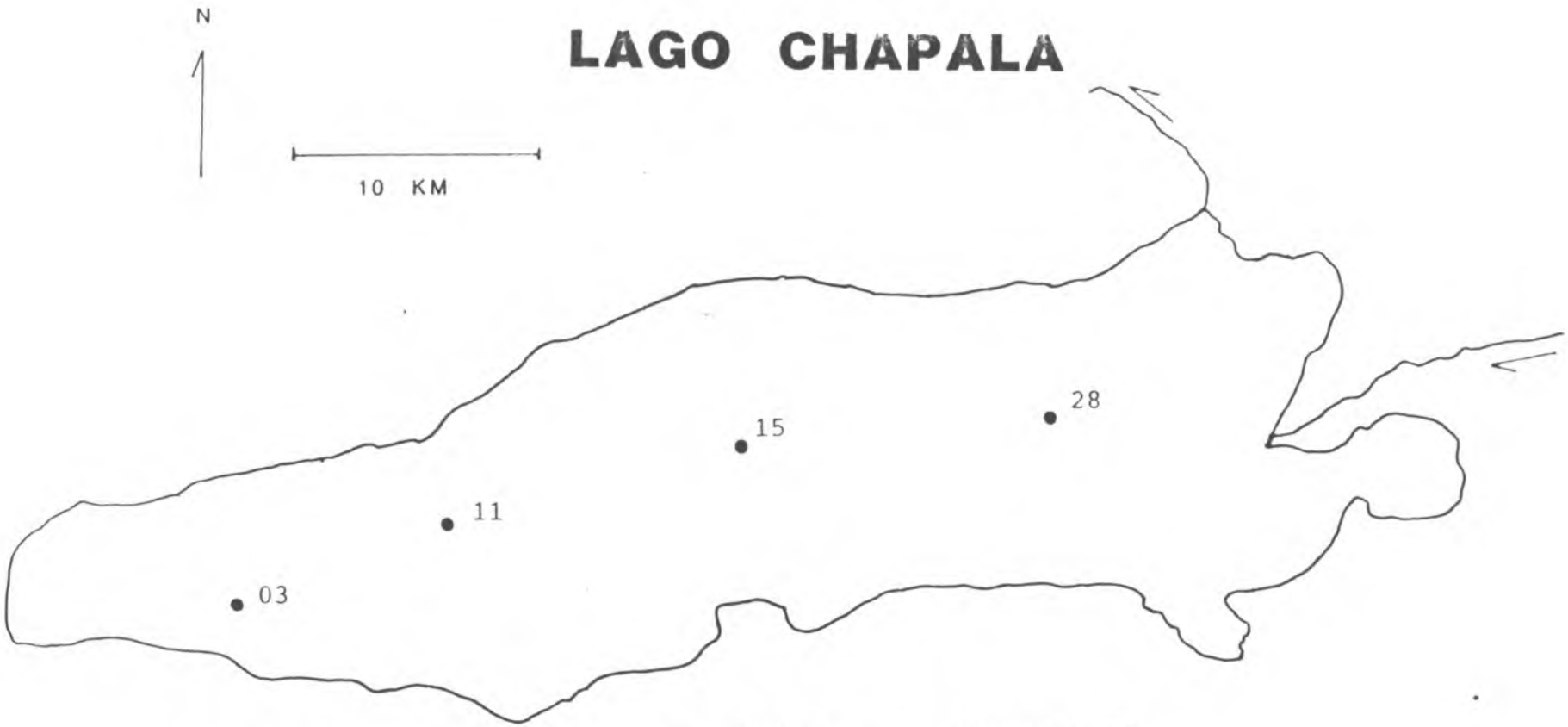
METHODS AND MATERIALS

Incubation Materials

Before beginning experiments, I tested clear plastic tubing to determine its suitability as an enclosure material. Other investigators have used similar materials (Redfield 1980; Lehman 1980a), but tests were conducted to determine if ammonia-nitrogen (NH_3-N) loss might occur at the relatively high pH of lake waters (pH = 7.7 to 8.6). I tested three concentrations of NH_3-N (50, 150, and 500 ug/l) each at three pH values (6.2, 8.3, and 10.3). Bags were filled with solution, sealed, and left in the incubation tank for 3 days. Then I removed the test bags, performed chemical analyses, and compared results with initial values to determine percent change from the initial concentration.

Field Collections

Samples were taken at four stations from September to December 1983 (Figure 1). Each station was sampled five times, for a total of 20 experimental series. Additionally, station 11 was sampled in late August to develop and evaluate methods used in the field and in the laboratory. Since several modifications were made,



STATION 03	STATION 11	STATION 15	STATION 28
12 Sept.	26 Aug.	13 Sept.	6 Sept.
10 Oct.	7 Sept.	11 Oct.	28 Sept.
1 Nov.	26 Sept.	31 Oct.	24 Oct.
17 Nov.	25 Oct.	18 Nov.	7 Nov.
10 Dec.	8 Nov.	12 Dec.	8 Dec.
	5 Dec.		

Figure 1. Lake Chapala with sampling dates and stations.

these data are not comparable, and therefore not used.

Water was collected using an electric pump, from four depths. Depths sampled were those at 50%, 25%, 10%, and 1% of surface illumination as determined by an irradiance meter. All sampling was done between 11:00 am and 1:00 pm. I filled four 50 liter plastic containers for each experimental series. Each container received one quarter of its volume from each depth. Containers were acid rinsed before each collection series.

I excluded macrozooplankton from two of the containers (PB - control and RG - control) by filtering water through 64-um-mesh netting. A third container (PB - experimental) received unfiltered water. The fourth container (RG - experimental) received water that was unfiltered and was enriched with zooplankton filtered from the control containers (except there was no enrichment in sampling period #1).

Zooplankton samples for identification and counting were taken along with water samples. Before moving the pump to the next sampling depth, 12 liters of water were collected and poured through a 64 um mesh net. I repeated this procedure at each sampling depth for a total of 48 liters of water filtered. Zooplankton retained in the net were rinsed into a collection bottle

with 75% ETOH, labeled and returned to the laboratory for enumeration.

I used a compound microscope (mag. = 400x) and identification keys in Freshwater Biology (Edmondson 1959) to make identifications. Counts were made with a binocular dissecting microscope on four replicate 1 ml subsamples. Lengths were measured using an ocular micrometer when counts were made. Length values do not include spines, mucros, or caudal setae. Mean length values reported include both immature and adult individuals.

Sample Incubation

The 50-l-sample containers were returned to the CEL laboratory (located between Guadalajara and Lake Chapala) to begin the experimental procedures. The elapsed time between collection and start of experiments was approximately 2-4 hours. RG containers were spiked with NH_4Cl to increase their ammonia concentration by 250 ug/l. Each sample container was thoroughly mixed before filling the enclosures.

Enclosures were constructed of clear polyethylene. The material was purchased as a "tube." The ends were heat sealed except for a small opening in the top corner (Figure 2) used for sampling. This opening was closed

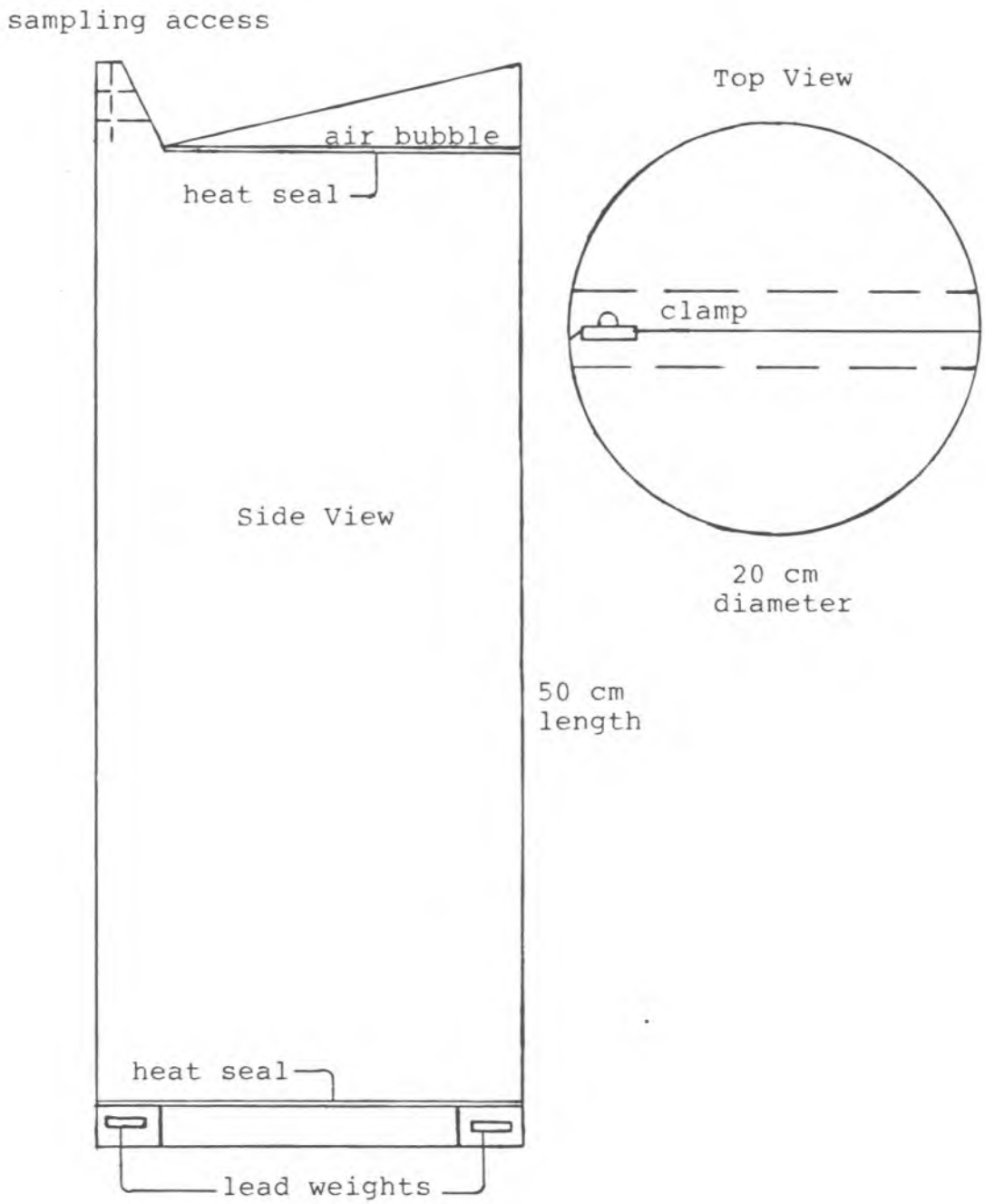


Figure 2. Enclosure bag design.

with a spring clamp during incubations. Small lead weights were sealed in the bottom and an air bubble was sealed on top to maintain proper orientation.

The enclosures, which were approximately 50 cm long and 20 cm in diameter, were filled with 10 l of appropriate lake water. Before filling, I first rinsed each enclosure with a 5% acid solution and then demineralized water. Enclosures were used only once.

Incubation was in a large (2000 l), round, fiberglass tank, heated to approximate lake temperatures. The average temperature for the entire study period was 22.7 $\pm$ 3 C. Within any sampling period the maximum temperature fluctuation was 3 C.

The incubation tank was maintained outdoors in an alcove between two buildings. It was shaded by a translucent roof, out of direct sunlight (Figure 3). Illumination on the incubation tank was approximately 5% of lake surface illumination, as measured by an irradiance meter.

Twice a day, I mixed enclosure contents by inverting top and bottom several times. Compressed air from a large air stone in the incubation tank helped to keep enclosures circulating within the tank.

Daily NH_3-N sampling was done in the early evening, after first mixing enclosure contents. A small

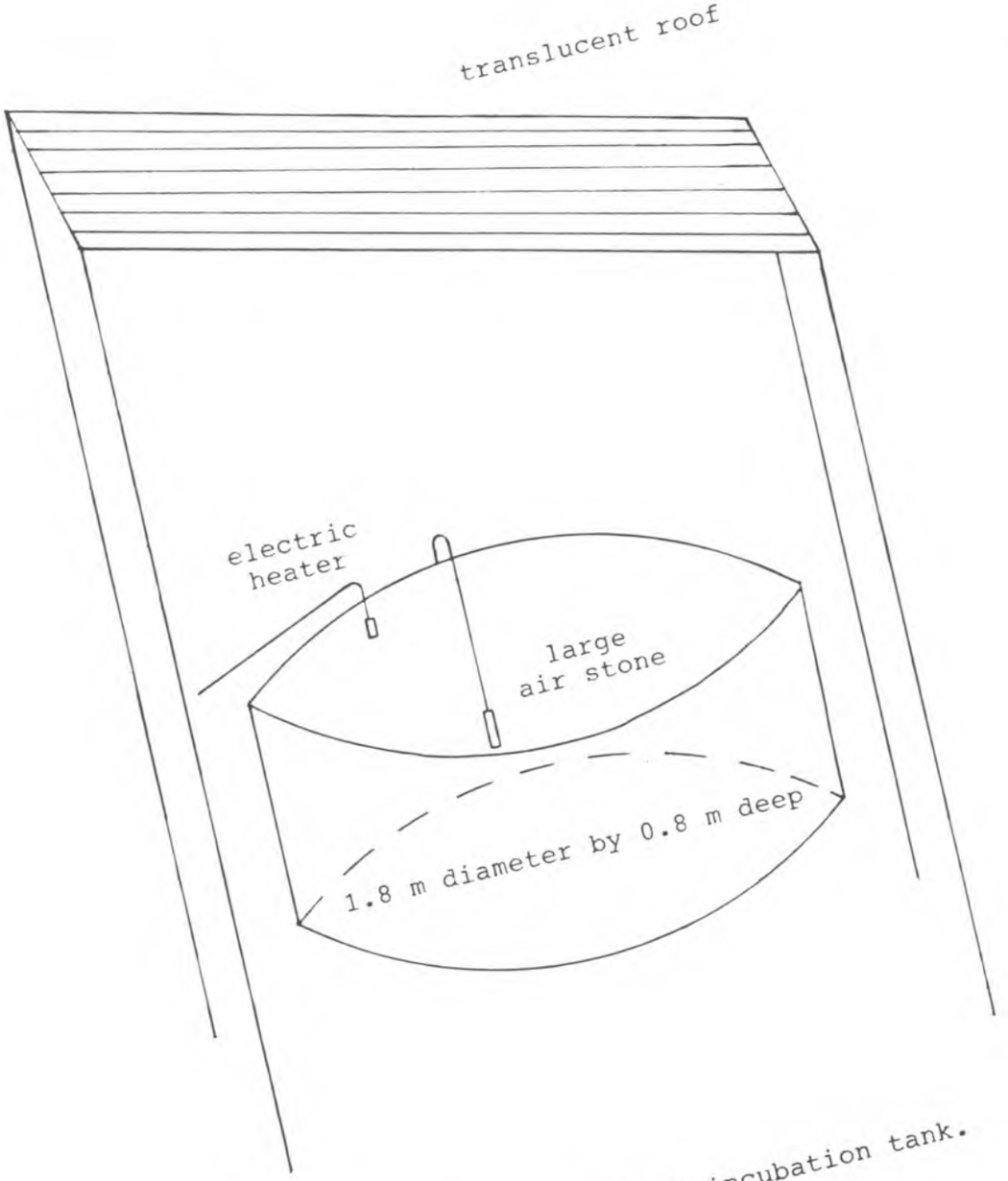


Figure 3. Enclosure incubation tank.

glass tube (1 cm O.D. by 30 cm long) attached to the end of a 50 ml plastic syringe was used to sample enclosures. I removed the clamp from the enclosure opening and inserted the glass tube into the bag. Water was drawn into the syringe then put in a labeled test tube. Samples for ^{14}C- production also were taken in this manner.

At termination of each experimental series I removed enclosures from the incubation tank and returned them to the laboratory. Final samples were then taken to determine NH_3-N, total Kjeldahl nitrogen (TKN), nitrate-nitrogen (NO_3-N), Chlorophyll *a* - phytoplankton biomass, ^{14}C-production, and zooplankton biomass.

Laboratory Analyses

NH_3-N was determined by the indophenol method (Lind 1979). Initial analyses were made within 2-4 hr of collection from the lake on triplicate samples. Duplicate 25 ml samples were taken from each enclosure daily thereafter.

To monitor other forms of nitrogen, NO_3-N, and TKN analysis were conducted on initial samples and at the termination of each series, for all but the last four series. Samples for both of these were acidified

to pH = 6.0 and frozen until analysed. NO_3-N was determined by a cadmium reduction batch method (Davison and Woof 1978), and TKN was determined by micro-Kjeldahl digestion (E.P.A. 1976). The ammonia formed was measured using a selective ion electrode (Orion).

Phytoplankton production was determined using the ^{14}C method on initial PB samples, on samples taken mid-way through the experiment, and at termination. Two 37 ml light bottles and one dark bottle from each enclosure were incubated under flourescent lights. Bottles were placed in an 85 l aquarium which had its sides covered with aluminum foil. A small flourescent lamp was suspended above the samples, which were just covered with water, and incubated for two hours. Production values were adjusted to daily production in the large tank, based on total daily light input.

Incubated samples were filtered through 0.45 um pore membrane filters, placed in vials, and dried in a dessicator. Samples were then returned to Baylor University for counting. Counts were made on a Beckman Liquid Scintillation Counter Model # LS 1800. Total inorganic carbon was calculated from alkalinity and pH which were determined at the time of sampling.

Chlorophyll *a*, as an estimate of phytoplankton biomass, was determined spectrophotometrically (Lind

1979) on initial and final samples from each PB enclosure. One liter samples were filtered on glass fiber filters (GF/C), sealed in plastic, frozen and maintained in the dark until the extraction and analysis could be made. Samples were then ground, extracted in acetone, centrifuged, and absorbance measured on a Shimadzu UV-Visible Model #240 spectrophotometer.

P/B ratios were calculated directly from the phytoplankton production and biomass data.

The effect of zooplankton on phytoplankton production, biomass, and P/B ratio was tested by a group T - test ($p \leq .05$). For each of these variables, the mean value of the control enclosures was subtracted from the value of each experimental enclosure to obtain the relative change between experimentals and controls (equation 6). The relative change in each experimental enclosure was then divided by its zooplankton biomass to adjust for differences in zooplankton weight between experimental enclosures, and then tested statistically.

The estimate of nitrogen required was calculated from initial phytoplankton production values. Estimated N-required values were based on an assumed phytoplankton tissue C:N:P ratio of 40:7:1 by weight.

Zooplankton biomass was determined at the termination of each series. Four to 8 l of water were

filtered through a 64-um-mesh net for each RG experimental enclosure. Zooplankton retained in the filter were rinsed onto a pre-weighed glass fiber filter which had been dried at least 4 hr at 100 C before pre-weighing. Filters with zooplankton were dried at 90 C for a minimum of 24 hr and then re-weighed.

Ammonia nitrogen regeneration by zooplankton was calculated from the relative change in NH_3-N concentration (equation 3) between experimental and control groups (Figure 4). The mean change in controls was subtracted from the change in experimentals to determine total NH_3-N regeneration. Total regeneration was divided by zooplankton biomass and the regeneration rate found by regression (Figure 5). NH_3-N regeneration rates for each series were determined by dividing the total regeneration in each enclosure by its zooplankton biomass and performing a regression on these data over the time of the experiment (Figure 6). The results of the regression were tested by a one-tailed T-test for a slope greater than zero. Only significant slopes ($p \leq .05$) were used in determining zooplankton regeneration rates.

To check the assumptions that the food supply was not depleted by zooplankton grazing and that phyto-

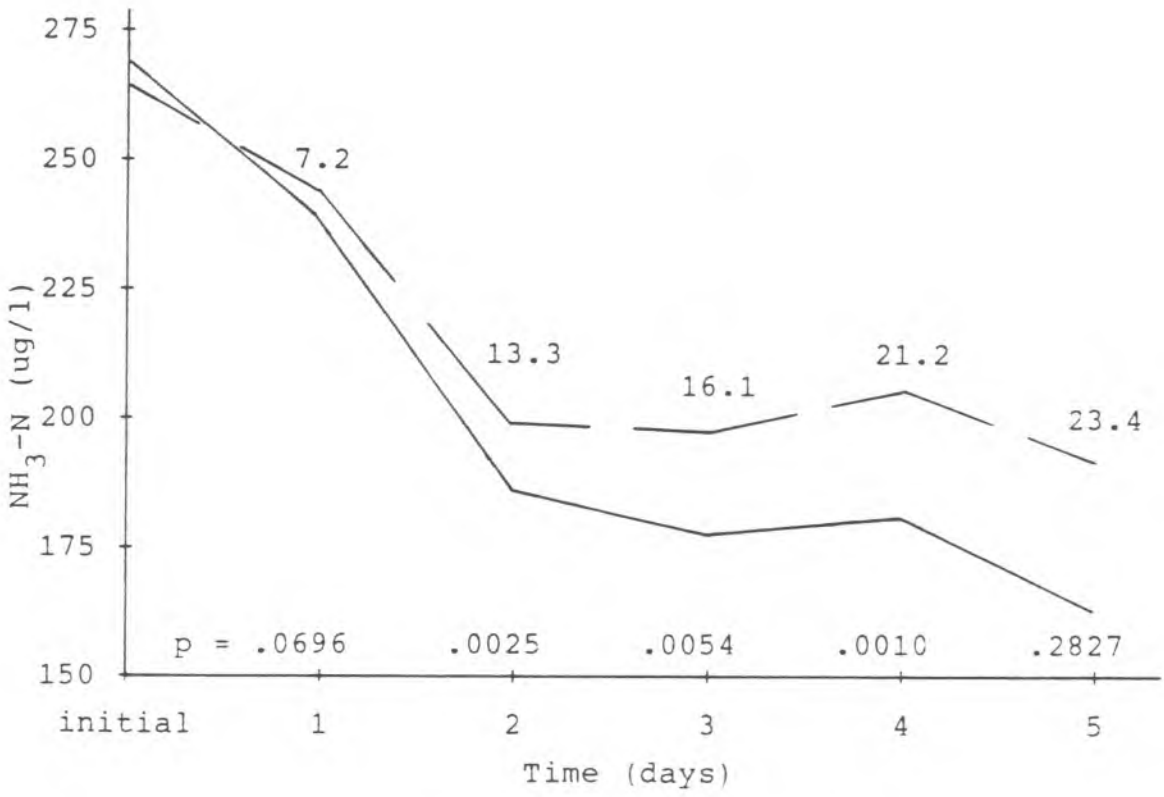


Figure 4. Mean daily NH_3-N concentration for all series, experimentals (— —), and controls (———). Numbers along the top are differences between means. Values at bottom are p - values for a T - test of means.

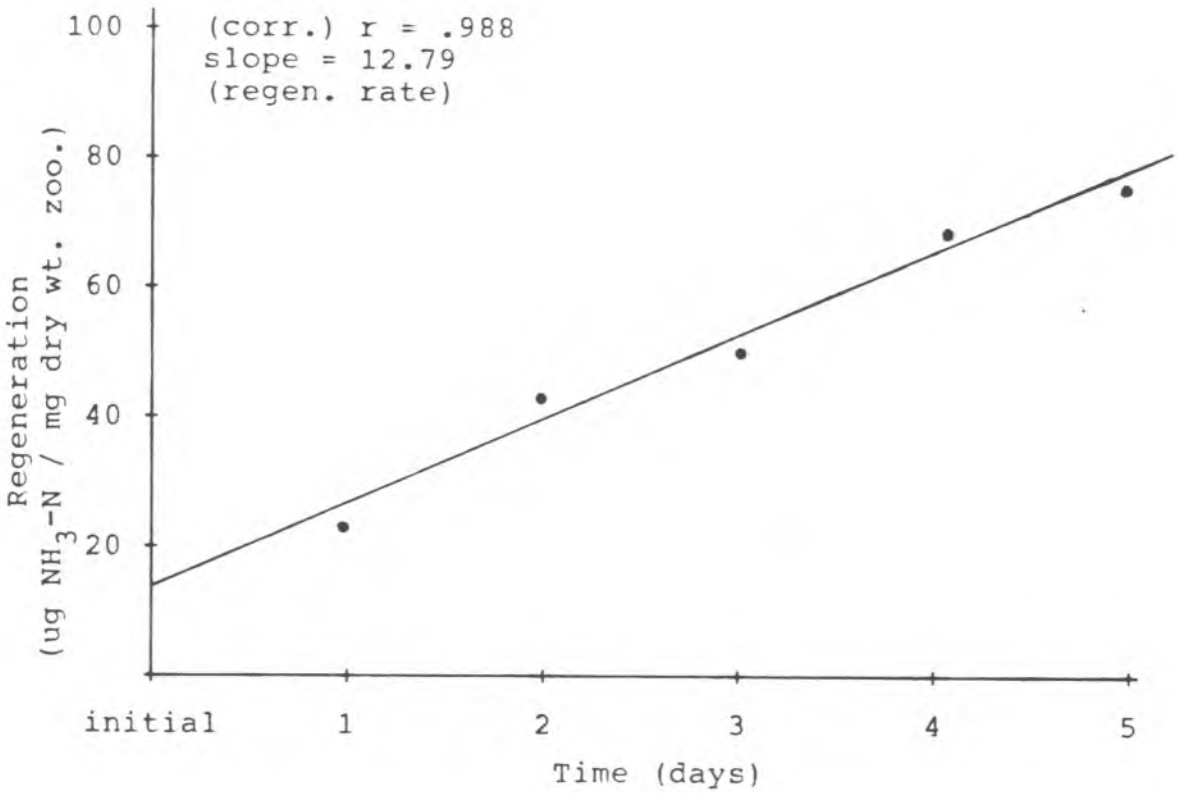


Figure 5. Regresssion of NH_3-N regeneration per mg dry weight zooplankton versus time for all experimental series. (Slope of the regression line equals regeneration rate).

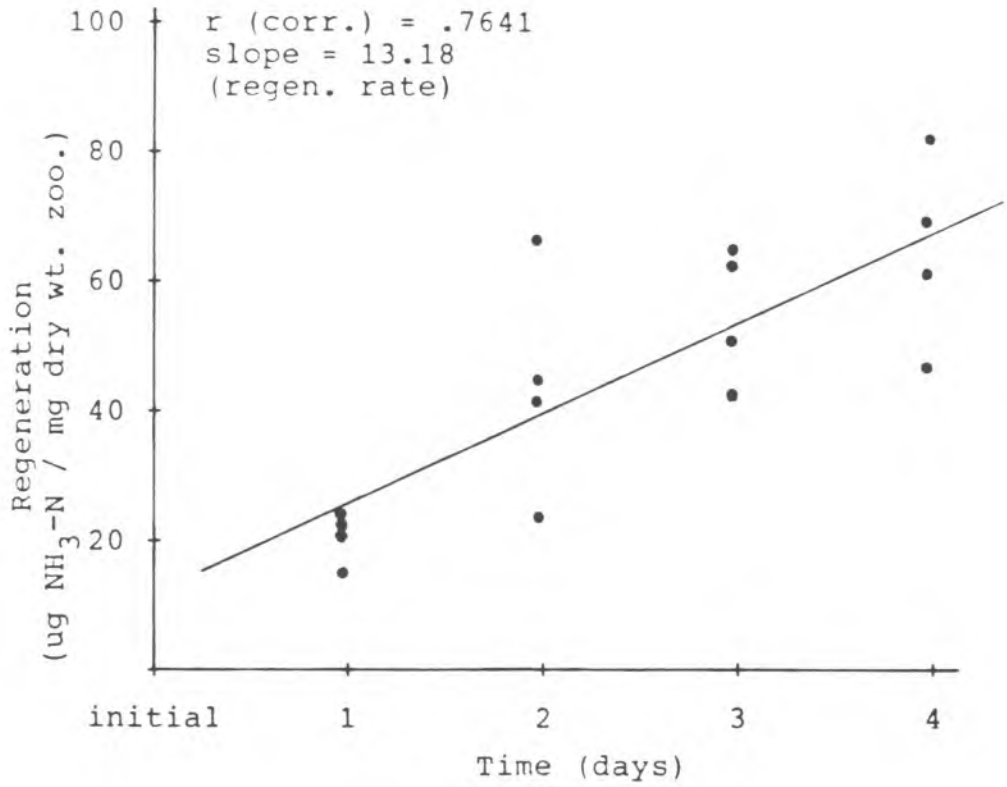


Figure 6. Regresssion of NH_3-N regeneration per mg dry weight zooplankton versus time for Series #7. (Slope of the regression line equals regeneration rate).

plankton biomass remained relatively stable, chlorophyll concentrations were monitored daily using a flourometer (Turner Designs).

To check the assumption that zooplankton biomass remained stable, organism counts and dry weight measurements were made at the initiation and termination of the last three experimental series.

To check the assumption that zooplankton were removed from controls, organism counts were made on initial samples from control groups for the last four experimental series.

Phytoplankton NH_3-N uptake was calculated by using the zooplankton regeneration rate for each series. The measured zooplankton biomass within each PB experimental enclosure multiplied by the regeneration rate gave total regeneration (equation 1). Because NH_3-N concentration change and regeneration were known, total phytoplankton uptake could be calculated. Uptake values were calculated from NH_3-N concentration changes measured only during the first day to minimize any changes in phytoplankton biomass which may have occurred.

Specific uptake was calculated after phytoplankton biomass was determined. Initial phytoplankton biomass values were utilized to determine specific uptake, and

flourescence chlorophyll readings were taken to monitor the assumption that biomass remained relatively stable for the one day period.

RESULTS

Initial concentrations for NH_3-N, NO_3-N and TKN are presented in Table 3. NO_3-N values were more variable among stations than TKN or NH_3-N. NH_3-N concentrations were low throughout the study. NO_3-N began to decline after sampling period #2 while TKN generally increased (Figure 7).

The zooplankton community was represented by 11 taxa (Table 4). The calanoid copepod Diaptomus albuquerquensis was the dominant species overall, but the cladocerans Bosmina coregoni, Ceriodaphnia lacustris and C. pulchella were very abundant at station 11 (Table 4[b]). Station 03 was unique with the lowest abundance of organisms, and very strongly dominated by copepods.

There was considerable difference in species abundance among sampling periods (Table 5). Copepods were at their lowest abundance when the study began. Their numbers increased in sampling period #2, decreased in period #3 (except nauplii), and reached peak numbers during sampling period #4.

Cladoceran abundance was more variable. B. coregoni abundance was very low initially, but steadily increased to 22.92/l in sampling period #5.

Table 3. Initial NH_3-N, NO_3-N, and TKN concentrations for Lake Chapala, Sept. to Dec., 1983.

Sampling Date	Sampling Station	NH_3-N ug/l	NO_3-N ug/l	TKN mg/l
9/6	28	41.6	160.4	0.072
9/7	11	29.3	38.8	0.200
9/12	03	66.2	8.3	-
9/13	15	35.8	445.1	0.106
mean	period #1	43.2	163.2	0.126
9/26	11	19.3	7.7	0.163
9/28	28	22.1	550.5	0.143
10/10	03	30.4	121.8	0.394
10/11	15	34.5	-	-
mean	period #2	26.6	226.64	0.233
10/24	28	28.2	162.8	0.671
10/25	11	28.8	47.0	0.796
10/31	15	42.6	262.9	0.483
11/1	03	48.5	55.9	1.222
mean	period #3	37.0	132.2	0.793
11/7	28	13.8	156.3	0.804
11/8	11	6.7	29.4	0.718
11/17	03	19.6	9.5	0.838
11/18	15	4.9	136.1	1.256
mean	period #4	11.2	82.8	0.904
12/5	11	31.5	-	-
12/8	28	34.3	-	-
12/10	03	10.0	-	-
12/12	15	16.5	-	-
mean	period #5	23.1	-	-

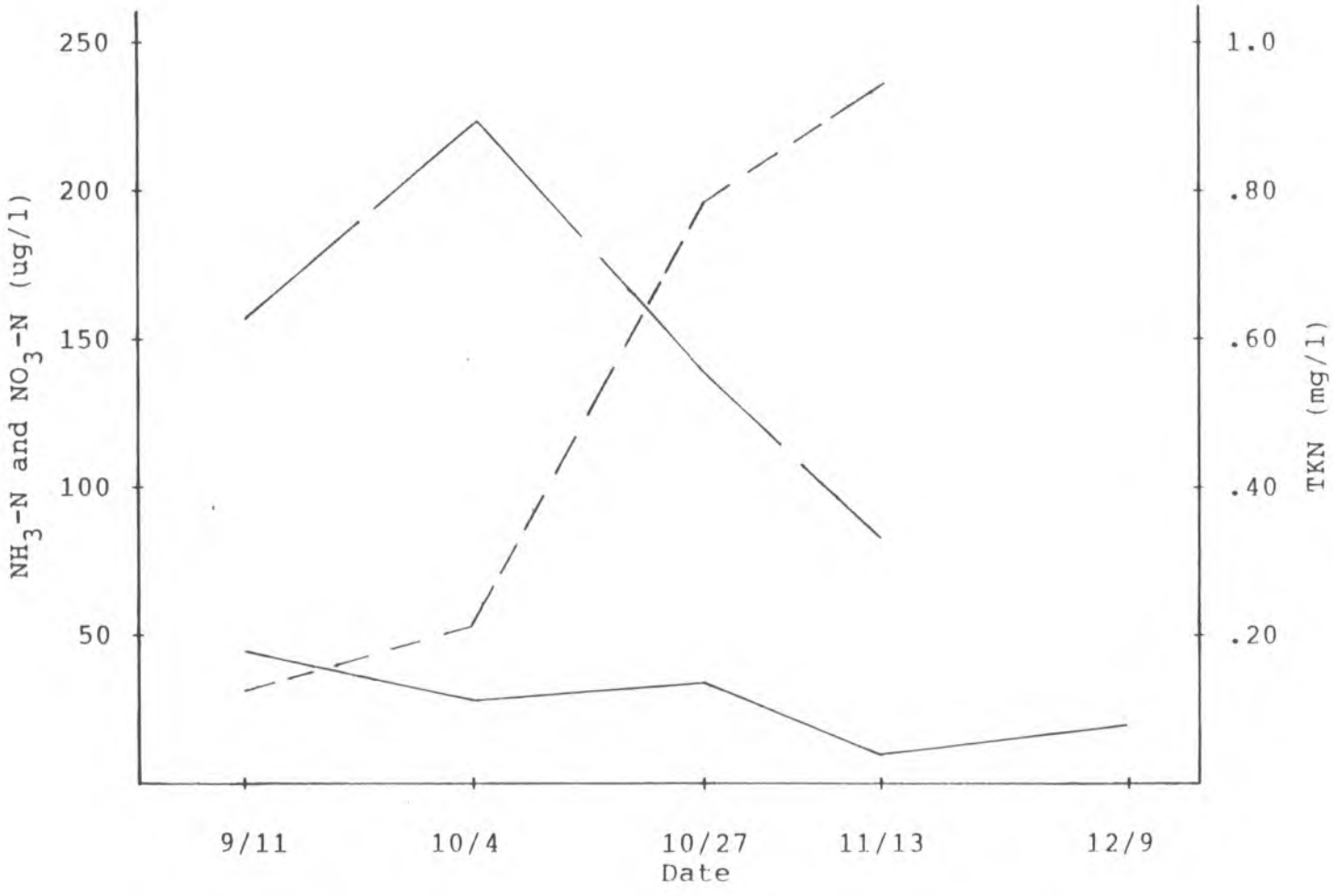


Figure 7. Mean initial concentrations for NH_3-N (———), NO_3-N (— —), and TKN (— — —). (Dates are mid-points for each sampling period).

Table 4. Mean zooplankton abundance and size by sampling station.

Species	mean length (mm)	number measured (N)	number per liter
Diaptomus albuquerquensis	.703	335	35.00
Mesocyclops inversus	.534	98	10.21
Nauplii (all)	.218	367	65.10
Bosmina coregoni	.337	19	1.98
Ceriodaphnia lacustris	.411	38	3.96
Ceriodaphnia pulchella	.346	46	4.79
Daphnia parvula	.500	10	1.04
Daphnia ambigua	.536	5	0.52
Diaphanosoma leuchtenbergianum	.533	24	2.50
Keratella spp.	.125	46	4.79
Brachionus spp.	-	-	0.00
Filinia spp.	.205	12	1.35

(a) station 03

Table 4. Mean zooplankton abundance and size by sampling station.

Species	mean length (mm)	number measured (N)	number per liter
Diaptomus albuquerquensis	.705	267	26.33
Mesocyclops inversus	.593	106	10.22
Nauplii (all)	.215	389	105.75
Bosmina coregoni	.359	231	23.70
Ceriodaphnia lacustris	.405	232	21.42
Ceriodaphnia pulchella	.363	359	34.81
Daphnia parvula	.582	99	9.84
Daphnia ambigua	.540	34	3.48
Diaphanosoma leuchtenbergianum	.578	27	2.72
Keratella spp.	.131	154	16.12
Brachionus spp.	.176	10	0.98
Filinia spp.	.212	29	3.02

(b) station 11

Table 4. Mean zooplankton abundance and size by sampling station.

Species	mean length (mm)	number measured (N)	number per liter
Diaptomus albuquerquensis	.710	251	26.15
Mesocyclops inversus	.613	49	5.21
Nauplii (all)	.207	377	117.39
Bosmina coregoni	.327	85	8.85
Ceriodaphnia lacustris	.361	41	4.27
Ceriodaphnia pulchella	.343	104	11.04
Daphnia parvula	.513	39	4.06
Daphnia ambigua	.504	14	1.46
Diaphanosoma leuchtenbergianum	.467	18	1.87
Keratella spp.	.129	140	14.69
Brachionus spp.	.174	11	1.15
Filinia spp.	.206	41	4.27

(c) station 15

Table 4. Mean zooplankton abundance and size by sampling station.

Species	mean length (mm)	number measured (N)	number per liter
Diaptomus albuquerquensis	.726	373	38.43
Mesocyclops inversus	.562	141	14.54
Nauplii (all)	.196	316	93.33
Bosmina coregoni	.328	119	12.37
Ceriodaphnia lacustris	.390	184	18.85
Ceriodaphnia pulchella	.351	307	31.61
Daphnia parvula	.551	69	7.13
Daphnia ambigua	.560	27	2.77
Diaphanosoma leuchtenbergianum	.469	18	1.84
Keratella spp.	.131	189	19.61
Brachionus spp.	.172	11	1.14
Filinia spp.	.204	63	6.56

(d) station 28

Table 4. Mean zooplankton abundance and size by sampling station.

Species	mean length (mm)	number measured (N)	number per liter
Diaptomus albuquerquensis	.712	1226	31.48
Mesocyclops inversus	.557	394	10.04
Nauplii (all)	.210	1449	95.39
Bosmina coregoni	.344	454	11.72
Ceriodaphnia lacustris	.396	495	12.12
Ceriodaphnia pulchella	.355	816	20.56
Daphnia parvula	.556	217	5.52
Daphnia ambigua	.540	80	2.06
Diaphanosoma leuchtenbergianum	.520	87	2.23
Keratella spp.	.130	529	13.80
Brachionus spp.	.174	32	0.82
Filinia spp.	.206	145	3.80

(e) all stations

Table 5. Mean zooplankton abundance and size by sampling period.

Species	Number Per Liter For Each Station (station number) 28	11	03	15	Values For Entire Sampling Period: mean length (mm)	number meas. (N)	number per liter
Diaptomus albuquerquensis	25.48	23.32	9.90	16.15	.771	162	18.71
Mesocyclops inversus	8.65	12.02	1.04	3.12	.606	57	6.21
Nauplii (all)	68.75	74.04	32.81	65.10	.208	276	60.12
Bosmina coregoni	1.44	2.88	-	-	.298	12	1.08
Ceriodaphnia lacustris	37.98	33.17	1.56	9.38	.376	191	20.52
Ceriodaphnia pulchella	28.36	32.93	1.04	5.73	.344	161	17.02
Daphnia parvula	3.36	9.13	0.52	1.56	.530	33	3.64
Daphnia ambigua	2.40	0.72	0.52	0.52	.518	9	1.04
Diaphanosoma leuchtenbergianum	1.92	2.64	0.52	2.60	.440	16	1.92
Keratella spp.	4.81	1.44	-	1.56	.135	16	1.95
Brachionus spp.	0.48	0.24	-	-	.160	2	0.18
Filinia spp.	0.48	-	0.52	-	.180	2	0.25

(a) sampling period #1

Table 5. Mean zooplankton abundance and size by sampling period.

Species	Number Per Liter For Each Station (station number) 11	28	03	15	Values For Entire Sampling Period: mean length (mm)	number meas. (N)	number per liter
Diaptomus albuquerquensis	17.71	56.77	48.44	31.77	.760	296	38.67
Mesocyclops inversus	5.21	22.40	5.73	2.08	.553	68	8.86
Nauplii (all)	47.40	53.12	54.69	157.81	.219	310	78.26
Bosmina coregoni	13.02	6.25	0.52	21.35	.327	79	10.28
Ceriodaphnia lacustris	14.06	37.50	16.15	5.73	.398	141	18.36
Ceriodaphnia pulchella	19.27	32.29	11.98	20.83	.347	162	21.09
Daphnia parvula	3.12	15.10	1.04	2.08	.606	41	5.33
Daphnia ambigua	2.08	4.68	-	0.52	.624	14	1.82
Diaphanosoma leuchtenbergianum	3.65	2.08	4.69	1.56	.528	23	3.00
Keratella spp.	1.04	4.69	0.52	9.38	.133	30	3.91
Brachionus spp.	0.52	-	-	3.65	.172	8	1.04
Filinia spp.	-	-	-	3.65	.203	7	0.91

(b) sampling period #2

Table 5. Mean zooplankton abundance and size by sampling period.

Species	Number Per Liter For Each Station: station number 28	11	15	03	Values For Entire Sampling Period: mean length (mm)	number meas. (N)	number per liter
Diaptomus albuquerquensis	25.00	42.71	14.58	23.44	.675	203	26.43
Mesocyclops inversus	10.94	14.58	3.12	1.04	.591	57	7.42
Nauplii (all)	80.21	92.19	140.62	34.90	.202	298	86.98
Bosmina coregoni	18.23	19.27	10.94	-	.331	93	12.11
Ceriodaphnia lacustris	10.42	51.56	3.65	1.56	.427	128	16.80
Ceriodaphnia pulchella	71.88	81.77	16.15	7.29	.359	339	44.27
Daphnia parvula	1.04	15.11	-	-	.603	31	4.03
Daphnia ambigua	1.04	4.17	0.52	-	.525	11	1.43
Diaphanosoma leuchtenbergianum	-	5.21	1.04	2.08	.668	16	2.08
Keratella spp.	35.94	7.81	19.79	1.04	.132	124	16.14
Brachionus spp.	1.56	1.04	1.56	-	.175	8	1.04
Filinia spp.	10.42	1.04	7.81	1.04	.207	39	5.08

(c) sampling period #3

Table 5. Mean zooplankton abundance and size by sampling period.

Species	Number Per Liter For Each Station (station number 28)	(11)	(03)	(15)	Values For Entire Sampling Period: mean length (mm)	number meas. (N)	number per liter
Diaptomus albuquerquensis	51.04	14.06	75.00	57.81	.670	380	49.48
Mesocyclops inversus	14.58	6.77	25.52	12.50	.553	114	14.84
Nauplii (all)	169.79	236.46	101.04	116.67	.219	298	155.99
Bosmina coregoni	22.92	12.50	5.73	7.81	.335	94	12.24
Ceriodaphnia lacustris	4.17	1.04	-	2.60	.354	15	1.95
Ceriodaphnia pulchella	24.48	14.58	2.60	9.38	.349	97	12.76
Daphnia parvula	2.60	1.56	3.65	11.46	.486	37	4.82
Daphnia ambigua	3.65	1.04	1.04	5.73	.507	22	2.86
Diaphanosoma leuchtenbergianum	2.08	1.04	3.12	2.08	.499	16	2.08
Keratella spp.	19.27	24.48	11.46	8.85	.130	122	16.02
Brachionus spp.	3.65	1.04	-	0.52	.172	10	1.30
Filinia spp.	12.50	5.73	4.69	7.81	.211	59	7.68

(d) sampling period #4

Table 5. Mean zooplankton abundance and size by sampling period.

Species	Number Per Liter For Each Station: station number 11	28	03	15	Values For Entire Sampling Period: mean length (mm)	number meas. (N)	number per liter
Diaptomus albuquerquensis	33.85	33.85	18.23	10.42	.712	185	24.09
Mesocyclops inversus	12.50	16.15	17.71	5.21	.567	98	12.89
Nauplii (all)	78.65	94.79	102.08	106.77	.199	267	95.57
Bosmina coregoni	70.83	13.02	3.65	4.17	.367	176	22.92
Ceriodaphnia lacustris	7.29	4.17	0.52	-	.416	20	3.00
Ceriodaphnia pulchella	25.52	1.04	1.04	3.12	.395	57	7.68
Daphnia parvula	20.31	13.54	-	5.21	.548	75	9.76
Daphnia ambigua	9.38	2.08	1.04	-	.538	24	3.12
Diaphanosoma leuchtenbergianum	1.04	3.12	2.08	2.08	.460	16	2.08
Keratella spp.	45.83	33.33	10.94	33.85	.128	237	30.99
Brachionus spp.	2.08	-	-	-	.190	4	0.52
Filinia spp.	8.33	9.38	0.52	2.08	.202	38	5.08

(e) sampling period #5

C. lacustris was most abundant during sampling period #1 and generally declined thereafter, while the number of C. pulchella increased from sampling period #1, peaked in period #3, and declined to their lowest value in period #5. Abundance of Daphnia spp. was somewhat variable, due partly to their relatively low occurrence, but both species were least abundant when the study began and most abundant during sampling period #5. Diaphanosoma leuchtenbergianum was not abundant, but its abundance was the least variable.

Rotifers were relatively scarce early in the study and reached their peak abundances during sampling periods #4 (Brachionus spp. and Filinia spp.) and #5 (Keratella spp.).

Organism counts for each species were variable among sampling stations over the course of the study (Table 5). Species abundances at individual stations were different from one another among sampling periods.

Zooplankton biomass was also variable (Table 6) throughout the study and was generally consistent with total abundance (Figure 8). Zooplankton biomass was variable but it was at its highest when the study began while phytoplankton biomass was at its lowest (Figure 9).

Phytoplankton biomass and production values

Table 6. Mean zooplankton biomass and total abundance.

Experimental Series	Station Number	Zoo. Biomass (mg/l)	Zoo. Abundance (#/l) *
1	28	.245	187.11
2	11	.252	192.53
3	03	.596	48.43
4	15	.440	105.72
mean	period #1	.383	132.64
5	11	.189	127.08
6	28	.192	234.88
7	03	.479	143.76
8	15	.329	260.41
mean	period #2	.297	191.45
9	28	.375	266.68
10	11	.375	336.46
11	15	.158	219.78
12	03	.179	72.39
mean	period #3	.272	222.38
13	28	.329	330.73
14	11	.242	320.30
15	03	.478	233.85
16	15	.308	243.22
mean	period #4	.339	282.02
17	11	.400	315.61
18	28	.257	224.47
19	03	.279	157.81
20	15	.204	172.91
mean	period #5	.285	217.70

* Total for Copepods, Cladocerans, and Rotifers.

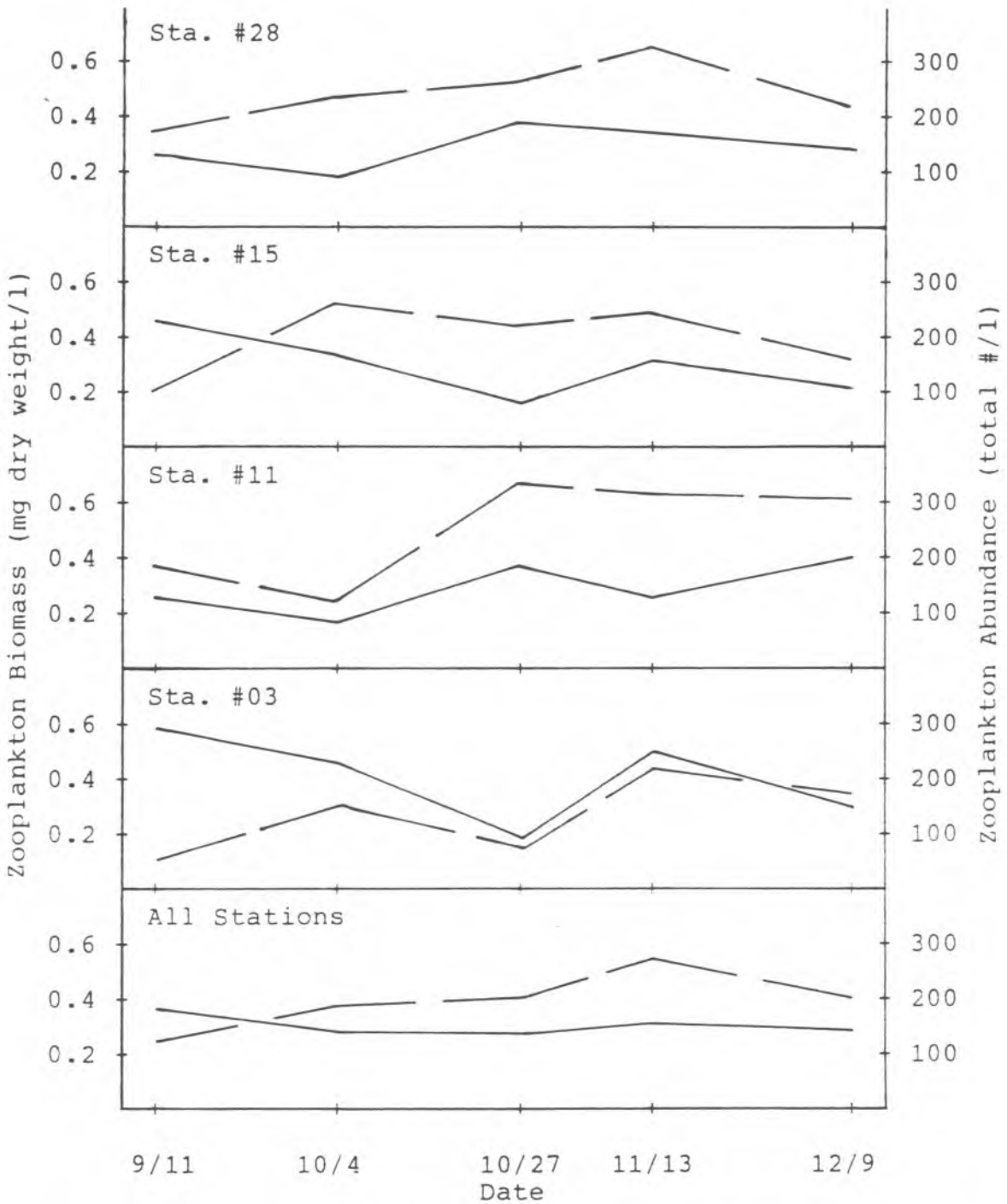


Figure 8. Zooplankton biomass (———) and abundance (— —) in Lake Chapala, Sept. to Dec. 1983. (Dates are mid-points for each sampling period).

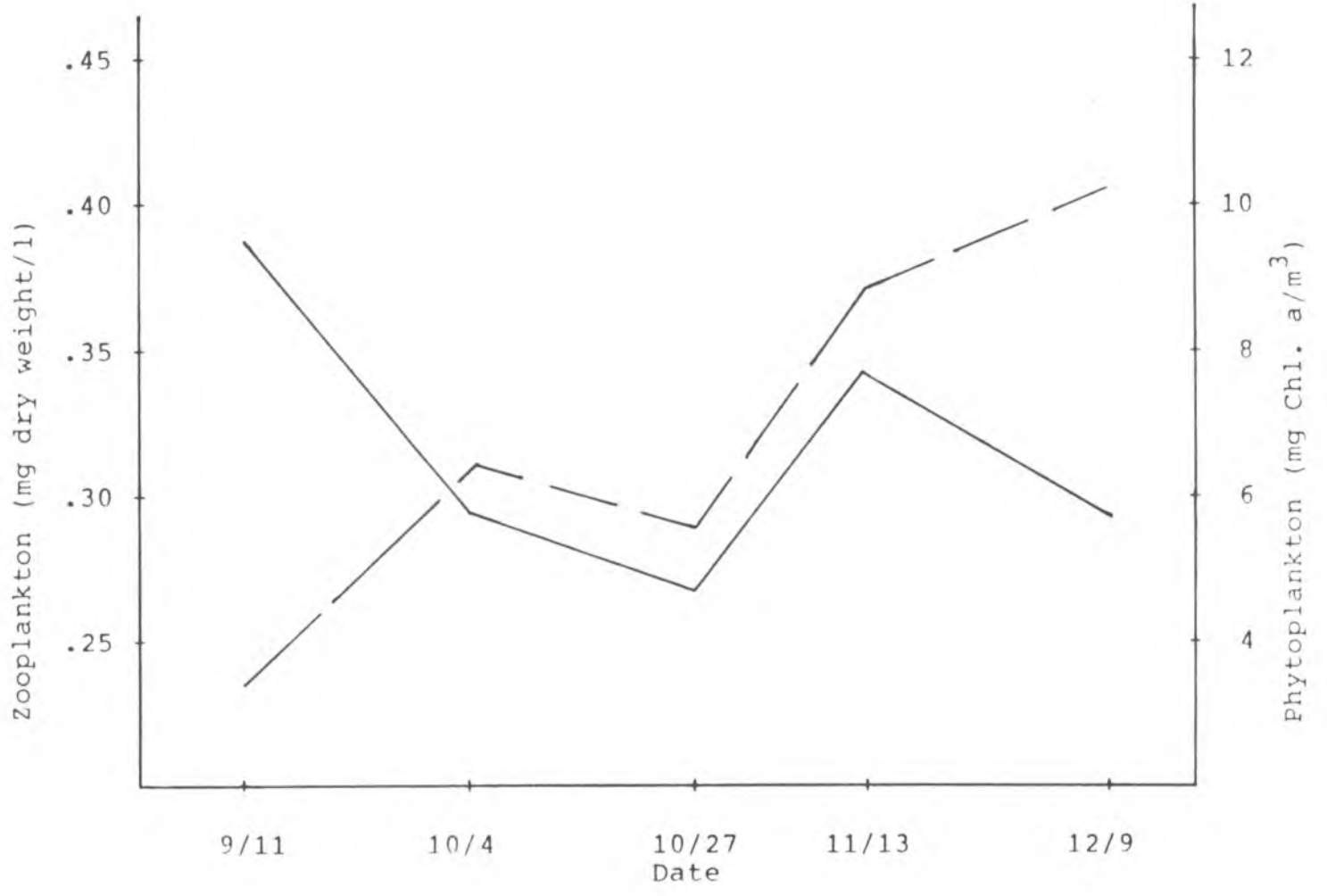


Figure 9. Mean zooplankton (———) and phytoplankton (— —) biomass in Lake Chapala, Sept. to Dec. 1983. (Dates are mid-points for each sampling period).

(Table 7) were low at the beginning of the study. Production peaked in sampling period #4 at all stations (Figure 10) while biomass either continued to increase from period #4 to #5 or declined slightly.

Zooplankton NH_3-N regeneration rates for each series are presented in Table 8 along with the calculated phytoplankton uptake and specific uptake values. Regeneration rates have been summarized (Table 9) and compared to ambient NH_3-N concentration. The greatest percentage contribution from regeneration to the NH_3-N pool was in period #4, the least in period #1. Turnover time, the number of days required to supply the ambient concentration at the given rate, is a reciprocal measure of percent ambient from regeneration and averaged 7.8 days.

Phytoplankton uptake values are summarized in Table 10. Total uptake was highest during period #1 and lowest during period #4, but uptake as a percent of ambient NH_3-N concentration was highest in period #4, 96.1% of ambient. Zooplankton regeneration provided 47.4% of phytoplankton NH_3-N uptake during period #4, the highest percentage contribution.

Specific uptake generally declined from sampling period #1 to period #5 (Table 10) and paralleled NH_3-N concentration (Figure 11). Maximum specific

Table 7. Mean phytoplankton biomass, production, and estimated required nitrogen.

Series Number	Station Number	Phyto. Biomass (ug Chl. a/l)	Phyto. Prod. (ug C/l/d)	Est. N-Required * (ug/l/d)
1	28	2.50	7.64	1.34
2	11	5.03	20.16	3.53
3	03	4.43	7.63	1.33
4	15	2.91	17.28	3.02
mean	period #1	3.71	13.18	2.30
5	11	5.11	8.82	1.54
6	28	5.35	9.20	1.61
7	03	9.10	25.99	4.55
8	15	7.10	24.68	4.32
mean	period #2	6.66	17.17	3.00
9	28	7.23	30.92	5.41
10	11	7.30	41.63	7.28
11	15	3.29	26.52	4.64
12	03	6.28	50.11	8.77
mean	period #3	6.02	37.30	6.52
13	28	5.53	34.17	5.98
14	11	10.22	53.47	9.36
15	03	12.41	65.40	11.44
16	15	7.67	43.27	7.57
mean	period #4	8.96	49.08	8.59
17	11	9.98	27.63	4.84
18	28	9.00	22.51	3.94
19	03	8.94	25.91	4.53
20	15	12.28	24.82	4.34
mean	period #5	10.05	25.22	4.41

* Based on carbon production and a 40:7 ratio of C:N by weight.

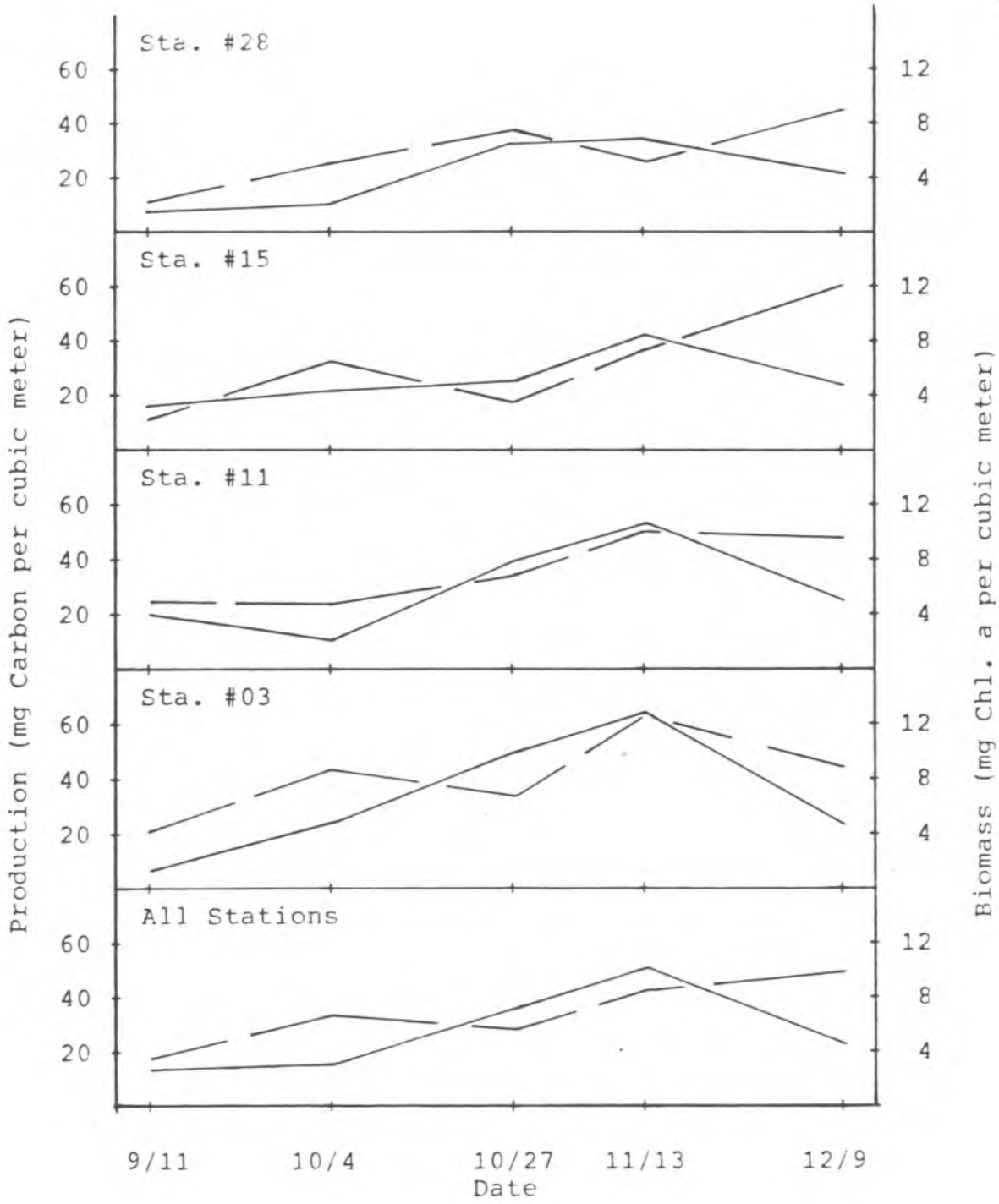


Figure 10. Phytoplankton initial production (———) and biomass (— —). (Dates are mid-points for each sampling period).

Table 8. Zooplankton NH_3-N regeneration and phytoplankton NH_3-N uptake.

Experimental Series	Station Number	Zoo. Regeneration (ug/mg dry wt./d)	Phyto. Uptake (ug/l/d)	Specific Uptake (v/d)*
1	28	-	12.90	5.12
2	11	-	14.28	2.84
3	03	7.95	45.11	10.19
4	15	13.63	14.48	4.99
mean	period #1	5.40	21.69	5.96
5	11	22.50	9.17	1.79
6	28	9.92	13.08	2.45
7	03	13.18	12.46	1.37
8	15	27.32	18.48	2.60
mean	period #2	18.23	13.30	2.05
9	28	12.64	5.48	0.76
10	11	26.78	17.19	2.35
11	15	12.23	10.68	3.24
12	03	-	19.66	3.13
mean	period #3	12.91	13.25	2.37
13	28	18.77	15.45	2.79
14	11	9.57	9.00	0.88
15	03	7.95	15.74	1.27
16	15	9.20	2.84	0.37
mean	period #4	11.37	10.76	1.33
17	11	12.35	17.77	1.78
18	28	11.49	16.84	1.87
19	03	23.86	5.74	0.64
20	15	-	4.90	0.40
mean	period #5	11.92	11.31	1.17

* Specific Uptake, v = (ug NH_3-N/ug Chl. a)

Table 9. Summary of zooplankton regeneration, mean values for each sampling period.

Sampling Period	Ambient NH_3-N (ug/l)	Regen. rate (ug/mg dry wt zoo./d)	NH_3-N supplied (ug/l/d)	Per Cent from zoo.	Turnover time (days)
1	43.2	5.4	2.7	6.2	16.1
2	26.6	18.2	5.4	20.2	5.0
3	37.0	12.9	4.2	11.3	8.8
4	11.3	11.4	3.8	33.6	3.0
5	23.1	11.9	3.6	15.8	6.3
mean	28.2	12.0	3.9	14.5	7.8

Table 10. Summary of phytoplankton uptake, mean values for each sampling period.

Sampling Period	Ambient NH_3-N (ug/l)	NH_3-N Uptake (ug/l/d)	Uptake as % of Ambient	Regen. as % of Uptake	Specific Uptake (v/d)
1	43.2	21.7	47.1	13.0	5.96
2	26.6	13.3	50.3	32.9	2.05
3	37.0	13.2	36.2	40.8	2.37
4	11.3	10.8	96.1	47.4	1.33
5	23.1	11.3	48.2	30.9	1.17
mean	28.2	14.1	55.6	33.0	2.58

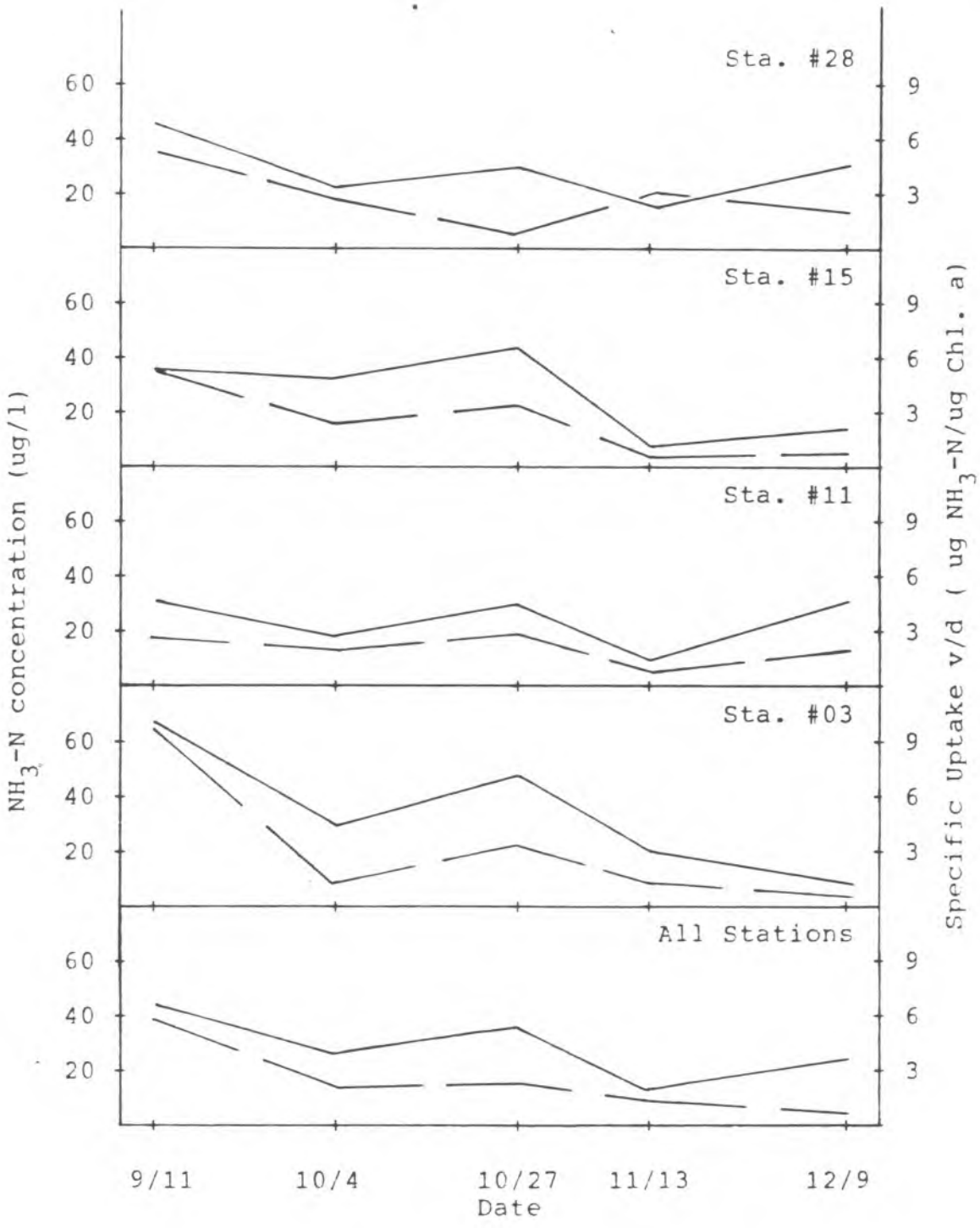


Figure 11. Specific uptake (— —) and NH_3-N concentration (———). (Dates are mid-points for each sampling period).

uptake was calculated from spiked control enclosures, and changed considerably throughout the study (Table 11). Specific uptake was at its greatest percentage of maximum specific uptake when the study began (44.2%), and was at its lowest in sampling period #4 (27.4%).

The estimated amount of nitrogen required to provide for the measured phytoplankton production (Table 7) is summarized in Table 12. Zooplankton regeneration was capable of supplying all of the nitrogen needed for phytoplankton production in the early part of the study, but by period #4 only 50% of the required nitrogen was supplied by zooplankton regenerated NH_3-N. The demand for nitrogen in this sampling period was at its highest, fully 99% of the ambient NH_3-N concentration was required daily to support phytoplankton production and over 120% of uptake was required.

The relationships between nitrogen regeneration, phytoplankton uptake and estimated N - required relative to ambient concentration changed during period #4 (Figure 12). Regeneration and N-required were both substantially less than uptake during the first three sampling periods. During sampling period #4, even though nitrogen regeneration was at its maximum percentage input, it increased much less relative to the increased phytoplankton demand for nitrogen and the

Table 11. Mean specific uptake and maximum specific uptake by sampling period.

Sampling Period	Ambient NH_3-N (ug/l)	Specific Uptake (v/d)	Specific Uptake (% of Max.)	Maximum Specific Uptake (v/d)
1	43.2	5.96	44.2	13.47
2	26.6	2.05	28.2	7.28
3	37.0	2.37	31.9	7.43
4	11.3	1.33	27.4	4.86
5	23.1	1.17	39.4	2.97
mean	28.2	2.58	34.2	7.20

Table 12. Summary of estimated nitrogen required for phytoplankton production, mean values for each sampling period.

Sampling Period	Ambient NH_3-N (ug/l)	Estimated N Required (ug/l/d)	N Required as % of Ambient	Regen. as % of N Required	N Required as % of Uptake
1	43.2	2.30	6.4	138.8	14.7
2	26.6	3.00	10.7	142.6	22.2
3	37.0	6.52	18.4	66.8	57.3
4	11.3	8.59	99.0	49.7	120.5
5	23.1	4.41	24.6	69.1	54.5
mean	28.2	4.96	31.8	93.4	53.8

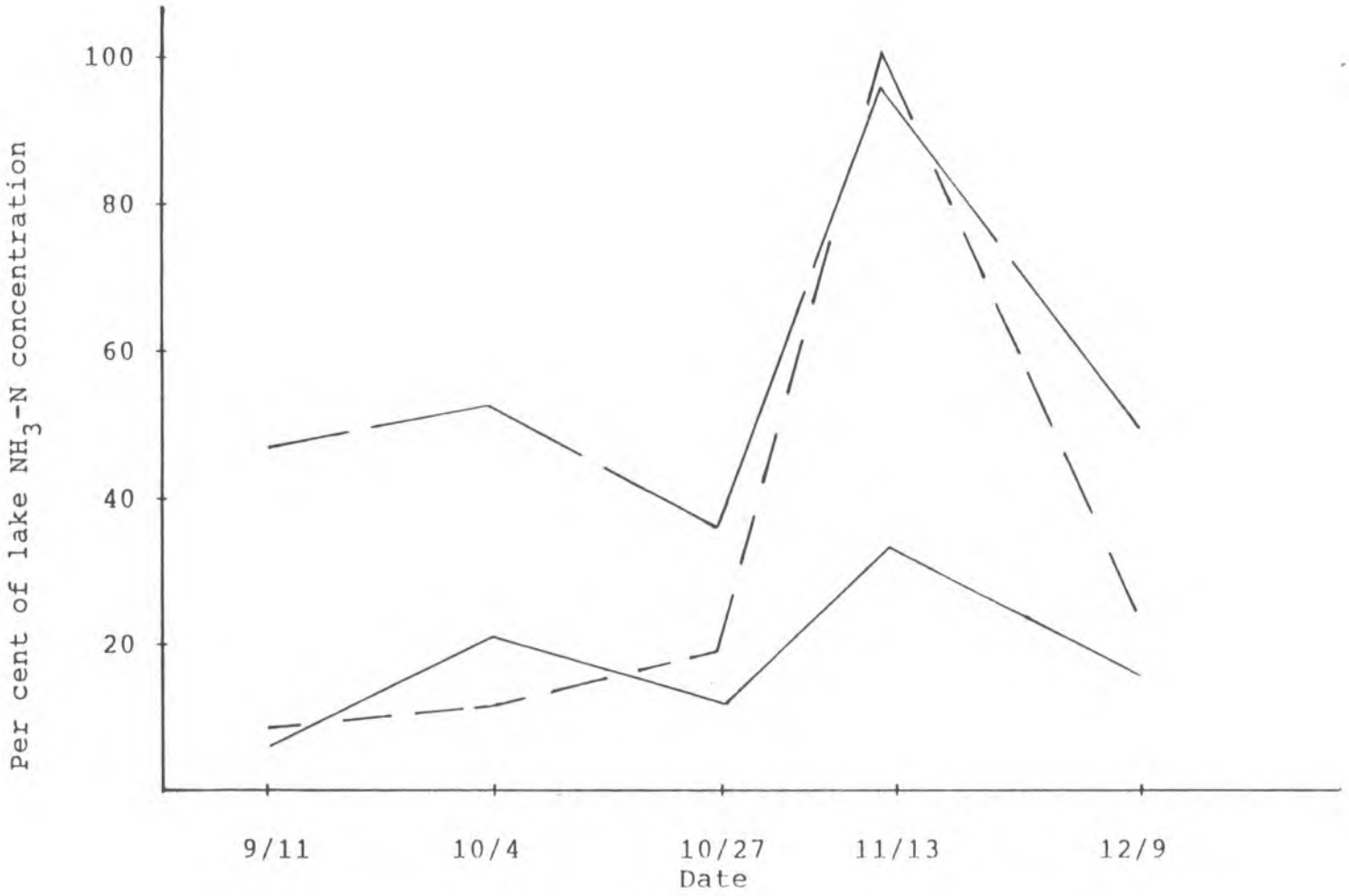


Figure 12. Regeneration (———), uptake (— —), and estimated required nitrogen (— — —) as per cent of ambient lake concentration. (Dates are mid-points for each sampling period).

increased uptake of NH_3-N. During sampling period #4 N-required far exceeded regeneration and NH_3-N uptake.

The effect of zooplankton grazing and nutrient regeneration on phytoplankton was not clear (Table 13). The change per day per mg dry weight zooplankton in phytoplankton production and biomass was both positive and negative within sampling periods. In general, zooplankton had a negative impact on phytoplankton production and biomass in sampling period #1, and a negative impact on production in sampling period #5. Zooplankton had a positive effect on phytoplankton production in sampling period #2. Phytoplankton production and biomass values in sampling periods #3 and #4 were less consistent. The response of phytoplankton production and biomass to zooplankton varied at each station (Figure 13). Production changes were more pronounced than biomass changes.

The effect of zooplankton on the P/B ratio was less variable (Table 13), but no significant ($p \leq .05$) changes in P/B ratio were observed. Overall the P/B ratio increased from the beginning to the middle of the study, and then declined from periods #3 or #4 to period #5 (Figure 14). Zooplankton were beneficial in improving phytoplankton production efficiency (P/B) during the

Table 13. Effect of zooplankton on phytoplankton production, biomass, and P/B ratio, relative change between experimental and control groups. (Values are mean relative change per day per mg dry weight zooplankton).

Exp. Series	Sta. Number	Production Values Short (ug Carbon/l/d)	Production Values Long (ug Carbon/l/d)	Biomass (ug Chl. a per liter)	P/B Ratio (ug Carbon/ ug Chl. a)
1	28	0.86	-0.45	0.14	-0.17
2	11	1.13	-8.34	-2.27**	-0.25
3	03	0.35	0.27**	0.35**	-0.23
4	15	-2.62**	-4.13**	-0.52*	-0.41
period #1		-0.07	-3.16**	-0.58*	-0.27
5	11	1.70	2.91	0.88	0.33
6	28	-2.21*	0.40	0.19	0.00
7	03	2.77	0.66**	0.10	0.07
8	15	3.76**	2.74*	0.24	0.38
period #2		1.50*	1.68**	0.35	0.20
9	28	0.12	0.23	-0.01	0.06
10	11	5.78	0.10	-1.13**	0.58
11	15	-16.17*	-5.30**	-1.92	0.66
12	03	14.86**	8.13**	1.19*	0.22
period #3		1.15	0.79	-0.47	0.38
13	28	1.27	-1.91	-0.90	0.24
14	11	1.72	3.57**	1.43*	-0.27
15	03	0.56	-1.64**	-0.29	-0.03
16	15	-2.11	-0.32	-1.93**	0.47
period #4		0.36	-0.08	-0.42	0.10
17	11	-3.95*	-5.20**	-1.18**	-0.21
18	28	2.45	-1.42	1.49	-0.41
19	03	-5.08	0.27	1.31	-0.39
20	15	-	3.88	1.50	0.04
period #5		-0.68	-2.12**	0.54	-0.24

* = $.05 < p < .1$, ** = $p < .05$
Production Short - relative change in production measured midway through experimental incubation.
Production Long - relative change in production measured at termination of experimental incubation.
Biomass and P/B - relative changes measured at termination of experimental incubation.

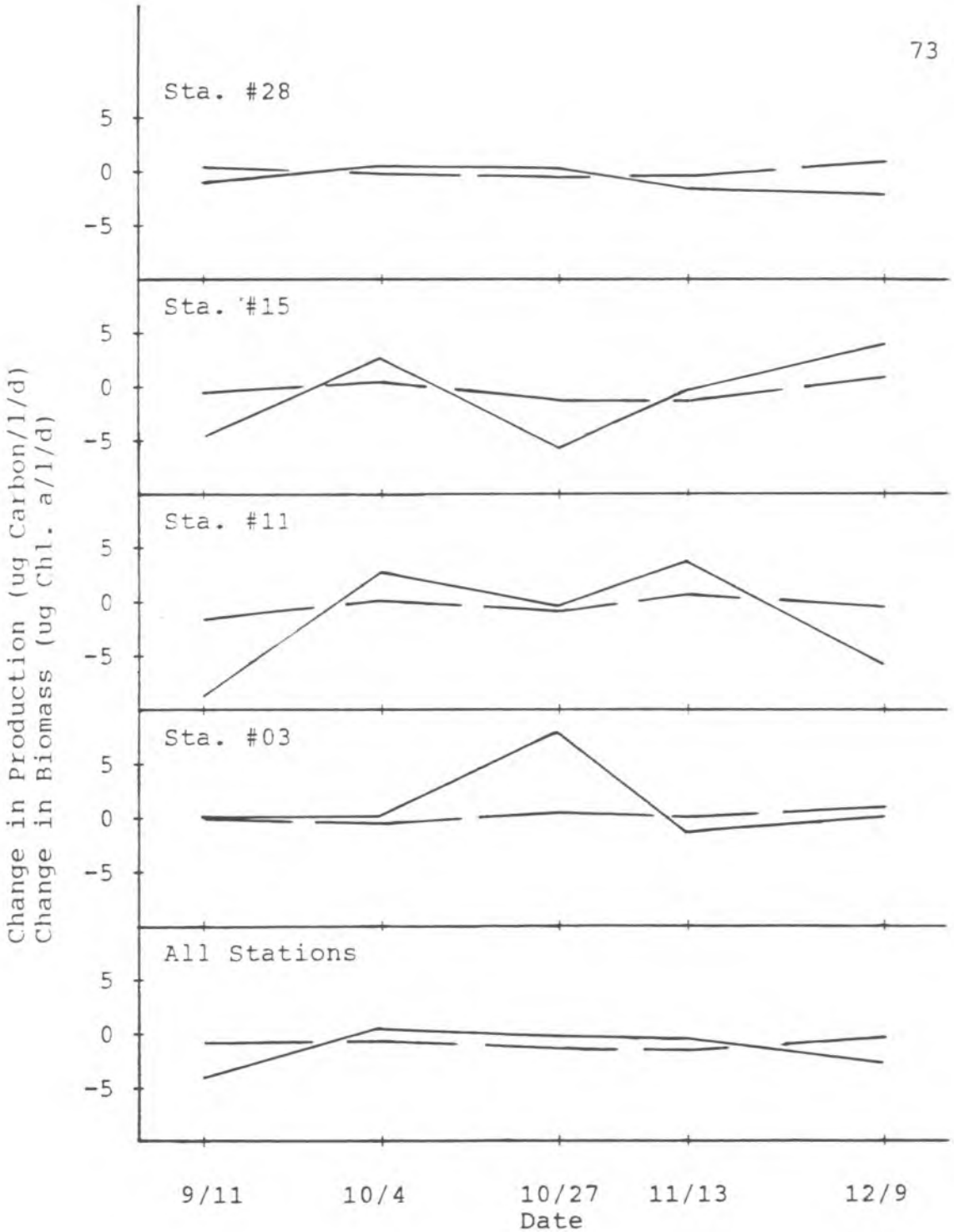


Figure 13. Effect of zooplankton on phytoplankton production (———) and biomass (— —). (Values are mean relative change per day per mg dry wt. zoo. between initial and final values). (Dates are mid-points for each sampling period).

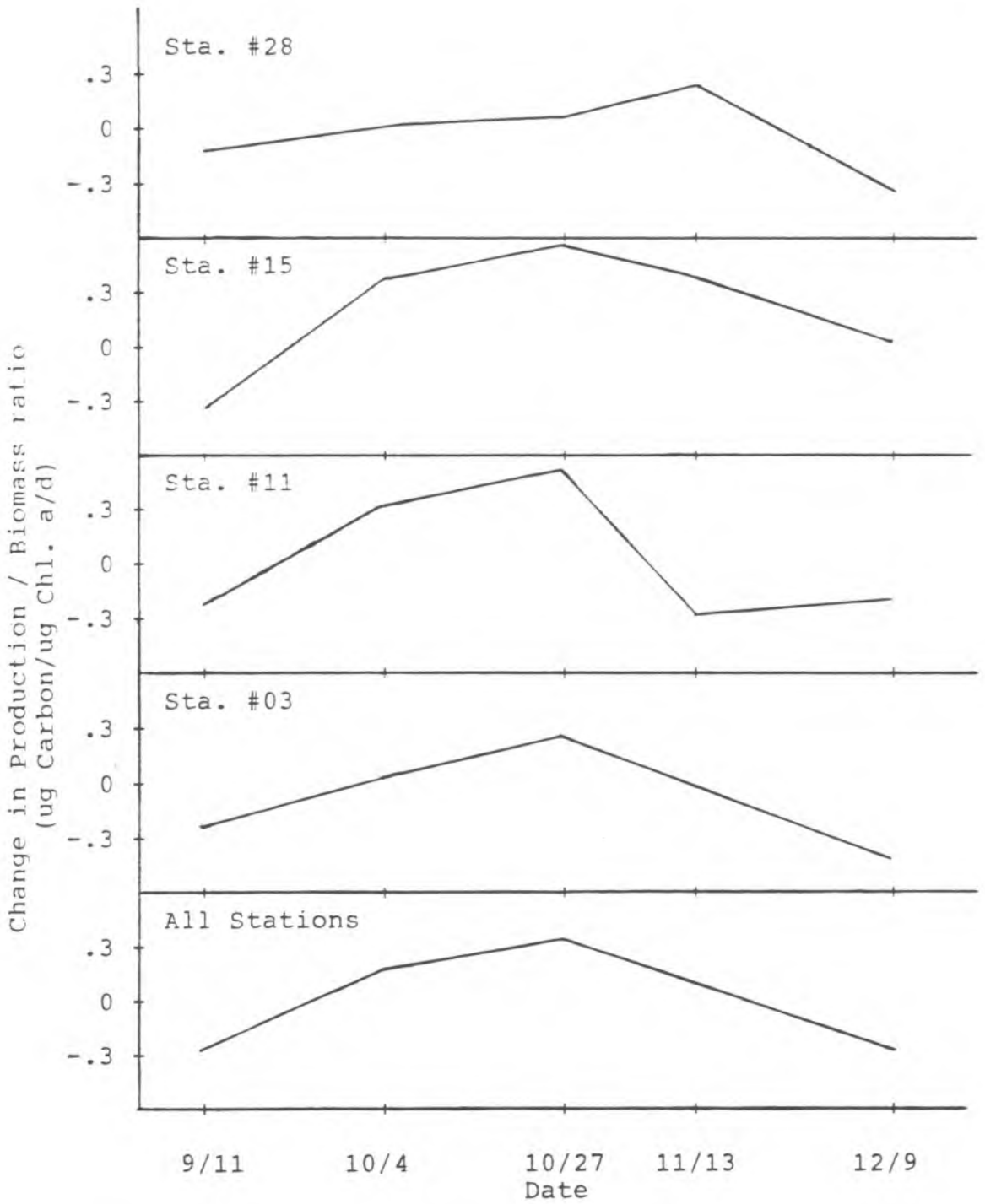


Figure 14. Effect of zooplankton on phytoplankton P/B ratio. (Values are mean relative change per day per mg dry wt. zoo. between initial and final values). (Dates are mid-points for each sampling period).

middle part of the study, though not significantly.

The change in P/B ratio (Table 14) relative to zooplankton biomass changed throughout the study (Figure 15). Initially, the percent change in P/B was negatively correlated with zooplankton biomass, but by sampling period #3 there was a positive correlation. Between sampling period #3 and #5 the correlation between change in P/B and zooplankton biomass became increasingly negative.

Table 14. Mean relative change between experimentals and controls in P/B ratio as a per cent of initial P/B values. (No adjustments for differing zooplankton biomass have been made on these values).

Experimental Series	Station Number	Initial P/B (ug C/ ug Chl. a)	Rel. Change in P/B (Change/d)	Per Cent Change (%)
1	28	3.06	-0.04	-1.5
2	11	4.01	0.00	0.0
3	03	1.73	-0.13	-7.8
4	15	5.95	-0.18	-3.0
mean	period #1	3.69	-0.09	-3.0
5	11	1.73	0.04	2.1
6	28	1.72	-0.04	-2.2
7	03	2.84	0.00	0.0
8	15	3.48	0.11	3.1
mean	period #2	2.44	0.03	0.7
9	28	4.28	-0.01	-0.2
10	11	5.70	0.20	3.4
11	15	8.06	-0.05	-0.6
12	03	7.98	0.04	0.4
mean	period #3	6.51	0.04	0.8
13	28	6.18	0.06	0.9
14	11	5.23	-0.04	-0.7
15	03	5.27	-0.02	-0.3
16	15	5.64	0.12	2.2
mean	period #4	5.58	0.03	0.5
17	11	2.77	-0.09	-3.1
18	28	2.50	-0.09	-3.6
19	03	2.90	-0.08	-2.6
20	15	2.02	0.00	0.0
mean	period #5	2.55	-0.06	-2.3

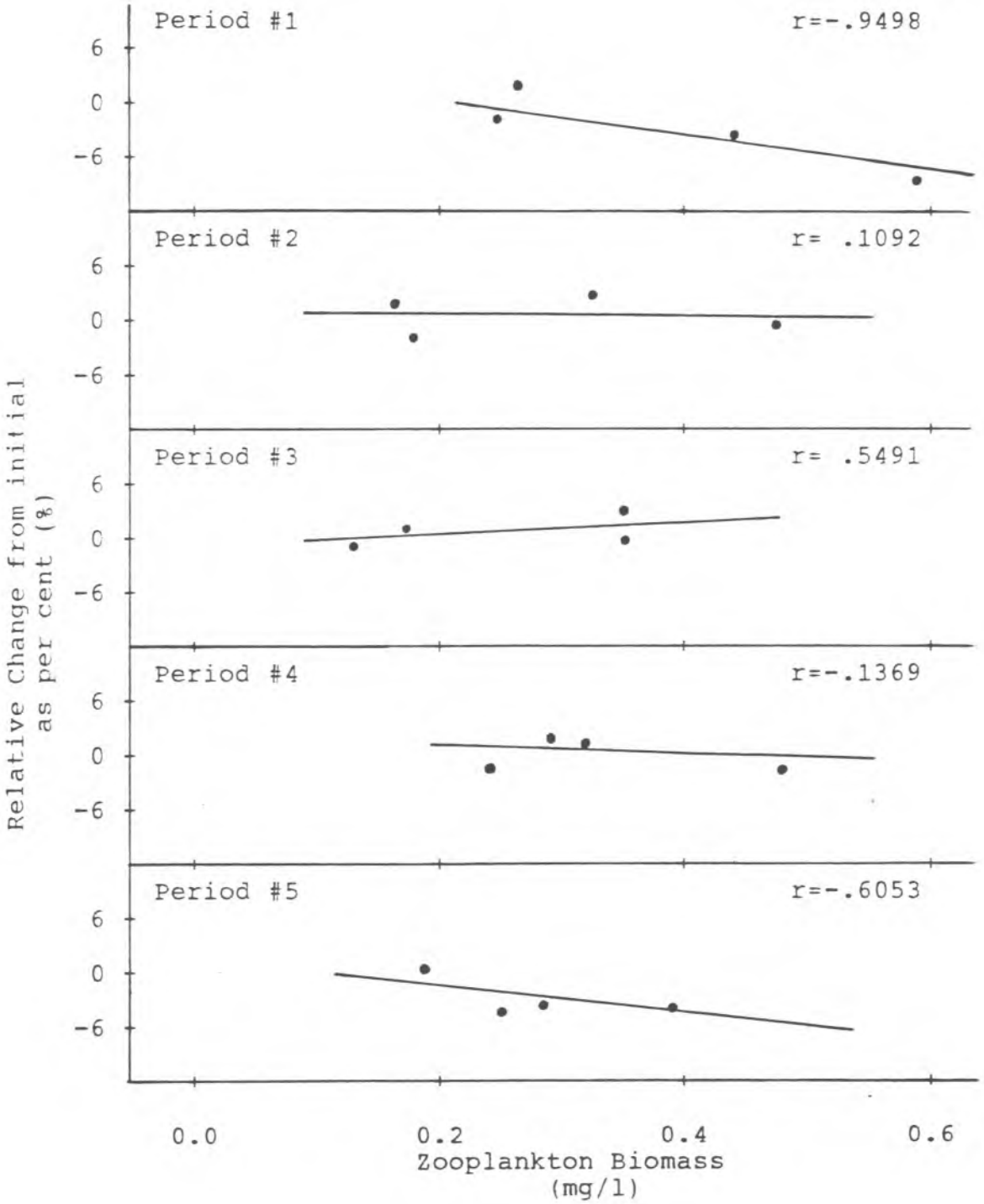


Figure 15. Mean relative change in P/B ratio as a per cent of initial P/B values relative to zooplankton biomass. (Values not adjusted for differences in zooplankton biomass within enclosures).

DISCUSSION

To understand zooplankton - phytoplankton interactions in Lake Chapala the first step was to determine zooplankton regeneration of essential nutrients and the extent regenerated nutrients were utilized by phytoplankton. The extent to which phytoplankton utilize nutrients regenerated by zooplankton is an indication of nutrient recycling. Nutrient recycling, and therefore regeneration, is important only if nutrients are limiting phytoplankton production. As nutrients become less available nutrient regeneration and recycling become more important. Phytoplankton uptake and the estimated nitrogen required for production are measures of nutrient demand. If uptake and estimated nitrogen requirements are high relative to ambient concentrations, then nutrient demand is high. If nutrient demand is slight, nutrient recycling and therefore zooplankton regeneration of nutrients are unimportant.

The next step was to determine the direct effects of zooplankton on phytoplankton production and biomass. Zooplankton regenerate nutrients by grazing. Zooplankton grazing can negatively affect phytoplankton biomass and therefore production. Zooplankton grazing

and nutrient regeneration interact to affect phytoplankton biomass and production. The overall effect of zooplankton on phytoplankton biomass and production is in part dependent upon nutrient demand.

Zooplankton Community Structure

Though stations showed considerable individuality throughout the study in organism abundances (Table 5) all 11 taxa were represented at each station (Table 4) except for Brachionus spp. at station 03. This reflects the similarity in stations (Figure 1). All were open water locations.

Except for Mesocyclops inversus and Diaphanosoma leuchtenbergianum all genera were reported previously from the lake by Ortiz et al. (1982). In addition they found one other genus of Cladocera, two other genera of Copepoda, and seven other genera of Rotifera. Many of their sampling stations were near shore and a total of 24 locations were sampled. They sampled a greater variety of lake habitat and throughout the year which probably explains the greater variety of organisms encountered.

Station 03 had the highest zooplankton biomass relative to abundance (Figure 8, Table 6). This was partly due to the dominance of larger-bodied copepods at

this station (Table 5). Station 15 was also dominated by copepods during sampling period #1. The dominant copepod, Diaptomus albuquerquensis, was largest during this sampling period as well. Additionally, although accurate counts were not made, both station 03 and 15 had much higher numbers of an unidentified testate amboeba than the other two stations, especially in the early part of the study.

Length measurements included immature individuals and therefore may be more reflective of overall population age at the time of sampling than anything else. These values fluctuated somewhat during the study in no discernable manner, and gave the impression of a dynamic, constantly changing population.

Zooplankton abundance and biomass were dynamic as well. Cladoceran abundances peaked in October or November, copepods in November, and rotifers in November or December (Table 5). These peaks, which follow the wet season and precede the longer dry season, generally coincide with changes in phytoplankton biomass. This seasonal pattern agrees with the results of Ortiz et al. (1982). An overall seasonal pattern in zooplankton abundance was identifiable, but the variability among stations throughout the study was considerable.

Zooplankton biomass and abundance was dynamic not

only seasonally but spatially. Abundances for any given species would frequently increase at one station and decline at the next within a sampling period.

While an overall seasonal pattern in zooplankton abundances seemed to exist, this pattern was modified by differences at the widely separated stations. Though stations were very similar in species represented, the abundances of those species at any given moment were quite different. Zooplankton populations in Lake Chapala were neither static nor homogenous, but were more dynamic and patchy. This is very different from Lake George, where zooplankton biomass was strongly dominated by a single species and changed little throughout the year.

Nutrient Recycling

The enclosure material was suitable. NH_3-N changes in the polyethylene test bags during preliminary testing averaged -2%, with no pattern of change due to pH or concentration.

NH_3-N regeneration measurements were made assuming a constant regeneration rate. Since incubation tank temperatures were relatively stable, this assumption would be met if food supplied remained

constant. Flourometer readings indicated only a slight decrease in chlorophyll throughout the incubation period in RG experimental enclosures (-6.6%). Phytoplankton biomass was relatively stable, and hence food supply constant.

I assumed zooplankton biomass did not change through the incubation period. Dry weight measurements and organism counts for the last three experimental series indicated that this assumption was reasonably met. The average change from initial to final for dry weight measurements was a 15.1% decline with an average increase of 12.0% in organism counts. Copepods declined, rotifers increased, and cladocerans were relatively unchanged, thus the numbers increased overall with a decline in biomass.

The mortality of copepods is of some concern because they were the dominant organisms, even though nauplii mortality accounted for most of the loss. Damaged individuals were noted in these samples although healthy individuals were frequently observed at termination of experiments. The decline in zooplankton would tend to increase regeneration rate estimates, assuming all mortality did not occur at the initiation of the experiment.

It was also assumed that regeneration in controls

was zero, and therefore regeneration was found by the relative change between control and experimental enclosures. This assumption was reasonably met also. Organism counts from control enclosures for the last four series revealed that only copepod nauplii and rotifers were not completely removed. On average, 86.3% of nauplii were removed, while only 35.4% of rotifers were removed. Even though most of the larger organisms were effectively removed from controls, the failure to remove all zooplankton from controls would tend to underestimate regeneration rates.

I assumed total phytoplankton uptake was equal in experimental and control RG enclosures. Since both enclosure sets were spiked with NH_4Cl to saturate uptake, the rate of phytoplankton uptake was made equal. Phytoplankton biomass did not remain equal however, and so total uptake was not exactly equal. Changes in chlorophyll content, as measured by flourometer readings, indicated a slight increase in phytoplankton biomass in RG control enclosures (4.6%) and a slight decrease in experimentals (-6.6%). This difference is attributable to grazing impact by zooplankton. Although phytoplankton biomass did not remain equal between experimental and control enclosures the difference between them was slight, only 10.7%, so this assumption

has been relaxed somewhat. This difference in phytoplankton biomass and therefore total uptake tends to lower regeneration estimates.

In calculating phytoplankton uptake from NH_3-N concentration changes and zooplankton regeneration rates I assumed that phytoplankton biomass remained relatively stable during the one day measuring period. Flourometer readings indicated little change in biomass in the PB experimental enclosures, and so this condition was met.

If zooplankton NH_3-N regeneration rates were incorrectly estimated then estimates of phytoplankton uptake rates were likewise incorrect. In considering the sources of error in estimating zooplankton regeneration rates, it is likely that my estimates maybe be somewhat lower than actual regeneration rates, and therefore phytoplankton uptake may be underestimated as well.

Zooplankton NH_3-N regeneration rates (Table 8) were similar to values reported from other freshwater locations (Axler et al. 1981; Lehman 1981a; Ganf and Blazka 1974). Lake George, Uganda, is morphologically similar to Lake Chapala but is seasonally stable. The daily mean NH_3-N regeneration rate reported for Lake George was 23.1 ug/mg dry wt. zoo (Ganf and Blazka 1974), while the daily rate for Lake Chapala was 12.0

ug/mg dry wt. zoo. Zooplankton in Lake George are believed to be responsible for regenerating all the nitrogen necessary to maintain phytoplankton production. The turnover time for NH_3-N in Lake George is approximately 1 day, while in Lake Chapala turnover time averages 7.8 days. Still, zooplankton regeneration is important in Lake Chapala. While only 14.5% of ambient NH_3-N was supplied by zooplankton regeneration (Table 9), regeneration accounted for an average of 33% of phytoplankton uptake (Table 10), and over 93% of the estimated N-required (Table 12).

The relative effect of zooplankton regeneration to the NH_3-N pool changed in Lake Chapala (Figure 12). Regeneration supplied nearly all the nitrogen required during the early part of the study. Phytoplankton uptake during this time was approximately 50% of ambient, much higher than the estimated N-required. This indicates some luxury uptake early in the season. In the middle of the season however there was a great change. Even though zooplankton regeneration was at its greatest contribution to the NH_3-N pool, the gap between supply and demand was at its widest. Regeneration supplied 46% of ambient, but phytoplankton uptake was 96% of ambient and N-required reached 99% of available NH_3-N. Phytoplankton production and

biomass were high late in the season (Figure 10). Demand for nitrogen greatly exceeded zooplankton regeneration. Indeed, it appears that the demand for nitrogen exceeded availability, or at least the ability of phytoplankton to effectively uptake sufficient nitrogen, as production rates declined at the end of the study.

Maximum specific uptake of NH_3-N by phytoplankton, measured from spiked RG control enclosures, changed throughout the study (Table 11). This may indicate a change in phytoplankton species composition, lake temperature, physiological state of the algae, or a combination of factors. Whatever the cause, maximum specific uptake declined, and by the end of the study was less than a quarter the value at the beginning.

NH_3-N specific uptake seemed to change with concentration (Figure 11) and when concentrations are relatively low, as in sampling period #4 (Table 3, Figure 7), phytoplankton uptake becomes increasingly less efficient. Even though maximum specific uptake (v), had declined to only 4.86 v/d by sampling period #4, phytoplankton uptake efficiency was at its lowest value, only 27.4% of maximum (Table 11).

This is an apparent "no win" situation. The lower the concentration the lower the specific uptake and

hence the lower the uptake efficiency. The greater the demand the less NH_3-N available, and the less efficiency at obtaining it. Such a cycle could not continue indefinetly. The discrepancy between supply and demand became critical during sampling period #4.

Demand for nitrogen during sampling period #4 was high (Table 7) but the ambient NH_3-N pool was at its lowest. The demand reduced supply which in turn intensified demand. Nitrogen was not only becoming scarce but the ability of phytoplankton to efficiently uptake NH_3-N was diminished by the scarcity.

Because the demand for nitrogen was not steady (Table 7), the relative importance of zooplankton regenerated NH_3-N was not constant. Zooplankton regeneration reached its highest percentage contribution to the NH_3-N pool in period #4 (Table 9) when demand was greatest. However, at its highest this amounted to only 33.6% of ambient, a turnover time of 3.0 days. While this is a valuable contribution by zooplankton regeneration it is not comparable to that reported for Lake George, where turnover time averages 1.0 days.

Zooplankton regeneration as a percentage of phytoplankton uptake was also highest in sampling period #4 (Table 10), at 47.4%. Nearly half of the NH_3-N uptake was supplied by zooplankton regeneration.

The importance of zooplankton NH_3-N regeneration as a percentage of N-required was just the opposite of its contribution to ambient and phytoplankton uptake. One-half (49.7%) of the estimated N-required was supplied by zooplankton during sampling period #4, the lowest percentage contribution (Table 12).

During sampling period #4 zooplankton regeneration reached its highest percentage contribution to the ambient NH_3-N pool and to phytoplankton uptake, and its lowest contribution to the estimated N-required. Demand was much greater than supply. Neither zooplankton regeneration nor nitrogen from other sources were sufficient to satisfy demand, and the available NH_3-N was reduced.

The value of zooplankton regenerated NH_3-N in Lake Chapala is not as constant or sustained as in tropical Lake George, nor is zooplankton regeneration sufficient to supply the N-required to maintain or extend phytoplankton production late in the growing season as is the case in some temperate lakes (Axler et al. 1981; Redfield 1980).

Zooplankton NH_3-N regeneration in Lake Chapala, while important during the "high demand" part of the season, may be more important early in the season when

concentrations and phytoplankton uptake are high relative to demand. Near the end of the rainy season NH_3-N concentration is as high as it is likely to be. The long dry spell, both literally and in terms of available nitrogen, is over. Phytoplankton NH_3-N uptake is high, much higher than required to maintain production. Zooplankton regeneration during this time helps to redistribute this resource for later use. Excess phytoplankton uptake is resupplied to the NH_3-N pool by zooplankton regeneration, making it available for later use when demand is much greater.

Nitrogen does appear to be limiting at times in Lake Chapala. Flourometer readings from NH_3-N spiked (RG) enclosures usually showed a substantial increase over readings from non-spiked (PB) enclosures. Nitrogen demand based on phytoplankton production values also indicated a shortage, at least late in the growing season. While zooplankton NH_3-N regeneration does not eliminate the nitrogen shortage in Lake Chapala, it is important in redistributing this resource.

Production/Biomass

There did not appear to be a close coupling of zooplankton - phytoplankton interactions in Lake Chapala like that in Lake George. The effect of zooplankton

grazing and nutrient regeneration on phytoplankton biomass and production changed throughout the season. Changes in phytoplankton production values due to zooplankton were negative early in the study, probably a result of zooplankton grazing impacting phytoplankton biomass (Table 13). Zooplankton biomass was high relative to phytoplankton biomass during sampling period #1 (Figure 9). Changes in phytoplankton production values and biomass were positive in sampling period #2 (Table 13) and generally mixed thereafter. P/B ratios, though not significantly changed by zooplankton, displayed the same pattern.

The effect of zooplankton on phytoplankton production and biomass was variable among stations (Figure 13) throughout the study. However, the change in phytoplankton production per unit biomass (P/B) due to zooplankton was similar at all stations, positive through the middle part of the study (periods #2 - #4) and negative at the beginning and end (Figure 14).

Zooplankton grazing may have had a negative impact initially but as phytoplankton biomass increased this impact was negated. Zooplankton improved phytoplankton production efficiency during the middle part of the study.

The mean relative change in P/B (Table 14) as a

function of zooplankton biomass (Figure 15) supports the conclusion of a seasonal impact on phytoplankton by zooplankton. The initial negative correlation between zooplankton biomass and change in P/B became increasingly positive until sampling period #3, and then increasingly negative again. This is similar to the results reported by Redfield (1980) for temperate Castle Lake. He found the effect of increased zooplankton biomass on phytoplankton production became increasingly more negative later in the growing season.

The influence of zooplankton grazing and nutrient regeneration on phytoplankton production and biomass in Lake Chapala was neither stable nor sustained. In contrast to Lake George where phytoplankton production and biomass are relatively stable throughout the year, Lake Chapala has considerable seasonal variation. Zooplankton - phytoplankton interactions in Lake Chapala change accordingly.

The response of phytoplankton production and biomass to zooplankton grazing and nitrogen regeneration in Lake Chapala is more similar to that of a seasonally affected temperate lake than a seasonally stable tropical lake. Zooplankton - phytoplankton interactions would seem to be regulated more by local environmental variations than similarity in latitude. Though tropical

lakes may inherently be more likely to have little seasonal variation, it is not always the case. Lake Chapala and Lake Titcaca, Peru (Vincent et al. 1984) are not seasonally stable.

Zooplankton - phytoplankton interactions in Lake Chapala are dynamic and seasonal. The effects of zooplankton grazing and nutrient regeneration on phytoplankton production and biomass change seasonally in response to changing environmental conditions, chief of which is rainfall.

SUMMARY AND CONCLUSIONS

Lake Chapala is a large tropical lake which experiences two seasons, a wet season (May to September), and a dry season (September to May). Nutrient input occurs in the wet season.

Phytoplankton production and biomass increase after nutrient inputs in the summer wet season, and peak in November or December. Available nitrogen is diminished as phytoplankton biomass increases. At some time nitrogen begins to limit phytoplankton production.

Zooplankton populations are dynamic. Zooplankton abundances peak in November but are not homogenous within the lake. Open-water sampling stations are uniform in species represented but are variable with respect to species abundances.

Regeneration by zooplankton is an important contribution to the NH_3-N pool in Lake Chapala. Zooplankton regeneration is valuable in redistributing available NH_3-N. Though regeneration, on average, can supply all the nitrogen required to maintain phytoplankton production, it is insufficient by itself to meet nitrogen demands at all times of the year.

The importance of zooplankton NH_3-N re-

generation in Lake Chapala is variable, as ambient nitrogen declines and demand for nitrogen increases. While zooplankton regeneration can not supply sufficient nitrogen to meet peak phytoplankton production demands, it adequately meets nitrogen requirements early in the season. Because phytoplankton uptake exceeds demand early in the season, regeneration during this time helps to redistribute NH_3-N to the lake, making it available for later use.

Zooplankton regeneration in Lake Chapala is not closely coupled to N-requirements of phytoplankton production, nor is it sufficient to maintain or extend phytoplankton production later in the season when nitrogen becomes scarce. It is, however, important in releasing NH_3-N early in the production season making that NH_3-N available for recycling later when demand is greater.

The effect of zooplankton grazing on phytoplankton biomass is negative very early in the season. Zooplankton reduce phytoplankton biomass and consequently production. As phytoplankton biomass and production increase though, the negative effect of zooplankton is reduced.

Phytoplankton production efficiency (P/B ratio) changes in response to zooplankton as the seasons

change. At the end of the wet season (September), when nitrogen was more available, production efficiency declines. Early in the dry season (October - November), as nitrogen becomes less available, production efficiency generally improves. Later in the dry season (December), after production has peaked, the effect of zooplankton on phytoplankton production efficiency is again negative.

The interactions between zooplankton grazing and NH_3-N regeneration, and phytoplankton production and biomass in Lake Chapala changes seasonally (Figure 16). Initial negative grazing impacts from zooplankton, give way to positive regeneration effects, which then become less important than grazing effects again as phytoplankton production declines.

Nutrient dynamics and production processes in Lake Chapala are not entirely known. Zooplankton NH_3-N regeneration in the later half of the dry season (December - May) and during the wet season (May - September) warrants further investigation. Also worthy of consideration in understanding the nutrient dynamics of the lake are microbial remineralization and resuspension of nutrients from the sediments. Lake Chapala is large, shallow, warm, and frequently windy. These processes may prove to be very important. Never-

theless, zooplankton - phytoplankton interactions are important to the nutrient dynamics and production processes within Lake Chapala.

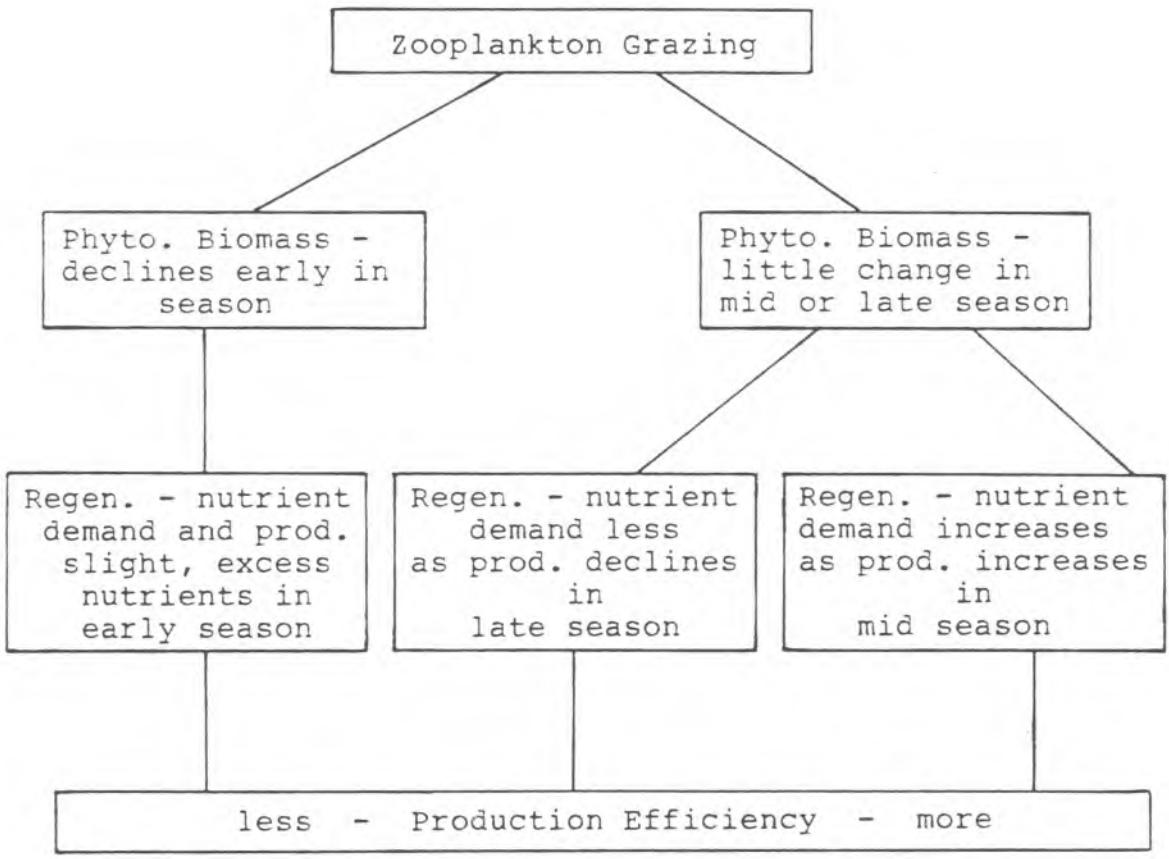


Figure 16. Relative interactions between zooplankton grazing and NH_3-N regeneration, and phytoplankton production and biomass.

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