The Impact of Nutrient Pulses on Trophic Interactions in a Farm Pond

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Abstract

We placed eight 1500 L mesocosms in a 0.2 ha eutrophic cattle pond during summer 1991 to determine if zooplankton grazing, nutrients, or both control algal biomass and productivity. The three treatments: + zooplanktivorous fish (39 bluegill, mean total length = 36 mm); + zooplankton (10x ambient); and + N + P (160 μM NH_4^+ and 10.0 μM PO_4^{3-}) were duplicated and compared to ambient pond conditions and two control mesocosms. In the + N + P treatment, chl *a* concentrations increased 700% in four days and then decreased to initial levels; further nutrient enrichments failed to create an algal response, probably because of grazing associated with an eightfold increase in large cladocerans. After nutrients were added to the + fish treatment, the NH_4^+ and soluble reactive phosphorus concentrations rose and then decreased rapidly, whereas chl *a* concentrations and rotifer numbers increased. When nutrients were added to the + zooplankton treatments, chl *a* increased, but less than when either fish or nutrients alone were added. In small eutrophic ponds, trophic manipulations may have little effect during equilibrium conditions but do alter algal responses during nutrient pulses. An increase in large cladocerans in response to a nutrient pulse may control nuisance algal blooms, even with subsequent nutrient additions.

Introduction

Biomanipulation, first proposed by Shapiro et al. (1975), is based on the idea that a decrease in algal blooms and an increase in water clarity in lakes and ponds can be achieved through food web manipulations. The cascading trophic interactions hypothesis of Carpenter et al. (1985) accounted for the roughly 50% observed variability in primary production not explained by nutrient loading. The concept of biomanipulation when applied to lakes is that an increase in piscivorous fish will result in a decrease in planktivorous fish; an increase in zooplankton; and, ultimately, a decrease in algal biomass and primary production.

Many studies have tested the effectiveness of biomanipulation. DeMelo et al. (1992) examined the results in 50 papers encompassing 44 separate studies involving biomanipulation. They found agreement with the cascading trophic interactions hypothesis to be 100% at the level of the piscivore-planktivore interaction, 72% at the level of the planktivore-zooplankton interaction, 20% at the level of the zooplankton-chl *a* interaction, and 21% at the level of the zooplankton-Secchi depth interaction. The apparent weakening of the trophic

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cascade at the zooplankton-phytoplankton link has raised questions regarding the general effectiveness of biomanipulation management. However, this weakening may be related to the trophic state of the lake.

The impact of lake trophic status on the zooplankton-phytoplankton interaction has received a great deal of attention. Of the 22 studies summarized by DeMelo et al. (1992) that reported trophic status of lakes, 16 were eutrophic to hypereutrophic, two were mesotrophic, and four were oligotrophic. In a model proposed by McQueen et al. (1986), zooplankton should have the most prominent effect on phytoplankton in oligotrophic lakes where top-down effects are not buffered strongly by bottom-up effects (nutrient availability). Elser et al. (1990a) suggested that the effects of zooplankton on phytoplankton are most significant in mesotrophic lakes and weak in lakes with either extremely low or high productivity. In eutrophic lakes or fertilized enclosures, an increase in filter-feeding zooplankton usually can initially control phytoplankton biomass. However, after extended periods, the zooplankton ultimately can fail at reducing algal populations (Gliwicz 1990). Very few, if any, studies have looked at the importance of the zooplankton-phytoplankton interaction in relation to nutrient pulses.

Grover (1990) hypothesized that a lack of equilibrium caused by nutrient pulses might explain higher species diversity in ecosystems with more than one resource. Therefore, nutrient pulses may allow for a more diverse phytoplankton assemblage and, thus, maintain the presence of smaller, more edible phytoplankton. This then may increase the ability of zooplankton to decrease phytoplankton biomass.

Small ponds (farm ponds) are important aquatic habitats in the midwest United States. For example, small farm ponds make up 46% of the total surface lake area in Kansas, because few natural lakes occur. These types of impoundments often are supplied by ephemeral streams, which can induce short-term nutrient pulses during periods of flow. In addition, many of these ponds also are used as water sources for cattle. A common practice in cattle ranching is to periodically move cattle from one pasture to another, thereby supplying the watering ponds with periodic nutrient pulses. Few studies have been conducted on the potential for trophic controls of algal blooms in these impoundments (except see Arruda 1979). The purpose of this study was to determine if top-down effects (grazing by zooplankton), bottom-up effects (nutrient availability), or both control the response of algal biomass and primary production in small ponds that receive short-term (days) pulses in nutrient supply.

Methods and Materials

Fry's Pond (0.2 ha) is a shallow (max. depth = 2 m) eutrophic pond located 2 km north of Kansas State University in the northeast Kansas tallgrass prairie and is used exclusively as a water source for cattle. Four 10 L translucent polyethylene carboys were used for nutrient deficiency bioassays. The carboys were filled with surface water collected from the center of the pond. The four deficiency bioassay treatments were control (no nutrient addition), + N (160 μM NH_4Cl), + P (10 μM NaH_2PO_4 H_2O), and + N + P (160 μM

NH_4Cl and 10 μM NaH_2PO_4). Carboys were suspended in the center of the pond at a depth of approximately 0.5 m, recovered after seven days, and taken to the laboratory. Within one hour, three 100 mL aliquots from each carboy were filtered onto Whatman GF/C filters and frozen for later analysis of chl *a*. Phaeophytin-corrected chl *a* was analyzed fluorometrically with the acid addition method (APHA 1989).

Eight, 1500 L mesocosms were placed in the center of Fry's Pond (3 September 1991) for the biomanipulation study. The mesocosms (cylinders 1 m in diameter, 2 m deep) were made of semitransparent, layered, reinforced, low-density, polyethylene sheeting sealed with Griff-tape and held rigid externally with 1 m diameter hoops of 13 mm PVC pipe at the top and bottom. The bottom hoop was filled with concrete for negative buoyancy. The open mesocosm bottoms were inserted 0.2 m into the sediments and anchored with galvanized wire stakes. The tops were supported by an anchored wooden frame with styrofoam added for extra buoyancy.

The mesocosms contained one of three duplicate treatments: + fish, + zooplankton, or + N + P; the final two mesocosms were left as controls (see details in Table 1). Bluegill for the + fish treatments were obtained by seining the shoreline of the pond. Zooplankton for the + zoo treatments were collected by hauling a 32 cm diameter, 160 μm mesh plankton net for 50 m (10 times the volume of each enclosure passed through plankton net) for each + zoo enclosure.

Table 1. Description and timing of additions to 1500 L mesocosms placed in Fry's Pond from 5 September 1991 until 1 October 1991.

	Day		
Treatment	1	7	12
Control	-	-	-
+ N + P	160 μM NH_4Cl 10.0 μM NaH_2PO_4	160 μM NH_4Cl 10.0 μM NaH_2PO_4	Micronutrients[a]
+ Fish	39 bluegill (*Lepomis macrochirus*) mean TL = 36 mm	-	160 μM NH_4Cl 10.0 μM NaH_2PO_4
+ Zoo	10 x ambient	-	160 μM NH_4Cl 10.0 μM NaH_2PO_4

[a] Woods Hole MBL, pH 7.2, 1 mL L^{-1} (Stein 1973); included Na_2 EDTA, $FeCl_3$, $CuSO_4$, $ZnSO_4$, $CoCl_2$, $MnCl_2$, and Na_2MoO_4.

Secchi depth measurements and water samples were collected every two or three days from 5 September 1991 until 1 October 1991. Aliquots (100 mL) from the water samples were filtered through Whatman GF/C filters and frozen

for later analysis of NH_4^+, NO_3^- + NO_2^-, and soluble reactive phosphorus (SRP). NH_4^+ was measured by the phenol hypochlorite method (Solorzano 1969), and SRP and NO_3 were measured using the acid molybdate (Strickland and Parsons 1972) and the cadmium reduction (Eppley 1978) methods, respectively. Chl *a* was measured in the same manner as described above for the carboys. Photosynthetic rate measurements were started in the laboratory within 1 h of collection. Six aliquots from each mesocosm were placed in 60 mL borosilicate BOD bottles; three bottles were placed in the dark and three under cool white fluorescent lights (150 μmol quanta m^{-2} s^{-1}, similar to light at about 0.75 m in the pond, under full sunlight) for 4 h at 25 °C. Oxygen was measured by titration using the azide modification of the iodometric method of APHA (1989).

Zooplankton samples were collected at day 26 by a single vertical haul of an 11 cm diameter, 61.2 μm mesh plankton net from the sediments to the surface within each enclosure and in the pond. Net contents were rinsed into a 1 L bottle, and all samples were raised to a constant volume with reverse osmosis water. Samples were preserved with 4% formaldehyde (final concentration) for later analysis. A 1 mL subsample from each sample was used for zooplankton enumeration and identification. Dry weight of different zooplankton types was obtained directly by weighing. Individuals of each zooplankton group (cladocerans, copepods, nauplii, and rotifers) were extracted from each sample and placed into vials containing 15 mL of reverse osmosis water. The contents of each vial were filtered through a 3 μm polycarbonate membrane filter and rinsed with an additional 50 mL of reverse osmosis water. The filters were dried at 60 °C for 24 h and weighed to the nearest 10^{-6} g to estimate zooplankton biomass.

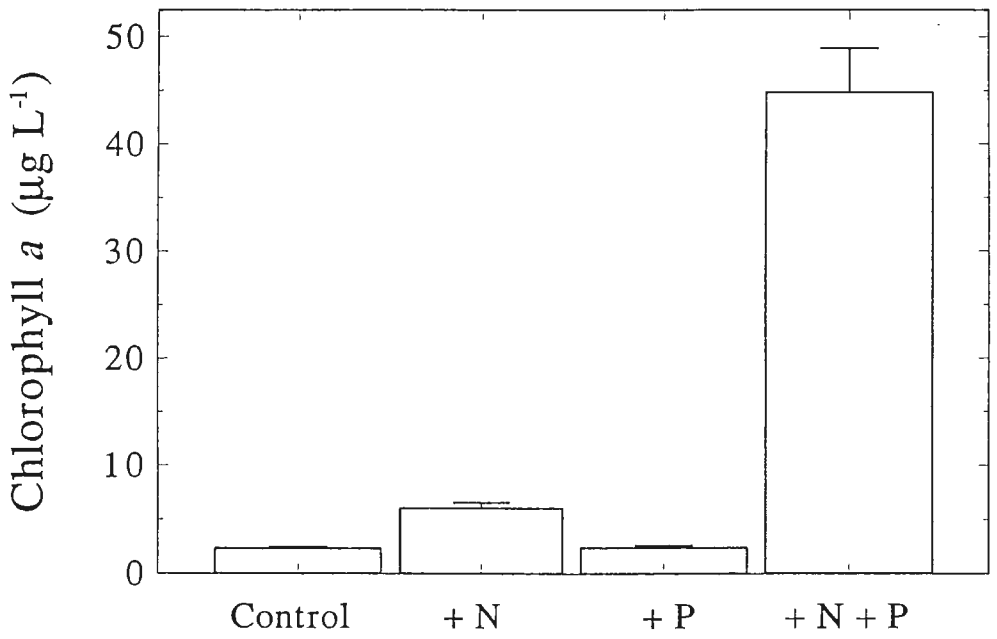

Figure 1. Chl *a* concentrations from 10 L microcosms suspended in Fry's Pond for 7 days after nutrient addition. Control = no nutrient addition; + N = 160 μM NH_4Cl; + P = 10 μM $NaH_2PO_4 \cdot H_20$; + N + P = 160 μM NH_4Cl and 10 μM NaH_2PO_4. Error bars = 1 std. dev. Note, error bars indicate variance in a single carboy for each treatment.

Results

In the 10 L carboys, the chlorophyll *a* concentration was only increased in the + N and the + P treatments by 2.60 fold and 1.03 fold, respectively, compared to that in the control carboy (Fig. 1). However, the chl *a* concentration in the + N + P carboy was 19.31 times greater than that in the control. These results suggested that the phytoplankton were colimited by nitrogen and phosphorus and, thus, justified using a + N + P treatment in the mesocosms to stimulate algal growth.

In the + N + P treatment of the 1500 L mesocosms, the NH_4^+ and SRP concentrations decreased rapidly after the first addition. The nutrients were added again in an attempt to simulate a nutrient pulse (Figs. 2a, b). The rates of NH_4^+ and SRP disappearance were significantly less following the second addition ($P < 0.01$, comparison of slopes from linear regression), possibly indicating lower phytoplankton demand for the nutrients. The NH_4^+ and SRP concentrations in all the other treatments were not significantly different from those of the control and lake treatments, until nutrient additions were made to the + fish and + zoo treatments on day 12. Then NH_4^+ and SRP concentrations increased in these treatments. However, the concentrations of these nutrients in the + fish treatment never reached the levels observed in the + zoo treatment (Figs. 2a, b). Microbial nitrifiers apparently oxidized much of the added NH_4^+ to NO_3^- with an approximately seven day time lag (Fig. 2c). Nutrient levels in the controls were similar to those in the pond, which suggests minimal container effects.

The chl *a* level in the + N + P treatment peaked early (day 4), declined, and never recovered, even after the second nutrient addition on day 7 or micronutrient addition on day 12 (Fig. 3). In the + fish treatment, the chl *a* levels exhibited a steady increase after the nutrients were added and reached a maximum after 14 days. The chl *a* level in the + N + P treatment required only four days to reach a maximum. This may have been a result of a decrease in temperature over the period of the study (data not shown). The only increase in chl *a* levels in the + zoo treatment occurred at the end of the experiment and was less than that observed in the + fish treatments.

Rates of photosynthesis in the + N + P treatments increased substantially during the first days of the experiment and then decreased to levels not significantly different than those of the control and pond for the remainder of the study (Fig. 4). Rates in the + fish treatment showed a gradual increase throughout the experiment. No change in photosynthetic rate occurred in the + zoo treatment. The photosynthetic rate in the control initially dropped slightly below but later exceeded the pond rate.

Cladoceran density on day 26 (the last day of the experiment) was eightfold higher in the + N + P treatments and threefold higher in the + zoo treatments than the control (Fig. 5a). An 11 fold increase in rotifers was observed in the + fish treatment compared to the control (Fig. 5a). Other zooplankton groups in all treatments changed little. Analysis of variance on zooplankton biomass (Fig. 5b) on day 26 gave marginally significant results for cladocerans ($P = 0.0646$) and rotifers ($P = 0.0562$).

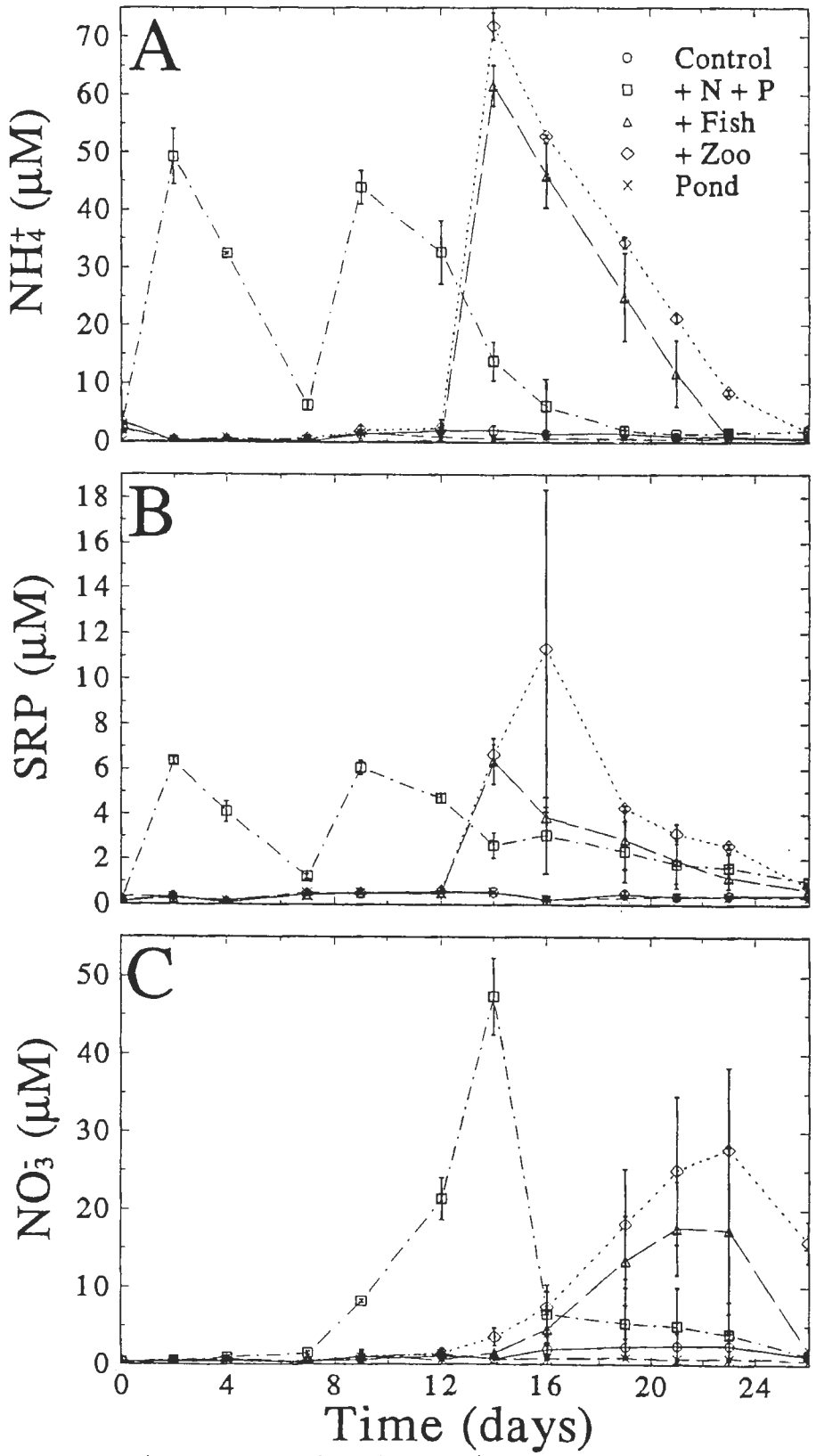

Figure 2. Nutrient concentrations (A, NH_4^+; B, SRP; C, NO_3^-) from 1500 L mesocosms placed in Fry's Pond from 5 September 1991 - 1 October 1991. Treatment abbreviations and explanations as in Table 1. Error bars = 1 std. dev.

An increase in Secchi depth was observed in all treatments except for + N + P by day 2. This increase probably was due to the settling of suspended sediments (Fig. 6). Secchi depth in the + N + P treatment declined, paralleling the increase in algal biomass (Fig. 3). After the initial decrease, Secchi depth increased steadily until it reached the bottom of the pond on day 12, where it remained until the end of the experiment. The Secchi depth in the + fish treatment reached its maximum (pond bottom) by day 7 and gradually decreased and became significantly less ($P < 0.05$) than that of all other treatments (except pond) on day 23. This decrease corresponds to the gradual increase in chl *a* in the + fish mesocosms (Fig. 3). The Secchi depth in the + zoo treatment oscillated in the middle of the water column and demonstrated no observable response to the nutrient additions.

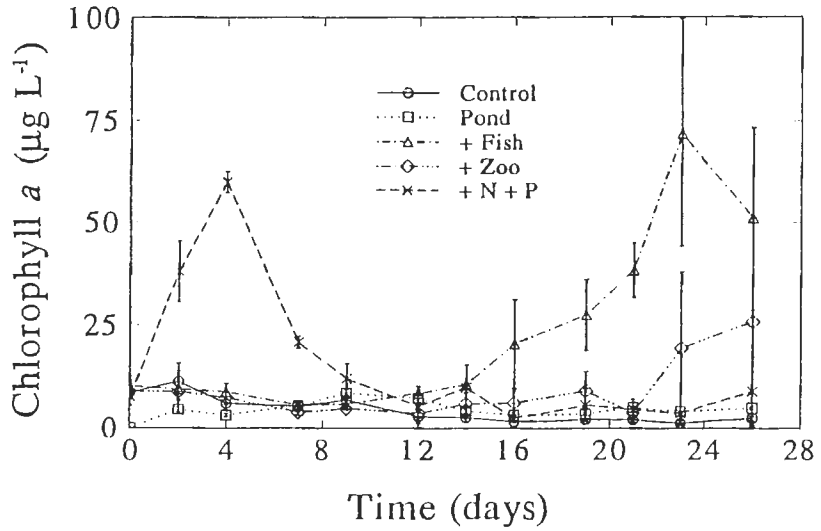

Figure 3. Chl *a* concentrations from 1500 L mesocosms placed in Fry's Pond from 5 September 1991 - 1 October 1991. Treatment abbreviations and explanations as in Table 1. Error bars = 1 std. dev.

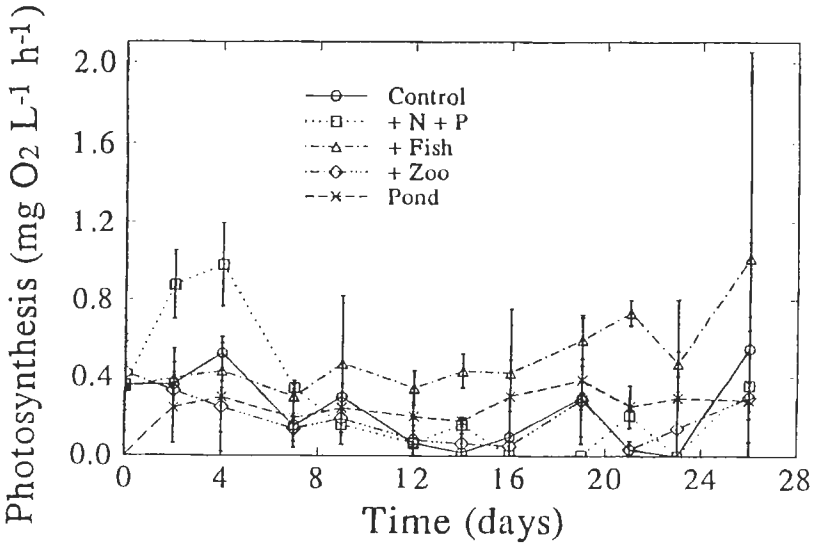

Figure 4. Photosynthetic rate from 1500 L mesocosms placed in Fry's Pond from 5 September 1991 - 1 October 1991. Treatment abbreviations and explanations as in Table 1. Error bars = 1 std. dev.

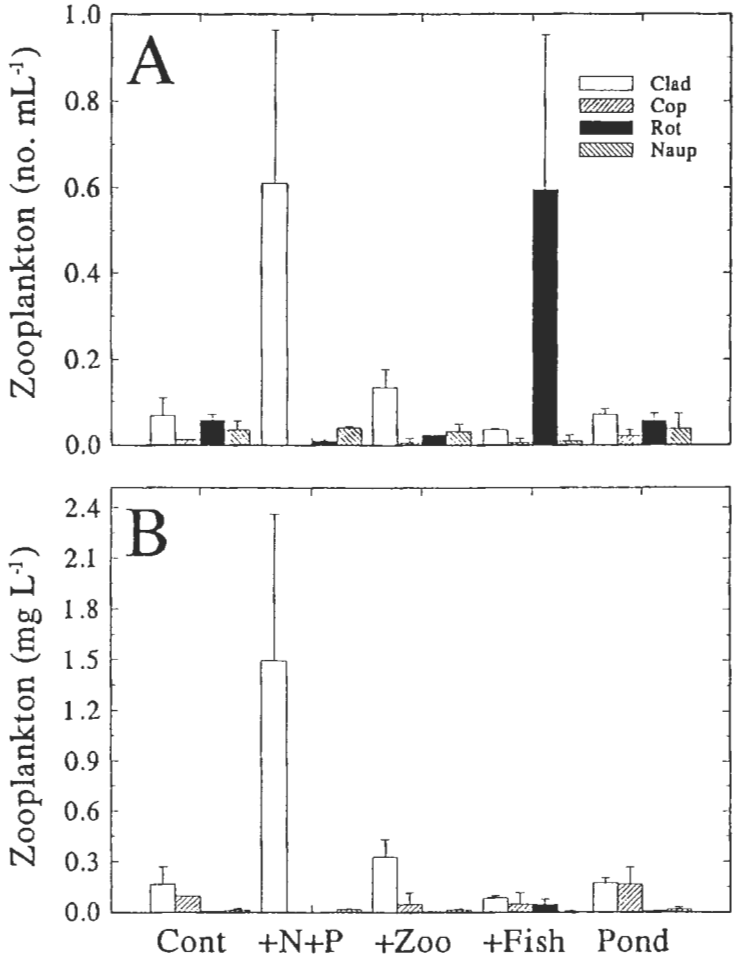

Figure 5. Zooplankton counts (A) and zooplankton biomass (B) taken on day 26 from 1500 L mesocosms placed in Fry's Pond from 5 September 1991 - 1 October 1991. Treatment abbreviations and explanations as in Table 1. Clad, cladocerans; Cope = copepods; Rot = rotifers; Naup = nauplii. Error bars = 1 std. dev.

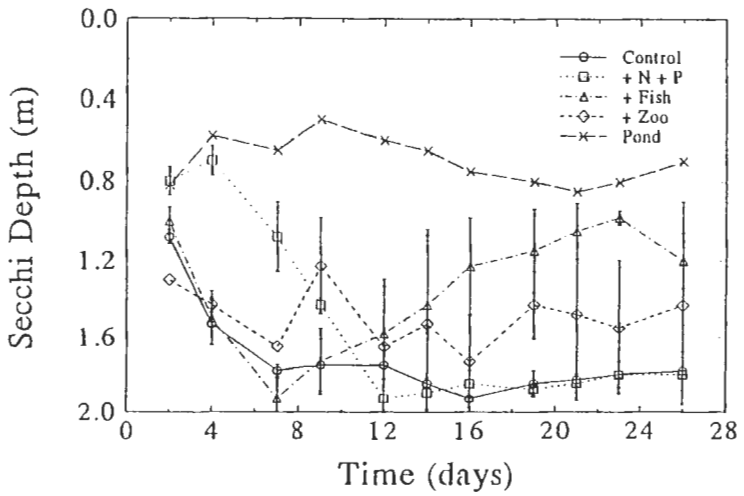

Figure 6. Secchi depth measurements from 1500 L mesocosms placed in Fry's Pond from 5 September 1991 - 1 October 1991. Treatment abbreviations and explanations as in Table 1. Error bars = 1 std. dev.

Discussion

Colimitation of phytoplankton by N and P as seen in this experiment has been found to be a typical response in many oligotrophic, mesotrophic, and eutrophic lakes (Suttle and Harrison 1988, Dodds et al. 1989, Dodds et al. 1993, Dodds and Priscu 1990, Elser et al. 1990b). However, because chl *a* and photosynthetic rate did not respond to the second nutrient addition or the micronutrient addition in the + N + P treatment, a more complex control of phytoplankton biomass than simple nutrient deficiency is indicated. The possibility of light limitation can be discounted because of increased Secchi depth.

It has been well documented that small planktivorous fish alter zooplankton community structure toward smaller types (Lazarro 1987, Northcote 1988). This effect was also evident in our study. First, an increase of rotifers occurred in the + fish treatment. This increase in rotifers is consistent with other studies in which numbers of planktivorous fish were increased (Gilbert 1988, Christoffersen et al. 1993, Telesh 1993). Second, an increase in large cladocerans occurred in the + N + P and + zoo treatments. This is also consistent with other studies (Shapiro and Wright 1984, Vanni 1986, Carpenter et al. 1987, Vanni et al. 1990).

Large daphnids and other cladocerans are more efficient at grazing phytoplankton than copepods and rotifers because of their high filtering rates and ability to capture a wide range of particle sizes (Brooks and Dodson 1965, Haney 1973, Porter 1977). Thus, a shift toward larger zooplankton might alter the response of phytoplankton to nutrient additions. Elser et al. (1988) demonstrated that transitions between N or P limitation of phytoplankton could be induced by manipulations of zooplankton biomass or size. The + fish treatment had fewer high efficiency grazers and, thus, had higher chl *a* than the + zoo treatment following the nutrient additions. The highest number of large cladocerans was in the + N + P treatment, which again had no observable algal response after the first nutrient addition. However, the zooplankton in the + zoo treatment could not completely suppress the chl *a* response to the nutrient addition. This suggests that there might be a weakening in the trophic cascade at the zooplankton-phytoplankton link, as suggested by DeMelo (1992). But, nonetheless, a definite top-down effect on the phytoplankton was observed.

The cascading effects through the food web did not extend to the nutrients. Nutrient concentrations responded to nutrient additions but not to fish or zooplankton additions. Dodds (1993) hypothesized that nutrient levels are maintained at equilibrium by interaction between nutrient uptake and remineralization. In this study, the trophic cascade apparently did not alter this relationship. Although nutrient concentrations were elevated after additions they always returned to pretreatment levels. Adding fish or zooplankton amounts to a nutrient enrichment, but even this had little effect on the equilibrium level of dissolved nutrients.

The transient nature of the biomass response to nutrients may be a common feature in small ponds. Such ponds may regularly experience pulses of nutrients, because they are fed by ephemeral streams and storm runoff may contain elevated nutrient concentrations. In addition, the temporally variable use

of the pond by cattle may cause pulses in nutrient availability. Our data suggest that a short-term algal bloom will occur in response to such a pulse, but this bloom will stimulate herbivorous zooplankton. A second bloom probably will not be possible until large herbivorous zooplankton populations are reduced.

The observation that a nutrient pulse resulted in only a brief increase in productivity brings into question the use of short-term carboy measurements to study the effects of nutrient addition. Such measurements commonly are made by investigators to determine nutrient deficiency (e.g., Elser et al. 1990b, Dodds and Randel 1992, Dodds et al. 1993). These measures may be a sufficient way to determine nutrient deficiency in algal primary producers, but may not indicate which factors ultimately control productivity.

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