EFFECTS OF PREDATION BY FATHEAD MINNOWS, PIMEPHALES PROMELAS, ON PLANKTONIC COMMUNITIES IN SMALL, EUTROPHIC PONDS

Dissertation for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
LOUIS A. HELFRICH
1976

ABSTRACT

EFFECTS OF PREDATION BY FATHEAD MINNOWS, *Pimephales promelas*, ON PLANKTONIC COMMUNITIES IN SMALL, EUTROPHIC PONDS

By

Louis A. Helfrich

This experiment was designed to examine the effects of predation by fathead minnows, *Pimephales promelas* Rafinesque, on planktonic communities in a series of eight artificially enriched ponds. Replicate fish populations were established in half of the ponds and the remaining ponds were kept unstocked for reference. Physical, chemical and biological parameters, including phytoplankton and zooplankton densities, were measured at weekly intervals. The fish populations and their food habits are described.

Fish predation significantly reduced the densities of both small and large zooplankton species. The gut contents of fatheads suggest a size selection of prey that was related to the size of the minnow. The decrease in the total abundance of herbivorous zooplankters permitted an increase in the total standing crop of algae, primary productivity and turbidity and ultimately effected a shift in algal composition from one dominated by edible green algae, diatoms and cryptomonads to one dominated by inedible blue-green algae. There was a strong inverse relationship between the average density of blue-green algae and the average concentration of free carbon dioxide.

EFFECTS OF PREDATION BY FATHEAD MINNOWS, *Pimephales promelas*,

ON PLANKTONIC COMMUNITIES IN SMALL, EUTROPHIC PONDS

By

nthony
Louis A. Helfrich

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

1976

ACKNOWLEDGMENTS

I wish to express my gratitude to my major professor, Dr. C. D. McNabb, who advised and encouraged me throughout this study, and to my graduate committee members, Dr. T. G. Bahr, Dr. W. T. Porter, Dr. E. W. Roelofs, and Dr. P. I. Tack for their thoughtful review and suggestions concerning this thesis.

I would particularly like to thank Dr. R. A. Cole and Diana L. Weigmann for their special attention to the problems involved in this study and for their continuing advice, criticisms and encouragement throughout this study. Special thanks is also extended to Joan Duffy, who helped in the field sampling and zooplankton enumeration with an appreciation for detail and accuracy that was outstanding.

Finally, I wish to acknowledge the understanding, interest and inspiration of my family.

Financial support was provided by the Michigan Agricultural Experiment Station and the Rockefeller Foundation under funds administered by the Institute of Water Research at Michigan State University.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The potential role of fish as regulators of plankton communities has been recognized at least since Clements and Shelford (1939) proposed that carnivorous fish may ultimately control plant and animal planktonic densities. Although physical and chemical attributes more often are credited as important regulators of algal abundance and species composition; biological mechanisms, including fish predation, zooplankton grazing, competition and parasitism, also have been recognized as potentially important (Edmondson, 1972; Hutchinson, 1973; Lund, 1965; Hrbacek *et al.*, 1961; Porter, 1973). Hurlbert *et al.* (1972) believed that excessive phytoplankton growth, a principal symptom of eutrophication, may be more directly attributable to man-caused alterations in fish populations than to nutrient influx. Although previous workers recognized the potential role of planktivorous fish as regulators of phytoplankton populations, little published work has directly addressed the problem.

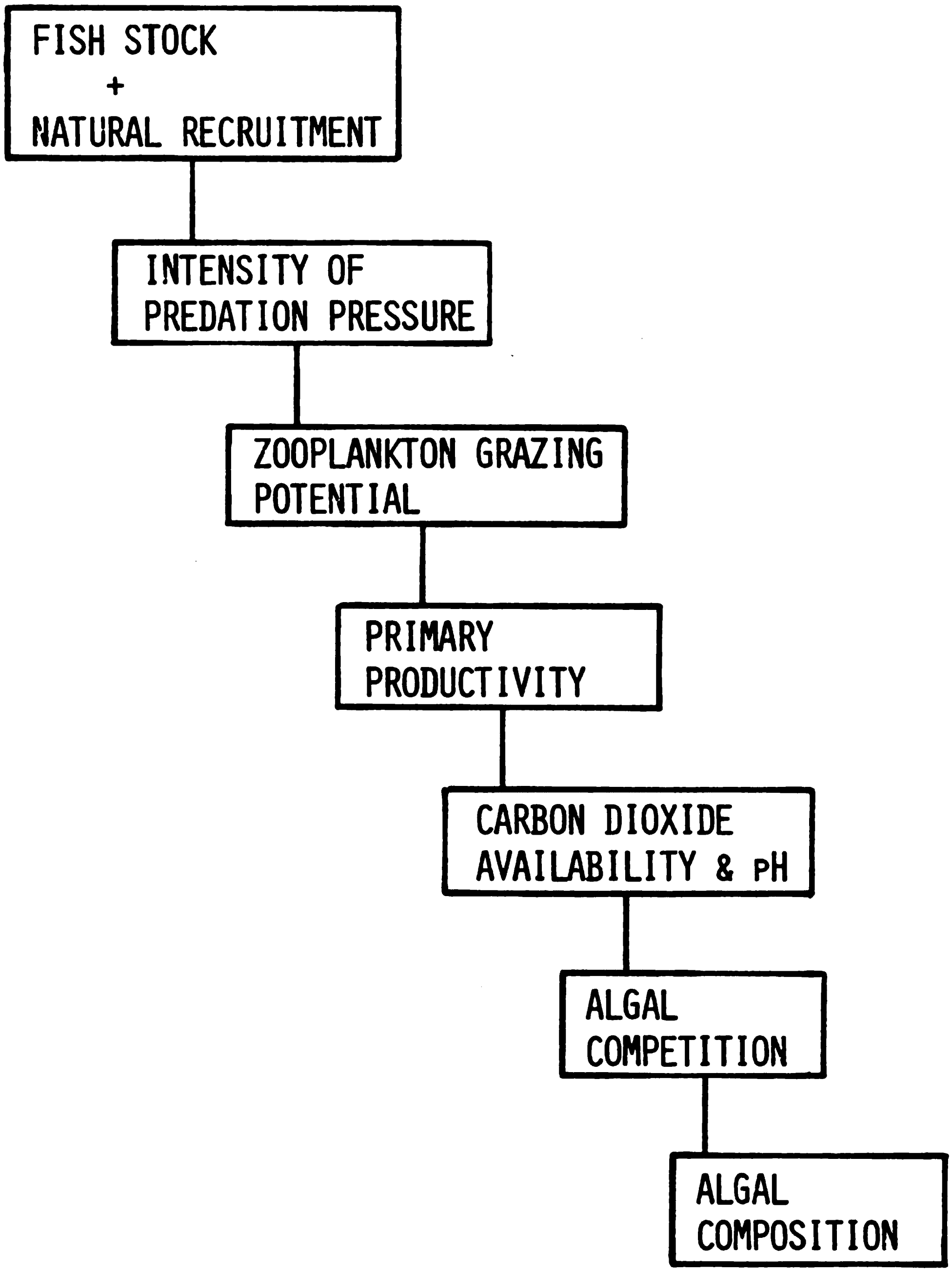
This experiment was designed to clarify some of these trophic relationships. The general purpose was to test the impact of zooplanktivorous fish on the plankton community, with particular emphasis on algal dynamics and associated changes in nutrient chemistry.

This study addresses a sequence of hypotheses that are designed to test the premise that zooplanktivorous fish can influence phytoplankton productivity which, in turn, may modify water quality and cause successional changes in algal composition. The model schematized in Figure 1 was structured from observations and speculations of previous investigators. Among them, Hrbacek (1962) considered fish as the decisive factor influencing the composition and quantity of plankton and possibly several physical and chemical properties of water. Many authors, including most outstandingly, Hrbacek and Novatna-Dvorakova (1965), Brooks and Dodson (1965) and Galbraith (1967), have established that certain species of fish are capable of altering zooplankton composition. Others, Fryer (1957), Burns (1968), Jorgensen (1966), Porter (1973), have found that crustacean zooplankters exhibit selective feeding behavior. In at least some instances zooplankton grazing has had a measurable depressive impact on algal abundances and productivity (Cushing, 1958; Menzel and Ryther, 1961; Hargrave and Geen, 1970; Haney, 1971).

Another group of investigators have noted that primary productivity in eutrophic systems may become limited by carbon dioxide availability (King, 1970, 1972; Shapiro, 1973), and that blue-green algae tend to be favored in nutrient enriched environments where carbon dioxide is scarce. Development of blue-green algal blooms is usually one of the least desirable consequences of eutrophication.

Presumably, then, blue-green algal dominances in enriched environments may be favored by restricting zooplankton grazing which, in turn, increases primary productivity and promotes the rapid development of large algal standing crops that are often referred to as "blooms." Algal composition could change as a consequence of carbon dioxide scarcity generated by the increased rate of carbon incorporation in an otherwise unlimited aquatic environment (King, 1972).

Figure 1. Proposed interrelationships between planktivorous fish, herbivorous zooplankters, plankton algae and chemical parameters in eutrophic ponds.


FISH STOCK + NATURAL RECRUITMENT
INTENSITY OF PREDATION PRESSURE
ZOOPLANKTON GRAZING POTENTIAL
PRIMARY PRODUCTIVITY
CARBON DIOXIDE AVAILABILITY & pH
ALGAL COMPETITION
ALGAL COMPOSITION

Hypothetically, uninhibited zooplanktivorous fish populations have the capacity to decimate zooplanktonic herbivores, at least during the short term, as long as all sizes and species of grazers are readily consumed. Planktivorous fish populations of diverse age and size structure probably would be required to obtain this result.

With these hypotheses in mind, I stocked four of eight physically and biologically similar ponds with adult fathead minnows (*Pimephales promelas*) Rafinesque, which soon developed a diversified age and size structure through natural recruitment. Subsequent to fish stocking, data were gathered on fish populations, fish stomach contents, zooplankton and algal density, primary productivity, carbon dioxide and other limnological parameters. The results generally confirm the predictions of the model.

MATERIALS AND METHODS

The Experimental Ponds

Eight identical ponds, 7.2 x 7.2 x 1.8 m deep, previously used as wastewater treatment ponds served as the experimental units. The ponds were constructed of concrete and had a bottom of peastone gravel. Three months before the experiments, each unit was filled to a depth of 1.5 m with a mixture of untreated well water and domestic sewage. Constant, identical water levels and similar fertilities were maintained in all experimental ponds during the study period by the weekly addition of a homogeneous mixture of domestic wastewater.

Wastewater applications were carefully conducted to insure that each pond received identical volumes and equivalent nutrient enrichment. Wastewater was pumped from a municipal sewage line into a head tank, thoroughly mixed and then uniformly distributed over the surface of each pond through a network of suspended PVC tubing. The total phosphorus and ammonia concentrations of the influent wastewater were measured weekly; ancillary data on pH and temperature were taken and spot checks for heavy metals were conducted. Throughout the study, the pH of the influent wastewater remained relatively constant at 7.8, the average temperature was 22 C, copper and chromium concentrations remained below detectable levels, total phosphorus values (as P) ranged from 5.8 to 7.2 mg/liter, and ammonia nitrogen levels ranged from 16.1 to 17.4 mg/liter. All ponds were similar in their chemistry and biology at the initiation of the treatment.

Fish Populations

On July 1, 1974, 200 adult fathead minnows (*Pimephales promelas*), 4.5 to 6 cm total length, were introduced into each of four randomly selected ponds. The remaining four ponds were kept unstocked for reference. The initial stocking density, 38,500 fish/ha, was chosen to provide a relatively high level of predation pressure on the zooplankton community. The adult stock was in spawning condition; I assumed that natural reproduction and the consequent recruitment of larval fish in early summer would provide a size structure capable of utilizing the full-range of food particle sizes available and increase the intensity of predation through the summer.

The fathead minnow has received considerable attention as a forage fish well suited for pond culture. This minnow is widely distributed and extensively propagated in the United States; it is a popular bait fish which is commonly used as food for hatchery-reared game fish. Fathead minnows were selected for use in this study because of their potential influence on plankton communities. This species has generalized food habits encompassing the majority of herbivorous zooplankton. These minnows are characteristic of small warmwater ponds, often are found in wastewater lagoons and are quite tolerant of the chemical conditions that typically occur in hypereutrophic waters. The initial stock used in this study was obtained from a waste stabilization pond at Belding, Michigan.

Food habits were determined for 100 fathead minnows seined during the second weeks of July, August and September. Large minnows (>45 mm) were injected with a 50% alcohol solution to retard digestive processes and all fish were preserved in a 10% formalin solution. Total lengths of individual fish were recorded and gut contents were rinsed into a circular counting chamber where food items were identified and enumerated.

During the second week of September, the total fish populations were harvested from two ponds chosen randomly from the four stocked ponds. These ponds were cleared of macrophytes, treated with rotenone solution and repeatedly seined. The fish were immediately preserved in formaldehyde solution. Later they were counted, measured to the nearest 1 mm, and separated into two size categories; small, larval minnows (<45 mm) and large, adult minnows (>45 mm). Subsamples from each of these groups were dried in a forced-air oven for 24-hours and weighed to estimate production.

Water Samples

The sampling regime provided for replicate physical, chemical and biological samples for each pond during every week of the study. To determine sampling points, a grid was established for each pond and random numbers were selected to determine the sampling area. All samples for water chemistry and phytoplankton analysis were collected with a one liter PVC Kemmer bottle at mid-depth between 10:00 a.m. and 1:00 p.m. the day before wastewater application.

Chemical Analysis

Total phosphorus (as phosphate) was measured by the stannous chloride method (American Public Health Association, 1965). Nitrate nitrogen measurements were made by the brucine method of Jenkins and Medesker (1964). Ammonia nitrogen was determined by the direct Nesslerization test (American Public Health Association, 1965). The hydrogen ion concentration was measured using a Corning Glass electrode pH meter; total alkalinity was determined by acid titration (American Public Health Association, 1965). Free carbon dioxide concentrations were estimated by nomograph using alkalinity, pH and temperature determinations (American Public Health Association, 1965). Temperature and oxygen profiles were measured each week over a 24-hour period in all ponds with a YSI oxygen meter which was periodically standardized against Winkler determinations of oxygen. In addition, continuous 24-hour temperature and oxygen measurements using a Rustrak Temperature-Oxygen Recorder and probe (Model 192), were made each week in one randomly selected pond.

Primary Productivity

Gross primary productivity was calculated from the diurnal oxygen curves by the single station method of Odum (1956). The values for the gas transfer coefficient (K) across the air-water interface were calculated from the rate of change of oxygen concentrations for each diurnal curve and corrected for temperature (Odum, 1956). Water clarity was estimated by measuring the percent transmission at mid-depth using a Schueler Submarine Photometer.

Phytoplankton

Duplicate whole water samples were collected from each pond during every week of the study at the same time samples for chemical analysis were taken. One sample was preserved with a 5% formalin solution and the other with a 1% Lugol's killing and fixing solution. Two preservatives were used because of their differential disruptive properties; the formalin fixative may destroy small flagellates while Lugol's may disrupt the integrity of colonial algae (O'Brien, 1970). Individual phytoplankters were counted on membrane filters following the technique of McNabb (1960); the filters were examined at 200X and 450X using a dark phase microscope. Diatoms were identified on separate, permanent mounts which were prepared according to Weber (1971). Phytoplankton taxonomy was based on the keys of Smith (1950) and Prescott (1962). A list of the planktonic algae encountered in the experimental ponds is given in Appendix I.

Zooplankton

Triplicate zooplankton samples were collected each week in all ponds with a Wisconsin-style plankton net (74μ, No. 20 mesh size). Vertical tows were made to integrate samples over depth. To reduce distributional errors, all samples were taken at night, beginning one hour after sunset, when the vertical distribution of the animal plankters was assumed to be more uniform. All zooplankton densities undoubtedly were underestimated since the efficiency of the No. 20 plankton net has been estimated at 40-60% (Hall *et al.*, 1970). The values presented represent the actual estimates obtained, since any correction factor for net efficiency would not change trends in the data. All samples were immediately preserved in a 70% ethanol and 3% formalin solution. Subsamples, 1-10 ml, were enumerated in a zooplankton counting wheel under a dissecting microscope. Crustaceans were identified according to Brooks (1959), Wilson (1959) and Yeatman (1959) and rotifers according to Edmondson (1959). A list of the zooplankton species encountered in the experimental ponds is given in Appendix II.

Data Analysis

The results were arranged to show differences between the stocked and unstocked ponds. The sampling regime provided for duplicate phytoplankton and physicochemical samples and triplicate zooplankton collections from each of the 8 ponds every week. Phytoplankton and physicochemical means for a given date represent 8 samples for each of the two sets of ponds. Similarly, zooplankton means for a given date represent 12 samples for each of the two groups of ponds. A one-way analysis of variance was applied to most of the data. Logarithmic transformations of the plankton values were used to reduce heterogeneity among variances and percentage values were normally distributed by an arc sine transformation. The plankton data were analyzed with standard parametric statistical techniques because the short generation times of planktonic organisms made autocorrelation between the sampling dates unlikely. Standard errors presented in association with treatment means contain several sources of variation. No attempt was made to separate within-pond variation, which was high since the area sampled is a small fraction of the total pond area, from within-treatment group variation. A large component of the variation in the plankton data was the result of asynchronous population trends. The following results clearly demonstrate that among the factors measured, there were major, consistant trends and significant differences between the stocked and unstocked ponds.

RESULTS

Fish

Population Changes

Changes in the populations of introduced fathead minnows were investigated in two ponds which were chosen randomly from the four stocked ponds. The data on total numbers, biomass, production of fry and adult survivorship were similar for both ponds. I assumed that changes exhibited by these two ponds adequately represent population changes for all of the four ponds stocked with minnows at the beginning of the experiment. In establishing the minnow populations each pond received 200 fathead minnows (38,500 fish/ha) weighing 400 grams in total (77 Kg/ha). The total numbers and biomass in both ponds increased as a result of high survivorship of the initial stock and natural reproduction through the summer. At the termination of the study in September, 8888 minnows weighing 2264 grams (435 Kg/ha) were recovered from Pond 2 and 6188 minnows weighing 1913 grams (349 Kg/ha) were recovered from Pond 5. Total biomass of fish had increased at least 5 fold in each pond over the study period.

Large numbers of 5-12 mm larval fish first appeared in the zooplankton samples on 22 July (fourth week) in all of the stocked ponds. The larvae were apparently only susceptible to the plankton net in this size range, as fish larger than 12 mm were never caught. Since newly hatched fathead minnows are about 5 mm long, the first major reproductive pulse probably occurred during the third week of July. The size-frequency distribution of fish populations in September indicated that reproduction continued throughout the study and that there was no recruitment of larval fish into the size-classes of the initial stock (Figure 2). The mode of the fry size distribution was about 15 mm; the maximum length attained by young-of-the-year fish was 35 mm.

The total number of larval fish recovered in September from the two ponds, 8758 and 6125, undoubtedly were underestimates of the total larval fish populations, particularly of larvae less than 20 mm. These smaller larvae were especially susceptible to entrainment by the pumps used to regulate the water levels, and despite precautions to screen them from the intake, many small fish were not recovered. Therefore, the estimate of fish biomass in the ponds was conservative.

Survivorship of adult minnows was determined for all four stocked ponds. Of the total 200 fish stocked in each pond, 59-82% were recovered in September. The survival rates obtained are somewhat higher than those determined for natural populations (Isaak, 1961). Evidently, the high post-spawning mortality commonly reported for this species (Markus, 1934; Hasler *et al.*, 1946) did not occur in this experiment.

Stomach Contents

The relative importance and monthly variation in utilization of food items for large (>45 mm) and small (<20 mm) fathead minnows collected from all four stocked ponds during the second weeks of July, August and September are listed in Table 1. Crustacean species were dominant in

Figure 2. Size-frequency distribution of the minnow populations harvested in September.

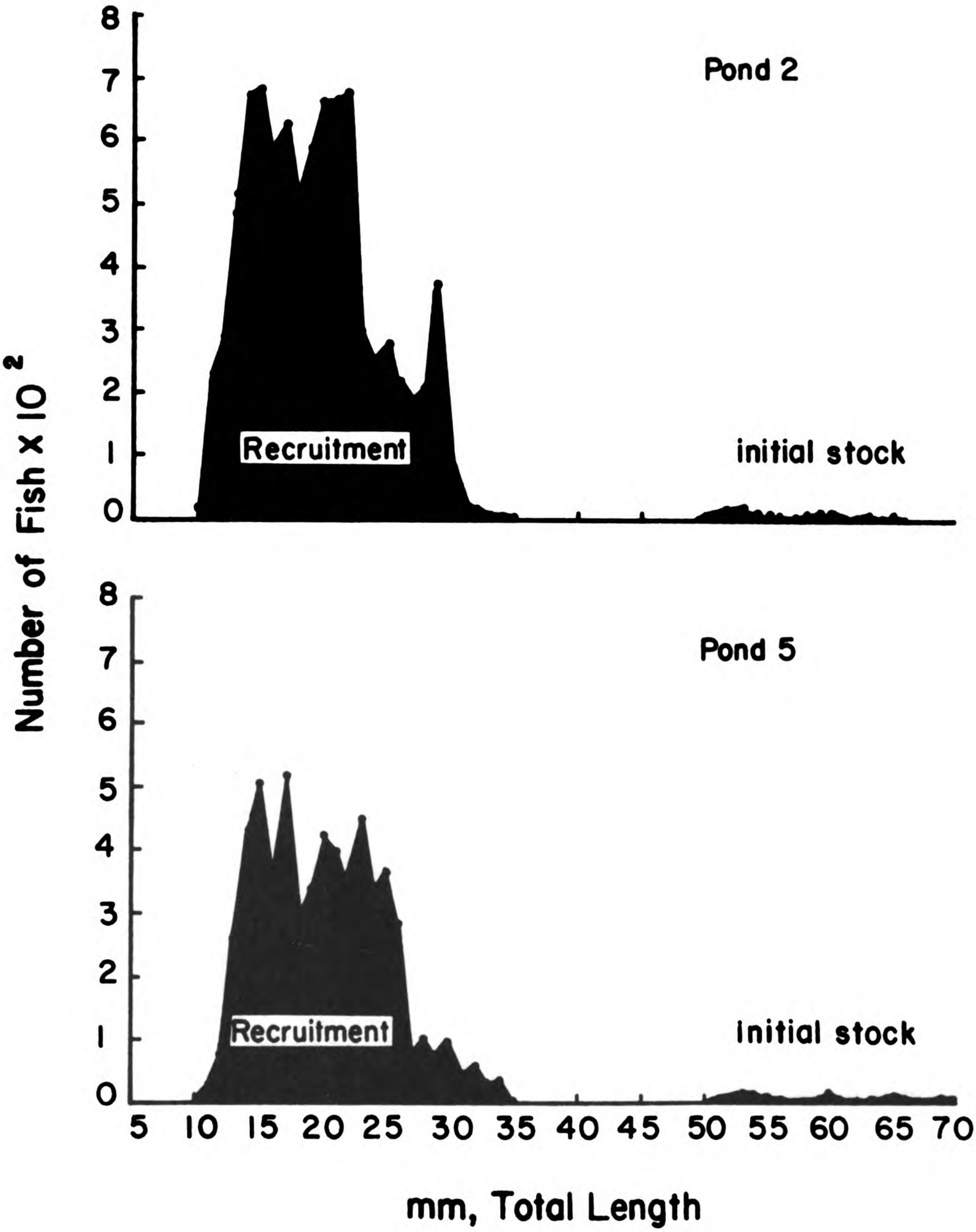

Pond 2
Recruitment
initial stock
Pond 5
Recruitment
initial stock
Number of Fish X 10²
mm, Total Length
0
1
2
3
4
5
6
7
8
5
10
15
20
25
30
35
40
45
50
55
60
65
70

Table 1. Relative importance and seasonal variation in utilization of food items for large (>45 mm) and small (<20 mm) fathead minnows collected from four experimental ponds during the second weeks of July, August and September. (n = 20 in all cases).

	July		August				September			
	Large[a]		Large[b]		Small[c]		Large[d]		Small[e]	
Food Item	No.	%	No.	%	No.	%	No.	%	No.	%
Daphnia	270	53	60	9	0	0	13	8	0	0
Diaphanosoma	0	0	87	13	0	0	19	12	12	5
Ceriodaphnia	73	14	20	3	0	0	0	0	0	0
Bosmina	5	1	0	0	48	5	0	0	0	0
Chydorus	28	6	146	22	110	11	7	4	0	0
Diaptomus	60	12	0	0	0	0	0	0	0	0
Cyclopoids	18	4	80	12	10	1	10	6	0	0
Copepod nauplii	0	0	0	0	272	28	0	0	0	0
Keratella	0	0	0	0	494	51	5	3	42	19
Ostracoda	37	7	181	27	29	3	13	8	25	11
Midge larvae	9	2	27	4	0	0	95	59	141	63
Others	5	1	67	10	6	1	0	0	4	2
Total	505	100	668	100	969	100	162	100	242	100

[a] 7 with empty digestive tracts.
[b] 4 with empty digestive tracts.
[c] 5 with empty digestive tracts.
[d] 2 with empty digestive tracts.
[e] 5 with empty digestive tracts.

the stomachs of 100 fathead minnows collected during the study; they comprised about 65% of the total number of all food items. Of the crustacea, cladocerans were the most important prey item, accounting for 36% of the total number. Cladocerans were followed in numerical importance by the copepods, including nauplii (18%), and the rotifer, *Keratella quadrata* (18%). Ostracods and chironomid larvae each accounted for 11% of the total number of prey items. Minor food organisms included other rotifers, amphipods, mayfly and dragonfly larvae, snails and algae. Few phytoplankton cells occurred in the digestive tracts examined during the summer. However, filamentous algae, primarily species of *Cladophora* and *Spirogyra*, and detritus were common in the intestinal contents toward the end of the study, in September.

Comparisons of the stomach contents of large fathead minnows (>45 mm) and small minnows (<20 mm) suggests that fish size was an important determinant in the selection of prey items. Cladocerans predominated in the stomachs of the large fathead minnows, accounting for 54% of the total number of all prey items. In contrast, the rotifers, essentially *Keratella quadrata*, and copepod nauplii were the most frequently utilized food organisms for the small minnows; they comprised 45 and 23% respectively of the total stomach contents.

Distinct changes in the utilization of food organisms by the two size categories of minnows were observed during the study. In early July, the large cladoceran, *Daphnia pulex*, was the most important prey species, accounting for 53% of the total food items. At this time no larval fish were available for food habit analysis. During the second week of August, *Chydorus sphaericus*, and the ostracods were the

the major food organisms of the large minnows, representing 22 and 27% of the total diet. At the same time larval fish were feeding primarily on the rotifer, *Keratella quadrata* (51%), and secondarily on copepod nauplii (28%). In September, all minnows switched from a planktophagous to a benthophagous habit and chironomid larvae became the most important food organism for all sizes of fathead minnows, comprising 59% of the total number of food items taken by the large minnows and 63% of the total stomach contents for the small minnows.

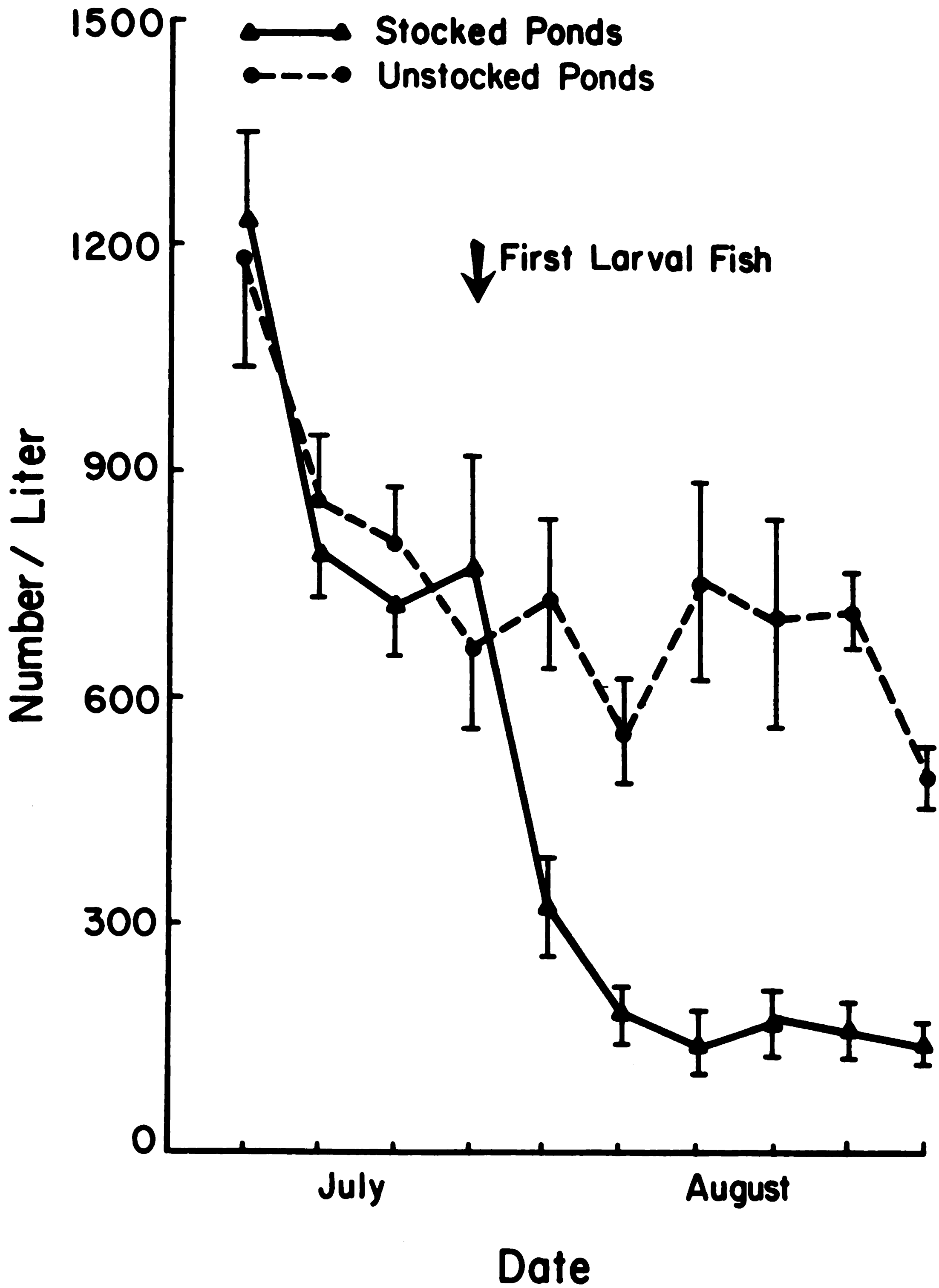
In summary, the initial stock of fathead minnows introduced to four treatment ponds reproduced and their biomass increased by at least 5-fold. Analysis of the stomach contents of fathead minnows revealed that the majority of zooplankton species present in the ponds were consumed. In general, the mean size of the zooplankton species found in the stomachs was directly related to the size of the fish. Fathead minnows represented the dominant planktivore in the experimental ponds and, unlike natural systems with an array of piscivorous fishes and other natural predators to limit their densities, the minnow populations were virtually unrestrained. Potentially, the fathead minnow population had the capacity to severely limit zooplankton population abundances.

Zooplankton

Total Zooplankton Density

The results of the zooplankton studies indicated that fathead minnows significantly reduced the total populations of crustacean zooplankters (Figure 3). Initially, the mean total numbers of

Figure 3. Mean zooplankton densities (± one standard error) in the stocked ponds and the unstocked ponds.



Stocked Ponds
Unstocked Ponds
First Larval Fish
1500
1200
900
600
300
0
Number / Liter
July
August
Date

zooplankters in all eight experimental ponds were relatively similar with average maximum densities for both stocked and unstocked ponds in excess of 1000 individuals/liter. During the first four weeks of July, the mean total number of zooplankton declined rapidly in all eight ponds; throughout this period the zooplankton densities in the stocked ponds were statistically indistinguishable from those in the unstocked ponds. Thereafter, total numbers of zooplankton in the stocked ponds were significantly ($p < 0.05$) lower than those in the unstocked ponds. The total number of zooplankton during the last six weeks of the study averaged 665±45 (mean ± one standard error) individuals/liter in the unstocked ponds and 196±28 individuals/liter in the stocked ponds.

Zooplankton Composition

The zooplankton community was numerically dominated by the large cladoceran, *Daphnia pulex,* the smaller rotifer, *Keratella quadrata,* and copepod nauplii. Combinations of these two species and the immature copepods accounted for about 78% of the total number of zooplankters in the experimental ponds during the study. Most major differences in zooplankton densities occurring between the stocked and the unstocked ponds can be attributed largely to shifts in the relative abundance of these three taxa.

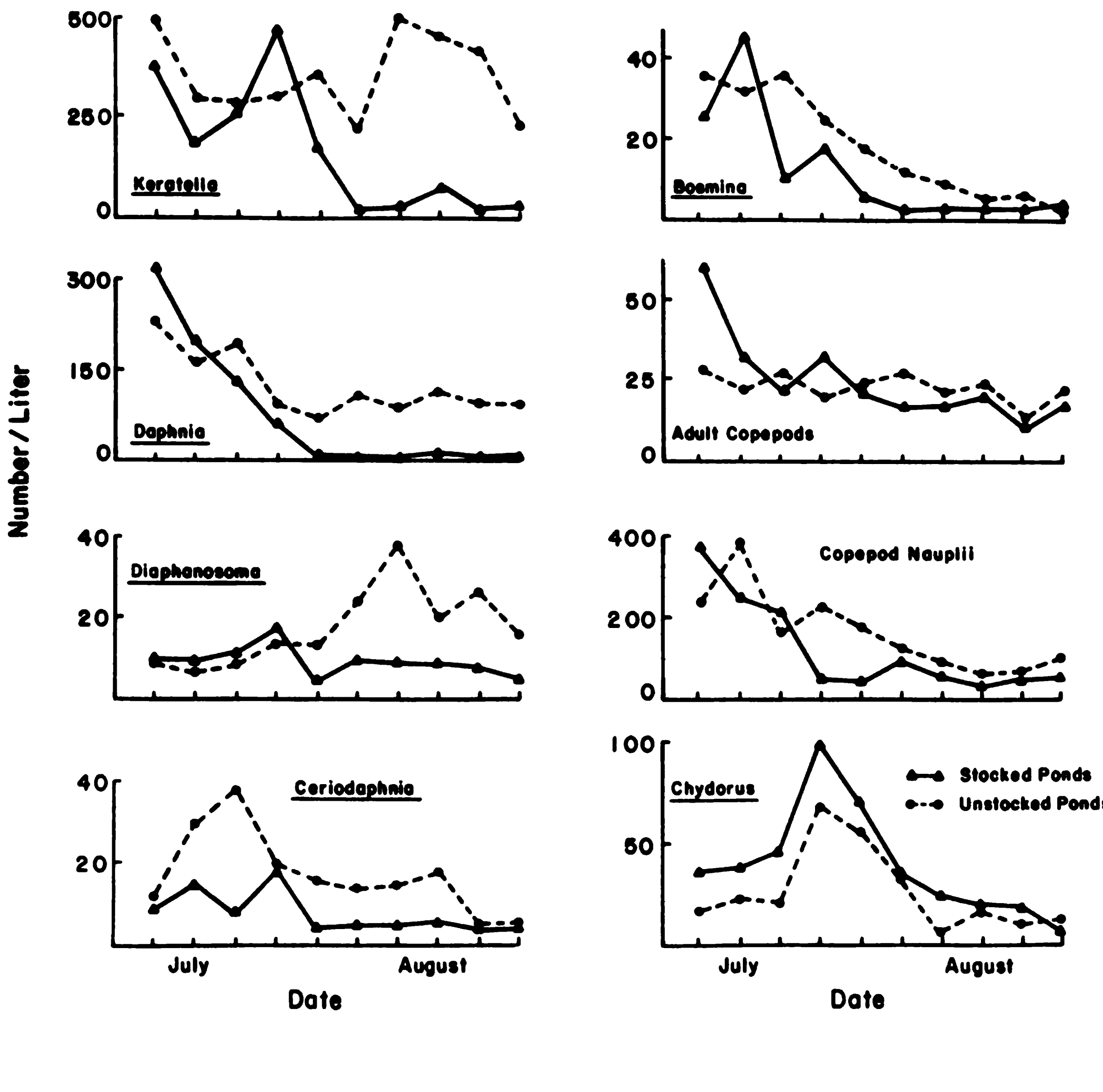
The total number of zooplankton species occurring in the experimental ponds was relatively low. Only nine species of cladocerans, seven species of copepods, nine species of rotifers and two species of ostracods were encountered in the samples (Appendix II). Since the majority of these species exhibited only sparse and isolated

occurrences, no clear differences in species diversity could be detected between the two groups of ponds. Quantitative changes of the zooplankton species and groups which occurred most frequently in the samples are illustrated in Figure 4.

The rotifer, *Keratella quadrata*, was the most abundant animal plankter in the experimental ponds; this species constituted 34% (8-65%) of the total number of all zooplankters and about 98% of the total number of rotifers in the experimental ponds. The remaining species of rotifers contributed few individuals, seldom exceeding 10/liter. During the first five weeks of the study, *K. quadrata* populations fluctuated asynchronously; their densities in the stocked ponds were indistinguishable from those in the unstocked ponds. After July, the populations of *K. quadrata* increased in the unstocked ponds, to densities 4 to 25 times greater and significantly ($p < 0.05$) different from those in the stocked ponds. The number of *K. quadrata* during the last five weeks of the study averaged 364/liter in the unstocked ponds and 40/liter in stocked ponds. In the stocked ponds, *K. quadrata* populations reached maximum abundances (400/liter) during the fourth week then suddenly declined; this period of rapid depression coincides with the appearance of large numbers of minnow larvae. Analysis of the stomach contents revealed that *K. quadrata* accounted for 51% of the total diet of larval fish at this time.

The cladoceran, *Daphnia pulex*, represented the largest zooplankton species and the most numerous cladoceran in the ponds; this species comprised an average of 17% (11-25%) of the total number of zooplankters in all ponds during the study. *D. pulex* was most abundant during the first week of the study when the mean densities in all ponds exceeded

Figure 4. Mean numerical densities of the major zooplankton species in the stocked and unstocked ponds.


Number / Liter
500
250
0
Keratella
300
150
0
Daphnia
40
20
Diaphanosoma
40
20
Ceriodaphnia
July
August
Date
40
20
Bosmina
50
25
0
Adult Copepods
400
200
0
Copepod Nauplii
100
50
Chydorus
Stocked Ponds
Unstocked Ponds
July
August
Date

200/liter. Shortly after the introduction of fathead minnows the population of *D. pulex* declined. By the end of July (fifth week) *D. pulex* populations in the stocked ponds were significantly ($p < 0.05$) lower than those in the stocked ponds. During the last six weeks, the number of *D. pulex* averaged 102/liter in the unstocked ponds and 7/liter in the stocked ponds. Stomach analysis of the large fathead minnows at this time showed that *D. pulex* was the dominant prey item, accounting for 53% of the total number of all stomach contents. Similarly, Hrbacek (1962), Brooks and Dodson (1965) and Galbraith (1967), all found that large *Daphnia* were the preferred prey of planktivorous fish and the first zooplankton species to decline at high levels of fish predation.

The copepod nauplii were considered separately from the adult copepods since they represented a numerically important group. Copepod nauplii comprised 27% (9-52%) of the total number of zooplankters in the ponds during the study. The only statistically significant differences in nauplii densities between the stocked and the unstocked ponds occurred during mid-summer (7/22, 7/29). Immature copepods became particularly abundant during late summer when the populations of *K. quadrata* and *D. pulex* had been substantially reduced.

The adult copepods and ostracods contributed little to the total number of zooplankters in any of the experimental ponds. Comparisons of these two taxa between the stocked and unstocked ponds were characterized by asynchronous fluctuations of little magnitude with small non-significant differences.

Subtle, statistically non-significant, but consistent differences in the densities of the small cladocerans appeared between the stocked and the unstocked ponds. The average numbers of *Bosmina longirostris, Ceriodaphnia reticulata,* and *Diaphanosoma leuchtenbergiana* were generally lower in the stocked ponds than in the unstocked ponds; while the mean densities of *Chydorus sphaericus* were consistantly greater in the stocked ponds than in the unstocked ponds.

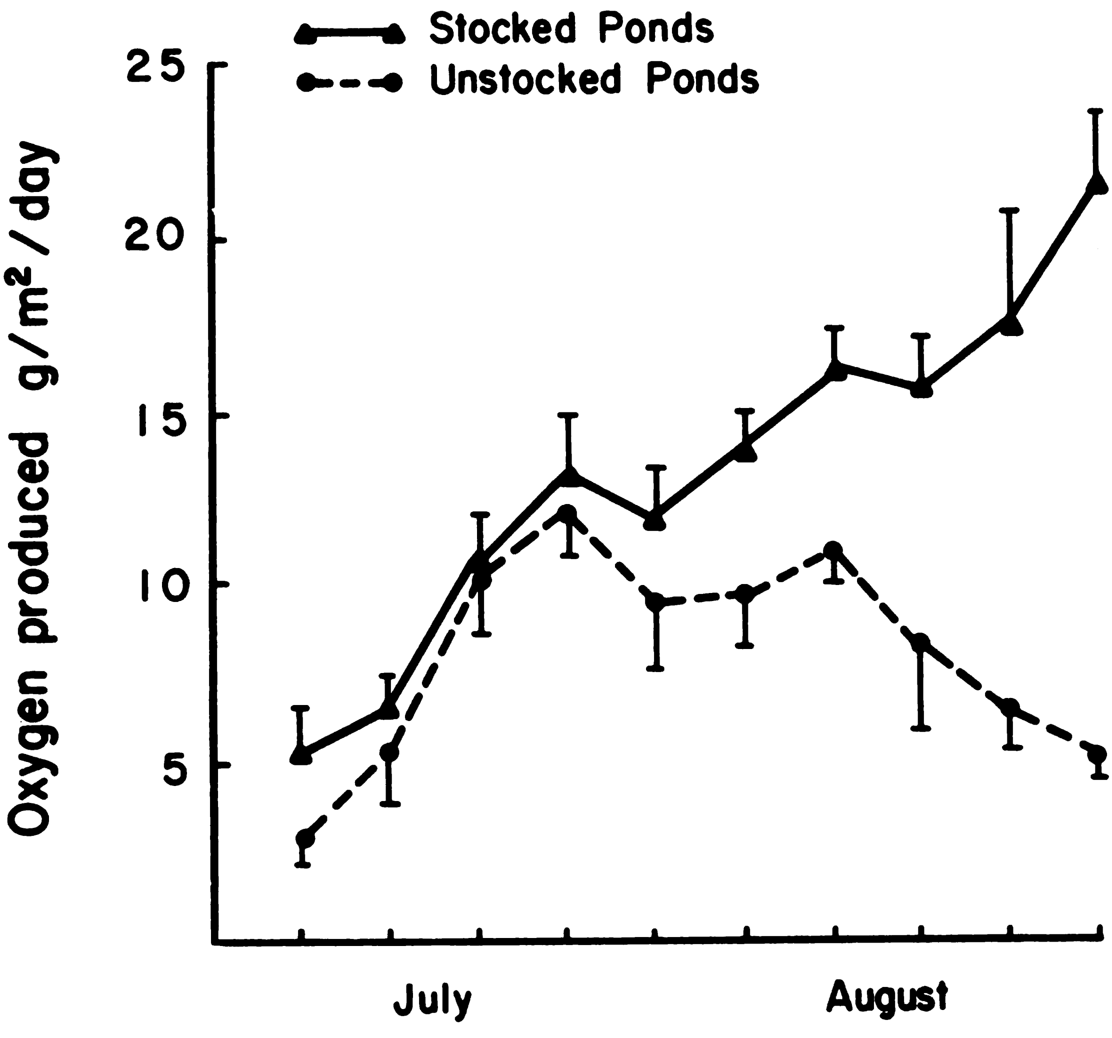
In summary, the populations of certain zooplankton species were strongly reduced following the introduction of fathead minnows and the subsequent recruitment of larval fish. Other zooplankton species decreased less obviously, but somewhat constantly over the study period. *Chydorus sphaericus* seemed to show a positive response to increasing levels of fish predation. The overall effect of stocking fathead minnows was a significant reduction of the total abundance of herbivorous zooplankters and presumably grazing pressure. Most of the zooplankton species present in the experimental ponds are considered relatively efficient filter feeders (Jorgensen, 1966). Potentially, the zooplankton populations have the capacity to limit algal growth and influence primary productivity.

Phytoplankton

Gross Primary Productivity

Gross primary productivity, calculated from diurnal oxygen curves, was used to estimate the total phytoplankton response to the introduction of planktivorous fish (Figure 5). Primary productivity corresponded closely with the total phytoplankton development in both groups of experimental ponds. Gross primary productivity was consistently higher in the stocked ponds. Primary productivity increased throughout the

Figure 5. Average gross primary productivity (± one standard error) in the stocked and unstocked ponds.



Stocked Ponds
Unstocked Ponds
25
20
15
10
5
Oxygen produced g/m² /day
July
August
Date

study in the stocked ponds; whereas productivity in the unstocked ponds declined during the last half of the experimental period. After July, the average weekly primary productivity was significantly ($p < 0.05$) higher in the stocked ponds. During the last five weeks of the study, gross primary productivity averaged 17 ± 1.3 g O_2/m^2/day in the stocked ponds and 8.3 ± 1.0 g O_2/m^2/day in the unstocked ponds.

Phytoplankton Densities

The total standing crop and community composition of the phytoplankton demonstrated marked differences between the stocked and unstocked ponds by the end of the study period. Initially, all eight ponds had relatively similar cell densities and similar species representation.

The total number of phytoplankton cells remained consistently lower in the unstocked ponds while the number of algal cells increased dramatically in the stocked ponds (Figure 6). The mean total weekly cell counts were statistically ($p < 0.05$) higher in the stocked ponds after July. Phytoplankton densities during this period averaged 30,486 cells/ml in the stocked ponds and 2,818 cells/ml in the unstocked ponds.

Phytoplankton Composition

Weekly differences in the numerical densities of the major phytoplankton taxa between the stocked and the unstocked ponds are illustrated in Figure 7. In general the successional composition of the phytoplankton in the stocked ponds shifted from an early summer dominance of mixed greens, to a mid-summer association of diatoms and cryptomonads

Figure 6. Mean total phytoplankton densities (± one standard error) in the stocked and unstocked ponds.

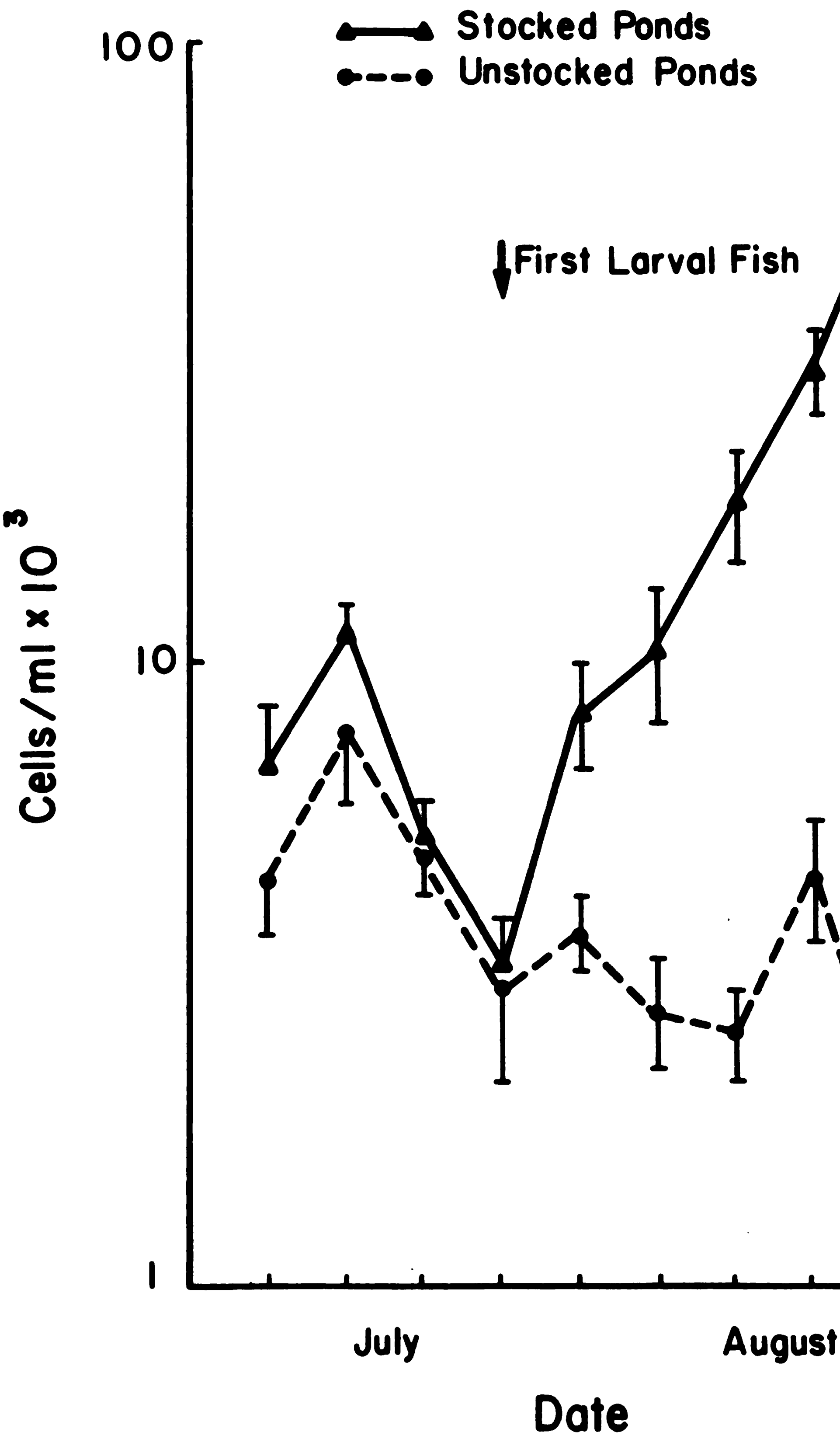
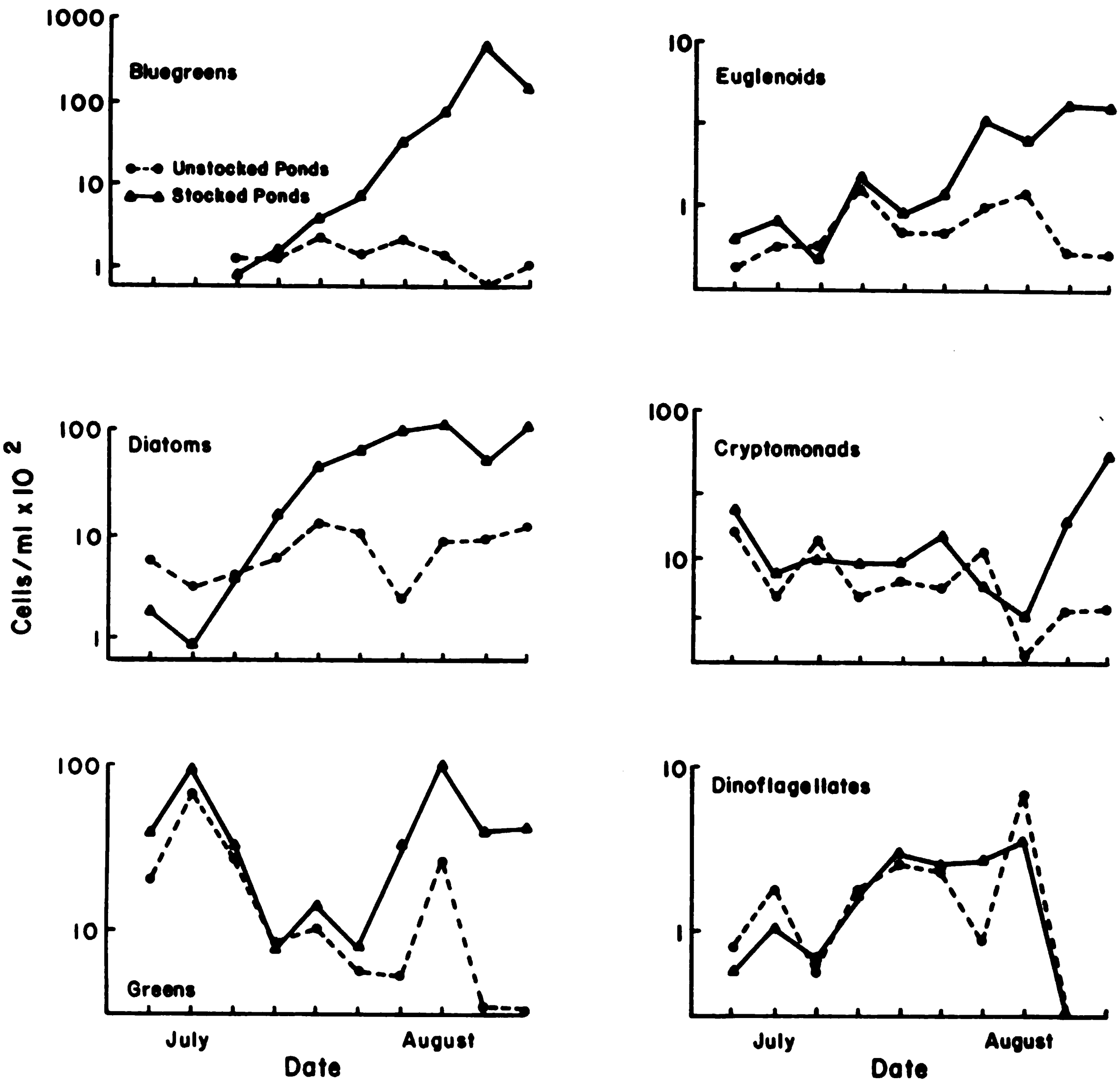

Stocked Ponds
Unstocked Ponds
100
10
1
First Larval Fish
Cells/ml x 10^3
July
August
Date

Figure 7. Mean numerical densities of the major phytoplankton taxa in the stocked and the unstocked ponds.



1000
100
10
1
Bluegreens
Unstocked Ponds
Stocked Ponds
10
1
Euglenoids
100
10
1
Diatoms
Cells/ml x 10 2
100
10
Cryptomonads
100
10
Greens
July
August
Date
10
1
Dinoflagellates
July
August
Date

and finally to a dominance of blue-green algae in late summer. The unstocked ponds were also initially dominated by mixed green algae which progressed to a mid-summer association of diatoms and cryptomonads that continued into late summer. In contrast to the stocked ponds, no substantial development of blue-greens occurred in any of the unstocked ponds.

The green algae (Chlorophyta) of the orders Volvocales and Chlorococcales dominated the phytoplankton community during the first three weeks of July; they comprised 46-86% of the total number of algae in the unstocked ponds and 60-90% in the stocked ponds. The mean total number of green algae fluctuated in a bimodal pattern with peak abundances in early July and late August in both groups of ponds. The early summer maximum was comprised mostly of *Schroederia sp.* and *Chlamydomonas spp.*, while the main participants in the late summer pulse were *Scenedesmus quadricauda*, *Gonium pectorale* and *Chlamydomonas spp.* Although the mean total number of green algae was consistantly higher in the stocked ponds, differences between the stocked and the unstocked ponds were statistically identifiable ($p < 0.05$) only during the final two weeks of the study. At that time densities averaged 4,092 cells/ml in stocked ponds and 366 cells/ml in the unstocked ponds.

The diatoms (Bacillariophyceae) reached dominant proportions in mid-summer when they comprised 43-66% of the total number of all phytoplankton cells. In the unstocked ponds, the diatoms did not clearly dominate the phytoplanktonic community until the last two weeks of the study when they accounted for 50-51% of the total number of phytoplankton. Individuals of the genera *Cyclotella*, *Stephanodiscus* and *Nitzschia* were the major representatives of the mid-summer planktonic

algae in all ponds. The mean total number of diatoms in the stocked ponds (8,992 cells/ml) was significantly ($p < 0.05$) higher than in the unstocked ponds (867 cells/ml) after July.

The cryptomonads (Cryptophyceae) exhibited similar patterns of development in both sets of experimental ponds throughout most of the study. They consistently represented about 20% of the total phytoplankton community during mid-summer in all ponds. The cryptophycean flagellates, *Rhodomonas spp.* and *Cryptomonas spp.* were the sole representatives of this taxa found in the ponds. The mean total number of cryptomonads in the stocked ponds (3,943 cells/ml) was significantly ($p < 0.05$) higher during the last two weeks of the study than (567 cells/ml) in the unstocked ponds.

Blue-green algae (Cyanophyta) were not found in the ponds during the first weeks of the study, but by late summer they comprised 41-80% of the total phytoplanktonic community in the stocked ponds. In the unstocked ponds, the blue-greens never exceeded 9% of the total number of the phytoplankton. The large filamentous species *Anabaena flos-aquae* and *Anabaena affinis* and the colonial blue-green *Microcystis aeruginosa* were the major representatives of this taxa in both sets of experimental ponds. During the last four weeks of the study, the mean total number of blue-greens (17,850 cells/ml) in the stocked ponds was significantly ($p < 0.05$) higher than that (130 cells/ml) in the unstocked ponds.

The dinoflagellates (Dinophyceae) and the euglenoids (Euglenophyceae) never exceeded 8% of the total phytoplanktonic community during the study. The dinoflagellates were represented by *Ceratium hirundinella, Peridinium sp.* and *Gymnodinium sp.* and the euglenoids by

Euglena spp., Phacus sp. and *Trachelomonas sp.* The average summer concentrations were about 171 dinoflagellates/ml and 229 euglenoids/ml. The mean weekly densities for both taxa in the stocked ponds and the reference ponds were statistically indistinct through the summer, except for a sudden pulse of euglenoids in the stocked ponds during the final two weeks of the study.

Physical Conditions

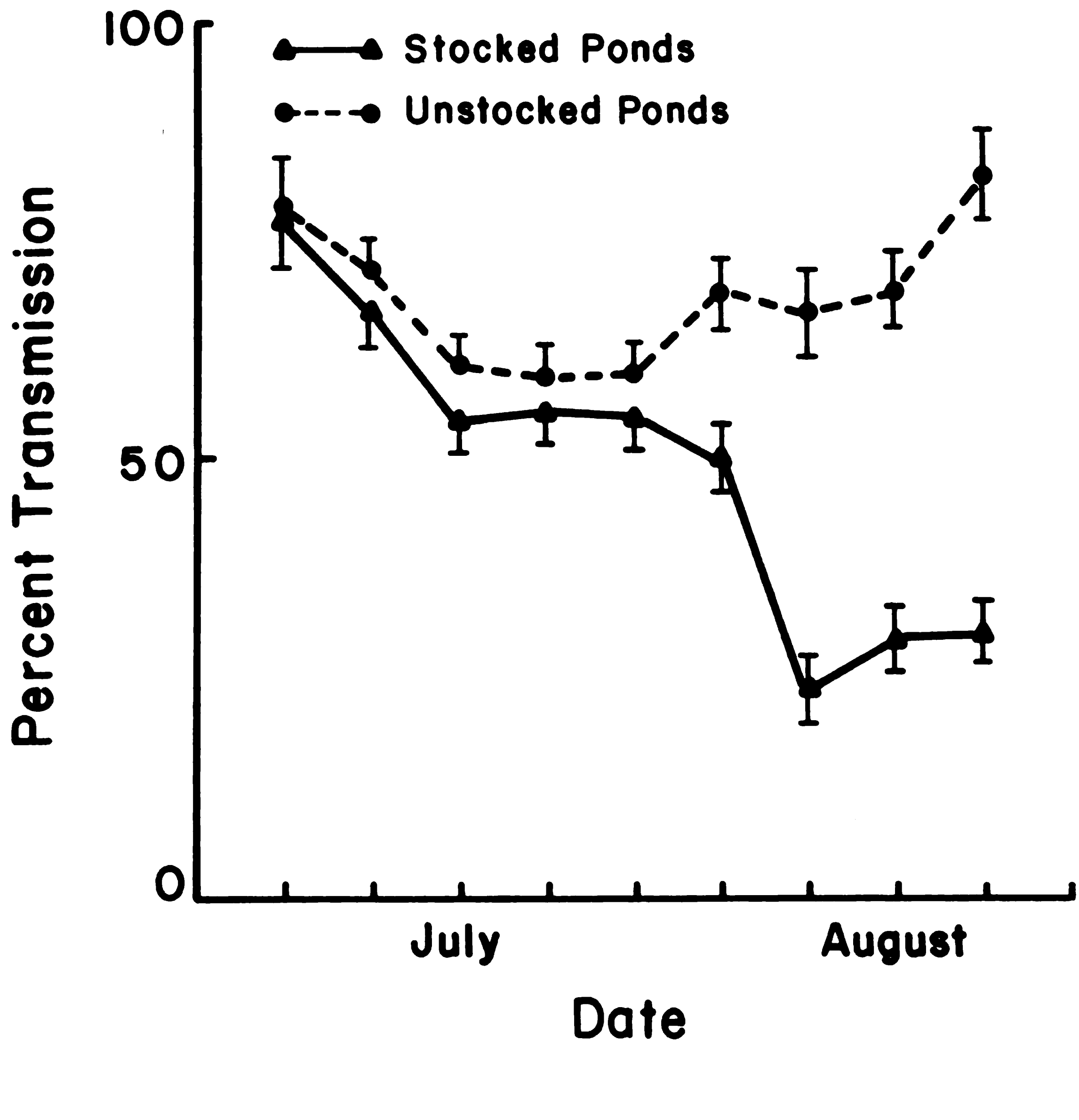
There was no meaningful difference in the water temperatures between the stocked and the unstocked ponds during the study. The average daily summer temperature was about 22 C in the unstocked ponds and 23 C in the stocked ponds. The maximum temperature recorded was 25 C; the average daily range was about 2 C.

The percent transmission of light (water clarity) was consistently lower in the stocked ponds than in the unstocked ponds (Figure 8). During the last half of the study the stocked pond waters were significantly ($p < 0.05$) more turbid than the unstocked pond waters. The mean percent transmission at mid-depth (± one standard error) for the last five weeks of the study was 70.57 ± 3.13 in the unstocked ponds and 32.22 ± 4.65 in the stocked ponds.

Chemical Conditions

All ponds were heavily enriched with domestic wastewater to produce relatively high nutrient levels. Based on phosphorus and nitrogen concentrations all ponds were eutrophic according to the classification of Vollenweider (1968). Of the phosphorus and nitrogen compounds

Figure 8. Mean percent transmission values ($\pm$ one standard error) in the stocked and the unstocked ponds.



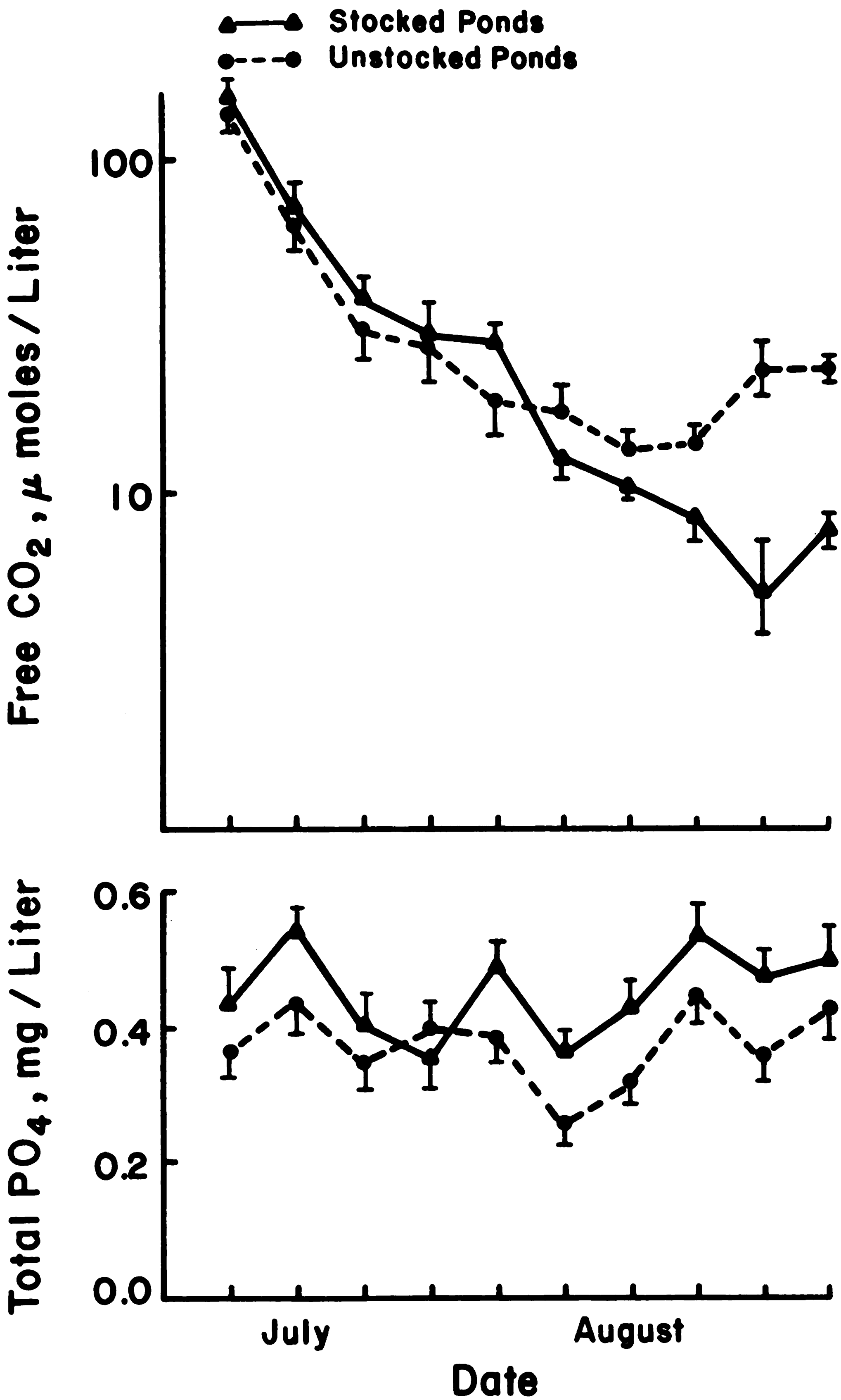
100
50
0
Stocked Ponds
Unstocked Ponds
Percent Transmission
July
August
Date

measured, no statistically significant differences were determined between the stocked and the unstocked ponds. However, mean total phosphorus values were consistently higher in the stocked ponds with only one exception, during the fourth week of the study (Figure 9). During the study, total phosphorus (as phosphate) averaged 0.46 ± 0.04 mg/liter in the stocked ponds and 0.38 ± 0.03 mg/liter in the unstocked ponds. Nitrogen values sampled at irregular intervals through the study averaged about 0.42 mg/liter nitrate nitrogen and 0.31 mg/liter ammonia nitrogen over all ponds during the study.

Free carbon dioxide concentrations decreased substantially in all experimental ponds throughout the study period (Figure 9). During the last half of the study period, when blue-green algae were abundant in the stocked ponds, the free carbon dioxide values were consistently lower in the stocked ponds than in the unstocked ponds. Statistically significant ($p < 0.05$) differences between the two sets of experimental ponds occurred only during the final two weeks of the study, when free carbon dioxide values averaged 24.77 ± 3.57 μ moles/liter in the unstocked ponds and 7.37 ± 1.79 μ moles/liter in the stocked ponds. The average density of blue-green algae for each experimental pond during every week of the study showed a strong negative correlation ($r = -0.83$) with the average concentration of free carbon dioxide in each experimental pond (Figure 10).

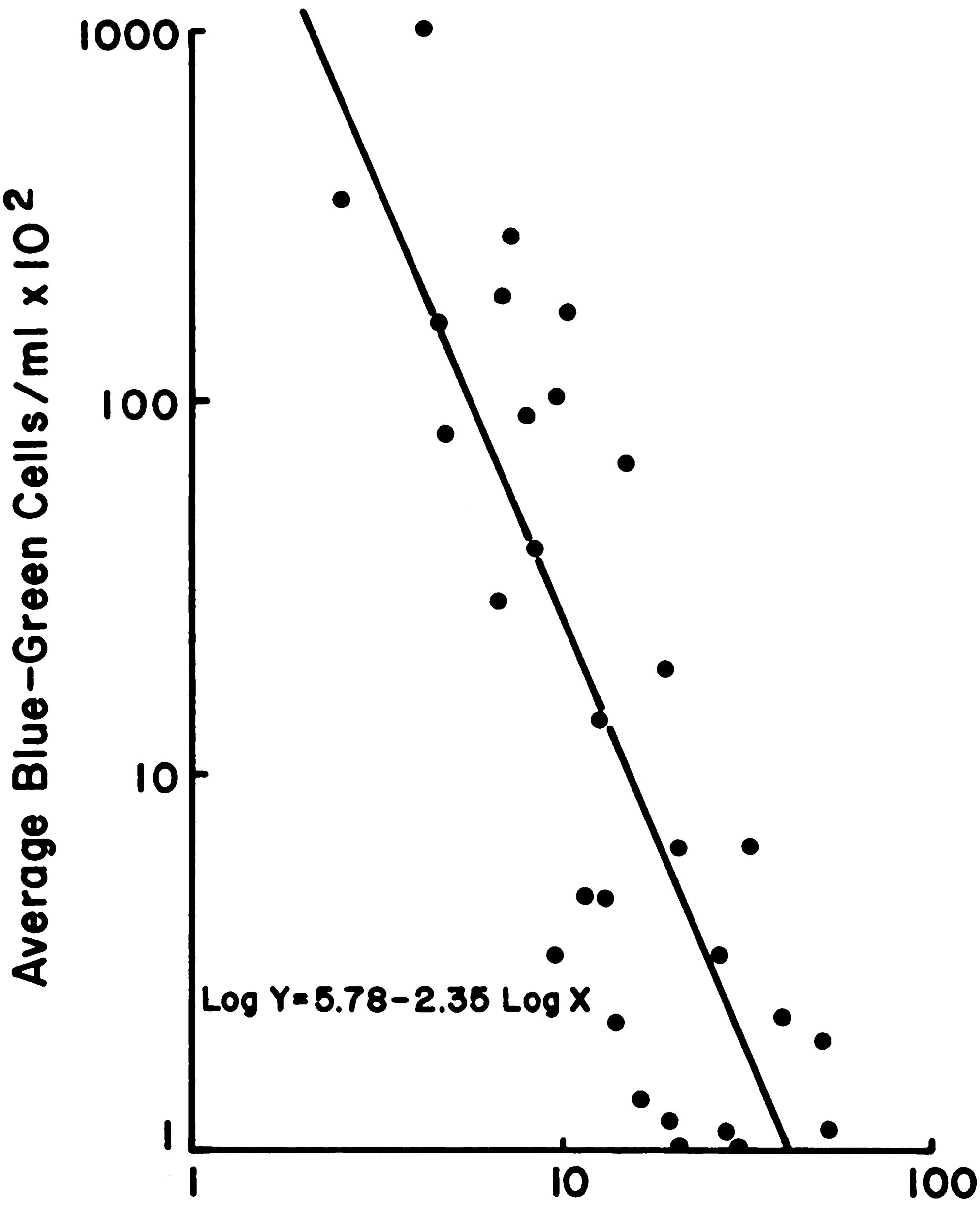
Alkalinity and the hydrogen ion concentrations in the two sets of ponds were statistically indistinguishable. The total alkalinity (as $CaCO_3$) ranged from 232 to 146 mg/liter and mid-day pH values varied from 7.6 to 9.5 units. The highest pH values and the lowest alkalinities were recorded in the stocked ponds during late summer when algal

Figure 9. Mean total phosphorus (as PO_4) and free carbon dioxide values (± one standard error) in the stocked and unstocked ponds.



Stocked Ponds
Unstocked Ponds
Free CO_2, μ moles / Liter
100
10
Total PO_4, mg / Liter
0.6
0.4
0.2
0.0
July
August
Date

Figure 10. Relationship between the log of the average free CO_2 concentration and the log of the average density of blue-green algae. The straight line was fitted using the least squares method.


1000
100
10
1
1
10
100
Average Blue-Green Cells/ml x 10 2
Log Y=5.78-2.35 Log X
Average Free CO2 μ moles/Liter

productivity was maximum. In general, the pH values in the stocked ponds were slightly higher than in the unstocked ponds, but well below lethal thresholds for zooplankton (O'Brien and deNoyelles, 1972).

DISCUSSION

The results of this study point to the potential role of planktivorous fish as regulators of planktonic communities in eutrophic environments. In this experiment, stocking of fathead minnows in otherwise fish-free ponds led to a significant reduction in the total number of zooplankton and the associated grazing pressures. The depression of zooplankton, in turn, allowed an increase in the total density of phytoplankton and ultimately effected a shift in algal composition from one dominated by green algae, diatoms and cryptomonads to one dominated by blue-green algae. These changes were associated with increased primary productivity and reduced water clarity. This transition resembles the frequently described succession of lakes from mesotrophic to eutrophic stages.

It is unlikely that the changes observed in the stocked ponds were due to water quality alterations unrelated to stocking since this experiment was designed to minimize extraneous effects. The nutrient concentrations, exposure to overhead light, temperature and sediments were indistinguishable among ponds at the beginning of the experiment. Temperature and overhead light remained the same in all of the ponds during the experiment. Slight changes in nutrient concentrations originated from the stocking of fathead minnows alone.

Several species of invertebrate predators were also present in the ponds including: *Asplanchna sp., Cyclops vernalis, Macrocyclops albidus* and *Chaoborus sp.* as well as a few hemipterans, odonates and beetles. Zooplankton predators were no more abundant in the stocked ponds than in the unstocked ponds, so their effect was considered constant in all ponds. Holling (1965), Hall *et al.* (1970) and Kaczynski (1970) all discounted the relative impact of invertebrate predation on zooplankton populations as compared to food availability and fish predation.

Fathead minnows were the dominant planktivores in the experimental ponds. The significant reduction of zooplankton populations in the stocked ponds was considered a direct effect of predation rather than the result of other environmental changes. Independent evidence from fish stomach analysis supports this conclusion. Crustacean zooplankters and rotifers were the most important summer food items for fathead minnows in the stocked ponds. Similarly, Held and Peterka (1974), Dobie *et al.* (1966) and Pearse (1918) all found predominating quantities of zooplankton and aquatic insects in the guts of fathead minnows. The fish in this experiment exhibited the capacity to influence the zooplankton composition of the ponds.

The impact of fish predation has been investigated primarily in regard to the effect on prey diversity and size distribution. Although no previous authors have remarked on size-selection by fathead minnows, the gut contents of stocked fatheads suggest a size-selection of prey that was related to the size of the minnow. Other species of fish are strongly food-size selective according to Hrbacek (1962), Hrbacek and Novatna-Dvorakova (1965), Brooks and Dodson (1965), and Galbraith (1967). Large fatheads recovered from the stocked ponds in this study contained relatively large zooplankters, particularly *Daphnia pulex,* while small minnows appeared to select smaller food items like

Keratella quadrata and copepod nauplii. However, it is possible that fathead minnows were simply selecting the most abundant zooplankters within a size range they could easily consume, since *D. pulex* and *K. quadrata* were the most numerous species in the ponds.

Most previous investigators have shown that predation by planktivorous fish results in decreased proportion of large zooplankton species, probably because of size selection and a complimentary increase in the abundance of smaller zooplankters (Hrbacek, 1958; 1962; Hrbacek and Novatna-Dvorakova, 1965; Grygierek *et al*, 1966; Brooks and Dodson, 1965; Hall *et al*., 1970; Losos and Hetesa, 1973). Hall *et al*. (1970) found that even though fish predation increased the diversity of zooplankton, the compensatory response of the small zooplankters maintained the biomass of the original population, so that, in terms of biomass alone, there was no persistent effect from fish predation.

Unlike the results of most previous studies, the density of both large and small species of zooplankton in this study was depressed by stocked fish while diversity remained relatively unchanged. However, in the sequence of events that followed stocking, the density of smaller *K. quadrata* at first seemed to increase and did not begin to decline until several weeks after the study began. The larger *D. pulex* began to decline immediately after stocking. The decline in small zooplankton corresponded to the time when large numbers of larval fish appeared in the ponds and began consuming *K. quadrata* in particular. The combined impact of a high initial stocking with adult fish, high adult survivorship, and a high reproductive potential with continuous recruitment produced a diverse size structure in the predator population which enabled it to decimate all size categories of zooplankton relatively uniformly. In a similar study, Hurlbert *et al.* (1973) found that mosquito fish, *Gambusia affinis*, eliminated *D. pulex* and greatly reduced other crustacean and rotifer populations.

The intensity of predation and the structure of the predator population appears to determine the zooplankton response to fish predation. At low and intermediate levels of fish predation, the abundance of large zooplankters such as *Daphnia pulex*, has been known to increase (Archibald, 1975). Grygierek *et al.* (1966) examined the effect of different stock density of carp fry and noted that the total abundance of zooplankton increased with increasing fish stock up to a critical stock density (about 22,500 fry/ha) beyond which total abundance decreased. Hall *et al.* (1970) concluded that predation by bluegills at low to moderately high intensities strongly depressed mean prey size and increased diversity without markedly altering the total biomass of the zooplankton. However, Hall *et al.* (1970) were using a fish species with discontinuous, single-cohort recruitment in a "weedy" habitat which was more spatially complex than the ponds used in this study. Larval bluegills which feed on small zooplankters exist in the population only for two or three weeks of the year. Bluegill population size structure is relatively simple compared to that of fathead minnows.

It may be generally assumed that when planktivorous fish effect changes in zooplankton populations there will be corresponding changes in the primary producers. Although data on fish-zooplankton-phytoplankton interrelationships are sparse and often inconclusive, some fish-induced changes in the composition and abundance of the phytoplankton community have been reported after the introduction of zooplanktivorous fish have

effected a change in zooplankton species composition (Hrbacek *et al.*, 1961; Brooks, 1969; Straskraba, 1965; Grygierek *et al.*, 1967; Hurlbert *et al.*, 1972; Losos and Hetesa, 1973). In experiments where man served as the predator, manipulation of zooplankton densities significantly altered algal standing crops and determined the relative proportions of algal species (Pennington, 1941; Ehrlich, 1964; Porter, 1973).

Most significant differences in the plankton (quantity and composition) found in stocked and unstocked ponds occurred during the latter half of the study period when larval fish were abundant. At this time, the development of the phytoplankton was directly proportional to the increase in the number of minnows and indirectly proportional to the density of herbivorous zooplankters. Among the major phytoplankton taxa, both the diatoms and blue-green algae were consistently more dense in the stocked ponds. Similar increases in the total standing crop of phytoplankton and blue-green algae were reported in ponds following the introduction of planktivorous fish (Losos and Hetesa, 1973; Hurlbert *et al.*, 1972).

The genera of algae which increased in the stocked ponds, with the exception of the blue-green algae, are commonly found in the guts of grazing zooplankton (Mullin, 1967; Fryer, 1957; Porter, 1973). Depressed grazing pressure appears to have permitted the increased abundance of these edible species. However, it is unlikely that the strong development of blue-greens, essentially *Anabaena* and *Microcystis*, was a direct response to lower grazing pressure. The rejection of large filamentous and gelatinous blue-greens, notably *Anabaena* and *Microcystis* (Burns, 1968), has been attributed to their large size and

unmanageable dimensions. There also is evidence that certain blue-green species produce substances which inhibit feeding by zooplankton. Arnold (1971) found that *Anabaena flos-aquae* and several coccoid species reduce ingestion, assimilation, survivorship and reproduction in *D. pulex*. Shangenberg (1960) found that *Microcystis aeruginosa* was very toxic to *D. pulex*.

Among the numerous adaptive characteristics of blue-green algae that have been suggested to explain why blue-greens reach maximum abundance in eutrophic waters, tolerance to low carbon dioxide tension (King, 1970) appears to be the most reasonable explanation for their success in the stocked ponds. Blue-green algae may also gain competitive advantages because at least some species are more tolerant of high light intensities and temperatures (Jackson, 1965), are able to regulate their bouyancy to remain in the nutrient-rich photic zone (Reynolds, 1965), can chemically inhibit the growth of other algae (Boyd, 1973), and can fix atmospheric nitrogen (Dugdale and Neess, 1961). All of the experimental ponds in this study were enough alike in all respects other than carbon dioxide concentrations to disregard these other explanations for blue-green development. During the last four weeks of the study, free carbon dioxide concentrations in the stocked ponds averaged less than 10 μ moles/liter, a value which is considered limiting to most green algae but adequate for blue-greens (King, 1972). Therefore, it is proposed that depressed grazing pressure, which allowed an increase biomass and productivity and an accelerated consumptive uptake of carbon dioxide by the edible planktonic algae, indirectly generated the conditions (limiting CO_2 concentrations) which favored the development of blue-green algae.

Evidence gathered from eutrophic ponds in this study indicate that a planktivorous fish population can severely limit zooplankton and that the relative abundance of algal species is, in part, dependent on the resultant depression of grazing by herbivorous zooplankters. Therefore, accelerated primary productivity accompanied by succession to blue-green algal dominances may result from changing trophic relationships between primary and secondary consumers.

The success of future water quality management strategies oriented toward the regulation of objectionable growths of planktonic and filamentous algae requires not only the ability to accurately access the physicochemical processes involved, but a more complete understanding of and appreciation for biological forces which drive aquatic ecosystems. The elimination of all nutrient inputs and complete control of other abiotic factors is not usually practicable. The potential importance of biological controls is evident from this study, although further investigations are required before phytoplankton densities can be routinely manipulated by management of consumer populations.

LITERATURE CITED

LITERATURE CITED

American Public Health Association. 1965. Standard methods for the examination of water and wastewater. 12th edition. APHA, New York. 769 p.

Archibald, C. P. 1975. Experimental observations on the effects of predation by goldfish (*Crassius auratus*) on the zooplankton of a small saline lake. J. Fish. Res. Bd. Canada 32: 1589-1594.

Arnold, D. E. 1971. Ingestion, assimilation, survival and reproduction by *Daphnia pulex* fed seven species of blue-green algae. Limnol. Oceanogr. 16: 906-920.

Brooks, J. L. 1959. Cladocera, p. 587-656. *In* W. T. Edmondson (ed.), Fresh-water Biology, 2nd edition. Wiley, New York.

__________. 1969. Eutrophication and changes in the composition of zooplankton, p. 236-255. *In* Eutrophication: Causes, Consequences, Correctives. Nat. Acad. Sciences.

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

Boyde, C. E. 1973. Biotic interaction between different species of algae. Weed Science 21: 31-37.

Burns, C. 1968. The relationship between body size of filter feeding Cladocera and the maximum size of particles ingested. Limnol. Oceanogr. 13: 675-678.

Clements, F. E. and F. E. Shelford. 1939. Bioecology. Wiley, New York. 356 p.

Cushing, D. H. 1958. The effect of grazing in reducing primary production: a review. Rapp. Proces-Verbaux Reunions Cons. Perma. Int. Explor. Mer. 144: 149-154.

Dobie, J., O. L. Meehan, S. F. Snieszko, and G. N. Washburn. 1956. Raising bait fishes. Fish and Wildl. Serv., U. S. Dept. Interior Circ. 35: 1-124.

Dugdale, R. C., and J. C. Neess. 1961. Recent observations on nitrogen fixation in blue-green algae, p. 103-106. *In* Algae and metropolitan wastes. R. A. Taft Sanitary Eng. Center, Cincinnati, Ohio.

Edmondson, W. T. 1972. Nutrients and phytoplankton in Lake Washington. *In* G. Likens (ed.), Nutrients and Eutrophication, ASLO Special Symp. 1: 1172-1188.

__________. 1959. Rotifera, p. 14-21. *In* W. T. Edmondson (ed.), Fresh-water Biology, 2nd edition. Wiley, New York.

Ehlrich, S. 1966. Two experiments in the biological calarification of stabilization pond effluents. Hydrobiologica 28: 70-80.

Fryer, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. J. Animal Ecology 26: 263-286.

Galbraith, M. G. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Amer. Fish. Soc. 96: 1-10.

Grygierek, E., A. Hillbricht-Ilkowska, and I. Spodniewska. 1966. The effect of fish on plankton community in ponds. Int. Ver. Theor. Angew. Limnol. Verh. 16: 1359-1366.

Hall, D. J., W. E. Cooper and E. E. Werner. 1970. An experimental approach to the production, dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839-928.

Haney, J. F. 1971. An *in situ* method for the measurement of zooplankton grazing rates. Limnol. Oceanogr. 16: 970-977.

Hargrave, B. T. and G. H. Geen. 1970. Effects of copepod grazing on two natural phytoplankton populations. J. Fish. Res. Bd. Canada 27: 1395-1402.

Held,, J. W. and J. J. Peterka. 1974. Age, growth, and food habits of the fathead minnow, *Pimephales promelas,* in North Dakota saline lakes.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45. 60 p.

Hrbacek, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Rozpr. Cesk. Akad. Ved., Rada Mat. Prir. Ved. 72: 11-116.

__________, M. Dvorakova, V. Korinek, and L. Prochazdova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Int. Ver. Theor. Angew. Limnol. Verh. 14: 192-195.

__________, and M. Novotna-Dvorakova. 1965. Plankton of four backwaters related to their size and fish stock. Rozpr. Cesk. Akad. Ved., Rada Mat. Prir. Ved. 75: 1-65.

Hurlbert, S. H., J. Zedler, and D. Fairbanks. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Science 175: 639-641.

Hutchinson, G. E. 1973. Eutrophication. Am. Sci. 61: 269-279.

Isaak, D. 1961. The ecological life history of the fathead minnow, *Pimephales promelas* (Rafinesque). Ph.D. Thesis, Univ. Minnesota, 150 p.

Jackson, D. F. 1965. Ecological factors governing blue-green algae blooms, p. 402-420. *In* Proceedings of the 19th Industrial Waste Conference. Engineering Extension Series 117, Purdue Univ., WesT Lafayette, Ind.

Jenkins, D. and L. Medsker. 1964. Brucine method for determination of nitrate in ocean, estuarine and fresh waters. Anal. Chem. 36: 610-612.

Jorgenson, C. J. 1966. Biology of suspension feeding. Pergamon Press, New York. 357 p.

Kaczynski, V. W. 1970. Population ecology of the anostrachan, *Eubranchipus bundyi*. Ph.D. Thesis, Cornell Univ., Ithaca, New York. 89 p.

King, D. L. 1970. The role of carbon in eutrophication. J. Water Pollut. Contr. Fed. 42: 2035-2051.

__________. 1972. Carbon limitation in sewage lagoons. *In* G. Likens (ed.), Nutrients and Eutrophication, ASLO Special Symp. 1: 98-110.

Losos, B. and J. Hetesa. 1973. The effect of mineral fertilization and carp fry on the composition and dynamics of plankton. Hydrobiol. Stud. 3: 173-217.

Lund, J. W. G. 1965. The ecology of freshwater phytoplankton. Biol. Rev. 40: 231-293.

Markus, H. C. 1934. Life history of the blackhead minnow, *Pimiphales promelas*. Copeia 1934: 116-122.

McNabb, C. D. 1960. Enumeration of freshwater phytoplankton concentrated on the membrane filter. Limnol. Oceanogr. 5: 57-61.

Menzel, D. W. and J. H. Ryther. 1961. Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production. J. Cons. Perma. Int. Explor. Mer 26: 250-258.

Mullin, M. M. 1967. On the feeding behavior of planktonic marine copepods and the separation of their ecological niches, p. 955-964. *In* Proceedings of Symposium on Crustacea, Part III, Mar. Biol. Ass., India.

O'Brien, J. W. 1970. The effects of nutrient enrichment on the plankton community in either experimental ponds. Ph.D. Thesis, Michigan State Univ., E. Lansing, Michigan. 180 p.

__________ and F. deNoyelles. 1972. Photosynthetically elevated pH as a factor in zooplankton mortality in nutrient enriched ponds. Ecology 53: 605-614.

Odum, H. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1: 102-117.

Pearse, A. S. 1918. The food of the shore fishes in certain Wisconsin lakes. Bull. U. S. Fish. 35: 249-290.

Pennington, W. 1944. The control of numbers of freshwater phytoplankton by small invertebrate animals. J. Ecol. 29: 204-211.

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

Prescott, G. W. 1962. Algae of the western Great Lakes area. W. C. Brown, Dubuque, Iowa. 977 p.

Reynolds, C. S. 1972. Growth, gas vacuolation and buoyancy in a natural population of planktonic blue-green algae. Freshwater Biol. 2: 87-106.

Shapiro, J. 1973. Blue-green algae: why they become dominant. Science 179: 382-384.

Smith, G. 1950. The freshwater algae of the United States. McGraw-Hill, New York. 719 p.

Strangenberg, M. 1968. Toxic effects of *Microcystis aeruginosa* Kg. extracts on *Daphnia longispins* O. F. Muller and *Eucypris virens* Jurine. Hydrobiol. 32: 81-87.

Straskraba, M. 1965. The effect of fish on the number of invertebrates in ponds and streams. Mitt. Int. Ver. Theor. Angew. Limnol. 13: 106-127.

Vollenweider, R. A. 1970. Scientific fundamentals of eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Organization for Economic Co-operation and Development Ex. 40105. Paris, France, 159 p.

Weber, C. I. 1971. A guide to the common diatoms at water pollution surveillance stations. U. S. Environmental Protection Agency, Cincinnati, Ohio. 101 p.

Wilson, M. S. 1959. Calanoida, p. 738-795. *In* W. T. Edmondson (ed.), Fresh-water Biology, 2nd edition. Wiley, New York.

Yeatman, H. C. 1959. Cyclopoida, p. 795-815. *In* W. T. Edmondson (ed.), Fresh-water Biology, 2nd edition. Wiley, New York.

APPENDICES

APPENDIX I. Species list of the phytoplankton in the experimental ponds encountered during quantitative counts.

Chlorophyceae:

Actinastrum sp.
Ankistrodesmus falcatus
Carteria sp.
Chlorella vulgaris
Chlorella sp.
Chlamydomonas spp.
Closterium sp.
Cosmarium spp.
Golenkinia sp.
Gonium pectorale
Kirchneriella sp.
Micractinium sp.
Pandorina morum
Pediastrum boryanum
Scenedesmus quadricauda
Scenedesmus spp.
Schroederia sp.
Selenastrum sp.
Staurastrum sp.
Tetraedron spp.
Volvox sp.

Bacillariophyceae:

Achnanthes lanceolata
Amphora ovalis
Cyclotella meneghiniana
Cyclotella stelligera
Cyclotella spp.
Cocconeis placentula
Gomphoenema sp.
Melosira granulata
Melosira spp.
Navicula spp.
Nitzschia acicularis
Nitzschia palea
Nitzschia spp.
Rhoicosphenia curvata
Stephanodiscus spp.
Synedra ulna
Synedra spp.

Cyanophyceae:

Agmenellum sp.
Anabaena affinis
Anabaena flos-aquae
Anabaena sp.
Gomphosphaeria lacustris
Microcystis aeruginosa

Cryptophyceae:

Cryptomonas sp.
Rhodomonas sp.

Euglenophyceae:

Euglena spp.
Phacus sp.
Trachelomonas sp.

Dinophyceae:

Ceratium hirundinella
Peridinium sp.
Gymnodinium sp.

Chrysophyceae:

Mallomonas sp.

APPENDIX II. Species list of the zooplankton in the experimental ponds encountered during quantitative counts.

Cladocera:

Alona sp.
Bosmina longirostris
Ceriodaphnia reticulata
Chydorus sphaericus
Daphnia pulex
Diaphanosoma leuchtenbergiana
Pleuroxus denticulatus
Scapholeberis kingi
Simocephalus ventulus

Copepoda:

Copepod nauplii
Cyclops vericans rubellus
Cyclops vernalis
Diaptomus pallidus
Eucyclops agilis
Macrocyclops albidus
Mesocyclops edax

Rotifera:

Asplanchna sp.
Brachionus sp.
Keratella cochlearis
Keratella quadrata
Lecane sp.
Lepadella sp.
Monostyla sp.
Platyius sp.
Synchaeta pectinata

Ostracoda:

Cypridopsis sp.
Physocypria sp.