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EFFECTS OF ZOOPLANKTON ON ALGAE IN WESTHAMPTON LAKE

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ABSTRACT

Natural assemblages of algae and various concentrations of zooplankton were confined in aquariums in Westhampton Lake, Richmond, Virginia. Properties of the water, algae, and zooplankton inside and outside the aquariums were measured in order to ascertain the effects of the zooplankton on the algae.

Rotifers, zooplankton which underwent no consistent vertical migrations, decreased photosynthesis of the algae by 22% daily. Copepods and cladocerans, zooplankton which underwent consistent daily vertical migrations, had no significant influence on photosynthesis. None of the zooplankton significantly affected photosynthetic efficiency (photosynthesis per unit chlorophyll) of algae.

Daily variations in photosynthesis were significantly related to rainfall. Photosynthesis increased several days after rainfall. The increase resulted not from increased chlorophyll, but from increased photosynthetic efficiency of the algae.

INTRODUCTION

Impounded streams are among the most common bodies of water in Virginia. They have many uses, but often develop undesirable features because of the large growths of algae they support. Blooms of algae may create unpleasant sights and odors (Edmondson, 1967), accumulations of organic matter and anaerobic conditions (Barlow, Lorenzen, and Myren, 1963), and even inhibit activities of other organisms (Burns and Rigler, 1967; Ryther, 1954).

Zooplankton, weakly swimming microscopic animals, are potentially important regulators of algae. They eat algae (Bogatova, 1965; Cushing, 1958), and supply algae with nutrients (Barlow and Bishop, 1965; Martin, 1968). The purpose of the present study was to measure the extent to which zooplankton regulated photosynthesis by algae in Westhampton Lake, Richmond, Virginia.

Previous studies of effects of zooplankton on algae usually followed one of two approaches: (1) field observations, or (2) laboratory experiments. The first involves correlations between the abundances of zooplankton and algae in their natural habitats. Such studies demonstrate that under certain conditions, as after a bloom of algae, the two are inversely related (Raymont, 1963). This approach is most useful when changes in the abundances of the zooplankton and algae are large, but is not applicable when the sizes of the populations are stable. The second approach is useful regardless of the stability of the populations. Effects of zooplankton on algae are measured under controlled laboratory conditions and applied in mathematical formulas to predict effects in the natural habitat (Riley, 1965). Activities measured in the laboratory, however, may not adequately describe those in the natural habitat. Burns and Rigler (1967) for example, showed that *Daphnia* fed nearly five times faster in laboratory cultures of food than in lake water. Most laboratory experiments also deal with one kind of algae and zooplankton at a time, a unique event in nature.

In the present study, experiments were conducted in the field. The experiments were similar to those of Strickland and Terhune (1961) and Stepanek (1966) in that the organisms were confined in plastic containers in the natural habitat. One advantage of the present method over previous in situ studies of zooplankton and algae by Gliwicz (1968) and Nauwerk (1963) was that the zooplankton were relatively free to undergo vertical migrations.

PROCEDURES

The study was conducted in Westhampton Lake, a freshwater impoundment on the campus of the University of Richmond, Virginia. The surface area of the lake at the time of the study was about 20 acres, and mean and maximum depths were 5 feet and 12 feet (Figure 1). The major tributary entered into the northeast corner of the lake. In summer it flowed during, and shortly after rainstorms. The experiments were done in the deepest area near the southwest corner of the lake.

Algae with different concentrations of zooplankton were enclosed in aquariums, which were cylinders of polyethylene and plexiglass, in the lake. Properties of the water, algae, and zooplankton inside and outside the aquariums were measured over several days.

Pilot studies in the summer of 1968, dealt with general features of the lake (bathymetry, temperature, light), algae (kinds, vertical distribution of chlorophyll a, and photosynthesis), zooplankton (kinds and vertical distribution) and structure of the aquariums. These studies were used to design routine experiments conducted in the summer of 1969.

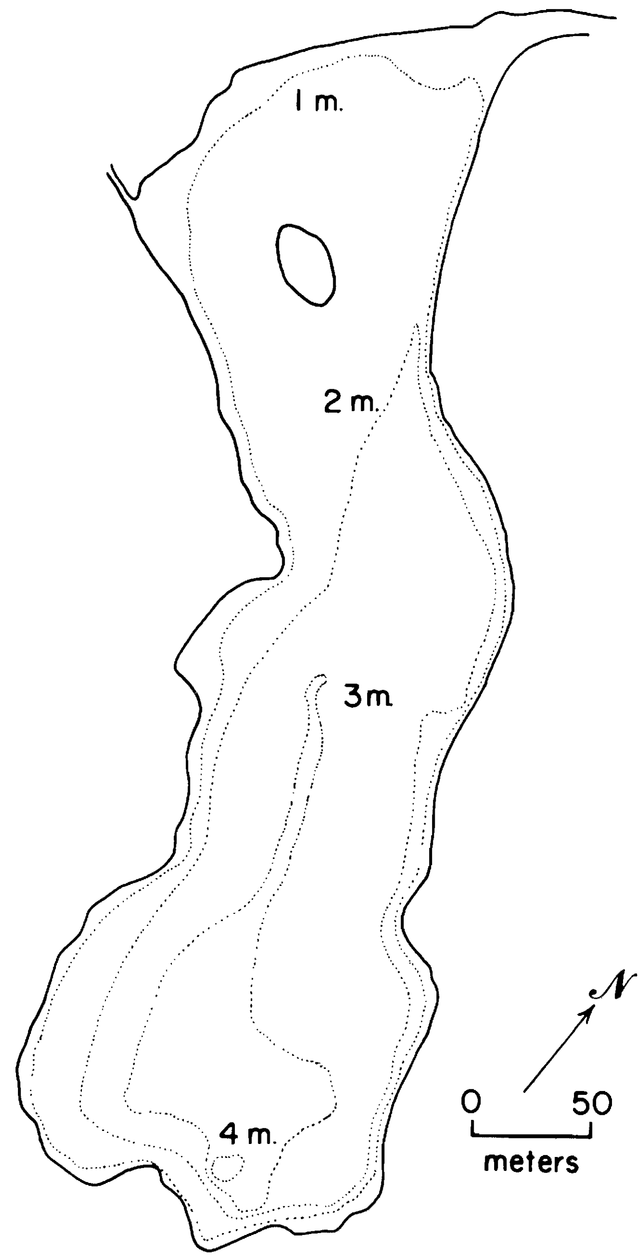
Bathymetry was measured with lead lines for depths and transits and alidades for positions. Temperatures and light intensities were measured with a thermistor thermometer and submarine photometer. Identification of algae was done with living specimens and samples treated with Lugol's iodine. Zooplankton were treated with formalin.

The vertical distributions of chlorophyll a and photosynthesis were measured for samples collected with a van Dorn bottle. Chlorophyll a samples were treated and analyzed according to the method of Lorenzen (1967). Photosynthesis was measured by the oxygen evolution method. Samples were siphoned into three BOD bottles, one opaque and two translucent, and suspended at their original depths. After about 8 hours, they were retrieved and analyzed for oxygen with an oxygen meter.* Differences in concentrations of oxygen between the opaque and translucent bottles were measures of photosynthesis. Vertical distributions of zooplankton were measured for samples collected with a sewage sampler and concentrated with a No. 20 mesh plankton bucket.

During each routine experiment, natural populations of algae with different concentrations of zooplankton were enclosed in aquariums that were

Figure 1

Bathymetry of Westhampton Lake, Richmond, Virginia.



suspended in the lake. Each aquarium was a cylinder 3 feet in diameter and 3 feet in length. It consisted of polyethylene sides, a plexiglass bottom, and an upper rim buoyed at the surface with styrofoam. The aquariums were filled with surface water from the lake and anchored in position. They were filled and suspended in pairs – one pair during the day (day aquariums) to exclude zooplankton that migrated out of surface waters during the day, and one pair during the night (night aquariums) to include zooplankton that migrated into surface waters at night.

Samples were taken from the upper 1.5 feet from inside and outside the aquariums for several days. Zooplankton were collected every 3 hours beginning at different times on different days so that all 24 hours of the day were represented during each experiment. Samples for photosynthesis, chlorophyll a, and algal cell counts were collected at 0800 on each day of an experiment.

Zooplankton were strained from one liter of water with a No. 20 mesh plankton bucket, rinsed from the bucket, preserved with formalin, and counted under a dissecting microscope. Photosynthesis was measured by the oxygen evolution method described above. These samples, however, were placed on a rotating rack in an incubator at a temperature of 27°C, which was about the average lake temperature, and light intensity of 800 foot-candles, which was within the range in the upper 3 feet of the lake. Chlorophyll a was measured according to the method of Lorenzen (1967). Cell counts of algae were made from 40-milliliter samples of lake water treated with Lugol's iodine. Subsamples were placed in a Palmer chamber and analyzed under a compound microscope.

RESULTS AND DISCUSSION

Temperature and Light

The average temperature of the lake was the same, 29°C, down to a depth of six feet and decreased to 20°C at a depth of nine feet (Figure 2). The intensity of light was attenuated to 0% incident radiation by a depth of six feet.

The temperature inside and outside the aquariums was the same (Table I). Light intensities, however, were 2 to 8% lower inside than outside the aquariums. The lower intensities inside the aquariums resulted from scattering and absorption of light by the polyethylene sides of the aquariums, approximately 3%, and shading by buoys and materials that adhered to the sides of the aquariums.

Table I

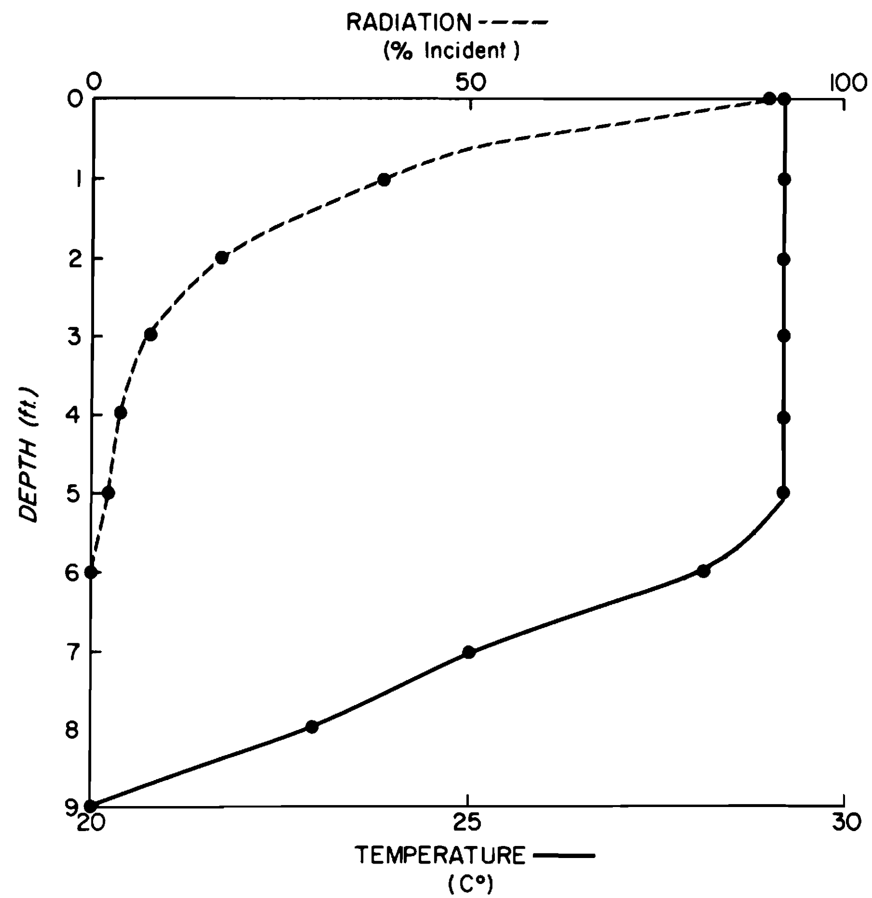
Average temperatures and intensities of light at various depths inside and outside aquariums.

Depth, ft	Temperature, C		Intensity of Light, % incident	
	Inside	Outside	Inside	Outside
0	29	29	83	87
1	29	29	31	39
2	29	29	10	17
3	29	29	5	7
4	–	29	–	4
5	–	29	–	2
6	–	28	–	0
7	–	25	–	0
8	–	23	–	0
9	–	20	–	0

Readings were taken one to several days after aquariums were suspended in the lake during summer of 1968.

Figure 2

Temperatures and intensities of light at various depths in Westhampton Lake. Measurements taken near deepest portion of the lake during summer of 1968. Average values given.



Chlorophyll a and Photosynthesis at Various Depths

Chlorophyll a was homogeneously distributed within the upper three feet of the lake (Figure 3). It consistently increased between four and seven feet. The average concentration of chlorophyll a was greatest at five feet. The increase in chlorophyll a at middle depths coincided with the decline in temperatures at those depths. Algae produced within the surface waters most likely sank toward the middle depths and were retained there in the denser water.

Photosynthesis was greatest at the surface. Secondary increases in photosynthesis at middle depths coincided with increased chlorophyll a at these depths. Algae at middle depths, therefore, were not all dead. Their low rates of photosynthesis probably resulted from the low intensities of light to which they were exposed.

Samples for routine experiments were taken from the upper 1.5 feet. The above data show that these samples included algae which underwent about 60% of the photosynthesis in the lake.

Photosynthesis Inside and Outside Aquariums

Photosynthetic rates varied nearly 20-fold throughout the summer (Figure 4). They were low in early July, reached a maximum in early August, and declined during the latter part of August. The rates were slightly greater inside than outside the aquariums, but there was no significant difference between the rates within the day and night aquariums (Table II).

Table II

Rates of photosynthesis (ppm O_2 hr^{-1}) inside and outside aquariums.

	Outside		Inside			
			Day Aquarium		Night Aquarium	
	Mean	SD*	Mean	SD	Mean	SD
Rates	0.57	0.24	0.51	0.24	0.50	0.27

Measurements taken throughout summer of 1969.
*Standard Deviation

The photosynthetic rates were significantly related to photosynthetic efficiency, photosynthesis per unit chlorophyll ($r = 0.64$, $p < 0.05$). The efficiencies were low in early July, reached their greatest values in early August, and declined throughout the latter part of August (Figure 5). The photosynthetic rates were not significantly related to concentrations of chlorophyll a.

Algal Cell Concentration

Algae belonging to the Chlorophyta were abundant throughout August (Table III). Those belonging to the Cyanophyta were abundant in early and middle August, but decreased during late August. Algae belonging to the Chrysophyta, mostly diatoms, increased from early to middle August and decreased during late August.

From August 5 to 8 an increase in cell numbers coincided with increased photosynthesis and photosynthetic efficiency. The largest gains in cells occurred in *Golenkinia* sp., diatoms, and *Anabaena spiroides*. Cell numbers decreased in most species between August 12 and 15. During this time, photosynthesis also decreased and photosynthetic efficiency remained relatively constant. The greatest decreases occurred in *Golenkinia* sp. and *A. spiroides*, and greatest increases occurred among diatoms. Between August 26 and 28, most species increased in the day aquariums and decreased in the night aquariums. In the day aquariums, the greatest increases occurred for the Chlorophyta and the greatest decreases occurred for small diatoms. In night aquariums, the greatest decrease occurred among diatoms and *Staurastrum* sp.

Abundance of Zooplankton Inside and Outside Aquariums

The most abundant zooplankton were rotifers of the genera *Polyarthra, Keratella*, and *Brachionus*. Copepods, almost wholly *Mesocyclops edax*, were next in abundance. Cladocerans, mostly *Daphnia ambigua* and *Bosmina coregoni*, were the least abundant.

Outside the aquariums, the concentrations of rotifers varied nearly 30-fold (Figure 6). They were low early in July, reached a maximum early in August, and declined throughout the latter part of August. The concentrations of copepodid and adult copepods followed a similar trend, but increased during the latter part of August. The concentrations of nauplii (the youngest larvae

Figure 3

Concentrations of chlorophyll a and photosynthetic rates at various depths in Westhampton Lake. Measurements taken near the deepest portion of the lake during summer of 1968. Average values given.

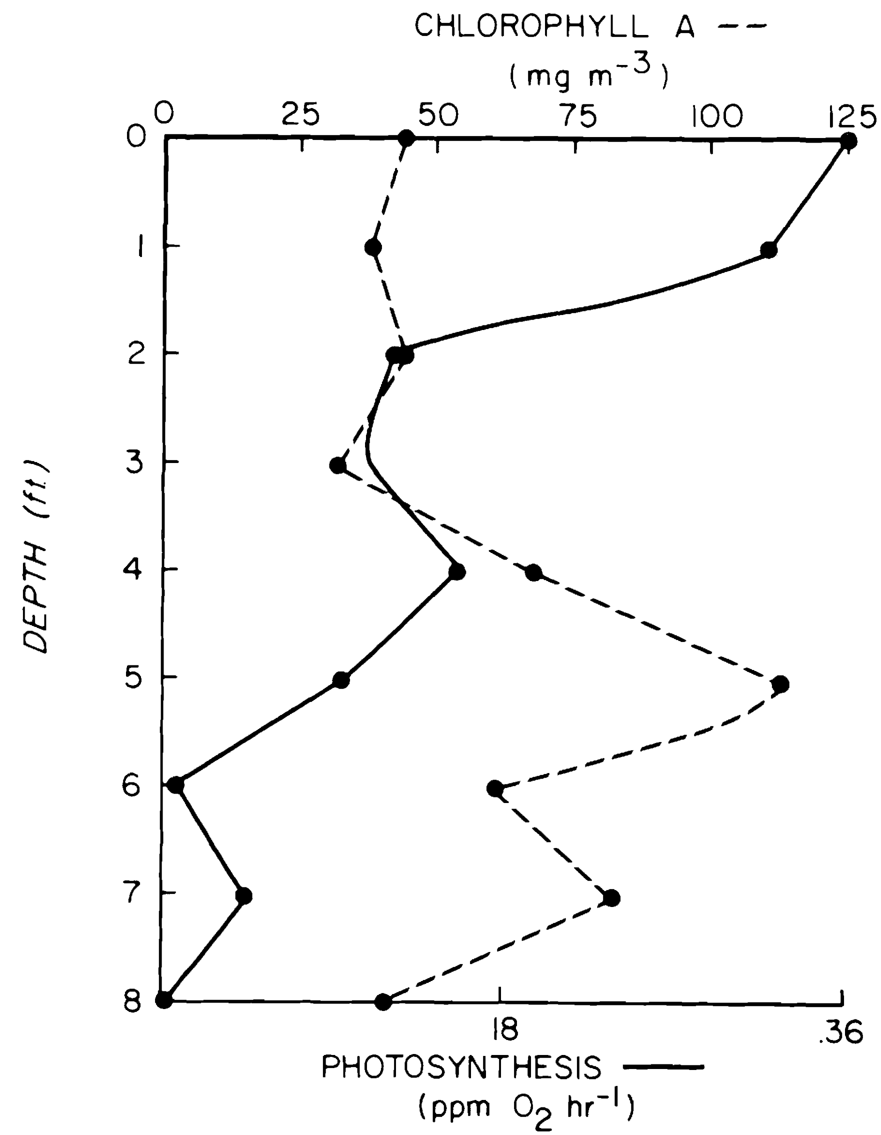


Figure 4

Rates of photosynthesis on various dates during the summer of 1969. Measurements are of gross photosynthesis of samples taken from upper 1.5 feet and held in incubator.

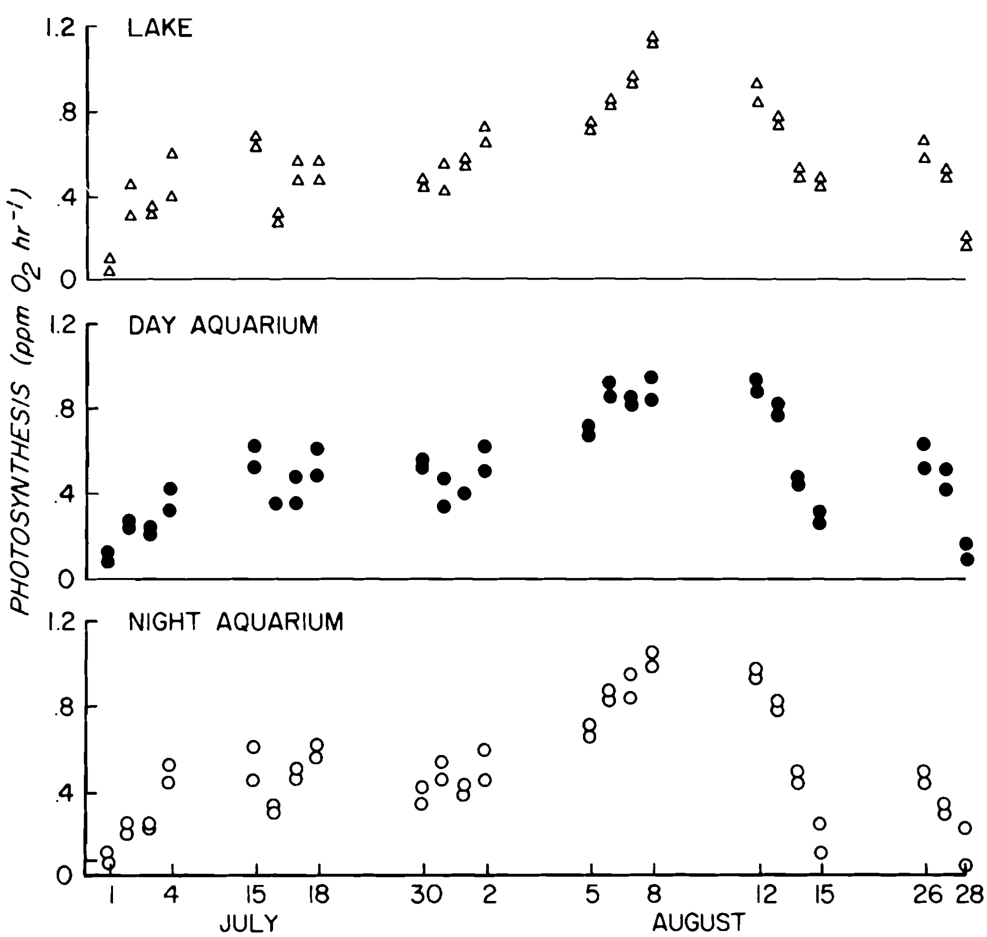


Table III

Concentrations of algae (number of cells and colonies ml-1) in day and night aquariums.

	Experiment I				Experiment II				Experiment III			
	August 5		August 8		August 12		August 15		August 26		August 28	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Chlorophyta												
Closterium	500	0	620	0	120	120	0	360	0	360	120	0
Eudorina	380	120	240	500	500	1400	0	240	1260	360	420	640
Gleocystis	0	0	0	0	1140	0	500	380	0	1280	1140	500
Golenkinia	9400	9540	27760	13620	3560	4960	120	700	2920	5720	5720	4840
Pandorina	1400	1140	1880	2140	1000	1280	620	500	1000	620	420	900
Pediastrum	3020	1260	3680	2280	1280	1920	1780	1800	1280	3180	2300	2560
Scenedesmus	2020	1520	900	1260	2440	4420	1920	2300	3440	4860	4820	2920
Staurastrum	2780	3440	2400	360	1160	1280	1640	1280	1020	4180	1520	1400
Euglenophyta												
Phacus	120	0	0	0	500	0	120	420	240	240	360	120
Trachelomonas	240	1780	380	0	240	0	240	120	360	0	900	240
Cyanophyta												
Anabaena	2260	2040	4200	3820	3680	4820	640	1160	0	0	240	120
Chrysophyta												
Lg pennate*	1780	2680	3420	3440	1140	900	1800	900	2280	2420	2160	1000
Sm pennate**	1280	1520	12600	3160	9140	6620	43880	27580	9020	9160	4080	4320
Centrate	240	0	2280	2680	3560	11440	9920	5560	5580	6620	6700	3680

*Large pennate diatom, length greater than 5 μ
** Small pennate diatom, length less than 5 μ

of copepods) varied only three-fold, and reached a maximum in the middle of August. The concentrations of cladocerans were high early in July, reached a minimum in the middle of July, and increased to a maximum during late August.

Inside the aquariums, rotifers were slightly more concentrated in the day than in the night aquariums (Table IV). The other zooplankton were more concentrated in the night than in the day aquariums. Compared with concentrations of zooplankton outside the aquariums, the differences between concentrations in the day and night aquariums were quite appreciable. They were 10% for rotifers, 65% for nauplii, 54% for adult and copepodid copepods, and 86% for cladocerans. Significant effects of zooplankton on the algae in the lake, therefore, should have been possible to detect by comparisons between the day and night aquariums.

Table IV

Average concentrations of zooplankton (number liter^{-1}) inside and outside aquariums.

Zooplankton	Outside	Inside	
		Day Aquarium	Night Aquarium
Rotifers	839	1,238	1,148
Copepods			
Nauplii	32	15	36
Copepodids and Adults	13	6	13
Cladocerans	14	3	15

Samples taken during summer of 1969.

The zooplankton showed two different patterns of vertical migration. Cladocerans and copepods underwent distinct migrations into surface water during the night and toward greater depths during the day (Figure 7). Such a pattern is common among crustaceans (Bainbridge, 1960). Rotifers showed no consistent pattern of migrations, and occasionally were more abundant at the surface during midday than at night and early morning. The migrations of

Figure 5

Rates of photosynthesis per unit chlorophyll a on various dates during the summer of 1969. Samples taken from upper 1.5 feet inside and outside aquariums.

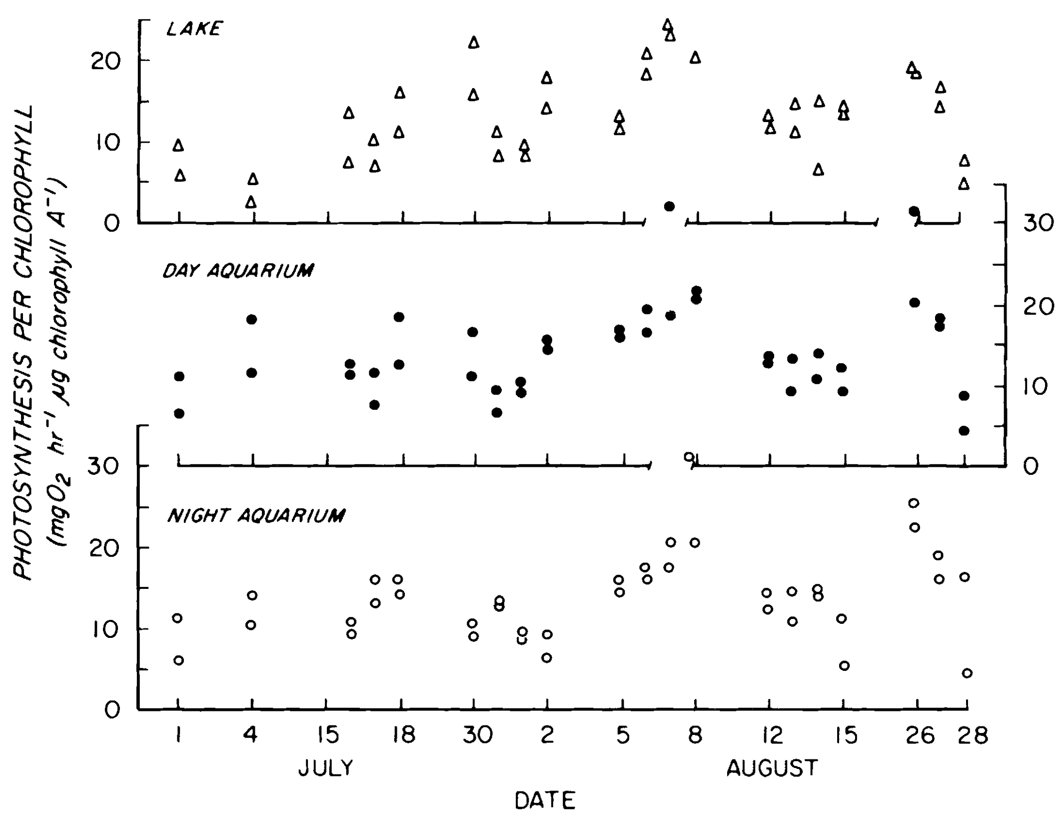


Figure 6

Concentrations of zooplankton outside aquariums. Samples taken from upper 1.5 feet of lake during summer of 1969.

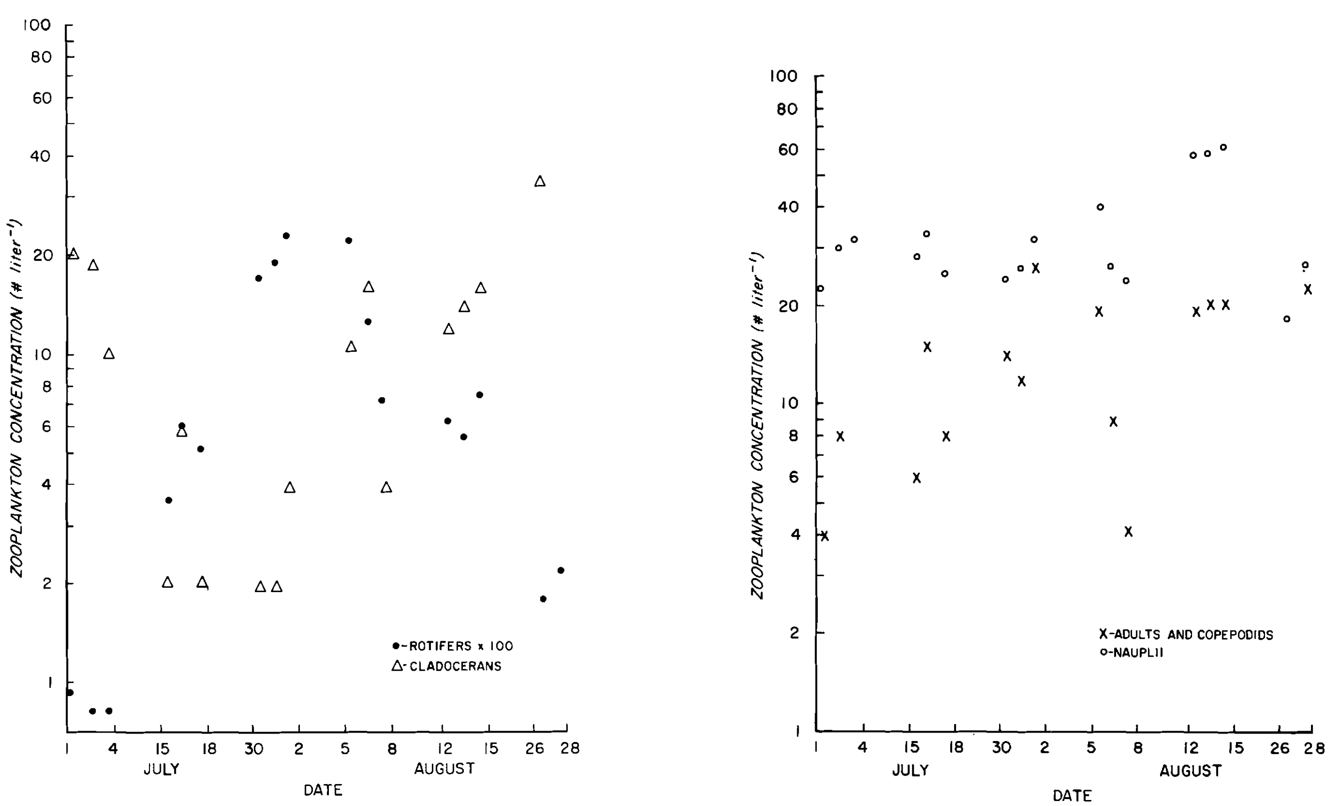
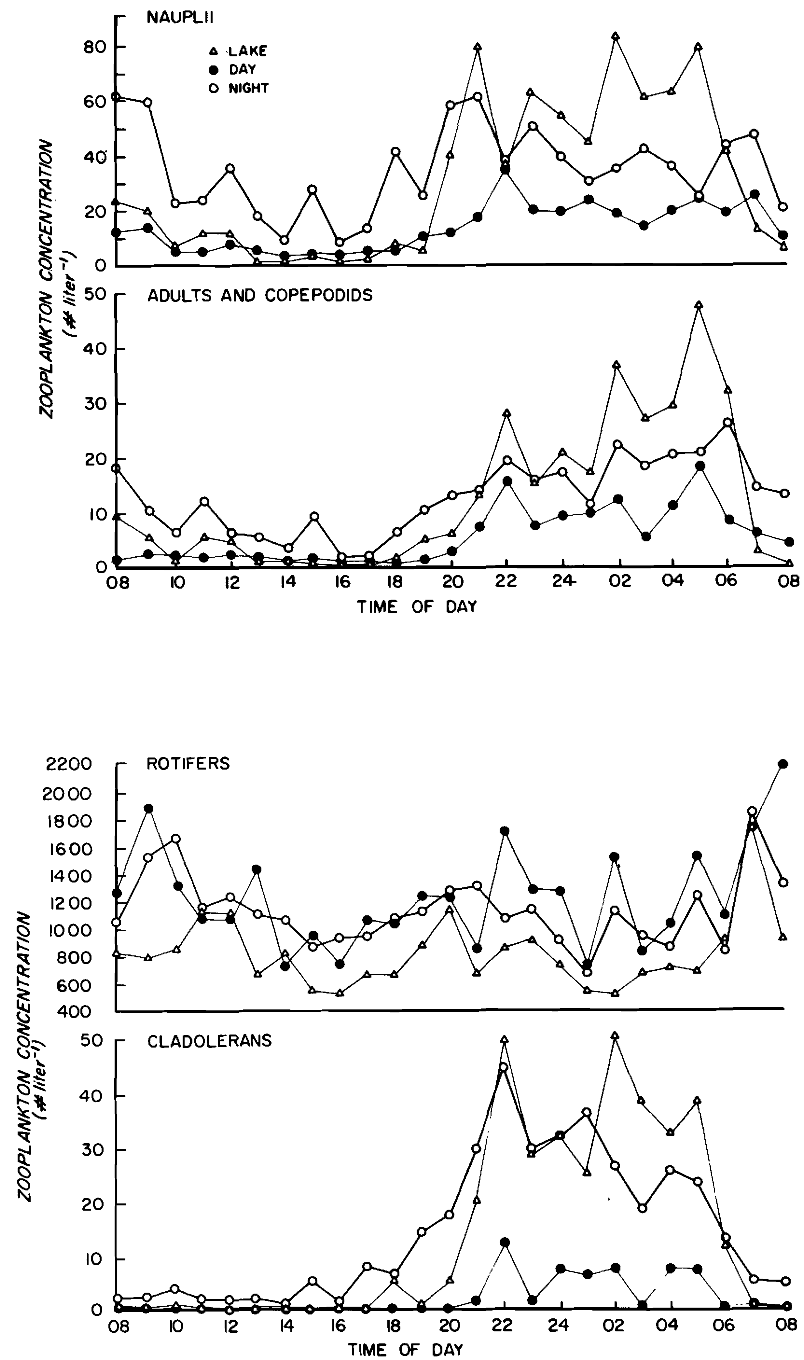


Figure 7

Concentrations of zooplankton during various times of the day inside and outside aquariums. Data represents average values for the summer of 1969. Samples taken from upper 1.5 feet.



the zooplankton inside and outside the aquariums were similar to one another. Such similarity indicated that the behavior of the zooplankton was not adversely influenced by confinement of the animals within the aquariums.

Effects of Zooplankton on Photosynthesis

Despite the differences between the concentrations of zooplankton in the day and night aquariums, photosynthetic rates inside the day and night aquariums were remarkably similar to one another. Such similarities indicated that the effects of zooplankton on photosynthesis were small compared with effects of other factors. In order to detect possible effects of the zooplankton, statistical techniques of analysis of covariance and analysis of variance were used (Dixon and Massey, 1957). These techniques made it possible to estimate the relationships between the concentrations of zooplankton and the changes in photosynthetic rate inside the four aquariums, two day and two night, over each day. These analyses showed that of the zooplankton examined, rotifers, nauplii, copepodid and adult copepods, and cladocerans, only rotifers had a significant effect on photosynthesis (Tables V and VI). Rotifers at a concentration of 1,000 animals liter^{-1}, about the average, were estimated to decrease photosynthesis 0.125 ppm O_2 hr^{-1} daily. This value represents 22% of the average photosynthesis and 78% of the average absolute value of daily change in photosynthesis.

Table V

Analysis of covariance of daily change in rates of photosynthesis (ppm O_2 hr^{-1} day^{-1}) and concentration of rotifers (number ml^{-1}) inside aquariums.

Source	d.f.*	Σx^2	Σxy	Σy^2
Inside	51	1,158.0	-5.4	0.23
Among	16	43,053.0	99.0	1.91
Total	67	44,211.0	93.6	2.14

Concentrations of rotifers are the cumulative values of 25 samples over a day. Measurements taken throughout summer of 1969.

*degree of freedom

Table VI

Analysis of variance of regression between daily changes in photosynthesis and concentrations of roifers inside aquariums.

Source	d.f.	s.s.	m.s.	F
Total	51	0.23	–	–
Regression	1	0.02	0.02*	5.0
Error	50	0.21	0.004	–

*Statistically Significant: $F_{0.95}$ (1,50) = 4.04

Analysis of covariance and analysis of variance showed no significant relationship between daily changes in photosynthetic efficiency and concentration of zooplankton.

The strong relationship between rotifers and photosynthesis and the poor relationship between other zooplankton and photosynthesis are surprising in light of several previous studies of zooplankton feeding. According to Nauwerk (1959), the filtering rates of rotifers are about 0.04 ml animal^{-1} day^{-1}. Based on this value, rotifers at a concentration of 1,000 animals liter^{-1} should decrease algae by 4% within that liter. The present study indicated that the rotifers decreased photosynthesis 5 times faster than would be predicted for feeding rates alone. Filtering rates by the other zooplankton, cladocerans, and nauplii, which may feed on algae, are about 1.0 ml animal^{-1} day^{-1} (Jorgensen, 1966). The older copepods probably are carnivores (Fryer, 1957). Based on this value, cladocerans and nauplii at a concentration of 46 animals liter^{-1}, the average, should have decreased algae by 5% daily within that liter. The present study demonstrated, however, no significant effect of these zooplankton on photosynthesis. One possible explanation for the poor relation between cladocerans, nauplii, and photosynthesis is that these zooplankton did not feed only on algae within the natural habitat. Evidence in support of such an explanation has been presented by Nauwerk (1963) and more recently by Gliwicz (1968), who showed that the bulk of food of natural zooplankton communities was not algae, but rather bacteria and detritus.

Effects of Zooplankton on Kinds of Algae

The effects of zooplankton on the various kinds of algae are indicated in Table VII. The table shows the differences between the concentrations of zooplankton and changes in cell concentrations inside the day and night aquariums. Positive values for cell concentrations occurred when the cells increased more or decreased less in the day than night aquariums. Positive values for zooplankton concentrations occurred when zooplankton were more abundant in the day than night aquariums.

Copepods and cladocerans were less abundant in the day than night aquariums on all three occasions. Rotifers were less abundant in the day aquariums during Experiment II, from August 26 to 28. Only three kinds of algae, *Golenkinia* sp., *Staurastrum* sp., and pennate diatoms had positive values on all three occasions. Cladocerans and copepods appear, therefore, to decrease the concentrations of cells of these three kinds of algae. The sizes of these algae are within the range eaten, but not within the range selected by some cladocerans according to studies by Bogatova (1965) and Burns (1969).

Only two kinds of algae, *Eudorina* sp. and *Pandorina* sp., had negative values during the first and last experiments and a positive value during the middle experiment. Rotifers, therefore, appear to decrease the cell concentrations of these algae. Feeding alone probably does not account for this decrease. Gliwicz (1968) showed that zooplankton communities which contain relatively large proportions of rotifers select algae within the size range of 3 to 6 μ. The above algae have colony sizes between 50 and 100 μ.

Rain and Photosynthesis

As mentioned above, variations in photosynthesis were not clearly related to most zooplankton; the main concern of this study. An environmental factor which could have influenced photosynthesis was rain. It could have decreased photosynthesis by draining algae from the lake. It could have increased photosynthesis by mixing the highly concentrated algae at 4 feet into the surface and/or by adding nutrients required for growth of the algae.

A statistical analysis, Kendall rank correlation (Siegel, 1956), showed that photosynthesis in Westhampton Lake was significantly correlated with rain (Table VIII). Photosynthesis increased for several days following rain. Such an increase probably did not result from mixing of the algae. If mixing were the cause, photosynthesis would have been related to chlorophyll

Table VII

Differences in the concentrations of zooplankton (number liter^{-1}) and changes in the concentrations of algal cells (number ml^{-1}) between the day and night aquariums.

	Algae		
	Experiment I	Experiment II	Experiment III
Chlorophyta			
Closterium	+120	-360	+480
Eudorina	-520	+660	-1120
Gleocystis	0	-1020	+1920
Golenkinia	+14280	+820	+3680
Pandorina	-520	+400	-860
Pediastrum	-360	+620	+1640
Scenesdesmus	-860	+1600	+3320
Staurastrum	+2700	+480	+3280
Euglenophyta			
Phacus	-120	-800	+240
Trachelomonas	+1920	-120	+300
Cyanophyta			
Anabaena	+160	+620	+120
Chrysophyta			
Lg pennate	+880	+660	+1300
Sm pennate	+9680	+13780	-100
Centrate	-640	+12240	+4060
	Zooplankton		
Rotifers	+1400	-5600	+400
Copepods			
Nauplii	-920	-240	-400
Copepodids and Adults	-280	-80	-160
Cladocerans	-120	-120	-600

Positive values for algae indicate that algae increased more or decreased less in the day than night aquariums. Positive values for zooplankton indicate that the zooplankton were more concentrated in the day than night aquariums.

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