PRIMARY PHOTOSYNTHETIC PRODUCTIVITY OF TWO MICHIGAN PONDS

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ABSTRACT

PRIMARY PHOTOSYNTHETIC PRODUCTIVITY
OF TWO MICHIGAN PONDS

By

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The primary photosynthetic productivity of two ponds was studied. Two methods of estimating the productivities of the ponds were employed. First the changes in the dissolved oxygen content of the waters were monitored and the resulting data converted to productivity values in terms of gm. cal./m^2/day. Secondly, the three groups of primary producers, plankton, macrophytes, and periphyton, were sampled periodically to determine their role in the total photosynthetic production of each pond.

There existed a close relationship between the light intensity and the rate of primary production. Periods of cloudiness brought about a drop in the primary production while periods of higher light intensities resulted in an increase in the productivity of the ponds.

The efficiency with which the photosynthetic organisms fixed solar energy was found to decrease with increasing light intensities up to a saturation level of light intensity.

In both ponds primary production slightly exceeded community respiration, thereby classifying them as autotrophic communities.

A probable relationship existed between macrophyte and periphyton growth with the former inhibiting the growth of the latter by means of nutrient limitations or direct inhibiting action.

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By

John R. Gehring

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TABLE OF CONTENTS

TABLE OF CONTENTS--continued Page

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The problem of determining the primary productivity of aquatic ecosystems has been foremost in the minds of many aquatic biologists. Although scientific investigation into this field of aquatic biology has only relatively recently begun a considerable amount of data has been accumulated and new techniques have been developed.

The study of primary productivity in ponds has not received the attention of investigators as have some of the other aquatic habitats such as the open seas.

The primary objectives of this investigation were to measure the primary productivity of two ponds by implementing two techniques, one of which is relatively new and the other being somewhat older. The former method, that of measuring the dissolved oxygen content of the water over a period of time, will give an index of the total primary productivity of the ponds and the latter method, that of sampling the standing crops of primary producers will identify which groups of primary producers are the dominant ones. Environmental factors were also investigated and their effect upon primary productivity determined.

LITERATURE REVIEW

Energy fixation and transfer in an aquatic ecosystem is complex and difficult to quantify. The study of the first step in the bio-energetic cycle involving fixation of solar energy by attached algae (periphyton), planktonic algae, and higher aquatic plants (macrophytes) is a somewhat less formidable task.

Saijo and Ichimura (1961) credit Thieneman as being the first modern author to attempt a critical assessment of the concept of primary biological productivity. He defined primary production as the total amount of organic matter produced in a given space during a given period.

According to Saijo and Ichimura (op. cit.) Lohmann made one of the first attempts to estimate primary production by noting changes in a standing crop, taking into account rates of reproduction and the effects of grazing. This method was followed by many well-known limnologists in the 1940's such as Juday and Lindemann, who studied energy flow through producer and consumer levels of the aquatic ecosystem.

The majority of research conducted with small ponds has been designed to measure various physical and chemical

parameters. Changes in these parameters have been associated with changes in biological activity; however, relatively few attempts were made until recent years to quantify the results.

Birge and Juday (1914) observed that heavy concentrations of photosynthetic organisms produced a substantial increase in the pH of the water; however, no effort was made to calculate productivity on the basis of this change in alkalinity. Phillip (1927) observed pH fluctuations in a lake thought to be caused by vegetation in the water, but again no attempt was made to calculate photosynthetic productivity.

Oxygen

Calculation of photosynthetic rates from changes in the oxygen content of waters followed the use of changes in pH and carbon dioxide by several years.

The original idea of estimating production from the photosynthetic rate of phytoplankton was first introduced by Gaarder and Gran (1927). The light and dark bottle method which they used, though usually giving overestimates of gross production, has been widely employed by researchers.

Wiebe (1931) recorded data which showed a daily increase from 1.66 ppm. oxygen to 16.9 ppm. oxygen and believed that the increases were roughly proportional to

the amount of algae present. Whitney (1942) measured pH and oxygen changes in small ponds and a stream and proposed that these fluctuations were dependent upon photosynthetic and respiratory activity of the aquatic organisms.

The use of diurnal oxygen pulses to determine the rates of primary or photosynthetic productivity became widespread after publication of work by Odum (1956). He outlined a method whereby diurnal oxygen curves could be analyzed and the component rates of production, respiration and diffusion, determined. Ryther (1956), Verduin (1956), Odum and Hoskin (1957), Odum and Hoskin (1958), Odum and Wilson (1962), and Duffer and Dorris (1966) are a few of those who have refined techniques and added to the data already accumulated. Saijo and Ichimura (1961) review various techniques for measuring primary production in both fresh and salt waters. Doty (1961) gives a bibliography of articles pertinent to primary production in both fresh and salt water.

The majority of research dealing with productivity in ponds has been directed at estimating fish growth and related topics of fish management. More recently, however, researchers have made an attempt to estimate the rates of primary production in ponds and other smaller bodies of water.

Copeland and Whitworth (1963) and Butler (1964) both used diurnal oxygen curves to measure the primary productivity of two different sets of Oklahoma farm ponds. Knight,

Ball and Hooper (1962) estimated the primary production of the three groups of primary producers--plankton, periphyton, and macrophytes--in four Michigan ponds.

Manual sampling and testing of various parameters such as oxygen concentrations are very time consuming and impossible to maintain on an around the clock basis. What was needed was a robot-monitor device. One of the first robot monitors was the original conception of Edward J. Cleary (1967) of the Ohio River Valley Water Sanitation Commission. His investigations were begun in 1956 and by 1960 a monitor designed to measure ten different water quality characteristics was placed in operation on the Ohio river. Availability of such monitoring devices will undoubtedly be a tremendous aid to the production biologist of the future.

Periphyton

Periphyton is defined by Odum (1953) as: "organisms both plant and animal attached or clinging to stems and leaves of rooted plants or other surfaces projecting above the bottom." In shallow ponds such as the ones used in this study the littoral zone extends to all depths. Aquatic habitats, within which the littoral zone is all encompassing frequently possess periphyton communities that play a very important role as primary producers (Wetzel, 1964).

Cooke (1956) credits a 1915 Swedish publication as giving the first description of a specific technique whereby artificial substrates could be introduced into the water for the collection of aquatic organisms.

The majority of the papers written that incorporated the artificial substrate method were primarily concerned with taxonomy studies and surveys of various aquatic communities (Bissonnette, 1930). Ecological studies were also undertaken to determine the distribution of various algal and other life forms using the artificial substrate as a collection device (Miller, 1936).

Extensive reviews of studies conducted that made use of artificial substrates as a collection device have been compiled by Cooke (1956) and Sladecokova (1962).

One of the first researchers that used artificial substrates in estimating productivity was Newcomb (1949). He reported that the organic matter collected from vertically and horizontally placed substrates was in the ratio of 1 to 6.6 respectively. In view of these findings, Newcomb (1950) stated that horizontal placement of substrates appeared to be the most advantageous. Newcomb (1949) noted that most of the evidence tended to indicate that the growth forms present on the glass artificial substrates were representative of those occurring on the natural substrates such as aquatic plants and detritus.

The relationship between chlorophyll concentrations and photosynthetic productivity led early workers,

especially marine researchers, to develop methods of phytopigment extraction. Kreps and Verjbinskaya (1930) were among the first to develop a suitable technique. They were later followed by Harvey (1934) and Manning and Juday (1941) whose works further sophisticated phytopigment extraction methods and, in the case of Manning and Juday (1941), applied these methods towards the estimation of primary productivity.

The application of the artificial substrate method to determining periphyton productivity is dependent upon the ability of the worker to quantitatively assess the amount of organic matter accumulated on the substrate. Numerous methods have been employed. Direct microscopic observations and counting of the material collected has been widely used in the past. When dense growths of periphyton make direct observations impossible, the growth has been scraped from the substrate and various volume and weight measurements have been made.

More recently, however, the use of phytopigment extracts have been employed to estimate the amounts of periphyton growing on artificial substrates. Grzenda and Brehmer (1960) credit Hooper, Ball, and Hayne with being the first to estimate periphyton production by combining the artificial substrate and phytopigment extraction methods. Grzenda and Brehmer (1960) found that a linear relationship existed between a given number of phytopigment units and the organic

weight of the periphyton from which the phytopigments were extracted. It was found that one regression was capable of making year-round predictions of organic periphyton weight from chlorophyll absorbency readings. This technique represents a significant advancement which enabled succeeding workers to more rapidly assess periphyton productivity.

The problem of determining what portion of the periphyton growth curve on artificial substrates most precisely represents that growth which occurs on natural substrates is discussed in a paper by Kevern, Wilhm and Van Dyne (1966). They discuss a method whereby measurement of the standing crop of periphyton over a period of time provides an instantaneous growth rate which is comparable to the growth of periphyton actually taking place on the natural substrates.

Macrophytes

The initial research, dealing with higher aquatic plants in America, is credited by Pieters (1894) to Professor Douglas Campbell who conducted a study of aquatic plant distribution in the Detroit river. Pieters (1894) also sampled aquatic plants in the Detroit River by pulling a drag with a sailboat which scooped plants from the river bottom. Denniston (1922) worked with higher aquatic plants in Lake Mendota but also confined his work, as did the majority of his contemporaries, to taxonomic surveys and

distribution studies.

Rickett (1920) was one of the first to make a quantitative survey of higher aquatic flora. Working on Lake Mendota he estimated the total standing crop of various higher aquatic species.

Primary productivity estimates of higher aquatic plants have only been made during the recent past. Penfound (1956) measured the productivity of some larger aquatic plants and compared their productivities with those of other plant forms in other ecosystems. Odum (1957), Smally (1959), Knight, Ball, and Hooper (1962), and Vannote (1964) are a few of those who have contributed much needed data on the productivity of different species of aquatic plants in a wide variety of aquatic habitats.

Plankton

Planktonic organisms have long been studied from a taxonomic aspect. Birge and Juday (1922) credit Hensen's work of 1882 as being the first involving plankton to be of a quantitative nature.

Birge and Juday (1922) conducted extensive research on the planktonic organisms of several Wisconsin lakes. Their work, being quantitative in substance, enabled them to assess the primary productivity of the planktonic community. Many other workers such as Riley (1939) contributed more data and refined techniques developed by Birge and Juday.

The majority of these early workers measured the standing crop of planktonic organisms and then estimated the rate of population turnover before computing productivity indices. More recently attempts by such workers as Manning and Juday (1941) have been made to utilize the chlorophyll content of water as an index of phytoplankton productivity. The most convenient and reliable method for the estimation of phytoplankton productivity has proven to be the carbon-14 method introduced by Steeman-Nielson (1952).

DESCRIPTION OF STUDY AREA

This project was conducted at the Lake City Experimental Station which is located in the west central area of Missaukee County two miles south of Lake City, Michigan. The station is owned by Michigan State University, and here research projects are conducted by the College of Agriculture.

The area for study consisted of four experimental ponds which were constructed near the headwaters of Mosquito Creek. A dam, located west of the ponds on the stream, forms a six and one-half acre reservoir which is used for filling the ponds. Each pond has a separate inlet and outlet and can be filled and drained independently into the creek which flows below and behind the ponds.

The ponds were excavated in an area of sandy soil. However, since their formation (1943-1945), their bottoms have become covered with several inches of small twigs, mud, and detritus. The land surrounding the ponds is flat and covered with grass which holds surface runoff to a minimum.

The ponds are designated alphabetically A, B, C, D from west to east. The ponds used in this study are B

and D. Both ponds have an average depth of one meter. Pond B has an area of 0.43 acres and pond D an area of 0.18 acres.

Figure 1 shows the positioning of the ponds and laboratory areas.

Figure 1. A map of the Lake City experimental ponds.

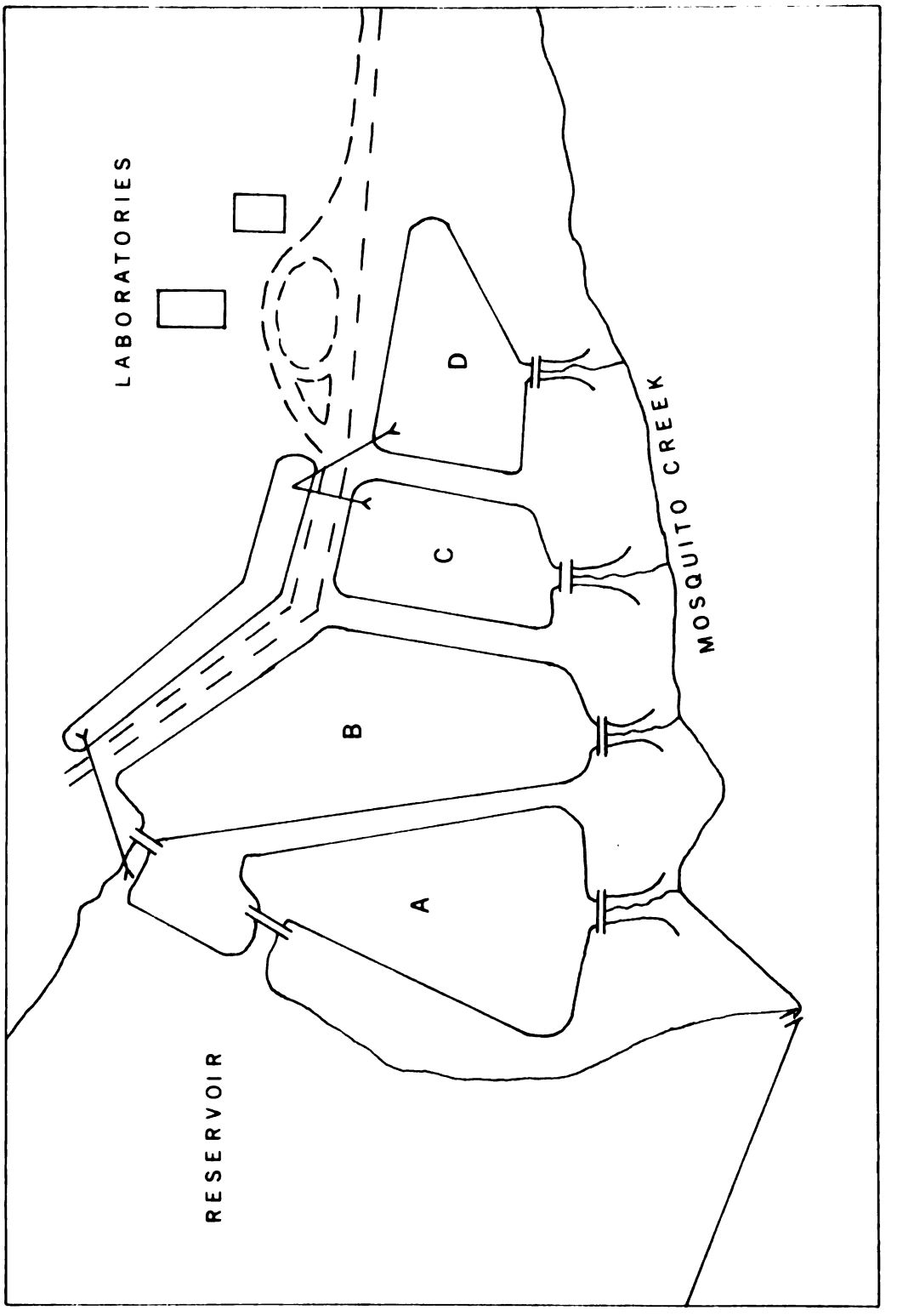

Figure 1

TECHNIQUES AND EQUIPMENT

Physical Measurements

Oxygen Monitoring System

Ponds B and D used in this study were located south of the building where laboratory work was conducted. In order to continuously monitor changes occurring within the two ponds, water from them was pumped into the laboratory. Installed in each pond was a Little Giant Pump housed in a square wire cage which supported it one meter below the surface. The wire mesh enclosure prevented small fish from obstructing the intake port of the pump. Water was pumped through 3/4 inch Tygon tubing into a cylindrical Plexiglass "submarine" located on a workbench in the laboratory. The top of the submarine was fitted with openings into which probes used to monitor various physical and chemical parameters could be inserted.

The dissolved oxygen content of the two ponds was measured continuously for seventy-eight days from July 1, 1965 through September 16, 1965. Beckman Oxygen Analyzers (Model 777) were used to monitor the dissolved oxygen content of the water. Oxygen concentrations in parts per million were recorded on Sargent MR and SR recorders.

Oxygen concentrations used for the calibration of the monitoring system were determined by the Alsterberg (azide) modification of the Winkler method, as given in Standard Methods for the Examination of Water, Sewage, and Industrial Wastes (APHA, AWWA, WPFC, 1960).

Each instrument was calibrated daily upon arrival at the laboratory and again at night before leaving the laboratory. Oxygen concentrations, as monitored in the laboratory, were the same as those found in the test ponds.

Solar Energy Measurement

Solar radiation in gram calories per centimeter squared was measured with an Eppley Pryheliometer, which was located on the west side of Pond D, and was recorded on a Bristol recorder.

Water Temperature

Water temperature in pond D was measured and recorded for weekly periods by a Taylor thermograph. The temperature probe was located in one meter of water and was covered with a wooden roof to prevent an increase in the recorded temperature due to insolation.

Gravimetric Measurements

All weighings were made on an analytical balance. When two consecutive readings of ± 0.5 mg. were obtained after

an interval of twelve hours, the sample was said to be at a constant weight.

Dry weight was assumed to be the weight of a sample after drying in an oven at 55°C. for twelve hours.

Organic weights (ash-free dry weight) were determined after sample ignition at 550°C. in a muffle furnace.

Calorimetry

The caloric content of the aquatic macrophytes was determined with a series 1300 Parr Oxygen Bomb Calorimeter.

Each sample analyzed for caloric content was first powdered with mortar and pestle then pressed into pellets and finally oven dried at 55°C. to a constant weight. The calorimetric procedures used were those outlined in Oxygen Bomb Calorimetry and Combustion Methods (Parr Instrument Company, 1960).

Pain (1965) suggested that endothermic reactions accompanying the combustion process would affect the determination of the caloric content of a sample when the biological materials possessed a high ash content. Corrections for this factor was made for all samples processed according to the method described by Pain (op. cit.).

Biological Measurements

Periphyton

A periphyton or aufwuchs community is composed primarily of non-planktonic epiphytic organisms which are found

growing on most exposed surface areas in an aquatic environment.

Periphyton production has been measured in several ways. The method chosen for use in this study is that of phytopigment analysis of periphyton collected upon artificial substrates.

Plexiglass shingles with dimensions of 5x2x$\frac{1}{4}$ inches and a total exposed surface area of 1.5 decimeters were used as the artificial substrates. The Plexiglass plates were attached to a horizontal rod by means of spring operated metal clips. The horizontal rod was in turn supported approximately one meter below the surface of the pond by a stake driven into the pond basin.

The study of periphyton production began with the placement of one rack of shingles in each pond. Each rack held twenty-four shingles which were placed in a horizontal position. Paired substrates were removed in the evening every four days until all the shingles had been removed from a rack. Twelve days after the first racks were placed in the ponds another similar set of racks was positioned in the ponds and the usual removal process was continued.

Periphyton shingles were removed from the pond with considerable care taken to avoid loss of the loose clinging growth. Upon removal from the pond, the shingles were placed in marked plastic freezer bags and put into a deep freeze. Freezing of the samples served a two-fold purpose. First large numbers of samples could be held and then

processed more efficiently at one time. Freezing also ruptures the algal cells thereby facilitating the removal of the plant pigments.

After freezing the periphyton was removed from the thawed substrate with a spatula. The shingles were then rinsed with 50 ml. of 95% ethanol and the periphyton-alcohol mixture was then transferred to a 2 oz. bottle. The phytopigment solution was allowed to remain in the dark for a minimum of forty-eight hours. The bottles were then taken out and shaken vigorously to ensure that the entire periphyton mass was adequately exposed to the alcohol and that all the chlorophyll was extracted. The bottles were then returned to the dark and allowed to settle for at least another 24 hours.

After settling, the bottles were removed and 25 ml. of the phytopigment extract was carefully pipetted into a colorimeter cell. The absorbency of the phytopigment solution was then measured, using a Klett-Summerson colorimeter equipped with a red filter (640-700 mu.). If at any time some of the algal cells were accidentally taken up or disturbed with the pipette, the sample was allowed to settle one day before another reading was attempted.

Experiments have shown that the relationship between absorbancy and phytopigment concentrations of 95% ethanol extracts is not linear above one-hundred units when read on a Klett-Summerson colorimeter. This deviation from the

Lambert-Beer law presented no problems with regard to this study as all instrument readings were well below one hundred.

All phytopigment units (optical density) were multiplied by 10^3 to avoid the use of a decimal point.

Algae Identification

Algae used for taxonomic purposes was collected on Plexiglass plates similar to those being used in determining periphyton productivity. The algae was scraped from the plates and stored in 95% ethanol for identification at a later date.

Identifications were made using a Wild phase contrast binocular microscope. Algae were examined from plates having colonization periods from eight to twenty-four days.

Macrophytes

The net primary productivity of the aquatic macrophytes was measured by employment of the harvest method.

The macrophytes were taken from randomly selected locations using a Petersen dredge which removed the vegetation from an area of 0.08 m^2. During the study period the higher aquatic vegetation was sampled twice in pond D and three times in pond B. Forty samples were removed during each sampling period. Each sample was washed until the mud, silt, sticks, and all other detritus was removed. The plants were then placed in an oven, dried at 55°C., and then weighed. This figure was recorded as dry weight.

Plankton

Planktonic organisms to be used in computation of productivity estimates were collected once per week throughout the entire study period. Water samples containing the plankton were collected from both test ponds at random locations and depths with a Kemmerer water sampler. The sixteen liter samples collected from each pond were removed at approximately 10 A.M. on each sampling day.

The water samples once obtained were passed through a revolving-bowl type Foerst electric centrifuge. The sixteen liter samples were centrifuged at a rate of four to six liters per hour. Welch (1948) reports that when operated at 20,000 r.p.m. 98 percent of the plankton will be removed plus 25 to 50 percent of the bacteria.

The planktonic organisms so collected were then placed in 50 ml. of 95 percent ethanol. The samples were later dried at 55°C. to a constant weight and then transferred to an electric furnace at 550°C. for 30 min. The difference in weight between the dry sample and the sample after ignition represents the organic weight of the plankton sample.

PRIMARY PRODUCTION

RESULTS AND DISCUSSION

Diurnal Oxygen Curves

Gross Primary Productivity

Diurnal oxygen curves for both ponds B and D were analyzed by computer and the component rates of primary productivity and community respiration were obtained.

Gross primary production is defined by Odum (1956) as "the sum of the net plant production and community respiration during the daytime." Net primary production, as used in this text, is defined by Odum (1953) as "the rate of storage of organic matter in plant tissues in excess of the respiratory utilization by the plants during the period of measurement."

Data from the entire study showed the gross primary productivity in pond B ranged between 1.42 and 6.71 gm. $O_2/m^2/day$ with a mean productivity of 3.73 gm. $O_2/m^2/day$. The gross primary productivity in pond D ranged between 0.56 and 7.18 gm. $O_2/m^2/day$ with a mean productivity of 3.03 gm. $O_2/m^2/day$. Rates of primary productivity for both ponds throughout the study period are illustrated in Figure 1.

Productivity values cited by other authors using diurnal oxygen curves and L-D bottle methods in similar environments

Figure 2. The gross photosynthetic productivity in the test ponds during the summer of 1965.

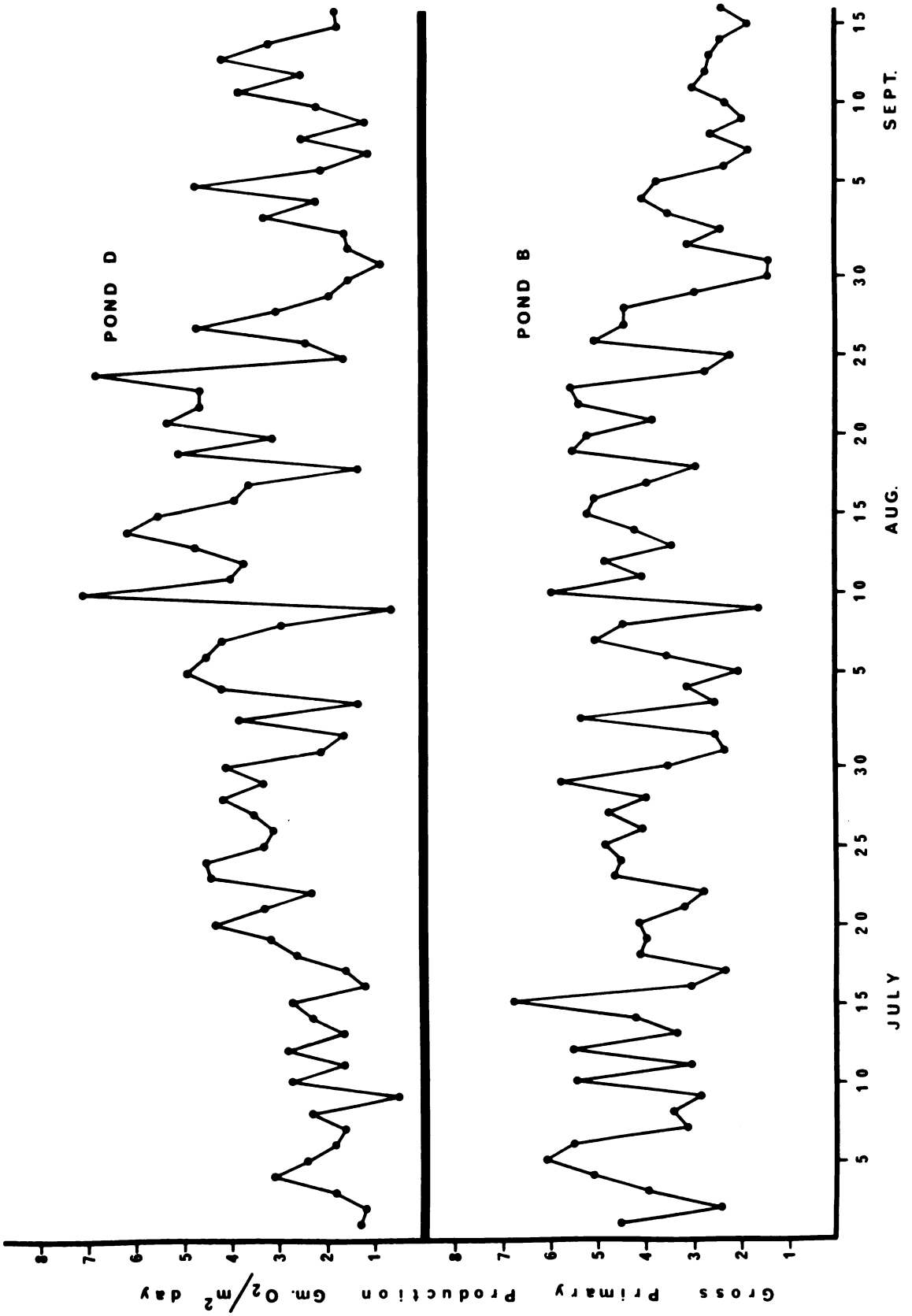
POND D
POND B
Gross Primary Production Gm. O_2/m^2 day
JULY
AUG.
SEPT.

Figure 2

are shown in Table I. Reference to Table I shows that the values of gross primary productivity for the Lake City ponds are in general agreement with values reported by other authors.

Inspection of Figure 1 indicates that there is a marked difference in the productivity of the two ponds during the beginning of the study period. The data revealed that the productivity of pond B was significantly greater than that of pond D as determined by a paired t-test of the productivity estimates for the first thirty-one days of the investigation (Table II). It is most probable that this difference in productivity was partially due to the removal of the higher aquatic plants (macrophytes) from pond D prior to the initiation of the study. Draining of the test pond would severely deplete the periphyton population which would also in turn contribute to the low productivity values observed in pond D.

The data also revealed that there was no significant difference between the productivity of the two ponds as determined by a paired t-test of the productivity estimates for the second thirty-one days of the study period (Table III). By the second month of study lush growths of higher aquatic plants, primarily Chara, had established themselves to an extensive extent over the bottom of pond D. The periphyton growth had also recovered from the initial draining and was now clinging to most of the available substrates.

TABLE I

PRODUCTIVITY ESTIMATES OF PONDS AND OTHER SMALL AQUATIC HABITATS

Author	Year	Habitat	Productivity $gm.O_2/m^2/day$
Butler	1964	Pond	2.4 - 16.1
Copeland and Whitworth	1963	Pond	4.4 - 27.4
Odum and Hoskin	1958	Tank	1.16
Copeland and Dorris	1962	Polluted Pond	23.4
Copeland, Butler and Shelton	1961	Pond	1.1 - 7.3
Hepher	1962	Pond	4.4 - 22.6
Minter and Copeland	1962	Pond	0.0 - 5.9

TABLE II

PAIRED t-TEST OF THE PRODUCTIVITIES OF PONDS B AND D DURING THE FIRST THIRTY-ONE DAYS OF STUDY

$N = 31$	$\Sigma d = 48.01$
$\Sigma d^2 = 114.79$	$(\Sigma d)^2 = 2304.96$
$s^2_d = 1.34$	$s^2_{\bar{d}} = 0.043$
$s_{\bar{d}} = 0.205$	$\bar{d} = 1.54$
$t = 7.55^*$	

*Significantly different at the 0.05 level (d.f. = 30).

TABLE III

PAIRED t-TEST OF THE PRODUCTIVITIES OF PONDS B AND D DURING THE SECOND THIRTY-ONE DAYS OF STUDY

$N = 31$	$\Sigma d = 6.07$
$\Sigma d^2 = 67.59$	$(\Sigma d)^2 = 36.84$
$s^2_d = 2.21$	$s^2_{\bar{d}} = 0.712$
$s_{\bar{d}} = 0.845$	$\bar{d} = 0.19$
$t = 0.22^*$	

*Not significantly different at the 0.50 level (d.f. = 30).

The noticeable increase in the abundance of these two important groups of primary producers most probably accounts for the increase in productivity of pond D during the second thirty-one days of measurement.

The Role of Light, Primary Productivity

A close correspondence between light intensities and variations in primary productivity has been noted by several authors. Odum and Hoskin (1958) present diurnal oxygen curves which indicate that decreasing light intensities caused by cloud cover cause a decrease in the photosynthetic rate of the aquatic primary producers. Odum and Wilson (1962) state that diurnal oxygen curves have the same general hump shape as that of the incident solar radiation. A diurnal oxygen curve is also presented which shows a sharp drop in the dissolved oxygen accompanying the passage of a cold frontal squall line.

Observations similar to the above were made during the course of this study. Figure 3 shows a diurnal oxygen curve for pond D and below it the corresponding graphic representation of the solar radiation levels occurring in the vicinity of the Lake City Experiment Station. Inspection of Figure 3 shows that the rises and falls in solar radiation intensity are remarkably reflected in corresponding rises and falls in the dissolved oxygen concentration of pond D.

Figure 3. The changes in solar radiation and dissolved oxygen concentrations in pond D, August 8, 1965.

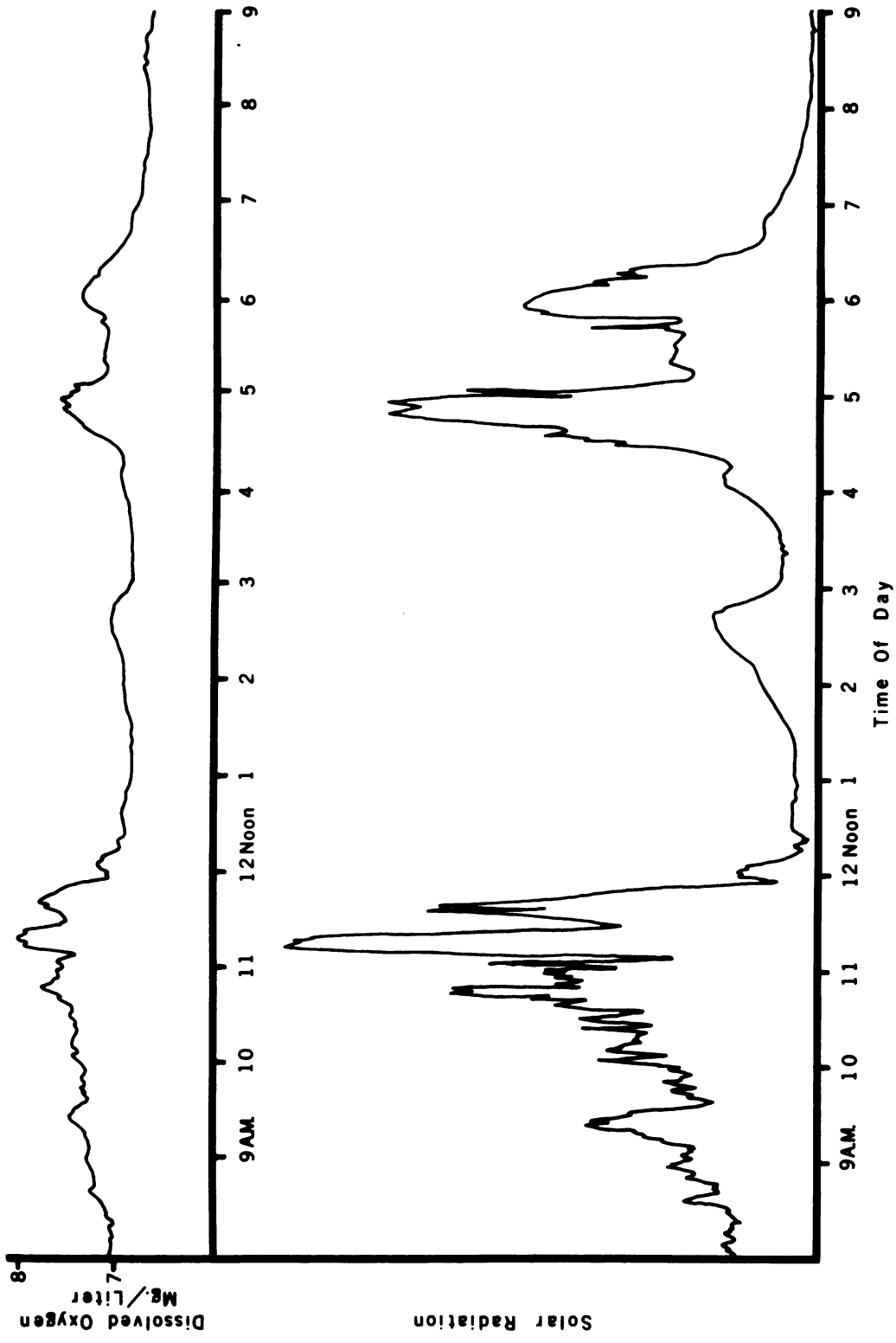
Dissolved Oxygen
Mg./Liter
8
7
Solar Radiation
9AM
10
11
12 Noon
1
2
3
4
5
6
7
8
9
Time Of Day

Figure 3

Efficiency

The efficiency of the primary producers in converting solar energy into chemical energy was calculated from gross oxygen production and solar radiation data. During the computation of efficiencies it was assumed that there was an approximate conversion of 4 kg. cal./gm. of oxygen metabolized (Odum and Wilson, 1962). It was also assumed that approximately fifty percent of the incident solar radiation was available at the surface for photosynthesis (Edmondson, 1955; Forsythe, 1954; and List, 1951).

Table IV lists several efficiencies reported for a diverse range of aquatic habitats. The efficiency of solar energy utilization in pond B ranged between 0.3 and 2.1% with a mean efficiency of 0.7%. The efficiency of pond D ranged from 0.1 to 1.61% with a mean efficiency of 0.6%. The efficiencies observed in the test ponds generally correspond with those values reported by the more recent studies of similar habitats.

Figure 4 illustrates the efficiencies observed in both ponds for the entire testing period. As one would expect, noting the method for calculation of efficiencies, pond B is clearly more efficient for the first nineteen days of study. From this time until the end of the test period the efficiencies of the two ponds come closer to approximating each other. The probable reason for the observed differences in the efficiency levels would be similar to that

TABLE IV

EFFICIENCY OF SOLAR ENERGY UTILIZATION
FOR VARIOUS AQUATIC HABITATS

Author	Year	Habitat	Percent Efficiency
Druffer and Dorris	1966	River	0.1 - 2.7
Odum	1957	Spring	4.0
Odum and Wilson	1962	Sewage Lagoon	6.0
Odum and Hoskin	1957	Microcosm	1.0 - 8.0
Butler	1964	Pond	0.2 - 1.8
Kohn	1956	Coral Reef	1.1
Clarke	1939	Lake	0.04 - 0.3
Juday	1940	Lake	0.40
Lindeman	1942	Bog Lake	0.10
Dineen	1953	Pond	0.04
Teal	1957	Cold Spring	0.20

Figure 4. The efficiency values for ponds B and D during the summer of 1965.

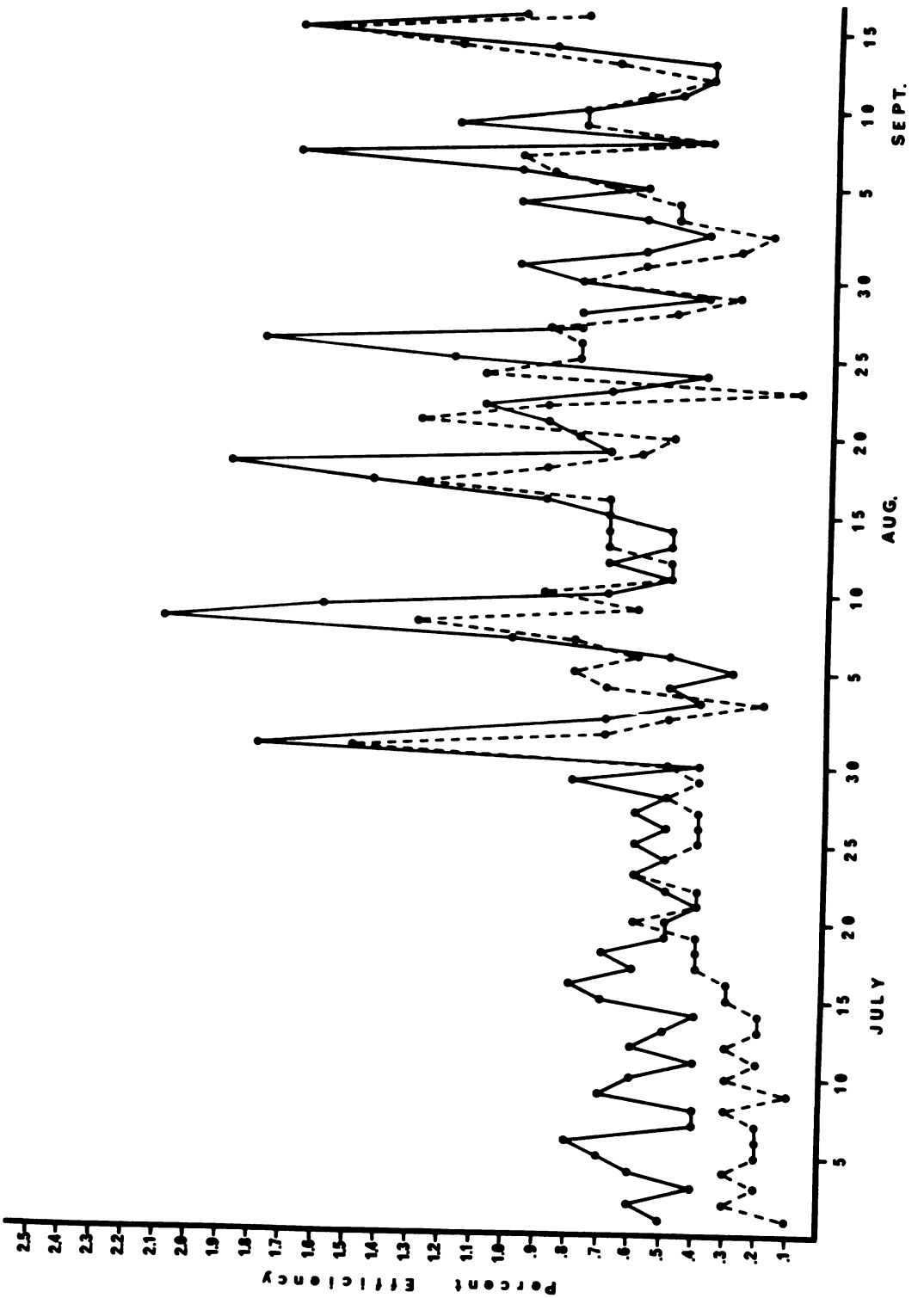

Figure 4

given for explaining the observed differences in the gross primary productivities of the two ponds.

The relationship between light intensity and efficiency has been shown by Odum and Wilson (1962) and Druffer and Dorris (1966) to be an inverse one, with efficiency decreasing with increasing light intensities. Inhibition of photosynthesis at high light intensities has also been shown to exist. Rabinowitch (1951) states that there is a general trend in most cases towards a linear increase in photosynthesis with a corresponding increase in light intensity only to a saturation point. Beyond this saturation level higher light intensities do not increase photosynthesis but eventually result in its inhibition. Steeman-Neilsen (1952) also states that in exceedingly bright light photo-oxidation of enzymes interfere with part of the photochemical mechanisms involved in photosynthesis.

Examination of Figure 5 shows a situation similar to the one described by Rabinowitch (1951) existed in pond B. There appears to be a steady decrease in photosynthetic efficiency up to a saturation energy of approximately 475 gm./cal./cm^2/day. Beyond this solar energy level decreases in efficiency, with increasing energy levels, become less pronounced.

P/R Ratios

The ratio of photosynthetic productivity to community respiration, P/R ratio, was used by Odum (1956) to classify

Figure 5. The relationship between efficiency and incident solar radiation in pond B during the summer of 1965.

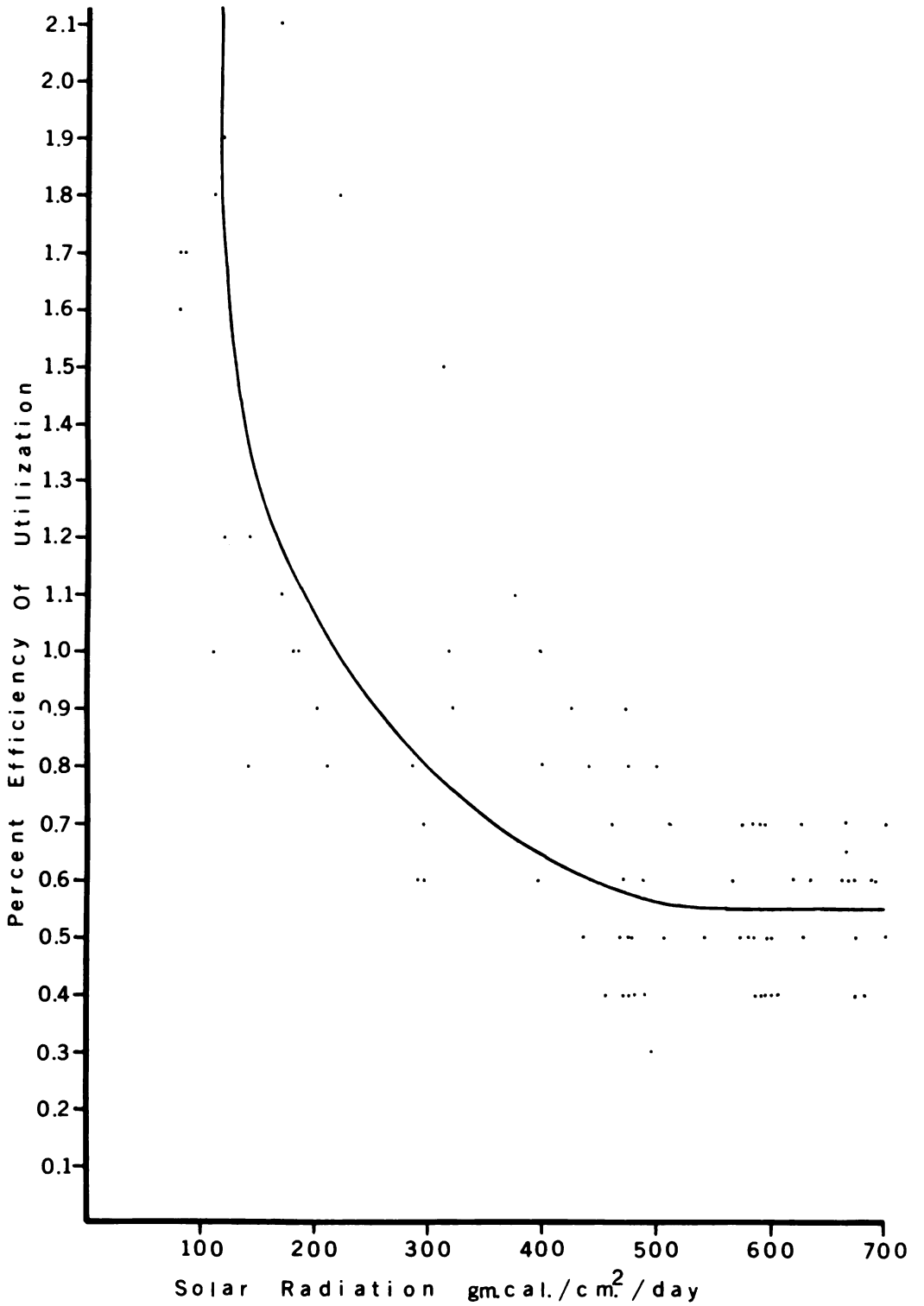
Percent Efficiency Of Utilization
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
100
200
300
400
500
600
700
Solar Radiation gm.cal./cm.2/day

Figure 5

communities according to their total metabolism and the relative dominance of autotrophic and heterotrophic metabolism. P/R ratios that are less than one occur when community metabolism exceeds photosynthetic production. P/R ratios greater than one are found where photosynthesis exceeds community respiration. Examination of the P/R ratio of a community makes it possible to classify it as either heterotrophic or autotrophic.

The P/R ratios varied between 0.59 and 2.64 in pond B and 0.30 to 3.00 in pond D. With mean P/R ratios for both ponds B and D being 1.01 and 1.04, respectively, we can classify them both as autogrophic communities producing approximately as much organic matter as they are using.

PERIPHYTON PRODUCTIVITY

The net photosynthetic productivity of the periphyton communities in the test ponds was measured by the employment of artificial substrates as collecting agents.

Periphyton shingles were examined at random during the summer to determine which genera of algae composed the periphyton community of the Lake City ponds. It has been noted by Castenholz (1960) that the artificial substrates are non-selective and do not favor the establishment of one particular type of algae. A list of the genera of algae found to be present in the periphyton of the test ponds is given in Table V. Although no quantitative measurements were made, there did not appear to be any one particular genus or genera of algae that dominated the periphyton community at any one particular part of the summer or during any specific part of the substrate exposure period.

The experiments of Grzenda (1960) showed that the number of phytopigment units in a given sample of periphyton extract could be used to quantitatively predict the organic weight of that particular sample.

TABLE V

THE GENERA OF ALGAE FOUND IN THE PERIPHYTON COMMUNITY OF THE LAKE CITY PONDS

Genera	Genera	Genera
Actinotaenium	Elakatothrix	Oscillatoria
Anabaena	Euastrum	Pandorina
Ankistrodesmus	Eudorina	Pediastrum
Aphanothece	Fragilaria	Penium
Apiocystis	Franceia	Peridinium
Botryococcus	Geminella	Pleurotaenium
Bulbochaete	Gloeocapsa	Quadrigula
Calothrix	Gloeocystis	Radiofilum
Ceratium	Gomphosphaeria	Rhabdoderma
Chaetosphaeridium	Hormidium	Scenedesmus
Chroococcus	Kirchneriella	Sphaerocystis
Closterium	Lyngbya	Spondylosium
Coelastrum	Micrasterias	Staurastrum
Coelosphaerium	Mougeotia	Staurodesmus
Coleochaete	Nephrocytium	Stipitococcus
Cosmarium	Nostoc	Tetraedron
Crucigenia	Oedogonium	Tolypothrix
Cylindrocapsa	Onychonema	Trachelomonas
Desmidium	Oocystis	Vaucheria

An attempt was made to establish a phytopigment-organic weight relationship for the periphyton growth in the experimental ponds using the method described by Grzenda (1960).

The data in Figure 6 was derived from forty-four samples taken at random from periphyton collections made throughout the summer. The formula used for the regression model was:

$$Y = a + bx$$

where Y = the mean organic weight estimate in milligrams,

a = the intercept of the Y axis,

b = the point estimator of the population slope,

and X = the observed phytopigment reading in phytopigment units x 10^3.

The predictive equation obtained by substituting the computed constants is:

$$Y = -0.26 + 0.47X$$

Range of X = 7 to 114

n = 44

r = 0.98.

The equations for computing the confidence regions on the linear regression (Figure 6) are given by Snedecor (1956). The 0.95 confidence limits for the Y (mean estimates) is denoted by CB (Figure 6). The 0.95 confidence

Figure 6. The relationship between phytopigment units and organic weight. Ninety-five percent confidence limits for Y (mean estimates) are BC and for individual estimates AD.

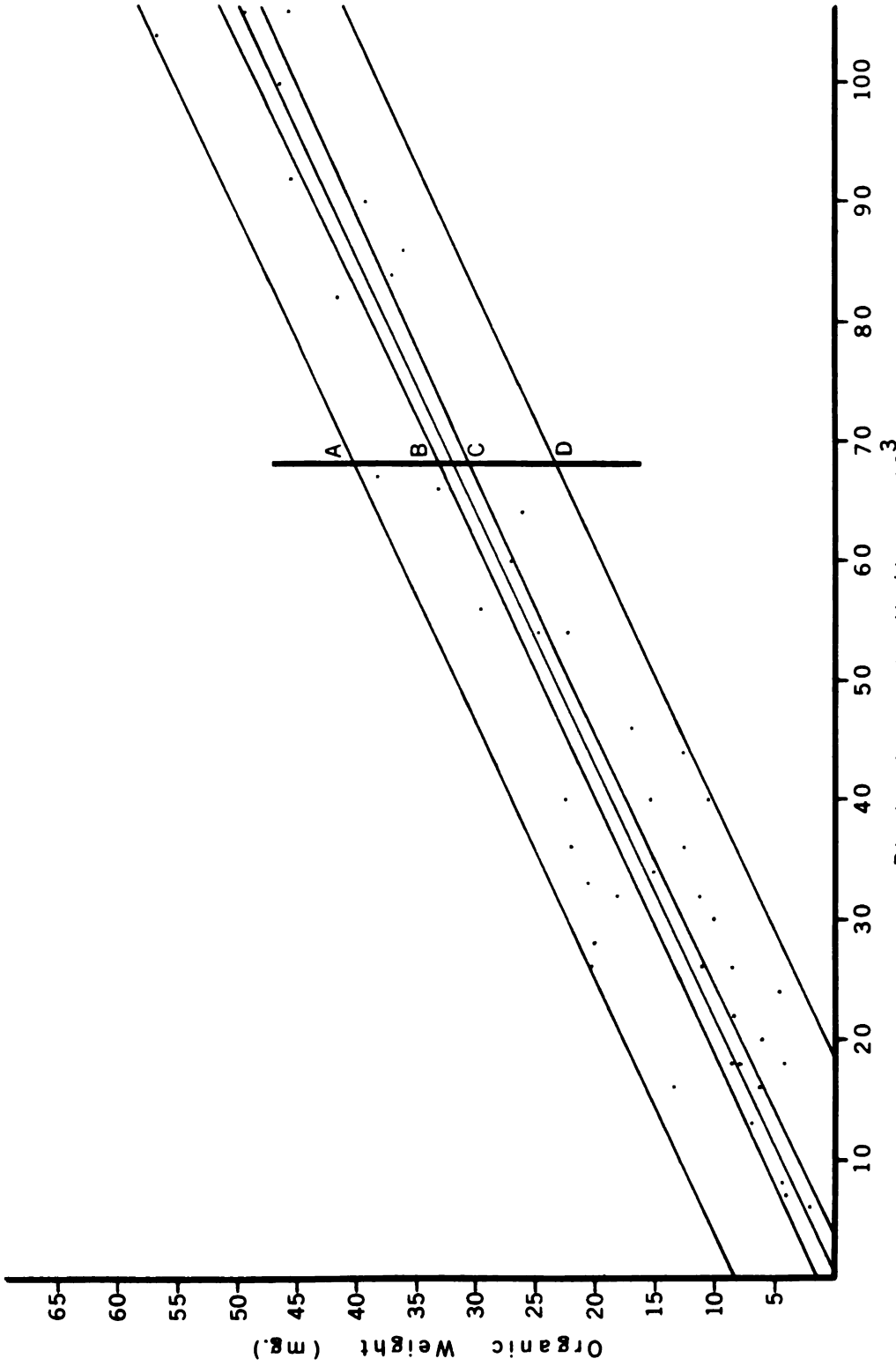
Organic Weight (mg.)
65
60
55
50
45
40
35
30
25
20
15
10
5
10
20
30
40
50
60
70
80
90
100
Phytopigment Units x 10^3
A
B
C
D

Figure 6

limits for the Y (individual estimates) is represented by AD (Figure 6). The confidence limits for the mean and individual estimates appear as lines with slightly curved borders. These curved borders illustrate the hazard of making predictions of Y at an X far removed from $\bar{X}$ (the mean of the X's). The minimum and maximum 95% confidence limits for individual estimates of Y are ± 8.43 mg. and ± 8.56 mg. respectively. The minimum and maximum 95% confidence limits for the mean estimates of Y are ± 1.24 mg. and ± 1.94 mg., respectively. Minimum values are located at $\bar{X}$ (mean of the X's), and maximum confidence limits occur at the maximum value for X which is 114 phytopigment units x 10^3.

Figure 7, line CD, shows the linear regression as calculated by Grzenda (1960) for the phytopigment organic weight relationship of the periphyton occuring in the Red Cedar River. Phytopigment organic weight regressions calculated by Kevern (1962) for an artificial stream also approximate those reported by Grzenda (1960). Line AB (Figure 7) is the linear phytopigment organic weight regression calculated for the periphyton community of the Lake City ponds. Examination of the two regressions reveals that there is a greater quantity of organic matter per any given number of phytopigment units in the test ponds as opposed to the Red Cedar River. This difference in the chlorophyll content of the two periphyton communities is most probably due to

Figure 7. The phytopigment-organic weight regression for the Lake City ponds, line AB, for the Red Cedar river (Grzenda, 1960), line CD.

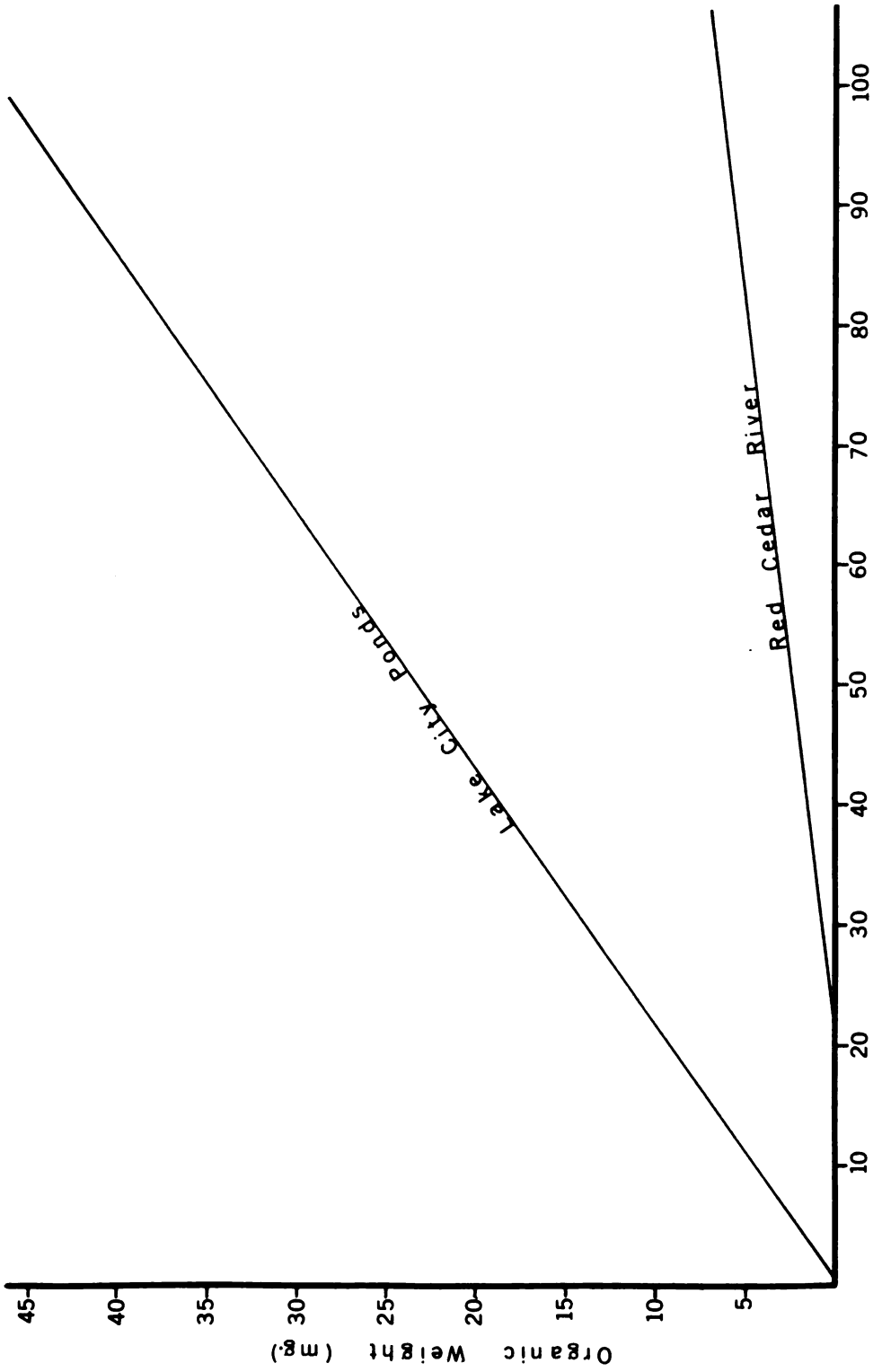
Organic Weight (mg.)
45
40
35
30
25
20
15
10
5
Lake City Ponds
Red Cedar River
10
20
30
40
50
60
70
80
90
100
Phytopigment Units x 10^3

Figure 7

differing species composition of the two algal communities and to the different conditions under which they are growing. These observed variations between the phytopigment organic weight relationships of various habitats illustrates the necessity of workers who wish to use this method to construct regression equations for the particular habitat in which they are working. Only then will a regression equation have any predictive value.

When attempting to measure the photosynthetic productivity of a periphyton community by employing the use of artificial substrates as collecting agents, one must determine which portion of the periphyton growth on these substrates is most representative of the growth taking place on the naturally occurring substrates. Kevern (1962) stated that periphyton productivity could be estimated by using artificial substrates as collecting devices only if the exposure period was long enough for the collected periphyton to approach a growth phase similar to that occurring on natural substrates. He also indicated that his investigations showed that productivity estimates based on the growth accumulated during the last few days of the exposure period yield the most reliable productivity estimates.

The substrates used to make productivity estimates were exposed for a minimum of four days before removal from the pond and for a maximum of twenty-four days. A new series of periphyton shingles was placed in the ponds sixteen days after placement of the preceding rack.

The growth curve of the periphyton on the substrates exhibited a J-shaped form in all cases except one, which occurred at the end of the summer when periphyton production was greatly reduced. Figure 8 shows a growth curve typical of those found for the periphyton growth on the collecting shingles. The decline in total biomass of periphyton clinging to the substrate usually began on the 16th or 20th day of exposure. The decline in biomass was caused by the sloughing off of the periphyton coating. This sloughing off may be caused by the accumulation of oxygen bubbles during the day time which would cause the loose periphyton growth to float away. During the latter part of the substrate exposure period the periphyton covering the Plexiglass plate became very fuzzy with growth extending out away from the substrate. Undoubtedly some of this very loose growth was lost when the substrate was removed from the supporting rack. This sampling error would also contribute to the J-shaped form of the growth curve.

Periphyton production was estimated by subtracting the total amount of organic matter accumulated on a pair of substrates at the end of the fourth day of exposure from the total organic biomass present on another pair of substrates at the removal date immediately prior to the beginning of the sloughing off period. This difference was then divided by the total time elapsed to give the periphyton production in terms of grams of organic matter accumulated

Figure 8. A representative growth curve of periphyton accumulating on artificial substrates in a Lake City test pond during the summer of 1965.

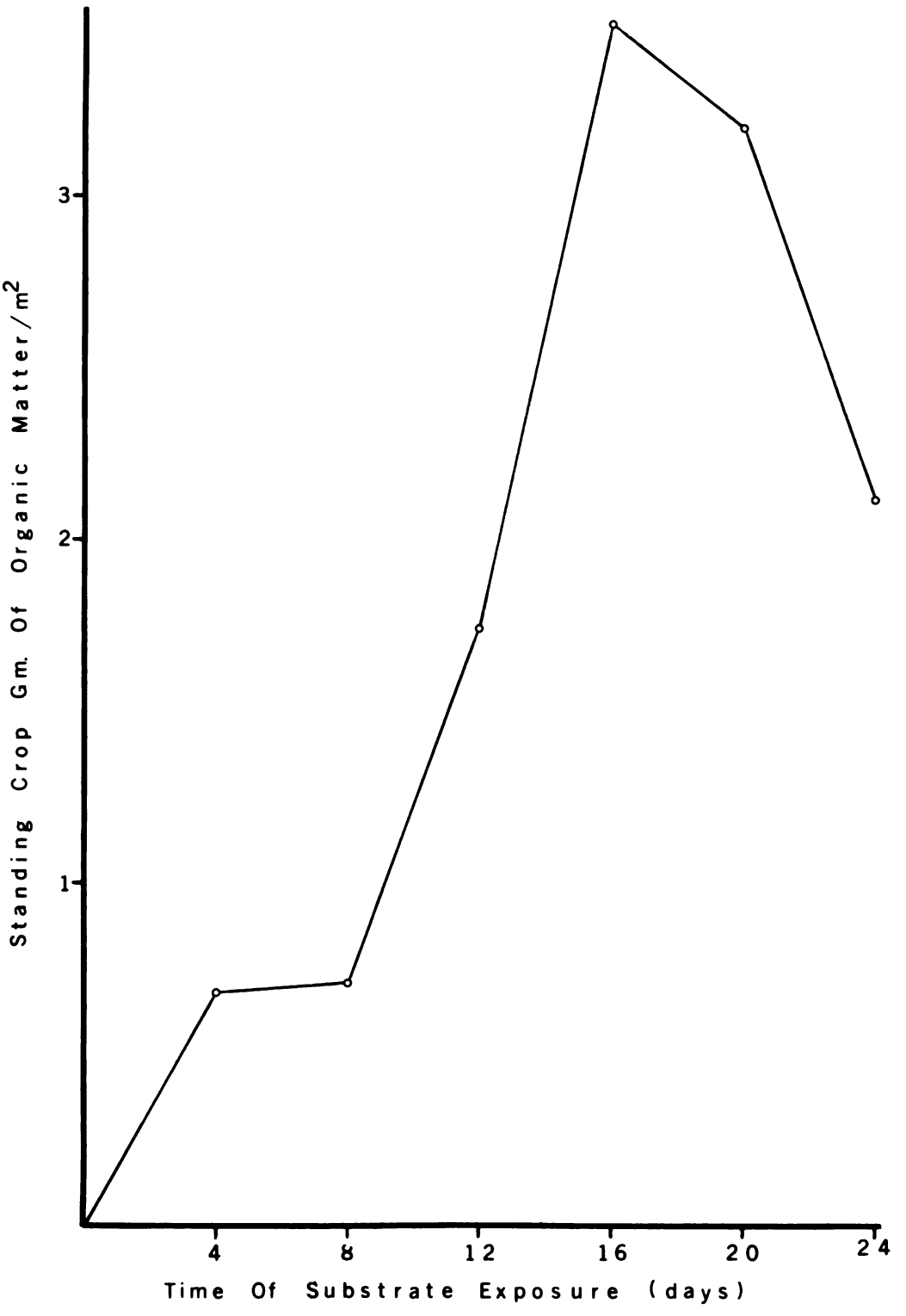
Standing Crop Gm. Of Organic Matter/m2
3
2
1
4
8
12
16
20
24
Time Of Substrate Exposure (days)

Figure 8

per sq. meter per day. Use of the time period described above for periphyton productivity estimates enables one to eliminate incorporation of the colonization period in the calculations thereby providing an estimate of periphyton production more closely approximating the production occurring on natural substrates in the ponds themselves.

The periphyton production ranged from 0.12 to 0.30 gm. organic matter/m^2/day in pond B and from 0.04 to 0.20 gm. organic matter/m^2/day in pond D. Mean productivity values for ponds B and D were 0.17 and 0.11 gm. organic matter/m^2/day respectively. The productivity values for the entire study period are given in Table VI.

The efficiency of the periphyton community in converting or transferring the photosynthetically active solar radiation (50% of incident solar radiation or $\frac{1}{2}$Li) into organic matter (P_n) was estimated for both test ponds (see Table VII). The equation used to convert the organic weight of the algae into caloric values was developed by Kevern (1962) who determined the energy content of periphyton, using bomb calorimetry. The conversion equation used is:

$$\text{gm. cal.} = \text{organic weight} \times 4500$$

Inspection of Figure 9 shows that the periphyton community of pond B was, with but one exception, more efficient in its utilization of solar energy. It is also evident that the efficiencies are more widely divergent during the latter part of the summer.

TABLE VI

NET PRIMARY PERIPHYTON PRODUCTIVITY
OF PONDS B AND D

Date	Net Primary Productivity (ash-free dry wt. gm./m^2/day)	
	Pond B	Pond D
7-1 thru 7-19	0.30	0.20
7-20 thru 7-31	0.22	0.16
8-1 thru 8-12	0.16	0.15
8-13 thru 8-24	0.13	0.05
8-25 thru 9-5	0.12	0.04
9-6 thru 9-16	0.14	0.08
Mean	0.17	0.11

TABLE VII

PERCENT EFFICIENCY OF UTILIZATION OF PHOTOSYNTHETICALLY ACTIVE SOLAR ENERGY BY POND PERIPHYTON COMMUNITIES

Date	Pond B	Pond D
7-1 thru 7-19	0.04%	0.03%
7-20 thru 7-31	0.03%	0.02%
8-1 thru 8-12	0.03%	0.03%
8-13 thru 8-24	0.02%	0.01%
8-25 thru 9-5	0.03%	0.01%
9-6 thru 9-16	0.04%	0.02%
Mean	0.03%	0.02%

Figure 9. The efficiency of periphyton communities B and D in transferring photosynthetically active solar energy into organic matter.

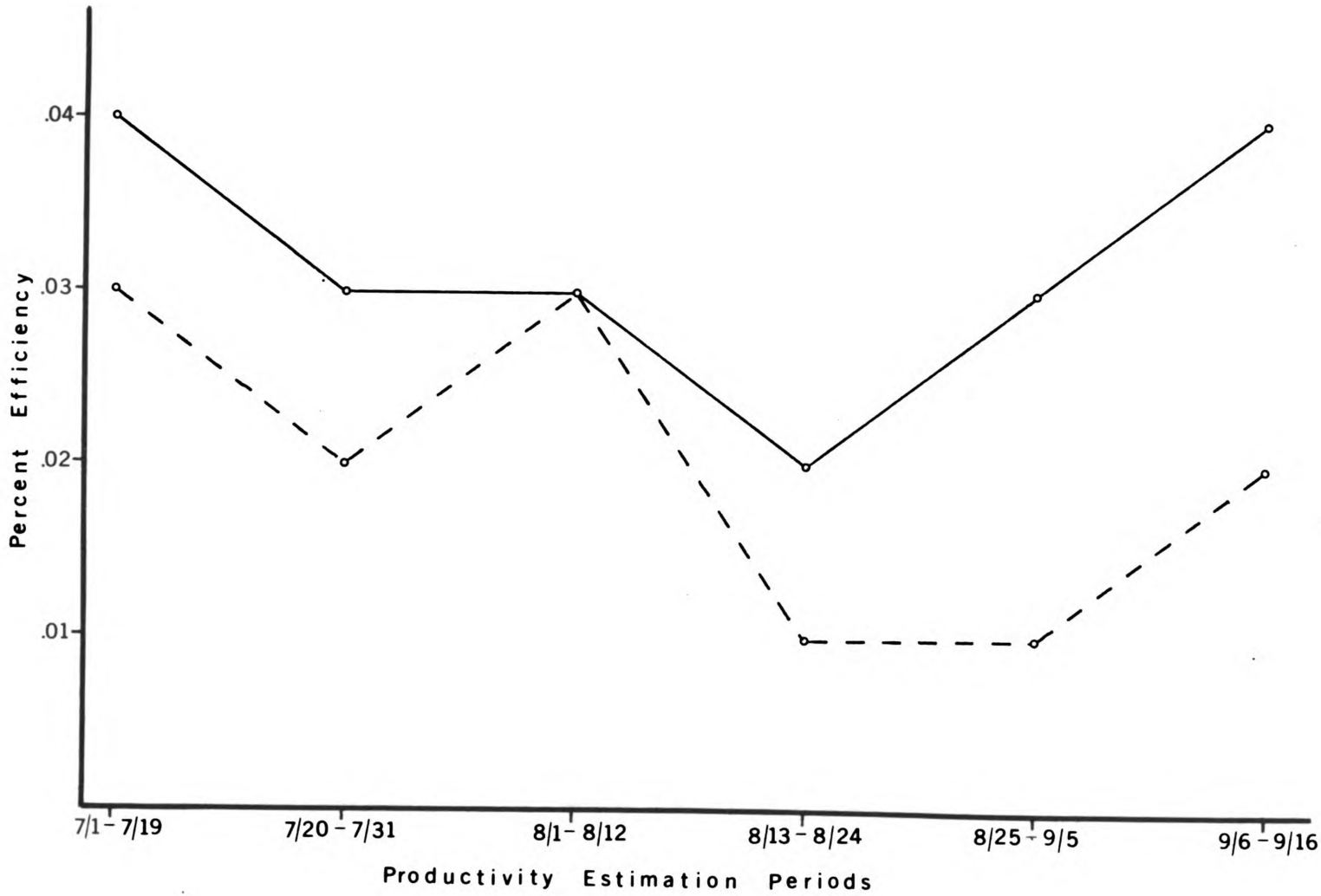
.04
.03
.02
.01
Percent Efficiency
7/1 - 7/19
7/20 - 7/31
8/1 - 8/12
8/13 - 8/24
8/25 - 9/5
9/6 - 9/16
Productivity Estimation Periods

Figure 9

Hasler and Jones (1949) found that large growths of aquatic plants had an inhibiting effect upon the growth of phytoplankton and rotifers. Moore (1952) suggested that low phytoplankton productivity was caused by the use of the nutritive materials by the higher aquatics.

From approximately August 1st until the end of the test period there was a substantial die-off of higher aquatic plants in pond B. Pond D, on the other hand, was experiencing rapid growth of its late flourishing macrophyte population.

Although no positive relationship between a decreasing macrophyte population and an increasing periphyton production rate can be authoritatively established from these data, one could speculate as to the fact that periphyton growth in pond D was affected by nutrient limitations or availabilities placed upon it by the rapidly growing macrophyte population.

It should be noted that production rates occurring on artificial substrates are only indices of production rates occurring on the natural substrates. Pond D, in fact, may have possessed a greater total amount of periphyton production due to its greater surface area available for colonization.

MACROPHYTE PRODUCTIVITY

The second source of primary productivity in the test ponds was that of the macroscopic aquatic plants. The net photosynthetic productivity of the macrophytes was measured by employment of the harvest method.

Forty samples were removed from randomly selected locations in pond B upon initiation of the productivity study. Pond D had previously been drained and ranked clear of all higher aquatic growth making an initial sampling unnecessary. The macrophytes were again sampled in pond B on August 1, 1965 and finally on September 10, 1965. Macrophytes were sampled in pond D on August 3, 1965 and September 10, 1965.

During the final sampling period the aquatic plants removed from pond D were separated according to genera and weighed to determine the composition of the plant population. The most abundant macrophyte was Chara sp. with 91.0% of the dry weight of the population being comprised of this particular genera. The second most abundant macrophyte was Elodea sp. which comprised 5.9% of the total dry weight. The remainder of the population was composed of Potamogeton sp. 2.9%. Very small amounts of Najas flexilis were also noted in some of the samples.

Plans were originally made to conduct a similar survey of the macrophyte population of pond B, however, at the time the attempt was made the population was so severely depleted that any results would have proved highly unreliable. Inspection of dried samples from the first and second samplings of pond B did show that the three genera of macrophytes were present in approximately the same ratios as those found in pond D.

The caloric content of the three genera of macrophytes was determined by analysis of five or more samples of each type. The caloric content of Chara sp., after corrections were made for endothermy was 1882.6 ± 93 cal./gm. dry weight. The caloric content of Elodea sp., and Potamogeton sp., are 3470.5 ± 68 cal./gm. dry weight and 3961.6 ± 233 cal./gm. dry weight respectively.

Inspection of Figure 10 shows that the average biomass of macrophytes decreased in pond B throughout the study period while the biomass of the macrophyte population in pond D steadily increased over the same time period. This fact also reflects itself in the net productivity rates of the two ponds. This difference was undoubtedly due to the fact that pond D was drained on June 21, 1965 prior to initiation of the study. The macrophyte population of pond B, which was not drained had passed its maximum growth phase by the time the study was begun.

The rates of net primary productivity of the macrophytes in pond D varied from 0.43 to 0.92 gm. dry weight/m^2/day.

Figure 10. The rates of net production and biomass accumulation of the aquatic macrophytes in ponds B and D.

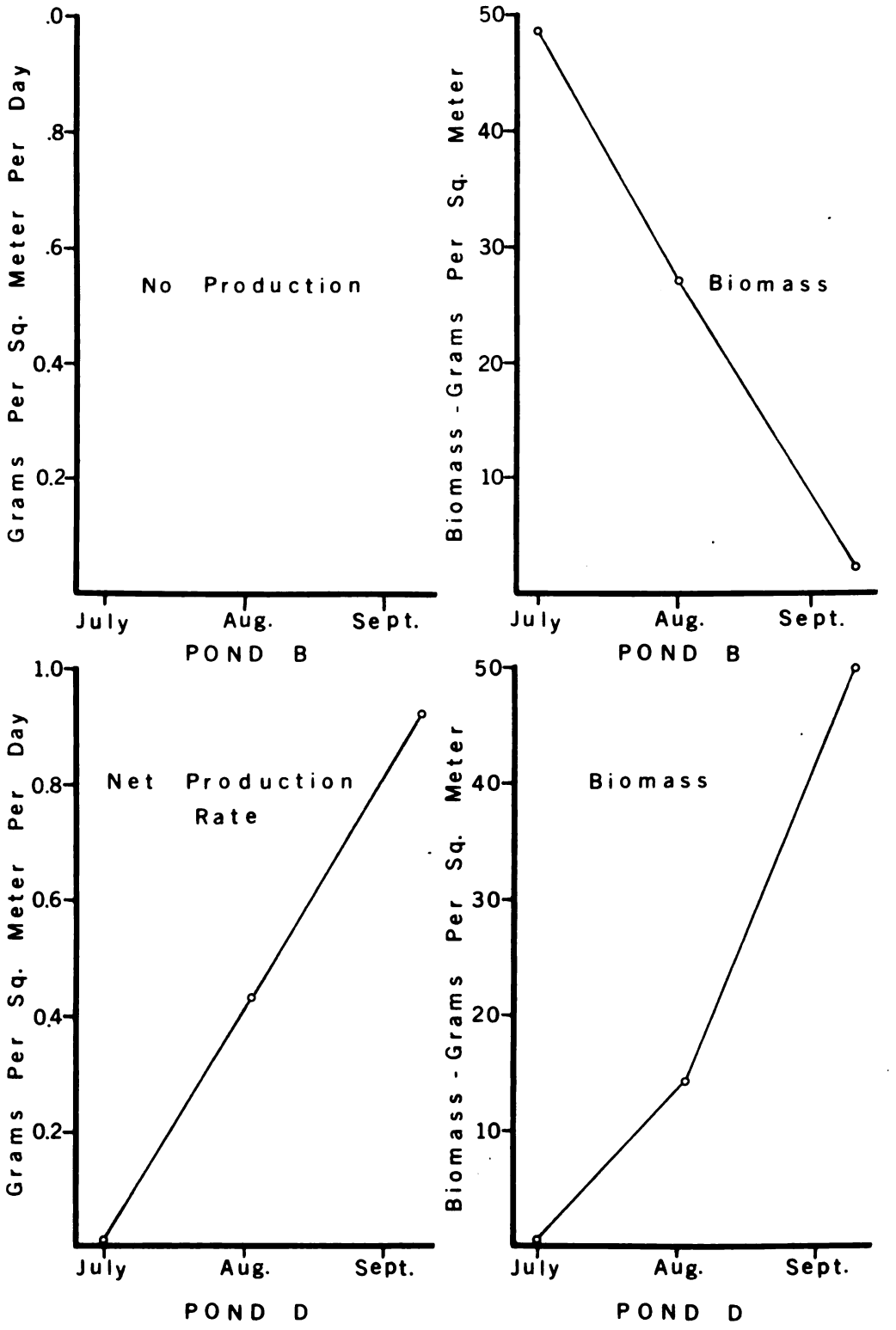
Grams Per Sq. Meter Per Day
.0
.8
.6
0.4
0.2
No Production
July
Aug.
Sept.
POND B
Biomass - Grams Per Sq. Meter
50
40
30
20
10
Biomass
July
Aug.
Sept.
POND B
Grams Per Sq. Meter Per Day
1.0
0.8
0.6
0.4
0.2
Net Production Rate
July
Aug.
Sept.
POND D
Biomass - Grams Per Sq. Meter
50
40
30
20
10
Biomass
July
Aug.
Sept.
POND D

Figure 10

Knight, Ball, and Hooper (1962) reported the same pond to have a net productivity of 6.00 gm. dry weight/m^2/day for the entire growing season of 1960. Vannote (1963) reported production rates of 0.41 and 1.37 gm. dry weight/m^2/day for a Vallisneria community in the Red Cedar River.

The dry weight estimates of the macrophyte populations were converted to caloric content by the following relationship:

$$\text{gm. cal.} = \text{dry weight} \times 2036$$

The net productivity rates in terms of gm. cal./m^2/day are given in Table VIII for the macrophyte communities of the two ponds.

The efficiency of the macrophyte community in converting the photosynthetically active solar radiation, $\frac{1}{2}Li$, into organic matter, Pn, was estimated for pond D, with results also being given in Table VIII. Efficiencies in pond D ranged from 0.03 to 0.1% with a mean efficiency of 0.08%. Vannote (1963) reported mean annual Pn/Li efficiencies from 0.03 to 0.07%.

TABLE VIII

NET PRIMARY PRODUCTIVITY AND PERCENT EFFICIENCY OF UTILIZATION OF PHOTOSYNTHETICALLY ACTIVE SOLAR ENERGY OF POND MACROPHYTES

Pond	Date	Grams per sq. meter per day	Gram calories per sq. meter per day	Percent Efficiency Pn/½Li
D	7-1 thru 8-2	0.43	875.5	0.03%
	8-3 thru 9-9	0.92	1873.2	0.10%
B	7-1 thru 7-31	0.00	0.0	0.00%
	8-1 thru 9-9	0.00	0.0	0.00%

Pn = Net primary production.

½Li= Photosynthetically active solar radiation.

PHYTOPLANKTON PRODUCTIVITY

The phytoplankton are the third and final group of photosynthetic organisms found in the experimental ponds. The dominant group of phytoplankters appeared to be the desmids.

The C^{14} method of measuring the productivity of the phytoplankters, although generally accepted, was not used in this study. An attempt was made to estimate the productivity of the phytoplankton by measuring the standing crop of organisms and estimating their rate of turnover.

Standing crops of plankton were sampled weekly from both ponds B and D throughout the study period. Plankton samples once collected were dried, weighed, ignited and the loss of weight upon ignition determined and recorded as the organic weight of the sample.

The average standing crop of planktonic organisms in pond B was 1.44 gm. organic matter/m^2. The standing crop of planktonic organisms in pond D averaged 1.14 gm. organic matter/m^2. These values are similar to those average values reported by Birge and Juday (1922).

Birge and Juday (1922) estimated that approximately 25 percent of all the planktonic material is composed of

zooplankton. Riley (1940) in a study of the plankton of a New England pond stated that the mean phytoplankton to zooplankton ratio, which he considered to be somewhat high, was 4.5 to one.

For the purpose of estimating the standing crop of phytoplankton in the test ponds it was assumed that the phytoplankton to zooplankton ratio was 3:1. The average estimated standing crop of phytopoankton in pond B was 1.08 gm. organic matter/m^2 and 0.85 gm. organic matter/m^2/ in pond D.

Birge and Juday (1922) indicate that the turnover rate of the plankton population falls somewhere between one and two weeks. Riley (1939) estimated that the phytoplankton production was 2.02 crops per week in surface waters. Since the entire area of both ponds are within the euphotic zone a turnover rate of two crops per week was used to estimate the mean phytoplankton production of the two test ponds. The estimated average production of organic matter by the phytoplankton population of pond B is 0.30 gm. organic matter/ m^2/day. The average rate of energy fixation by the phyto-plankton of pond D is somewhat less rapid with 0.24 gm. organic matter being fixed m^2/day. These values though some-what lower are in general agreement with those reported by Knight, Ball, and Hooper (1962) for the same test ponds.

If it is assumed that the caloric content of the phyto-plankton is 4500 cal./gm. organic weight, the average

efficiency of conversion of photosynthetically active solar energy, $\frac{1}{2}$Li, into organic material would be 0.05 percent for pond D and 0.06 percent for pond D.

SUMMARY

The primary productivity of two ponds was measured by monitoring the dissolved oxygen content of the water and by the collection of the three groups of primary producers.

The mean net productivity rates of ponds B and D were 3.73 gm. O_2/m^2/day and 3.03 gm. O_2/m^2/day respectively.

A close correspondence was noted between the level of light intensity and the rate of primary production. Periods of decreased light intensities even though quite short produced a decrease in primary production while increases in light intensity brought about an immediate increase in primary production.

There was a relationship between the light intensity and the efficiency with which the photosynthetic organisms fixed the available solar energy. Efficiency of utilization of solar energy was found to decrease with increasing light intensities up to approximately 475 gm. cal./cm^2/day. Above this light intensity increases in solar energy produced little decreases in efficiency levels. This decrease in efficiency accompanying increases in light intensity is thought to be due to photo-oxidation of enzymes essential to photosynthesis.

The mean P/R ratios for ponds B and D were 1.01 and 1.04 respectively, thereby classifying them as autotrophic communities.

A linear relationship between ethanol phytopigment extracts of periphyton and the organic weight of the sample was established.

In pond B the phytoplankton was the leading primary producer (0.30 gm. organic matter/m^2/day) with periphyton being second (0.17 gm. organic matter/m^2/day) and the macrophytes fixing no solar energy during the study period. In pond D the macrophytes were the leading primary producers (0.67 gm. organic matter/m^2/day) with the phytoplankton second (0.24 gm. organic matter/m^2/day) and periphyton last (0.11 gm. organic matter/m^2/day).

A relationship appears to exist between macrophyte, periphyton and phytoplankton growth. Increased levels of macrophyte growth coincide with decreased levels of periphyton and phytoplankton growth in pond D, while decreased macrophyte growth concurs with increased production of phytoplankton and periphyton in pond B. It is possible that nutrient limitations placed upon the periphyton and phytoplankton populations by the flourishing macrophyte growth occurring in pond D resulted in the lower rate of productivity of the periphyton and phytoplankton. The macrophytes may also have had a direct inhibiting action upon the growth of the periphyton and phytoplankton.

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APPENDIX

Solar energy measured at the Lake City Experiment Station during the summer of 1965. Values are expressed as gram calories per square centimeter per day.

Date	Gram cal. cm^{-2} day^{-1}	Date	Gram cal. cm^{-2} day^{-1}
7-1	702.9	8-9	80.4
7-2	296.3	8-10	625.7
7-3	673.2	8-11	597.2
7-4	672.6	8-12	512.5
7-5	664.4	8-13	478.0
7-6	501.0	8-14	673.0
7-7	601.1	8-15	593.0
7-8	593.6	8-16	424.4
7-9	295.7	8-17	312.1
7-10	659.3	8-18	117.0
7-11	603.0	8-19	589.0
7-12	687.6	8-20	476.1
7-13	507.7	8-21	321.0
7-14	683.2	8-22	373.1
7-15	699.8	8-23	574.0
7-16	285.0	8-24	488.1
7-17	291.1	8-25	142.6
7-18	460.6	8-26	221.1
7-19	628.8	8-27	297.5
7-20	572.7	8-28	440.4
7-21	596.0	8-29	475.8
7-22	436.0	8-30	140.3
7-23	567.9	8-31	110.8
7-24	628.2	9-1	394.0
7-25	633.7	9-2	470.9
7-26	580.0	9-3	470.4
7-27	620.0	9-4	318.9
7-28	600.0	9-5	485.6
7-29	560.0	9-6	185.5
7-30	590.0	9-7	85.8
7-31	110.0	9-8	471.0
8-1	170.0	9-9	120.8
8-2	586.6	9-10	210.9
8-3	285.7	9-11	475.7
8-4	468.0	9-12	485.6
8-5	495.0	9-13	455.5
8-6	542.2	9-14	202.9
8-7	394.2	9-15	87.8
8-8	168.7	9-16	181.1

Gross primary productivity of the Lake City ponds expressed as grams of oxygen per meter squared per day--Summer, 1965.

Date	Pond B	Pond D	Date	Pond B	Pond D
7-1	4.58	1.37	8-9	1.66	0.64
7-2	2.42	1.20	8-10	5.95	7.18
7-3	3.93	1.80	8-11	4.09	4.03
7-4	5.12	3.10	8-12	4.89	3.70
7-5	6.19	2.40	8-13	3.47	4.75
7-6	5.51	1.85	8-14	4.27	6.29
7-7	3.12	1.66	8-15	5.28	5.51
7-8	3.40	2.34	8-16	5.05	3.90
7-9	2.82	0.56	8-17	3.98	3.60
7-10	5.45	2.72	8-18	2.91	1.35
7-11	3.05	1.63	8-19	5.58	5.14
7-12	5.55	2.80	8-20	5.28	3.14
7-13	3.30	1.38	8-21	3.80	5.30
7-14	4.26	3.27	8-22	5.33	4.63
7-15	6.71	2.73	8-23	5.58	4.65
7-16	3.06	1.20	8-24	2.79	6.84
7-17	2.30	1.67	8-25	2.21	1.60
7-18	4.10	2.63	8-26	5.03	2.41
7-19	3.95	3.25	8-27	4.45	4.70
7-20	4.19	4.38	8-28	4.43	3.08
7-21	3.20	3.32	8-29	2.93	1.91
7-22	2.75	2.37	8-30	1.42	1.56
7-23	4.63	4.40	8-31	1.44	0.84
7-24	4.53	4.50	9-1	3.19	1.59
7-25	4.88	3.33	9-2	2.41	1.68
7-26	4.06	3.11	9-3	3.55	3.35
7-27	4.71	3.51	9-4	4.08	2.26
7-28	3.92	4.26	9-5	3.77	4.73
7-29	5.76	3.36	9-6	2.37	2.17
7-30	3.50	4.12	9-7	1.89	1.15
7-31	2.35	2.13	9-8	2.60	2.55
8-1	2.54	1.62	9-9	1.92	1.21
8-2	5.36	3.84	9-10	2.32	2.27
8-3	2.57	1.35	9-11	3.08	3.82
8-4	3.15	4.28	9-12	2.76	2.58
8-5	2.03	4.98	9-13	2.64	4.20
8-6	3.56	4.51	9-14	2.45	3.25
8-7	5.02	4.22	9-15	1.89	1.77
8-8	4.49	2.92	9-16	2.45	1.84

Community respiration of the Lake City ponds expressed as grams of oxygen per meter squared per day--Summer, 1965.

Date	Pond B	Pond D	Date	Pond B	Pond D
7-1	4.05	0.60	8-9	2.53	2.13
7-2	3.45	1.95	8-10	4.66	6.53
7-3	2.70	0.60	8-11	4.13	3.33
7-4	5.40	3.60	8-12	5.60	4.00
7-5	6.75	2.40	8-13	4.53	3.73
7-6	5.70	1.35	8-14	4.13	7.33
7-7	3.12	1.95	8-15	5.33	5.46
7-8	4.32	2.55	8-16	5.20	4.00
7-9	2.40	1.65	8-17	3.46	3.60
7-10	6.96	2.70	8-18	4.40	2.00
7-11	1.80	1.05	8-19	3.86	3.73
7-12	6.26	2.40	8-20	5.33	4.13
7-13	5.46	1.86	8-21	4.40	3.60
7-14	4.26	2.40	8-22	5.20	5.46
7-15	2.53	2.26	8-23	5.46	2.66
7-16	3.86	1.86	8-24	2.80	6.40
7-17	2.53	2.00	8-25	4.00	3.60
7-18	2.80	2.26	8-26	3.46	2.53
7-19	5.20	2.53	8-27	4.53	5.46
7-20	2.93	5.06	8-28	3.86	2.80
7-21	3.20	3.06	8-29	2.66	1.46
7-22	4.40	3.06	8-30	2.40	1.32
7-23	4.40	4.26	8-31	1.92	1.32
7-24	5.46	5.73	9-1	2.88	1.08
7-25	6.40	3.06	9-2	2.64	1.44
7-26	3.75	3.15	9-3	4.32	2.52
7-27	4.65	3.30	9-4	4.32	3.36
7-28	3.90	3.30	9-5	3.48	7.32
7-29	4.65	3.45	9-6	3.00	3.12
7-30	4.50	3.00	9-7	2.16	1.56
7-31	3.60	3.90	9-8	1.32	1.20
8-1	2.80	2.13	9-9	2.83	3.05
8-2	3.73	2.80	9-10	2.07	3.05
8-3	2.93	1.20	9-11	3.16	2.29
8-4	2.80	3.86	9-12	3.27	1.85
8-5	2.93	4.13	9-13	3.38	4.14
8-6	4.53	5.73	9-14	2.04	6.10
8-7	4.93	4.80	9-15	1.96	2.94
8-8	5.86	3.73	9-16	1.63	0.76

P/R ratios found in ponds B and D during the summer of 1965.

Date	Pond B	Pond D	Date	Pond B	Pond D
7-1	1.13	2.29	8-9	0.65	0.30
7-2	0.70	0.61	8-10	1.27	1.09
7-3	1.45	3.00	8-11	0.99	1.20
7-4	0.94	0.86	8-12	0.87	0.92
7-5	0.91	0.76	8-13	0.76	1.27
7-6	0.96	1.37	8-14	1.03	0.85
7-7	1.00	0.85	8-15	0.99	1.00
7-8	0.78	0.91	8-16	0.97	0.97
7-9	1.17	0.34	8-17	1.15	1.00
7-10	0.66	1.00	8-18	0.66	0.67
7-11	1.59	1.55	8-19	1.44	1.37
7-12	0.88	1.16	8-20	0.99	0.76
7-13	0.60	0.73	8-21	0.86	1.47
7-14	0.99	0.98	8-22	1.02	0.84
7-15	2.64	1.20	8-23	1.02	1.74
7-16	1.79	0.64	8-24	0.99	1.06
7-17	0.91	0.83	8-25	0.55	0.44
7-18	1.97	1.16	8-26	1.45	0.95
7-19	0.76	1.28	8-27	0.98	0.86
7-20	1.42	0.86	8-28	1.14	1.10
7-21	1.00	1.08	8-29	1.09	1.30
7-22	0.88	0.77	8-30	0.59	1.18
7-23	1.05	1.03	8-31	0.75	0.64
7-24	0.82	0.78	9-1	1.10	1.47
7-25	0.76	1.08	9-2	0.91	1.16
7-26	1.08	0.98	9-3	0.82	1.32
7-27	1.01	1.06	9-4	0.94	0.67
7-28	1.00	1.29	9-5	1.08	0.64
7-29	1.24	0.97	9-6	0.79	0.69
7-30	0.77	1.37	9-7	0.87	0.74
7-31	0.65	0.54	9-8	1.96	2.12
8-1	0.90	0.76	9-9	0.67	0.39
8-2	1.43	1.37	9-10	1.12	0.74
8-3	0.87	1.12	9-11	0.97	1.66
8-4	1.12	1.10	9-12	0.84	1.39
8-5	0.69	1.20	9-13	0.78	1.01
8-6	0.78	0.78	9-14	0.83	0.53
8-7	1.01	0.88	9-15	0.96	0.60
8-8	0.76	0.78	9-16	1.49	2.41