PRIMARY PRODUCTIVITY—PHYTOPLANKTON RELATIONSHIPS, HODGSON LAKE, PORTAGE COUNTY, OHIO[1]

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ABSTRACT

Primary productivity-phytoplankton relationships were studied for one year (1963–64) in Hodgson Lake, Portage County, Ohio. The lake was found to be a "blue-green—diatom" reservoir of moderate productivity, but containing a large phytoplankton standing crop, dominated by the cyanophycean, *Oscillatoria rubescens* Decandole. Average cell volumes ranged from 1.4 mm^3 $liter^{-1}$ in September to approximately 88.6 $mm^3 liter^{-1}$ in June, over 80 percent of which were *O. rubescens.* Diatoms, including *Cyclotella* sp, *Fragilaria* sp. *Asterionella formosa* Hass, and *Synedra delicatissima* W. Sm., usually accounted for <10 percent of the total cell volume. Photosynthesis ranged from 4–5 mgC m^{-2} day^{-1} during the winter to approximately 2600–2700 mgC m^{-2} day^{-1} in June and October, with an annual mean of 847.5 mgC m^{-2} day^{-1}. Photosynthesis per unit cell volume ranged from $<1 \mu gC$ day^{-1} mm^{-3} during the winter to 172.8 μgC day^{-1} mm^{-3} in October, averaging 10.5 μgC day^{-1} mm^{-3} annually.

INTRODUCTION

Photosynthetic carbon fixation by phytoplankton represents the major part of the organic production in most lakes. The rate of carbon fixation at the primary level currently provides the best assessment of the result of physical, chemical, and biological interactions determining the actual fertility of any environment (Goldman, 1963). Changes and differences in quality and quantity of basic productivity within a lake may be expected to influence, although not always directly, the quality and quantity of organic accumulation in successive trophic levels.

Although considerable work has been done in recent years on rates of phytoplankton photosynthesis, less is known about the relationship between biomass or standing crop and photosynthesis (Findenegg, 1965). When relating productivity to biomass, most workers have used rapid measurements of standing crop, such as packed cell volume, wet or dry weights, and chlorphyll *a* estimates. Much less attention has been given to species identification of the standing crop and microscopically determined cell volumes.

This paper compares photosynthetic rates to the volume and species composition of the phytoplankton standing crop for one year in Hodgson Lake, Portage

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County, Ohio. Possible relationships between photosynthetic rates and the seasonal succession of phytoplankton are discussed.

STUDY AREA

Hodgson (Muddy) Lake, part of the upper Cuyahoga River-Lake Erie watershed, is located 3.2 km southwest of Ravenna, Portage County, Ohio. The lake has a surface area of approximately 437 ha and a maximum depth of 21 meters. The original basin was a kettle type depression formed in glacial moraine, but the volume and surface area have been increased to their present dimensions by the construction of a small dam.

TABLE 1

Mean annual chemical analyses, euphotic zone, Hodgson Lake, Ohio 1961, 1963, 1964.

	PPM
Oxygen	10.3
Total Alkalinity	72.0
Total Hardness	175.0
Chlorides	15.7
Silica	1.0
Phosphates	tr
Iron	tr
pH	7.7

Temperatures during the study ranged from 0–25°C in the surface waters, 4–15°C in the lower photic zone (at a depth of six to eight meters), and 4–10°C from ten meters to the bottom. Thermal stratification is prominent from May until October. Ice up to 36 cm thick usually covers the lake from late December until early March. The photic zone extends to approximately ten meters, with the 1 percent light level occurring at a depth of six to eight meters. Values for mean annual euphotic-zone oxygen, total alkalinity, total hardness, chlorides, silica, phosphates, iron concentrations, and pH are shown in table 1.

METHODS

Phytoplankton was sampled two to five times each month from July 1963 to June 1964 at 0.5, 3, 6, and 12 m depths in Hodgson Lake, Ohio. An opaque polyvinyl chloride Van Dorn-type water sampler was used. Each sample was divided into two parts.

One portion of the sample was used to identify the species present and to calculate the volume of the phytoplankton standing crop. The latter estimate was obtained by counting the organisms concentrated from a known volume of water on a Millipore filter (McNabb, 1960) and multiplying by the cell volume of each species. Average cell volumes for each species were determined from cell measurements made with a calibrated ocular micrometer and compound microscope.

The second portion was placed into duplicate 260 ml glass-stoppered, light and dark bottles. Two microcuries of ^{14}C sodium carbonate of specific activity 2.99 mc/mM were added to each bottle. The bottles were then suspended and exposed from sunrise to sunset at the depth from which the phytoplankton had been removed. After exposure, samples were filtered immediately on Millipore 47 mm, type AA filters and radioassayed using a Tracerlab Versamatic V scaler equipped with a 2-inch gas-flow thin-window detector (counting efficiency = 16%). Productivity rates were calculated according to the procedures of Saunders, Trama, and Bachmann (1962) except that, when inorganic ^{14}C precipitation was noted, radioactivity remaining after a dilute acid wash was used in the computations.

Chemical analyses were made according to APHA *Standard Methods* (1961). Light measurements were taken with a GM Mfg. submarine photometer.

RESULTS

Total photosynthesis, cell volumes, and photosynthesis per unit cell volume are shown in table 2. Blue-green algae and diatoms formed over 99 percent of the standing crop at all seasons. *Oscillatoria rubescens* DeCandole was present at all times and usually accounted for over 80 percent of the total cell volume in both upper and lower photic zones. From late April to September, *O. rubescens* accounted for 99 percent of the total cell volume in the lower photic zone (six meters). Other blue-green algae, including *Aphanizomenon sp*, *Anabaena* sp, and *Merismopedia sp*, were abundant in later summer, but their bulk never approached that of *O. rubescens*. Diatoms occurring during the study period included *Cyclotella sp*, *Asterionella formosa* Hass, *Fragilaria sp*, and *Synedra delicatissima* W. Sm. The latter organisms formed a considerable bloom in late March and early April, accounting for up to 20 percent of the total cell volume, but were not present at any other time. *Cyclotella* was present at all times, although no blooms occurred. *Asterionella formosa* also appeared in most samples, and in December formed a small bloom. Many other species were observed during the study, but their volume never approached that of the organisms listed above. Pecora (1966) found approximately 55 species during an annual cycle in Hodgson Lake.

TABLE 2

Total photosynthesis, cell volumes and photosynthesis per unit cell volume, 0–10 m depth, July 1963 to June 1964, Hodgson Lake, Ohio

Month	Photosyn mgC m^{-2} day^{-1}	Cell Vol. mm^3 $Liter^{-1}$	Photosyn/unit Cell Vol. μgC day^{-1} mm^{-3} cells
Jan 1964	5	7.1	.07
Feb 1964	4	8.4	.04
Mar 1964	162	19.5	.83
Apr 1964	491	29.8	1.64
May 1964	1116	65.7	1.70
Jun 1964	2655	88.6	3.00
Jul 1963	802	24.5	3.28
Aug 1963	790	22.2	3.56
Sep 1963	1134	1.4	81.00
Oct 1963	2766	1.6	172.87
Nov 1963	184	3.7	5.01
Dec 1963	61	5.5	1.11
Mean	847.5	26.2	10.52

DISCUSSION

Annual Mean Primary Productivity

Productivity in Hodgson Lake was moderate, but phytoplankton cell volumes were high, resulting in low rates of photosynthesis per unit cell volume (relative photosynthesis). The mean annual productivity of 847 mgC m^{-2} day $^{-1}$ was considerably less than the approximate 2 gC m^{-2} day^{-1} reported by Verduin (1956) for eutrophic western Lake Erie, and somewhat higher than the approximate 400 mgC m^{-2} day^{-1} reported for an oligotrophic marl lake in Indiana (Wetzel 1965). Compared to eleven California and European lakes compiled by Wetzel (1964), mean annual primary productivity in Hodgson Lake is slightly above the median value of 675 mgC m^{-2} day^{-1}. Also compared to seven other European lakes ranging from oligotrophic to eutrophic (Elster 1965), primary productivity in Hodgson Lake lies near mid-range between the approximate 150–1400 mgC m^{-2} day^{-1} extremes (latter values obtained from Elster (1965) by multiplying hourly rates times ten).

Annual Mean Cell Volumes

The annual mean cell volume of 26.2 mm^3 $liter^{-1}$ was somewhat greater than values reported by Elster (1965) for any of seven European lakes and also greater than the average phytoplankton density of 3–6 mm^3 $liter^{-1}$ reported by Verduin (1962) for western Lake Erie. The reason for this is the extremely high concentration of *O. rubescens* occurring in the lower photic zone of Hodgson Lake during thermal stratification (fig. 1). Phytoplankton density at Hodgson Lake appears comparable to that reported from the Wörthersee by Findenegg (1965).

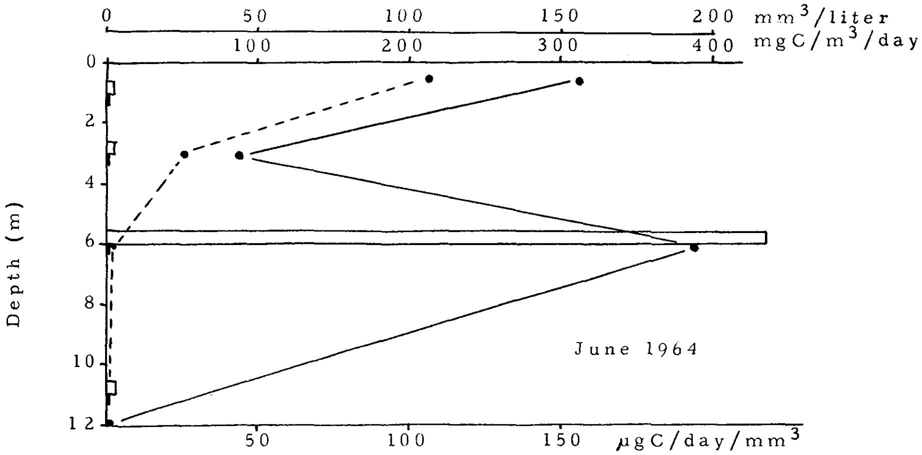

FIGURE 1. Comparison of total photosynthesis (——— lines), relative photosynthesis (- - - - lines), and cell volumes (clear bars—*Oscillatoria rubescens;* solid bars—diatoms). Hodgson Lake, June 1964.

Large, deep, relatively unproductive lakes in temporate regions usually exhibit a rise in total phytoplankton in the spring and early summer, reaching a maximum in summer. In smaller, more productive lakes, there are usually more complicated successional patterns, with maxima and minima occuring throughout the year (Hutchinson 1967). Because of the unusual distribution of *O. rubescens*, total cell volumes reached a maximum during the summer (table 2), as in the large unproductive lakes. However, the oxygen profile (Ruttner 1963), primary productivity, and the presence of *O. rubescens* all indicate that Hodgson Lake is moderately productive rather than unproductive, and probably in the early stages of eutrophy.

Seasonal Productivity—Phytoplankton Relationships

During periods of ice cover (Jan.-Feb.) the phytoplankton was dominated by *O. rubescens*, which accounted for 5–10 mm^3 cells $liter^{-1}$. No pronounced stratification of organisms was apparent. Total photosynthesis and relative photosynthesis were low, the latter amounting to less than 1 μgC day^{-1} mm^3 cell volume.

In March and April, both *O. rubescens* and diatoms, including *Asterionella, Fragilaria, Cyclotella,* and *Synedra* increased rapidly (figs. 2, 3). The increase in diatoms was greater (in proportion to) than the increase in *O. rubescens*, but the diatoms never exceeded more than 20–25 percent of the standing crop. Increased phytoplankton growth was accompanied by both increased rates of total photosynthesis and of photosynthesis per unit cell volume, probably because of more favorable light and temperature conditions. In mid-March, soon after the ice melted, total and relative photosynthesis in the middle and lower photic zones (three to six meters) were approximately double that encountered in the upper photic zone (0.5 m) (fig. 2), although no thermal stratification was evident. A possible explanation is that, while under ice, phytoplankton were dark-adapted throughout the photic zone, and a rapid thaw, as occurred during the study, exposed the organisms to sudden high light intensity, causing photoinhibitions in phytoplankton occupying upper photic levels (Talling 1961). In the lower photic zone, however, illumination was nearer optimal for photosynthesis in the dark-adapted population, resulting in higher photosynthetic rates at six meters.

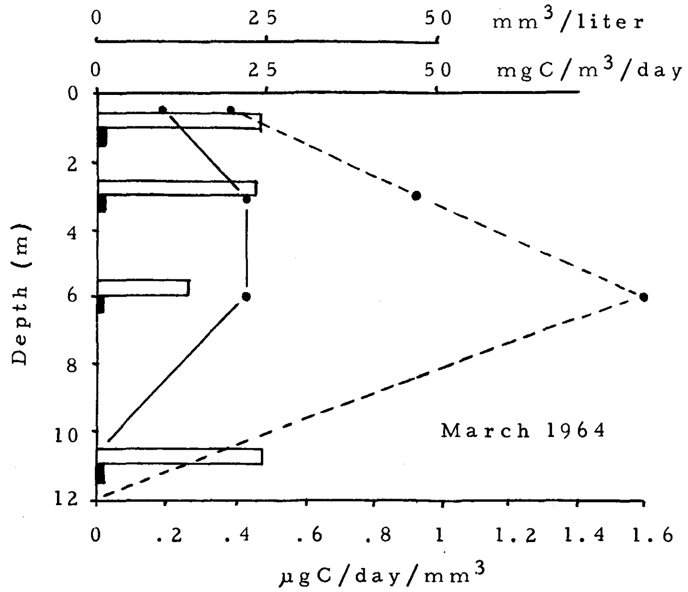

FIGURE 2. Comparison of total photosynthesis (———— lines), relative photosynthesis (- - - - lines), and cell volumes (clear bars—*Oscillatoria rubescens;* solid bars—diatoms). Hodgson Lake, March 1964.

Beginning the first of May, a thermocline developed at six to eight meters, corresponding to the region of one percent incident illumination. Thermal stratification was accompanied by (1) a rapid decline in cell volume in the upper photic zone and (2) a rapid increase in cell volume in the lower photic zone, the result of cells settling from upper levels. Cell volume increased from 27 to 416 mm^3/liter at six meters, while declining from 28 to 3mm^3/liter at 0.5m between 23 April and 4 May. This increase at six meters was due almost entirely to *O. rubescens*, which accounted for up to 99 percent of the cell volume. Although the standing crop declined sharply in the upper photic zone, approximately 80 percent of the remaining crop was also *O. rubescens.*

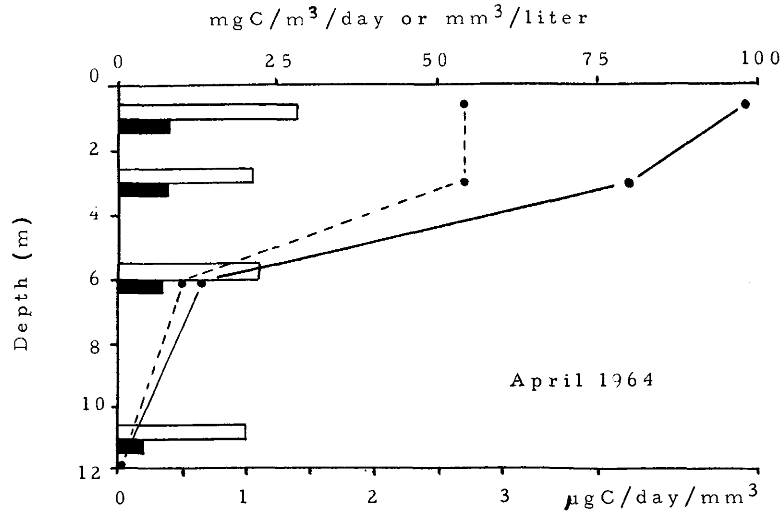

FIGURE 3. Comparison of total photosynthesis (——— lines), relative photosynthesis (- - - - lines), and cell volumes (clear bars—*Oscillatoria rubescens;* solid bars—diatoms, mostly *Synedra delicatissima*). Hodgson Lake, April 1964.

As *O. rubescens* accumulated at six meters, phycoerythrin synthesis increased, causing the organism to become red, while in the upper photic zone they remained brownish-green. Pigmentation variations have been commonly observed in algal cultures (Fogg 1965). In our laboratory, cultures of *O. rubescens* turned brownish-green under high light intensity, but became brownish-red under low illumination. Several workers have reported environmentally induced variations in phycoerythrin-phycocyanin ratios in blue-green algae. Both low illumination (Halldal 1958) and increased green light (Hattori and Fujita 1959; Fujita and Hattori 1960) have been shown to induce formation of phycoerythrin, whereas higher light intensities and more red light stimulates formation of phycocyanins.

In Hodgson Lake, as in most lakes, higher percentages of green light penetrate to six to eight meters than does red light (table 3). The six-to-eight-meter depth also corresponds to the one-to-five-percent white-light level, suggesting that a combination of low intensity green light may induce phytocerythrin synthesis in the *O. rubescens*. Formation of this pigment may permit more effective absorption of the prevailing blue-green light at this depth. This suggestion was made by early investigators as an explanation for chromatic adaptation in marine red

TABLE 3

Light penetration, Hodgson Lake March-April 1964

	Percent light penetration		
Depth	White	Red	Green
0	100	100	100
2	64	32	70
4	21	6	26
6	5	1	7
8	1	0	1
10	0.1	0	0.2
12	0	0	0

algae (Haxo 1960), but Haxo believes that these and other environmental factors interact in a complex way to control the vertical distribution of algae. For example, reduced temperatures in the lower photic zone may favor development of *O. rubescens* at this depth. These organisms appear to thrive best in water below 10°C. In addition to the extensive growth at six to eight meters, they also increased in number during January at temperatures of 1–4°C.

Relative photosynthesis increased at six meters during early June to the level encountered in March, probably as a result of more efficient use of available light following phycoerythrin synthesis. However, these values were considerably lower than those noted in the upper and middle photic zones. Relative photosynthesis in the upper photic levels during May-June was the highest recorded for the year (figs. 1, 4), however; large volumes of *O. rubescens* at six meters gave overall low values for relative photosynthesis at this time (table 2). The standing crop in the upper three to four meters, although small, consisted mainly of *O. rubescens* and *Anabaena* sp. Very few diatoms were present.

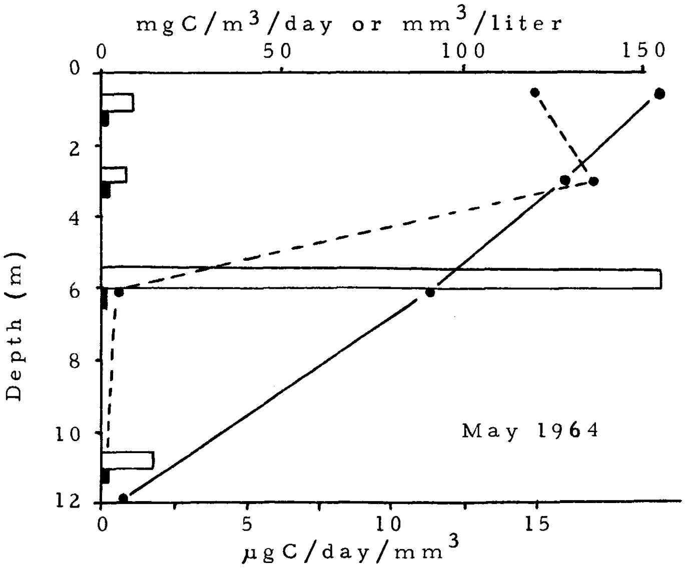

FIGURE 4. Comparison of total photosynthesis (———— lines), relative photosynthesis (- - - - lines), and cell volumes (clear bars—*Oscillatoria rubescens;* solid bars—diatoms). Hodgson Lake, May 1964.

Oscillatoria rubescens was concentrated in the lower photic zone throughout the summer, although in reduced numbers from the June peak. Relative photosynthesis remained fairly constant at 3 μgC day^{-1} mm^{-3} because the rate of photosynthesis dropped to approximately 800 mgC m^{-2} day^{-1} during July and August. Growth in filament length of *O. rubescens* was noted during this period, but because of cell settling and possible zooplankton grazing, a relatively constant population density was maintained.

During September and October, as thermal stratification disappeared, cell volume in the entire photic zone declined to the lowest point of the year (table 2). Absolute photosynthesis increased sharply, resulting in high relative photosynthetic rates. *Oscillatoria rubescens* still accounted for most of the cell volume, but other blue-green algae, including *Anabaena, Merismopedia,* and *Aphanizomenon,* also were abundant. Several investigators have suggested that large algae with low surface area:volume ratios do not assimilate carbon as rapidly as smaller species with higher surface:volume ratios (Rodhe, 1958; Findenegg, 1965). *Oscillatoria rubescens* is a relatively large species and, although it represents over 80 percent of the total cell volume, it may not account for most photosynthesis at this time.

Blue-green algae (mostly *O. rubescens*) continued to increase slowly during the winter under ice cover, reaching approximately 8.4 mm^3 $liter^{-1}$ during February. This growth, accompanied by low rates of photosynthesis, suggests either increased efficiency in use of products of immediate photosynthesis or accelerated utilization of dissolved organic materials as first suggested by Rodhe (1955) and later supported by Fogg (1958).

Findenegg's (1943) data on *Oscillatoria rubescens* in the Keutschacher See, the Längsee, and the Wörthersee, and Eberly's (1966) work in Indiana lakes, indicates that this species behaves in these lakes in much the same manner as it does in Hodgson Lake. That is, it appears to be a cold-water shade plant thriving under ice in winter, then decreasing in the upper photic levels during the spring, and subsequently accumulating in large quantities in the lower photic zone during the summer.

Numerous factors are known to affect seasonal succession of phytoplankton. In addition to temperature and light, turbulence, inorganic nutrients, vitamins, antibiotics, parasitism, predation, and competition play an important role in regulating seasonal cycles (Hutchinson 1967). No attempt has been made in this study to determine the relative effectiveness of each of these factors in explaining the periodicity of phytoplankton in Hodgson Lake.

Diatoms, especially *Asterionella formosa*, also grew briefly in December prior to the winter freeze, forming approximately 20 percent of the total cell volume. Under ice, the population declined to approximately two to four percent of the total until the spring thaw in mid-March. The periodicity of *Asterionella* probably has been studied more intensively than any other phytoplankter. Recent studies performed in the English Lake district by Lund (1949a, b; 1950a, b) and by Lund, Mackereth, and Mortimer (1963) are probably the most extensive undertaken and illustrate the most prevalent type of cycle. It usually consists of a rapid increase in late winter, reaching a pronounced maximum in spring, followed by a rapid decline in early summer. In most cases, the maximum is reached and the decline initiated when the soluble silicate has been reduced to 0.4–0.5 ppm. Considering that *Asterionella* is a true photoautotroph in culture, it seems reasonable to attribute this spring maximum to the increasing illumination at a time when the water is rich in silicate and other inorganic nutrients. Lund's experiments indicate that silica, rather than nitrate or phosphate, probably limits the spring increases.

Autumnal maxima have been observed by Lund (1949b) and by Tucker (1957), among others, but never completely explained. In general these maxima may be attributed to the renewal of nutrients, particularly silicates, in the photic zone, following the autumn overturn. The magnitude of these maxima probably depends upon illumination, which quite often is reduced by turbulence during the overturn. In Hodgson Lake, although no precise measurements were taken, the overturn was accompanied by high turbidities, thus reducing illumination sufficiently to prevent a fall diatom maxima. Under these conditions, silica may have remained in relatively high concentration and then, as the turbidity decreased in December, illumination may have increased enough to trigger the small *Asterionella* pulse observed at this time.

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