SUMMER PHYTOPLANKTON PHOTOSYNTHESIS IN A NORTHEASTERN OHIO GLACIAL LAKE[1]

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ABSTRACT

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Approximately fifty species of phytoplankton were found in Sandy Lake during the summer and early autumn of 1971. Euglenophyta including species of *Euglena*, *Phacus*, and *Trachelomonas* were the dominant organisms frequently accounting for more than 50 percent of the phytoplankton volume. Blue-green algae, especially *Aphanothece nidulans* and *Oscillatoria prolifica*, at least 14 species of green algae, and 14 species of diatoms also appeared in the phytoplankton, but seldom accounted for large proportions of the total cell volume. *Ceratium hirundinella*, *Glenodinium*, and *Dinobryon* appeared in brief pulses during the study and occasionally accounted for large fractions of the total cell volume. The total volume of phytoplankton ranged from 21,500 to 55,800 mm^3 m^{-2}. Mean cell volumes at depths of 1-, 2-, 4-, and 6 m were 7.3-, 6.3-, 4.1-, and 3.5 mm^3 l^{-1} respectively. The daily rate of integral photosynthesis averaged 944 mgC m^{-2} ranging from 210 to 1750 mgC m^{-2}. Relative photosynthesis in the upper photic zone averaged 7.9 μgC mm^{-3} hr^{-1} ranging from 1.2 to 16.9 μgC mm^{-3} hr^{-1}. The most striking feature of the pattern of photosynthesis in Sandy Lake was an abrupt decline and prolonged depression in the rates of photosynthesis after August 23. The major causes of this decline in photosynthesis probably were a reduction in the phosphorus supply and toxic conditions resulting from the diffusion of hydrogen sulfide from the hypolimnion into the epilimnion.

The purpose of this study was to analyze the relationships between phytoplankton photosynthesis, the composition of the summer phytoplankton community and selected physical-chemical factors in a small glacial lake in northeastern Ohio. The rate of photosynthesis in phytoplankton communities is the result of many interrelated physical, chemical, and biological factors including light and temperature conditions, the chemical and physiological state of the phytoplankton standing crop, and various interactions among components of the aquatic community.

Studies of phytoplankton photosynthesis which consider the standing crops seldom include the species composition of the phytoplankton community or provide biomass measurements for component species (Findenegg, 1965). Instead standing crops usually are regarded as homogenous units described in terms of dry weights, fresh weights, packed cell volumes, or chlorophyll *a* content. For a clearer understanding of factors affecting phytoplankton photosynthesis in lakes more information is needed about the composition and biomass of phytoplankton communities in relation to photosynthetic rates. This information is needed especially for lakes in northeastern Ohio where very few studies of this nature have been made.

THE STUDY AREA

This study was conducted in Sandy Lake, a small glacial lake situated within the Cuyahoga River watershed. The lake is located approximately 19 km east of Akron, a few kilometers southwest of the city of Ravenna in Portage County.

The surface of the lake is somewhat oval in shape and covers about 40 hectares at an elevation of 1083 ft (330 m). The single basin is a simple, relatively shallow depression with a maximum depth of approximately 7 m. The water is relatively hard (180–210 ppm) and alkaline

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(75–160 ppm) with hydrogen ion concentrations in the epilimnion ranging from pH 7.4–8.9. The maximum suface temperature is approximately 27°C. A thermocline develops in late spring at a depth of 5–6 m and persists until early September. The epilimnion is well-oxygenated throughout the summer, but the hypolimnion becomes anoxic from midsummer to the autumnal overturn (fig. 1). In addition to run-off from the immediate watershed, water enters the lake from Congress Lake Outlet and Breakneck Creek through a feeder canal. This canal was constructed in the mid-1800's to ensure an adequate water supply for the Ohio Canal system. Water exits the lake through a small outlet to the northeast into Hodgson Lake from where it reenters Breakneck Creek. Twenty-six cottages and homes are located on the north shore of Sandy Lake. At the time of this study wastewater from all dwellings but one had been recently connected to a central wastewater treatment facility that bypassed the lake. Most of the immediate watershed (80–90%) has been cleared of the original deciduous forests for agricultural purposes.

METHODS

Water samples were taken from a single station near the center of the lake from depths of 1, 2, 4, and 6 m. Portions of these water samples were used for determining photosynthetic rates; for identification of the phytoplankton, for determination of phytoplankton biomass; and for analysis of selected physical-chemical properties of the water. Sampling was conducted approximately twice each week between June 28 and October 8, 1971.

Phytoplankton photosynthesis was measured

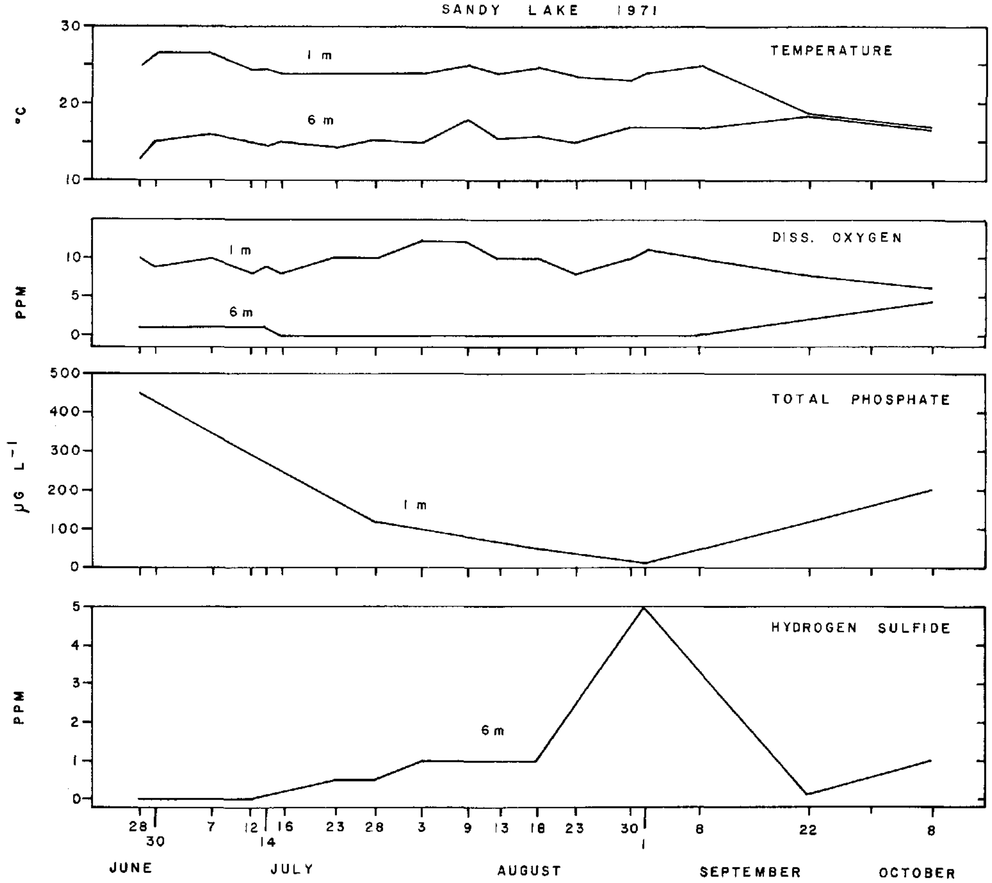

FIGURE 1. Selected physical-chemical conditions in Sandy Lake between June 28 and October 8, 1971.

in situ by the ^{14}C technique (Steeman Nielsen, 1952; Goldman *et al.*, 1969). Aliquots from each sample depth were placed into two 250 ml clear glass-stoppered bottles; 2 μCi of sodium bicarbonate were added; and the bottles were incubated near mid-day for a period of four hours at the depths from which the phytoplankton had been collected. Following incubation the phytoplankton was filtered on 0.8 μm membrane filters, exposed to HCl fumes for 20 minutes to remove inorganic carbon, dried, and radioassayed. Carbon assimilation rates were calculated according to methods used by Goldman *et al.* (1969).

Phytoplankton was identified from living samples and from samples preserved in Merthiolate (Am. Pub. Health Assn., 1971). Brightfield and phase-contrast microscopy at magnifications up to 1000× were used in the identification process. The major taxonomic references used were Algae of the Western Great Lakes Area (Prescott, 1962), and *The Diatoms of the United States* (Patrick and Reimer, 1966).

Phytoplankton biomass was determined from estimates of the volume of phytoplankton present. Volume-based estimates were determined from cell counts for each species and from measured volumes of ten randomly selected organisms of each species. Cell counts were made with a nanoplankton counting chamber (Palmer and Maloney, 1954). Prior to counting phytoplankton samples were concentrated by sedimentation. Some organisms especially several blue-green algae, did not readily settle so an additional 25 ml aliquot was filtered through a 0.8 μm membrane filter. The filter was cleared and the organisms that would not settle were counted on the filter (McNabb, 1960).

Selected chemical-physical analyses of the water were made periodically during the summer. Water temperatures and the concentration of dissolved oxygen, hydrogen ions (pH), and total alkalinity were measured on each sampling date. The concentrations of total phosphates, nitrates, silicates, hydrogen sulfide, and total hardness were determined periodically, but less frequently than other chemical analyses. Methods for all chemical-physical water analyses were in accordance with *Standard Methods for the Examination of Water and Wastewater* (Am. Pub. Health Assn., 1971).

RESULTS AND DISCUSSION

The Phytoplankton Communities

Species composition.—The major groups of algae found in the upper photic zone of Sandy Lake and the quantity (volume basis) of each group are shown in fig. 2. Approximately fifty species of phytoplankton representing forty-one genera were recorded for Sandy Lake during the summer-early autumn study period. These totals did not include one or more species of photosynthetic sulfur bacteria which appeared in the phytoplankton in late summer.

Species of *Euglenophyta* representing the genera *Euglena*, *Phacus*, and *Trachelomonas* were the dominant organisms. Euglenophyta were present throughout the summer frequently accounting for more than 50 percent of the phytoplankton standing crop in either the upper or lower photic zones. *Trachelomonas lacustris* was the single most important species occurring throughout the water column. This organism because of its brownish color may be partly responsible for the brownish color of Sandy Lake water. Species of *Euglena* and *Phacus* were found mainly in the lower photic zone. Because of the motility of euglenophytes, considerable diurnal vertical migrations undoubtedly occurred, but our single near mid-day sampling procedures could not have verified these movements.

Cyanophyta were present throughout the study period and, except for late June, seldom accounted for a large proportion of the total cell volume. In terms of cell numbers, however, blue-green algae were often the dominant organisms. *Aphanothece nidulans* was one of the most abundant blue-green algae forming a relatively dense bloom in the upper photic zone on July 7. One month later *Oscillatoria prolifica* pulsed in the upper photic zone while a moderate-sized population of *O. rubescens* developed in the lower photic zone. Unlike other lakes in the region this metalimnetic bloom of *O. rubescens* was short-lived (Olive et al., 1968; Long, 1971). In late August and throughout September, species of *Merismopedia* were abundant in the lower photic zone and in the upper aphotic zone (6 m). *Anabaena flos-aquae* and *Dactylococcopsis* also occurred frequently in the phytoplankton.

The Chlorophyta of Sandy Lake included at least fourteen species, but on the basis of number and cell volume were of little importance. The major forms included *Phacotus lenticularis* and species of *Chlorella*, *Lagerhaemia*, and *Scenedesmus*.

Two dinoflagellates, *Ceratinum hirundinella* and at least one species of *Glenodinium*, were present during the summer. Characteristically these organisms, especially *Glenodinium*, appeared in brief pulses throughout the summer. At the peak of each pulse they often accounted for a large proportion of the total phytoplankton biomass. At least four such pulses occurred with approximately 2–3 weeks between pulse maxima.

The Chrysophyta in Sandy Lake were represented by fourteen species of diatoms and by one Chrysophycean. In spite of

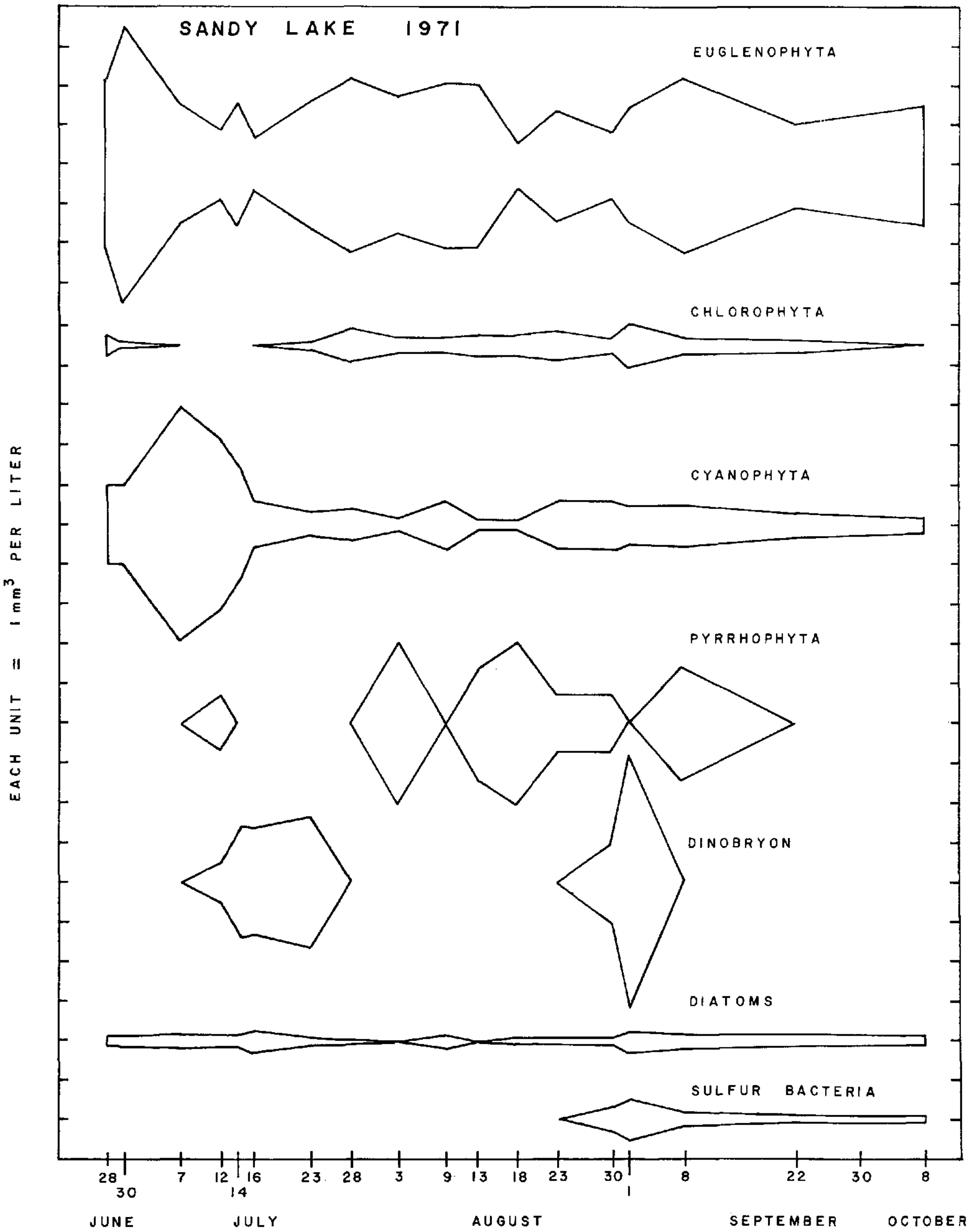

FIGURE 2. Periodicity and volume of major groups of phytoplankton at 1 m depth in Sandy Lake between June 28 and October 8, 1971.

the large number of species present, diatoms never accounted for more than 10 percent of the total phytoplankton volume. Among the most common species were *Melosira italica*, *Melosira granulata*, *Cyclotella meneghiniana*, *Synedra ulna*, *Asterionella formosa*, *Stephanodiscus astrea*, and *Nitzschia palea*. One or more species of *Navicula* and *Synedra* also were noted during the summer. Most of the summer diatom species that occurred in Sandy Lake probably were remnants of much larger spring populations that characterize many temperate zone lakes (Fogg, 1965; Hutchinson, 1967).

Dinobryon appeared in the upper photic zone twice during the summer for periods of approximately two weeks each —once in mid-July and once in late August and early September. On September 1 these organisms accounted for approximately one half of the total phytoplankton volume in the upper photic zone (fig. 2). The behavior of *Dinobryon* in Sandy Lake is similar to its behavior in other lakes of the world (Hutchinson, 1967). In general *Dinobryon* increases in the summer after the major nutrients present in the spring are used by the vernal phytoplankton. In fact large amounts of phosphorus probably inhibit *Dinobryon*. Rodhe (1948) found that 5 mg m^{-3} $P-PO_4$ inhibits *Dinobryon divergens* in culture.

In Sandy Lake the large pulse of *Dinobryon* on September 1 coincided with near depletion of the phosphate supply (fig. 1). The mid-July pulse, however, probably was associated with relatively high levels of phosphates. The latter relationship cannot be verified for certain because phosphate levels were not determined during the pulse; only measurements before and after the pulse were available. In any event the relationship of *Dinobryon* to the phosphate supply probably was complicated by other environmental factors.

Phytoplankton biomass.—The volume of phytoplankton per square meter of surface in Sandy Lake ranged from 21.5 to 55.8 x 10^3 mm^3 (fig. 3). The largest quantities occurred in mid-August and consisted primarily of dinoflagellates and euglenophytes. Total phytoplankton volumes usually were largest in the upper photic zone and gradually diminished with increasing depth. The volume and composition of phytoplankton at four sample depths in Sandy Lake are shown in figs. 4, 5, 6, and 7. Average cell volumes at depths of 1, 2, 4, and 6 meters

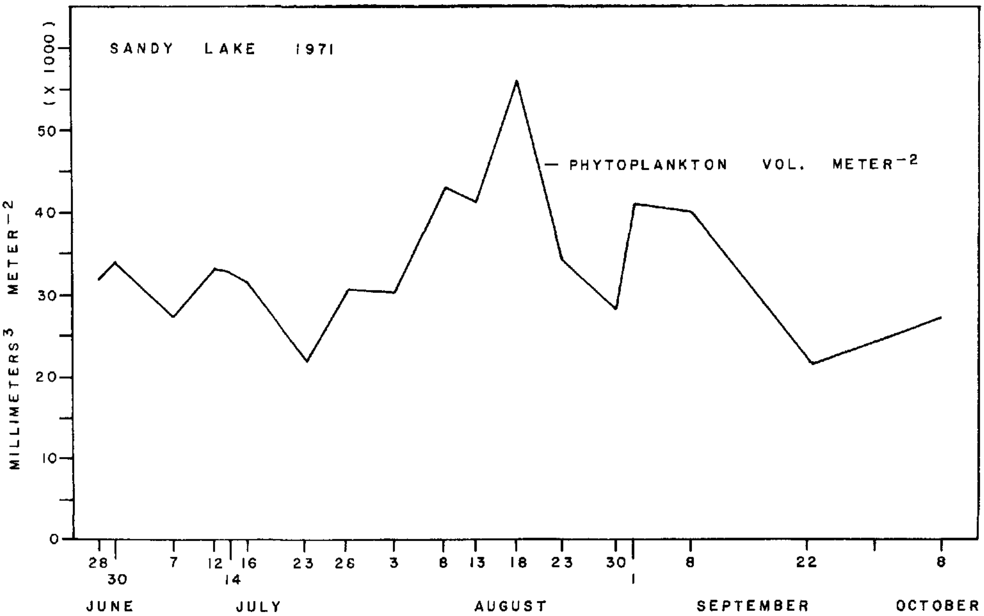

FIGURE 3. Volume-based total phytoplankton biomass m^2 in Sandy Lake.

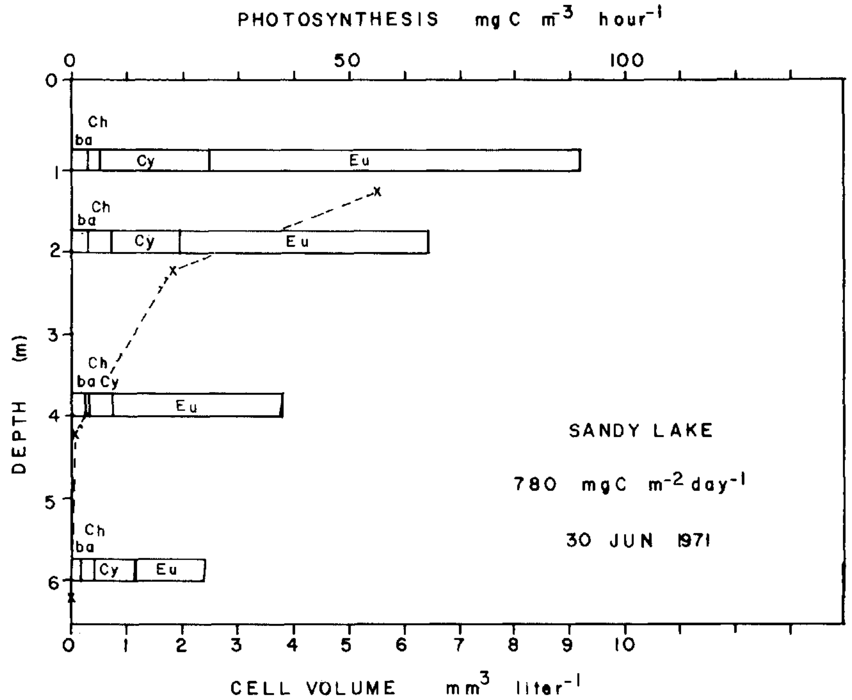

FIGURE 4. Vertical distribution of phytoplankton cell-volumes (bars) and absolute rates of photosynthesis (broken lines) at four depths in Sandy Lake, 30 June 1971. Code: ba = bacillariophyceae, Cr = Chrysophyceae (*Dinobryon*), Ch = Chlorophyta, Eu = Euglenophyta, Py = Pyrrhophyta, Cy = Cyanophyta, B = sulfur bacteria.

were 7.3, 6.3, 4.1, and 3.5 mm^3 l^{-1} respectively. Occasionally large quantities of algae consisting mostly of *Trachelomonas lacustris* and *Ceratium hirundinella* occurred in the lower photic zone (4 m). Because these communities consisted mostly of flagellated organisms the lower photic zone accumulations were quite transitory and seldom persisted from one sampling date to the next. In early autumn following temperature equalization at all depths the phytoplankton was more uniformly distributed in the water column.

In comparison to neighboring lakes that have been studied the summer phytoplankton of Sandy Lake contains larger proportions of Euglenophyta and dinoflagellates and correspondingly smaller proportions of blue-green and green algae (Kraatz, 1931, 1941; Smith, 1961; Marshall, 1965; Pecora, 1966; Heinz, 1971; Long, 1971). According to Palmer (1962) phytoplankton dominated by Euglenophyta is characteristic of hard-water lakes without an outlet. This characterization fits Sandy Lake quite well because the water is relatively hard and because the rate of flow through the lake is usually small despite the presence of an inlet and outlet.

The organic content of Sandy Lake also may be relatively high compared to other lakes in the area because certain species of Euglenophyta are often associated with small bodies of water with high organic content (Hutchinson, 1967). Such conditions probably favor euglenophytes because most species are facultatively heterotrophic and require an outside source of certain vitamins.

The source of nitrogen in Sandy Lake also may be an important factor in the success of Euglenophyta. Sandy Lake was deficient in nitrates which probably limited the growth of nitrate dependent organisms. Apparently alternate sources of nitrogen in the form of organic com-

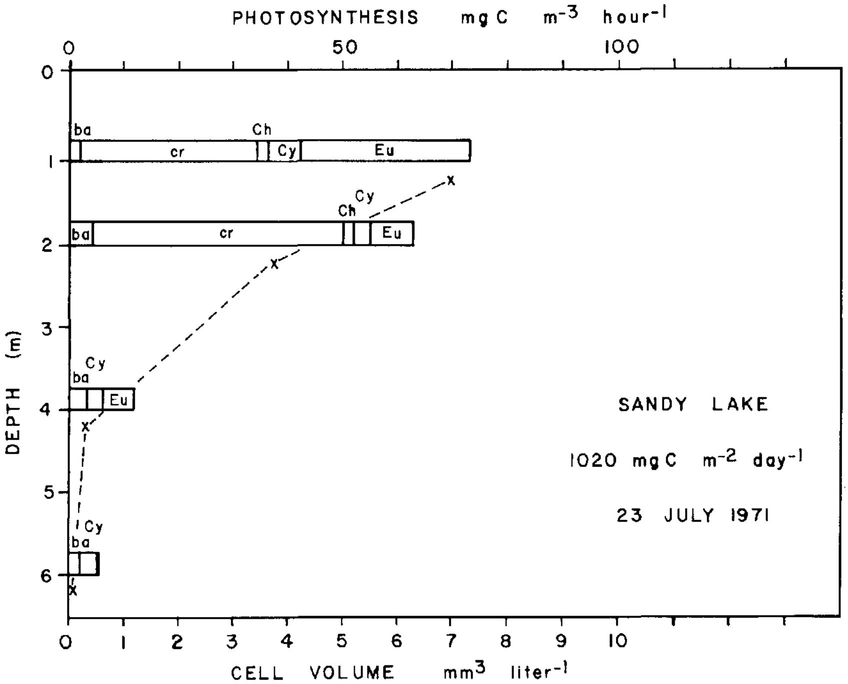

FIGURE 5. Vertical distribution of phytoplankton cell-volumes (bars) and absolute rates of photosynthesis (broken line) at four depths in Sandy Lake, 23 July 1971. See Fig. 4 for code to symbols.

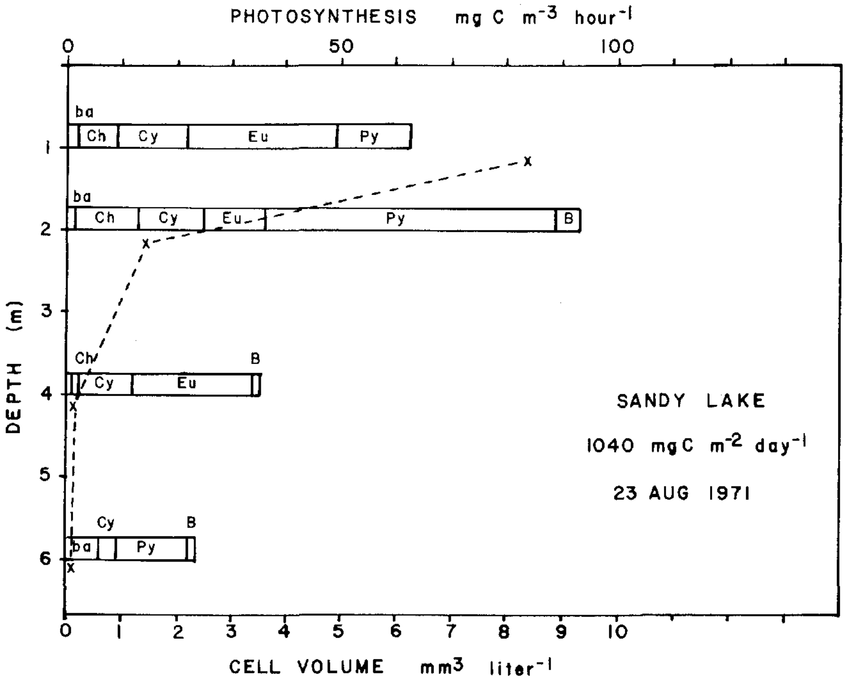

FIGURE 6. Vertical distribution of phytoplankton cell-volumes (bars) and absolute rates of photosynthesis (broken line) at four depths in Sandy Lake, 23 August 1971. See Fig. 4 for code to symbols.

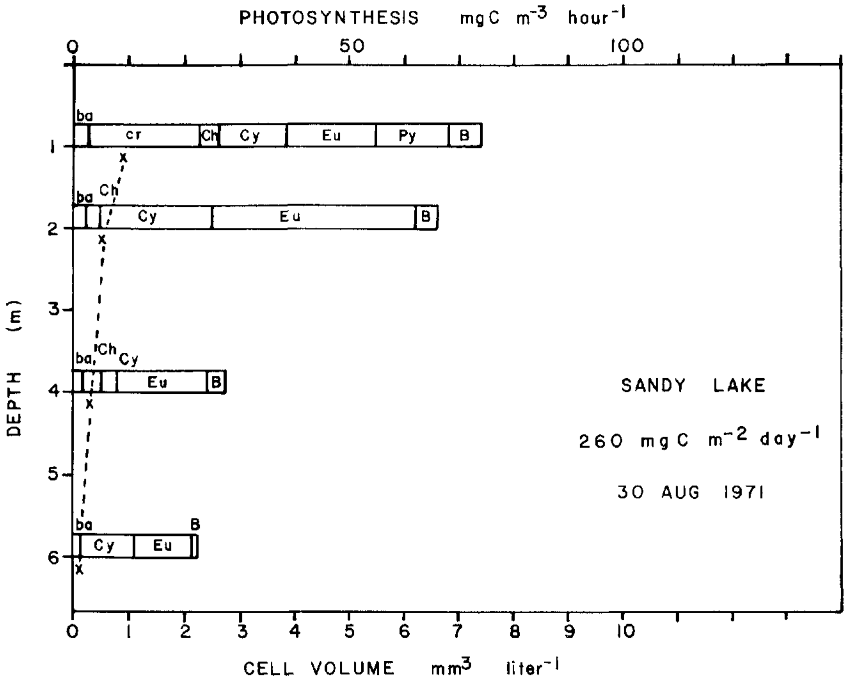

FIGURE 7. Vertical distribution of phytoplankton cell-volumes (bars) and absolute rates of photosynthesis (broken line) at four depths in Sandy Lake, 30 August 1971. See Fig. 4 for code to symbols.

pounds and ammonia were available giving the euglenophytes a slight competitive advantage and enabling them to maintain dominance throughout the summer. Because of species differences, the vertical distribution of algae differs considerably between Sandy Lake and some other lakes in the area. For example metalimnetic blooms of blue-green algae did not develop in Sandy Lake as reported for nearby Hodgson Lake (Olive et al., 1968; Pecora, 1966) and for West Twin Lake (Long, 1971). Also blue-green algae did not dominate the late summer phytoplankton as reported for East and West Reservoirs near Akron (Kraatz, 1931), Turkeyfoot Lake (Kraatz, 1941), Muzzy Lake (Smith, 1961), Aurora Lake (Marshall, 1965), East Twin Lake and West Twin Lake (Heinz, 1971; Long, 1971). In most of these studies the relative importance or dominance of certain species was based on cell numbers rather than cell volume and, therefore, the latter statement needs some qualification.

Phytoplankton Photosynthesis

The daily rate of integral photosynthesis during the study averaged 944 mgC m^{-2} ranging from 210 to 1750 mgC m^{-2} (fig. 8). The highest rates of photosynthesis occurred in July and August and the lowest rates occurred in late August and early September. More than 75 percent of the total photosynthesis usually occurred in the upper 3 meters of Sandy Lake.

Relative photosynthesis followed a similar pattern. In the upper 1 meter photosynthesis per unit volume averaged 7.9 μgC mm^{-3} hr^{-1} ranging from 1.2 to 16.9 μgC mm^{-3} hr^{-1} (fig. 9). The rate at 2 m depth usually averaged about half the rate at 1 m. In general these rates of photosynthesis were comparable to values reported from other lakes in the area and from other north temperate regions of the world (e.g. Jackson and McFadden, 1954; Wright, 1959; Verduin, 1962; Elster, 1965; Findenegg, 1965; Olive et al., 1968; Long, 1971; Kalff, 1972; Hickman, 1973).

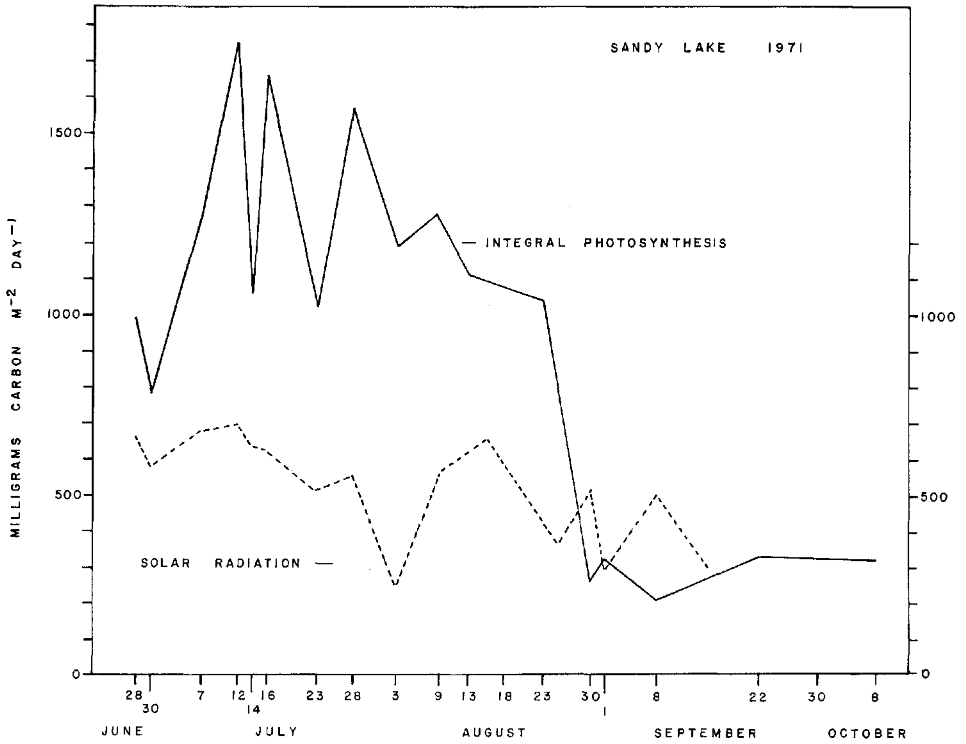

FIGURE 8. Relationship of absolute photosynthesis per square meter and solar radiation in Sandy Lake between June 28 and October 8, 1971. Solar radiation data obtained from U.S. Weather Bureau, Cleveland, Ohio.

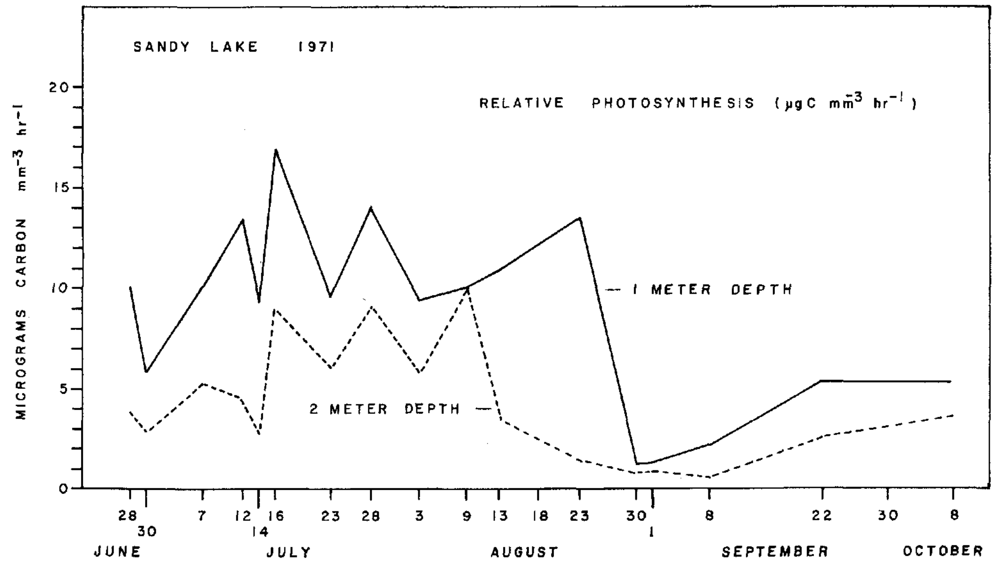

FIGURE 9. Relative photosynthesis (μgC mm^{-3} hr^{-1}) at 1 m and 2 m depths in Sandy Lake.

Many chemical, physical, and biological factors were involved in determining photosynthetic rates. These included light and temperature conditions, the content of nutrients, the nature and physiological state of the phytoplankton, and interactions among the components of the aquatic community. Of the various factors investigated in this study of Sandy Lake, the species composition, the quantity of light available, the nutrient supply, especially phosphorus; and the presence of hydrogen sulfide appeared to be the most important factors controlling the rate of photosynthesis.

The most striking feature of the pattern of primary productivity in Sandy Lake was the abrupt decline and prolonged depression in photosynthesis after August 23 (fig. 8). Prior to late August daily productivity ranged from 760 to 1750 mgC m^{-2}, but after August 23 the daily rate declined sharply, ranging from 210 to 330 mgC m^{-2} through October 8, 1971.

During early and mid-summer the rate of photosynthesis usually fluctuated in proportion to the amount of light available (fig 8). This was an indication that other physical-chemical factors were at least non-limiting, if not optimal, during this period. Over the entire period of study, however, the correlation between integral photosynthesis and light (as solar radiation) was relatively weak ($r = +.44$). This relatively poor correlation was caused by the depletion of phosphates and possibly by the toxic effects of hydrogen sulfide which greatly reduced the rate of photosynthesis in late summer.

The species composition of the phytoplankton during early summer did not appear to greatly affect the rates of photosynthesis. No particular species or combination of species were associated consistently with unusually high or unusually low rates of photosynthesis. For example, relative photosynthesis at 1 m exceeded 10 μgC mm^{-3} hr^{-1} on four occasions during July and August (fig. 9), but each time the phytoplankton community consisted of a different combination of species (fig. 2).

A difference in species composition between 1 and 2 m depths on August 9 probably had an important effect on relative photosynthesis. On this date relative photosynthesis at 2 m equaled the rate at 1 m. Usually relative photosynthesis at 2 m was about half the rate at 1 m in early summer (fig. 9). Since the species composition during this period was similar between levels and the water was well mixed, the difference in photosynthetic rates between depths was the result of differences in light intensity. On August 9, however, *Glenodinium* and *Euglena* accounted for 26.7% and 28.2% of the cell volume respectively at 2 m, but were absent at 1 m. At 1 m *Trachelomonas* and *Oscillatoria prolifica* accounted for approximately 58% of the standing crop, but at 2 m only a few filaments of *O. prolifica* were present and *Trachelomonas* was absent. Thus, despite the attenuation of light at 2 m, relative photosynthesis was unusually high because of the presence of certain photosynthetically active species.

Changes in phytoplankton biomass in Sandy Lake during early summer did not greatly affect absolute or relative rates of photosynthesis. Other studies of temperate zone lakes have shown that absolute photosynthesis rates usually increase proportionally to the algal volume while relative photosynthesis rates decline with larger densities of phytoplankton (Elster, 1965; Findenegg, 1965). Although similar trends were observed in Sandy Lake, correlations between absolute and relative photosynthesis and the volume of phytoplankton at 1 m depth over the entire study period were relatively weak ($r = +.12$ and $-.24$ respectively). The large proportion of motile phytoplankton in Sandy Lake could have been a major reason for these relative poor correlations. Because of their great mobility, flagellated organisms quickly adjust population densities to prevailing light and nutrient conditions minimizing the changes in photosynthetic rates.

In late August and September other factors assumed greater prominence in regulating photosynthesis. Two factors which probably were of greatest importance were a reduced supply of phosphorus and toxic conditions as a result of the diffusion of hydrogen sulfide into the photic zone. From the early summer period of relatively high productivity through September 1, the supply of phosphorus gradually diminished in the euphotic zone (fig. 1). The importance of phosphorus as a limiting-nutrient to phytoplankton productivity is widely known and well documented (Hutchinson, 1957). Considerable attention has been given to the role of phosphorus in lake eutrophication problems (e.g. see G. E. Likens, 1972; Peterson et al., 1974; Schelske et al., 1974; Middlebrooks et al., 1973). In one of the most recent and conclusive studies Schindler (1974) demonstrated the vital role of phosphorus in eutrophication by fertilizing one basin of an experimental lake with phosphorus, nitrogen, and carbon while a second (control) basin, separated by a plastic curtain from the experimental basin, received only nitrogen and carbon. The basin fertilized with all three elements developed a large algal bloom within two months while no increase in algae or species changes were observed in the control basin that received similar quantities of nitrogen and carbon, but no phosphorus.

Despite the demonstrated importance of phosphorus to photosynthesis, the reduction in phosphorus supply in Sandy Lake probably did not solely account for the abrupt decline and prolonged depression in photosynthesis. As shown in fig. 1, relatively high phosphorus levels were restored to the euphotic zone following thermal destratification, which occurred sometime between September 8 and 22. Despite this replenishment of phosphorus, integral photosynthesis remained depressed through October 8 when the study ended (fig. 8).

A second factor which appeared to be implicated in this late summer depression in photosynthesis was the molecular diffusion of hydrogen sulfide from the hypolimnion into the autotrophic zone. Hydrogen sulfide is generally regarded as highly toxic to aquatic animals (McKee and Wolf, 1963) and may be toxic to sulfur bacteria in undissociated form (Baas-Becking, 1925). The compound also is presumably toxic to most algae although we are unaware of any major studies that support this conclusion. Sulfur metabolism of algae has not been studied extensively in blue-green algae (Wolk, 1973). According to Nakamura (1938) photoassimilation of carbon dioxide was not decreased in *Oscillatoria* by 10^{-4} M H_2S, but oxygen evolution was almost eliminated.

In Sandy Lake the concentration of H_2S gradually increased at 6 m depth from early to late summer as shown in Fig. 1. The increase began sometime after July 12 and continued until at least September 1 after a peak of 5 mg 1^{-1} had been reached. Near this peak build-up of H_2S the abrupt decline in integral and relative photosynthesis occurred (fig. 8 and 9).

Direct evidence for the diffusion of H_2S from the hypolimnion into the upper levels of Sandy Lake was obtained on only one occasion, when 0.1 mg 1^{-1} of H_2S was detected at 4 m on August 18. The absence of detectable quantities of H_2S in the epilimnion, however, was not surprising since H_2S can be rapidly oxidized by molecular oxygen and by bacterial metabolism (Hutchinson, 1957). Indirect evidence for the molecular diffusion of H_2S into upper lake levels, however, was indicated by the appearance of sulfur bacteria (fig. 2), first in the hypo- and metalimnion and later in the epilimnion (figs. 6 and 7) and by the decline in relative and absolute photosynthesis on August 23 at 2 m depth where sulfur bacteria were present while photosynthesis at 1 m increased in the absence of sulfur bacteria (figs. 6 and 9).

During early summer relative photosynthesis at 1 and 2 m nearly always remained directly proportional. The greater rates of photosynthesis at 1 m usually were the result of greater light intensity at 1 m, because most other environmental conditions at 1 m were similar to conditions at 2 m. Also during early summer the species composition usually was similar between levels (figs. 4 and 5). For these reasons the divergence in rates of photosynthesis between depths probably is best explained by the presence of a toxin such as hydrogen sulfide at the 2 m depth. This conclusion was further supported by the appearance of photosynthetic sulfur bacteria at 2 m on August 23 and by their absence at 1 m (fig. 6).

Sulfur bacteria were not observed in the phytoplankton until August 23. On that date these organisms accounted for a small proportion of the phytoplankton at 2, 4, and 6 meters (fig. 6). By August 30 sulfur bacteria were present throughout the water column and for the remainder of the study period these organisms accounted for an important proportion of the phytoplankton (fig. 7). The appearance of sulfur bacteria at 1 m on August 30 coincided with the sharp drop in photosynthesis at 1 m on that date (fig. 7). Sulfur bacteria remained in the phytoplankton through October 8.

These results indicate that H_2S may play an important role in determining the pattern of photosynthesis in small dimictic lakes. For example, it may prevent the appearance of the autumnal phytoplankton maximum that often occurs in temperate zone lakes in response to nutrient enrichment following the fall overturn. Prevention of an autumnal phytoplankton maximum probably would result in a seasonal phytoplankton cycle with a single spring or early summer peak. This contrasts with Hutchinson's (1967) speculation that a single phytoplankton pulse, "is characteristic of large, deep, cold, unproductive lakes," which presumably lack physical mechanisms for enriching the autotrophic zone with nutrients. Further studies of Sandy Lake on a year round basis will be necessary to adequately establish the existence of a single annual phytoplankton pulse.

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