PHOTOSYNTHESIS AND RESPIRATION

OF THE PHYTOPLANKTON

IN SANDUSKY BAY

DISSERTATION

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By

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INTRODUCTION

The present paper concerns a study of photosynthesis and respiration of the phytoplankton in Sandusky Bay, conducted from February 2 to June 18, 1954. S_andusky Bay, a drowned embayment, has conditions of great turbidity that are peculiar to itself and in contrast to those of western Lake Erie. Because of the important role of photosynthesis in the energy relations of the aquatic environment, an intensive study of this process was considered desirable under these conditions.

Laboratory facilities were established at Winous Point, located at the point of a peninsula projecting into the upper Eay. At this position the Eay is approximately one mile in width and the water is essentially a mixture of the effluent of the tributaries with that of the embayment.

Sandusky Eay lies in Ottawa, Sandusky and Erie Counties in northern Ohio. It is the principal indentation of the southern shore line of western Lake Erie, Figure 1. The Bay is approximately 14 miles in length and has an average width of nearly 4 miles. The long axis lies nearly in an east-west direction and consequently is exposed to the maximum influence of the prevailing winds. The shore line is characterized by great regularity, there being 0.788 mile of shore line per square mile of area (Wil-



Figure 1

A map of Sandusky Bay modified from the U.S. Lake Survey Map (1949) by the Corps of Engineers of the U.S. Army. The location of Winous Point is indicated by (x). Tributaries flowing into the Bay are (1) Muddy Creek, (2) Sandusky River, and (3) South Creek. son, 1938).

The Bay is crossed midway by the Bay Bridge causeway which comprises a land-fill with openings for the passage of water. The Bay is shallow, seven feet (2.1 m) being the maximum depth shown by the topographical map of the U. S. Geological Survey (1901) and verified by Wilson (1938); 33% of the basin has a depth between 6 and 7 feet. The upper portion of the Bay (west of the bridge), with which this study is concerned, has an area of 27.97 square miles, a maximum length of 7.7 miles and an average width of 3.7 miles (Wilson, 1938). The average depth of water in the vicinity of Wincus Point is approximately one meter; however, due to frequent strong seiches the depth may vary from one half meter to two meters.

A basin as long and shallow as Sandusky Bay, lying in the direction of the prevailing winds, and with low, regular shore lines, is subject to considerable disturbance of the water. These disturbances bring bottom sediments into suspension and attack the clay banks along both the north and south shores. During a "blow" the water becomes very turbid. Most of the shore line has clay banks, a small portion has superficial gravel or stone rip-rap cover (Langlois, 1954). Rapid erosion of the clay banks along the north and south shores is evidence of the effectiveness of the attack. There are only a few small patches of

rooted vegetation remaining in the Bay.

Three converging tributaries discharge their effluents into the upper end of the Bay. The Sandusky River is the principal tributary, the others are Muddy Creek and South Creek. The drainage area of the Sandusky River is 1421 square miles (Langlois, 1954), and lies in fertile, agricultural soils which formerly comprised the extinct glacial Lake Maumee basin. The total discharge (secondfoot-days) of the Sandusky River for the period October 1950 to September 1951 was 507,624 and the total load of suspended sediment for the period was 269,024 tons. Large volumes of available nutrients, eroded from the agricultural soils, are carried into the Bay (Lake Erie Pollution Survey, 1953).

Considerable marsh land surrounds the upper end of the Bay and this is the only portion of the shore line with any significant amount of rooted aquatic vegetation. Small bays and open pockets in these marshes provide excellent cultural grounds for plankton which are carried into the Bay and eventually reach the waters of Lake Erie.

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METHODS

The method used for determination of rates of photosynthesis and respiration was described by Verduin (1951). In brief, it consists of measuring the change in pH of water samples upon removal of carbon dioxide by photosynthesis or upon evolution through respiration. The equilibrium equations published by Moore (1939) and the nomographs by Dye (1944) provide the theoretical basis for the determinations of carbon dioxide exchange. Verduin has observed (unpublished) that Dye's nomographs do not give a true picture of total carbon dioxide change in waters containing substances of considerable buffering effect. Therefore, an actual buffer-curve was constructed by stepwise titration of a liter of the water sample with NaOH of known normality; the relationship so established was used in computing CO2 change.

A pail of water of approximately ten liters, removed from the surface of the Bay at 8 am, provided the water to

fill the series of test bottles and also the sample for the estimation of the phytoplankton population. The temperature of the water and the initial pH were immediately recorded.

The capacity of the test bottles was 140 ml. glass stoppered, and they were filled by being submerged and stoppered under water in order to eliminate air bubbles. Seven clear and two blackened bottles were used. After filling, each bottle was attached in a horizontal position to a cord and suspended in the Bay with the bottles at 0.1 m intervals in a vertical series at such a place that they received unobstructed exposure to the light. The first bottle was at the surface of the water and the two black bottles were at the bottom of the series. The support, to which the cord was fastened, was anchored to the concrete pier, except on those occasions when seiches would flood the pier. At such times the bottles were suspended from a bridge.

The experimental run was for six hours (9 am to 3 pm). The bottles were then removed from the Bay, submerged in a pail of Bay water to prevent change in temperature, and carried to the laboratory where the pH (average of three determinations) was recorded for each bottle. The pH and the temperature of the open water were also taken at the end of the experimental run so that

apparent photosynthesis in the open water could be compared with that of the closed system in the test bottles. - : : -

Using standard water-sampling bottles of 300 ml., samples of water were taken at 8 am with a modified Hale's water sampler (Welch, 1948) for the determination of dissolved oxygen, free carbon dioxide, phenolphthalein and methyl orange alkalinities (Standard Methods for the Examination of Water and Sewage.- 8th Ed.).

General weather conditions, including temperature, wind direction and velocity, precipitation and light conditions were observed and recorded.

Light intensity at the surface of the water and at O.1 m intervals were measured at 10 am and at 2 pm by means of a Weston photronic cell, Model 256 RR, enclosed in a water-ticht case which was lowered into the water by a water-proof electric cord. The electric impulse was recorded in microamperes from readings of an ammeter. The light intensities were plotted on semi-log paper and the decimal reduction distance (DRD), or depth to which 10% of the surface light penetrates, was recorded for each experimental run.

About midway through the period of investigation, it became apparent that a simultaneous experimental run for the measurement of oxygen exchange should be instituted as a check on the carbon dioxide data. Consequently, a series

of three water-sampling bottles, one of which was lightproof, was filled with the sample water and suspended in the Bay for a six-hour experimental run. One bottle was held at the surface, another at 0.2 m, and the blackened bottle was lowered to the bottom. All dissolved oxygen analyses were made by the Winkler method (Standard Methods for the Examination of Water and Sewage .- 8th Ed.). Considerable difficulty was encountered at first in correctly determining the amount of dissolved oxygen. Later, it was discovered that the formula for the titration reagent, sodium thiosulfate as described by Welch (1948) "6.205 Na2S203" was in error, when compared to the formula for sodium thiosulfate prescribed by Standard Methods for the Examination of Water and Sewage .- 8th Ed., as follows: "6.205 g. of Na₂S₂O₃•5H₂O". The dissolved oxygen computations were 50% too low until correction was made for this reagent.

At first, estimation of the phytoplankton population was attempted by filtering a measured liter of sample water through a No. 25 silk bolting cloth filter. The filter was washed with 10 ml. of distilled water and one milliliter of the concentrate was placed in a Sedgwick-Rafter cell. Ten fields were counted by using a Whipple ocular counting disc, averaged, and 3-dimensional measurements made of the abundant species (Welch, 1948). It was soon

apparent that this method was not accounting for a significant portion of the population, as it was observed that the most abundant organisms were unicells and too small to be retained by the filter. These were so abundant that a direct count could be made from one milliliter of water in the Sedgwick-Rafter cell. Consequently, the phytoplankton population was estimated volumetrically (μ^3 per liter) by adding the count of colonial and filamentous forms obtained from the concentrated sample to that of the unicells obtained by the direct method. All zooplankters were ignored in this study.

The total suspensoids and ash-free dry weight of organic matter per liter were determined gravimetrically by centrifuging a liter of the sample water in a Foerst centrifuge, drying the concentrate in a constant-temperature electric oven at 60° C, weighing, igniting and reweighing (Welch, 1948). For these weighings a chemical balance with a sensitivity of 0.1 mg. was used. To correct for organic and inorganic matter in solution in the Bay water, a blank was run using the same amount of centrifuged water as was used to transfer the concentrate from centrifuge to crucible.

RESULTS

The dissolved oxygen in the Bay water ranged from a maximum of 14.25 ppm in February at 0.0° C to a minimum of

5.92 ppm in June at 25.0° C, and averaged 10.3 ppm, or 88.6% of saturation.

The initial pH varied from day to day, the minimum of 7.74 was recorded in April and maximum of 9.06 in early March, with an average of 8.25 for the period. Free carbon dioxide was present when the pH dropped below 8.3 and varied from 0.0 to 11.0 ppm. During the period of March 26 through April 29, the pH was consistently low and was associated with the presence of free carbon dioxide. Aside from this prolonged period, free carbon dioxide was intermittently present throughout the entire period.

The alkalinity of the Sandusky Bay water is due almost entirely to bicarbonates. The methyl orange alkalinity varied from 79 ppm to 210 ppm and averaged 132 ppm. The maximum was recorded on February 5, after which the total alkalinity showed a steady decline until mid-April, then an increase to a relatively consistent average to the end of the study. Only once did the total alkalinity drop below 100 ppm, April 19, when the DRD was 0.11 m, suggesting an important injection of turbid water.

Normal carbonate values were irregular from week to week and ranged from 0.0 to 15.0 ppm. There may be experimental error involved here due to the difficulty of judging the end-point in the color change. Invariably there was no measurable phenolphthalein carbonate below

pH 8.3. Normal carbonates were consistently absent from March 26 through May 5, then present until May 28, after which they were intermittently present.

The waters of Sandusky Bay are characterized by high turbidity. This condition is primarily due to (1) wind and resulting wave action which erodes the clay shore lines and causes a resuspension of bottom sediments in the shallow basin, and (2) the silt and detritus-laden discharge of the tributaries. Throughout the period of the study, the decimal reduction distance varied from 0.03 m to 0.92 m and averaged 0.36 m.

The temperature of the water was uniform from surface to bottom. There was no thermal stratification. Water temperatures approximated that of the atmosphere within a few degrees.

Gravimetric determinations of total suspensoids and their ash-free dry weight began the first week of May and continued to the end of the study. The data obtained on May 3 followed a period of precipitation and high winds, resulting in extreme turbidity. The total oven-dry suspensoids for this day were 1128 mg. per liter and the ashfree dry weight of organic matter was 300 mg. per liter. This day was exceptional during this part of the study, and it was assumed that the major portion of the organic matter consisted of non-living detritus, hence these

weights are not included in the averages during this seven weeks. The oven-dry suspensoids varied from 30.0 to 233.8 mg. per liter; the net ash-free dry weights ranged from 6.0 to 27.8 mg. per liter with an average of 11.78 mg.

In figure 2, the rates of total photosynthesis (micromoles CO_2 absorbed per hour per $10^{10}\mu^3$) on five different days are plotted against light intensity. Comparing the data points of the different days, there is a rather wide scatter, the highest curve showing maxima about 2.5 times the values of the lowest curve. The data for each day present a fairly smooth curve. All the curves show some degree of inhibition at the surface, regardless of the surface light intensity. In each case the maximum rate appears in the second bottle of the series 0.1 m below the surface. The rates on any single day cannot be considered a representative sample, but the mean of several days represents a more reliable estimate of average performance.

In figure 3, the photosynthetic rates, based on micromoles CO₂ absorbed per mg. ash-free dry weight of suspensoids for the same five days as in figure 2, are plotted against light. In this graph, similar curves appear but the scatter is reduced considerably. The maxima of the highest curve being only 1.7 times those of the lowest curve. These data suggest that ash-free dry weight of





Total photosynthesis (μ moles CO₂ absorbed /hour /10¹⁰ μ^3) graphed against light (μ amps Weston photronic cell x 10⁻⁵). The broken lines represent rates on five different days. The solid line indicates the average of the five days.



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Total photosynthesis (μ moles CO₂ absorbed /hour /mg ash-free dry weight) graphed against light (μ amps Weston photronic cell x 10⁻³). The broken lines represent rates on five different days. The solid line indicates the average of the five days.

suspensoids was a better index of photosynthetic capacity than was the volumetric standing crop of phytoplankton for these five samples.

Total photosynthesis, as based on carbon dioxide consumption, is graphed against temperature in figure 4. Means are indicated by open circles. The average photosynthetic rate for the temperature range 0.0° C to 10.0° C was 8.22 µ moles CO2 removed per hour per 1010µ3. The average rate for the temperature range 15.0° C to 25.0° C was 14.01 μ moles per hour per $10^{10}\mu^3$ or roughly twice the rate at the lower temperatures. Both of these rates are associated with large standing crops; however, they are related to different communities, the former being nearly a pure stand of Cyclotella and the latter predominately Melosira. The photosynthetic rates for the temperature range 5.0° C to 15.0° C average much higher than the rates on either side of this interval and apparently are not attributable to temperature. They were observed during a period of extremely low populations and low decimal reduction distances.

Figures 5 and 6 show photosynthesis rates per $10^{10}\mu^3$ per hour graphed against standing crop of phytoplankton per liter. In figure 5 the rates are determined from CO₂ change, and in figure 6 the rates are based on O₂ change. The scatter diagrams in these figures are essentially



Figure 4

Relationship of CO₂ removal (μ moles /hour /10¹⁰ μ^3) at optimal light intensity to temperature °C. Means are indicated by open circles.





Total photosynthesis (μ moles CO₂ absorbed /hour /10¹⁰ μ^{3}) at optimal light plotted against the volume of phytoplankton naturally present in one liter of water (μ^{3} /liter/ x 10⁻¹⁰).



Figure 6

Total photosynthesis (μ moles O_2 evolved /hour /10¹⁰ μ^3) at optimal light graphed against the volume of phytoplankton naturally present in a liter of water (μ^3 /liter/ x 10⁻¹⁰).

alike. indicating that these two separate methods of determining photosynthesis yield similar estimates. The average values (open circles) were used in drawing curves, and the high values mentioned below, which go off scale, justify the upward extensions of the curves. The means show a gradual downward slope over most of the graph but a sharp bend and a rapidly ascending rate appears at the population level of about 0.3 x $10^{10}\mu^3$. The data indicate an inverse ratio between photosynthesis rates and the standing crop. The rates approached phenomenal values during the periods of extremely low populations. The following sequence of rates were obtained on a sequence of days from April 20 to May 3: 323.0, 632.0, 356.0, 904.0, 711.6 micromoles CO2 removed per 10¹⁰µ3 per hour. The average photosynthetic rate for the entire period, inclusive of the above high rates, was 74.0 micromoles per 10¹⁰µ³ per hour. Excluding the period of high rates, the average rate was 15 micromoles CO2 removed per 10¹⁰µ3 per hour. The ratio of CO_2 consumed to O_2 evolved (CO_2/O_2) was 0.87.

Photosynthesis rates were also computed per mg. of ash-free dry weight of suspensoids. The rates so expressed varied from 1.05 to 3.45 micromoles CO₂ absorbed per hour, and averaged 2.4. On the basis of oxygen evolution, the rates ranged from 0.49 to 3.33 micromoles O₂

per hour, and averaged 2.3. The photosynthetic quotient (CO_2/O_2) was 1.04.

In figure 7, total photosynthesis (μ moles CO₂/hour/ liter of water) is plotted against ash-free dry weight of suspensoids. These data were obtained during the period May 5 to June 18. The photosynthetic rates in experimental bottles ranged from 14 to 42 micromoles per hour per liter, with an average of 26. A line drawn through the means of the scatter-diagram indicates that the relationship appears linear; a correlation coefficient of 0.604 was obtained, and this is statistically significant at the 5% level. Correlation of CO₂ consumption with standing crop was 0.388; of O₂ evolution with standing crop was 0.457. The broken line shows the influence of one low reading taken subsequent to a storm, when total suspensoids were unusually high.

The rates of apparent photosynthesis in the open water for the period indicated above were calculated from the initial pH and from the pH taken six hours later. This varied from a -5 to a +38 micromoles CO_2 per hour per liter and averaged 12. For the entire period, February to June, the average total photosynthesis at optimal light in the experimental bottles was 17 micromoles CO_2 consumed per hour per liter, and the average apparent



Figure 7

Total photosynthesis (μ moles CO₂ absorbed /hour /liter) at optimal light graphed against ash-free dry weight of suspensoids in water (mg. per liter).

photosynthesis was 13. These data indicate close agreement between changes in the open water and changes in the experimental bottles, with apparent photosynthesis accounting for about three-fourths of total photosynthesis.

The euphotic zone, or depth to which 1.0% of the surface light penetrates, comprised approximately 70% of the water mass, on the average. For the period of May 5 to June 18, the average photosynthesis rate within the euphotic zone was 12 micromoles CO_2 per hour per $10^{10}\mu^3$ and 2 micromoles per mg. ash-free dry weight. The average for the total water mass was 5.9 micromoles CO_2 per hour per $10^{10}\mu^3$ and 0.9 micromoles per mg. ash-free dry weight.

Figures 2 and 9 show respiration rates per $10^{10}\mu^3$ graphed against standing crop. In figure 8 the rates determined from CO₂ change are portrayed; in figure 9 the rates represent O₂ changes. Again, the average values (open circles) were used in drawing the curves, and the high values go off scale, justifying the upward extension of the curves. A comparison of these figures shows a much larger scatter in the CO₂ data than in the O₂ data. The shape of the curve in both graphs is similar and contains the same sharp increase at low populations that was observed in the photosynthesis data, but the level of the CO₂-based curve lies distinctly above













that of the O₂-based curve, indicating that respiration rates based on CO₂ changes are several times higher than those based on O₂ change. The average CO₂ evolution was $4.72 \ \mu$ moles/hr/10¹⁰ μ^3 ; O₂ consumption was 1.7 μ moles/hr/ $10^{10}\mu^3$, giving a respiration quotient (CO₂/O₂) of 2.7. When related to ash-free dry weight of suspensoids, the average CO₂ evolution was 0.887 μ moles/hr/mg; the O₂ consumption was 0.267 μ moles/hr/mg, and showed a respiratory quotient of 3.3.

In figure 10, respiration rates relating to oxygen consumption per hour per $10^{10}\mu^3$ are plotted against temperature. A line drawn through the means indicate that the rates of oxygen consumption decrease with increasing temperature. This is somewhat surprising because temperature increases are usually associated with increased metabolic activity.

The time distribution of the standing crop is portrayed in figure 11. The study began with the standing crop receding from the crest of a pulse, followed by a steady decline to very low levels in April, then a rather rapid rise to a maximum in mid-June. The configurations of the population and DRD curves are similar and suggest that the standing crop is significantly influenced by light supply.

Figure 11 also shows the decimal reduction distances against time. This curve reflects the extent and changes





Respiration (μ moles 02 absorbed/hour/10¹⁰ μ^3) graphed against temperature ^{o}C .





Comparison of phytoplankton populations $(\mu^3/\text{liter/x }10^{-10})$ and decimal reduction distance (DRD) in meters. Each point on the graph represents the average of three determinations made during a week. The standing crop is indicated by the solid line and light penetration by the broken line.

in turbidity. Light penetration was at a maximum in February; a sharp decline was followed by a moderate rise in early March. Both of these crests were associated with an ice sheet and the declines were related to the disappearance of the ice, exposing the water to wind influence. Maximum turbidity and the minimum of light penetration occurred in April, caused by strong winds, precipitation and the resulting turbid effluent of the tributaries. Week to week fluctuations prevailed through May into June but with general lessening of turbidity accompanied by increasing light penetration.

The light absorption coefficient was calculated by the application of the Lambert-Beer's Law to the data obtained, beginning with the first week of May. This varied from 0.07 to 0.15 and averaged 0.12 for the period. The average value of this coefficient was very close to the average reported for Lake Erie (Verduin 1954), although the concentration of suspensoids is 10 times greater in Sandusky Bay than in western Lake Erie.

The distribution of phytoplankton populations in relation to decimal reduction distances is portrayed in figure 12. Fopulation means are plotted for each 0.1 m interval. This graph reveals a positive correlation of the standing crop with light penetration between abscissa values of 0.0 - 0.4, but beyond this point the correlation





Population of phytoplankton $(\mu^3/\text{liter x 10-10})$ plotted against decimal reduction distance (DRD) for the period February 2 to June 18. Means for each 0.1 m are indicated by open circles.

between light penetration and standing crop disappears. These data suggest that when DRD is reduced to less than one-third of the total depth, light becomes severely limiting and the size of the standing crop is largely determined by light penetration, but when the DRD is greater than one-third of the water column, factors other than light supply exert a controlling influence on the size of the standing crop.

The average population for the temperature range 0.0° to 10.0° C was l.l x $10^{10}\mu^3$ and Cyclotella was the predominant genus. For the range of $15.0^{\circ} - 25.0^{\circ}$ C, the average population was $2.4 \times 10^{10}\mu^3$ and Melosira was the major component.

At the start of this study on February 2, the phytoplankton population apparently holdeen or was at the crest of a pulse as the crop was $2.54 \times 10^{10} \mu^3$ per liter. Minety three percent of the crop consisted of Cyclotella, the largest component of which was identified by the author as Cyclotella michiganiana Skvortzow and this identification was confirmed in private communication by L. H. Tiffany. This genus was represented by 25 million cells per liter. The low crop in April, 0.007 x $10^{10}\mu^3$ per liter, comprised a mixture of diatoms with 36,000 cells per liter. The June pulse attained a crest of 5.73 x $10^{10}\mu^3$ per liter of which Melosira varians C. A.

Agardh and M. granulata (Ehrenberg) Ralfs. comprised 65% of the population with 5,150,000 units per liter (100 u in length equals 1 unit).

The Bacillariophyceae comprised 96.7% of the February crop and 93.5% of the June crop. The phytoplankton population, while abundant in number of individuals, showed a scarcity of genera. In addition to the two predominant genera mentioned, the following genera of diatoms were present in lesser fractions; Asterionella, Tabellaria, Fragellaria, Navicula, Gyrosigma, Pinnularia and Synedra.

The Chlorophyceae were represented by Pediastrum, Actinastrum, Staurastrum, Coelastrum, Tetrastrum, Scenedesmus, Ulothrix, Eudorine and Closterium. These represented less than 1% of the plant volume present.

Oscillatoria, Microcystis and Aphanizomenon were the only genera of the Myxophyceae. Euglena, Phacus and Lepocinclis of the Euglenophyceae were fairly common in early spring; Dinobryon of the Chrysophyceae was observed at the lower temperatures; and Peridinium was the only representative of the Dinophyceae.

DISCUSSION

In the respiration graphs, figures 8 and 9, the discrepancy between carbon dioxide evolution and oxygen consumption poses a problem upon which the author can only speculate. Because of the photosynthetic rates for carbon

dioxide consumption and oxygen production (figures 5 and 6) show a ratio near unity, one would expect a similar correlation of respiratory exchanges. The data indicate that a condition, or combination of factors, results in appreciable changes in pH either (1) through CO, production in excess of 02 consumption, or (2) the formation of some other acid, or (3) a non-biological chemical reaction that produces a drop in pH during the six-hour enclosure in the black bottles. This phenomenon has not been recorded be-Throughout this period, average to excessive turbifore. dity prevailed, affecting high concentrations of organic and inorganic suspensions from the bottom sediments. The situation suggests release from the bottom muds of heterotrophic bacteria active in the fermentation of organic matter with the production of CO2, or some other acid (Henrici 1939). Little is known regarding the extent of bacterial populations in bottom muds or of the magnitude and quality of their metabolic products. The reports of Beaver (1942) and Weeks (1943) on the bacteria of Lake Erie do not appear to be pertinent to this study.

The effect of the difference between O_2 consumption and CO_2 production upon estimates of net photosynthesis (total photosynthesis minus respiration) is that the rates computed from CO_2 data will be much smaller than rates computed from O_2 data. For example, net photosynthesis

for the entire water mass computed from CO_2 data is -66 micromoles per liter per day and from O_2 data +77 micro-moles per liter per day. More investigation is needed in this area of possible bacterial influence on rates.

In figures 5 and 6, the phenomenon of sharply increasing photosynthesis per $10^{10}\mu^3$ appears with low levels of standing crop and the entire curve shows an inverse relation to the phytoplankton population. For several weeks during the summer of 1953, studying samples taken from Fut-in-Bay, I observed similar inverse ratios between photosynthetic rates and standing crop with rapidly rising rates associated with low populations. Experiments with Lake Erie water from which the phytoplankton had been removed by a No. 25 silk bolting cloth filter, showed average photosynthetic rates of 2.3 µ moles CO2 removed per liter per hour. Obviously, these rates are attributable to a component of the phytoplankton not retained by the No. 25 bolting cloth filter. Henrici (1939) suggests that "autotrophic bacteria are very probably of great importance in the metabolism of lakes. They fall into two divisions: the chemosynthetic species which obtain energy from the oxidation of inorganic elements or compounds (hydrogen, sulphur, iron, ammonia, carbon monoxide) and the photosynthetic species. The latter, the red and green sulphur bacteria, possess pigments

which, like chlorophyll, trap the energy of sunlight, and use it to transform carbon dioxide and hydrogen sulfide into organic matter". van Niel (1935) in summarizing observations of photosynthesis in bacteria states "with regard to a concept of the mechanism of the photosynthetic conversion of various H-donors and CO₂ into bacterial cells, nothing stands in the way of the hypothesis that fundamentally this conversion follows the same path as green plant photosynthesis".

It seems reasonable to suspect that the flora of the Bay contains a significant fraction of chemosynthetic and photosynthetic bacteria, the metabolic activities of which may explain both the inverse correlation between photosynthesis per unit plant volume and standing crop, and the high CO_2/O_2 respiratory ratio. This problem needs considerable study before there can be a thorough understanding of phytoplankton metabolism.

The average total photosynthetic rate for the entire water column, May 5 to June 18 was 12 micromoles O_2 evolved per liter per hour, or 144 micromoles evolved in 12 hours of daylight. The average rate of respiration was 2.8 micromoles O_2 consumed per liter per hour, or 67 micromoles consumed in 24 hours. Photosynthesis presents a net gain of 77 micromoles of O_2 per liter in 24 hours.

Riley (1940), for Linsley Fond, reported an average rate of 1.065 mg. O_2 evolved per liter per week for the entire water mass, which amounts to 4.75 micromoles per liter per day; and he reports 1.357 mg. O_2 consumed per liter per week, which amounts to 6.07 micromoles consumed per day. A net loss of 1.32 micromoles O_2 per liter per day is indicated.

Wright (1954) reported a photosynthetic rate of 0.39 mg. O_2 produced per liter per 48 hours in Atwood Lake, which amounts to 6.1 micromoles O_2 per liter per day; and a respiration rate of 0.54 mg. O_2 absorbed per liter per 48 hours, which amounts to 8.4 micromoles O_2 consumed per day. This represents a net loss of 2.3 micromoles O_2 per liter per day.

There is considerable difference in the period of exposure of test bottles in the above-mentioned experiments (Riley 7 days, Wright 2 days, present study 6 hours) and some of the differences appearing in the above comparisons may be due to that fact. But the shallow waters of Sandusky Fay, with high phytoplankton crops (about 3 times as high as in Linsley Pond) and high values of suspensoid ash-free dry weight (about 5 times as high as in Linsley Pond) are associated with a 24-fold greater total photosynthesis per liter, and it seems unlikely that the difference is entirely an artificial one resulting from

the difference in methods.

It is interesting to compare the photosynthesis per unit area in Sandusky Eay with data computed from the literature. On this basis, the average total photosynthesis in Sandusky Bay was 144 millimoles O2/m2/day, which is equivalent to the production of 4 grams of glucose/m²/day. Manning and Juday (1941) reported an average total photosynthesis for Weber Lake of 57 millimoles 0,/ m²/day. This was the highest of 9 lakes studied. Rabinowitch (1945) quotes an annual average amounting to 85 millimoles $0_2/m^2/day$ for marine phytoplankton. Wright (1954) reported an average gross photosynthetic rate of 28 millimoles 02/m2/day for Atwood Lake. Riley (1940) obtained rates of 67 millimoles 02/m2/day in Linsley Pond. Jackson and McFadden (1954) reported rates amounting to 210 millimoles $0_2/m^2/day$. The author obtained rates (unpublished) of 150 millimoles $0_2/m^2/day$ in western Lake Erie waters in the summer of 1953. These comparisons show that although photosynthesis per liter, the standing crop of phytoplankton, the ash-free dry weight of suspensoids, the chlorophyll content of water, etc., may vary over several orders of magnitude, the photosynthetic rates per unit area within these widely different environments lie within the same order of magnitude. The similarity of correlation coefficients in the

 O_2 and CO_2 data plotted against ash-free dry weight and standing crop indicate that the method using pH change as an index of photosynthesis is as reliable as the Winkler method of following O_2 change. These correlation coefficients are notably higher than those obtained by Riley (1940) for O_2 production plotted against ash-free dry weight and standing crop which were 0.051 and 0.150 respectively.

Populations may vary in protoplasmic content (Verduin, 1952) and Sedgwick-Rafter type counts do not include the bacterial and fungal flora which would be contained in the measurements of ash-free dry weight. Rates per unit ash-free dry weight reported by various authors show less disparity than with rates pertaining to phytoplankton volume. The average maximum results obtained in this study were 2.3 micromoles O₂ evolved/hr/mg ash-free dry weight; Jackson and McFadden (1954) obtained average rates in Sanctuary Lake of 1.34 micromoles CO₂ absorbed /hr/mg; and Riley (1940) in Linsley Pond obtained an average surface rate of 0.32 micromoles O₂ produced/hr/mg ash-free dry weight of organic matter.

Since different bodies of water present a wide variance in organic seston, it is important that more extensive studies be made to indicate the range of photosynthetic values per unit of ash-free dry weight. This was

apparent in the study on Sandusky Bay where the organic matter varied from 5.8 to 300 mg. ash-free dry weight per liter.

The phytoplankton populations in this study represented two rather distinct communities. Cyclotella during February and March, and Melosira in May and June. The photosynthetic rates of these two communities vary by a factor of 1.7. The organisms comprising the separate communities differ in cell volume, protoplasmic content and perhaps physiological activity. They also occurred at different environmental temperatures. It is important that data be obtained pertaining to the metabolic activity of phytoplankton communities rather than being lumped as "standing crop". Such rates may be obtained in relatively short periods of 4 to 6 hours and the methods used in the present study require no more effort than the accepted methods of determining standing crop. Contributions have been made in this direction by Verduin (1952) and Jackson and McFadden (1954).

SUMMARY

A study of the photosynthetic and respiratory activity of the phytoplankton of Sandusky Bay was made from February 2 to June 18, 1954.

The waters of Sandusky Bay are characterized by high turbidity. The decimal reduction distance averaged 0.36 m.

The light absorption coefficient averaged 0.12. The average euphotic zone comprised 70% of the water column.

Oven-dry suspensoids averaged 121.8 mg. per liter and ash-free dry weight of suspensoids averaged 11.78 mg. per liter. Phytoplankton population ranged from 0.007 x $10^{10}\mu^3$ to 5.73 x $10^{10}\mu^3$ per liter and averaged 1.3 x $10^{10}\mu^3$ per liter; diatoms were the predominant component.

The average photosynthetic rate in optimal light, based on CO_2 consumption per $10^{10}\mu^3$ was 15 micromoles per hour; the ratio of CO_2 consumption to O_2 evolution was 1.16.

The total productivity on an area basis was 144 millimoles $O_2/m^2/day$, or the equivalent of 4 grams of glucose per square meter per day.

pH changes in surface samples from the Bay during the 6-hour test periods indicated CO₂ absorption amounting to 75% of the average total photosynthesis at optimal light observed in the bottles.

Photosynthetic rates at periods of low levels of phytoplankton population indicate the presence of important quantities of organisms that are not detected by observation under 100x magnification. Chemosynthetic and photosynthetic bacteria may be responsible for this phenomenon.

A respiratory quotient of 3.3 was obtained, indicating CO₂ evolution considerably in excess of O₂ con-

sumption. This phenomenon also suggests the activity of a bacterial or fungal component causing production of CO₂ or some other acid in the dark. More information is needed regarding the bacterial and fungal components of phytoplankton.

The correlation of CO_2 consumed per liter with ashfree dry weight of suspensoids was 0.604; with phytoplankton volume was 0.388. The correlation coefficient of O_2 evolved per liter with ash-free dry weight of suspensoids was 0.413; with phytoplankton volume it was 0.457. These coefficients of correlation indicate that phytoplankton volume and ash-free dry weight are of the same order of reliability as indices of productivity in Sandusky Eay. Only one of these correlations (CO_2 consumed with ash-free dry weight of suspensoids) is significant at the 5% level. These correlations indicate further, that measurements of photosynthesis by means of pH determinations are as reliable as those based on oxygen determinations using the Winkler method. The latter method is considerably more tedious and time-consuming.

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AUTOBIOGRAPHY

I, Arthur George McQuate, was born in Huntington, Lorain County, Ohio, March 31, 1896. I received my secondary education in the public schools of Litchfield and Medina, Ohio. My undergraduate training was obtained at Denison University, from which I received the degree Bachelor of Science in 1920. From the University of Michigan, I received the degree Master of Science in 1948. In 1951 I registered at The Ohio State University, where I have specialized in the field of Hydrobiology at the Institute of Hydrobiology while completing the requirements for the degree Doctor of Philosophy.

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