LIMNOLOGY, PRIMARY PRODUCTIVITY, AND CARBONATE SEDIMENTATION OF MINNESOTA LAKES

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INTRODUCTION

This is a report of an investigation of the regional limnology of Minnesota. The work has involved 3 phases: first, a mobile limnological laboratory was designed and outfitted; second, standard field and laboratory techniques were modified wherever necessary to make them more compatible with the mobility of the laboratory; and third, a study was begun of the primary productivity and general limnology of 14 lakes in various parts of the state.

The mobile laboratory has been described elsewhere (Megard and Shapiro, 1966). This progress report is a compilation of limnological data from the various lakes. Not enough productivity measurements have yet been obtained for adequate comparison of most of the lakes, although productivity data from the lakes studied most intensively have been utilized in an analysis of carbonate sedimentation and have been compared with the content of plant pigments in sediments to illustrate how productivity data can aid in understanding problems of lake chemistry.

Most of its work was supported by funds from the United States Department of Interior as authorized by the Water Resources Act of 1964, Public Law 88-379. The author wishes to thank Dr. Joseph Shapiro for frequent advice and for invaluable assistance with laboratory techniques. The work on carbonate sedimentation was stimulated by Dr. K. S. Deffeyes. The efforts in the field

and laboratory of student assistants Douglas Hall, Paul Richmond, and Lynn Henrickson have contributed substantially to the project.

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The lakes in a region must be compared with each other and with lakes in other parts of the world to determine which chemical and biological conditions are normal and which conditions result from cultural activity. It is extremely difficult, however, to describe lakes and to compare them with each other. They vary in geologic and geographic setting and in depth, area, and volume. The quantities of dissolved substances vary from lake to lake and from season to season; furthermore, highly complex biological variables are superimposed on the physical and chemical variables. Descriptive data are therefore laborious to compile and difficult to interpret, particularly where lakes are numerous and scattered over a large area.

To overcome these difficulties, this investigation utilizes an analytic method to supplement traditional descriptive methods for comparing lakes. The study is based on the premise that the primary productivity, that is, the rate of photosynthetic production of organic matter by planktonic algae, integrates the physical variables on one hand and the biological variables on the other. Measurements of the primary productivity should therefore provide an index for comparing lakes in terms of the

fertility of the water.

Most of the seasonal chemical changes in lake waters are either caused or modified by biological activity. The changes are very large in productive lakes and smaller in unproductive lakes. It is therefore necessary to know the rates of biological activity in order to understand the chemistry of lake waters; conversely, knowing the chemistry of the environment is a first step toward understanding the distribution and abundance of organisms.

Several techniques may be used to measure the rate of production. Most of the organic matter is produced by photosynthesis of planktonic algae. It is usually not feasible to measure directly the amount of organic matter produced in a time unit, so the rate of assimilation of carbon dioxide, the major raw material of photosynthesis, may be measured. The most sensitive method is to measure the carbon dioxide consumption, using radioactive carbon-14 as a tracer. This method requires complex apparatus and considerable skill in radiochemistry on the part of the investigator. The oxygen method is simpler, but it is also less sensitive. No special skills, apparatus, or reagents beyond those for standard water analysis are required for the oxygen method, although careful analytic technique is mandatory.

THE OXYGEN METHOD FOR MEASURING PHOTOSYNTHESIS

The oxygen method was found to be adequate for most of the lakes in Minnesota; therefore considerable effort has been devoted to designing the experimental procedure and developing field techniques so that the method might be utilized by others. The experiments measure the rate of photosynthesis by algae at

successive depths down to the limit of light penetration. Thus, the method is a bioassay of light penetration as well as of photosynthesis. It also measures respiration rates of the zooplankton, bacteria, and algae in the water.

The experimental procedure involves collecting water samples at depth intervals and dividing the sample into three bottles. One subsample is used to determine the initial oxygen concentration, and the other two subsamples are used for the experiment. One experimental bottle is of normal transparent glass (light bottle), but the other is opaque to light (dark bottle). The light and dark bottles from each depth are suspended during an incubation period at the depths from which the samples were collected. The oxygen change (net photosynthesis) in the light bottle after incubation is due to oxygen production during photosynthesis minus an amount of oxygen consumed by respiration. In the dark bottle there is only an oxygen decrease because of respiration. The total amount of oxygen produced during the experimental period (gross photosynthesis) is obtained by adding the oxygen decrease in the dark bottle to the increase in the light bottle. The amount of organic matter produced at each depth during the experiment is then computed from the oxygen changes.

Although the ultimate goal is to compare lakes in terms of the rate of production per unit surface area of water, the shapes of the curves in themselves are instructive. Some lakes have very high rates of photosynthesis near the surface, but the rates decrease rapidly with increasing depth. Other lakes have relatively low photosynthetic rates near the surface, with slower decreases as depth increases. In others the maximum photosynthesis

is many meters beneath the surface. Another potential use of the experiments, not yet attempted, is as bioassays for the effect of dissolved substances contributed to lakes by streams and sewage effluents.

The oxygen light-and-dark-bottle method of measuring photosynthetic rates has been criticized frequently because long incubation periods, up to 24 hours or longer, have been utilized to obtain measurable changes in oxygen concentration in the light bottles. (The precision of the Winkler oxygen analysis is about 0.03 mg/l; thus the purely analytical error is uncomfortably large if the maximum oxygen changes are less than 0.2 mg/l.) Critics point out that enclosing the algae in bottles for long periods deprives them of the turbulence they require to continue floating; the algae consequently tend to sink to the bottoms of the bottles, and they are no longer planktonic. A second difficulty is that bacterial growth and respiration is enhanced, both because of a lack of turbulence and because of the surface area provided by the bottle walls. Finally, the supply of nutrients in the bottles may become depleted during long incubation times. Long incubation periods are therefore to be avoided because the experiment imposes an abnormal environment on the algae.

In spite of these disadvantages the early experiments in this study were 24 hours long, from noon of one day to noon the next, so that relatively large oxygen changes could be obtained. Short-term variations in physiological rates and illumination are integrated during 24-hour experiments, and the results may be expressed on a daily basis. All the experiments from July, 1965, to May, 1966, were for periods of 24 hours. These

experiments demonstrated that the light-and-dark-bottle technique could be employed profitably on most Minnesota lakes. In late June, 1966, an experiment was performed at Lake Itasca in order to determine if it was feasible to reduce the duration of the experiments.

At 8:00 a.m. a water sample was divided among 4 pairs of light and dark bottles, and the bottles were suspended at a depth of 1 m. The oxygen change in one pair was measured after 4 hours, in 2 pairs after 8 hours, and in the fourth pair after 24 hours. The oxygen increase in the light bottles after 8 hours was greater than the increase after 24 hours, and the hourly rate of respiration increased from 0.015 mg per hour after 4 hours to 0.031 mg per hour after 24 hours (Table 1).

The respiration rate in Lake Itasca is rarely this high in 24-hour experiments, however. The mean respiration rate in the upper 5 m of the lake during a 24-hour experiment on August 2, 1965, was only 0.020 mg/hour. In 6-hour experiments on June 28 and July 21, 1966, they were 0.025 and 0.021 mg/hour. In these experiments the respiratory rates of 24-hour experiments were nearly identical to the rates of 6-hour experiments. Thus, the respiration rates apparently do not alway increase in 24-hour experiments.

An analysis of the oxygen budget during photosynthesis reveals that the net oxygen increase in 24-hour experiments can be no more than 50% greater than in 6-hour experiments begun at noon to include half a solar day. The main effect is that the oxygen decrease in the black bottles after 24 hours is 4 times greater than after 6 hours, and therefore the respiration rate can be measured more accurately; but the oxygen decrease in the

dark bottles may be even greater than this if bacterial growth is stimulated, and the oxygen increase in the light bottles would be proportionately smaller. For example, if the mean rate of gross photosynthesis is 0.1 mg/hour, then total oxygen production during 12 hours daylight will be 1.2 mg. With a respiration rate of 0.02 mg/hour the met oxygen production will be 0.96 mg after 12 hours and 0.72 after 24 hours (Fig. 1a). The net oxygen production in a 6-hour experiment begun at noon will be 0.48 mg. If the respiration rate were to increase to 0.03 mg/hour in the 24-hour experiment, however, then the net oxygen would be the same as in a 6-hour experiment (Fig. 1b).

A 12-hour experiment from morning to evening therefore provides the maximum reliability, with the precision of the oxygen analysis amounting to about 3% of the typical maximum oxygen change for Lake Itasca. The precision is 4% in 24-hour experiments and about 6% in 6-hour experiments. The loss of accuracy in 6-hour experiments is not excessive in view of the errors that may be introduced and the time required for longer periods of incubation. All experiments since July, 1966, have therefore been 6 hours long.

The results of 6-hour experiments begun at noon are used to compute production during a 24-hour day by assuming that there are 12 hours daylight, that the amount of photosynthesis after noon equals the amount before noon, and that the respiration rate in light is the same as in darkness (Table 4). The gross photosynthesis after 24 hours (G_{24}) must equal the gross photosynthesis after 12 hours (G_{12}), which is twice the gross photosynthesis after 6 hours (G_6). Hence,

$$(1) \quad G_{24} = G_{12} = 2\ G_6$$

Net photosynthesis after 24 hours (N_{24}) must equal the net photosynthesis after 12 hours ($2N_6$) minus the respiration during the night ($2R_6$)

$$(2) \quad N_{24} = 2N_6 - 2R_6$$

If it is assumed that glucose is the sole product of photosynthesis, then each mole of oxygen produced represents one mole of carbon assimilated, and the weight of carbon fixed may be computed as follows:

$$(3) \quad \frac{\text{mg C}}{\text{mg } O_2} = \frac{\text{mol. wt. C}}{\text{mol. wt. } O_2}$$

$$(4) \quad \text{mg C} = .375\ (\text{mg } O_2)$$

Actually, however, the organic matter produced contains a smaller proportion of oxygen than does glucose, and consequently more oxygen is produced than carbon consumed. The carbon fixation in Table 4 was computed from a photosynthetic quotient $\left(\frac{\Delta O_2}{\Delta C}\right)$ of 1.2, as recommended by Ryther (1956) and Strickland (1966).

$$(5) \quad \frac{\text{mg C}}{\text{mg } O_2} = \frac{\text{mol. wt. C}}{1.2\ (\text{mol. wt. } O_2)}$$

$$(6) \quad \text{mg C} = 0.312\ (\text{mg } O_2)$$

The photosynthesis experiments involve culturing algae and measuring their metabolism. Minute traces of many substances may inhibit algal metabolism. This may be significant in the oxygen method, because the analysis at the end of the experiments involves liberating iodine in the bottles. Iodine is very toxic, and the results of an experiment might be affected by traces of iodine from the previous experiment. Initially the

bottles were thoroughly washed after each experiment by inverting them over jets of tap water for several minutes. In several experiments the results in bottles washed this way were compared with the results in bottles that were soaked in dichromate cleaning solution for 1 hour before rinsing (Table 2). The rates of both photosynthesis and respiration were generally lower in the bottles that were only rinsed, suggesting that traces of iodine remained. Subsequently all experimental bottles were soaked in cleaning solution for 1 hour before they were washed.

It would be most desirable to test the light-dark bottle method by comparing complete photosynthesis profiles from simultaneous experiments, but this has not been possible for logistical reasons. However, it is almost as instructive to compare profiles obtained from lakes within several days of each other under virtually identical weather conditions.

Six-hour experiments were performed on Lake Itasca beginning at noon on June 28 and June 30, 1966 (Fig. 2). The shapes of the photosynthesis curves were remarkably similar to each other, and both of them had inflections at 1 m. A peak in the respiration curve near the bottom of the photic zone occurs frequently in Lake Itasca and in other lakes at comparable depths. This peak probably represents the respiration of dense zooplankton populations. Daphnia were obviously more abundant in the bottles at 6 m than at other depths in the experiment on June 30.

The results of a pair of experiments on July 5 and 7, 1966, at Long Lake, which is about 5 km northwest of Lake Itasca, were also similar to each other (Fig. 3). Rates were uniformly low in the epilimnion (0 - 4 m), higher in the top of the metalimnion (5 - 7 m), and highest at the bottom of the metalimnion (11 m).

The experiments are therefore reproducible. The irregularities in the photosynthesis curves probably are not experimental artifacts but real variations in photosynthetic rates. The high rates at 0.5 and 2 m in Lake Itasca, with lower rates at 1.0 and 1.5 m, represent either variable physiologic responses by a homogenous algal population or microstratification of discreet algal populations. Microstratification because of low turbulence in the metalimnion is probably responsible for the profile irregularities in Long Lake and also for the high oxygen concentration in the metalimnion (Fig. 12), which will be described in a later section.

METHODS

A comprehensive regional limnological survey requires many items of field equipment and laboratory instruments and apparatus, combined with careful field and laboratory technique. The oxygen analyses required for the light-and-dark-bottle experiments must be performed within several hours after the samples are collected, and ideal laboratory conditions are required to attain the necessary precision. Other analyses, particularly for nutrients, should also be performed within several hours after collection if they are to be meaningful, because concentrations may change significantly soon after samples are collected. For these reasons a mobile limnological laboratory was designed (Megard and Shapiro, 1966) that permits most of the usual limnological analyses to be performed at the shores of all but the most inaccessible lakes. The laboratory is normally connected to the electrical and water supplies of lake-side resorts while analyses are performed, but

on some occasions it uses its own electrical generator and water supply. Field equipment is stored during transit in exterior compartments. The laboratory can be stocked with enough reagents and supplies for several months of operations in the field. A 14-ft boat is towed on a trailer behind the laboratory. All of the analyses described here are routinely performed in the mobile laboratory.

The usual procedure has been to arrive at a lake in mid-morning in order to set up the laboratory and to begin an experiment at solar noon. The experiment was usually performed at the deepest part of the lake. First the temperature and oxygen profiles are determined with a Precision Scientific Co. galvanic-cell oxygen analyser. This information is often required to determine the depth intervals for the experiment. Water samples are collected with a 3-liter Van Dorn plastic water sampler. Samples are taken from 0.5-m intervals in the upper 3 m, where the light gradient is steepest, and at 1-m or sometimes 2-m intervals at greater depths to the bottom of the photic zone. After each sample is brought to the surface, the sampler is inverted several times to homogenize the sample, and 3 standard 300-ml B.O.D. bottles are filled for the experiment. One bottle for determining the initial oxygen content, one clear bottle, and one dark bottle are filled with water from each depth. The dark bottles are covered with an inner layer of plastic electrical tape and an outer layer of aluminum foil. The necks and stoppers of the dark bottles are also covered with foil after the bottles are filled. Each pair of filled light and dark bottles is then immediately clamped in a plexiglass bottle-holder that holds the stoppers in place and the bottle-holder is attached to a brass chain and

lowered to the depth in the lake from which the sample was obtained. Usually from 10-13 depths are utilized for each experiment.

Water samples for chemical and phytoplankton analyses are taken in 500-ml plastic bottles from many of the samples used for the photosynthesis experiments and from selected additional depths.

The azide modification of the Winkler oxygen analysis is used to determine the oxygen concentrations in the light and dark bottles. Samples to be titrated are poured from the B.O.D. bottles into a volumetric flask cut off at the neck to contain exactly 203 ml, which is the volume of sample required to correct for the dilution by reagents. Each sample is then transferred quantitatively to a 250-ml Erlenmeyer flask for titration. By titrating thiosulphate from a 10-ml semi-micro burette and using a magnetic stirrer during the titration, one can obtain a precision of ± 0.03 mg/l. All oxygen titrations are completed within 1-3 hours after the samples were removed from the lake.

Dissolved inorganic phosphate was determined colorimetrically (American Public Health Association, 1960) on 100-ml unfiltered water samples. One ml acid ammonium molybdate solution (25 g per liter 28% H_2SO_4) and 1 ml $SnCl_2$ solution (100 mg pre-weighed crystalline $SnCl_2$ dissolved in 25 ml 10% HCl) were added to each sample, and the optical density at 650 mμ was determined after 12 minutes with a double-beam filter photometer with a 5-cm light path. The optical density of a 100-ml color blank to which 1 ml 28% H_2SO_4 had been added and of a 100-ml reagent blank were subtracted from the optical density of each sample. The optical density of a series of standards was determined at the same time

as the unknown samples were analyzed; the concentration of the unknown samples was then obtained from a graph of the optical density of the standards.

Silica was also measured colorimetrically (American Public Health Association, 1960). Two ml 10% ammonium molybdate and 0.2 ml 50% H_2SO_4 were added to 50-ml unfiltered samples, and the optical density of 525 mμ was determined after 12 minutes. The optical density of a color blank, to which 0.2 ml H_2SO_4 was added, and of a reagent blank was subtracted from the optical density of each sample. The silica concentration was obtained from a calibration curve as in the phosphorus analyses.

Alkalinity was determined by titrating a 50-ml sample with 0.02 N H_2SO_4 to an end-point of pH 4.4, as determined with a pH meter.

Total hardness and calcium were determined with EDTA, using Eriochromeblack-T as an indicator for hardness and hydroxy-naphtol-blue for calcium.

A carbonate saturometer was used to determine the degree of calcium carbonate saturation at different times of year and depths in the lakes. An important requirement for studying carbonate saturation is that the analyses should be performed soon after samples are collected, before plankton metabolism, temperature, pH, and carbon dioxide content have changed. The virtue of the carbonate saturometer in this respect is that a qualitative measurement of carbonate oversaturation or undersaturation requires only a little more time than is required to measure pH.

The carbonate saturometer is basically a sensitive, portable, battery-operated pH meter (Weyl 1961). The instrument used in

this study is a modification of a design by K. S. Deffeyes. Saturation measurement involves measuring the pH change after crystalline calcite is placed in contact with the glass electrode in a water sample. If the sample is exactly saturated with calcium carbonate, then there is no pH change. If the water sample is oversaturated with carbonate, the added calcite provides nuclei for carbonate precipitation, hydrogen ions are released, and the pH decreases. Conversely, hydrogen ions are consumed when calcite is added to a sample that is undersaturated, and the pH increases. The magnitude of the pH deflection is a qualitative index of the degree of oversaturation or undersaturation. Because of its simplicity, the method may be used in the field to study carbonate saturation of both water and sediments. Most of the data discussed here, however, were obtained in the mobile laboratory with 1-2 hours after the water samples were collected.

The saturometer was developed for use with sea water, so it was desirable to determine its response in fresh water. For this purpose a sample of unaltered lake water and 80%, 50%, 40%, and 30% dilutions of this water with CO_2-free distilled water were tested after the diluted samples had equilibrated for 26 hours (Fig. 4). The initial pH of the undiluted sample was 8.60. The pH decreased to 8.23 within 2 minutes after calcite addition, stabilized for a minute, and slowly increased again after 3 minutes. The sample was therefore oversaturated with carbonate. The pH deflection of 40% lake water was negligible and the sample was therefore nearly saturated. The pH of 30% lake water was 8.18. Within 2 minutes after calcite addition the pH increased to 8.42, but it also began to increase again after 3 minutes. Data for sea water presented by Weyl indicated similar responses,

and therefore the pH-change 2 minutes after calcite addition is the proper indication of the degree of oversaturation or undersaturation of both fresh water and sea water.

When the saturometer deflection (ΔpH) after 2 minutes in a series of similar dilutions is plotted against the calcium content of the water, a sigmoid curve results (Fig. 5). The point where the curve intersects the line of 0 ΔpH corresponds to the saturation concentration, in this case 15.6 mg/l. It has not yet been determined if this procedure for measuring quantitatively the degree of oversaturation is theoretically sound, but it is much simpler than the approach Weyl initially proposed. To measure quantitatively the undersaturation of a sample, standard sodium carbonate may be added to obtain a pH change equivalent to the saturometer deflection.

RESULTS

Four lakes were studied near the University of Minnesota Biological Station in northwestern Minnesota (Fig. 7). Ten other lakes were selected from among those in which the ionic composition, dissolved organic materials, sediment pigments, and phytoplankton are being studied by others associated with the Limnological Research Center. The location of the lakes with respect to the distribution of the major vegetation formations in Minnesota is shown in Figure 6, and the area, depth, and volume are shown in Table 3. The lakes are generally small, ranging in area from 22.8 ha (57 acres) to 1,570 ha (3936 acres). Depths range from 3 m (9 ft) to 41 m (135 ft).

Lake Itasca

The data from Lake Itasca are from the north arm of the lake, where the maximum depth is 11 m. The north arm is oriented parallel to the prevailing southwesterly winds in spring and early summer, and this prevents it from becoming thermally stratified until water temperatures exceed about 15°C. The north arm is not deep enough to have a hypolimnion; consequently there is usually oxygen in the deep water throughout the summer (Figs. 8 and 9). Silica in the epilimnion was higher in spring (9 mg/l) than in summer (5 - 6 mg/l), but dissolved phosphorus was lower in spring (2 µgm/l) than in summer (6 - 11 µgm/l). The alkalinity in the epilimnion decreased from about 170 mg/l in May to about 145 mg/l in late July. This corresponded to a calcium decrease of about 10 mg/l. The pH and carbonate oversaturation of the epilimnion both increased during this interval, but the metalimnion became

undersaturated with carbonate. Calcium, silica, and phosphorus all accumulated in the deep water after the lake became stratified.

The productivity experiments indicate that photosynthesis may occur down to depths of 6 to 9 m, but the compensation depth (the depth where the rate of respiration equals the rate of photosynthesis) varied from 4 m in May to 5.5 m in summer. In the photosynthesis curve for 30 June, 1966, the inflection suggests that the algal population in the epilimnion may have been stratified with low population densities at 1 m; a very similar curve for net photosynthesis was obtained in an experiment conducted 2 days earlier (see above and Fig. 2). The respiration curve also indicated low metabolic rates at 1.0 m.

High respiration rates often occurred slightly below the compensation depth in Lake Itasca and in other lakes. The only experiment on Lake Itasca without a respiration peak near the compensation depth was performed on 2 August, 1965, which was a cloudy day (Fig. 8). These high rates probably were due to concentrations of zooplankton, such as Daphnia, which migrate downward in response to daylight.

Depletion of oxygen beneath the ice indicated that respiration was the dominant metabolic process in Lake Itasca during the winter. Oxygen was virtually absent in late March in depths below 5 m (Fig. 8). Carbon dioxide production reduced the pH to 7.4 - 7.6, from a pH of 8.5 in October. Another index of carbon dioxide production was the alkalinity increase, from about 140 mg/l at all depths in October to more than 200 mg/l at the bottom in March. The water at all depths also became undersaturated with respect to calcium carbonate in late winter, although the calcium concentration in deep water increased from 29 mg/l in

October (when the water was probably oversaturated at all depths) to 54 mg/l. The slope of the alkalinity, hardness, and calcium curves indicate that these substances came from carbonate dissolution in the surficial sediments. The implications of the seasonal changes of alkalinity, calcium, and carbonate saturation will be discussed in the section describing the environment of carbonate sedimentation.

The primary productivity of Lake Itasca is higher than in any of the other lakes in the vicinity (Table 4). Rates varied from 0.74 g C/m^2 per day (5 October, 1965) to 1.53 g C/m^2 (30 June, 1966), with a mean for 5 experiments of 1.24 g C/m^2 per day.

Long Lake

Long Lake is located about 6 km northwest of Lake Itasca (Fig. 7). It is much smaller than Itasca but the mean depth is more than twice that of Itasca.

The long axis of the lake is perpendicular to the prevailing wind in summer. Also, a steep ridge parallels the southern shore and protects the lake from the wind. Consequently little heat is transmitted to the deep water in spring, and thermal stratification prevents water below depths of 15 m from becoming warmer than 6 or 7°C (Figs. 10, 11, and 12). The lake warmed so quickly in 1966 that the epilimnion was only 4 m thick in July.

The oxygen profiles in Long Lake are particularly interesting because oxygen concentrations in the metalimnion during summer are higher than in the epilimnion. Data for 19 May, 1966, only about 10 days after the ice melted, indicate that the oxygen concentrations above 15 m in spring range from 8 to 10 mg/l. Oxygen concentrations in the epilimnion decrease as the water

becomes warmer, but the metalimnetic oxygen concentrations remain high or increase. They may exceed 12 mg/l at depths of 9-11 m in mid-July. This is about 125% saturation with respect to pressure of one atmosphere at the altitude of the lake (425 m) at 10°C. The hydrostatic pressure at at 10-m depth is approximately equivalent to another atmosphere, however, so the metalimnion is undersaturated with oxygen.

The summer oxygen concentrations in the metalimnion exceed the oxygen concentrations in the spring. The metalimnetic oxygen maximum must be caused by photosynthesis, and this conclusion is substantiated by the photosynthesis experiments. On 7 July, 1966 (Fig. 12), rates of photosynthesis were low in the epilimnion, but there were 2 zones of high oxygen production in the metalimnion. A small peak at 5 m was at the top of the metalimnion, and a large peak was near the bottom at 11 m, which was also the depth where the oxygen concentration was highest. The highest rate of photosynthesis on 5 August, 1965, was also at the depth containing the most oxygen (Fig. 11).

Two discreet algal populations were probably responsible for the metalimnetic oxygen maximum in Long Lake: an upper population tolerant of low light intensity but requiring high temperatures, and a lower population tolerant of very low light intensity and temperature. Algal and oxygen stratification of this type occurs in the metalimnion of Meyers Lake, Indiana (Eberly 1959, 1964), where there is an upper population of Aphanizomenon and Melosira and a lower population of Oscillatoria. Algal populations may become stratified in the metalimnion because it is a region with low turbulence. If the surface waters are relatively transparent so that light intensities in the metalimnion exceed 1-5% of the

surface light intensity, then photosynthetic rates in the metalimnion may be greater than in the epilimnion because of more favorable nutrient conditions. The best conditions for accumulation of oxygen in the metalimnion are when the thermocline is above the center of gravity of the lake and the zone of oxygen production lies below the center of gravity (Eberly 1964).

Quantitative phytoplankton samples were taken from each of the water samples used for the photosynthesis experiment on 7 July, but they have not yet been examined to determine if the algal populations were in fact stratified.

The seasonal chemical changes in Long Lake are more subdued than in Lake Itasca. Dissolved phosphorus varies from 3 to 10 µgm/l at most depths, although concentrations may rise to 25 µgm/l near the bottom. Calcium concentrations decreased at all depths between July and November, 1964, and smaller decreases of both calcium and alkalinity occurred during the same period in 1966. Calcium, alkalinity, and hardness all increase during the winter and spring. In 1964 the water above the thermocline was oversaturated with calcium carbonate and the water below was undersaturated (Fig. 10). In 1966, however, the water in both the epilimnion and metalimnion was oversaturated (Fig. 12), probably because there was photosynthetic consumption of carbon dioxide at least to depths of 12 m and perhaps even to 15 m. The water below 15 m is undersaturated with carbonate in spring and summer but oversaturated in autumn.

Although photosynthesis per unit volume in Long Lake is typically lower than in Lake Itasca, Long Lake is almost as productive as Itasca because photosynthesis occurs to much greater depths. Daily gross photosynthesis varied from 0.56 to

1.78 g C/m^2, with a mean for 5 experiments of 1.03 g C/m^2 (Table 4).

Mary Lake

Mary Lake is a small lake less than 1 km south of the east arm of Lake Itasca (Fig. 7). A small creek flows from Mary Lake into Itasca.

The depth of Mary Lake (Table 3) is about the same as the depth of the north arm of Lake Itasca, but the fetch of the wind on Mary Lake is very small, and the lake is therefore well stratified in summer. There is a steep chemical gradient across the thermocline (Figs. 13 and 14). Data from October, 1965, indicate that the hardness of the water in Mary Lake is about 20 mg/l less than in Lake Itasca, and about 30 mg/l less than in Long Lake. Oxygen is absent or is present in very low concentrations below depths of 5 or 6 m in mid-summer and again in winter. Oxygen depletion in the deep water is accompanied by accumulations of hardness, alkalinity, and dissolved phosphorus and low pH values. The epilimnetic water is oversaturated with calcium carbonate in mid-summer, but the hypolimnion is very undersaturated. Oversaturation in the epilimnion decreases in late summer, and all depths are undersaturated in autumn and winter. Two photosynthesis experiments in 1965 yielded a mean value of 0.38 g C/m^2 per day (Table 4), indicating that Mary Lake is less productive than either Long Lake or Itasca.

Elk Lake

Elk Lake is only several hundred meters south of the west arm of Lake Itasca (Fig. 7), and a small creek flows from it into

Itasca. The mean depth (11 m) is similar to the mean depth of Long Lake (12.9 m) and more than twice the mean depth of Itasca (5.2 m) and Mary (5.7 m). In contrast to Long Lake, Elk Lake has no metalimnetic oxygen maximum, and oxygen disappears from the hypolimnion by mid-July. The rapid oxygen depletion indicates that the lake is very productive. A photosynthesis experiment on 11 July, 1966, also indicated moderately high productivity, with a daily rate of 1.05 g C/m^2 (Table 3). As in Long Lake, production per unit volume of water is low, but the trophogenic zone is relatively thick.

The maximum rate of photosynthesis in this experiment was at 3 m, near the bottom of the epilimnion, rather than at depths of 1 or 2 m as in Itasca and Mary, or in the metalimnion as in Long Lake. A secondary peak at 6 m, in the metalimnion, may be analagous to that at Long Lake, however, although it is based on only a single pair of bottles. Photosynthetic carbon dioxide consumption reduced the alkalinity and calcium concentrations in the epilimnion during summer and autumn.

The hypolimnion of Elk Lake was much different from the hypolimnion in Long Lake because it had no oxygen during most of the summer and early autumn. Phosphorus liberation from the sediments in the reducing environment increased phosphorus concentrations in deep water to 70 µgm/l just before autumnal overturn.

Sallie Lake

Sallie Lake is about 45 mi (72 km) southwest of Lake Itasca, near the city of Detroit Lakes (Fig. 6). Whereas the lakes near Itasca are in the coniferous forest, Lake Sallie is on the border

between deciduous forest and prairie. It is one of the larger lakes studied (528 ha, 1,320 acres), but the mean depth is only 6.2 m (Table 3).

When Sallie Lake was visited on 13 July, 1966, the surface water temperature was 25°C and the bottom was only 4° cooler (Fig. 16). Although the thermal gradient across the metalimnion was very small, chemical stratification was well defined. Oxygen was virtually absent at depths greater than 7 m, and phosphorus, silica, hardness, and alkalinity concentrations were higher in the hypolimnion than in the epilimnion.

A conspicuous difference between Sallie Lake and the Itasca Lakes is phosphorus concentration. Dissolved phosphorus in the epilimnion of Sallie Lake was about 60 µgm/l in July, 5 to 10 times greater than the dissolved phosphorus concentration in the surface waters in the lakes near Itasca.

The photosynthesis experiment yielded 2.42 g C/m^2 per day, which indicates that Sallie Lake is more productive than any other lake in this survey. Photosynthesis decreased rapidly below 0.5 m depth, and the compensation depth was only 4 m. Respiration rates were very high at 6 m, probably, as in Lake Itasca, because of zooplankton trapped in the experimental bottles.

The pH in the epilimnion was 9.1, which was also higher than the Itasca Lakes, and the carbonate oversaturation was also greater than any other lake studied, both of which are consequences of rapid carbon dioxide uptake by photosynthesis. Even the hypolimnion was oversaturated with carbonate.

The lake was also visited in late October, during the fall overturn. Oxygen concentrations were about 115% saturation at

all depths, but phosphorus concentrations had decreased to between 11 and 14 µgm/l. Between mid-July and late October the dissolved inorganic phosphorus content of the lake decreased from 5.15 metric tons (Table 5). The phosphorus lost may have been incorporated into organic matter, lost to the mud as an inorganic precipitate, or possibly the lake was simply receiving less phosphorus in the fall than in the summer. Although the productivity was not measured in October, photosynthetic rates were probably very high because the pH was even higher and carbonate oversaturation greater than in July. As in Lake Itasca, carbonate oversaturation increased as the calcium concentration decreased.

Nokay Lake

Nokay Lake, about 10 miles northwest of Mille Lacs Lake (Fig. 6), is about half as large (264 ha, 660 acres) as Sallie Lake, but the mean depth of the two lakes is about the same (Table 3).

The water chemistry of Nokay Lake resembles Mary Lake, however, except temperatures in the hypolimnion of Nokay Lake are somewhat higher (Fig. 17). The concentration and seasonal variation of oxygen, phosphorus, hardness, alkalinity, and pH are very similar in the two lakes. The mean productivity of two photosynthesis experiments was 0.92 g C/m^2 per day (Table 4), and Nokay appears, therefore, to be more productive than Mary Lake.

Ball Club Lake

Ball Club Lake, in Itasca County northwest of Grand Rapids (Fig. 6) is the largest (1,570 ha, 3936 acres) lake visited,both

in area and volume (Table 3). Maximum depth is 26 m (85 ft), mean depth is 10.8 m, and the volume is 165.5 x 10^6 m^3.

The lake was visited only once, and a photosynthesis experiment was performed (Fig. 18). The epilimnion was much thicker than in the smaller lakes described thus far. The highest rate of photosynthesis was at 2 m. Net photosynthesis decreased to zero at 4 m, but there was a second zone of production in the lower epilimnion and upper metalimnion. Although the productivity per unit volume was relatively low, the trophogenic zone was thick and it yielded 1.12 g C/m^2 (Table 4).

Clearwater Lake

Clearwater Lake is in Cook County in northeastern Minnesota (Fig. 6). It is the deepest (40 m, 130 ft) lake studied (Table 3), and it occupies a basin in igneous rock, in contrast to the lakes described thus far, which are in calcareous glacial drift.

The concentration of dissolved substances in Clearwater Lake in only about 10 - 15% of the concentration in lakes in regions with calcareous drift (Fig. 19). The alkalinity was about 14 mg/l, and the calcium concentration was between 5 and 6 mg/l at all depths. The pH was lower than in lakes with harder water; it varied between 7.5 and 8 in the epilimnion and between 7.2 and 7.4 in the hypolimnion. Phosphorus concentrations varied between 2 and 4 µgm/l at all depths in late July, but there was no measurable dissolved phosphorus below 2 m in August.

Photosynthetic rates were comparatively low at all depths. The highest rates both in July and August, were at 2 m in the epilimnion and at 9 m in the metalimnion. Photosynthesis may therefore be responsible for maintaining the relatively high

oxygen concentrations in the metalimnion. The productivity was 0.38 mg C/m^2 per day for the experiment in July and 0.39 mg C/m^2 in August (Table 4).

Trout Lake

Trout Lake, in northeastern Minnesota, is also in the region of igneous bedrock (Fig. 6). The area of the lake is 103 ha (257 acres), the maximum depth is 23 m (77 ft), and the mean depth is 10.6 m (Table 3).

The chemical content of the lake is very similar to that of Clearwater Lake, except that the pH in the hypolimnion is slightly acidic (Fig. 20). As in Clearwater Lake, oxygen concentrations in the metalimnion in July were higher than at other depths, but photosynthesis experiments have not been performed to determine whether this was the result of photosynthesis or whether this was residual from the high oxygen concentrations during spring circulation. In November, 1966, 2 pairs of light and dark bottles were suspended for ½ day at a depth of 1 m, but there was no measurable oxygen change in any of the bottles.

Francis Lake

Francis Lake is in Le Sueur County, near the southern border of the deciduous forest in southeastern Minnesota (Fig. 6). The area of the lake is 370 ha (926 acres), and the maximum depth is 15 m (50 ft), but the mean depth is only 3.5 m.

The concentration of dissolved substances in the water is similar to the concentration in the northwestern lakes (Fig. 21). Oxygen in the hypolimnion disappears soon after the lake becomes thermally stratified. Phosphorus concentrations were mostly

between 5 and 10 µgm/l in May, before the lake became stratified. They increased in the epilimnion to between 8 and 15 µgm/l in June, July, and September, and they increased even more in the hypolimnion to a maximum of 320 µgm/l in late September. The calcium in the lake decreased from 550 x 10^6 g in early May, 1966, to 403 x 10^6 g in late September. The water at all depths was slightly oversaturated with carbonate in May. The epilimnion became very oversaturated in late spring, but it was only slightly oversaturated again in early autumn. The hypolimnion was always weakly undersaturated with calcium carbonate.

The mean of 4 photosynthesis experiments is 0.87 g C/m^2 per day.

Linwood Lake

The basin of Linwood Lake is in the Anoka Sand Plain in eastern Minnesota (Fig. 6). The maximum depth and area are less than for Francis Lake, but the mean depth (3.4 m) is about the same (Table 3).

Linwood Lake was visited only once, in May, 1966, when it was unstratified (Fig. 18). The total hardness and alkalinity at all depths were both about 10 mg/l less than in Francis Lake. The calcium concentration was about 40 mg/l, and the water at all depths was oversaturated with calcium carbonate. The gross photosynthesis was 1.42 g C/m^2 per day.

Christmas Lake

Christmas Lake, in Hennepin County, is smaller (105 ha, 257 acres) than the other two lakes studied in eastern Minnesota but deeper (24 m maximum depth, Table 3). The mean depth (12.5 m) is

similar to the mean depth of Long Lake, which is somewhat smaller.

The lake was thermally stratified when it was visited in late September, 1966, and oxygen was absent below 14 m (Fig. 22). The hardness of the water in Christmas Lake was greater than in Francis Lake, which was visited 6 days earlier; calcium concentrations in the epilimnion were 40 mg/l, or 10 mg/l higher than in Francis Lake. The phosphorus concentrations in Christmas Lake were very similar to those of Francis Lake, however. Epilimnetic concentrations were between 14 and 18 µgm/l, while hypolimnetic values were much higher, reaching 220 µgm/l near the bottom.

Gross photosynthesis was only 0.37 g/m^2 per day. This is the lowest rate of production measured in this study, but this is probably because the experiment was performed on a dull day in late September.

Big Kandiyohi and Shetek Lakes

Big Kandiyohi Lake is near the boundary between deciduous forest and prairie in west-central Minnesota, and Shetek Lake is on the prairie in southwestern Minnesota (Fig. 6). Big Kandiyohi is 5-m deep and Shetek is only 3 m (Table 3), and, like most of the lakes in the region, neither is deep enough to be thermally stratified in summer.

Each lake has been visited only once. The concentration of dissolved substances is higher in these lakes than in lakes elsewhere in the state, as indicated by the total hardness, which was about 330 mg/l in Kandiyohi and 340 mg/l in Shetek (Fig. 23).

Concentrations of dissolved phosphorus in the surface waters in these lakes were higher than in the other lakes except Sallie Lake, amounting to 28 µgm/l in Big Kandiyohi Lake and 82 µgm/l in

Shetek Lake.

The productivity of both lakes was high, even in late September. Gross photosynthesis was 1.20 g C/m^2 per day in Kandiyohi Lake (Table 4). Although only surficial photosynthetic rates were measured at Shetek Lake, it appears that it may be the more productive.

PHOTOSYNTHESIS AND CARBONATE DEPOSITION

During photosynthesis, plants remove carbon dioxide from the environment and produce organic matter and oxygen according to the generalized photosynthesis equation.

$$(7) \quad 6CO_2 + 6H_2O \longrightarrow C_6H_{12}O_6 + 6O_2$$

The equation may be simplified by dividing all terms by 6.

$$(8) \quad CO_2 + H_2O \longrightarrow CH_2O + O_2$$

When the pH of the water exceeds 8.3, as it generally does in the epilimnion of the lakes in regions with calcareous drift, then the quantity of free carbon dioxide in the water is negligible. Dissolved calcium bicarbonate may therefore be regarded as the source of carbon for phytoplankton photosynthesis, and photosynthesis may be considered as a type of calcium bicarbonate decomposition:

$$(9) \quad Ca(HCO_3)_2 \longrightarrow CH_2O + CaCO_3 + O_2$$

Thus, when bicarbonate is the carbon source, one mole of calcium carbonate is formed for each mole of carbon assimilated by the phytoplankton. Calcium carbonate is relatively insoluble, and large quantities become incorporated in the sediments as marl.

Not all of the carbonate reaching the sediments is preserved, however. It may be dissolved by carbonic acid produced by respiration, which is the dominant metabolic process in and near the sediments.

$$(10) \quad CO_2 + H_2O \longrightarrow H_2CO_3$$

$$(11) \quad CaCO_3 + H_2CO_3 \longrightarrow Ca(HCO_3)_2$$

This discussion implies that carbonate formation and dissolution in these lakes depends more upon photosynthesis and

respiration than upon the calcium concentration of the water. The premise is substantiated by data from the carbonate saturometer discussed previously, which show that water in which there is net photosynthesis, generally epilimnetic water, is oversaturated with carbonate. Furthermore, the oversaturation of the epilimnion increases during the summer, even though the calcium concentration decreases (compare the data for 30 June and 21 July at Itasca Lake, Fig. 9). In contrast, the hypolimnion is generally undersaturated, even though calcium concentrations are higher than in the epilimnion, as in Christmas Lake (Fig. 22). Also in late winter, when calcium concentrations are highest and respiration exceeds photosynthesis, the water is undersaturated at all depths (Figs. 8 and 13). Photosynthetic rates are high soon after the ice melts, and the water becomes oversaturated again, even though the calcium concentration is somewhat lower than in late winter (Itasca Lake, 8 May 1966, Fig. 9).

The relationship between photosynthesis and calcium carbonate sedimentation may be elucidated further by examining the calcium budget of several lakes.

Long Lake contained 217 x 10^6 g calcium on 9 July, 1964, but only 182 x 10^6 g on 6 November (Table 6). This was a 16% decrease. The calcium loss was 9.6% during a similar period in 1966. On an areal basis the loss amounted to 50.7 g/m^2 (452 lbs/acre) in 1964 and 42.6 g/m^2 in 1966. The rate of calcium depletion during these two intervals were 499 and 387 mg/m^2 per day, respectively.

The computed losses of calcium from Long Lake are probably minimal values. Analyses of well-water near the lake indicate that calcium concentrations in the groundwater are about double

the concentrations in the lake. Thus groundwater entering the lake may have delivered twice as much calcium as the effluent removed. The difference between calcium removed and calcium delivered must also have been lost to the sediments. The calcium budgets for Mary, Elk, Francis, and Sallie lakes for various time intervals have also been computed (Tables 7-10). Summer depletion rates for these lakes range from 55 mg/m^2/day for Mary Lake in 1965, to 482 mg/m^2/day for Sallie Lake in 1966.

Although the calcium content of a lake may decrease 20% or more in summer, it increases again in winter (Table 7). Between late July and late September, 1964, the calcium content of Mary Lake decreased from 41.7 x 10^6 g to 33.5 x 10^6 g. The rate of decrease was 571 mg/m^2 per day in 1964, but it was only 55 mg/m^2 per day in 1965. Between late October and early February, however, the calcium content increased again, at a rate of 140 mg/m^2 per day. During this interval the oxygen concentration at depths below 5 m decreased from about 8 mg/l to a trace. During the next 5 weeks the oxygen disappeared below 6 m and the rate of calcium increase was almost 10 times greater than earlier, 1,106 mg/m^2 per day. The total calcium in the lake increased during the fall and winter from 45.2 x 10^6 g to 59.5 x 10^6 g, an increase of almost 32%. Probably very little of the calcium in the water was contributed by the groundwater, because the outlet discharge is very low in winter. Most of the calcium in the water probably came from the dissolution of carbonate in the sediments. It also appears quite probably that more calcium was dissolved in the winter of 1965-66 than was deposited the previous summer.

If the calcium carbonate deposited during a summer is redissolved in winter, then how does carbonate eventually get into

the sediments? Data from late winter and spring in Itasca Lake (the complete budget has not yet been computed) suggests that the ultimate deposition of carbonate formed in a summer may not occur until the following spring, after the ice breaks up and before the lake becomes thermally stratified. The calcium concentration in Itasca decreased more rapidly between late March and mid-May than during any other season (Figs. 8 and 9). The entire water column was oversaturated with carbonate and therefore the environment at all depths favored carbonate preservation. Net carbon dioxide consumption by photosynthesis in spring is higher than at any other time in Itasca (Table 4) and in lakes generally. In fact, the high alkalinity resulting from winter carbonate dissolution is probably an important stimulant for phytoplankton growth in the spring. A massive layer of calcium carbonate is probably deposited over the entire floor of the basin in the spring, more than can be dissolved by the undersaturated hypolimnetic water during the summer.

If the calcium carbonate deposition in a lake depends upon the rate of photosynthesis, then the rate of calcium depletion in different lakes should be directly related to their primary productivity. This is demonstrated in Figure 24, in which the rate of calcium depletion in five lakes is plotted against measurements of net photosynthetic carbon uptake. The date for net photosynthesis are used, because the rest of the carbon assimilated as gross photosynthesis each day is soon returned to the water by respiration, and it has only a transient effect on the water chemistry. The photosynthesis values for Mary, Elk, Francis, and Long Lakes are means of 2 or 3 experiments performed during the corresponding interval of calcium depletion. The

value for Sallie Lake is from only one experiment. The data suggest that approximately one mole of calcium is removed from these lakes for every 4 moles of carbon converted to organic matter, whereas equation 9 would lead us to expect one mole of calcium to be removed for each mole of carbon. The reasons for the discrepancy are unknown, but the 1:4 ratio is probably real because it is exhibited by such a diverse array of lakes. The ratio for Sallie Lake is somewhat low, but this is probably because the datum for carbon uptake is based on a single experiment at the beginning of the time interval, and it is probably higher than the average for the period. The ratio for Mary Lake is also low, but in this case the estimated rate of calcium depletion may be defective; the rate of depletion in 1965 was only about 10% of the rate in 1964.

If additional measurements also indicate a constant ratio between calcium depletion and carbon uptake, then analyses of the calcium budget could become an important adjunct to productivity studies. Photosynthesis experiments measure instantaneous rates, but calcium depletion evidently integrates day-to-day variations in photosynthesis, and it might therefore provide a long-term estimate of production. Furthermore, since the calcium removed is probably not recycled immediately, measurements of its depletion are not subject to many of the difficulties encountered when productivity estimates are based on consumption of nutrients or other ions actually incorporated into protoplasm. Another possibility is that the productivity of a lake could be computed from the calcium content of the sediments, but this prospect is complicated by the fact that the sediment content depends as much on the environment of preservation as it does upon the rate of

sedimentation.

PHOTOSYNTHESIS AND PLANT PIGMENTS PRESERVED IN LAKE SEDIMENTS

The quantity of chlorophyll derivatives and other plant pigments in surficial sediments from some of these lakes has been determined by Dr. Eville Gorham and Jon Sanger. It is postulated that the quantity of pigments in the sediments should depend upon the general organic productivity of the lake and its watershed, and, to an unknown degree, upon the environment of preservation, as with carbonate in sediments. Thus it is desirable to compare the productivity data with unpublished pigment data generously provided by Dr. Gorham (Table 11 and Fig. 25).

When the lakes are listed in their rank order on the basis of productivity, there is a perfect correlation with the pigment content of the sediments except in those lakes where there has been only a single productivity measurement. The production figure for Big Kandiyohi Lake is undoubtedly too low, because it is based on only one experiment in September. The value for Linwood Lake is probably too high, because it is based on an experiment in early spring. In view of the generous supply of nutrients in Sallie Lake, however, the estimate of pigment in the sediments may be too low and not representative of the productivity of the lake.

The data indicate that there may be two categories of lakes with respect to plant pigments in sediments. In the first category are lakes with oxygen in the hypolimnion throughout the summer, represented in Figure 25 by Clearwater Lake. In these lakes organic production is low and only a small proportion of

the plant pigments produced are preserved in the sediments. In the second category are lakes with anaerobic hypolimnia, in which organic production is high and a large proportion of the plant pigments are preserved.

The correlation between photosynthetic carbon fixation and both calcium depletion and pigment content of the sediments indicates that all three are potential indices of productivity. It also suggests that the mean of only four or five photosynthesis experiments may be sufficient to evaluate the productivity of a lake, provided that the experiments are performed at intervals during the open-water season.

SUMMARY

1. A mobile water chemistry laboratory has been designed and outfitted for studying regional limnology in Minnesota.

2. The laboratory permits water samples to be analyzed at lakeside before nutrient concentrations are altered by biological activity. It also provides facilities for measuring the growth-rates of algae and determining the fertility of lake water.

3. The oxygen light-dark-bottle method is being used to compare the algal productivity of 14 lakes in different parts of the state. The method was tested to evaluate its sensitivity, precision, and reproducibility and to determine the effects of different incubation periods.

4. The response of the carbonate saturometer in freshwater was tested, and the instrument was used to determine the degree of calcium carbonate saturation at different times of the year and at various depths in the lakes.

5. The seasonal chemical changes in the lakes are described and the productivity data assembled, but there are not yet enough data for a detailed comparison of the lakes.

6. Data obtained with the saturometer indicate that the epilimnion of lakes in regions with calcareous drift is oversaturated with calcium carbonate and that the hypolimnion is undersaturated, even though the calcium concentration is higher in the hypolimnion. The water at all depths in these lakes is undersaturated in winter but oversaturated in spring. The rate of calcium depletion and presumably also of calcium carbonate deposition is highest in the lakes with the highest rate of photosynthetic carbon uptake by algae. One mole of calcium is removed for

every four moles of carbon assimilated. There is also a correlation between gross photosynthesis and the quantity of plant pigments preserved in surficial lake sediments.

7. The mean of only four or five photosynthesis experiments may be sufficient to evaluate the primary productivity of a lake, provided that the experiments are performed at suitable intervals during the season.

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TABLE CAPTIONS

Table 1. Photosynthetic and respiratory rates in light and dark bottles after incubation for 4, 8, and 24 hours

Table 2. Effects of cleaning experimental bottles with dichromate cleaning solution.

Table 3. Area, depth, and volume of the lakes studied. The morphometric data was obtained from maps prepared by the Minnesota Department of Conservation

Table 4. Primary productivity of the lakes

Table 5. Dissolved inorganic phosphorus content of Lake Sallie in summer and autumn.

Table 6. Calcium budget for Long Lake

Table 7. Calcium budget for Mary Lake

Table 8. Calcium budget for Elk Lake

Table 9. Calcium budget for Francis Lake

Table 10. Calcium budget for Sallie Lake

Table 11. Gross productivity and total plant pigments preserved in surficial lake sediments

Table 1

Duration (hours)	Net photosynthesis (mg O_2)		Respiration (mg O_2)		Gross photosynthesis (mg O_2)	
	ΔO_2	ΔO_2/hr	ΔO_2	ΔO_2/hr	ΔO_2	ΔO_2/hr
4	0.32	0.080	0.06	0.015	0.40	0.100
8	0.60	0.075	0.16	0.020	0.76	0.095
8	0.63	0.079	0.13	0.016	0.76	0.095
24	0.50	---	0.75	0.031	1.25	---

Table 2

Duration of experiment	Net Photosynthesis Mg/L Oxygen/hour		Respiration Mg/L Oxygen/hour	
	Rinsed	Cleaned with dichromate	Rinsed	Cleaned with dichromate
8 hours	0.078	0.080	0.018	0.018
6 hours	0.040	0.062	0.010	0.017
6 hours	0.076	0.083	0.030	0.037

Table 3

Lake	County	Latitude and Longitude	Area (ha)	Area (acres)	Maximum Depth (m)	Maximum Depth (ft)	Mean Depth (m)	Total Volume ($m^3 \times 10^6$)
1. Itasca	Clearwater	47°14'N, 95°12'W	436	1,077	14	45	5.2	22.9
2. Long	Clearwater	47°17'N, 95°16'W	60	145	24	80	12.9	7.6
3. Elk	Clearwater	47°12'N, 95°12'W	101	252	30	97	11.0	11.2
4. Mary	Hubbard	47°11'N, 95°10'W	23	57	12	41	5.7	1.3
5. Sallie	Becker	46°46'N, 95°55'W	528	1,320	13	43	6.2	32.7
6. Nokay	Crow Wing	46°23'N, 93°58'W	264	660	13	42	5.6	14.8
7. Ball Club	Itasca	47°22'N, 93°12'W	1,533	3,835	26	85	10.8	166
8. Clearwater	Cook	48°05'N, 90°20'W	522	1,302	40	130	15.0	78.4
9. Trout	Cook	47°52'N, 90°10'W	103	257	23	77	10.6	10.9
10. Francis	Le Sueur	44°13'N, 93°43'W	370	926	15	50	3.5	12.9
11. Linwood	Anoka	45°23'N, 93°06'W	223	559	13	42	3.4	7.9
12. Christmas	Hennepin	44°52'N, 93°32'W	104	260	24	87	12.5	13.0
13. Big Kandiyohi	Kandiyohi	45°00'N, 94°56'W	273	684	5	18	3.6	9.8
14. Shetek	Murray	44°07'N, 95°41'W	1,390	3,480	3	9	1.6	21.8

Table 4

Lake	Date	Hours Duration of Experiment	Net Photosynthesis (24 hours)			Gross Photosynthesis (24 hours)		
			G O_2/m^2	G C/m^2	$\bar{\Sigma}$ G C/m^2	G O_2/m^2	G C/m^2	$\bar{\Sigma}$ G C/m^2
Itasca	2 Aug 65	24	2.02	0.63		3.78	1.18	
	13 Oct 65	24	1.13	0.35		2.36	0.74	
	17 May 66	24	2.56	0.80	0.44	4.64	1.45	1.24
	28 Jun 66	6	1.00	0.31		4.92	1.53	
	21 Jul 66	6	0.46	0.14		4.22	1.32	
Long	5 Aug 65	24	1.08	0.36		1.78	0.56	
	19 May 66	24	2.47	0.77	0.50	3.02	0.95	1.03
	7 Jul 66	6	2.60	0.82		5.72	1.78	
	30 Oct 66	6	0.18	0.05		2.70	0.84	
Elk	11 Jul 66	6	1.39	0.43	0.27	3.36	1.05	0.76
	29 Oct 66	6	0.36	0.12		1.40	0.47	
Mary	9 Jul 65	24	0.45	0.14	0.14	1.26	0.39	0.38
	14 Oct 65	24	0.43	0.14		1.23	0.38	
Sallie	13 Jul 66	6	2.12	0.66		7.76	2.42	
Nokay	18 Jul 66	6	1.70	0.53	0.53	3.54	1.10	0.92
	5 Oct 66	6	1.68	0.53		2.36	0.74	
Ball Club	26 Jul 66	6	0.32	0.10		3.60	1.12	
Clearwater	23 Jul 65	24	0.97	0.30	0.19	1.21	0.38	0.38
	19 Aug 65	24	0.25	0.08		1.25	0.39	
Francis	18 Jul 65	24	0.82	0.26		3.22	1.00	
	3 May 66	24	0.90	0.28	0.29	1.74	0.54	0.87
	6 Jun 66	24	0.54	0.17		1.98	0.62	
	23 Sep 66	6	1.44	0.45		4.20	1.32	
Linwood	9 May 66	24	0.57	0.17		4.54	1.42	
Christmas	28 Sep 66	6	0.10	0.03		1.18	0.37	
Big Kandiyohi	20 Sep 66	6	2.68	0.84		3.84	1.20	

Table 5

SALLIE LAKE, Dissolved Phosphorus

Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	13 Jul 1966 $P\text{-}PO_4$ Concentration (mg/m^3)	13 Jul 1966 $\Sigma P\text{-}PO_4$ ($mg \times 10^6$)	27 Oct 1966 $P\text{-}PO_4$ Concentration (mg/m^3)	27 Oct 1966 $\Sigma P\text{-}PO_4$ ($mg \times 10^6$)
0 - 3.0	0-10	12.9	60	774	11.5	148
3.0- 6.1	10-20	9.3	130	1209	12.0	112
6.1- 9.1	20-30	7.1	300	2125	12.0	85
9.1-12.2	30-40	2.8	370	1036	13.0	36
12.2-13.1	40-43	0.7	370	26	14.0	10
Total		32.7		5170 = 5.17 metric tons		391 = 0.39 metric tons

Table 6

Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	9 Jul 1964 Ca^{++} Concentration (g/m^3)	9 Jul 1964 ΣCa^{++} ($g \times 10^6$)	20 Sep 1964 Ca^{++} Concentration (g/m^3)	20 Sep 1964 ΣCa^{++} ($g \times 10^6$)	6 Nov 1964 Ca^{++} Concentration (g/m^3)	6 Nov 1964 ΣCa^{++} ($g \times 10^6$)
0 - 3.0	0-10	1.72	27.3	47.2	23.5	42.5	24.2	41.6
3.0- 6.1	10-20	1.48	28.0	41.4	22.6	33.5	24.2	35.8
6.1- 9.1	20-30	1.28	28.8	36.9	23.7	30.4	24.2	31.0
9.1-12.2	30-40	1.11	29.1	32.3	24.5	27.2	24.2	26.9
12.2-15.2	40-50	0.90	30.2	27.2	26.2	23.6	24.2	21.8
15.2-18.3	50-60	0.65	30.5	19.8	27.3	17.7	24.2	15.7
18.3-21.3	60-70	0.39	31.1	12.2	28.0	10.9	24.2	9.4
21.3-24.4	70-80	0.08	--	--	--	--	--	--
Total		7.61		217.0		186.8		182.2

Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	5 Jul 1966 Ca^{++} Concentration (g/m^3)	5 Jul 1966 ΣCa^{++} ($g \times 10^6$)	30 Oct 66 Ca^{++} Concentration (g/m^3)	30 Oct 66 ΣCa^{++} ($g \times 10^6$)
0 - 3.0	0-10	1.72	33.0	56.9	30.6	52.6
3.0- 6.1	10-20	1.48	34.0	50.4	30.6	45.3
6.1- 9.1	20-30	1.28	34.0	46.9	31.2	40.0
9.1-12.2	30-40	1.11	33.0	36.7	31.2	34.6
12.2-15.2	40-50	0.90	33.5	30.2	30.9	27.8
15.2-18.3	50-60	0.65	35.5	23.1	30.7	19.9
18.3-21.3	60-70	0.39	35.5	13.8	31.2	12.3
21.3-24.4	70-80	0.08	--	--	--	--
Total		7.61		257.8		232.5

Interval	Ca^{++} Depletion $g \times 10^6$	Ca^{++} Depletion g/m^2	Ca^{++} Depletion $mg/m^2/day$
9 Jul - 20 Sep 64	30.2	50.7	714
20 Sep - 6 Nov 64	4.6	7.7	108
9 Jul - 6 Nov 64	34.8	58.4	499
5 Jul - 30 Oct 66	25.3	42.6	387

Table 7

MARY LAKE, calcium budget

Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	17 Jul 64 Ca^{++} Concentration (g/m^3)	17 Jul 64 ΣCa^{++} ($g \times 10^6$)	20 Sep 64 Ca^{++} Concentration (g/m^3)	20 Sep 64 ΣCa^{++} ($g \times 10^6$)	9 Jul 65 Ca^{++} Concentration (g/m^3)	9 Jul 65 ΣCa^{++} ($g \times 10^6$)
0 - 3.0	0-10	.605	30	18.3	26	15.7	34	20.6
3.0- 6.1	10-20	.450	34	15.3	26	11.7	34	15.3
6.1- 9.1	20-30	.225	36	8.1	27	6.1	41	9.2
9.1-12.2	30-40	.030	--	--	--	--	44	1.3
Total		1.310		41.7		33.5		46.4

Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	14 Oct 65 Ca^{++} Concentration (g/m^3)	14 Oct 65 ΣCa^{++} ($g \times 10^6$)	10 Feb 66 Ca^{++} Concentration (g/m^3)	10 Feb 66 ΣCa^{++} ($g \times 10^6$)	24 Mar 66 Ca^{++} Concentration (g/m^3)	24 Mar 66 ΣCa^{++} ($g \times 10^6$)
0 - 3.0	0-10	.605	34	20.6	35	21.2	41	24.8
3.0- 6.1	10-20	.450	35	15.7	38	17.2	50	22.5
6.1- 9.1	20-30	.225	35	7.9	41	9.2	48	10.8
9.1-12.2	30-40	.030	35	1.0	45	1.3	48	1.4
Total		1.310		45.2		48.9		59.5

Interval	No. Days	ΔCa^{++} ($g \times 10^6$)	ΔCa^{++} (g/m^2)	ΔCa^{++} $mg/m^2/day$
17 Jul - 20 Sep 64	63	- 8.2	-35.9	-571
9 Jul - 14 Oct 65	95	- 1.2	- 5.3	- 55
14 Oct 65 - 10 Feb 66	116	+ 3.7	+16.2	+140
10 Feb - 24 Mar 66	42	+10.6	+46.5	+1,106
14 Oct 65 - 24 Mar 66	158	+14.3	+62.7	+397

Table 8

ELK LAKE, calcium budget

Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	11 Jul 66 Ca^{++} Concentration (g/m^3)	11 Jul 66 ΣCa^{++} ($g \times 10^6$)	29 Oct 66 Ca^{++} Concentration (g/m^3)	29 Oct 66 ΣCa^{++} ($g \times 10^6$)
0 - 3.0	0-10	2.96	32	95	31	92
3.0- 6.1	10-20	2.46	33	81	31	76
6.1- 9.1	20-30	2.12	35	74	32	68
9.1-12.2	30-40	1.47	35	51	32	47
12.2-15.2	40-50	.88	36	32	32	28
15.2-18.3	50-60	.60	36	22	32	19
18.3-21.3	60-70	.41	36	15	33	13
21.3-24.4	70-80	.27	35	9	35	9
24.4-27.4	80-90	.12	--	--	--	--
27.4-29.6	90-97	.01	--	--	--	--
Total		11.17		379		352

Interval	No. Days	Ca^{++} Depletion ($g \times 10^6$)	Ca^{++} Depletion (g/m^2)	Ca^{++} Depletion ($mg/m^2/day$)
11 Jul - 29 Oct	108	27	26.7	.248

Table 9

FRANCIS LAKE, calcium budget

Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	3 May 1966 Ca^{++} Concentration (g/m^3)	3 May 1966 ΣCa^{++} ($g \times 10^6$)	22 Sep 1966 Ca^{++} Concentration (g/m^3)	22 Sep 1966 ΣCa^{++} ($g \times 10^6$)
0 - 3.0	0-10	7.39	42.5	314	30.4	224
3.0- 6.1	10-20	3.56	42.5	151	31.7	113
6.1- 9.1	20-30	1.61	45.0	72	32.8	53
9.1-12.2	30-40	.23	45.0	10	41.0	9
12.2-14.0	40-50	.08	43.0	3	50.0	4
Total		12.87		550		403

Interval	No. Days	Ca^{++} Depletion ($g \times 10^6$)	Ca^{++} Depletion (g/m^2)	Ca^{++} Depletion ($mg/m^2/day$)
3 May - 22 Sep 66	139	147	39.8	270

Table 10

SALLIE LAKE, calcium budget

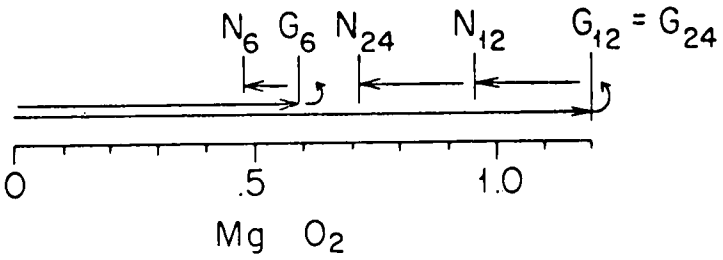
Depth (m)	Depth (ft)	Volume ($m^3 \times 10^6$)	13 Jul 66 Ca^{++} Concentration (g/m^3)	13 Jul 66 ΣCa^{++} ($g \times 10^6$)	27 Oct 66 Ca^{++} Concentration (g/m^3)	27 Oct 66 ΣCa^{++} ($g \times 10^6$)
0 - 3.0	0-10	12.9	34.5	44.5	27.5	35.5
3.0- 6.1	10-20	9.3	35.0	32.6	28.0	26.0
6.1- 9.1	20-30	7.1	37.5	26.6	27.3	19.4
9.1-12.2	30-40	2.8	39.0	10.9	28.0	7.9
12.2-13.1	40-43	0.7	39.2	2.7	28.0	1.9
Total		32.7		117.2		90.7

Interval	No. Days	Ca^{++} Depletion $g \times 10^6$	g/m^2	$mg/m^2/day$
13 Jul - 27 Oct 66	104	265	50.2	482

Table 11

Lake	Number of Experiments	Mean Gross Productivity g $C/m^2/day$	Total Pigments units/g loss on ignition
Kandiyohi	1	0.37	15.8
Clearwater	2	0.38	4.3
Francis	4	0.87	18.3
Nokay	2	0.92	24.0
Long	4	1.03	41.9
Ball Club	1	1.12	50.0
Itasca	5	1.24	63.1
Linwood	1	1.42	25.5
Sallie	1	2.42	32.0

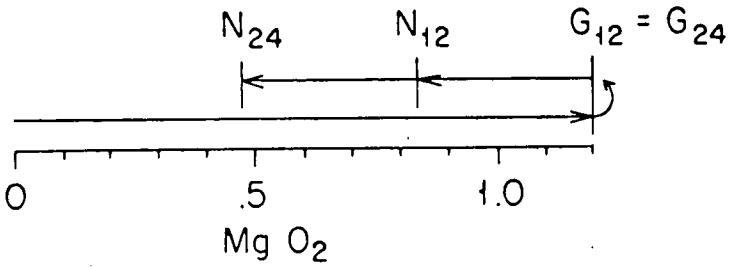
A.



Photosynthesis rate = 0.1 mg O_2/hr.

Respiration rate = 0.02 mg O_2/hr.

B.



Photosynthesis rate = 0.1 mg O_2/hr.

Respiration rate = 0.03 mg O_2/hr.

Legend:

N_6 , N_{12} and N_{24} = net photosynthesis after 6, 12, and 24 hours.

G_6 , G_{12} and G_{24} = gross photosynthesis after 6, 12, and 24 hours.

Fig. 1. The oxygen budget during photosynthesis experiments of various durations; A, assuming a respiration rate of 0.02 mg O_2/l per hour, and B, assuming a respiration rate of 0.03 mg O_2/l per hour

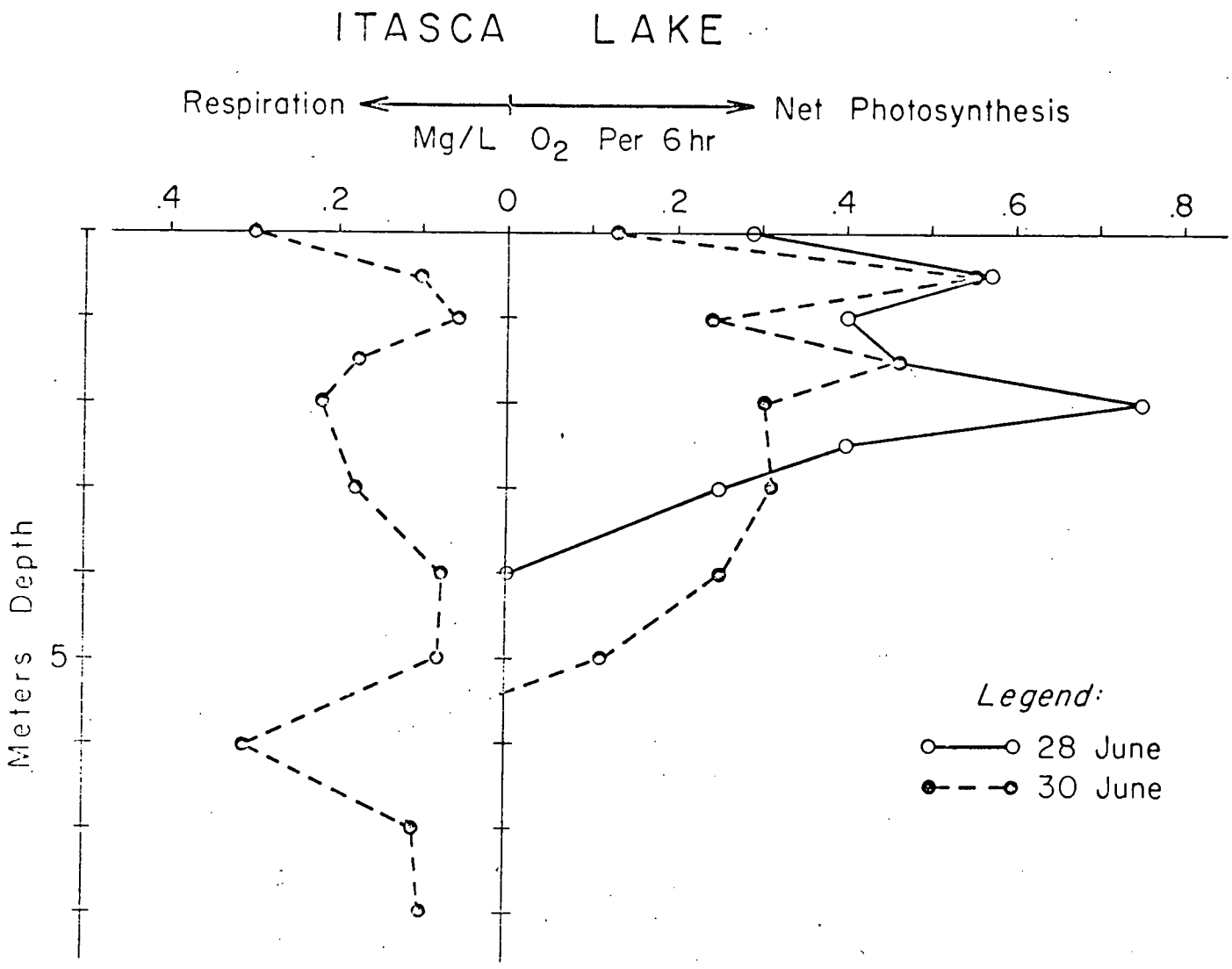


Fig. 2. Net photosynthesis for 6-hour experiments begun at solar noon on 28 and 30 June, 1966, in Lake Itasca. The respiration rates for 30 June are shown by the curve at the left

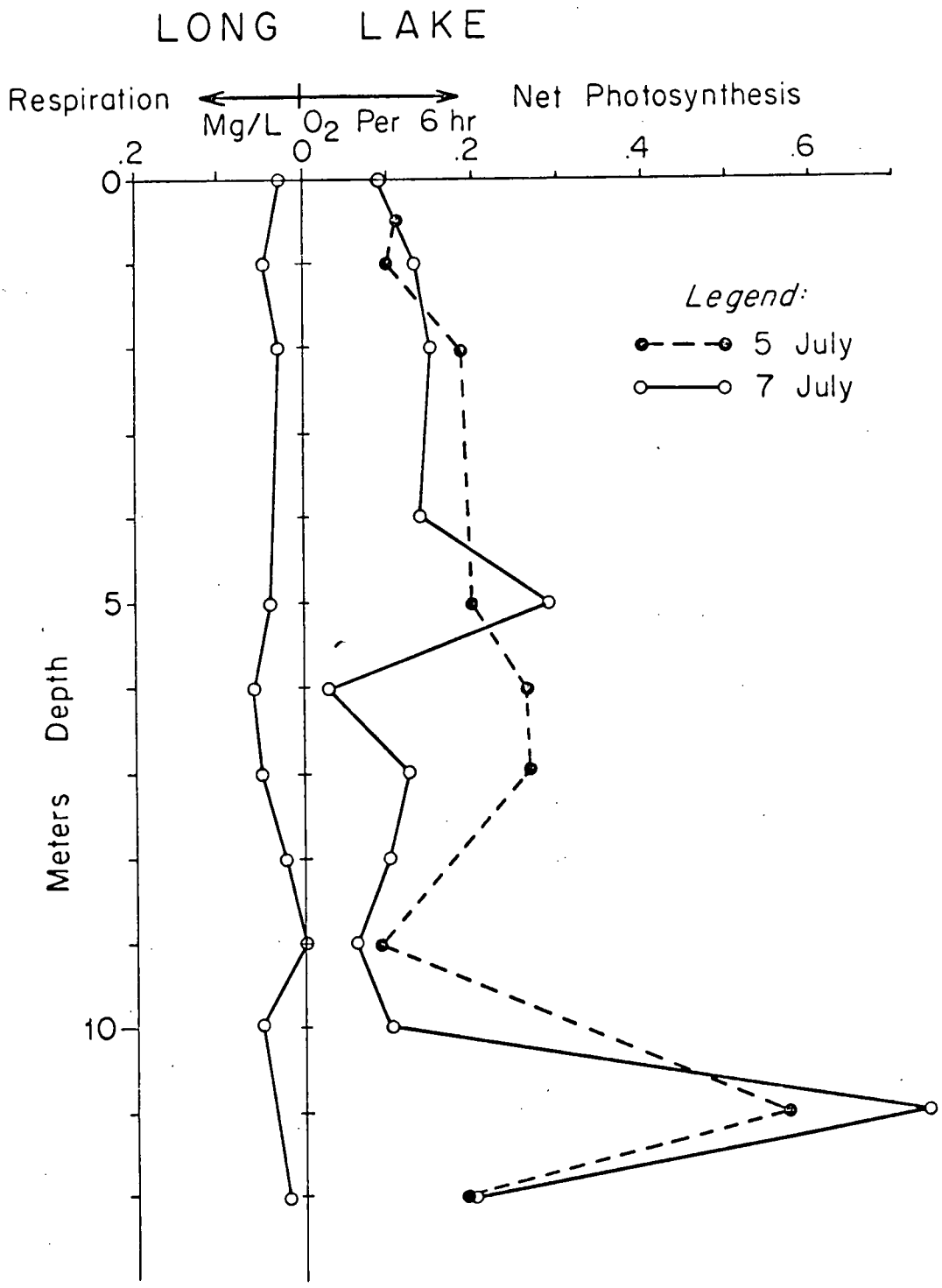


Fig. 3. Net photosynthesis for 6-hour experiments begun at solar noon on 5 and 7 July, 1966 in Long Lake

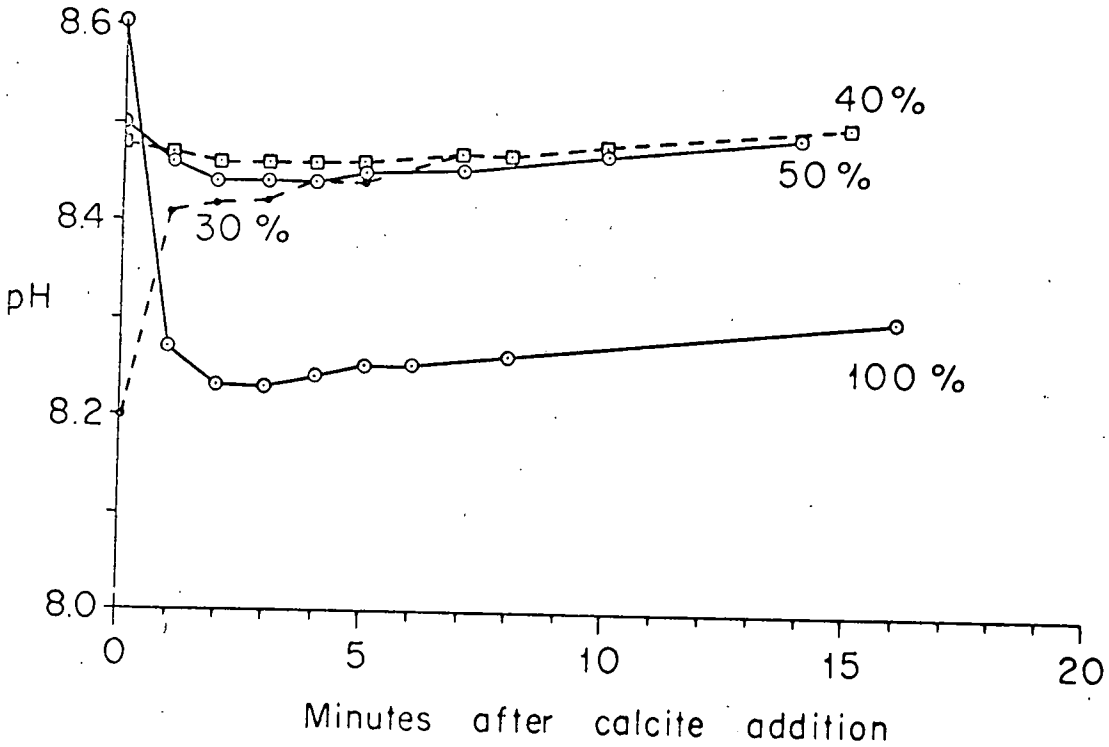


Fig. 4. Initial pH and pH at time intervals after placing calcite in contact with the glass electrode in 100% lake water and in 3 dilutions with CO_2-free distilled water. Sample collected 11 February, 1966, at 4-m depth in Long Lake

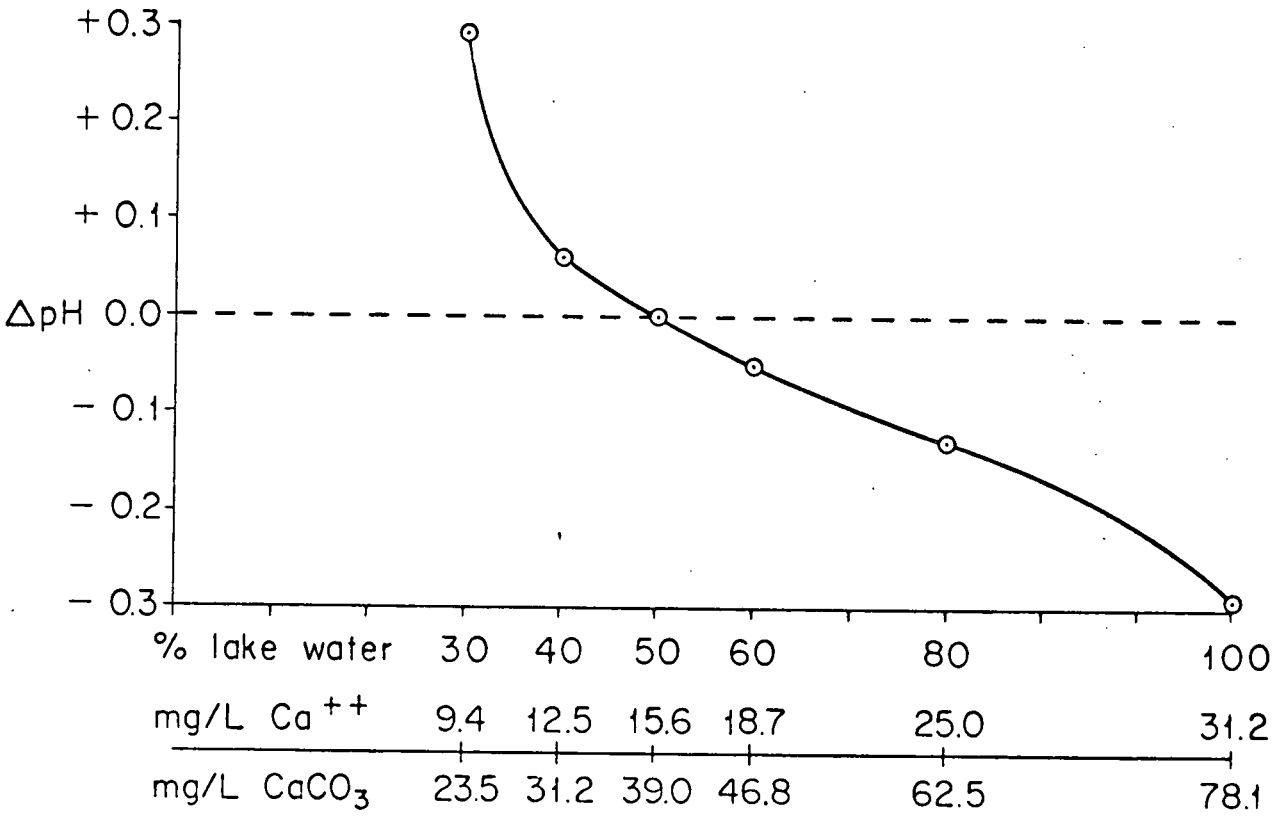


Fig. 5. Saturometer values for water from Long Lake, collected 11 February, 1966, 26 hours after the sample was diluted with CO_2-free distilled water

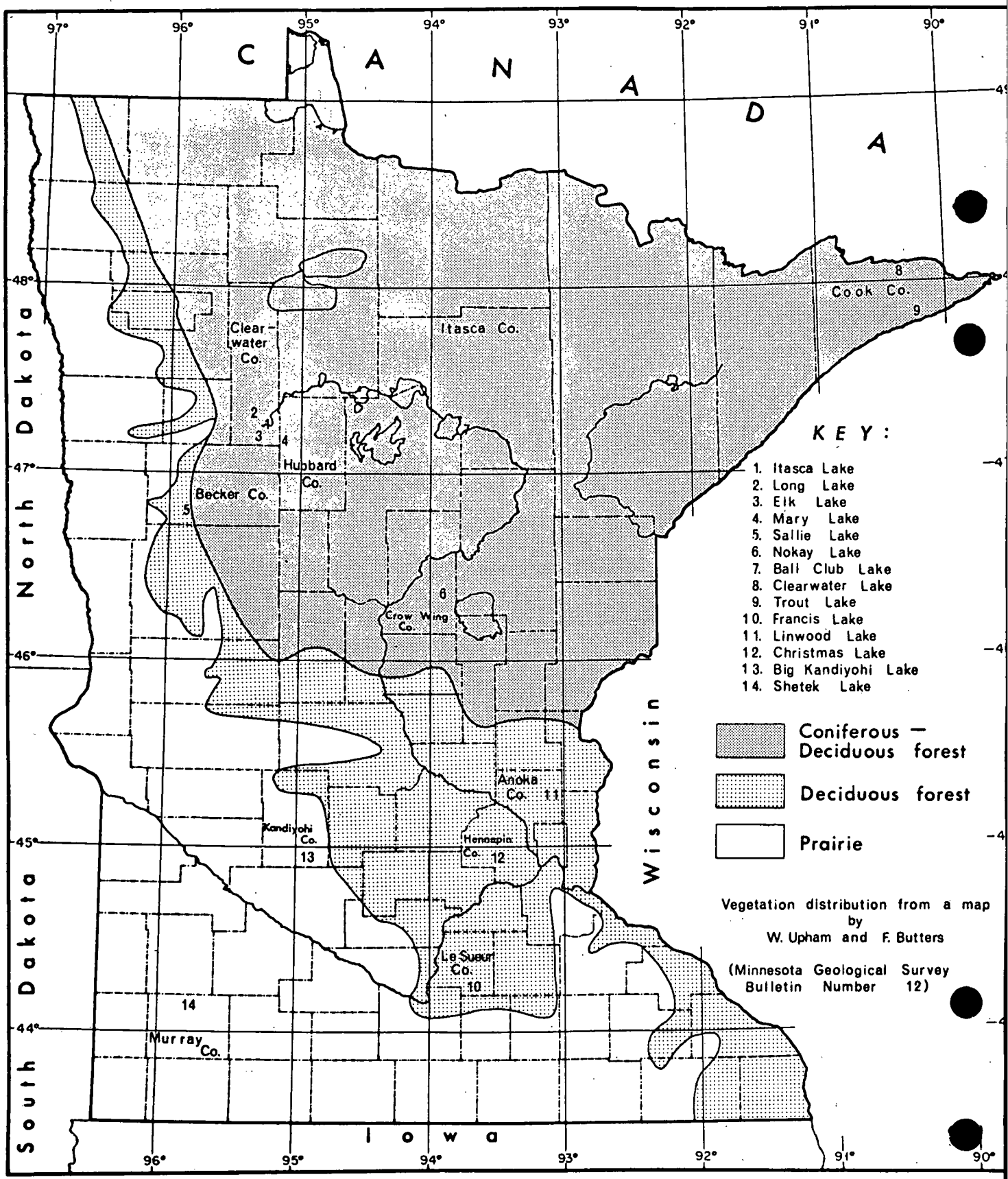


Fig. 6. The geographic distribution of the lakes studied, and their distribution with respect to the major types of vegetation in Minnesota

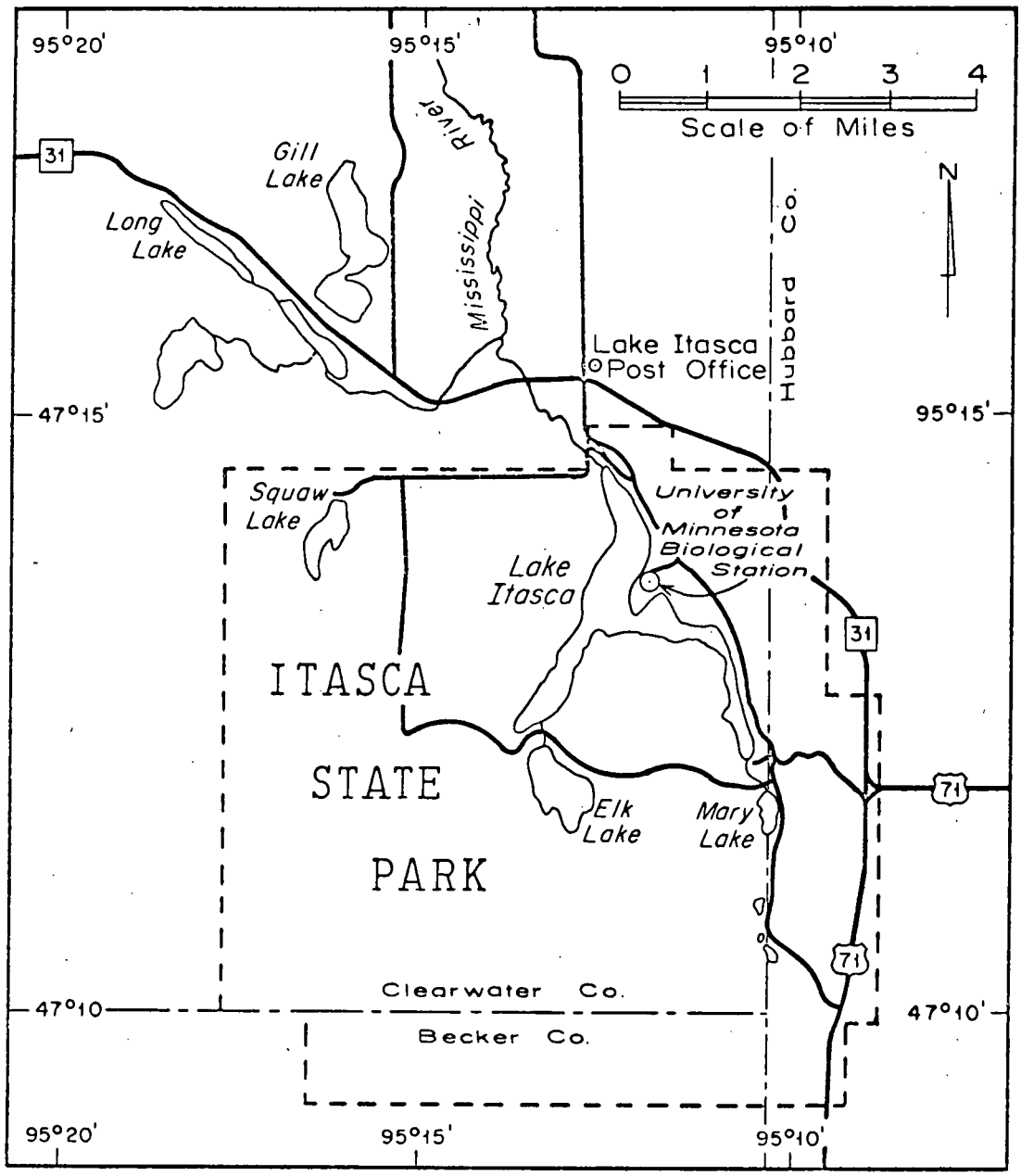


Fig. 7. Itasca State Park and vicinity, showing the location of Lake Itasca, Long Lake, Mary Lake, and Elk Lake. Map modified from Minnesota State Highway Department county road maps

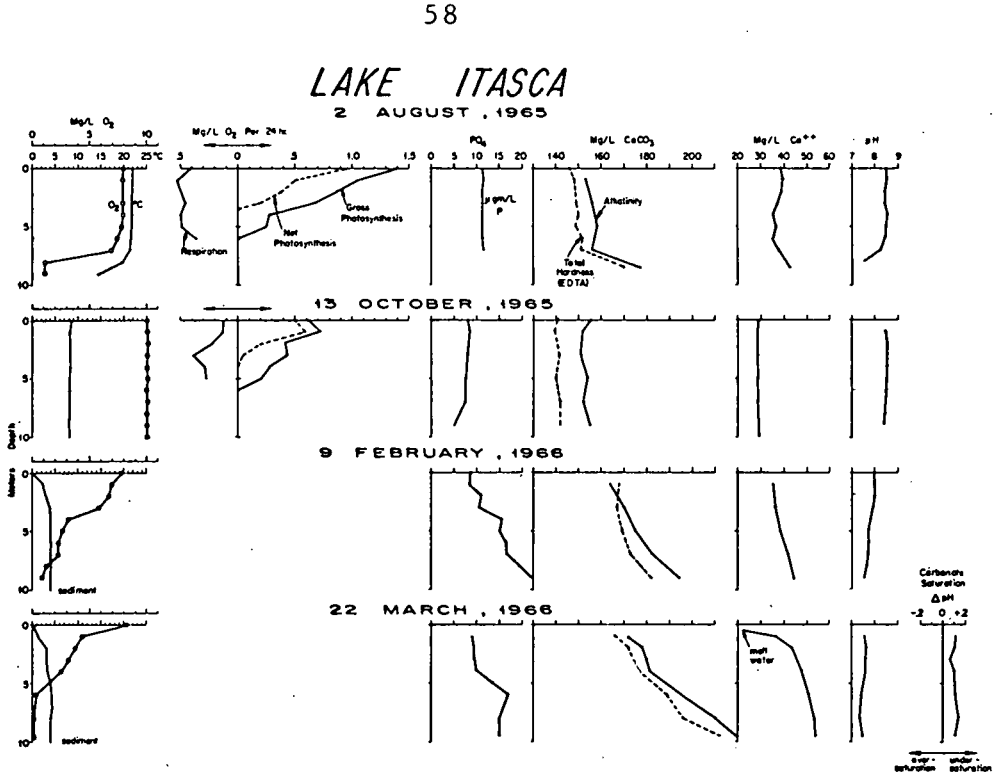


Fig. 8. Water chemistry and productivity of Lake Itasca, 1965-66

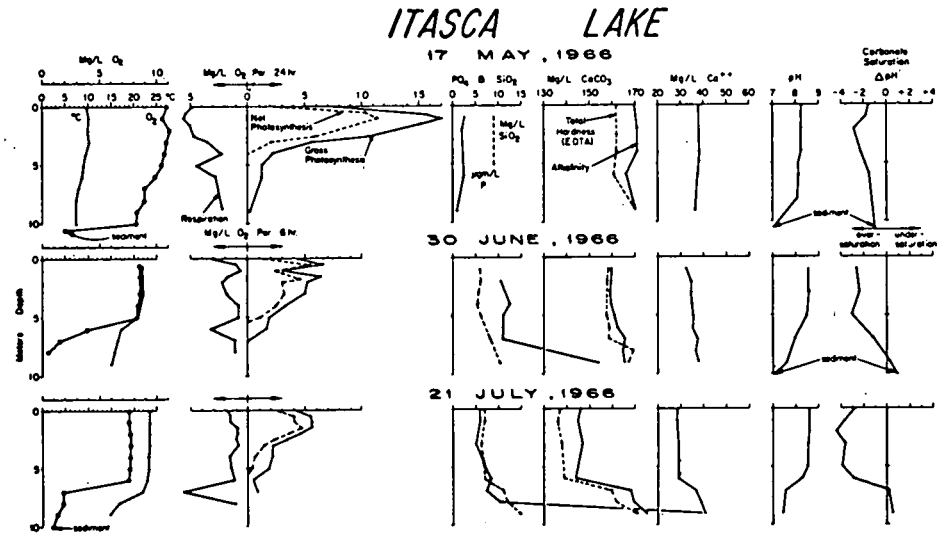


Fig. 9. Water chemistry and productivity of Lake Itasca, spring and summer, 1966

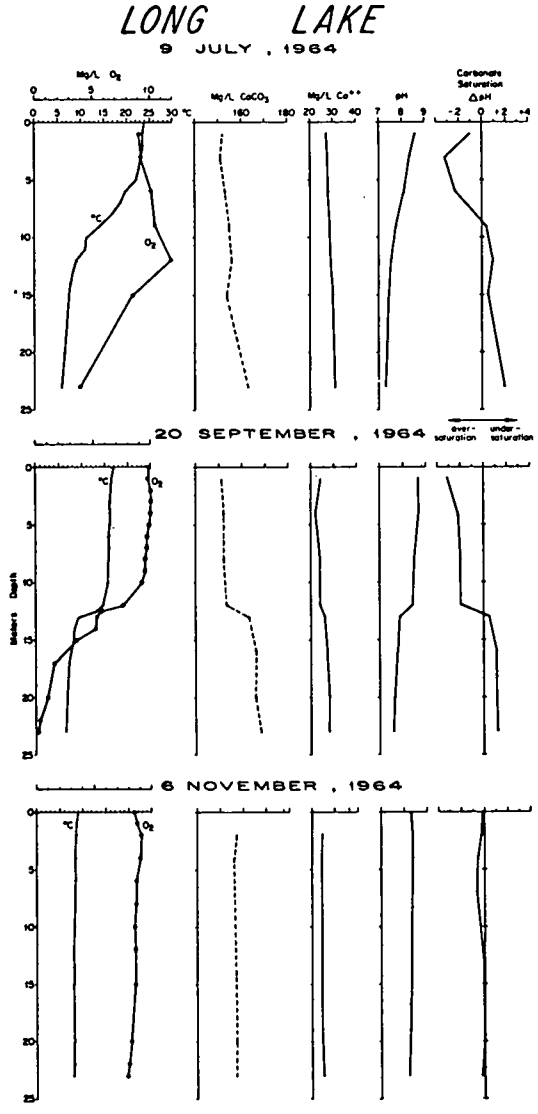


Fig. 10. Water chemistry of Long Lake, 1964

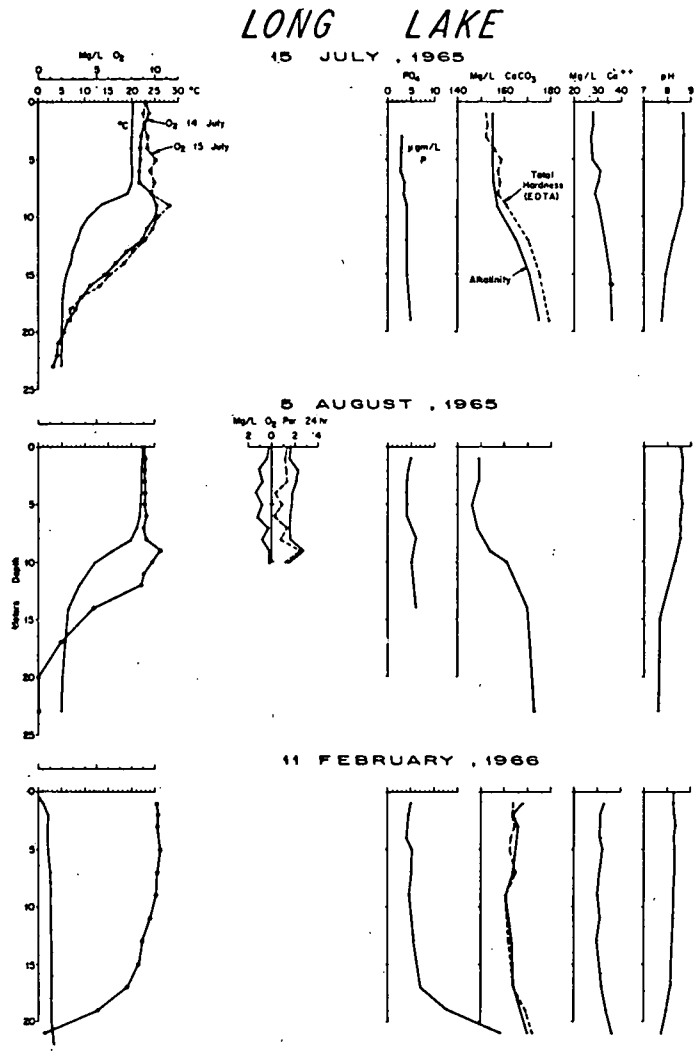


Fig. 11. Water chemistry and productivity of Long Lake, 1965-66

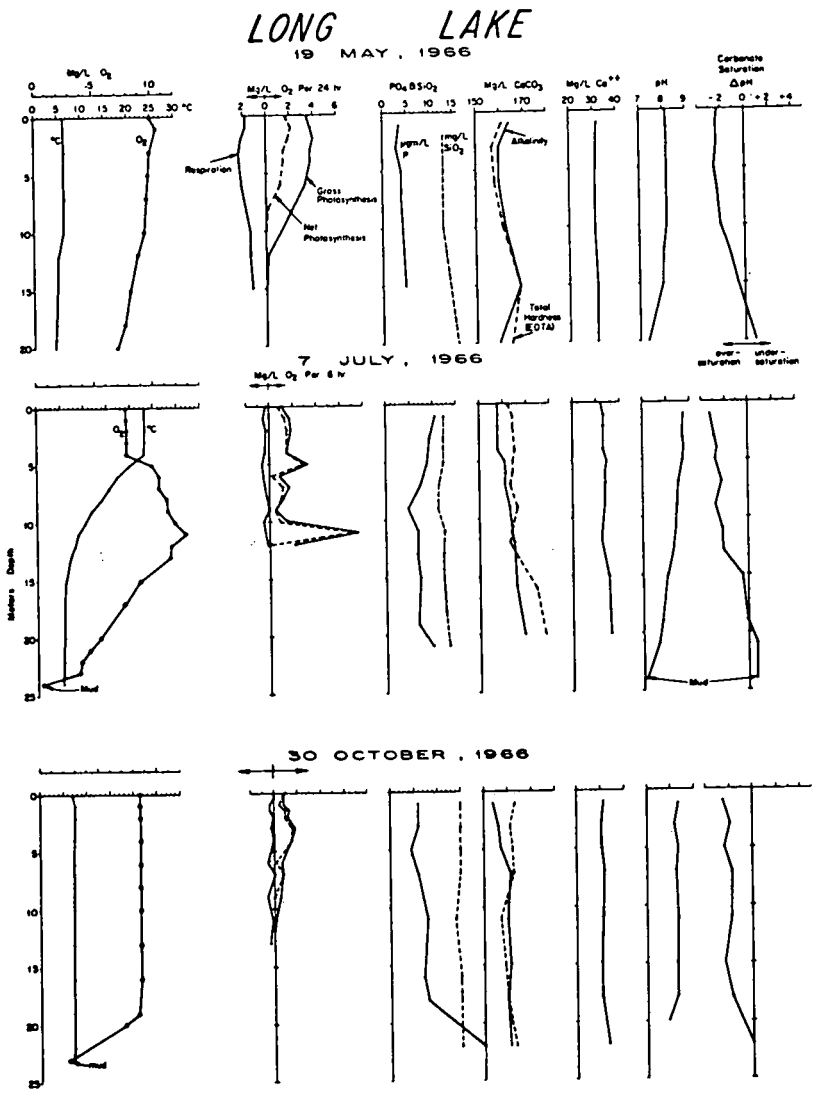


Fig. 12. Water chemistry and productivity of Long Lake, 1966

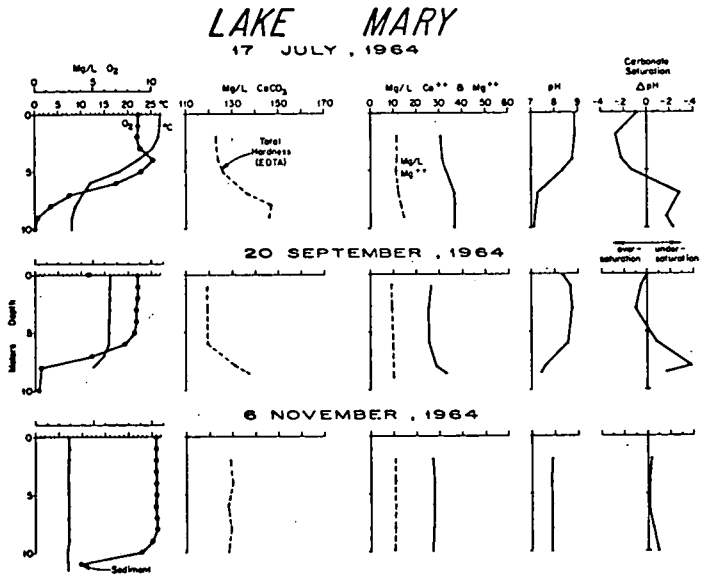


Fig. 13. Water chemistry of Lake Mary, 1964. Oxygen and temperature data for 17 July were obtained by Dr. J.C. Underhill

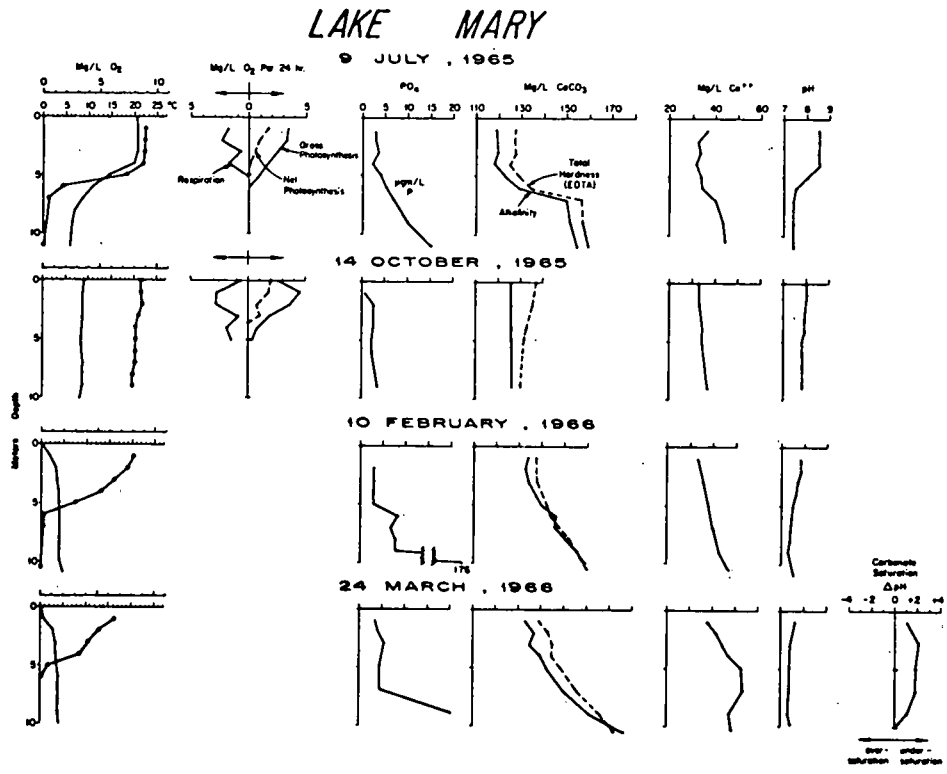


Fig. 14. Water chemistry and primary productivity of Lake Mary, 1964-66

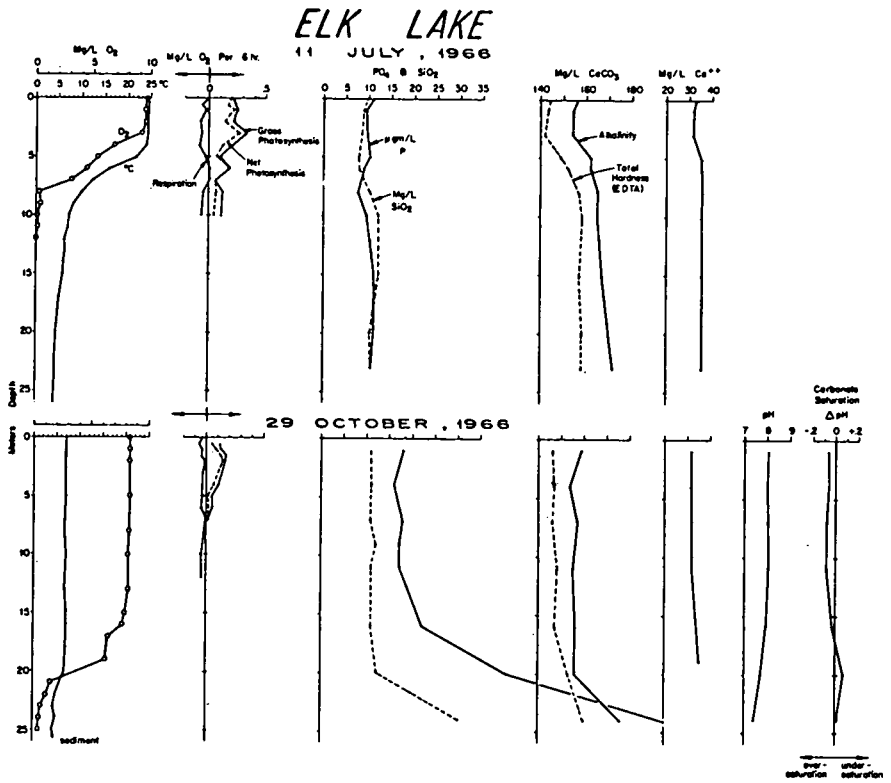


Fig. 15. Water chemistry and primary productivity of Elk Lake

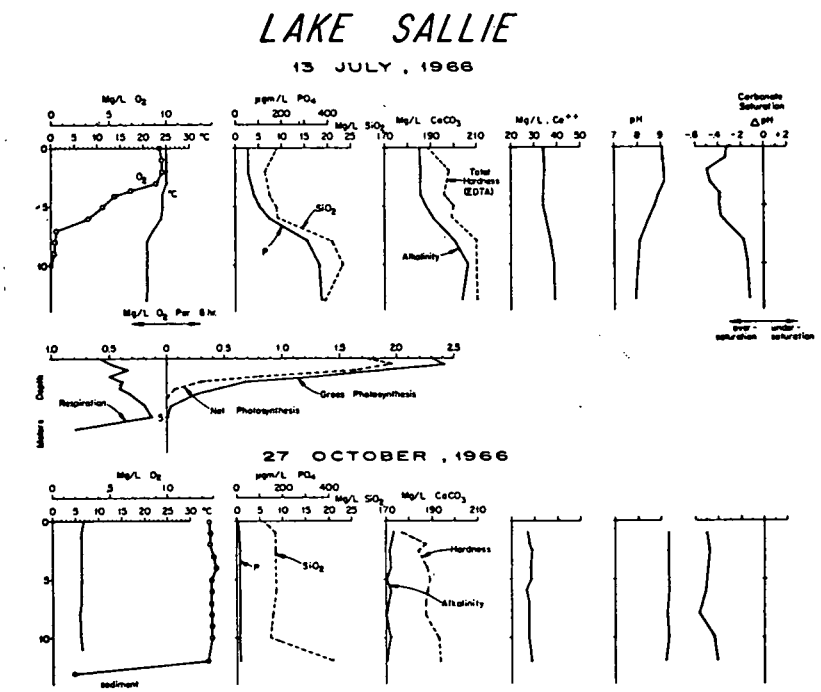


Fig. 16. Water chemistry and primary productivity of Lake Sallie

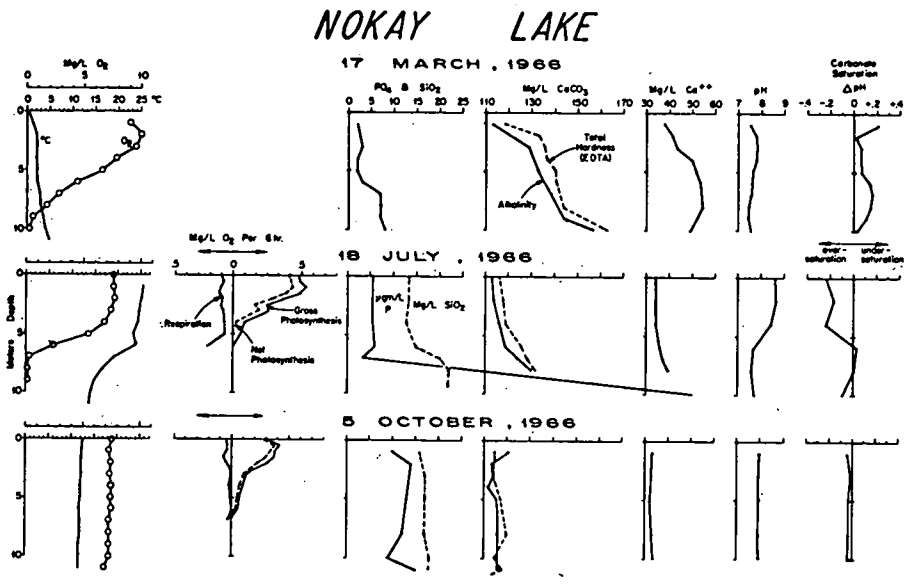


Fig. 17. Water chemistry and primary productivity of Nokay Lake

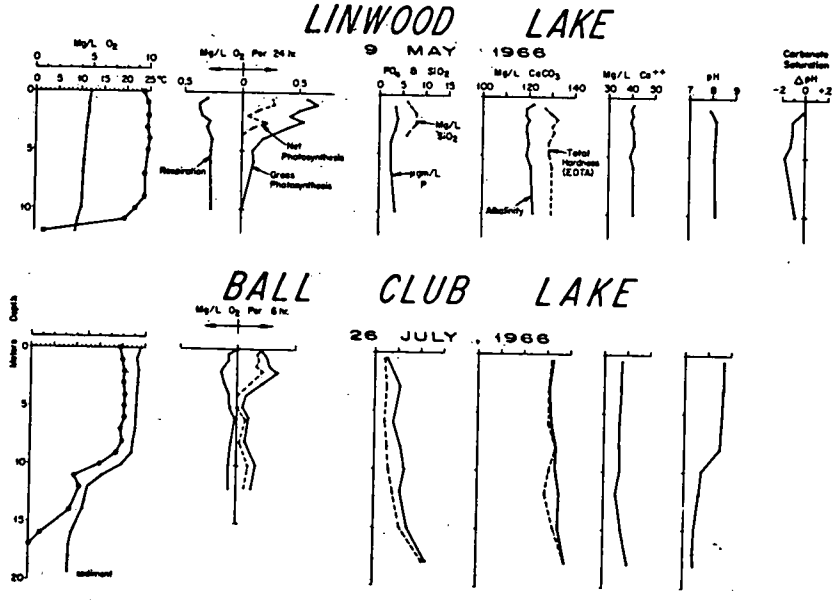


Fig. 18. Water chemistry and productivity of Linwood and Ball Club Lake

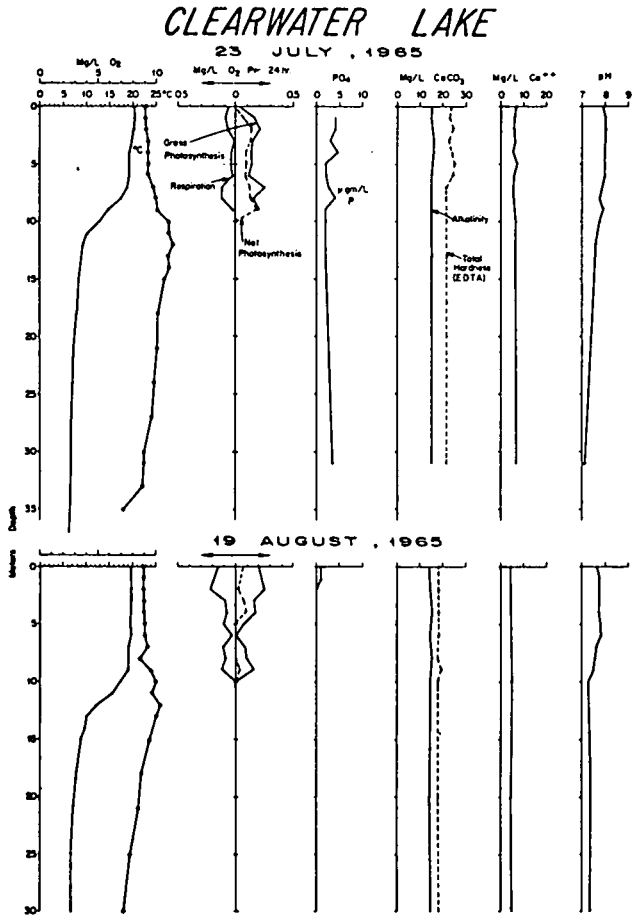


Fig. 19. Water chemistry and productivity of Clearwater Lake

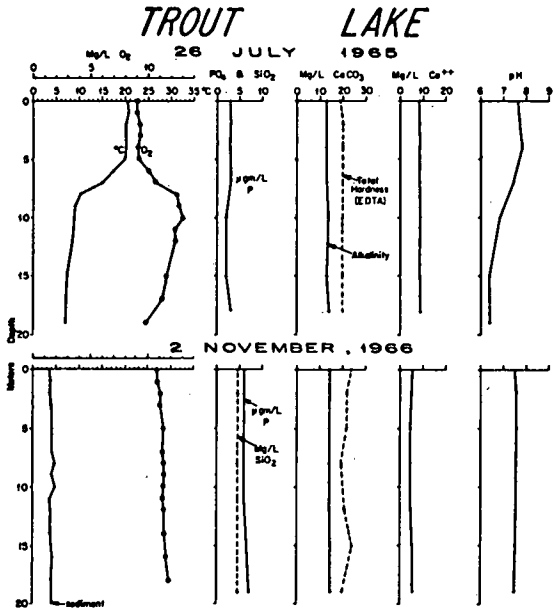


Fig. 20. Water chemistry of Trout Lake

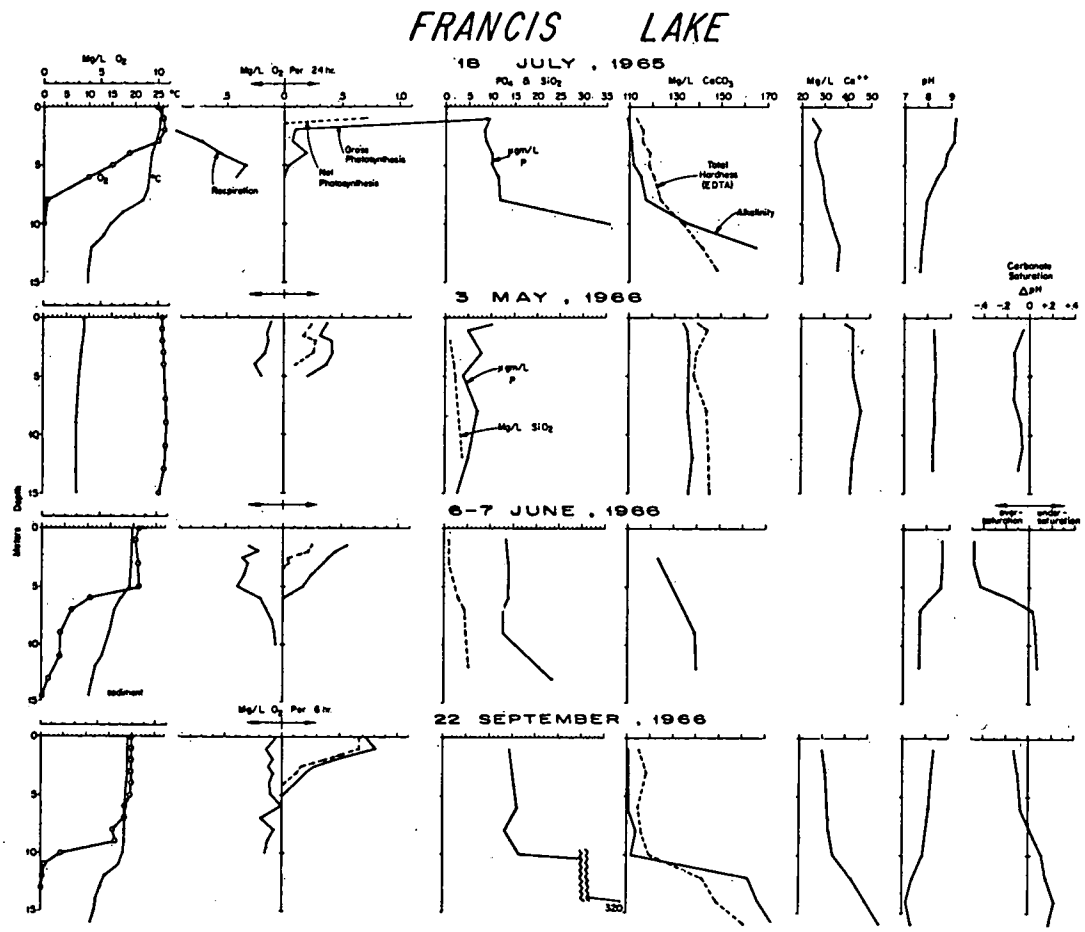


Fig. 21. Water chemistry and productivity of Francis Lake

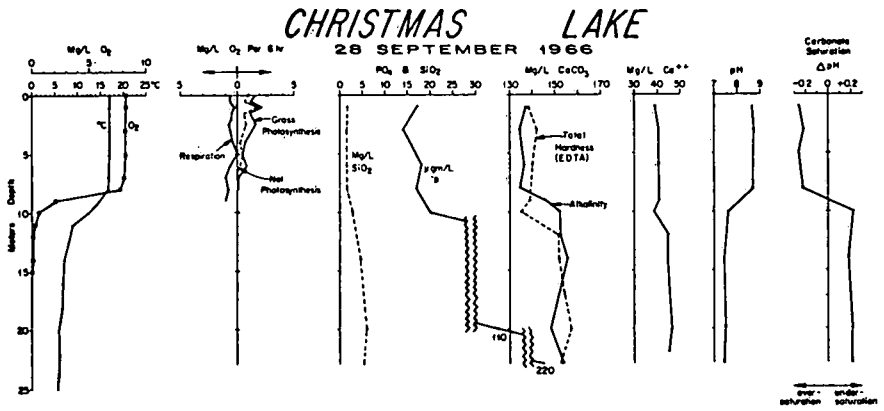


Fig. 22. Water chemistry and productivity of Christmas Lake

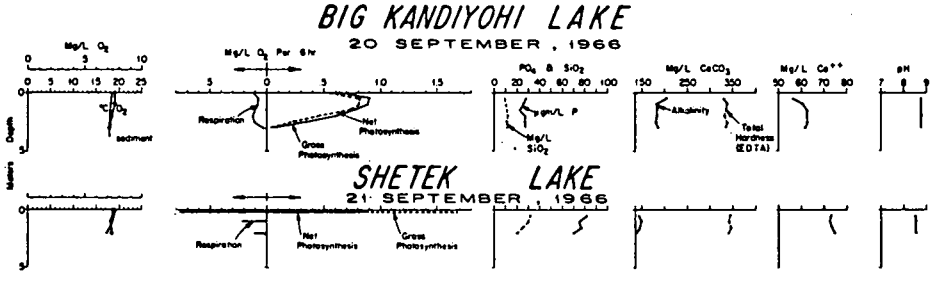
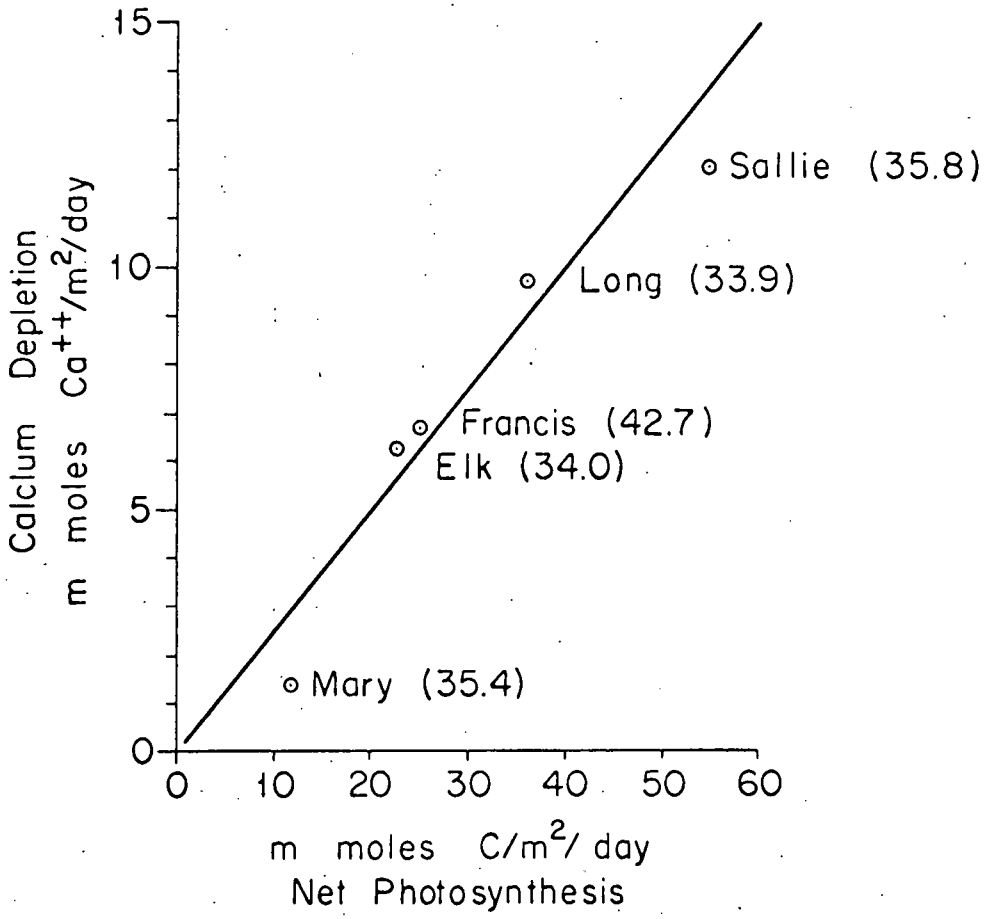


Fig. 23. Water chemistry and productivity of Big Kandiyohi and Shetek lakes

Fig. 24. Photosynthetic carbon consumption and calcium depletion in five Minnesota lakes. The mean initial calcium concentration as mg/l Ca for each lake at the beginning of the corresponding time interval is shown in parentheses after the name of each lake. The time intervals are as follows: Mary Lake, 9 July - 14 October, 1965; Elk Lake, 11 July - 29 October, 1966; Francis Lake, 3 May - 22 September, 1966; Long Lake, 5 July - 30 October, 1966; Sallie Lake, 13 July - 27 October 1966



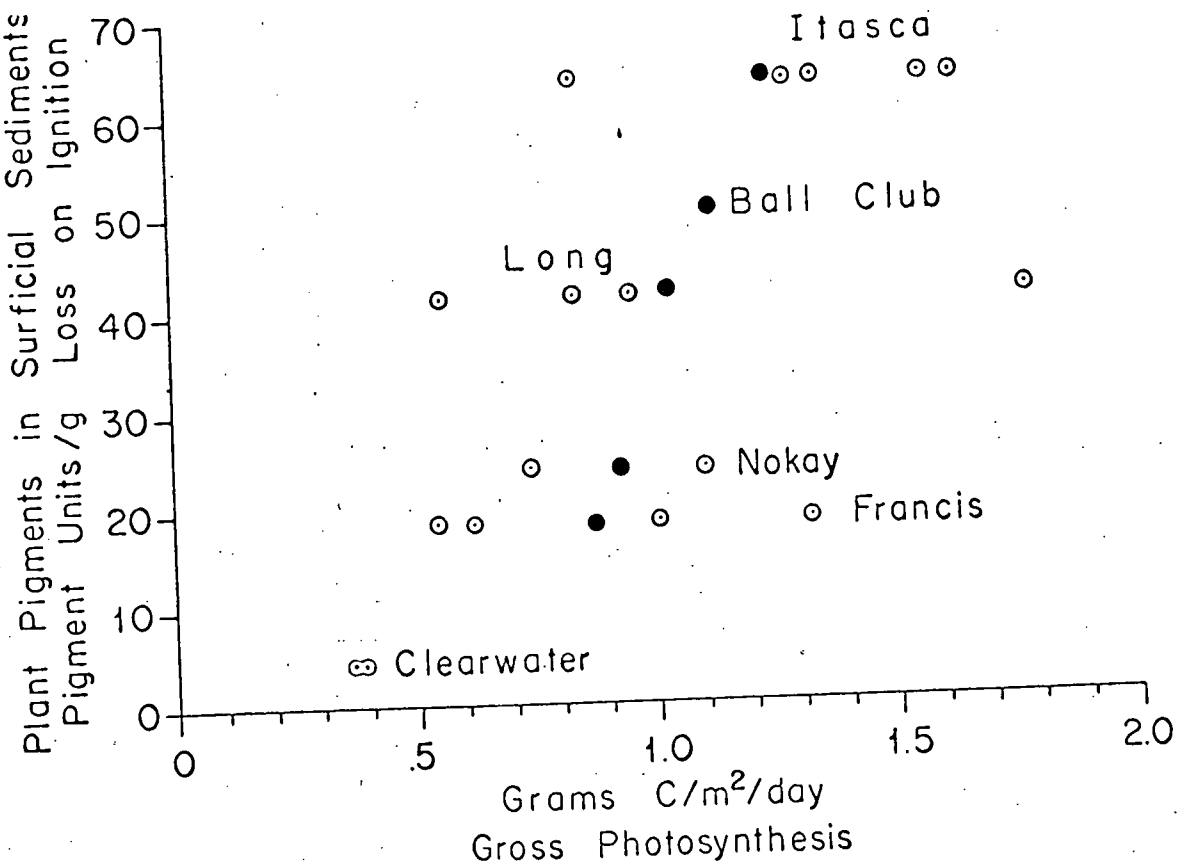


Fig. 25. Gross productivity and plant pigments preserved in surficial sediments from 6 Minnesota lakes. Open circles are the results of individual experiments on a lake, closed circles are the means of all experiments from a lake. Productivity and pigment data from Big Kandiyohi, Linwood, and Sallie lakes, which are included in Table 11, are excluded from the graph for the reasons given in the text.