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PRIMARY PRODUCTIVITY (C^{14}) AT TWIN LAKES COLORADO: 1973–81 STUDY RESULTS

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16. ABSTRACT

Primary productivity and its limiting factors were studied in Twin Lakes, Colorado, during 1973-81, to characterize the lakes limnologically before operations began at the pumped-storage powerplant then under construction on the lower lake. The lakes are a pair of connected, dimictic, montane, drainage lakes of glacial origin. They are classified as oligotrophic. The upper lake receives spring runoff directly, and its volume strongly influences the limnology of both lakes. Both lakes also receive unknown, but limited, amounts of local runoff which – like spring runoff – contains nutrients that support primary production in Twin Lakes.

Based on 82 observations, the range of primary production rates in the upper lake is 1 to 104 mg C/($m^2 \cdot d$). That in the lower lake, based on 86 observations, is 5 to 312 mg C/($m^2 \cdot d$). The mean daily production rate for the same number of observations from 1973-81 was 33.6 and 63.9 mg C/($m^2 \cdot d$) for the upper and lower lakes, respectively. The range for oligotrophic lakes, based on the literature, is 50 to 300 mg C/($m^2 \cdot d$). The average annual productivity over the 9 years of study was 11.3 and 25.8 g C/($m^2 \cdot a$) for the upper and lower lakes, respectively. The maximum rates of primary production were observed at spring and fall circulation periods. The lowest production rates were observed during winter, under the ice, especially in those years when snow and ice cover were thickest.

Runoff transports nutrients that are at other times limited; the years with greatest runoff were observed to have the highest rates of primary production in Twin Lakes. However, these higher rates were observed only in the lower lake, because the increased turbidity and flushing caused by heavy spring runoff severely limits primary production in the upper lake.

The data in this report, with other limnological and fishery data from Twin Lakes, will be used with postconstruction data now being collected to evaluate the effects of pumped-storage powerplant operation on the ecology of Twin Lakes.

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December 1985

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UNITED STATES DEPARTMENT OF THE INTERIOR ★ BUREAU OF RECLAMATION

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INTRODUCTION

This report discusses the results of C^{14} primary productivity studies conducted at Twin Lakes, Colorado, before operation of the Mt. Elbert Pumped-Storage Powerplant. It is one of a series of reports describing the preoperational limnology and fishery of Twin Lakes.

"All production within an ecosystem stems from the energy in organic substances that autotrophic organisms create from inorganic raw materials" (Cole, 1979) [1].* Cole goes on to point out that there are two main kinds of autotrophs, or primary producers: chemosynthetic bacteria, which derive their production energy from inorganic chemical bonds, and photosynthetic organisms, which use light as the energy source for production of organic substances. In a living ecosystem, like Twin Lakes, primary production is mainly the result of photosynthetic fixation of atmospheric carbon dioxide into starches, sugars, and other cellular materials.

Primary production is routinely measured at Twin Lakes using a C^{14} radioisotope tracer method. This method enables us to determine the rate at which carbon is converted (fixed) by algae into cellular substances by photosynthesis. The carbon fixation rate determined is a relatively precise measure of the photosynthesizing activity of the standing crop of algae under existing environmental conditions (light, nutrient availability, temperature, etc). It reflects the present or future abundances of algae and zooplankton, and the eventual biomass of fish in the lakes. The C^{14} studies over a long period (e.g. 2 to 3 yrs) become good indicators of cycles in zooplankton and fish population densities. Estimates of primary production are important to managers of recreation and fisheries in USBR (Bureau of Reclamation) reservoirs.

APPLICATION

The results from this study are being used to determine the average annual primary production rates for each of the Twin Lakes. These data characterize the ecology of Twin Lakes before operation of the Mt. Elbert Pumped-Storage Powerplant began in late 1981. Preoperation limnological studies are now being repeated to quantify the changes that are occurring in the lake's ecology. The results of the study on Twin Lakes and those of other studies on pumped-storage effects, will be used by planners, designers, and operators to predict the impacts of constructing and operating future projects.

The results of this study can be valuable to anyone interested in the limnology of lakes, particularly high-mountain lakes. This group includes fishery managers who are responsible for montane fisheries. The results of limnological studies at Twin Lakes can be applied to other lakes and reservoirs in the Rocky Mountain region. Interpretation of the limnological data indicates a wide variability in the potential of these lakes and reservoirs to support fisheries. By using this limnological data, more efficient stocking plans can be developed. Thus, the fisheries of lakes and reservoirs can be improved. Other scientists studying lake and reservoir limnology can also use the data and conclusions in this report.

* Numbers in brackets refer to entries in the bibliography.

SUMMARY

Primary production in Twin Lakes before operation of the Mt. Elbert Pumped-Storage Powerplant seems to have been mainly influenced by runoff volume, light, and nutrients. Algal biomass and water temperature were less important, perhaps having had more subtle and interactive, rather than limiting, effects.

The smaller upper lake is directly affected by annual spring runoff. In average and above-average runoff years, this lake is subjected to increased flushing and turbidity for a 6-8 week period. This period coincides with decreases in carbon fixation rate, chlorophyll *a* concentration, and plankton density. The upper lake also functions as a settling basin for suspended sediments in average and above-average runoff years, buffering the lower lake from the direct effects of runoff. Generally, the upper lake is less productive in average and above-average runoff years than in below-average runoff years.

The larger lower lake is less directly affected by the annual spring runoff event. In average and above-average runoff years, enough nutrients are flushed from the upper lake to sustain the increased levels of production in the lower lake. Generally, the lower lake is more productive in average and above-average runoff years than in below-average runoff years.

Thus, the runoff volume seems to be responsible for the pattern of productivity observed in Twin Lakes; that is, either lake, but not both lakes simultaneously, experiences increased production.

Production rates in the upper lake vary inversely with runoff volume. The upper lake traps nutrients in below-average runoff years and with the lessened turbidity, which means more light and warmer water, it supports maximum production during late summer and fall. In average and above-average runoff years, the upper lake experiences increased flushing and turbidity during runoff, and the runoff period is longer.

As a result, nutrients are flushed into the lower lake or are diluted by the volume of runoff, and maximum water temperatures may be 3 °C cooler than those in below-average runoff years. Generally, the upper lake does not exhibit increased or maximum production until after fall turnover in average and above-average runoff years.

Production rates in the lower lake vary directly with runoff volume. In below-average runoff years, production seems to be nutrient-limited, with maximum production occurring after spring and fall turnovers. Production in the lower lake seems to be more dependent upon autochthonous nutrient cycling in below-average runoff years, and is generally less in below-average than in average and above-average runoff years. Production in the lower lake has an allochthonous nutrient cycle pattern in average and above-average runoff years, when it is supported by nutrients flushed from the upper lake. Generally, the production rates in the lower lake are higher when nutrient input is increased by greater runoff volume.

Light limitation at Twin Lakes tends to be a critical factor at two main periods of the year. The first period is when the amount of winter snow and ice cover severely limits the amount of light reaching plankton populations. However, when the ice is clear, and there is little or no snow, production continues under the ice. In the upper lake a significant percentage of the yearly total production may occur during the ice-covered season if the ice remains clear and snow cover is light. However, in years when the ice and snow cover are heavy, and little light is available to plankton populations into April, a biological "crash" may occur, caused by release of toxic concentrations of heavy metals from the sediments in the lakes. The second time of year when light becomes limiting to primary production is during spring runoff, when turbidity levels are high, especially in the upper lake.

Nutrient concentrations also vary directly with runoff. They are trapped by the upper lake in low runoff years and flushed into the lower lake in high runoff years. The allochthonous cycle displayed by the lower lake in high runoff years compared with the autochthonous cycle observed in low runoff years is a clear indication of the effect nutrients have on primary production in Twin Lakes. The limiting nutrient at Twin Lakes appears to be phosphorus.

DESCRIPTION

Location and Geology

Twin Lakes are located on Lake Creek at the eastern foot of the Sawatch Range in the upper Arkansas River Valley of central Colorado (fig. 1). The lakes are 2802 m above mean sea level. The present topography of the western side of the Arkansas River Valley in the Twin Lakes area is largely the result of glacial action on earlier alluvial deposits (Buckles, 1973) [2]. Twin Lakes probably originated with the moranic damming of Lake Creek (Sartoris et al., 1977) [3]. The shoreline and bottom topography of Twin Lakes are shown on figure 2.

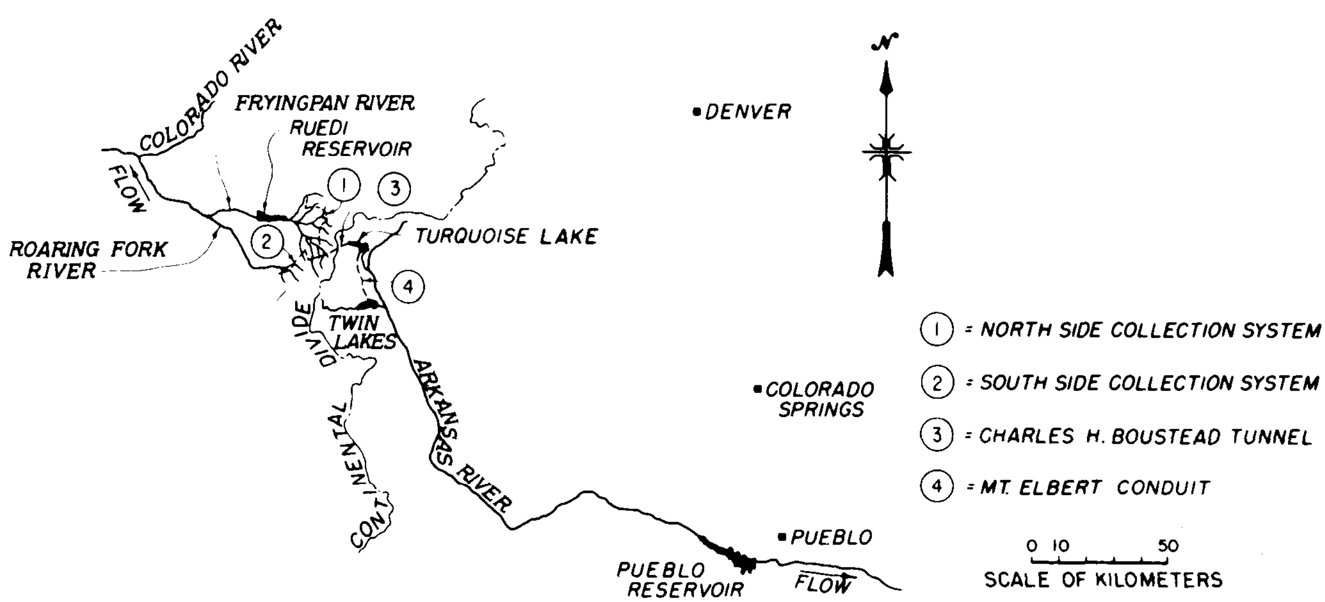


Figure 1. – Location map of Twin Lakes, Colorado.

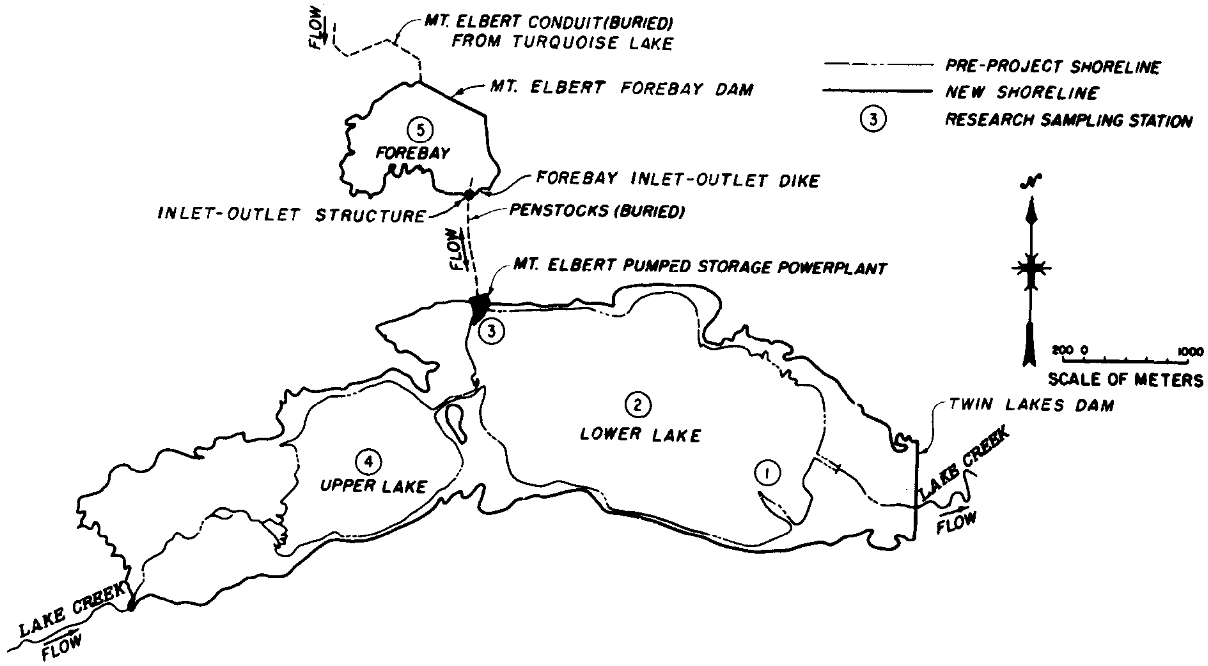


Figure 2 (a) Twin Lakes shoreline.

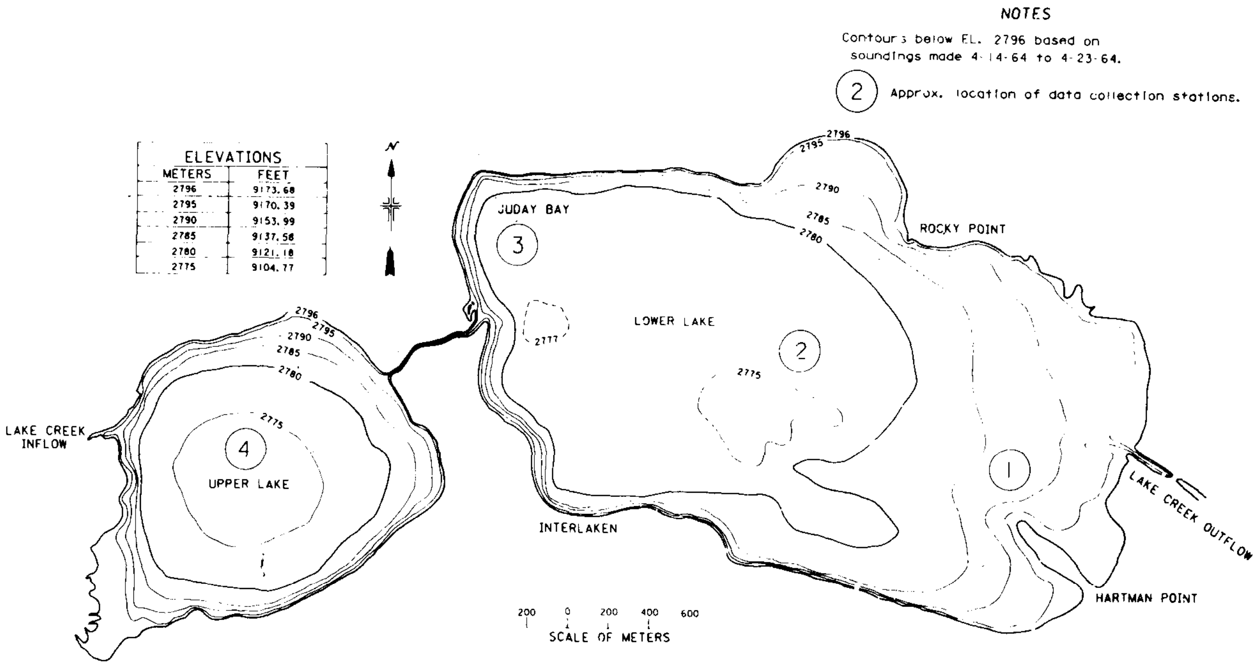


Figure 2(b) Bottom topographic map of Twin Lakes.

Beginning at the turn of the century, the lakes were hydraulically modified to convert them into irrigation storage reservoirs. These modifications included damming of the original lower lake outlet and construction of a deeper, controlled outlet works. The stream connecting the two lakes was dredged, allowing them to fluctuate essentially as one. In addition, flows in Lake Creek were augmented with water diverted from the Western Slope by the Twin Lakes Tunnel under the Continental Divide. The increased flows and greater hydraulic gradient resulted in the erosion of the marshy area above the lakes and the deposition of a significant amount of woody organic debris on the bottom of the upper lake.

The bathymetric map on figure 2 shows the configuration of Twin Lakes before the new dam was constructed. Maximum water surface elevation of the lakes before closure of the new dam was 2802 m above mean sea level. Maximum surface areas were about 263.4 ha for the upper lake and 736 ha for the lower, with corresponding maximum depths of about 28 and 27 m, respectively. Area-capacity data for Twin Lakes are summarized in table 1.

Hydrology

Twin Lakes receives most of the runoff from the Lake Creek drainage basin and additional flows diverted from the Roaring Fork drainage by the Twin Lakes Tunnel. Nearly all of this water enters the lakes via Lake Creek, the principal tributary and sole outlet. The Lake Creek drainage basin covers an area of about 238 km^2, as shown on figure 3.

Figure 4 is a plot of average monthly inflow volume to Twin Lakes from Lake Creek, 1971-81. Mean annual inflow to Twin Lakes from October 1971 through December 1981, was 140.13×10^6 m^3, which is approximately 91 percent of the total capacity of the lakes before closure of the new Twin Lakes Dam (table 1).

Annual inflow volume fluctuates widely from year to year. For example, annual inflow volume ranged from a low of 70.19×10^6 to a high of 186.28×10^6 m^3, depending mainly on winter snow conditions in the basin (table 2). Ninety percent of the annual runoff occurs from May through August, usually peaking in June (mean = 24.2 m^3/s). Minimum inflows usually occur in March, which has a mean rate of 0.30 m^3/s.

Annual releases from Twin Lakes from October 1971 through September 1981, averaged about 140.13×10^6 m^3, which is about 100 percent of the mean annual inflow (table 2). Releases varied widely from year to year in response to irrigation demands of users in the lower Arkansas River Valley of Colorado.

Table 1. – Twin Lakes area-capacity data.

Surface	Upper Lake		Lower Lake	
elevation, m	Area, ha	Capacity, m^3	Area, ha	Capacity, m^3
2774.0	0	0	0	0
2776.7	70.0	1 078 079	105.6	1 105 216
2779.8	103.6	3 742 439	246.1	6 752 179
2782.8	125.4	7 245 579	328.6	15 584 039
2785.9	143.7	11 355 601	386.1	26 482 012
2788.9	155.4	15 922 018	438.7	39 069 879
2792.0	164.7	20 804 211	476.3	53 018 297
2795.0	174.8	25 975 043	533.0	68 330 966
2798.0	206.4	31 834 168	616.7	85 813 362
2801.1	248.1	38 739 301	710.2	106 039 061
2802.0	263.4	41 078 017	736.5	112 653 088

Ninety percent of the annual outflow is released during the irrigation season, generally from May through October. Maximum flows, averaging 13.8 m^3/s, are usually released in June; while minimum releases usually occur in December and average 0.33 m^3/s.

The annual inflow-outflow cycle at Twin Lakes consists of high flows and rapid flushing from May through September, followed by greatly reduced flows and low lake levels until spring runoff begins in May. Lake levels are often at their lowest just after ice-off in early May, because releases are made in April to make room for storing anticipated runoff.

Physical-Chemical Limnology

Twin Lakes are relatively clear; the mean light extinction coefficients from 1972-79 were 0.51 m^{-1} and 0.40 m^{-1} for the upper and lower lakes, respectively. Light extinction coefficients are inversely proportional to water clarity. They increase as the water becomes less clear and decrease as the water becomes more clear.

Clarity of the upper lake during the ice-free season displays a good correlation with the volume of inflow (r = 0.88). The highest light extinction coefficients are observed in late spring and early summer, coinciding with maximum runoff. Clarity of the upper lake during winter is independent of the amount of flow. A small December increase in light extinction coefficient is apparently a result of biological activity under the ice immediately after ice-on. Extinction coefficients in the lower lake follow the same general trends as those seen in the upper lake, with two main differences. First, the increase in extinction coefficients associated with maximum runoff lags that of the upper lake by about a month. Second, the overall variability in annual and monthly mean is much reduced in the lower lake. Both of these differences illustrate that the upper lake is much more directly influenced by the Lake Creek inflow. The upper lake functions as a settling basin in the Twin Lakes system.

Twin Lakes are second-class, dimictic lakes; that is, they circulate twice a year and bottom temperatures during summer stratification are well above 4 °C. The average date of ice-off has been May 6. Thermal stratification is usually established by early June and reaches its maximum by late July to mid-August. Maximum surface temperatures in the lower lake average approximately 17 °C, about 2 °C higher than those in the upper lake. Associated bottom temperatures average about 9 °C and 6 °C in the lower and upper lakes, respectively. The cooler temperatures at the bottom of the upper lake reflect the influence of Lake Creek, which enters at 3 to 4 °C lower than the surface temperature of the upper lake. The upper lake acts as a warming pond for the lower lake. Fall turnover in the lower lake occurs in mid-October, when the surface to bottom water temperature is approximately 10 °C (isothermal).

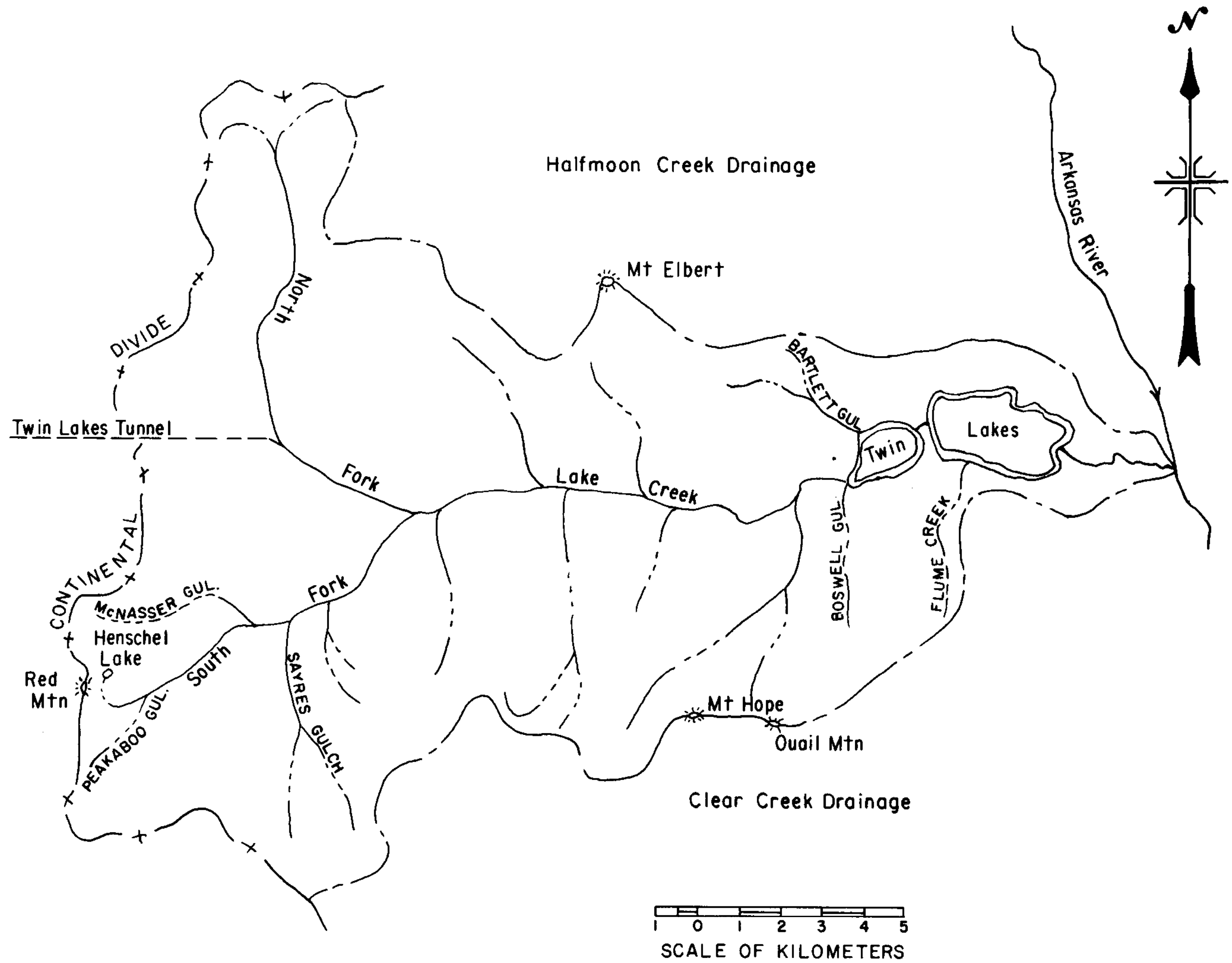


Figure 3. – Lake Creek drainage basin.

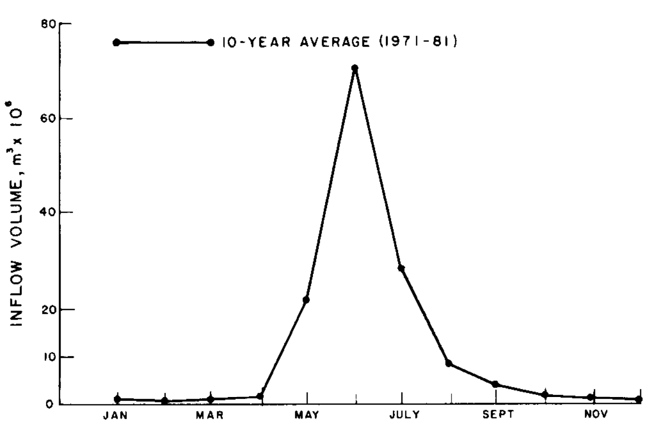


Figure 4. – Average monthly inflow volume to Twin Lakes from Lake Creek, 1977-81.

Depending on the intensity of winds in late November, the lakes may continue to circulate freely, losing heat to the cold atmosphere, while ice cover may be delayed until the second week in December (average date of ice-on is December 6). When this occurs, bottom temperatures after ice-on are as low as 1 to 2 °C and do not reach 4 °C until just before ice-off the following May. In less windy years when ice forms early, bottom temperatures usually reach 4 °C by early January. Maximum ice thickness during this study ranged from 610 to 762 mm. Snow cover on the ice varies in depth and duration depending upon the severity of the winter. In 1974-75, and again in 1979-80, for example, snow depths on the ice exceeded 610 mm; whereas, in 1976-77, the ice was essentially clear all winter. Because it limits light availability, winter snow cover has an important influence on primary productivity and related water chemistry during winter stratification at Twin Lakes. This influence is discussed in more detail below.

The pH (hydrogen ion concentration) of both lakes is generally neutral to slightly basic. Epilimnetic pH values as high as 8.0 to 8.3 were observed during high summer photosynthesis, and bottom pH values have

Table 2. – Twin Lakes, Colorado total annual inflow and outflow.[1]

Water year	Total inflow, m³	Total outflow, m³	Outflow / Inflow, %
Oct. 1971-Sept. 1972	164 688 163	[2]157 280 280	96
Oct. 1972-Sept. 1973	169 375 916	[2]175 895 594	104
Oct. 1973-Sept. 1974	122 967 162	144 950 256	118
Oct. 1974-Sept. 1975	160 493 858	[2]149 761 371	93
Oct. 1975-Sept. 1976	123 855 368	152 351 971	123
Oct. 1976-Sept. 1977	70 192 932	40 376 356	58
Oct. 1977-Sept. 1978	186 276 499	165 428 335	89
Oct. 1978-Sept. 1979	178 049 558	158 628 100	89
Oct. 1979-Sept. 1980	126 791 465	125 069 499	99
Oct. 1980-Sept. 1981	97 397 160	131 588 547	135

[1] Based on data provided by State of Colorado Division of Water Resources.

[2] Authors' estimate, winter data record incomplete.

Table 3. – Average concentrations of the principal ions in Twin Lakes.

Ions	Mean concentrations, mg/L
Anions	
Bicarbonate, HCO_3^{-1}	26
Sulfate, SO_4^{-2}	14
Chloride, Cl^{-1}	1.4
Cations	
Calcium, Ca^{+2}	11
Magnesium, Mg^{+2}	1.9
Sodium, Na^{+1}	1.1
Potassium, K^{+1}	0.8

dropped as low as 6.6 during peak summer and winter stratification.

Conductivity averaged 71 µS/cm in the lower lake and 75 µS/cm in upper lake. Although these mean values are quite similar, the range of variation in the upper lake is about twice that in the lower (standard deviation of 15 µS/cm in the upper lake compared with 8 µS/cm in the lower lake). On the other hand, TDS (total dissolved solids) was very nearly the same in both lakes, with a mean of about 68 mg/L and an observed range from 10 to 120 mg/L. The trend in mean monthly TDS is generally the inverse of that displayed by inflow volume (fig. 4), because low TDS values usually coincide with high June inflows, and higher TDS values are observed during the low flow months.

The principal ions in Twin Lakes and their approximate mean concentrations are listed in table 3.

Carbonate (CO_3^{-2}) is rarely detected in these waters because the pH is usually below 8.3, the level at which carbonate ions are formed.

The sediments of Twin Lakes are mainly unconsolidated deposits of very fine-grained glacial rock flour. These sediments have accumulated large amounts of heavy metals, including iron, manganese, zinc, copper, and lead, which are ultimately derived from naturally exposed mineral deposits in the Lake Creek watershed. Sediments of the upper lake also contain the allochthonous deposit of woody debris.

D.O. (dissolved oxygen) concentrations remain generally high (i.e., at or near saturation) throughout the year, with some depletion near the bottom in both lakes during summer and winter stratification. This stagnation can become especially pronounced in the upper lake during severe winters from the combined effects of (1) the higher oxygen demand of the organic deposit on the bottom of the lake and (2) the exclusion of light needed for photosynthesis by a deep and persistent snow cover. At such time, the oxidation-reduction potential (E_7) near the sediment-water interface may drop well below 300 mV, signaling the onset of reducing conditions in the hypolimnion. Under these conditions, biologically significant amounts of iron and manganese and, later, copper and zinc are released from the sediments. Although these metals are reoxidized and precipitated during and after spring turnover, they have a deleterious effect on the biota and productivity of the lakes. The situation described above was observed in the upper lake during the winter of 1974-75, and documented by Sartoris et al., 1977 [3]. This situation may also be approached in the lower lake during the late summer.

In summary, the physical limnology of Twin Lakes is that of a relatively clear, cool, second-class dimictic lakes. The lakes are characterized chemically as relatively soft, dilute calcium bicarbonate lakes. They have been subject to periodic biological "crashes" as a result of extreme reducing conditions and associated metal releases during long periods of thermal stratification coupled with deep snow cover on the ice. This situation has been especially pronounced in the upper lake, apparently because the allochthonous organic debris deposited on the bottom has a higher oxygen demand.

Biological Limnology

Twin Lakes are biologically similar to other oligotrophic montane lakes, although they now have a biota different from that originally found (Jordan, 1891 and Juday, 1906) [4, 5]. Historically, Twin Lakes contained perhaps five kinds of cladocerans and two species of native trout (the yellow-finned and Colorado cutthroat). Today, an abundance of cladocerans is rare, and the two native trouts are gone. The biological assemblege now consists of a naturally reproducing lake trout and a stocked rainbow trout game fishery. Both species were introduced early in the 20th century. Brown and brook trout, longnose and white suckers, and dace also live in Twin Lakes. Suckers are particularly abundant.

The zooplankton fauna is dominated by the introduced freshwater opposum shrimp, *Mysis relicta*, which was introduced in 1958 as a food source for young lake trout. The establishment of opposum shrimp in Twin Lakes has resulted in a complete absence in the pelagic zone of such large cladocerans as *Daphnia* sp. Smaller cladocerans, such as *Bosmina* sp., are found occasionally in Twin Lakes during the summer, and benthic species of *Daphnia* have been found in the stomachs of suckers (Krieger, 1980) [6].

Besides *Mysis*, the dominant kinds of zooplankton in Twin Lakes today include copepods (*Cyclops* spp., *Diaptomus* sp.) and rotifers (*Keratella* sp., *Polyarthra* sp., and *Kellicotia* sp.). Lieberman, 1983 [7] lists the most common zooplankton and algal species in detail. The abundance of these zooplankters varies seasonally and annually. Average zooplankton abundance in the lower lake has exceeded 120 organisms per liter during summer months. However, an average abundance of less than one organism per liter is common in the upper lake, especially during spring runoff.

Diatoms and chrysophyceans dominate the phytoplankton in Twin Lakes. Particularly abundant are the diatoms *Synedra* sp., *Asterionella* sp., and the chrysophyte *Dinobryon* sp. When conditions have been favorable, some species of green algae and an occasional blue-green species (e.g. *Oscillotoria* sp.) have been found. Average concentrations of algae in Twin Lakes of over 13 000 individuals per liter have been found during late summer when stratification is strong. Average concentrations of less than 100 individuals per liter are common in the upper lake during late winter or early spring.

The benthos of Twin Lakes is dominated by chironomids, oligochaetes, and sphaeriid (or pea) clams. Densities of 0 to >3000 chironomids, 0 to >3000 oligochaetes, and 0 to >1000 clams per m^2 of lake bottom are found in Twin Lakes. These organisms are a food for suckers and help break down organic detritus in the benthic environment.

METHODOLOGY

Limnological surveys at Twin Lakes include measurement of the following physical-chemical parameters: temperature, pH, D.O., conductivity, oxidation-reduction potential, light penetration, and light transmittance. The surveys also include the collection of water samples for chemical analyses. Biological samples are routinely collected for chlorophyll *a*, plankton, and benthos. Methods for collecting and processing these parameters are detailed in Sartoris et al., 1977 [3], LaBounty and Sartoris, 1982 [8], Lieberman, 1983 [7], and Campbell and LaBounty, 1985 [9].

Measurement of Primary Production Rates

At monthly intervals, if not with each limnological survey, the C^{14} primary productivity test is performed in each lake using a modified technique reported by Steemann-Nielsen, 1952 [10].

The standardized C^{14} test performed at Twin Lakes is a three phase operation. The first phase is field collection, inoculation, and incubation. The second phase is field filtration, preservation, bicarbonate alkalinity titration, and relative efficiency determination. The third phase is laboratory processing, scintillation counting, and calculation of carbon fixation rates.

Phase 1. – Two 5-mL inoculation vials, each containing 50 µCi of C^{14}-tagged NaHCOs (sodium bicarbonate) solution, are diluted from 1 mL to 5 mL using 9.5-pH distilled water. The alkaline dilution reduces conversion of $NaHCO_3$ to CO_2 when the rubber seal of the vial is breached.

Water is collected from each lake at five standard depths for each C^{14} test. The depths are 1, 3, 5, 9, and 15 m. Four 300-mL BOD (Biological Oxygen Demand) bottles are filled with water from each of the five depths. Two of the BOD bottles are clear, or light bottles, and two are black coated, or dark bottles. Before inoculation, all BOD bottles are kept in a dark, insulated box. The two light bottles and one of the dark bottles from each depth are inoculated with the C^{14}-tagged $NaHCO_3$ at a standard rate of 3 µCi per 300 mL water. The remaining dark bottle is a blank that is used to determine bicarbonate alkalinity in phase 2. After inoculation, the bottles are suspended from a rack and incubated at the original sampling depth for 2 to 6 h. Recently, 4 h, has been the minmum time in each lake. When the bottles are removed from the lake, they are kept in the dark, insulated boxes until they are filtered.

Phase 2. – Filtration of C^{14} samples is performed in the field laboratory facility at Twin Lakes, usually within an hour or two after their removal from the lakes. The water from each of the inoculated light and dark bottles is filtered through a membrane filter (0.8 µm pore size) in a pressure filtering manifold at 2.76×10^5 to 4.19×10^5 Pa. Each filter is then folded in half (sample surface inside) and placed between two filter papers. The stack of filter papers is held overnight in a dessicator. The next day the dried filters are frozen to prevent water absorption until processed in our Denver E&R (Engineering and Research) Center laboratory.

The determination of bicarbonate alkalinity is a critical part of the C^{14} test procedure. Bicarbonate alkalinity is determined by the titration of 100 mL of lake water (from the remaining dark sample at each depth) to pH 4.5 using 0.02-normal H_2SO_4.

Control aliquots are taken each time the C^{14} test is performed to determine the relative efficiency of the C^{14}-tagged $NaHCO_3$ solution. Differences in this relative efficiency from the manufacturer's listed efficiency may result from losses of C^{14} to the atmosphere and technical error during the dilution of the $NaHCO_3$ solution. Five replicate 5 to 10 µL aliquots are obtained from each of the $NaHCO_3$ vials used for field inoculation. First, 1 mL of quaternary ammonium hydroxide tissue solubilizer is pipetted into each of five quality control samples containing 10 mL of xylene-based fluor. Then each aliquot of C^{14}-tagged $NaHCO_3$ is injected into a quality control sample, capped, and swirled gently to mix. These samples are returned to the E&R Center to be counted along with the other test samples after processing.

Phase 3. – Final processing of the C^{14} productivity filters is done in the E&R Center laboratory. Each filter is placed in a borosilicate 20-mL scintillation vial and dissolved in 1 mL of tissue solubilizer. After the filters have completely liquified (4 to 6 h), 10 mL of fluor are added to each vial. A reaction between the tissue solubilizer and fluor occurs during mixing, which causes a temporary chemiluminescence[1] in the samples. If the samples were counted immediately, erroneously high rates of carbon fixation would result. Therefore the samples are allowed to stand, and are shaken briskly each day, for 3 to 4 days. During this time the chemiluminescence gradually decreases. The samples are then placed in a liquid scintillation counter where the radioisotope activity is counted.

After counting, carbon fixation rate and relative efficiency of the C^{14}-tagged $NaHCO_3$ solution are calculated using the formulas reported in Vollenweider, 1969 [11]:

$$\underset{\text{mgC/(m}^3\cdot\text{h)}}{\text{Carbon fixation}} = \frac{\text{net count/min}}{\text{total ampoule count}} \underset{\text{of incubation}}{\left(\frac{1}{\text{h}}\right)} \frac{\text{mg C}}{\text{L}} \left(\frac{100}{1000-\text{I}}\right) 1000$$

where:

$$\text{net count/min} = \frac{\text{raw count}}{\text{quench correction percent}}$$

total ampoule count = 3 µCi (relative efficiency),
mg C/L = (bicarbonate alkalinity) × (listed factor based on temperature and pH in situ), and
I = isotope effect, (ca. 6.79 percent).

[1] Chemiluminescence – Emission of light as a result of a chemical reaction without apparent change in temperature.

$$\text{Relative efficiency} = \frac{C/Q}{C_t}$$

where:
C = raw count in dpm (disenterations per min),
Q = quench correction percent, and
C_t = theoretical count at 100 percent efficiency (22 000 dpm/L).

Modifications to the Steemann-Nielsen C^{14} technique include discontinuing the use of glacial acetic acid in the processing procedure and not rinsing the filters to remove unfixed radioisotope tracer during the filtering process.

Use of glacial acetic acid to quickly reduce the chemiluminescence was determined by experimentation to increase color quenching.[2] Carbon fixation rates were underestimated by 25 to 30 percent when 0.1 mL of 1:1-normal glacial acetic acid was added to each sample. This practice was discontinued in 1978, and a compensating factor was applied to all pre-1978 data.

Experimental filtration of subsample volumes of the 300-mL C^{14} samples has determined that the filters do not retain unfixed radioistotope tracers when 200 mL or more is filtered. McMahon, 1973 [12] found that 100 mL of sample should be filtered to obtain consistent values. Two experiments were performed on Twin Lakes samples: one on in situ C^{14} samples and one at the E&R Center laboratory using native Twin Lakes algae cultures. The results of the cultured algae experiment are plotted on figure 5. Volumes of less than 150 mL do show that unfixed radioisotope tracer is retained by the membrane filter. The results of filtering small volumes from in situ C^{14} samples at Twin Lakes (March 12, 1979) are plotted on figure 6. As in the previous experiment, smaller volumes had higher activities, indicating retention of unfixed radioisotope tracer. If at least 200 mL of sample is filtered, rinsing the filters seems to be unnecessary.

RESULTS AND DISCUSSION

Seasonal Trends in Primary Production

Figures 7 and 8 contain primary production rate profiles for the upper and lower lakes from most of the C^{14} primary production tests performed at Twin Lakes since 1976. Sampling methods and depths were not standardized until 1977. Some of the earlier results are not displayed in profile; however, a complete list of all C^{14} data from Twin Lakes can be found in the appendix.

The profiles of carbon fixation rate versus sample depth displayed on figures 7 and 8 illustrate the seasonality of production; during some years (e.g.,

[2] Quenching — Any process causing a reduction in the amount of light incident upon the photocathodes of a liquid scintillation counter.

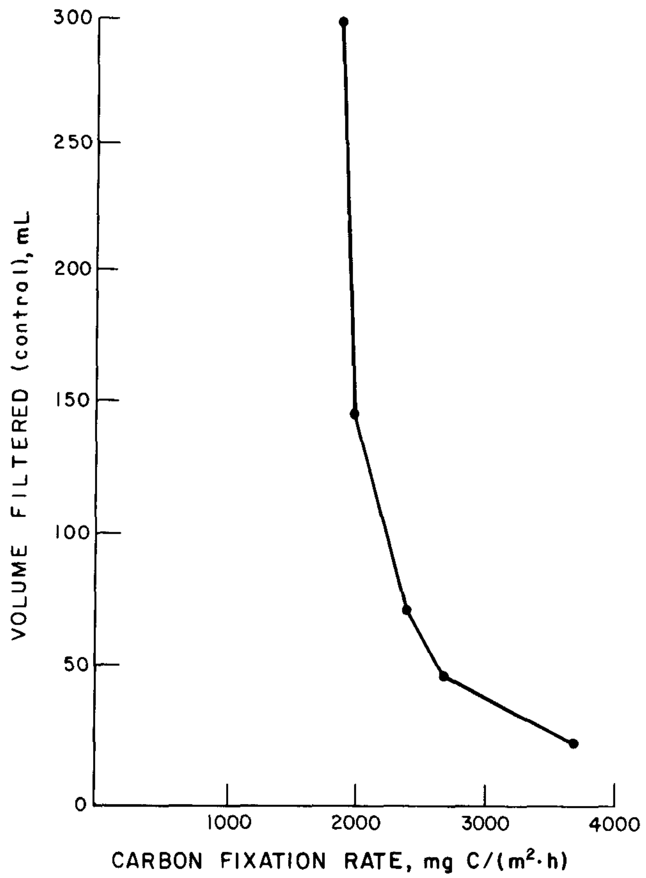


Figure 5. – Carbon fixation rate versus volume filtered using rates measured in the E&R Center laboratory.

1979, in the lower lake), this is particularly obvious (fig. 8). The influence of snow and ice cover can also be seen. In years (e.g., early 1980) when snow and ice were thickest, production rates were lowest. Ice and snow cover severely limit light penetration. This is probably the major limiting factor for phytoplankton production during winter. The profiles (figs. 7 and 8) also indicate that primary production rates vary greatly with depth; they are usually greatest just below the surface and least at the bottom of the profiles. In some cases (e.g., summer 1981, in the upper lake), production is near or at zero below a certain depth when light is limited by the shading from the plankton population above (fig. 7).

Average monthly carbon fixation rates in Twin Lakes are summarized by year in table 4. Figures 9 and 10 are plots of the average monthly primary production rates in the upper and lower lakes from 1973-81. One standard deviation on either side of the mean is indicated for each monthly average.

The following is a general description of annual events at Twin Lakes based on the data on figures 9 and 10. Rates of production are generally less in the upper lake than in the lower lake. Primary production decreases during the winter when the lakes are covered with snow and ice. The mean carbon fixation rate in the upper lake was 135.6 mg C/(m^3·h) during the ice-covered season, and 333.0 mg C/(m^3·h) during the ice-free season. In the lower lake, carbon fixation rates were 202.2 and 582.9 mg C/(m^3·h) for the ice-covered and ice-free seasons, respectively. Production rates in the lower lake were generally highest just after spring or fall turnover; whereas, rates dropped off during midsummer, when stratification was strongest and runoff had subsided. The maximum spring mean carbon fixation rate observed in Twin Lakes was 1418.8 µg C/(m^3·h), in the lower lake, on May 16, 1979. The maximum fall mean carbon fixation rate observed in Twin Lakes was 1328.2 µgC/(m^3·h), also in the lower lake, on October 5, 1978 (table 4). Although primary production rates in the upper lake are lowest during winter, there is also a noticeable drop during June. This drop is associated with the flushing and increased turbidity of runoff. Rates remain generally steady in the upper lake through November.

Greater variability in primary production rates is more characteristic of the lower than the upper lake. The extreme variability in primary production rates measured during May is reflected in the large standard deviation (Figure 10). Rates become progressively lower and somewhat less variable through August. As the thermocline sinks and stratification begins to break down in September and October, rates progressively increase, as does the variability.

Autumn turnover of the lakes generally occurs in mid-October. Because turnover causes redistribution of nutrients, primary production increases after turnover, resulting in a fall peak. The rate of primary production then decreases until ice forms and remains generally low through at least January, although exceptions have been observed. There is some significance in the small rise in production rate in the upper lake during February, when the snow is generally not deep enough to severely limit light, and the small inflow still supplies some nutrients. Rates in the upper lake are lowest in March, when thick snow and ice cover limit light penetration.

Figures 11 and 12 are plots of the total primary production for 7 of the 9 years of study, including the 9-yr averages. Primary production during the ice-free months is distinguished from that during the months when the lakes were covered with ice. Overall average annual production rates for the upper and lower lakes are 11.3 and 25.8 g C/(m^2·a), respectively. The upper lake is more productive during the ice-free season in below-average runoff years (1977 and 1981). The lower lake is less productive during the ice-free season in below-average runoff years than in above-average runoff years (1978-79). This tends to support the hypothesis that the upper lake acts as a nutrient trap in below-average runoff years; whereas, the lower lake benefits from the flushing of nutrients from the upper lake in above-average runoff years.

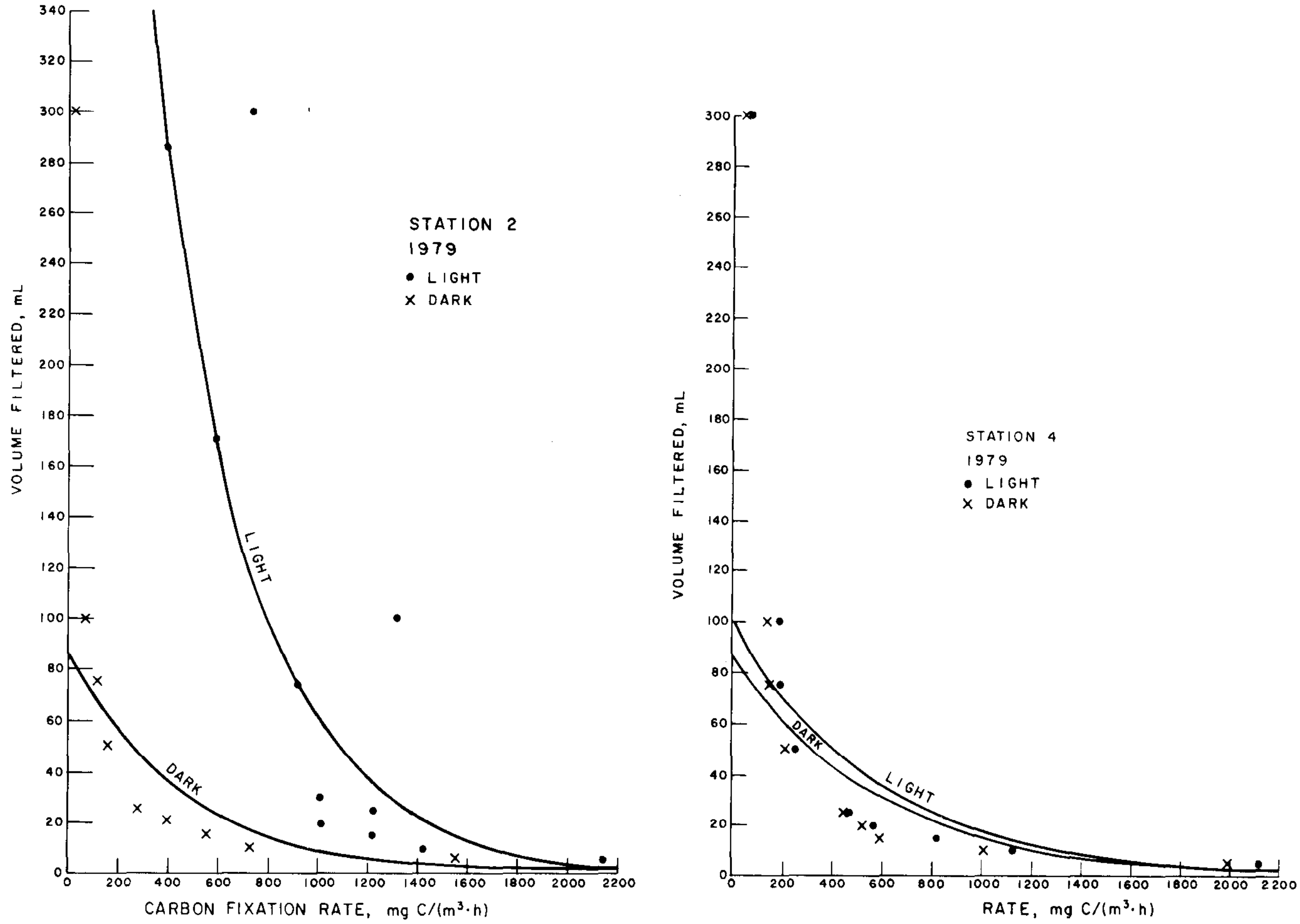


Figure 6. – Carbon fixation rate versus volume filtered using rates measured in situ, Twin Lakes.

Relationship to Other Aquatic Systems

The rate at which primary production occurs in Twin Lakes is generally quite low by most standards. The highest single rate of primary production we have measured at Twin Lakes is 21 696 µg C/($m^3 \cdot h$). Table 5 shows a comparison of primary production rates at Twin Lakes with those at other locations selected from Wetzel, 1975 [13]. The mean daily and annual production rates are displayed along with the observed ranges from each locality. The net primary productivity of Twin Lakes is compared with values for the three major trophic categories, as defined by Likens, (1975) [14], in table 6. From these comparisons, the lower lake compares favorably with those from other oligotrophic lakes. However, the upper lake falls into the category of ultra-oligotrophic, even when values from "growing season" alone are averaged.

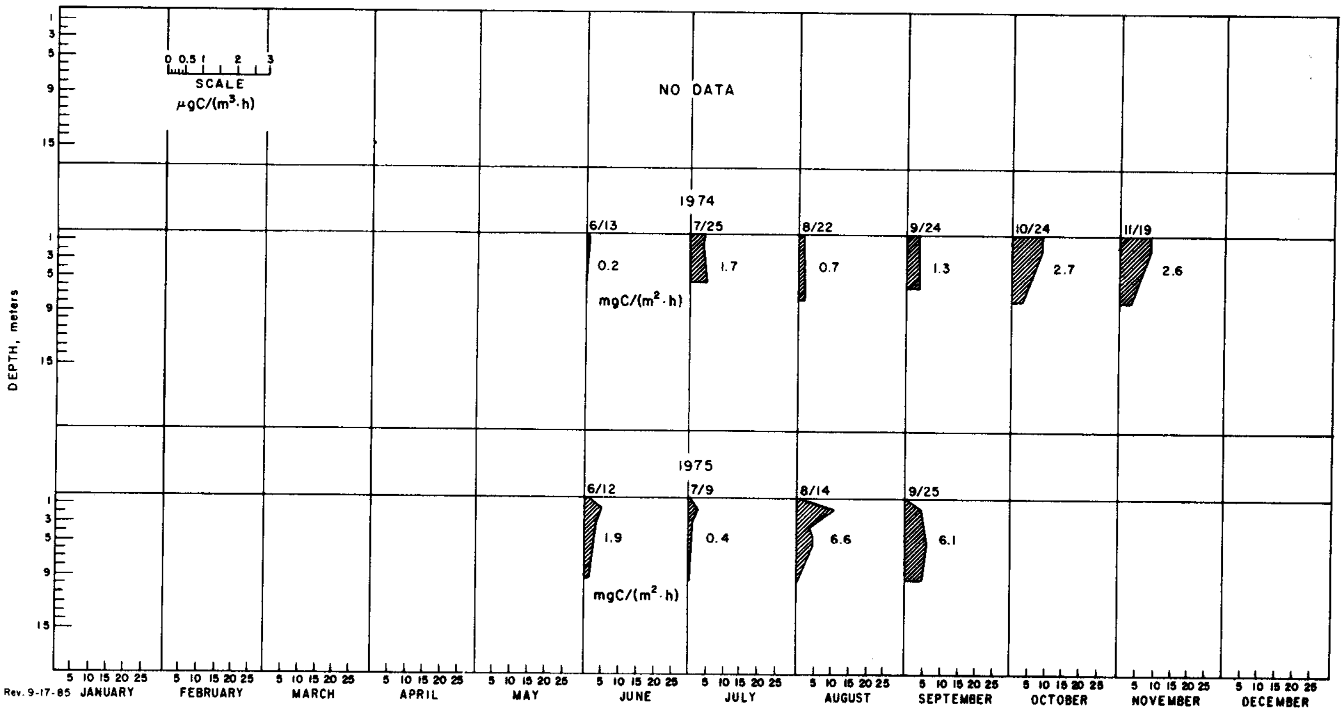
Factors Affecting Primary Production in Twin Lakes

Primary production in Twin Lakes is affected by a number of factors. The most significant are runoff volume, light, nutrients, algal biomass, and water temperature.

Runoff volume. – The influence of the annual runoff on the rate of primary production in Twin Lakes cannot be overemphasized. Annual inflow and outflow volumes are displayed on figures 13 and 14. As previously discussed, the lower lake has been, on the average, more than twice as productive as the upper lake. However, the annual rate of primary production in the upper lake was significantly higher during years of low runoff than during years of high runoff.

The upper lake is directly influenced by spring runoff, while the lower lake is not so directly affected. High runoff years, such as 1978 and 1979, which were above the 10-yr average, reduce primary production in the upper lake (fig. 13). Sediment-laden inflow during maximum runoff in June reduces water clarity and flushes the upper lake. The combination of turbidity and increased flushing varies with the amount of runoff in any given year. Low runoff years, such as 1977 and 1981, benefit the upper lake (fig. 13): Turbidity is reduced and flushing rate decreases, so that nutrients tend to remain instead of being carried to the lower lake. The reduced inflow of colder water in low runoff years also makes the upper lake generally warmer than in high runoff years. Approximately 30 percent of the total annual production in both lakes

UPPER LAKE, 1973



UPPER LAKE, 1976

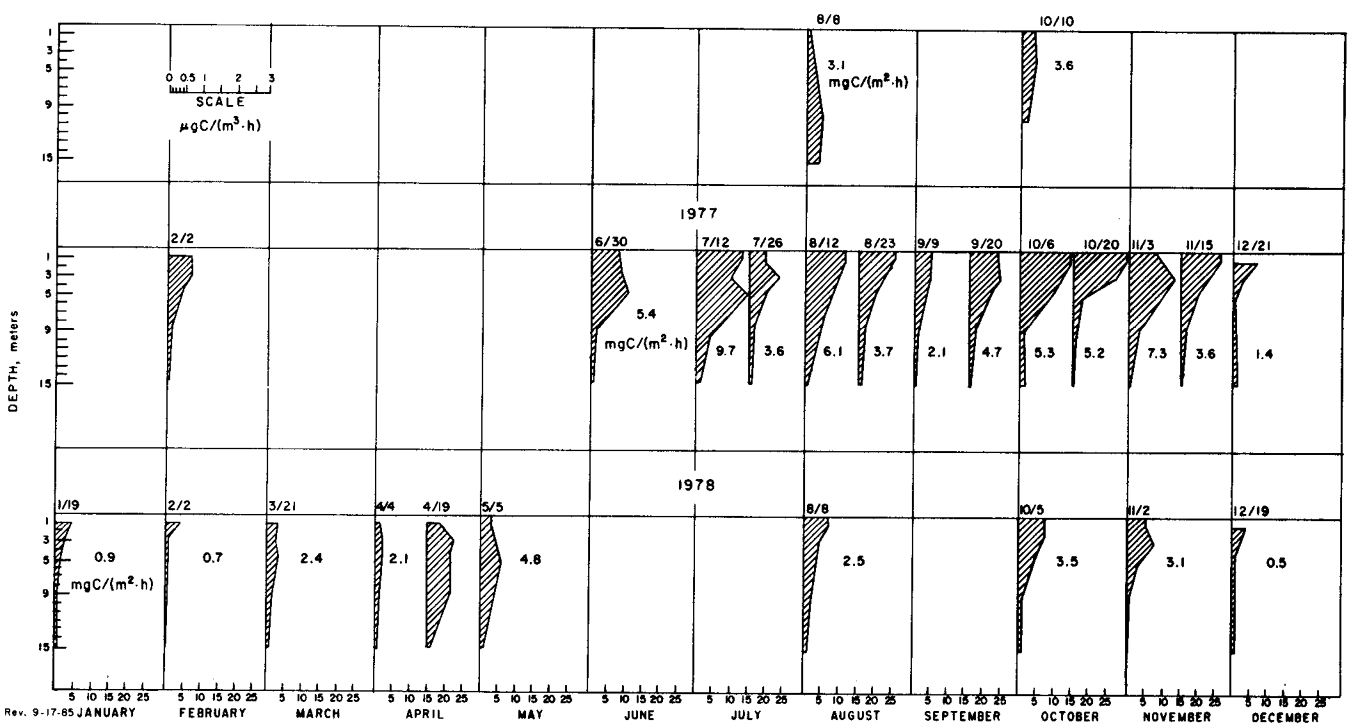


Figure 7. – Profiles of carbon fixation rates in the upper lake, 1973-81.

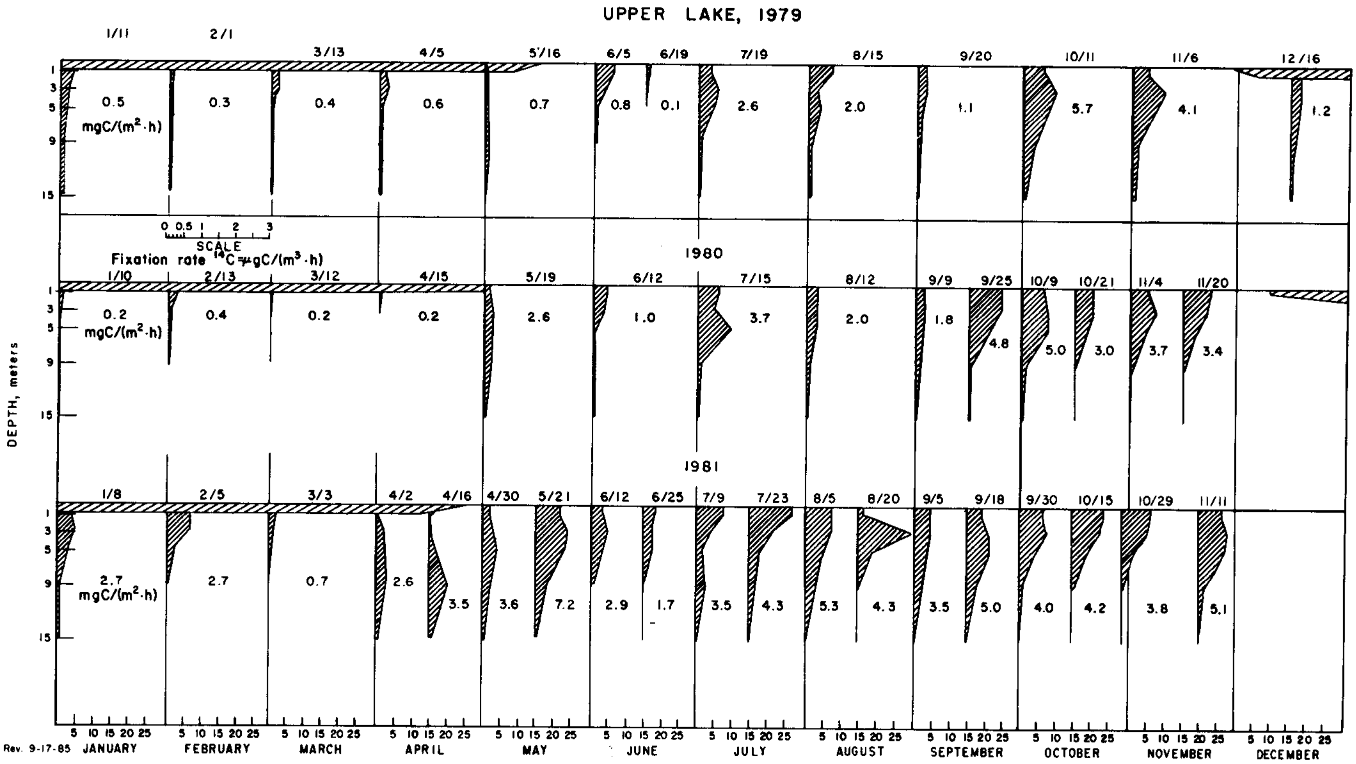


Figure 7. – Profiles of carbon fixation rates in the upper lake, 1973-81 – continued.

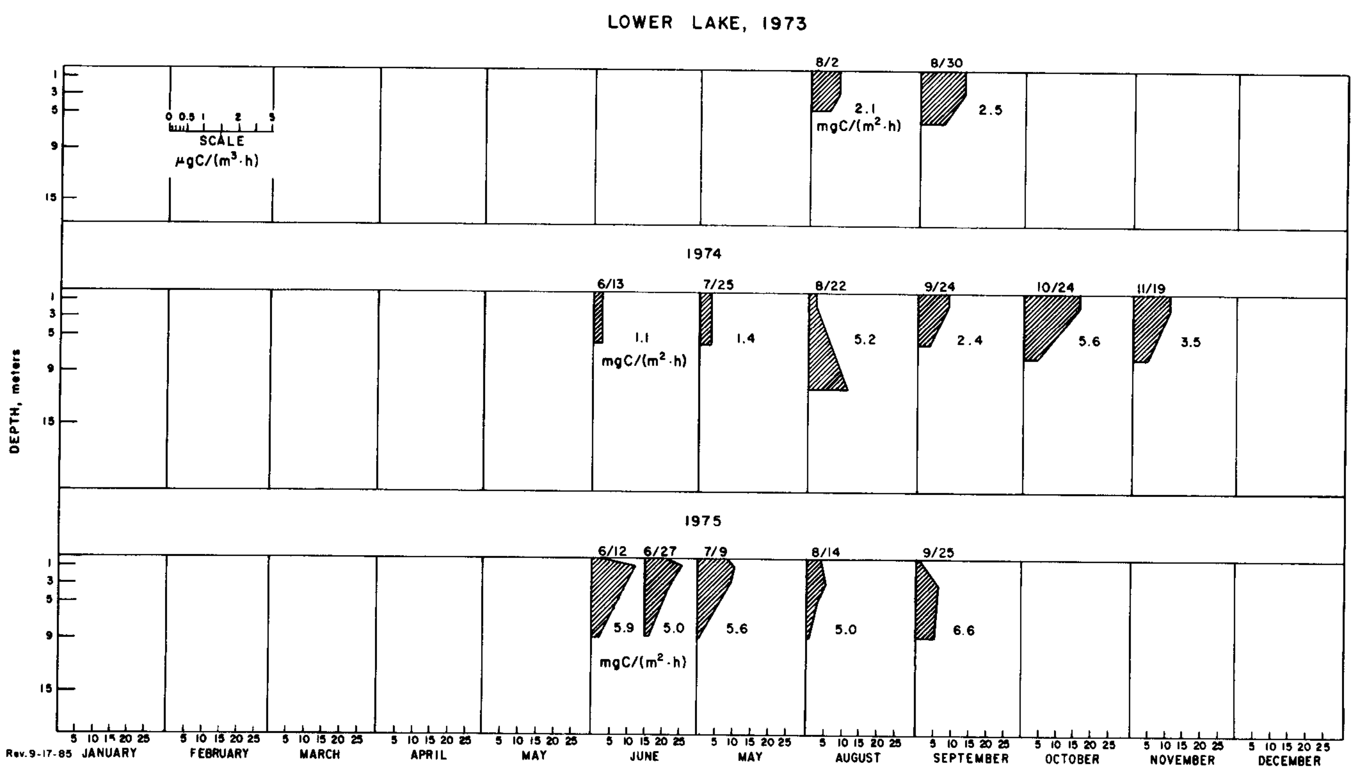


Figure 8. – Profiles of carbon fixation rates in the lower lake, 1973-81.

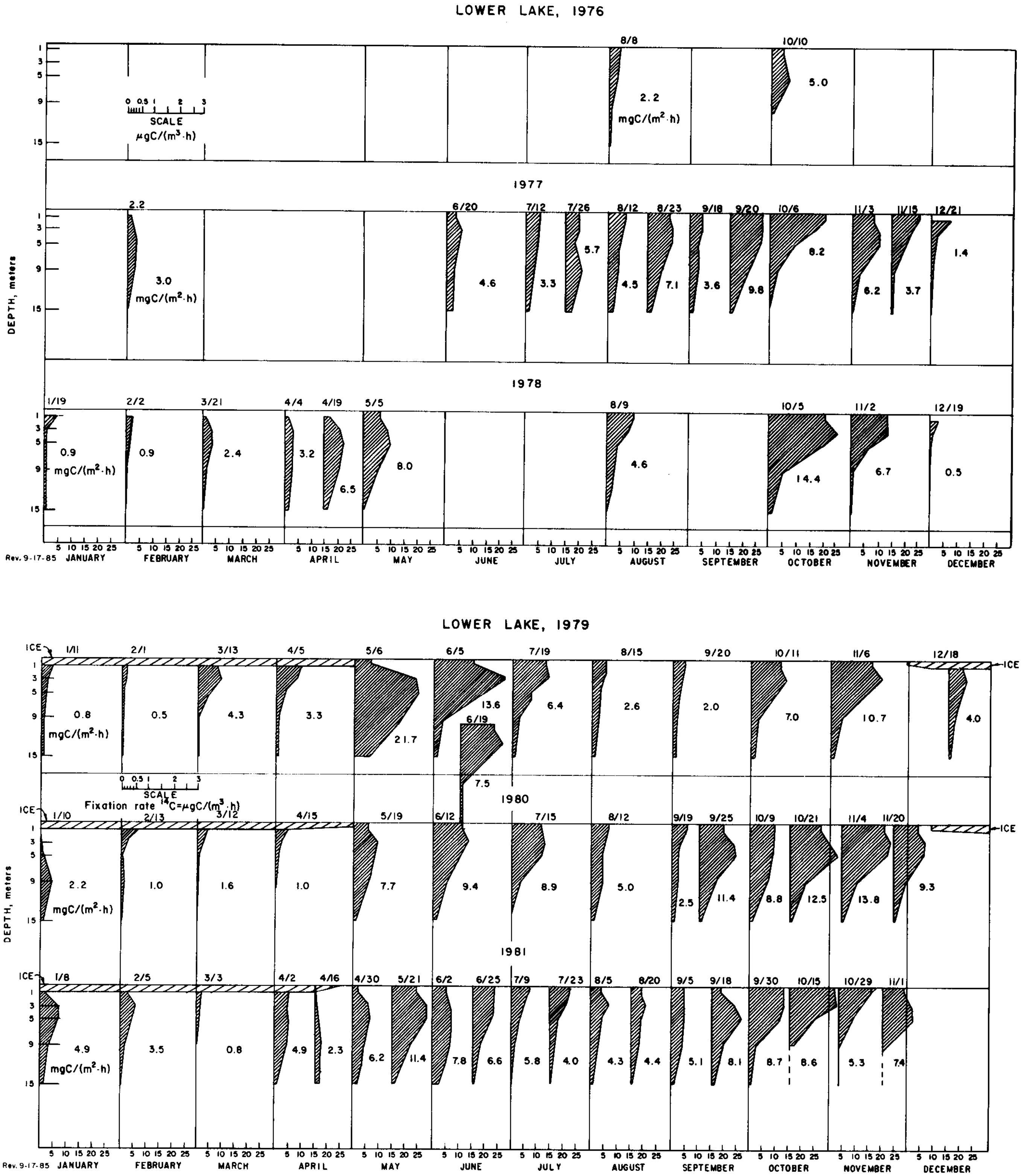


Figure 8. – Profiles of carbon fixation rates in the lower lake, 1973-81 – continued.

Table 4. – Average monthly carbon fixation rates (µg C/(m³·h) in Twin Lakes, Colorado 1973-81.

Month	Lake*	1973	1974	1975	1976	1977	1978	1979	1980	1981
Jan.	U*						167.4	80.0	16.3	260.3
	L*						133.2	124.9	96.3	358.4
Feb.	U					347.4	103.6	49.4	48.7	305.1
	L					191.4	93.5	52.8	146.7	286.0
Mar.	U						194.4	47.2	27.9	79.0
	L						168.2	431.7	173.4	86.4
Apr.	U						304.8	68.0	39.0	193.0
	L						313.5	381.9	152.2	304.7
May	U						326.2	43.0	176.1	591.0
	L						588.7	1418.8	567.0	879.2
June	U		46.2	203.9		498.5		71.2	102.1	215.0
	L		230.3	581.0		344.5		995.0	761.5	554.1
July	U		372.1	56.8		569.1		240.3	334.7	399.7
	L		310.2	688.3		334.0		641.4	780.3	372.6
Aug.	U		111.7	412.5	187.2	459.8	249.5	330.0	181.5	435.0
	L	796.7	565.6	348.2	171.2	460.4	446.8	304.7	392.1	339.6
Sept.	U		278.4	364.6		332.4		103.6	322.4	364.0
	L		519.9	387.3		542.2		190.1	564.6	590.2
Oct.	U		449.8		242.1	577.4	364.3	469.7	377.3	426.9
	L		913.4		338.9	796.3	1328.2	644.0	841.3	730.5
Nov.	U		426.6			535.7	329.1	366.4	365.3	447.6
	L		581.0			478.2	594.3	990.5	978.8	639.6
Dec.	U					184.5	105.3	110.0		
	L					207.2	82.8	346.4		

* U = upper lake, L = lower lake.

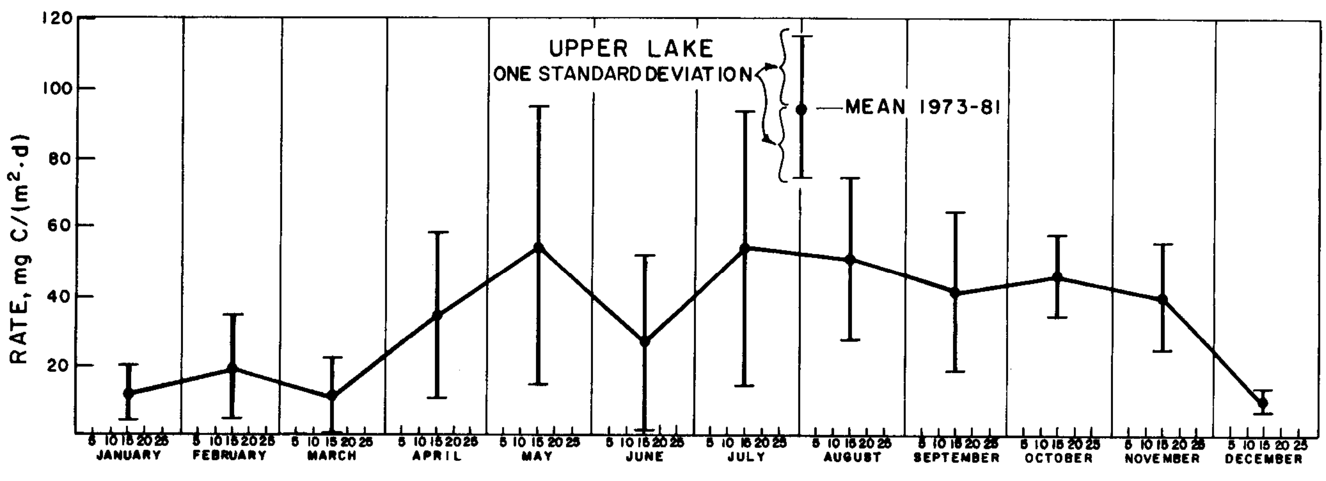


Figure 9. – Average monthly primary production rate in the upper lake, Twin Lakes, 1973-81.

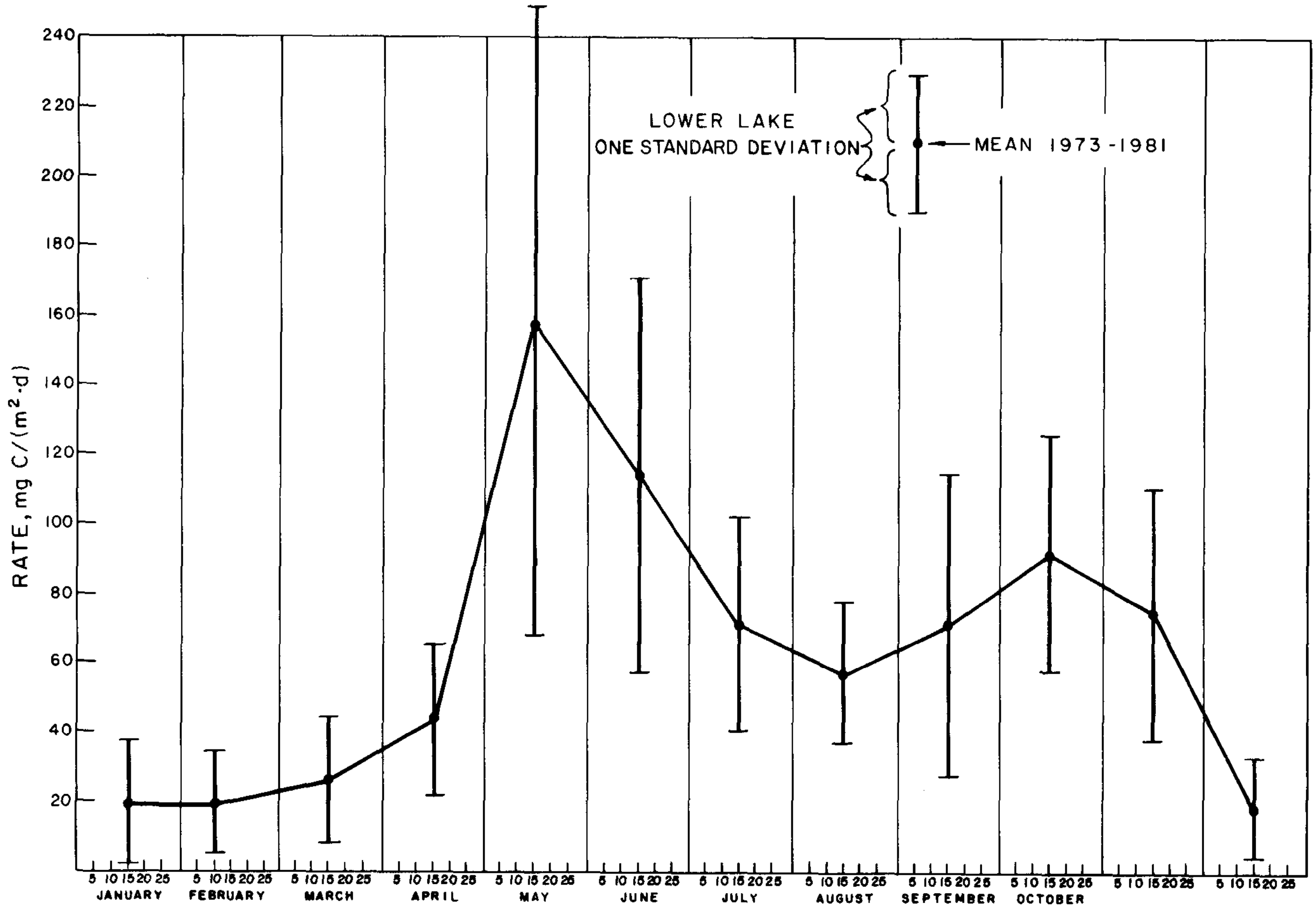


Figure 10. – Average monthly primary production rate in the lower lake, Twin Lakes, 1973-81.

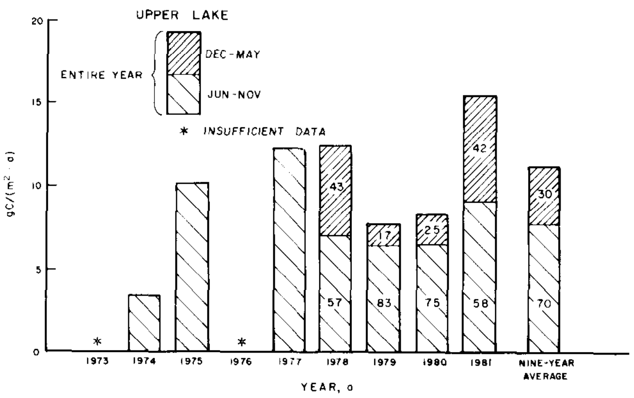


Figure 11. – Total annual primary production rate in the upper lake, Twin Lakes, 1973-81.

occurs during the winter months. In dry years, about 40 percent of the total annual production in the upper lake occurs in winter. The reasons for this increased winter production in the upper lake are not completely clear, but lack of snow cover on the ice, which increases light penetration, may be a factor.

Correlation coefficients were calculated on annual primary production and inflow data. The *r* value between annual inflow volume and annual rate of primary production in the lower lake is +0.81, indicating

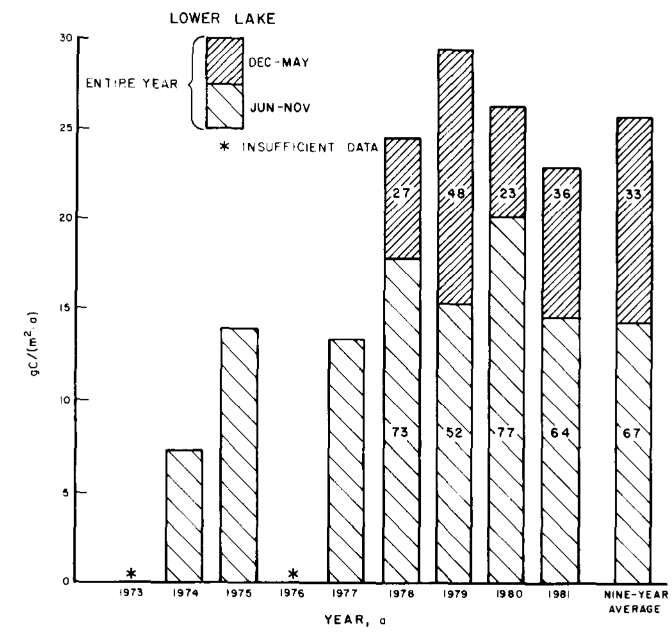


Figure 12. – Total annual primary production rate in the lower lake, Twin Lakes, 1973-81.

a strong positive relationship between runoff and rate of production. However, the *r* value between annual

Table 5. – Comparison of primary production rates for phytoplankton in Twin Lakes, (1973-81) with other selected lakes.

Lake	Remarks	Mean daily productivity, 1973-81, mg C/(m²·d)	Range observed, mg C/(m²·d)	Annual production, g C/(m²·a)
Twin Lakes – upper lake (No. = 82)	12 months	33.6	1 to 104	11.3
Twin Lakes – upper lake (No. = 54)	Ice-free or "growing season"	43.7	3 to 104	15.9
Twin Lakes – lower lake (No. = 86)	12 months	63.9	5 to 312	25.8
Twin Lakes – lower lake (No. = 58)	Ice-free or "growing season"	80.0	17 to 312	29.4
Castle (California)	Deep, alpine	98	6 to 317	36
Lawrence (Michigan)	Small, hard water; 7-year average	112.6	5 to 497	41.1
Char (Canada)	80% of total production by benthic flora	1.1	0 to 35	4.1
Meretta (Canada)	Polluted by sewage	3.1	0 to 170	11
Clear (California)	Very large, shallow	438	2 to 240	160
Erken (Sweden)	Large, deep, naturally productive	285	40 to 2205	104
Minnetonka (Minnesota)	Extremely complex basin, large, deep	[1]820		[1]300

[1] Estimated.

Table 6. – Comparison of net primary productivity values for Twin Lakes with those for regional aquatic ecosystems, as presented by Likens, 1975 [14].

Twin Lakes – upper lake[1]	43.7	15.9
Twin Lakes – lower lake[1]	80.0	29.4
Ultra-oligotrophic lakes	<50	
Oligothropic lakes	50 to 300	
Mesotrophic lakes	250 to 1000	
Eutrophic	600 to 8000	

[1]Averaged over ice-free season.

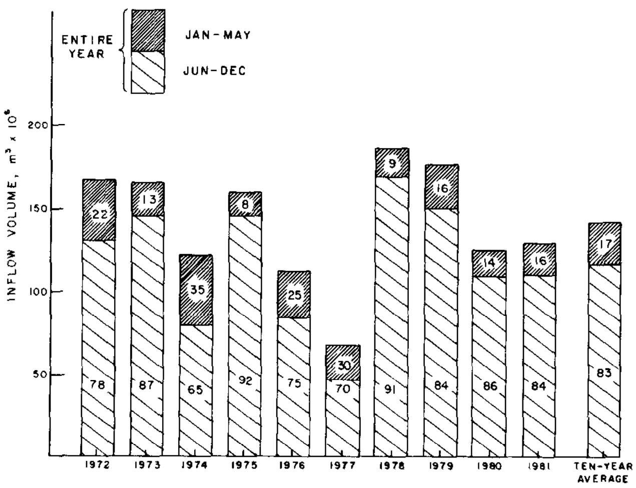


Figure 13. – Twin Lakes inflow volume, 1972-81.

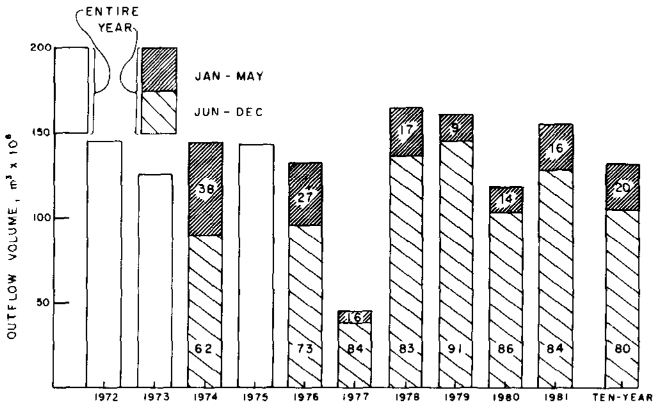


Figure 14. – Twin Lakes outflow volume, 1972-81.

inflow volume and the annual rate of primary production in the upper lake is −0.58, indicating a negative relationship between runoff and production.

Probably the most revealing of the correlation statistics is the *r* value of −0.91 between the annual rate of primary production in the upper lake and the annual rate of primary production in the lower lake. This value indicates a very strong negative relationship between the production rates of these lakes. That is, when annual production is high in one, it is low in the other.

All of the above facts and descriptions may be summarized quite simply as follows. The amount of production in Twin Lakes depends very strongly on the amount of inflow from Lake Creek. The greater the spring runoff, the lower the annual production in the upper lake, because it is acts as a settling basin. High inflows flush necessary nutrients from the upper lake to the lower lake where other limnological conditions favor greater production. These high inflows also tend to be turbid; which induces the light available for photosynthesis in the upper lake. During years of low inflow, reduced flushing of the upper lake means more retention of nutrients, less turbidity and, often, warmer temperatures. Therefore, production in the upper lake is greater when inflows are less. In low flow years, the lower lake is not only deprived of the greater supply of nutrients provided by higher runoff, it is also deprived by the upper lake of the small amounts of nutrients that the lower volume of runoff provides.

Numerous factors favor or hinder primary production in Twin Lakes; however, none are more important than the runoff volume.

Light. – Light has a major effect on aquatic ecosystems. It affects a wide range of biological processes from photosynthesis to fish vision.

The quantity of light is important to primary production. This section considers light at Twin Lakes in three ways: average available light for the dates on which C^{14} surveys were performed at Twin Lakes, light extinction coefficients in each of the lakes, and transmissivity data from Twin Lakes.

Figure 15 shows the 5-d ambient light flux at Twin Lakes between 0900 and 1500 hours, from late June to mid-November 1980. The dashed line connects points representing 5-d periods that were nearly or completely cloud free. The maximum average insolation, about 44 g-cal/(cm^2·h) (fig. 17), occurred during the 5-d period July 16-20. After that period, the theoretical curve declined to a low average insolation of about 26 g-cal/(cm^2·h) during the 5-d period November 9-13. The solid line on figure 15 connects the data points collected by instrumentation on a raft moored in the northwest corner of the lower lake. These data indicate the variability in the amount of light available from day to day and from season to season at Twin Lakes. For example, the average insolation during the 5-d period of September 9-13, was about 22 g-cal/(cm^2·h). Theoretically, if the skies had been mostly clear during that period, the insolation value would have been about 40 g-cal/(cm^2·h). Observed insolation values were about 50 percent of the potential values for that period. Variations in cloud cover are characteristic of the area, and significant loss of energy for primary production in the lakes can occur.

Figure 16 is a bar graph displaying the average available light on the times and dates, in 1979, 1980, and 1981, when C^{14} surveys were performed. The variability that occurs at Twin Lakes is again apparent, verifying that the surveys were made under the typical variety of light conditions. The peak available light appears to occur in late June and in early July, as expected.

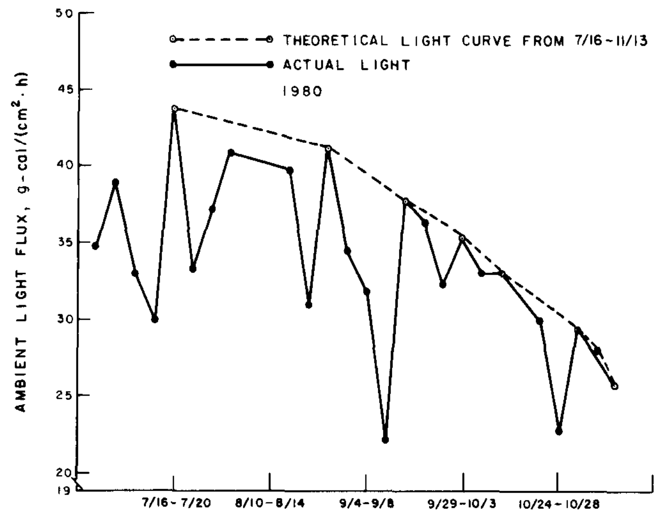


Figure 15. – Five-day average ambient light flux at Twin Lakes, June to November, 1980.

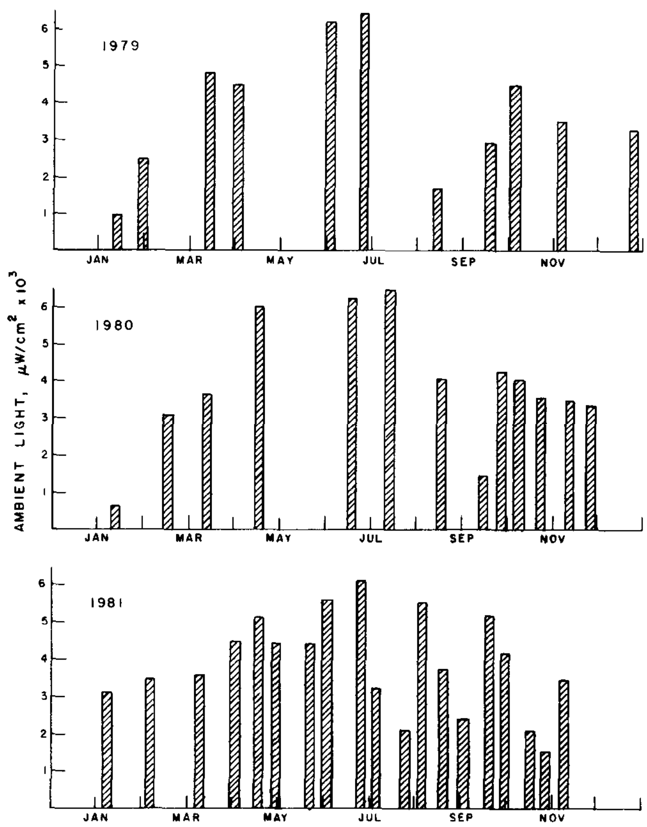


Figure 16. – Average available light during C^{14} surveys at Twin Lakes, 1979-81.

In addition to the available light above the surface of Twin Lakes, the attenuation of light below the surface of the lakes is also significant. This is the net light available for photosyntheses.

Figure 17 shows average monthly light extinction coefficients for the 8-yr period, 1974-81. The light extinction coefficient is inversely proportional to the water clarity; lower values mean greater water clarity and vice versa. The influence of the sediment-laden inflow that peaks in late June is obvious, especially in the upper lake.

Other generalizations can be made about Twin Lakes from the data on figure 17. The clarity of the upper lake is generally much less than that of the lower lake. This is because the upper lake acts as a settling basin for the Lake Creek inflow. It has been well established that the clarity of the upper lake is directly proportional to the volume of runoff. Therefore, during years of greater runoff, the difference in clarity between the two lakes is even more pronounced. Turbidity caused by this inflow reduces the amount of light available in the water column and along with the increased flushing, significantly reduces primary production in the upper lake.

Figures 18 and 19 display production rates and the limnological factors that affect these rates for 1981. Any other year could have been chosen; however, more data are available from 1981, than from any other year. Parameters plotted on figures 18 and 19 include the following: rates of primary production, light extinction coefficients, water temperatures at 1 m, ambient light available during each of the surveys, orthophosphorus concentrations, and total organic nitrogen concentrations. The only obvious relationship from the data on figure 18 (upper lake) is that between rates of primary production and light extinction coefficient. When the light extinction coefficient is greatest, meaning less light is entering the water column, the rate of primary production is lowest. This same relationship, to a lesser degree, can be seen on figure 19 for the lower lake.

Figure 20 includes profiles of light transmittance for the upper and lower lakes for 15 sampling dates in 1981. (Few transmissivity data are available for previous years.) The data on figure 20 were obtained by passing a beam of light from a lamp to a photocell mounted on the opposite end of a rigid frame. The frame was lowered into the lake, and the percentage of transmitted light received at the photocell was recorded for each given depth. This "percent transmittance" is a measure of the optical clarity of the water at a particular depth. Although the profiles on figure 20 may not be typical for all years at Twin Lakes, their analysis reveals many significant qualities of the lakes not revealed by light extinction data.

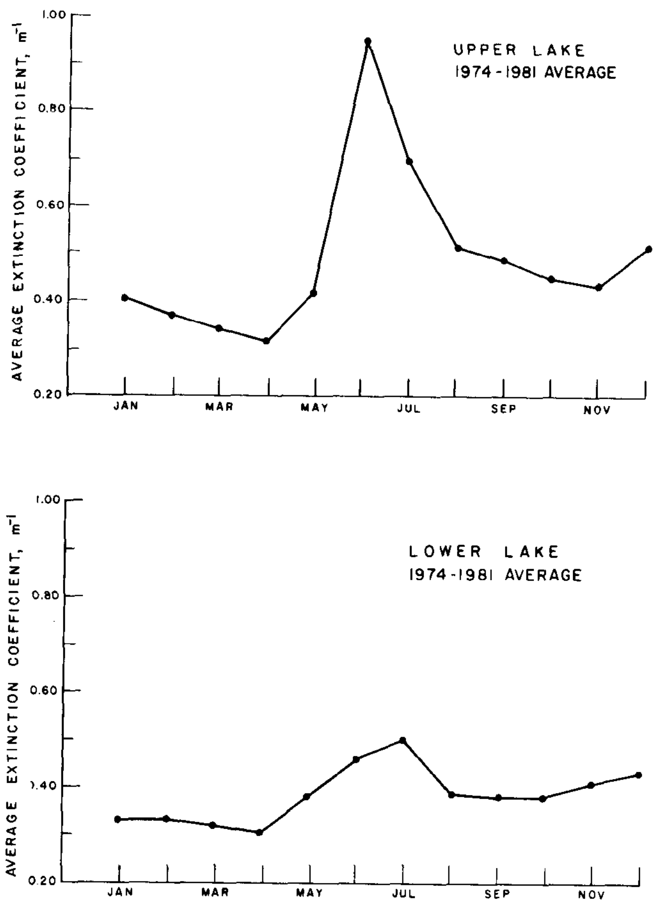


Figure 17. – Average light extinction coefficients at Twin Lakes, 1974-81.

Several factors can cause percent transmittance to decrease. These include allochthonous sediment, zooplankton, phytoplankton, and resuspended material from bottom sediments. The thermocline, when it was present, is depicted as a shaded area on figure 20.

Under winter ice (January 7-April 1 on fig. 20), transmittance near the bottom of both lakes was decreased. This indicates the buildup of either resuspended material from bottom sediments or of a layer of particulates that settled after the lake became ice covered. In months when spring turnover occurs, transmittance is relatively uniform with depth. After runoff begins, the increased turbidity of the lakes is reflected in decreased transmittance at all depths, especially in the upper lake. Wind action stirring the isothermal lakes and the increased concentration of plankton decreases light transmittance in the spring. Before the onset of runoff, the transmittance in the lower lake can be less than that in the upper lake. The lower lake has a much larger surface area and is influenced more by wind action than the upper lake. In addition, the lower lake has

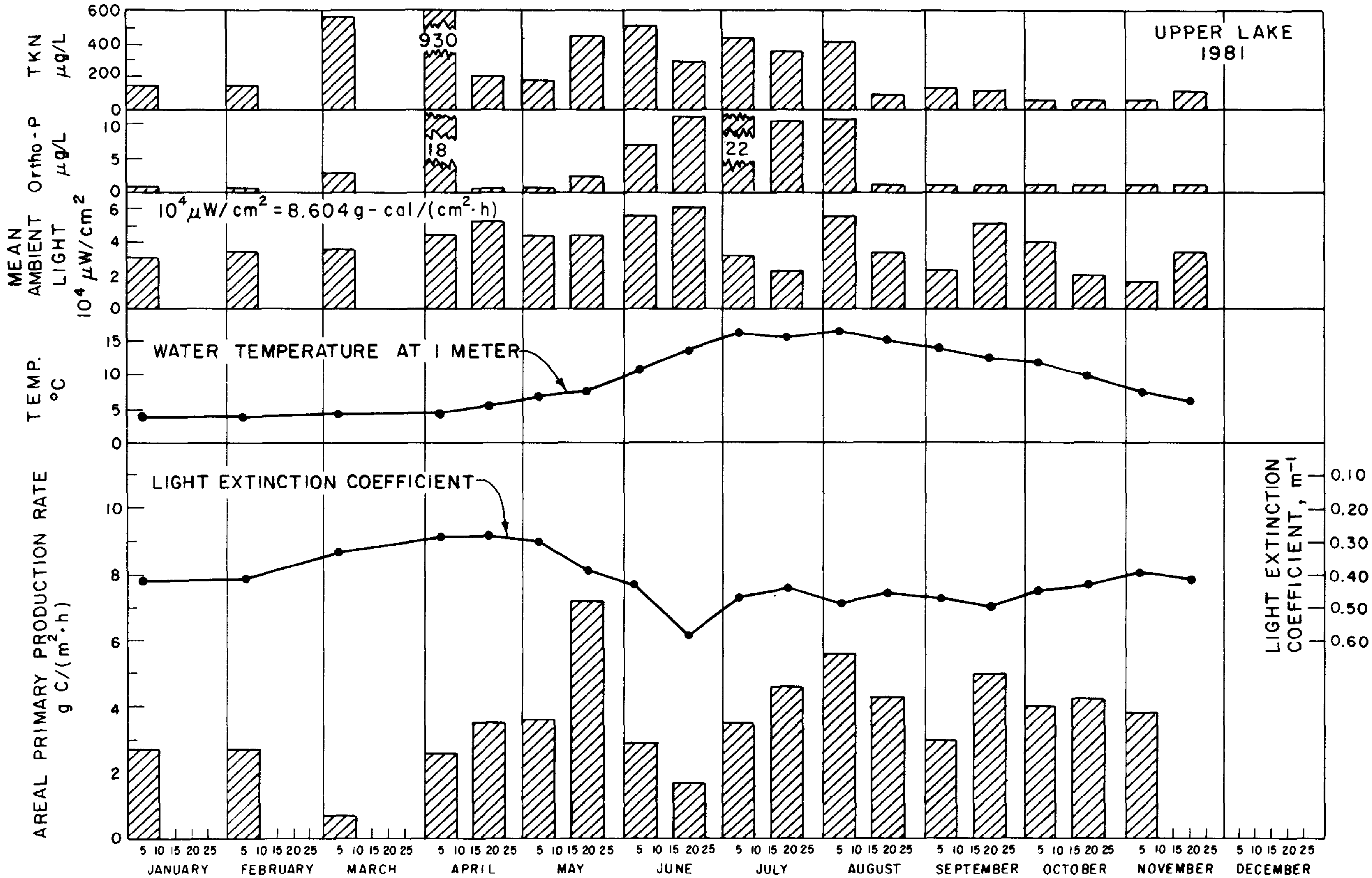


Figure 18. – Primary production rate and five related limnological factors for the upper lake during 1981, Twin Lakes.

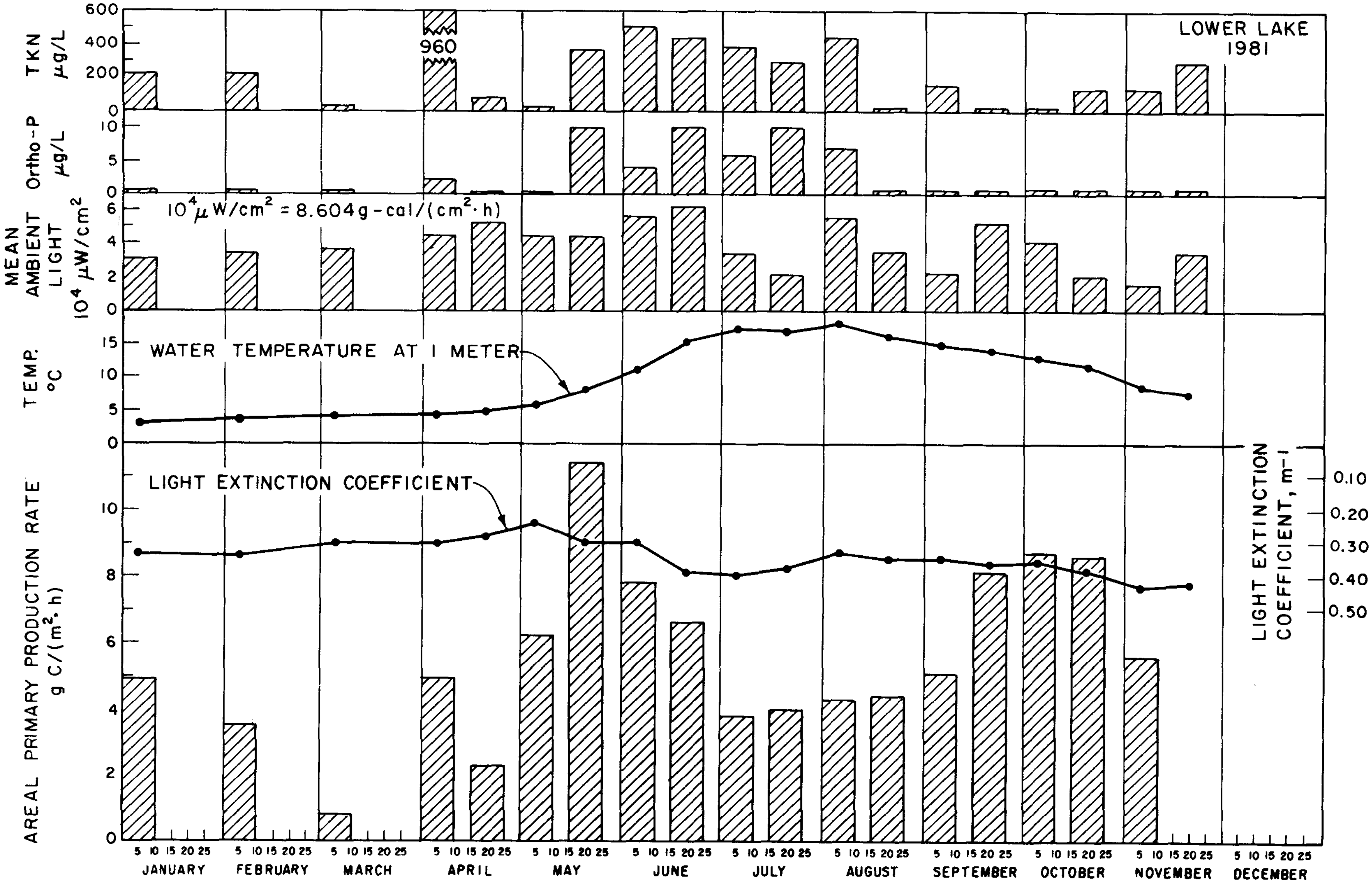


Figure 19. – Primary production rate and five related limnological factors for the lower lake during 1981, Twin Lakes.

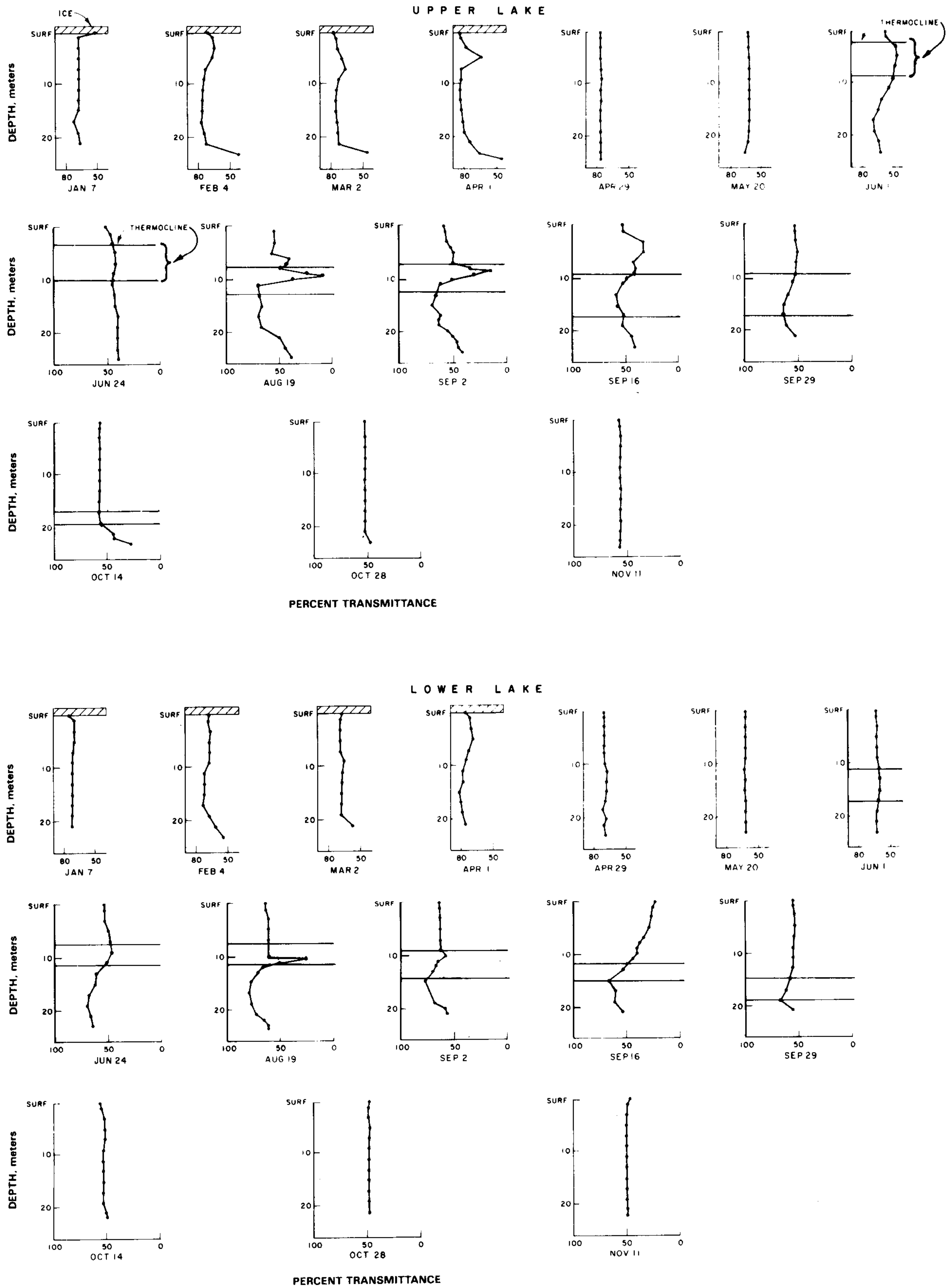


Figure 20. – Transmissivity profiles during 1981, Twin Lakes.

a higher plankton concentration. Both of these factors may contribute to the observed cases of lower transmissivity in the lower lake before runoff.

Strong thermal stratification in summer seems to be the limnological parameter that relates best to transmissivity in Twin Lakes. Data displayed on figure 20 for June 1 through September 29, 1980, are classic examples of the many events accompanying strong thermal stratification that influence transmittance in Twin Lakes. First, and perhaps most significantly, within the thermocline, a phytoplankton bloom began in both lakes in early June, and became well-developed by mid-August. By mid-September, these algae had either died or dispersed. Just above the thermocline (see August 19 profile), zooplankton accumulated. Below the thermocline, densities of plankton were generally less, causing an increase in water clarity. Examination of plankton samples from these dates show an abundance of *Synedra* in the lower lake and *Dinobryon* in the upper lake, in the area of lowest transmittance within the thermocline. Late in the season, as the thermocline sank below the euphotic zone, these algae became more dispersed and transmissivity increased. Second, there was a decrease in percent transmittance in the 4 to 5 m closest to the bottom. This decrease was caused by either the turbulence at the bottom from the influx of colder water, the resuspension of material from bottom sediments, or the accumulation of sinking debris.

The third observation from data on figure 20 relates to conditions after fall turnover. Profiles from this period resemble those from the spring turnover; however, transmittance was generally 10 to 25 percent less than that during spring turnover because the abundance of plankton is greater in the fall.

Nutrients. – Table 7 presents the average concentrations of various nutrients at Twin Lakes during the study. This table also lists the value or range that describes, (according to the literature) oligotrophic lakes by concentrations of total phosphorus, total organic nitrogen, silica, and total organic carbon. The average concentrations of samples collected from Twin Lakes all fall in the listed ranges. Only 55 percent of the samples for total phosphorus were above the 1 µg/L detection limit, and the average concentrations of total phosphorus were at the very low end of the range presented for oligotrophic lakes. Therefore, it must be concluded that the lakes are limited in kind and quantity of phytoplankton species by phosphorus. The concentration of total organic nitrogen, although it was in the lowest third of the range reported for oligotrophic lakes, seems adequate because values were above the detection limit of 10 µg/L about 87 percent of the time. Neither silica nor carbon seems to be limiting; silica concentrations

Table 7. – Average concentration of nutrients in samples collected from Twin Lakes, 1977-1981.

Nutrient	Sta. 2 mean	Sta. 4 mean	Concentration value or range of oligotrophic lakes
Orthophosphorus (µg/L)	<1.00	<1.00	–
Total phosphorus (µg/L)	1.54	1.34	[1]<1 to 5; [2]<14
Total organic nitrogen (µg/L)	65.6	57.9	[1]<1 to 250
Ammonia nitrogen (µg/L)	10.46	15.89	– –
Nitrate nitrogen (µg/L)	14.3	57.3	– –
Nitrite nitrogen (µg/L)	<10	<10	– –
Silica (mg/L)	4.85	5.29	[3] <5
Total organic carbon, (mg/L)	2.05	1.73	[1] 1 to 3

[1] From Likens, 1975 [14].
[2] From Taylor et al., 1980 [15].
[3] From Wetzel, 1975 [13].

averaged at the high end of the range for oligotrophic lakes, and total organic carbon concentrations fell in the middle of the range.

Further evidence to support the idea that Twin Lakes are relatively phosphorus poor is seen when the C:N:P (carbon:nitrogen:phosphorus) ratio in Twin Lakes water is compared with that within plant material itself. The C:N:P ratio of aquatic plants is roughly 40C:7N:1P by weight (Wetzel, 1975) [13]. The C:N:P ratio, based on data collected thus far, for Twin Lakes water is 1890C:55N:1P. These calculations indicate a shortage of phosphorus. The carbon:nitrogen ratio in Twin Lakes water is about 34C:1N compared with about 6C:1N in aquatic plants. Wetzel, 1975 [13] states that nitrogen exceeds phosphorus in most lakes by an order of magnitude. These estimates also indicate a relative abundance of carbon and a scarcity of phosphorus. Because the average concentration of carbon (2 mg/L) is in the middle of the range reported by Wetzel, 1975 [13] for oligotrophic lakes, it is assumed that it is not limiting, and may in fact be in abundant supply.

Phosphorus concentrations may not always be limiting in Twin Lakes, but the concentrations of total phosphorus in water samples collected from Twin Lakes are at or below the 1 µg/L detection limit more than 55 percent of the time. Perhaps more importantly, of 240 samples collected through 1979 and analyzed for orthophosphate, which is the form most immediately available to aquatic plants, only two had detectable amounts (1 µg/L) of this nutrient. Therefore, it seems realistic to conclude that the species composition or the quantity of aquatic plant life in Twin Lakes is heavily dependent on the available phosphorus. Although this will be discussed in detail in another report, an analysis of the samples of phytoplankton collected during the past few years from Twin Lakes supports the idea of a phosphorus-limited environment there.

The chrysophycean *Dinobryon* sp. and the diatom species *Asterionella* and *Synedra* are the three dominant kinds of phytoplankton at Twin Lakes. Each is known to grow best in water where phosphorus concentrations are lower than 20 µg/L (Wetzel, 1975) [13]; (Cole, 1979) [1]. These diatoms are considered very efficient at using low levels of phosphorus and are, in fact, ecologically favored by these low levels. In addition, the ability of *Asterionella* to utilize phosphorus is greatest at pH values between 6 and 7 (MacKereth, 1953) [16]. These pH values are not uncommon in Twin Lakes, especially during spring turnover. At this time, *Asterionella* is usually dominant but *Dinobryon* replaces or succeeds *Asteronella*, during the summer. If higher phosphorus levels (e.g., > 10 µg/L) occurred in Twin Lakes, this balance would surely change. In fact, with higher phosphorus levels, as the water temperature of Twin Lakes increased during the summer, the two species could be totally replaced by other, perhaps ecologically less desirable, species of algae. Of course, other factors, such as temperature, other nutrients, and available light, would also affect this change. However, the amount of available phosphorus now seems paramount to the current composition of algal species.

Algal biomass. – Table 8 is a general summary of average monthly chlorophyll *a* concentration and total phytoplankton densities in Twin Lakes from 1977-81. These data are plotted on figures 21 and 22, respectively. These parameters are the two measures of algal biomass routinely measured at Twin Lakes. Chlorophyll *a* concentration in Twin Lakes is the subject of another report (Campbell and LaBounty, 1985) [9]. Only the relationship of chlorophyll *a* to carbon fixation rates will be discussed here. Generally, chlorophyll *a* concentrations in Twin Lakes reach a maximum in the fall. However, this situation may continue into late winter if snow and ice cover are light (fig. 21). A peak in chlorophyll *a* concentration is sometimes observed in summer in either lake, but not in both lakes at the same time (fig. 21).

A correlation was run between carbon fixation rate and chlorophyll *a* concentration. Campbell, 1981 [17] found an overall correlation between the two parameters of r = 0.56 in the lower lake and r = 0.67 in the upper lake, for the period 1977-80. It seems that in some years, factors other than chloraphyll *a* concentration influence carbon fixation rates.

Phytoplankton populations in Twin Lakes plotted on figure 22 display general trends in algal growth throughout the year. Algal density in the upper lake in above-normal or normal runoff years (1978-80) tends to be greatest after fall turnover. In below-normal runoff years (1977-81), increases in algal density may occur in early spring and summer in the upper lake. Light snow and ice cover, reduced flushing and turbidity during runoff, and the normal increase after fall turnover are important factors that influence algal density trends in below-average runoff years.

The lower lake also has a trend toward increased algal densities in the fall, after turnover. In above-average or average runoff years (1978 and 1980), a late spring to midsummer increase in algal density may be observed. In low runoff years (1977 and 1981), an increase in late winter and early spring may be observed. The trend in algal density in the lower lake in 1981, may be closely tied to nutrient availability. The spring peak followed by a decline until after spring turnover, and another increase followed by a decline until after fall turnover, followed by yet another increase seems to indicate a nutrient-limiting situation. The algal population during low runoff years may be more dependent on autochthonous nutrient cycling in the lower lake, when the upper lake acts as a trap for nutrient input from spring runoff.

The overall 1977-81 correlation between carbon fixation rate and total phytoplankton density is $r = 0.31$ in the lower lake and $r = 0.60$ in the upper lake. Table 9 is a summary of correlation coefficients in both lakes for this relationship.

The poor correlations in 1977 and 1978 may result from a combination of incomplete data sets, sampling and counting error. Before 1977, plankton sampling was performed using a No. 10 (153 micron mesh) Clarke Bumpus net. Beginning in 1977, a closing net with a No. 20 (80 micron mesh) was used for plankton sampling. The variation between individuals doing the sampling was found to be quite significant and, after some experimentation, the speed at which the net was hauled through the water column was standardized in late 1978 and early 1979. This standardization significantly reduced the variability. Plankton identification and counting procedures were also improved and standardized at the same time. The strong positive correlation between carbon fixation and total phytoplankton density seen in both lakes for 1979 and 1980, may be the result.

The poor correlation between carbon fixation and total phytoplankton density in both lakes during 1981, cannot be precisely explained. Campbell and LaBounty, 1985 [9] speculate that chlorophyll *a* and phytoplankton density did not correlate well because the discrete depths sampled for chlorophyll *a* estimation missed algal concentrations that occurred at

Table 8. – Average monthly chlorophyll *a* concentration and total phytoplankton densities in Twin Lakes, 1977-81.

		Average areal chlorophyll *a*, mg/m²					Average total phytoplankton density, No./L				
Month	Lake	1977	1978	1979	1980	1981	1977	1978	1979	1980	1981
Jan.	upper	129.6	43.0	39.8	29.2	70.8	1 705	1 854	2 799	239	3 053
	lower	72.4	39.2	33.6	87.2	55.7	7 970	3 377	4 032	7 417	28 717
Feb.	upper	176.2	72.8	15.4	12.8	76.3	3 279	1 343	529	89	4 775
	lower	86.3	27.8	27.5	32.1	74.3	17 132	2 499	3 761	502	38 097
Mar.	upper	96.0	31.2	11.1	12.5	56.6	–	1 909	120	14	8 530
	lower	*	25.0	39.6	23.1	61.0	–	2 570	7 862	111	72 755
Apr.	upper	71.4	36.4	6.8	8.8	30.1	473	1 679	154	86	9 507
	lower	–	29.2	32.8	19.4	36.6	–	1 755	14 582	131	53 770
May	upper	66.2	47.9	20.1	20.0	35.6	746	884	244	183	6 471
	lower	31.9	20.7	56.9	31.1	40.5	789	1 296	28 777	2 552	9 009
June	upper	40.0	–	8.9	17.1	31.7	–	–	185	364	5 425
	lower	33.9	62.9	69.2	41.5	48.6	–	–	19 591	5 185	20 745
July	upper	122.4	13.8	11.5	14.8	69.2	2 863	–	167	618	12 188
	lower	39.1	64.0	66.9	38.9	50.9	1 261	–	23 247	11 309	15 852
Aug.	upper	44.8	64.6	46.0	55.0	130.7	1 006	795	2 585	760	6 525
	lower	29.8	76.9	186.1	40.6	33.4	937	11 537	18 027	52 372	5 903
Sept.	upper	26.8	–	22.7	93.7	91.9	90	–	4 678	2 473	11 702
	lower	36.1	–	35.6	46.8	38.1	2 834	–	9 217	10 905	7 941
Oct.	upper	36.7	64.2	40.7	98.2	62.4	1 554	1 936	7 772	2 866	5 115
	lower	49.5	69.4	81.4	47.9	72.8	3 318	18 116	4 652	15 019	25 876
Nov.	upper	34.5	60.4	48.0	66.1	65.3	4 098	6 577	7 033	3 251	4 639
	lower	55.3	79.7	82.9	69.0	65.4	10 333	22 427	16 534	16 703	10 450
Dec.	upper	56.3	76.8	33.2	–	–	2 748	8 078	1 766	–	–
	lower	59.3	69.6	78.3	–	–	7 877	8 915	10 479	–	
Annual mean:	upper	75.1	51.1	25.4	38.9	65.5	1 956	2 784	2 336	995	7 085
	lower	48.9	51.3	65.9	43.4	52.5	5 050	8 055	13 397	11 110	26 283
		5-year mean upper 51.2					5-year mean upper 3 031				
		5-year mean lower 52.4					5-year mean lower 12 779				

* No data.

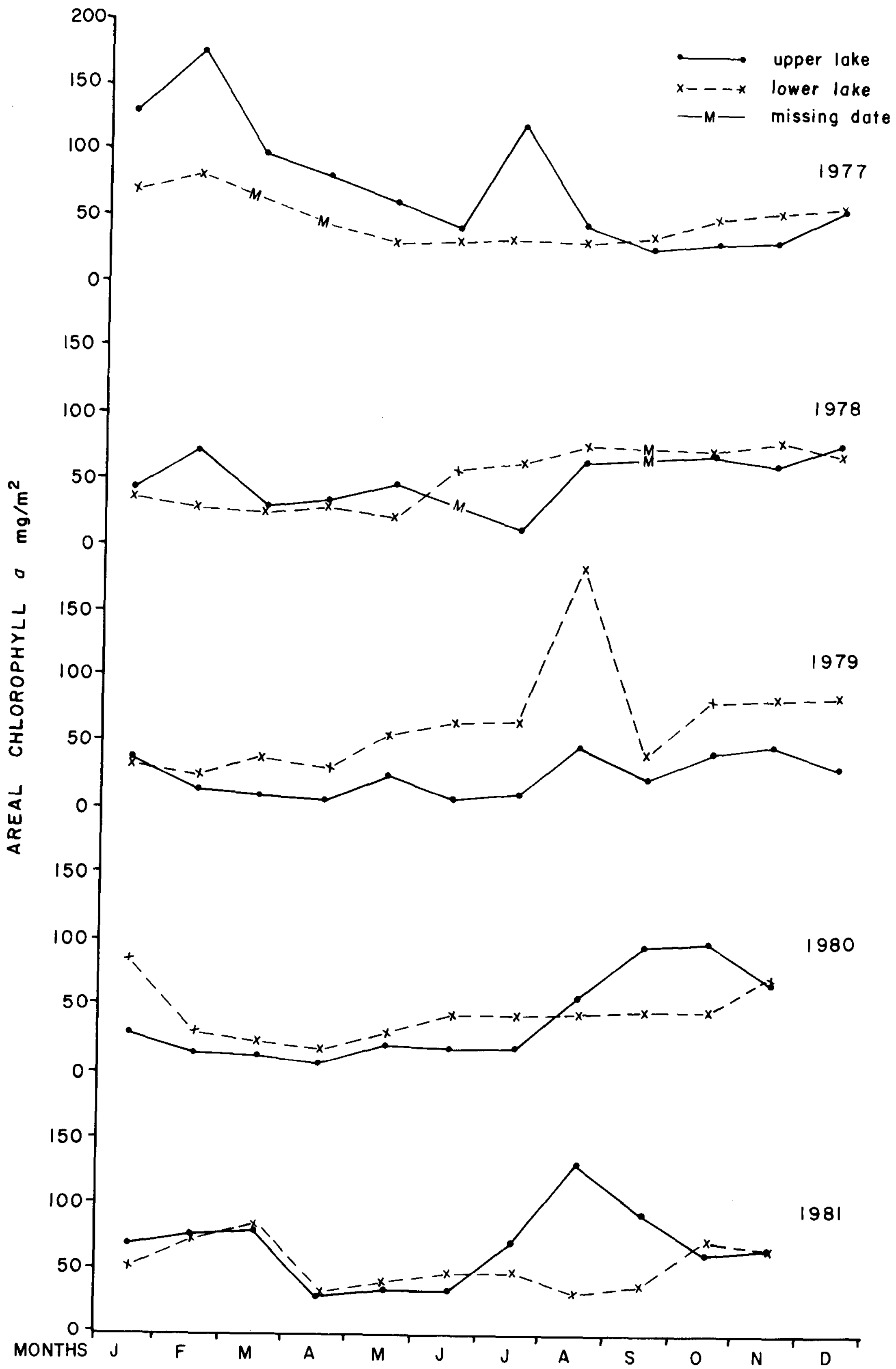


Figure 21. – Average monthly areal chlorophyll *a* concentration in Twin Lakes, 1977-81.

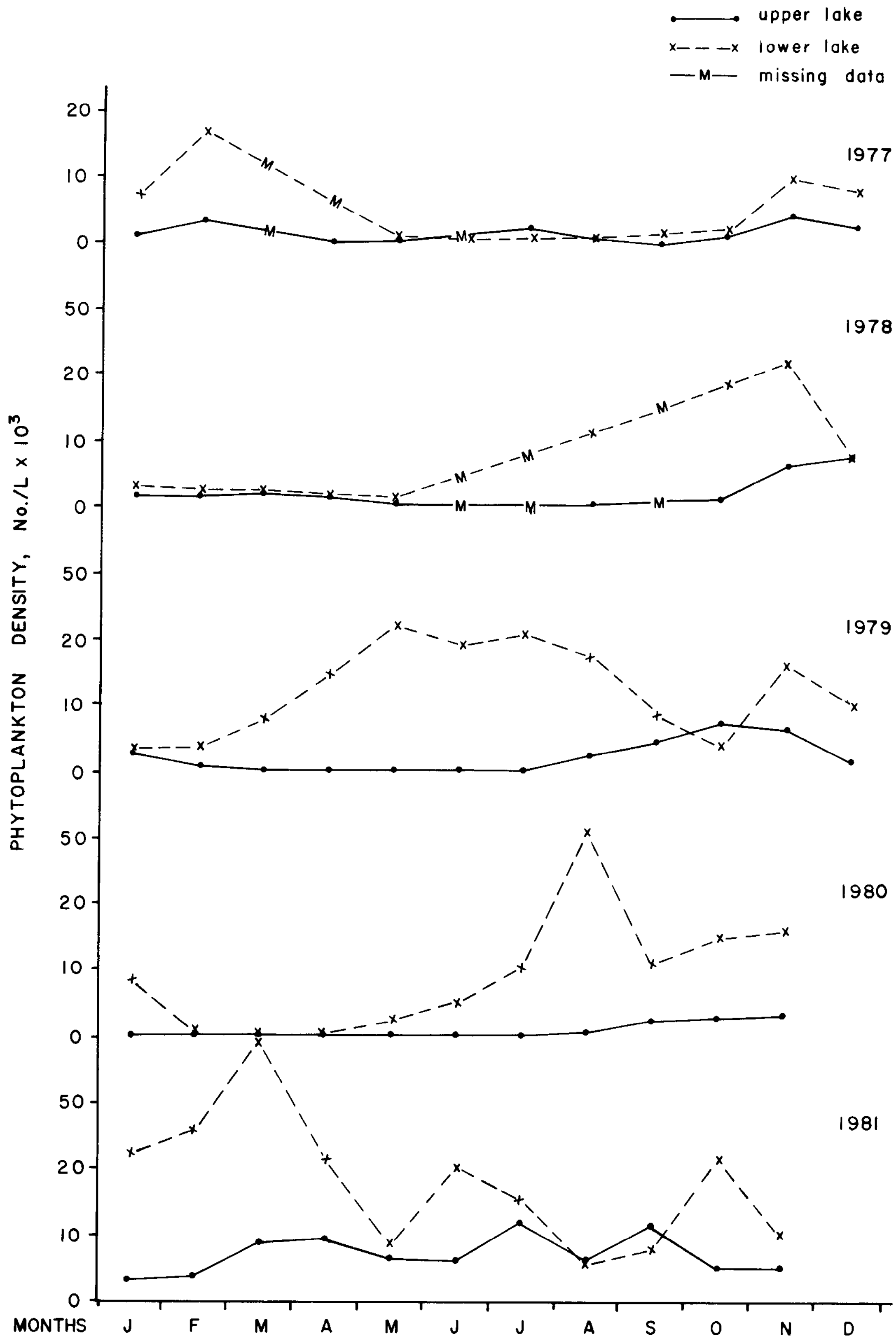


Figure 22. – Average monthly total phytoplankton density in Twin Lakes, 1977-81.

Table 9. – Correlation coefficient, *r*, for carbon fixation and total phytoplankton density in Twin Lakes, 1977-81.

Lake	1977	1978	1979	1980	1981	5-year
Upper	0.01	−0.06	0.73	0.79	0.02	0.60
Lower	−0.53	0.21	0.71	0.77	−0.59	0.31

depths other than those sampled. If this is true, then carbon fixation rate sampled at the same discrete depths as chlorophyll, may have the same errors. Another hypothesis is the presence of an unknown quantity of subnet-sized algae, which are retained by filters in carbon fixation rate and chlorophyll *a* biomass estimations, but escape measurement in our plankton enumeration procedure. These nanoplankton (subnet-sized organisms) may make significant contributions towards total algal production and biomass (Watson and Kalff, 1981) [18]. In a study of Lake Cachuma, California, Boehmke (unpublished) found that 79 to 98 percent of chlorophyll *a* biomass came from subnet-sized plankton, while net-sized plankton contributed only 2 to 21 percent of total chlorphyll biomass.

Water temperature. – Twin Lakes are cool, with a range of surface temperatures from 1 to 17 °C. In attempting to develop light-chlorophyll primary productivity models from Twin Lakes data, Sartoris (unpublished) has found that temperature is not a critical factor in these relationships.

Rhee and Gotham, 1981 [19] found that temperature is interactively important. That is, temperature is not important when considered alone, but becomes increasingly important when combined with light, daylength, season, depth, etc. They also found that nutrient requirements for many algae were higher when the temperature was suboptimal. The carbon fixation rates in Rhee and Gotham's cultures remained the same, but chlorophyll *a* concentrations per cell increased as temperatures decreased. Twin Lakes are phosphorous-limited. In winter (under ice cover) it may be possible for chlorophyll *a* to increase, while the carbon fixation rate remains the same or even decreases. It is also possible that chlorophyll *a* increases or remains the same as the algal density decreases as a function of temperature. It seems that temperature, although not critical at Twin Lakes, may have some subtle interactive effect on primary production.

BIBLIOGRAPHY

[1] Cole, G.A., *Textbook of Limnology*, 2d ed., 426 pp., The C.V. Mosby Company, St. Louis, MO., 1979.

[2] Buckles, W.G., "Archeological Salvage for the Fryingpan-Arkansas Project in Lake, Chaffee, and Pitkin Counties, Colorado, in 1972," National Park Service Contract No. 2-929-P-20073, 157 pp., Anthropology Laboratory, Southern Colorado State College, Pueblo, CO, 1973.

[3] Sartoris, J.J., J.F. LaBounty, and H.D. Newkirk, *Historical, Physical, and Chemical Limnology of Twin Lakes, Colorado*, Bureau of Reclamation Report No. REC-ERC-77-13, 86 pp., Denver, CO, 1977.

[4] Jordan, D.S., "Explorations in Colorado and Utah During the Summer of 1889 With an Account of the Fishes Found in Each of the River Basins Examined," Bulletin of the U.S. Fish Commission, vol. 9, 1889, pp. 1-40, 1891.

[5] Juday, C., "A Study of Twin Lakes, Colorado, With Aspectual Consideration of the Food of the Trouts," Bureau of the Fisheries, Document No. 616, pp. 148-178, 1906.

[6] Krieger, D.A., *Ecology of Catostoimids in Twin Lakes, Colorado, in Relation to a Pumped-Storage Powerplant*, Bureau of Reclamation Report No. REC-ERC-80-2, 56 pp., Denver, CO, 1980.

[7] Liberman, D.M., *Common Plankton of Twin Lakes, Colorado*, Bureau of Reclamation Report No. REC-ERC 82-21, 17 pp., Denver, CO, 1983.

[8] LaBounty, J.F., and J.J. Sartoris, *Effects of Operating the Mt. Elbert Pumped-Storage Powerplant on Twin Lakes, Colorado: 1981 Report of Findings*, Bureau of Reclamation Report No. REC-ERC-83-2, Denver, CO, 1982.

[9] Campbell, S.G., and J.F. LaBounty, *Chlorophyll a Concentration and Distribution in Twin Lakes, Colorado, Prior to Operation of the Mt. Elbert Pumped-Storage Powerplant, 1977-1981*, Bureau of Reclamation Report No. REC-ERC-85-6, Denver, CO, 1985.

[10] Steemann-Nielsen, E., "The use of radioactive carbon (C^{14}) for measuring organic production in the sea," *Journal du Conseil*, 18:117-40, 1952.

[11] Vollenweiden, R.A., ed., *A Manual on Methods for Measuring Primary Production in Aquatic Environments*, International Biological Program Handbook No. 12, 225 pp., Blackwell Scientific Publications, London, 1969.

[12] McMahon, J.M., "Membrane Filter Retention – A Source of Error in the C^{14} Method of Measuring Primary Production," *Limnology and Oceanography*, vol. 18, No. 2, pp. 319-324, 1973.

[13] Wetzel, R.G., *Limnology*, 743 pp. W.B. Saunders Company, New York, NY, 1975.

[14] Likens, G.E., "Primary Productivity of Inland Aquatic Ecosystems," In: *Primary Productivity of the Biosphere*, H. Leith, and T. H. Whittaker, editors, pp. 185-202, Springer-Verlag, New York, NY, 1975.

[15] Taylor, W.D., V.W. Lambou, L.R. Williams, and S.C. Hern, *Trophic State of Lakes and Reservoir*, Technical Report E-80-3, 26 pp., U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS., 1980.

[16] MacKereth, F.J.H., "Phosphorous Utilization by *Asterionella formosa* Hass.," Jour. Exp. Bot., vol. 4, pp. 296-313, 1953.

[17] Campbell, S.G., "Proposed Change for Chlorophyll Computation and Resulting Correlation with Carbon Fixation Rate at Twin Lakes, Colorado," ARSM 81-2-15, September 28, 1981.

[18] Watson, S., and J. Kalff, "Relationships between Nanoplankton and Lake Trophic Status," *Canadian Journal of Fishery Aquatic Science*, 38:960-967, 1981.

[19] Rhee, G., and I. J. Gotham, "The Effect of Environmental Factors on Phytoplankton Growth: Temperature and the Interactions of Temperature With Nutrient Limitation," *Limnology and Oceanography*, 26(4), 635-648, 1981.

APPENDIX A

CARBON FIXATION RATES OF TWIN LAKES, COLORADO, 1973-81 RAW DATA

Table A1. – Carbon fixation rates μgC/(m³·h) in the lower lake, Twin Lakes, Colo., 1973-81.

Date	Meters					Areal 1 to 15 m μgC/(m²·h)
	1	3	5	9	15	
1973						
8-02	*799.1	*731.0				2 150.9
8-30		*1249.7	*407.0			2 485.0
1974						
6-13	*218.9		*241.6			1 059.1
7-25	*322.2		*298.2			1 427.0
8-22	*116.2			*1015.0		5 203.2
9-24	*783.7		*256.0			3 291.3
10-24	*1538.9			*287.8		5 571.5
1975						
11-19	*908.3			*253.7		3 544.2
6-12	*176.7	*1118.3	*953.0	128.2		5 897.3
6-27	*482.0	*995.6	*724.8	69.4		2 782.5
7-09	*781.0	*1020.8	*935.3	16.2		5 620.3
8-14	*324.1	*406.5	*486.0	*434.6	*89.8	5 037.1
9-25	*57.7	*226.8	*579.1	*580.0	*492.7	6 626.6
1976						
8-08	*353.8		290.4	*39.0	1.4	2 245.1
10-10	*417.9		628.9	*31.0	277.7	4 968.3
1977						
2-02	97.5	226.0	318.1	279.4	36.1	3 009.3
6-30	320.5	509.8	398.5	286.9	207.0	4 591.3
7-12	439.9	361.4	367.6	174.4	44.7	3 271.3
7-26	431.1	479.0	322.4	576.9	142.5	5 668.3
8-12	495.1	390.5	366.1	333.9	136.4	4 452.6
8-23	741.3	838.0	787.6	407.0	108.3	7 139.7
9-08	420.7	403.4	257.3	271.6	81.9	3 603.1
9-20	1118.7	1118.2	1056.2	593.7	99.8	9 791.2
10-06	2035.0	1497.2	845.7	240.2	0.0	8 765.5
10-20	1007.5	1023.8	945.1	345.4	22.3	7 684.5
11-03	719.8	905.4	876.4	205.8	12.1	6 225.2
11-15	939.0	646.2	430.7	26.4	19.9	3 715.5
12-21	688.6	193.8	129.5	0.0	24.2	1 406.3
1978						
1-05	441.3	70.7	33.5	23.2	26.6	879.1
1-19	472.1	121.6	61.7	10.8	0.0	930.2
2-02	207.0	152.6	83.0	15.2	9.9	867.0
3-21	122.1	315.2	296.2	105.2	2.4	2 174.4
4-04	94.1	307.2	305.3	257.3	105.1	3 226.0
4-19	173.2	483.3	729.6	561.9	117.9	6 491.7
5-15	554.6	855.6	948.5	553.6	31.1	7 972.4
8-08	781.0	686.9	453.0	256.7	0.0	4 796.3
8-09	935.2	780.2	383.6	191.5	0.0	4 597.4
10-05	1959.3	2391.3	1850.1	415.3	25.2	14 444.4
11-02	1332.8	1401.2	692.4	102.9	0.0	6 682.0
11-30	833.1	836.7	622.2	114.7	7.2	4 968.2
12-19	299.7	95.1	10.9	8.1	0.0	540.3

Table A1. – Carbon fixation rates μgC/(m³·h) in the lower lake, Twin Lakes, Colo., 1973-81 – Continued.

Date	Meters					Areal 0 to 15 m μgC/(m²·h)
	1	3	5	9	15	
1979						
1-11	386.8	101.5	44.8	4.5	4.3	759.6
2-01	132.7	97.4	20.0	11.9	1.9	452.8
3-13	689.0	880.0	541.3	47.3	0.9	4 312.1
4-05	861.4	735.3	281.1	31.6	0.3	3 334.0
5-16	426.8	2189.2	2318.8	1728.2	431.2	21 696.1
6-05	1440.3	2601.5	1918.9	234.4	9.2	13 599.7
6-19	1167.8	1498.0	1022.6	55.3	1.6	7 512.9
7-19	1138.2	1265.2	621.4	182.2	0.0	6 432.8
8-14	751.1	437.6	140.5	184.5	9.8	3 000.1
9-02	368.6	275.5	208.6	83.8	14.0	2 006.5
10-11	953.3	1136.3	944.7	187.7	0.0	6 988.9
11-06	1467.5	1854.8	1325.6	304.6	0.0	10 655.7
12-18	481.4	582.4	475.1	181.8	11.5	4 014.8
1980						
1-10	0.0	1.7	14.4	402.1	63.2	2 243.0
2-13	563.4	103.0	16.5	34.1	16.5	1 038.6
3-12	408.4	298.3	114.4	36.4	9.4	1 558.1
4-15	463.4	194.2	92.4	10.9	0.0	1 150.9
5-19	512.6	896.8	795.3	540.9	89.4	7 664.9
6-12	1020.0	1273.9	1017.4	486.2	10.0	9 081.1
7-15	1169.3	1249.6	1145.8	336.8	0.0	8 689.3
8-12	618.5	483.9	380.9	412.3	64.8	4 985.2
9-09	509.4	311.0	234.3	112.6	34.4	2 500.6
9-25	935.3	1339.4	1414.5	630.7	123.9	11 382.5
10-09	944.1	890.2	891.1	658.9	50.7	8 844.5
10-21	1117.7	1415.1	1770.4	631.0	44.2	12 546.5
11-04	1665.0	1896.1	1753.8	590.5	41.6	13 795.6
11-20	953.3	1247.6	1152.1	464.5	23.4	9 297.7
1981						
1-08	197.5	606.2	681.2	268.9	38.4	4 913.2
2-05	274.2	543.7	434.4	152.2	25.7	3 502.8
3-03	199.1	151.7	45.4	30.1	5.6	805.8
4-02	492.4	420.8	490.2	395.6	39.9	4 901.9
4-16	55.9	77.9	103.8	254.2	164.5	2 287.1
4-30	200.3	591.2	635.3	475.7	171.6	6 181.8
5-21	963.3	1308.3	1331.8	720.9	71.9	11 395.6
6-02	484.3	627.9	697.7	655.1	238.2	7 822.9
6-25	875.0	810.1	775.5	325.2	51.7	6 602.7
7-09	694.1	526.6	358.1	180.8	27.1	3 806.5
7-23	767.7	661.4	311.0	183.5	15.4	3 987.8
8-06	332.3	656.4	392.8	263.5	41.6	4 266.0
8-20	409.8	529.0	393.4	314.6	62.8	4 409.5
9-02	430.5	475.6	474.5	399.2	93.5	5 081.7
9-17	371.9	893.7	1157.6	433.0	116.8	8 147.4
9-30	1284.8	1284.8	1146.8	259.7	25.9	8 681.3
10-15	1634.2	1700.8	939.0	147.5	4.3	8 603.2
10-29	1275.0	930.9	589.0	82.5	1.3	5 319.8
11-11	770.8	1072.3	1142.0	212.9	0.0	7 389.1

* Sampled at nonstandard depths, but closest to depth indicated.

Table A2. – Carbon fixation rates μgC/(m³·h) in the upper lake, Twin Lakes, Colo., 1973-81.

Date	Meters 1	3	5	9	15	Areal 1 to 15 m μgC/(m²·h)
1974						
6-13	*76.3		*16.1			212.7
7-25	*336.4		*407.7			1711.6
8-22	*116.0			*107.4		681.4
9-24	*285.6		*271.1			1 280.2
10-24	*726.0			*173.5		2 743.3
11-19	*650.3			*202.8		2 601.9
1975						
6-12	*72.8	*422.8	*252.7	67.1		1859.4
7-09	*26.1	*170.7	*30.5	0.0		381.4
8-14	*254.8	*1047.0	*284.3	*401.5	*75.0	5434.6
9-25	*37.0	*386.7	*462.5	*543.9	*392.9	6096.3
1976						
8-08	45.3	87.3		*338.6	277.7	3164.0
10-10	*225.2		342.5	*122.8	277.7	3555.4
1977						
2-02	603.3	682.2	350.7	82.4	18.3	3486.6
6-30	705.2	768.7	959.2	48.8	10.7	5396.2
7-12	1148.0	851.0	1700.2	358.7	0.0	9683.1
7-26	332.1	715.7	373.5	21.4	190.0	3560.9
8-12	874.1	859.8	619.0	338.7	0.0	6121.1
8-23	816.7	610.6	350.1	101.9	25.7	3674.5
9-09	441.5	355.9	236.0	47.1	1.6	2101.6
9-20	739.7	830.3	528.9	132.4	11.0	4682.0
10-06	1446.1	412.5	843.5	36.1	101.3	5286.4
10-20	1384.6	1123.3	287.5	120.1	18.8	5150.6
11-03	901.5	1221.3	888.5	249.1	3.1	7264.3
11-15	1026.9	679.8	341.6	34.7	10.8	3617.0
12-21	628.4	198.2	45.2	11.7	39.0	1336.0
1978						
1-05	374.3	100.3	32.2	32.9	12.5	873.6
1-19	465.2	457.2	105.0	43.1	51.1	2063.1
2-02	413.6	54.6	28.3	5.4	16.1	683.4
3-21	289.0	252.1	285.5	136.5	8.7	2357.8
4-04	123.5	217.0	196.2	167.4	33.7	2083.8
4-19	337.2	743.1	623.5	530.8	75.4	6574.1
5-15	252.3	427.2	505.2	403.2	43.3	4768.2
8-08	526.4	332.3	292.0	90.1	6.5	2537.1
10-05	708.2	651.1	389.1	58.5	14.8	3514.5
11-02	524.8	746.9	324.6	33.4	0.0	3132.6
11-30	586.2	505.1	483.0	63.0	24.1	3433.0
12-19	350.8	146.1	15.2	14.2	0.0	707.0

Table A2. – Carbon fixation rates μgC/(m³·h) in the upper lake, Twin Lakes, Colo., 1973-81 – Continued.

Date	Meters 1	3	5	9	15	Areal 0 to 15 m μgC/(m²·h)
1979						
1-11	276.0	95.8	22.8	5.5	0.0	505.6
2-01	150.7	47.1	22.7	0.0	26.3	337.4
3-13	73.9	109.8	51.4	1.0	0.0	443.3
4-05	118.1	159.8	51.7	10.4	0.0	642.4
5-16	23.3	68.5	32.5	77.1	13.8	684.2
6-05	438.8	173.4	17.8	0.0	0.0	803.4
6-19	57.1	18.8	2.4	3.5	0.0	99.6
7-19	300.2	476.1	404.3	20.7	0.0	2561.3
8-14	657.3	459.8	485.3	43.8	3.9	3263.5
9-20	193.4	165.7	118.3	40.5	0.3	1083.0
10-11	534.0	813.9	718.6	282.0	0.0	5714.4
11-06	378.0	797.0	547.9	93.5	15.6	4130.2
12-18	167.2	204.4	141.2	37.0	0.2	1185.1
1980						
1-10	29.4	37.1	1.3	8.9	4.9	166.6
2-13	144.5	43.3	32.4	23.1	0.0	435.1
3-12	56.7	54.2	26.9	1.8	0.0	235.7
4-15	87.5	79.2	19.8	5.3	3.3	341.9
5-19	131.1	220.2	254.4	200.7	73.9	2559.6
6-12	284.1	210.4	7.0	3.4	5.5	759.5
7-15	464.6	364.3	844.8	0.0	0.0	3727.6
8-12	299.7	272.8	269.5	65.7	0.0	1982.1
9-09	207.1	260.9	175.5	92.5	32.1	1813.8
9-25	904.7	875.4	596.9	67.0	11.9	4816.8
10-09	664.5	730.7	754.2	126.2	0.0	5019.4
10-21	541.3	536.5	342.7	67.1	10.0	3008.1
11-04	555.0	734.9	465.4	60.7	2.8	3733.0
11-20	724.8	684.5	378.7	32.0	13.8	3431.4
1981						
1-08	392.9	492.2	297.7	45.1	73.4	2721.8
2-05	632.2	652.2	217.2	22.5	1.6	2705.5
3-03	187.2	110.5	80.8	14.1	2.2	727.7
4-02	15.4	201.9	231.4	289.9	28.8	2649.2
4-16	17.4	44.7	177.8	529.9	85.8	3547.0
4-30	208.7	301.0	400.5	283.7	77.3	3662.7
5-21	716.9	986.2	867.5	362.6	21.8	7170.2
6-02	330.6	475.8	376.4	106.0	0.0	2937.9
6-25	355.3	239.7	242.7	21.3	1.9	1675.1
7-09	776.6	426.9	192.4	259.7	0.0	3499.0
7-23	1201.9	632.8	334.3	170.7	1.4	4327.8
8-06	761.0	719.5	530.9	307.4	1.7	5335.0
8-20	181.8	1457.5	380.3	10.1	0.0	4279.4
9-02	470.9	455.6	355.2	207.4	5.4	3501.0
9-17	419.0	627.7	652.2	273.5	4.1	5010.4
9-30	659.6	762.7	479.4	82.0	4.5	4047.0
10-15	900.3	757.9	466.8	76.2	0.8	4200.1
10-29	871.4	746.1	386.4	60.1	2.7	3831.3
11-12	600.3	756.4	690.9	189.8	10.5	5136.2

* Sampled at nonstandard depths, but closest to depth indicated.

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