RPI – FWI – 72-72

RENSSELAER

Fresh Water Institute

AT LAKE GEORGE

PRIMARY PRODUCTIVITY OF LAKE GEORGE, NEW YORK:
ITS ESTIMATION AND REGULATION

By

Raymond G. Stross
Department of Biological Sciences

November, 1972

FWI 72-72

Rensselaer Polytechnic Institute Troy, New York 12181

PRIMARY PRODUCTIVITY OF LAKE GEORGE, NEW YORK: ITS ESTIMATION AND REGULATION

submitted to

Union Carbide Subcontract No. 3566 for the
Eastern Deciduous Forest Biome, IBP, Lake George Site.
Annual Report - Year II - IBP - EDFB

by

Raymond G. Stross

Department of Biological Sciences

November, 1972

FWI Report #72-72

Eastern Deciduous Forest Biome
Memo Report #72-72

PRIMARY PRODUCTIVITY OF LAKE GEORGE, NEW YORK: ITS ESTIMATION AND REGULATION

A final technical report for Union Carbide Subcontract No. 3566 for the Eastern Deciduous Forest Biome, IBP, Lake George Site.

Annual Report - Year II - IBP-EDFB

Raymond G. Stross
Department of Biological Sciences

Research supported in part by the Eastern Deciduous Forest Biome, U.S. International Biological Program, funded by the National Science Foundation under Interagency Agreement AG-199, 40-193-69, with the Atomic Energy Commission, Oak Ridge National Laboratory.

November 1972

State University of New York at Albany
Albany, New York

ABSTRACT

Primary Productivity of Lake George, New York: Its Estimation and Regulation

R. G. Stross
Department of Biological Sciences
SUNY, Albany
Albany, New York 12222

Rates of production were estimated for the phytoplankton and the attached macrophytes. Daily rates of net carbon assimilation for the phytoplankton are calculated from measurements of hourly rates at expected light saturation, total daily insolation and coefficient of light attenuation.

Mean daily rates for the years 1970-1972 show a 50% increase in the maximum summertime rate.

The macrophytes are primarily Nitella flexilis which grows in the depth zone of 7 and 12 meters, or on some 20% of the bottom. Evidence suggests two crops per year. Daily rates, estimated from seasonal growth patterns and annual accumulation, suggest intervals in June and September when macrophyte and plankton contribute equally to productivity on an areal basis. Growth morphology and oospore formation suggest that (red?) light strongly influences the Nitella beds on Lake George.

KEY WORDS: Biological productivity, phytoplankton production, primary productivity, macrophyte productivity, photoecology.

The objective of this report is to present the estimates of primary production in Lake George, New York that have been made since 1969.

The studies of primary productivity in Lake George have had several objectives since its inception in 1969. One of these is to estimate the combined rate of primary production for both the phytoplankton and macrophytes in Lake George. This report is devoted to giving the first comprehensive estimate of this kind for Lake George.

Acknowledgements

I wish to thank the many students who assisted with various parts of the program. On the SUNYA campus I must thank T. A. Downing for carrying on most of the field measurements on macrophytes with the aid of Nancy Liptak. S. W. Chisholm did most of the direct modification of the necessary computer programming. Others who lent assistance are J. W. Sutherland, M. Acosta, and John King. Mr. Ronald Stewart, SUNYA-ASRC, allowed use of the July 1971 through August 1972 solar radiation data. Plant identifications were done by Dr. Eugene Ogden of New York Science Service. The Nitella and Chara species were identified by Dr. Ogden and confirmed by Dr. R. D. Wood of the University of Rhode Island. On the RPI campus there are also a number of individuals who played a vital role. Mr. R. Kohberger supplied light data from the data library. He and Dr. John Wilkenson also performed statistical analysis on the phytoplankton data. Dr. Donald Aulenbach lent generously of his time on phytoplankton cruises. Special acknowledgement is due the Site Director for allowing use of the facilities at Lake George and for retaining the interest of the primary producers despite a spartan budget.

I. PHYTOPLANKTON

Productivity of phytoplankton was estimated with a single approach from measurements of light-saturated photosynthesis and light intensity data which consists of extinction coefficients and total daily radiation at the lake surface. The techniques involved in measuring light-saturated photosynthesis of P_{max} are standard. Since they have been described elsewhere they will be only summarized here.

Methods and Materials

The basis of the measurement is the short term rate of photosynthetic uptake of carbon as determined with the addition of carbon-14 (Steemann-Nielsen, 1952). Lake water was incubated in 165 ml bottles in an illuminated revolving drum incubator. Light intensity maximum was 1500 ftc and the temperatures were those of the lake surface. The rate of photosynthesis is reported with corrections being made for dark uptake of carbon and for loss of photosynthate in extracellular excretion. Mean extinction coefficients were calculated from profiles of white light attenuation as measured with the submarine photometers (G. M. Manufacturing and Montedoro).

Surface light intensity was measured at the SUNYA-ASRC Laboratory in Lake George Village. The interval from July 1971 through August 1972 was the only data available at the time this report was prepared. The data were obtained from Mr. Robert Kohberger in the IBM card form provided to him by Mr. Ronald Stewart. Hourly rates of photosynthesis (P_{max}) are converted to daily rates for the entire water column. The formula was supplied by Mr. Paul Nobbs of San Diego State University as was the computer program to calculate day length. The formula for depth integration of hourly rates and for conversion to rates per day:

$$P_{(mg/C/m^2/day)} = (P_{max}/\epsilon)\frac{\lambda}{2} \text{ Arctan } \left[(D-Z)(Io)\right] - \text{Arctan } \left[(-Z)(Io)\right]$$

where: P_{max} = photosynthesis at light saturation

$\mathcal{E}$ = light extinction coefficient

D = maximum lake depth

Z = depth of optimal light intensity

I_o = incident light intensity

λ = daylength (sunset-sunrise)

The formula yielded results very nearly that of the standard Vollenweider (1966) equation (see last year's report) when surface light is intense but tends to give larger estimates on dim days.

The correction for daily asymmetry in hourly rates of photosynthesis was obtained from the following formula (also supplied by Nobbs):

$$P_{max} = \text{Measured } P_{max} / 0.5 \sin\left[\pi/2\left(\frac{1-T}{P}\right)\right] + 0.5$$

where $T = t_{pmeas} - t_{pmax}$

and $P = t_{ss} - t_{pmax}$

The formula for daily asymmetry replaces last year's technique which was found to be greatly in error (Stross, 1971).

Spatial-Temporal Patterns

Much effort has been devoted to the measurement of P_{max}. The question was asked: What is the minimum number of samples necessary for a reasonable estimate of the mean? At the same time it was necessary to know both what variance resulted from local or small-scale patchiness and from vertical stratification of the algal assemblage. Finally, the question was also asked: Is there a significant difference in rate of photosynthesis at light saturation that is associated with location in the axial gradient of Lake George?

Results

The spatial temporal pattern of photosynthesis in Lake George as

determined from estimates of P_{max} has already been described (Stross, 1970 1971; Stross and Kohberger, ms) and will be only summarized here. Hourly rates of P_{max} ranged from 4.4 to 31.1 mg $C/m^3/hr$ during the ice-free part of the year. Photosynthetic rates are much more stable than the range indicates, however. Most of the variability is removed when the major sources of variance are removed. When variance due to season, location in the lake (station), and time of day is removed, the metabolic activity of the algae in Lake George is remarkably stable. At a single station the amplitude of daily oscillation may be in the range of 1.6 and 2.0. Seasonal variability at a station is in the range of 2.2 and 3.0 if the winter period of ice cover is excluded; a small amplitude indeed if one realizes that the solar input at 45^{o} has an annual range of 2.0. The other variable is location or station in the lake. Rates at Station 1 in the southern end of Lake George are usually 2.0 or more times larger than photosynthetic rates in samples at Station 7 near the northern end. Station 4, which is immediately north of the narrows that separates southern and northern basins, may have rates that agree with Station 1 or 7, or be intermediate to the extremes. Combined, the various sources of variability suggest a strongly fluctuating P_{max} when in reality the local variability at any one station is remarkably small indeed.

Local variability in P_{max} is quite small with exception. In the overall analysis, profile and depth were set up with station as the main sources of variance. In all but one cruise the only main source of variance was station and that was consistently significant. The only other main source of variance in the analysis was the effect of depth. During the late summer intervals there was often an accumulation of photosynthetic standing crop (Newhouse, et.al., 1967) in the thermocline at 10 and 15 meters depth.

Local variation was rarely if ever significant. In both the horizontal, as measured by comparison of profiles, and the vertical, as measured at five depths, variability in P_{max} was not significant in a Station-Profile-Depth thruway analysis of variance with exceptions. Vertical stratification of the photosynthetic standing crop was often associated with thermal stratification, especially in late summer. The larger than the mean P_{max} from depths of 10 and 15 meters were eliminated from the mean P_{max} for each station however. Error variance was always smaller than 10 percent of the variance at a station and usually near 5 percent.

Daily Rates of Phytoplankton Production

Three variables necessary to calculate the daily rate of primary production are the standard P_{max}, surface light intensity, and an attenuation coefficient of light intensity with depth. The calculation program, prepared by Paul Nobbs and Miss S. W. Chisholm, was designed to give an output value for each day on which there was a datum for daily input of solar radiation (shortwave). P_{max} estimates were interpolated from the estimates shown in Figure 1. Light extinction coefficients are introduced as mean monthly values. They may be based on actually measurement, as during the ice-free period, or based on an assumed attenuation of 99 percent in the first 2 meters beneath the ice which may be realistic when the ice is covered with snow.

Light saturated rates of photosynthesis are summarized for the interval July 1969 to September 1972 in Figure 1. Mean values are shown for each of three stations on Lake George. The general annual trend is apparent. Maximum rates for each year are to be found in the summer and autumn. P_{max} is usually largest at the southern end of the lake at Station 1 and smallest at the northern end of the lake at Station 7. Considering Station 1 only for the moment, there is an interesting pulse that seems to occur in the

summers of 1970, 1971 and 1972. The pulse interval seems to be restricted to the late July-August interval and repeated each year (Fig. 2). The summer maximum of P_{max} recorded in 1970 was in July at 17.7 mg C/m^3. In 1971 the summer maximum was measured in August at 20.6, and in 1972 it was recorded also in August at 31.1 mg $C/m^3/hr$. That is, there was a measurable increase in hourly rate over the three year period.

The calculation program described above permitted the conversion of hourly rates applicable to a depth where light intensity is at saturation to daily rates for the entire water column. Two months, July 1971 (Fig. 3) and August 1972 (Fig. 4) were chosen arbitrarily for display of day-to-day trends. In the first comparison (Fig. 3) the daily rates at Stations 1 and 7 show reversing trends. That is in July 1971 the rate at Station 1 declined from 1.2 g $C/m^2/day$ to approximately 0.7 before reversing the trend. The rate at Station 7 increased from 0.4 to 0.7 g $C/m^2/day$ during the same interval (Fig. 4). Since the same solar input was employed in both cases, the trends are obviously determined by the estimates of P_{max} for the respective stations. In August of 1972 the rates at both Stations 1 and 7 declined from maximum values at the beginning of the month. The daily fluctuations in solar intensities seemed more severe in the August 1972 comparison. As a result the fluctuations in production rates also have greater amplitude. It is to be noted that the estimated daily rates at Station 1 approach 2.5 g $C/m^2/day$, an all time single-day high for the 3-year interval of study.

Daily rates are combined to give a mean daily rate for each month in Figure 5. The period from July 1970 to August 1972 is included in the calculations. Although the P_{max} are new for each year, the solar radiation data for Lake George was at first available for the single year of from July 1971 to August 1972 only. As a consequence, the same light data are

used for both years. The net result of using the same annual radiation data is to observe that each summer from 1970 through 1972 there is a progressive increase in the mean daily production rate that approached a 50 percent overall increase in mean daily rate of photosynthesis. The second pattern to emerge from the mean daily estimates is a distinct bimodal distribution for the spring-summer interval. Since the effect is restricted to Station 1, it seems unlikely that use of the same solar radiation data for both years should account for the bimodal pattern.

II. MACROPHYTES

Production and Growth Regulation

Reported by Needham, Juday and associates (1922), the extensive beds of Nitella flexilis are well known for Lake George. The objective of the present study was 1) to determine the precise distributions of the Nitella beds; 2) to determine whether or not Nitella is the only species of macrophytes found at the bottom in the sub-littoral of Lake George; 3) to measure the annual production; and 4) to determine the senstivity of the macrophytes to the major components of their environment.

Large plants and animals obviously contain larger quantities of nutrient ions and are likely to exchange the ions at a slower rate than their microscopic counterparts. Conceivably large plants take up and retain nutrients that may, without such a sink, normally recycle within the planktonic community. Whether or not the macrophytes in Lake George compete with the phytoplankton for nutrients may be suggested with the present approach.

In addition to the Needham (Needham, et.al., 1922) report there are specific studies of the macrophytes in Lake George. Fenlon (1971) and Traver (1971) sampled extensively with an Ekman dredge in depths reportedly up to 25 meters. Fenlon reports finding an identified species of Potamogeton in depths ranging up to 12 meters, but this is almost certainly a misidentification of Nitella flexilis. Mean quantities of dried plant matter was given at 21.88 g per m^2 for the southern portion of Lake George's south basin. Ogden (1971) has made an extensive analysis of the species represented in Lake George. This project is grateful to him for identifications of all species described in the report.

Methods and Materials

The total annual production of rooted and attached macrophytes was

estimated from standing crops and rates of replacement. Short term rates of carbon uptake were also measured and these data may serve as a second type of estimate of annual production, aside from their utility for evaluating the environment.

Standing crops were estimated from samples collected with an Ekman dredge. The macrophytes were removed from the dredge, washed, dried at 105°C and weighed on an analytic balance. The collections were made at depth intervals of 1.0 meter from either the 3- or the 7.0 -meter contour to the 12-meter contour.

The sampling locations were restricted to the south basin of Lake George. Tea Island (Fig. 6) was settled as the major reference station and the samples necessary to evaluate the seasonal development of Nitella were taken from a transect at Tea Island. A general analysis of quantitative distribution was undertaken in the whole of the south basin of Lake George. Complete transects, that is samples taken from 3- to the 12-meter contour, were established at seven locations. These were Tea Island, Dunham Bay, Warner Bay, Speaker Heck Island, Diamond Island, Dome Island (west shore) and Northwest Bay. In all cases the most gently sloping bottom was selected so as to extend the distance between the one-meter contours. The steep slopes were examined to verify presence by scuba divers on underwater sleds, a vehicle that allowed extensive coverage of the bottom. Both types of slopes were compared photographically.

The general survey was for the purpose of measuring both qualitative and quantitative distributions of species populations in the sub-littoral bottom of Lake George, or primarily from 7 through 12 meters of depth. The fractional area of the lake in the depth range of 3 and 12 meters was determined from planimetric measurement of the standard Lake George map as supplied by the Power Squadron on the lake.

Rates of carbon assimilation were measured with short term incubation in the presence of carbon-14 labelled CO_2 and bicarbonate (or as with the phytoplankton). Only the sub-littoral macrophyte, Nitella flexilis was subjected to photosynthesis measurements. Usually individual plants, collected by dredge or diver, was suspended in lake water contained in a standard milk dilution bottle of 165 ml capacity. The bottle were then suspended on the revolving drum of the standard PECCER photosynthesis chamber.

Following incubation of normally two hours duration, the plants were removed from the incubator, placed on dry ice, and transported to the fuming hood. After fuming, the plants were dried at 105° and weighed. The amount of carbon-14 label assimilated was measured by converting the organic carbon to free CO_2 in controlled combustion chambers (Adams pers. communication). The CO_2 was absorbed in ethanolamine. A standard scintillation cocktail was added to the vial, and the contents counted in a liquid scintillation spectrometer (Packard Mo. 3375). Calculation of the rate of carbon uptake was standard and based on the ratio of carbon-14 absorbed to that in the incubation vessel. The amount of carbon-12 available in the incubation vessel was determined from titration of alkalinity, pH determination, temperature and conversion tables (Saunders, et.al., 1962). Uptake is expressed per gram dry weight of plant.

The photosynthesis measurements served two functions. One was to determine the times of maximum photosynthetic activity of Nitella in the field. The second function was to evaluate light intensity, nutrient (phosphate and nitrate) concentrations, temperature and time of day on the rates of photosynthetic incorporation of carbon. Nitella has already been shown to be sensitive to turbulence (see below) and the plants were routinely tested in an environment made turbulent by the agitation of the

incubation vessels in the incubator.

Results

Attached or rooted plants grow extensively on the bottom of Lake George. In that part of the bottom within the 3- and 12-meter contours is a vast, almost continuous covering of plants. The species Nitella flexilis is the singularly most abundant member. In fact it is essentially the only macrophyte species in the zone of 7 to 12 meters. Plant densities are rather uniform on the bottom from 3 through 9 meters at 35.0 grams (dry weight)/m^2 and from 10 through 12 meters at 119.5 g/m^2. The much greater luxuriance in the deeper water is confirmed by a variety of techniques that consist of photography, morphological analysis of the plants, etc. and will be a special topic (see below). The growth form of the Nitella and its rather striking delimitation along depth contours illustrate the precise way the environment controls the growth of the macrophytes. Most observed species of plants and animals found on the bottom show rather precise depth distribution as observed by the divers and in the photographs of the bottom.

Seasonal Standing Crop at Tea Island

An argument is presented to the effect that the standing crop of Nitella, the principal species, seems to be replaced at least twice each year. There is evidence for both a winter and a summer population of Nitella. Three types of individual plants were recognized. Old plants contained only dark green or green-brown cells; many of these plants contained segments that were dead or necrotic. New plants were light green and finer textured. A third category consisted of old plants with young or newly generated or light green terminal sections. Most of the observations fall in the interval of June to October. Within this interval there is clearly replacement taking place in June and again in September.

In early June two easily distinguished groups of Nitella plants are present in the dredge samples from the Tea Island area. At 12 meters the old plants are 42 cm tall and the young plants are 5 to 10 cm tall (Fig. 7). The old plants have disappeared by the end of July while the young plants have grown to a length of 30 cm. The same thing happens in shallower water at 7 and 8 meters depth although the length of the plant is much less, reaching maximum lengths of 10 and 18 cm, respectively.

The summer plants also appear to die in August and September. At the end of September there is a new crop of plants whose length is now much greater than that of the summer plants. The autumn populations were in October 1972 approximately 62 cm tall at 12 meters and 32 cm tall at 7 and 8 meters depth. The length of Nitella plants at 12 meters is roughly twice that of plants at 7 and 8 meters. And the late summer population is approximately twice the length of the early summer population at both the shallow and deep end of the zone inhabited.

The existence of two distinct replacements each year seems reasonably well demonstrated with the observations based on both change in length of the plant and color of the plants. There is also some indication of partial if not complete replacement taking place in the winter interval. In January and February 1972, plants brought to the surface with divers and dredges contained partially regenerated segments. There is no good evidence for the extent or amount of replacement, however.

Annual Production of Macrophytes in the South Basin

The basis of the annual production estimates is the measurements of standing crop in the south basin. The Nitella population will be assumed to be replaced twice each year. The late spring-early summer crop is estimated from the values obtained at Tea Island. The second crop of late summer-early autumn is estimated from the measurements taken at Tea Island

and at 5 other locations in the south basin of Lake George. Macrophytes other than Nitella are estimated only once during the summer and are assumed to be replaced only once each year.

The densest populations of Nitella existed in the zone of 10 to 12 meters and the added biomass is consistent with the observations of length of the individual plants. In the interval from June through July, crops at 12 meters were estimated to be in the range of 73.6 and 117.1 g (dry weight)/m^2. During the same interval at 7 and 8 meters depth biomass ranged from 9.8 to 42.5 g C/m^2 (Table 1).

The fall population was similarly denser in the deeper water although the difference was less dramatic, possibly owing to location of sampling rather than real increases at the shallower locations. Considering only the Nitella first, mean values range from 43.8 to 133.0 g/m^2 with some suggestion that the deeper zone is the more productive (Table 2). The macrophytes that exist in depths shallower than 7 meters were also sampled in the September period. Biomass is shown for these as a composite of all taxa which consisted of species of Potamogeton, Valisneria, Ranunculus and Elodea (see Appendix 1 for a breakdown of biomass according to species). Generally, the biomass at 3 and 4 meters depth is nearly that at 10 and 12 meters, with intermediate depths having lesser quantities.

Early and late summer populations of Nitella are combined with the late summer biomass of other species of aquatic macrophytes in Table 3. Annual production ranges from 40 g/m^2 at 5 meters depth to and estimated 190 g/m^2 at a depth of 10 meters. Estimated rates for the area of the bottom actually covered with plants were converted to an estimated rate per m^2 of surface. Total production in the south basin within the depth range of 3 and 12 meters was 2,286.92 x 10^6 g (dry weight). The southern basin is estimated at 21.745 $miles^2$ or 54.653 x 10^6 m^2. The estimated annual

production in the south basin would then be 34.72 g (dry weight)/m^2 of Lake George surface.

MACROPHYTE PHOTOSYNTHESIS

All experimental measurements of photosynthetic rates were carried out in on the same rotating drum incubator that is employed for estimating P_{max} of phytoplankton. Agitation, as one might expect, is a serious factor in the observed rate. Two types of techniques were employed to provide circulation of the medium about the plants. One was the revolving drum. The second techniques was to recirculate the water through a closed incubation chamber via a peristaltic pump (Cole-Parmer Pump Mo. 7015). The second type of circulating device provided a variable rate of circulation, although the results are in relative units. Circulation is quite influential as shown by Adams and Schmidt, 1972. Experiments indicated a twofold increase in rate resulting from agitation. In the unagitated control the rate was 9.1 mg C/g/hr and at the equilibrium level of agitation the rate was approximately 20 mg C/g/hr (Fig. 8). The twofold increase resulting from a saturating level of agitation was apparently achieved by the rotating drum approach since the tests with that technique also gave values that were twofold larger. The rotating drum was apparently able to give saturating agitation as determined by comparison of values in a similar experiment with it.

Seasonal Trends

The seasonal growth form of the summer Nitella population and the seasonal trend in rate of carbon assimilation show a parallel pattern. Hourly rates of photosynthesis were 32.0/mg/C/g (dry weight)/hr in early June 1972 when the plants were small (Fig. 9). The rate declined to 10.0./mg/C/g/hr in mid-July at which time the Nitella plants were nearing equilibrium length. The rate was again higher than the July value in September during the time at which the autumn population was developing. Although estimates were not available for August 1972, some estimates are available from the 1971 experiments in which Wetzel (1966) chambers were employed. Estimates in August 1971

were approximately 0.6/mg/C/g/hr in the no-motion chambers of Wetzel, but would probably be not greater than 2 or 3 times that value had the revolving drum technique of 1972 been employed. Thus it seems safe to assume that during August 1972 the hourly rate of photosynthesis was greatly reduced in August or when the Nitella plants in the shallow end of the bed had complet fruiting.

Experiments were carried out to measure if, and the extent of, nutrient limitation. Both phosphate and nitrates were tested. Individual Nitella plants were placed in milk dilution bottles along with water from the Lake George and specifically from the depth at which the plants were growing. Sets of triplicate bottles were incubated in the rotating drum chamber in the presence of carbon-14 labelled inorganic carbon. The water was either unenriched or was supplemented with various concentrations of sodium (primary) phosphate or sodium nitrate. The results of the 2-hour incubation are shown in Figure 10. Phosphate was shown to limit photosynthesis. Concentrations of 0.1 and 0.2 micromoles phosphate increased the rate of photosynthesis although to an insignificant extent. Larger concentrations either definitely stimulated or inhibited photosynthesis. At 0.5 and 1.0 uM PO_4/liter photosynthesis was stimulated from 50 to 100 percent over the unenriched controls. At 5.0 and 10.0 u Molar there was a 2- or 3-fold inhibition over the maximum stimulation achieved at 2.0 uM/liter phosphate. The addition of nitrate appeared to have no stimulating effect in the range of 0.1 and 10.0 uMoles nitrate (Fig. 10).

The depth distribution of Nitella in Lake George is apparently rather exact beginning at or about 7.0 meters at all locations in the southern basin, or so the divers reported in 1972. The lower limit of the bed is also exact with the plants ending abruptly at depths slightly deeper than 12.0 m. These observations agree within 0.3 meters of those reported in

1922 (Needham, et.al., 1922). Light or one of its facets; intensity, quality, duration, may be of considerable significance in determining the depth distribution. A single experiment was carried out to test the effect of light intensity on short term rates of photosynthesis. Replicate samples were incubated at 14, 100, 200, 400, and 1000 ftc. All were incubated in the revolving drum incubator with reduced light intensity achieved by wrapping the bottles in cheese cloth. The results are ambivalent and highly questionable (Table 5). Nevertheless, the indication is that at 14 ftc the rate is only 8 percent of saturation. The large spread in data points was reduced at 100 ftc by splitting the results into two sets of results. When this is done, the indication is that either 100 or 400 ftc is saturating.

The results from incubating at 200 ftc would suggest that the saturation is achieved somewhere in the neighborhood of 400 ftc. The experiment also revealed a tremendous level of inhibition at 1000 ftc incubation intensity, inhibition which must be erroneous. Since the results could not be worked up until the oxidizer was prepared, most of the experiments were carried out before the results of a single experiment was known. Since all of the experiments were routinely done at full light intensity, or 1500 ftc, at which intensity the rates were up to 50 mg C/g/hr (e.g. the phosphate limiting experiment), there seems little evidence to suggest that inhibition at 1500 or even 1000 ftc is general.

Combined Production of Phytoplankton and Macrophytes

Annual production of macrophytes ranges from 40 to 190 g/m^2 in the areas of the bottom actually occupied by the plants. For the entire south basin of Lake George the annual rate in 1972 was estimated at 34.7 g/m^2, or approximately twice the actual accumulation of standing biomass. Phytoplankton production on an annual basis has little functional value, since the plant constituents are recycled. A better comparison might be had if

the daily production of phytoplankton were added to an estimated daily production of macrophytes. Daily macrophyte production, if it is assumed that total growing period is approximately 30 days would be approximately 1.0 gram per day, which is equal to the daily rate of phytoplankton production on all but the most productive days (at Station 1) and about twice the mean daily rate.

III. DISCUSSION AND CONCLUSIONS

Phytoplankton, macrophytes, periphyton and microscopic benthic algae are the principal primary producers in Lake George, as in most, if not all, lakes. The first two may be equally productive in the southern basin of Lake George during the period of the year when the macrophytes, especially the Nitella beds, are growing rapidly. Short term estimates of Nitella photosynthesis and rate of elongation in situ indicate the intervals of rapid growth to be in June and September. Most of the annual macrophyte production of 34.7 g C/m^2 of lake surface must be synthesized at that time, and the guess is that the growth intensity may be in the range of 0.5 and 1.0 g C/m^2/day. Since the macrophyte beds are under no more than 20 percent of the lake surface, the growth rates in the plant beds must be very high indeed. Certainly, they are likely to be much larger than the daily rate for the phytoplankton in the water column above the beds. At its peak the rate of photosynthesis is no more than 1.2 g C/m^2/day and usually equal or less than 0.6 g C/m^2/day.

Light, nutrients and turbulence were found to be strong influences in the growth environment of the principal species of macrophyte. Rates of photosynthesis in Nitella were dependent on the concentration of phosphate with a maximum response at 2.0 uMoles/liter. Lesser concentrations gave intermediate values. Photosynthesis in the phytoplankton also has been shown to be phosphate limited in Lake George (Stross, 1971). Turbulence is a necessary part of the environment. Without it, rates in Nitella are halved, as shown in this report, or reduced to 1/3 (Adams and Schmidt, 1972) in the Wingra principal, Myriophyllum. Light also acts as a limiting factor to the growth of the principal macrophyte, Nitella, but in an unusual and exciting way.

The one experiment measuring light saturation in Nitella suggested

that saturation intensity is at least 100 ftc and probably closer to 400 ftc. Yet shading cannot explain the depth distribution of the Nitella biomass which is maximum at the lower end of the depth distribution at 12 m where intensities are surely less than 100 ftc.

Two annual trends can be compared as a result of this study. The depth distribution of the Nitella beds is almost exactly like that given 50 years earlier in the Needham-Juday report of Lake George. On a much shorter time scale, the preliminary evidence is that summer time rates of phytoplankton production have increased from 1970 to 1972 possibly by as much as 50 percent. However, the increase may be due entirely to an increase in the August value for P_{max}. The August interval may or may not be the most stable indicator of annual change. Hourly rates are a maximum for the summer at this time. The peak interval is also reasonably narrowly restricted in time to the late July-August interval. Although certainty of its reliability demands that one know the explanation for the August maximum, it would be convenient to chart the annual change in Lake George from a smaller than heretofore series of samples.

In conclusion, the macrophytes in Lake George are potential competitors with the phytoplankton for a limiting supply of phosphate. A mathematic model describing the growth rates of the two may want to force the outcome with both variable concentrations and variable rates of nutrient input. To achieve the necessary reality, the Michaelis constants for uptake of the limiting nutrient, e.g. phosphate will be needed for principal species of phytoplankton and Nitella. Equally important will be the rates of nutrient input for they will determine the standing crop of the phytoplankton and consequently the light environment at the depth of the Nitella beds.

Adams, M. and A. Schmidt, 1972. Annual Report for Primary Production of Macrophytes in Lake Wingra, Madison, Wisconsin.

Fenlon, M.W., 1971. Macrophytes of the southern basin of Lake George. In: Aquatic plants in the southern basin of Lake George. SUNY - ASRC Publ. 149 (June 1971) p. 8-22.

Needham, J.G., C. Juday, E. Moore, C. Sibley and J.W. Titcombe, 1922. A Biological Survey of Lake George, N.Y. Conservation Comm. Special Report, J.B. Lyon Co., Printers, Albany, N.Y. 78 p.

Newhouse, J., M.S. Doty and R.T. Tsuda, 1967. Some diurnal features of a neritic surface plankton population. Limnol. Oceanogr., 12: 207-212.

Ogden, J.C. and S.J. Smith, 1971. Preliminary checklist of the vascular aquatic plants of Lake George, New York. NYS Museum and Science Service, Albany, N.Y., 16 p.

Steemann-Nielsen, E., 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. J. Cons. Explor Mer., 18: 117-140.

Stross, R.G., 1970. Primary productivity of Lake George, New York: A final report of preliminary estimates. Annual Report, pp. 1-50.

Stross, R.G., 1971. Primary productivity in Lake George, New York: It's Estimation and Regulation. Annual Report, Yr. I, IBP-DPB Eastern Deciduous Forest Biome, Memo Report 71-115, pp. 1-46.

Traver, S.W., 1971. Aquatic plant site identification in the southern portion of Lake George. In: Aquatic plants in the southern basin of Lake George, 4 p. SUNY-ASRC Publ. 149 (June 1971).

Wetzel, R.G., 1966. Techniques and problems of primary productivit measurements in higher aquatic plants and periphyton. pp. 249-267. C.R. Goldman, Ed., In: Primary Productivity in Aquatic Environments. Univ. of California Press, Berkeley.

Figure 1. Seasonal trends in light saturated rates of phtosynthesis (P_{max}) at three stations in Lake George. The interval spanned is from July 1969 to September 1972. Station 1 is located two miles north of the south shore at Tea Island. Station 4 is immediately north of the Narrows off French Point (center lake) and Station 7 is several hundred yards off shore of Rogers Rock at the northern end of the 30-mile long lake. Each value is the mean of normally 30 estimates at each station. The measured value were obtained from water samples incubated at 1500 ftc and lake surface temperature of the lake. (See methods for more details).

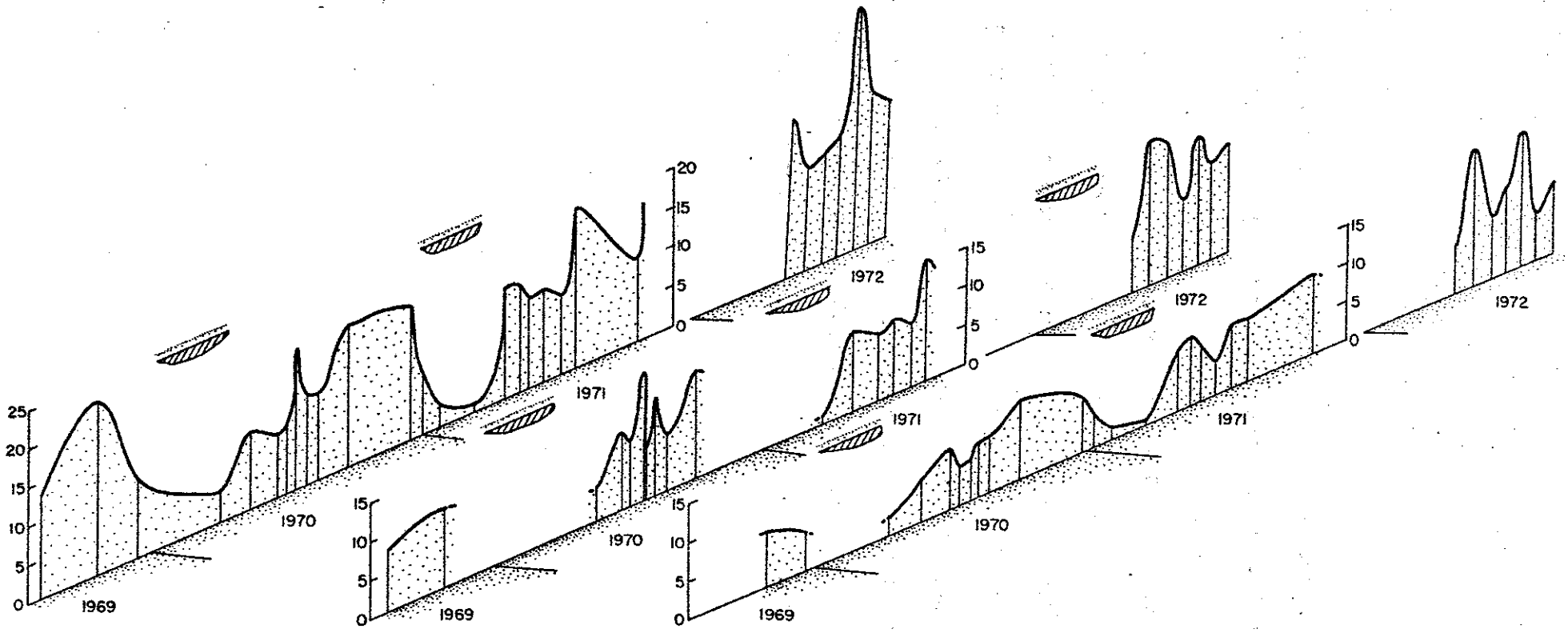

25
20
15
10
5
0
1969
1970
1971
1972
I
15
10
5
0
1969
1970
IV
20
15
10
5
0
1971
1972
15
10
5
0
1969
1970
1971
1972
VI and VII

Figure 2. Summer time estimates for P_{max} at Station 1 in Lake George, New York for the years 1970 through 1972. Each measurement, shown as a vertical line consists of a minimum of 15 estimates (see methods for further details).

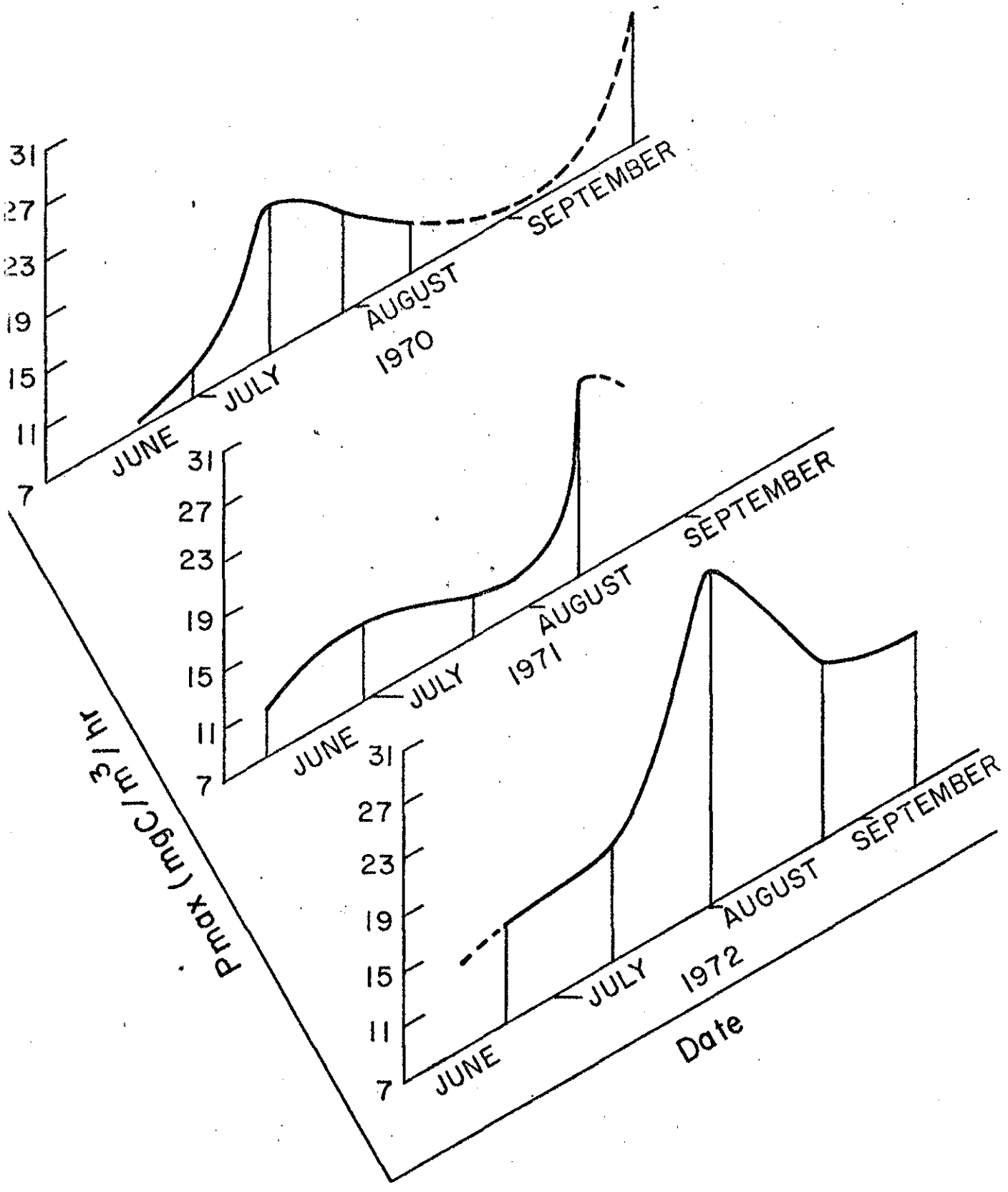

31
27
23
19
15
11
7
JUNE
JULY
AUGUST
SEPTEMBER
1970
1971
1972
Date
pmax (mgC/m³/hr)

Figure 3. Daily rates of phytoplankton photosynthesis for the month of July 1971 at Stations 1 and 7 in Lake George, New York. Also shown is the solar radiation for that month (see Figure 1 legend for location of stations).

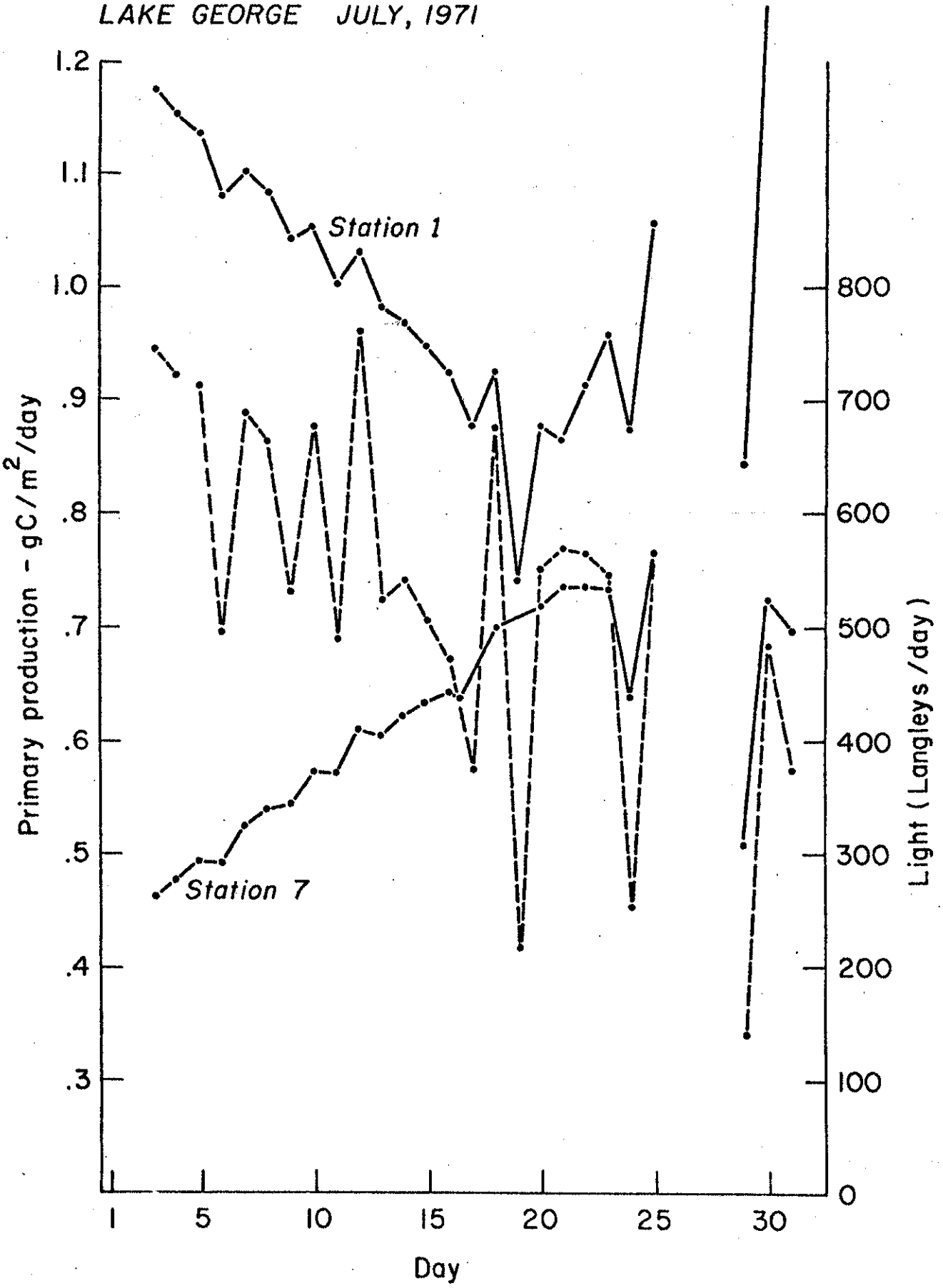

LAKE GEORGE JULY, 1971
Station 1
Station 7
Primary production - gC/m²/day
Light (Langleys/day)
Day
1.2
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
800
700
600
500
400
300
200
100
0
1
5
10
15
20
25
30

Figure 4. Daily rates of phytoplankton photosynthesis for the month of August 1972 at Stations 1 and 7 in Lake George, New York. (Also shown is the solar radiation for the month of August).

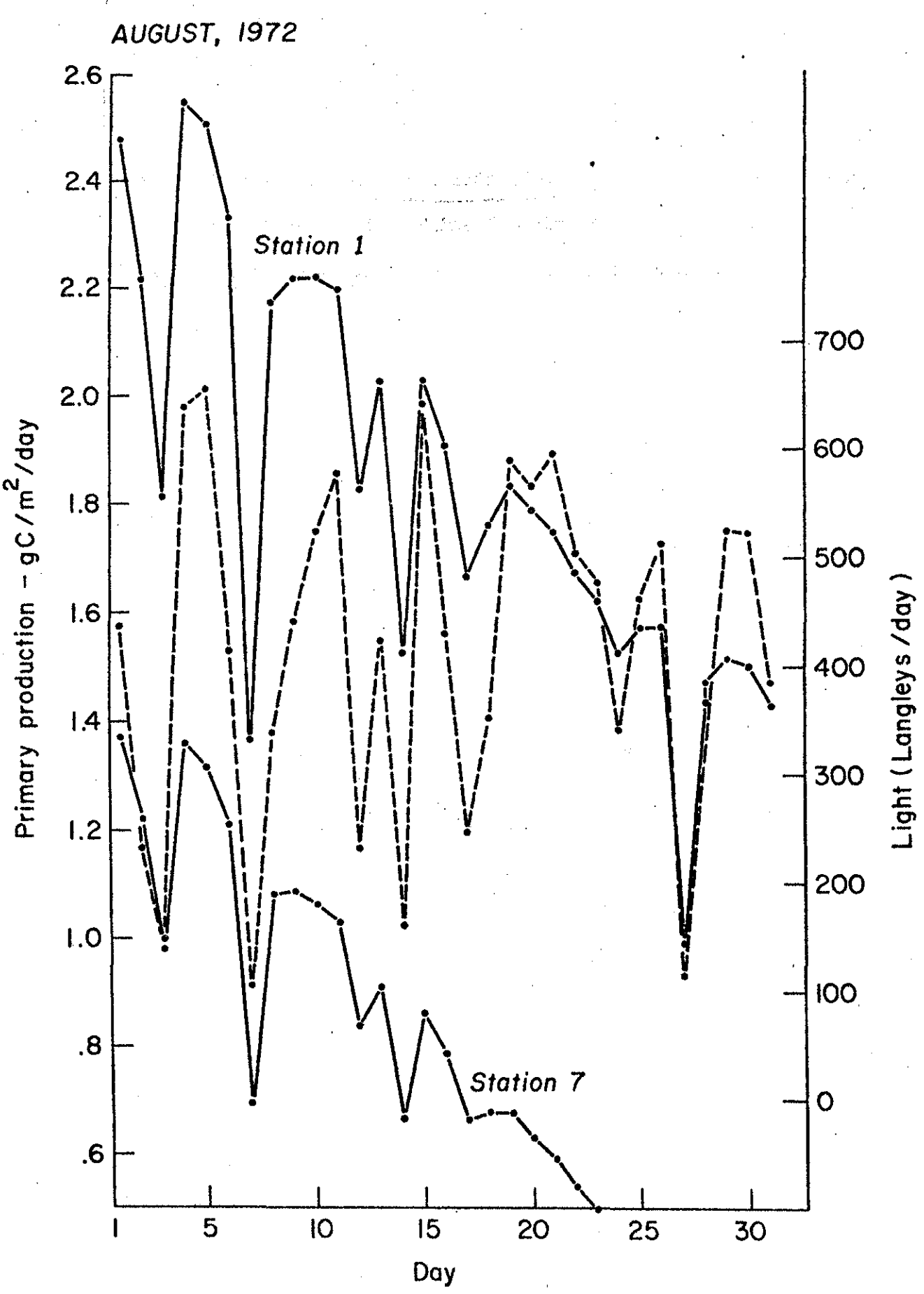

AUGUST, 1972
Station 1
Station 7
Primary production - gC/m²/day
Light (Langleys/day)
Day
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
.8
.6
700
600
500
400
300
200
100
0
1
5
10
15
20
25
30

Figure 5. Mean daily rates of phytoplankton photosynthesis for each month during the interval of July 1970 through August 1972. Data are shown for Stations 1 and 7. The solar radiation data for the interval July 1971 to August 1972 was also employed to calculate daily rates for the interval July 1970 through June 1971. The bimodal pattern in mean daily rates at Station 1 for all summers is probably not the result of employing the same solar data; the lack of bimodality in the rates at Station 7 would argue against that. An alternative postulate is that the bimodality is real and that it results from a predictable set of events that occur annually in the lake.

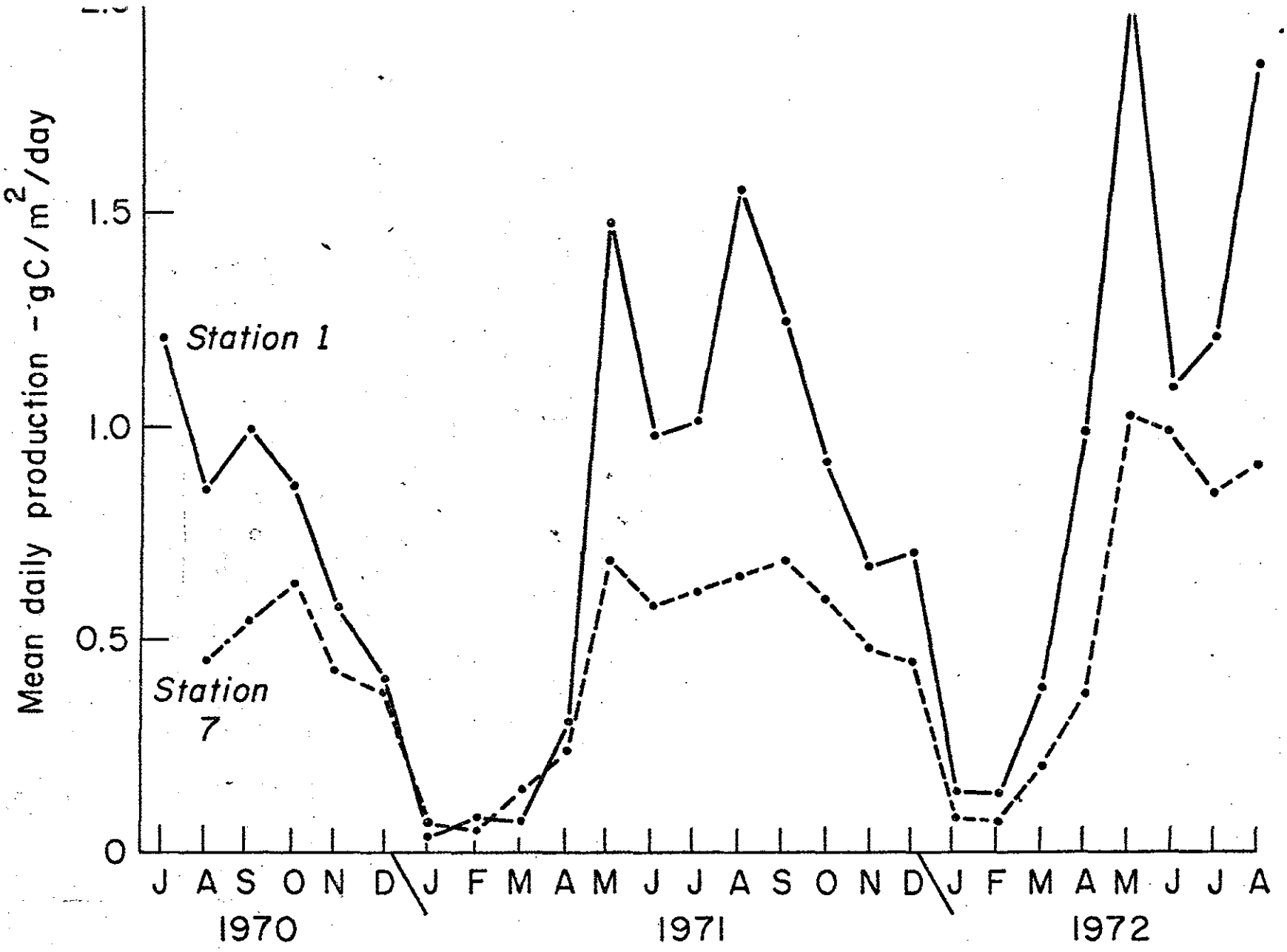

Mean daily production - gC/m²/day
1.5
1.0
0.5
0
Station 1
Station 7
J A S O N D J F M A M J J A S O N D J F M A M J J A
1970
1971
1972

Figure 6. Location of transects in the south basin of Lake George that were employed to measure the density of macrophytes.

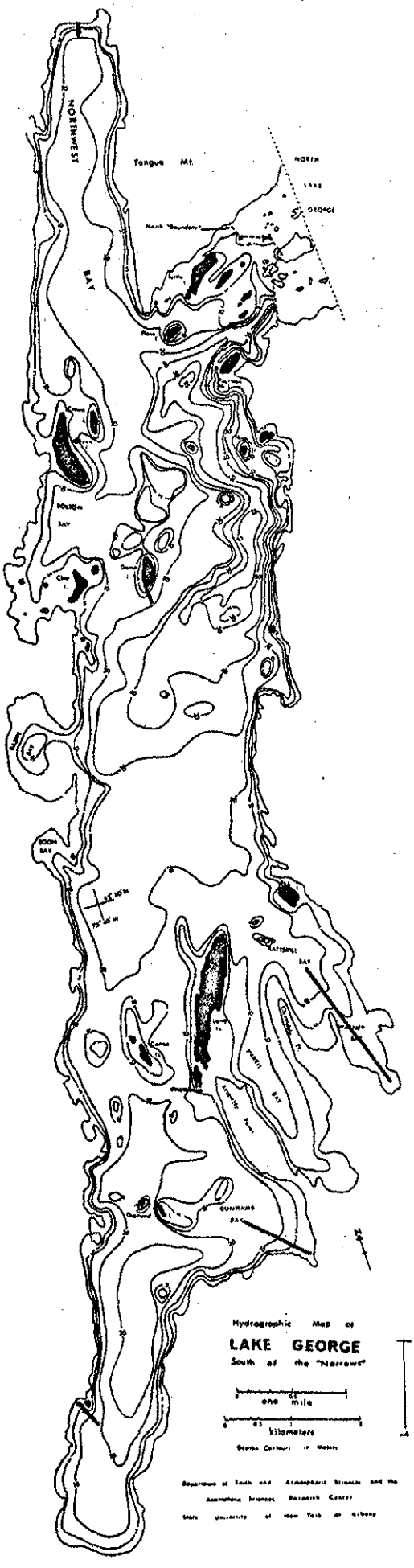

NORTHWEST BAY
Tongue Mt.
NORTH LAKE GEORGE
BOLTON BAY
BOOM BAY
DUNHAMS BAY
Hydrographic Map of
LAKE GEORGE
South of the "Narrows"
one mile
kilometers

Figure 7. Size distribution of old and young plants of Nitella flexilis in Lake George as determined by inspection of samples dredged from 7 and 12 meters depths. The criterion for age of the plant is the presence of light green coloration or otherwise indicated evidence of recent growth.

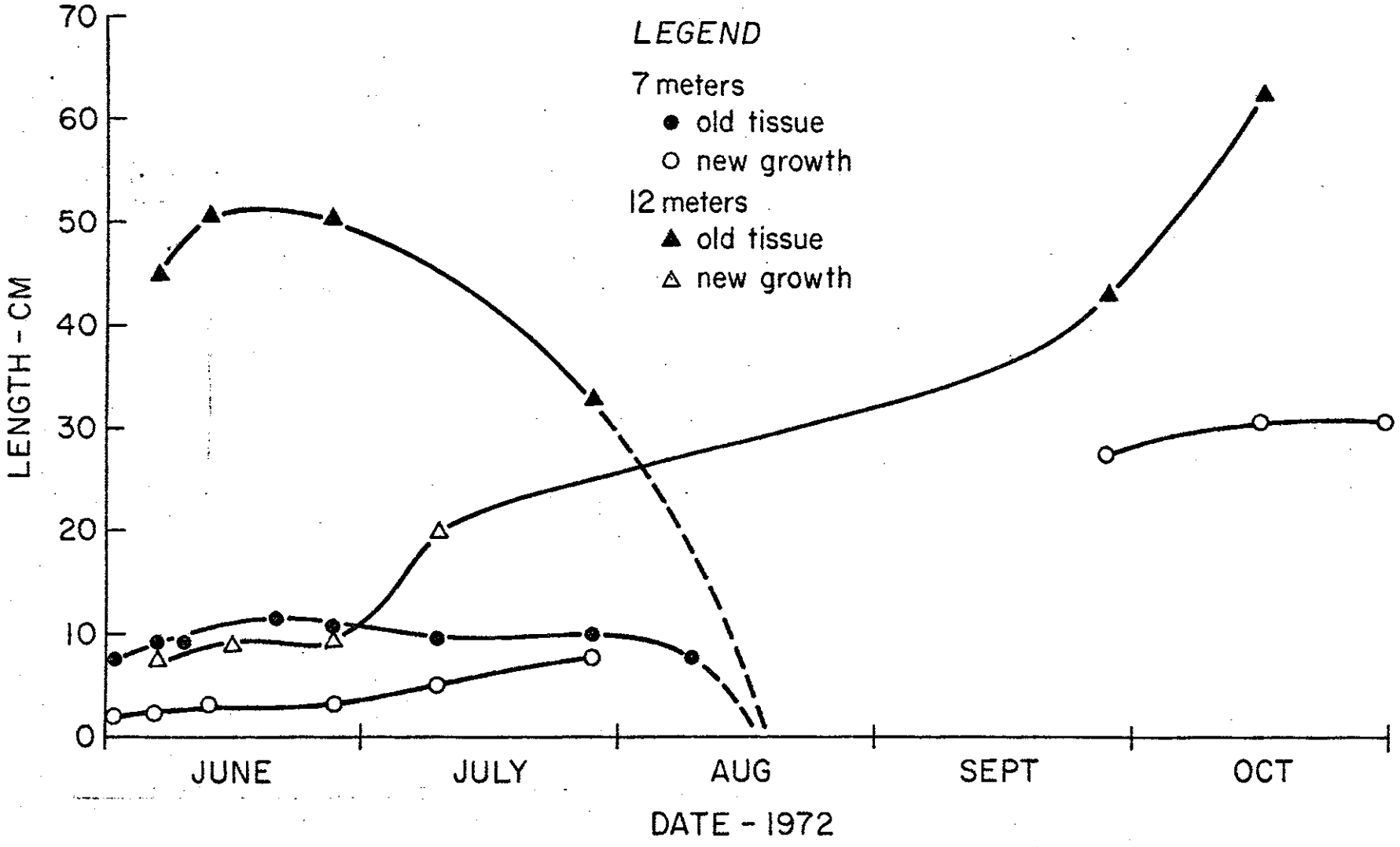

LEGEND
7 meters
old tissue
new growth
12 meters
old tissue
new growth
70
60
50
40
30
20
10
0
LENGTH - CM
JUNE
JULY
AUG
SEPT
OCT
DATE - 1972

Figure 8. Rate of carbon fixation in individual plants of Nitella flexilis in response to agitation at various velocities. Light and temperature are held constant at 500 ftc and 14 ± 2.0°C. The plants were removed from Lake George (Tea Island transect) and transported to the laboratory for the experiments.

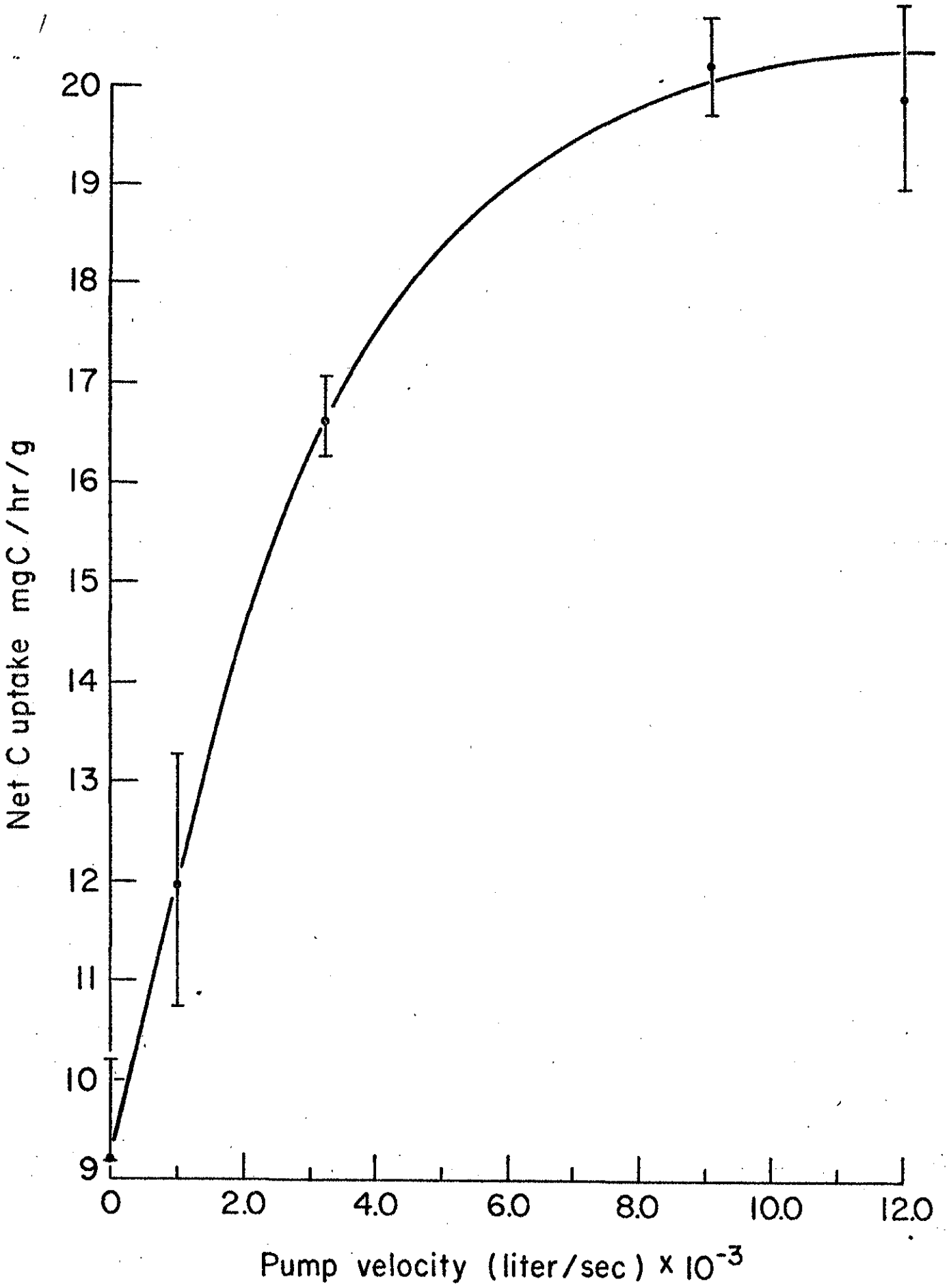
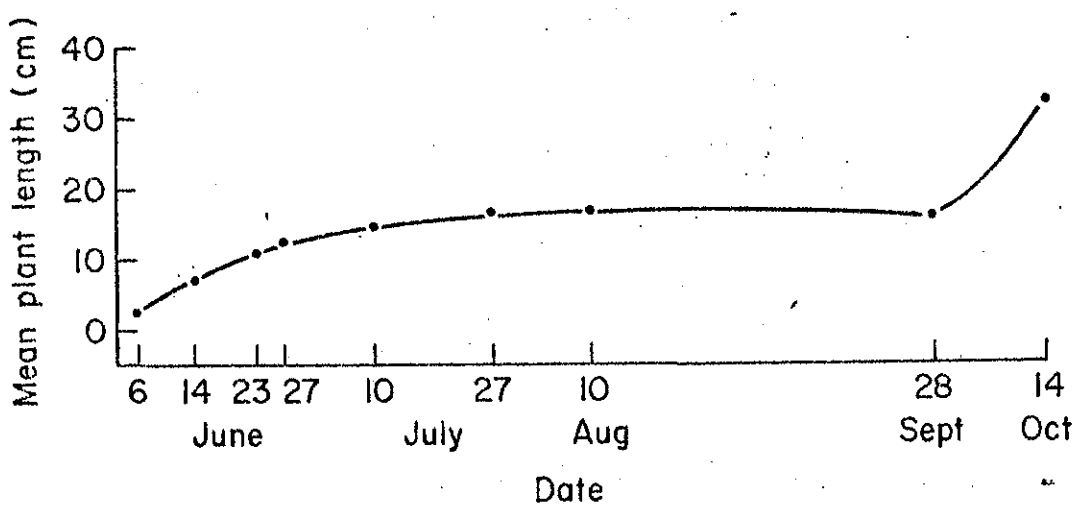

20
19
18
17
16
15
14
13
12
11
10
9
Net C uptake mgC / hr / g
0
2.0
4.0
6.0
8.0
10.0
12.0
Pump velocity (liter/sec) x 10^{-3}

Figure 9. Seasonal trend in hourly rates of photosynthesis by plants of Nitella flexilis when incubated in vitro under a constant environment of light, temperature, and agitation as provided on a rotating drum within a constant light incubator. Compared is the mean length of the plants in samples from Lake George that were collected at the time of the photosynthesis measurements. Collections from a standard station off Tea Island in the southern end of the south basin of Lake George (see Fig. 6 for location).


Mean plant length (cm)
40
30
20
10
0
6
14
23
27
10
27
10
28
14
June
July
Aug
Sept
Oct
Date

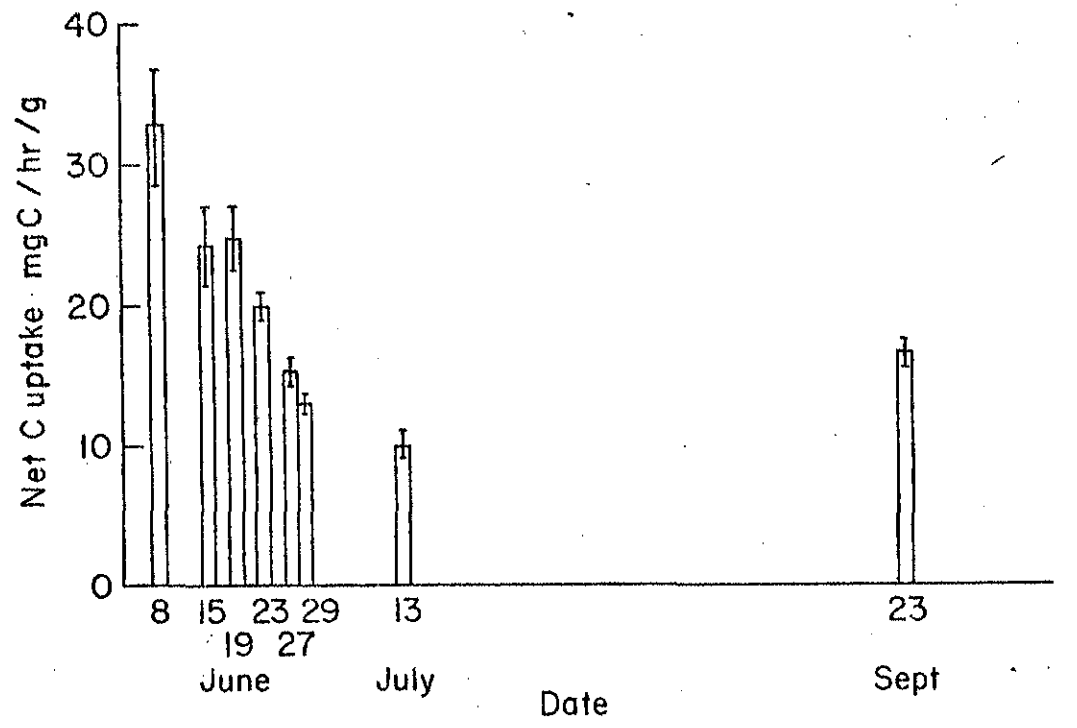

Net C uptake · mgC / hr / g
40
30
20
10
0
8
15
19
23
27
29
13
23
June
July
Sept
Date

Figure 10. Rates of photosynthesis of Nitella flexilis in response to the addition of various concentrations of primary sodium phosphate or sodium nitrate. Experiment carried out on June 19 in incubator at 1500 ftc and 16.5° with standard rate of agitation on the revolving drum (6 rpm/min).

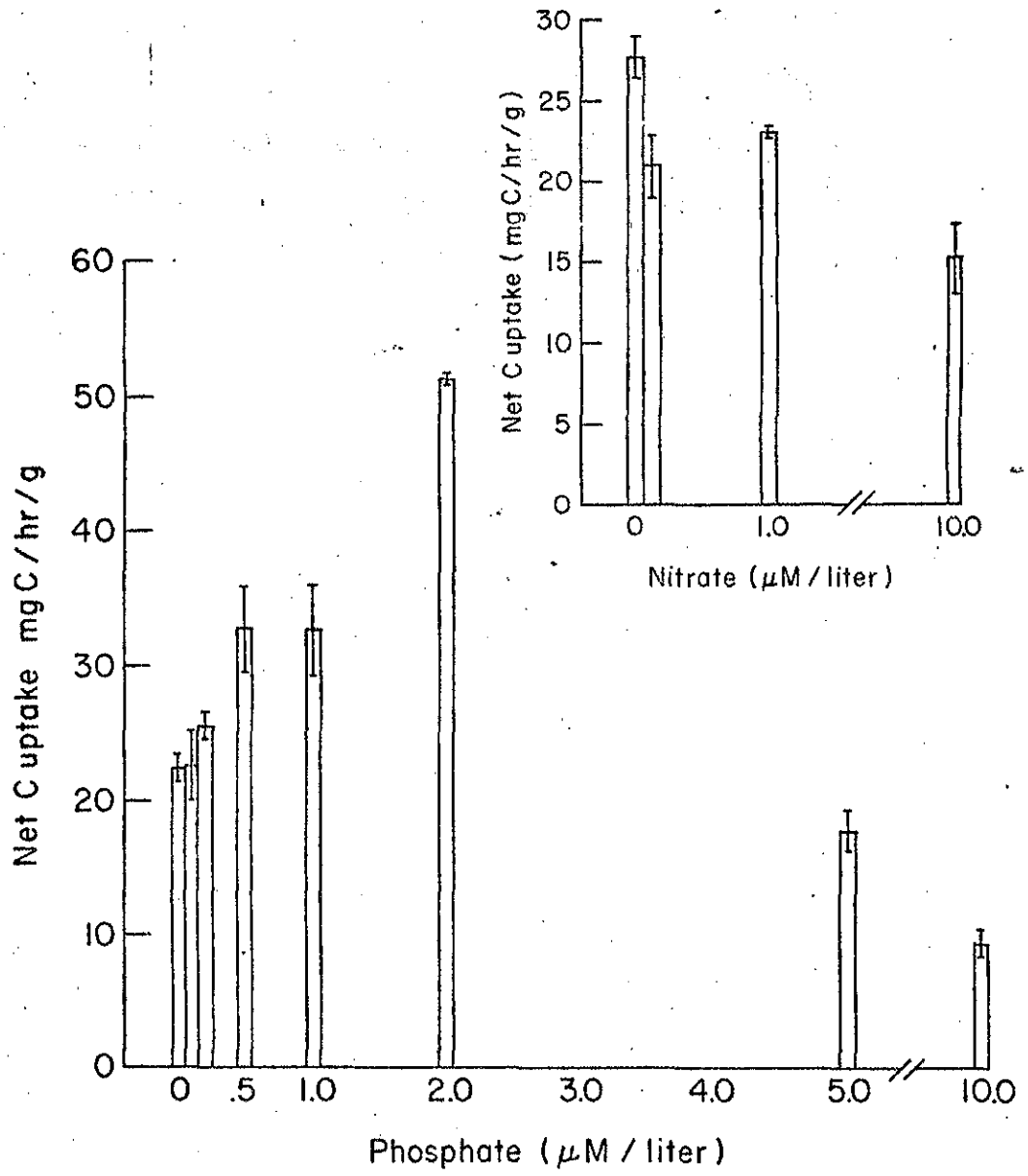

Net C uptake mg C / hr / g
60
50
40
30
20
10
0
0
.5
1.0
2.0
3.0
4.0
5.0
10.0
Phosphate (μM / liter)
Net C uptake (mg C / hr / g)
30
25
20
15
10
5
0
0
1.0
10.0
Nitrate (μM / liter)

Table 1. Macrophyte Standing Crop for transect at Tea Island, Lake George at depths and dates indicated. Samples collected with Ekman dredge, washed and dried at 105°C. Weights expressed as $g/m^2 + 1$ S.E.$_{\bar{y}}$.

	Depth									
Sampling Date	3M	4M	5M	6M	7M	8M	9M	10M	11M	12M
6/6/72	-	-	-	-	22.59 ± 5.76	9.76 ± 1.44	-	-	-	73.62 ± 17.83
7/27/72	-	-	-	-	10.91 ± 3.45	33.68 ± 5.74	-	-	-	117.16 ± 28.34
8/10/72	-	-	-	-	23.27 ± 5.37	42.54 ± 14.68	-	-	-	98.56 ± 21.58
9/8/72	122.63 ± 27.08	163.00 ± 34.37	165.77 ± 46.97	144.98 ± 18.15	79.65 ± 3.96	18.77 ± 4.70	- -	- -	- -	113.30 ± 12.69

Table 2. Macrophyte Standing Crop on various transects of bottom for the Southern Basin of Lake George during September 1972 for the depths and locations indicated. Values as g (dry wt)/m^2 + S.E.$_{\bar{y}}$.

Location	Depth (Measurements in g dry tissue/m^2 + S.E.)									
	3M	4M	5M	6M	7M	8M	9M	10M	11M	12M
Tea Island Bay	122.6 + 27.08	163.0 + 34.4	165.8 + 47.0	145.0 + 18.20	79.6 + 4.0	18.8 + 4.7	-	-	-	113.3 + 12.70
Dunham Bay	126.7 + 116.3	57.6 + 45.5	6.08 + 5.90	76.9 + 15.4	19.6 + 5.10	0.3 + 0.3	-	168.6 + 17.7	-	-
Warner Bay	127.6 + 40.4	177.9 + 16.8	5.0 + 4.8	23.9 + 0.9	64.2 + 38.8	164.9 + 3.7	-	175.0 + 3.	-	205.6 + 58.7
Dome Island	-	18.2 + 9.9	11.6 + 10.4	6.9 + 4.	23.0 + 5.0	180.4 + 12.6	76.9 + 16.6	55.4 + 4.4	20.2 + 5.8	-
Northwest Bay	13.7 + 12.2	58.8 + 32.9	8.4 + 8.1	10.7 + 1.4	144.3 + 54.7	-	1.8 + 0.8	-	86.5 + 26.2	69.6 + 9.8
Mean	97.6 + 28.0	95.1 + 31.8	39.4 + 31.6	33.6 + 22.4	62.4 + 19.0	82.5 + 37.6	39.4 + 37.5	133.0 + 39.3	53.4 + 34.4	106.0 + 36.9

Table 3. Annual production of Nitella flexilis and other macrophytes in the south basin of Lake George, New York for the year 1972. All measurements are in grams (dry wt.)/m^2 ± Standard Error.

Depth (meters)	Nitella flexilis June	Nitella flexilis Sept.	Other Species Sept.	Annual Production
3.0	-	-	97.65 ± 28.0	97.65 ± 28.0
4.0	-	-	95.10 ± 31.8	95.10 ± 31.8
5.0	-	-	39.38 ± 31.6	39.38 ± 31.6
6.0	-	43.79 ± 10.1	42.42 ± 15.9	130.00 ± 26.0
7.0	16.41 ± 2.3	53.68 ± 19.8	32.95 ± 18.1	103.04 ± 40.2
8.0	30.42 ± 7.9	73.48 ± 31.5	3.67 ± 3.5	107.57 ± 42.9
9.0	44.06 ± 5.1	76.93 ± 16.55	-	120.99 ± 21.6
10.0	57.69 ± 5.0	133.00 ± 39.3	-	190.69 ± 43.3
11.0	57.83 ± 5.1	53.39 ± 34.4	-	111.22 ± 39.5
12.0	57.91 ± 5.2	105.96 ± 36.9	-	163.93 ± 43.1

Table 4. Annual production of macrophytes within the 3 to 12-meter contour limits. Rates expressed as grams (dry wt.)/m^2/yr. ± Standard Error.

Depth (meters)	Annual Rate/m^2	Surface area (mi^2)	Production g x 10^6/contour
3.0	97.65 ± 28.0	0.95	233.16
4.0	95.10 ± 31.8	0.70	167.31
5.0	39.38 ± 31.6	0.80	79.18
6.0	130.00 ± 26.0	0.80	261.39
7.0	103.04 ± 40.2	0.75	194.23
8.0	107.57 ± 42.9	0.80	216.29
9.0	120.99 ± 21.65	0.80	243.27
10.0	190.69 ± 43.3	0.75	359.45
11.0	111.22 ± 39.5	0.80	223.63
12.0	163.93 ± 43.1	0.75	309.01
		TOTAL:	2,286.92

Table 5. Light intensity and rate of carbon assimilation in Nitella flexilis from Lake George, New York. Samples incubated with C-14 for 2.0 hours on rotating drum incubator at light intensities indicated. Light source was fluorescent strips (cool white and daylight).

Light Intensity (ftc)	mg C/g (dry wt.)/hr. $\bar{x} \pm SE_{\bar{x}}$	
14.0	3.8	1.9
100	46.4*	11.8
200	33.0	5.2
400	60.5	9.1
1000	6.3**	1.1

*Two means are pooled at 100 ftc. Omitting two of five estimates, the mean is 27.9 ± 2.0.

**I doubt this. These values were obtained on June 12, 1972 during which time the seasonal rates as measured at 1500 ftc were giving values of 25 mg C or more.

Appendix I. Macrophytes in the 3 one of 3 to 6 meters in Lake George, New York as determined from dredge sampling in September, 1972. Values are in g (dry wt.)/m^2.

DEPTH (All measurements are in grams dry tissue/meter^2 bottom area ± 95% comb. 1 m.)

Location	Date	Species	3M	4M	5M	6M	7M	8M	9M	10M	11M	12M
Tea Is. Bay	9/8/72	Nitella flexilis	0	0	0	0	78.15 ± 7.51	18.77 ± 14.10				
		Potamogeton Robinsii	64.67 ± 50.44	26.59 ± 6.57	135.74 ± 160.62							
		Valisneria americana	57.94 ± 30.75	131.14 ± 82.94	4.37 ± 6.48							
		Elodea canadensis	.02 ± .06	0.22 ± .63			1.51 ± 4.37					
		Potamogeton praelangus		5.05 ± 14.64								
		Najas flexilis			25.46 ± 73.82							
		Isoetes macrospora				144.99 ± 54.44						
	9/1/72	Nitella flexilis					13.7302 ± 25.86	32.5035 ± 13.84				113.3046 ± 38.07
Dunham Bay	9/8/72	Ranunculus longirostris	.85 ± 2.46									
		Potamogeton bercholdii	1.23 ± 3.56									
		Valisneria americana	22.18 ± 54.99	53.60 ± 124.91								

Location	Date	Species	3M	4M	5M	6M	7M	8M	9M	10M	11M	12M
		Potamogeton Robinsii	102.42 ± 288.35	4.03 ± 11.70	6.08 ± 17.65							
		Nitella flexilis				76.87 ± 46.27	19.65 ± 15.39	.29 ± .82		168.58 ± 53.07		
Warner Bay	9/8/72	Potamogeton amplifolius	54.51 ± 103.46									
		Valisneria americana	73.04 ± 17.74	3.85 ± 11.16	4.37 ± 12.67							
		Elodea canadensis		.51 ± 1.50								
		Potamogeton longirostris		1.04 ± 3.01								
		Potamogeton praelangus		6.92 ± 20.07								
		Potamogeton Robinsii		5.41 ± 15.70		23.89 ± 2.73	64.16 ± 116.38					
		Najas flexilis			.68 ± 1.97							
		Nitella flexilis						164.90 ± 11.11		174.97 ± 9.59		205.57 ± 176.16
Dome Island	9/16/72	Valisneria americana		18.20 ± 29.77	11.60 ± 31.29	6.89 ± 12.50						
		Nitella flexilis					23.05 ± 15.10	180.43 ± 37.70	76.93 ± 49.74	55.44 ± 13.25	20.24 ± 17.55	

Location	Date	Species	3M	4M	5M	6M	7M	8M	9M	10M	11M	12M
Northwest Bay	9/21/72	Chara globularis	.10 ± .29									
		Isoetes macrospora	1.63 ± 1.95	.01 ± .04								
		Potamogeton Robinsii	.28 ± .81	38.64 ± 58.33	8.38 ± 24.31							
		Nitella flexilis				10.71 ± 4.15	144.32 ± 164.17	0.00 ± 0.00	1.85 ± 2.54	0.00 ± 0.00	86.53 ± 78.59	69.63 ± 29.51
		Potamogeton perfoliatus	11.72 ± 33.99									
		Valisneria americana		20.12 ± 40.38								
Tea Is. Bay (did not dredge entire depth range)	9/28/72	Nitella flexilis				2.10 ± 6.09	43.15 ± 38.23	43.99 ± 28.12				35.34 ± 31.01
		Isoetes macrospora				29.42 ± 42.82						
		Cladophora				7.00 ± 20.29						
		Najas flexilis					.23 ± .67					
		Chara globularis						3.67 ± 10.63				