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PHYTOPLANKTON PRODUCTIVITY AND RESPONSE TO ALTERED NUTRIENT CONTENT IN LAKES OF CONTRASTING TROPHIC STATE

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ABSTRACT

Lakes Findley, Chester Morse and Sammamish, Washington, are characterized by one major outburst of phytoplankton productivity and biomass (mainly diatoms) with usually no or low fall activity. Vernal outbursts were often delayed in some lakes and years probably by unfavorable climate (snow cover and cloudy-rainy conditions). Mean spring-summer productivity ranged from 270 mgC/m² day in the most oligotrophic lake, Findley, to nearly 1000 mgC/m² day in mesotrophic-eutrophic Lake Sammamish. The range in mean Chlorophyll α content was 0.8 to 10 μ g/l for the same lakes respectively. Mean biomass within and between the lakes was related to winter phosphorus content but not to nitrogen. However, nitrogen (N) and phosphorus (P) were simultaneously limiting productivity increase in the three lakes in summer. Carbon assimilation in response to added P showed increasing half-saturation constants for the natural phytoplankton progressing from oligotrophy to eutrophy.

While diversion of over 1/2 the phosphorus from nearby Lake Washington during 1963-1967 was followed by reduction in winter mean P content and a rapid shift from eutrophy to mesotrophy (Edmondson 1970), mean winter P content and measured characteristics of plankton response have not changed significantly in Lake Sammamish following a diversion of similar magnitude. P availability in the water column (winter mean content) appears to be controlled by precipitation with Fe to a greater extent than in Lake Washington.

INTRODUCTION

The need to understand aquatic ecological processes in order to predict the impact of man's activity is rapidly increasing. To a large extent, this is a result of accelerated regional planning for water resource use. An area of major concern in this planning is the impact of man's activity through the cultural eutrophication of aquatic ecosystems, particularly lakes since standing water usually responds slower to corrective action than does running water. The eutrophication process, to be sure, is poorly understood in general quantitative sense. Some lakes seem to respond to nutrient manipulation as expected while others show little or no response. To be useful for management and water resource planning, predictive models of nutrient cycling and biomass change must meet the criteria of generality by containing the modifications that account for the important differing characteristics among lakes and consequently their different behavior.

To accomplish the goal of general models that are useful to the management of man's water resources first requires the development of basic functions that compose the model. The lack of such functions that define the important processes may explain the reluctance of many to accept models as useful management tools. Cultural eutrophication is caused by an increase in external nutrient supply and most of the undesirable effects are a result of the extent to which phytoplankton utilize that increased nutrient supply. The research covered here will hopefully provide the important functions defining phytoplankton dynamics which will result in a general predictive model for the timing and magnitude of phytoplankton biomass in the Cedar River drainage lakes of differing characteristics, in particular, nutrient supply.

This report summarizes past work that has three general aims; 1) to define the seasonal patterns of phytoplankton productivity, biomass, species composition and nutrient content in Findley and Chester Morse Lakes and Lake Sammamish (Cedar River drainage), Washington, for the purpose of providing general understanding of the systems as well as process and validation data for phytoplankton biomass and growth rate models; 2) to determine the limiting nutrients and define the relationships between phytoplankton growth and nutrient assimilation rates in the three lakes and the seasonal generality of such relationships and 3) to define the relationship between external nutrient supply and various trophic status indicators, particularly plankton biomass and productivity, and the rate at which such indicators may change as a result of altering the external nutrient supply.

Findley Lake has been sampled for one year and Chester Morse Lake for two and although analyses are incomplete much of the resulting data are illustrated here. Experimental procedures for defining relationships of growth and nutrient assimilation rate with nutrient content have been worked out and example data are presented here. But again full evaluation is not possible at this time because sample analysis is incomplete. Lake Sammamish has been sampled for three years following the diversion in 1968 of sewage and dairy wastes from Issaquah, Washington. The lake was sampled by Seattle Metro during the pre-diversion years 1964-65 and those data are compared with data from 1970-72 to determine if trophic status of the lake has changed.

For the purposes outlined, a minimum of three years data from each lake is considered necessary and four years desirable because annual variations of two fold have been observed. Variation among lakes has not been proportional so productivity rates have overlapped between oligotrophic and mesotrophic-eutrophic lakes. Thus, four years data are desirable for realistic mean values for variables. Because recovery of Lake Sammamish has been so slow, processes should be monitored there for at least three more years.

MATERIALS AND METHODS

Sampling

The three lakes were sampled at least twice monthly during the spring and monthly during summer and fall. Winter sampling was less frequent since biomass and productivity of phytoplankton is lowest at that time. In some instances sampling was more frequent than described. Lake Sammamish has been sampled from 1964-65 by Seattle METRO and from 1970 to 1972 by us. Chester Morse was sampled in 1971 and 1972 and Findley only in 1972.

Water was collected from the most centralized and deepest location in each lake at about six depths through the water column. Judging from results from as many as five stations sampled for a year in Lake Sammamish, one station (612) was ultimately considered adequate to represent pelagic conditions in the lakes. Four sampling depths in the photic zone conformed to 95, 60, 25 and 1 percent of incident light intensity for purposes of *in situ* measurement of productivity. The remaining two depths were located at the top and bottom of the hypolimnion.

Oxygen and temperature were measured at frequent depth intervals in the water column with a polarographic electrode and thermistor (Yellow Springs Instruments). These results were occasionally compared to measurements using the wet chemical method (Winkler) for oxygen.

Nutrient supply to Lake Sammamish from surface waters was estimated by monthly sample collection and flow measurements from 2 major and 11 minor tributary streams entering the lake (Figure 1). Ammonia and organic nitrogen results are still incomplete so the nitrogen budget includes only nitrate and is thus tentative.

Analyses

Primary productivity was determined *in situ* according to procedures described by Goldman (1961). Water samples inoculated with ^{14}C were incubated at four depths for four hours and the results reported as integrated productivity in the photic zone extrapolated to daily rates assuming a 1:1 relationship with incident light. Productivity of three size groups of organisms was determined by filtration of the samples through 50μ (net plankton), 5μ (nano plankton) and 0.5μ (ultra plankton).

Methods of Strickland and Parsons (1968) were followed for N, P, and Chlorophyll *a* (Chl *a*) analyses in water. Total and ortho-phosphate phosphorus were determined spectrophotometrically as a phosphomolybdate complex. Reactive silicate was also determined from a silico-molybdate complex. Nitrate and nitrite were determined spectrophotometrically following reduction in a cadmium-copper filled column and are reported together as $\text{NO}_3\text{-N}$. Chl *a* was determined with a Turner Model 110

fluorometer. All chemical analyses except for total P were performed on filtered (0.45 μ poresize) water samples. These concentrations are reported as weighted means in the photic zone.

Experiments in situ

Bioassays to determine the limiting nutrient(s) were conducted in Lake Sammamish in large (0.21 m² x 5 m) plastic cylinders submerged in the lake for seven days. N, P, C and Si were added to experimental bags separately and in combination. Phytoplankton response was determined by daily measurements of productivity and Chl *a* concentration. Significance of response was judged from results of analysis of variance using a factorial design and Dunnett's test at the 95% level of confidence.

Experiments in vitro

Experiments with lake water and natural phytoplankton were conducted in flasks in the laboratory to determine; 1) which nutrients were limiting growth, and 2) the growth rate (and assimilation rate)--limiting nutrient concentration relationship. Three experiments were conducted in water from Chester Morse Lake, two from Findley Lake and one each from Lakes Sammamish and Washington. Each of the assimilation rate experiments included the measurement of 10 variables in 30 assay flasks every two days for a period of about two weeks. Following determination of the limiting nutrient ten flasks were set up at each of three light levels (4000, 2000 and 100 lux). Experiments were set up as soon as possible after collection of the lake water. Protection of the phytoplankton from direct sunlight was found to be important so water was transported in opaque containers. This prevented reduced photosynthetic rates for the first three days as was observed when clear containers were used. The nutrients NO₃, PO₄, Si, C and a complete medium were added to determine the limiting nutrient. Constant amounts of NO₃ and varying amounts of PO₄ were added in the subsequent nutrient assimilation, growth rate studies to determine the response to PO₄ only. PO₄ was varied from 0-10 μ g/l in Chester Morse and Findley Lakes and 0-40 μ g/l in Lakes Sammamish and Washington. Among other variables measured, ¹⁴C assimilation (conducted on separate subsamples), Chlorophyll *a*, nitrate, ammonia, phosphate, inorganic carbon and particulate carbon were determined. Samples were also preserved to inspect for changes in species dominance.

Analyses are incomplete at the time of this writing so example results from only three experiments will be presented and only nutrient content based on amount added can be used. Because of the large number of analyses necessary the phytoplankton were fractionated into three size groups only for the Lake Washington experiment.

Two additional experiments were conducted with Lake Sammamish water only to study the interaction of NO₃ and PO₄ additions on the growth rate and nutrient assimilation rates of the natural phytoplankton. In this experiment,

the response to three separate additions was tested; 75 μ g/l NO₃-N, 250 μ g/l PO₄-P and both additions combined. The ¹⁴C and nutrient assimilation rates were then determined.

RESULTS AND DISCUSSION

Productivity - Nutrients

Findley Lake. The seasonal patterns of phytoplankton productivity and biomass change in Findley Lake is regulated to a large extent by snow and ice cover. After melt off in late June and early July a rapid increase in productivity (780mgC/m² day) occurs to be followed by a biomass increase (2 μ g/l Chl *a*). As shown in Figure 2, the growing season as far as primary productivity is concerned is probably restricted to July and August. This means that annual primary production in this lake is very low compared to the other lakes in the drainage.

Ortho phosphate (PO₄-P) concentrations ranged from 2-4 μ g/l during the study period and total phosphorus (P-tot) from 5 to 10 μ g/l (Figure 3). PO₄-P did not appear to be depleted below pre-melt levels as a result of phytoplankton activity. Nitrate (NO₃-N) on the other hand reached a peak of 42 μ g/l before snow melt and then declined to 6 μ g/l in inverse relation to phytoplankton activity. The loss of 36 μ g/l of NO₃-N without a proportionate loss in PO₄-P according to a ratio of 7-10/1 is surprising. This implies that PO₄-P is being constantly supplied from elsewhere. On the other hand data on ammonia may show larger amounts of this N form appearing as NO₃ declines, which would suggest levels are adjusted to the ratio in cells by recycling. Ammonia analyses are incomplete at present.

A nutrient limitation experiment *in vitro* with Findley Lake phytoplankton (8 August) suggests that the ratio of available N:P is adjusted to that required by growing cells. The addition of N and P together provided the greatest productivity (¹⁴C assimilation). Productivity as a measure of response is actually a product of growth rate and biomass. In this manner the week long test is an indicator of "long term" response to raised nutrient supply and allows time for adaptation of the plankton community. Thus, the nutrient that not only limits growth rate at sample time, but also would become most limiting to ultimate biomass increase and productivity is determined. Even though NO₃-N reached 6 μ g/l and PO₄-P reached a previous low of 2 μ g/l, resulting in a ratio of N:P probably much lower than required by cells, suggesting that N was limiting, the experiment demonstrated that both nutrients were limiting to further growth. Carbon and silicon showed much reduced stimulation and a complete media including trace elements equaled the response by N and P.

In Findley Lake the thermocline occurred between 3 and 6 meters. The lowest oxygen concentration was 6.9 mg/l at 25 m on 8 September. The photic zone depth was greatest of all three lakes--extending to the bottom 27 m.

Chester Morse Lake. The seasonal cycle of phytoplankton productivity and biomass in Chester Morse Lake is typical of other monomictic lakes in the drainage having one large peak and a much smaller fall peak (Figure 4). The large peak is shifted more into the summer in Chester Morse--by as much as two months--compared to the Lakes Sammamish and Washington. The productivity peak in 1971 is about twice that in 1972 and even though the peak does not come until June or July, there is still considerable activity present in April and May. These two points probably indicate an effect of light--more total radiation in 1971 than 1972 and a scarcity of consecutive sunny days since Chester Morse is located in the mountains and higher rainfall area than the lower lakes--Sammamish and Washington. Test of the validity of this supposition must await the installation of insolation recorders at Lakes Sammamish and Chester Morse, which is planned.

The delayed productivity peaks until July is probably not caused by a lack of macronutrients since concentrations of NO_3 and PO_4 are no greater during June and July 1971, when productivity reached $1400 \text{ mgC/m}^2 \text{ day}$ than during March to May 1972, when productivity only reached $200 \text{ mgC/m}^2 \text{ day}$ (Figure 5). In spite of the June-July productivity peak in 1972, biomass reached the highest level in April--about $1.5 \mu\text{g/l}$. The subsequent increased productivity without an accompanying increase in biomass may suggest that biomass increase is limited by a low nutrient supply, but that nutrient regeneration by grazing zooplankton is supplying nutrients to sustain high photosynthetic rates. On the other hand, the low nutrient content during June and July 1971 (following onset of thermal stratification in mid-May) gives little hint as to where the nutrient supply came from to produce the large biomass of phytoplankton ($9.5 \mu\text{g/l Chl } a$) resulting from the high rates of productivity.

In any case, alteration of the rates of productivity that can be observed seasonally in Chester Morse Lake must be largely related to light intensity. The small changes in nutrient content during the periods just preceding peak productivity could hardly be expected to cause those peaks through changed plankton growth rates. However, only nutrient content is known, which is simply the residual difference between uptake and supply, and is hardly indicative of nutrient supply. Until more is known of the nutrient supply rates as a function of vertical mixing rates and vertical zooplankton migrations and nutrient regeneration, little can be concluded accurately as to the cause for these detailed seasonal changes in phytoplankton activity.

As was the case in Findley Lake, greatly increased levels of biomass and productivity in Chester Morse Lake on 15 June and 5 September 1972 was limited by both N and P. Some previous experiments indicated that P added above gave as much stimulation as any other combination of N, Si, C and complete media. However, these 1972 experiments show that during the period of minimum nutrient content in Chester Morse, all other nutrients except N and P are adequate to produce a much larger biomass and productivity.

The thermocline in Chester Morse is established in late May, breaks up in mid November and occurs between 5 and 7 meters. The lowest oxygen content was 5.8mg/l observed at 30 m on 13 October 1972.

Lake Sammamish. The seasonal cycle of biomass in Lake Sammamish does not appear greatly different from that of Chester Morse Lake in that there is only one large peak although the fall peak may be a little more developed in Lake Sammamish (Figure 6). The point of most interest is that during two years (1965 and 1971) the outburst of diatoms came in April, two months earlier than in Chester Morse. The other two years (1970 and 1972) the increase in biomass was more gradual and the peak was not reached until June. Even though the April outbursts resulted in twice the biomass maximum as the later peaks, total productivity was much less during an outburst year than in the year of late maximum (Figure 7).

Of interest also, is the high levels of productivity in October even though biomass is low. This could well be related to a high grazing rate that prevents accumulation of phytoplankton biomass. Further sample analysis, particularly of the zooplankton should allow evaluation of such dynamic factors.

The early spring outbursts seem to be related to available light as determined by mixing depth. The two years when early outbursts occurred, 1965 and 1971, were also characterized by thermal stratification of the upper waters setting in at about the same time. Figure 8 shows that stratification in the upper 5 m occurred in April in 1971, but similar stratification occurred in April coincident with the diatom outburst. The importance of this early, shallow, stratification is that of increasing the average light intensity available to mixed plankton cells. This was evident during a sampling trip in early April 1971 when Chl *a* content at the surface was 30µg/l and NO₃-N had been reduced to undetectable levels. This was possible because of a 2°C temperature increase in the upper couple of meters. Stratification was probably broken up at night because water at 20 m was super saturated with oxygen--the only way water at that depth could gain so much oxygen is by photosynthesis in the lighted zone and then be mixed down to that depth when the water column is destratified.

Nutrient content (Figure 9 and 10) decreased during the spring outburst period, except for total P in 1970. For the latter there is no explanation. Nitrate in particular was found to decrease inversely to phytoplankton biomass. Only total P is shown in Figure 10 because ortho P was not determined by Seattle Metro in 1965. If ortho P depletion is compared with NO₃-N depletion during 1970-71, N and P were depleted in a rate ratio of 60/1. This suggests that to supply the ratio required by cells, 7-10/1, considerable regeneration of P must have occurred during the spring.

Although the N:P ratio drops slightly below 7/1 at times in the summer, and N would be expected to limit growth, both *in situ* experiments in large plastic bags and *in vitro* experiments have shown that N and P simultaneously limit further increase in biomass and productivity. Results of the *in situ* experiments are shown in Figure 11. Thus, even though the N:P ratio suggests that N limits, there is so little P around (1-2 μ g/l), that in order to utilize the added N more P is required.

In contrast to the other two lakes, the Lake Sammamish hypolimnion loses nearly all of its oxygen during the stratified period (Figure 12). Although the productivity is not that much greater than in the other lakes, the volume of the hypolimnion (and available oxygen) relative to the lake surface area (and potential organic matter) is much less.

Comparison of Lakes. Table 1 shows that Findley and Chester Morse Lakes are very similar in winter nutrient content (which should indicate supply for summer growth), productivity and biomass. Lake Sammamish contains about twice the productivity, biomass and P content as the other two lakes. Nitrate is more like ten times greater in Sammamish. Also there seems to be annual variations in productivity and biomass within the lakes of two times. Because of the greater photic zone depth in Chester Morse Lake and particularly Findley Lake, areal productivity is much greater than might be expected from the mean photic zone nutrient content and biomass.

Effects of Nutrient Income Change

Sewage was diverted from Lake Washington during 1963-67 and from Lake Sammamish in 1968, by the Municipality of Metropolitan Seattle. The diversion removed about 55 percent of the annual external P supply and 12 percent of the inorganic N from Lake Washington. P and N external supply into Lake Sammamish was reduced by about 46 and 22 percent, respectively (Table 2). The N and P supplies to Lake Washington are not greatly different than those to Lake Sammamish. Initial estimates (Welch and Spyridakis 1972) suggested that Lake Washington received about twice the supply of P as Lake Sammamish before diversion and that such a difference was still maintained after diversion. The most recent estimates of the diversion effect on the P supply are shown in Table 3. The accuracy of these estimates can be improved only by continuous monitoring of nutrient supply which is presently underway on Issaquah Creek.

The diversion brought the P supply to Lake Washington to near Vollenweider's (1968) danger limit for eutrophication but it remains well above the danger limit in Lake Sammamish (Table 2). The pre-diversion N supply did not exceed the danger limit nearly as much as did P in either lake so N diversion may be considered less significant than P.

The mean winter (December to April) total P concentration in the surface waters of Lake Washington decreased over 60 percent following

sewage diversion (Edmondson 1970, 1972). Although diversion was not complete until 1967, winter P concentrations began gradually decreasing soon after the four year diversion process was initiated in 1963. In contrast, little difference can be seen in the 1971 winter mean P concentrations in Lake Sammamish three years after diversion in 1968 (Table 1).

Phytoplankton biomass quickly responded to the reduction in mean winter PO_4 -P content in Lake Washington as shown by Edmondson (1970). Chl α decreased in direct proportion to PO_4 -P, while the other macronutrients, C and N, varied independent of Chl α . A significant decrease in phytoplankton biomass or production has not been observed in Lake Sammamish (Table 1).

In one respect this is gratifying because winter mean NO_3 -N and total P concentration, which should indicate available supply, also have not decreased to conform with the income decrease. In fact, summer biomass and phosphorus content have increased in Lake Sammamish and are related. In another respect, the delayed responses of winter mean P content to diversion of about one half the annual supply to the lake suggests that factors controlling these winter levels in the two lakes are different in either kind or magnitude. This is indicated in Figure 13 where Vollenweider (1969) has shown that for most lakes, whether oligotrophic or eutrophic, lake concentration is related to supply. One of the exceptions is Lake Sammamish.

Factors controlling winter P concentrations in Lake Sammamish are not yet understood, but comparison of seasonal changes in total P and morphological characteristics between the two lakes offers a hypothesis. Winter P content remained high until the spring diatom pulse in Lake Washington following which a moderate decrease was observed (Emery et al. 1971). In Lake Sammamish, total P content normally increased to peaks as high as 70 - 100 $\mu g/l$ following turnover in November. Instead of remaining high until the spring diatom pulse in April, as it does in Lake Washington, total P usually decreased during the winter in Lake Sammamish before the diatom pulse. The surface water in Lake Sammamish has been observed to become cloudy with particulate matter during turnover and remain that way for a month or two before clearing. P may be absorbed by this particulate matter and removed in shallower Lake Sammamish (mean depth 17.7 m), while in deeper Lake Washington (mean depth 37 m) particulate matter from the bottom is not so readily mixed to the surface. In support of this, iron content during the following turnover is higher in Lake Sammamish than in Lake Washington particularly in the hypolimnion. The lower residual P content in late winter in Lake Sammamish is undoubtedly due to P sedimentation through interaction with relatively greater amounts of iron (Horton 1972, Shapiro et al., 1971).

Recovery rate in Lake Sammamish may be slower than in Lake Washington because the quantity of nutrient diverted from the former still left the external supply above the danger limit. Thus, the relationship

between nutrient supply and trophic state may not be linear, even if corrected for depth. There may exist a control threshold level of P supply to a lake, above which alteration by manipulation of external supply would be relatively rapid while below that level the responses would be very slow. Internal control mechanisms for P such as hypothesized for Lake Sammamish could affect such a control threshold.

Slight improvements have been noted in water clarity and community composition of the phytoplankton, although the latter may be only natural variation. Table 4 shows an increase in mean Secchi disk of about one meter during the summer during the two study years following diversion. Figure 14 shows a decrease in the myxophycean (blue green algae) portion of the phytoplankton following diversion, however considerable variation in the timing and magnitude of the spring diatom outburst was observed which may also be reflected in the myxophycean abundance.

Recovery Rate

Predictions of recovery rates for lakes having altered conditions of nutrient income are possible using a model by Vollenweider (1969). His model is based on determinations of wash-out and sedimentation coefficients. The model can provide a preliminary and tentative estimate of a "half-life period," or the time required to reduce the concentration of material in the lake to one-half of the sum of the original plus the expected new material concentration. To reach full recovery or equilibrium with the external supply, the "half-life period" is multiplied by three. The expression used is

$$\text{Recovery Time} = 3 T \frac{1}{2} = 3 (\ln 2) / \phi, \quad (1)$$

where $\phi = \sigma + \rho$. σ is the sedimentation coefficient and ρ the wash-out coefficient. The sedimentation coefficient σ must be estimated for a lake by calculating the net exchange of material between the water and the sediment or the net loss of nutrients through the system. The wash-out coefficient ρ is calculated by dividing the lake's flushing rate by the lake's volume or for stratified lakes an effective wash-out coefficient is calculated.

The estimated time required for complete material recovery in Lake Washington is 3.4 years. The actual recovery time estimated for phosphate-phosphorus concentrations is 4.1 years. This estimate does not account for the period through which the diversion project was carried out, and would likely be reduced if such an accounting were made. Thus, Vollenweider's model appears reasonably close to an estimate of the actual time of restoration for Lake Washington. The estimated recovery period for Lake Sammamish is 2.8 years. This estimation for Lake Sammamish is approximately equal to that for Lake Washington. From the standpoint of Vollenweider's model then, a similar prompt recovery for Lake Sammamish that was observed for Lake Washington should

be expected. This expectation coupled with the absence of amelioration suggests even further that Lake Sammamish's response to nutrient diversion is unusual. See Emery et al. (1971) and Emery (1972) for details of these calculations.

If maximum concentrations of total P at overturn time are considered instead of mean winter values, a considerable reduction following diversion occurred (Table 20). The lake typically mixes completely in October and November. Comparing mean surface total P in 1964 and 1965 with similar data from the same months in 1970 and 1971 shows a 50 to 60 percent reduction. If the entire period, October to January, is considered a reduction of about 40 percent occurred. It is tempting to reason that since Fe probably removes much of this regenerated P from the surface water prior to spring algal growth and thus controls the winter concentrations, then maximum P at overturn may best represent effects of diversion. If this hypothesis is further substantiated then Lake Sammamish may be recovering at a predictable rate if maximum P at overturn is used as an indicator. Recovery of the other trophic indicators may be delayed in a lake with an anaerobic hypolimnion like Sammamish which may require weighting in the recovery model.

Growth Rate - Nutrient Relationships

Carbon assimilation of natural phytoplankton collected from Findley Lake and exposed for 11 days to $50\mu\text{g/l NO}_3\text{-N}$, 0 to $20\mu\text{g/l PO}_4\text{-P}$ and three levels of light are shown in Figures 15 to 17. The response was greatest to $10\mu\text{g/l PO}_4\text{-P}$ at all light levels, but the greatest assimilation occurred at the lowest light intensity - 1000 lux. Although not represented here replicates were run and showed excellent agreement. The medium light intensity (2000 lux) was found to be the average photic zone light intensity to which phytoplankton were exposed in the lake. Actually the difference among light intensities was not great. These results were typical of those from the other two lakes when the collected phytoplankton were protected from direct sunlight. When collected water was transported in clear containers a decreased assimilation occurred for the first two to three days until the plankton readapted and then a more typical response occurred.

The ^{14}C assimilation data in counts per minute were converted to assimilation rates in uptake (carbon/l day) per unit biomass (carbon/l). These data were then plotted against added P content to determine how well they followed a hyperbola according to Michaelis-Menton kinetics. Except for Findley Lake and the surprising increase at $10\mu\text{g/l P}$, the relationships were reasonable at the medium, light intensity (2000 lux and average for photic zone) (Figures 18-20).

When sample analyses are complete assimilation rate versus actual P content will be known, which will improve the realism of the relationship and hopefully the form. Although, only the mean assimilation rate for the first three days of each experiment is represented here, other values

such as the maximum rates were plotted. The first 3-day mean rate, however, seems most justified to us, because evidence of species composition change was noted in later stages of experiments.

If results of the medium light intensity are considered, and for the time being the interaction of uptake with light intensity seems relatively unimportant, some interesting and predictable differences among the three lakes are apparent. Growth or assimilation rates appear saturated at lower concentrations of P for Findley than for Chester Morse Lake and Lake Sammamish phytoplankton. Rough estimates of half-saturation constants are 0.13, 0.38 and 0.43 $\mu\text{g/l}$ P for Findley, Chester Morse and Sammamish, respectively. This would be expected since the more eutrophic the lake becomes the better adapted to higher nutrient content is the phytoplankton.

Much is left to be done in terms of developing sound relationships for these lakes and understanding seasonal changes in phytoplankton response to nutrient change. However, these results are encouraging, at least to the extent of showing the differences between the lakes that were expected. How well developed assimilation or growth rate - nutrient relationships can be generalized to predict actual changes in phytoplankton biomass in the lakes remains to be seen. As far as we know this is the first attempt to develop Michaelis-Menton kinetic parameters from static culture experiments with natural phytoplankton. If successful, it should be a valuable tool for water management since continuous flow culture experiments are much less practical under most conditions.

An additional objective in these experiments was to determine the interaction between N and P on assimilation rates of nutrient poor phytoplankton. Results from one experiment has been analyzed and results expressed in one form are shown in Table 4. The interesting point here is that addition of NO_3 alone did not stimulate the assimilation rate of PO_4 , however, the addition of PO_4 alone did stimulate the assimilation of NO_3 and to nearly the same level as with NO_3 added. Another interesting point is that the assimilation rate of PO_4 was nearly as great as that of NO_3 even though 7-10 times more N is required for growing cells than P. Hopefully, these results along with those from another experiment will provide a basis with which to guide the linkage of assimilation rate models of P and N interacting together. Initially, at least, we want to determine if the form often used is valid;

$$\mu = \mu_m \frac{P}{P + K_p} \cdot \frac{N}{N + K_N} \cdot \frac{L}{L + K_L}$$

where μ is the growth rate constant, μ_m is the maximum growth rate and P, N and L are phosphorus, nitrogen and light with K as the respective half-saturation levels.

Table 1. Mean winter (Feb-May) content of nutrient and summer (May-Aug) content of Chlorophyll *a* in $\mu\text{g/l}$ (weighted mean in photic zone) and phytoplankton productivity in mgC/m^2 day for three lakes in the Cedar River drainage.

Year	$\text{NO}_3\text{-N}$	P_{tot}	$\text{PO}_4\text{-P}$	Chl <i>a</i>	Productivity
<u>Findley Lake</u>					
1972	27.4	9.0	3.0	0.8	272
<u>Chester Morse Lake</u>					
1971	-	-	-	2.3	525
1972	53.0	10.0	3.6	0.9	288
<u>Lake Sammamish</u>					
1965	473.7	19.9	-	3.9	-
1970	450.7	37.7	7.6	10.6	963
1971	331.3	24.2	6.6	4.8	499

Table 2. Comparison of nutrient supply in Lake Sammamish and Washington before and after diversion with special reference to Wollenweider's (1968) nutrient supply limitations with respect to mean depth (from Emery, Moon and Welch 1971).

	Sammamish	Washington
Area (km ²)	19.8	87.615
Volume (km ³)	0.350	2.884
Maximum depth (m)	31	64
Mean depth (m)	17.7	32.9
Flushing rate (year)	2.2	3.0
Pre diversion annual total P supply (kg)	20,170	92,600
Pre diversion annual total P supply per surface area (g/m ² /yr)	1.09	1.06
Percent total P income diverted	46*	55
Post diversion annual total P supply (kg)	11,800	41,700
Post diversion annual total P supply per surface area (g/m ² /yr)	0.60	0.48
Vollenweider's danger limit of P supply for respective mean depth (g/m ² /yr)	0.26	0.42
Pre diversion annual inorg. N supply (kg)	49,100	246,100
Pre diversion annual total N supply per surface area (g/m ² /yr)**	4.96	5.63
Percent inorg. N diverted	22	12
Post diversion annual inorg. N (NO ₃ -N) supply (kg)	38,298	216,568
Post diversion annual total N supply per surface area (g/m ² /yr)**	3.87	4.33
Vollenweider's danger limit of N supply for respective mean depth (g/m ² /yr)	4.00	6.00

* Estimated on the basis of population equivalent nutrients diverted and pre diversion annual income to the lake. The error in estimating income may be 20-30 percent.

** Total N values are estimated by doubling inorg. N values.

Table 3. Observed and theoretical (determined from known waste composition and population equivalents) estimates of P income in surface water to Lake Sammamish before and after waste water diversion (from Moon 1972).

Prediversion Nov 1964 - Nov 1965		
	Theoretical	Observed
Issaquah Cr.	50.3 kg/day	43.3 kg/day
	17,900 kg/yr	15,800 kg/yr
	0.9 g/m ² /yr	0.8 g/m ² /yr
Total Lake	59.3 kg/day	52.3 kg/day
	20,170 kg/yr	19,100 kg/yr
	1.09 g/m ² /yr	0.97 g/m ² /yr
Post diversion Nov 1970 - Nov 1971		
Issaquah Cr.	23.2 kg/day	23.2 kg/day
Total Lake	32.2 kg/day	32.2 kg/day
	11,800 kg/yr	
	0.6 g/m ² /yr	
Percent diverted of total income	46	39

Table 4. Nutrient assimilation rates per unit biomass (Chlorophyll *a*) for Lake Sammamish phytoplankton (*Synedra* dominant) exposed to added N, P and N + P.

Flask No.	Nutrient added in $\mu\text{g/l}$	assimilation rate (day^{-1})	
		$\text{NO}_3\text{-N/Chl } a$	$\text{PO}_4\text{-P/Chl } a$
1	750 $\text{NO}_3\text{-N}$	15.6	0
2	750 $\text{NO}_3\text{-N}$	20.1	0
3	250 $\text{PO}_4\text{-P}$	16.4	10.0
4	250 $\text{PO}_4\text{-P}$	13.5	9.3
5	750 $\text{NO}_3\text{-N}$ + 250 $\text{PO}_4\text{-P}$	12.7	10.4
6	750 $\text{NO}_3\text{-N}$ + 250 $\text{PO}_4\text{-P}$	8.0	4.1

Table 5. A comparison of pre- and postdiversion surface water total P concentrations during and following fall overturn in Lake Sammamish.

	SURFACE WATER* TOTAL P ($\mu\text{g}/\text{l}$)						Difference Between Means	Per Cent Change
	PRE-DIVERSION			POST-DIVERSION				
	1964-65	1965-66	2 Yr. Mean	1970-71	1971-72	2 Yr. Mean		
Oct	24.6	36.0	32.3	12.8	17.2	15.0	-17.3	-53.6
Nov	72.5	99.0	85.8	24.6	28.1	26.3	-59.5	-69.3
Dec	33.5	13.0	23.2	37.8	24.8	31.3	+ 8.1	+34.9
Jan	23.5	30.5	27.0	37.9	24.0	30.9	+3.9	+14.4

*Station 612

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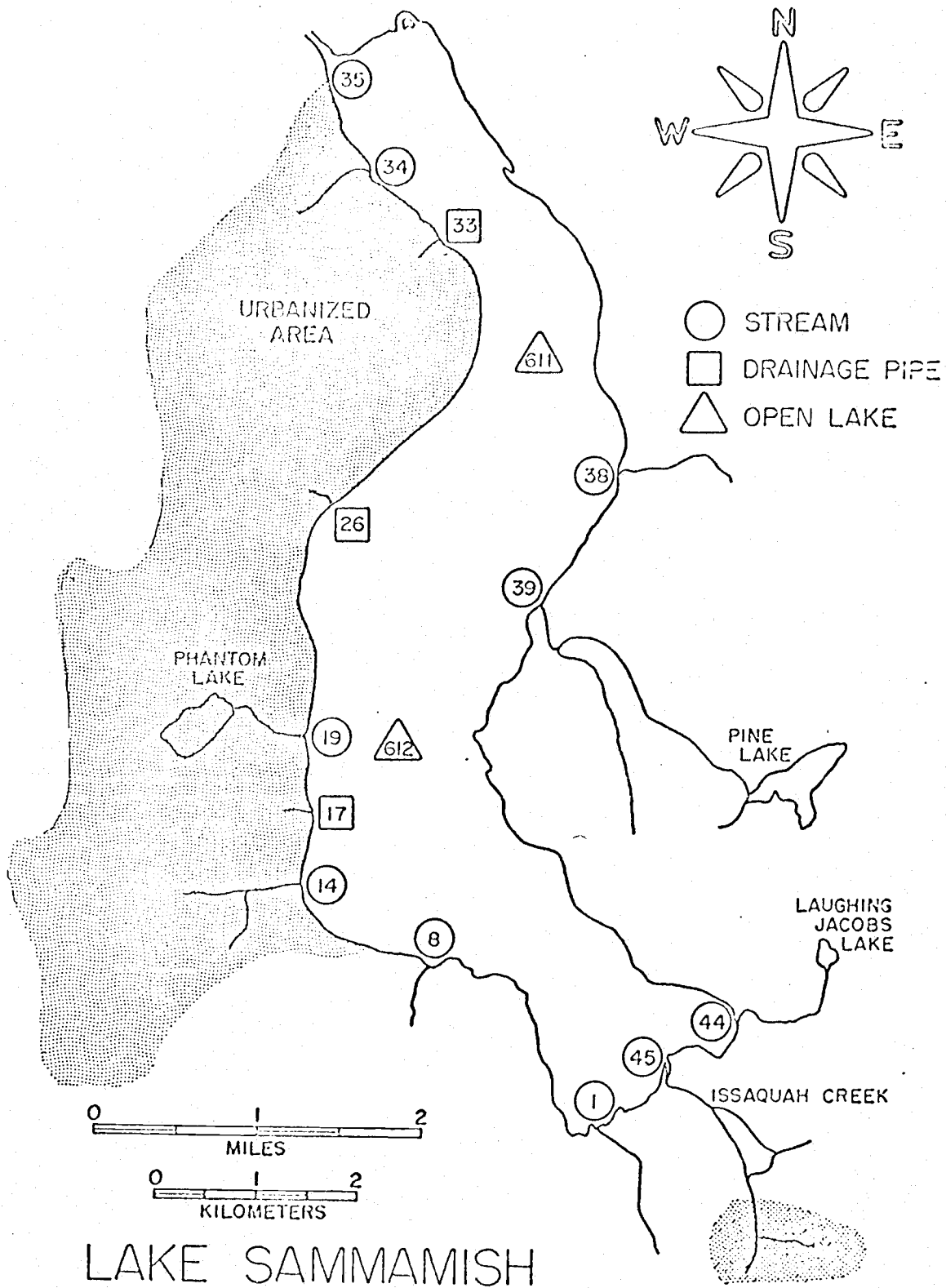


Figure 1. Lake Sammamish and vicinity showing study streams, open lake stations, and urbanized areas to the east and south of the lake.

FINDLEY LAKE

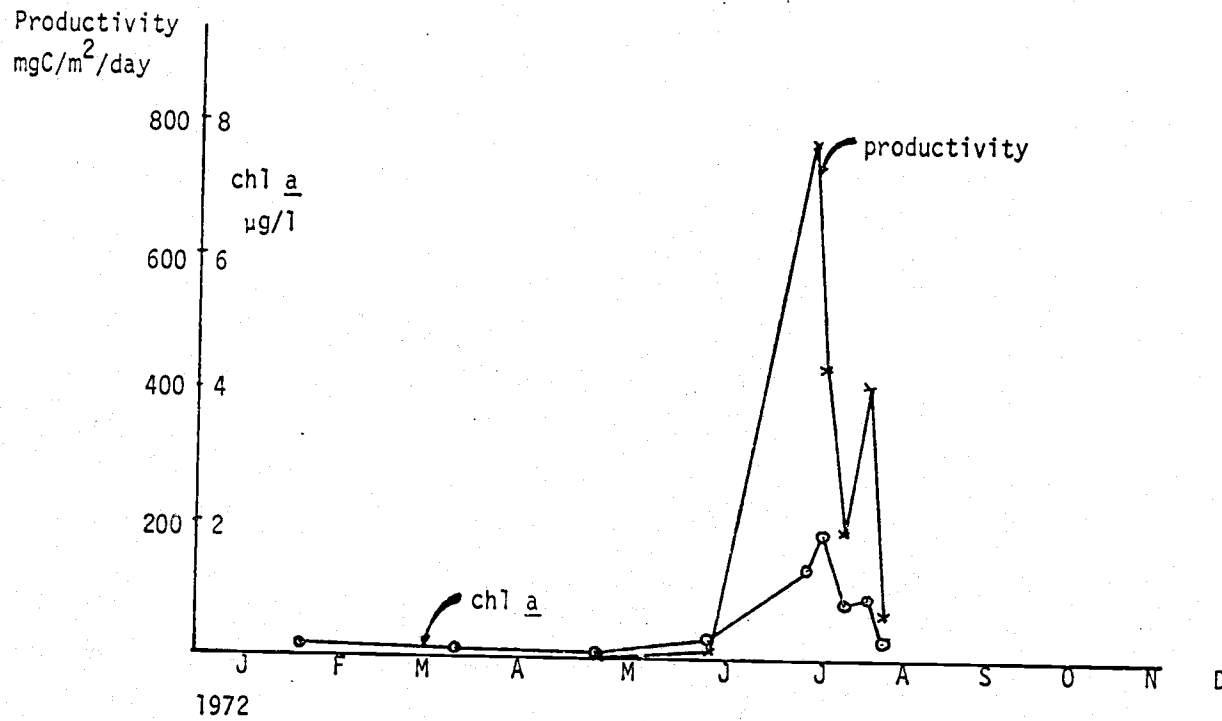


Figure 2. Phytoplankton productivity and Chlorophyll a (weighted mean for photic zone) in Findley Lake, Washington, 1972.

FINDLEY LAKE

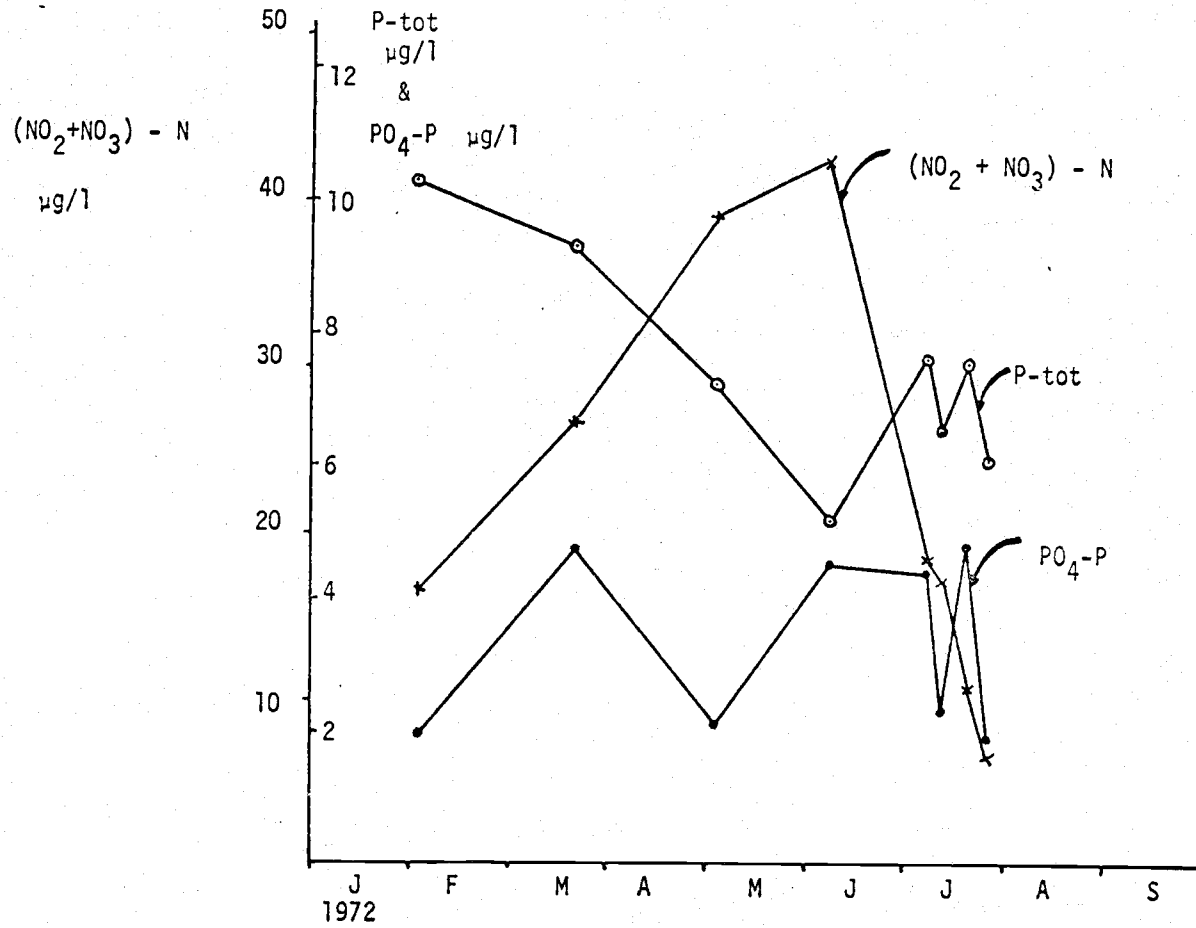


Figure 3. Nitrate, orthophosphate and total phosphorus content in Findley Lake, Washington, 1972.

CHESTER MORSE LAKE

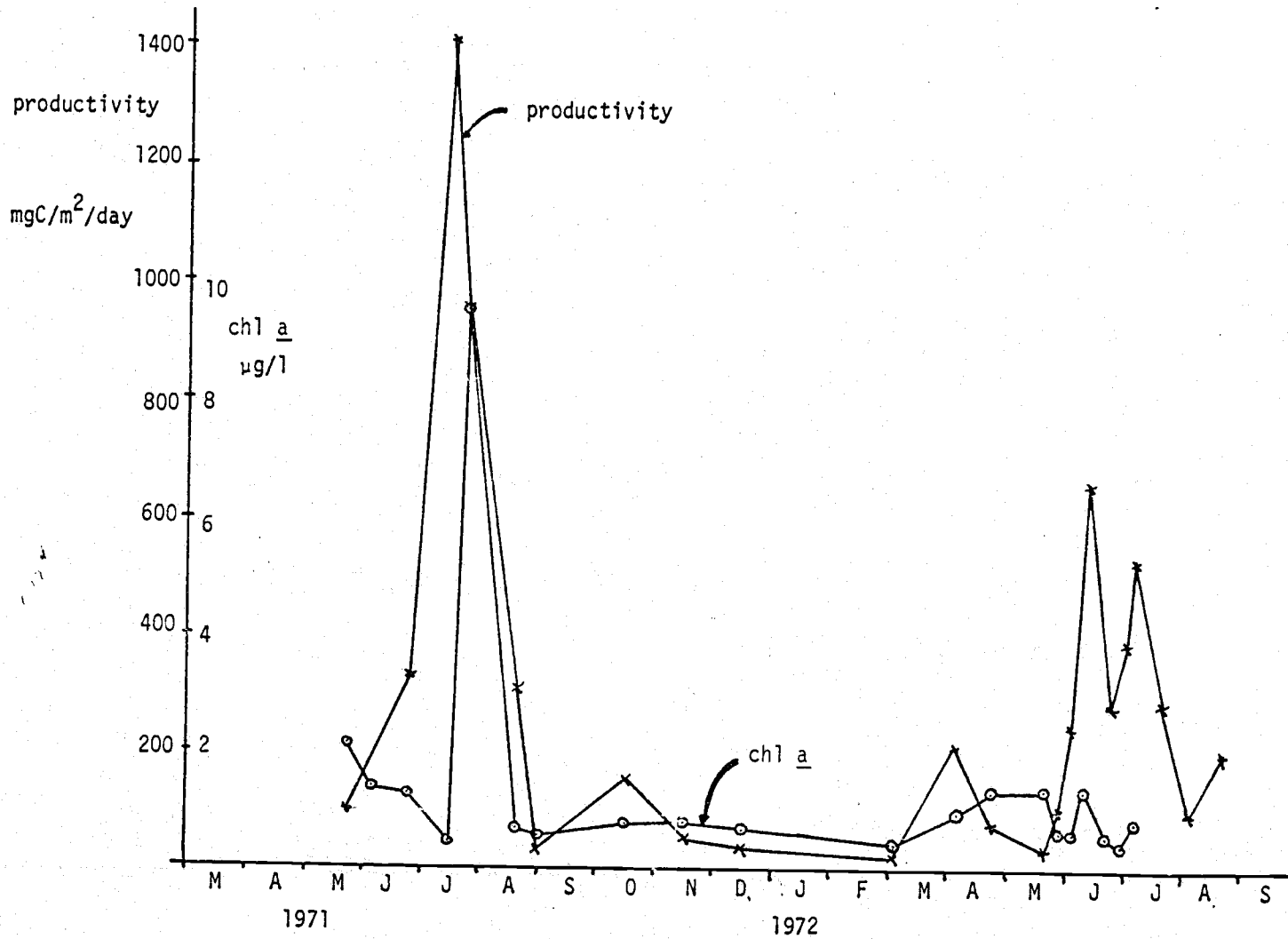


Figure 4. Phytoplankton productivity and Chlorophyll a content (weighted mean for photic zone) in Chester Morse Lake, Washington, 1971-72.

CHESTER MORSE LAKE

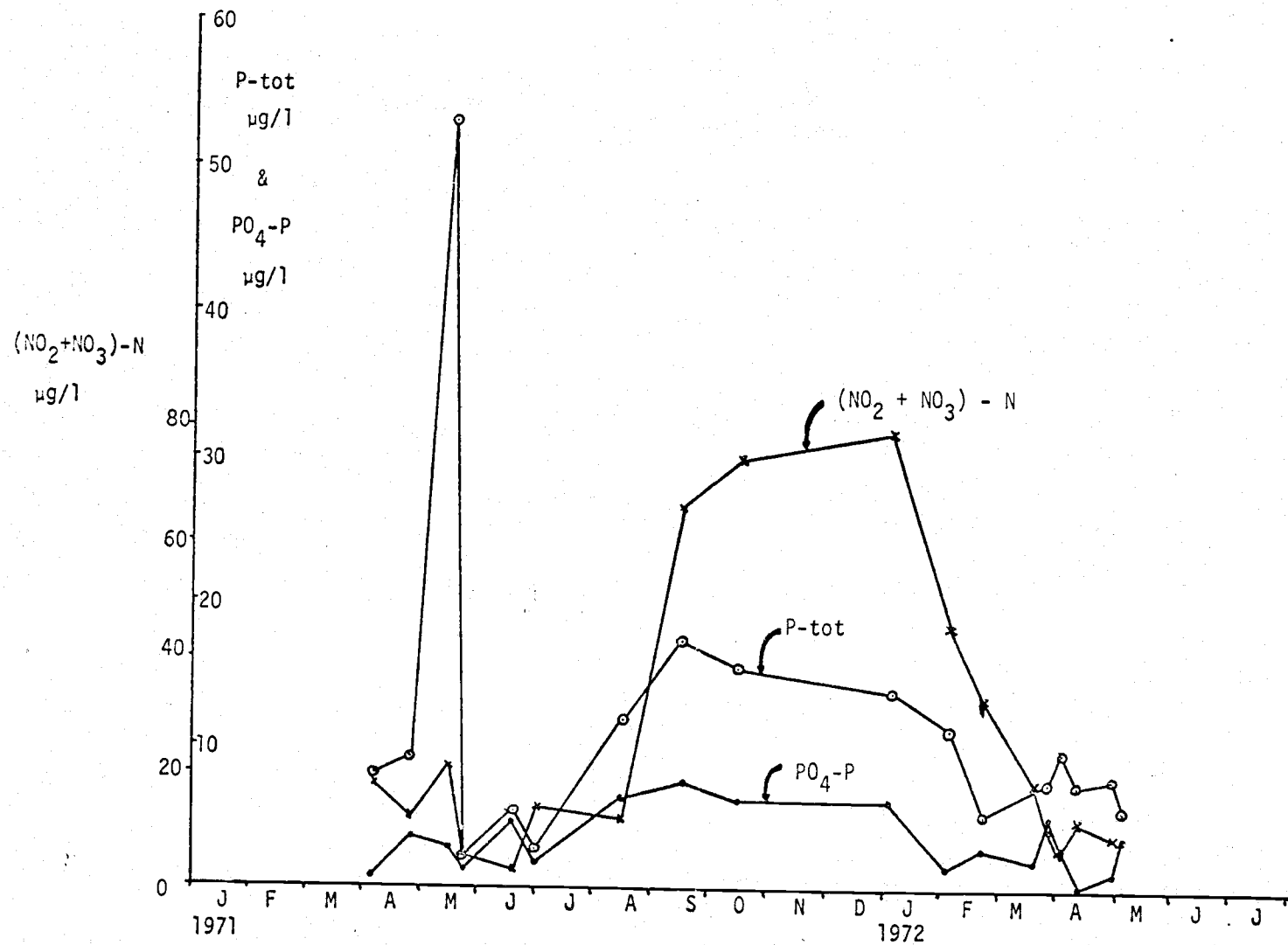


Figure 5. Nitrate, orthophosphate and total phosphorus content (weighted mean in photic zone) in Chester Morse Lake, Washington, 1971-72.

LAKE SAMMAMISH

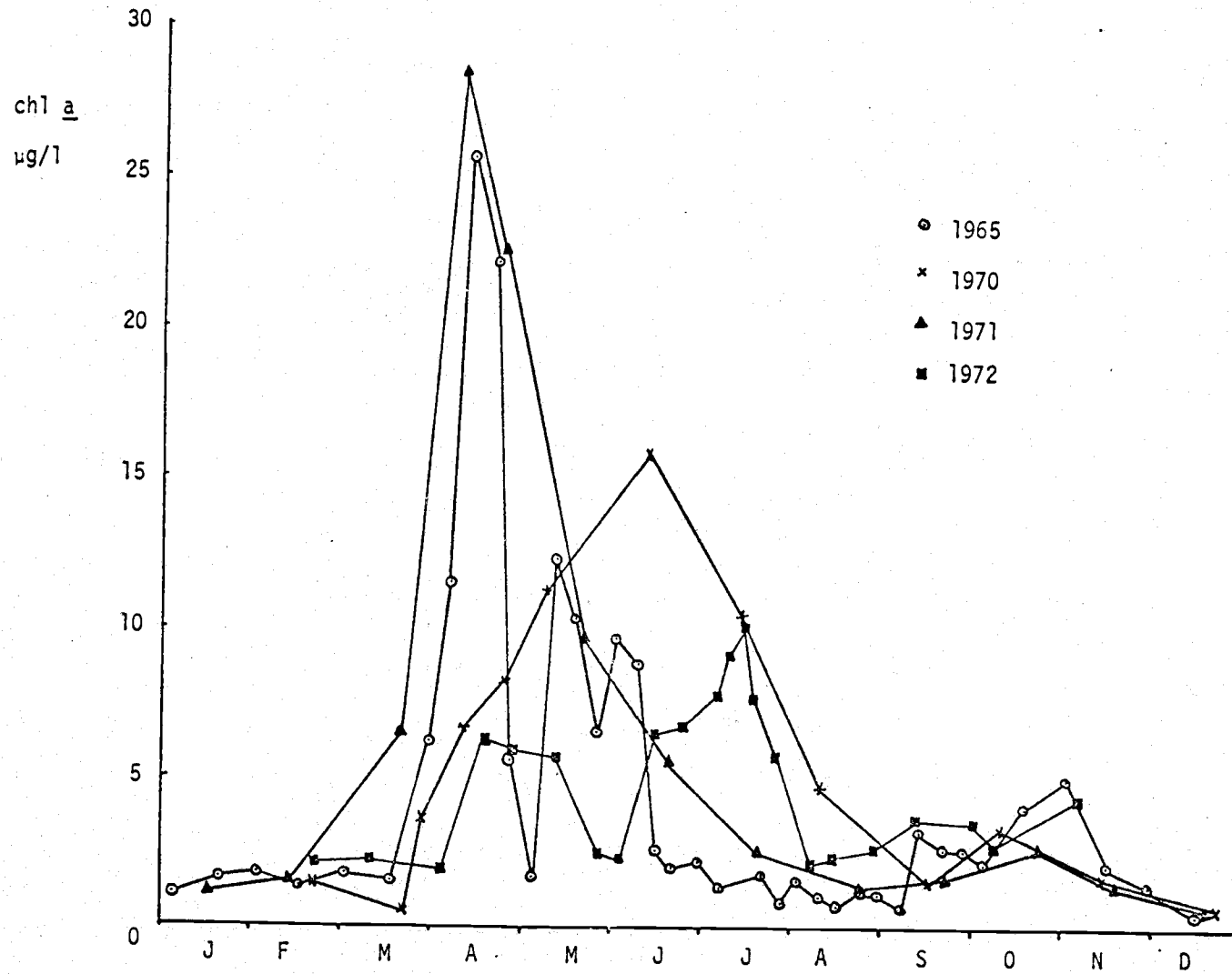


Figure 6. Chlorophyll a content (weighted mean in photic zone) in Lake Sammamish during 1965 and 1970-72.

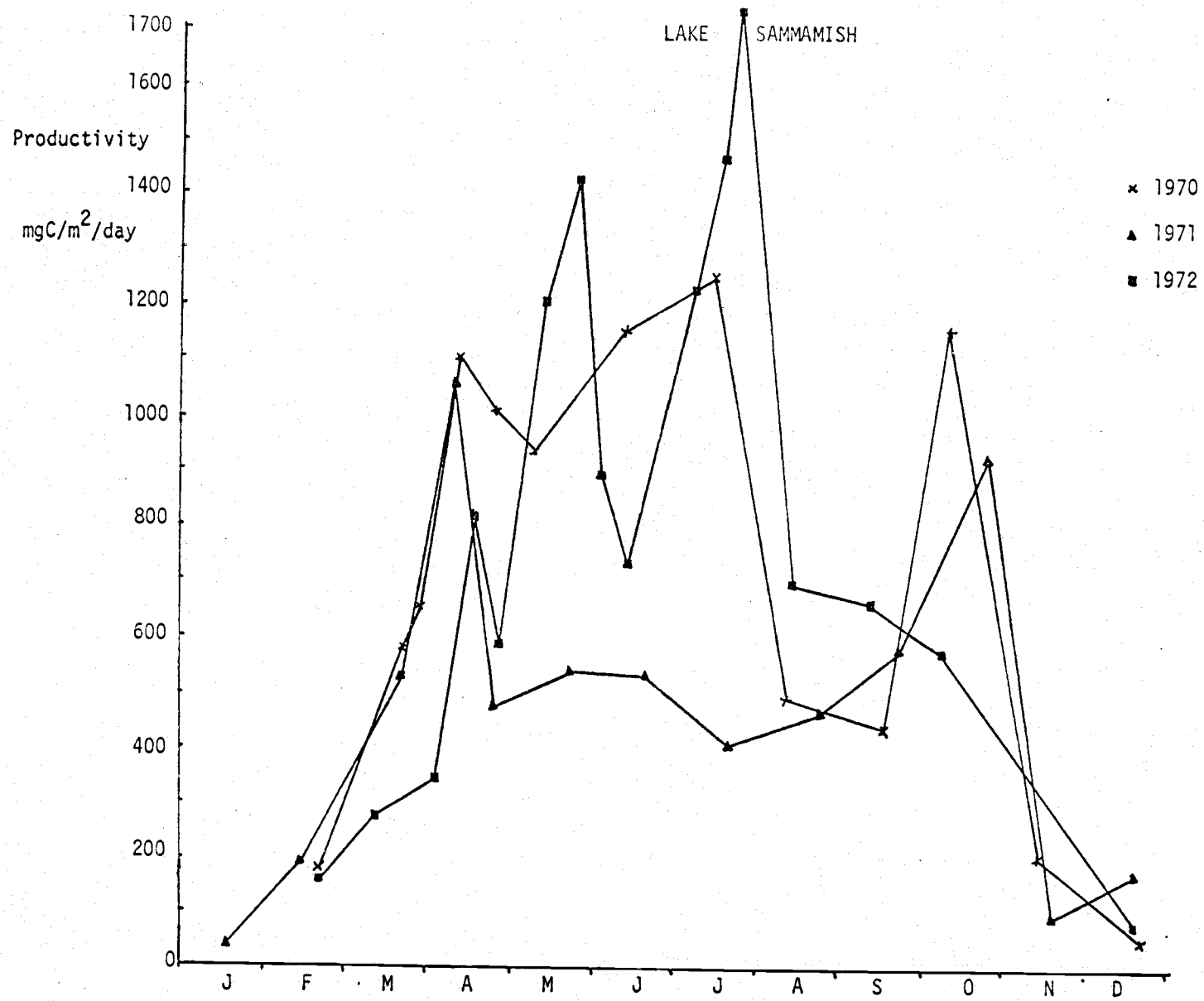


Figure 7. Phytoplankton productivity in Lake Sammamish during 1970 to 1972.

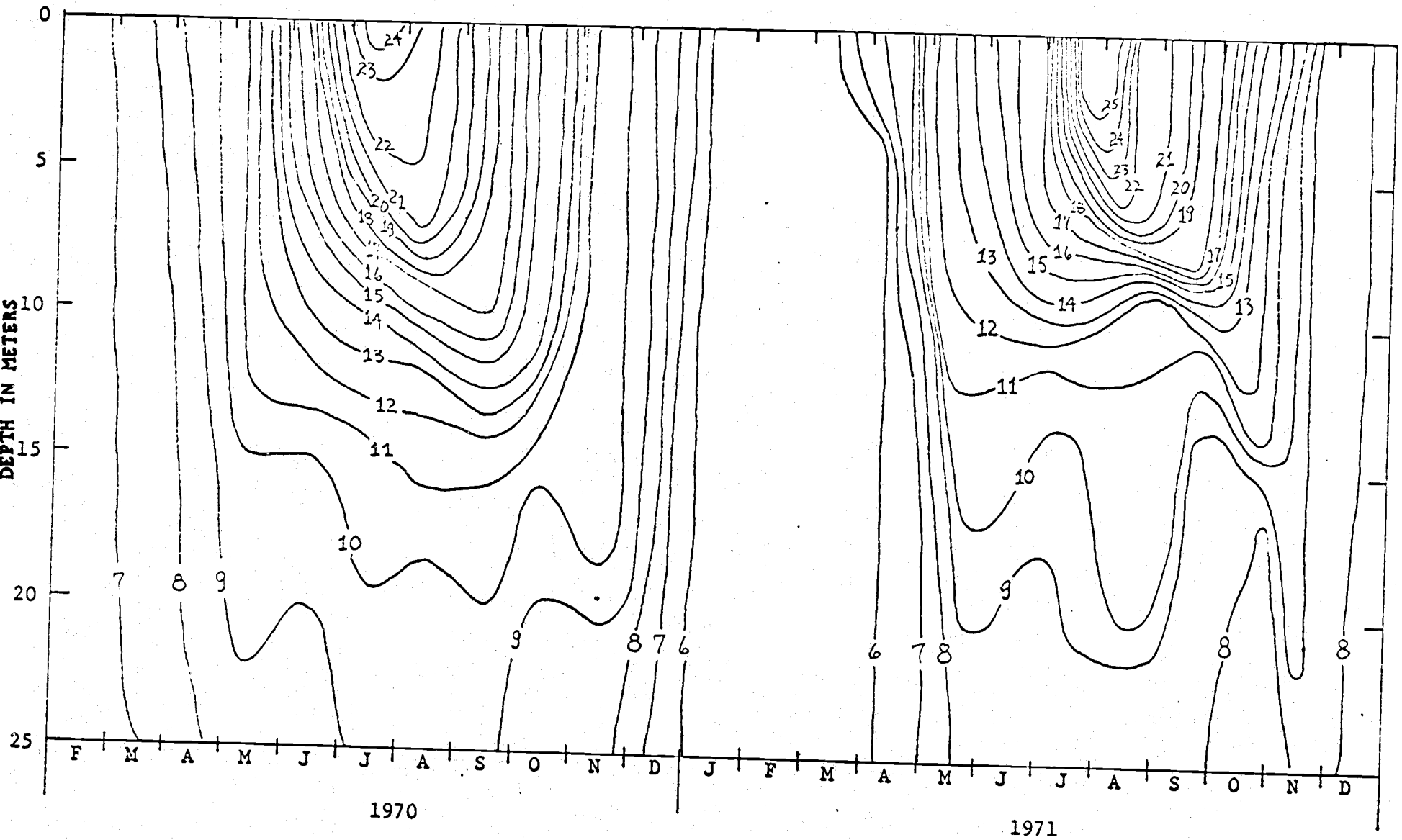


Figure 8. Isotherms in Lake Sammamish during 1970-71.

LAKE SAMMAMISH

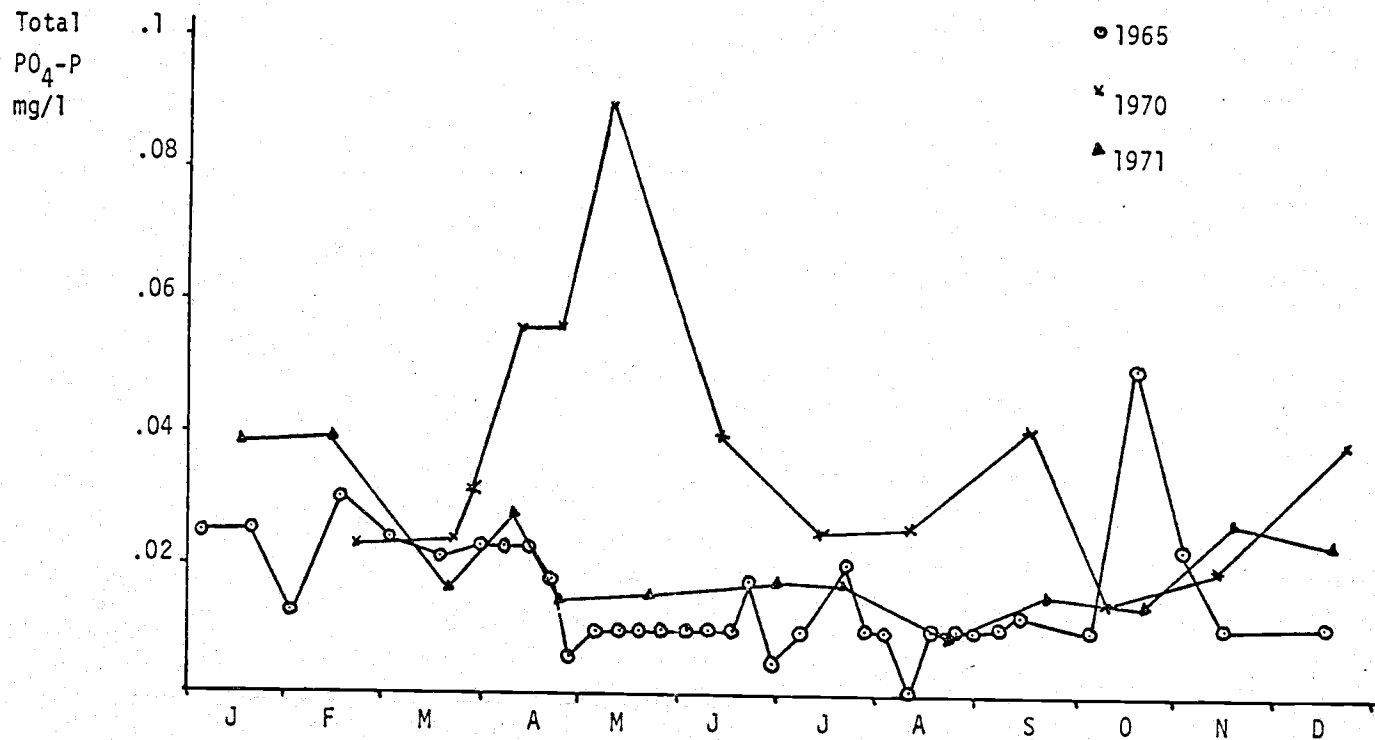
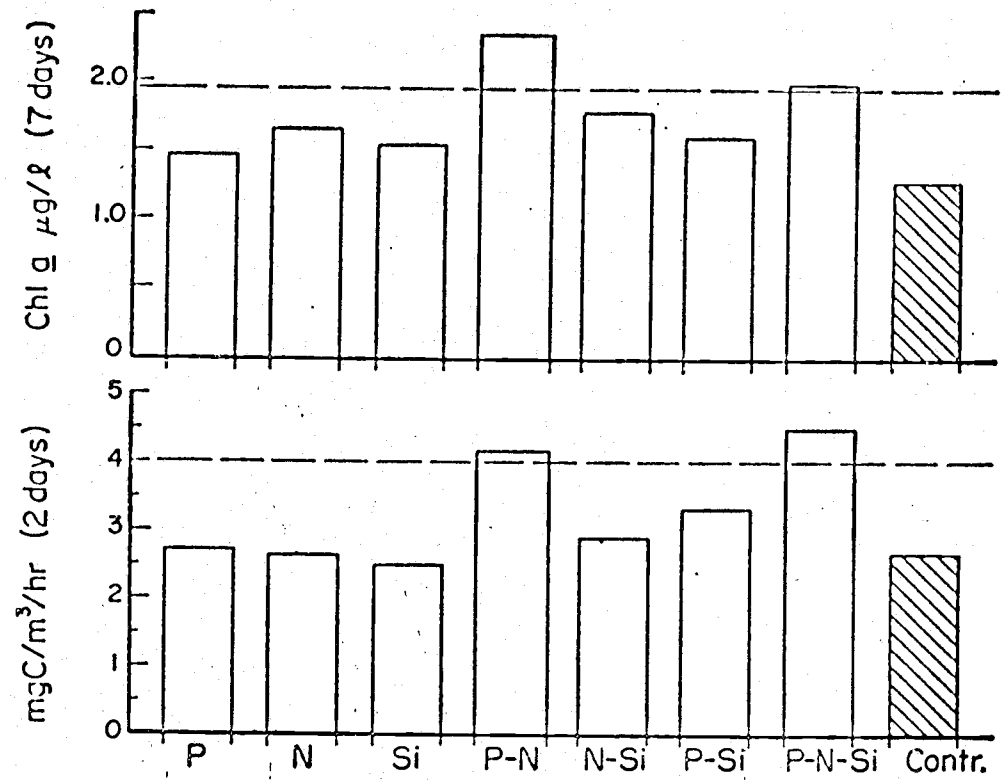
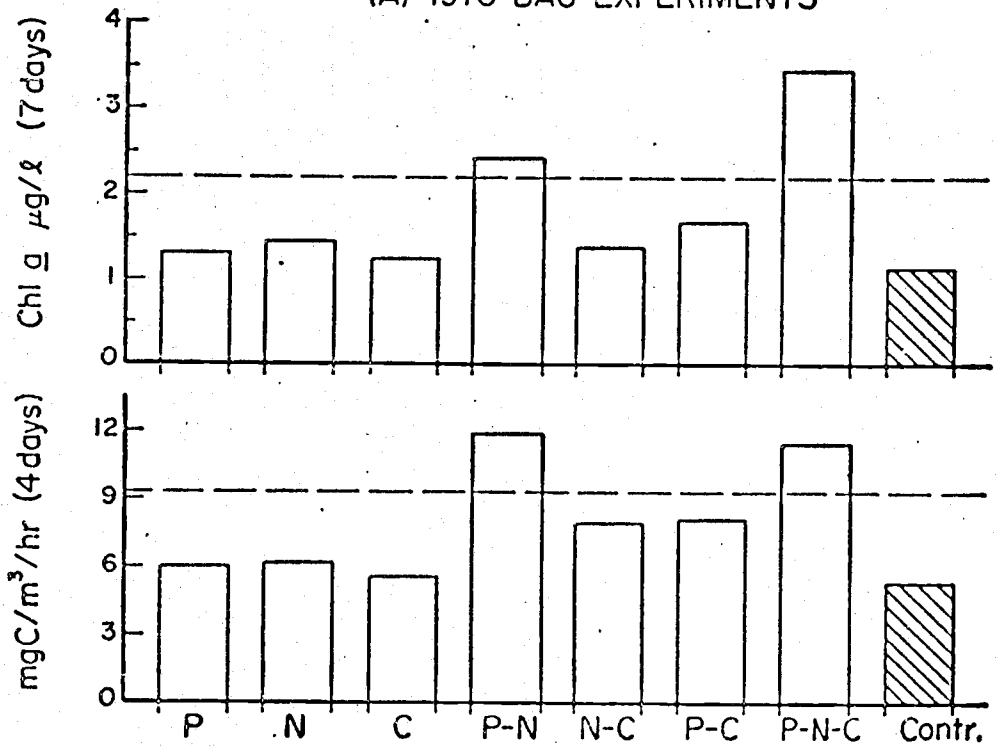


Figure 10. Total phosphorus content (weighted mean in photic zone) in Lake Sammamish in 1965 and 1970-71.

MEAN ALGAL BIOMASS AND PRODUCTIVITY



(A) 1970 BAG EXPERIMENTS



(B) 1971 BAG EXPERIMENTS

Figure 11. Plastic bag experiments *in situ* in Lake Sammamish showing the response of natural phytoplankton to added P, N, C and Si.

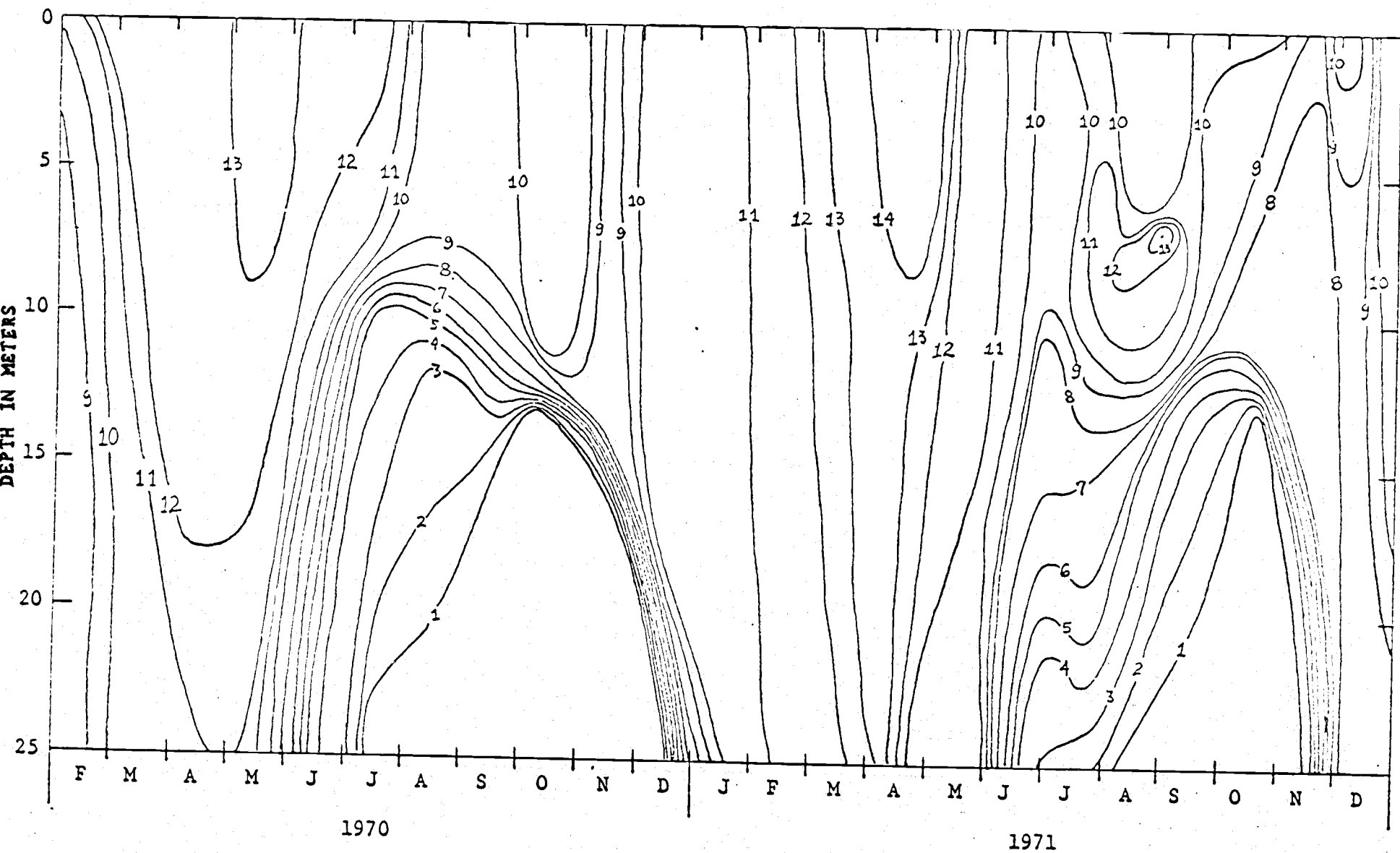
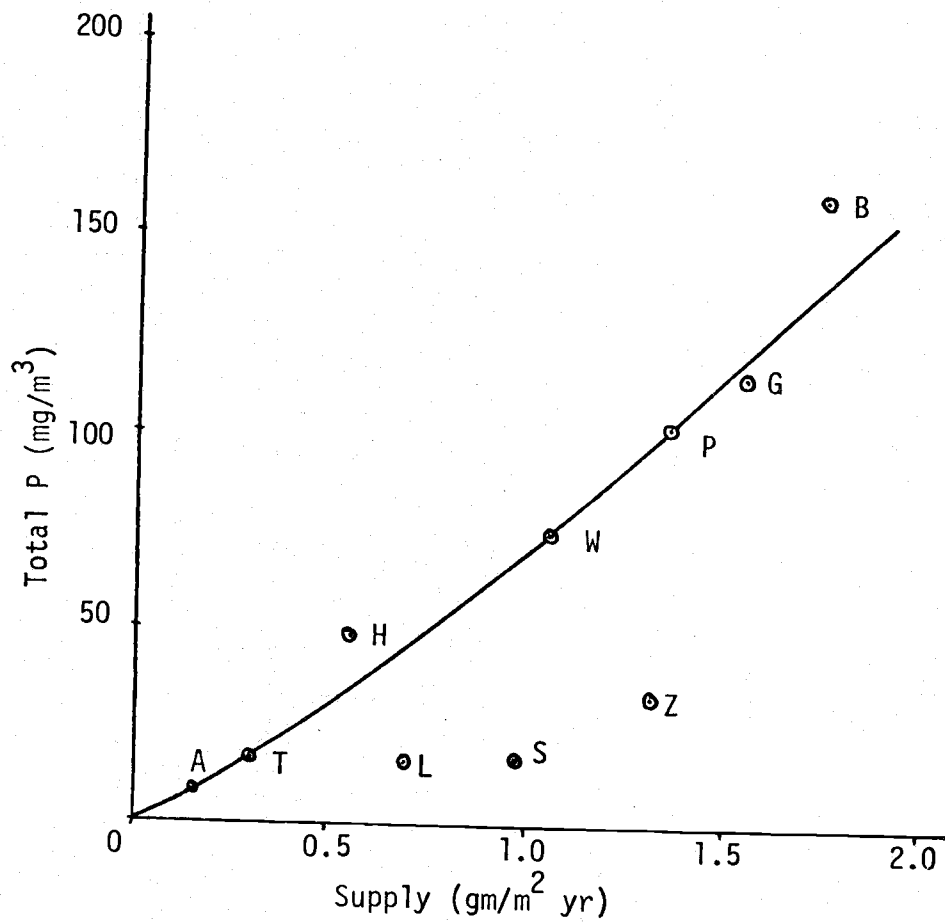


Figure 12. Oxygen Isopleths in Lake Sammamish during 1970-71.



- A = Aegerisee (Oligo)
- B = Baldeggersee (Eu)
- G = Greifensee (Eu)
- H = Hallwilersee (Eu)
- L = Lac Lemman (Geneva) (Oligo)
- P = Pfäffikersee (Eu)
- S = Sammamish (Meso)
- T = Turlersee (Meso)
- W = Washington (Eu)
- Z = Zurichsee (Eu)

Figure 13. Relationship of external phosphorus supply and lake phosphorus concentration for lakes of various trophic state (Vollenweider 1969).

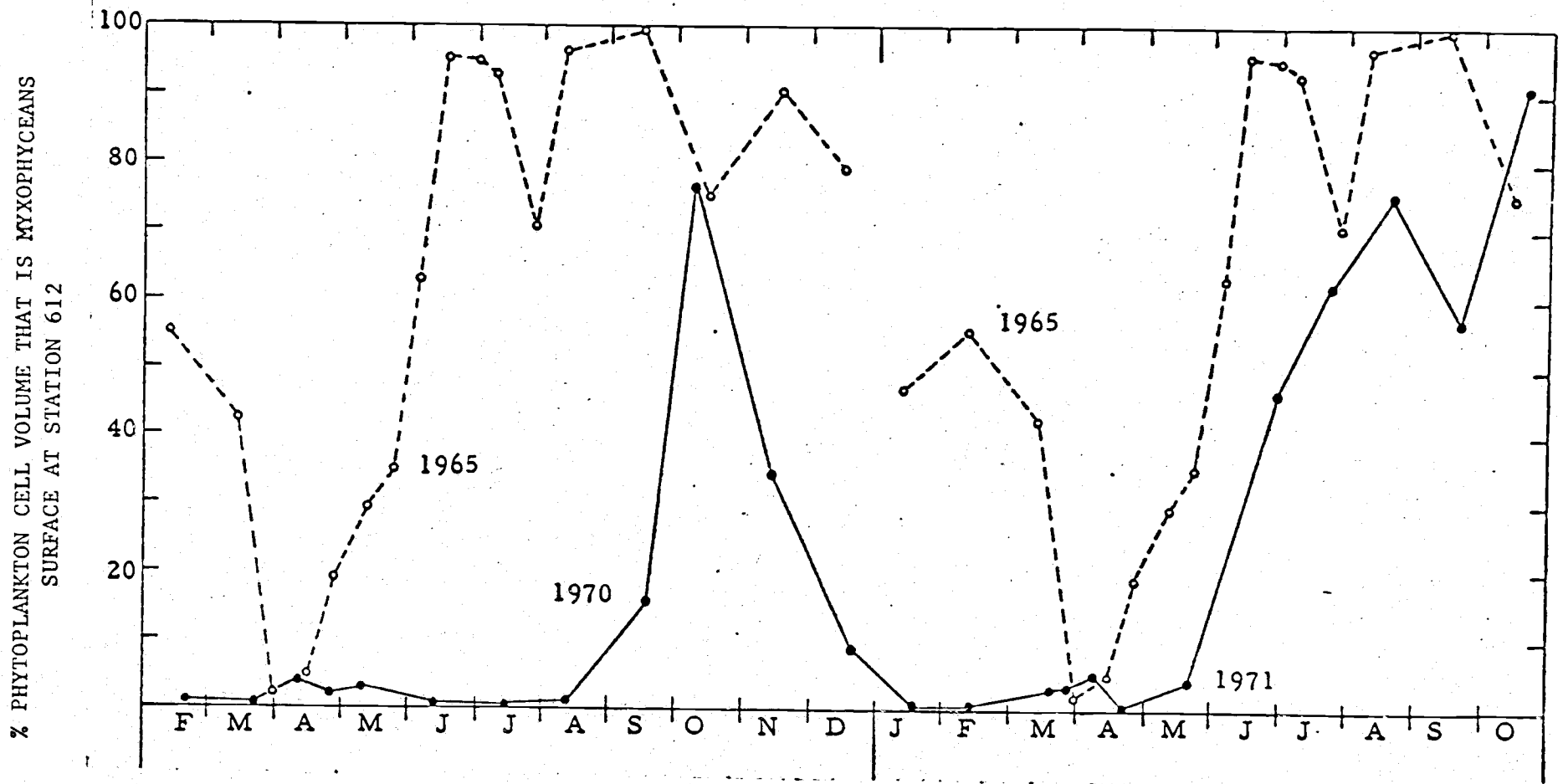


Figure 14. A comparison of percent total volume that were blue green algae between 1965 (prenutrient diversion) and 1971-72 (postnutrient diversion) in Lake Sammamish.

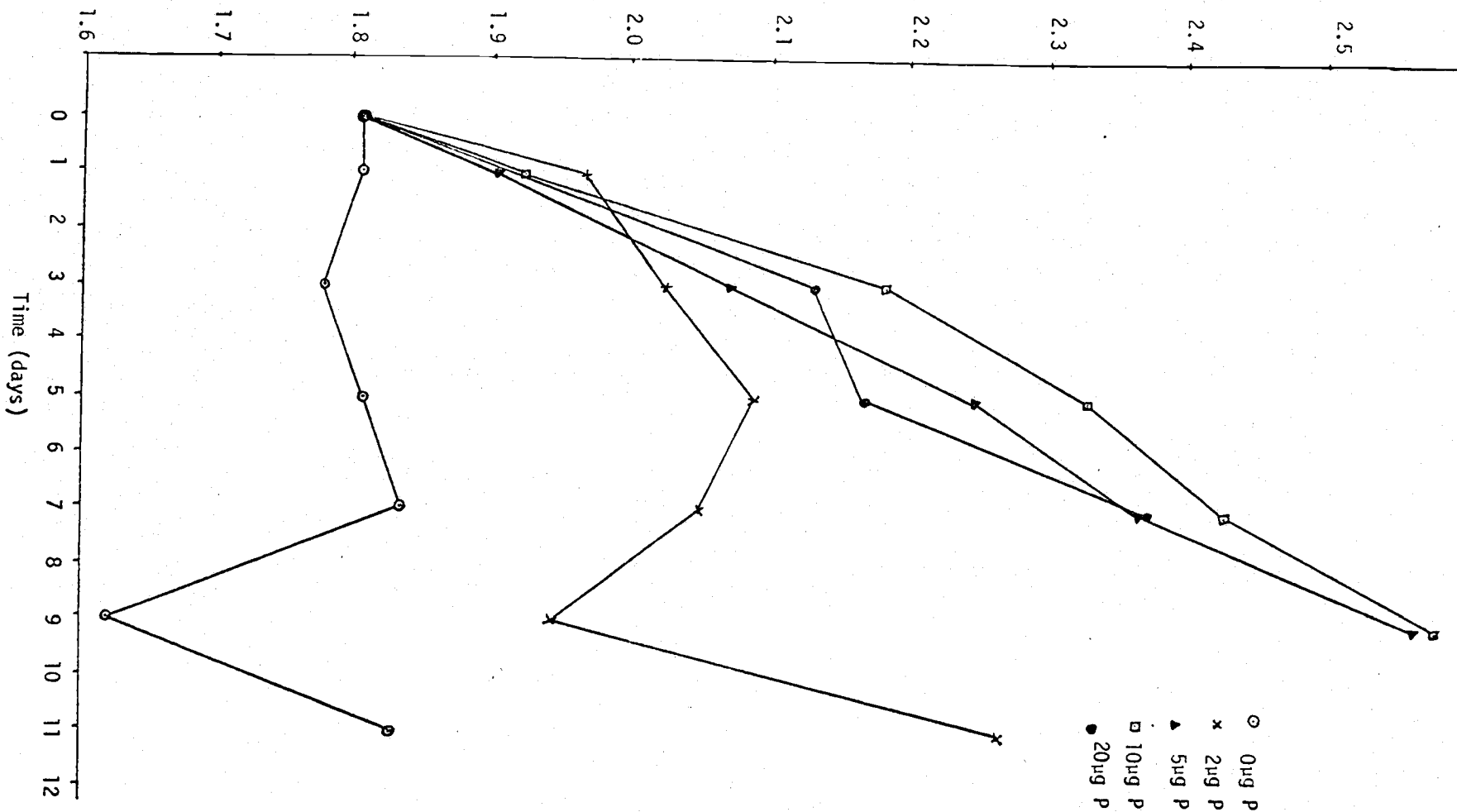


Figure 15. C^{14} assimilation in cultures of Findley Lake phytoplankton exposed to a light intensity of 1000 lux and nutrient additions of $50\mu\text{g}/\text{l}$ N and $0\text{-}20\mu\text{g}/\text{l}$ P.

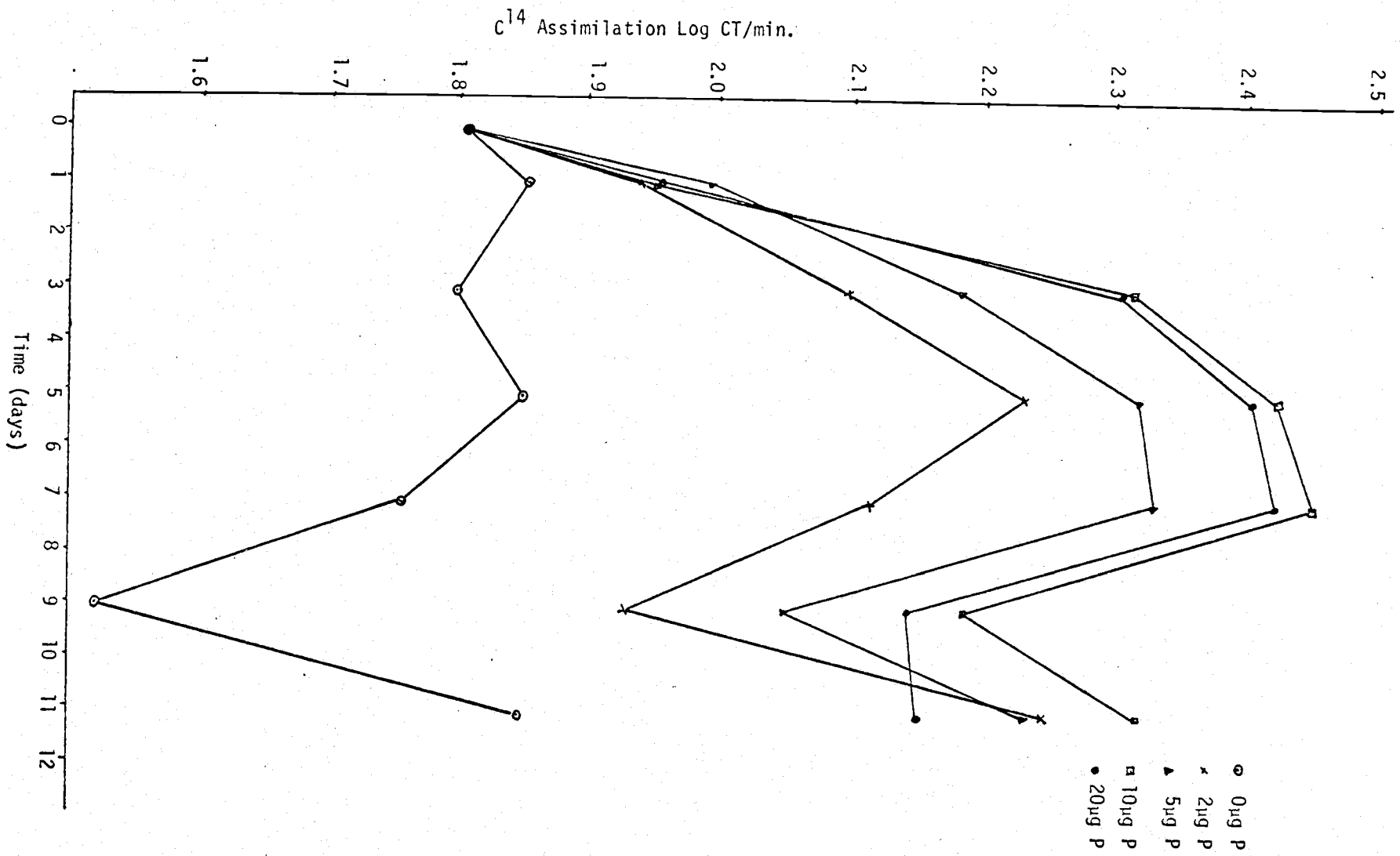


Figure 16. C^{14} assimilation in cultures of Findley Lake phytoplankton exposed to a light intensity of 2000 lux and nutrient additions of 50 µg/l N and 0-20 µg/l P.

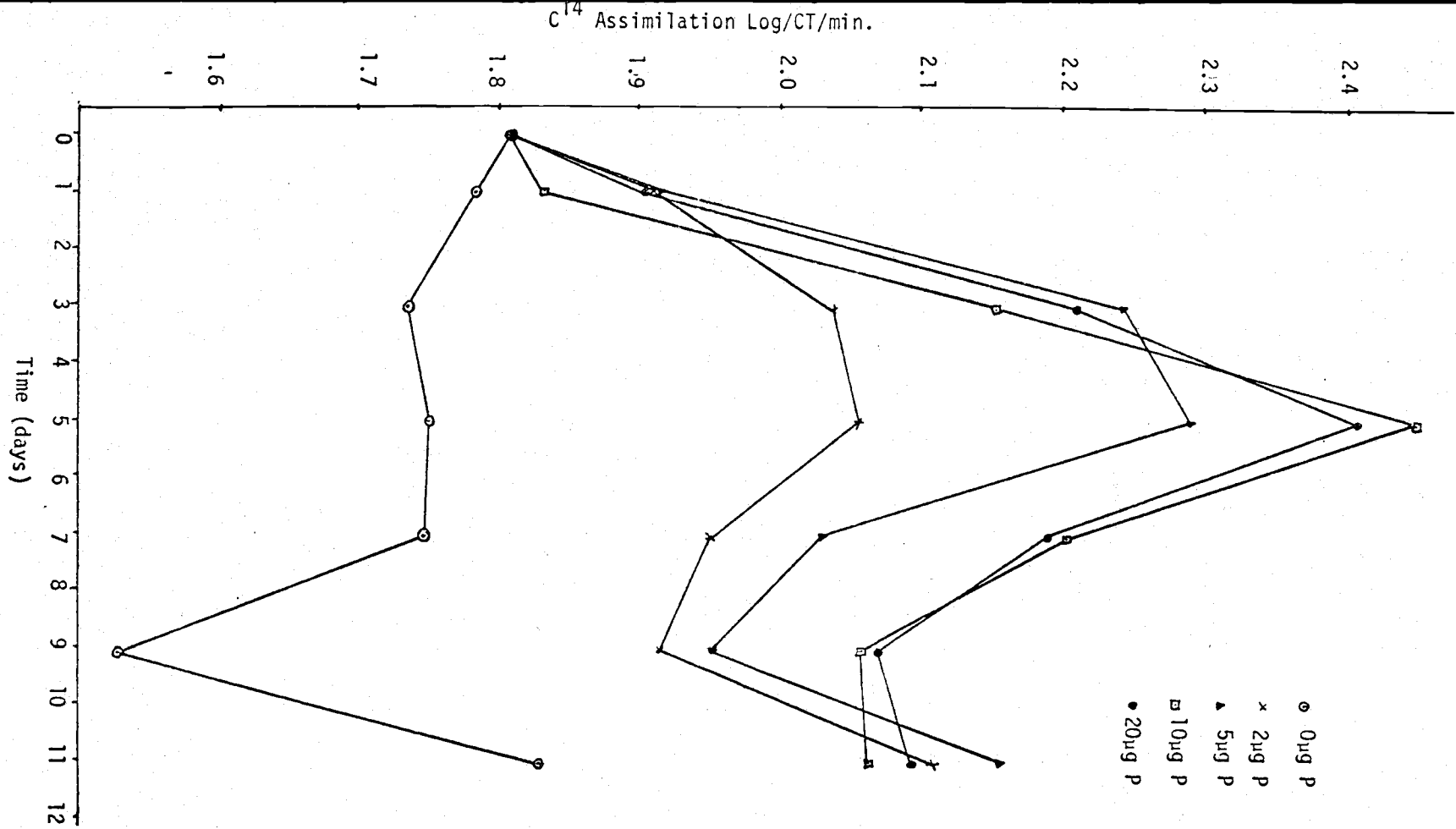


Figure 17. C^{14} assimilation in cultures of Findley Lake phytoplankton exposed to a light intensity of 4000 lux and nutrient additions of 50 $\mu\text{g/l N}$ and 0-20 $\mu\text{g/l P}$.

FINDLEY LAKE

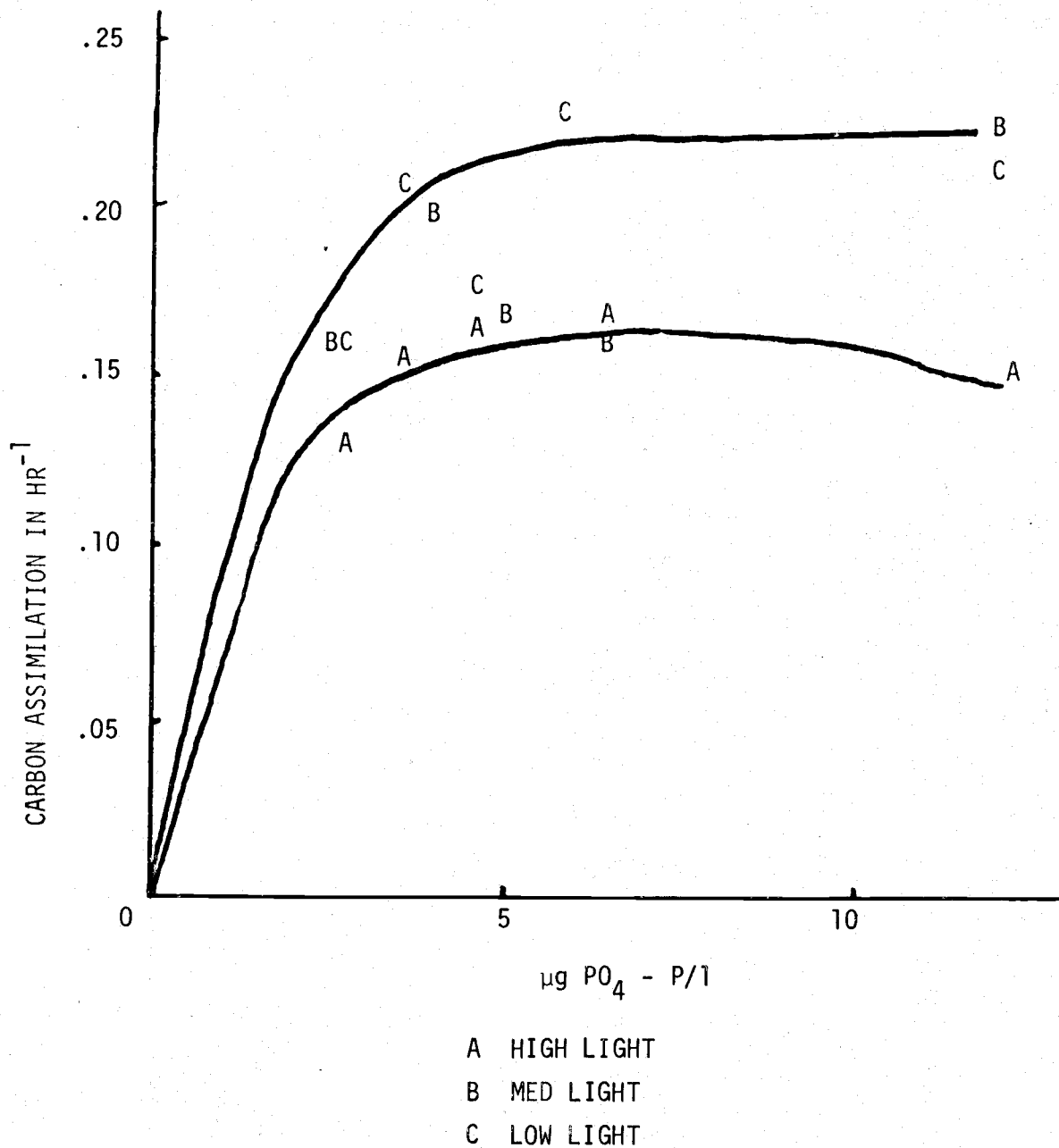


Figure 18. Carbon assimilation rate ($\frac{\mu\text{gC/l}\cdot\text{hr}}{\mu\text{gC/l}}$) by Findley Lake phytoplankton exposed to 4000, 2000 and 1000 lux light intensity and nutrient additions of 50µg/l N and 0-10µg/l P on 30 Aug. 1972

CHESTER MORSE (9-15-72)

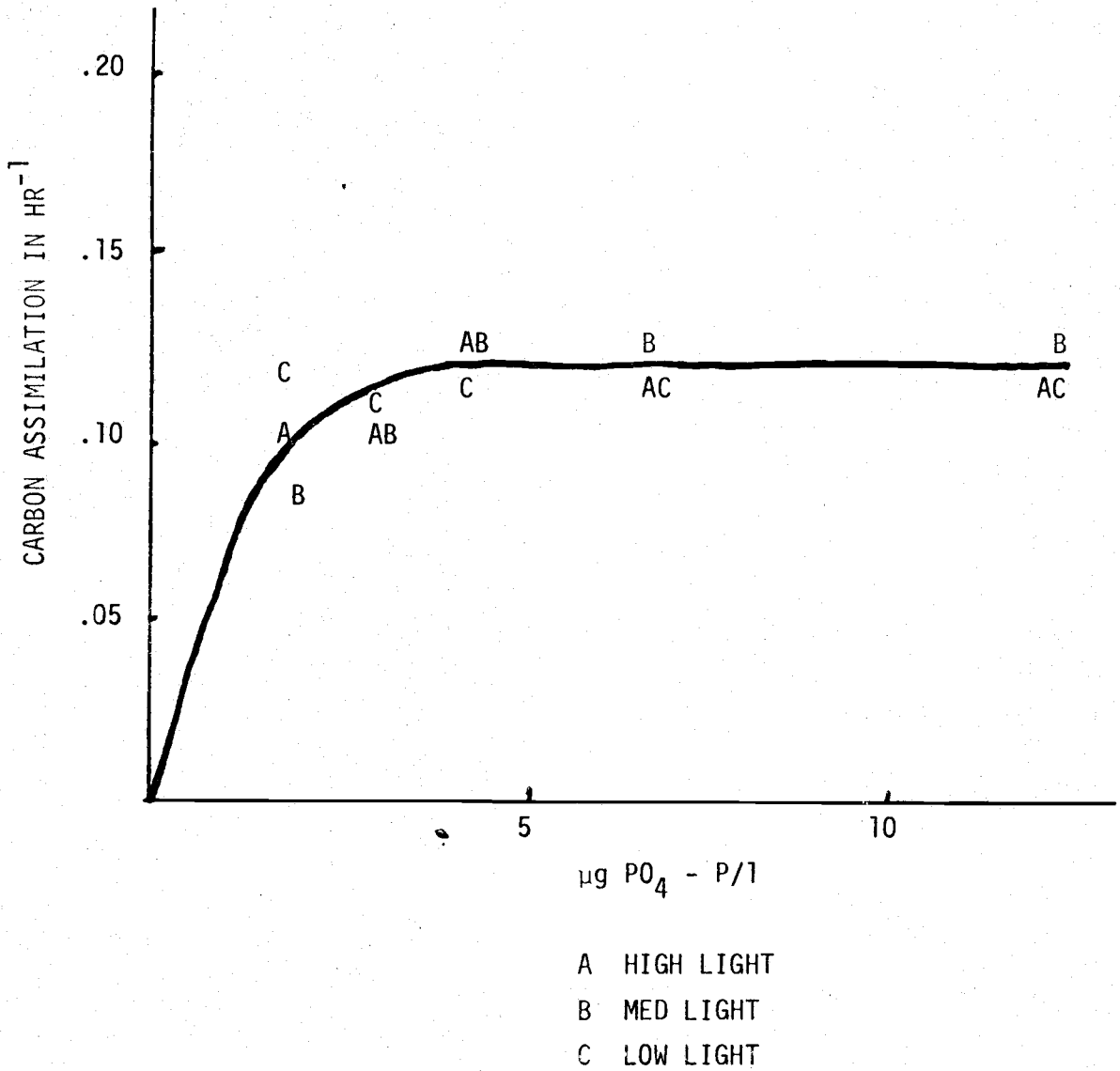


Figure 19. Carbon assimilation rate ($\frac{\mu\text{gC/l}\cdot\text{hr}}{\mu\text{gC/l}}$) by Chester Morse Lake phytoplankton exposed to 4000, 2000 and 1000 lux light intensity and nutrient additions of 50 $\mu\text{g/l}$ N and 0-10 $\mu\text{g/l}$ P on 15 Sept. 1972.

LAKE SAMMAMISH (8-3-72)

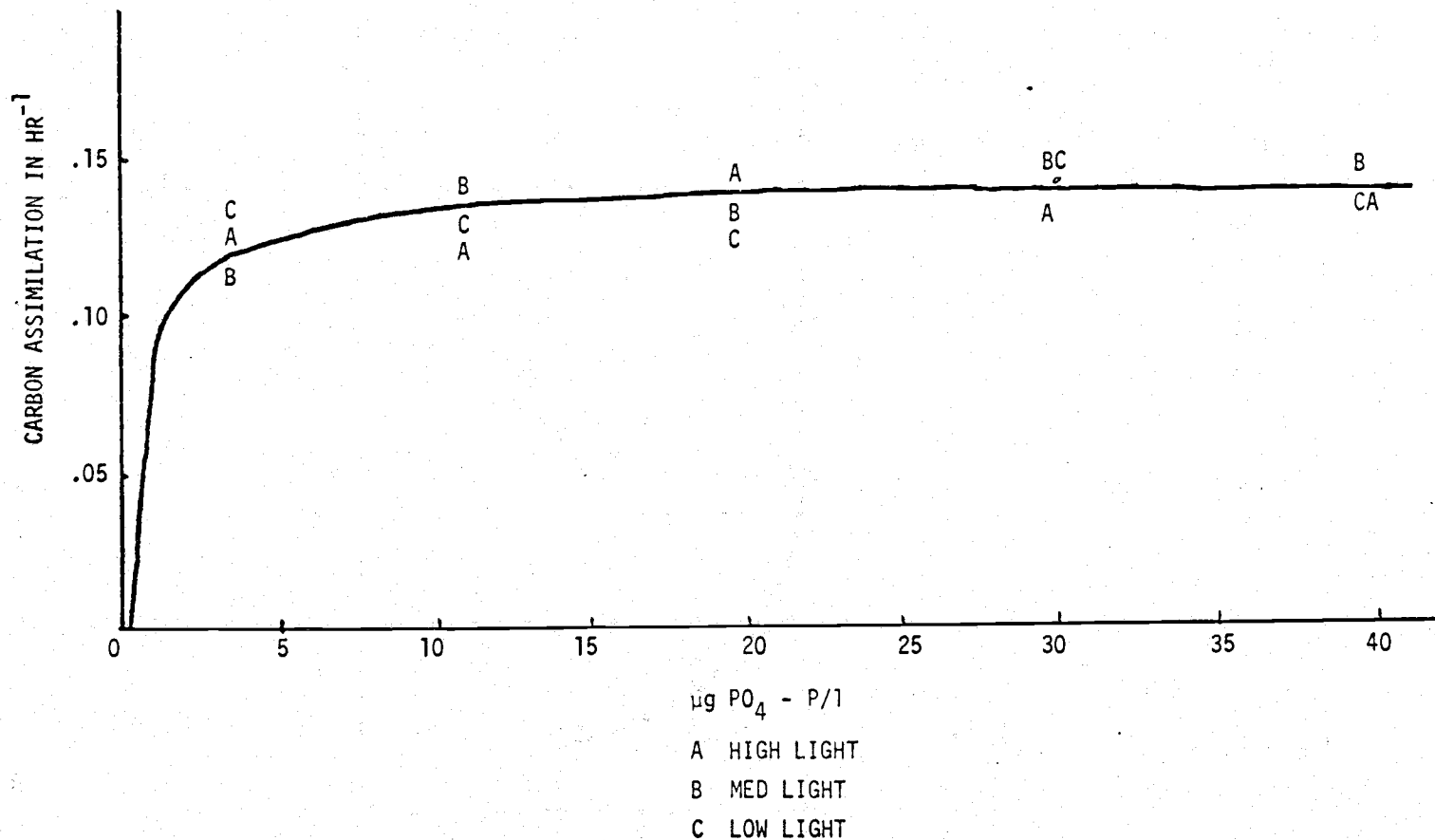


Figure 20. Carbon assimilation rate ($\frac{\mu\text{gC/l}\cdot\text{hr}}{\mu\text{gC/l}}$) by Lake Sammamish phytoplankton exposed to 4000, 2000 and 1000 lux light intensity and nutrient additions of 100 $\mu\text{g/l}$ N and 0 to 40 $\mu\text{g/l}$ P on 4 August 1972.