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PHYTOPLANKTON PRODUCTIVITY AND GROWTH RATE KINETICS IN THE CEDAR RIVER LAKES

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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 the monomictic lakes by inadequate light because of unfavorable climate and/or a lack of thermal stratification. Strong inhibition by light (probably u.v.) was observed in Findley such that average maximum productivity occurred at 10% of surface intensity while maximum was customarily at 60% in the other lakes. Annual productivity was 369C/m^2 in Findley, 479C/m^2 in Chester Morse and 1989C/m^2 in Sammamish. The range in mean chlorophyll *a* content was 0.8 to 10 µg/ℓ for the same lakes respectively. Although more than three fourths of the productivity in the four lakes was contributed by nanoplankton (5-50µ), a tendency for increased contribution from netplankton was observed with increasing trophic state.

In vitro experiments during all parts of the growing season show that nitrogen (N) and phosphorus (P) were simultaneously limiting productivity increase in the three lakes. Growth rate kinetics experiments showed increasing half-saturation constants for P (0.17 to 2.8µgP/ℓ) for the natural phytoplankton progressing from oligotrophy to eutrophy. Growth rate models using these parameters were evaluated in Findley Lake subsequent to iceout in 1973. The best agreement was obtained with a model using light (with a function that included inhibition) N and P in contrast to several other combinations of those variables. Light was the most important factor and adaptation problems to low experimental light necessitated increasing the maximum growth rate by a factor of 10 in order to obtain the best agreement with *in situ* growth rate.

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 a general quantiative 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. At the same time, models of finer resolution are needed for study purposes to better understand the mechanisms of principal lake processes.

To accomplish these goals of general models that are useful to the management of man's water resources as well as detail models for study purposes first requires the development of basic functions that compose the model parts. 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 a 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 growth kinetics of natural phytoplankton in response to nutrient concentration 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 two years and Chester Morse Lake for three. Analyses are incomplete for all of 1973 and therefore will not be presented at this time. However, more in depth analysis of 1971-72 data are presented. Experimental procedures for defining growth rate kinetics of the natural phytoplankton have been worked out and complete analysis of the 1972 data is presented. Model evaluation in Findley in 1973 is presented.

Lake Sammamish has been sampled for four 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. Those data were compared with data from 1970-72 in 1972 (Welch, et al., 1972) to determine if trophic status of the lake has changed and will not be repeated here.

For the purposes outlined, a minimum of three years data from each lake is considered necessary 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. However, the three years of data should provide reasonably reliable means for the different lakes. Future efforts should be concentrated on short term intensive monitoring for purposes of validating finer resolution models of nutrient uptake, growth kinetics and nutrient cycling. This is proposed for 1974.

Because recovery of Lake Sammamish has been so slow, processes should be monitored there for at least three more years. The effort on Lake Sammamish is being partly supported by EPA for purposes of modeling long term recovery and phosphorus cycling.

METHODS AND MATERIALS

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 1973 by us. Chester Morse was sampled during part of 1971 and all of 1972 and 1973 and Findley in 1972 and 1973. The sampling in Findley was intensive in 1973, being as frequent as three times per week after iceout.

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 per cent 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. Findley Lake, however, was sampled at every 5 meters, because nearly the whole water column was in the photic zone.

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. These results have been reported elsewhere (Welch et al., 1972; Hendrey, 1973; Emery, 1972).

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 NO_3-N and PO_4-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 NO_3-N. NH_3-N was determined by the phenolhypochlorite method of Solo'rzano (1969). Chl *a* was determined with a Turner Model 110 fluorometer. All chemical analyses except for total P were performed on filtered (0.45μ poresize) water samples. These concentrations are reported as weighted means in the photic zone.

Growth Kinetics Experiments

Experiments with lake water and natural phytoplankton were conducted in flasks in the laboratory to determine; (1) which nutrient was limiting growth, and (2) the growth rate kinetics related to increase in limiting nutrient concentration. Three experiments were conducted in water from Chester Morse Lake, two from Findley Lake and one each from Lakes Sammamish and Washington during late summer in 1972. In 1973, experiments were conducted in each lake following the spring diatom outburst. In 1972, 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 1000 lux). In 1973, only one light intensity was used because little variation with *in vitro* light was noted in 1972.

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 NO_3, PO_4, Si, C and a complete medium were added to determine the limiting nutrient. Constant amounts of NO_3 and varying amounts of PO_4 were added in the subsequent nutrient concentration, growth rate studies to determine the response to PO_4 only. PO_4 was varied from 0-10μg/ℓ in Chester Morse and Findley Lakes and 0-40μg/ℓ in Lakes Sammamish and Washington. Among other variables measured, ^{14}C 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.

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 reaches a maximum of 780mgC/m^2 day followed by a biomass increase that peaks at 2μg/ℓ chl *a*. The growing season as indicated by primary productivity is probably restricted to July and August although lower rates still occur into November (Figure 1). This suggests that annual primary production of Findley Lake is low in comparison to other lakes in the drainage which do not freeze and sustain high productivity

rates as early as April. Annual production in Findley Lake during 1971-72 was 36gC/m^2.

Ortho phosphate (PO_4-P) concentrations ranged from 2-4µg/ℓ during the study period and total phosphorus (P-tot) from 5 to 10µg/ℓ. PO_4-P did not appear to be depleted below pre-melt levels as a result of phytoplankton activity (Figure 1). Nitrate (NO_3-N) on the other hand reached a peak of 42µg/ℓ before snow melt and then declined to 6µg/ℓ in inverse relation to phytoplankton activity. The loss of 36µg/ℓ of NO_3-N without a proportionate loss in PO_4-P according to a ratio of 7-10:1 is surprising. This implies that PO_4-P is being recycled at higher rates than nitrogen. Including ammonia (NH_3-N) does not change the picture (Figure 1). NH_3-N and NO_3-N together as available N shows a decrease following iceout of about 60µg/ℓ while PO_4-P decreased only a few µg's/ℓ.

In vitro nutrient limitation experiments with Findley Lake phytoplankton (1972-73) suggest that P is the principal controlling nutrient during late summer. The addition of N and P together caused the largest increase in ^{14}C assimilation while the second greatest stimulation was with P alone. The response to complete media was equal to that of N and P while single additions of Fe, Mo, C and N were similar to controls. NO_3-N levels of 6µg/ℓ and PO_4-P low of 2µg/ℓ resulted in a N:P ratio that was possibly lower than required by cells and suggests that N should have been most limiting. However, the experiment demonstrated that both nutrients were limiting to further growth and indicated that recycling influenced N and P levels.

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. Therefore, we determined the nutrient that not only limits growth rate at sample time but at maximums of biomass increase and carbon fixation.

The response of the phytoplankton to declining nutrient resources in late summer is shown in Figure 2. The peak in biomass (chl *a*) occurred in July 1972 shortly after the peak in productivity. C uptake per unit biomass, an index of growth rate, was closely correlated with biomass in productivity during the initial outburst and decline in activity. However, in late summer when biomass and productivity were low, assimilation rate per unit biomass reached the highest level. The same tendency has been observed in Chester Morse and Sammamish and no doubt indicates increased efficiency of photosynthesis in response to reduced nutrient levels. This could be a result of changed species dominance and/or increased adaptation of the same dominant species. As table 1 shows, the results are probably a combination of both factors. *Cyclotella* was important throughout the growing season although the smaller celled *Oocystis* and *Gloeocystis* are also important in late summer.

Light plays a different and possibly more important role in Findley Lake than in the other lakes. Maximum productivity occurs in the hypolimnion in Findley. Figure 3 shows that productivity is distributed throughout the entire depth of the lake, but that the maximum rate occurs at 15 m. These

values represent percents of mean rates at each depth during the growing season. The mean light intensity at this depth was only 10 percent of surface intensity (I_0). This suggests that light inhibits photosynthesis in the upper water column while light saturation and maximum productivity occur at depths which receive 30 to 70 percent of I_0. The other lakes in the Cedar drainage show maximum productivity at about 60 percent of I_0. The inhibition is hypothesized to have been caused by deep penetration of near ultraviolet light (300-400 m) into the very clear Findley Lake waters (Hendrey and Welch, 1973).

In Findley Lake the thermocline occurred between 3 and 6 meters. The lowest oxygen concentration was 6.9 mg/ℓ at 25m on September 8. Thus, even though the D.O. dropped near the bottom it was completely aerobic at all times. The photic zone depth was greatest of all three lakes--extending to the bottom (27m) at the deepest point.

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 principally one large peak in the spring. The large peak is shifted more into early summer in Chester Morse--by as much as two months--compared to the Lakes Sammamish and Washington. The productivity peak in 1971 was about twice that in 1972. Daily productivity in Chester Morse ranged from 24mgC/m^2 day to 1680mgC/m^2 day. The mean growing season productivity, May to August, in 1971 was 570mgC/m^2 day while in 1972 it was 260mgC/m^2 day. The total annual production was 47g/m^2 from October 1971 to October 1972.

Seasonal changes in rates of productivity in Chester Morse Lake can be related to light intensity (Figure 4). The small differences in nutrient content preceding peaks in productivity are not necessarily related to increases in carbon assimilation. Since only the nutrient content is known, which is simply the residual difference between uptake and supply, and it is hardly indicative of nutrient supply. Figures 4 and 5 show this pattern of NO_3-N and PO_4-P removal during the growing season and regeneration during autumn and winter mixing. NO_3-N is the principal available N form in Chester Morse; NH_3-N remains fairly constant. However, NH_3-N actually appears more important in summer.

Figure 4 indicates the difference in light intensity is insufficient to account for the reduced productivity in 1972 as compared to 1971. Secchi disk depths show no difference suggesting that water transparency was similar. Although one can expect light intensity to be closely related to productivity the magnitude of productivity is probably more nearly dependent upon nutrient supply. As was the case in Findley Lake, increased biomass and productivity in Chester Morse Lake was limited by both N and P on June 23 and September 5, 1972. An experiment in August 1973 indicated that P was as stimulatory as any other combination of N, Si, C and a complete medium. However, these experiments plus another in May 1973 show that throughout the growing season in Chester Morse Lake, all other nutrients except N and P were in adequate supply. Of the two, P probably controls productivity more than N.

Table 2 shows an account of dominant phytoplankton genera in Chester Morse during 1971-72. Although this lake is clearly oligotrophic, the

blue green algae *Anacystis* is present in appreciable numbers in late summer. Diatoms are most important, but very small green algae (<3μ) are also abundant. However, these small forms are not important in 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 October 13, 1972. Thus, the pattern of O_2 change in Chester Morse is similar to Findley - they both remain totally aerobic throughout the year.

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. 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. Annual production in 1970 was 234gC/m^2 and 162gC/m^2 in 1971.

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. Stratification in the upper 5 m occurred in April in 1971, but similar stratification did not occur in 1970 until June. Likewise in 1965 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 has been described in earlier reports (Welch et al., 1972).

Species composition of the outbursts shows interesting trends. The April peak is composed entirely of diatoms - usually *Fragilaria* is dominant with some *Stephanodiseus* and *Asterionella* However, when the peak is delayed, then the blue green *Anabaena* is dominant although *Fragilaria* is important. This difference could be related also to the differing mixing characteristics and light availability - floating forms being more able to compete for light during periods of poor stratification.

Nutrient content decreased during the spring outburst of diatoms in each year of study in Lake Sammamish. Nitrate in particular was found to decrease inversely to phytoplankton biomass. If ortho P depletion is compared with NO_3-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. A detailed accounting of the phosphorus cycling in the water column in Lake Sammamish during the stratified period shows that in order to meet the demand of photosynthesis by the phytoplankton, 80% of the required supply must come from regeneration. Probably most significant to this regeneration process are the zooplankton and the phytoplankton themselves (Welch, 1973).

Although the N:P ratio drops slightly below 7:1 at times in the summer, and N would be expected to be most limiting to growth, *in vitro* experiments during spring summer and fall have shown that N and P simultaneously limit further increase in biomass and productivity. Sammamish, in this regard shows no real difference in response from Findley and Chester Morse. Thus, even though the N:P ratio suggests that N limits in Sammamish, there is so little P around (1-2µg/ℓ), that in order to utilize the added N more P is required. Furthermore, Staley[1] has measured N fixation rates in Sammamish as high as 0.25µg/ℓ hr in summer which is sufficient to equal the NO_3-N pool in a few days time in late summer when NO_3 is low. Considering this and the foregoing P is probably the most long term controlling nutrient.

In contrast to the other two lakes, the Lake Sammamish hypolimnion loses nearly all of its oxygen during the stratified period (Welch et al., 1972). 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.

Cell Size and Productivity

Nanoplankton (5-50µ) contribute most of the productivity in the lakes (Table 3). An increased contribution from the netplankton would be expected with an increase in productivity - that is the ratio of net:nano plus ultra should increase progressing from Findley to Lake Washington. As Table 3 shows, the lower three lakes conform to this quite well, but Findley has a greater contribution from netplankton. Hendrey (1973) has suggested that this may be a mechanical artifact since the size separations were performed by sequential filtration which would result in more centric chain diatoms counted as netplankton in more wind-protected Findley, whereas they would tend to pass through the 50µ net in the lower lakes where wind-driven turbulence is greater. Such characteristic differences in chain lengths were in fact observed.

Another artifact affecting this distribution is the tendency for 5µ millipore filters to effectively filter particles to near 1µ. This would account for an underestimation of ultra plankton productivity. However nanoplankton, both through productivity, chlorophyll content and actual cell counts clearly dominate in these lakes showing a tendency toward more netplankton as trophic state increases.

Growth Rate Kinetics

For all of the kinetic experiments the changes in the P/B ratios tended to be rather erratic over the first few days of growth. This may have been due to handling effects such as changes in temperature and some change in light intensity.

[1]J. Staley, Dept. of Microbiology, U. of W., personal communication

To provide a consistant treatment of the experimental data the mean P/B ratios over the first three measurements, made on days 0, 1, and 3 or days 1, 3, and 5 of the incubation, were used for a particular treatment. To obtain kinetic parameters this P/B value for each flask in a light treatment group was plotted against the initial P concentration of the flask, S.

A significant result is that the natural phytoplankton responded to such low concentrations of added phosphorus. The Findley Lake test results provided very nice Michaelis-Menten type curves, with the lower two initial nutrient levels 0.5 and 1.5 g/ℓ, respectively, resulting in suboptimal growth. A maximum specific growth rate was clearly indicated with the P/B plateau being observed at the upper two or three nutrient levels. The effect of light intensity is also obvious. Figure 7 shows growth rate as a function of light according to $\mu = R/R_o\ e^{(1-R/R_o)}$, utilizing the mean P/B ratios observed for each of the five nutrient treatments. Figure 8 indicates the growth rate as a function, $\mu = \mu_m\ S/k_t+S$, utilizing the mean P/B ratios observed at the three light intensities (see Hendrey, 1973, for model explanation).

The Chester Morse Lake phytoplankton results were less like an ideal Michaelis-Menten response. Figures 9 and 10 indicate the P/B ratios as functions of light intensity and nutrient concentration respectively. From Figure 10 it can be seen that the original concentrations of P were slightly suboptimal, at 2.0 µg/ℓ, but with the P concentration raised to 3.0 µg/ℓ the μ_m plateau was attained. The Lake Sammamish experimental results were similar, with the initial concentration of 3.1 µg/ℓ being slightly suboptimal. Figures 11 and 12 illustrate growth rate kinetics for Lake Sammamish as plots of the P/B ratios with respect to light and P concentration.

The response of the Lake Washington total phytoplankton community followed a typical Michaelis-Menten function. Nutrient levels up to 6.1 µg/ℓ were suboptimal but the response was tending toward a μ_m plateau. Figures 13 and 14 illustrate the effects of light intensity and nutrient concentration on the total phytoplankton community.

An initial hypothesis of this research was that the k_t values of natural populations are related to the productivity of the ambient waters in such a fashion that as productivity increases so does k_t. Table 4 compares the estimated parameters k_t, μ_m, R_o and annual production for the four lakes. The direct correlation between trophic state and k_t confirms this behavior for the natural phytoplankton communities in these lacustrine environments.

The effect of light was found to be significant, as demonstrated by analysis of variance on the data (including R = 0), but the response of the algae to different light regimes was less than had been anticipated. This probably resulted from physiological adaptation of the algal cells to the light to which they were exposed. Steeman Nielsen, et al., (1962) were able to show that plankton algae adapt to new light intensities within 17 to 48 hours when light intensities of 3000 to 30,000 lux were used. The light levels used in these experiments were quite low in comparison, 1000 to

4000 lux, so that only slight changes in algal physiology would have been needed in adapting to the 3 light intensities used. Subsequent, short term experiments (hour) with natural phytoplankton and these same three light levels have shown a very clear response to light intensity indicating that several days' exposure does result in some adaptation to light.

Light intensity produced the most variation in growth response at the lowest nutrient level. Unenriched flasks incubated at 4000 lux consistently had higher P/B ratios than those receiving 2000 or 1000 lux. At higher nutrient levels this was not always the case, and the difference between responses to different light intensities was less pronounced. Cells at higher nutrient concentrations were probably close to or at their maximum specific growth rates regardless of light exposure because of adaptation to the light regime. On the other hand, cells which were not given nutrient enrichment were in a relatively nutrient starved condition and may have been unable to make physiological adaptations to the various light regimes as rapidly as the nutrient rich cells.

The function which related the effects of light intensity and nutrient concentration to the P/B ratios,

$$\mu = \mu_m \left(\frac{S}{k_t + S}\right) \frac{R}{R_o} e^{(1-R/R_o)}$$

provided a good fit to the observed data at the 0.95 confidence level, when the function was forced through P/B = 0 at light intensity = 0 and at phosphorous content = 0. The R^2 statistic, indicating the portion of total variance in μ explained by the model, ranged from 0.95 for the upper three lakes to 0.91 for the whole phytoplankton community in Lake Washington.

Effects of Light Intensity and Nutrient Concentration on Net- and nanoplankton When the fractions of the phytoplankton community were considered in the Lake Washington experiment, the R^2 statistic was 0.95 for the nannoplankton, but only 0.75 for the netplankton. The unexplained variations in the netplankton data may be due to uneven clumping of the phytoplankton algae so that large bundles appeared at random on net filters.

In Lake Washington the R_o value for the netplankton was 5360 lux, while the nanoplankton R_o was 1840 lux (Figures 15 and 17). The larger cells were able to utilize light at higher intensities than were the smaller nanoplankton. This might be explained by the physical limitations of cell size restricting chlorophyl content, and analagous situation to enzyme content and temperature response discussed by Jorgensen and Steemann Nielsen (1965).

Figures 16 and 18 show the P/B ratios as a function of nutrient content for the net- and nanoplankton, respectively. The corresponding k_t values are 4.6 µg/ℓ and 2.9 µg/ℓ. We had hypothesized that smaller cells would be found to have lower k_t values and the data supports that hypothesis.

Long Term Changes in Community Composition. We were also interested in the long term effects on the natural phytoplankton communities of the nutrient additions and light intensities utilized in these experiments. The Lake

Sammamish cultures were allowed to continue growing for two weeks under the same light regimes described above. At the end of this period the relative abundance of each of three categories of algae, greens, blue-greens, and diatoms was evaluated. Table 5 lists the organism counts observed as averages of replicate flasks with three light treatments at a particular phosphorous level presented as rows, and the five phosphorous treatments at a particular light level presented as columns. By comparing the row means the effect of the various P treatments can be observed, while a comparison of column means reveals the effect of light intensity.

The green algae were favored by higher phosphorous enrichment and higher light intensity. The blue-green algae were also favored by increasing phosphorous content but grew best at the lowest light level. The diatoms responded best at the highest light level and all of the phosphorous enrichments produced much greater diatom growth than was seen in the control, but essentially the same response was observed for the four nutrient enrichments. The diatoms seem to have reached a growth plateau with the additions of the lowest level of phosphorous enrichment, 10 µg P/ℓ, and the addition of more phosphorous in excess of this level did not stimulate more growth as was the case for the greens and blue-greens.

These results have particular significance with regard to Lake Sammamish. It may be expected that if the phosphorous income to the lake increased, production of all algal forms would accelerate but a resultant increased biomass would cause a reduction of light penetration into the lake. This combination of conditions would favor the development of populations of the blue-green algae.

Model Evaluation

Several growth rate models were evaluated in 1973 by comparing prediction with observed growth rate in Findley Lake. Findley was sampled each two to three days following iceout for most of June and part of July, and the existing levels of light intensity, PO_4-P, NO_3-N, chl *a* and productivity were measured at 5 m intervals throughout the deepest water column.

The growth rate models evaluated were the Michaelis Menton type as follows:

A. $$\mu = \mu_m \frac{P}{K_t + P}$$

B. $$\mu = \mu_m \frac{P}{K_t + P} \frac{R}{R_o} e^{(1-R/R_o)}$$

C. $$\mu = \mu_m \frac{P}{K_t + P} \frac{N}{K_t + N}$$

D. $$\mu = \mu_m \frac{P}{K_t + P} \frac{N}{K_t + N} \frac{R}{R_o} e^{(1-R/R_o)}$$

where μ is the growth rate, μ_m is the maximum growth rate, P is soluble ortho phosphorus, N is nitrate nitrogen, R is the observed light intensity and R_o is the optimum light intensity.

Modification of *in vitro* determined parameters for light (R_o) and μ_m were necessary because of the apparent adaptation phenomenon described in the previous section. Growth rates observed in the lake were about an order of magnitude greater than the μ_m's measured in laboratory. Considering this the following parameters were used to evaluate the different models.

$\mu_m = 0.06\ hr^{-1}$

K_t for P = 0.2 µg/ℓ

K_t for N = 2.8 µg/ℓ

R_o @ 10 m = 30,000 lux

20 m = 1,500 lux

Only predicted growth rates using model D including light, nitrogen and phosphorus showed a reasonable agreement with the observed values. Model A with phosphorus alone shows much poorer agreement (Figures 19 and 20) and with phosphorous and nitrogen (model C), although not plotted, the agreement was only slightly improved. With this model the relative fit improved as depth increased. The agreement was reasonably good at 10 m and below as illustrated in Figures 19 and 20. The strong light inhibition of photosynthesis in the upper 5 to 10 meters in Findley Lake may account to some extent for the poorer agreement between observed and predicted values near the surface. The model has light inhibition built into it, but inhibition due to u.v. wavelengths in Findley may require additional modification.

This limited evaluation indicated that to show the best agreement with observed growth rate, functions for both limiting nutrients N and P and light are required, with the light function showing the biggest effect. Without the light function and inhibition built in, the growth rate in most of the Findley water column would be overestimated by about a factor of two. Thus, a light function such as:

$$\mu = \mu_m \frac{L}{K_t + L}$$

which is frequently used would overestimate growth rates particularly in a lake like Findley where light inhibition is so pronounced.

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Table 1. Dominant genera of phytoplankton in Findley Lake, observed at the depth of maximum production, exclusive of small green algae of 1 - 3 μ.

Date	Genera	Relative abundance*
10/10/71	Cyclotella	100
11/18/71	Cyclotella	100
6/ 7/72	Cyclotella	33
	Melosira	33
	Gymnodinium	33
7/ 7/72	Trachelomonas	67
	Gymnodinium	33
8/29/72	Cyclotella	70
	Oocystis	15
	Gloeocystis	15
10/21/72	Gloeocystis	25
	Cyclotella	25
	Oocystis	25
	Melosira	25

*Percent

Table 2. Relative contributions of several genera of phytoplankton to the total number of cells in Chester Morse Lake. This list does not include small algae of less than 3μ diameter nor genera which contributed less than 5% of the total.

Date	Percent	Genus
5/22/71	15	Melosira
	10	Cyclotella
6/25/71	30	Chroomenas
	5	Melosira
	5	Oocystis
8/31/71	25	Melosira
	10	Chroomonas
10/15/71	40	Chroomonas
	20	Anacystis
4/ 5/72	5	Melosira
	5	Cyclotella
	5	Chroomonas
6/11/72	48	Melosira
	7	Cyclotella
	6	Fragilloria
8/ 4/72	30	Melosira
	10	Chroomonas
	5	Oocystis
8/18/72	15	Anacystis
	15	Melosira
	5	Gloeocystis
9/ 1/72	20	Melosira
	10	Chroomonas
10/13/72	40	Melosira
	15	Chroomonas
	5	Anacystis

Table 3. Mean relative contributions of the net-, nano.-, and ultra-plankton content per square meter to daily productivity and chlorophyll *a* during the growing season in 4 lakes of the Cedar River drainage basin.

Lake	Mean % of daily productivity/m^2			Mean % of chl *a*/m^2		
	net-	nano.	ultra-	net-	nano.	ultra-
Findley	11.0	87.5	1.3	5.6	82.6	12.0
Chester Morse	3.9	92.3	3.5	3.6	99.0	7.4
Sammamish	10.3	85.3	4.4			
Washington	17.6	76.1	6.4			

Table 4. The estimated values for k_t, μ_m, and R_o are compared to the May through August mean daily productivities of four lakes of the Cedar River drainage system.

Lake	Mean Productivity mg C m^{-2} day^{-1}	k_t µg P/ ℓ	μ_m hr^{-1}	R_o lux
Findley	220 (1972)[a]	0.17	0.011	1900
Chester Morse	260 (1972)	0.36	0.007	2300
Sammamish	499 (1971)[b]	0.42	0.008	2200
Washington (whole)	1070 (1971)[c]	2.83	0.131	1851
Washington (net.)		4.55	0.135	5329
Washington (nano.)		2.82	0.167	1585

[a]July through October, the period of maximum production in Findley Lake.

[b]C. A. Rock, personal communication.

[c]W. T. Edmondson, personal communication to E. B. Welch.

Table 5. Variation in the Relative Abundance of Greens, Blue-Greens, and Diatoms Resulting from Five Levels of Phosphorous Enrichment at Three Light Intensities

	µg P/ℓ Added	Light Intensity in Lux 4000	2000	1000	Row Means
GREENS (No. of Cells)	0	43	58	32	44
	10	132	196	57	128
	20	211	143	65	141
	30	243	285	86	204
	40	334	232	92	219
	Column means	193	183	85	
BLUE-GREENS (µ of Filament Length)	0	1220	1748	2680	1883
	10	1860	4540	4160	3520
	20	3120	5010	5620	4583
	30	1840	3980	6000	3940
	40	2840	6960	5440	5080
	Column means	2176	4448	4780	
DIATOMS (No. of Cells)	0	5	2	9	5
	10	153	69	30	84
	20	91	35	24	50
	30	168	86	15	90
	40	135	30	13	59
	Column means	110	44	18	

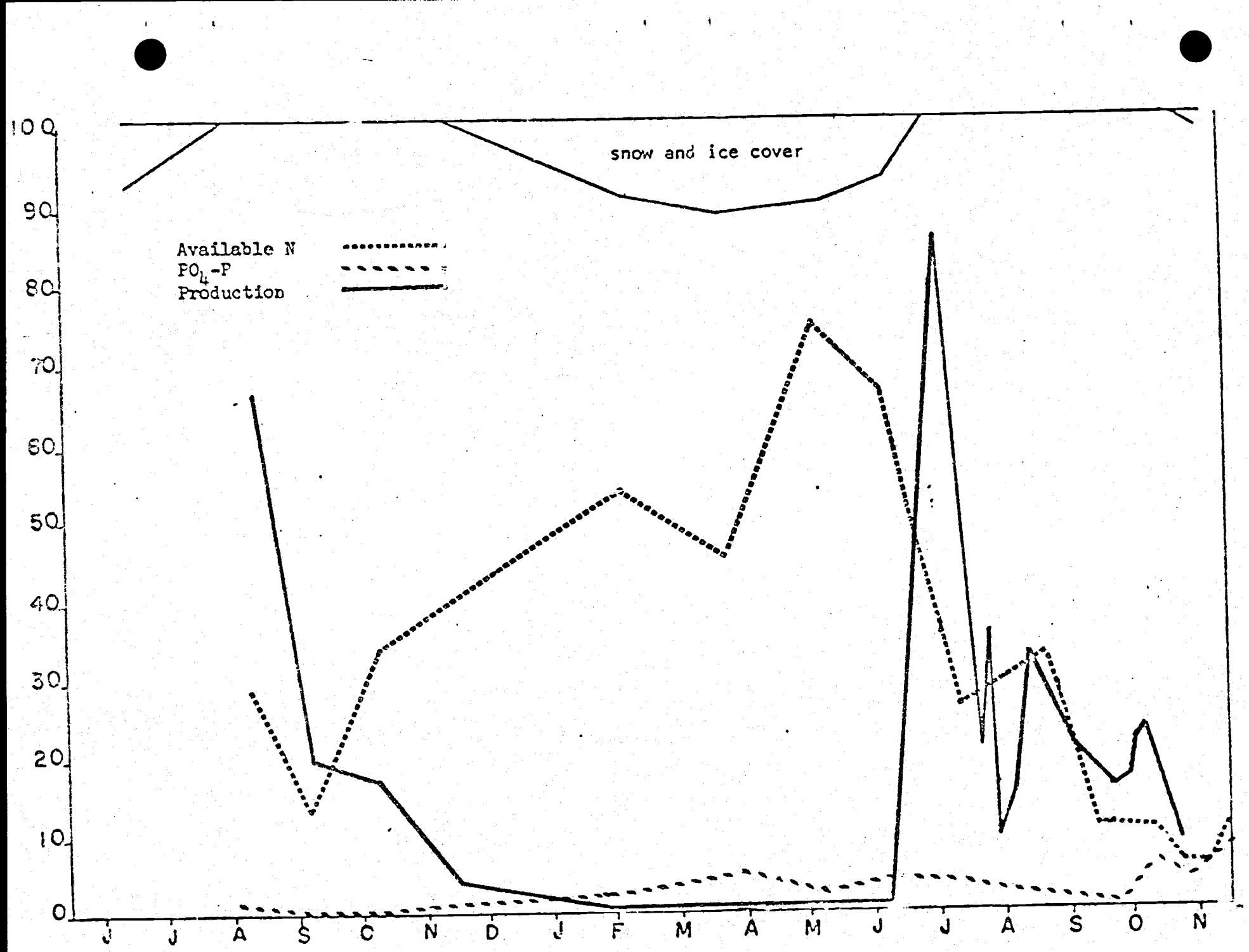

Figure 1. Findley Lake, 1971-72. Relationship between production and weighted mean nutrient concentrations. Nutrient values are in mg/m^3 and production is in mg C $m^{-2}hr^{-1}$.

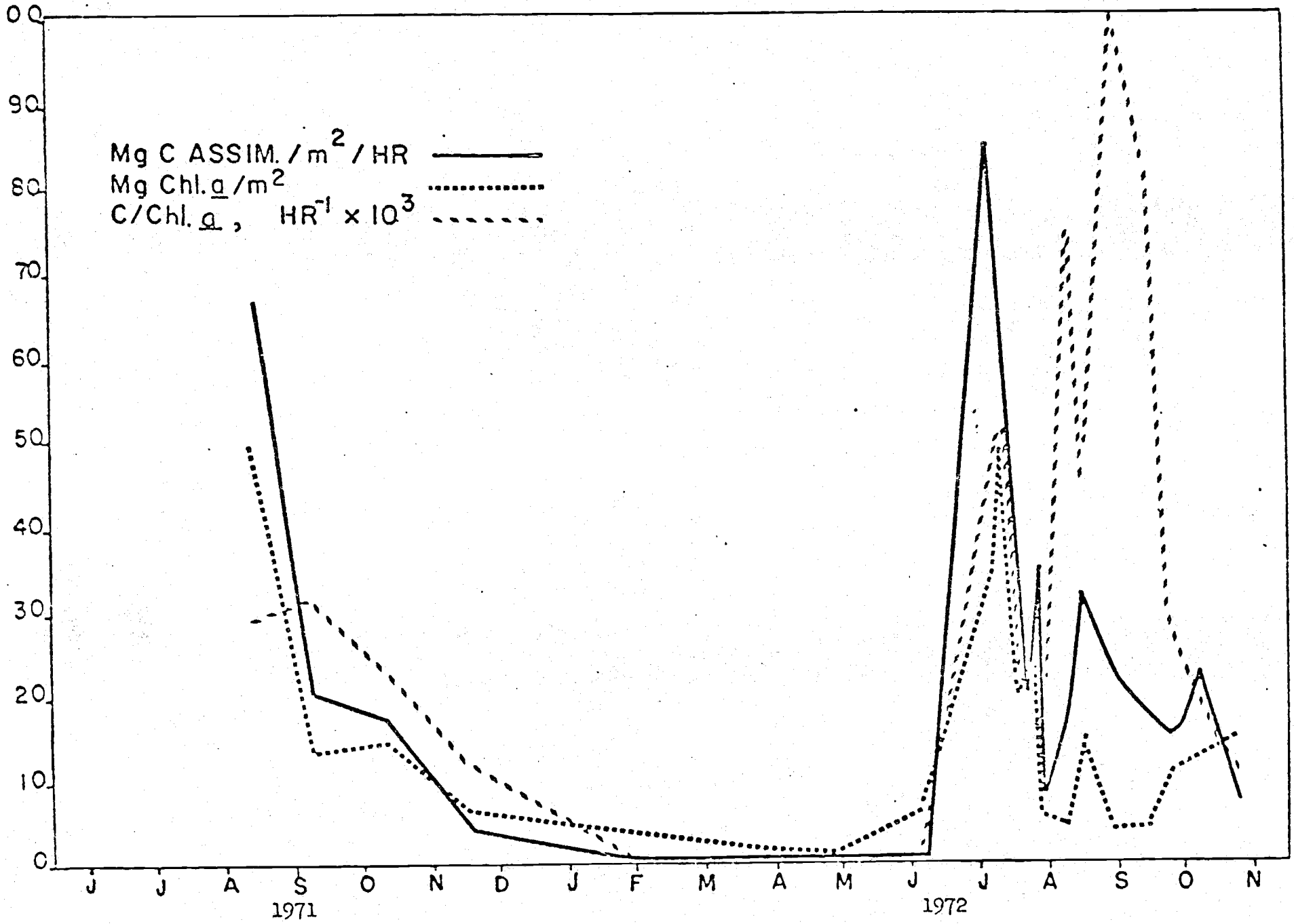

Figure 2. Findley Lake productivity, chlorophyll a content, and the carbon assimilated to chlorophyll a ratio, plotted over the period of investigation, in months.

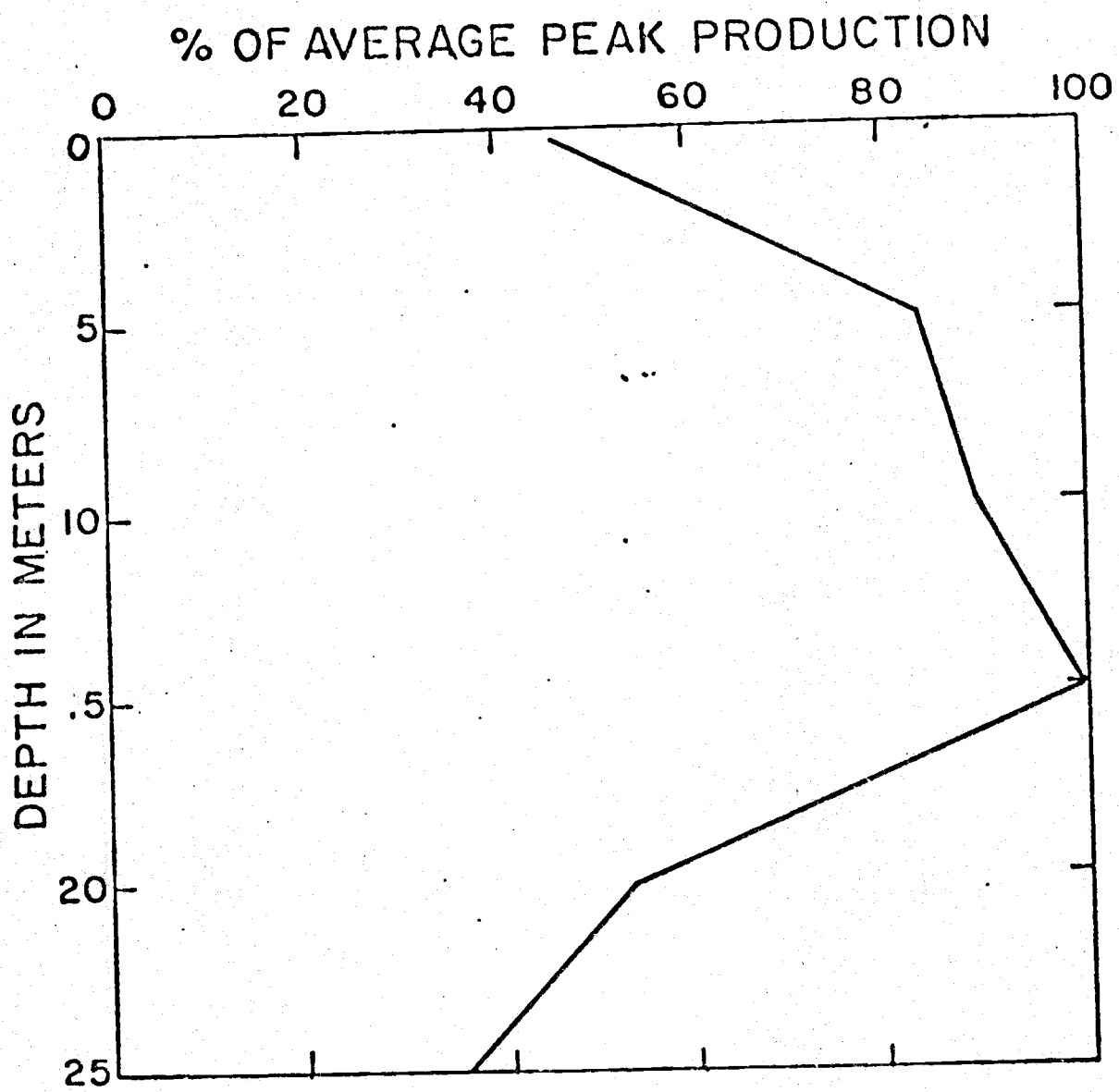

Figure 3. Findley Lake, 1972. Phytoplankton production ($mg \cdot m^{-3} \cdot hr^{-1}$) at each incubation depth is averaged over the period 7 July to 21 October, 1972. Each average is then plotted as a percent of the peak value which occurred at 15 m.

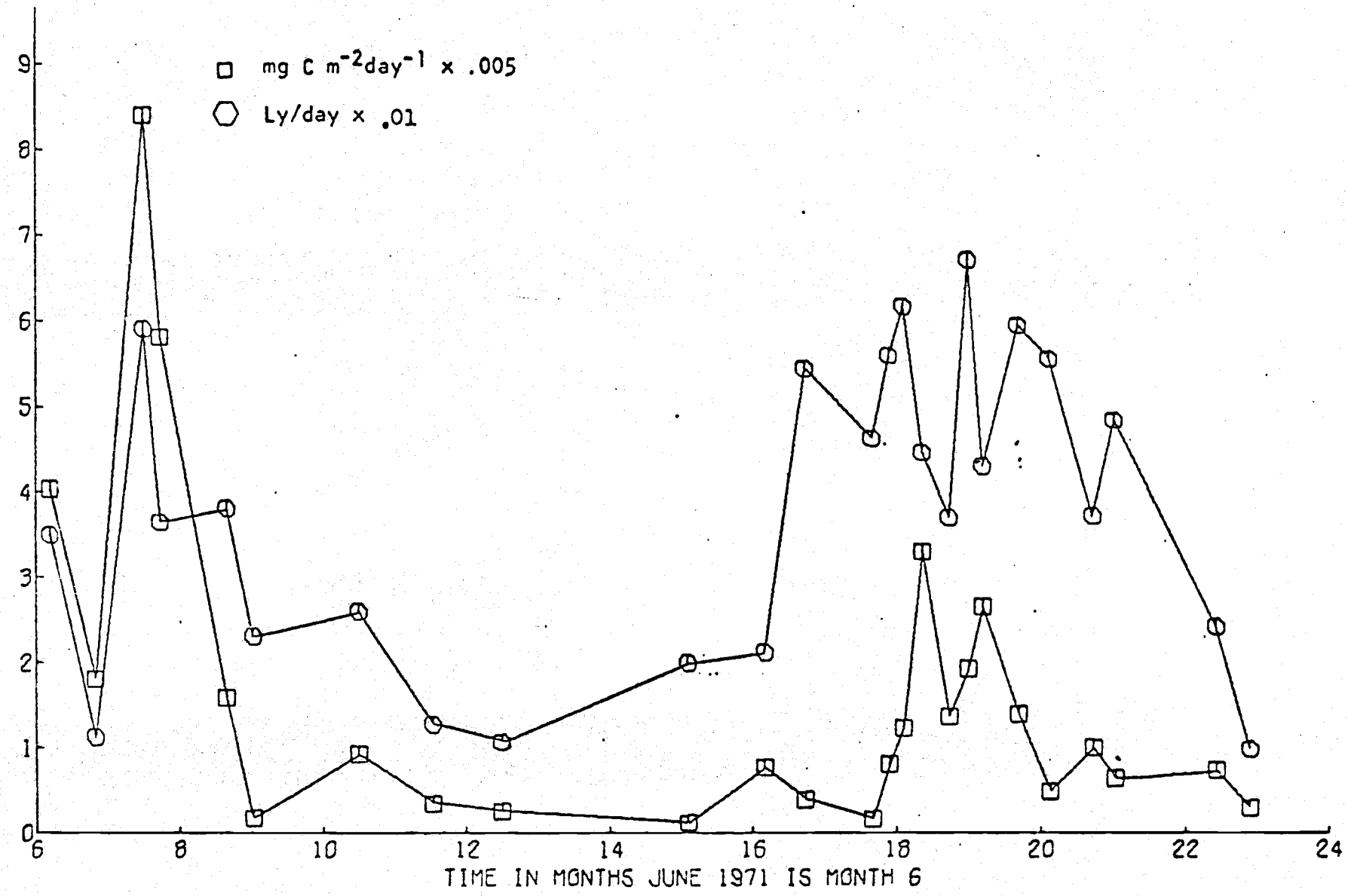

Figure 4. Chester Morse Lake, 1971-72. Comparison of aereal productivity and daily insolation.

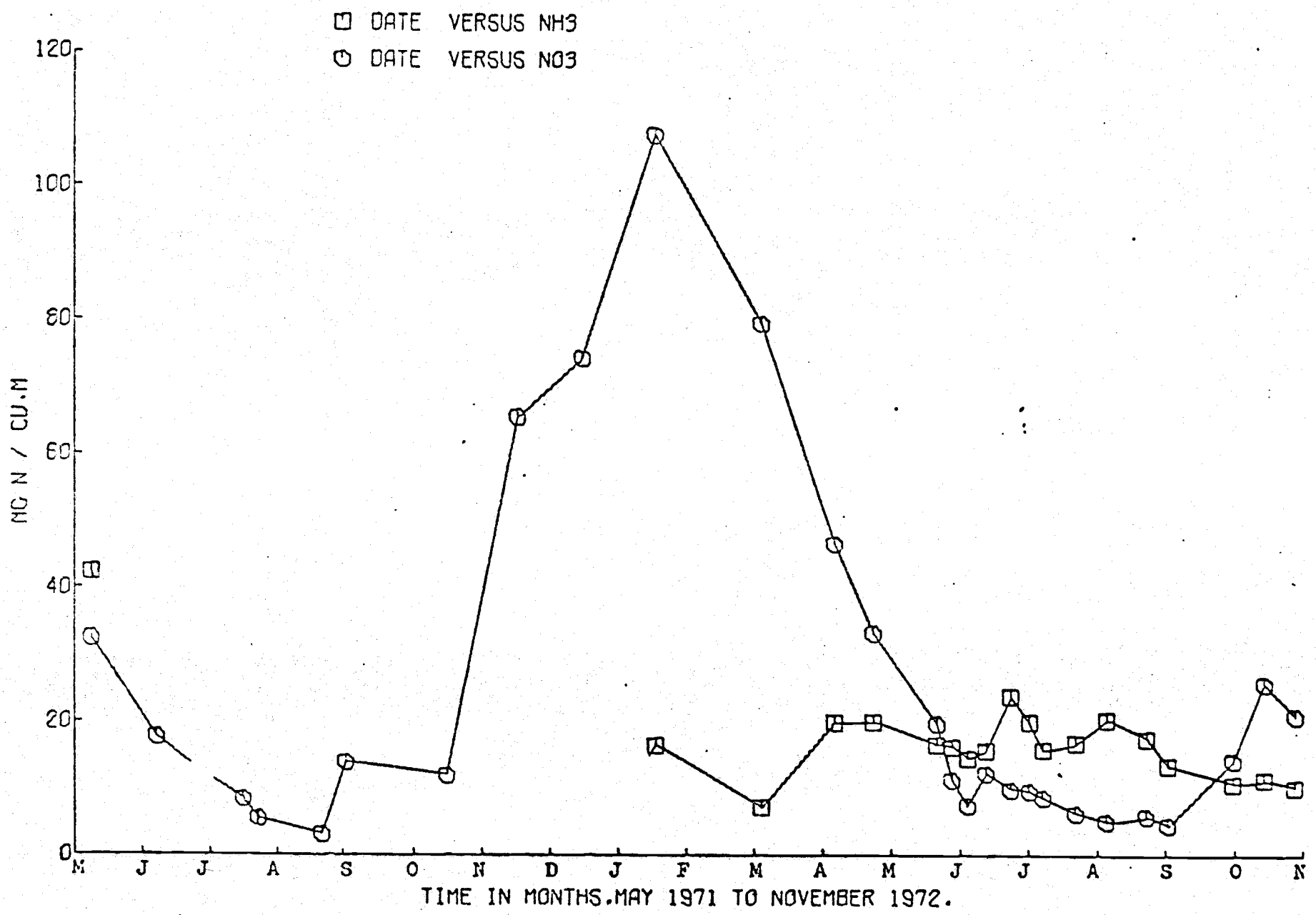

Figure 5. Chester Morse Lake. NO_3 and NH_3 nitrogen.

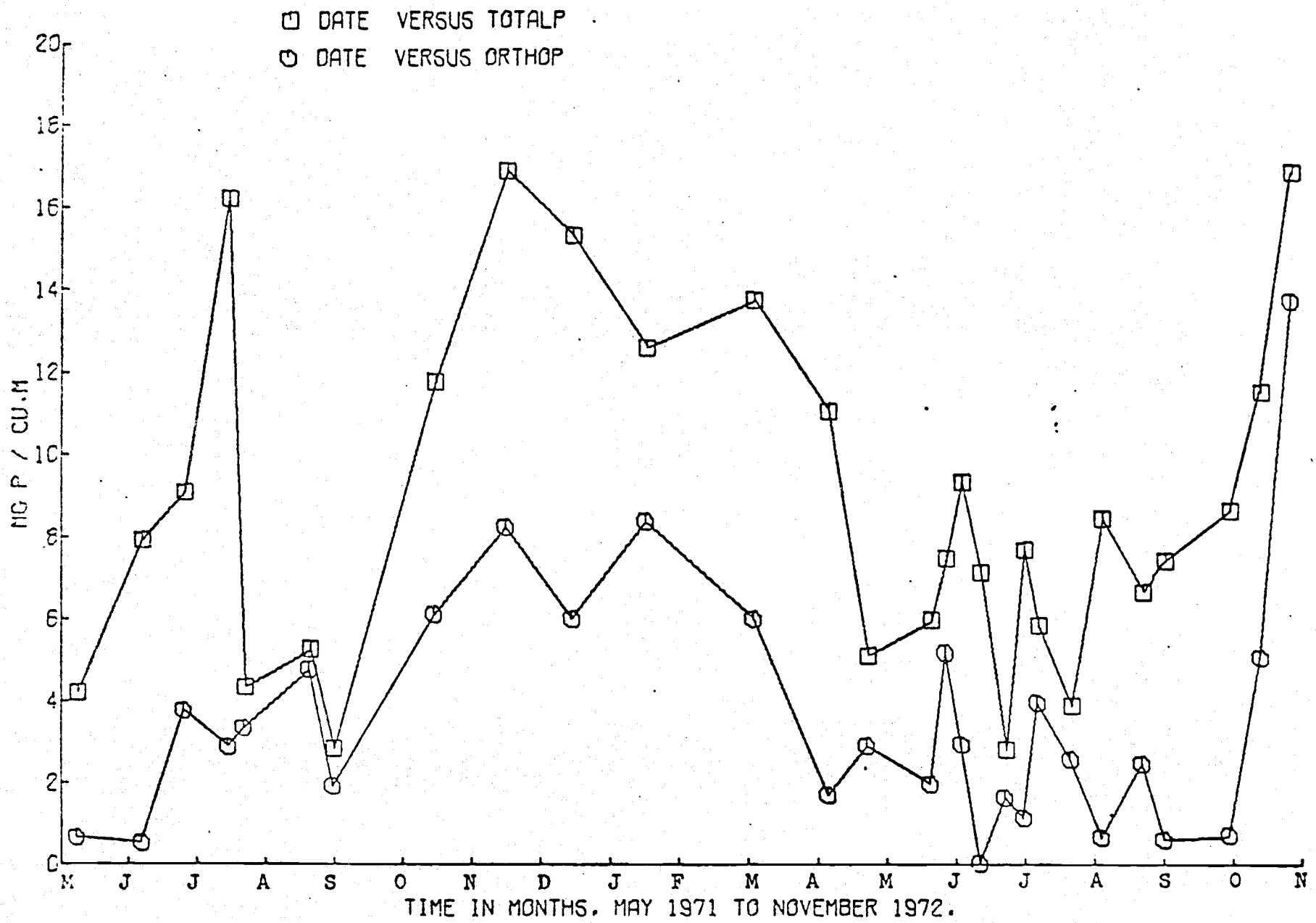

Figure 6. Chester Morse Lake. Ortho- and Total-P.

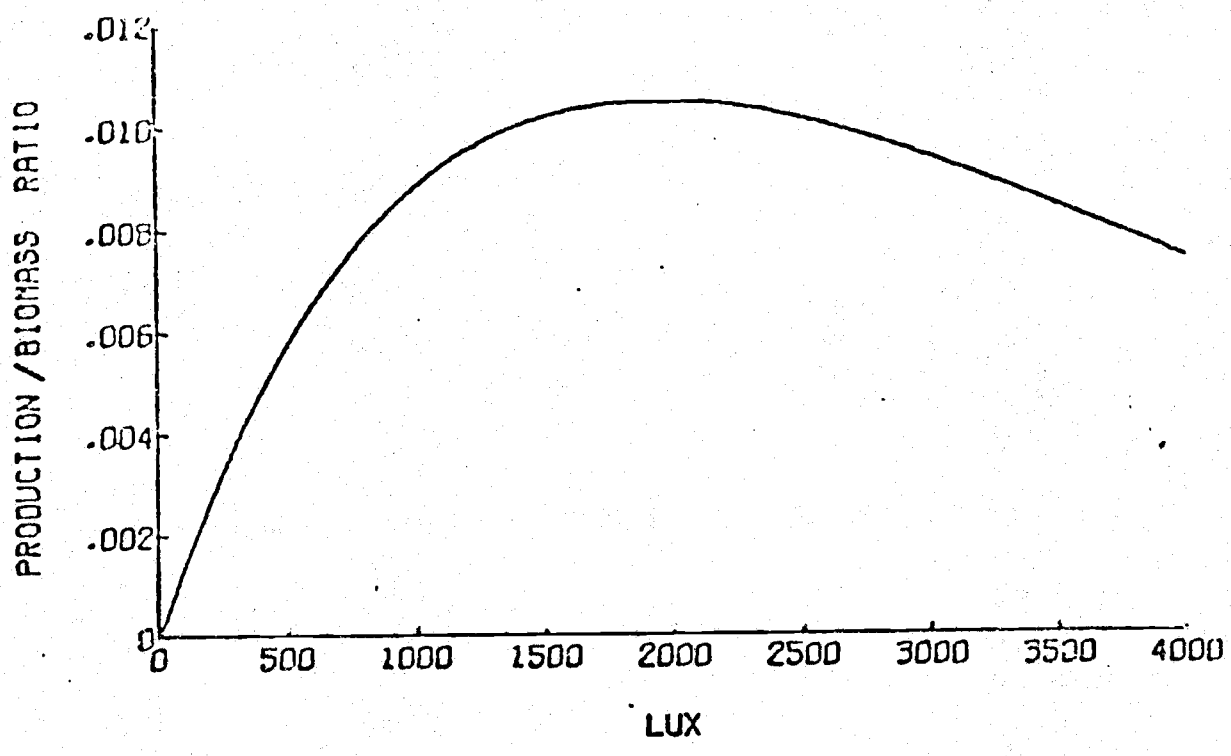

Figure 7. Findley Lake growth kinetics experiment, plot of the P/B ratio as a function of light intensity.

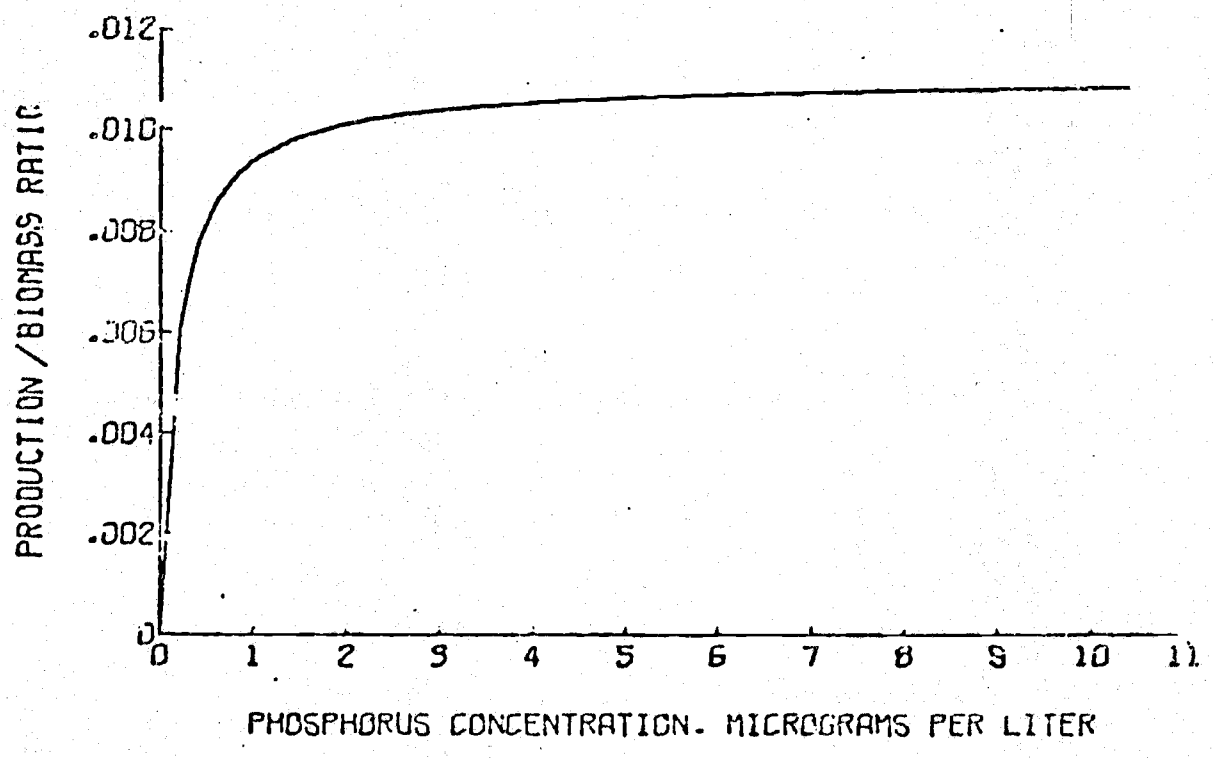

Figure 8. Findley Lake growth kinetics experiment, plot of the P/B ratio as a function of nutrient concentration.

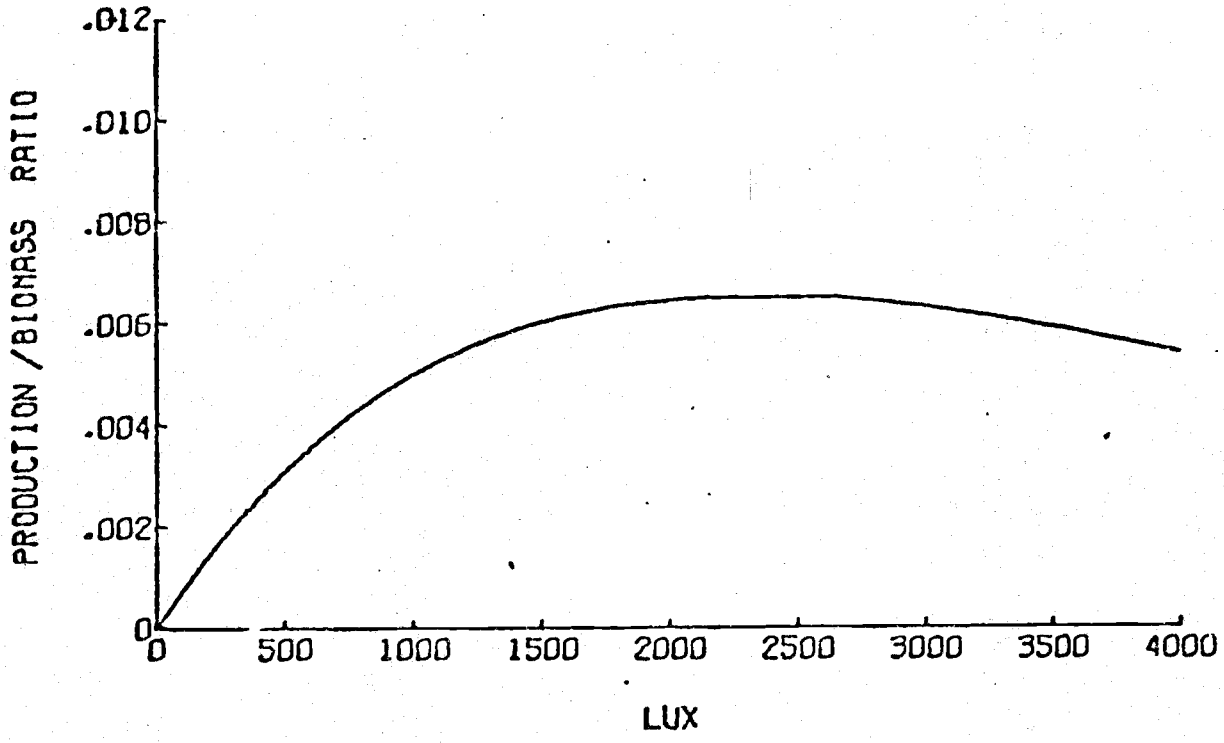

Figure 9. Chester Morse Lake growth kinetics experiment, plot of the P/B ratio as a function of light intensity.

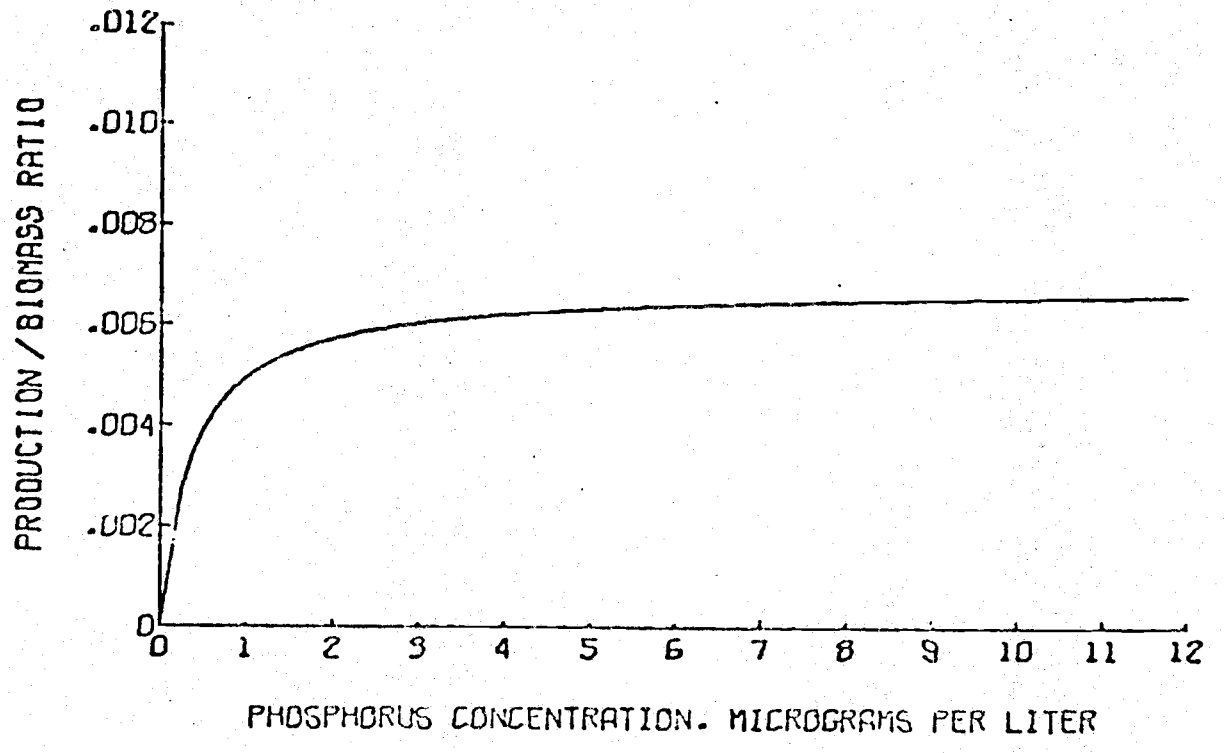

Figure 10. Chester Morse Lake growth kinetics experiment, plot of the P/B ratio as a function of nutrient concentration.

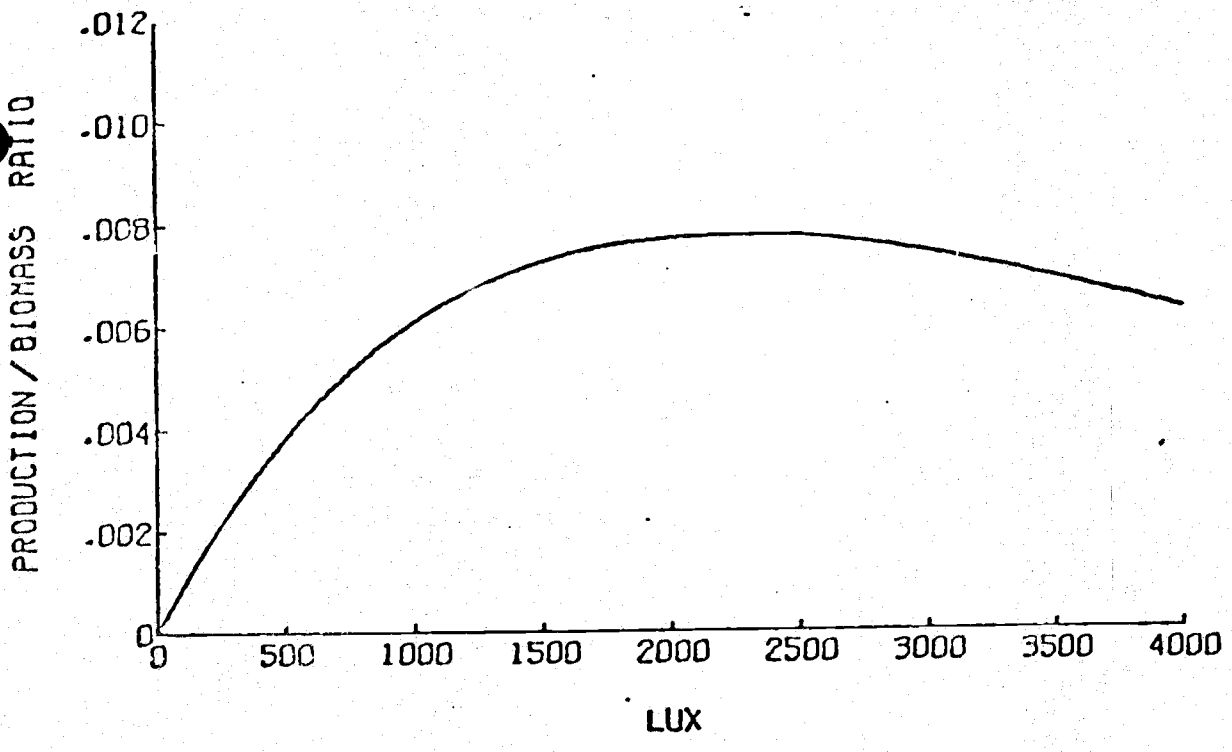

Figure 11. Lake Sammamish growth kinetics experiment, plot of the P/B ratio as a function of light intensity.

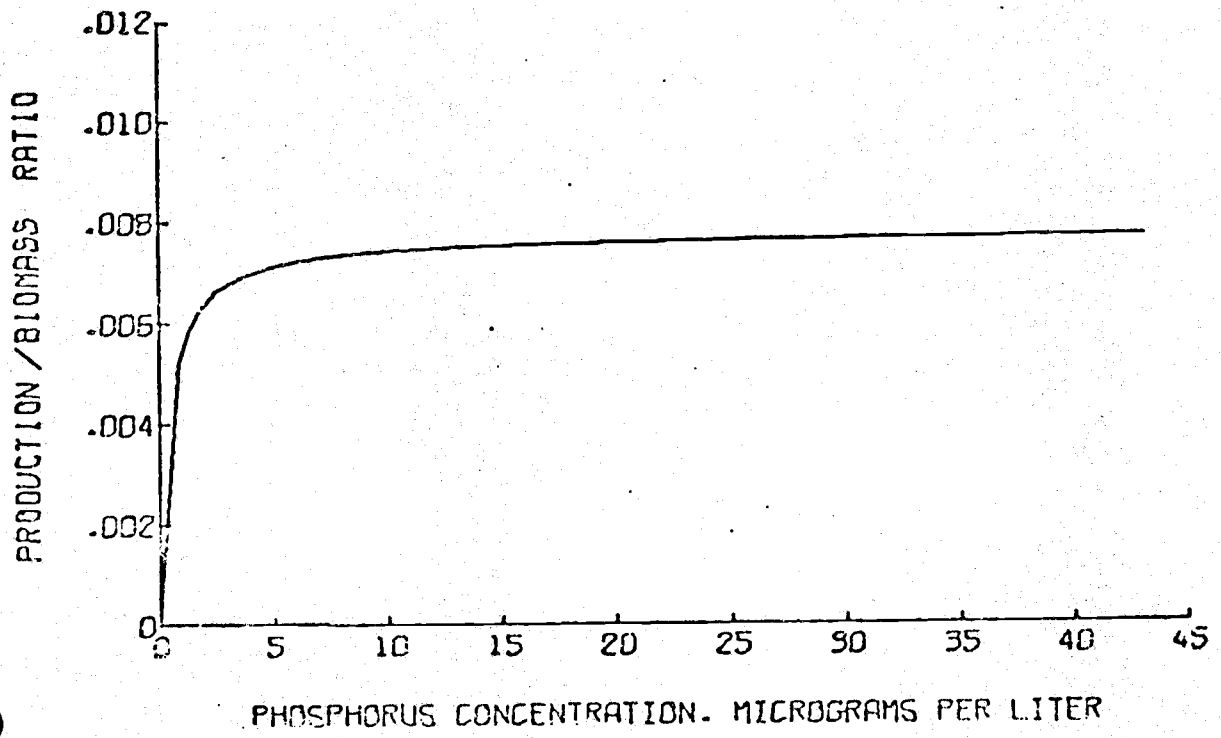

Figure 12. Lake Sammamish growth kinetics experiment, plot of the P/B ratio as a function of nutrient concentration

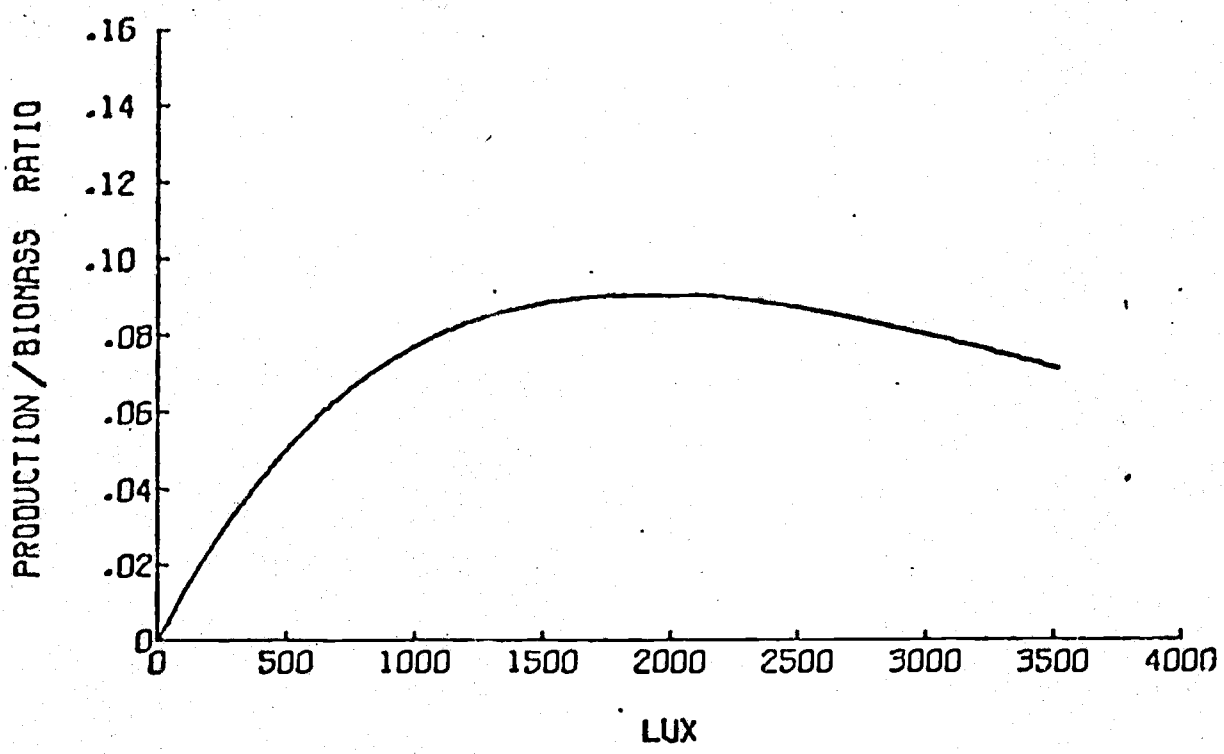

Figure 13. Lake Washington (whole) growth kinetics experiment, plot of the P/B ratio as a function of light intensity.

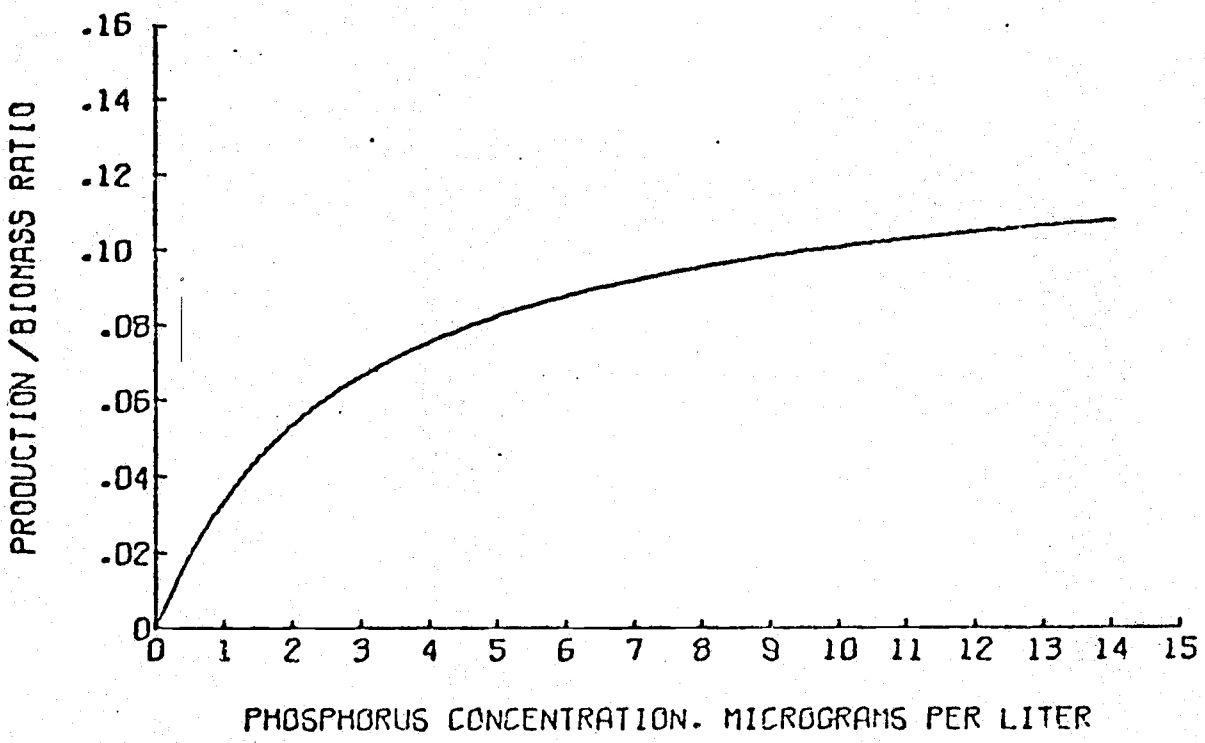

Figure 14. Lake Washington (whole) growth kinetics experiment, plot of the P/B ratio as a function of nutrient concentration.

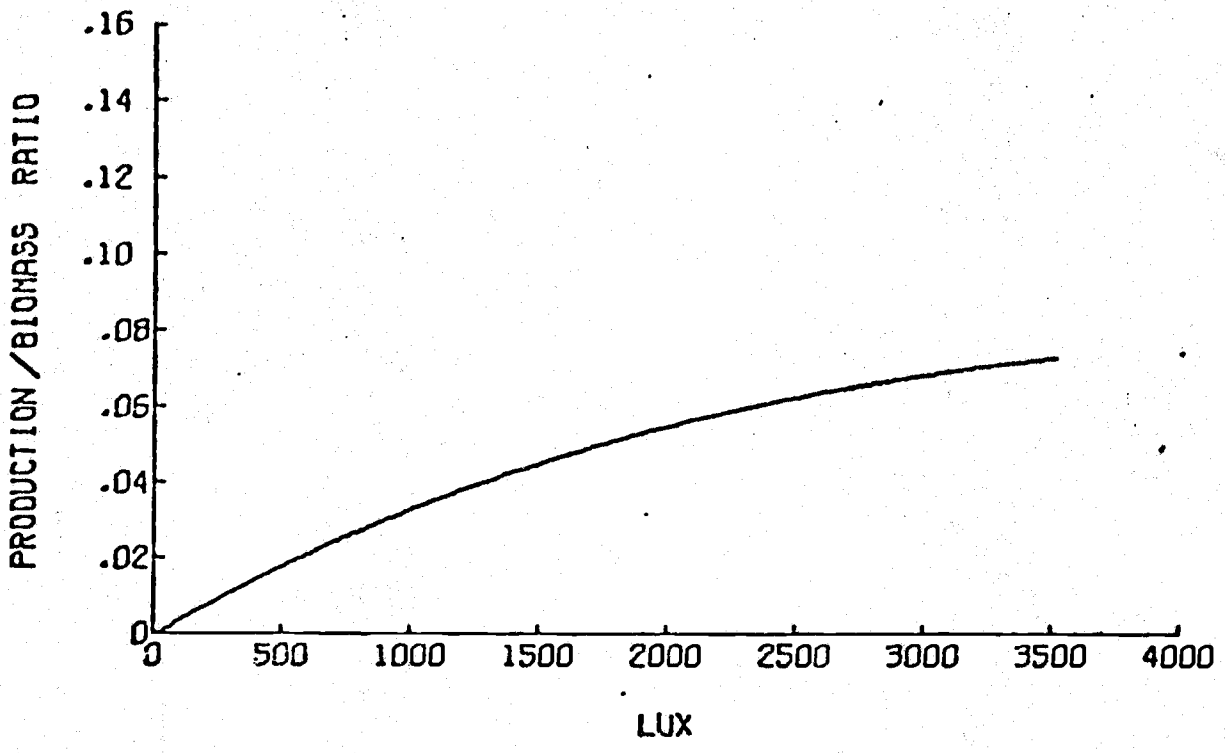

Figure 15. Lake Washington (netplankton) growth kinetics experiment, plot of the P/B ratio as a function of light intensity.

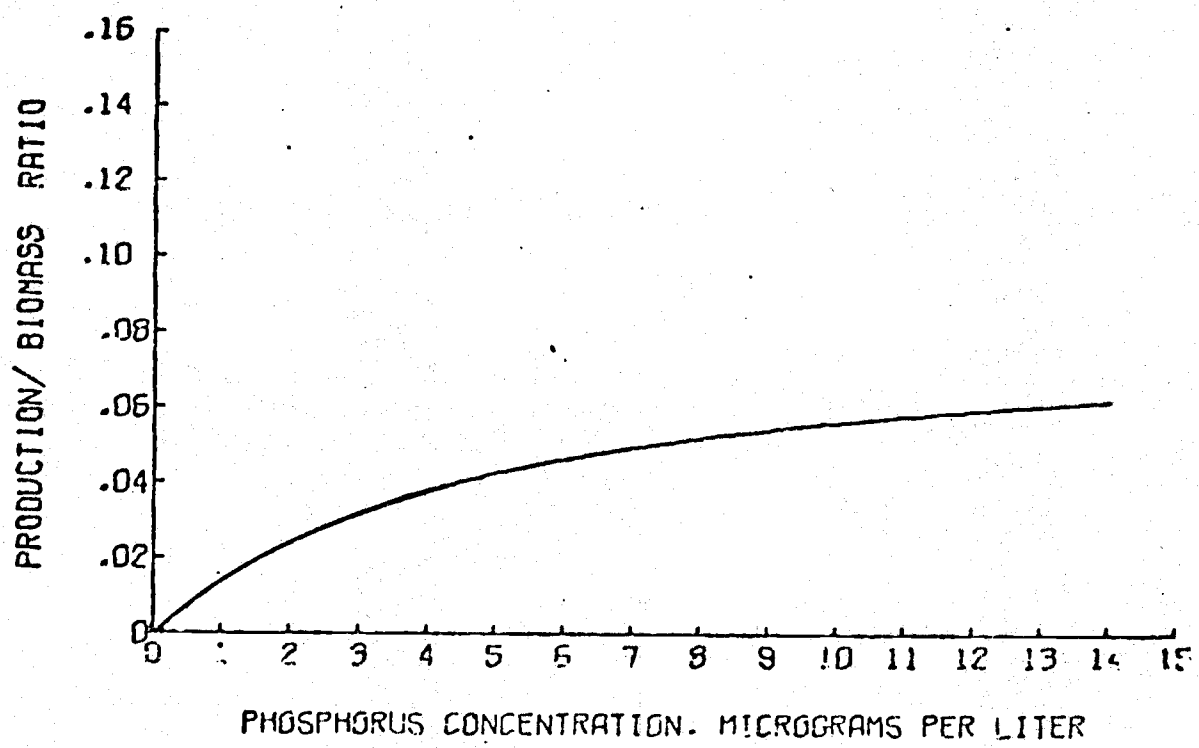

Figure 16. Lake Washington (netplankton) growth kinetics experiment, plot of the P/B ratio as a function of nutrient concentration.

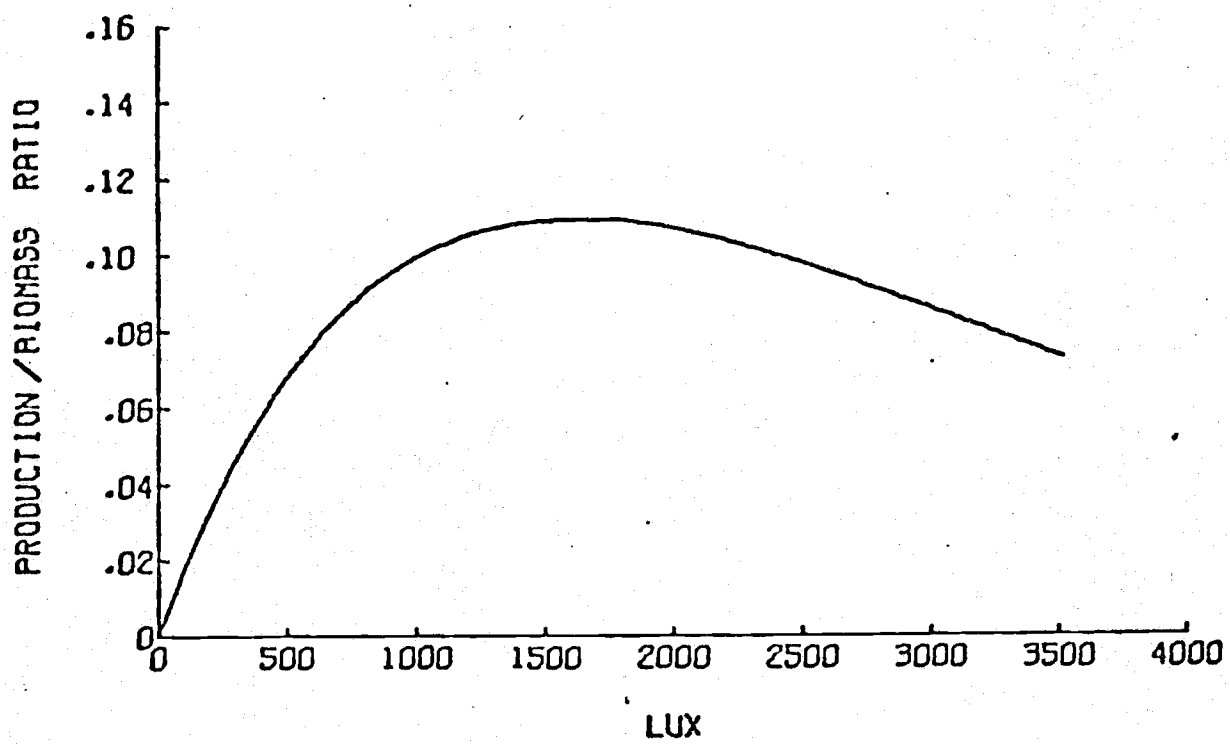

Figure 17. Lake Washington (nannoplankton) growth kinetics experiment, plot of the P/B ratio as a function of light intensity.

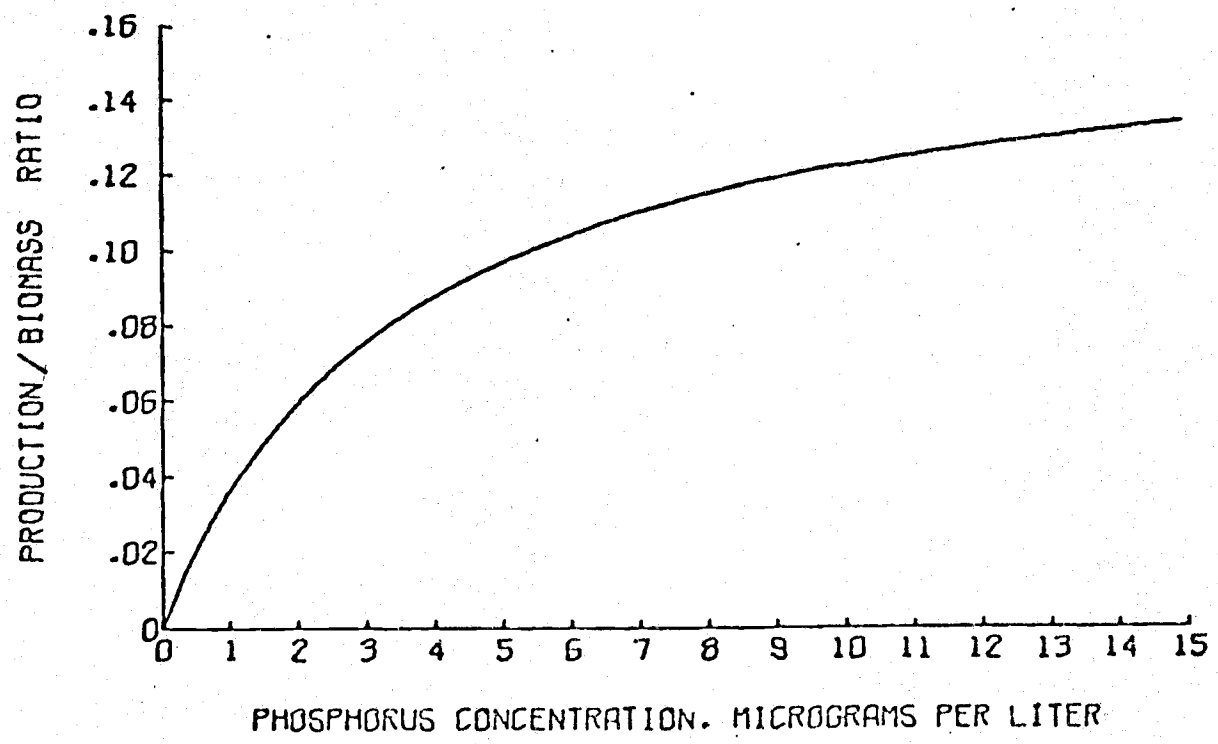

Figure 18. Lake Washington (nannoplankton) growth kinetics experiment, plot of the P/B ratio as a function of nutrient concentration.

Fig. 19. Observed (---) versus predicted (—— model D and —·— model A) growth rate at 10 meters depth during June and July, 1973, following iceout in Findley Lake.

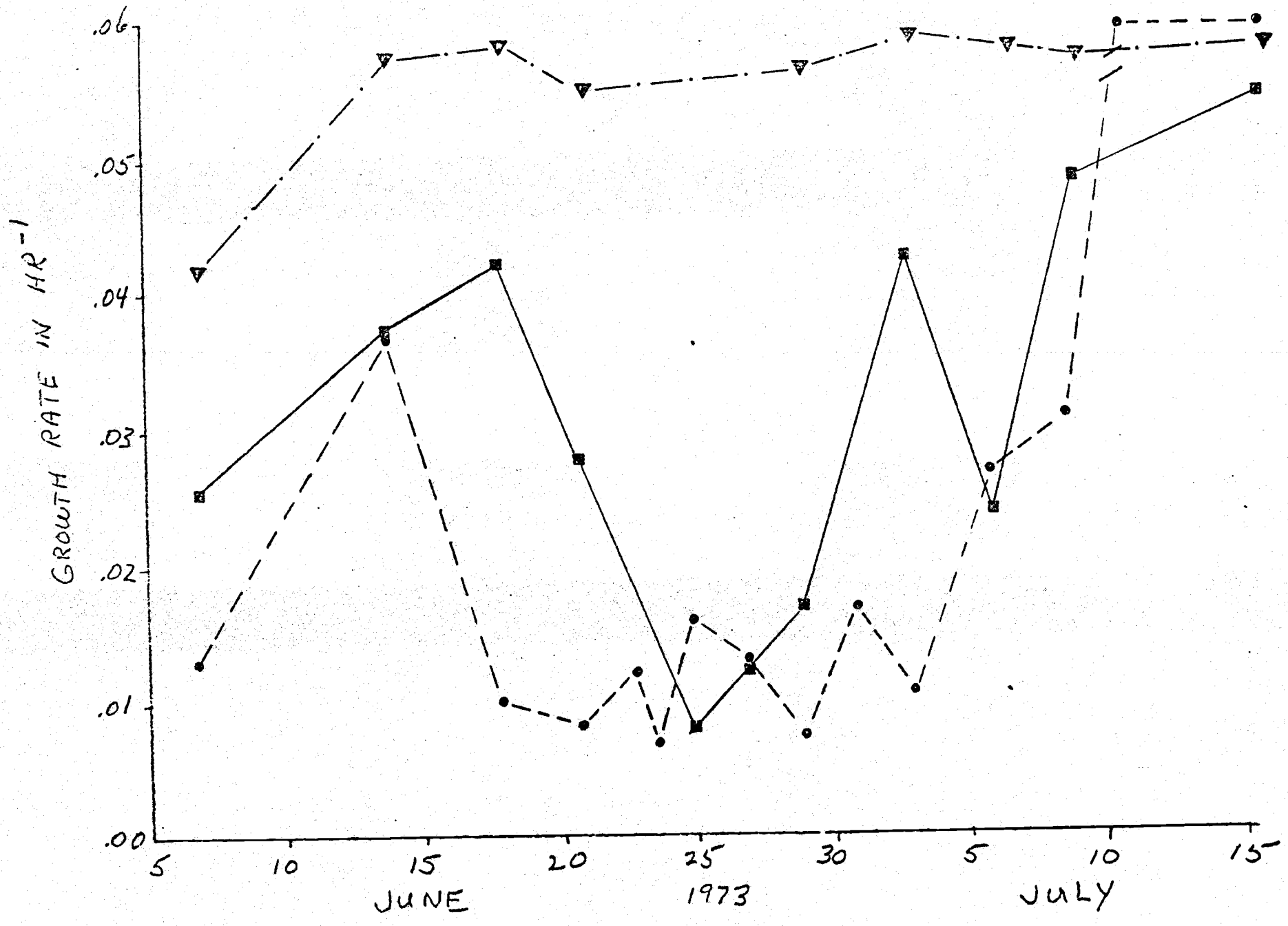

Fig. 20. Observed (---) versus predicted (—— model D and —·—model A) growth rate at 20 meter depth during June and July 1973 following iceout in Findley Lake.