INTERNAL REPORT 145

A MATHEMATICAL AND EXPERIMENTAL MODEL OF THE PHOSPHORUS CYCLE IN CASTLE LAKE, CALIFORNIA

Jeffrey E. Richey*
University of California, Davis

ABSTRACT

A study of the phosphorus dynamics in Castle Lake, California, is presented. The approach is (1) to identify the important phosphorus parameters, (2) to develop and apply methods measuring the parameters in the field and (3) to develop a computer model of the phosphorus cycle. This model will be used to test hypotheses concerning the functioning of the phosphorus cycle and to suggest future research.

The cellular metabolism of phosphorus and its different forms and flows in lakes are discussed to identify the important parameters needed to build a model. The method for measuring these parameters involves determining chemically the size of the phosphorus pools and using the tracer ^{32}P to measure the fluxes. Bioassays and stoichiometric approximations provide further data.

The concentrations of phosphorus in Castle Lake from 14 August to 18 September 1972 were extremely low: in $\mu g\ \ell^{-1}$, dissolved inorganic 0.1, total dissolved 1-3, and total 1-4, with a maximum 0.5 m off the sediments of 10. There was no measureable polyphosphate, but there was a detectable increase in alkaline phosphatase activity with depth. The rate of ^{32}P uptake was constant over depth and time, with an increase under conditions of high photosynthesis. The rate of evolution of ^{32}DOP was quite variable, being the greatest under high photosynthesis and decreasing with depth. Phosphorus was no limiting in bottle bioassays and was even inhibitory on occasion at additions as low as 1 $\mu g\ \ell^{-1}$.

The model of the phosphorus cycle was derived from expected rates of phosphorus flux and pool size derived from stoichiometric calculations of phytoplankton, bacteria and zooplankton carbon masses and fluxes and functions derived from the literature or experimentation. Model output was compared against the field-measured values and good agreement was found. A steady-state model was modified to include the case of a sudden addition of phosphorus fertilizer under different conditions. The lessons learned from and the shortcomings of the model are discussed. The direction for future research into phosphorus dynamics is outlined.

---

* Present address: University of Washington

INTRODUCTION

Phosphorus may be an important agent in regulating primary production in some lakes, but the relationship between phytoplankton growth and phosphorus utilization is perplexing. Dugdale (1967) suggested that a basic problem in evaluating the relationship between nutrients and production is the lack of suitable models that could be tested in the field. Analyzing how phosphorus limits production and determines the species composition of the plankton community requires understanding of the forms of phosphorus available for utilization, the kinetics of uptake and regeneration of available phosphorus and the details of the phosphorus cycle within the plankton community (Rigler 1973). To make quantitative predictions on the relationship between phosphate input and aquatic plant production, a reasonable detailed mathematical model describing the rates of transformation of the important forms of phosphorus present in natural waters should be developed (Lee 1973).

This paper describes a model of the flow of the different phosphorus compounds in Castle Lake, California, during summer steady-state conditions. The approach is threefold: (1) to identify the parameters that would be important in formulating a model of the phosphorus cycle, (2) to develop sensitive methods to simultaneously measure the pertinent parameters in the field, and (3) to develop the mathematical model. Finally this model will be used to suggest the direction for future experimental work. There are at least two benefits to be gained from developing mathematical models from field work: (1) it is an excellent tool for determining what factors are indeed important and, (2) with enough sophistication such a model might be useful in predicting the degree of response of an aquatic system to a nutrent diversion or input.

The term "model" will be defined in this paper as the expression of its author's understanding of the system in question, both with a schematic diagram and as a set of mathematical equations. A model indicates what parameters ought to be measured, solves for quantities that would be difficult to measure directly, and suggests a framework for further research. Finally a model allows the author to test different hypotheses. For example, is it important to know the flux as well as the concentration of phosphate in determing its importance in a lake? How important is dissolved organic phosphorus as an alternate phosphorus source? How is phosphate regenerated?

THE PHOSPHORUS CYCLE

Phosphates are defined as those chemical structures with a phosphorus atom surrounded tetrahedrally by four oxygen atoms. Their key properties include (1) hydrolytic degradation of esters and condensed polyphosphates, (2) precipitation to form materials of low solubility, (3) sorption onto surfaces, and (4) formation of soluble complexes with metal ions (Van Wazer 1973). Phosphorus is present in cells in a wide variety of compounds, in part as a basic structural element of materials and in part as a mobile entity of cell metabolism (Vollenweider 1970).

A primary use of cell phosphate is in photosynthesis (cf. Kuhl 1962, 1968, Jagendorf 1973). Phosphates are important in the formation of the energy-rich compound adenosine triphosphate (ATP) and of the phosphorylated intermediate compounds of photosynthesis. A second role for phosphorus is as a

constituent of some electron carriers that mediate biological redox reactions. Less mobile forms of phosphorus include the techoic acids which give strength and rigidity to cell walls and the nucleic acids which hold and duplicate the genetic code.

It first became practical to measure the concentration of phosphorus in lakes and thus start studies of the phosphoruse cycle when Atkins (1923) applied to colorimetric method of Denige (1920) to water chemistry. Since then, studies of the different aspects of the phosphorus cycle in lakes have proliferated (reviewed in Rigler 1973; Richey 1973). The pools and interactions identified as being important in characterizing the phosphorus cycle in the water column of a lake may be summarized in the conceptual model of Figure 1. The model is composed of a series of individual pools, or compartments. At any particular instant in time, any compartment i is characterized by its volume V_i and quantity of solute Q_i (hereafter Q_i will be considered the quantity of solute per unit volume, or concentration). The solute exchanges with another compartment j, at a rate J_{ij}. The fraction of Q_i transferred per unit time is given by the rate constant $r_{ij} = J_{ij}/Q_i$ (Solomon 1960, Riggs 1963). The model uses the sumbols of Odum (1971). Representative literature will be cited [furthur justification for the processes included is provided in Richey (1973)].

Dissolved inorganic phosphorus (Q_1) is taken up through active transport by phytoplankton (J_{13}) and bacteria (J_{14}), where it becomes fixed in the metabolic pathways and cell structure as particulate phosphorus (Q_3 and Q_4, respectively) (Kuhl 1962, Pomeroy 1963, Sommer and Blum 1965). Bacteria and phytoplankton may compete for available phosphate (Rigler 1956, Phillips 1964, Rhee 1972). If there is not enough phosphate to maintain the minimum cell phosphorus necessary for photosynthesis (Fuhs 1969, Carpenter 1970, Soeder et al. 1971), then the (hypothetical) photosynthesis demand switch (s_1) will induce the ecto enzyme alkaline phosphatase (AP). This enzyme catalyzes the hydrolysis of a variety of monoesters and anhydrides, thus allowing some use (J_{23}) of dissolved organic phosphorus ((Q_2) for photosynthesis. (Kuenzler 1965, 1970, Reichardt et al. 1967). If enough phosphate builds up, s_1 switches off or represses the formation of AP, and the phosphate alone is used. If excess phosphate is present, then s_1 allows the storage (J_{16}) of polyphosphate (Q_7), an orthophosphate polymer, through the process known as "luxury consumption" (Keck and Stich 1957, Harold 1966, Rhee 1972). If external concentrations of orthophosphate become low, the polyphosphate may supply photosynthesis (J_{61}). If none of these mechanisms are enough to supply sufficient phosphate for photosynthesis, then the system may become phosphorus-limited. As part of metabolism, dissolved organic phosphorus (DOP) is excreted by phytoplankton (J_{32}). If Lean's (1973a,b) hypothesis is correct, then the DOP is an immediate excretory product XP which polycondenses, forming a colloidal fraction and giving off phosphate in the process. DOP may also be used by bacteria as a phosphate source (Harrison et al. 1972). Zooplankton (Q_5) graze phytoplankton and bacteria (J_{35}, J_{45}) and excrete phosphate in turn (J_{51}) (Gardiner 1937, Rigler 1961, Peters and Lean 1973). The smaller the zooplankter the greater the percentage of excretion (Joannes 1964, Peters and Rigler 1973). Phytoplankton, bacteria, and zooplankton die (J_{37}, J_{47}, J_{57}), forming the detrital phosphorus pool (Q_7). Within several hours after

death, 25-75% of cell phosphate may be released through autolysis (Golterman 1964, Johannes 1968). The remaining cell phosphates, mostly slow degrading nucleic acids, sediment out (J_{79}) (Scharpa 1973, Golterman 1973). Depending on pH, iron and phosphate concentrations, some phosphate will be removed through physical complexation and precipitation processes (J_{18}, J_{19}) (Mortimer 1941, Stumm and Morgan 1970). Other ligands, such as calcium, magnesium, and aluminum may also enter these reactions (Otsuki and Wetzel 1972, Brown 1973). Light and temperature affect the metabolic rates and thus the phosphorus demands of the organisms. In some lakes allochthonous inputs, sediment recharge, and a littoral macrofaunal community may be important in the phosphorus cycle, but were shown to be insignificant during the summer in Castle Lake (Richey 1973).

The processes or pools indicated in Figure 1 occur at varying levels or intentities down the water column and change over time. Translating Figure 1 into a field program and subsequently into computer models requires the measurement of the different Q_i's J_{ij}'s and r_{ij}'s and the different factors that influence them. Phosphorus is a particularly ephemeral substance to work with, as it is present in a number of different forms at extremely low concentrations and it is quickly recycled. Thus it was most important to work out techniques sensitive enough to simultaneously monitor the rates of change of the phosphorus system to work out a meaningful, testable model. Perturbing or disordering one of these fractions or flows experimentally might provide insight into what could happen to the system under some sudden stress, such as pollution.

The large number of parameters outlined in Figure 1, and the inaccessibility to direct measurement of some of these parameters (e.g. J_{18}, J_{37}, J_{47}, J_{57}), precluded complete experimental measurement during this study. However, the primary goal here is not only to provide direct measurements, but to outline an approach that might be used in suggesting quantitative models. Such models, if validated against field data, might then indicate the magnitude of those quantities difficult to measure directly.

FIELD MEASUREMENTS

Castle Lake is a mesotrophic, glacial cirque lake at an elevation of 1708 m in the Klammath Mountains of northern California (T.39N., R.5W, S13). The lake has a surface area of 19.7 ha and is divided into a shallow end over a terminal moraine, with an average depth of about 4 m, and a deep end off the cirque face with a depth of 35 m. During the summer there is virtually no rain, inflows are minimal, and there is no significant littoral community.

Total (TOTP), total dissolved (TDP), and soluble reactive (SRP) phosphorus were measured directly, If DIP is assumed to be SRP (see Chamberlin and Shapiro 1973 for a discussion of DIP versus SRP), the TDP = DOP + DIP and TOTP = TDP = PP, where PP = particulate phosphorus. The molybdate blue technique was used, with ascorbic acid as the reducing agent, antimony as the catalyst, butyl acetate for extraction, and sulfuric acid for hydrolsis of total fractions. Samples were read on a Beckman DU spectrophotometer with a 10-cm cell. The dissolved phase was defined as that phosphorus passing through an acid-soaked 47-mm GFC filter. Precision and sensitivity were taken as the 95% confidence interval about the regression equation of the standard curve

and as defined by Strickland and Parsons (1968). Results were comparable, yielding SRP values ±0.1µg ℓ^{-1} PO_4-P and TOTP and TDP values ±1.1 µg ℓ^{-1} PO_4-P. Polyphosphate was extracted using 5% trichloroacetic acid (Harold 1966) and alkaline phosphatase was measured using para-nitrophenolphosphate (Reichardt et al. 1967). TOTP, TDP and SRP were measured at the central sampling station every 5 days from 14 August to 18 September 1972 at 3, 7.5, 12.5, 17.5 22.5 30, and 32.5 m and at varying depths and time intervals from April 1972 through February 1973. POP was measured on three dates in August and AP once in September 1972.

Once the concentrations of the different solutes Q_i have been determined, the flux between compartments must be measured. A traditional approach to the study of nutrient dynamics in water is to use Michaelis-Menten kinetics (Dugdale 1967). This method requires the nutrient in question to be present in limiting amounts, an assumption not met in Castle Lake for phosphorus (see below). Instead a ^{32}P technique was used to measure the rate of uptake of phosphate by the seston ($J_{13} + J_{14}$). Samples were collected from their respective depths in duplicate 125-ml dark bottles, injected with 2 µ Ci of carrier-free, ampulated ^{32}P and incubated for 3 min. Then 10 ml were filtered through 0.45-µg Millipore filters, dried and counted on a G-M counter. An absorption corraction was taken by treating a sample with Lugol's solution to half biological activity and subtracting the counts from the untreated samples. Results were taken as the average of the two replicates minus the adsorption. Error was calculated by proagating the error associated with each step of the technique (Beers 1953). Sampling was concurrent with the phosphorus chemistry analyses from 19 August to 18 September 1972.

The possible importance of DOP as a phosphate source has been discussed above. The accumulation of $DO^{32}P$ in the samples injected with $DI^{32}P$ might then be an indication of the use of organic phosphorus by phytoplankton and bacteria in Castle Lake. The method used here is a modification of Kuenzler's (1965) technique, using butyl acetate instead of isobutanol. Several compartmentalkinetics analysis experiments were done to determine light versus dark uptake of phosphate and to determine the relative importance of DIP and DOP as phosphorus sources.

A series of bioassay experiments were conducted, using the addition of phosphorus and sulfur (previously shown to be limiting on occasion in Castle Lake, Goldman 1964) to enclosed flasks with ^{14}C (Goldman 1960). Though the biota of a lake will usually change with a prolonged nutrient addition, this short-term method is useful as a relative indicator of immediate nutrient limitation. Additions of 1, 3, and 6 µg ℓ^{-1} of PO_4-P, 50 µg ℓ^{-1} SO_4-S and 3 µg ℓ^{-1} PO_4-P plus 50 µg ℓ^{-1} SO_4-S were made at 3 m and 12.5 m on three different occasions. Flasks were sampled daily for 4 days. One 4-hr bioassay was conducted.

The measurement of primary productivity was made in situ using the ^{14}C method of Steeman Nielsen (1952), with the Goldman (1963) modifications as applied to Castle Lake (Goldman 1969). Phytoplankton samples were collected from each sampling depth and preserved immediately in Lugol's solution. Samples were returned to the Davis laboratory and counted by species (Goldman 1969). Zooplankton samples were taken by filtering 7 ℓ from each sample

depth through a 75 μm net and preserving immediately with several drops of formalin. Samples were counted according to species, size class, and sex (Williams 1973). Jassby (1973) measured biomass and activity of bacteria. Light at depth was measured with a Rigosha submarine photometer and incident light with an Eppley pyroheliometer.

CONVERSION OF CARBON TO PHOSPHORUS DATA

The carbon content of the phytoplankton was obtained by converting cell volume to carbon (Mullin et al. 1966) for the phytoplankton data. Bacteria carbon was calculated by Jassby (1973) from cell counts and ATP biomass minus phytoplankton biomass. Zooplankton carbon was calculated from zooplankton individual volume estimates, where cell carbon in mg is 0.045 of volume in mm^3 (Williams 1973).

The phosphorus contained in phytoplankton, bacteria, and zooplankton (Q_3, Q_4 and Q_5) was not measured directly (it would be a most difficult task). Rather, these fractions were calculated from biomass and count data from the general sampling day and stoichiometric ratios. The ratio of phosphorus to carbon in phytoplankton is about 0.01. (Redfield et al, 1963, Stumm and Morgan 1970). The ratio is considered most accurate when phosphorus is not limiting and polyphosphate is not present, both conditions of which are met in Castle Lake (see below). Estimates for zooplankton range from 0.0075-0.0132 (Beers 1966) to 0.0278 (Baudouin and Ravera 1972), depending on the species, age class, season, and location. Thus the ratio 0.01 was used to convert the carbon biomass data of phytoplankton, bacteria and zooplankton to phosphorus mass. Error of each assumption was propagated, yielding error estimates of $\Delta Q_3 = 0.40Q_3$, $\Delta Q_4 = 0.35Q_4$, and $\Delta Q_5 = 0.40Q_5$.

RESULTS OF FIELD MEASUREMENTS AND CARBON-PHOSPHORUS CONVERSIONS

Data will be discussed only for the period 19 August through 18 September 1972 because the most complete measurements are for this period and the lake is in summer steady-state. TOTP and TDP did not change over this time. The statistically most significant measurement of SRP was obtained on 19 August. Accordingly a phosphorus profile is presented for that date (table 1). These extremely low concentrations of phosphorus were too close to the limits of detection to separate PP from TOTP. SRP concentrations were about 0.1 $\mu g\ \ell^{-1}$ through the water column. This is close to the 0.09 $\mu g\ \ell^{-1}$ that Lean (1973a) calculated for Heart Lake. At no time was any polyphosphate detected in Castle Lake. Detectable alkaline phosphatase was found on 9 September, but it was not possible to calculate how much DOP may have been converted to phosphat by the enzyme.

A detailed description of the phytoplankton and zooplankton communities over this time period is provided By Williams (1973) and of the bacterial community by Jassby (1973). The error associated with the indirect calculations used to convert carbon to phosphorus are approximately 40%, thus no great faith may be placed in the exact numbers nor do the data warrant close scrutiny for subtle patterns. Nonetheless such an analysis may give order-of-magnitude approximations into pools not otherwise accessible, which may provide useful guides to future experimental work. The stoichiometric approximations to phytoplankton phosphorus (Q_3), bacteria phosphorus (Q_4), zo-

oplankton phosphorus (Q_5), and their sum as total particulate phosphorus were calculated (Table 1). The values compare closely to the total phosphorus measured chemically, within the error estimates. This as a first approximation these datas are reasonable.

The uptake of phosphate as measured by ^{32}P is shown in Table 2. Most of the error in the calculation results from the uncertainty of the SRP measurement. There was no significant variation in phosphate uptake over depth on any one day in Castle Lake. Pronounced vertical variations have been demonstrated in Lake Tahoe (Perkins unpubl. data) and in Lake Washington (Richey unpubl.). Perhaps increased bacterial activity with depth compensates for decreased photosynthetic demand. To compare between sampling depths, the results from any one day were averaged and compared. The rate of uptake on 19 August was significantly ($P < 0.05$) greater than the uptake of any of the other sample days. The turnover times r_{13} and r_{14} varied between 0.39 to 1.24 hr^{-1}. These values are comparable to those reported for mesotrophis waters by Pomeroy (1960) and Rigler (1973).

$DO^{32}P$ relative results are presented in Table 3. Due to the uncertain kinetics of DOP evolution it was not possible to calculate the $\mu g\ \ell^{-1}$ the amount of DOP excreted in the regular sampling period. The evolution of $DO^{32}P$ showed a pronounced vertical variation, with high counts at the surface on the 18th and 24th of August and the 13th and 18th September. This might be due to maximal phytoplankton numbers and thus excretion and less use of DOP by phytoplankton and bacteria in the shallower waters. In the deeper waters there are fewer phytoplankton to excrete DOP and more bacteria to use what is there. There is considerable variation in $DO^{32}P$ evolution between sampling days. Yang (1973) found much variation in release of extracellular products of photosynthesis (ECPP) on different days. As the excretion of ECPP and DOP are probably related, the varied results of the $DO^{32}P$ might be expected. The results of the compartmental analysis experiment showed that DOP was not an important source of phosphorus to the phytoplankton and bacteria, at least at the time of the experiment. Lean (1973a) confirmed that DIP is the most important form in Heart Lake. However, the evidence given here is inclusive. Further experimentation is needed before the role of DOP in Castle Lake is adequately defined. It should also be noted that the greatest uptake of $DI^{32}P$ and release and uptake of $DO^{32}P$ occurred on 19 August, which was also the day of the greatest photosynthetic activity (see below). On all other days there were not significant differences in either carbon or phosphorus flux. From this it would seem that there is a distinct relation between the metabolism of waters and the rate of phosphorus flow.

Bioassay results showed that the addition of phosphorus to Castle Lake at 3 m and 12.5 m was rarely stimulatory and on occasion may have been inhibitory. Bioassays conducted by Jassby on Castle Lake in 1971 (unpublished data) showed the same pattern. There may be several possible explanations for this phenomena at even such low additions of 1 $\mu g\ PO_4\ \ell^{-1}$. As the ambient DIP levels are extremely low, less than 0.1 $\mu g\ \ell^{-1}$, even the addition of 1 $\mu g\ \ell^{-1}$ represents a tenfold increase over ambient levels, which could easily be toxic. The phytoplankton populations, particularly at their level of greatest activity at 3 m, are probably well-adapted to their steady-state levels and any additional single nutrient increase might be disruptive.

Alternatively, cellular processes may be diverted from fixing carbon to the luxury consumption of this sudden surplus PO_4 as polyphosphate. Or perhaps there is some complex competition between phytoplankton and bacteria that is disturbed. Of course, the bioassays discussed here measured only short term changes in the rate of carbon fixation. Populations or biomasses may have been changing under the influence of an altered nutrient regime. Also the truepicture of nutrient limitation lies in the spectrum of a variety of complex nutrient interactions and only rarely as one single nutrient, such as phosphorus.

Primary production from 14 August to 18 September 1972 showed an approximate steady-state, with a bimodel profile (Table 4). A maximum production of 3-5 mgC m^{-3} hr^{-1} at 3 or 5 m was seen, with a second peak of 1-3 mgC M^{-3} hr^{-1} at 17.5 to 20 m. Total daily area production of 662 mgC M^{-2} day^{-1} on 19 August was significantly $P<.05$ greater than the production on the other sampling days, while none of the other days differed significantly amount themselves.

A MODEL OF THE PHOSPHORUS CYCLE OF CASTLE LAKE

The rate of change of a substance Q_i in some cube of water at a depth z at any instant in time t may be given by the equation

$$\frac{\partial Q_i}{\partial t} = \left(\frac{\partial}{\partial z}\right) K_h \left(\frac{\partial Q_i}{\partial z}\right) + \left(\sum J_{ji} - \sum J_{ij}\right)$$

where K_h is the coefficient of eddy diffusivity and $(\sum J_{ji} - \sum J_{ij})$ is the sum of the the biological transformations. The model presented below will ignore the turbulence term, which probably is valid only over short time intervals, as phosphorus cycling is a much more rapid process than transport [see Jassby (1973) and Williams (1973) for discussions of the effects of turbulent transport on the biological community]. The remaining terms will be assessed below are presented in Table 5.

The dependent variables in a lake include the rates of growth of the phytoplankton, zooplankton, and bacteria and the flux of the different nutrients. Independent driving variables (forcing functions) include mass transport mechanisms, temperature, and solar radiation. As mentioned above transport processes may be neglected over short time periods for nutrient considerations. Lowering the temperature has no effect on the rate of absorption of light quanta by chlorophyll, thus in the light-limited state the rate of photosynthesis does not depend on temperature (Rabinwitch and Govindjee 1969). In lakes, then, temperature would affect photosynthesis only when light was not limiting, but in these zones light inhibition is a problem (see below). Bacteria and zooplankton metabolism are, however, affected by temperature. Solar radiation is, of course, the driving force of photosynthesis. In Castle Lake, phosphorus itself is not limiting to short-term photosynthesis even at its almost unmeasurably low concentrations. As the results of the tracer experiments show, phosphorus flux increased with primary production. As phosphorus flux appears to be dependent on photosynthesis and not vice versa, a model of photosynthesis is a necessary inclusion in a model of the phosphorus cycle.

There have been a variety of photosynthesis models reported in the literature (as reviewed by Patten 1968, Kelly 1974). The model used here

was developed to predict photosynthesis per unit volume as a function of phytoplankton carbon and light.

The second peak in primary production at the vastly reduced light intensity implies perhaps that the deep water population has adapted its enzyme system to become much more efficient at utilizing quanta of light. Indeed Goldman (1969) showed that during the summer of 1968 in Castle Lake efficiency (defined as mgC fixed m^{-3} ly^{-1}) increased greatly with depth. This phenomona can be described by equation 1a. Goldman (1963, 1969) reviews some of the mechanisms and reported intensities of inhibition. One explanation is that if total sunlight is above 0.2 ly min^{-1} depression occurs. Another possibility is that depression is caused by the extreme wavebands of ultraviolet (UV) and infrared (IR) radiation. Mechanisms might include inactivation of light and/or dark reactions and photolytic destruction of pigments. In Castle Lake maximum photosynthesis occurs at about 0.2 ly min^{-1} between 3 and 5 m. The light spectrum in Castle Lake was broken down into wavebands, with the energy of each band and extinction coefficient calculated. The combined extinction coefficient of UV plus IR was 1.32, indicating that this portion of the spectrum extincts by 5 m. Thus either explanation of photosynthetic inhibition is possible for Castle Lake. The surface primary production averaged 0.41 times the maximum. An inhibition term was then derived as a function of UV + IR by normalizing maximum, uninhibited photosynthesis to 1 and taking inhibition as a function of available UV and IR (Equation 1C).

Light saturation (Equation 1C) was taken as developed elsewhere (Talling 1957, Vollenweider 1965, Fee 1969). The effect of a single limiting nutrient [(Equation (1d)] is expressed through the familiar Michaelis-Menten formulation, as this expression describes a curve similar to the pattern of nutrient addition to a system previously limited by that nutrient. Multiplication of Equation 1 by 0.01 yields the amount of phosphate required to support photosynthesis [Equation (2)], assuming that J_{23} is negligible.

The phosphorus uptake required to support bacteria was calculated by modifying the bacteria generation time equation of Jassby (1973) (again assuming that J_{24} is negligible). The doublings per day would indicate a certain phosphorus demand (Equation 3).

Williams (1973) derived feeding rate equations for the three dominant zooplankters in Castle Lake. For *Daphnia rosea* and *Holopedium gibberum* the filtering rate in ml individual $^{-1}hr^{-1}$ is given by $0.51\ L^2\ (0.44 + .05T)$ and for *Diapotmus novamexicanus* by $0.0034\ L^2T$, where L = body length in mm and T = temperature in °C. The amount of phytoplankton and bacteria phosphorus removed by the zooplankton will be the volume filtered times the phosphorus concentration. This model will ignore size preference and assume that all Q_3 and Q_4 is available for grazing. The total amount of phytoplankton and bacteria phosphorus grazed is given by Equation 4, where i = 3 is phytoplankton and i = 4 is bacteria grazed, k = 1 is *Daphnia* k = 2 is *Holopedium*, and k = 3 is *Diatomus*, and j = 1,5 are size classes.

The model for zooplankton excretion reported by Peters and Rigler (1973) appears to account for the ranges of excretion reported in the literature, so it was used here. They describe the rate of phosphorus release (with this author's correction for the phosphorus content of the zooplankton population) as given in Equation 5 where T = temperature in °C, C = cell food concentration (cells ml^{-}), P = food phosphorus concentration, W is dry weight (mg) of the individual zooplankers, and Q_{5j} is the sum by individual of the zooplankton phosphorus mass.

There are several approaches to determining the size of the detrital phosphorus pool (Q_7). The direct approach is to subtract, $Q_7 = \sum_{i=3}^{8} Q_i - (\sum_{i=3}^{6} Q_i + Q_8)$. This would give only the residual phosphorus, mostly nucleic acids, left after autolysis had liberated the more labile fractions from the cell shortly after death. Therefore the rate of accumulation of this fraction would be J_{79}, the contribution of the detrital pool to the sediments. Error analysis showed that this fraction was insignificant, thus will be ignored. The total detrital phosphorus is actually a function of the death rates of the phytoplankton, bacteria, and zooplankton, as autolysis releases much of the cellular phosphorus very quickly in an inorganic form available for assimilation. In fact Jassby (1973) demonstrated that the death rate of bacteria was almost as great as the growth rate, thus a large fraction of bacteria phosphorus might be made available through death. The death rates were taken as 10% of the population day^{-1} for the plankton and 70% of the bacteria day^{-1}. Regeneration from the detrital pool P_7 was taken as the autolysis of the inputs to that pool of 75% hr^{-1}.

As discussed above, physical complexation and precipitation processes affect the concentration and biological availability of the different phosphorus species. It is assumed here that the protonation of the phosphate ions does not affect their availibility. The equations of Table 6 calculate the distribution, complexation, and precipitation of the different species as a function of iron and pH (after Stumm and Morgan 1970).

DOP and its associated fluxes and enzymes were excluded from the model. The compartmental analysis experiments performed in this study indicated that DOP is probably not an important factor in Castle Lake (similarly Lean 1973a,b). As there was no polyphosphate detected in Castle Lake it was excluded from the model. Vertical processes such as sedimentation (J_{79}) were not included because they did not immediately affect short-term cycling.

The model tests a set of postulated relationships concerning the functioning of the phosphorus cycle in Castle Lake. Comparison of model to field results checks the validity of the model assumptions. If the data match, the postulates may be correct, whereas breakdown indicates a need for further understanding. The outcome of the primary productivity model with no nutrient limitation is shown with the field data (Figure 2). On 14 and 19 August and 19 September the agreement throughout the water column is quite close, within the error of the methods. On the remaining days the agreement is close in the upper 3-5 m, but then the model failed by giving values far greater than the observed rates of carbon fixation. The biomass estimates for those occasions appeared to be considerably higher than surrounding values. Also the percentage of dead, or non-photosynthetically active plankton that are counted increases with depth, giving an over-estimate of viable plankton. This model might then be a method of checking the validity of the count data, and it highlights the necessity for obtaining accurate estimates of viable plankton biomass.

Figure 3 compares the observed rate of phosphate uptake with the model results ($J_{13} + J_{14}$) and with the model calculations of phosphate regeneration ($J_{51} + J_{51}$). Within the error boundaries the three catgories are comparable. Zooplankton excretion appears to be particularly important in the epilimnion. It is implied that because uptake predicted by the model and measured in the field should be close and should be balanced in turn by regeneration, the general procedure outlined here may be a valid first approximation to understanding some of the aspects of the phosphorus cycle. It also implies that the system was in a steady-state at the time of study. With this justification a steady-state solution to the system of equations in Table 5 may provide insight into the behavior of some of the other terms of the model.

Under steady-state conditions, the net flows into and out of each compartment must balance to give an equilibrium solution. This solution was provided by taking representative values as discussed above and solving the model equations for the different Q_i (Table 7). Grazing of bacteria phosphorus by zooplankton results in a minor depletion of bacteria, but bacterial autolysis is considerable. If Jassby's (1973) hypothesis that bacteria death is almost equal to bacteria growth is correct, and if autolysis is rapid, then the phosphorus released by bacteria through autolysis is almost enough to sustain bacteria growth. The turnover of zooplankton phosphorus via excretion is significant enough to supply the demands of phytoplankton under steady-state conditions. Perhaps, then, the competition of phytoplankton and bacteria for phosphorus is less than supposed, as each can meet its needs via alternate sources. These calculations show that the mechanisms for the regeneration of phosphorus are sufficient to supply the community, without DOP. Thus the exclusion of DOP from this model does not appear to have caused serious error. However the error inherent in the model does not permit precise enough calculations to say that for sure.

It might be interesting to see what would happen to this steady-state phosphorus cycling system if a sudden input of phosphorus were to be made. For example, what would have been the result if a plane loaded with phosphate fertilizer were to have crashed at 3 m in the lake on 19 August 1972?

The phosphorus model equations were expressed in the explicit difference form

$$Q_{i,t+1} = Q_{i,t} + (\sum J_{ji} - \sum J_{ij})_t \Delta t$$

and solved. It was assumed that the fertilizer was instantly diffused to a concentration of 10 $\mu g\ \ell^{-1}$, as orthophosphate. At a pH of 7 and an Fe^{3+} concentration of $10^{-6.7m}$, over 50% of the addition was precipitated out, leaving only 4.14 $\mu g \ell^{-1}$ as phosphate (Q_1). The results show that the additional phosphorus remains in the Q_1 pool. At first the author was surprised that none showed up elsewhere. But none of the other compartments are limited by Q_1, thus there should be no change in the flows into and out of these compartments. Where the addition does show up is the difference in turnover rates. The turnover r_{13} went from 0.314 hr^{-1} to 0.008 hr^{-1} and r_{14} went from 0.015 hr^{-1} to 0.001 hr^{-1}. Thus there is no direct relation between the amount of a solute present and its rate of utilization. This further supports the concept that knowing the mere ambient concentration

of a nutrient tells one little about the importance of that nutrient in the system.

To test what might happen to the phosphorus cycle in Castle Lake if phosphate were added and phosphorus was limiting the following scenario was constructed. Assume in equation (1) that $v = 2$ and $K_m = 0.1$. Then the addition of phosphate should result in an increased demand for phosphorus.

Figure 4 shows the results of the addition of 10 $\mu g\ \ell^{-1}$ phosphate to the phosphorus limited system. Again only 4 $\mu g\ \ell^{-1}$ of Q_1 is left after precipitation with iron. After 48 hr the Q_1 pool is reduced to 2.67 $\mu g\ \ell^{-1}$, while the phytoplankton phosphorus Q_3 increases from 1.65 to 2.96 $\mu g\ \ell^{-1}$. Zooplankton (Q_5) increases from 0.23 to 0.39 $\mu g\ \ell^{-1}$, presumably due the increased availability of phosphorus in algae. Detrital phosphorus Q_7 also increases. Bacteria phosphorus Q_4, however did not change. Zooplankton did not increase enough to exert a significantly-increased grazing pressure on the bacteria. The formulation for bacteria uptake depends only on the concentration of dissolved organic carbon and temperature, thus increased phosphorus would not directly affect the bacteria. In real life the increased phytoplankton population would probably excrete more carbon as extracellular products of photosynthesis or as dissolved organic phosphorus, which would increase the bacterial activity. This is another argument for further research into the role of excreted organic products by phytoplankton. This model predicts only those changes that might occur shortly after the nutrient addition. In nature the populations would change and a complete new system would evolve (c.f. Schindler et al. 1973).

SUMMARY AND CONCLUSIONS

To predict the response of a lake to an altered nutrient regime involves the understanding of the dynamics of the limiting nutrient(s). As phosphorus is often such a limiting nutrient, this author chose to study phosphorus dynamics in Castle Lake, California, with an eye toward future studies of modeling whole lake processes. The following points were made:

(1) The cellular metabolism of phosphorus and its different forms and flow in lakes are discussed to identify the important components of the phosphorus cycle.

(2) Methods were developed for the simultaneous field measurement of several of these parameters, including chemical and ^{32}P isotope techniques.

(3) The concentrations of phosphate were extremely low. Dissolved inorganic phosphorus averaged about 0.1 $\mu g\ \ell^{-1}$, total dissolved phosphorus 1-3 $\mu g\ \ell^{-1}$, and total phosphorus about 1-4 $\mu g\ \ell^{-1}$ in the water column and 10 $\mu g\ \ell^{-1}$ off the sediments. There was no detectable polyphosphate, but there was alkaline phosphatase activity. The rate of phosphate uptake was constant over depth and time, with an increase under conditions of increased photosynthesis, averaging about 0.04-0.12 $\mu g\ \ell^{-1}$. The rate of evolution of $DO^{32}P$ was quite variable, being the greatest under high photosynthesis and decreasing with depth. Phosphorus was not limiting and was even inhibitory on occasion at additions as 1 $\mu g\ \ell^{-1}$.

(4) A model of the phosphorus cycle was constructed based on derived equations of processes and stoichiometric approximations of phytoplankton, zooplankton, and bacteria data. The agreement between model calculations of fluxes and pools agreed with field measurements.

Approaching the study of phosphorus dynamics in Castle Lake with a modeling perspective served several purposes:

(1) Formulating an understanding of the phosphorus cycle as a whole was aided by a conceptual model, which indicated what parameters ought to be measured in the field.

(2) Comparison of the field data to model output is a check on the validity of the model assumptions and thus on the author's understanding of the system, as expressed through the equations.

(3) Steady-state solutions to the equations allowed estimates of parameters difficult to measure experimentally. The field data and the model suggest that the regeneration of phosphate is adequately accounted for by zooplankton excretion. Autolysis from bacteria may also be a significant source of phosphate. Physical complexation and precipitation processes may remove considerable amounts of phosphate from solution. Dissolved organic phosphorus may be an important source of phosphate in some systems, but in Castle Lake there appear to be enough alternate sources of phosphorus to maintain the population in a nonphosphorus limited state, even at extremely low ambient nutrient levels. This highlights the importance of obtaining nutrient flux rates as well as quantity to assess the importance of a nutrient to the system.

(4) The model provided insight into what might happen to Castle Lake if a pollution stress occurred, under both phosphorus-limiting and not-limiting conditions.

Further model manipulation would serve little purpose, as the data is not available to verify the results. Rather the model highlights a number of problems that need further investigation, before an adequate dynamic model of the phosphorus cycle is completed. The accurate and sensitive chemical analysis of the different phosphorus pools is needed. The partitioning of phosphorus uptake between phytoplankton and bacteria must be resolved. The role of dissolved organic phosphorus, in particular, needs careful study. Accurate determination of death rates and the subsequent nutrient release is important. Zooplankton excretion needs further work if the hypothesis that it is the main source of phosphate renewal is to be accepted. Also of great importance is the necessity to properly determine through a variety of bioassay techniques the degree of phosphate and phosphate plus other nutrients limitation in a lake.

The agreement between the model and field measurements suggest that the interaction between models and field experimentation may provide a powerful tool for the study of aquatic nutrients. These methods are applicable to to the study of whole lake ecosystems and could lead to models of the eutrophicaton processes. Such models would be invaluable tools in water quality management.

ACKNOWLEDGEMENTS

Drs. C. R. Goldman, D. W. Schindler, C. A. Hall, F. Taub, and E. P. Richey made valuable comments on the manuscript. P. N. Neame, F. Sanders, N. Williams, and A. Jassby provided field support.

LITERATURE CITED

ATKINS, W. R. G. 1923. The phosphate content of fresh and salt waters in its relationship to the growth of algal plankton. J. Mar. Biol. Assoc. U.K. 13:119-150.

BAUDOUIN, M. F., and O. RAVERA. 1972. Weight, size and chemical composition of some freshwater zooplankters: Daphnia hyalina (Leydig). Limnol. Oceanogr. 17:645-649.

BEERS, Y. 1953. Introduction to the Theory of Error. Addison-Wesley Press, Reading, Mass. 167 p.

BEERS, J. R. 1966. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. Limnol. Oceanogr. 11:520-528.

BROWN, W. 1973. Solubilities of phosphates and other sparingly soluble compounds, p. 203-239. In E. Griffith, A. Beeton, J. Spencer, and D. Mitchell [eds.], Environmental phosphorus handbook. John Wiley and Sons, New York.

CARPENTER, E. J. 1970. Phosphorus requirements of two planktonic diatoms in steady-state culture. J. Phycol. 6:28-30.

CHAMBERLIN, W., and J. SHAPIRO. 1973. Phosphate measurements in natural waters: a critique, p. 355-366. In E. Griffith, A. Beeton, J. Spencer, and D. Mitchell [eds.], Environmental phosphorus handbook. John Wiley and Sons, New York.

DENIGE, G. 1920. Reaction de coloration extremenent sansibles des phosphates et des arsenates. Cr. Acad. Sci. 171:802-804.

DUGDALE, R. C. 1967. Nutrient limitation in the sea: dynamics, identification and significance. Limnol. Oceanogr. 12:685-695.

FEE, E. J. 1969. A numerical model for the estimation of photosynthesis production, integrated over depth and time in natural waters. Limnol. Oceanogr. 14:90.

FUHS, G. W. 1969. Phosphorus content and the rate of growth in the diatoms Cyclotella nana and Thalassiosira fluviatilis. J. Phycol. 5:312-321.

GARDINER, A. C. 1937. Phosphate production by planktonic animals. J. Cons., Cons. Perm. Int. Explor. Mer 12:144-146.

GOLDMAN, C. R. 1960. Molybdenum as a factor limiting primary productivity in Castle Lake. Science 132:1016-1017.

GOLDMAN, C. R. 1963. The measurement of primary productivity and limiting factors in freshwater with carbon-14, p. 103-113. In M. S. Doty [ed.]. Proc. Conf. Prin. Prod. Meas., Mar. and Freshwater. U.S.A.E.C. TID-7633.

GOLDMAN, C. R. 1964. Primary productivity and micronutrient limiting factors in some North American and New Zealand lakes. Int. Ver. Theor. Angew. Limnol. Verh. 15:365-374.

GOLDMAN, C. R. 1969. Photosynthetic efficiency and diversity of a natural phytoplankton population in Castle Lake, California. Proc. IBP/PP Tech. Meet., Trebon, 14-21 Sept. 1969:507-517.

GOLTERMAN, H. 1964. Mineralization of algae under sterile conditions by bacterial breakdown. Int. Ver. Theor. Angew. Limnol. Verh. 15:544-548.

GOLTERMAN, H. 1973. Natural phosphate sources in relation to phosphate budgets: a contribution to the understanding of eutrophication. Water Research 7:3-17.

HAROLD, F. M. 1966. Inorganic polyphosphates in biology: structure, metabolism, and function. Bacteriol. Rev. 30:772-788.

HARRISON, M. T., R. E. PACHA, and R. Y. MORITA. 1972. Solubilization of inorganic phosphates by bacteria isolated from Upper Klamath Lake sediment. Limnol. Oceanogr. 17:50-57.

JAGENDORF, A. T. 1973. The role of phosphate in photosynthesis, p. 381-392. In E. Griffith, A. Beeton, J. Spencer, and D. Mitchell [eds.], Environmental phosphorus handbook, John Wiley and Sons, New York.

JASSBY, A. 1973. The ecology of bacteria in the hypolimnion of Castle Lake, California. Ph.D. thesis. Univ. Calif., Davis. 186 p.

JOHANNES, R. E. 1964. Phosphorus excretion and body size in marine animals, microzooplankton and nutrient regeneration. Science 146:923-924.

JOHANNES, R. E. 1968. Nutrient regeneration in lakes and streams, p. 203-213. In M. Droop and E. Wood [eds.], Advances in the microbiology of the sea. Academic Press, London and New York.

KECK, K., and H. STICH. 1957. The widespread occurrence of polyphosphate in lower plants. Ann. Bot. 21:611-622.

KELLY, ROBERT. 1974. C. Hall and J. Day [eds.], Models as ecological tools: theory and case histories. William Kaufmann Inc., Los Altos.

KUENZLER, E. J. 1965. Glucose-6-phosphate utilization by marine algae. J. Phycol. 1:156-164.

KUENZLER, E. J. 1970. Dissolved organic phosphorus excretion by marine phytoplankton. J. Phycol. 6:7-13.

KUHL, A. 1962. Inorganic phosphorus uptake and matabolism, p. 211-229. In R. Lewis [ed.], Physiology and biochemistry of algae. Academic Press, New York.

KUHL, A. 1968. Phosphate metabolism of green algae, p. 37-52. In D. F. Jackson [ed.], Algae, man and the environment. Syracuse Univ. Press, Syracuse, N. Y.

LEAN, D. R. S. 1973a. Phosphorus dynamics in lake water. Science 179:678-680.

LEAN, D. R. S. 1973b. Movements of phosphorus between its biologically important forms in lake water. J. Fish. Res. Board Can. 30:1525-1530.

LEE, G. F. 1973. Role of phosphorus in eutrophication and diffuse source control. Water Research 7:111-128.

MORTIMER, C. H. 1941. The exchange of dissolved substances between mud and water in lakes. Vol. I, J. Ecol. 29:280-329.

MULLIN, M. M., P. R. SLOAN, and R. W. EPPLEY. 1966. Relationship between carbon content, cell carbon and area in phytoplankton. Limnol. Oceanogr. 11:307-311.

NIXON, SCOTT, and KRAMER. C. Hall and J. Day [eds.], Models as ecological tools: theory and case histories. William Kaufmann Inc., Los Altos.

ODUM, H. T. 1971. Environment, power, and society. John Wiley and Sons, New York. 331 p.

OTSUKI, A., and R. G. WETZEL. 1972. Coprecipitation of phosphate with carbonates in a marl lake. Limnol. Oceanogr. 17:763-767.

PATTEN, B. C. 1968. Mathematical models of plankton production. Int. Rev. ges. Hydrobiol. 53:357-408.

PETERS, R., and D. R. S. LEAN. 1973. The characterization of soluble phosphorus released by limnetic zooplankton. Limnol. Oceanogr. 18:270-279.

PETERS, R. H., and F. H. RIGLER. 1974. Phosphorus release by Daphnia. Limnol. Oceanogr. In press.

PHILLIPS, J. E. 1964. The ecological role of phosphorus in waters with special reference to microorganisms, p. 61-81. In H. Haukelekian and N. Dondero [eds.], Principles and applications in aquatic microbiology. John Wiley and Sons, New York.

POMEROY, L. R. 1960. Residence time of dissolved phosphate in natural waters. Science 131:1731-1732.

POMEROY, L. R. 1963. Experimental studies of the turnover of phosphate in marine ecosystems, p. 163-166. In V. Schultz and A. Klement [eds.], Radioecology. Reinhold Publ. Corp., New York.

RABINOWITCH, E., and GOVINDJEE. 1969. Photosynthesis. John Wiley and Sons, New York. 273 p.

REDFIELD, A. C., B. H. KETCHUM, and F. A. RICHARDS. 1963. The influence of organisms on the composition of sea-water, p. 26-77. In M. N. Hill [ed.], The Sea, Vol. II. Interscience Publ., New York.

REICHARDT, W., J. OVERBECK, and L. STEUBING. 1967. Free dissolved enzymes in lake waters. Nature 216-1345-1347.

RHEE, G-YULL. 1972. Competition between an alga and an aquatic bacterium for phosphate. Limnol. Oceanogr. 17:505-514.

RICHEY, J. E. 1973. Phosphorus dynamics in Castle Lake, California. Ph.D. thesis, Univ. Calif., Davis. 160 p.

RIGGS, D. S. 1963. The mathematical approach to physiological problems. Williams and Wilkens, Baltimore. 445 p.

RIGLER, F. 1956. A tracer study of the phosphorus cycle in lake water. Ecology 37:550-562.

RIGLER, F. 1961. The uptake and release of inorganic phosphorus by Daphnia magna Straus. Limnol. Oceanogr. 6:165-174.

RIGLER, F. 1973. A dynamic view of the phosphorus cycle in lakes, p. 539-568. In E. Griffith, A. Beeton, J. Spencer, and D. Mitchell [eds.], Environmental phosphorus handbook. John Wiley and Sons, New York.

SCHARPA, L. 1973. Transformations of naturally occurring organophosphorus compounds in the environment, p. 393-412. In E. Griffith, A. Beeton, J. Spencer, and D. Mitchell [eds.], Environmental phosphorus handbook. John Wiley and Sons, New York.

SCHINDLER, D. W., H. KLING, R. V. SCHMIDT, J. PROTOPOWICH, V. E. FROST, R. A. REID, and M. CAPEL. 1973. Eutrophication of lake 227 by addition of phosphate and nitrate: the second, third and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30:1415-1440.

SITARAMAIAH, P. 1967. Water nitrogen and calorific values of freshwater organisms. J. Cons. Perm. Int. Explor. Mer 31:27-30.

SOEDER, C., H. MULLER, H. PAYER, and H. SCHULLE. 1971. Mineral nutrition of planktonic algae; some considerations, some experiments. Mitt. Int. Verein. Limnol. 19:39-58.

SOLOMON, A. K. 1960. Compartmental methods of kinetic analysis, p. 119-167. In C. L. Comar and F. Brunner [eds.], Mineral metabolism: an advanced treatise. Vol. 1 (A). Academic Press, New York.

SOMMER, J. R., and J. J. BLUM. 1965. Lytochemical localization of acid phosphatases in Euglena gracilis. J. Cell. Biol. 24:235-254.

STEEMAN NIELSEN, E. 1952. The use of radioactive carbon (C14) for measuring primary production in the sea. J. Cons. Perm. Int. Explor. Mer 18:117-140.

STRICKLAND, J. D. H., and T. R. PARSONS. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. No. 167. Ottawa. 311 p.

STUMM, W., and J. MORGAN. 1970. Aquatic chemistry. Wiley Interscience, New York. 583 p.

TALLING, J. F. 1957. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater racliation. New Phytol. 56:29-50.

VAN WAZER. 1973. The compounds of phosphorus, p. 169-178. In E. Griffith, A. Beeton, J. Spencer, and D. Mitchell [eds.], Environmental phosphorus handbook. John Wiley and Sons, New York.

VOLLENWEIDER, R. A. 1965. Calculation of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements, p. 435-437. In C. R. Goldman [ed.], Primary productivity in aquatic environments. Mem. Ist. Ital. Idrobiol. 18 Suppl., Univ. California Press, Berkeley.

VOLLENWEIDER, R. A. 1970. Water management research. Scientific fundamentals of the eutrophication of lakes and flowing waters with particular reference to nitrogen and phosphorus as factors in eutrophication. Tech. Rep. to the Organization for Economic Cooperation & Development, Committee for Research Cooperation, Paris. 159 p.

WILLIAMS, N. 1973. A mathematical model of plankton dynamics in Castle Lake, California. Ph.D. thesis, Univ. Calif., Davis.

YANG, Y. 1973. Primary production and extracellular release by phytoplankton in Castle Lake, California. Ph.D. thesis, Univ. Calif., Davis.

Table 1. Chemical and stoichiometric measurements for 19 August 1972, SRP ± 0.1, TOTP and TDP ± 1.1 μg ℓ^{-1}; Q_3, Q_4, Q_5 ± 40% ($p<0.05$)

	PHOSPHORUS FRACTION						
Depth (m)	SRP	TOTP	TDP	Q_3	Q_4	Q_5	PP
3.	0.1	3.0	2.2	1.8		0.9	2.7
7.5	0.1	1.6	3.6	1.6		0.7	2.3
12.5	0.1	0.8	0.9	1.1	0.1	0.5	1.7
17.5	0.1	2.0	1.5	0.5	0.0	0.4	0.9
22.5	0.1	1.8	1.1	0.5	0.2	0.3	1.0
30.0	0.1	5.5	1.9				
32.5	0.1	8.4	3.8				

Table 2. Phosphate uptake ($J_{13} + J_{14}$), in $\mu g\ \ell^{-1}\ hr^{-1} X 10^{-2}$. Average error = 102%, 19 August to 18 September 1972.

Depth (m)	19 Aug	24 Aug	3 Sept	8 Sept	13 Sept	18 Sept
3.	.124	.048	.034	.045	.031	.054
7.5	.101	.048	.053	.039	.053	.043
12.5	.103	.033	.035	.046	.036	.035
17.5	.109	.041	.036	.051	.035	.030
22.5	.106	.050	.043	.056	.038	.043
30.0	.110	.097	.107	.039	.051	.063

Table 3. $DO^{32}P$ evolution, in distintegrations per minute (DPM). Average error = 21%. 19 August to 18 September 1972.

Depth (m)	19 Aug	2[illegible] Aug	3 Sept	8 Sept	13 Sept	18 Sept
3.0	434,669	164,706	30,151	5,366	229,634	204,623
7.5	160,759	55,615	55,440	0	91,584	74,612
12.5	111,929	36,124	44,954	3,701	102,492	46,723
17.5	93,969	34,592	80,266	6,004	50,701	23,130
22.5	79,342	21,691	89,148	18,125	22,904	12,788
30.0	65,340	19,882			29,904	10,948

Table 4. Primary productivity, mgC m^{-3} hr^{-1}, 19 August - 18 September 1972. Average error of 10% with integrated daily production and insolation.

Depth (m)	19 Aug	24 Aug	3 Sept	8 Sept	13 Sept	18 Sept
0.0	1.65	1.57	0.87	1.36	1.34	1.38
1.0	2.14	2.82	1.66	2.97	2.58	2.04
2.0	3.66	3.30	2.99	4.30	3.42	2.50
3.0	4.64	3.19	4.30	4.70	3.90	3.17
5.0	5.40	4.15	4.39	4.92	4.35	3.30
7.5	4.69	4.87	2.45	4.60	4.16	3.21
10.0	2.98	2.27	1.57	3.00	2.91	2.11
12.5	2.79	1.48	1.17	1.98	2.18	1.85
15.0	2.44	1.34	0.84	1.71	1.60	1.30
17.5	3.24	1.12	0.59	1.92	1.50	1.01
20.0	2.65	1.87	1.85	2.68	1.96	2.06
25.0	1.49	1.15	1.00	1.13	0.99	0.76
30.0	0.49	0.17	0.17	0.22	0.10	0.10
mgC $M^{-2}day^{-1}$	662	448	398	522	427	362
lang day^{-1}	510	610	465	475	485	445

Table 5. Phosphorus model equations, J_{ij} expressed in μg liter^{-1}hr^{-1}.

	Equation		Curve
1	$dC/dt = (F\gamma)^{1/2}\rho\alpha P_{mod}$	carbon flux (mgC m^{-3} hr^{-1}), F = phytoplankton biomass	
1a	$\gamma = \exp(0.685I_z + 0.4)$	Increase of photosynthetic efficiency with decreased light (i.e., with depth)	Exponential
1b	$\rho = 1 - \frac{\ln[(UV + IR)_z + 5]}{[\ln(UV + IR)_o + 5](1.54)}$	Light inhibition as a function of UV and IR at surface (o) and depth (z)	Exponential
1c	$\alpha = (I_z/I_k)/[1 + (I_z/I_k)^2]^{1/2}$	Light saturation, I_z = light at depth z, I_k = light at onset of saturation	Hyperbola
1d	$P_{mod} = vQ_1/(k_m + Q_1)$	Michaelis-Menten expression for phosphate limitation (Q_1); k_m = half-saturation, v = maximum flux	Hyperbola
2	$J_{13} = 0.01\ dC/dt$	Phosphate required to support photosynthesis	
3	$J_{14} = Q_4[2.46S \exp(-0.76/T)]/[24(1.17 + S)]$	Phosphate required to support bacteria S = concentration of dissolved organic carbon, T = temperature	
4	$J_{i5} = Q_i[\sum_{k=1}^{2}\sum_{j=1}^{5} 0.51L_{kj}^2(0.44 + 0.05T) + \sum_{j=1}^{5} 0.0034L_{3j}^2T]$	Zooplankton grazing. See text for description	
5	$J_{51} = 0.0286Q_{5j}W^{-0.383} \exp(0.0387T + 10^{-5}C - 3.34P)$	Zooplankton excretion of phosphate. See text for description	
6	$J_{37} = 0.005Q_3/t$	Phytoplankton death per time t	
7	$J_{47} = 0.7J_{14}$	Bacteria death	
8	$J_{57} = 0.005Q_5/t$	Zooplankton death	
9	$J_{[illegible]} = 0.75Q_7/t$	Phosphate regeneration through autolysis	

Table 6. Model equations of distribution, complexation, and precipitation of phosphate species as a function of pH and iron. P_T = total species, DIP = phosphate left in solution, HPO_4S = HPO removed, HPO_4P = percentage removed, and [ ] = concentration of ion.

$[PO_4^{3-}]$	=	$P_T/(1 + [H+]/10^{-12.3} + [H^+]/10^{-19.5} + [H^+]^3/10^{-21.7})$
$[HPO_4^{2-}]$	=	$PT/(1 + (10^{-12.3}/[H^+] + [H^+]/10^{-7.2} + [H^+]^2/10^{-9.4})$
$[H_2PO_4^-]$	=	$P_T/(1 + [H^+]/10^{-2.2} + 10^{-7.2}/[H^+] + 10^{-19.5}/[H^+]^2)$
$[H_3PO_4]$	=	$PT/(1 + [H^+]/10^{-2.2} + [H^+]^2/10^{-9.4} + [H+]^3/10^{-21.7})$
HPO_4S	=	$10^{-11}[H^+]/[Fe^{3+}]$
HPO_4P	=	HPO_4S/HPO_4
[DIP]	=	$3.1 \times 10^7(P_T - [HPO_4^-](1-HPO_4S[HPO_4^-]$

Table 7. Steady-state solution to equations (1)-(9)

Pool ($\mu g\ liter^{-1}$)		Flux ($\mu g\ liter^{-1}\ hr^{-1}$)		Turnover (hr^{-1})	
Q_1	0.10	J_{13}	0.032	r_{13}	0.319
Q_3	1.65	J_{14}	0.005	r_{14}	0.050
Q_4	0.11	J_{35}	0.025	r_{35}	0.015
Q_5	0.24	J_{45}	0.002	r_{45}	0.015
Q_7	0.01	J_{51}	0.025	r_{51}	0.104
		J_{37}	0.007	r_{37}	0.004
		J_{47}	0.004	r_{47}	0.038
		J_{57}	0.001	r_{57}	0.004
		J_{71}	0.012	r_{71}	0.840

DIP (Q_1) = dissolved inorganic phosphorus
DOP (Q_2) = dissolved organic phosphorus
PPP (Q_3) = phytoplankton particulate phosphorus
BPP (Q_4) = bacteria particulate phosphorus
ZPP (Q_5) = zooplankton particulate phosphorus
POP (Q_6) = polyphosphate
DET (Q_7) = detrital phosphorus
PHY (Q_8) = ferric phosphate
SED (Q_9) = sediment phosphorus
AP = alkaline phosphatase
T = temperature
LT = light
J_{ij} = flow from pool Q_i to pool Q_j

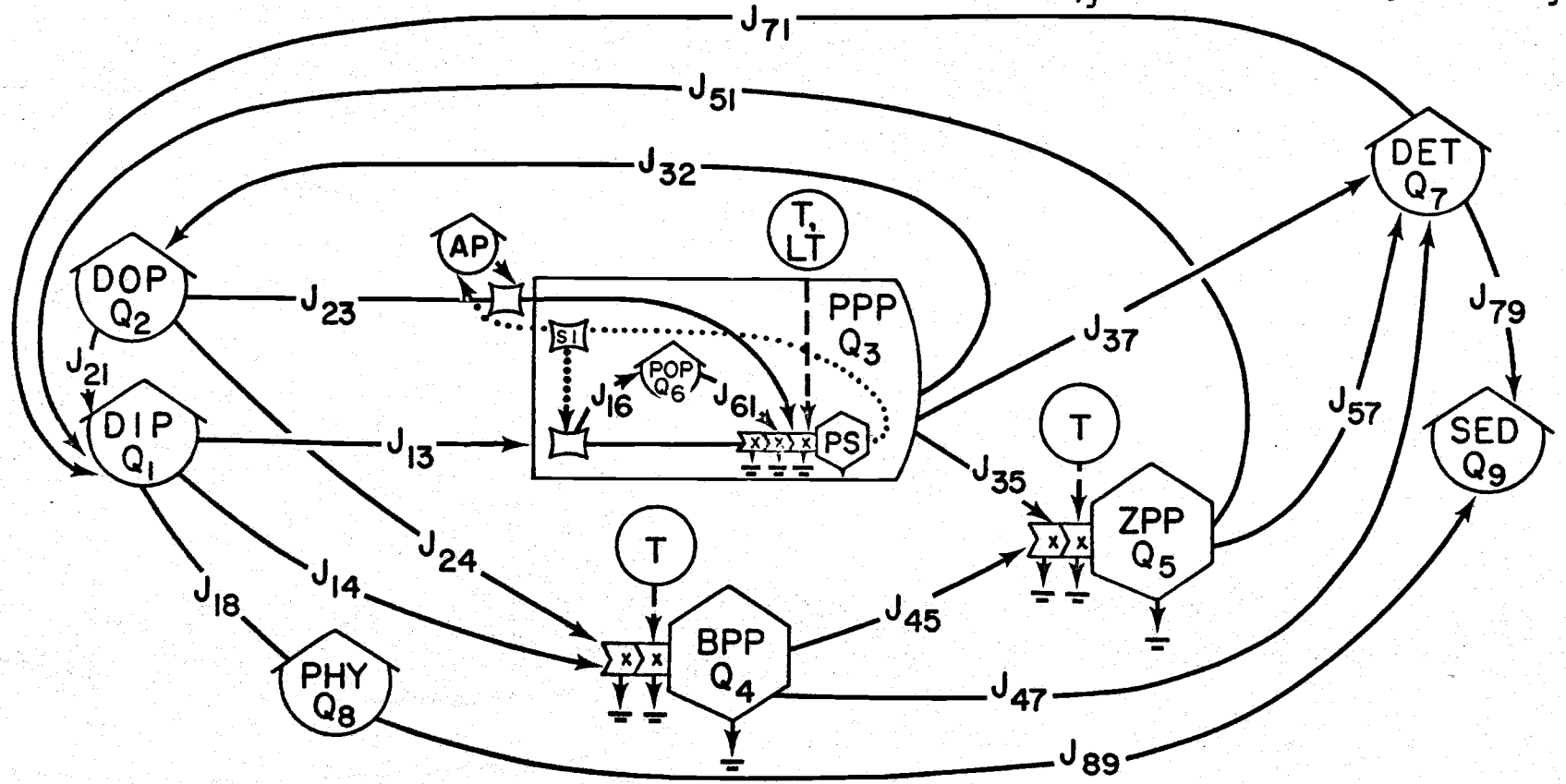

Figure 1. Conceptual model of the phosphorus cycle of Castle Lake during summer stratification (see text for discussion).

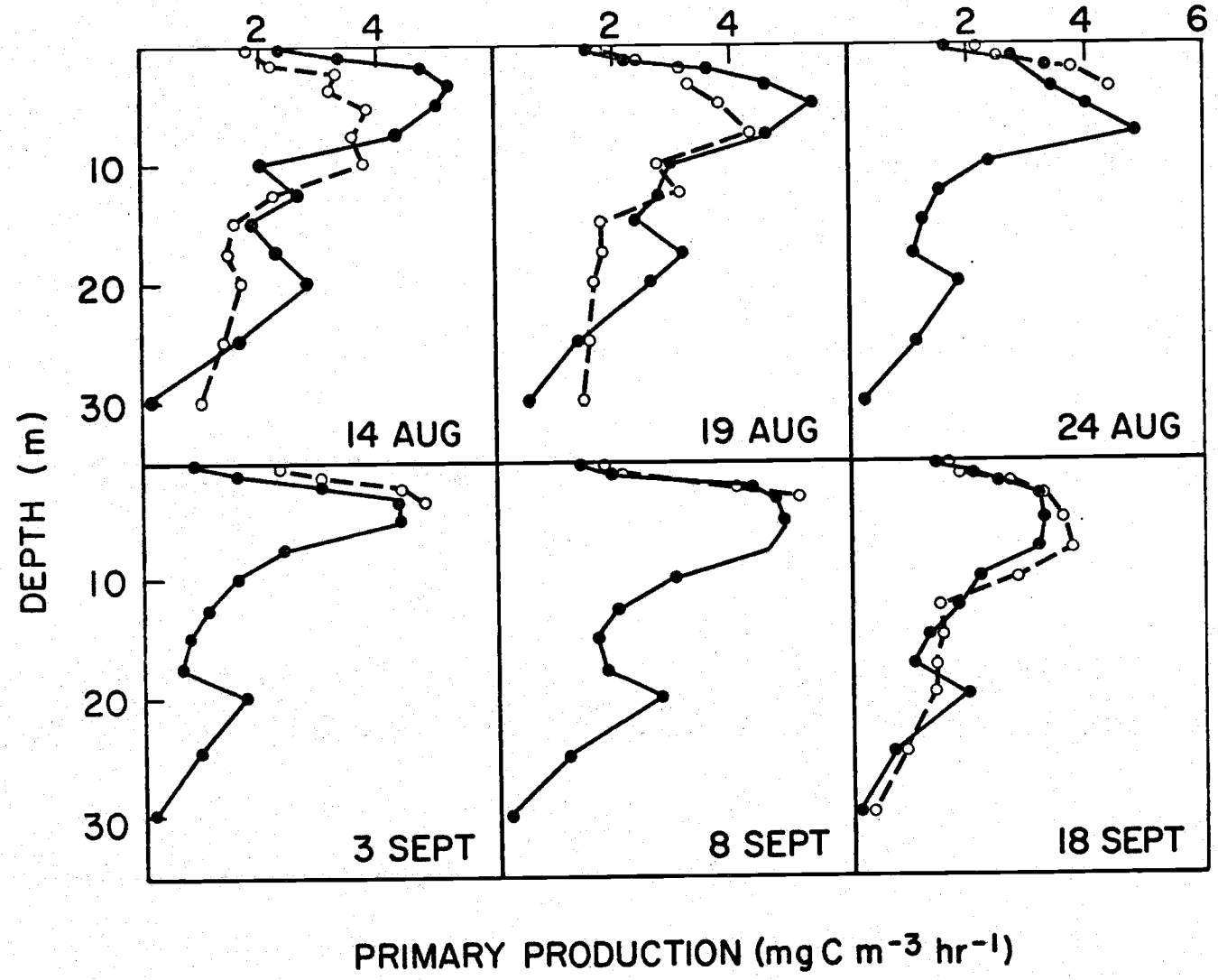

Figure 2. Observed (●—●) versus predicted (Equation 1, o---o) primary production. Absence of (o---o) indicates model failure.

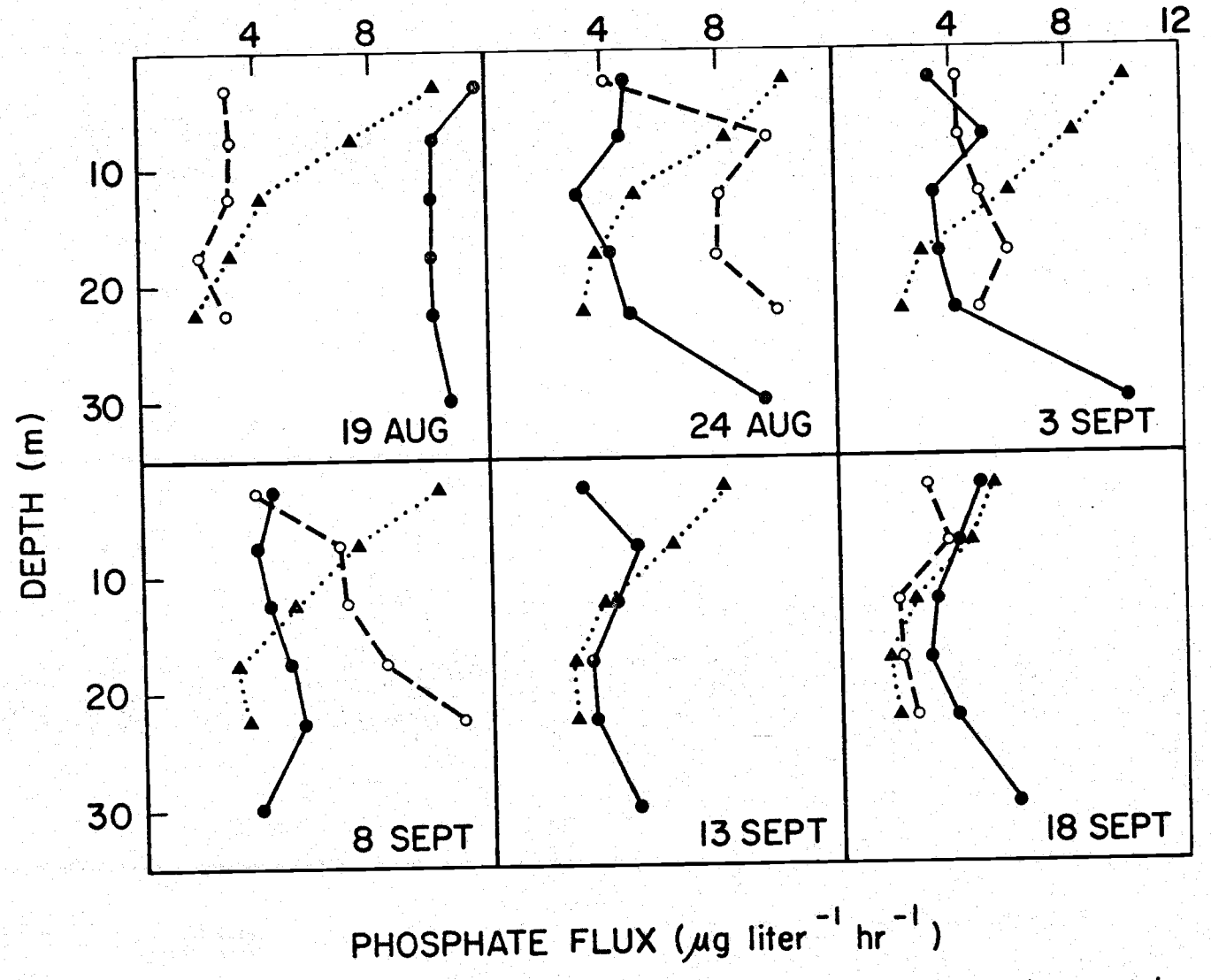

Figure 3. Observed phosphate uptake (●—●), predicted phosphate uptake ($J_{13} + J_{14}$, o---o) and model phosphate regeneration ($J_{51} + J_{71}$, ▲---▲). Absence of (o---o) indicates model failure.

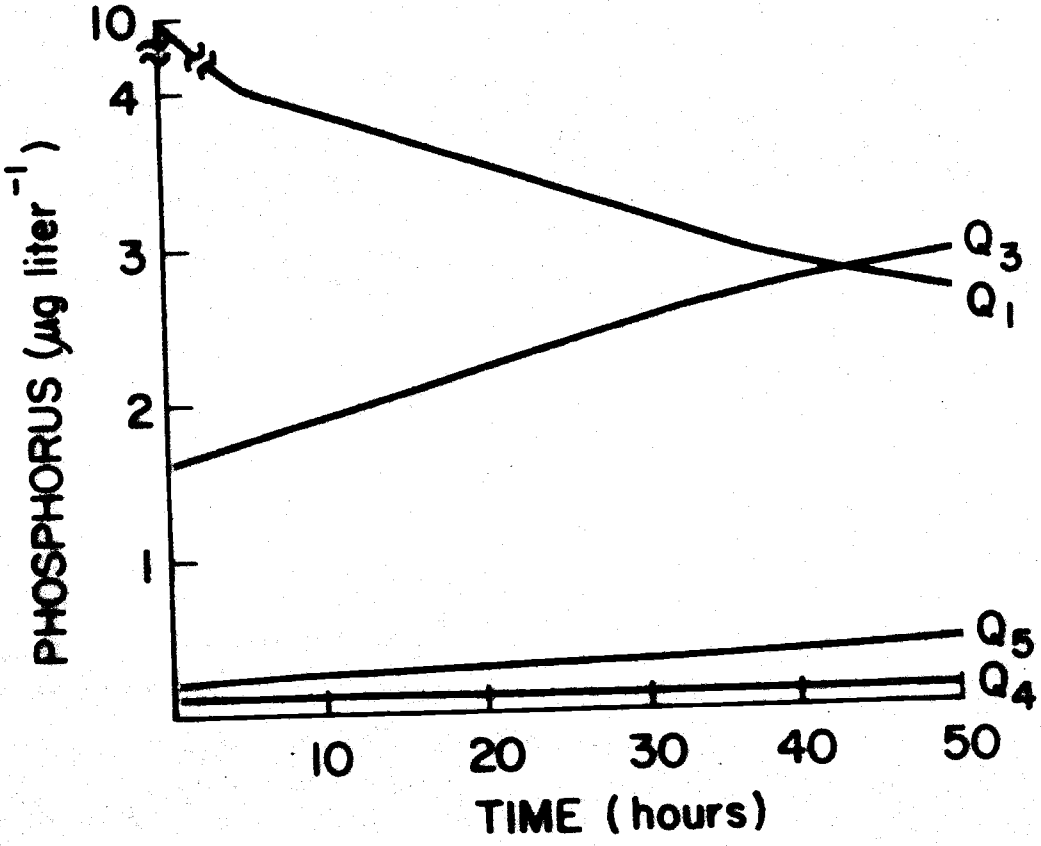

Figure 4. Response of phosphorus model under phosphate-limiting conditions to plane crash of fertilizer; phosphate (Q_1), phytoplankton (Q_3), bacteria (Q_4), zooplankton (Q_5), detritus (Q_7).