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Phosphorus Dynamics in a North Carolina Piedmont Reservoir

by

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ABSTRACT

A ten-month study of University Lake, a water-supply impoundment in the Piedmont Province of North Carolina, showed the patterns of phosphate uptake at different depths throughout the year. The lake underwent turnover in November but was temperature stratified again by mid-March. Oxygen depletion of the hypolimnion occurred by mid-April. Filterable reactive phosphate concentrations were low (0.006-0.045 mg $P \cdot l^{-1}$); phosphate made up about half of the total P in winter but less than a quarter in spring, summer, and fall. Inorganic nitrogen concentrations in surface waters were also low, less than 0.1 mg $N \cdot l^{-1}$ except for peaks (>0.3 mg $\cdot l^{-1}$) in ammonium in October-November and in nitrate in January-February. Chlorophyll-a values in surface waters ranged from <5 $\mu g \cdot l^{-1}$ in winter to >30 $\mu g \cdot l^{-1}$ during the warm seasons.

The phosphate uptake rate coefficient (k) ranged from about 0.06% removal from surface water per minute in January to 40% per minute in June. Gross rates of phosphate uptake by seston averaged >0.1 mg $P \cdot l^{-1} \cdot h^{-1}$ during May-October, although net uptake was only a fraction of this. Algal contribution to this uptake was negligible throughout the winter but became dominant in June. Although there was a good correlation between phosphate uptake and chlorophyll-a concentration, bacterial uptake exceeded algal uptake at all depths and on all dates except in the epilimnion in June. Unfortunately, "bacterial" uptake, assessed by antibiotic treatment, may have included blue-green algal uptake; therefore bacterial uptake may be overestimated and algal uptake underestimated. Suspended sediments dominated phosphate uptake in winter when they were most abundant, when phosphate concentrations were high, and when biological activity was low. Except in the hypolimnion, however, abiotic uptake did not contribute significantly to total phosphate uptake. During the stratified period suspended sediments were a source of phosphate to the water. Phosphorus is probably the major nutrient limiting phytoplankton growth in University Lake.

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SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

University Lake is a warm-monomictic or dimictic water supply impoundment in the Piedmont Province. It is oxygenated at all depths during the winter mixing period but the hypolimnion is deoxygenated during the summer stratified period. Because the watershed is mostly agricultural land and forest, inputs of algal nutrients are not excessive, concentrations in the water are not high, and the phytoplankton is only moderately productive. Turbidities are high, especially during the winter when heavy runoff brings in silt and clay from the watershed. This is the first study of nutrient kinetics in a Piedmont lake.

Nutrient concentrations measured during this 10-month study were low. Total P averaged 0.044 $mg \cdot l^{-1}$, of which filterable reactive phosphorus (phosphate) usually was about 25-50% in surface waters. Phosphate was especially low when phytoplankton was abundant in summer. Inorganic nitrogen concentrations were also low, less than 0.1 mg $N \cdot l^{-1}$ except for peaks of >0.3 mg $N \cdot l^{-1}$ in ammonium in October-November and nitrate in January-February. The ratios of inorganic N to inorganic P were much higher than the 16:1 Redfield ratio, averaging 68:1 in surface waters. Although the ratio approached the Redfield ratio closest during the growing season, phosphorus is more likely to be limiting than nitrogen on an annual basis. These ratios suggest that increased phosphorus inputs to the lake would tend to increase algal productivity more than increased nitrogen loadings.

Phosphate uptake rate varied with depth and season. The uptake rate coefficient (k), measured with radioactive phosphate tracer, in surface waters ranged from about 0.06% removal per minute in February to 40% per minute in June and October. The gross phosphate uptake rates by seston were highest during the period of lake stratification, ranging from 0.084-0.47 mg $P \cdot l^{-1} \cdot h^{-1}$ between May and October; no samples were taken in July and August when even higher rates might have occurred. Bacterial uptake, assessed by antibiotic treatment, usually dominated phosphate uptake. Algal uptake, however, exceeded bacterial uptake in the epilimnion in June, and abiotic (suspended sediment) uptake exceeded bacterial uptake in January and February and in the hypolimnion in May and June. "Bacterial" uptake may have included uptake by blue-green algae and therefore may have been overestimated at the expense of "algal" uptake. Algal uptake was found only in the surface waters (except in the metalimnion in March). Abiotic gross phosphate uptake rates were <0.003 mg $P \cdot l^{-1} \cdot h^{-1}$ except in the hypolimnion in May and June (0.015-0.018 mg $P \cdot l^{-1} \cdot h^{-1}$). Although suspended sediment uptake dominated total uptake during the winter when biological activity was low, it was much less important on an annual basis than algal and bacterial uptake. However, since net phosphate uptake rate has been shown to be substantially less than the gross rate, especially when biological activity is highest, suspended sediment uptake is undoubtedly more important than it appears here.

Phosphate potential curves showed that suspended sediments functioned as a sink for phosphate during the winter when they were abundant and phosphate concentrations were high, but that they were a source of phosphate

to the water during spring and early summer. Sediments sinking to the bottom during winter, and algae and bacteria settling out during the rest of the year, tend to strip phosphate out of surface waters and thereby maintain the high N:P ratio.

The Piedmont physiographic province with its rolling hills and clay soils covers a very large area from Georgia to Virginia. Piedmont lakes, mostly man-made, are important to local residents for water supply, recreation, and fishing. Their ability to serve adequately as a resource and their ultimate value is linked to water quality. It is therefore important that preventive and corrective measures be undertaken to protect the level of water quality and trophic state of impoundments such as University Lake.

One factor important to the trophic state of any lake is nutrient supply. Increased nutrients increase algal growth. Such increased growth is undesirable in University Lake, because abundant algae could increase filtration costs, create taste and odor problems in the drinking water supply, and cause unsightly surface blooms on the lake. Furthermore, an increase in algal productivity would almost certainly deplete the dissolved oxygen in the bottom waters to an even greater extent than presently occurs. Oxygen depleted water would reach higher into the surface waters and extend over a longer period. Hypolimnetic oxygen depletion often severely damages fish populations and causes chemical release from the sediments into the water of iron and manganese which increase costs of water treatment. Careful consideration must therefore be given to restrict excessive loadings of phosphorus (and to a lesser extent nitrogen) to Piedmont impoundments if control of algal productivity is to be maintained.

Investigations which are needed to provide understanding necessary for proper management of Piedmont impoundments include the following:

1. A study of nutrient exchanges between the bottom sediments and the water so that nutrient budgets for the entire lake system may be constructed.
2. A study of nutrient loading to the lake from the entire watershed, with careful analysis of land use and nature of nutrient sources so that the functioning of the lake as a part of the entire drainage basin landscape can be established.

INTRODUCTION

Nutrient uptake and water quality

Impounded waters, including farm ponds, water supply reservoirs, and cooling ponds for electrical power plants, comprise the most important bodies of surface water in the Piedmont Province. As water consumption, water-based recreation, and industrial activity increase, the need for maintaining high quality in the waters increases. Intelligent management requires knowledge and understanding of the environmental factors which contribute to water quality problems. The factors which control nuisance algal blooms in the Piedmont have not been identified, and the relationships between nutrient availability and algal growth are not clearly understood.

Eutrophication is a term used to describe the sequence of changes in aquatic ecosystems caused by an increased rate of supply of nutrients to water (Vallentyne 1974). The immediate response of the ecosystem to increased nutrient load is an increase in the primary production rate and abundance of plants. This increase in primary production leads to long term changes in the chemistry and biology of the lake. There is generally a decrease in oxygen in the deep waters which causes progressive changes in the fauna. Lakes which are excessively productive are undesirable as water supplies (Downing 1970), recreational resources (Beeton 1969), and fishing grounds (Golterman 1975).

The most important nutrients in eutrophication of fresh waters are nitrogen and phosphorus. Many authors have been able to correlate N and P levels in a lake to chlorophyll-a (Lund 1970; Thomas 1973), and the correlation has been used for predicting the trophic state of lakes (Vollenweider 1968; Dillon and Rigler 1974; Carlson 1975; Weiss and Kuenzler 1976; Nicholls and Dillon 1978). In enrichment experiments, when phosphorus and nitrogen are added artificially to lakes, a dramatic increase in algal growth may ensue (Schindler, et al. 1973; Schindler 1974), and when nutrient loading to a lake is reduced, there may be a decrease in algal growth (Edmondson 1969, 1970).

There are, however, considerable difficulties in interpreting the exact relationships between nutrients and production. During phytoplankton blooms, for example, water is often stripped of its orthophosphate yet supports the algal population at high levels for days or weeks (Pearsall 1932). Often it is during summer, when the nutrients are largely depleted, that a lake supports its largest algal population of the year. Thus there is the paradoxical situation that the algae, which seem to be an indicator of eutrophy, often are abundant at the time when there is the least available plant food in the water (Hutchinson 1973).

The explanation of this paradox may lie in the fact that lakes are dynamic systems (Pomeroy 1960), and thus the single static measurement of nutrient concentration may not reflect the actual utilization of the nutrient by organisms of the lake. Nutrients are partitioned and re-

cycled at rapid rates, and the phosphate concentration at one time does not reflect the system's potential to provide phosphorus for growth. Exchange of dissolved orthophosphate with sediments and organisms is rapid (Hutchinson and Bowen 1947, 1950; Coffin, et al. 1949; Hayes, et al. 1952), and "organisms able to concentrate the phosphate may have a constant supply" (Pomeroy 1960). Even in the epilimnion, where exchanges between water and bottom sediments and water and aquatic macrophytes are minimal, the turnover time (time necessary for phosphorus in a given compartment to be replaced) between orthophosphate and suspended biotic and abiotic particles can be as short as one minute (Rigler 1956, 1964; Lean 1973). It has therefore been suggested that the uptake rate of phosphorus may be more indicative of the nutrient status of the plankton than is the phosphate concentration (Pomeroy 1960; Healy 1973; Peters and MacIntyre 1976; Peters 1979); a rapid flux rate of phosphate may be more important than a high phosphate concentration in maintaining high levels of primary production.

Factors controlling phosphorus uptake by micro-organisms

Both ecological and physiological factors are important in controlling the uptake rate of phosphorus by micro-organisms. One physiological factor important to uptake rate is the nutritional state of the algae; polyphosphates stored at a time of phosphorus abundance in the water generally inhibit phosphorus uptake (Fitzgerald 1969; Fuhs 1969; Rhee 1972), although there is evidence that stored polyphosphate will not inhibit P uptake in natural ocean plankton or P-starved cultures (Perry 1976).

Cell size is also of importance in phosphorus uptake ability. Munk and Riley (1952) provided a theoretical basis which predicted that smaller cells would have a higher uptake rate, and this prediction was confirmed in a laboratory study by Fuhs et al. (1972). Friebele, Correll, and Faust (1978) confirmed the importance of cell size in rate of uptake in their field work in Chesapeake Bay; uptake rate per unit biomass was found to be inversely proportional to cell size.

One environmental factor which governs the rate of phosphorus uptake is the concentration of phosphate in the water; increasing amounts of phosphate increase the rate of uptake according to Michaelis-Menton kinetics (Fitzgerald 1969; Fuhs 1969; Rhee 1972). Other factors include temperature, light, and diurnal cycle. An increase in temperature increases P uptake rate (Kuenzler, Stanley, and Koenings 1979), although the effect of light is controversial. Healy (1973) and Kuenzler and Ketchum (1962) found P uptake was stimulated by light but not dependent on it. Fuhs et al. (1972), in their laboratory work, and Perry (1976) and Faust and Correll (1976), using natural populations, found light to have no effect at all, although the latter authors suggest that light could be important to some species but not to others. The phosphate uptake rate of estuarine seston in surface waters was increased about 25% by illumination whereas the rate in normally dark bottom waters

was increased about 60% compared to experiments performed in darkness (Kuenzler, Stanley and Koenings 1979). No consistent diurnal variation in uptake of P was observed by Richie, Devol, and Perkins (1976) or Perry (1976) in field work, although laboratory findings of Chisolm and Stross (1976) suggest life stage of the cell may be important; uptake rate is highest immediately before cell division.

Generally, there is a distinct seasonal variation in the uptake rate of phosphorus in open systems. Phosphate turnover times are affected by annual cycles of phosphate concentration, algal and bacterial density, and temperature. In freshwater systems, turnover times are shortest (less than 1 minute) in the summer when phosphorus reserves are depleted and longest (over 30 hours) in the winter when there is little biological demand (Rigler 1964; Halmann and Stiller 1974; Levine 1975). In estuarine systems, summer algal blooms in the Chesapeake Bay (Taft, Taylor, and McCarthy 1975; Faust and Correll 1976) and winter blooms in the Pamlico River (Kuenzler, Stanley, and Koenings 1979) caused rapid turnover rates.

Biotic competition for phosphorus

An additional factor which may affect the rate of uptake of phosphorus by a species of micro-organism is competition for the nutrient by other micro-organisms. Studies of competition for phosphorus among different species of algae in culture reveal that species found in oligotrophic waters can often successfully outcompete species found in eutrophic waters under conditions of phosphorus scarcity; the same species are outcompeted by the eutrophic algae under conditions of phosphorus abundance (Titman 1976).

Bacterial competition with algae for phosphorus has been studied both in culture and in open systems. Rhee (1972) and Fuhs, et al. (1972) found that the competitive success of algae or bacteria depended on the phosphate concentration in the medium; bacteria successfully competed with diatoms at the higher phosphate concentrations. Although the bacterial densities used by Fuhs, et al. and Rhee were several orders of magnitude greater than those found in open water systems, most field work supports laboratory conclusions that bacteria dominate the uptake of phsophorus (Harrison, et al. 1977; Taft, et al. 1977; Friebele, et al. 1978). Other studies (Taft, et al. 1975; Kuenzler, et al. 1979), however, found algae to be responsible for most of the phosphorus uptake. Faust and Correll (1975) found a seasonal variation in the relative importance of algae and bacteria to the uptake of phosphorus in the Chesapeake Bay. Algae were important contributors to P uptake in the spring and summer months of May, June, and July.

Less work has been done to partition the biotic uptake of phosphorus in freshwater lake systems than in estuarine systems. Rigler (1956), in his pioneer work on P uptake, concluded that bacteria were the major organisms responsible for the removal of P in the water column. Pearl

and Lean (1976) confirmed this by examining P uptake in freshwater using autoradiographs of ^{33}P experiments. Bacteria became visible after two minutes, whereas phytoplankton could be seen only after 10 minutes. Specific activity of the algae (radioactivity per unit biomass) was 30% of that for bacterial cells at the end of the experiment. All phosphorus kinetic work in freshwater has been done using epilimnetic water only; there are therefore no data on the importance of organisms at other depths to phosphorus cycling in lakes.

Interpretation of tracer measurements of phosphorus uptake

Radioactive isotopes of phosphorus have been widely used as tracers in experiments designed to measure the flux of phosphate from water to phytoplankton or other particles in suspension (e.g., Hutchinson and Bowen 1947; Hayes, et al. 1952; Rigler 1956; Kuenzler and Ketchum 1962; Rhee 1972; Halmann and Stiller 1974). These tracer experiments may produce erroneous or misleading results due to errors in chemical analysis for phosphate (e.g., Kuenzler and Ketchum 1962; Rigler 1968; Lean 1973) and in underestimating the importance of phosphate efflux from algal cells (Rice 1953). Nalewajko and Lean (1978), grew algae with ^{33}P as a phosphorus source and then added ^{32}P to cultures for short-term uptake experiments. The rates of uptake of the ^{32}P were much more rapid than the uptake of the ^{33}P in which the algae were grown. In their experiment, there was no possibility for errors in assessing the rate of change of ambient FRP, since the ambient FRP was radioactive and the authors did not need to rely on chemical analysis for orthophosphate. The authors concluded that short-term experiments represented gross uptake only and did not account for release of phosphorus from cells. Kuenzler, et al. (1979) demonstrated that gross uptake rates of phosphate, as measured with short-term tracer experiments, were often much higher than the net uptake rates, measured by the change in phosphate concentration, of estuarine phytoplankton populations.

Suspended sediment contribution to phosphorus dynamics

The influx of suspended sediment is potentially important to the phosphorus dynamics of lake systems, especially where the watershed soils are rich in clay, as in the Piedmont. Sediments can act either as a phosphorus source or a phosphorus sink depending on the chemical composition and nutrient status of the sediment and the concentration of phosphate in the water column (Carritt and Goodgall, 1954; Taylor and Kunishi 1971; Butler and Tibbits, 1972; Kunishi, et al. 1972). Generally, it is reported that sediments act as a sink (Hayes and Phillips 1958; Pomeroy, et al. 1965; Harter 1968; Fitzgerald 1970; Lincoln 1971), adsorbing phosphate ions loosely at first and later incorporating them into crystalline lattice of the sediment (Harter, 1968).

Although sediments are generally sinks for phosphate, algae have been shown to be able to use loosely sorbed sediment phosphorus as they

deplete the phosphate in the water column (Olsen 1958, 1964; Porcella and Bishop 1975). Most algal bioassay work with both aerobic and anaerobic muds have shown that up to 30% of the total P associated with the sediment is potentially available to algae for growth (Golterman, et al. 1969; Helfrich and Kevern 1973; Cowen and Lee 1976), although Fitzgerald (1970) reported no growth in cultures with phosphorus supplied only as aerobic sediments. Thus the living plankton and the non-living suspended sediments (collectively termed the seston) must both be considered in studies of phosphorus cycling.

This report describes a study of the partitioning of phosphorus and rate of phosphorus cycling in a Piedmont impoundment. Seasonal changes of several important forms of phosphorus were monitored, and radioactive tracers were used to measure the rates at which biotic and abiotic particles removed phosphorus from the water column. The reservoir was studied at three depths during spring and summer stratification to elucidate differences between surface, middle, and bottom waters. Results provide data on the effects of phytoplankton, bacteria, and suspended sediments on the seasonal and vertical distribution of phosphorus during a ten-month period. This research was the basis of a technical report by Linda E. Greer to the Department of Environmental Sciences and Engineering as part of the Master of Science in Public Health degree, December 1979.

The research site

University Lake was selected for this research partly because of its accessibility, its size, and the amount of research which has already been carried out there, but mainly because it typifies a Piedmont impoundment. It serves as the water supply for Chapel Hill and Carrboro, North Carolina. University Lake is a warm-monomictic or dimictic lake, depending on the severity of the winter, with an area of 73 ha, a maximum depth of 9 m, an average depth of about 3 m. Its capacity is approximately 2.2×10^6 m^3 and it receives 4.9×10^4 m^3 of water per day (mean annual rate) from 80 square kilometers of an agricultural watershed (Weiss and Oglesby 1962) on the Carolina slate belt. Its main tributary is Morgan Creek, a headwater stream which flows into the Haw River and then into the Cape Fear River.

University Lake is oxygenated at all depths during winter, but thermal stratification beginning in March prevents oxygen transport to the hypolimnion; the hypolimnion is therefore normally anoxic from about May until November (Weiss and Oglesby 1960, 1962; Weiss and Breedlove 1973). High levels of iron, manganese, and sulfide are reached in the hypolimnion in summer (Weiss and Oglesby 1960, 1962; Weiss and Breedlove 1973). Although phosphate concentrations in the lake are relatively low (0.009 to 0.025 mg $P \cdot l^{-1}$), chlorophyll values range from 1 to 35 $mg \cdot m^3$ during the year and total phosphorus values are high (0.075 to 0.129 mg $P \cdot l^{-1}$) (Weiss and Breedlove 1973). Using criteria of total P, conductivity, and pollution index, Weiss and Kuenzler (1976) in their study of

North Carolina lakes rated the lake mesotrophic. The lake is moderately productive (2.7 and 47 $mgC \cdot m^{-3} \cdot h^{-1}$ in winter and summer, respectively). The normal algal flora includes greens, euglenophytes, diatoms, blue-greens, chloromonads, and others (Heath 1968; Soyak 1970). An interesting phenomenon is the summer bloom of Oscillatoria tenuis in the metalimnion; high bacterial numbers were also found in this layer (Heath 1968; Weiss and Oglesby 1960). Heterotrophic utilization of glucose and acetate resulted in turnover times of 0.2-5 h for these substrates (Francisco 1970). Oxygen demand in the hypolimnion was about 8.4 g $O_2 \cdot m^{-2} \cdot d^{-1}$ with large quantities of methane being released (Haywood 1968). Midges (Chironomidae) are the dominant benthic animals because of their microaerophilic tendencies (Hartley 1971).

METHODS

Sampling

University Lake was sampled periodically from September 1978 through June 1979 at the dam (Station 1) and the Jones Ferry Road bridge (Station 3) (Figure 1). A Guzzler hand pump (Cole Parmer, Inc.) was used to obtain water samples; its intake hose was covered with a #30 plankton net to exclude zooplankton and macroinvertebrates. Large (10-15 liter) carboys were filled with lake water and taken back to the laboratory within one hour of collection for chemical analyses and kinetic measurements. Because the guzzler pump aerated samples as it filled the jugs, an alternate method was used in May and June 1979 to obtain hypolimnion and metalimnion samples when the dissolved oxygen concentration was less than 1 $mg \cdot l^{-1}$. An APHA stream sampler fitted with a #30 plankton net screening was lowered quickly to the desired depth where BOD bottles rinsed and filled. This procedure was repeated by lowering the sampler again to the same depth and location until enough water was obtained for uptake measurements and nutrient and chlorophyll analyses. The anaerobic bottles were stored and transported to the laboratory in a cooler at the temperature of the water depth sampled. All sampling was done between 0830 and 0930 to control for diurnal population variability in the lake.

Concurrently with water collection at Station 1, various chemical and physical limnological data were obtained. Conductivity and temperature were measured at 0.5 m intervals with a YSI Model 33 conductivity meter. Dissolved oxygen was measured at three depths in the lake (upper epilimnion, metalimnion, and hypolimnion) using a YSI Model 54 oxygen meter which was calibrated before use. Turbidity measurements at 1 m were made routinely by the Orange Water and Sewer Authority Analytical Laboratory.

Water was obtained from a depth of 0.5 m at least once monthly. Sampling at other depths was occasional until March 1979 when monthly sampling at three depths at Station 1 was begun. Epilimnion samples came from 0.5 m and hypolimnion samples from 7.0 meter depths. Depth of the mid-metalimnion sample varied with the depth of the thermocline but was usually between 3 and 4 meters.

At the laboratory, water was prepared for various analyses. Filtered (using 0.4 µm Nuclepore or 0.45 µm Gelman filters prerinsed with 10% HCl and deionized water) and unfiltered water was collected in clean polyethylene bottles and frozen until later analysis for nutrients. Samples for chlorophyll were passed through Gelman GF/C glass fiber filters and processed by the procedure of Lorenzen (1967). Other unfiltered samples of water were used to measure phosphate uptake.

Uptake of phosphate by seston

Samples (200 ml) of lake water were dispensed into glass BOD bottles and placed in incubators in the laboratory at ambient lake temperatures

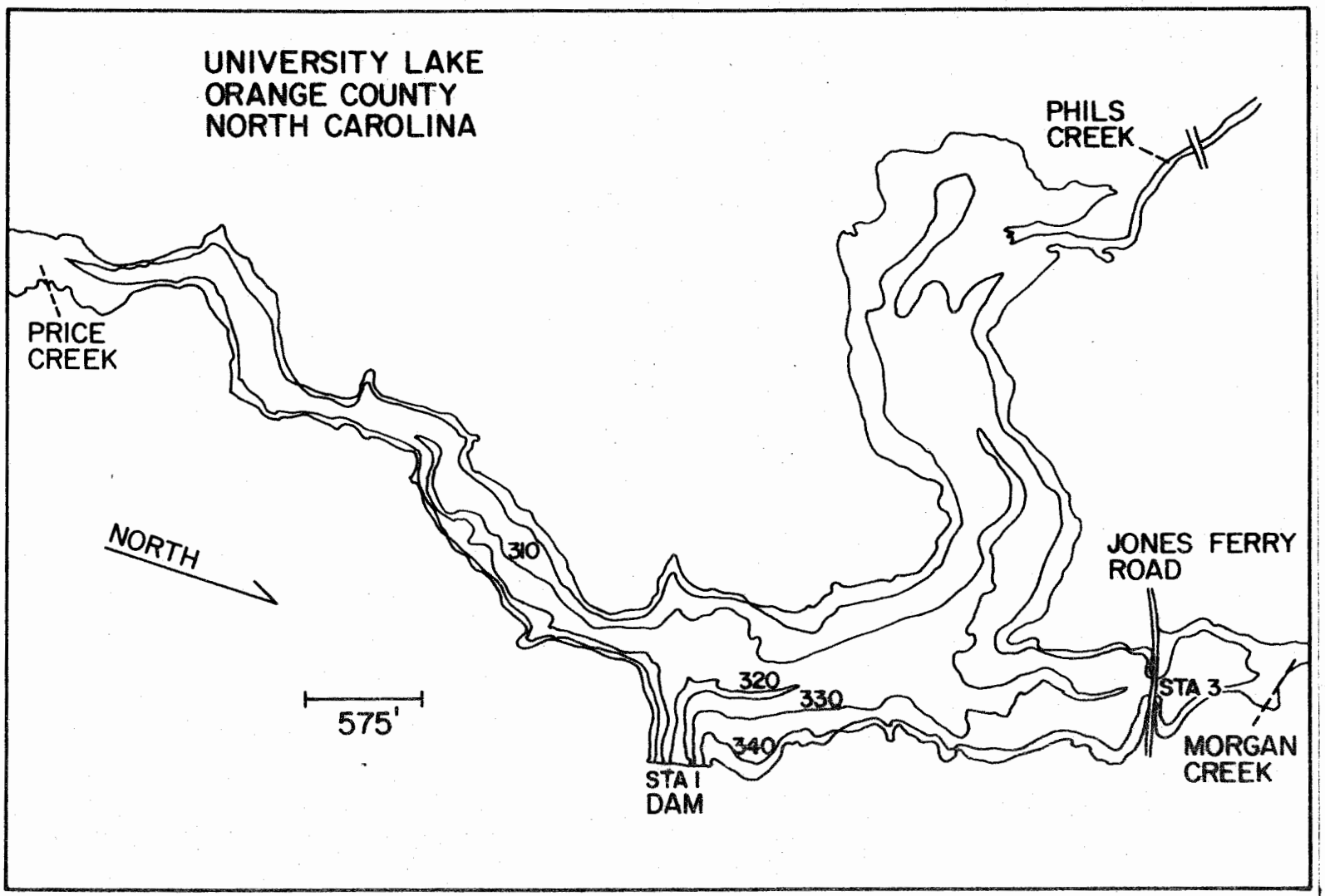

Fig. 1. Map of University Lake showing location of sampling stations. Bathymetric contours are in feet above MSL; spillway elevation = 346'.

± 2°C. During stratified conditions, three temperatures corresponding to the epilimnion, metalimnion, and hypolimnion were required, whereas during unstratified conditions only one temperature was required. Light of intensity 6 x 10^2 foot candles (17% of average ambient light as measured by the same meter) was provided to epilimnion samples. Metalimnion and hypolimnion samples were incubated in the dark by covering the bottles with aluminum foil; these depths received less than 1% light penetration throughout the study period in the lake. Samples were preincubated at least one hour before radioactive tracer was added to begin the kinetic experiments; all experiments were complete within eight hours of collection of the water. Uptake rate was measured in triplicate throughout most of the study.

Rate of gross phosphate uptake was measured primarily through the use of radioactive tracer. Carrier-free ^{32}P-labeled orthophosphate (6-7 μCi) was added to 200 ml of lake water. Samples were incubated, and 5 ml subsamples were removed over a period of time appropriate to the rate of uptake. The subsample was gently filtered to remove particulates, and the filter and/or the filtrate was placed in a scintillation vial for counting by Cerenkov radiation (Haberer 1965) on a Packard Tri-carb Model 3320 liquid scintillation counter.

The rate of net phosphorus uptake was occasionally measured concurrently by a second method which monitored the change in filterable reactive phosphorus (FRP, also termed phosphate) with time. Lake water was incubated as in the tracer experiments, although no tracer was added. Subsamples (50 ml) were removed over time and filtered and frozen for later chemical analysis of FRP. (See below.)

When samples were obtained from anaerobic waters, a modified procedure for tracer work was employed. Additions of antibiotic, formaldehyde, and ^{32}P were made under nitrogen gas to BOD bottles which had been filled to the top with lake water in the stream sampler. As 5 ml subsamples were removed, nitrogen gas was used to displace the air before bottles were recapped. Because of the shape of the BOD bottles and the small (20 ml) amount of water removed, little surface area was available for oxygen exchange. There was no visual evidence of precipitation in bottles which were under nitrogen during the experiments.

The rate constant, k, for phosphate uptake was obtained by the formula:

$$-k = \ln(A_t/A_o)/t$$

where A_o = initial activity of filterable ^{32}P, A_t = activity at time t of filterable ^{32}P, and t = elapsed time.

This equation assumes that the phosphorus in and on particulate matter (phytoplankton, bacteria, suspended sediments) is in steady state with phosphate in the water and that removal of tracer P is a first order reaction. Where k was not linear throughout the experiment, only the rapid, initial linear uptake was used in the calculations. The rate constant reflects the relative uptake rate of FRP, per unit of time.

Turnover time (1/k) is the time necessary to replace once the amount of P in the water, assuming a steady-state concentration of P. The uptake rate, v, was calculated by multiplying k by the ambient filterable reactive phosphorus concentration in the lake water at the beginning of the experiment:

$$v = k \cdot (FRP)$$

Units for v are mg $P \cdot l^{-1} \cdot t^{-1}$.

Statistical analysis was used to compare the velocities of uptake (v) by each fraction at each depth for individual sampling dates. Analysis of Variance (ANOVA) was used to find the overall significance of depth, treatment, and station on each date (Barr et al., 1976; Kleinbaum and Kupper, 1978). Where overall F-tests revealed significance, the Tukey pairwise procedure was used to uncover statistical differences at Station 1 among treatments at a given depth and differences among depths for a given treatment (Kleinbaum and Kupper, 1978). Uptake differences between the two stations were also assessed using the Turkey comparison procedure.

Fractionation of uptake

Abiotic and bacterial uptake were differentiated from algal uptake of phosphate using both chemical treatment and physical separation methods. Antibiotics (Pennicillin G, at 50 µg/ml and Streptomycin sulfate at 100 µg/ml final concentrations) were added to some water samples to inhibit bacteria, and the uptake of ^{32}P was considered to be primarily algal and abiotic. Since blue-green algae as well as bacteria are probably inhibited, the "algal" uptake and "bacterial" uptake might more correctly be called eucaryotic uptake and procaryotic uptake. Formaldehyde (0.74% final concentration) was added to other bottles to measure the rate of abiotic uptake of phosphate.

There was no evidence for phosphorus contamination by the addition of formaldehyde. Streptomycin sulfate, however, was found to be buffered with phosphate and contributed up to 0.017 mg $P \cdot l^{-1}$ to the lake water samples at the concentration used in the experiments. The contamination was not considered significant in light of phosphate addition experiments performed on 3 occasions during the year (Table 1). These experiments showed that an increase in phosphate concentration did not cause an increase in the velocity of uptake of phosphorus. The algae were taking up phosphorus at their fastest possible rate (Vmax) at ambient and higher phosphate concentrations; rate of uptake was not clearly substrate limited on any occasion during the addition experiments.

Physical size separation was done by filtering subsamples through an 8 µm filter followed directly in series by a 0.4 µm filter. In January, an experiment to compare the adsorption and particle retention capacity of Gelman and Nuclepore filters was performed. One sample of lakewater was pre-filtered through a pre-washed 0.45 µm Gelman filter before tracer

was added as described above. In a second sample, tracer was added to whole lake water. Subsamples (5 ml) were passed through each type of filter in triplicate. Counts on filters from the filtered water were considered to be from adsorption, and counts from whole lake water were considered to be from particle retention. After January 12, 1979, Gelman filters were replaced with Nuclepore filters for size separation work. Uptake of ^{32}P by particles trapped on the 8 μm filter was considered to be largely algal and by particles trapped on the 0.4 μm filter was considered to be bacterial and abiotic.

Table 1. The effect of phosphate addition on the velocity of uptake of P.

Date	Phosphate Concentration (mg $P \cdot l^{-1}$)	Velocity (μg $P \cdot l^{-1} \cdot h^{-1}$)
1/12/79	.036	1.33
	.061	1.71
	.071	1.42
	.14	2.1
	.39	5.1
4/06/79	.005	4.8
	.016	2.9
	.043	12.0
	.088	9.0
6/07/79	.005	75.3
	.007	53.8
	.013	58.5
	.024	72.0

Role of suspended sediments in phosphorus exchanges

The role of sediments as a phosphorus source (contributing phosphate to lake water) or a phosphorus sink (removing phosphate from the water) was defined by constructing phosphate buffer capacity curves (Taylor and Kunishi, 1971; Kunishi, et al., 1972). Suspended sediment was obtained by continuous centrifugation of large quantities (8-18 liters) of lake water after heavy rains and runoff had increased the turbidity of the lake; centrifuged material was stored in 0.74% formaldehyde as a slurry. This sediment was later added in concentrations of 10X ambient to flasks containing a gradient of phosphate concentrations in distilled water and equilibrated by stirring for six hours. The experiments were done at ambient lake water temperatures and at winter

temperatures (5°C) for comparison. After six hours, sub-samples were filtered through pre-washed 0.45 μm Nuclepore filters, and the filtrate was frozen for later FRP analysis. The amount of phosphate adsorbed or desorbed was calculated and plotted. On the plot, the intersection of the curve with the concentration axis gave the equilibrium phosphate concentration, the concentration in the water at which no net uptake or release of P would take place.

Nutrient analyses

Nutrient analyses were performed using a Technicon Autoanalyzer for total phosphorus (TP), total filterable phosphorus (TFP, also termed soluble P or total dissolved P), filterable reactive phosphorus (FRP, also termed orthophosphate or soluble reactive P), ammonia (NH_3), nitrite (NO_2), and nitrite + nitrate ($NO_2 + NO_3$). Particulate phosphorus (PP) was calculated as TP - TFP. Filterable unreactive phosphorus (FUP) was calculated as TFP - FRP. Methods for analysis (Table 2) were EPA approved, all samples were run in duplicate, and EPA controls were run at the beginning and end of nearly every run. Occasionally standards and spikes were included for quality control; recovery of spikes in lake water was generally excellent (95-100%).

Table 2. Methods used for N and P analyses.

Nutrient	Method	Reference
Ammonia	Automated Colorimetric Method, Phenolate	EPA*, p. 168
Nitrite	Automated Colorimetric	EPA, p. 215
Nitrate	Automated Cadmium Reduction	EPA, p. 207
Filterable Reactive P	Automated Ascorbic Acid Reduction	EPA, p. 256
Total Filterable P	Persulfate Digestion; Automated Ascorbic Acid Reduction	EPA, p. 256
Total P	Persulfate Digestion; Automated Ascorbic Acid Reduction	EPA, p. 256

*Environmental Protection Agency, 1974

RESULTS

Physical and chemical characteristics of lake water

University Lake retained thermal stratification through November in 1978. Because sampling was done early in the morning, epilimnion temperatures were low and the temperature profile was weak by the end of the fall sampling (Figure 2). Throughout the fall, temperatures ranged between 17 and 21 C. Depth of the thermocline was approximately 4 m. Mixing took place from November through March, and temperatures during this period were around 4-5 C. Thermal and chemical stratification began slowly in March, becoming well-established by April of 1979.

Stratification was more marked in the conductivity than in the temperature data. Conductivity ranged from 80-90 $\mu mho \cdot cm^{-1}$ in the hypolimnion during the fall (Figure 3). Whereas epilimnetic readings varied little from September through November, hypolimnetic readings increased steadily from 250 in September to over 400 $\mu mho \cdot cm^{-1}$ in November. During the winter mixing period, conductivity readings ranged from 60-80 $\mu mho \cdot cm^{-1}$ and were uniform with depth. As the lake restratified, conductivity values increased in the hypolimnion, reaching 150 $\mu mho \cdot cm^{-1}$ by the end of June.

Turbidity in the lake varied seasonally. It averaged 24 Jackson units before overturn (Figure 4). Winter turbidities were high, reflecting an increased loading of suspended sediments from the watershed. In the spring, turbidity readings were irregular but generally higher than fall readings.

Dissolved oxygen concentration varied widely over the year in the hypolimnion; oxygen was undetectable in the fall, replenished during mixing, and depleted again by June (Figure 5). At the surface, oxygen concentrations were more constant. They were always higher than hypolimnion concentrations, even during mixing, but they were not supersaturated until late spring and early summer.

There were also distinct seasonal changes in the total phosphorus and its constituents during the year at University Lake (Figure 6). Filterable reactive phosphorus (FRP) concentrations in the epilimnion averaged 0.015 mg $P \cdot l^{-1}$ during the fall. During mixing, FRP in the epilimnion was approximately twice fall levels, averaging 0.031 mg $P \cdot l^{-1}$. Although thermal and chemical stratification was gradual, FRP concentrations dropped sharply (to 0.006 mg $P \cdot l^{-1}$) by March and remained low for the duration of the study. Filterable unreactive phosphorus (FUP) concentrations generally followed those of FRP throughout the year. The particulate phosphorus concentration (PP) showed more variation than other constituents of total P. It peaked in late fall, early spring, and early summer. Total phosphorus averaged 0.044 mg $P \cdot l^{-1}$ in the epilimnion during the fall and was fairly constant until turnover when it went up approximately 1.5 fold. At the end of the mixing period,

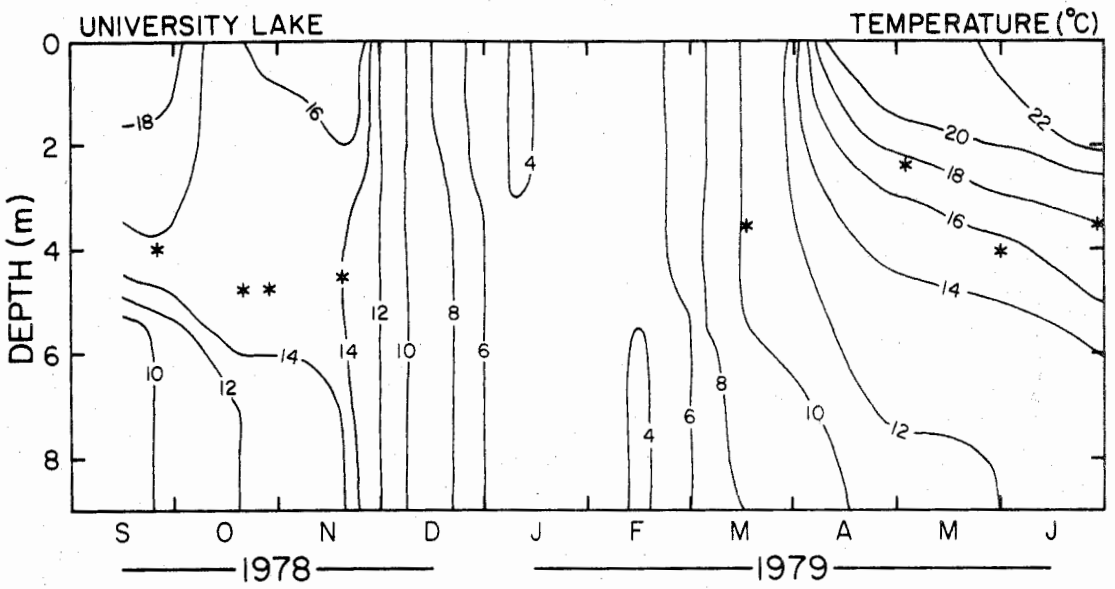

Fig. 2. Isotherms of University Lake, 1978-1979. Asterisks indicate the assumed depth of the metalimnion.

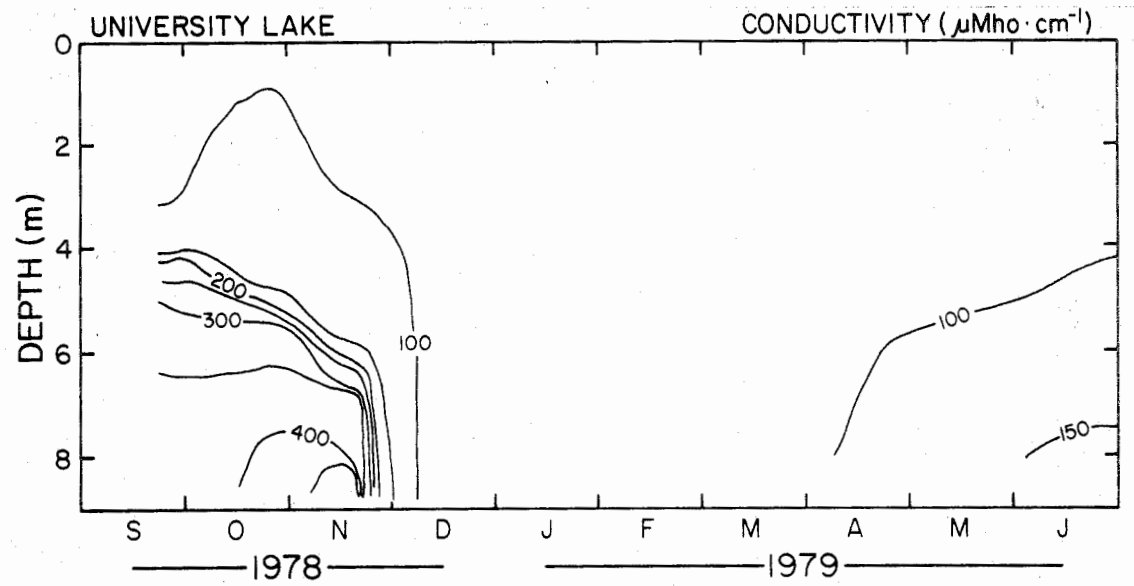

Fig. 3. Specific conductivity isopleths of University Lake, 1978-1979.

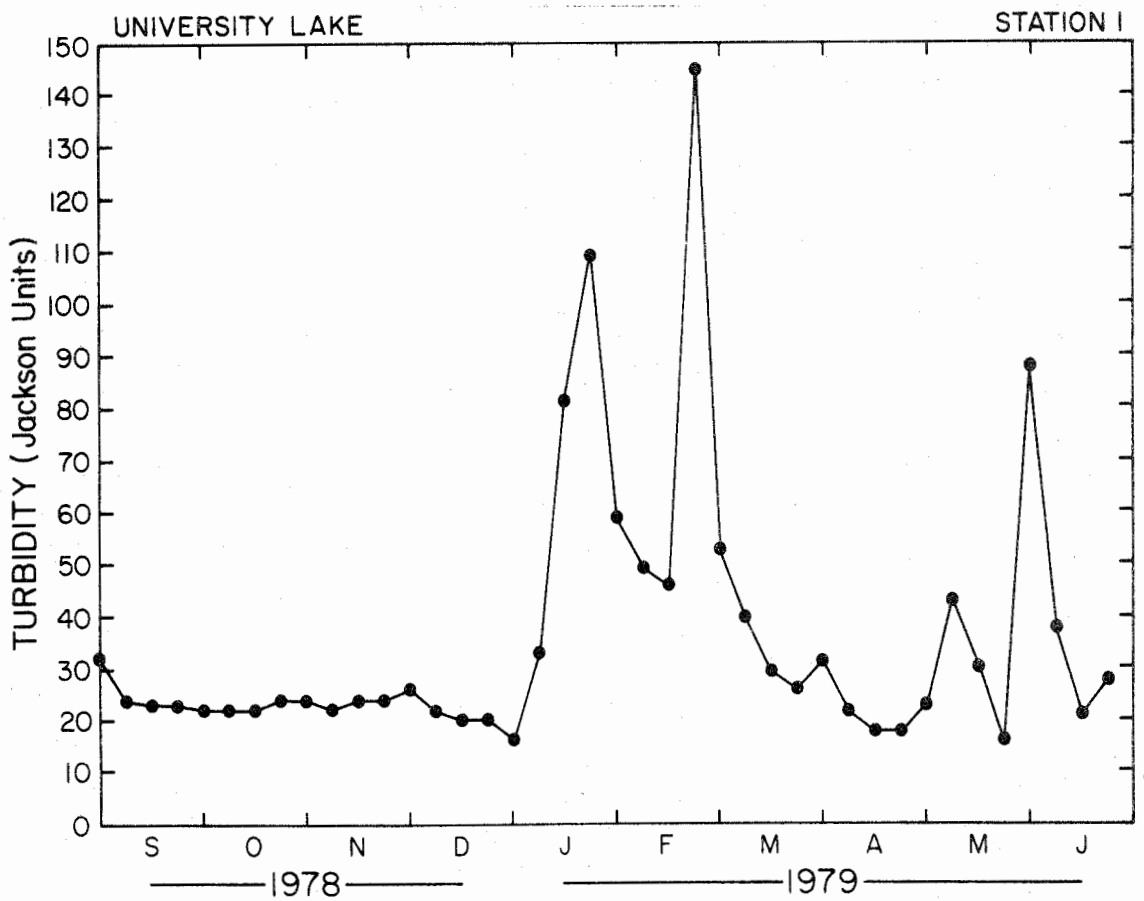

Fig. 4. Turbidity levels at 1 m depth in University Lake, 1978-1979. Data from Orange Water and Sewage Authority, Chapel Hill, NC.

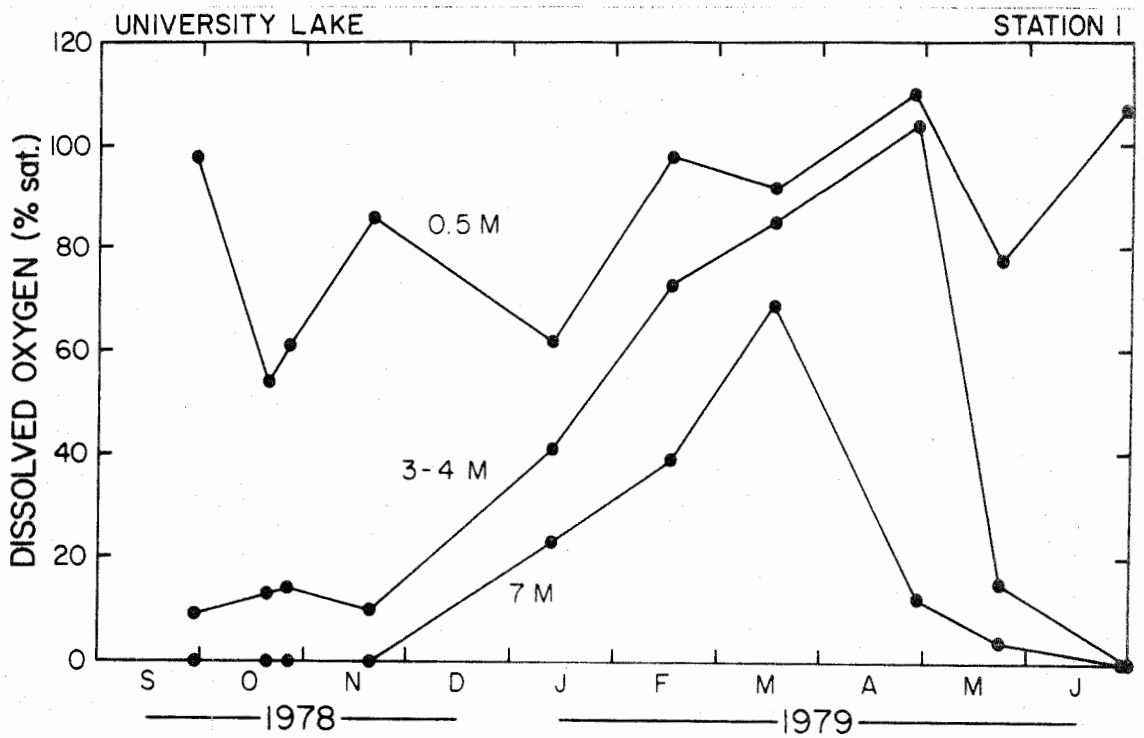

Fig. 5. Percent oxygen saturation at three depths in University Lake.

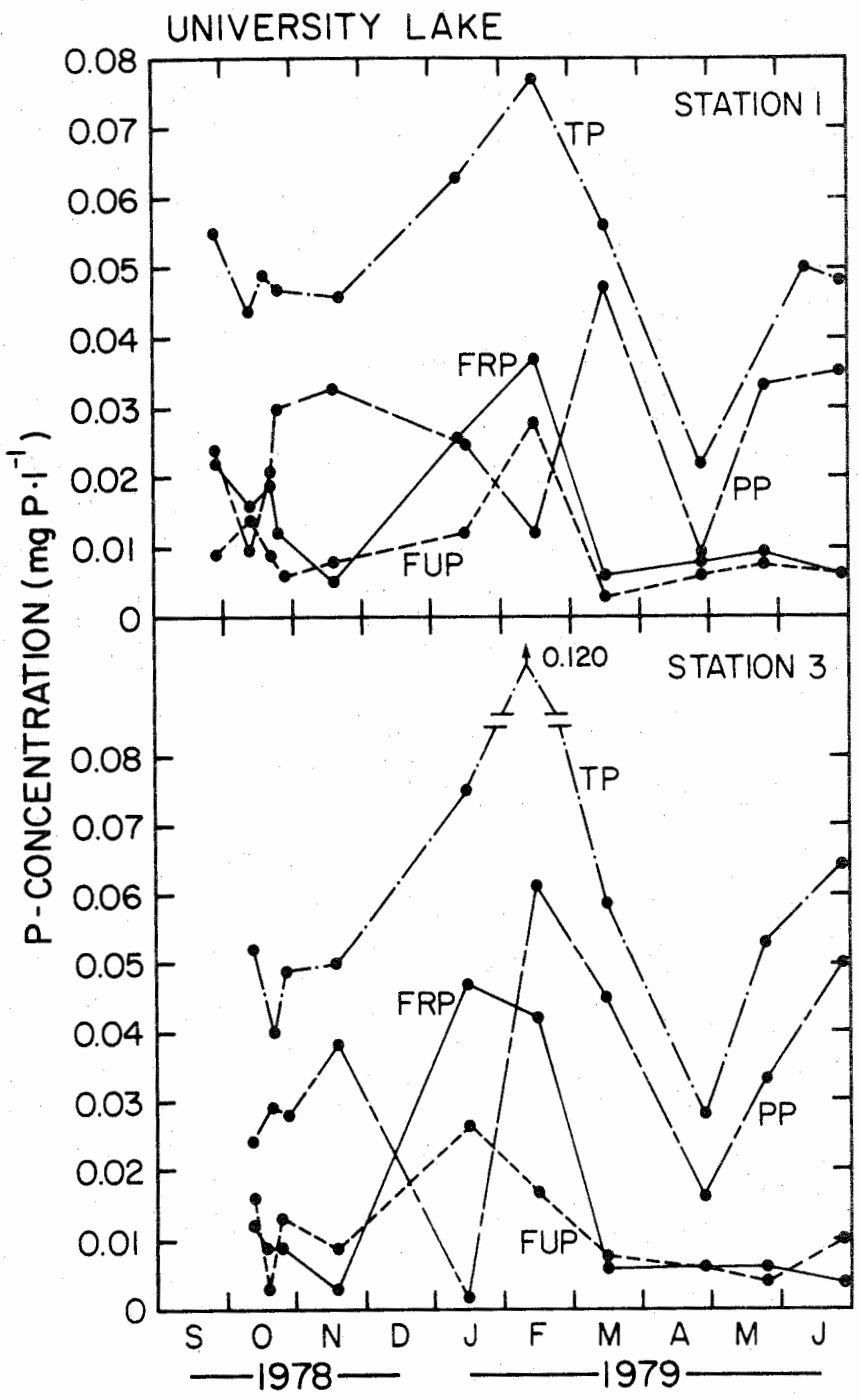

Fig. 6. Seasonal pattern of total P, particulate P, filterable reactive P, and filterable unreactive P in surface waters at Stations 1 and 3.

TP dropped to fall levels again and remained lower through the spring and early summer. Station 1 and Station 3 had similar phosphorus concentrations on most dates sampled (Figure 6). Total P and FRP were consistently higher at Station 3 during winter, however.

Ammonia-N (NH_3) was the predominant form of inorganic N in the epilimnion at both stations throughout the fall and decreased during the winter mixing period (Figure 7). Nitrite (NO_2) (not shown separately) always was at undetectable levels. Nitrate (NO_3) was low throughout the fall in the epilimnion. During winter, ammonia values declined slightly, but nitrate went far above the fall levels. Ammonia and nitrate levels dropped more slowly than the levels of FRP in the lake with the onset of stratification, reaching low levels comparable to the fall at the end of April rather than the middle of March.

When the lake was stratified, the epilimnion, metalimnion, and hypolimnion nutrient concentrations distinguished themselves (Figure 8). TP always increased with depth. In October, April, and June, this was mostly because of higher PP in the hypolimnion; in other months FRP and FUP accounted for most of the increase in TP with depth. Ammonia generally increased with depth, especially in the fall and early summer. Nitrate remained rather constant with depth throughout the year.

Chlorophyll-a and phaeophytin concentrations varied over the seasons and with depth in the lake. In the epilimnion, chlorophyll-a decreased from 37 $\mu g \cdot l^{-1}$ in October to 4 $\mu g \cdot l^{-1}$ in February and then increased steadily to fall levels by the end of June (Figure 9). Chlorophyll-a concentrations were rather constant with depth during mixing, and the lake maintained chlorophyll levels in the hypolimnion which were comparable to those of the epilimnion through the month of April (Figure 10). Levels in the hypolimnion later, however, dropped, and those in the epilimnion increased by late June. Phaeophytin levels were usually lower than chlorophyll-a and did not vary as much over the seasons (Figure 9). Values were, however, consistently higher in the metalimnion and hypolimnion than the epilimnion as spring stratification proceeded (Figure 10).

Phosphate uptake by seston

1. Gross uptake rates by total seston

The relative rate of uptake of phosphate tracer (k) showed wide variations through the year (Table 3). Highest rates, >0.10 min^{-1} (i.e., >10% removal per minute) occurred only in the epilimnion before mid-November and after mid-May at both stations. Very low rates (<0.0008) occurred in January and February when temperatures and chlorophyll-a levels were low (Fig. 2,9). Metalimnion and hypolimnion rates were similar to, or lower than, rates near the surface (Table 3). Standards errors tended to be an order of magnitude below the means. Gross uptake rates (v) by total seston also varied greatly, from 0.6 to 470 $\mu g\ P \cdot l^{-1} h^{-1}$ (Table 4), mostly because of variability in biotic uptake (Fig. 11).

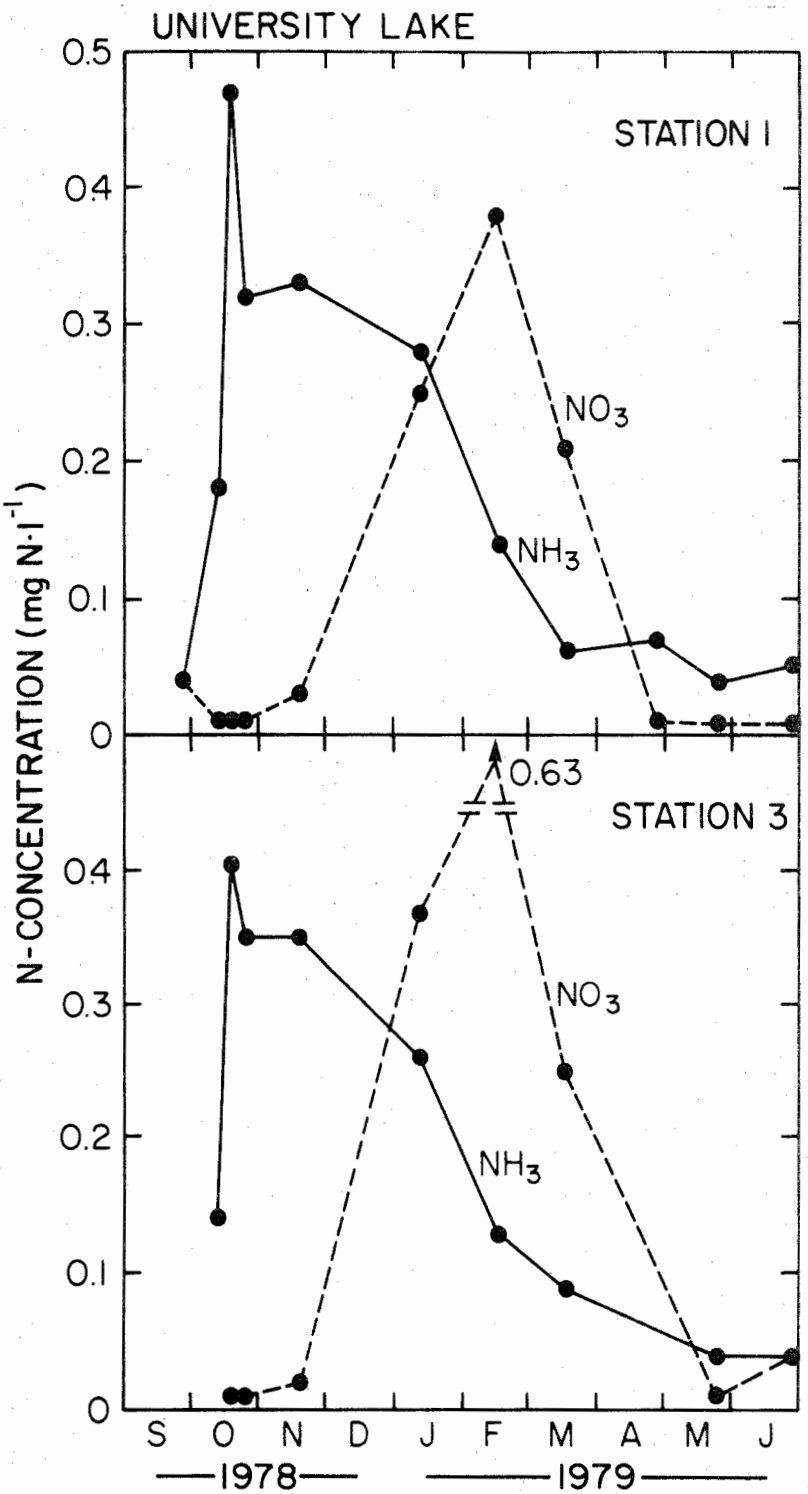

Fig. 7. Seasonal patterns of ammonia and nitrate in surface waters of University Lake, 1978-1979.

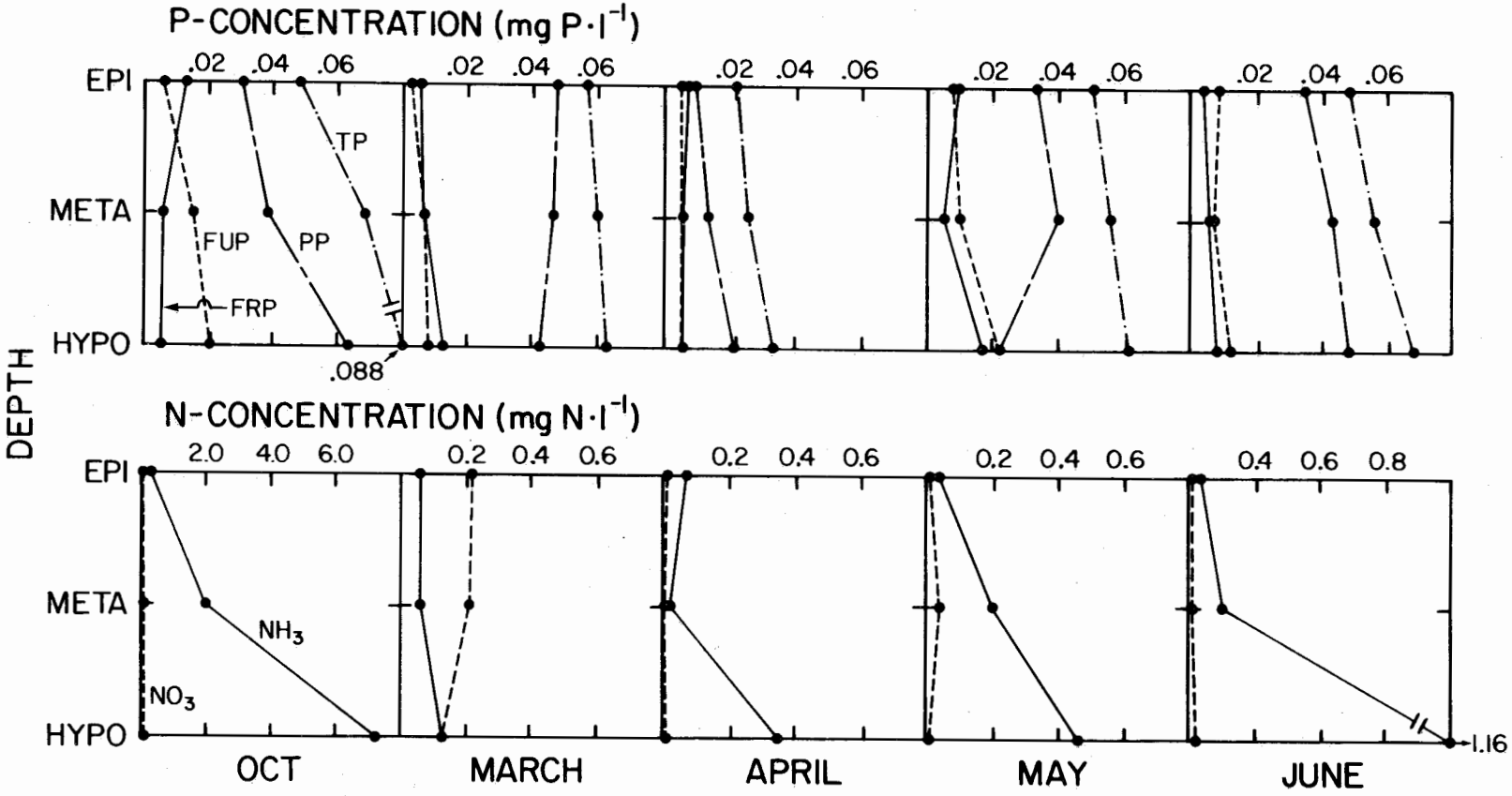

Fig. 8. Distribution of total P, particulate P, filterable reactive P, filterable unreactive P, ammonia, and nitrate with depth during stratified periods in University Lake, 1978-1979.

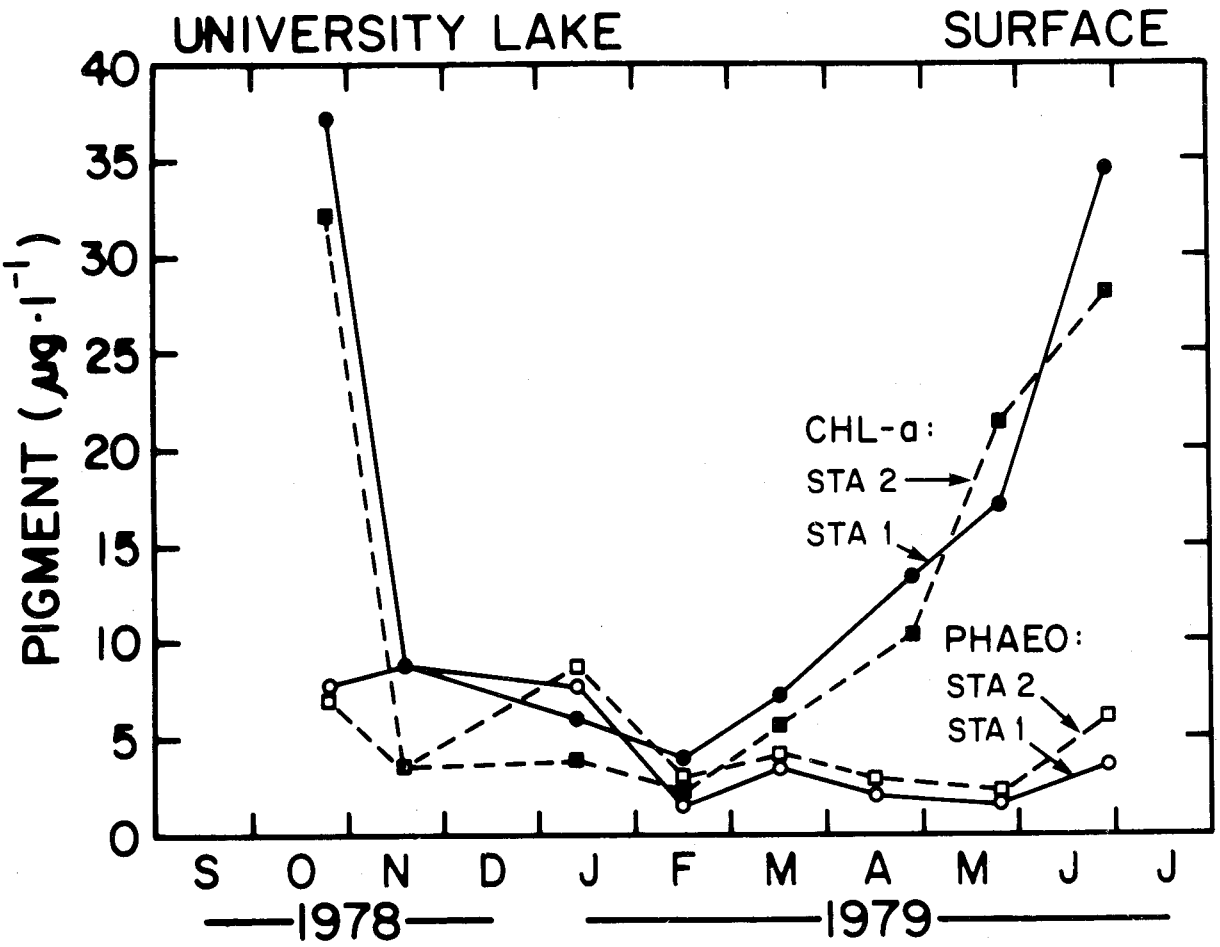

Fig. 9. Concentrations of chlorophyll-a and phaeophytin in the surface waters of University Lake, 1978-1979.

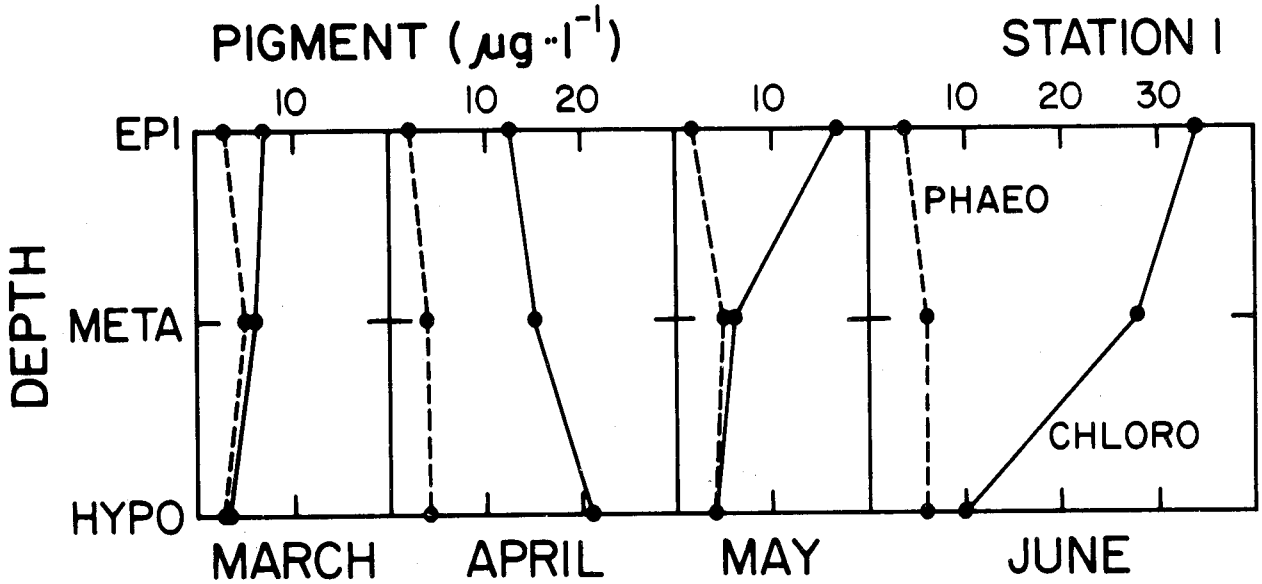

Fig. 10. Distribution of chlorophyll-a and phaeophytin with depth during stratified periods in University Lake, 1978-1979.

Table 3. Phosphate uptake constant (k) in the epilimnion or surface, metalimnion, and hypolimnion of University Lake ($\bar{k}$ ± S.E. where n = 3; units = min^{-1}, except h^{-1} in January and February).

Date	Station 1			Station 3
	Epi	Meta	Hypo	Epi
09/27/78	.275	--	--	--
10/13	.087	--	--	--
10/18	.421	--	--	--
10/25	.132	--	--	--
11/18	.146 ± .030	--	--	.167 ± .020
01/12/79	.037 ± .006*	--	--	.033 ± .002*
02/16	.046 ± .005*	--	--	.044 ± .004*
03/16	.0026 ± .0002	.0028 ± .0009	.0018 ± .0009	.0029 ± .0001
04/27	.013 ± .001	.015 ± .009	.048 ± .007	.024 ± .006
05/23	.320 ± .080	.020 ± .001	.020 ± .002	.221 ± .052
06/27	.400 ± .052	.089 ± .029	.056 ± .006	.350 ± .019

*h^{-1}

Table 4. Seasonal variation in gross uptake rate (v) ($\mu g\ P \cdot l^{-1} \cdot h^{-1}$) at 3 depths and 2 stations in University Lake.

Date	Station 1			Station 3
	Epi	Meta	Hypo	Epi
09/27/78	363	--	--	--
10/13	84	--	--	--
10/18	474	--	--	222
10/25	96	--	--	96
11/18	42	--	--	30
01/12/79	0.9	--	--	1.5
02/16	1.7	--	--	1.8
03/16	0.6	1.1	1.2	1.0
04/27	5.4	5.4	16.8	9.6
05/23	168	5.9	18	78
06/27	96	30	24	84

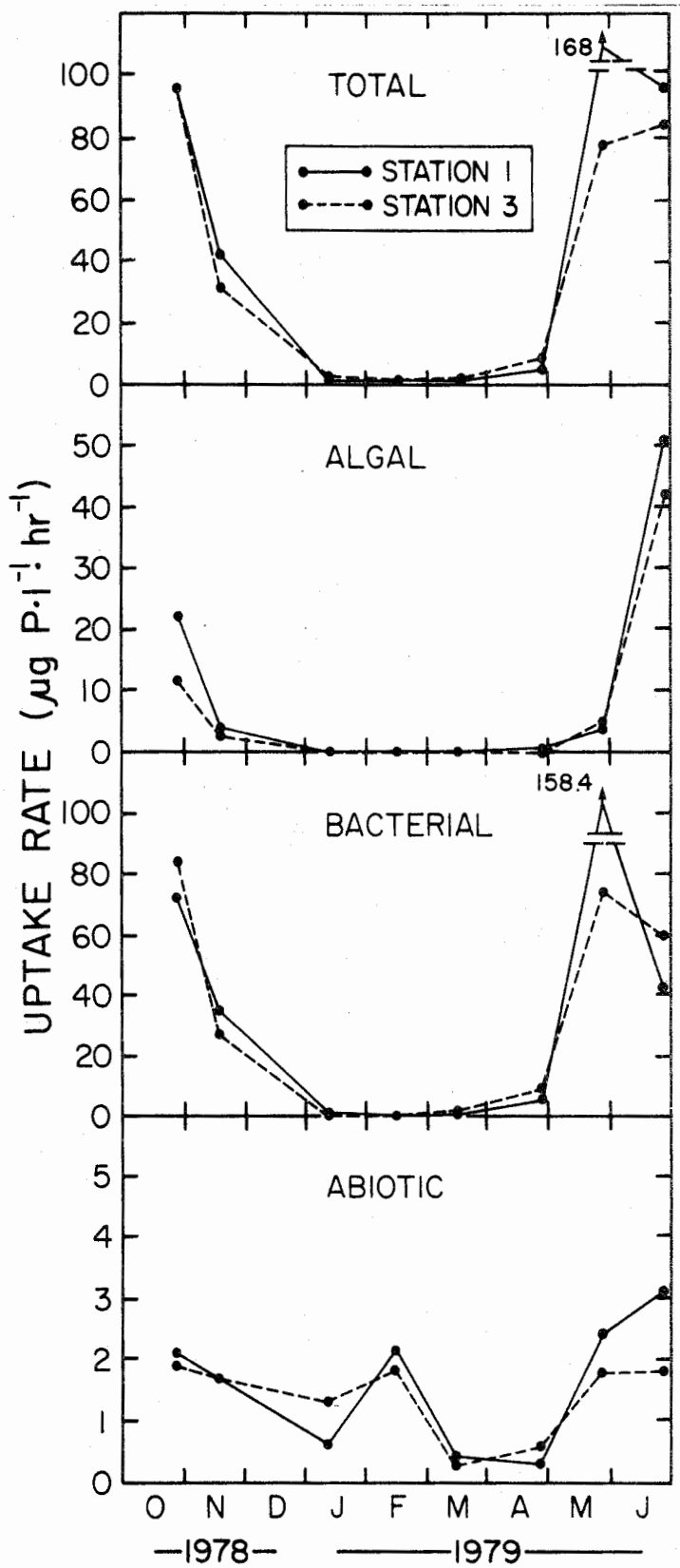

Fig. 11. Total and partitioned gross phosphate uptake rates in surface waters of University Lake, 1978-1979.

2. Discrimination between algal, bacterial, and abiotic uptake

Algal uptake, defined as the amount of uptake which persisted in antibiotic-treated bottles minus the killed sample uptake, varied seasonally at the dam from 0-52% of the total uptake (Figure 11, 12). The average contribution was slight, only 11.4%. Throughout the winter, the algal contribution was negligible. The highest contribution of algae to phosphate uptake (47 and 52%) took place in the late June sampling date at both stations. Bacterial uptake, defined as the amount of uptake in ambient bottles minus the amount of uptake in antibiotic bottles (both after subtracting killed uptake) varied from 0-97% of the total uptake, with the mean contribution being 52% at the dam. Bacteria were important contributors to the uptake of phosphate on all but one occasion in the winter when temperatures were low and total uptake was slow.

An attempt was made to distinguish algal and bacterial uptake by a second method, size-fractionating the samples using Nuclepore filters. Seston greater than 8 μm contributed between 2 and 20% to the uptake of phosphate in the epilimnion and between 4 and 29% in the metalimnion and hypolimnion of the lake (Table 5). Although data are limited, "large size-fraction" uptake assessed by differential filtration exceeded "algal" uptake assessed by chemical treatment (Table 6). There was no detectable uptake by the algal fraction, except in March, at the depths of the meta- or hypolimnion, and the algal fraction exceeded the large size fraction in epilimnetic water only at Station 3 in May and at both Stations in June. The date of peak algal uptake corresponded to the date of peak uptake of the large size fraction, although the rate of uptake measured by each method differed (Table 6).

Table 5. Relative contribution of large (>8 μm) size fraction of seston to gross uptake of labeled orthophosphate from lake water.

Date	Station 1			Station 3
	Epi	Meta	Hypo	Epi
02/16/79	2.9%	--	--	2.0%
03/16	20.0%	4.9%	5.0%	7.0%
04/27	17.8%	10.6%	3.9%	6.2%
05/23	5.3%	29.2%	10.0%	5.2%
06/27	12.5%	24.0%	22.5%	17.6%

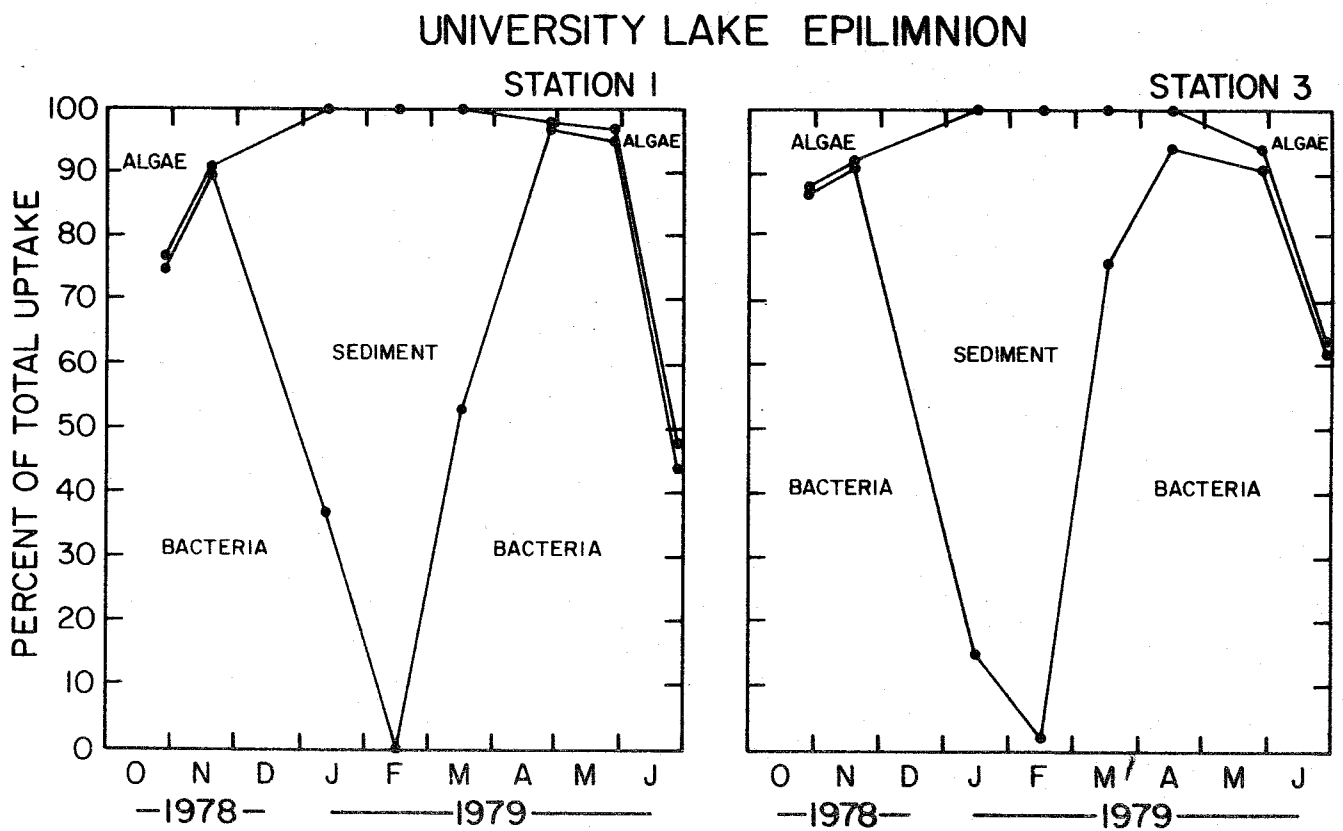

Fig. 12. Relative contributions of algae, bacteria, and suspended sediments to the total uptake of radiophosphate in surface waters.

Table 6. Comparison of uptake rates ($\mu g\ P \cdot l^{-1} \cdot h^{-1}$) by the algal fraction and the large size fraction of the seston.

Date	Station	Depth	Algal	Large Size
02/16/79	1	Surface	0	.05
	3	Surface	0	.17
03/16	1	Epi	0	.12
	1	Meta	.18	.06
	1	Hypo	0	.06
	3	Epi	0	.07
04/27	1	Epi	.08	.96
	1	Meta	0	.58
	1	Hypo	0	.66
	3	Epi	0	.60
05/23	1	Epi	5.5	9.0
	1	Meta	0	1.7
	1	Hypo	0	1.8
	3	Epi	5.1	4.1
06/27	1	Epi	53.	12.0
	1	Meta	0	7.2
	1	Hypo	0	5.4
	3	Epi	31.	18.0

Abiotic uptake, presumably mostly by suspended sediments, varied from almost none to almost all of the total phosphate uptake in the epilimnion at both Stations (Figure 12). It was important relative to biotic uptake only during the winter when suspended sediments in the water were high (Figure 3) and biotic competition was low. Although during some winter samplings sediment apparently was responsible for all of the uptake, this uptake was very small in comparison to total uptake during the rest of the year when the biotic compartment was active (Figure 11).

Additional evidence that sediment played a role in the exchange of phosphate in the water column was obtained by spiking killed samples with concentrated sediment. In these experiments, the addition of sediment

increased the amount of radioactivity taken up by the killed particulate fraction (Table 7).

Table 7. Effect of sediment additions on rate of gross phosphate uptake from lake water using radioactive tracer technique.

Date	Sediment Concentration	v ($\mu g\ P \cdot l^{-1} \cdot h^{-1}$)
02/16/79	Ambient	1.6 ± .02
	5X	1.8 ± .07
	10X	3.0 ± .1
06/07	Ambient	2.5 ± .006
	5X	9.7 ± 0
	10X	18.0 ± .01

3. Effect of depth on gross phosphate uptake rate.

University Lake was sampled at three depths from March through June 1979 to assess the change in uptake patterns with depth as the lake stratified. Sampling depths of 0.5 m and 7.0 m were chosen to represent the epilimnion and hypolimnion respectively. The depth of the metalimnion varied between 2.5 and 4.0 m depending on the stratification in the lake (Figure 2).

In March, when the lake was only weakly stratified, uptake rates were slightly lower in the epilimnion than in the meta- or hypolimnion. After April, uptake was highest in the epilimnion (Table 4). As stratification proceeded, all depths increased their P-uptake rate, with the epilimnion increasing the fastest. Hypolimnetic uptake of P was generally higher than metalimnetic uptake during times of lake stratification except in late June when the rates were similar.

Algal uptake at Station 1 was found only in the epilimnion, except in March when it contributed 8% to total P uptake in the metalimnion (Table 8). In the epilimnion, the algal contribution to total uptake increased steadily from April (2.3% of uptake) to June (52%) (Figure 12, Table 8).

Bacterial uptake was more evenly distributed in the water column than algal (Table 8). During March, the hypolimnion sample had greater bacterial uptake in the water column than the epilimnion sample, but bacterial epilimnetic uptake increased rapidly;in May and June, the epilimnion was the dominant depth for bacterial as well as algal uptake.

Table 8. Rates of algal, bacterial, and abiotic gross uptake of phosphate with depth ($\mu g\ P \cdot l^{-1} \cdot h^{-1}$). Station 1.

Date	Depth	Algal	Bacterial	Abiotic
03/16/79	Epi	0	.17	.43
	Meta	.18	.54	.42
	Hypo	0	.48	.72
04/27	Epi	.08	4.9	.29
	Meta	0	5.1	.29
	Hypo	0	17	.96
05/23	Epi	5.5	160	1
	Meta	0	4.7	1.2
	Hypo*	0	3	15
06/27	Epi	52	42	3
	Meta*	0	25	5
	Hypo*	0	6	18

* = Samples incubated anoxically

Abiotic uptake was highest in the hypolimnion on all sampling dates and increased with time (Table 8). Although the absolute abiotic rates also increased in the epilimnion, their relative importance decreased during the period of stratification.

4. Phosphate uptake rate measured chemically.

Experiments which measured the concentration of filterable reactive phosphorus (FRP) in incubated lake water showed that, on all occasions except one, the concentration of FRP during the course of the tracer experiments did not change significantly (Table 9). In April, although the uptake rate in the epilimnion as measured chemically was only 10% of that measured with tracer, it was statistically different from zero (Table 9). At no other time was any increase or decrease from the starting FRP concentration statistically significant.

Table 9. Rate of change of filterable reactive phosphorus concentration (net P uptake) during incubation of University Lake water and statistical significance of the rate.

Date	Depth	k (h^{-1})	Difference from Zero (α>.05)
01/12/79	Surface	-.0008	NS
02/16	Surface	+.0014	NS
03/16	Epi	-.00003	NS
04/27	Epi	-.0005	*
	Meta	-.0001	NS
	Hypo	-.0003	NS
05/23	Epi	-.0005	NS
	Meta	+.0003	NS
	Hypo	-.0009	NS

* $\alpha \leq .05$

5. Phosphate buffer capacity of the sediments.

Phosphate potential curves showed that the role of the suspended sediment coming into University Lake varied seasonally. In February when lake water was rich in FRP (Figure 6, Table 10), the equilibrium phosphate concentration was relatively low (Figure 13, Table 10). Consequently there was potential for transfer of P from the water (x-axis) to the sediment (y-axis, Figure 13) even at phosphate concentrations below 0.01 $mg \cdot l^{-1}$, and the sediment acted as a sink. After March, however, ambient FRP levels dropped (Figure 6, Table 10) while the equilibrium concentration increased (Figure 13, Table 10), and the suspended sediments became potential phosphorus sources for the water.

The same amounts of sediment were used for experiments on a given date, so sorptive capacities may be compared at different temperatures. During March and May, experiments were attempted at ambient temperature and 5 C to assess the effect of temperature on the sorption of phosphate on sediment. Increasing temperatures increased the adsorptive capacity (longer arrows) of the sediments in these two months (Figure 13). Increasing temperatures raised the equilibrium phosphate concentration in March but not in May (Figure 13). Note that on the March sampling date, the incubator failed to maintain the ambient temperature, 14 C, and the

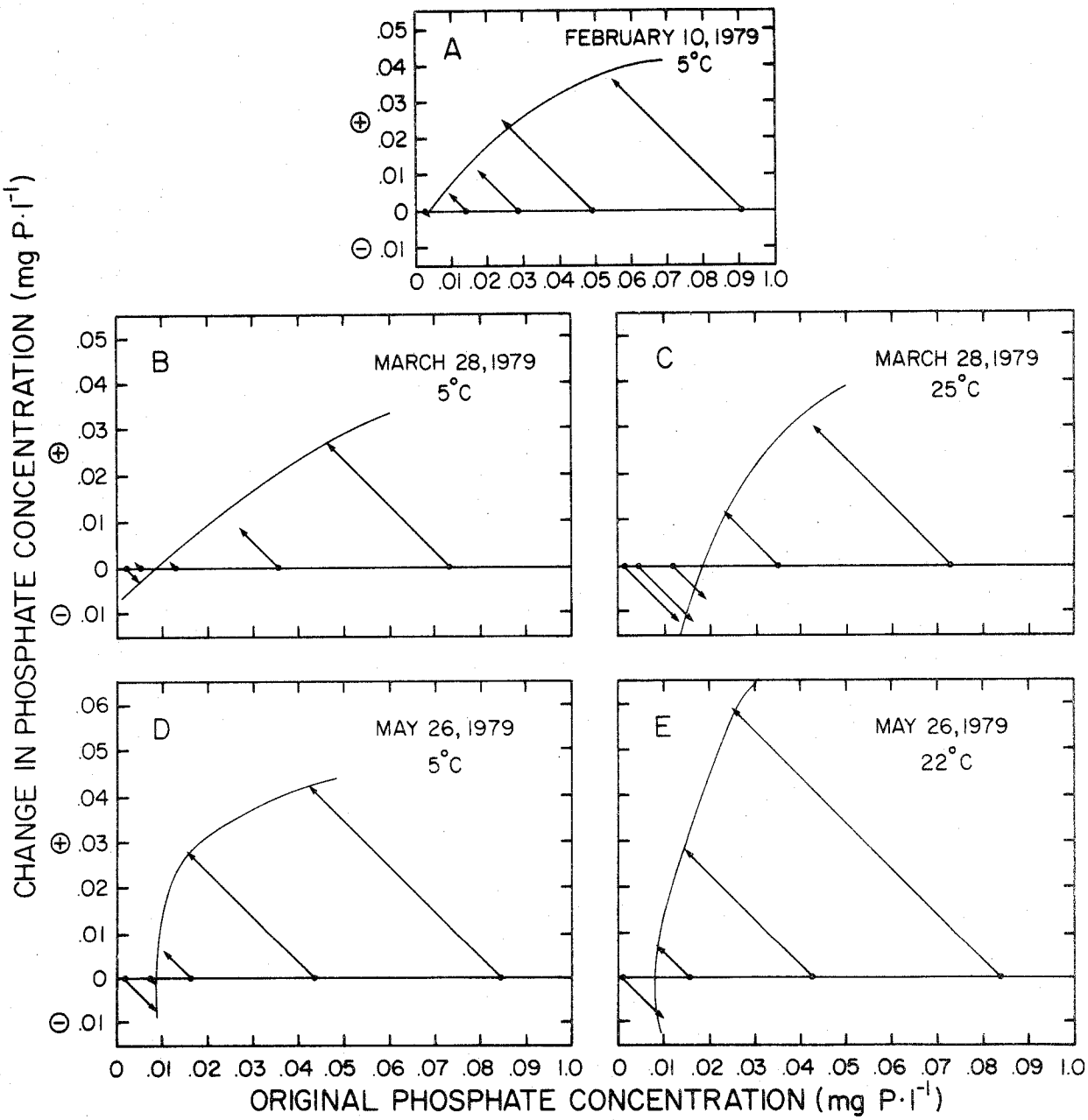

Fig. 13. Phosphate potential curves showing the role of sediment in the P dynamics of University Lake. At concentrations where the curve is above the abscissa, the sediment is acting as a P-sink; at concentrations where the curve is below the abscissa, the sediment is acting as a P-source. The length of the line is the sediment's sorptive capacity, and the intercept of the curve with the X axis is the equilibrium phosphate concentration.

temperature rose to 25 C. The functioning of the sediment as a source (Table 10) at ambient temperatures (14 C) was assumed to be the same as at 25 and 5 C.

Table 10. Effect of suspended sediments on filterable reactive phosphorus concentration in the water column. FRP concentrations in $mg \cdot l^{-1}$.

Date Date	Experimental Temp. (C)	Ambient FRP ($mg \cdot l^{-1}$)	Equilibrium FRP ($mg \cdot l^{-1}$)	Estimated Effect
2/02	5	.042	.01	sink
2/10	5	.042	.004 - .006	sink
3/28	5	.006	.008	source
	25	.006	.02 - .025	source
5/26	5; 22	.006	.008 - .010	source

DISCUSSION

Nutrient and chlorophyll distributions

Chemical and biological data were examined for station-to-station differences in University Lake. Overall, the nutrient differences between the two stations were slight (Figure 6, 7), as first documented by Heath (1968). There was no evidence of any eutrophication gradient in the lake, which is probably attributable to the few point sources of pollution in the watershed.

Seasonal differences between the stations, however, were apparent. FRP, TP, and NO_3 were generally higher at Station 3 than Station 1 in the winter runoff season (Figure 6, 7), suggesting that phosphorus and nitrogen were coming into the lake from the watershed at this time. The seasonal pattern in ammonium concentration (Figure 7) is not different from that found by Heath (1968); the early autumn increase at the surface is attributable to injections of richer waters from the hypolimnion. The nitrate concentrations and seasonal pattern (Figure 7) were also not different from an earlier report (Weiss and Breedlove, 1973). The peak values of PP did not coincide at each station; during periods of high hydraulic loading, the lake apparently was not uniform in its suspended particulate concentration. Visual observations from the bridge at Station 3 often strongly indicated higher turbidities on the upstream side after rain storms.

Chlorophyll-a was generally lower at Station 3 (Figure 9), possibly because water at this station had not been in the lake long enough to experience much algal growth. Heath (1968) reported similar findings in total algal numbers from Station 1 to Station 3; although he found differences in the species composition of the phytoplankton from station to station, total cell numbers were generally highest at the dam. Our data do not show the marked increase in chlorophyll in the metalimnion resulting from the usual bloom there of Oscillatoria tenuis in summer (Weiss and Oglesby, 1962; Heath, 1968; Weiss and Breedlove, 1973), perhaps because our sampling ceased in June.

Patterns of seasonal and spatial variation in phosphate uptake

Data was analyzed using ANOVA to assess statistically the effects of station, treatment, and depth on the uptake of phosphorus in University Lake over the year. From November through March, two-way ANOVAs were employed, as only epilimnetic samples were taken from each station. From March through June, samples were obtained from three depths at Station 1, and data was analyzed using a 3-way ANOVA to assess the depth effect. The Tukey paired-comparison procedure was used as a follow-up to the ANOVA on those dates where the source of statistical difference was of interest.

The data used in the statistical analysis differed in form from that used in the RESULTS section of this report. Subtraction of Killed uptake

Table 11. ANOVA tables showing the effect of treatment, station, and depth on the uptake of phosphorus.

Date: 11/18/78

Source	df	SS	MS	F	Pr >F
Model	5	1.3×10^{-6}	2.7×10^{-7}	20.15	.0001
Error	12	1.6×10^{-7}	1.0×10^{-8}		
Total	17	1.5×10^{-6}			

Source	df	Type IV SS	F	Pr >F
Treatmt	2	1.3×10^{-6}	17.32	.0001
Station	1	1.6×10^{-8}	2.54	.1369
Tr x Sta	2	1.5×10^{-8}	1.79	.2083

Date: 1/12/79

Source	df	SS	MS	F	Pr >F
Model	5	3.1×10^{-6}	6.3×10^{-7}	16.31	.0001
Error	12	4.6×10^{-7}	4.0×10^{-8}		
Total	17	3.6×10^{-6}			

Source	df	Type IV SS	F	Pr >F
Treatmt	2	1.7×10^{-6}	21.62	.0001
Station	1	1.2×10^{-6}	35.53	.0001
Tr x Sta	2	2.2×10^{-7}	2.9	.0938

Date: 2/16/79

Source	df	SS	MS	F	Pr >F
Model	5	2.6×10^{-6}	5.3×10^{-7}	9.77	.0007
Error	12	6.5×10^{-7}	5.0×10^{-8}		
Total	17	3.3×10^{-6}			

Source	df	Type IV SS	F	Pr >F
Treatmt	2	2.4×10^{-6}	22.67	.0001
Station	1	3.0×10^{-8}	2.54	.1369
Tr x Sta	2	5.0×10^{-8}	1.79	.2083

Table 11 (cont.)

Date: 3/16/79

Source	df	SS	MS	F	Pr >F
Model	11	$<1 \times 10^{-8}$	$<1 \times 10^{-8}$	113.25	.0001
Error	24	$<1 \times 10^{-8}$	$<1 \times 10^{-8}$		
Total	35	$<1 \times 10^{-8}$			

Source	df	Type IV SS	F	Pr >F
Treatmt	2	$<1 \times 10^{-8}$	257.5	.0001
Station	1	$<1 \times 10^{-8}$	2.2	.1553
Depth	2	$<1 \times 10^{-8}$	88.3	.0001
Tr x Sta	2	$<1 \times 10^{-8}$	1.6	.2190
Tr x Depth	4	$<1 \times 10^{-8}$	5.0	.0044

Date: 4/27/79

Source	df	SS	MS	F	Pr >F
Model	11	2.5×10^{-7}	2.0×10^{-8}	15.09	.0001
Error	24	4.0×10^{-8}	1.3×10^{-9}		
Total	35	2.8×10^{-7}			

Source	df	Type IV SS	F	Pr >F
Treatmt	2	1.2×10^{-7}	40.91	.0001
Sta	1	$<1 \times 10^{-8}$	.94	.3417
Depth	2	3.0×10^{-8}	9.98	.0007
Tr x Sta	2	$<1 \times 10^{-8}$	.94	.4042
Tr x Depth	4	5.0×10^{-8}	8.09	.0003

Date: 5/23/79

Source	df	SS	MS	F	Pr >F
Model	11	2.4×10^{-5}	2.1×10^{-6}	13.64	.0001
Error	24	3.8×10^{-6}	1.6×10^{-7}		
Total	35	2.7×10^{-5}			

Table 11 (cont.)

Date: 5/23/79 (cont.)

Source	df	Type IV SS	F	Pr >F
Treatmt	2	2.4×10^{-7}	.75	.4845
Station	1	1.3×10^{-6}	7.97	.0094
Depth	2	4.8×10^{-6}	15.31	.0001
Tr x Sta	2	2.4×10^{-6}	7.49	.0030
Tr x Depth	4	9.6×10^{-6}	15.14	.0001

Date: 6/27/79

Source	df	SS	MS	F	Pr >F
Model	11	9.2×10^{-6}	8.4×10^{-7}	15.26	.0001
Error	24	1.3×10^{-6}	5.0×10^{-8}		
Total	35	1.0×10^{-5}			

Source	df	Type IV SS	F	Pr >F
Treatmt	2	1.5×10^{-6}	13.51	.0001
Station	1	1.4×10^{-7}	2.53	.1249
Depth	2	2.1×10^{-6}	19.45	.0001
Tr x Sta	2	5.0×10^{-8}	.46	.6375
Tr x Depth	4	2.1×10^{-6}	9.5	.0001

from Ambient and Antibiotic uptake could not be performed without altering the within-treatment variance of the ANOVA. Because of this limitation, statistical differences between "algal" (antibiotic-formaldehyde treated bottles), "bacterial" (ambient-formaldehyde) - (antibiotic-formaldehyde), and "killed" (formaldehyde) could not be assessed. Statistical analysis allowed comparison of only the uncorrected uptake rates obtained in Ambient, Antiobiotic, and Formaldehyde treatments.

Differences in the uptake rates of phosphorus between Station 1 and Station 3 were generally slight (Table 4, Figure 12). ANOVA showed that the station effect was significant (α=.05) on only two dates (01/12/79 and 05/23/79) where data were adequate for comparison (Table 11). Seasonally, there were some interesting trends, however. Until overturn, total uptake was generally higher at the dam (Table 4). During the winter (January, February, and March), when the uptake was largely abiotic,

uptake was slightly higher at Station 3. Algal uptake was lower at Station 3 on all but one occasion (Figure 11), a finding which corresponded with lower chlorophyll concentrations at Station 3 (Figure 9). Bacterial uptake and abiotic uptake fluctuated in magnitude between Station 1 and Station 3. Perhaps the abiotic fluctuation is attributable to uptake by both suspended sediments (higher at Station 3) and killed algal and bacterial cells (more abundant at Station 1).

Depth and treatment, however, did affect phosphate uptake rates. ANOVA suggested that depth was a significant factor in controlling the rate of total uptake on all occasions from March through June in the study (Table 4, 11). Treatment made a statistical difference in the rate of uptake on all occasions except in May (Table 11). Analysis of the data by ANOVA, however, did not segregate out the specific effects of antibiotic and formaldehyde treatments.

The Tukey Pairwise Comparison test was used to aid in interpreting the specific treatment effects. Several assumptions were necessary in order to render statistical results ecologically meaningful:

1. If the ambient uptake rate was statistically different from the rate after formaldehyde treatment, it was concluded that the biotic (algal and bacterial) uptake rate was significant (i.e., distinguishable from the abiotic (suspended sediment) uptake rate).

2. If the antibiotic treatment gave an uptake rate statistically different from the ambient rate, it was concluded that the bacterial uptake was significant (i.e., distinguishable from algal plus abiotic uptake).

3. If the antibiotic treatment gave rates statistically different from the formaldehyde treatment, it was concluded that the algal uptake rate was significant (i.e., distinguishable from the abiotic plus bacterial uptake rates).

Pairwise comparisons of phosphate uptake rates showed differences between treatments which confirmed the patterns in Figures 11 and 12. In the epilimnion or surface samples, biotic uptake was statistically significant on all dates except in February (Table 12) when suspended sediment uptake predominated (Figure 12). An apparent lack of significance in April arose from the treatment-depth interaction term in the ANOVA on which the Tukey test was based; the same was true for the bacterial uptake in April. A t-test using epilimnion data only, however, demonstrated significant ($\overline{P}<0.01$) bacterial uptake on this date. Bacterial uptake in the epilimnion appeared significant on all dates except June. Apparent bacterial uptake in February, however, cannot be interpreted critically because formaldehyde treatment resulted in somewhat greater P uptake rates than ambient treatment (difference not significant) or antibiotic treatment. Finally algal uptake was not statistically distinguishable until June (Figure 11, 12; Table 8, 12). In the metalimnion bacterial uptake was significant in March but not in later months (Table 12)

because of depth-treatment interaction in the Tukey test; t-test at this depth only, however, showed significant differences between ambient and antibiotic treatment (cf. Table 8). The hypolimnion showed significant bacterial uptake in both March and April. There was never any statistically significant algal contribution to P uptake in the metalimnion or hypolimnion.

Table 12. Tukey pairwise comparisons between treatments upon the phosphate uptake rate (v) at Stations 1 and 3 (November - February) and at Station 1 only (March - June) at three depths. Biotic = ambient - formaldehyde; bacterial = ambient - antibiotic; algal = antibiotic - formaldehyde. NS, $P>0.05$; *, $P\leq0.05$; **, $P\leq0.01$; (**), $P\leq0.01$ using t-test at one depth only.

Depth	Nature of Uptake	Date						
		11/18/78	1/12/79	2/16	3/16	4/27	5/23	6/27
Epilimnion or surface	Biotic	**	*	NS	**	(**)	**	**
	Bacteria	**	**	**	**	(**)	**	NS
	Algal	NS	NS	(-)	NS	NS	NS	*
Metalimnion	Biotic	--	--	--	**	NS	(**)	NS
	Bacteria	--	--	--	**	NS	(**)	(*)
	Algal	--	--	--	NS	NS	NS	NS
Hypolimnion	Biotic	--	--	--	**	**	NS	NS
	Bacteria	--	--	--	**	**	NS	NS
	Algal	--	--	--	NS	NS	NS	NS

The results of this attempt to separate bacterial, algal, and abiotic uptake rates must be used with caution because the treatments do not distinguish perfectly between these fractions of the seston. Furthermore, the interactions between terms in the ANOVA must be considered. Finally, the variability inherent in taking biological samples from a natural system sometimes keeps ecologically significant differences from emerging as statistically significant.

Relative importance of algae and bacteria in phosphate uptake

Experiments using antibiotic treatment showed that bacteria were more important than algae for uptake of phosphate in University Lake (Table 8; Figure 12). Bacterial uptake was important in winter (Figure 12; Table 12)

when light limited algal growth. Furthermore, bacterial uptake rates below the surface waters may be expected to resemble surface rates (Figure 11) during the mixing period. There was some evidence of bacterial stratification in the lake as the water warmed; whereas in March the uptake of P by bacteria was rather constant with depth, by May bacterial uptake was highest in the epilimnion (Table 8). The use of antibiotics to discriminate bacterial and algal metabolism has inherent difficulties. In the first place, antibiotics may not have stopped phosphate uptake by bacteria by the end of the preincubation period so that "algal" uptake is overestimated. On the other hand, some photosynthetic planktonic organisms, the blue-green algae, may be inhibited by antibiotics; the blue-green fraction of algal phosphate uptake will therefore by attributed to bacteria in the sample, thereby giving an underestimation of algal uptake. This problem may not be important in certain waters where blue-green algae are relatively scarce, such as the Pamlico River (Kuenzler, et al. 1979). In University Lake, however, blue-greens such as Microcystis aeruginosa, Anabaena affinis, and Oscillatoria tenuis are sometimes abundant (Heath 1968, Weiss and Breedlove 1973) along with active bacterial populations (Francisco 1970). There is usually a peak in Oscillatoria and bacteria in the metalimnion during summer (Weiss and Oglesbee 1960, 1962; Heath 1968) and even greater numbers of bacteria in the hypolimnion by mid-summer. Therefore it might be more nearly correct to term bacterial uptake "procaryotic uptake" and algal uptake "eucaryotic uptake" when the activity of these populations are distinguished by the response to antibiotics.

Francisco (1970) found that bacterial uptake of glucose in University Lake increased with depth; V_{max} was greatest at 7.0 m, least at 0.5 m, and intermediate in the metalimnion. Not all authors have found such a trend in other bodies of water, however (Hobbie 1967; Rodhe 1969). It is likely that glucose uptake is not intimately linked to phosphorus uptake in the same organisms, for glucose is used for both growth and respiration and phosphorus is used for growth. Furthermore, those organisms dominating glucose uptake in the hypolimnion may not be the same species dominating phosphorus uptake in the epilimnion. Literature on the depth profile of bacteria in lakes shows that physiologically distinct bacteria are found in different strata (Overbeck 1975).

Algal (or eucaryote) importance in P uptake was essentially limited to the epilimnion of the lake. Chlorophyll values were rather evenly distributed during the mixing period, but increased dramatically in the epilimnion during the spring (Figure 9, 10). Algae contributed most to the uptake of P in University Lake (52%) in late June (Figure 10) when chlorophyll-a levels were high and the FRP concentration was low. Faust and Correll (1975) found similar seasonal variation in the relative importance of algae and bacteria in the uptake of FRP in Chesapeake Bay. For most of the year in the Chesapeake (August through April), algae contributed less than 6% to the uptake of radioactive phosphate. In May, June, and July, however, the algal contribution increased, reaching a July high of 42% of the total phosphate uptake. At two of the three times algae were important to uptake in the Chesapeake, there were dinoflagellate blooms in the estuary. High chlorophyll values at the time that algal uptake

was important in University Lake suggest that in this study, too, dense algal populations coincided with greater algal uptake of FRP.

Although algae did not dominate the uptake of P in University Lake for most of the year, the correlation between overall uptake and chlorophyll-a in the epilimnion was good (r^2=.70). Hickman and Penn (1977) note that high bacterial numbers are often observed during times of algal blooms in open systems, a finding which suggests that conditions conducive to high algal uptake rates are also good for bacterial uptake rates. However, there is evidence in University Lake that when the algal populations were large, there was increased competition between algae and bacteria for orthophosphate reserves, and each fraction was capable of suppressing the uptake rate of the other fraction. In June, the algal uptake rates had increased about 10-fold from the previous month, whereas bacterial (or procaryote) uptake rates decreased by 74% (Table 8); probably algal uptake increased at the expense of the bacteria and perhaps blue-green algae, as the levels of FRP were quite low at this date (0.005 mg $P \cdot l^{-1}$). On the other hand, uptake of ^{32}P by the large (>8 μm fraction) increased 50% with the addition of antibiotics, suggesting that bacteria were obstructing algal uptake of phosphorus. The good correlation between overall uptake and chlorophyll-a, therefore, may be misleading because it suggests that algal uptake and bacterial uptake of phosphorus follow the same seasonal trends during the year; the confounding of bacteria and blue-green algae by the antibiotic treatment (see above) probably also contributes to this problem.

Much field work comparing the relative importance of bacteria to algae in the uptake of phosphorus has shown bacteria to be more important, both in estuaries (McCarthy, Taylor, and Loftus 1974; Faust and Correll 1975; Taft, Loftus, and Taylor 1977; Friebele, Correll, and Faust 1978) and in freshwater systems (Rigler 1956; Pearl and Lean 1976; Peters and MacIntyre 1976). Other studies (Taft, Taylor, and McCarthy 1975; Kuenzler, Stanley, and Koenings 1979) have found algal uptake to be dominant, at least some of the time. More work needs to be done to assess the conditions under which one fraction of the plankton can compete successfully against another for phosphorus. The concentration of phosphate, quantity and type of organisms in the population, temperature of the water, and physiological state of the organisms are possible parameters of importance in governing the rate of P uptake and growth.

Role of suspended sediment

The rate of both sediment and phosphorus loading to a lake from its watershed is not constant throughout the year but instead is related to stream flow. During periods of high flow, streams carry surface runoff which is generally higher in suspended sediment and total phosphorus than base flow (Cowen and Lee 1976). The suspended matter, predominantly silt, clay, and organic matter (Porcella 1975), is that which has eroded from the surface layer of the watershed's soil. Soil top layers contain more nutrient per unit mass and are also more susceptible to erosion than

lower layers (Porcella 1975); therefore, there is potential for eroded soil to contribute large quantities of phosphorus to aquatic systems.

As sediment enters a lake, it begins approaching equilibrium with the existing phosphate concentration in the water column. If the concentration of phosphate in the water is high and that on the sediment is low, the sediment will adsorb phosphate. If the sediment carries higher phosphate than the surrounding water, it will release phosphorus to achieve equilibrium with the water. Incoming sediments thus can serve as a P-source or a P-sink depending on a number of environmental parameters. Sediment can be considered a phosphate "buffer" in that it removes or adds phosphorus to solution in response to changes in water phosphate concentration.

During three periods of heavy rain (February, March, and May), University Lake was sampled to assess the role that the sediments were playing in the lake. Two techniques were used. In one, concentrated suspended sediment was equilibrated in the laboratory with various concentrations of phosphate in distilled water (Taylor and Kunishi 1971; Kunishi, et al. 1972). A seasonal variation was found in the role that the suspended sediment played. In winter, when FRP and suspended sediments were abundant, these particles constituted a sink for phosphate (Figure 13; Table 10). From March on, however, they became a source, releasing phosphate to the water and therefore to the growing phytoplankton populations (Figure 9). Note that suspended sediments in March tended to be a net source of phosphate to the water (Table 10) even though tracer experiments suggested that abiotic uptake was about half of the gross rate (Figure 12). As discussed below, for biotic uptake, the net rate may be far smaller than the gross rate measured with tracer phosphate, and in the case of suspended sediments the net rate may even be negative.

Suspended sediments may buffer phosphate concentrations in solution (Carritt and Goodgal 1954; Taylor and Kunishi 1971; Butler and Tibbits 1972; Kunishi, et al. 1972). The sediment's capacity to adsorb or release P is governed by such environmental parameters as pH, temperature, and sediment composition, as well as the phosphorus concentration of the water (Golterman 1973). Although the role of lake bottom sediments in contributing or removing phosphorus from the water column is controversial (Schindler 1974), most authors have found that suspended sediments act as a sink for P in the water column in both fresh and salt water systems (Hayes and Phillips 1958; Pomeroy 1965; Fitzgerald 1970; Lincoln 1971). Phosphorus may come into a lake mostly as soluble or as organic forms, however, independent of the actual sediment influx into the lake.

Although the role the suspended sediment played in the lake over the seasons changed, the equilibrium phosphate concentration -- that is, the concentration at which no net uptake or release of phosphate would take place -- did not vary widely. This finding implies that the nutrient status of the incoming sediment was rather constant from February through May, a reasonable conclusion since the watershed surrounding University

Lake is largely undeveloped. Temperature was also disqualified as a cause for the change in the sediment's role; experiments showed that increasing temperatures actually increased the adsorptive capacity of the sediment, rather than decreasing it. It is most likely that the change in the role of the sediment from a phosphate sink to a phosphate source was largely dictated by the rapid change in the orthophosphate concentration in the water column; water in the spring and summer was depleted of much of its orthophosphate, and thus the suspended sediment lost some of its sorbed phosphate in order to equilibrate to conditions in the water column.

In a second technique, sediment spikes were added to lake-water samples to assess their effect on the abiotic uptake of ^{32}P (Table 7). Both sediments and water had been treated with formaldehyde. The samples took up more ^{32}P than unspiked samples regardless of the apparent role of the sediment according to the phosphorus potential curve data. It appears that the tracer shows an exchange of ^{32}P for ^{31}P on the adsorptive sites on the sediments and thus did not measure net uptake (Golterman 1973). Experiments should have been run longer to assiss uptake as the ^{31}P and ^{32}P on sediment and in solution came to equilibrium in the system.

The technique of using P-potential curves to assess the role sediment plays in the phosphorus dynamics of lake phytoplankton assumes that the only form of phosphorus available to algae is ortho-phosphate. Although phosphate is the form of phosphorus most readily available to plankton (Rigler 1964), other forms of the element may also be available to algae, especially when concentrations of phosphate are low. Many species of phytoplankton have the ability to produce alkaline phosphatase which allows them to use dissolved organic phosphorus when the supply of phosphate in the water column is low (Watt and Hayes 1963; Johannes 1964; Rigler 1964; Kuenzler 1965; Kuenzler and Perras 1965; Berman 1970; Perry 1976). Colloidal phosphorus is also a possible phosphorus source for micro-organisms (Pearl and Downes 1976).

When concentrations of phosphate are low, phosphate may desorb from sediment to replace phosphate taken up by plankton (Olsen 1958, 1964; Porcella 1975). Golterman (1969) found that 5-30% of the total P in his mud (which had been anaerobic but was directly suspended in his assay) could be used as a phosphorus source by algae. Cowen and Lee (1976) and Helfrich and Kevern (1973) confirmed that sediment would release about 30% of its total P to cultures when needed, although Fitzgerald (1970), using aerobic muds in dialysis tubes, could not detect growth in his phosphorus-starved Selenastrum and Cladophora cultures.

Effect of suspended sediments on water quality

High concentrations of suspended sediments in a water supply are generally considered undesirable for two reasons: (1) sediment transports algal nutrients and pesticide residues from the watershed to the lake, and (2) the suspended sediment impedes water filtration. Although sediment may be undesirable from a filtration point of view, preliminary results from

this study showed that sediment transport of phosphorus may not be a serious problem in University Lake in the winter months of the year. Suspended sediments seemed to act in a buffer capacity in the lake over the year, adsorbing P during winter when the concentration of P in the water was high and releasing P in the spring and summer when the concentration of P in the water was low. This adsorption-desorption process is not balanced; far more sediment is in suspension in winter. Most of the sediment apparently settles to the lake bottom and thereby removes phosphorus from the water column. The seasonal nature of the role of sediment in University Lake should be explored in future studies to develop an appropriate erosion control scheme for the lake.

Interpretation of phosphorus uptake kinetics

The rate of uptake of ^{32}P over time shows a biphasic pattern of initially rapid uptake followed by a slower uptake (Figure 14). Taft, Taylor, and McCarthy (1975) offer two possible explanations for the curve: (1) the entire curve represents net uptake which slows with the duration of the experiment as the level of available orthophosphate approaches the uptake limiting concentration, or (2) the initial uptake is only an exchange of unlabelled P for labelled P and represents gross uptake rate rather than net uptake rate.

Interpretation of the biphasic curve for ^{32}P uptake is difficult. In this study, as many others (Kuenzler and Ketchum 1962; Faust and Correll 1975; Levine 1975; Kuenzler, et al. 1979), the rapid first phase was used to assess the rate of P uptake. However, Taft, Taylor, and McCarthy (1975), comparing the N:P ratio of the plankton in Chesapeake Bay with their P uptake rates, concluded that the composition of the plankton was better fit by the slow uptake phase than the fast one. The authors felt that the rapid P uptake was only an exchange phenomenon of unlabelled P for labelled P and represented gross uptake rate rather than net uptake rate.

In order to clarify the pattern of ^{32}P uptake, the concentration of FRP was measured concurrently during some tracer experiments to see if the FRP and tracer concentrations would decrease together. No statistically significant change in FRP concentration was apparent over time (Table 9), however, even when uptake rates of ^{32}P were quite high.

The discrepancies between the apparent rate of uptake by using tracers and by monitoring chemical changes were noted early by Rigler (1956). Although ^{32}P was rapidly lost from the upper two meters of Rigler's lake, there was no concurrent loss of epilimnetic unlabelled phosphate. The phosphate in the epilimnion, in fact, increased slightly over the course of the experiment. Kuenzler, et al. (1979), monitoring FRP concurrently during tracer experiments, found a discrepancy between ^{32}P uptake rate and FRP uptake rate, with the latter rate being less than 30% of the ^{32}P uptake rate on all occasions. Perry (1976), on the other hand, reported good agreement between estimates of uptake and changes in ambient FRP concentrations. Because she used P-starved cells in her work, it is

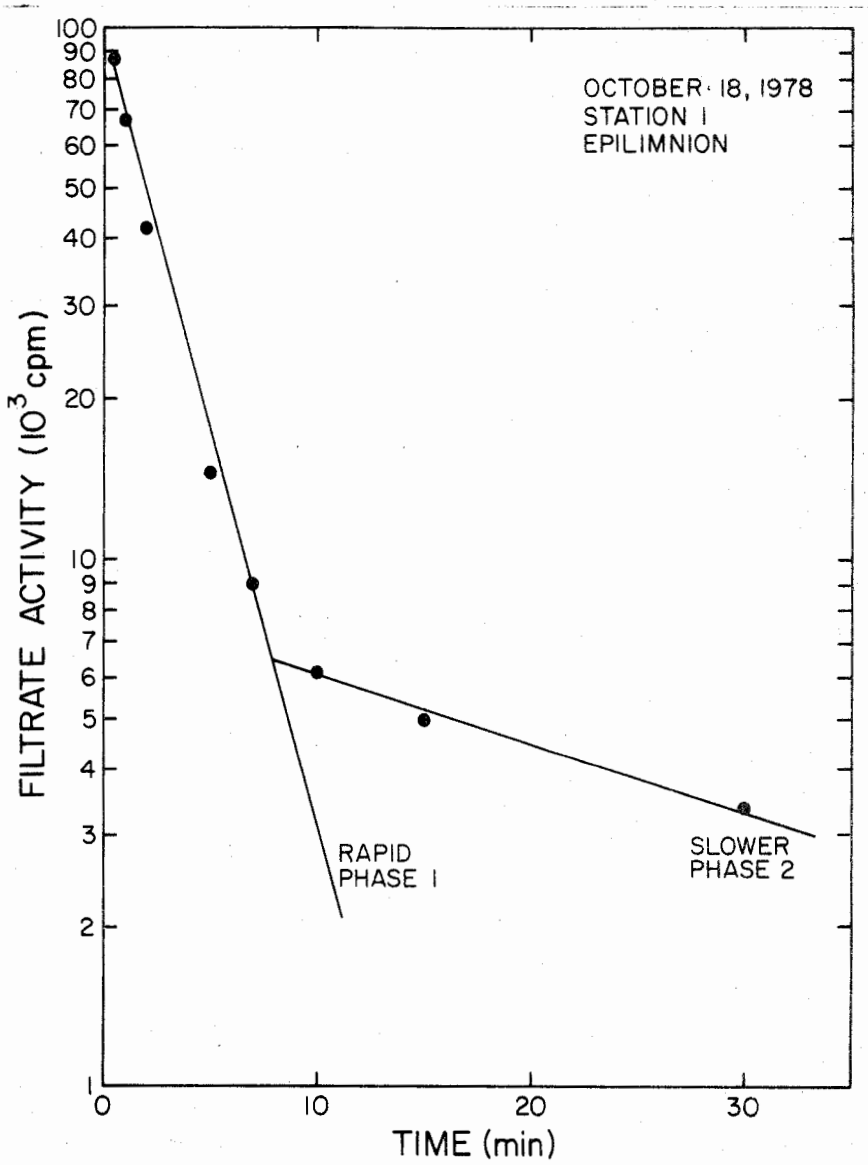

Fig. 14. Biphasic pattern of uptake of radiophosphate over time.

possible that phosphate uptake measured chemically and radiochemically were comparable.

There are two reasons why the rates of tracer uptake and FRP uptake do not agree. First, the problem may lie in the analysis of FRP. A significant portion of the phosphorus in natural waters measured by standard methods as orthophosphate is not actually orthophosphate (Kuenzler and Ketchum 1962). Low molecular weight P, high molecular weight P, and colloidal P have all been found to react with molybdenum blue as simple orthophosphate in the standard analysis for phosphate (Rigler 1964, 1968; Schindler, et al. 1973; Lean 1973; Peters 1978). These phosphorus compounds are not as readily available as orthophosphate to micro-organisms for uptake (Pearl 1978). Although arsenate is also assayed as phosphate in natural waters (Whitnack and Martens 1971), arsenic levels were found to be extremely low in University Lake in June, 1979 (1 ppb) and probably were not a problem here. It is therefore possible that the rapid uptake of ^{32}P reflects the actual uptake of rapidly-available orthophosphate. Residual phosphorus compounds less available to the micro-organisms but which are assayed by the chemical analysis may be responsible for the constant or slowly changing "FRP" concentrations which remain in solution throughout the duration of the tracer experiment.

A second possibility is that the ^{32}P initially traces only the phosphorus that the micro-organisms take up and not the amount that they keep. It therefore does not distinguish between gross uptake rate and net uptake rate (Taft, Taylor, and McCarthy 1977; Nalewajko and Lean 1978; Kuenzler, et al. 1979). Algae are known to release or excrete phosphorus compounds as well as take them up, even under limiting conditions (Rice 1953; Kuenzler 1970), and the ^{32}P may initially monitor only what is taken up and not the efflux back to the medium. The initial "uptake" may largely represent an exchange of ^{32}P for unlabelled P as the tracer reaches an equilibrium with various components of the system.

Separation of algal and bacterial uptake

An attempt was made to distinguish algal and bacterial uptake by two methods in this study, treatment with antibiotics and separation of plankton by differential size filtration. Although the two techniques are theoretically comparable (because most algae are greater than 8 μm and most bacteria are susceptible to treatment with antibiotic), there is a discrepancy between results obtained by the two methods. Generally, uptake activity which persisted in the presence of antibiotics was not as great as that trapped on an 8 μm filter (Table 6). In addition, the uptake of phosphorus by the larger size fraction was reduced to some extent by the addition of antibiotics (Table 13). Results similar to these are reported by Harrison, et al. (1977) in their work on the Chesapeake Bay Estuary.

There are two possible explanations for the discrepancies between the two methods: antibiotics may affect algal physiology and reduce their ability to take up phosphorus, or bacteria may have been trapped along

with algae on the 8 μm filter and may therefore have been contributing to the uptake by the 8 μm particles.

Table 13. Reduction by antibiotics of P-uptake by seston particles greater than 8 μm.

Date	Depth	Station	Uptake Rate ($\mu g\ P \cdot l^{-1} \cdot h^{-1}$) Ambient	Antibiotic	% Reduction
2/16	Surface	1	.049	.037	24
		3	.17	.04	77
3/16	Epi	1	.12	.017	86
	Meta		.06	.018	68
	Hypo		.06	.028	53
	Epi	3	.07	.012	83
4/27	Epi	1	.96	.096	90
	Meta		.58	.044	92
	Hypo		.66	.21	68
	Epi	3	.60	.066	90
5/23	Epi	1	9.0	4.0	55
	Meta		1.7	.26	85
	Hypo		1.8	1.1	40
	Epi	3	4.1	4.6	+12
6/27	Epi	1	12.0	18.0	+50
	Meta		7.2	1.2	83
	Hypo		5.4	2.4	55
	Epi	3	18.0	18.0	0

Little work has been done on the effect of antibiotics on the uptake of phosphorus by algae. Spencer (1952), Rigler (1961), and Hargrave and Geen (1968) all report that Pennicillin G (50 units per ml) and Streptomycin sulfate (100 units per ml) are effective in eliminating bacterial activity but do not address the issue of their effect on algal activity. Kuenzler, et al. (1979) found that antibiotics did not affect the ability of phytoplankton to take up ^{14}C-bicarbonate, a finding which suggests that the antibiotics did not injure the algae. However, algae do not

take up phosphorus as they do carbon; for example, phosphorus uptake can take place in the dark (Kuenzler and Ketchum 1962; Faust and Correll 1975), whereas carbon uptake cannot. The potential effect of antibiotic effects on blue-green algae was discussed above.

Evidence exists to support the theory that bacteria can be trapped on a coarse filter. Although free bacteria are smaller than 8 μm, bacteria are often found closely associated with algae (Faust and Correll 1975; Pearl 1975; Goulder 1977) or attached to abiotic particles (Pearl 1975), and are susceptible to being caught on the coarse filter. The reduction of the uptake of the 8 μm fraction by antibiotics suggests that this entrapment of bacteria is responsible for the discrepancy (Table 13) or that blue-green algae trapped on the filter are affected by antibiotic treatment.

In addition, there is evidence that the nominal porosity of the filter may not reflect the filter's actual performance in fractionating particles (Hobbie, et al. 1977; Burnison 1975; Pearl, pers. comm.). The discrepancy of the nominal porosity of Gelman filters was documented in this study as in others (Table 14). From September through January, Gelman filters were used to fractionate plankton. In February, a switch was made to Muclepore filters because of their documented superiority in size fractionation (Burnison 1975). Table 14 reveals the differences in the behavior of the two filters in January, 1979, a time of year when algal uptake was not important. Gelman filters consistently overestimated the amount of uptake by the large fraction of plankton, although they were comparable to Nuclepore filters in their 0.4 μm retention. ^{32}P adsorption to Gelman filters was responsible for part of this inflated retention figure. A correction factor for the difference between the two filters was not developed, because such a factor could not be a constant; it would change through the seasons with algal and bacterial population succession. Only size separation data from Nuclepore filters was included in this report.

Table 14. Performance of Nuclepore and Gelman filters in size fractionation of University Lake plankton.

Filter Type	Size	Adsorption cpm	Retention cpm
Nuclepore	8 μm	64 ± 9	339 ± 23
Gelman	8 μm	899 ± 96	1418 ± 393
Nuclepore	0.4 μm	197 ± 29	9660 ± 786
Gelman	0.45 μm	1383 ± 62	9990 ± 630

Relative importance of N and P in University Lake

In most lakes the major nutrients regulating trophic state are nitrogen and phosphorus. Because algae need about 16 moles of inorganic N for every mole of P (Redfield 1934), a system containing an N:P molar ratio greater than 16:1 will tend to be P limited. The N:P ratios (NO_3 + NH_4/FRP) available in University Lake calculated on each sampling date were generally much higher than 16:1, averaging 68:1 in the surface waters. These data indicate that phosphorus is potentially limiting to algal growth in the lake, perhaps in part because of sorption of P onto suspended sediments which settle to the bottom.

Sources of nutrients into University Lake

There is little evidence here of significant point source pollution in the University Lake watershed and no evidence of a eutrophication gradient in the lake during most of the year. Nonpoint pollution, from natural causes (soil erosion, deposition of leaves and animal wastes, and solution of minerals) and from human activities (fertilization of farmland, development of roads, and septic tanks), is thought to be the major contributor of sediments, nutrients, and organic matter to the lake. Therefore, future nutrient abatement plans should be directed towards nonpoint sources of pollution, especially phosphorus. A nutrient budget for University Lake would be helpful in identifying the most important nonpoint sources of nutrients to the lake.

Little is known about the ultimate fate of the phosphorus coming into the lake. Although this report covered the phosphorus recycling in the epilimnion, it is not known how much of the phosphorus associated with biotic and abiotic particles which settles to the hypolimnion of the lake recirculates again into the water column during overturn. The importance of iron in binding phosphate during overturn is also important to the P-cycle and is unexplored in University Lake. Further studies of the internal cycling of phosphorus in the lake would be useful because they would elucidate the relative importance of recycling of P to P loading to the lake.

Management implications of P-uptake experiments

The uptake rate of phosphorus in University Lake was generally in the range of values reported in the literature for other lakes in Canada, Israel, and the U.S. (Rigler 1964; Halmann and Stiller 1974; Levine 1975). The relationship between P-32 uptake rate and trophic state is controversial. Although some authors have found that uptake rate constants and patterns in the uptake of P are constant over lakes with a wide range of water quality (Rigler 1964), others have more recently found that where

orthophosphate concentrations were high, uptake rate was slow and where concentrations were low, uptake rates were fast (Peters and MacIntyre 1976; Peters 1979). More work needs to be done relating uptake of P to the concentration and distribution of nutrients in open systems before the results of kinetic studies can be directly useful to management of water bodies.

Recently it has been postulated that the uptake rate of P may be symptomatic of the nutritional state of the algae and hence symptomatic of the trophic state of the lake. Richey (1979) found that under conditions of adequate nutrient supply, P-32 is taken up at a rate which is required for the given rate of photosynthesis. Conversely, when nutrients are depleted and the algae are P-stressed, uptake is rapid and there is little correlation between uptake and utilization. Further experiments with dual labeling with C-14 and P-32 might help elucidate the nutritional state of the plankton in University Lake.

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