Lake Water and Sediment

IV. Radiophosphorus Equilibrium with Mud, Plants, and Bacteria under Oxidized and Reduced Conditions

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ABSTRACT

The phosphorus equilibration pattern and rate between mud and water was the same in natural Jenkin sampler cores, in artificial cores, and in bottles in which dredged surface mud was packed by centrifuge. Thus any specific natural physico-chemical or bacteriological layering of the surface muds of lakes is relatively unimportant in phosphorus exchange. Phytoplankton or bacterial cells equilibrate within a few minutes after addition. When antibiotics are used the P\(^{32}\) remains as inorganic PO\(_4\) and is rapidly taken up by higher plants, or in the absence of plants, there is a rapid loss of P\(^{32}\) to the mud. With one exception, in over 100 artificial systems tested, the amount of P\(^{32}\) remaining in the water at equilibrium was greater in the presence of bacteria than where antibiotic had been added. This was true whether the system was treated with nitrogen or air, i.e., was aerobic or anaerobic. After a week less than 10% of the P\(^{32}\) remained in the water of an antibiotic treated sample, while two thirds remained in the control.

The remarkable ability of bacteria to hold phosphorus in the water might be accomplished in two ways:

1) By an acceleration of the rate of P\(^{32}\) return from the sediment to the water by bacteria in the mud. In all experiments while the turnover time of water was generally of the same order of magnitude for all systems, the turnover time for mud was much shorter in the controls than in the antibiotic treated systems.

2) By the rapid uptake of radiophosphate by water bacteria and their ability to hold the radiophosphorus from the chemical or colloidal adsorption mechanism of the mud, which would be accomplished by incorporating the phosphate into non-participating organic compounds. An affinity, or holding back by water bacteria of P\(^{32}\) would be indistinguishable from an accelerated return to the water from the mud.

Dead plankton deposited on the mud decay and greatly increase the removal of P\(^{32}\) from the water. This reaction also is blocked by antibiotics. In bottle experiments there is a natural fallout of bacterial cells of about 1/10 per day. Neither the redox state of the system nor the level of lake productivity could be shown to influence either living or inorganic exchanges. The events following addition of radiophosphorus can be described as a modified first order consecutive reaction in which PO\(_4\) yields organic P in the bodies of bacteria which in turn yields organic soluble phosphorus to the water.

The rate of exchange is measured as turnover time, which is the time required for the appearance or disappearance of as much phosphorus as is present in the test material, say phytoplankton or water or mud. Some turnover times are: water of a whole lake, one week; water in a bottle over mud, 0.5 week; return from lake sediment in nature including rooted aquatics, 1 month; from mud in a bottle, 0.5 week; from bottle mud without bacteria, 2 weeks. Equilibration of PO\(_4\) between water and the inside of bacterial or phytoplankton cells is almost immediate, say 5 minutes, but conversion to the organic state is slower with average turnover time 0.3 days. Rooted aquatics, probably cannot take up organic P; with inorganic P their time is 0.5 week. Zooplankton are opposite in behavior, unable to use phosphorus until bacteria have made it organic; their time is then 1 day.

INTRODUCTION

When phosphorus is added to a lake as fertilizer nearly all of it disappears in a few days (Smith 1945, Orr 1947, Pratt 1949).

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The decline, taken together with the known effects of fertilization of agricultural land, might be attributed to new growth, although no immediate algal blooms appeared. The theory of growth stimulation demanded reconsideration when it was discovered that tracer phosphorus atoms, measured as radio-
activity, declined in the water in the same way as large masses of fertilizer (Hayes et al. 1952, Rigler 1956). It now appears that there is a single pool of phosphorus belonging to lake water and solids, which is distributed between them in a dynamic equilibrium or steady state. Disappearance from water is a consequence of an experimental arrangement in which phosphorus is added to the water phase. Were the opposite technique followed, of taking up phosphorus from the lake water on, say, ion-exchange resins, a continuous replacement from the solids would be expected.

The foregoing interpretation does not deny the general observation that addition of fertilizers to lakes stimulates growth. Obviously after equilibration there will be more nutrient in the system than before. The point is that the decline of phosphorus in the water phase is not a measure of increased productivity, since its rate will tend to be independent of the quantity added.

The oxygen relations of red blood cells in their plasma provide a simple analogy to the lake nutrient system. Oxygen is distributed between the phases in dynamic equilibrium. Under ordinary conditions nearly all the oxygen is in the cells. Any disturbance of either phase will cause an appropriate rearrangement of the system. For example, the addition of oxygen to the plasma would be followed by a "loss" to the cells and vice versa. To a physiologist the plasma, or fluid phase, is merely an innocuous transporter between the active parts of the system.

The dynamic equilibrium of a lake might be represented as

\[
\text{Phosphorus in aqueous phase, a small fraction of the whole} \Rightarrow \text{Phosphorus in solid phase, a large fraction of the whole.}
\]

with a constant value for each phase but with a continuous exchange between them. The radioactive tracer technique makes it possible to measure the rate of exchange, which is given as the turnover time, defined by convention as the time for as many atoms to move through the phase as are present in the phase. To illustrate turnover time, one might imagine a country of 16 million people (say Canada) in tourist equilibrium with a country of 160 million people (say U.S.A.). Suppose there are 32 million people crossing the border each way each year. The turnover time for Canada would be \( \frac{1}{32} \) yrs or 6 months; for the U.S. it would be \( \frac{1}{160} \frac{1}{2} \) or 5 yrs. It will be noticed that there is no uptake of tourists by the U.S. although there would erroneously appear to be such if the only observation made were a count of persons leaving Canada. Also, it is not implied that every Canadian moves across twice a year. Many persons will not cross at all, others several times per year and still others will go over once and stay. Turnover time is not obtainable by counting the populations of the two countries, however frequently, for the counts do not change. It is necessary to detect persons actually crossing the border.

In limnological work the P\(^{32}\) is an identifiable sample moving one way, like Rotarians leaving Canada. Extra mathematics, over and above tourist-like counts, are made necessary by lack of knowledge of the total populations of phosphorus atoms in the two phases, so that indirect means must be used to secure turnover times.

The purpose of this paper is to discuss the effect on the exchange reaction of some natural variants in lakes, namely the level of productivity, the state of oxidation or reduction, and the presence of green plants and bacteria. In a lake all these will be acting together to produce the observed equilibrium, but in the laboratory the components can be separated. An account of preliminary experiments is given by Hayes (1955), and the results to follow are an amplification and in one respect a modification of that report. Whereas the dominant role in exchange was previously attributed to the state of oxidation or reduction with bacteria playing a supplementary part, the results to follow indicate that bacteria are decisive and can to a considerable degree suppress the classical inorganic mechanism.

**MATERIAL AND METHODS**

Of the lakes whose sediments were studied, one was judged eutrophic (Southport Pond),
two were acid bog (Punchbowl and Silver), and five were unproductive or marginal (Copper, Black Brook, Grand, Lily, Bluff). For descriptions see Hayes and Anthony (1958).

Methods of handling and counting $^{32}$P, calculations of turnover times, handling of Jenkin sediment cores, etc. are given by Coffin et al. (1949), Hayes (1955), Hayes et al. (1952), and Harris (1957). Methods for measuring oxidation-reduction and for counting bacteria are given respectively in papers II and VI of this series.

In previous work (Hayes 1955) Jenkin core samples were collected to measure the radiophosphorus exchange between mud and water from lakes. This method is relatively exacting and inconvenient when many samples are required, and a simpler one was developed for the present investigation. Mud was collected in an Ekman dredge, the water was decanted off, and the surface mud was scooped into a sterile quart bottle. The remaining mud was put into a second sterile bottle. Lake water was also collected, and the samples were chilled and transported back to the laboratory as quickly as possible, generally within three or four hours. Here they were kept, in the dark at $4^\circ$C until use, which was within a week or less. Before use the lake water was filtered through Whatman number 42 paper to remove large mud particles and plankton.

Artificial systems, as shown in Figure 1, were set up and maintained at $4^\circ$C. Before being used they were allowed to stand for five to seven days, to give the bacteria time to reach a stable number, under aerobic or anaerobic conditions, and to allow the whole system to reach biological and chemical equilibrium. When it was desired to inactivate bacteria the antibiotic terramycin, or later the more powerful tetracycline, was used. A quantity of 100 mg of terramycin was needed per bottle but only 15 mg of tetracycline. In practice 30 mg of the latter was used, to allow a safety factor. This concentration was found to inactivate the bacteria for at least a week. A further advantage of tetracycline was the absence of any observable deposit on the mud surface. The antibiotic was dissolved in a few ml of distilled water and then passed through a millipore filter to remove any resistant bacteria or moulds. It was added to the artificial system a day before the experiment was to begin. This interval was found to be sufficient to inactivate the bacterial population almost entirely.

In order to discover whether there was any appreciable uptake and exchange of phosphorus by bacteria on the glass surface of the bottle, water blanks were set up in each experiment without the addition of mud. There was no loss of $^{32}$P in the glass.
blanks to which tetracycline was added. Further evidence of the effectiveness of tetracycline in inhibiting bacterial activity is seen in the investigation of qualitative changes in the radiophosphate added to Grand Lake and Punchbowl systems (see below). The culturing of water microorganisms by the millipore technique indicated that moulds are relatively unimportant numerically in lake water.

Attempts that were made to sterilize samples by heat under standard autoclaving conditions, were successful in killing all organisms, but produced such changes in the appearance and evident colloidal properties of the mud that they could not be taken as representative of natural conditions. Nevertheless, reactions with P32 agreed well with those of antibiotic sterilized samples.

Radiophosphate in dilute HCl, as obtained from Atomic Energy of Canada Ltd., was diluted with distilled water to give a count of 500,000 c.p.m. per ml and at once sterilized to kill bacteria and to permit storage for future use without the formation of organic radiophosphate by microorganisms. About one ml of the dilute radiophosphate was added to each artificial system, and duplicate samples were taken at intervals for counting.

From paper I, Table 2, the average total P in lakes is 18.5 ppb and the inorganic fraction amounts to 2.8 ppb. The added 500,000 counts in 150 ml water works out at 5.6 × 10⁻⁵ ppb. Thus the phosphorus increase in the samples by reason of added P32 amounted to 0.0003 % of the total P already present or 0.002 % of the inorganic P.

To separate the radiophosphate fractions a sample of water was passed through a millipore filter, which retained bacteria and particulate matter. The filtrate contained total phosphorus in solution, from which the inorganic P was precipitated. It was possible to find in a sample the c.p.m. per ml of radiophosphorus (a) in bacteria, (b) in particulate matter, (c) as inorganic P32 in solution, and (d) as total P32 in solution. The bacterial fraction could be estimated by comparing the counts in particulate matter with and without tetracycline treatment. There is a possibility that the small particulate fraction in the tetracycline-treated artificial systems might be incorporated in tetracycline-resistant bacteria or moulds, rather than in non-living particulate matter, although as already noted, moulds were not observed.

It was important to make sure that reduced conditions were secured in artificial systems by bubbling nitrogen through the water for a week. The cylinder nitrogen used was stated to contain not over 0.05 % oxygen, which at equilibrium would give a dissolved oxygen level of 0.03 ppm. According to Mortimer (1941–2) ferrous iron was found in artificial systems below 0.1 ppm and in lakes below 0.5 ppm. Thus our oxygen level is theoretically low enough. Winkler tests on water through which nitrogen was bubbled were indistinguishable from zero oxygen.

Reduced conditions, however, are not attained merely by withdrawal of oxygen, but require the action of microorganisms, or of a suitable catalyst. The decisive test is the redox potential which, as paper II points out, is not easy to measure or interpret.

In an artificial Silver Lake oxidized mud-water system the initial potential was 0.33 volts for mud and the pH was 4.7. The water was then bubbled with nitrogen for four days, whereupon the potential of the mud fell to 0.14 volts. After bubbling with air for 12 hours, the mud potential rose to 0.40 volts. The same result was obtained with tetracycline treatment indicating probably that the antibiotic did not penetrate the mud to kill the bacteria there, but allowed them to reduce the system.

Further results on the Punchbowl are

<table>
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<th>Duration of</th>
<th>Potential in volts</th>
<th>Potential in volts</th>
</tr>
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<tr>
<td>bubbling in</td>
<td>(Nitrogen)</td>
<td>(Air)</td>
</tr>
<tr>
<td>days</td>
<td>Water Mud</td>
<td>Water Mud</td>
</tr>
<tr>
<td>0</td>
<td>0.45 0.06</td>
<td>0.45 0.12</td>
</tr>
<tr>
<td>0.5</td>
<td>0.27 0.27</td>
<td></td>
</tr>
<tr>
<td>3.0</td>
<td>0.17 0.14</td>
<td></td>
</tr>
<tr>
<td>4.0</td>
<td>0.38 0.38</td>
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</tbody>
</table>

The mud was initially reduced and the water oxidized. These results show that the mud-water system was well oxidized or reduced before the antibiotic was added and the experiments started.
given in Table 1 showing that here also reduced conditions can be produced. With Grand Lake however, bubbling with nitrogen for over two weeks failed to bring about a corresponding reduction in four oxidized mud-water systems, to two of which antibiotic had been added. The mean initial potential of these systems was 0.42 volts for mud and 0.65 volts for water. The potential was measured every three or four days, the lowest reading after 15 days being 0.3 volts for mud and water. Other Grand Lake systems, when bubbled with air, remained oxidized at values between 0.4 and 0.5 volts for mud. It appears probable, in the light of these results and those in paper II, that the reduction achieved in these tests was as effective as would be found in nature in the sub-surface mud.

EXPERIMENTAL RESULTS

Natural and artificial cores compared

It was necessary for purposes of interpretation to know whether the mud-water radiophosphorus exchange in artificial systems represented the exchange under conditions more closely approaching those in the lake itself. The preparation of an artificial system involves the destruction of the natural physico-chemical and biological layering of the surface muds. If this layering were in any way peculiar and important to the phosphorus exchange in lakes, different results would be expected with natural Jenkin cores in which the mud-water interface is undisturbed. Two Jenkin cores were collected from Grand Lake and set up in the laboratory at 4°C. Water was siphoned off the cores until approximately 200 ml of water remained over the mud. Two artificial systems were set up by placing stirred bottom and surface mud in Jenkin cores and adding 200 ml of surface water over the mud in the usual manner. Tetracycline was added to the water of one natural and one artificial core. All cores were air bubbled.

The loss of \( {\text{P}}^{32} \) from the water is shown in Figure 2. It is apparent that natural and mocked-up Jenkin cores react similarly both in the presence and absence of bacteria. These results are almost identical to those for the eight-ounce bottle, artificial system results with the same lake. Any heterogeneous structure of the natural mud-water interface, if it is essential, was obviously reestablished in the artificial systems before the \( {\text{P}}^{32} \) was added.

This experiment illustrates a general finding, namely that when bacteria are inactivated with antibiotic (or by heat sterilization) there is a rapid loss of \( {\text{P}}^{32} \) to the mud. With one exception, in more than 100 artificial mud-water systems tested the amount of \( {\text{P}}^{32} \) remaining in the water at equilibrium was greater in the controls in which bacteria were present than in the corresponding system to which antibiotic had been added. This was true whether the system was treated with nitrogen or air, i.e., was aerobic or anaerobic. In the treated example under discussion, after a week less than 1.0% of the radiophosphate remained in the water. In the control two-thirds remained after the same period. This remarkable ability of bacteria to hold phosphorus in the water might be accomplished in two ways:

1) By an acceleration of the rate of \( {\text{P}}^{32} \)
return from the sediment to the water by bacteria in the mud. In all experiments, while the turnover time of water was generally of the same order of magnitude for all systems, the turnover time for mud was generally much shorter in the controls than in the antibiotic treated systems.

2) By the rapid uptake of radiophosphate by water bacteria and their ability to hold the radiophosphorus from the chemical or colloidal adsorption mechanism of the mud, which would be accomplished by incorporating the phosphate into non-participating organic compounds. An affinity, or holding back by water bacteria of $P_{32}$ would be indistinguishable from an accelerated return to the water from the mud.

The marked atoms which were added follow along with the rest of the inorganic phosphate in solution. The test being in the dark, there is no green plant effect to consider, but only bacteria which are putting inorganic phosphate rapidly through their bodies, changing most of it en route to the organic form. The organic fraction does not enter into non-living exchange reactions, of the kind described in earlier papers of this series. There is at the same time a regeneration of the inorganic phosphate by breakdown of the organic fraction, so that in the steady state of nature about 10 to 20% of the phosphorus in solution is inorganic.

When we prevent bacteria from entering the reaction by addition of antibiotic, the $P_{32}$ remains in the inorganic state and is free to participate in, say, an adsorption equilibrium as discussed in paper III. This is the lower curve of Figure 2, showing the $P_{32}$ atoms leaving the water. As each one leaves it is replaced by a conventional or $P_{31}$ atom coming out of the mud, but these ordinary atoms have no identification marks.

A culture of phytoplankton

A side experiment with a culture of Chlamydomonas dysosmos illustrates the speed with which microorganisms can pass phosphorus through their bodies. It was a pure strain culture, bacteria free, and was well supplied, indeed over supplied, with nutrient in the medium so that no excess uptake due to possible starvation could occur. The phosphate concentration was 0.015% in the form of $KH_2PO_4$. The organisms made up 5% of the volume of the culture. Three-hundred counts per minute per ml of radiophosphorus was added to the medium, and its transfer from water to organisms followed, organisms being centrifuged from the medium before they were counted. In the final equilibrium the counts amounted to about 190 per minute per ml for the water and 1,760 counts per minute per ml for the cells. At the time of the first count, 2.5 minutes after the start of the experiment, equilibrium had already been established. On general grounds it is known that the turnover time for water is about one-third of the time for substantial completion of equilibration. Thus we can say that the turnover time for the phosphorus in the water was probably not more than 1 minute and may have been considerably less. At equilibrium the cells contained about half as much radiophosphorus as the water, and they had to return an atom to the water for every one they took out in exchange. It would thus appear that the turnover time for the phosphorus in Chlamydomonas cells must be not more than 0.5 minutes. Thus under natural conditions in a lake such microorganisms could very rapidly make over any inorganic phosphorus present into the organic form and return it to the water.

Competition between bacteria and plants

We turn now to the 8-oz bottle experiments, beginning with the competition for phosphorus between bacteria and higher plants. The mud layer at the bottom is omitted and the duplicates set up include a control of filtered lake water, the same plus one or other of the plants tested, and the same plus plant and antibiotic. Results on two lakes are shown in Figure 3.

The flowering plant Eriocaulon, which is very abundant over the bottom of Bluff Lake, was collected, and 1 g of sprigs was placed in each of two aerated bottles of Grand Lake water. The loss of $P_{32}$ from the water is shown in Figure 3 at left. In the absence of bacteria Eriocaulon very rapidly takes up radiophosphate and reaches an equilibrium at which 10% of the $P_{32}$ is left
RADIOPHOSPHORUS EQUILIBRIUM WITH LAKE MUD AND ORGANISMS

60 - ERIOCAULON UTRICULARIA

PUNCHBOWL -

A ANTIBIOTIC

Sphagnum

FIG. 3. Radiophosphorus remaining in aerated water (without added mud) from Grand Lake (primitive) and Punchbowl (acid bog) containing plants with and without antibiotic. The plants used were the pipewort (Eriocaulon), the bladderwort (Utricularia), and the peat moss (Sphagnum).

in the water. The phosphorus turnover times for Eriocaulon and water, in the absence of bacteria, were calculated to be 3.0 days and 0.34 days, respectively. The effect of bacteria is to hold phosphorus in the water and prevent the large loss to the bottom plants. When bacteria are present, the equilibrium between radiophosphorus in water and in mud was reached with two-thirds of the radiophosphorus in the water, including its bacterial population. This is because bacteria hold such large quantities of phosphorus in their cell bodies. A second cause is the production by the bacteria of soluble organic radiophosphorus, which the plant presumably cannot assimilate. This experiment was repeated with the plants Sphagnum and Utricularia in Punchbowl water, Figure 3 right. One and one-half grams of Sphagnum sprigs or 0.5 g of Utricularia sprigs were placed in 150 ml of water. Unfortunately tetracycline caused the Utricularia to turn brown, and there was little uptake by this plant in the presence of the antibiotic. Because of the adverse effect only the non-treated Utricularia result is plotted, which is similar to that for the other plants. In the absence of bacteria Sphagnum took up 97% of the radiophosphate in the water within half a day, the turnover times for Sphagnum and water being 3.5 days and 0.09 days, respectively. In the presence of bacteria 50% of the phosphorus remained in the water after 5 days. Although no turnover time for Utricularia and water in the absence of bacteria was obtained, the fact that the loss of radiophosphorus from the water in the presence of bacteria was greater for Utricularia than Sphagnum suggests that the former plant is as active as Sphagnum in exchanging phosphorus with water.

There was also a Grand Lake experiment including mud, to which Eriocaulon was added, and a Bluff Lake test including mud and Utricularia. This is placing all three components in competition. The two lake systems agreed well, that for Grand (Fig. 4A) showing that the addition of Eriocaulon to the control resulted in a loss of 70% of the radiophosphate from the water after six days. The ability of the plant to remove so
great a quantity of radiophosphate from the water when the mud control was unable to do so in the presence of bacteria indicates the affinity of Eriocaulon for phosphate. The control curve in Figure 4A is an extreme illustration of another phenomenon which was common to most experiments. While a control mud-water system seemed to reach equilibrium after three to eight days, a gradual loss of radiophosphorus continued over a period of weeks until practically none remained in the water. Evidence will be presented later which suggests this decline is due to a fall out of radiophosphorus in the bodies of bacteria. In the present example the turnover time would be calculated from the curve values before the sixth day.

In summary, when bacteria and higher plants compete for inorganic phosphorus the bacteria get there first and change a part of it to organic forms which are apparently unavailable to plant use. In the absence of bacteria the aquatic plants tested take up enormous quantities of $^{32}$P within 12 hr, indicating a rapid exchange and the establishment of an equilibrium with most of the phosphorus in the plant body.

**Effect of plankton fallout**

A large fallout of plankton following a bloom, might be expected to affect bacterial activity at the mud surface of a lake and thus alter the exchange of phosphorus. Plankton was netted from Grand Lake, autoclaved, and approximately 0.3 g was pipetted into duplicate mud-water systems from the same lake. The plankton sedimented immediately to the mud surface. Equal quantities of dead plankton were placed in two antibiotic treated glass blanks, omitting mud. Results are shown in Figure 4B. Obviously sterile dead plankton, of itself, is unable to adsorb significant quantities of phosphate by a colloidal mechanism or by other means. The addition of dead plankton to a mud-water system resulted in an enormous and rapid loss of $^{32}$P from the water. This greater uptake at the mud surface, as compared with the control in Figure 1A, was evidently caused by increased bacterial activity there, due to the large amount of readily decomposable organic matter. An uptake of phosphate by bacteria attached to falling organic matter in lakes is probably of importance in the natural cycle.

**Effect of the state of oxidation**

It is a matter of fact, repeatedly verified, that the removal of oxygen either over the lake bottom or in laboratory tubes will allow inorganic P to come up out of the mud. In
nature this will take place in the dark below the green plant zone. A large fraction though presumably not all of the new $P$ remains inorganic. The conditions of stagnation which are prerequisite to oxygen lack also operate to keep the new $P$ in a close layer a few cm thick over the bottom where it may reach a high concentration. Any increase which might be observed if the new $P$ were dispersed through the whole lake, would depend on both the volume of the lake and the quantity of $P$ produced. The latter measurement has hitherto been too difficult to make (as far as we know). The new $P$ may formerly have been adsorbed on a gel which was destroyed when reduced, (paper III) or (as Einselc stresses) it may exist as a salt of which the reduced form (ferrous phosphate) is more soluble than the oxidized (ferric phosphate).

How would the above considerations affect the behavior of $P^{32}$ in the water? We know that under ordinary aerobic conditions the loss to the mud is kept small through the intervention of bacteria. The effect of removing oxygen is unpredictable because of competition between two processes: (a) bacterial conversion to organic $P$ will be if anything diminished, and this would enhance removal of $P^{32}$ from the water (see Fig. 2), and (b) the general flow of ordinary $P$ out of the mud would so affect the exchange mechanism as to leave most $P^{32}$ in the anaerobic water. Turning to actual results, in four out of ten experiments, the per cent of radiophosphorus in the water at equilibrium was higher under aerobic than under anaerobic conditions. The average difference between the equilibrium values in these four experiments was 5.5%, the highest being 11.0%.

When antibiotics are added to prevent bacterial synthesis one might hope to observe the inorganic mechanism, (b) of the previous paragraph. In ten out of twelve experiments the average per cent of radiophosphorus in the water at equilibrium was indeed higher under anaerobic conditions. In four out of these ten experiments however the difference was less than 5%. It was maximal in the two Punchbowl experiments in which there was twice as much radiophosphorus in anaerobic water at equilibrium (Fig. 5).

**Effect of trophic level and lake type**

Tests such as those described above have been carried out on eight lakes, with results expressed as turnover times for mud and for water and as $P^{32}$ left at equilibrium. The data are in Table 2, in which the lakes are arranged in productivity groups. This judgment is in large measure qualitative, particularly as regards the separation between "marginal" and "unproductive."

A complete experiment would number 12 to 16 bottles each arranged as in Figure 1. Four artificial mud-water systems were bubbled with air and four with nitrogen. Antibiotic was added to two bottles in each
Table 2. Turnover times for mud and water in 8-oz bottle experiments, and $P^{32}$ concentration left at the equilibrium time

The symbols are: $A_e$ aerobic control; $A_t$ aerobic test with tetracycline added to inactivate bacteria; $N_e$ anaerobic or nitrogen control; $N_t$ nitrogen with antibiotic added. Some heat sterilization results are also included, being placed for economy under the antibiotic values with which they are to be compared. The values are averages of duplicate tests or, in several instances, pairs of duplicates done at different times.

A mathematical limitation may be mentioned here, for illustration of which attention is directed to the upper curve of Figure 4. Suppose the flattening of this curve at 6 days and its subsequent decline were described by points with a little more scatter. The line marked “control” would then have to be drawn straight, a treatment which would make little difference to the turnover calculation for water, but would make the mud value read as infinity. The per cent left in water at equilibrium would come out to be zero. Such results, being meaningless, have been omitted from the table.

The treatment just described, involving the assumption that the decline, when plotted logarithmically, is linear, was the first way to calculate turnover time (Zilversmit et al. 1943). When applicable however, the complete method in which allowance is made for a two-way flow of phosphorus, yields more information.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Turnover time for mud</th>
<th>Turnover time for water</th>
<th>% $P^{32}$ left in water at equilibrium</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>$A_e$</td>
<td>$A_t$</td>
<td>$N_e$</td>
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<tr>
<td>Productive</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southport</td>
<td>3.2</td>
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<tr>
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<td></td>
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</table>

group. In the Punchbowl and Lily Lake experiments heat-sterilized systems were also set up to compare with the effect of antibiotics. Each experimental arrangement was thus prepared in duplicate. Glass blanks (150 ml of water without mud) were set up under each condition in all experiments with the exception of Copper Lake and Bluff Lake. After the addition of $P^{32}$ between eight and eighteen duplicate samples of water were taken from each bottle at intervals until equilibrium was reached or approached, and from these samples the turnover times for water and mud were calculated, as given in Table 2. They are averages of duplicate mud-water systems, the mean probable deviation of the two values corrected by the $t$-test being less than 20%. The per cent of the initial radiophosphorus concentration remaining in the water at equilibrium is also given.

The first conclusion to be drawn from Table 2 must be negative. Looking vertically at the columns, there is no clear relation between trophic level and the exchange reaction. Only the acid bog differs from the rest of the groups in the antibiotic or heat-treated "$t$" columns. Here the turnover time for mud is shorter and for water longer, and more $P^{32}$ is left at equilibrium than in the others. Since the difference is in the sterile samples it is evidently related to the physical properties of the sediment rather than microorganisms. The brown water of bog lakes is carrying in and depositing large quantities of foreign organic material from surrounding swampy country which may account for the $P^{32}$ effects.

The absence of differences in laboratory tests may not reflect behavior in nature, where phytoplankton enters the scene. These plants will not only compete with
bacteria for phosphorus, but may suppress them by their own antibiotics (Steemann Nielsen 1955).

Table 2 shows that the turnover time for mud, i.e., the rate at which mud can put phosphorus back into the water, becomes greatly lengthened when microorganisms are inactivated. We may postulate a normal cycle in which there is (a) an uptake and synthesis of organic P$^{32}$ in the water, followed by (b) a fall out to the sediment surface, where (c) a breakdown to inorganic P$^{32}$ occurs under bacterial action, so that (d) the P$^{32}$ is restored to the water. Under the tetracycline treatment an inorganic mechanism is in operation with different time relations.

Looking at the center block of Table 2, the horizontal values have no trend. Thus the turnover time for water is not shown to be affected by bacteria or by the state of oxidation-reduction.

The right block however, does indicate bacterial action, in that the columns $A_e$ and $N_e$ have higher values respectively than $A_i$ and $N_i$. This means that when bacteria are present they hold extra phosphorus in the water. To look for an oxidation-reduction effect we compare column $A_e$ with $N_e$ and $A_i$ with $N_i$. No convincing behavior pattern can be discerned, i.e., there is no indication of more P$^{32}$ left in the water under one state than the other. The one lake, Punchbowl, which clearly obeys theoretical demands, has already been illustrated in Figure 5.

No appreciable loss of radiophosphorus was noted from the water of over thirty glass blanks, both anaerobic and aerobic, to which antibiotic had been added. This is evidence that the loss from the water of mud-water systems was not due to precipitation of phosphate as ferric phosphate.

The agreement between heat sterilization and antibiotic treatment of mud-water systems suggests that: (a) the effect of antibiotic on P$^{32}$ exchange is due to the inactivation of bacteria; (b) moulds and other antibiotic-resistant microorganisms are relatively unimportant in the mud-water exchange; (c) the physico-chemical adsorption mechanism of the mud is not drastically affected by the very harsh treatment of heat sterilization.

A look at the whole of Table 2 suggests that the action of bacteria is to suppress the underlying inorganic exchange mechanism, which is thereby relegated to a subsidiary role. We may suppose that in nature the phytoplankton behaves in the same way.

Loss from the water of control glass blanks

There was a loss of radiophosphate from the water of over thirty control blanks, that is, blanks in which the bacteria had not been killed. This loss was generally much less and occurred at a slower rate than that from corresponding mud-water systems.

Some blanks showed an equilibrium with a solid phase, evidently periphytic or sedimented organisms. In most cases the decline was arithmetic during the time of sampling. Often there was no decline during the first few days followed by slow loss of radiophosphorus. Full data dealing with these results are not presented here because of their voluminous and diverse nature. The loss of radiophosphorus from Grand Lake and Punchbowl glass blanks is shown in Figure 3.

Haukelekian and Heller (1940) report that the bacterial population of stream water is increased by addition of clean sand, while ZoBell (1943) found that increased bacterial activity in stored sea water is directly proportional to the ratio of glass area to water volume. According to Taylor and Collins (1949) growth is stimulated by Bohemian glass but not by Pyrex or fused silica. These reports led us to enquire whether the loss of P$^{32}$ in the control glass blanks was due to bacteria on the sides of the glass bottles. If this were so it would be a source of error in the mud-water systems. If however, the loss were due to fallout of bacteria from the water to the bottom of the bottle, or to accumulation by sessile bacteria on the bottom, there would be no error introduced.

Tests were conducted on Punchbowl mud-water systems in which the water volume was reduced from the usual 150 ml to 100 ml and 50 ml, and to which pieces of glass tubing were added to double the glass surface. Tabular data will be omitted since all
results were negative, i.e., there was no difference in behavior of P\textsubscript{32} caused by changed surface-volume ratios.

It is known (Fig. 3, lines marked "control") that some loss occurs from water even when mud is not present. To discover whether such loss of radiophosphorus might be due to a fallout of bacteria, a glass filter disc was placed on the bottom of an aerobic Grand Lake preparation. After 15 days 50\% of the radiophosphorus remained in the water. The sintered glass disc, when it was removed and its activity tested, accounted for 89\% of the P\textsubscript{32} which had disappeared from the water. Thus most of the loss of P\textsubscript{32} is to the bottom of the bottles, and the effect is not a source of error where the mud surface replaces the glass bottom of the blank. It is concluded that periphytic bacteria, if they are present on the glass walls, are not active in taking up radiophosphorus.

**Consecutive forms of phosphorus**

It has already been suggested that tracer phosphate is soon taken up by bacteria and changed into the organic state, and that later some of it leaks out into the water again as soluble organic phosphate. We may now consider the time and equilibrium relations of the process which may be compared and contrasted with a consecutive reaction, \( A \rightarrow B \rightarrow C \), as shown in the left block of Figure 6, in which the two reactions are proceeding simultaneously. If events were followed by analyzing for A, curve A would be obtained; if periodic measurements were made of the end product C, curve C would result; finally if only the intermediate product B were determined, the course of the reaction would rise to a maximum and fall off as shown by curve B.

The course of events with a P\textsubscript{32} experiment differs from the reaction described in that there is a gradual loss of the total, \( A + B + C \), from the water both by reason of fallout, etc., as already described, and by inorganic exchange with mud if mud is present. Also the lake water reaction does not proceed to virtual completion, but to an equilibrium in which appreciable quantities of all forms remain. As already mentioned general water analyses show 10 to 20\% of the phosphate as inorganic, i.e., corresponding to A.

Three aerated bottle series were set up, with and without mud, in which the P\textsubscript{32} in several fractions was followed. Two were on Grand Lake material, collected in January and July and the third on Punchbowl collections made in July. Results agreed very well, and the Punchbowl, for illus-
Rapid changes were observed in the $^{32}P$ which had been introduced as inorganic $PO_4$. Figure 6, center, shows the water blank for the first nine days. Water bacteria rapidly incorporated 50% of the $^{32}P$ as part of their body protoplasm, and reached virtual equilibrium within 12 hours. (The same equilibrium at 12 hours was observed in a test on Black Brook water by which time two-thirds of the $^{32}P$ was in the bacteria.)

There was a rapid formation of soluble organic radiophosphorus (C) reaching a maximum by the time of the first observation at twelve hours. This fraction then fell to an equilibrium value after two days. The maximum might be due to a very rapid production via bacteria and a slower loss from the water to mud or sessile microorganisms. The subsequent change in C was slight with a possible rise at right. While the increase at 7 days is not proven by the single analysis, it is made plausible by the theoretical necessity that the total $A + B + C$ should sum up to the value for the top line. The turnover time for the bacteria was calculated at 5 hr.

When mud is added to the system (Fig. 6, right) the uptake of $^{32}P$ by water bacteria is considerably diminished. The reason is apparent in the difference between the topmost or "total" curves showing the great loss from the water when mud is present. In other words there is introduced with the mud a great number of competing bacteria as well as an inorganic exchange mechanism. The soluble organic fraction (C) in the water is also smaller when mud is present. It appears that the two experiments are showing the same phenomena but that the mud one is modified by the steep down slope of the $A + B + C$ curve. The turnover time for water bacteria worked out at four days, nearly an order of magnitude larger than when mud is absent. Evidently the mud is pulling for $^{32}P$ against the water bacteria, which tend, as a consequence, to hold on to what they can get.

In Grand Lake tests the mud has diminished effectiveness as a $^{32}P$ remover (see Fig. 4A, top line). For this reason the turnover time for water bacteria was about the same as that of the Punchbowl water blank, 4 hr or less. As a further consequence there was a greater uptake by the water bacteria (B). In other words the Grand Lake complete system was not unlike the Punchbowl water blank in behaviour.

INTEGRATION

There are now sufficient data, as assembled in Table 3, to warrant a preliminary assessment of the time relations of the several phosphorus reactions.

For the water of a whole lake, the turnover time averages about a week (center col., blocks A and B). For a bottle experiment it is nearly half a week (block C, 1st 4 entries). The bottle experiments lack phytoplankton and rooted aquatics. The two results are surprisingly alike, and they seem at first to contradict the tourist analogy of the introduction, according to which a lake of infinite depth (compared to a bottle) would have an infinite population of phosphorus atoms, hence an infinitely long turnover time. The fact seems rather to be that in these lakes the exchanging mechanism builds up with the water volume, perhaps because the littoral zone is large and phytoplankton is proportional to volume of water. In our analogy the tourists are proportional to the population of the country.

The return from solids (left col.) is an order of magnitude slower in lakes than in bottles, presumably because of extra competition from rooted aquatics, phytoplankton, and zooplankton in the natural state. We suggest provisional acceptance of the bottle results as describing the behavior of mud alone. The lack of difference between oxidized and reduced systems and the four-fold slowing of the response when bacteria are inactivated has already been discussed.

The remainder of Table 3 deals with reactions between aquatic life and water in absence of mud. With microorganisms a sharp time distinction exists between two processes. There is a quick reaction, evidence for which rests mainly on Rigler's results with freshly collected lake water in-
The first three lake experiments are with large quantities of phosphate as fertilizer; all the others are with tracer amounts of radiophosphorus. Although added as inorganic $\text{PO}_4$, the phosphorus is soon changed to organic compounds when bacteria are present. Times are given in days except for equilibria between outside water and cells, which are given in minutes (shown by italics in table). Table 3. *A collection of turnover times*

<table>
<thead>
<tr>
<th>Turnover time for 1st mentioned component</th>
<th>Equilibrium system</th>
<th>Turnover time for 2nd mentioned component</th>
<th>Lake, location, experiment</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Whole lakes. Addition of dry phosphate fertilizer</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Solids, <em>i.e.</em>, mud + plants, <em>vs.</em> water incl. bacteria</td>
<td>3.2</td>
<td>Unstrat. marine Loch Craighlin, Scotland</td>
<td>Orr 1947</td>
</tr>
<tr>
<td>B. Whole lakes. $\text{P}^{32}$ tracer experiment</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>37</td>
<td>Solids, <em>i.e.</em>, mud + plants, <em>vs.</em> water incl. bacteria</td>
<td>7.6</td>
<td>Punchbowl, N. S. epilimnion</td>
<td>Coffin <em>et al.</em> 1949</td>
</tr>
<tr>
<td></td>
<td>Solids, <em>i.e.</em>, mud + plants, <em>vs.</em> water incl. bacteria</td>
<td>3.6</td>
<td>Toussaint, Ont. epilimnion</td>
<td>Rigler 1956</td>
</tr>
<tr>
<td>29</td>
<td>Solids, <em>i.e.</em>, mud + plants, <em>vs.</em> water incl. bacteria</td>
<td>10.2</td>
<td>Toussaint, recalculated by us from Rigler data.</td>
<td></td>
</tr>
<tr>
<td>C. Laboratory experiments with $\text{P}^{32}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mud <em>vs.</em> water, with bacteria present, oxidized system</td>
<td>2.7</td>
<td>Average of values in Table 2</td>
<td>Orig.</td>
</tr>
<tr>
<td>3.6</td>
<td>Same, but reduced system</td>
<td>2.6</td>
<td>Average of values in Table 2</td>
<td>Orig.</td>
</tr>
<tr>
<td>15.5</td>
<td>Mud <em>vs.</em> water, with bacteria absent, oxidized system</td>
<td>2.6</td>
<td>Average of values in Table 2</td>
<td>Orig.</td>
</tr>
<tr>
<td>12.5</td>
<td>Same, but reduced system</td>
<td>2.9</td>
<td>Average of values in Table 2</td>
<td>Orig.</td>
</tr>
<tr>
<td>1.1</td>
<td>Inorg. phosphorus in sol. &amp; in bact. <em>vs.</em> org. phosphorus in sol. &amp; in bact.</td>
<td>0.79</td>
<td>Filtered surf. water from Chocolate, a polluted lake near Halifax</td>
<td>Harris 1957</td>
</tr>
<tr>
<td>0.21</td>
<td>Inorg. phosphorus in sol. &amp; in bact. <em>vs.</em> org. phosphorus in sol. &amp; in bact.</td>
<td>0.21</td>
<td>Same from Punchbowl N. S.</td>
<td>Orig.</td>
</tr>
<tr>
<td>0.2</td>
<td>Inorg. phosphorus in sol. &amp; in bact. <em>vs.</em> org. phosphorus in sol. &amp; in bact.</td>
<td>0.2</td>
<td>Same from Grand, N. S.</td>
<td>Orig.</td>
</tr>
<tr>
<td>4.5</td>
<td>Bacteria &amp; algal cells <em>vs.</em> water</td>
<td></td>
<td>Surf. water freshly collected from Toussaint, Ontario</td>
<td>Rigler 1956</td>
</tr>
<tr>
<td></td>
<td>Bacteria &amp; algal cells <em>vs.</em> water</td>
<td>3.6</td>
<td>Same from Oiseau, Ont.</td>
<td>Rigler 1956</td>
</tr>
<tr>
<td></td>
<td>Bacteria &amp; algal cells <em>vs.</em> water</td>
<td>2.6</td>
<td>Same from Maskinonge, Ont.</td>
<td>Rigler 1956</td>
</tr>
<tr>
<td></td>
<td>Phytoplankton culture <em>vs.</em> water</td>
<td>1.0</td>
<td>Pure <em>Chlamadomonas</em> in laboratory nutrient solution</td>
<td>Orig.</td>
</tr>
<tr>
<td></td>
<td>Flowering plant <em>Eriocaulon</em> <em>vs.</em> water</td>
<td>0.34</td>
<td>1 g sprigs in 150 ml lake water; bacteria absent</td>
<td>Orig.</td>
</tr>
<tr>
<td></td>
<td>Peat moss (<em>Sphagnum</em> <em>vs.</em> water</td>
<td>0.09</td>
<td>1.5 g sprigs in 150 ml lake water; bacteria absent</td>
<td>Orig.</td>
</tr>
<tr>
<td></td>
<td>Brine shrimp (<em>Artemia</em>) <em>vs.</em> sea water</td>
<td></td>
<td>Naturally occurring bacteria present</td>
<td>Harris 1957</td>
</tr>
<tr>
<td></td>
<td>Same, but bacteria absent</td>
<td>1.8</td>
<td>Naturally occurring bacteria present</td>
<td>Harris 1957</td>
</tr>
<tr>
<td></td>
<td>Beach flea (<em>Gammarus</em> <em>vs.</em> sea water</td>
<td></td>
<td>$\text{P}^{32}$ remains in inorganic state</td>
<td>Harris 1957</td>
</tr>
<tr>
<td></td>
<td>Same, but bacteria absent</td>
<td></td>
<td>$\text{P}^{32}$ remains in inorganic state</td>
<td>Harris 1957</td>
</tr>
</tbody>
</table>
including natural phytoplankton, and presumably some bacteria; there is also a slow reaction observed in our laboratory results with bacteria but not including phytoplankton. These are resolved below (Fig. 7) into a harmonious scheme, for the validity of which further proof is desirable. In the scheme it is supposed that PO₄ in water goes in and out of the bodies of phytoplankton and bacteria with a turnover time of the order of 5 min. Most of it is chemically unchanged. (One is tempted to think about the way glucose or urea crosses cell walls in a higher animal.) The process of conversion to the organic form is about two orders of magnitude slower, with a turnover time averaging 0.3 days.

Two plants tested had the same turnover times as natural mud. As previously noted they were apparently unable to take up organic phosphorus, although we have not yet proved this. Proof would consist in offering plants organic P³² in solution with no inorganic fraction present.

Finally, two marine invertebrates are reported which may be considered to indicate the expected behavior of zooplankton. They are unable to take up inorganic phosphorus, but when bacteria are present to serve as food, their turnover time is of the order of one day.

In Figure 7 the data on turnover are combined in a single plan. The numbers are all days except for one 5-min entry. Four kinds of line are used as qualitative indicators of time. It is seen that upon addition of phosphate to water the immediate reaction, within minutes, is a transfer through the bodies of unicellular floating forms of life (heavy lines to right). Next, as shown by the light solid lines to the left, there occurs within a matter of hours, i.e., two orders of magnitude slower than the above, an exchange in which the floating cells and the higher aquatics compete on approximately equal terms for the PO₄. This they make into their own body structures, throwing some of it back to the water as soluble organic phosphorus. We have cancelled out the virtually instantaneous passage through floating cells and set the process down as an equilibrium between inorganic and organic phosphorus in solution, for which the turnover time is 0.3 days.

At top left is indicated a doubt as to whether higher plants can utilize organic phosphorus, and at top right the feeding of zooplankton is given a turnover time, and their inability to utilize inorganic P is noted.

The lower part of Figure 7 brings in the sediment surface. At right bacteria are noted to fall out at a few per cent per day. This is in bottles and not to be read as net fallout in lakes, which is subject to wide variation. The fallout at right probably describes the same phenomenon as the line leading down at left, i.e., the settling of organic matter to be reduced again by bottom microorganisms for regeneration to the water. The turnover time for leaving the water and for return is here 3 days, an order of magnitude slower than for exchanges with floating life.

The inorganic mechanism, which can be observed when bacteria are suppressed, is shown at lower center. There are variants for reduced and for oxidized conditions which have been described in papers II and III of this series. As already noted, the observed time relations are not affected by the redox state. In taking out inorganic P
the mechanism has the same turnover as
the bacterial action just described, namely
3 days. The return to water however is
much slower, at 15 days. This means that
there is about \( \frac{15}{3} = 5 \) times as much par-
ticipating inorganic P in the mud phase as
in the water (as in our tourist example the
U. S. has a larger population than Canada).
Now as previously noted, the ratio of soluble
organic to inorganic P in the water is also
5 to 1. Putting the ratios together we con-
clude that the P exchanging in the mud by
the inorganic mechanism is about equal to
the total P in the water. Thus if we could
get it all released it would double the lake
supply. (However the removal of the partici-
pating mud pool would trigger a further
equilibration reaction by which more phos-
phorus in the mud would become available
and so on \emph{ad infinitum}, like the flow of
ink out of a fountain pen.)

The final level of total exchangeable
phosphorus in a lake is eventually deter-
mined by: (1) The net rate at which phos-
phorus in solution and in particulate matter
enters the lake through drainage and rain-
fall. Ruttner (1953) states that the spring
waters entering Lunz Lake contain 0 to 3\( \gamma \)/L
of phosphate, while rain water occasionally
contains 10\( \gamma \)/L of phosphorus originating in
dust. This inflow is dependent on the
goalogy, fertility, and size of the drainage
area, and on the amount of rainfall. (2)
The rate at which exchanging phosphorus is
lost from further metabolism by incorpora-
tion into inorganic insoluble precipitates and
undecayed organic matter in the lake
bottom. Phosphorus in sediments amounts
to about 0.05% dry wt of which two-thirds
is organic. The largest concentrations and
highest organic fractions are in surface sedi-
ments of recent geological formations
(Kleeckoper 1957). (3) The morphometric
properties of a lake. The volume deter-
mines the extent to which phosphorus is
diluted. The area and depth influence the
thermal stratification and relative size of the
photosynthetic zone, which in turn affect the phosphorus cycle.

Within the limits set by these properties
the various parts of the phosphorus cycle
will operate. For example rooted aquatics
are probably unimportant in large deep
lakes where the littoral region is negligible
compared to the total volume. In smaller
and shallower lakes, in which the profundal
zone is minimal, the growth and bacterial
decay of rooted aquatics probably dominates
the phosphorus exchange. It is even pos-
sible for the whole productive capacity to
be occupied by rooted aquatics, leaving no
nutrients to spare for support of phyto-
plankton (Prowse 1955).

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