Advances in understanding phosphorus cycling in inland waters – their significance for South African limnology

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ABSTRACT

The definitions of the different phosphorus compound fractions present in inland waters are reviewed and the limitations of the definitions discussed. The development of models of phosphorus cycling is summarized. Attempts to establish their applicability to South African inland waters have been unsuccessful. The exchange processes involved in the phosphorus cycle are influenced by the biota, by phosphorus enzymes and by the presence or absence of littoral vegetation. These processes are poorly understood, however. It is not known to what extent phosphorus exchange between sediment and water takes place in South African inland waters, but these exchange processes are influenced by the presence of a variety of soluble phosphorus fractions, dissolved oxygen and other chemical constituents in the water and by the nature of the sediments and sedimentation processes. The influence of external loading on phosphorus cycling and its significance in the prediction of algal growth is discussed. It is concluded that in South Africa factors such as shallowness, mixing and silt-loading make it desirable to study phosphorus cycling in local impoundments; existing knowledge is based primarily on deep, stratified and clear north temperate lakes. In addition, there is a need to standardize terminology and analytical techniques.

UITTREKSEL

'n Oorsig word gegee van die verskillende fraksies van fosfor verbindings wat in binnelandse waters voorkom en die beperkings van die definisies word bespreek. Die ontwikkeling van modelle van fosforsirkulering word bespreek. Pogings om hul toepasbaarheid in Suid-Afrikaanse binnelandse waters te bevestig was onsuksesvol. Die uitruilingsprosesse word deur die biota, deur fosfor-ensieme en deur die teenwoordigheid, al dan nie, van littorale plantegroei beïnvloed. Daar is egter onvoldoende kennis oor die prosesse. Die omvang van fosfor-uitruiling tussen sediment en water in Suid-Afrikaanse binnelandse waters is onbekend maar die uitruilingsprosesse word deur die teenwoordigheid van 'n verskeidenheid oplosbare fosforfraksies, deur opgeloste suurstof en ander chemiese bestanddele in die water en deur die aard van die sedimente en sedimentasie beïnvloed. Die invloed van eksterne belading op die sirkulering van fosfor en die betekenis daarvan in die voorspelling van alggroei word bespreek. Die gevolgtrekking word gemaak dat in Suid-Afrika faktore soos vlakheid, menging en slikbelading dit wenslik maak om sirkulering van fosfor in plaaslike damme te bestudeer; bestaande kennis is hoofsaaklik op diep, gestratifiseerde en helder gematigde mere gebaseer. Verder is daar ook 'n behoefte vir die standardisering van analitiese tegnieke.

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INTRODUCTION

Phosphorus (P) is an essential element for plant and animal growth. It occurs in low concentrations relative to other essential elements in the environment (Wetzel 1975) and has special significance as an element controlling biological activity. In common with most other elements it may be combined into a variety of ionic, molecular and colloidal forms, often mediated by biological processes (Rigler 1973). The variety and quantities of the forms in which phosphorus can exist may therefore be expected to be related to the quantitative extent of these biogenic processes. Where turnover in these processes is increased, for example during eutrophication, the implications for phosphorus fractionation may be considerable.

In a body of water, changes in the concentrations of different phosphorus fractions result from processes which can be categorized into three distinct but nevertheless interdependent spheres of influence:

- Phosphorus cycling in the water

- Phosphorus exchange between sediment and water

- Allochthonous phosphorus loading.

These three categories are considered separately below in outlining some recent advances in the study of phosphorus cycling and in considering their significance for South African limnology. This paper is not a comprehensive review, but is rather a summary of current concepts in phosphorus cycling which may be unfamiliar to limnologists not directly involved in this field.

Such a discussion of concepts raises problems in terminology. These result from limitations in analytical techniques which have hindered the identification and measurement of the variety of phosphorus fractions occurring in water. The consequence of this in South Africa has been that most limnologists have considered all soluble reactive phosphorus to be orthophosphate phosphorus (PO_4-P), in spite of the trend elsewhere (Rigler 1973) and more recently in South Africa (Howard-Williams and Allanson 1978) to recognize this fraction as being comprised of a variety of forms and hence to refer to it as soluble reactive phosphorus (SRP). These problems of terminology are described before proceeding to a discussion of phosphorus cycling.

TERMINOLOGY

Early analyses indicated that phosphorus levels in inland waters were low and it was only after the introduction of colorimetric analytical procedures in 1923 that the presence of a number of phosphorus fractions became apparent (Hutchinson 1957). The following categories of phosphorus were used by Hutchinson:

- Soluble phosphate phosphorus

- Acid soluble sestonic phosphorus

- Organic soluble (and colloidal) phosphorus

- Organic sestonic phosphorus.

However, the techniques used to separate seston from the soluble phosphorus fractions varied, resulting in confusion in the literature. This was highlighted by Rigler (1956) who duplicated the entire range of soluble organic phosphorus levels reported in the literature by varying the method of separating seston from Foerst centrifugation to filtration through 0,1µ membrane filters. He showed that if methods were standardized the percentage of soluble organic phosphorus remained constant for a variety of lakes; this implied that much of the variation in early data on phosphorus reflected variations in the separative techniques used.

Recently, use of 0,45µ membrane filters has become standard practice in limnological research. This is reflected in the definitions of phosphorus fractions measured in inland waters. These fractions were outlined in the review by Rigler (1973) as follows:

- Soluble reactive phosphorus (SRP) refers to the value when membrane filtered water is analysed by one of the variants of the molybdenum blue technique. This term implies neither that the orthophosphate measured was in solution before addition of the reagents nor that the intensity of the blue color is exclusively a function of orthophosphate concentrations rather than that of interfering ions. When orthophosphate phosphorus (PO$_4$-P) is used it will not refer to the results of chemical analyses but to free orthophosphate in solution, the concentration of which is assumed to be as yet unmeasurable in the trophogenic zone of most lakes.

- Soluble phosphorus (SP) refers to the value obtained when membrane filtered water (0,45µ) is analysed after being digested with an oxidizing acid solution.

- Soluble unreactive phosphorus (SUP) is the difference between SP and SRP.

- Total phosphorus (TP) is obtained by analysing whole lake water after acid digestion. It is assumed that the values obtained by this technique are indicative of the true phosphorus content of the sample.

This terminology is based on analytical methodology and does not refer to definite phosphorus compartments that are equivalent to morphologically and chemically distinct components of lake water (Rigler 1973). This is especially true of the SRP, which is frequently regarded as being synonymous with PO_4-P, particularly by South African limnologists. There is however increasing evidence which indicates that SRP includes forms which are not PO_4-P.

As early as 1966 it was suggested that SRP was greater than PO_4-P (Rigler 1966) and this has been confirmed in Canada (Lean 1973, Peters 1978) and New Zealand (Paerl and Downes 1978). Similarly, SUP could be a considerable underestimation of soluble organic phosphorus in inland waters.

The difference between PO_4-P and SRP is due to the hydrolysis of soluble organic phosphorus and colloidal phosphorus during the acid conditions of the molybdate blue procedure (Paerl and Downs 1978). Although characteristic of all inland waters (Rigler 1973), soluble organic phosphorus and colloidal phosphorus are of biological origin and are thus more abundant in systems where primary productivity is high (Lean and Rigler 1974).

There are therefore limitations in the use of data derived from analytical techniques that are currently in use. This limitation will also apply to predictive modelling of the relation between phosphorus loading and changes in lake metabolism where it is necessary both to identify discrete phosphorus forms of biological importance and to measure the fluxes between them (Lean 1973).

PHOSPHORUS CYCLING IN WATER

Development of phosphorus cycling models

While PO_4-P is the only form in which phosphorus is freely available for uptake by the primary producers in inland waters, it represents only one of the important phosphorus compartments in water.

Before radio-isotopes were introduced into limnological research, phosphorus cycling in inland waters was studied by monitoring temporal and vertical changes in the concentrations of organic or inorganic phosphorus. As early as 1939 it was postulated that the dissolved phosphorus could be in colloidal form rather than in solution and that the sestonic phosphorus consisted of both organic and inorganic forms (Able 1939 cited in Hutchinson 1957). However, analytical limitations prevented direct investigation of the rates of flux between the phosphorus compartments, or of the mechanisms involved (Rigler 1956).

The pioneering ^{32}P tracer studies have been reviewed by Hutchinson (1957). These involved the addition of $^{32}PO_4$-P to lakes and made a major contribution to the understanding of phosphorus cycling in inland waters, emphasizing the extreme mobility and rapid exchange kinetics of phosphorus between soluble and particulate (solid) compartments. Similar techniques were then applied to isolated surface water samples to study the exchange kinetics between soluble and particulate phosphorus fractions (Rigler 1956). These kinetics often conform to

those predicted by a two-compartment (monophasic) exchange model in which ^{32}P in solution decreases exponentially to an equilibrium level, and are explained by postulating the following simple exchange of PO_4-P between a soluble and a particulate compartment:

SOLUBLE

$$\boxed{PO_4\text{-}P} \rightleftharpoons \boxed{PARTICULATE\ P}$$
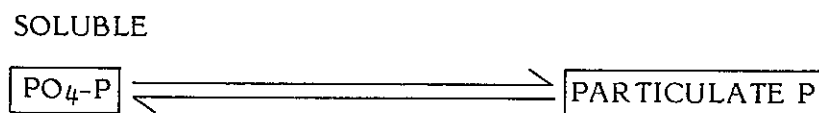
(Rigler 1956)

In contrast, Chamberlain (1968, cited in Rigler 1973) reported occasional ^{32}P uptake kinetics which were better described by a diphasic exponential equation. He demonstrated that, in a short time after addition of tracer to the lake water, a fraction of ^{32}P in solution had become something other than PO_4-P. This was confirmed by Rigler (1968) who postulated a second soluble phosphorus compartment, which he could not identify, to explain the diphasic uptakes, as follows:

SOLUBLE

$$\boxed{PO_4\text{-}P} \rightleftharpoons \boxed{PARTICULATE\ P}$$
$$\updownarrow$$
$$\boxed{\begin{array}{c}UNIDENTIFIED\\FRACTION\end{array}}$$
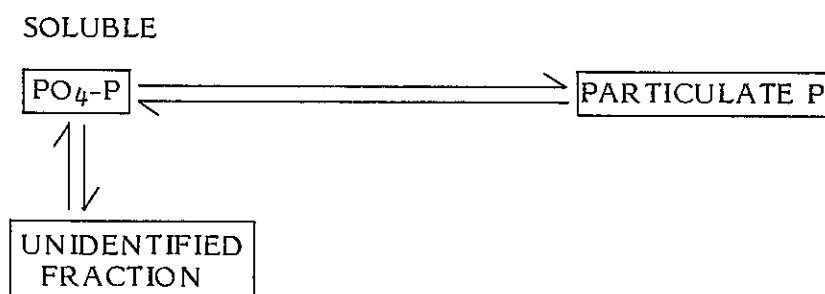
(Rigler 1968)

By combining ^{32}P uptake experiments with gel-filtration analysis, Lean (1973) identified four phosphorus fractions in lake water which were particulate phosphorus plus three soluble phosphorus fractions. The soluble fractions were PO_4-P, a low molecular mass organic phosphorus compound, and a macromolecular colloidal phosphorus compound. The soluble molecular fractions were shown to be of biological origin and formed important components of the following four-compartment model proposed by Lean:

SOLUBLE
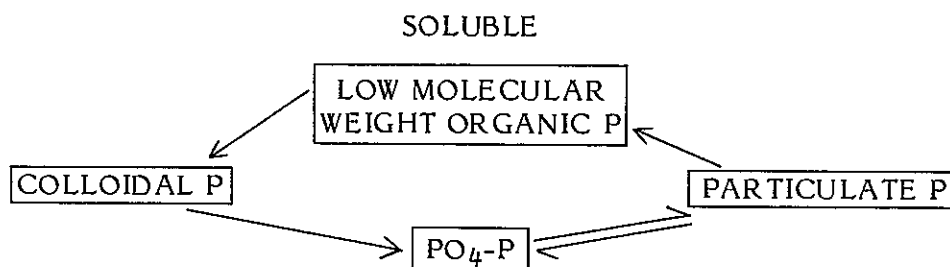
(Lean 1973)

Under natural conditions the number of recognizable compartments comprising the particulate phosphorus is large and it has been suggested that Lean's model requires modification to account for this diversity (Norman and Sager 1978, Halfon et al 1979). At least two different rates of exchange with the particulate phosphorus compartment appear to be necessary to make the model consistent with experimentally observed diphasic phosphorus curves, one comprising the smaller organisms through which phosphorus cycles rapidly, and the other comprising the larger organisms through which phosphorus cycles slowly (Rigler 1973):

SOLUBLE

| LOW MOLECULAR |
| WEIGHT ORGANIC P |

PARTICULATE P

| COLLOIDAL P |

| NANOPLANKTON |

| NET PLANKTON |

PO_4-P

(Lean 1973 modified by
Norman and Sager 1978)
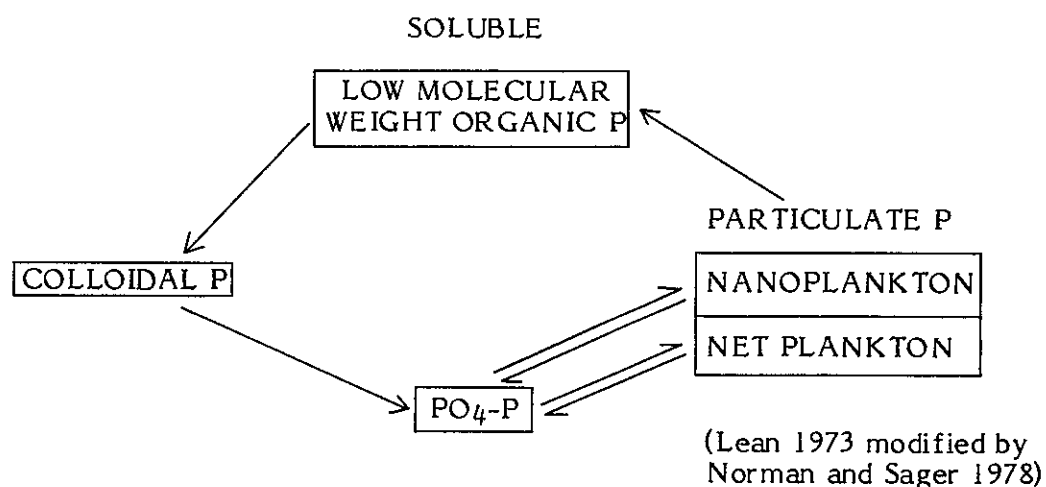
Applicability of five-compartment phosphorus model

The general applicability of Lean's four-compartment model has not been confirmed. Norman and Sager (1978) have reported infrequent diphasic ^{32}P uptake curves in Lake Michigan associated with rapid decreases in phytoplankton, and diphasic kinetics have been shown to be more common during the more productive summer months in Canadian lakes (Lean and Rigler 1974). In Midmar Dam a total of twelve ^{32}P uptake experiments were conducted during the summer of 1978-79 all of which could be described by a single exponential equation (Twinch 1980). This does not imply that the uptake kinetics were monophasic, but rather that differences in exchange rates were not great enough to be detected using present methods (Norman and Sager 1978). The applicability of Lean's model cannot therefore always be assessed purely on the ^{32}P uptake kinetics.

Lean's model was formulated specifically to describe diphasic phosphorus exchange which characterized some Canadian lakes during the summer. A study of soluble phosphorus fractions in New Zealand lakes (Downes and Paerl 1978) revealed only two distinct fractions - PO_4-P, and a reactive high molecular mass (>5000) fraction corresponding to colloidal phosphorus in Lean's model. Similar results have been obtained in fractionated Midmar Dam water (Twinch 1980). Thus the low molecular mass compound identified by Lean (1973) may not be characteristic of all freshwaters. The presence of only three distinct fractions involved in phosphorus exchange in Midmar Dam indicates that Lean's model is not generally applicable to inland waters in South Africa, but further studies, including the investigation of more productive systems are necessary before this can be categorically stated.

Relative importance of biological components

While rapid exchange of ^{32}P between seston and water has frequently been demonstrated, the relative importance of the particulate components in these exchanges is not clear. The importance of the phytoplankton in this exchange appears to vary considerably between lakes. In Toussaint Lake (Canada) Rigler (1964) showed that only 5 percent of the ^{32}P taken up by seston could be accounted for in the zooplankton and larger phytoplankton while 68 percent was taken up by ultraplankton (bacteria). Peters (1975) suggested that the converse was true in Lago Maggiore (Italy) where ^{32}P uptake rates did not correlate with estimates of bacterial populations but did correlate with estimates of phytoplankton populations.

Lean and Nalewajko (1976), using axenic cultures of phytoplankton, showed that rapid phosphorus turnover and the excretion of colloidal phosphorus and low molecular mass organic phosphorus can occur in the absence of bacteria. However, phosphorus retention and excretion varied amongst the species studied, supporting the view that a single particulate phosphorus compartment cannot adequately describe a diverse phytoplankton population. Comparable studies on bacteria have not been undertaken, but it seems probable that they would be characterized by a similar variability in soluble phosphorus exchange.

Zooplankton can also form an important component in the phosphorus cycle but, because of their secondary and tertiary trophic status, are probably more important in the regeneration of soluble phosphorus from particulate phosphorus than in direct uptake of soluble phosphorus. Following quantitative studies of phosphorus release by zooplankton, Rigler (1973) concluded that direct release of phosphorus from ultraplankton and excretion by zooplankton are equally important in regenerating phosphorus in the trophogenic zone of eutrophic lakes during summer stratification. The forms in which phosphorus is released by zooplankton have been studied (Peters and Lean 1973) and it appears that approximately 90 percent of the released soluble phosphorus is PO_4-P while the balance is made up largely of colloidal phosphorus.

The importance of abiotic particles in the exchange of phosphorus between particulate and soluble forms is not well understood. Paerl and Lean (1976) used autoradiographic techniques to study the movement of phosphorus between algae, bacteria and abiotic particles in Heart Lake, Canada. Bacteria and phytoplankton were labelled most rapidly but after two hours tracer was also evident on detrital aggregates harbouring bacteria. In the South African context, where many fresh waters are characterized by high levels of suspended inorganic material, the rôle of abiotic phosphorus exchange may possibly be more important. The availability of silt-associated phosphorus to phytoplankton is thought to be a major factor in some turbid waters in the Amazon River system (Grobbelaar in press). A similar situation is likely in turbid waters in South Africa, either by direct exchange of PO_4-P by the clay particles, or by bacteria harboured on silt particles as shown by Paerl and Lean (1976).

It must be concluded that little is known about the specific rôles of various biotic and abiotic factors in the phosphorus exchange processes outlined in Lean's model.

Rôle of phosphatase enzymes

Another process involved in phosphorus cycling in inland waters is enzymatic hydrolysis of phosphorus compounds to PO_4-P. Phosphatase enzymes are produced by bacteria, algae and zooplankton and provide a means of converting organically bound phosphorus into available PO_4-P in the water. Phosphatase production is related to the levels of available phosphorus in the water and consequently production is highest under phosphorus limiting conditions while being repressed when phosphorus availability is high (Fitzgerald and Nelson 1966). Jansson (1976 and 1977) concluded that in subarctic lakes seston constitutes an important phosphorus source as a result of phosphatase activity. In systems characterized by high silt loads but low soluble phosphorus levels, the rôle of phosphatase could be important. The full implications of the phosphatases in the phosphorus cycle are not clear, however, and their relative importance in comparison with other phosphorus cycling mechanisms has not been measured.

Rôle of the littoral zone

Littoral vegetation is an important component of the phosphorus cycle in many inland waters. Hutchinson and Bowen (1950) demonstrated both liberation of phosphorus into the epilimnion and uptake of phosphorus from the epilimnion by the littoral vegetation. In systems where extensive macrophyte beds can establish, such as Swartvlei (Howard-Williams and Allanson 1978) and some pans on the Pongolo River floodplain (Breen unpublished data), they have been shown to play a significant rôle in the phosphorus cycle. Biological production in the littoral zone can be much higher than in open water; in Swartvlei the annual mean production of the phytoplankton is 74 mg C m^{-2} day^{-1} while the combined productivity of littoral algae and hydrophytes is 3114 mg C m^{-2} day^{-1} (Howard-Williams and Allanson 1978). Thus a small area of littoral vegetation can have a large influence on the overall metabolism of a water body.

In the majority of South African impoundments the establishment of extensive macrophyte beds is prevented both by marked seasonal and shorter term fluctuation in water levels and by high water turbidity. Consequently the littoral zone may only be of minor importance in phosphorus cycling in these water bodies.

The rôle of phytobenthos in the littoral zone is little understood. In the P K le Roux Dam, phytobenthos is thought to be an important food source for benthic rock-scraping fish and to be more widely grazed than the phytoplankton (Hart pers comm). Furthermore, in contrast to the rooted hydrophytes, the phytobenthos can to some extent accommodate fluctuations in water level and may therefore be important in relation to phosphorus cycling. This aspect requires further investigation in the South African context.

PHOSPHORUS EXCHANGE BETWEEN SEDIMENT AND WATER

Since the classical study of mud-water nutrient exchange in Lake Windermere (Mortimer 1941), much attention has been given to the rôle of sediments in phosphorus cycling in inland waters. The exchange processes have been shown to be complex and the rates and extents of the phosphorus fluxes across the sediment-water interface vary with sediment structure and nutrient status (Syers et al 1973). Considerable differences may therefore be expected between water bodies. Large deep lakes are characterized by substrates of deep organic gytta (Hesse 1973), while in many impoundments the substrate consists of drowned terrestrial soil overlain by a layer of recently deposited sediment of thickness varying with the age of the impoundment.

The mechanisms which may influence rates and directions of phosphorus fluxes in South African inland waters are described in this section. For further information on these mechanisms please refer to Stumm and Leckie (1970), Golterman (1973) and Syers et al (1973).

Phosphorus uptake and release by sediments

Most lake sediments are capable of adsorbing large amounts of PO_4-P from the water when concentrations in solution are increased, and desorbing some PO_4-P when concentrations in the water are reduced by biological uptake (Golterman 1973). The result is a dynamic equilibrium similar to that first proposed by Hayes and Phillips (1958) whereby a large proportion of the total pool of exchangeable phosphorus in a lake is bound by the sediments (Stumm and Leckie 1970).

Inorganic clay minerals, because of their large adsorptive surfaces, play an important rôle in the exchange of PO_4-P across the sediment-water interface (Syers et al 1973). This exchange is further complicated by the presence of organic matter, both living and dead, because of its varied exchange characteristics. Furthermore, since bacteria are major contributors to the process of nutrient regeneration, their activity is often of more significance than inorganic exchange reactions, particularly in systems of high productivity (Hesse 1973). The relative importance of processes such as inorganic exchange and release associated with bacterial activity is dependent upon the proportions of inorganic and organic material in the sediment, the nutrient status of the sediments and overlying water, the stability of the mud-water interface, the rate of sedimentation and the nature of the sedimenting material. The implication of all this is that as impoundments become eutrophic bacterial processes may be expected to become more important. Under South African conditions however this may be counteracted to some extent by the high inorganic silt loads entering impoundments.

The ability of lake sediments to buffer changes in PO_4-P levels in the water explains the frequent observation that freshwater systems can tolerate substantial loading with PO_4-P without great increase in the dissolved phosphorus. However, with the heavy and prolonged loading of many eutrophic systems, the buffering of the sediments is insufficient to maintain stable PO_4-P levels. As the degree of saturation of sediments increases so does their potential to release phosphorus (Schindler 1976).

The influence of dissolved oxygen concentration at the sediment-water interface on PO_4-P fluxes was first reported by Mortimer (1941). Anaerobic conditions favoured the release of PO_4-P from sediments through their influence on the solubility of iron. Subsequently phosphorus release from sediments came to be regarded as a predominantly anaerobic phenomenon. Aerobic release has however also been demonstrated, but at markedly slower rates, and has therefore been regarded as being of less importance (Kamp Nielsen 1974, Syers et al 1973, Viner 1975).

The $Fe-PO_4$-S and the $Ca-CO_3-PO_4$ systems have been implicated in the vertical exchange of PO_4-P in different types of water bodies (Golterman 1973). In the former system PO_4-P co-precipitates as $FePO_4$ or is adsorbed into $Fe(OH)_3$ under aerobic conditions, but under anaerobic conditions $Fe(OH)_3$ is made soluble by the reduction of ferric iron at low redox potential, which results in the release of PO_4-P into the water. In hard water the Ca^{++} content of the water can influence phosphorus content through precipitation of calcium phosphates or through co-precipitation of phosphates with $CaCO_3$ precipitate (Stumm and Leckie 1970). PO_4-P adsorption-desorption interactions with the clay fractions, which are pH dependent, are also important in the overall exchange of phosphorus between sediments and overlying water (Syers et al 1973).

While recent evidence indicates that the iron-phosphate interaction is not as universally important in phosphorus release as previously thought, Golterman et al (1976) have suggested that aerobic phosphorus release plays a dominant rôle in the chemistry of lakes and impoundments. The evidence is largely from studies of eutrophic systems and shows that aerobic phosphorus release is related to mineralization processes where bacterial breakdown of organic phosphorus results in the release of PO_4-P into the water (Lee 1976). This process is enhanced by a rapid rate of organic sedimentation.

The importance of phosphorus loading from sediments has been demonstrated in rehabilitation studies in eutrophic systems which have had nutrient loads reduced through management. Responses have varied between marked improvement (Edmondson 1972) and no apparent improvement (Larsen et al 1975), the latter being due to phosphorus loading from the sediments. The duration and intensity of previous loading is important in this regard and the longer the loading with high levels of phosphorus, the more extensive the deposition of phosphorus-rich sediments and consequently the longer the recovery time (Schindler 1976). In South Africa the residence time of most impoundments is relatively short compared with that of lakes, and rapid flushing may result in more rapid recovery.

The occurrence of internal phosphorus loading from sediments in oligotrophic systems has received less attention and its importance has not been established. Evidence of significant phosphorus loads from the sediments has been obtained under aerobic conditions in Midmar Dam (Twinch and Breen 1978a). In view of the well established concept of a phosphorus equilibrium between sediment and water and the resultant PO_4-P releasing potential of the mud during periods of PO_4-P depletion in the water, this could be important in the shallow, well mixed impoundments in South Africa.

Anaerobic conditions, and associated increases in the rate of phosphorus release from the sediment, occur in the hypolimnia of lakes during periods of marked stratification and result in phosphorus accumulation below the thermocline. The phosphorus released does not reach the epilimnion and is therefore not available to the phytoplankton at the time of maximum demand during the summer (Golterman et al 1976). A similar phenomenon has been shown in the Swartvlei estuary where salinity gradients prevent PO_4-P released into the anaerobic zone from reaching the phytoplankton (Howard-Williams and Allanson 1978). The release of PO_4-P under anaerobic conditions may therefore not be as important to primary production in the epilimnion as was previously thought because, as stratification breaks down and the hypolimnion again becomes aerobic, a large proportion of the released PO_4-P would be fixed by the oxidized sediments before it is taken up by primary producers. Conversely PO_4-P release from sediments in contact with a well mixed epilimnion may be more important than was previously thought. This requires investigation as there are implications in South Africa where the majority of impoundments are shallow water bodies (Noble and Hemens 1978) and consequently have large areas of oxidized surface sediments.

Phosphorus compounds released from sediments have not been well characterized. It seems likely, particularly when decomposition rates at the mud-water interface are high, that the soluble phosphorus released could be in the form of colloidal phosphorus, low molecular mass organic phosphorus or PO_4-P. The relative proportions of these under varying conditions could be of considerable ecological significance because of their differences in exchange kinetics with the sediments and their rôle in phosphorus cycling in the water.

Influence of sedimentation

Lake sediments are formed as a result of the deposition of particulate material from the water column. This material can be of either autochthonous or allochthonous origin and consists of both living and dead organic matter as well as inorganic matter. The composition of the allochthonous material depends on the geology, soils, vegetation, land-use practices and domestic and industrial development in the drainage basin, while the composition of the autochthonous material is largely dependent on the morphometry, trophic status and chemistry of the water body.

The continuous processes of sedimentation and resuspension result in ever changing conditions at the mud-water interface, and the rate and extent of the sediment deposition reflects limnological conditions at the time. In this regard bioturbation can result in homogenization of surface sediments, and this can influence exchange of nutrients between sediment and water (Petr 1976). However the development of benthic faunal communities is dependent upon a fairly stable mud-water interface. The processes of sedimentation and resuspension, common in South African impoundments in particular, probably limit the extent of bioturbation by benthic fauna. Little is known of the effects of benthic feeding fish on the sediment-water interface but this could be of significance in South Africa.

Associated with the changes which occur at the sediment-water interface are changes in the phosphorus status, and thus in the exchange kinetics between the sediments and the overlying waters. As has already been discussed, the most obvious demonstration of this has been in the failure of some rehabilitation programmes to improve the trophic status of eutrophic systems because of phosphorus release from the highly enriched surface sediments (Schindler 1976).

In contrast to most lakes, impoundments are characterized by substrates of drowned terrestrial soil which are overlain by recent deposits of lake sediment of differing thickness. Most soils have the ability to fix or retain PO_4-P (Russell 1961) and even under waterlogged conditions this property is maintained (Syers et al 1973, Furness and Breen 1978, Twinch and Breen 1978b). Thus at the time of construction all impoundments are characterized by PO_4-P fixing substrates. If the subsequent development of surface sediments is due largely to organic deposition, the PO_4-P fixing potential at the mud-water interface will be reduced. When the surface layer becomes thick enough to form an effective barrier between the water and the original soil the rôle of the substrate may be shifted from being a sink to being a source of phosphorus. This occurs more readily in eutrophic systems. Alternatively, in systems where sediment formation is due largely to eroded inorganic material the PO_4-P fixing capacities of the substrate may be maintained or even enhanced. Results supporting this suggestion have been obtained in the Maumee River basin (Green et al 1978, McCallister and Logan 1978) and may be relevant to the turbid systems in South Africa. However, sediment formation is usually the result of a combination of varying proportions of both organic and inorganic sedimentation.

If exchange of phosphorus between sediment and water is to be taken into account in the future management strategies used in South Africa, much closer attention will have to be given to the transformations which occur at the mud-water interface following the construction of impoundments and in older impoundments being subjected to excessive nutrient loading.

Exchange of soluble phosphorus fractions with the sediments

The presence of at least three soluble phosphorus fractions, all of which are at least partially biologically available, has been established in inland waters (Lean 1973, Peters 1978). However their comparative exchange kinetics with lake sediments are not understood.

Eisenreich and Armstrong (1978) showed that aluminium hydroxide effectively removes PO_4-P from lake water while having very little influence on soluble organic phosphorus, indicating that the sediment-water exchange kinetics of these two fractions differ widely. This suggests that soluble phosphorus fractions exhibit markedly different exchange kinetics from lake sediments. Support for this has been obtained during studies in Midmar Dam which showed that $^{32}PO_4$-P exchanged freely with intact sediment cores while colloidal ^{32}P did not (Twinch 1980).

This observation could be of significance in the phosphorus cycle in inland waters. As already discussed, lake sediments are characterized by high PO_4-P fixing capacities. Therefore any mechanism whereby phosphorus availability in the water overlying the sediment can be increased would influence organisms, particularly algae and bacteria, living under conditions where the growth rate is limited by phosphorus availability. One possible mechanism is the biological production of colloidal phosphorus and organic phosphorus, which are not fixed by sediments, via the pathways envisaged by Lean (1973). Enrichment experiments in isolated columns of water in Midmar Dam have provided indirect evidence for this (Twinch 1980). In view of the implications such a finding would have in relation to phosphorus cycling the whole concept should be investigated in more detail on a series of systems providing a range of trophic levels.

Differential uptake of soluble phosphorus fractions by sediments also has implications when assessing the impact of external phosphorus loads on freshwater bodies. Peters (1978) showed that the soluble phosphorus load entering a Canadian lake consists largely of PO_4-P and colloidal phosphorus (each contributing approximately 40 percent of the total) while traces of lower molecular mass organic fractions were also present. If this is typical of river inputs, it is possible that a large proportion of the PO_4-P may be rapidly fixed by the sediments while the colloidal phosphorus may remain in solution, thereby contributing significantly to the available phosphorus via the exchange pathways outlined in Lean's model.

ALLOCHTHONOUS PHOSPHORUS LOADING

River loading

The phosphorus inputs into lakes and impoundments via river inflows are a major factor in eutrophication and result predominantly from human activities (Toerien 1977). Reduction of this load has been shown to be effective in reducing primary production in some lakes. Models for the prediction of permissible loads have been developed. Of these the Vollenweider model has been adopted for setting standards for prevention of excessive loads of phosphate into South African impoundments (Toerien 1977). This model can be used to predict the phosphorus concentration in water bodies from simple parameters such as input and output rates, residence time and lake morphometry (Rigler 1973). In this model TP is the form selected to describe the load.

Walmsley et al (1979) have developed an empirical model relating phosphorus loading described as SRP and chlorophyll concentrations in South African impoundments, which appears to have a greater predictive capacity than the Vollenweider model. The new model, which is valid in impoundments where phosphorus is growth limiting, is also designed to compensate for variations in turbidity. Since the model ignores processes occurring within the impoundments, research is required to verify the observed relationships and to assess the reliability of its predictions.

The TP in the inflow to impoundments is made up of some or more of the following phosphorus fractions - crystalline, occluded, adsorbed, particulate organic, soluble organic and soluble inorganic. Suitable analytical procedures are not available for separate determination of these fractions (Schaffner and Oglesby 1978), as has already been discussed in the section dealing with terminology.

It is generally believed that the SRP represents a biologically available fraction of TP (Walton and Lee 1972, Lean 1973), but some of the SUP is also available to the phytoplankton via the exchange processes outlined in Lean's model (Lean 1973) and through the action of phosphatase enzymes (Berman 1970). Moreover, some of the organic particulate phosphorus could be transformed into more available soluble phosphorus forms during decomposition.

Conflicting opinions have been expressed about the availability of suspended inorganic phosphorus. According to Schaffner and Oglesby (1978) "there seems to be no valid rationale, or published evidence, to support the contention that all, or even a significant fraction, of phosphorus bound by soil particles, or in crystalline form, is of potential biological availability when introduced into lakes", while other workers have reported varying degrees of availability of suspended inorganic phosphorus (Green et al 1978, Grobbelaar in press). This aspect has particular relevance in the numerous turbid impoundments of South Africa.

There is also evidence that PO_4-P retention may be an important characteristic of suspended inorganic particles. The involvement of inorganic clay particles in PO_4-P retention has frequently been demonstrated (Golterman 1973, Shukla et al 1971, Syers et al 1973), and Green et al (1978) and McCallister and Logan (1978) showed that PO_4-P adsorption maxima of composite suspended samples and bottom sediments in the Maumee River basin were higher than those for the surface soils from which they were derived. This implies that PO_4-P in the river water could be removed from solution by the silt.

In view of the problems surrounding the characterization of phosphorus loads, Schaffner and Oglesby (1978) have adopted the term biologically available phosphorus (BAP) which, by their definition, includes SRP, SUP and labile phosphorus. Labile phosphorus is the fraction of phosphorus associated with silt, which desorbs into an aqueous solution as determined by the adsorption isotherm method of Taylor and Kunishi (1974). In a comparison of TP and BAP in run-off entering thirteen New York lakes, it was shown that TP was usually about twice the BAP concentration and labile phosphorus contributed about 5 percent of the BAP (Schaffner and Oglesby 1978).

Peters (1978), using ^{32}P tracer experiments in combination with gel filtration analysis, attempted to characterize the soluble phosphorus fractions of the phosphorus load entering Lake Memphremagog via river inlets, and estimated that approximately 8 percent of the TP consisted of PO_4-P with an equivalent amount of colloidal phosphorus and traces of lower molecular mass organic phosphorus. The availability of particulate phosphorus and dissolved organic phosphorus were

estimated and incorporated with PO_4-P to give a rough index of available phosphorus. The relationship between TP and available phosphorus was highly variable, particularly at higher phosphorus loading rates, and Peters concluded that further studies should concentrate on attempting to quantify available phosphorus in rivers with high TP loads. At low loading rates the available phosphorus represented a large proportion of the TP.

Of particular importance in turbid waters of South Africa is the contribution of silt load in river inputs to TP. Silt load is related to turbulence and varies temporally. The calmer conditions provided by impoundments result in rapid sedimentation of the silt transported by the river and the bulk of the sediment load is soon deposited on the substratum. A large fraction of the TP entering an impoundment via a silt-laden river probably remains in suspension for too short a period to contribute significantly to biological uptake. Bottom deposits do however have the potential to exchange phosphorus with the overlying water either directly or by resuspension; sedimentation of silt may therefore be an important factor in assessing the overall impact of phosphorus loads. This must be separated from the concept of TP load as used in the Vollenweider model because the exchange processes are complex and dependent on many factors.

The use of TP to define phosphorus loads via river inputs will be of dubious value in South African impoundments. The amount of available phosphorus is well below the TP concentration, and the phosphorus binding potential of the silt load may be a more important consideration if it is associated with other sources of PO_4-P enrichment.

Atmospheric loading

The importance of atmospheric fallout as a source of phosphorus in inland waters has been recognized (Peters 1977, Toerien 1977). A range of fallout values reported from around the world compiled by Toerien (1977) showed that levels recorded in Pretoria were among the highest. The major source of phosphorus in atmospheric fallout is from dust generated over land from wind erosion of soil, and from urban and industrial atmospheric contamination. The rôle of atmospheric inputs in South African impoundments generally has not been studied, but the influence of atmospheric pollution should not be overlooked.

The value of TP determinations in atmospheric fallout may be limited in relation to the control of primary production in fresh waters for reasons similar to those discussed under the section on river loading. The biological availability of phosphorus estimated as SRP in the fallout has varied between 7 percent and 32 percent in North America (citations in Peters 1977). However SRP measurements may not adequately reflect the availability of atmospheric phosphorus to algae because Peters (1977), using a modification of the Rigler radiological bioassay (Rigler 1966) to estimate availability of atmospheric phosphorus, found that an average of 38 percent of the TP was biologically available.

CONCLUSIONS

Phosphorus is a major factor in eutrophication (Rigler 1973) and this accounts for the attention it has received in limnological studies. Despite this a number of problems which are fundamental to understanding phosphorus cycling, and consequently to the setting of limits to loading, remain unresolved. Since South Africa has mainly shallow, monomictic impoundments which are often subject to silt-laden inflows, the components within the phosphorus cycling system may well be ranked in a different order of importance from those in deeper, cool, temperate, clear lakes where most studies have been done. Therefore it is necessary to study phosphorus cycling in South African impoundments. At the same time, attempts should be made to resolve the differences in terminology and techniques for measurements so that data produced by different research groups can be compared directly.

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