The Role of Phosphorus in the Eutrophication of Receiving Waters: A Review

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ABSTRACT

Phosphorus (P) is an essential element for all life forms. It is a mineral nutrient. Orthophosphate is the only form of P that autotrophs can assimilate. Extracellular enzymes hydrolyze organic forms of P to phosphate. Eutrophication is the overenrichment of receiving waters with mineral nutrients. The results are excessive production of autotrophs, especially algae and cyanobacteria. This high productivity leads to high bacterial populations and high respiration rates, leading to hypoxia or anoxia in poorly mixed bottom waters and at night in surface waters during calm, warm conditions. Low dissolved oxygen causes the loss of aquatic animals and release of many materials normally bound to bottom sediments including various forms of P. This release of P reinforces the eutrophication. Excessive concentrations of P is the most common cause of eutrophication in freshwater lakes, reservoirs, streams, and headwaters of estuarine systems. In the ocean, N becomes the key mineral nutrient controlling primary production. Estuaries and continental shelf waters are a transition zone, where excessive P and N create problems. It is best to measure and regulate total P inputs to whole aquatic ecosystems, but for an easy assay it is best to measure total P concentrations, including particulate P, in surface waters or N/P atomic ratios in phytoplankton.

Society normally wishes to maintain a reasonable level of productivity in our lakes, rivers, and estuaries and this requires the presence of modest levels of mineral nutrients. Historically, many of these water bodies have progressed from low productivity or oligotrophic settings to productive mesotrophic conditions to overenriched hypertrophic or eutrophic conditions. The results are often algal or cyanobacterial mats, anoxia, and fish kills leading to greatly reduced biodiversity (e.g., Carpenter et al., 1969; Jaworski, 1981; Likens, 1972). The relationships among P input, primary production, dissolved oxygen, biodiversity and trophic status are shown conceptually in Fig. 1. From the human perspective it is desirable to prevent or minimize eutrophication of receiving waters for aesthetics and to maintain the productivity of animal species preferred for recreation and commercial fisheries. Examples of the overenrichment of receiving waters with nutrients have occurred frequently all over the world. Questions that most often arise with respect to eutrophic conditions include: (i) Which nutrients are the most frequent cause of this eutrophication?, (ii) What nutrient concentrations are acceptable to society?, and (iii) Can we control eutrophication by limiting a key nutrient?

The causes and affects of eutrophication are very complex. The causes also vary somewhat for different aquatic systems. Thus, lakes and reservoirs behave somewhat differently than streams and rivers, while all of these differ from estuaries and other coastal waters. Any one system will also exhibit high variation in behavior both seasonally and interannually. These facts make it difficult to assess the eutrophication impacts of human interventions on the watershed and receiving waters and the mechanisms of these impacts. Changes over time due to human activities must be extricated from those due to variations in weather and, sometimes, due to natural successional processes.

Despite these complexities, there are some generalizations that can be made regarding eutrophication, based on the large body of scientific literature on this topic. It is my goal to summarize our knowledge of the role of P in the eutrophication of lakes, reservoirs, streams, rivers, and estuaries.

CHARACTERISTICS OF PHOSPHORUS

Phosphorus is an essential component of nucleic acids and many intermediary metabolites, such as sugar phosphates and adenosine phosphates, which are an integral part of the metabolism of all life forms. With the exception of trace emissions of phosphines from volcanoes, the P compounds found on the surface of the Earth are not volatile and transport through the atmosphere is primarily in dust or aerosols. Atmospheric

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Abbreviations: NASQUAN, National Stream Quality Accounting Network; NES, National Eutrophication Survey.

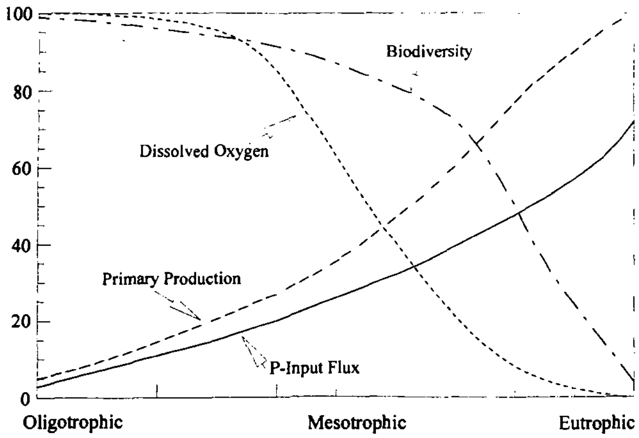

Fig. 1. Conceptualization of freshwater eutrophication.

flux rates are slow compared with those in surface waters (Hutchinson, 1957). With few exceptions surface waters receive most of their P in surface flows rather than in groundwater, since phosphates bind to most soils and sediments. The exceptions are where watersheds are of volcanic origin or where soils are water-logged and anoxic.

Phosphorus only occurs in the pentavalent form in aquatic systems. Examples are orthophosphate, pyrophosphate, longer-chain polyphosphates, organic phosphate esters and phosphodiesters, and organic phosphonates. Phosphorus is delivered to aquatic systems as a mixture of dissolved and particulate inputs, each of which is a complex mixture of these different molecular forms of pentavalent P.

However, P is a very dynamic, biologically active element. After these P inputs arrive in a receiving water, the particulates may release phosphate and organic phosphates to solution in the water column and various P compounds may be chemically or enzymatically hydrolyzed to orthophosphate, which is the only form of P that can be assimilated by bacteria, algae, and plants. Particulates may be deposited in the bottom sediments, where microbial communities gradually use many of the organic constituents of the sediments, ultimately releasing much of their P contents back to the water column as orthophosphate (Fig. 2). Hence, one should not assume that particulate P or dissolved organic P are inert in these aquatic systems because under appropriate conditions these forms of P can be converted to dissolved orthophosphate.

Once delivered to a lake, reservoir, or estuary, P is usually retained fairly efficiently by a combination of biological assimilation and the deposition of sediments and biota to the bottom sediments (Fig. 2). This efficient trapping of P inputs makes these systems sensitive to pollution with excessive amounts of P. If the system is oligotrophic (low primary production), the bottom waters will remain oxygenated throughout the year and most of this P will be stored in the bottom sediments. However, in eutrophic systems (excessive primary production), bottom waters often become anoxic during the growing season and even shallow waters may become diurnally anoxic overnight during warm, windless weather. When these conditions occur, much of this P in bottom sediments is released and diffuses back into the water column.

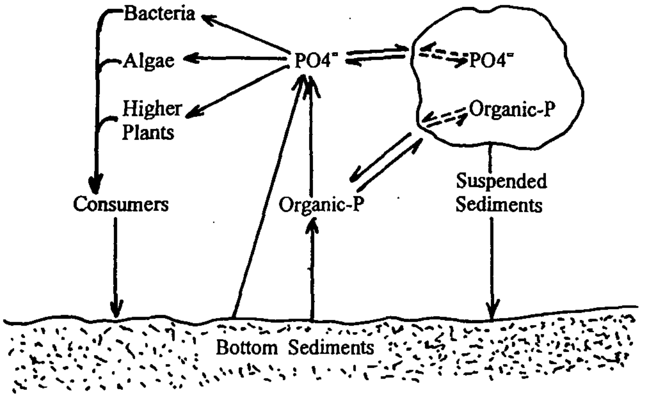

Fig. 2. Phosphorus cycle diagram.

EVIDENCE OF THE KEY ROLE OF PHOSPHORUS

Over time ecologists developed the concept that plant and bacterial growth in an aquatic system would ultimately become limited by the availability of an essential element. This would then constitute the limiting nutrient for that system at that time, and inputs of that nutrient could be managed to limit eutrophication. The term limiting nutrient has been used in somewhat different ways, sometimes meaning limiting the growth of the present population, sometimes the limitation of growth over time with species composition changes, sometimes limiting the ultimate primary or net production of an ecosystem (Howarth, 1988). Here I mean the ultimate limitation of ecosystem primary production.

The diatom *Cyclotella nana*, grown in P-limited chemostats could only reach biomass atomic ratios of C to P of 480 and N to P of 35 (Fuhs et al., 1972). This diatom had reached its limits of growth with the available P. In a series of bioassays of lake waters from the Great Lakes region of the USA using the Provisional Algal Assay Procedure (USDA, 1969), *Selenastrum capricornutum* cell number was found most often to respond to the addition of phosphate, rather than N (Maloney et al., 1972), indicating that most of these lake waters contained limiting concentrations of P. Mesocosm experiments in which 320 L of Minnesota or Oregon lake water were enclosed in clear plastic bags and then enriched with various nutrients, found that P was the primary controlling nutrient when positive responses were found (Powers et al., 1972). Mesocosm experiments in which 1000 to 4000 L of water from Lake Michigan were enclosed in clear plastic bags found that when P was added, silica was reduced to levels that limited algal growth but N was not (Schelske and Stoermer, 1972). They concluded that P was the limiting nutrient in Lake Michigan, but that silica was becoming limiting for diatoms.

Somewhat later, Lean and co-workers introduced the concept of an "index of P deficiency" (Lean and Nalewajko, 1979; Lean and Pick, 1981). They used radioactive tracers to measure the turnover times of dissolved orthophosphate in lake surface waters. High turnover rates (short turnover times) indicated more P limitation. This was further developed by measuring the ratio of C fixation to phosphate uptake under various conditions. Atomic ratios of C fixation to phosphate uptake varied from 1.2 to 206 depending on the degree of P deficiency prior to the measurement. If the algae had previously been highly P limited, they would fix a higher amount of C per P fixed.

A more direct measure of the key importance of P in lake eutrophication was the work at the Experimental Lakes research area in northwestern Ontario. Whole lakes were enriched with P for a period of years. These P-enriched lakes used atmospheric N and C for algal production and this resulted in significant increases in ecosystem primary production. Phosphorus additions triggered undesirable cyanobacterial blooms unless N was also added. However, if C or N were added, in the absence of P enrichment the effects were minor (Schindler, 1974, 1975, 1977). In another "whole lake" experiment, Lake

Washington near Seattle, WA, had been heavily loaded with nutrients in sewage outfalls for many years and had become severely eutrophic. Then, in 1963 the sewage effluent was diverted away from the lake. By 1969, chlorophyll in the summer and phosphate in the winter had declined to only 28% of previous years, but nitrate declined by only 10 to 20%. Lake Washington returned to a mesotrophic status. This was interpreted to mean that P was the key limiting nutrient (Edmondson, 1970). Another example is Lake Erie that began experiencing dissolved oxygen depletion due to eutrophication. In 1968, its annual P input was estimated to be 20 000 t and surface waters had an average of 22 μg of total P/L. By 1982, improved wastewater treatment had reduced annual P inputs to 11 000 t and surface waters averaged only 12 μg of total P/L (Boyce et al., 1987).

Many years of research on the effects of nutrient additions on lake productivity have led to a simple model that related algal biomass (Cl_a in mg/m^3) to total P input rates (L_p in g/m^2 d^{-1}), mean water depth (z in m), and outflow per unit of lake surface area (Q_s in m/acre); $Cl_a = (L_p/Q_s)/[1 + (z/Q_s)^{0.5}]$ (Vollenweider, 1976). This model fit the data from most of the lakes and reservoirs that had been studied in the world and accurately predicted trophic status based only on input rates of one nutrient (P). This was very strong support for the importance of P in the eutrophication of lakes. The Vollenweider model is still widely used by lake water quality managers, partly because of its simplicity. More sophisticated models often require more data than is available for a given lake.

If we accept that P is usually the limiting nutrient in lakes, the next question is what is the relationship between P enrichment and primary productivity. Prairie et al. (1989) analyzed data from 133 lakes for overall chlorophyll a relationships with total N and total P in the surface waters. The 133 lakes were selected from a larger set so that there was an even distribution of lakes that had ratios of total N to total P in surface waters, which varied from about 5 to 75. The LOWESS (a locally weighted regression) best fits for chlorophyll a concentrations in the various lakes were different functions for total P and total N. LOWESS regression slopes and intercepts shifted with changing N/P atomic ratios with slopes maximized and intercepts minimized at an N/P ratio of 22. Similar analyses for data from 1041 lakes, not selected for N/P ratios, found that the log of chlorophyll a vs. log of summer total P concentrations in surface waters was a sigmoid relationship that tended to flatten out at very high P concentrations (McCauley et al., 1989), rather than the linear one often assumed in the literature. It is apparent, therefore, that if a lake is already highly enriched with P, then adding more will have little effect, while adding N will bring about major additional eutrophication (e.g., Elser et al., 1990).

Thus, for lakes it seems quite clear that P is the nutrient most likely to be potentially limiting. But can we make the same statement about streams and rivers, reservoirs, or estuaries and coastal waters? Certainly, for estuaries and coastal waters the situation with respect to P-limitation of primary production is different. One of the first papers to conclude that there is a shift from P to N limitation as we move from fresh water to coastal waters was Ryther and Dunstan (1971). Their view has become widely accepted (e.g., review by Nixon, 1981). However, Hecky and Kilham (1988) have challenged the basis for this conclusion. They felt that the generality and severity of N limitation in the oceans had not been rigorously established. Most scientists have put their efforts into determining why this apparent shift from P limitation to N limitation occurs. Some of the more obvious reasons are the widely observed more efficient recycling of P in estuaries, the high losses of fixed N to the atmosphere due to denitrification in coastal waters (Nixon, 1981), and the role of sulfate in recycling P in coastal sediments (Caraco et al., 1989). They found that a strong positive correlation existed between primary production and sulfate concentration in lakes and estuaries. The increases in primary production with increased sulfate concentrate had a higher slope in systems with anaerobic sediments, such as most estuaries. Under these conditions some of the sulfate is reduced to sulfides, which might bind the ferrous ions that are also produced in anaerobic sediments, preventing the ferrous ions from diffusing to the sediment/water column interface. In less reduced sediments a layer of oxidized sediments at the surface of the bottom sediments, coated with ferric hydroxide, is believed to form a barrier that traps diffusing phosphate before it can reach the overlying water column. Regenerated phosphate is sufficient in Delaware Bay to supply almost all of the plankton P demand except during the spring bloom (Lebo and Sharp, 1992). Estuaries, especially at their upstream ends, are transition zones. Sometimes they are P limited in the spring, and N limited in the summer and fall (Fisher et al., 1992; Lee et al., 1996).

If lakes are primarily P limited, the oceans are primarily N limited, and estuaries are transition zones, how about streams, rivers, and reservoirs? Although they are perhaps the least understood with respect to nutrient limitation, one might reasonably assume that they behave somewhat like lakes. However, unlike many lakes, unless they are highly enriched with nutrients they do not undergo anaerobic periods and thus are unlikely to release high concentrations of phosphate from bottom sediments. If they have long enough retention times, a given volume of water moving downstream in a large river should behave much as though it were surface water in a lake or reservoir. Some differences include the "spiraling" of P down the channel (Newbold et al., 1981; Elwood et al., 1983). This is the result of uptake of P by attached bacteria and algae (periphyton) and vascular plants and the binding of P compounds in bottom sediments. When these P compounds are released back into the water column, either from bottom sediments or attached biota, they move further down stream, before becoming attached again as the P is cycled among the system components. Each such P movement downstream in the water column is referred to as a "spiral." One of the earliest experimental studies of P limitation in streams involved continuous addition for 8 d of diammonium phosphate to a stream in Michigan (D.L.Correll. 1958. Alteration of the productivity of a trout stream by the addition of phosphate. M.S. thesis. Michigan State University). This resulted in an increase from <8 μg total P/L to about 70 μg total P/L immediately downstream. Increased P concentrations were observed for 4 km downstream and periphyton concentrations on artificial substrates increased threefold. Stream water was diverted from a stream in British Columbia to a series of wooden troughs (Stockner and Shortreed, 1978). One was enriched with phosphate, one with nitrate, and one with both. Background dissolved phosphate was 3 μg P/L and the treatment raised this to 9 μg P/L. Chlorophyll a in periphyton increased over fourfold in those enriched with P. In Tennessee two reaches of a wooded stream were continuously enriched with 60 and 450 μg phosphate P/L for 95 d (Elwood et al., 1981). Background was about 4 μg of P/L. The result was increased periphyton chlorophyll, higher rates of decomposition of leaf litter, and increased populations of snails and leaf-shredding macroinvertebrates. When phosphate was continuously added to a stream on the north slope of Alaska to increase the concentration in the stream by 10 μg total P/L (Peterson et al., 1985), periphyton chlorophyll increased for 10 km downstream and the stream shifted from a heterotrophic to an autotrophic system. Effects ramified to increased bacterial activity and increases in the mean size of aquatic insects. These studies, although less numerous than was the case for lakes, strongly indicate that P is also a key element controlling productivity of streams and rivers.

Are streams and rivers in the USA often highly polluted with P? The answer is yes. A trend analysis of 381 riverine sites in the USA from 1974 to 1981 (Smith et al., 1987) found that the average total P concentration was 130 μg P/L, much higher than the levels attained in most of the fertilization experiments discussed above. Are these rivers improving with respect to P concentrations? Fifty of these sites, mostly in the Great Lakes and upper Mississippi drainages, had declines in P concentrations at 8.1% per year, mostly due to point source controls. Forty-three sites had increases at 7.4% per year, mostly due to increased diffuse sources of P.

An interesting study by Soballe and Kimmel (1987) analyzed data from 345 streams from the National Stream Quality Accounting Network (NASQUAN) and 812 lakes and reservoirs from the National Eutrophication Survey (NES). A canonical discriminant analysis of algal cell abundance and nutrient status found that natural lakes and rivers formed end member populations, while reservoirs were intermediate and overlapping. Multiple regressions of algal cell abundance vs. total P concentrations were significant, but different for all three categories of receiving water. Statistical models for each of the three types of water found that residence time, water depth, and water clarity were all important factors ($r = 0.7$, 0.6, and -0.4, respectively). Algal abundance per unit of P increased from rivers to reservoirs to natural lakes. Thus, the effects of P additions were most pronounced in lakes, primarily due to the long residence times typical of most lakes.

THE REDFIELD RATIO CONCEPT

A series of studies of laboratory cultures of algae and natural marine phytoplankton populations from the 1930s to the 1950s (Redfield, 1958) led to a concept that algae, under reasonably good growth conditions, will have an elemental composition with relatively defined atomic ratios. These ratios have become known as the Redfield ratios. For N to P this ratio is about 15 to 16:1.

Natural systems in which the atomic ratio of other elements to P is greater than the Redfield ratio are often assumed to be systems in which algal growth or biomass is ultimately limited by P or at least that algal growth rates in such systems will be greatly reduced. It is well to be aware, however, that these Redfield ratios are approximations and that the assumptions implied are complex and not necessarily universally applicable. Thus, a pure culture of an alga growing in a constant and saturating supply of nutrients will vary its P content per biomass fourfold depending only upon what stage of the algal cell division cycle is present (Correll and Tolbert, 1962). Also, the ratio of N to P in algae can vary approximately twofold due only to variation in either light intensity or light quality (Wynne and Rhee, 1986). The N/P ratio of algal cultures in stationary growth phase varied from 5 to about 20 under N or P limitation, respectively (Terry et al., 1985). The optimum ratio of N/P of seven algal species averaged 17, but ranged from 7 to 30 (Rhee and Gotham, 1980). Laboratory cultures have also been shown to have approximately the Redfield ratio of N/P when their growth is light limited (Tett et al., 1985) and phytoplankton are often light limited in productive estuaries like Chesapeake Bay (Gallegos et al., 1990). Likewise, fourfold shifts in N/P ratios were shown to be due to changing only temperature or light (Jahnke et al., 1986) and N/P ratios varied threefold between algal species when all other variables were held constant (Wynne and Rhee, 1986). Algal cultures subjected to P deficiency shift from N/P ratios of about 15 to about 100, then upon exposure to phosphate shift to ratios of <10 (Sakshaug and Holm-Hansen, 1977). Algal cultures that had been deprived of adequate P also exhibited a 26-fold increase in cellular P contents (primarily as polyphosphates) within 1 h of exposure to phosphate (Sicko-Goad and Jensen, 1976). These are examples of the phosphate "overplus phenomenon." Algae that have been severely limited by P deficiency for some time become physiologically poised to assimilate phosphate efficiently. If they are then exposed to a phosphate supply the algae take up unusually large amounts per cell. As the algal cell population begins to multiply, the P content per cell returns to a more normal level. Thus, one must indeed be very cautious in using the Redfield ratios. Nevertheless, the atomic ratios of nutrients in algal cells and in the water are often useful clues when attempting to understand algal-nutrient interactions and are often the only tool available (Hecky and Kilham, 1988). A good rule of thumb is not to attempt to use the Redfield ratio concept when dealing with algal populations exposed to significant changes in concentrations of available N or P in the last day or two, or with populations whose growth rates are light limited.

What the limiting nutrient concept, with respect to P, really means is that algal cells have an absolute requirement for a minimum amount of P per cell. This idea was first published by Droop (1974) and further developed into what is now called the Droop Model (Droop, 1977; Sakshaug and Holm-Hansen, 1977; Goldman et al., 1979; Wynne and Rhee, 1986). These studies have found that under P-limiting conditions, algal growth rates (cell division rates) are proportional to their P-content per cell.

THE PHOSPHATE BUFFER

It has often been claimed or assumed that particulate P inputs to receiving waters have relatively little effect on algal growth (e.g., Sonzogni et al., 1982), but this is not true. It has been widely observed that the patterns of dissolved orthophosphate concentrations in receiving waters can only be explained if dynamic interactions with both suspended particulate P and bottom sediments are taken into consideration (Hutchinson, 1957; Edmond et al., 1981; Boynton and Kemp, 1985; Jordan et al., 1991). For suspended sediments these dynamic equilibria between particulate and dissolved P became known as the phosphate buffer mechanism (Carritt and Goodgal, 1954; Froelich, 1988). Kinetically, there are two populations of particulate P, rapidly and slowly equilibrating populations. The rapid population equilibrates within a few minutes, while the slower population takes a few days. The rapid reaction is believed to be due to reactions at the surface of particulates, while the slow reaction involves solid-state diffusion within the particulates. When a river bearing suspended sediments discharges into a lake or estuary, the particulate P in the suspended sediments begins to re-equilibrate with the receiving water's dissolved P. If the concentration of dissolved P is low, P is released from the suspended sediments and vice versa.

Once the particulates have settled to the bottom of the receiving water the situation becomes more complex. Biological activity gradually mineralizes organic P and releases P into the pore water surrounding the particles in the bottom sediments. This dissolved P may diffuse into the overlying water, but the phosphate may become bound to the surfaces of particulates before it can reach this overlying water. Binding to aluminum and ferric hydroxides is particularly strong. If the pore water becomes anoxic, due to respiratory activity in the sediments, the ferric ions are reduced to ferrous and binding is weakened, allowing phosphate to diffuse more freely (Chen et al., 1973; Crosby et al., 1984; Hutchinson, 1957; Wauchope and McDowell, 1984). Thus, the exchange of P between the water column and bottom sediments often occurs at different rates seasonally or may only occur during such events as the spring turnover of lakes.

WHAT CONCENTRATION OF PHOSPHORUS IS ACCEPTABLE?

As discussed above, the response of lakes to P can be predicted with the Vollenweider model from the rates of total P input to the lake. However, it is often desireable to predict whether a system will have excessive productivity based on water column concentrations of P. For one thing, it is a lot easier to measure concentrations in the water than fluxes into a system. If we elect to use this approach to assessing eutrophication status, it is important to measure total P (including particulate P) in the surface waters. Dissolved orthophosphate in eutrophic surface waters is often turning over every few minutes (e.g., Correll et al., 1975). In such cases, the turnover rate of the available phosphate is so rapid, that the pool size is often misleading. Thus, total P is usually more meaningful. For example, in Chesapeake Bay during a period of increasing eutrophication in the 1970s, total P in surface waters during the summer and fall increased in a period of 8 yr from 20 to 50 μg/L to 150 to 200 μg/L, but dissolved orthophosphate-P was only 5 to 8 μg/L and hardly changed at all (Correll, 1981). If one had only monitored dissolved phosphate concentration, no change would have been apparent. In a laboratory study of 11 species of freshwater algae the concentration of phosphate-P needed to maintain equilibrium algal growth rates varied from 0.003 to 0.8 μg/L (Grover, 1989). If phosphate-P levels were maintained at 15 μg/L in mesocosms of Lake Michigan plankton, chlorophyll concentration increases and photosynthetic C fixation were maximized. Phosphate-P levels of 5 μg/L had almost as great an effect in these mesocosms (Shelske et al., 1974). These studies all lead one to believe that a pool size of a few micrograms per liter of phosphate-P is sufficient to saturate algal growth in most systems. However, the recycling rate must be sufficient to maintain this pool size. This fact makes monitoring of dissolved phosphate a technique of limited value, if the goal is to measure eutrophication potentials. A study by Morris and Lewis (1988) compared nine nutrient limitation indices for eight mountain lakes in Colorado. They conducted microcosm nutrient enrichments in situ in 10-L bottles to assess the actual nutrient limitations. They found that the ratio of dissolved inorganic N to total P was the best predictor of chlorophyll responses in the mesocosms followed by particulate N to particulate P ratios. Some investigators now use a combination of tests to infer whether P or N is most limiting. For example, Fisher et al. (1992) used phosphate and ammonium turnover times, alkaline phosphatase activity, nutrient enrichment bioassays, and ratios of dissolved total N to total P in studies of Chesapeake Bay. It is best to measure P inputs to the whole system, but for an easy assay it is best to measure total P concentrations in surface waters or N/P ratios in phytoplankton.

What concentration of total P is acceptable? There is no clear, widely accepted answer to this question. Certainly, for most lakes, streams, reservoirs, and estuaries concentrations of 100 μg total P/L are unacceptably high and concentrations of 20 μg/L are often a problem.

CONCLUSIONS

Phosphorus plays a unique and important role in the eutrophication of receiving waters, especially lakes, reservoirs, streams, and the upper reaches of estuaries. While N and C can be obtained from the atmosphere, P is transported primarily by surface waters. In most aquatic ecosystems P is naturally present in more limiting amounts than the other essential elements. Human activities often result in large fluxes of P to receiving waters. Since P tends to be retained efficiently in these aquatic systems, this leads to higher primary production, especially in the summer and fall. High primary production, in turn, leads to high rates of decomposition and depletion of dissolved oxygen in bottom waters and surface waters at night in calm weather. These eutrophic conditions can result in fish kills and major shifts in the species composition at all trophic levels (Fig. 1). Lake primary production can be accurately predicted from data on input fluxes of P, but research and data synthesis are needed to establish reasonable standards for total P concentration in various types of receiving waters. Much of the dissolved organic P and particulate P inputs to receiving waters become available to the phytoplankton and bacteria as the result of phosphate buffering equilibria between the particulates and dissolved phases, the action of phosphatases, and biological activity in the bottom sediments. When receiving waters have limiting amounts of P the phytoplankton biomass has N/P atomic ratios significantly above the Redfield ratio of 15 to 16. When N is limiting the Redfield ratio is much lower. If one needs to assess the P status of a receiving water based only on P concentrations in the water column, it is better to measure the sum of dissolved and particulate total P than to rely on dissolved orthophosphate concentrations.

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