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A Review: Phosphorus-Plankton Dynamics and Phosphorus
Cycling in Aquatic Systems

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PREFACE

This report is a part of the proceedings of the Phosphorus-Plankton Dynamics Symposium. This international symposium convened May 28-30, 1984, at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ontario, to discuss current issues in phosphorus dynamics in freshwater and marine environments. Thirty-one scientists from North America and Europe presented papers. The first part of the proceedings, consisting of 16 scientific papers, has been published in the Canadian Journal of Fisheries and Aquatic Sciences (1986, Volume 43, No. 2, pages 293-443). This report, based on an exhaustive literature review, is intended to supplement the article entitled "Introduction to the Phosphorus-Plankton Dynamics Symposium" by S. J. Tarapchak and C. Nalewajko that serves as the preface to the published set of 16 Symposium articles. A report summary of the complete proceedings will be published as a GLERL Technical Memo in the fall of 1986.

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A REVIEW: PHOSPHORUS-PLANKTON DYNAMICS
AND PHOSPHORUS CYCLING IN AQUATIC SYSTEMS¹

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ABSTRACT. Phosphorus (P)-plankton dynamics is a scientifically challenging, continuously evolving discipline. Research historically has focused on the role of P as a limiting factor in primary and secondary production. Extensive efforts have been made to understand the eutrophication process, model P-limited phytoplankton growth, predict the outcome of species competition, and understand the regenerative mechanisms that resupply orthophosphate (Pi) to algae. In the Great Lakes, research on P has focused primarily on water-quality monitoring programs and the use of P budget models to predict future changes in trophic state. However, to model production dynamics accurately in the Great Lakes system, additional studies on P cycling are required. This report briefly traces the development of scientific investigation into cultural eutrophication, identifies major research themes and problems in P-plankton dynamics and in aquatic P cycling, and summarizes basic and applied research on eutrophication and P cycling in the Great Lakes.

1. INTRODUCTION

1.1 Cultural Eutrophication

The causes and consequences of cultural lake eutrophication have been recognized as a practical and scientific problem for over 50 years (NAS, 1969; Thomas, 1953, 1973; Vallentyne, 1974). Studies on P-plankton dynamics are rooted in the early attempts to understand the causes of phytoplankton blooms. For example, Einsele's (1941) classic study on the fertilization of Schleinsee with superphosphates initiated the era of whole-lake enrichment experiments. Similarly, Sawyer (1947) detected that blooms in the Madison lakes, Wisconsin, were largest in lakes receiving the greatest quantities of nitrogen (N) and phosphorus (P) from agricultural and urban drainage. Thomas (1955, 1957) attempted to correlate nutrient inputs to the trophic state of several Swiss and Wisconsin lakes. Recognizing the importance of P as a limiting nutrient, Hutchinson and Bowen (1947, 1950), among others, used radioactive tracers to investigate the P cycle in lakes.

The identification of P as the nutrient that drives the eutrophication process motivated a vast expenditure of financial resources in North America and Europe beginning in the mid 1960's (WHO, 1981). In North America this period is marked by two monumental studies. First, a long-term limnological

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'study of Lake Washington by Edmondson (1970, 1972, 1977) and associates has documented quantitative changes in lake chemistry and biology following sewage diversion. Second, research on artificially fertilized lakes in the experimental lakes region, Ontario, has provided unparalleled insights into lake eutrophication processes (Schindler, 1974, 1977; Schindler et al., 1977, 1980). These include the evolution of nutrient limitation, the role of sediments and the hypolimnion in P recycling, and the importance of atmospheric N₂ and CO₂ as limiting nutrients. Reports published by Middlebrooks et al. (1973) and EPA (1979, 1980) include important articles on eutrophication processes and lake restoration.

This period of research has also witnessed one of the most successful experiments in applied aquatic ecology--the development and application of P-loading models to predict lake response to P enrichment (Metz, 1985). This approach, pioneered in its theoretical development and application by Vollenweider (1968, 1975, 1976), is based on the concept that phytoplankton biomass is correlated with external P loadings once appropriate adjustments are made for lake depth and water residence time. The Vollenweider models have not only provided the first truly quantitative means of managing lakes on a worldwide basis (Vollenweider and Kerekes, 1981), but they have spawned other approaches to quantify the relationship between P concentrations and loadings (e.g., Dillon and Rigler, 1974a,b; Chapra, 1977; Imboden and Gachter, 1978).

1.2 Phosphorus-Plankton Dynamics

In addition to understanding how lakes respond to altered P loadings, a primary goal in aquatic science is to predict the spatial and temporal behavior of major biological and chemical components in natural systems. The crucial role of P **has motivated** numerous studies to understand how primary and secondary production in freshwater aquatic systems are controlled by limiting concentrations of this nutrient. Research efforts can be grouped into five major categories: P cycling in lakes; eutrophication processes and mathematical modeling; P measurement and chemical compartments; microbial growth' and cellular metabolism; and theories and hypotheses concerning P-phytoplankton dynamics. The papers cited in Appendixes A-G represent generally recognized pioneering efforts in the field of P-phytoplankton dynamics, or are more recent catalytic or substantive works that provide new insights into the subject (as reflected by examination of the citation index Biosis Previews Database, published by Bioscience Information Service). Reviews by Nalewajko and Lean (1980) and Cembella et al. (1984) provide entry points into the recent literature.

A major research thrust in P-plankton dynamics has been to determine how variable orthophosphate (Pi)* supply rates control the outcome of species competition under steady-state conditions (Appendix D, Cell Growth and P Uptake). This effort is embedded in the pioneering studies of Droop (1974) on experimentally-based models for P-limited algal cell growth. Droop's cell

*P₁' refers specifically to the orthophosphate compartment in Rigler's (1973) model (Fig. 1); orthophosphate (Pi) refers more generally to this nutrient in aquatic systems.

quota model has motivated additional studies for developing refined growth models based on internal and external P pools (e.g., Rhee, 1973, 1978), as well as generalized models integrating the enzyme-mediated kinetics of substrate transport, growth, and nutrient efflux (Button, 1978). These models, which also include moderating effects of physical factors (Rhee and Gotham, 1981; Tilman et al., 1982), form the theoretical basis for predicting the outcome of nutrient-based competition (e.g., Tilman and Kilham, 1976; Rhee and Gotham, 1980). Two significant advances in competition theory have recently been made. First, models based on species resource requirements have been developed (Tilman et al., 1982; Tilman, 1982). Second, competition under non-steady-state P_i supply rates, a condition that may better characterize P_i supplies in nature, is now being actively explored (e.g., Burmaster, 1979; Sommer, 1984).

A second thrust has been to develop bioassays to detect limiting nutrients in natural phytoplankton populations (Appendix E, Physiologic Indicators of P Deficiency). This approach, initiated by Gerloff and Skoog (1954), Potash (1956), Thomas (1961), and Hughes and Lund (1962), is based primarily on growth-related physiologic characteristics of P-limited algae. Detection of P limitation is usually based either on measurements of intracellular nutrient ratios (Redfield et al., 1963), surplus P or polyphosphate stores (Fitzgerald and Nelson, 1966), cell-surface alkaline phosphatase activity (Kuenzler and Perras, 1965), or the capacity of cells to take up limiting nutrients (Fitzgerald, 1970a,b).

Bioassay technology has been marked by two major advances. First, during the era of the carbon-P eutrophication controversy in the late 1960's (Vallentyne, 1970; Likens, 1972), Schindler (1971) demonstrated that conventional bioassays could yield false impressions of the nutrients causing accelerated lake eutrophication. Second, Healey (1979) demonstrated that short-term ^{14}C photosynthetic responses to P_i additions give misleading information. P-limited cells temporarily suppress photosynthetic rates, diverting cellular energy to support rapid P_i uptake. State-of-the-art bioassay approaches are illustrated in Healey and Hendzel (1980) and Lean and Pick (1981).

2. PHOSPHORUS CYCLING

2.1 Modeling the P Cycle

The intrinsic growth rates of microorganisms in P-limited systems are ultimately dependent on internal P recycling rates. Rigler (1973) and Golterman (1973) reviewed then-current understanding of the P cycle. A simplified compartment diagram, developed primarily from Rigler's (1973) article, shows the major components of the epilimnetic P cycle (Fig. 1). The model includes two primary biologic compartments (phytoplankton and zooplankton) and three abiotic compartments (orthophosphate, dissolved organic phosphorus, and detritus).

One of the earliest observations is that the P_i pool is exceedingly small and highly labile, with apparent turnover times on the order of minutes during

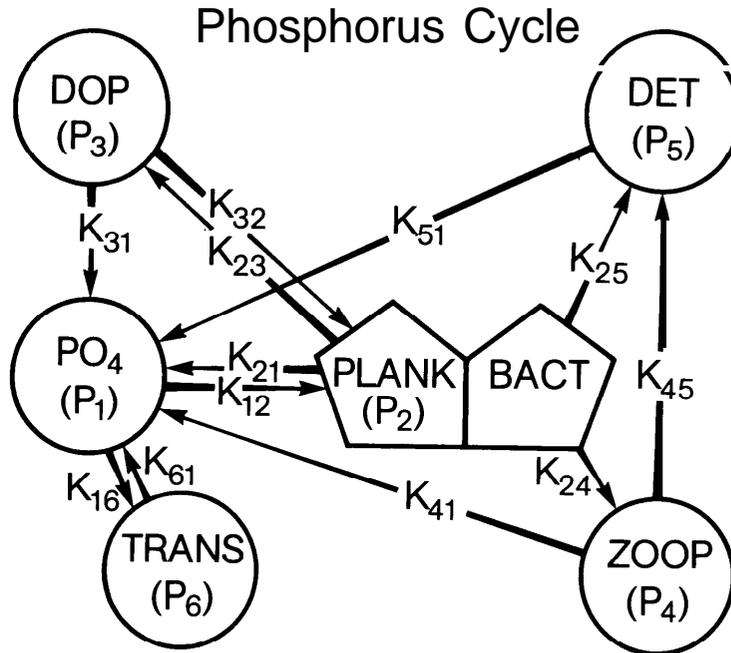


Figure 1.--A Conceptual diagram of the phosphorus cycle in freshwater lakes (after Rigler, 1973 and Golterman, 1973). Compartments are orthophosphate (P_1), phytoplankton (P_2), dissolved organic phosphorus (P_3), zooplankton (P_4), and detritus (P_5); transport (P_6) out of the epilimnetic zone. Bacteria are considered part of P_2 . K's are the rate constants for phosphorus movement among compartments.

summer in most natural environments (Pomeroy, 1960; Rigler, 1973). The kinetics of phosphorus movement in the epilimnion correspond best to a four-compartment model (Lean, 1973a,b). The dominant exchange is uptake and release of P_i by the particulate fraction, but some phosphorus is excreted by the microorganisms in the form of a low-molecular-weight compound (XP). Polycondensation of the low-molecular-weight compound produces a colloidal-size molecule and also releases P_i . Lean's model appears to have general validity, because similar results have been obtained for different lake types (e.g., Paerl and Downes, 1978; Stainton, 1980).

A principal impediment in modeling the P cycle is the difficulty of accurately measuring P_i and dissolved organic P (DOP) concentrations (Appendix C, Dissolved P Composition). For example, P_i pool size cannot be determined by standard procedures because molybdenum blue methods may grossly overestimate true P_i concentrations (Rigler, 1973). The reason for the discrepancy between true P_i concentrations and colorimetric estimates (i.e., soluble reactive P) was attributed to P_i release by acid hydrolysis of organic compounds. Rigler's (1966, 1968) work spawned numerous efforts to measure P_i or bioavailable P (Chamberlain and Shapiro, 1969; Peters, 1978; Pettersson, 1979; Nurnberg and Peters, 1984). To date, however, the problem remains unresolved (Stainton,

1980; Tarapchak, 1983). Rigler's (1966) radiobioassay approach, which only estimates maximum possible Pi concentrations, is the acknowledged standard. Similarly, procedures for determining DOP concentrations and composition are often based on operational definitions or imperfect techniques (Strickland and Parsons, 1972). Although some components of the DOP pool have been characterized, its precise chemical makeup is unknown (Minear, 1972; Koenings and Hooper, 1976; Francko and Heath, 1979, 1982).

2.2 Problems in Modeling the P Cycle

The cumulative research effort on aquatic P cycling through the 1980's has raised additional, even more challenging problems than those envisioned in the early 1970's. Several crucial issues are summarized here.

2.2.1 Orthophosphate Uptake by Phytoplankton

The starting point for modeling P cycling is the Pi pool (Rigler, 1973) (Appendix A). However, the rate at which Pi enters the lower food web (through phytoplankton and possibly bacteria) cannot be quantified for two reasons. First, conventional radiotracer techniques measure gross, not net, Pi uptake (Lean and Nalewajko, 1976; Lehman, 1984) (Appendix E, Kinetics of P Uptake in Natural Waters). Second, the size of the Pi pool, as pointed out above, cannot be measured accurately. The need to resolve this problem has been sharply focused by the fact that phytoplankton appear to be growing at maximal rates, despite the presence of only minute concentrations of the limiting nutrient (Goldman et al., 1979; Currie, 1984b). This apparent paradox may be explained in one or both of two ways: algae may have extremely high-affinity uptake systems (i.e., systems of natural populations are much more efficient than suggested by measurements on laboratory monocultures), or P may be obtained from sources other than bulk ambient Pi. Potential sources of non-bulk P include Pi from the DOP pool mediated by cell-surface alkaline phosphatase formation (Kuenzler, 1965; Kuenzler and Perras, 1965), or Pi from high-phosphate plumes generated by actively feeding zooplankton (Lehman and Scavia, 1982a,b). Rates of net Pi uptake by phytoplankton from the bulk Pi pool and the relative importance of other P sources must be quantified if significant advances are to be made in understanding how Pi functions as a limiting nutrient.

2.2.2 Bacterial P Sources

Recent studies on P utilization by heterotrophic bacteria and their production rates suggest that the assumed role of these organisms as primary consumers of DOP may have to be radically redefined (Appendix E, Phytoplankton-Bacterial Competition). Bacterial production rates in some systems can rival phytoplankton production rates (Pedros-Alio and Brock, 1982; Bell et al., 1983). Several reports since Rigler's (1956) pioneering study suggest that bacteria may not only use Pi but may, in fact, win the competition with phytoplankton at ambient Pi levels (e.g., Rhee, 1972; Faust and Correll, 1976; Paerl and Lean, 1976; Currie and Kalff, 1984a,b). Hence, if bacteria use primarily Pi, their assumed role as mineralizers of the DOP pool (which is

thought to provide P_i for algae) must also be critically evaluated.

2.2.3 Zooplankton P Recycle

The role of herbivorous zooplankton (P_4) in regenerating inorganic nutrients has been recognized ever since Gardiner's (1937) early experiments on nutrient release from marine plankton (Appendix A, Zooplankton). However, the contribution made by zooplankton to the total P budget is usually impossible to calculate because hydrologic budgets and fluvial fluxes for most lakes are unknown. Recent work, however, shows that epilimnetic zooplankton contribution to P_i recycling in the large lakes may be a primary regenerative mechanism. Lehman (1980a,b) used nutrient budgets and in situ grazing measurements to show that zooplankton in Lake Washington supply 10 times more P_i to the surface layer during summer than enters the lake from all other sources. Such results argue for additional studies on zooplankton contribution to P_i regeneration in relation to in situ phytoplankton demand. Another general assumption is that P_i is the primary form of P released by zooplankton (Rigler, 1973). However, this assumption must be validated because DOP compounds can test as P_i when measured by conventional methods (e.g., Stainton, 1980).

2.2.4 Dissolved Organic Phosphorus

The DOP pool (P_3) occupies a key position in P cycling because algae, zooplankton, and bacteria contribute to it (Fig. 1) (Appendix C, Dissolved P Composition). The pool is thought to be composed of numerous compounds, ranging from low-molecular-weight, highly labile compounds to large, biologically refractory compounds (Chamberlain, 1968; Hooper, 1973). However, the chemical composition of the pool and recycling rates of individual compounds are poorly understood. The major compounds and their fluxes, including recycling mechanisms for biologically refractory compounds, must be better known if the close coupling between nutrient-dependent bacteria-phytoplankton dynamics is to be better understood (Wetzel, 1983).

2.2.5 Alkaline Phosphatase

The importance of P_i regeneration by alkaline phosphatase, other dissolved enzymes, and physical-chemical processes is urgently in need of critical investigation, particularly in large lakes where most of the P_i supply during summer is recycled within the epilimnion (Wetzel, 1983). Intensive research over the last 10 years has identified three distinct regenerative mechanisms: release of P_i from colloids (Lean, 1973a,b); hydrolysis of dissolved low-molecular-weight organic P compounds by cell-surface alkaline phosphatase or other dissolved enzymes (Berman, 1970; Francko and Heath, 1979; Wetzel, 1981; Stewart and Wetzel, 1982); and photochemical P_i release from ferric iron-dissolved humic materials (Koenings and Hooper, 1976; Francko and Heath, 1983) (Appendix A, Regenerative Mechanisms). The overall importance of these mechanisms, relative to P_i regeneration by zooplankton, must be quantified in different lake types.

2.2.6 Detritus

The **role** of detritus (**P₅**) in epilimnetic P cycling has largely been ignored. Detritus, **produced** primarily by zooplankton grazing and by cell death, is a potentially important component. These materials serve as a temporary P sink, provide substrate for bacteria, and may remove relatively large quantities of P from the epilimnion by sinking into the hypolimnion.

3. THE DETERIORATED GREAT LAKES RESOURCE

The Great Lakes system, containing over **one-fifth** of the world's fresh surface water, represents an immensely valuable North American resource (Powers and Robertson, 1966; Ragotzkie, 1974; Sonzogni et al., 1983). The multipurpose use of this system can be dramatically illustrated as follows:

Commercial fisheries and sports fishery total \$160 million and over \$1 billion per year, respectively, with about 2 million people participating. Water withdrawals, supplying drinking water for nearly 25 million people, total 45 billion gallons per day. Great Lakes shipping, dominated by bulk cargoes of iron ore, coal, grain and limestone, total over 200 million tons per year. Waste disposal from municipal and industrial plants totals over 20 billion gallons per day. Water from the lakes is also used as coolant in nuclear and fossil fuel power generation in the multi-billion dollar energy industry. Recreation, sports fishing, and tourism in the Great Lakes basin represent an industry of \$1 billion per year (E. Aubert, Great Lakes Environmental Research Laboratory, Ann Arbor, MI, and C. Herdendorf, Ohio State University, Columbus, OH; personal communication).

Gradual increases in P loadings over the last 100 years resulting from human population increases have produced recognizable symptoms of deteriorating water quality that are especially severe in the lower Great Lakes (**Beeton**, 1965, 1969). For example, the lower portions of Green Bay, Saginaw Bay, and the western basin of Lake Erie showed severe signs of hypereutrophication by the early 1960's (Burns and Ross, 1972; Tarapchak and Stoermer, 1976). This problem, recognized by the governments of the United States and Canada, culminated in the Great Lakes Water Quality Agreements of 1972 and 1978. The objectives of the first plan were to restore year-round aerobic conditions in the bottom waters of Lake Erie's central basin, reduce algal growth in Lakes Erie and Ontario, and stabilize Lake Superior and Lake Huron as oligotrophic lakes (IJC, 1974). The second agreement was expanded to reduce P inputs from diffuse sources, reduce P in household detergents (to 0.5% by weight) where necessary to meet specified loading allocations, and maintain an active research program in P control (IJC, 1978). Large-scale P loading controls in the **1970's**, based on reformulating detergents to reduce their P content (especially in Canada) and improving sewage treatment facilities, have resulted in recent water quality improvements in Lakes Ontario and Erie (Dobson, 1981).

3.1 Great Lakes Research Focus

P research in the Great Lakes system has had a strong practical orientation with two primary thrusts: monitoring and water quality surveillance by the Environmental Protection Agency and Environment Canada, and the use of mathematical models to determine present and future trophic conditions in the lakes. The first effort to quantify the relationship between P loadings and lake response was that of Vollenweider et al. (1974) (Fig. 2). These and subsequent analyses (Appendix F, P Loading, Models, and Budgets) clearly demonstrate the pristine nature of Lake Superior relative to the polluted waters of western Lake Erie. Reports dealing with water quality, the overenrichment problem, and proposed remedial actions are contained in numerous IJC reports. Those cited in Appendix G serve as a point of entry to IJC literature.

The use of mathematical models to study plankton dynamics and eutrophication processes occupies a central theme in Great Lakes research (Loehr et al., 1980). Three classes of models have been applied. The first class center around the P-loading concept. These models, based on mass balances of P inflow, outflow, and sedimentation, are designed to assess trophic state as a function of past, present, and future loading rates (e.g., Chapra, 1977). They ignore the effects of internal dynamics. The second class, often termed "eutrophication models," are designed to simulate and predict phytoplankton biomass dynamics (e.g., Thomann et al., 1977; Thomann and Segna, 1980). These models normally predict biomass as a

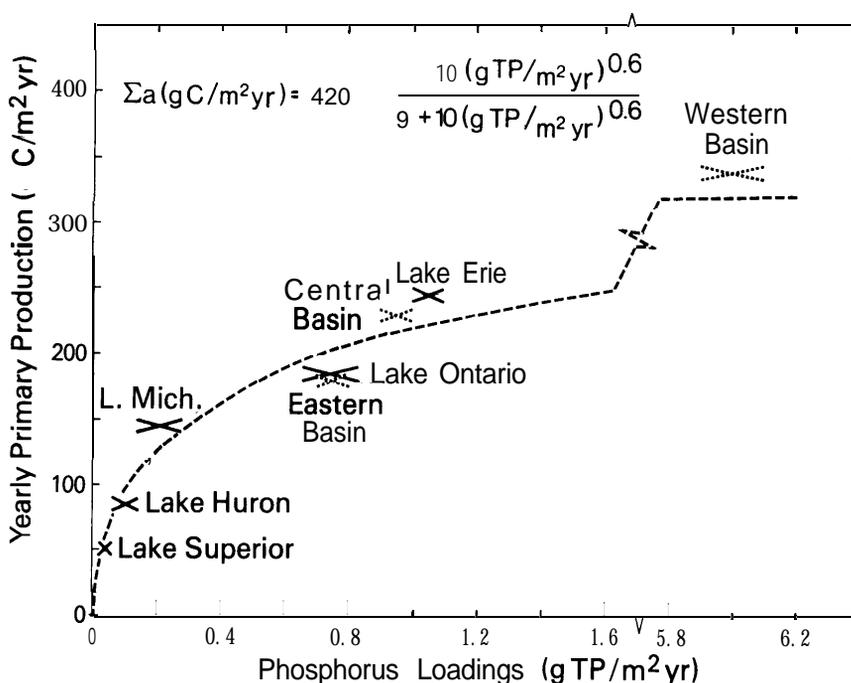


Figure 2.--The relationship between external phosphorus loadings and primary production in the Great Lakes (from Vollenweider et al., 1974).

function of first-order processes such as phytoplankton production, respiration, sinking, and nutrient cycling. The third class, complex ecosystem models, are designed to synthesize information on physical, chemical, and biologic processes and to analyze controls of system structure and function. These models have provided important insight into physical and chemical controls of plankton dynamics and nutrient regeneration processes in the Great Lakes (e.g., Scavia, 1979).

The use of P budget models to predict potential improvements in Great Lakes water quality resulting from P reductions has attracted immense interest. The IJC recommended that all point-source P discharges in the Great Lakes system be limited to 1 mg/L (IJC, 1976). Chapra's (1977) model illustrates the predictive capabilities of budget models (Fig. 3). His model, based on forcing functions such as population and land use (including wastes from domestic sources, land runoff, and the atmosphere), showed that the 1 mg/L effluent restriction would generally improve water quality over much of the Great Lakes. Only minor improvements would be

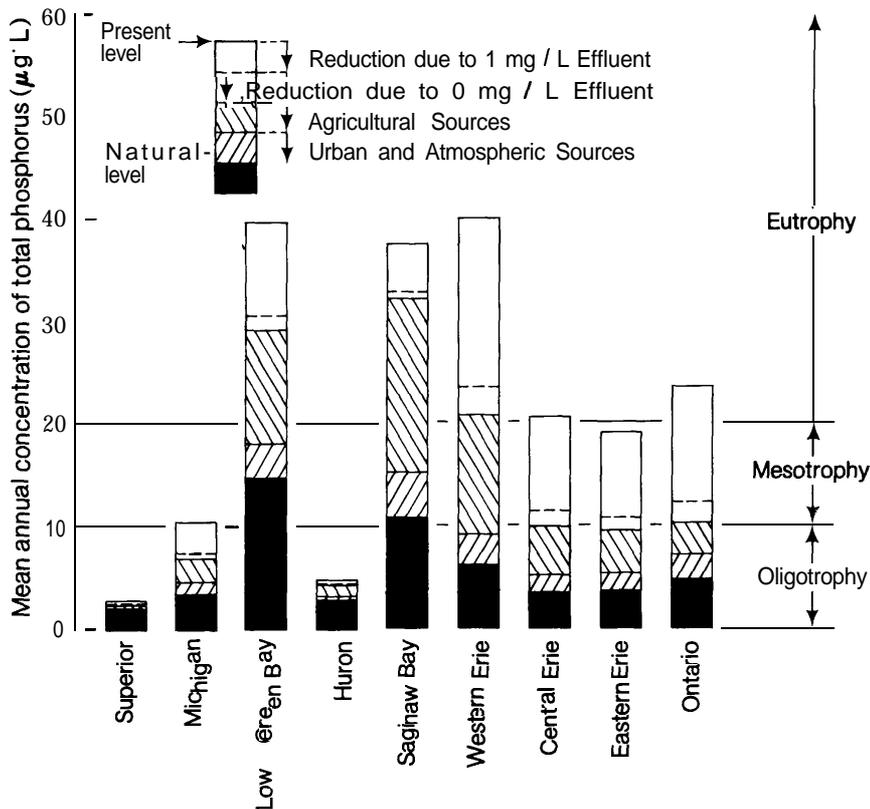


Figure 3.--Results of a budget model showing the effects of a 1 mg/L restriction on point source discharges of total phosphorus into the Great Lakes system (from Chapra and Robertson, 1977).

observed in Lake Superior and Lake Huron; Lake Michigan would return to its original oligotrophic state; and total P levels in central and eastern Lake Erie and Lake Ontario would decrease by about one-half. However, the 1 mg/L restriction would not result in major improvements in water quality in western Lake Erie, Green Bay, or Saginaw Bay because of high natural loadings in these areas.

3.2 Great Lakes Research Needs

The use of eutrophication and complex ecosystem models has clearly identified our incomplete understanding of P-plankton dynamics and P cycling in the Great Lakes system. Great Lakes research on P dynamics has focused largely on assessing eutrophication and predicting how changes in nutrient loadings will affect water quality (Appendix F). Unfortunately, basic research on P-related biologic and chemical processes needed to refine the predictive capabilities of mathematical models has lagged behind applied research efforts. For example, the only intensive long-term investigation into phytoplankton nutrient limitation and its effects on primary production and phytoplankton seasonal succession on the American side is that of Schelske and associates (Schelske and Stoermer, 1971, 1972; Schelske, 1975, 1979, 1984; Schelske et al., 1974). These collected works have demonstrated the role of P and silicon limitation in the Great Lakes eutrophication process and have also motivated studies to reconstruct the history of cultural eutrophication in the Great Lakes using nutrients and microfossils in lake sediments (Harris and Vollenweider, 1982; Schelske et al., 1983).

Efforts to correct the overenrichment problem in the Great Lakes motivated the formation of the Pollution from Land Use Activities Reference Group (PLUARG). This group, formed in 1972 under the auspices of the International Joint Commission, was established to carry out the Reference contained in the Great Lakes Water Quality Agreement of 1972, and was instrumental in refinement of management strategies based on P loading and budget models. PLUARG has had a major impact on the direction of P-related eutrophication research by focusing attention on the need for intensive studies on P bioavailability of particulate materials entering the lakes (Appendix F, Bioavailable P). This work has provided important information on the availability of different chemical forms of extractable P (e.g., Cowen and Lee, 1976; Williams et al., 1980). A comprehensive review of extraction schemes and the bioavailability of different chemical fractions has been presented by Sonzogni et al., (1982).

Basic research in the Great Lakes has provided only first-order insights into primary and secondary production controls. For example, internal recycling apparently supplies most of the P_i required for algal growth during summer (Stadelmann and Fraser, 1974). However, many questions regarding the subtle, but crucial, role of P cycling remain unanswered. What are the relative regenerative contributions of zooplankton, enzyme activity, and colloidal displacement, respectively, to the total P_i demand of the phytoplankton? How much of the required P_i diffuses from the nutrient-rich hypolimnion in Lakes Erie and Ontario into surface waters during summer? What fraction of this requirement is supplied by sediment resuspension at spring overturn? Do bacteria compete

with algae for the same P source, and do algae obtain significant Pi from organic compounds? What is the chemical composition of the DOP pool, and how is this material recycled if bacteria are using Pi? Obviously, answers to these questions are necessary if P cycling in the Great Lakes is to be understood.

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Appendix A. P Cycling In Lakes

Contribution	Authors
<u>Whole Lake</u>	
Classical Studies on Radiophosphorus Movement in Lake Waters	Hutchinson & Bowen, 1947, 1950; Coffin et al., 1949; Hayes et al., 1952; Hayes & Phillips, 1958
<u>Epilimnetic Cycling</u>	
P Cycling Among Chemical and Biotic Components	Pomeroy, 1960; Watt & Hayes, 1963; Rigler, 1964, 1968, 1973; Chamberlain, 1968; Golterman, 1973
Model for Epilimnetic P Exchange	Lean, 1973a
<u>Regenerative Mechanisms</u>	
Alkaline Phosphatase and Other Enzymes	
Regeneration of Orthophosphate From Dissolved Organic Compounds by Phosphatases and Other Enzymes	Berman, 1969, 1970; Perry, 1972; Yentsch et al., 1972; Heath & Cook, 1975; Herbes et al., 1975; Rivkin & Swift, 1979; Wetzel, 1981; Wynne, 1981; Stewart & Wetzel, 1982; Francko, 1984
Colloidal Displacement and Other Physiochemical Processes	
Release of Orthophosphate by Physiochemical Mechanisms and Abiotic Complexation	Otsuki and Wetzel, 1972; Lean, 1973b; Lean & Rigler, 1974; Koenings & Hooper, 1976; Downes & Paerl, 1978; Tarapchak et al., 1981; Francko & Heath, 1982, 1983

Sediments and Hypolimnion

P Regeneration in Sediments, and
the Sediments and the
Hypolimnion as a P Sink

Mortimer, 1941; Olsen, 1958;
Pomeroy et al., 1965;
Fitzgerald, 1970a; Serruya,
1971; Golterman, 1973;
Syers et al., 1973;
Kamp-Nielsen, 1974, 1975;
Ryding & Forsberg, 1976;
Ahlgren, 1977; Schindler
et al., 1977; Ulen, 1978;
Holdren & Armstrong, 1980;
Evans & Rigler, 1980;
DePinto, 1979; Bostrom et
al., 1982; Nurnberg, 1984;
Twinch & Peters, 1984;
Golterman, 1984

Zooplankton

Regeneration of P by Herbivorous
Zooplankton and Its Chemical
Composition

Gardiner, 1937; Harris, 1957;
Rigler, 1961; Ketchum, 1962;
Pomeroy et al., 1963;
Johannes, 1964; Barlow &
Bishop, 1965; Hargrave &
Green, 1968; Peters & Lean,
1973; Peters & Rigler,
1973; Ganf & Blazka, 1974;
Ferrante, 1976; Lehman,
1980a,b; Bartel, 1981;
Lynch & Shapiro, 1981;
Taylor, 1984

Appendix B. Eutrophication

Contribution	Authors
<u>Processes and Models</u>	
Classic P Loading-Lake Response Models, Application of Phosphorus Budgets and Loading Concepts to Lake Eutrophication	Vollenweider, 1968, 1975, 1976; Dillon & Rigler, 1974b; Jorgensen, 1976; Chapra, 1977; Chapra & Robertson, 1977; Lee et al., 1978; Imboden, 1974; Imboden & Gachter, 1978; Vollenweider & Kerekes, 1980, 1981; Ambuehl, 1980; Fricker 1980; Clasen & Bernhardt, 1980; Janus & Vollenweider, 1981; Rast et al., 1983; Reckhow & Chapra, 1983; Janus & Vollenweider, 1984; Lee & Jones, 1984
Total Phosphorus Concentration-Chlorophyll <u>a</u> Model	Sakamota, 1966; Dillon & Rigler, 1974a, 1975
The Lake Washington Recovery Experiment (Following Sewage Diversion)	Edmondson, 1970, 1972, 1977; Edmondson & Lehman, 1981; Smith & Shapiro, 1981
Whole-Lake P Enrichment Experiments (Experimental Lakes Area)	Schindler et al., 1973, 1978; Schindler, 1974, 1977
The Schelske-Stoermer Eutrophication Hypothesis (P and Silicon Limitation)	Schelske & Stoermer, 1971, 1972; Schelske et al., 1983
Complex Multicompartment Ecosystem Modeling	Bierman et al., 1973; Barsdate et al., 1974; Lehman et al., 1975; Bierman, 1976; DePinto et al., 1976; Richey, 1977; Reckhow, 1979; Scavia, 1979, 1980

Restoration Projects

Shagawa Lake, Minnesota (U.S.A.)	Bradbury & Waddington, 1973; Larsen et al., 1975, 1979
Madison Lakes, Wisconsin (U.S.A.)	Sonzogni et al., 1975
Lake Norrviken and Lakes Boren and Ekoln (Sweden)	Ahlgren I., 1972, 1977, 1978; Ahlgren G., 1978; Forsberg et al., 1975, 1978
Lake Muskoka (Gravenhurst Bag) (Canada)	Dillon et al., 1978

Contribution	Authors
<u>Analytical</u>	
Measurements of Phosphorus in Marine Waters (English Channel)	Harvey, 1948
Methods for Measuring Total Soluble-Reactive P (Ascorbic Acid Method)	Murphy & Riley, 1958, 1962; Stephens, 1963; Menzel & Corwin, 1965; Chamberlain & Shapiro, 1969
Method-Specific Differences in Soluble-Reactive P Estimation	Jones & Spencer, 1963; Jones, 1966; Olsen, 1967; Stainton, 1980; Tarapchak, 1983
<u>Orthophosphate Estimation</u>	
Bioassays for Estimating Orthophosphate and Biologically Available Phosphorus	Rigler, 1966; Chamberlain & Shapiro, 1969; Peters, 1977; 1978; Paerl & Downes, 1978; Pettersson, 1979; White & Payne, 1980; Nurnberg & Peters, 1984
<u>Dissolved P Composition</u>	
Chemical Composition and Characterization of the DOP Pool.	Kuenzler & Perras, 1965; Chamberlain, 1968; Solorzano, & Strickland, 1968; Rigler, 1968; Minear, 1972; Franco & Heath, 1979; Koenings and Hooper, 1976; Holm-Hansen & Booth, 1966; Ammerman & Azam, 1981; Peters, 1981; Francko & Wetzel, 1982; Francko & Heath, 1982; Tarapchak et al., 1982a; Persson, 1984

Appendix D. Cellular Growth, Physiology and Metabolism

Contribution	Authors
<u>P Uptake</u>	
Early Studies on Measurements of Cellular P Uptake	Ketchum, 1939; Rodhe, 1948; Mackereth, 1953; Kuenzler and Ketchum, 1962; Harvey, 1963
<u>Kinetics of Cellular P Uptake</u>	
Characterization of P Uptake Kinetics of Microorganisms	Harold et al., 1965; Blumm, 1966; Rosenberg et al., 1969; Carpenter, 1970; Medveczky & Rosenberg, 1971; Harold & Spitz, 1975; Perry, 1976; Chisholm & Stross, 1976a,b; Tomas, 1979; Burmaster & Chisholm, 1979; Robertson & Button, 1979; Rigby et al., 1980; Rivkin & Swift, 1982; Riegman & Mur, 1984a
<u>Metabolism and Intracellular P Composition</u> (Including Polyphosphates)	
Ecologically Significant Metabolic Events and Intracellular P Composition	Kuhl, 1962, 1974; O'Kelley, 1973; Rhee, 1973; Aitchinson & Butt, 1973; Harold, 1966; Healey, 1973; Jansen & Sicko, 1974; Tett et al., 1975; Kulaev, 1975; Stewart et al., 1978; Elgavish & Elgavish, 1980; Elgavish et al., 1980
<u>Alkaline Phosphatase Activity</u>	
Induction and Synthesis of Alkaline Phosphatase Activity in Algae	Kuenzler & Perras, 1965; Fitzgerald & Nelson, 1966; Bone, 1971; Feder, 1973; Aaronson & Patni, 1976; Rivkin & Swift, 1979; Karl & Craven, 1980

Organic P Utilization

Utilization and Excretion of
Organic P Compounds

Kuenzler, 1965, 1970;
Lean & Nalewajko, 1976;
Robertson & Button, 1979;
Rivkin, 1980; Rivkin &
Swift, 1982

P Influx and Efflux (including cell leakage)

Kinetics of P Uptake and Release
of Organic P Compounds

Lean & Nalewajko, 1976;
Berman & Skyring, 1979;
Robertson & Button,
1979; Brown & Button,
1979; Button & Kinney,
1980

P and Photosynthesis

Regulation and Cellular Energy
and P Requirements for
Photosynthetic

Kylin, 1966; Jagendorf,
1973; Healey, 1979; Lean
& Pick, 1981; Harris &
Piccinin, 1983

Cell Growth and P Uptake

Models for Cell Growth and Phosphate
Uptake (Including Cell Quota
Subsistence, and Non-Steady-State
Models)

Thomas & Dodson, 1968;
Fuhs, 1969; Fuhs et al.,
1972; Muller, 1972; Droop,
1973, 1974, 1975; Rhee;
1973, 1974; Harold &
Spitz, 1975; Goldman,
1977; Button, 1978, 1983;
Nyholm, 1978; Burmaster,
1979; Healey, 1980; Brown
& Harris, 1978; Nalewajko
and Lean, 1978; Shuter,
1978; Terry, 1980, 1982;
Riegman & Mur, 1984b

Contribution	Authors
<u>Early Studies</u>	
Phytoplankton Competition and Limiting Nutrients	Pearsall, 1930, 1932; Lund, 1950a,b; Hutchinson, 1967
<u>Competition--P Uptake and Growth Kinetics</u>	
Culture Studies	
Competition as Determinants of Species Seasonal Succession	Tilman & Kilham, 1976; Rhee & Gotham, 1980; Healey, 1980; Gotham & Rhee, 1981; Holm & Armstrong, 1981; Tilman et al., 1982; Smith & Kalff, 1982, 1983; Sommer, 1983.
Lake Studies	
Competition as Determinants of Species Seasonal Succession	Stross & Penrick, 1974; Friebele et al., 1978; Knoechel & DeNoyelles, 1980; Smith & Kalff, 1982, 1983
<u>Resource Competition Theory</u>	
Resource Requirements of Competing Species	Titman, 1976; Tilman, 1977, 1981, 1982
<u>Physical Factor Effects</u>	
Effects of Physical Factors on P Uptake, Growth, and Competition	Rhee & Gotham, 1981; Tilman et al., 1981, 1982; Nalewajko et al., 1981; Smith, 1983b; Nalewajko & Lee, 1983; Nalewajko & Garside, 1983; Reshkin & Knauer, 1979; Senft, 1978.

Kinetics of P Uptake in Natural Waters

Uptake Kinetics of P by Microorganisms
in Natural Waters

Fuhs & Canelli, 1970;
Halmann & Stiller, 1974;
Taft et al., 1975, 1977;
Brown et al., 1978;
Richey, 1979; Levine
& Schindler, 1980;
Perry & Eppley, 1981;
Lehman & Sandgren,
1982; Lean & White,
1983; Berman, 1983

Physiologic Indicators of P Deficiency ("Bioassays")

Photosynthetic Response to P
Enrichment

Hamilton, 1969; Schindler,
1971; Richey, 1979;
Healey, 1979; Lean & Pick,
1981

Intracellular Nutrient Ratios
and Nutrient Demand .

Gerloff & Skoog, 1954;
Potash, 1956; Thomas,
1961; Hughes & Lund, 1962;
Redfield et al., 1963;
Fitzgerald, 1970b; Haug et
al., 1973; Jensen &
Sakshaug, 1973; Banse,
1974; Peterson et al.,
1974; Rhee, 1978;
Healey & Hendzel, 1980;
Smith, 1983a

Alkaline Phosphatase

Fitzgerald & Nelson, 1966;
Berman, 1970; Perry, 1972;
Yentsch et al., 1972;
Megard & Smith, 1974;
Wynne, 1977; Rivkin &
Swift, 1979; Pettersson,
1980; Wynne & Berman,
1980; Wetzel, 1981;
Smith & Kalff, 1981

Kinetics of P Uptake
by Nutrient Deficient
Cells

Perry, 1976; Lean &
Nalewajko, 1979; Vincent,
1981

Phytoplankton-Bacterial Competition

Competition and Sources of
P for Algae and Bacteria

Rigler, 1956, Jones, 1972;
Rhee, 1972; Faust &

Correll, 1972;
Paerl & Lean, 1976;
Harrison et al., 1977;
Brown et al., 1981;
Krempin et al., 1981;
Currie & Kalff, 1984a,b,c

Microscale P Patchiness

Zooplankton Plumes as a High
Phosphate P Source

Lehman & Scavia, 1982a,b,
1984; Currie, 1984a,b;
Scavia et al., 1984

Contribution	Authors
<u>P Loading, Models, and Budgets</u>	
Classical P Loading Lake-Response Relationships	Vollenweider et al., 1974, 1980
P Budgets and Eutrophication and Water Quality Models	Snodgrass & O'Melia, 1975; Chapra, 1977, 1980a,b; Canale & Squire, 1976; Chapra & Robertson, 1977; Schelske, 1979; Reckhow, 1979; Snodgrass, 1979; Chapra & Sonzogni, 1979; DiToro & Matystik, 1979; Fraser, 1980; Chapra & Dobson, 1981; Janus & Vollenweider, 1981; Dolan et al., 1981; Berman et al., 1984.
<u>Atmospheric P Loading</u>	
Quantitative Importance of Atmospheric P Loadings	Kilham & Titman, 1975; Murphy & Doskey, 1976; Eisenreich et al., 1977; Parker et al., 1981
<u>Ecosystem Modeling</u>	
P Phytoplankton Dynamics	Thomann et al., 1977; Scavia & Chapra, 1977; Scavia, 1979, 1980; Thomann & Segna, 1980; DiToro, 1980; Bierman & Dolan, 1981
<u>Phosphorus Cycling,</u>	
Dissolved Phosphorus Composition	
SRP Measurements and Chemical Composition	Tarapchak & Rubitschun, 1981; Tarapchak et al., 1981; Tarapchak et al., 1982a,b,c; Tarapchak, 1983
Short-Term P Cycling	
P Cycling in the Bay of Quinte	Lean & Charlton, 1976

Appendix G. Selected IJC Reports* on Phosphorus Dynamics and Eutrophication

Report	Publ. Date
<u>General</u>	
1972 and 1978 Great Lakes Water Quality Agreements: A Bibliography - November 1983	1983
<u>Pluarg and Bioavailability</u>	
Availability of Phosphorus in Different Sources Entering the Great Lakes for Algal Growth	1979
Contribution of Phosphorus From Agricultural Land to Streams by Surface Runoff	1978
Biological Availability of Phosphorus	1978
Nonpoint Source Pollution Abatement in the Great Lakes Basin: An Overview of Post-PLUARG Developments	1983
<u>P Loading and Management Strategies</u>	
Phosphorus Load Reduction Supplement to Annex 3 of the 1978 Agreement Between the United States of America and Canada on Great Lakes Water Quality	1983
1981 Municipal and Industrial Phosphorus Loadings to the Great Lakes	1982
Report on Differences in the Great Lakes Phosphorus Load Estimates	1979
Relative Costs of Achieving Various Levels of Phosphorus Control at Municipal Wastewater Treatment Plants in the Great Lakes Basin	1978
Environmental Management Strategy for the Great Lakes System	1982
1981 Municipal and Industrial Phosphorus Loadings to the Great Lakes	1982
Supplement Report on Phosphorus Management Strategies	1981
Phosphorus Management for the Great Lakes: Final Report of the Phosphorus Management Strategies Task Force	1980
<u>Great Lakes Water Quality</u>	
1983 Report on Great Lakes Water Quality, Appendix, Great Lakes Surveillance 1983	1983

*Reports available from the International Joint Commission, Great Lakes
Regional Office Library, 100 Ouellette Avenue, Windsor, Ontario, CANADA N9A 6T3