Examination of Phosphorus Cycling and Control of Phytoplankton Dynamics in Lake Ontario with an Ecological Model[1]

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An ecological model of Lake Ontario was used to assist in interpretation of data collected during the International Field Year for the Great Lakes (March 1972–April 1973). The analysis indicated that in spring and fall phytoplankton biomass is controlled by the interaction of incoming solar radiation and vertical mixing, in summer by silica- and phosphorus-limitation, and in late summer by zooplankton grazing. The influence of $CaCO_3$ precipitation on the light climate in late summer was also demonstrated. During the period of stratification, available phosphorus concentration is controlled by recycling within the epilimnion, primarily through plant and animal excretion. Comparison of simulated available phosphorus concentrations and concentrations of total dissolved phosphorus and soluble reactive phosphorus in the epilimnion suggest that the composition of the soluble unreactive phosphorus pool changes dramatically during the year and that the large pool of dissolved unavailable phosphorus during summer is composed of end products of material cycled several times through the food web.

Key words: phytoplankton dynamics, phosphorus cycle, Lake Ontario, ecological model, nutrient recycling, phytoplankton production

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A l'aide d'un modèle écologique du lac Ontario, nous interprétons les données recueillies durant l'Année internationale d'étude des Grands Lacs (mars 1972–avril 1973). On constate à l'analyse que la biomasse phytoplanctonique de printemps et d'automne est réglée par l'interaction de la radiation solaire incidente avec le mélage vertical, en été par limitation de la silice et du phosphore et à la fin de l'été par le broutage du zooplancton. Nous démontrons aussi l'influence de la précipitation de $CaCO_3$ sur le climat lumineux en fin d'été. Durant la période de stratification, la concentration de phosphore disponible est réglée par recyclage dans l'épilimnion, surtout par excrétion végétale et animale. Une comparaison des concentrations de phosphore disponible simulées et de celles de phosphore dissous total et de phosphore réactif soluble dans l'épilimnion donne à penser que la composition du pool de phosphore non réactif soluble change de façon dramatique durant l'année et que le grand pool de phosphore non disponible dissous en été est composé des produits finals d'un matériel plusieurs fois recyclé dans le réseau alimentaire.

LAKE Ontario, the lowermost lake in the chain of Laurentian Great Lakes, has experienced considerable stress over the past several decades. Among the Great Lakes, the rate of eutrophication in Lake Ontario has been surpassed only by that in Lake Erie (Beeton 1965, 1969). It is important to understand the overall ecology of Lake Ontario to assess its present condition, to evaluate trends in its trophic status, and to suggest actions that might be taken to restore and protect this precious water body.

By necessity, a lake the size of Lake Ontario has been studied through discrete and often isolated research programs. Over the past decade, several excellent studies have been conducted illuminating the controls and mechanisms of several important ecological and physical processes. For example, there have been studies on primary production and phytoplankton turnover rates (e.g. Glooschenko et al. 1974; Stadelmann and Munawar 1974; Munawar et al. 1974; Stadelmann et al. 1974); diurnal migrations of crustaceans (Wilson and Roff 1973); phosphorus and nitrogen cycling (Stadelmann and Fraser 1974); vertical transport of heat (Sweers 1970) and of carbon and phosphorus (Burns and Pashley 1974); grazing by zooplankton (Gloos-

chenko et al. 1972); large-scale horizontal diffusion (Kullenberg et al. 1973) and current regimes (Pickett and Richards 1975; Pickett 1976a, 1977; Pickett and Bermick 1977); and benthic community metabolism (Johnson and Brinkhurst 1971). However, there have been few attempts to examine simultaneously several of these processes through field or laboratory experiments. Where combinations of processes have been examined, it has been done, by necessity, for only one or two stations (e.g. Lean et al. 1975; Lean and Charlton 1976). Information from these studies is important for understanding ecosystem controls; however, because Lake Ontario is neither homogenous horizontally nor simple hydrodynamically, it is not possible to extrapolate information from one or two stations to estimate lakewide conditions as, for example, Jassby and Goldman (1974) were able to do for Castle Lake, Calif. Thus, a comprehensive view of whole-lake processes for Lake Ontario has not been possible.

Because it is unlikely that a large field program designed to investigate important processes on a lakewide scale is tractable for Lake Ontario, some other method of synthesizing the available information and of processing that information to generate insight into whole-lake processes is needed. One method of synthesis is to summarize available information on Lake Ontario, to intuit qualitatively the interactions among ecosystem components, and to attempt to deduce the relative importance of specific processes where information on those processes exists. Another method is to develop some mathematical representation of the ecosystem and the interactions among its components, and thereby to produce some quantitative, yet theoretical, information on the processes. The method employed in this work was to use a model of the Lake Ontario ecosystem, based on theoretical concepts of nutrient cycles and food web ecology, together with data collected on Lake Ontario to combine the above two approaches.

Output from the model can never supplant information derived from experimental and observational programs; however, because the model simultaneously processes information from several interacting ecosystem components, it provides a larger, more systematic framework than is usually available from isolated experiments. By examining the processes that control a certain component of the model ecosystem, one can evaluate the magnitude and relative importance of these processes on a seasonal basis. Also, hypotheses concerning certain processes that are not presently understood very well can be tested. In essence, the model is merely a testing ground for hypotheses. As Steele (1974) has suggested, the model does not create any new information, but rather it forces a quantitative analysis of the system as a whole. This analysis very often results in identification of important areas requiring further experimental work, which then brings coupled modeling-experimental programs (see Mortimer 1975) around full circle. The model, designed originally to test hypotheses generated by experimental and ob-

servational studies, can then be used to generate further hypotheses that must be tested experimentally.

By using this approach of combined data analysis and mathematical modeling, three aspects of the Lake Ontario ecosystem were examined: (1) the factors controlling the dynamics of phytoplankton biomass, (2) the seasonal dynamics of available phosphorus and the relationship of these dynamics to control of phytoplankton production, and (3) the apparent changes in chemical composition of various phosphorus compartments.

Model and Data

Empirical relationships (e.g. Vollenweider 1968; Dillon and Rigler 1974a) and mass balance models (e.g. Dillon and Rigler 1974b; Imboden 1974; Chapra 1977), developed to relate gross properties in lakes, are useful in describing or predicting long-term trends in water quality. However, these models fall short of providing much insight into the interrelationships within, and the control of, the complex aquatic ecosystems they represent (Shapiro 1978). Therefore, if one wishes to use models to investigate processes within the ecosystem, then other, more realistic models must be used.

More mechanistic models exist for Lake Ontario. Thomann et al. (1975) developed a eutrophication model based on phytoplankton dynamics for the purpose of estimating the impact of variations in nutrient loads. The model was applied in that context to assess various management alternatives (Thomann et al. 1977). Simons (1976) also used the model, within a three-dimensional hydrodynamic framework, to examine the influences of physical processes on the simulation of phytoplankton dynamics. Concurrently, another model was developed to simulate the flow of carbon, nitrogen, and phosphorus through the food web of Lake Ontario (Scavia et al. 1976a). The generality of the framework of this model was tested through applications to the other Great Lakes (Scavia et al. 1976b) and by comparison with output from some of the simpler models mentioned above (Scavia and Chapra 1977). The model used herein is an extension of this latter model.

The purpose of the model is to synthesize information on process kinetics into equations describing the rate of change of ecosystem components as functions of the components themselves, of environmental variables, and of group-specific coefficients. Process equations posed by experimentalists over the past several years are used to describe specific biological and chemical processes. Granted, for some of the processes more than one theory or hypothesis has been espoused by researchers as a control or regulator. Use of a particular process equation in the overall framework is one way to test that theory or hypothesis in the context of the larger system. As such, the model is merely a tool allowing a quantitative evaluation of isolated process theories in a whole-system context.

The model (Fig. 1) includes phytoplankton; zooplankton; cycles of phosphorus, nitrogen, silicon, and carbon; an oxygen balance; and calculations of the carbonate equilibrium system. A sediment compartment includes benthic invertebrates as well as cycles of carbon, phosphorus, nitrogen, and silicon. The reason for segregating phytoplankton and zooplankton each into several groups is to allow for differences in functional requirements (e.g.
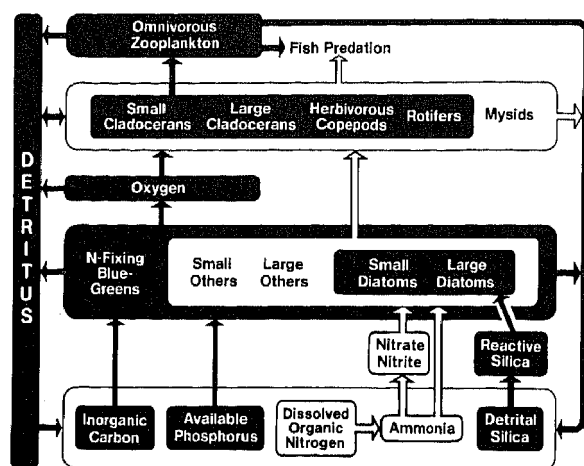
FIG. 1. Conceptualization of Lake Ontario ecological model.

TABLE 1. Lake Ontario phytoplankton and zooplankton functional groups used in the ecological model[a]

Small Diatoms		Small Cladocerans	
Melosira islandica		*Eubosmina coregoni*	
Stephanodiscus alpinus		*Bosmina longirostris*	
S. binderanus			
S. hantzschii		Large Cladocerans	
S. minutus			
S. subtilis		*Daphnia galeata*	
S. tenuis		*D. retrocurva*	
		D. longiremis	
Large Diatoms		*Ceriodaphnia lacustris*	
		Chydorus sphaericus	
Asterionella formosa		*Diaphanasoma*	
Diatoma tenue var. *elongatum*		*leuchtenbergianum*	
Fragilaria capucina			
F. crotonensis		Herbivorous Copepods	
Nitzschia bacata			
N. sp.		*Calanoid copepodites*	
Surirella angusta		*Diaptomus minutus*	
Taballaria fenestrata		*D. oregonensis*	
		D. sicilis	
		D. siciloides	
Small Others		*Eurytemora affinis*	
Flagellate #1	F	Carnivores/Omnivores	
Glenodinium and			
Gymnodinium spp.	Dn	*Cyclopoid copepodites*	
Gloecystis planctonica	G	*Cyclops biscuspidatus*	
Oocystis spp.	G	*C. vernalis*	
Oscillatoria limnetica	B	*Tropocyclops prasinus*	
Phacotus lenticularis	G		
Scenedesmus bicellularis	G	Blue-Green Algae with	
		Heterocyst	
Large Others			
		Anabaena flos-aquae	
Cryptomonas erosa	Cr	*A.* sp. #1	
Peridinium spp.	Dn	*A. variabilis*	
Staurastrum paradoxum	G		
Ulothrix subconstrictun	G		

[a]Algae other than blue-greens are only those whose annual average concentration is greater than 0.5 µg C/L (Stoermer and Ladewski 1978). Symbols are: B — blue-green without heterocyst; G — green; F — flagellate; Dn — dinoflagellate; Cr — cryptomonad. Zooplankton species from McNaught et al. (1975).

diatoms versus nondiatoms) and processes (e.g. size-selective filter feeders versus nonselective feeders). The major species of phytoplankton and zooplankton in Lake Ontario and their aggregation into functional groups are listed in Table 1.

Each model compartment is represented by a differential equation composed of important biological, chemical, and physical processes. For example, the phytoplankton equation includes terms for gross primary production, respiration, excretion, grazing, sinking, and vertical mixing, and the zooplankton equation includes terms for grazing, assimilation, respiration, excretion, defecation, and predation. Justification and rationales for the process equations used, as well as detailed documentation of the overall model are presented in Scavia (1979). What follows are general descriptions of the processes included in the model.

Gross phytoplankton production is considered a single-step process, which assumes, for the time-scale of the model (several days), that uptake and growth rates are equal. The process is modeled with a temperature-dependent, maximum growth rate times a reduction factor for light- and nutrient-limitation. Potential light-limitation is modeled after Vollenweider (1965) and Steele (1965) and potential nutrient-limitation is expressed as a Michaelis–Menten term for each nutrient. The threshold formulation is used to determine overall limitation. Phytoplankton respiration is considered as the sum of a low maintenance rate plus a term proportional to production, as well as being a function of temperature. To maintain constant nutrient stoichiometry within the plankton, nutrient excretion is proportional to respired carbon.

Zooplankton grazing is handled as a temperature-dependent Michaelis–Menten expression based on total food supply. The expression accounts for minimum thresholds for feeding as well as resource partitioning based on size-selection. Feeding and assimilation efficiency are regarded as food-specific constants. Food ingested but not assimilated is egested into the detritus pool. Respiration is a temperature-dependent process that is the sum of a low maintenance rate and a term proportional to the feeding rate. Nutrient excretion is proportional to respiration.

Transformation rates between detritus, dissolved organic nitrogen, ammonia, nitrate plus nitrite, available phosphorus, and available silicon pools all are temperature-dependent and first-order. Sinking rates of phytoplankton and detritus are size- and density-dependent. Vertical mixing is modeled as an exchange coefficient (see below) times the concentration gradient.

The model considers the lake to be homogeneous in the horizontal plane and to be segmented vertically into two layers representing the lake-wide average epilimnion and hypolimnion. A 1-dimensional, 18-layer diffusion model calibrated to temperature profiles measured in Lake Ontario is used to calculate depth of the thermocline and average epilimnion and hypolimnion temperatures. Values of the diffusion (or exchange) coefficient between the two layers are then calculated from temperature changes in
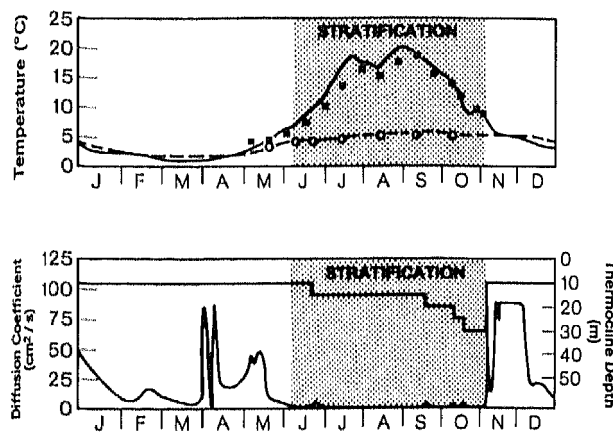
FIG. 2. Simulated and observed (Pickett 1976b) lakewide averaged temperatures. (*Top*): ■ — epilimnion, ○ — hypolimnion. Simulated thermocline depth and diffusion coefficients (*bottom*).

the two layers and from the extent of thermocline displacement (Fig. 2).

The ecological model was calibrated with data collected during the International Field Year for the Great Lakes (IFYGL) from March to November 1972. Documentation of the seasonal cycles of the IFYGL data and the model output, as well as detailed discussions of the model equations, coefficients, and sensitivity analyses, are presented elsewhere (Scavia 1979). Only the results of the analysis of phytoplankton production and phosphorus cycling are considered here. To ensure that the results that follow are not biased by a 1-yr simulation ·or impacted seriously by initial conditions, I ran the model to approach dynamic equilibrium (20–25 yr). I found the relative influence of the various controls of phytoplankton dynamics and phosphorus cycling at equilibrium to be not unlike those described here.

The data used in this paper were obtained from STORET, the data management system of the U.S. Environmental Protection Agency, and are based on data collected by the Canada Centre for Inland Waters as part of the Lake Ontario Organic Particle Study (Stadelmann and Fraser 1974).

Results and Discussion

Although the model includes detailed process equations describing the food web and nutrient cycles in Lake Ontario, it is still a crude representation of reality. Therefore, before this model was used to assist in the examination of lake-scale phytoplankton production and phosphorus cycling, it was tested, in this context, as to its adequacy as a representation of the seasonal changes in relevant lakewide averaged properties in Lake Ontario. This was done by comparisons between measured and simulated properties. The comparisons are best for those properties measured with least uncertainty (i.e. chemical properties) and worst for those properties difficult to measure (i.e. phytoplankton and zooplankton carbon concentrations); however, these comparisons resulted in general agreement between measured and
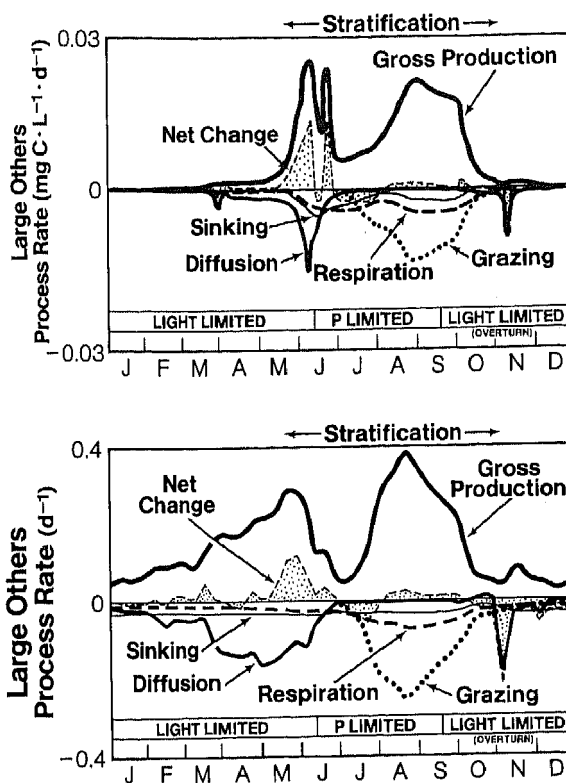

FIG. 3. Rate plots indicating simulated controls of epilimnion phytoplankton dynamics in Lake Ontario during 1972. Large Others represent nondiatoms greater than 20 μm. *Top* — Rates as d⁻¹, *bottom* — rates as mg C·L⁻¹·d⁻¹. Strippled area represents net growth rate.

simulated properties (Scavia 1979). These results demonstrate the model's ability to simulate the seasonal dynamics of phytoplankton, zooplankton, and the major nutrients; however, model output should also be compared to measurements of process rates to see how well the model simulates the internal dynamics of the system. Throughout the discussions that follow, both simulated and measured process rates are used to ensure that internal model dynamics are consistent with observations. I use process rates that were measured during IFYGL or measured in Lake Ontario during other years. Also, where certain processes were not observed in Lake Ontario, information from other field and laboratory studies are used for general comparisons. The simulated and measured rates were also in general agreement, which allows one to use the model to speculate about the relative importance of these processes.

PHYTOPLANKTON DYNAMICS

The simulated processes controlling the seasonal dynamics of the Large Others phytoplankton group in the epilimnion are shown in Fig. 3. The stippled area

on each graph indicates the net rate of change of the population biomass. In winter and early spring, this algal group, as well as the others, is controlled primarily by the balance between gross primary production and two physical processes, sinking and vertical mixing. During this time, phytoplankton gross production is limited mainly by the availability of light (Fig. 3), which is controlled both by the amount of incoming solar radiation and the depth to which the phytoplankters are mixed. Mixing between the two model layers becomes quite intense in early spring (Fig. 2), indicating that the mixing depth is the depth of the entire water column. This loss to the dark, deeper layers prevents substantial increases in algal biomass. Simons (1976) also found that even in three-dimensional simulations, the vertical mixing processes are very important in the early part of the year.

Riley (1942, 1946, 1963) and Riley et al. (1949) discussed the importance of the relationship between the depth of the euphotic zone and mixing depth. They suggested that phytoplankton can realize their productivity only after the thermocline begins to develop because it is only after this time that losses to the dark, non-productive strata are reduced. Significant increases in algal biomass occur only after midspring, when the surface waters in Lake Ontario begin to warm and the lake begins to stratify vertically (Fig. 3). At this time (early June), phytoplankton populations increase rapidly and the concentrations of the nutrients they assimilate begin to decrease. The concentrations of nutrients decrease because they also become relatively isolated from the nutrient-rich lower strata.

Diatoms, dominated by species (Table 1) with temperature optima in the lower range of Lake Ontario temperatures (Stoermer and Ladewski 1978), increase their productivity sooner than the other taxa. Consequently the diatoms assimilate available silicon and become limited by that nutrient before the other groups deplete the available phosphorus pool and become phosphorus-limited (Fig. 3). Late in the summer, phosphorus becomes limiting for diatoms as well. Phytoplankton production is limited by nutrients (silicon and phosphorus) from this time until the end of September, which has previously been suggested, based on mass balance considerations (Stadelmann and Fraser 1974) and on algal assays (Sridharan and Lee 1977).

During the same time period (late summer), grazing stress exerted by zooplankton becomes most intense (Fig. 3). This time history of simulated grazing pressure reflects the general seasonal pattern of crustacean zooplankton biomass (see Scavia 1979). All of the dominant species in Lake Ontario produced major biomass peaks during July or August in 1972 (McNaught et al. 1975). Also, for a previous year in Lake Ontario, Glooschenko et al. (1972) measured and compared the relative abundances of chlorophyll a and pheo-pigments and suggested that a high correlation between average percent pheo-pigment (relative to total chlorophyll a) and zooplankton abundance was probably a
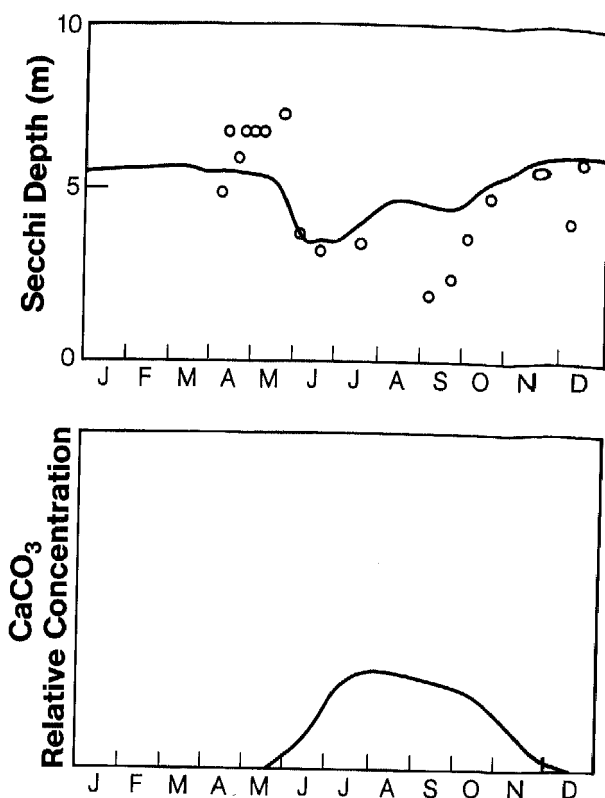

FIG. 4. *Top*: Simulated and observed Secchi depth. Simulation includes only effects of water color, algal carbon, and detrital carbon. *Bottom*: Simulated relative concentration of CaCO₃ precipitate forming in the epilimnion of Lake Ontario.

result of zooplankton grazing. On a lake-wide average basis, they found highest values for the percent of total chlorophyll a as pheo-pigments to occur in August–October. This further substantiates the simulation results in Fig. 3.

In late September the thermocline deepens (Fig. 2) and nutrient-rich, hypolimnetic water is mixed with epilimnetic water. Because of this increase in nutrient concentrations and the simultaneous increase in mixing depth, the algae again become limited by light. In early November the lake overturns and becomes vertically homogeneous and phytoplankton concentrations begin to approach winter values. Of course, this is a simplification of the three-dimensional effects discussed by Simons (1976); however in a one-dimensional model, all advective and dispersive processes are parameterized as vertical mixing.

Another factor in the control of phytoplankton production is the occurrence of "milky water" or CaCO₃ whitings in Lake Ontario. Kramer (1967) has demonstrated with equilibrium calculations that, for water temperatures greater than 13°C, Lake Ontario is saturated with respect to calcite. Eadie and Robertson
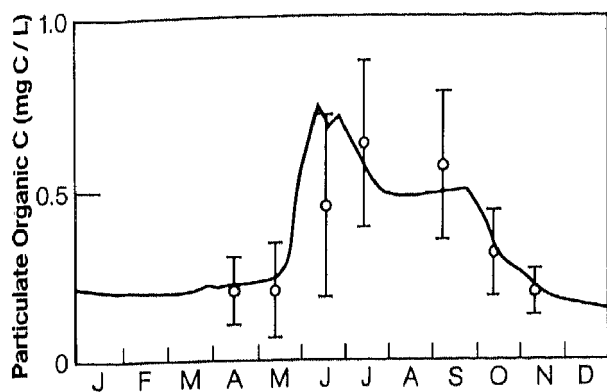
Fig. 5. Seasonal dynamics of data and model output for particulate organic carbon in the epilimnion (0–20 m) of Lake Ontario during 1972. Data are lakewide mean ± 1 SD.

(1976) discussed the seasonal trend in $CaCO_3$ saturation and indicated that in 1971–73 the epilimnion was highly supersaturated during the period of stratification. Satellite observations of these whitings (Strong and Eadie 1978) indicate that this phenomenon occurred in Lake Ontario during late August and September 1972. The whiting phenomenon has also been observed each year between 1972 and 1975, with the most intensive whitings observed in July–September 1973. Although the extent of the influence of these whitings on the lake's productivity is unclear at this time, Strong and Eadie suggest that the whitings may alter the light climate as well as scavenge nutrients, vitamins, and trace metals from the epilimnion.

Calculations of carbonate equilibrium, coupled with the ecological model, support the hypothesis that these whitings could have an impact on the lake's productivity and indicate that, if the whitings do affect primary production, they do so at a crucial time. Because the exact kinetics of crystal formation and dissolution are unknown and therefore not included in the model, the magnitude of the simulated concentration of $CaCO_3$ is not realistic; however, the timing of the peak of relative (or potential) concentration (Fig. 4) is consistent with theoretical considerations (Eadie and Robertson 1976) and observations (Strong and Eadie 1978). The potential impact of these whitings can be seen by examining seasonal variations in Secchi depth and concentration of particulate organic carbon (POC). Prior to and after the whitings, Secchi depths are accurately simulated by the model (Fig. 4). During these times, light extinction is due primarily to water color and particulate organic matter, both of which are accounted for in the Secchi depth calculations. The model, however, fails to simulate a 1.5-m decrease in Secchi depth in August. The concentration of POC (Fig. 5) during this time period also does not indicate that there should be a large change in transparency due to particulate organics. Simulation of the carbonate system (Fig. 4) indicates that the decreased trans-

parency may well be caused by formation of $CaCO_3$ crystals during this time period. Also, during the period of maximum potential crystal formation (August–September), the phytoplankton is already shifting from being nutrient-limited to being light-limited (Fig. 3), and thus the timing of the crystal formation may also be critical to production.

PHOSPHORUS CYCLING

Although it is clear from the above analysis that nutrient limitation does not solely control phytoplankton dynamics, the role of nutrients, especially phosphorus and silicon, is certainly critical during the period of stratification. The phytoplankters dominant during the summer months in Lake Ontario are limited primarily by phosphorus, as demonstrated in the simulations discussed above and as shown by recent experimental work (Sridharan and Lee 1977). Therefore, to understand better the control of phytoplankton dynamics in Lake Ontario, one must investigate the processes influencing the cycling of phosphorus.

Figure 6 illustrates the seasonal changes in the simulated concentration of available phosphorus and rate of gross primary production in the epilimnion. As discussed above, after spring the phytoplankton become limited by nutrients and thus the production rate decreases sharply. It is interesting to note that, although the production rate has decreased considerably, it does not approach low winter values and, in fact, after the initial drop, the rate increases gradually. This sustained production proceeds at the same time that available phosphorus concentrations, both actual and simulated (Fig. 6, 8a), are extremely low. One might expect that, with phosphorus concentrations this low ($<1 \mu g P/L$) and sustained phytoplankton production, phosphorus assimilation by algae would rapidly drive the concentration of phosphorus to virtually zero and thus severely limit further phytoplankton productivity. However, this is not the case. It appears that the supplies of phosphorus during this time period are sufficient to balance phytoplankton assimilation. Thus the importance of internal cycling of phosphorus (Golterman 1973; Rigler 1973) cannot be ignored. The sum of the rates of detritus remineralization, phytoplankton and zooplankton excretion, and diffusion input from the hypolimnion, is approximately equal to the rate of assimilation by phytoplankton. This analysis (Fig. 6) suggests that decomposer input is about one-fourth of the excretion input from algae and zooplankton during summer stratification and that phosphorus input from the lower strata is important only before and after stratification.

To examine more closely the relationships among the various processes in this conceptual phosphorus cycle, I constructed a phosphorus flow diagram (Fig. 7) from model output averaged over the period of July–September and compared the results to available information. The sizes of the five phosphorus compart-
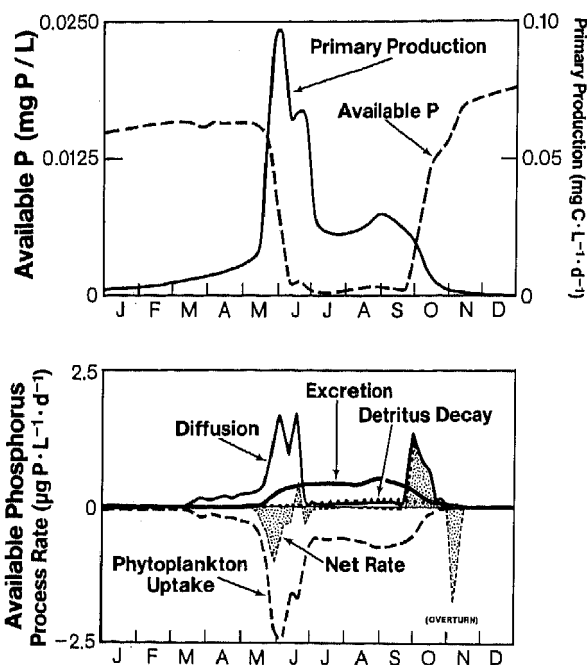
FIG. 6. *Top*: Simulated concentration of available phosphorus and rate of gross primary production in the epilimnion. *Bottom*: Rate plots indicating control of available phosphorus dynamics. Stippled area represents net rate of change.

TABLE 2. Lake-wide average relative recycle rates of phosphorus in the epilimnion of Lake Ontario during stratification (Total rate $= 0.629 \; \mu g \; P \cdot L^{-1} \cdot d^{-1}$).

	Percent of total recycle rate
Phytoplankton excretion	32.8
Zooplankton excretion	
Herbivores	27.3
Omnivores	10.2
Total	37.5
Detritus decay	17.0
External load	3.2
Hypolimnion load	9.5

ments are representative of Lake Ontario for this time period (Scavia 1979). The rate of conversion of available phosphorus to particulate phosphorus (Stadelmann and Fraser 1974) and the fluxes of phosphorus across the thermocline (Stadelmann and Fraser 1974; Burns and Pashley 1974) are also representative. Zooplankton grazing rates represent 50 and 53% of the animals' body phosphorus per day for omnivores and herbivores, respectively. This is consistent with general dry weight rations for small crustacean zooplankton (Parsons and Takahaski 1973). Zooplankton excretion rates represent 14 and 11% of body phosphorus per day for omnivores and herbivores, respectively. These rates agree with excretion rates summarized by Ganf and Blažka (1974) if one assumes for these animals a nitrogen to phosphorus body weight ratio of approximately 11 (cf. Parsons and Takahaski 1973). Quantitative information on other processes is not available and therefore, in those cases, model information alone will be used.

Figure 7 shows that it would take less than 1 d in the summer epilimnion for the phytoplankton to deplete the available phosphorus pool if there were no recycling and that external sources and hypolimnetic sources alone could not meet this algal phosphorus demand. In fact, this analysis indicates that 86% of the assimilated phosphorus is recycled within the epilimnion. Stadelmann and Fraser (1974) estimate this recycling to be

87–93% for the upper 20 m at a single station during the same time period.

Rigler (1973) suggested three possible sources for biological recycling of soluble PO_4-P: 1) direct release by ultraplankton (bacteria plus phytoplankton <30 μm), 2) excretion by zooplankton, and 3) enzymatic hydrolysis of organic compounds. Each of these sources has been studied separately and each has been cited as being very important. For example, Peters and Lean (1973), Peters and Rigler (1973), Ganf and Blažka (1974), Ferrante (1976), and others have examined the role of zooplankton excretion in the phosphorus cycle. Kuenzler (1970), Lean (1973a, b), Lean and Rigler (1974), and Lean and Nalewajko (1976) have demonstrated extracellular release of phosphorus by phytoplankton. The role of decomposers in nutrient cycling has been more difficult to quantify; however, in one study (DePinto and Verhoff 1977), incubation of laboratory phytoplankton cultures, when innoculated with a natural bacterial population from a eutrophic Michigan lake, resulted in remineralization of 74% of the algal phosphorus and nitrogen in 20–45 d. Golterman (1973) indicates that rates of autolysis may also be very high at times.

Rigler (1973) suggested that excretion by zooplankton and direct release from ultraplankton were equally important. The results of the present analysis (Fig. 7, Table 2) suggest that, for this five-compartment conceptualization, zooplankton excretion and direct release by phytoplankton are approximately equal and are the most important processes supplying phosphorus to the available pool. The rate of remineralization of detrital phosphorus is somewhat slower. This rate represents regeneration of approximately 1.7% of the detrital phosphorus per day, which is within the range measured by DePinto and Verhoff (1977). The general results (Fig. 7) are quite similar to Rigler's "provisional" model (his Fig. 5) when the different conceptualizations are considered and the relative phosphorus flows are compared.

The role of zooplankton in the phosphorus cycle must be emphasized. While the zooplankton has an obvious role in applying pressure to reduce algal con-

FIG. 7. Phosphorus flow diagram. Concentration in boxes are in μg P/L and in pipes in μg P·L^{-1}·d^{-1}. These values are averaged over the period of July–September for the top 15 m. Phytoplankton, zooplankton, and detritus are evaluated in the model in terms of carbon and are converted to phosphorus for this figure by assuming a C$_{106}$P$_1$ atomic ratio.

centrations (Fig. 3), it also appears to play a dual role in recycling phosphorus. Not only does the zooplankton input directly to the available nutrient pools through excretion, but it also serves as a supplier of detrital material (feces), which undergoes additional degradation by the decomposers and eventually adds to the available nutrient supply. Thus, it may well be that the zooplankton is principally responsible for the high recycling rates estimated by Stadelmann and Fraser in Lake Ontario.

PHOSPHORUS AVAILABILITY

The final aspect of the control of phytoplankton dynamics and phosphorus cycling to be considered here is phosphorus availability. It is commonly held that free orthophosphate (PO$_4$) is the phosphorus form most readily used by algae (Rigler 1973); however, assimilation of dissolved organic phosphorus (DOP), as demonstrated by Kuenzler (1970) and Paerl and Downes (1978), may also be important. Kuenzler showed reassimilation of DOP, through hydrolysis by extracellular alkaline phosphatase, by the same four marine algal species that had previously eliminated the DOP. Paerl and Downes demonstrated stimulation of P-starved *chlorella* when high molecular weight reactive P was added to the cultures. In addition to the direct use of DOP by algae, extracellular regeneration of PO$_4$ by other means also increases the potential supply of available phosphorus. Lean (1973a, b) demonstrated this regeneration of phosphorus in Heart Lake, and Peters (1978) estimated that available phosphorus in tributaries to Lake Memphremogog probably varied between 8 and 100% of total phosphorus. Cowen and Lee (1976) determined with algal assays that, of the phosphorus present in the tributaries to Lake Ontario, the fraction available for algal growth, on the average,
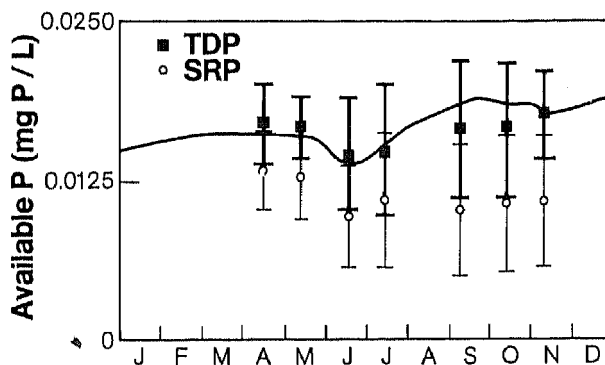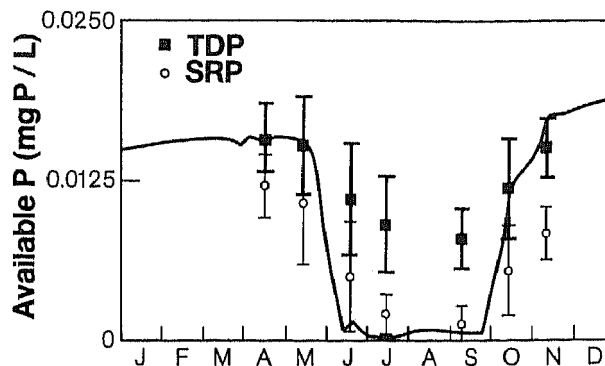

FIG. 8. Seasonal dynamics of TDP, SRP, and modeled available phosphorus (solid line) in the (a) epilimnion and (b) hypolimnion of Lake Ontario for 1972. Data are lake-wide mean ± 1 SD.

consists of the soluble reactive phosphorus (SRP) pool plus approximately 20% of the sum of all other phosphorus forms. This type of "availability" is a function of the time scales of interest. If one were only interested in phosphorus available at one particular instant, PO$_4$ (if it could be measured) would probably be the best estimate; however, the amount of phosphorus eventually available over a given time period is a function of the length of the time period (Chamberlain and Shapiro 1973) and the strength of the hydrolytic potential present during that period.

If one assumes that, under the time scale of interest in this work, particulate phosphorus is unavailable, then the concentration of available phosphorus lies somewhere between total dissolved phosphorus (TDP) and PO$_4$. Figure 8a illustrates the seasonal changes of epilimnetic concentrations of TDP, available phosphorus (by definition in the model), and SRP (which is likely to be an overestimate of PO$_4$, Rigler [1973], Paerl and Downes [1978]). Modeled phosphorus is separated simply into forms that are available, unavailable, and in living plankton. The results shown here suggest that a large fraction of soluble unreactive phosphorus (SUP = TDP — SRP) is available to the phytoplankton in early spring and after fall overturn. Paerl

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and Downes (1978) found, in a study of two New Zealand lakes, that higher molecular weight phosphorus was available for algal growth during 4-d incubations. It also appears from these simulations that most of the SUP, and in fact some of the SRP, is unavailable for algal growth during the period of summer stratification. These results imply that not only does the concentration of available phosphorus change seasonally (hence, phosphorus limitation), but the percent of TDP that is available also changes. This then implies that the composition of SUP, and thus the capacity to hydrolyze PO_4 from the SUP pool, changes seasonally.

In a study on Lake Kinneret, Berman (1970) found the extent of hydrolysis of organic phosphorus by natural phosphatases also changed seasonally. Hydrolysis in August, September, and November was lower than at other times; however, phosphatase activity in the lake was not severely reduced and, when phosphorus-laden water from a commercial fish pond was added to these samples, PO_4 was effectively released. He concluded that the lower rates of hydrolysis during August, September, and November were due to the existence of phosphorus forms resistant to enzymatic breakdown rather than due to a lack of enzymes in the lake. This may also be an explanation for the apparently large fraction of unavailable SUP in Lake Ontario during summer (Fig. 8a). The SUP pool may be composed of refractory compounds that are the end products of organic matter cycled several times through the food web. This suggestion of high rates of cycling was also evident from the analysis above (Fig. 7).

Berman also suggested that, under suitable conditions, gradual release of PO_4 from these more resistant phosphorus forms could occur. This may be occurring in the hypolimnion of Lake Ontario, where decomposition of unavailable phosphorus in the absence of primary production results in almost all of the dissolved phosphorus becoming available (Fig. 8b). This results in an increase in the availability of SUP in the epilimnion after fall overturn.

Summary

In other simulations of Lake Ontario phytoplankton, Thomann et al. (1975) and Scavia et al. (1976a) examined the relationship among modeled processes affecting phytoplankton and phosphorus dynamics. In the present study, an ecological model, based on process constructs posed by experimentalists over the past several years, driven by forcing functions that were measured and simulated specifically during IFYGL, and calibrated to lakewide averaged measurements of biological and chemical properties (Scavia 1979) was used in conjunction with in situ measurements and results from laboratory process studies to suggest important aspects of the control of phytoplankton production and phosphorus cycling in Lake Ontario during IFYGL.

The analysis indicated that, during 1972, Lake Ontario phytoplankton were controlled by several interacting processes. They were limited in spring by deep vertical mixing, in early summer by low phosphorus concentration, and in late summer by zooplankton grazing. Rapid internal recycle rates, especially due to zooplankton dynamics during late summer, provide phosphorus sufficient to maintain moderate phytoplankton production while SRP concentrations were generally low (1-2 μg P/L). Internal recycling rates of phosphorus were much higher than rates of external loading and influx from the hypolimnion. These controls of recycling and phytoplankton dynamics, estimated for IFYGL, are similar to controls suggested in the previous studies, which were based primarily on simulations.

It was also suggested, in the present study, that composition of the available phosphorus pool changes seasonally. It appears that the concentration of available phosphorus is most closely related to the total dissolved phosphorus pool in early spring and fall and is less than the concentration of the SRP pool during summer. The large fraction of soluble unreactive phosphorus that is unavailable to phytoplankton during summer may be composed of compounds relatively resistant to natural hydrolysis.

I have used an ecological model of Lake Ontario to synthesize information collected on individual ecosystem components and processes during IFYGL. Coupling this synthesis tool with traditional limnological analyses offered a more complete description of the control of phytoplankton dynamics and phosphorus cycling in Lake Ontario.

Acknowledgments

BEETON, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.
1969. Changes in the environment and biota of the Great Lakes, p. 150–187. In Eutrophication: causes, consequences, correctives. National Academy of Science, Washington, D.C.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 15: 663–674.

BURNS, N. M., AND A. PASHLEY. 1974. In situ measurement of the settling velocity profile of particulate organic carbon in Lake Ontario. J. Fish. Res. Board Can. 31: 291–297.

CHAMBERLAIN, W., AND J. SHAPIRO. 1973. Phosphate measurements in natural waters — A critique, p. 355–366. In. E. J. Griffiths, A. Beeton, I. M. Spencer, and D.

Mitchell [ed.] Environmental phosphorus handbook. Wiley, New York, N.Y.

CHAPRA, S. C. 1977. Total phosphorus model for the Great Lakes. J. Env. Eng. Div. (ASCE). 103: 147–161.

COWEN, W. F., AND G. F. LEE. 1976. Algal nutrient availability and limitation in Lake Ontario during IFYGL. Part 1. Available phosphorus in urban runoff and Lake Ontario tributary waters. U.S. Environ. Prot. Agency Rep. EPA-600/3-76-094a: 218 p.

DEPINTO, J. V., AND F. H. VERHOFF. 1977. Nutrient regeneration from aerobic decomposition of green algae. Environ. Sci. Tech. 11: 371–377.

DILLON, P. J., AND F. H. RIGLER. 1974a. The phosphorus–chlorophyll relationship in lakes. Limnol Oceanogr. 19: 767—773.

——— 1974b. A test of a simple model predicting the phosphorus concentration in lake water. J. Fish. Res. Board Can. 31: 1771–1778.

EADIE, J. B., AND A. ROBERTSON. 1976. An IFYGL carbon budget for Lake Ontario. J. Great Lakes Res. 2: 207–323.

FERRANTE, J. G. 1976. The role of zooplankton in the intrabiocenotic phosphorus cycle and factors affecting phosphorus excretion in a lake. Hydrobiologia. 49: 203—214.

GANF, G. G., AND P. BLAŽKA. 1974. Oxygen uptake, ammonia and phosphate excretion by zooplankton in a shallow equatorial lake (Lake George, Uganda). Limnol. Oceanogr. 19: 313–325.

GLOOSCHENKO, W. A., J. E. MOORE, AND R. A. VOLLENWEIDER. 1972. The seasonal cycle of pheo-pigments in Lake Ontario with particular emphasis on the role of zooplankton grazing. Limnol. Oceanogr. 17: 597–605.

GLOOSCHENKO, W. A., J. E. MOORE, M. MUNAWAR, AND R. A. VOLLENWEIDER. 1974. Primary production in Lakes Ontario and Erie: a comparative study. J. Fish. Res. Board Can. 31: 253–263.

GOLTERMAN, H. L. 1973. Vertical movement of phosphate in freshwater. p. 509–538. In E. J. Griffiths, A. Beeton, I. M. Spencer, and D. Mitchell [ed.] Environmental phosphorus handbook. Wiley, New York, N.Y.

IMBODEN, D. M. 1974. Phosphorus model of lake eutrophication. Limnol. Oceanogr. 19: 297–304.

JASSBY, A. D., AND C. R. GOLDMAN. 1974. Loss rates from a lake phytoplankton community. Limnol. Oceanogr. 19: 618–627.

JOHNSON, M. G., AND R. O. BRINKHURST. 1971. Benthic community metabolism in Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1715–1725.

KRAMER, J. R. 1967. Equilibrium models and the composition of the Great Lakes, p. 243–254. In Equilibrium concepts in natural waters. Adv. Chem. Ser. 67. Am. Chem. Soc., Washington, D.C.

KUENZLER, E. J. 1970. Dissolved organic phosphorus excretion by marine phytoplankton. J. Phycol. 6: 7–15.

KULLENBERG, G., C. R. MURTHY, AND H. WESTBERG. 1973. An experimental study of diffusion characteristics in the thermocline and hypolimnion regions of Lake Ontario, p. 774–790. In Proc. 16th Conf. Great Lakes Res. Int. Assoc. for Great Lakes Res.

LEAN, D. R. S. 1973a. Phosphorus dynamics in lake waters. Science 179: 678–680.

——— 1973b. Movements of phosphorus between its biologically important forms in lake water. J. Fish. Res. Board Can. 30: 1525–1536.

LEAN, D. R. S., AND M. N. CHARLTON. 1976. A study of phosphorus kinetics in a lake ecosystem, p. 283–294. In J. O. Nriagu [ed.] Environmental biogeochemistry: Vol. 1 Carbon, nitrogen, phosphorus, sulphur, and selenium cycles. Ann Arbor Science Publ., Ann Arbor, Mich.

LEAN, D. R. S., M. N. CHARLTON, B. K. BURNISON, T. P. MURPHY, S. E. MILLARD, AND K. R. YOUNG. 1975. Phosphorus: Changes in ecosystem metabolism from reduced loading. Verh. Int. Verein. Limnol. 19: 249–257.

LEAN, D. R. S., AND C. NALEWAJKO. 1976. Phosphate exchange and organic phosphorus excretion by freshwater algae. J. Fish. Res. Board Can. 33: 1312–1323.

LEAN, D. R. S., AND F. A. RIGLER. 1974. A test of the hypothesis that abiotic phosphate complexing influences phosphorus kinetics in epilimnion lake water. Limnol. Oceanogr. 19: 784–788.

McNAUGHT, D. C., M. BUZZARD, AND S. LEVINE. 1975. Zooplankton production in Lake Michigan as influenced by environmental perturbations. U.S. Environ. Prot. Agency Rep. EPA-600/3-75-021.

MORTIMER, C. H. 1975. Modeling of lakes as physico-biochemical systems — present limitations and needs, p. 217–232. In J. C. J. Nihoul [ed.] Modeling of marine systems. Oceanogr. Series, vol. 10. Elsevier, New York, N.Y.

MUNAWAR, M., P. STADELMANN, AND I. F. MUNAWAR. 1974. Phytoplankton biomass, species composition and primary production at a near shore and mid-lake station of Lake Ontario during IFYGL, p. 629–652. In Proc. 17th Conf. Great Lakes Res. Int. Assoc. for Great Lakes Res.

PAERL, H. W., AND M. T. DOWNES. 1978. Biological availability of low versus high molecular weight reactive phosphorus. J. Fish. Res. Board Can. 35: 1639–1643.

PARSONS, T., AND M. TAKAHASKI. 1973. Biological oceanographic processes. Pergamon Press, New York, N.Y.

PETERS, R. H. 1978. Concentrations and kinetics of phosphorus fractions in water from streams entering Lake Memphremagog. J. Fish. Res. Board Can. 35: 315–328.

PETERS, R. H., AND D. R. S. LEAN. 1973. The characterization of soluble phosphorus released by limnetic zooplankton. Limnol. Oceanogr. 18: 270–279.

PETERS, R. H., AND F. A. RIGLER. 1973. Phosphorus release by Daphnia. Limnol. Oceanogr. 18: 821–839.

PICKETT, R. L. 1976a. Lake Ontario circulation in November. Limnol. Oceanogr. 21: 608–611.

——— 1976b. Lake Ontario temperature and current profiles. IFYGL Bull. No. 18: 53–55.

——— 1977. The observed winter circulation of Lake Ontario. J. Phys. Oceanogr. 7: 152–156.

PICKETT, R. L., AND S. BERMICK. 1977. Observed resultant circulation of Lake Ontario. Limnol. Oceanogr. 22: 1071–1076.

PICKETT, R. L., AND F. P. RICHARDS. 1975. Lake Ontario mean temperature and currents in July 1972. J. Phys. Oceanogr. 5: 775–781.

RIGLER, F. H. 1973. A dynamic view of the phosphorus cycle in lakes, p. 539–572. In E. J. Griffiths, A. Beeton, J. M. Spencer, and D. T. Mitchell [ed.] Environmental phosphorus handbook. Wiley, New York, N.Y.

RILEY, G. A. 1942. The relationship of vertical turbulence and spring diatom flowerings. J. Mar. Res. 5: 67–87.

——— 1946. Factors controlling phytoplankton populations on Georges Bank. J. Mar. Res. 6: 54–73.

——— 1963. Theory of food-chain relations in the ocean,

p. 438–463. *In* M. N. Hill [ed.] The sea. Interscience, New York, N.Y.

RILEY, G. A., H. STOMMEL, AND D. F. BUMPUS. 1949. Quantitative ecology of the plankton of the western North Atlantic. Bull. Bingham Oceanogr. Coll. 12: 1–169.

SCAVIA, D. 1979. An ecological model of Lake Ontario. Ecol. Model. (In press)

SCAVIA, D., AND S. C. CHAPRA. 1977. Comparison of an ecological model of Lake Ontario and phosphorus loading models. J. Fish. Res. Board Can. 34: 286–290.

SCAVIA, D., J. B. EADIE, AND A. ROBERTSON. 1976a. An ecological model for Lake Ontario — model formulation, calibration, and preliminary evaluation. Natl. Ocean. Atmos. Admin. Rep. ERL 371-GLERL12. Boulder, Colo. 63 p.

1976b. An ecological model for the Great Lakes, p. 629–633. *In* W. T. Ott [ed.] Environmental modeling and simulation. U.S. Environ. Prot. Agency Rep. EPA-600/9-76-016. Washington, D.C.

SHAPIRO, J. 1978. The need for more biology in lake restoration. Contribution No. 183 from the Limnological Research Center, University of Minnesota, Minneapolis, Minn. 19 p.

SIMONS, T. J. 1976. Analysis and simulation of special variations of physical and biochemical processes in Lake Ontario. J. Great Lakes Res. 2: 215–233.

SRIDHARAN, N., AND G. F. LEE. 1977. Algal nutrient availability and limitation in Lake Ontario during IFYGL. U.S. Environ. Prot. Agency Rep. EPA-600/3-77-046a.

STADELMANN, P., AND A. FRASER. 1974. Phosphorus and nitrogen cycle on a transect in Lake Ontario during the International Field Year 1972–1973 (IFYGL), p. 92–107. *In* Proc. 17th Conf. Great Lakes Res. Int. Assoc. for Great Lakes Res.

STADELMANN, P., J. E. MOORE, AND E. PICKETT. 1974. Primary productivity in relation to temperature, structure, biomass, concentration, and light conditions at an inshore and offshore station in Lake Ontario. J. Fish. Res. Board Can. 31: 1215–1232.

STADELMAN, P., AND M. MUNAWAR. 1974. Biomass parameters and primary production at a nearshore and a mid-lake station of Lake Ontario during IFYGL, p. 109–119. *In* Proc. 17th Conf. Great Lakes Res. Int. Assoc. for Great Lakes Res.

STEELE, J. H. 1965. Notes on some theoretical problems in production ecology, p. 383–398. *In* C. R. Goldman [ed.] Primary productivity in aquatic environments. Univ. California Press, Berkeley, Calif.

1974. The structure of marine ecosystems. Harvard Univ. Press, Cambridge, Mass. 128 p.

STOERMER, E. F., AND T. B. LADEWSKI. 1978. Phytoplankton associations in Lake Ontario during IFYGL. Great Lakes Res. Div. Univ. Mich. Spec. Rep. 62: 106 p.

STRONG, A. E., AND B. J. EADIE. 1978. Satellite observations of calcium carbonate precipitations in the Great Lakes. Limnol. Oceanogr. 23: 877–887.

SWEERS, H. E. 1970. Vertical diffusivity coefficient in a thermocline. Limnol. Oceanogr. 15: 273–280.

THOMANN, R. V., D. M. DITORO, R. P. WINFIELD, AND D. J. O'CONNOR. 1975. Mathematical modeling of phytoplankton in Lake Ontario. 1. Model development and verification. Environmental Protection Agency. Corvallis, Oregon, 660/3-75-005.

THOMANN, R. V., R. P. WINFIELD, AND D. S. SMUSKI. 1977. Estimated responses of Lake Ontario phytoplankton biomass to varying nutrient levels. J. Great Lakes Res. 3: 123–131.

VOLLENWEIDER, R. A. 1965. Calculation models of photosynthesis-depth curves and some implications regarding day rate estimating in primary production measurements, p. 425–457. *In* C. R. Goldman [ed.] Primary productivity in aquatic environments. Univ. California Press, Berkeley, Calif.

1968. The scientific basis of lake and stream eutrophication with particular reference to phosphorus and nitrogen as eutrophication factors. Organ. Econ. Coop. Dev. Tech. Rep. DAS/DSI/68.27: 182 p.

WILSON, J. B., AND J. C. ROFF. 1973. Seasonal vertical distributions and diurnal migration patterns of Lake Ontario crustacean zooplankton, p. 190–203. *In* Proc. 16th Conf. Great Lakes Res. Int. Assoc. for Great Lakes Res.