

AN ECOLOGICAL MODEL OF LAKE ONTARIO *

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ABSTRACT

Scavia, D., 1980. An ecological model of Lake Ontario. *Ecol. Modelling*, 8: 49–78.

An ecological model of the epilimnion, hypolimnion and sediment of Lake Ontario is described. The model is based on realistic process equations posed by experimentalists over the past several decades and it simulates observations made of several phytoplankton and zooplankton groups; components of the phosphorus, nitrogen, silicon and carbon cycles; dissolved oxygen; and particulate sediment and pore water dynamics during the International Field Year for the Great Lakes (IFYGL). Model output is aggregated into a carbon flow diagram to illustrate the importance of detritus and herbivorous zooplankton in the ecology of Lake Ontario. The model serves as a synthesis tool for analysis of the large ecosystem.

INTRODUCTION

In 1972 the United States and Canada mounted an intense field program on Lake Ontario (Ludwigson, 1974). The International Field Year for the Great Lakes (IFYGL), a multi-million dollar program, focused about 600 scientists from over 70 federal, state, provincial, academic and private institutions into nearly 150 scientific tasks to study the meteorology, hydrology and physical, chemical and biological limnology of Lake Ontario. With this large amount of resources expended to collect and analyze environmental information, it is important to provide a means of synthesizing the information to allow a whole-system analysis of the field year. One such method is mathematical modeling.

During IFYGL three major biological and chemical modeling efforts were undertaken (Robertson and Scavia, 1978), each emphasizing a different aspect of the Ontario ecosystem. Thomann et al. (1975) developed a two-layer, horizontally homogeneous model incorporating one phytoplankton group, two zooplankton groups, and cycles of nitrogen and phosphorus. Their main objective was to simulate and predict eutrophication in Lake Ontario. Chen et al. (1975) developed an ecological model with seven layers

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and 42 horizontal segments simulating the seasonal and spatial dynamics of several groups of phytoplankton, zooplankton and fish, as well as the dynamics of carbon, phosphorus, nitrogen and silicon cycles. The major objective of this work was to examine the feasibility of these three-dimensional computations and to test the combined hydrodynamical—ecological model with field observations. Scavia et al. (1976a) developed an ecological model of Lake Ontario that simulates the seasonal dynamics of several phytoplankton and zooplankton groups; cycles of carbon, phosphorus and nitrogen; and the dynamics of benthic invertebrates in the epilimnion, the metalimnion, the hypolimnion and the lake sediment. The main objective of this work was to investigate the basic limnological and ecological properties of Lake Ontario on a lake-wide averaged basis.

The model developed by Thomann and co-workers has been used to predict Lake Ontario's response to various future load scenarios (Thomann et al., 1976; Hydrosience, 1976). The model produced by Chen and co-workers has been used to document the feasibility of three-dimensional ecological modeling (Chen and Smith, 1977) and to discuss some preliminary insights into such modeling efforts (Chen and Smith, 1979). The model developed by Scavia and co-workers has been tested by application to the other Great Lakes (Scavia et al., 1976b) and by comparison (Scavia and Chapra, 1977) to output from models of the phosphorus loading concept (Dillon and Rigler, 1974a and b), and a modified version has been used to examine specific aspects of the ecology of Lake Ontario (Robertson and Scavia, 1979; Scavia, 1979). The purpose of the present paper is to describe this modified version of the model (Scavia et al., 1976a), to document its usefulness in synthesizing much of the synoptic data amassed during IFYGL, and to demonstrate its use in analysis of whole-system functions.

THE MODEL

The model of Lake Ontario used in this work (Fig. 1) is an extension of an earlier model developed to simulate the flow of carbon, nitrogen and phosphorus through the food web (Scavia et al., 1976a). Process equations posed by experimentalists over the past several years are used here to describe specific biological and chemical processes. Below are outlined the process equations collected in the model, both those posed by experimentalists and those hypothesized from more qualitative information.

Phytoplankton

Five functional groups of phytoplankton are included in the model (Fig. 1, Table I); all require phosphorus and carbon, two require silicon (small and large diatoms), and all but one (nitrogen-fixing blue-green algae) require nitrate-nitrogen or ammonia. Carbon is assumed not to be limiting.

Recent studies have described phytoplankton growth as a two-step process

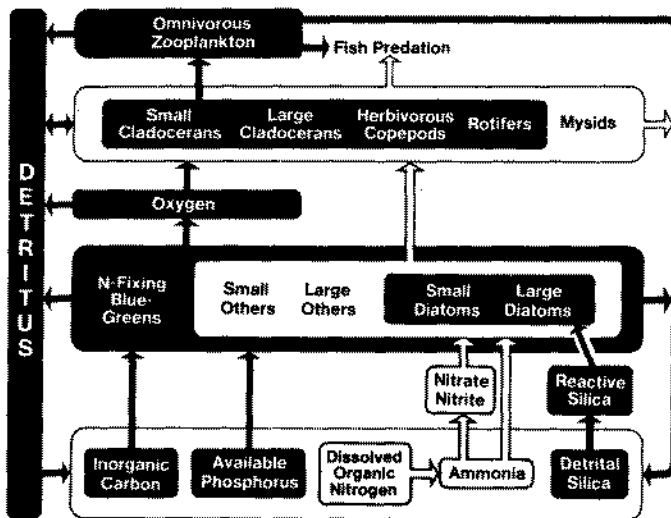


Fig. 1. Conceptualization of Lake Ontario ecological model.

including nutrient uptake and subsequent cell division. The reason for modeling the two processes separately (Lehman et al., 1975; Bierman, 1976) is to simulate the plankters' ability to create and use internal stores of nutrients. In the present model, however, phytoplankton growth rates are considered to be in steady state with nutrient uptake and thus growth can be related directly to the concentrations of nutrients in the water (Caperon and Meyer, 1972; Gavis, 1976). Growth rates are calculated with a temperature-dependent maximum rate times a reduction factor for nutrient and light limitation. The equation for temperature dependence provides a maximum rate at an optimum temperature, zero rate above a lethal temperature, and intermediate rates both above and below the optimum (Scavia and Park, 1976). Limitation of growth by a single nutrient is approximated by Michaelis-Menten expression. This expression has been used by others (Eppley and Thomas, 1969; Guillard et al., 1973; Kilham, 1975; Tilman, 1977) to describe phytoplankton growth as a function of ambient nutrient concentration. Light limitation is approximated by a time- and depth-integrated expression of the form used by Vollenweider (1965) and Steele (1965), which implies rate reductions both at low light intensities and at very high light intensities. Rhee (1978) has demonstrated that a threshold, or minimum, formulation is best for describing dual nutrient limitation in *Scenedesmus* cultures. We have extended this formulation to include light limitation as well. In this context, light in a water column is treated as a scarce resource rather than as an intensive rate controlling parameter such as temperature.

Phytoplankton respiration is described mathematically as the sum of two terms, one representing a low maintenance rate and one representing a potentially high rate that is proportional to primary production (Parsons and Takahashi, 1973; Platt et al., 1977). The overall respiration rate also varies

TABLE I

Phytoplankton and zooplankton groups *

Small diatoms		Small cladocerans	
<i>Melosira islandica</i>		<i>Eubosmina coregoni</i>	
<i>Stephanodiscus alpinus</i>		<i>Bosmina longirostris</i>	
<i>S. binderanus</i>			
<i>S. hantzschii</i>		Large cladocerans	
<i>S. minutus</i>		<i>Daphnia galeata</i>	
<i>S. subtilis</i>		<i>D. retrocurva</i>	
<i>S. tenuis</i>		<i>D. longiremis</i>	
		<i>Ceriodaphnia lacustris</i>	
Large diatoms		<i>Chydorus sphaericus</i>	
<i>Asterionella formosa</i>		<i>Diaphanasoma leuchtenbergianum</i>	
<i>Diatoma tenue</i> var. <i>elongatum</i>			
<i>Fragilaria capucina</i>		Herbivorous copepods	
<i>F. crotonensis</i>		Calanoid copepodites	
<i>Nitzschia bacata</i>		<i>Diaptomus minutus</i>	
<i>N. spp.</i>		<i>D. oregonensis</i>	
<i>Surirella angusta</i>		<i>D. sicilis</i>	
<i>Taballaria fenestrata</i>		<i>D. siciloides</i>	
		<i>Eurytemora affinis</i>	
Small others			
Flagellate no. 1	F	Carnivores/omnivores	
<i>Genodinium</i> and <i>Gymnodinium</i> spp.	Dn	Cyclopoid copepodites	
<i>Gloecystis planctonica</i>	G	<i>Cyclops bicuspidatus</i>	
<i>Oocystis</i> spp.	G	<i>C. vernalis</i>	
<i>Oscillatoria limnetica</i>	B	<i>Tropocyclops prasinus</i>	
<i>Phacotus lenticularis</i>	G	Blue-green algae with heterocyst	
<i>Scenedesmus bicellularis</i>	G	<i>Anabaena flos-aquae</i>	
		<i>A. spp. no. 1</i>	
Large others		<i>A. variabilis</i>	
<i>Cryptomonas erosa</i>	Cr		
<i>Peridinium</i> spp.	Dn		
<i>Staurostrum paradoxum</i>	G		
<i>Ulothrix subconstrictum</i>	G		

* Algae other than blue-greens are only those whose annual average concentration is greater than 0.5 $\mu\text{g C/l}$ (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).

with temperature in the same way as does the expression for growth rate.

Sedimentation out of the euphotic zone may or may not cause a significant loss of phytoplankton during different times of the year. Smayda (1970) has reviewed several mechanisms that affect phytoplankton buoyancy. These can be parameterized as three controls: (1) size/density, (2) shape, and (3) physiology. In this work size and density are used as follows in a basic Stokes for-

TABLE II
Sinking-rate coefficients

Group	Equivalent radius, r (μm)	Excess density $\Delta\rho$ (g/cm^3)	Shape correction
Small diatoms	5.0	0.19	1.3
Large diatoms	5.8	0.19	2.0
N fixers	3.2	0.027	1.0
Small others	9.0	0.027	1.0
Large others	10.0	0.027	1.0
Detritus	5.0	0.03	1.2

mulation for sinking:

$$S = \frac{2}{9} gr^2 \Delta\rho / \nu \quad (1)$$

Size, represented by the radius, r (Table II), of a sphere of equivalent volume, was estimated from typical sizes and shapes of the dominant phytoplankton species in each group (Stoermer and Ladewski, 1978). Excess density ($\Delta\rho$) is the difference between the densities of the water (~ 1.0) and the sinking particle. The density of diatoms is approximately 1.19 (Smayda, 1970) and the density of non-diatoms, assuming a composition of 90% water and 10% organic matter ($\rho \sim 1.27$), is estimated to be 1.027. The remaining factors in Eq. (1) are the gravitational constant (g) and the viscosity of water (ν). Sinking rates calculated from Eq. (1) are for inert spheres. Deviation from spherical geometry tends to increase structural viscosity and reduce sinking rates. Correction factors for substantially nonspherical particles (McNown and Malaika, 1950), based on representative shapes of dominant species, are also given in Table II.

The effects of physiological condition on phytoplankton sinking have been most recently investigated by Titman and Kilham (1976). They observed a four-fold increase in sinking rates of populations in a stationary growth phase over populations in an exponential growth phase. This factor from two to four also has been reported by Smayda and Boleyn (1965, 1966a and b), Eppley et al. (1967), Smayda (1970, 1974) and Boleyn (1972). For the purpose of relating sinking rates to physiological condition, the modeled sinking rate can be considered to be a linear function of the growth limitation terms such that, as the population becomes stressed due to the limitation by light or nutrients, the sinking rate increases. This mechanism was tested and the model was found to be insensitive to variations in sinking rates within the range of rates observed in the laboratory. The effect on sinking of the interaction between light and nutrients may, in fact, be more complicated (cf. Steele and Yentsch, 1960); however, sufficient information is not presently available to treat this phenomenon in greater detail.

Several authors have discussed the effects of water movement (usually

Langmuir circulation) on sinking rates of algae (Stommel, 1949; Hutchinson, 1967; Smayda, 1970; Titman and Kilham, 1976). If all water movements and diffusive processes were accounted for in a model, then sinking rates that have been measured under quiescent laboratory conditions would be appropriate to use for plankton at a given location in the water column. However, in horizontally averaged models, all water movements and diffusivities are represented by a single vertical dispersive term and, in this case, the sinking rate must represent losses from an average epilimnetic population rather than a population at a given depth. Use of this finite difference approximation will result in deviations from expected sinking losses if laboratory sinking rates are used, but these errors appear to be unimportant in these seasonal simulations.

Zooplankton

Six zooplankton types are considered in this analysis (Fig. 1, Table I). Herbivorous copepods are separated from cladocerans to allow for size-selective grazing (Mullin, 1963; Wilson, 1973); herbivorous cladocerans are divided into large (mainly daphnids) and small (mainly bosminids) groups to account for differential predation from carnivorous zooplankton and fish. Species in the omnivorous group are primarily cyclopoids (mainly *Cyclops bicuspidatus*), with cyclopoid copepodites making up a large fraction of the total biomass. The two remaining groups, rotifers and mysids, are included in order to investigate their potential importance in nutrient cycling and food chain structure. No provision is made to allow for different age classes within each modeled group.

Zooplankton feeding is described by a Michaelis-Menten expression with two modifications: (1) Feeding ceases when food concentration falls below a critical threshold value. This approximates Frost's (1975) observation that filtering rates are greatly reduced for food levels below a certain concentration. (2) Size-selective grazing coefficients are included in that they assign weights to the food types. Mullin et al. (1975) tested the ability of the Michaelis-Menten, Ivlev and rectilinear models to describe feeding by *Calanus pacificus*; they could not demonstrate statistical superiority for any of the expressions.

Selective grazing is modeled after O'Neill (1969). The expression allows animals to select (be it passive or active selection) certain types of food over others. The selectivity coefficient (W_i) represents the conditional probability that, if encountered, prey i will be eaten. The coefficients can be calculated from size-frequency ration data, filtering rates, feeding rates and Ivlev coefficients E and E' (Vanderploeg and Scavia, 1979). The selective grazing expression is

$$C_i = C_m \frac{\sum_i W_i X_i}{K + \sum_i W_i X_i} \frac{W_i X_i}{\sum_i W_i X_i} X_z = C_m \frac{W_i X_i}{K + \sum_i W_i X_i} X_z \quad (2)$$

where K is a half-saturation constant, X_i is the concentration of prey i , C_m is the temperature-dependent, weight-specific maximum feeding rate, $\sum_i W_i X_i$ is the concentration of total food "seen" by the predator, and X_p is the concentration of the predator. In the above expression, the first part can be recognized as the Michaelis-Menten term that relates grazing to the concentration of total food. The second factor is used to partition the total food eaten into each prey category. The value of C_i is set equal to zero if the concentration of food drops below the threshold value or if temperature exceeds an upper, lethal limit. Feeding (and assimilation) efficiency is a food-specific constant for each animal; food ingested but not assimilated is egested into the detritus pool.

Conover (1962), Blazka (1966), Comita (1968) and Omori (1970) observed that respiration rates are reduced in starved zooplankton; consequently, in this study, respiration is not only temperature-dependent, but also linearly related to the feeding rate. A low maintenance respiration rate is used during periods of decreased feeding. This expression allows for a reduction in the rate of metabolic losses during both cold and nutritionally poor periods.

Predatory pressures on the zooplankton are caused by carnivorous zooplankton and planktivorous fish. Zooplankton carnivory (including cannibalism) is modeled in the same way as described for herbivory. Fish predation is approximated by a prey specific, first-order loss rate for zooplankton concentrations above a threshold value and is equal to zero for zooplankton concentrations below the threshold.

Detritus

Food ingested by zooplankton but not assimilated becomes detritus, which also serves as a low quality food source for zooplankton. The chemical composition of detritus, as well as phytoplankton and zooplankton, is assumed to correspond to the atomic ratio $C_{106}N_{16}P_1$ (Redfield et al., 1963). To maintain this chemical composition, decomposition of detrital carbon is accompanied by stoichiometric remineralization of nitrogen and phosphorus and by stoichiometric consumption of oxygen. Here decomposition includes all processes that transform particulate organic matter into soluble inorganic nutrients except those processes included explicitly in the phytoplankton and zooplankton equations. Therefore, the transformations caused by bacteria, protozoa, zooplankton nauplii, and all other plankton not included in the 11 phytoplankton and zooplankton groups discussed above are simulated as temperature-dependent, first-order decay of detritus. Detritus sedimentation is handled the same as phytoplankton (see Table II) except no correction is made for physiological condition.

Phosphorus

Three general phosphorus compartments are considered (Fig. 1): (1) phosphorus in living organisms, (2) phosphorus in nonliving particles, and (3)

phosphorus available for phytoplankton assimilation. These categories account for all phosphorus fractions except particulate inorganic (assumed to be unimportant) and dissolved unavailable fractions. Clearly, the distinction between available and unavailable phosphorus is practical for this study; however, the fractions cannot be separated by standard analytical procedures (Rigler, 1973). The question of availability in this model's context is discussed in detail by Scavia (1979). Losses from the available phosphorus pool are proportional to phytoplankton growth since uptake and growth are assumed to be in steady state. The rate of phosphorus release by these organisms is made proportional to their respiration of carbon in order to maintain constant chemical composition of phytoplankton and zooplankton. This excreted phosphorus is assumed to be available for phytoplankton assimilation within one time step of model calculation.

Nitrogen

Five general nitrogen compartments are considered (Fig. 1): (1) nitrogen in living organisms, (2) nitrogen in nonliving particles, (3) dissolved organic nitrogen, (4) ammonia, and (5) nitrate plus nitrite. Detrital nitrogen decays into dissolved organic nitrogen; ammonification and then nitrification move nitrogen through the ammonia pool to the nitrate plus nitrite pool. Excreted nitrogen (proportional to respiration) is partitioned between the pools of dissolved organic nitrogen and ammonia (Corner and Newell, 1967; Butler et al., 1969).

Losses from the fixed nitrogen pool (ammonia and nitrate plus nitrite) are proportional to phytoplankton growth. It is well known that algae preferentially assimilate ammonia over nitrate (e.g., Caperon and Meyer, 1972); however, it is not clear if the presence of ammonia reduces nitrate uptake through suppressive (McIsaac and Dugdale, 1969) or competitive (Bienfang, 1975) processes. Preference for ammonia uptake over nitrate uptake is given by a Michaelis-Menten expression in terms of ammonia concentration. For cases where ammonia concentrations are low, nitrogen uptake is almost completely as nitrate. The preference for ammonia is reflected in the value of the half-saturation constant.

Silicon

Three general silicon compartments are considered (Fig. 1): (1) silicon associated with living diatoms, (2) silicon associated with dead diatoms (detrital silica), and (3) silicon available for diatom assimilation. In Lake Ontario, the fraction of the total phytoplankton community that is composed of diatoms changes considerably during the year (Stoermer and Ladewski, 1978) and therefore the C : Si ratio of zooplankton fecal material will also vary seasonally. Since the chemical composition of this input to the detritus pool cannot be considered constant, detrital silicon is modeled separately

from detrital carbon, nitrogen and phosphorus. All silicon ingested by zooplankton is immediately shunted to this detrital pool, which sinks like detrital carbon and dissolves according to a temperature-dependent, first-order reaction.

In addition to dissolution of detrital silicon, input to the pool of available silicon is through release from actively growing diatoms, which has been measured to be as high as 15% of the maximum silicon uptake rate for a marine diatom (Nelson et al., 1976).

Dissolved oxygen

Dissolved oxygen increases because of phytoplankton production and atmospheric gas exchange, and is consumed through phytoplankton and zooplankton respiration, detritus decomposition (decomposer respiration) and nitrification. The oxygen balance is related to respiration and phytoplankton production through an $O_2 : C$ mass ratio of 2.67 and to nitrification through an $O_2 : N$ mass ratio of 4.57. Atmospheric exchange rates are calculated as the product of the oxygen deficit, relative to saturation, and a reaeration coefficient that is a function of wind speed (Chen and Orlob, 1975).

Carbonate system

The major potential sources of dissolved inorganic carbon are phytoplankton and zooplankton respiration, detritus decay (decomposer respiration), and atmospheric exchange. Phytoplankton consume carbon at a rate proportional to their growth rate. Because the kinetics of speciation within the carbonate system are much faster than the biological kinetics under investigation in this study, all carbon is made available to the algae and no provision is made to differentiate between the use of H_2CO_3 and HCO_3^- (cf. King, 1972; Shapiro, 1973; Goldman et al., 1974; King and Novak, 1974).

In Lake Ontario, atmospheric exchange of CO_2 is a source of carbon during summer and a sink of carbon at other times (Eadie and Robertson, 1976). This process is described as the product of an exchange constant, which is a function of wind speed and CO_2 solubility, and the difference between the partial pressures of atmospheric and dissolved CO_2 (Kanwisher, 1963; Liss, 1973). Carbonate equilibrium calculations are coupled to the slower ecological kinetics to determine the partial pressure of dissolved CO_2 and to calculate the precipitation and dissolution of carbonates. The concentration of carbon is known at the end of each model time step and, by assuming that alkalinity remains constant, carbonate equilibrium can be re-established by solving a set of algebraic equations (Park, 1969). These equations provide estimates of the concentrations of H_2CO_3 , HCO_3^- and CO_3^{2-} , and of the pH. From H_2CO_3 , the partial pressure of CO_2 is calculated and, from CO_3^{2-} and average concentrations of Ca^{2+} , Mg^{2+} and Na^{2+} , the potential for carbonate precipitation or dissolution is calculated. Carbonate precipitation is assumed to occur

when the ion product of CO_3^{2-} and the appropriate cations are above 150% saturation. These precipitates are then subject to sinking and diffusion, as well as to dissolution, the last of which is assumed to occur when the ion product is below 67% saturation.

Physics

The important physical factors in a horizontally averaged, one-dimensional model are (1) incident solar radiation and the light extinction coefficient, (2) temperature, and (3) diffusion. Solar radiation is added as linearly interpolated weekly averages of output from a model that accurately simulates over-lake conditions during IFYGL (Atwater and Ball, 1974). The extinction coefficient is a base value (0.25 m^{-1}) plus a linear function of detrital carbon and phytoplankton carbon.

Detailed vertical profiles of temperature measurements were made during IFYGL except during some winter months. In order to provide a continuous record of temperature and to estimate effective diffusion coefficients, an 18-layer, horizontally averaged, one-dimensional diffusion model (after Sundaram and Rehm, 1973) was calibrated to available temperature profiles. Output from this model was used to obtain estimates of thermocline depth, average epilimnion and hypolimnion temperatures, and effective diffusion coefficients based on temperature gradients and thermocline displacement. As can be seen (Fig. 2), the seasonal dynamics of the average temperatures are simulated quite well. The results for diffusion coefficients are also con-

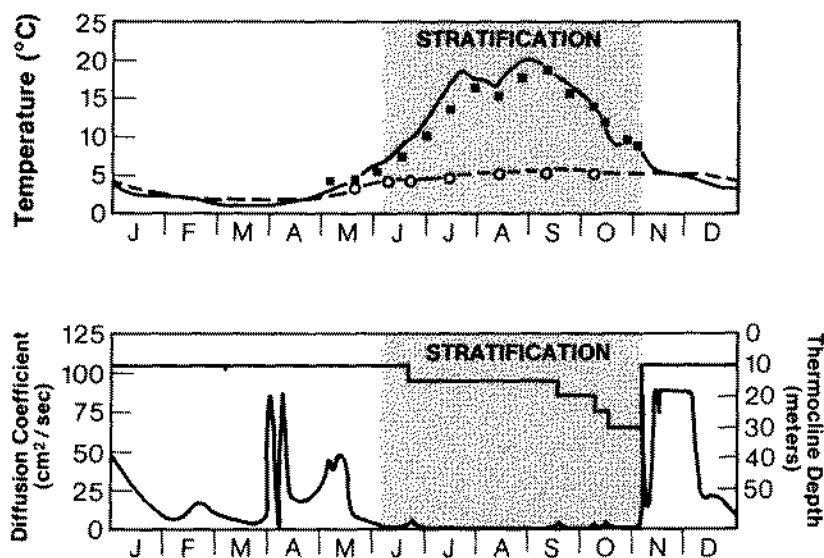


Fig. 2. Simulated and observed (Pickett, 1976) lake-wide averaged temperatures (top): ■ — epilimnion, ○ — hypolimnion. Simulated thermocline depth and diffusion coefficients (bottom).

sistent with those calculated by Sweers (1970) from previous years' summer data.

Sediment variables

Sediment dynamics are driven by sedimentation of phytoplankton and detritus (Fig. 3). The kinetics of the transformation from particulate organic compounds to dissolved nutrients are temperature dependent and first order. Consumption and respiration rates for benthic macro-invertebrates are empirical functions of temperature (Johnson and Brinkhurst, 1971), and excretion of phosphorus and nitrogen is related stoichiometrically to respiration. A sediment oxygen balance is calculated from rates of benthos respiration and of decomposition of organic matter and ammonia. The only source of oxygen is diffusion from the overlying hypolimnetic water. The dynamics are calculated for aerobic sediment (0–3 cm) under the influence of bioturbation and bottom currents. A fraction of the particulate material in this 3-cm zone is lost through burial.

The differential equations used to describe the dynamics of the system include, where appropriate, a sinking term, as described above; a diffusion term driven by concentration gradients and the calculated diffusion coefficients; and a group of biological and chemical kinetic terms, as described above and listed in Table III. Two boundary conditions are used: (1) no material flux (except for CO_2 and O_2 , as described above) is allowed at the air–water interface, and (2) continuity of flux at the sediment–water interface. The system of equations is programmed in FORTRAN on a CDC 6600 computer and is solved numerically with a forward step, Euler scheme using a time step of 0.5 day. All model output in this paper is reported as weekly averages of daily values. The model coefficients (Table IV) are generally based

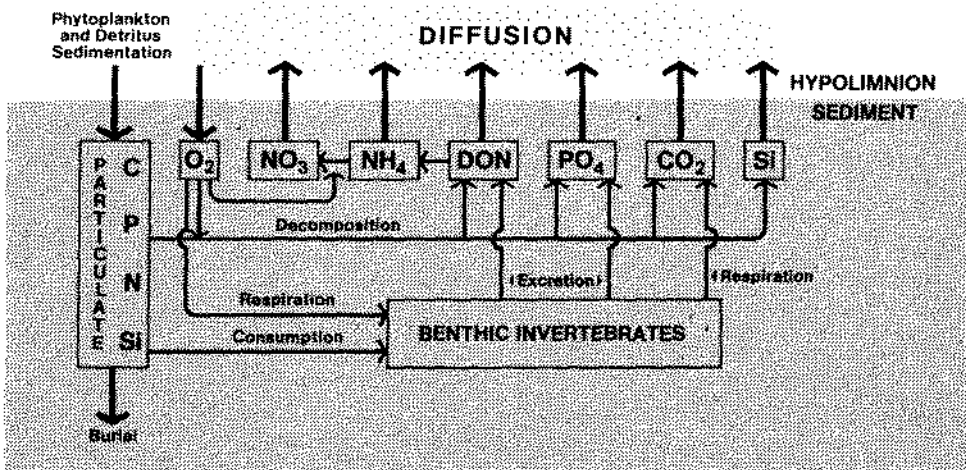


Fig. 3. Conceptualization of sediment model.

on representative values from the literature; however, in some cases, where information was lacking, rough estimates were made from a priori considerations. The final values of the model coefficients are a result of calibrating model output with field observations.

The calibration was accomplished by best-judgment "tuning" by the author, therefore the results of the calibration are not statistically optimal in a least-squares sense. The purpose of this work is to investigate limnological processes in Lake Ontario during IFYGL, not to make predictions pertaining to the response of the lake to possible management actions, thus, agreement between simulated and measured process rates are required. In order to obtain a calibrated model based on both state variables (addressed in this paper) and processes (Scavia, 1979), certain coefficient values that fell outside of the

TABLE IIIa

Model equations: state variables

Phytoplankton	Dissolved organic nitrogen
$\frac{dX_i}{dt} = P_i - R_i - \sum_j C_{ij}$	$\frac{dX}{dt} = \frac{N}{C} [D + B \sum_k R_k] - A$
Zooplankton	Ammonia
$\frac{dX_j}{dt} = \sum_n C_{nj} a_{nj} - R_j - C_{j,11} - F_j$	$\frac{dX}{dt} = \frac{N}{C} [(1 - B) \sum_i R_i - \sum_i P_i H_i] + A - N$
Detrital carbon	Nitrate and nitrite
$\frac{dX_c}{dt} = \sum_n \sum_j C_{nj} (1 - a_{nj}) - D - \sum_j C_{cj}$	$\frac{dX}{dt} = N - \frac{N}{C} \sum_i P_i (1 - H_i)$
Detrital silicon	Available phosphorus
$\frac{dX}{dt} = \frac{Si}{C} [\sum_d \sum_j C_{dj}] - D_s$	$\frac{dX}{dt} = \frac{P}{C} [D - \sum_i P_i + \sum_k R_k]$
Available silicon	Dissolved inorganic carbon
$\frac{dX}{dt} = D_s + \frac{Si}{C} [\sum_d R_d - \sum_d P_d]$	$\frac{dX}{dt} = \sum_k R_k + D - \sum_i P_i$
Dissolved oxygen	
$\frac{dX}{dt} = \frac{O}{C} [\sum_i P_i - \sum_k R_k - D] - \frac{O}{N} [A]$	

where summation indices are:

i = all phytoplankton
 j = all zooplankton

c = detritus
 k = all organisms

d = diatoms
 n = all food

Process equations and constant definitions are given in Table IIIb.

TABLE IIIb

Model equations: processes

Process	Symbol	Construct
Production	P	$P_m * \text{Min}[UI, UN, UP, US] * T_r * B$
P_m	= maximum growth rate	
T_r	= temperature factor	
B	= algal carbon	
$UI =$	$= \frac{2.178FP}{\epsilon \Delta Z} \left[\exp\left(-\frac{L}{I_s} \exp(-\epsilon Z_2)\right) - \exp\left(-\frac{L}{I_s} \exp(-\epsilon Z_1)\right) \right]$	
FP	= photoperiod	
L	= incident solar radiation	
ΔZ	= layer thickness	
Z_1, Z_2	= depth to top, bottom of layer	
I_s	= saturating light intensity	
ϵ	= $\epsilon^1 + \alpha \delta$	
ϵ^1	= extinction coefficient for filtered water	
δ	= particulate organic carbon	
α	= constant	
UN	= $(NH_3 + NO_3)/(NH_3 + NO_3 + K_n)$	
UP	= $P/(P + K_p)$	
US	= $Si/(Si + K_s)$	
K_n, K_p, K_s	= half-saturation constants	
Algal respiration	R	$(K_r + K_r^1 * \text{Min}(UN, UI, UP, US)) * T_r * B$
K_r	= base respiration rate	
K_r^1	= proportionality constant	
Zooplankton respiration	R	$K_r + K_r^1 \left[\frac{\sum W_i B_i}{K_g + \sum W_i B_i} \right] * T_r * Z$
K_g	= half-saturation constant	
Z	= zooplankton carbon	
$\sum W_i B_i$	(see Consumption)	

TABLE IIIb (continued)

Process	Symbol	Construct
Zooplankton consumption	C_{ij}	$C_m \left[\frac{W_i B_i}{K_g + \sum W_i B_i} \right] * T_r * Z$ (= 0 for $\sum W_i B_i < B_m$)
C_{ij}	= grazing rate of predator j on prey i	
C_m	= maximum grazing rate	
W_i	= selectivity coefficient for prey i	
B_i	= concentration of prey i	
B_m	= threshold concentration	
\sum	= summation over all prey	
Fish predation	F	$P_c * Z$ (= 0 for $Z < Z_m$)
P_c	= fish predation loss rate	
Z_m	= threshold concentration	
Decomposition	D	$\beta * T * X$
Dissolution	D_s	
Ammonification	A	
Nitrification	N	
β	= transformation rate	
T	= temperature	
X	= concentration of variable being transformed	

Temperature factor

$$T_r = V^x \exp(x(1 - v)) \quad \text{for } T < T_m$$

$$V = \frac{T_m - T}{T_m - T_o}$$

$$x = \left[\frac{W(1 + (1 + 40/W)^{0.5})}{20} \right]^2$$

$$W = \ln(Q)(T_m - T_o)$$

T_m = upper lethal temperature

T_o = optimal temperature

Q = Q_{10} value

Other constants

a_{ij} = feeding efficiency of predator j on prey i

$\frac{P}{C}$ = phosphorus to carbon ratio in plankton

$\frac{N}{C}$ = nitrogen to carbon ratio in plankton

$\frac{Si}{C}$ = silicon to carbon ratio in diatoms

$\frac{O}{C}$ = respiratory quotient by weight for carbon

$\frac{O}{N}$ = respiratory quotient by weight for ammonia

B = fraction of nitrogen excreted as organic N

H_i = preference of phytoplankton for NH_3 uptake over NO_3 uptake
 $= NH_3/(NH_3 + K)$ where K = preference constant

TABLE IV
Model constants

Parameters	Small diatoms	Large diatoms	Small others	Large others	Nitrogen-fixing blue-greens
Maximum growth rate (day^{-1})	2.5	2.5	2.5	2.5	2.0
Half-saturation constants					
mg P/l	0.004	0.004	0.004	0.004	0.010
mg N/l	0.025	0.030	0.030	0.035	0.000
mg Si/l	0.03	0.03	0.00	0.00	0.00
Saturating light (langley/day)	300	300	250	250	250
Optimal temperature ($^{\circ}\text{C}$)	20	20	23	23	30
Lethal temperature ($^{\circ}\text{C}$)	35	35	35	35	35
Q_{10}	2.0	2.0	2.0	2.0	1.9
Respiration rates					
Base rate (day^{-1})	0.05	0.05	0.05	0.05	0.05
Proportionality constant	0.2	0.2	0.2	0.2	0.2
Ammonia preference constant (mg N/l)	0.025	0.025	0.025	0.025	0.025
	<i>Detritus</i>	<i>DON</i>	<i>Ammonia</i>	<i>Silica</i>	
Decay rates ($(^{\circ}\text{C day})^{-1}$)	0.001	0.001	0.005	0.002	
Excretion partition		0.5	0.5		
Stoichiometric ratios	<i>P : C</i>	<i>N : C</i>	<i>Si : C</i>		
(by weight)	0.024	0.18	0.6		
Extinction coefficients					
Filtered water (m^{-1})	0.25				
Proportionality ($\text{m} \cdot \text{mg C/l})^{-1}$	0.4				

Parameters	Small cladocerans	Large cladocerans	Herbivorous copepods	Rotifers	Mysids	Omnivores
Maximum ingestion rate (mg C/mg C/day)	1.8	1.6	1.8	1.8	1.2	1.4
Half-saturation constant (mg C/l)	0.2	0.2	0.4	0.2	0.2	0.15
Threshold concentration (mg C/l)	0.02	0.02	0.02	0.02	0.02	0.001
Respiration rates						
Base rate (day^{-1})	0.1	0.1	0.1	0.12	0.05	0.08
Proportionality constant	0.25	0.25	0.25	0.28	0.23	0.25
Optimal temperature ($^{\circ}\text{C}$)	28	24	27	27	15	24
Lethal temperature ($^{\circ}\text{C}$)	40	32	35	40	17	32
Q_{10}	2.0	2.0	2.0	2.0	2.4	2.0
Fish predation constant (day^{-1})	0.001	0.005	0.002	0.0	0.08	0.005
Selectivity constants for feeding on:						
Small diatoms	1.0	1.0	1.0	1.0	1.0	0.4
Large diatoms	1.0	1.0	0.7	0.2	1.0	0.4
Small others	1.0	1.0	1.0	1.0	1.0	0.4
Large others	0.7	0.7	0.7	0.7	0.7	0.4
Blue-greens	0.2	0.2	0.2	0.2	0.2	0.2
Detritus	0.4	0.4	0.4	0.4	0.4	0.2
Selectivity constants for feeding by omnivores	0.5	0.5	0.5	0.5	0.0	0.3
Feeding efficiencies (%)	50	50	50	50	50	50
(on detritus and blue-greens)	20	20	20	20	20	20

range usually found in laboratory studies and adopted in models were required. (It should be noted that use of more "conventional" coefficient values resulted in good agreement between measured and simulated state variables but not between simulated and estimated process rates.)

DATA

The chemical variables reported here (Figs. 4 and 5) represent lake-wide averages ± 1 S.D. for the depth ranges 0–20 m and below 20 m. The data were obtained from the data management system of the U.S. Environmental Protection Agency, STORET, and are based on data collected by the Canada Centre for Inland Waters. Although data were only available for seven time periods, each lake-wide average represents between 200 and 500 samples from 32 stations and thus represent a massive effort. Particulate nitrogen was obtained from Stadelmann and Fraser (1974) and represents average values from a single north–south transect at mid-lake.

Phytoplankton cell counts (Stoermer et al., 1975) were converted to car-

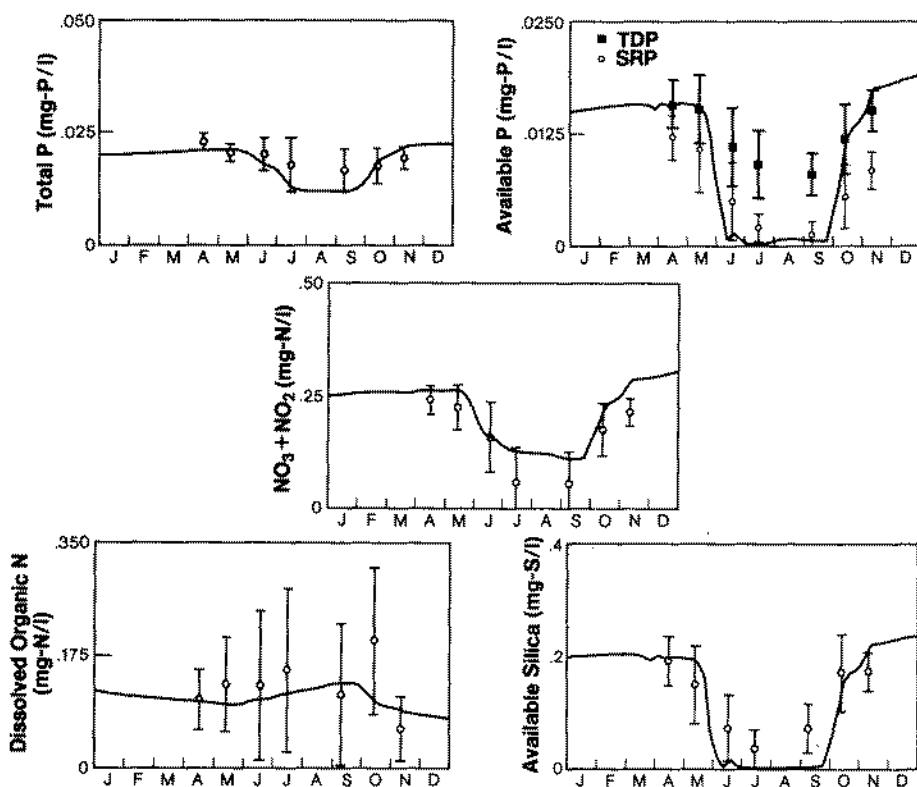


Fig. 4. Seasonal dynamics of data and model output for epilimnion (0–20 m) of Lake Ontario during 1972. (a) Total P; (b) filterable P; (c) nitrate and nitrite; (d) dissolved organic N; (e) soluble reactive Si. Data are lake-wide mean ± 1 S.D.

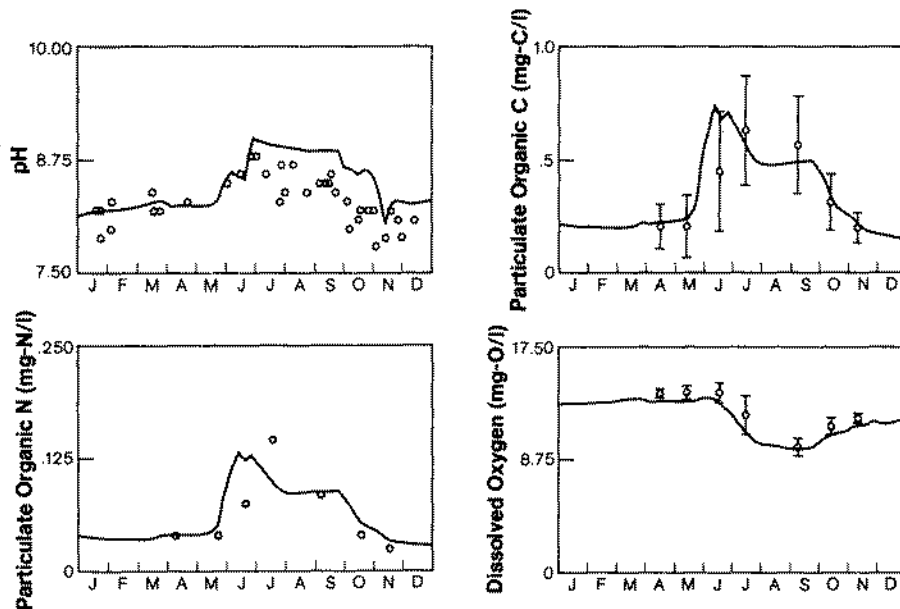


Fig. 5. Seasonal dynamics of data and model output for epilimnion (0–20 m) of Lake Ontario during 1972. (a) pH; (b) particulate organic C; (c) particulate organic N; (d) DO. Data are lake-wide mean ± 1 S.D.

bon concentrations (Stoermer and Ladewski, 1978) and aggregated into groups before lake-wide averages were calculated. "Large" and "small" species were separated at 20 μm (longest dimension) and the following taxonomic groups were provided by E.F. Stoermer (personal communication, 1977): diatoms, green algae, blue-green algae with heterocysts, blue-green algae without heterocysts, and others. For this study, green algae, blue-green algae without heterocysts, and Stoermer's others are grouped into large and small others categories. The dominant species in each of the five model compartments are shown in Table I. Because algal counts from the 60 lake stations appeared to follow a log-normal distribution, means and standard deviations were calculated with \log_e -transformed data and the variability is shown in Fig. 6 as the geometric mean \times the antilogarithm of the standard deviation for all surface samples (Parsons and Takahashi, 1973). Geometric means were also calculated with depth integrated values from five stations where depth profiles were obtained (~ 25 samples per time period).

Zooplankton species counts, collected by towing a plankton net from 5 m to the surface (McNaught et al., 1975) (ca 60 stations), were converted to carbon concentrations from estimates of individual mean weights supplied by D.C. McNaught (personal communication, 1977). Species compositions of the groups considered in this study are shown in Table I. Means and standard deviations were calculated with \log_e -transformed group concentrations. The variability in the data (Fig. 7) was calculated in the same manner as phytoplankton. Depth-integrated averages for the master stations were also calculated

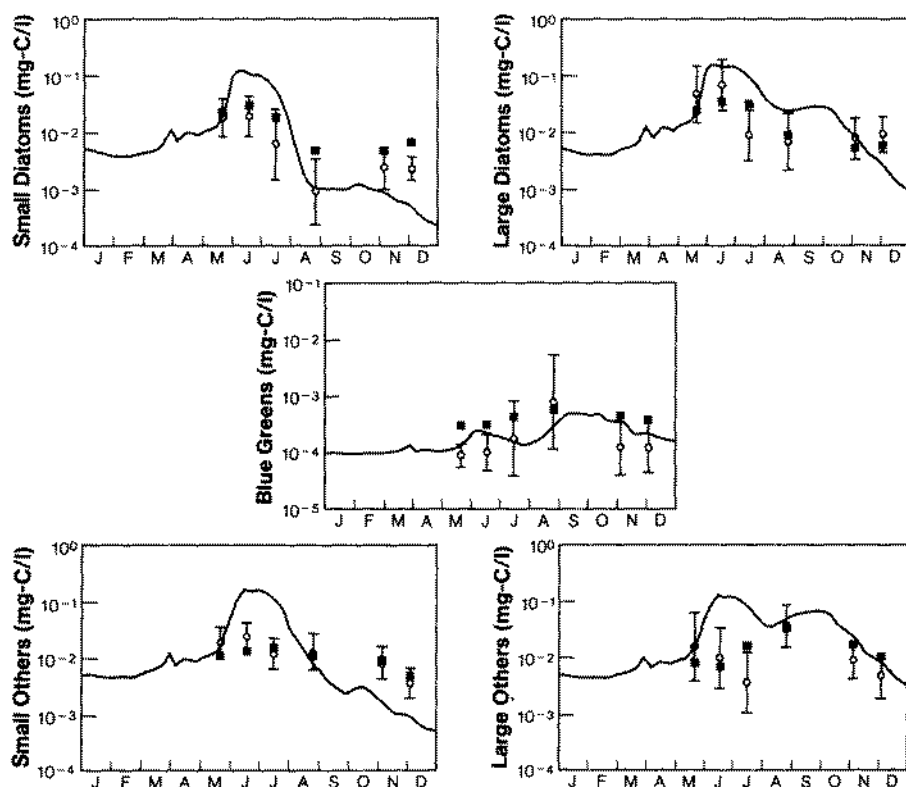


Fig. 6. Seasonal dynamics of data and model output from epilimnion (0–20 m) of Lake Ontario during 1972. (a) Small diatoms; (b) large diatoms; (c) blue-greens; (d) small others; (e) large others. \circ — lake-wide mean ± 1 S.D. for surface samples and \blacksquare — lake-wide mean for depth-integrated profiles.

with estimates from 0–5-m, 5–10-m, 10–15-m and 15–20-m depth ranges where data were available (D.C. McNaught, personal communication, 1977).

RESULTS AND DISCUSSION

The results of model calibration are shown in Figs. 4–7. As can be seen, chemical and biological properties measured in the epilimnion during IFYGL are simulated by the model. The comparisons between measured and simulated properties are best for those properties measured with most certainty (i.e. chemical properties) and worst for those properties that are difficult to measure accurately (i.e. phytoplankton and zooplankton carbon).

By considering both model output and lake-wide averaged observations, the seasonal dynamics of the ecology of Lake Ontario can be examined. The concentration of total phosphorus remains relatively constant (annual average epilimnion concentration = $18.6 \mu\text{g P/l}$) throughout the year with a slight decrease during summer (Fig. 4a). The decrease is due to the transformation of soluble phosphorus to particulate phosphorus and subsequent settling out

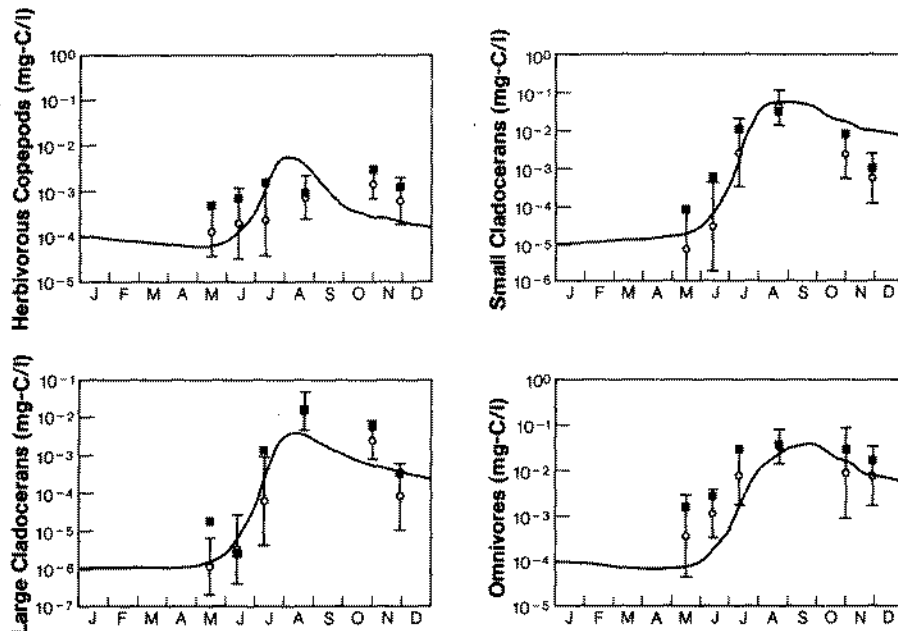


Fig. 7. Seasonal dynamics of data and model output for epilimnion (0–20 m) of Lake Ontario during 1972. (a) Herbivorous copepods; (b) small cladocerans; (c) large cladocerans; (d) omnivores. Symbols as in Fig. 6.

from the epilimnion. Concentrations of total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP) and simulated available phosphorus (AP) all follow seasonal trends typical of moderately productive, dimictic lakes (Fig. 4b). Concentrations are highest in winter and spring and decrease considerably during the warm productive summer months. Model estimates of available phosphorus are approximated best by TDP in spring and fall and are less than SRP in summer. The relatively large concentration of dissolved phosphorus that is unavailable during summer is likely composed of compounds resistant to natural hydrolysis. This phenomenon is discussed in more detail by Scavia (1979). Ammonia (NH) concentrations are relatively low (~ 0.01 mg N/l) throughout the year, with a maximum (~ 0.018 mg N/l) in mid-July. Nitrate-nitrogen plus nitrite-nitrogen (NO) follows a pattern similar to that of the dissolved phosphorus components (Fig. 4c); however, concentrations do not decrease as much until later in the summer. Stadelmann and Fraser (1974) and Thomann et al. (1975) suggest that nitrogen may become limiting in late summer. Dissolved organic nitrogen (DON) remains relatively constant (Fig. 4d), although concentrations become variable late in the year. Soluble reactive silicon (SRS) concentrations follow a seasonal pattern similar to that of SRP (Fig. 4e).

Observations of hypolimnetic concentrations of the above nutrients are all relatively constant and approximately equal to early spring epilimnion concentrations. Model output also agrees with those measurements.

All of the primary algal nutrients (AP, NH, NO and SRS) decrease with increasing rate of primary production. Increased production is indicated by increased pH (Fig. 5a) and increased concentrations of particulate organic carbon (Fig. 5b), particulate organic nitrogen (Fig. 5c) and algal carbon (Fig. 6). Changes in dissolved oxygen concentrations (Fig. 5d) appear to be most closely related to the temperature-dependent atmospheric transfer rate; primary production and community respiration contribute only slightly to the oxygen dynamics in the epilimnion.

Diatoms (Fig. 6a and b) bloom in late May and June, decrease during the summer, and remain relatively constant into fall. The concentration of nitrogen-fixing blue-green algae (Fig. 6c) is relatively low throughout the year, and increases only slightly in late summer. Of the remaining two phytoplankton groups, the small category (Fig. 6d) has a maximum in mid-summer and the large category (Fig. 6e) develops two peaks, one in spring and a second in fall. The seasonal dynamics and total abundance of phytoplankton are indicative of a moderately enriched temperate lake.

The concentration of herbivorous copepods (Fig. 7a) is low relative to the cladocerans and omnivores during summer. The seasonal dynamics of the two cladoceran groups and the omnivores are similar (Fig. 7b, c and d). Each has very low concentrations in early spring, exponentially increasing to a maximum in mid-summer. Small cladocerans and omnivores are each approximately twice as abundant (by weight) as large cladocerans. The two remaining zooplankton groups, rotifers and mysids, were also compared to sparse, available data. The rotifers followed dynamics similar to those of the small cladocerans, with a peak density of about 0.005 mg C/l in early August. These values are not unlike the densities observed in a nearshore area of Lake Ontario during the same year (McNaught et al., 1973). In the model, the density of mysids in the hypolimnion increased gradually to about 0.003 mg C/l in late July. These values are also similar to those that can be calculated from data in Lasenby and Langford (1972) and Carpenter et al. (1974).

The model is capable of simulating the exponential increase in zooplankton biomass over three orders of magnitude, as well as the eventual plateau and slight decrease of biomass into fall. A second year of simulation, however, did not reproduce exponential increases from very low concentrations. Concentrations in the second year began with the final values from the first year (Fig. 7) and remained rather steady until mid-summer, when they increased slightly to values similar to those in the previous year. This indicates that the resource-limited zooplankton dynamics in the model are capable of simulating peak biomass concentrations; however, large variations in total biomass, likely due to the dynamics of the plankters' life cycles, cannot be simulated with the single age-class conceptualization used in this work.

It should be noted that, of the variables simulated by the model, only one was not compared with observations — detrital silicon. The importance of comparing all simulated variables with observations cannot be overemphasized. Only in this way can one be assured that modeling errors are not accu-

TABLE V
Sediment properties

Property	Simulated	Measured	Reference
Net loss to sediment			
Total P ($\text{g P m}^{-2} \text{ year}^{-1}$)	0.16	0.434	Mass balance
Total N ($\text{g N m}^{-2} \text{ year}^{-1}$)	1.31	2.7	Mass balance
Total Si ($\text{g Si m}^{-2} \text{ year}^{-1}$)	-0.53		
Sedimentation rates			
Total P ($\text{g P m}^{-2} \text{ year}^{-1}$)	0.3	0.7	Kemp et al. (1974)
Total N ($\text{g N m}^{-2} \text{ year}^{-1}$)	2.0	2.5	Kemp et al. (1974)
Total organic C ($\text{g C m}^{-2} \text{ year}^{-1}$)	10.9	19.5	Kemp et al. (1974)
($\text{g C m}^{-2} \text{ day}^{-1}$)	0.013-0.074	0.02-0.18 *	Burns and Pashley (1974)
		0.03-0.15 **	Johnson and Brink- hurst (1971)
Sediment release rates			
P ($\text{mg P m}^{-2} \text{ day}^{-1}$)	0.2-0.4	0.03-0.80 $\bar{X} = 0.2$	Bannerman et al. (1975)
Si ($\text{g Si m}^{-2} \text{ year}^{-1}$)	3.1	7-48 †	Remmert et al. (1977)
O ₂ ($\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$)	0.02-0.04	<0.1 ††	Thomas (1975)

* One mid-lake station, using measured sinking rates, with POC near bottom assumed constant during March-October.

** Nearshore station near Bay of Quinte.

† Range of 26 cores from Lakes Erie, Huron and Michigan.

†† Sediment oxygen demand measurements over large area in Lake Ontario.

ulated, and compensated for, in unchecked compartments. It is assumed here that any discrepancy in the simulated values of detrital silicon are unimportant. Additional checks for other variables endowed with a high degree of uncertainty are also important. For example, accurate measurements of the carbon densities of individual phytoplankton and zooplankton species are difficult to make. Thus it is important to compare model output with both individual group observations (Figs. 6 and 7) and total organic matter associated with the particulates (Fig. 5b and c).

Some of the important properties of the sediment segment are compared with measurements in Table V. Concentrations of particulate material in the sediment and dissolved constituents in the pore water remain relatively constant during the year. High concentrations of nutrients in the pore water (e.g. $\sim 0.2 \text{ mg P/l}$) drive the diffusion processes in the direction of the overlying water and, as can be seen (Table V), simulated nutrient release rates are comparable to those measured in the Great Lakes. The large loss of organic matter to the sediment ($10.9 \text{ g C m}^{-2} \text{ year}^{-1}$) and subsequent decay of this material by both macro- and micro-benthos results in a sediment oxygen demand of about $0.03 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ as a lake-wide average. This low rate is indicative

of large offshore areas in lake Ontario. The release rates of dissolved silicon are low compared with rates measured in other Great Lakes; however, in the model there appears to be a net gain of total silicon from the sediment. The problems with the silicon cycle in the model may be due to inaccurate simulation of detrital silicon or to the inability to obtain adequate estimates of silicon loads during IFYGL.

Another useful method of displaying model output, as well as demonstrating synthesis of the diverse data set collected on Lake Ontario, is the construction of carbon flow diagrams. Robertson and Scavia (1979) suggest using such diagrams for examining ecosystem properties, especially those properties difficult to measure on a system as large as Lake Ontario. The purpose of the flow diagram is to show, in one figure, the relative sizes of specific ecosystem compartments and the relative magnitudes of carbon flows among the compartments. As can be seen in the flow diagram (Fig. 8) constructed to represent average conditions in the epilimnion (0–15 m) from July to September, carbon flow is quite active. The major pathways are from producers to herbivores and between herbivores and detritus rather than between herbivores and omnivores as might be expected. The role of detritus in the food web is shown clearly in the flow diagram. The size of the detrital pool is more than 1.5 times that of the phytoplankton pool. In fact, detrital carbon always constitutes over 50% of the total seston (Stadelmann and Munawar, 1974).

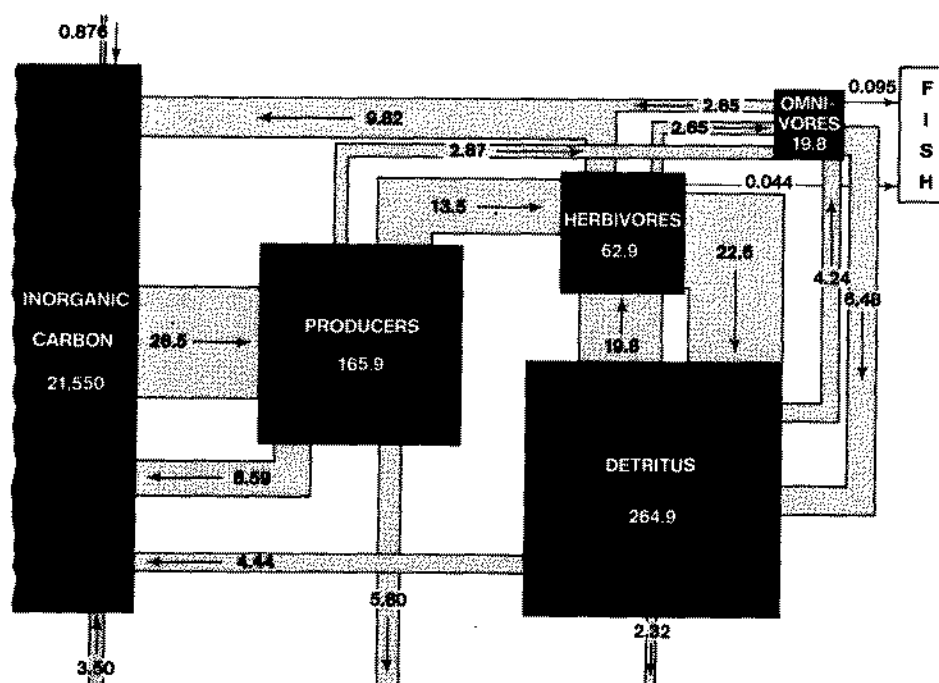


Fig. 8. Carbon flow diagram. Concentrations in boxes are as $\mu\text{g C l}^{-1}$ and in pipes as $\mu\text{g C l}^{-1} \text{ day}^{-1}$. These values are averaged over the period of July–September for the top 15 m.

This abundance of detrital particles is the reason carbon flows between detritus and the filter-feeding herbivores are the largest, albeit inefficient, flows during this time period. Because this major detrital food source is a relatively inefficient energy source, the ecological efficiency (Odum, 1971) of the herbivores with respect to the next higher trophic level is only 8%. Thus, if this upper trophic level were strictly carnivorous, it would benefit from only 8% of the food acquired by its prey. This information may help to explain the advantage of an opportunistic feeder over an obligate carnivore as the next highest trophic level above herbivores. The omnivore's food base is wider than the carnivore's and thus, in the model (Fig. 8), the ecological efficiency of the entire lower food web (producers, herbivores and detritus) with respect to omnivores is over 17%. This illustrates a competitive advantage for omnivores over carnivores in Lake Ontario.

One can also speculate, based on the information in the flow diagram, that herbivores are a very important component of nutrient cycles. High rates of production of fecal material (herbivores \rightarrow detritus) supply the decomposer community with organic matter that is subsequently degraded into inorganic nutrients. Also, high rates of respiration (herbivore \rightarrow inorganic carbon) are indicative of high metabolic activity and thus high rates of nutrient excretion. Therefore, the herbivores may be playing a dual role in nutrient cycling and are very important in the Lake Ontario ecosystem.

SUMMARY AND CONCLUSIONS

An ecological model of Lake Ontario was described. The three-layer model includes several phytoplankton and zooplankton groups; cycles of phosphorus, nitrogen, carbon and silicon; and sediment particulates and pore water nutrients. It was designed to simulate and synthesize chemical and biological data collected during a joint United States-Canadian field program, the International Field Year for the Great Lakes.

The model agrees with measurements made during IFYGL and is capable of simulating some of the ecological properties of Lake Ontario, as was demonstrated by comparisons between observations and all but one of the model state variables. Good agreement was also obtained between model output and observations of gross sediment and sediment-water interface properties.

Model output was aggregated to construct a carbon flow diagram to represent average epilimnion conditions during summer. With the flow diagram as a synthesis tool, the importance of detritus and herbivorous zooplankton in the ecology of Lake Ontario has been indicated. The information obtained from this analysis demonstrates how an ecological model is useful for synthesizing information and providing a whole-system framework for investigating disciplinary topics.

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