SIMPLE: A SIMPLIFIED ECOSYSTEM MODEL FOR LAKE GEORGE, NEW YORK

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ABSTRACT

A computer simulation model for oligotrophic lake systems is described. The variables included are organic matter, nutrients, phytoplankton, zooplankton, and fish. Sunlight, temperature, benthic organisms and nutrient loadings are treated as inputs. When calibrated using data from Lake George, N. Y., the model gives good results, differing from data primarily in absolute zooplankton biomass and lake behavior in autumn.

INTRODUCTION

Lake George is a large oligotrophic fresh water resource located in the Adirondack Mountains of New York State. Present activities within the Lake George watershed have the potential to significantly alter the quality of the lake and its value as resource.

Because Lake George is relatively unaffected by man's activities and, without proper environmental management would be modified adversely, it was chosen as a research site in the National Science Foundation's International Biological Program (IBP). The research program at the Lake George Site consisted of identification and measurement of the significant state variables and transfer rates between compartments of the ecosystem. The data collected was used to develop both process oriented models, e.g., a model for algal photosynthesis, as well as whole ecosystem models. One approach, to whole ecosystem modeling which incorporated data and models from Lake George as well as other IBP sites, was to couple the complex process models to form a whole ecosystem model, CLEAN. (2, 12)

The intent of the approach reported in this paper was to develop an ecosystem model similar in overall behavior to CLEAN, but greatly simplified and condensed. In order to accomplish this task, many significant process models were reduced in complexity; the remainder were ignored. The decisions were based upon estimates of the sensitivity of the whole system to each of the processes and upon the complexity of representation required by each.

The benefits which I and my co-workers hoped to achieve from this exercise were

- Emphasis of the important features of the data available to us.
- Computational efficiency which would allow the coupling of the ecosystem model with a transport model to obtain a spatial resolution of the behavior of the lake
- A condensation of expertise in lake ecosystem analysis to be useful as an educational device.
- Aid in selection of areas for future work--in the areas of both data collection and systems analysis.

Description of the Model

SIMPLE is a model of the mass flows between major compartments of the Lake George ecosystem. The model considers these flows within a well mixed volume of water. Each compartment may represent a biologically diverse assemblage of components that are functionally similar from the ecosystem viewpoint. Four inputs to the system are considered:

- Compounds of phosphorus (P_{in}), which results from precipitation, stream runoff and sewage treatment plant output. All other nutrients are assumed to exist in quantities that do not limit growth.
- Organic loading (O_{in}), which consists of dead plant and animal matter, which flows into the lake.
- Solar radiation (K).
- Water temperature (T), which in the modeled system affects all mass transfer rates uniformly.

The variables considered for inclusion within the system were (10):

x_1 = Biomass of phytoplankton (floating algae)

x_2 = Biomass of zooplankton (small floating invertebrate animals

x_3 = Biomass of macrophytes (rooted aquatic plants)

x_4 = Biomass of benthic organisms (bottom-dwelling insect larvae)

x_5 = Biomass of fish

x_6 = Level of orthophosphate (PO_4) in the water column

x_7 = Organic matter in shallow sediments and water

x_8 = Level of deep sediments

The processes by which the mass transfers between compartments occur, are:

- > Photosynthesis, an example of which is the combination of PO_4, sunlight and other minerals assumed to be amply present to form phytoplankton
- > Consumption, which is the transfer of mass by feeding; examples are the zooplankton grazing on the phytoplankton and the fish eating both zooplankton and insect larvae.
- > Defecation, which is the elimination of unassimilated food material
- > Respiration, which is the metabolic assimilation of oxygen and breakdown of organic compounds accompanied by the release of energy and carbon dioxide; respiration in this system formulation involves a mass transfer into the environment
- > Excretion, which is the elimination of metabolic wastes; this process transfers mass to the organic matter compartment from all compartments except PO_4 and the deep sediments.
- > Nonpredatory mortality
- > Decomposition, which is the metabolic breakdown of organic materials with the release of energy and simple organic and inorganic compounds; the example of this process is the decomposition of organic matter with transfer of mass to the phosphate compartment and into the environment.
- > Loss to deep sediments, which organic matter is lost to the remainder of the system.

SIMPLE is conceived as a "bare bones" compartment system, modeling the major mass flows in a lake ecosystem. It should be recognized that we proceed in the context of both a limited data set and a fairly primitive understanding of the basic biological processes that drive the system.

Not wishing to invest the model with greater complexith than our understanding allows, we only considered process models of order one, such as crude mortality and order two such as feeding terms which are multiplicative functions of predator and prey. Higher order terms, such as crowding factors, self-shading from algae and complex emergence terms for benthos were not considered.

The development of SIMPLE had two stages. The first, or process model stage treated each state variable separately. Various parameters, particularly the efficiency terms (those parameter representating losses in intercompartmental transfer) were estimated at the outset by Bloomfield (2) and held fixed thereafter.

The remaining terms (those dealing with feeding rates, mortality and organic decay) were estimated by decoupling each state variable in turn and using the data for the formerly coupled variables as inputs.

The process model parameters were then adjusted to give rough approximation to the data for that variation.

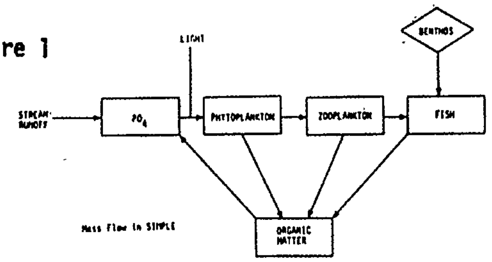
The second, or system calibration stage of model construction involved connecting the state variables and adjusting several selected parameters--primarily the feeding and mortality factors--to achieve a data fit. For the most part, the efficiency-excretion coefficients were left unchanged in both modeling stages, since these were the only parameters which seemed pacable of external estimation.

Three changes in model configuration were made at the process modeling state. Deep sediments and macrophytes were dropped as being unimportant to the behavior of an oligotrophic lake such as Lake George. Benthic organisms were shown to be too complex for simple treatment, and so were deleted as a state variable and treated as an input.

The necessity for the decoupling of benthos may be seen by the fact that the benthos subsection of CLEAN described by Zahorcak (15) is more complex than all of SIMPLE, and that Scavia (14) in reporting a pelagic zone model based on CLEAN also treats benthos as an input.

SIMPLE, therefore, as it is presently constructed, is a five state variable model (see Figure 1). There are three organism compartments: Phytoplankton zooplankton, and fish. The assumed limiting nutrient is phosphate (PO_4). Dissolved organic matter (DOM) and particulate organic matter (POM) are lumped together as a single species. Inputs consist of temperature, sunlight, runoff phosphate and organic matter. The complexity of SIMPLE may be compared to that of CLEAN, which has 28 state variables including three nutrients, 11 organisms and 5 organic material compartments.

Figure 1



Mass Flow in SIMPLE

MODEL EQUATIONS

Nutrient Cycling, Decomposition and Sedimentation Submodels

Nutrients are produced form decomposition or organic matter and removed by aquatic plants. A time varying phosporous loading is also included. The nutrient equation is

$$\frac{dX_6}{dt} = P_{in} + [E_{76}\emptyset_{76}\ 6 - E_{16}\emptyset_{16}X_1X_6]f(T)$$

where

$\emptyset_{16} = \hat{\emptyset}_{16}\ I_0(t)$

$\hat{\emptyset}_{16}$ = Biomass production constant for phytoplankton

$I_0(t)$ = Solar radiation

P_{input} = External phosphate loading

X_1 = Biomass of phytoplankton

E_{76} = Fraction of substrate that becomes dissolved inorganic phosphorus

E_{16} = Phosphorus fraction of phytoplankton

$\emptyset_{76}$ = Decomposition rate constant

$f(T) = \emptyset_{10}\ (T = T_{ref}/10)$

T = Water temperature

T_{ref} = Reference temperature at which Q_{10} is measured

Q_{10} = Temperature rate constant

E_{16} was taken to be 0.013, as calculated from the formula $C_{105}H_{145}O_{42}N_{21}P$ given by Bloomfield (2) as the stoichiometric composition of algae. We have adopted the convention that all organics (and hence all biomass) are of the same stoichiometric composition. By doing this we may have introduced a discrepancy into our predictions of the biomass of all compartments with stoichiometric composition different from algae--particularly with fish, whose biomass is probably overestimated as a result. However, this discrepancy is only that of a constant multiplicative factor. On the plus side, we are spared the need of introducing concentration factors into the mass flows between compartments. Also mass conservation is much easier to maintain when all of the mass flowing into the organics compartment is of the same composition.

The decomposition equation is simply a collection of all the inputs due to feces, dissolved organics, non-predatory mortality and external organic loadings, and losses due to remineralization of organics, and loss to deep sediments:

$$\frac{dX_7}{dt} = O_{in} + \sum_{j=1}^{n}\sum_{i=1}^{m} E_{ji}\emptyset_{ji}X_iX_j + \sum_{K=1}^{P}\emptyset_{7K}\ X_K$$

$$- (\emptyset_{76}X_7 + \emptyset_{87}X_7)]f(T)$$

where

O_{input} = External organics loading

E_{ji} = Assimilation efficiency of j^{th} consumer eating i^{th} food

$\emptyset_{ji}$ = ingestion constant of j^{th} consumer eating i^{th} food

$\emptyset_{7k}$ = Nonpredatory mortality constant of x^{th} organism

$\emptyset_{76}$ = Decomposition rate constant

$\emptyset_{87}$ = Sedimentation rate constant

X_i = Biomass of i^{th} food.

X_j = Biomass of j^{th} consumer

X_k = Biomass of k^{th} organism

The equation for loss of organic matter to the deep sediments is:

$$\frac{dX_8}{dt} = \emptyset_{87}\ X_7 \quad ;$$

$\emptyset_{87}$ = Sedimentation rate

PHYTOPLANKTON SUBMODEL

The phytoplankton submodel has four terms, corresponding to biomass production, predatory mortality, losses to organics and mass leaving the system. The latter two terms can be taken as reflecting the influences of non-predatory mortality, respiration and algal sedimentation. The form of the submodel is

$$\frac{dX_1}{dt} = [\emptyset_{16}X_6X_1 = (\emptyset_{01}X_1 + \emptyset_{71}X_1 + \emptyset_{21}X_1X_2)]f(T)$$

where

$\emptyset_{16} = \hat{\emptyset}_{16} \cdot I_0(t)$

$\emptyset_{16}$ = Biomass production constant

$I_0(t)$ = Solar radiation

$\emptyset_{01}$ = Algae loss from system (respiration, settling, etc.)

$\emptyset_{71}$ = Loss to organics (mortality)

$\emptyset_{21}$ = Zooplankton grazing facator

X_2 = Zooplankton

CONSUMER EQUATIONS

The equation for the system's consumers (fish and zooplankton) contains terms corresponding to ingestion, excretion, non-predatory and predatory mortality, and losses from the system such as respiration:

$$\frac{dX_j}{dt} = \sum_{i=1}^{n}\emptyset_{ji}X_iX_j(1 - E_{ji}) - (\emptyset_{7j}X_j + \emptyset_{0j}X_j)$$

$$- \sum_{K=1}^{m}\emptyset_{Kj}X_jX_K]f(T)$$

Where

$\emptyset_{ji}$ = ingestion constant of j^{th} consumer eating i^{th} food

e_{ji} = assimilation efficiency of j^{th} consumer eating i^{th} food

$\emptyset_{0j}$ = constant fo biomass lost from system

$\emptyset_{7j}$ = natural mortality constant

$\emptyset_{kj}$ = injestion constant of k^{th} predator on j^{th} consumer

X_i = biomass of i^{th} food

X_j = biomass of j^{th} consumer

X_k = biomass of k^{th} predator

The specific equations for zooplankton and fish are:

$$\frac{dX_2}{dt} = [\emptyset_{21}X_1X_2(1 = E_{21}) - (\emptyset_{72}X_2 + \emptyset_{02}X_2)$$

$$- \emptyset_{52}X_2X_5)]f(T)$$

$$\frac{dX_5}{dt} = [\emptyset_{54}X_4X_5(1 - E_{54} + \emptyset_{52}X_2X_5(1 - E_{52})$$

$$- (\emptyset_{75}X_5 + \emptyset_{05}X_5)]f(T)$$

Ingestion is assumed to be proportional to the product of consumer biomass and food biomass. Of this amount ingested, a fraction (E_{ji}) is excreted as feces or dissolved organics. Respiration and non-predatory mortality are strict linear functions of consumer biomass. Predatory mortality is identical in form to the ingestion term, except without as assimilation efficiency.

Although there are only two consumers in this version of SIMPLE (resulting in a food chain only three species deep) the consumer equation may easily be extended to include piscavores or more than one category of zooplankton and plankton feeding fish.

MODEL CALIBRATION AND RESULTS

In each calibration exercise the model was run for several simulated years in order that an equilibrium be established to eliminate the effects of initial conditions.

The parameters of the model were chosen (see Table 1) somewhat arbitrarily, to attempt a fit of the major changes in the phytoplankton and zooplankton data. The phytoplankton peak is easily fit (see Figure 2); the sudden increase in algae is caused by the icepack melt and subsequent increase in sunlight. The height of the algae peak is limited by the nutrients available and zooplankton grazing. The source of nutrients for the spring phytoplankton peak is the decay of organics within the lake; external nutrient inputs such as stream runoff are insufficient to supply the required observed biomass.

The secondary algae peaks seem to be due to food web oscillations and the effect of fish/benthos grazing; the algae peak is the 36th week can be approximated by adjusting the fish-benthos grazing parameter. Such a link (fish eat benthos, increased fish graze down zooplankton; fewer zooplankton allow algae growth) if correct, is an important result.

Other features of the data such as the algae minimum at the 44th week, the absolute populations of zooplankton (and to a lesser degree phytoplankton), and the summar PO_4 concentrations cannot be fit with SIMPLE. The data fit is similar to that achieved by CLEAN, however, suggesting that there are still unknown basic processes at work.

We might speculate at this point to suggest that the system behavior around the 44^{th} week, reflected in not only the algae data, but also the zooplankton and PO_4 data, may be related to physical changes in the lake such as upwelling. Our admitted inadequacies in the treatment of fish [our calculations are more representative of fish numbers than biomass (6)] may be responsible for underprediction of zooplankton.

Although our results are as good as any yet obtained at this scale of ecosystem modeling, we are clearly still short of a validated predictive model. So the question must be asked at this point, what have we gained by this exercise?

The first part of our answer is that we are further along the road to the predictive model than we were at the outset. We have a functioning, comprehensible model and clear directions for further work, both experimental and theoretical. We have directed our attention to four areas: benthic organisms, nutrient dynamics, the structure of the fish population, and the physical behavior of the lake.

Table 1

Model Parameters

$\emptyset_{16}$ = 2.0
$\emptyset_{76}$ = 0.0004
$\emptyset_{01}$ = 0.0
$\emptyset_{71}$ = 0.0
$\emptyset_{21}$ = 0.05
$\emptyset_{72}$ = 0.03
$\emptyset_{02}$ = 0.01
$\emptyset_{52}$ = 0.02

$\emptyset_{54}$ = 0.08
$\emptyset_{75}$ = 0.03
$\emptyset_{05}$ = 0.025
E_{76} = 0.013
E_{16} = 0.013
E_{21} = 0.5
E_{54} = 0.5
E_{52} = 0.5

Also, considering the inadequacies of the data, we believe that we have extracted a great deal of insight into the behavior of the lake. SIMPLE, therefore, can be claimed to have some utility as a tool for data analysis and pedagogy even in its present form.

Finally, a simplified ecosystem model can be of utility in other modeling applications. It is possible to test larger, more complicated process models (for instance, a model of benthos) by imbedding them within the simplified model of the whole ecosystem. Conversely, it may be possible to imbed the simplified ecosystem model within a larger hydrodynamic model, to ascertain the effect of spatial variations and mass flows from one part of the lake to another.

There is a natural tendency among modelers toward greater sophistication and complication of models. Carried to extremes this results in an ad hoc construct, too large to understand, with results that are difficult to assess for validity. SIMPLE is an attempt to demonstrate that pruning is at least as important as grafting. We believe that our results bear this out.

Figure 2

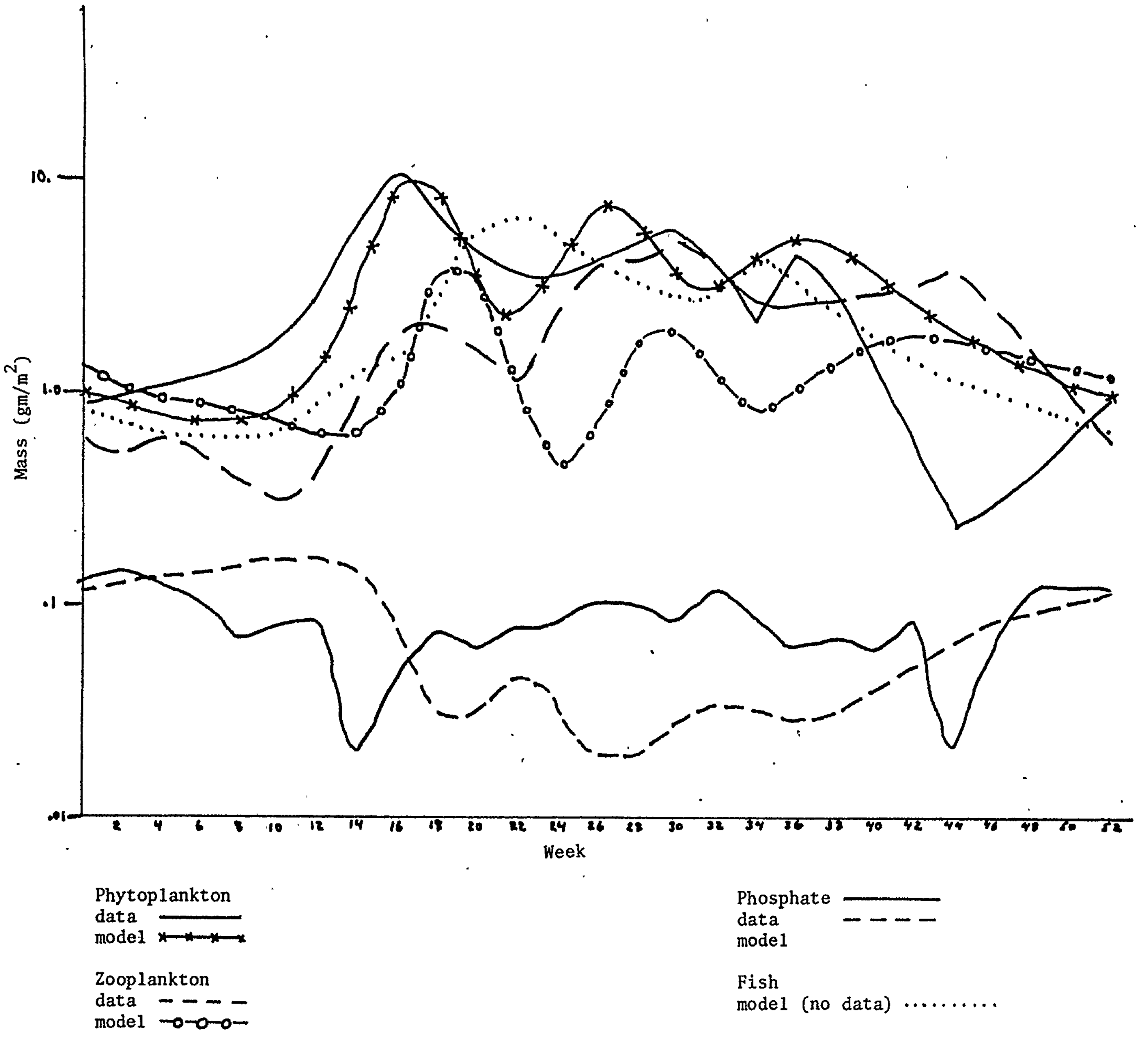


Table 2

		Data (gm/m^2)				Inputs		
Day	Week	Phy	Zoo	PO_4	Org	Benth (gm/m^2)	Light (arbitrary units)	$P(x10^{-5})$ gm/m^2 day
1	0	0.9	0.6	0.129	640	0.1	6	21
15	2	1.0	0.5	0.141	634	0.15	10	27
29	4	1.1	0.6	0.123	629	0.3	10	36
43	6	1.2	0.5	0.108	619	0.95	10	47
57	8	1.4	0.4	0.068	6.5	1.95	14	48
71	10	1.7	0.3	0.082	624	2.98	22	43
85	12	2.0	0.4	0.082	640	2.90	80	43
99	14	6.3	0.9	0.023	646	2.8	82	92
113	16	10.7	2.05	0.48	651	2.73	90	187
127	18	6.5	2.0	0.78	660	2.68	92	86
141	20	4.4	1.5	0.066	664	2.10	100	41
155	22	3.6	1.1	0.080	670	0.3	109	38
169	24	3.6	2.4	0.083	670	0.9	108	51
183	26	4.4	4.0	0.107	690	0.9	92	8
197	28	4.9	3.8	0.103	632	0.45	94	6
211	30	5.8	5.6	0.089	650	0.78	101	1
225	32	3.7	3.7	0.125	660	1.80	101	15
239	34	2.1	2.5	0.096	676	0.95	98	13
253	36	4.5	2.6	0.065	691	0.60	85	12
267	38	3.1	2.7	0.075	700	0.3	72	12
281	40	1.3	2.8	0.064	673	0.2	52	9
295	42	0.5	3.1	0.086	652	0.12	42	10
309	44	0.2	3.6	0.23	650	0.1	23	17
323	46	0.3	2.6	0.070	645	0.1	17	18
337	48	0.4	1.5	0.128	642	0.1	9	16
351	50	0.6	0.9	0.126	640	0.1	4	22
365	52	0.9	0.6	0.127	640	0.1	6	21

Sources

Phytoplankton	H. H. Howard (8)
Zooplankton	D. C. NcNaught (9)
Benthos	Henningson (7)
PO_4	Williams and Clesceri (12)
Organics	Wolfgang Fuhs (5)
Light	Emilo Colon (4)
P (PO_4 input)	D. B. Aulenbach (1)

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