

A GENERAL MODEL OF MICROBIAL GROWTH AND
DECOMPOSITION IN AQUATIC ECOSYSTEMS

By

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ABSTRACT

A model capable of simulating freely suspended and attached decomposers, particulate organic matter, labile and refractory dissolved organic matter, inorganic nitrogen, and phosphate in the open-water portion of lakes is presented. Examples are given showing the utility of the model when coupled to the whole-ecosystem model CLEANER.

INTRODUCTION

Mathematical models have come to be an important tool in the study of complex systems. They facilitate the organization of diverse data and the detection of conceptual weaknesses in our understanding of systems. As such they are well suited for the study of the role of microorganisms in the natural environment. However, with few exceptions,^{1,2} only the effects of microbial metabolism have been included in models of aquatic ecosystems.^{3,4,5,6}

We feel that it is important to model explicitly natural assemblages of microbial organisms, which we will refer to collectively as decomposers. Actual biomass of decomposers can serve as a food source for zooplankton and fish, thus affecting the dynamics of the aquatic food web. The sensitivity of decomposers to environmental controls can greatly affect the dynamics of remineralization of inorganic nutrients necessary for algal growth. And the relative utilization of different types of organic matter by the decomposers serves both to drive and to stabilize the aquatic ecosystem.

An aquatic ecosystem model incorporating realistic, functional terms for decomposers therefore seems necessary for understanding the interrelationships of the ecosystem and for predicting the consequences of various environmental-management decisions concerning the enrichment and removal of nutrients, thermal enrichment and the supply of organic material. However, development of such a model has been difficult because of lack of data on natural systems.

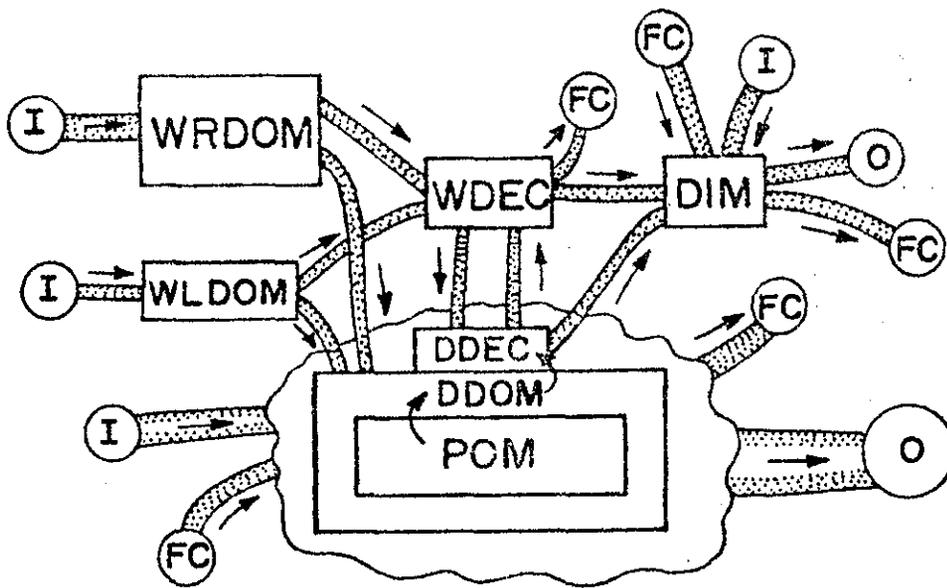
Elegant models have been developed to describe the growth of microbial populations in laboratory systems.⁷⁻⁹ The challenge is to generalize these models to describe natural assemblages and to incorporate them into large-scale ecosystem models suitable for studying natural aquatic systems.

This paper is a description of one such generalized microbial growth and decomposition model, developed as part of a large-scale aquatic modeling effort and designed to be incorporated

into the resulting whole-ecosystem model. The model represents the dual role of the microflora as a food source and as an agent of biogeochemical cycling in an aerobic, open-water portion of a freshwater lake. As such, it is a preliminary effort in modeling an exceedingly complex microbial system.

The historical basis for this model was set several years ago,¹⁰ but the ensuing whole-ecosystem model contained only one decomposer group, and two classes of organic matter.¹¹ Later versions included phosphorus cycling¹² and nitrogen cycling.¹³ These later versions gave adequate simulations of Lake George food-chain data; however, the behavior of the decomposer, organic matter and inorganic nutrient compartments is difficult to explain. The anomalies include dissolved orthophosphate being too drastically depleted during the warm months, and decomposer biomass exceeding estimates from data^{14,15} by over two orders of magnitude.

Therefore, in this study we have disaggregated the compartments in order to obtain the stabilizing effect of diverse substrates, including refractory dissolved organic matter which dominates most lake ecosystems.¹⁶ Figure 1 illustrates the resulting conceptualization of the model. Decomposition in the open-water zone is assumed to occur in the water and on suspended detritus. Freely-suspended decomposers (WDEC) utilize labile dissolved organic matter (WLDOM) and refractory dissolved organic matter (WRDOM). Attached, or detrital, decomposers (DDEC) utilize sorbed dissolved organic matter (DDOM) on particulate organic matter (POM).



- FC - CONNECTION WITH FOOD CHAIN.
 I - INPUTS FROM LAND, ATMOSPHERE, LITTORAL ZONE AND BOTTOM SEDIMENT.
 O - LOSSES TO ATMOSPHERE AND BOTTOM SEDIMENT

Figure 1. Diagram of compartments of microbial growth and decomposition model. WRDOM, refractory dissolved organic material in water; WLDOM, labile dissolved organic material in water; WDEC, decomposers in water; DDEC, decomposers on detritus; DDOM, dissolved organic material on detritus; POM, particulate organic material; DIM, dissolved inorganic material.

Other compartments simulated in the model include nannophytoplankton, net phytoplankton, blue-green algae, three types of zooplankton, and two types of fish. Driving variables include light, temperature, and external loadings for soluble inorganic nitrogen, orthophosphate, particulate organic matter, and labile and refractory dissolved organic matter.

DECOMPOSER SUBMODEL

Both attached and unattached decomposers are described by the same equation (see Table 1, Equation 1).

Uptake (V_{ij}) of DOM (Equation 1.1) is represented as a hyperbolic relationship similar to Monod kinetics, expanded to include multiple substrates. Although some individuals^{17,18} consider the hyperbolic model weak, others feel that the hyperbolic uptake function is an adequate model.¹⁹⁻²⁰ We are considering incorporation of a more complex process model to account for utilization of intracellular substrates,²¹ but are still using the hyperbolic model at this time.

Although most studies have been made of pure cultures of organisms growing on a single energy source at an optimal temperature, some evidence is available for growth on multiple energy sources. Cells appear to use the more efficient substrate first; they resort to the secondary energy sources only after the primary source is depleted.²²⁻²⁴ Even mixed cultures and natural assemblages of decomposers exhibit this sequential substrate utilization pattern.^{25,26} This can occur even at low substrate concentration.²⁷

The q_{ij} factor represents in a very general way a hierarchy

of substrate utilization. It embodies the influence of the nutritional balance of the substrates and the capability for producing nutritional balance through processes such as adsorption, nitrogen fixation and nitrate reduction. However, it permits representation of other effects of differential degradation as well. A more complete representation of nutrient-conservative metabolism is being elaborated upon in our continuing work.

As in classical Monod kinetics, uptake becomes proportional to the product of B_i and B_j as the effective DOM level becomes small in relation to $KDOM_i$. Whereas, under substrate-saturated conditions uptake is proportional only to B_i since decomposer biomass controls the rate of uptake. This situation, however, is rare in nature.²⁸

Mineral mobilization or remineralization (R_{ij}) is represented as two terms (Eq. 1.2). This functionality provides for some minimum loss of inorganic matter from endogenous respiration even when no uptake occurs, although in actuality the nitrogen and phosphorus may be immediately recycled. The maximum rate of release of elements bound in organic linkages is determined by the same factors that enter into the uptake term, i.e. q_{ij} and concentration.

Mortality (M_i) is assumed to occur at a constant rate, $KMORT_i$, a critical temperature, $TCRIT$, beyond which it is exponential (Fig. 2 and Eq. 1.3). Future versions of the model will have a substrate-dependent term for mortality, to represent the occurrence of osmotic fragility under conditions of poor nutritio

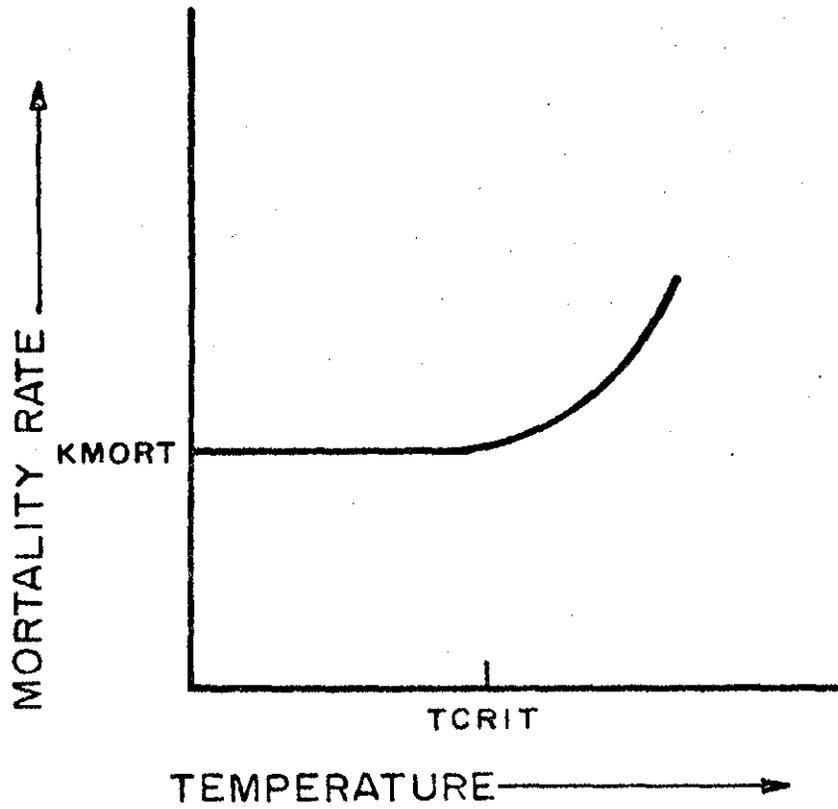


Figure 2. Relationship between mortality of microorganisms and temperature.

however, this idea has not yet been implemented.

Release of dissolved organic matter (U_i) is small for the aerobic conditions encountered in the open water zone, but cannot be considered zero since many organisms (especially pseudomonads) produce significant quantities of DOM as a result of their metabolism.³⁰ In modeling the anaerobic system this term takes on a more important role since organic fermentation products contribute to the value of U_i .

Sedimentation rate (S_i) is defined in Eq. 1.4. The $KSED_i$ parameter is a measure of the basal rate of sedimentation at 0° and reflects the effects of particle density and size. KDV_i represents the influence of temperature-dependent viscosity and density of water on the sedimentation rate. For decomposers and flocs of decomposers of approximately spherical shape sedimentation rate is essentially linear with respect to temperatures above 4° ; the slight nonlinearity due to decreasing density of water below 4° is ignored in the formulation.

The exchange of decomposers between water and suspended detritus is approximated by Eq. 1.5. The exchange process (D_i) is a direct function of the biomass of WDEC and the degree of colonization of the POM. Colonization and shedding depend on the availability of sites, b_{ij} (Eq. 1.51), where $(KSV_k \cdot B_k)$ is a measure of the total sites that can be colonized on the POM and $B_i / (KSV_k \cdot B_k)$ can be considered a measure of the occupied sites. KSV_k is the ratio of colonizable surface area to mass of POM, in other words a surface area coefficient.

$KSHED_i$ is an endogenous shedding rate that is independent of the availability of colonization sites. In future versions of this model it will be treated as a variable that is a function of growth rate, reflecting the loss of daughter cells that divide away from the plane of attachment on the particle.³¹ $KTRANS_i$ is a maximum colonization rate; colonization is increased by the availability of sites on the POM.

Consumption (C_i) of decomposers by detritus-feeding organisms is represented by a complex equation, based on general ecosystem modeling concepts.^{32,33} However, it is beyond the scope of this paper.

Equation 1 requires at least 26 parameters to predict one decomposer assemblage metabolizing one substrate and consumed by one higher organism. One parameter is required for uptake of each additional substrate (and at least nine parameters for each additional consumer).

ORGANIC MATTER SUBMODELS

The organic matter is divided into two classes, particulate and dissolved. The particulate material is defined as organic detritus that is retained on a 0.45 micron membrane filter; it is an aggregate consisting of three state variables: 1) particulate organic matter (POM), 2) sorbed organic matter (DDOM), and 3) attached decomposers (DDEC). The POM equation (Eq. 2.0) is shown in Table 2. Sorbed organic matter is treated in Eq. 3 with dissolved organic matter.

Most of the terms (E, M, I, C) in the submodel are dependent on the functioning of the ecosystem and are predicted by the whole-system model CLEANER.³³ The input term (I_k) is the organic loading to the system via air, water, and land. There are relatively few data quantifying these allochthonous inputs even though it is clear that they are important to the functioning of the aquatic ecosystem.³⁴ The relative importance of detrital-based versus algal-based food webs in a lake is determined by the loadings to the system. Those systems receiving high organic loadings in relation to inorganic loadings are inclined to be detrital based. Since the model being described is for the open water zone of a lake, the influence of the land is not direct but through the littoral zone. This coupling between open water and littoral zone is being developed in continuing work.

Sedimentation (S_k) is identical in form to Eq. 1.4. The only term of specific interest introduced in this submodel is that representing the enzymatic solubilization of POM by the attached heterotrophic microflora (H_{ik}).

The mediation of surfaces in the catalysis of chemical reactions is thought to be an important aspect of the decomposition process in lake water. Although never directly measured, concentration of nutrients at liquid solid, liquid-liquid, and gas-liquid surfaces has been repeatedly implicated by the accumulation of microorganisms at these interfaces. Chemotactic responses³⁵ to attachment sites at the interfaces coupled with

physico-chemical factors³⁶ are assumed to initiate the micro-colonization of POM. The subsequent metabolism of POM and DDOM results in the elaboration of DDEC on the surface of the aggregate. The solubilization of POM is actually a transfer from POM to DDOM mediated by the attached microflora (DDEC). This transfer is assumed to be a function of DDEC and POM (Eq. 2.1).

The microflora probably utilize the solid state as a substrate by means of membrane-bound, solubilizing enzymes. The solubilization of pure cellulose has been found to be very rapid and complete in aquatic environments.³⁷ Cellulose decomposition associated with sediments is also very rapid. This has been shown in studies performed in the development of this model. Decomposition was maximized by keeping the sediment suspended at 25°C. Under these conditions 85% of the cellulose was solubilized in 68 hours; in this way the value of HMAX for cellulose was determined. Under in situ conditions, the autumn load of finely divided cellulosic materials is reduced by 85% within 4 weeks; these data have proved useful in calibrating the model for the lake.

KSV_k describes how much surface area is associated with a given POM mass (B_k). $KPOM_k$ is the half saturation coefficient for POM. This is related to the chemical composition of the POM and would therefore be a low value for readily-degradable POM and a high value for less-readily degradable material.

The DOM equation is found in Table 3. This equation is used for sorbed (DDOM), as well as the two water-column dissolved organic matter variables (WLDOM, WRDOM) Eq. 3.0). The DOM equation introduces no new terms. However, the transfer term, D_j (Eq. 3.1), is different in that it incorporates a diffusion factor, a_j , as well as a measure of the availability of sites for sorption (b_j).

NUTRIENT SUBMODEL

The nutrient submodel includes four dissolved inorganic materials: carbon, nitrogen, oxygen, and phosphorus (DIM of Figure 1). Of greatest significance to the decomposition model is the relationship between the proximate mineral composition of organic compounds undergoing decomposition and the degree to which these minerals are mobilized and made available for photosynthetic uptake.

This obviously involves a consideration of the biodegradability and nutrient balance of the compounds undergoing decomposition and is therefore related to the q_{ij} factor discussed previously. It is also related to the level of chemical constituents in the surrounding water although this is not yet implemented. The model assumes release of a nutrient when the level of the nutrient exceeds the metabolic need of the decomposer.

As a simplifying assumption the mobilization of organically bound carbon, nitrogen and phosphorus is described by means of chemical stoichiometric equations for the oxidation of organic

compounds. This approach enables simulation of the remineralization produced by oxidative metabolism. By assuming a constant proximate composition of organic matter³⁸ or by considering specific organic materials, one can calculate remineralization constants for the carbon, nitrogen and phosphorus bound in organic linkages under conditions of total remineralization. The assumption that total remineralization occurs is another weakness since it is known that even with simple substrates, many microorganisms will produce incompletely oxidized end-products as a result of aerobic metabolism (see "Decomposer Submodel").

RESULTS AND DISCUSSION

The model provides a means for structuring our concepts of the decomposition processes within an unambiguous mathematical framework. As such it is amenable to detailed inspection for holistic relationships that are not evident when each process is considered separately under experimental conditions.

However, the model is probably most useful in simulating ecosystem responses to environmental perturbations and in determining the sensitivity of the ecosystem to variations in the components and processes that constitute the microbial decomposition subsystem. Thus the model suggests "emergent properties" that would be impossible to determine by direct observation of the ecosystem.

For example, the model can be used to consider the availability of various classes of dissolved organic matter and the

differential rates of uptake by decomposing microorganisms as modified by natural environmental variations throughout the year. As predicted by the model, the uptake of the various DOM classes in the southern end of Lake George, New York, changes drastically with time (Figure 3). Somewhat surprisingly, the model treats WRDOM as being of great importance as a substrate. However, that is a function of the large WRDOM pool in the lake ecosystem.

Sensitivity analyses can be performed quite readily using the interactive capability of the model on a time-sharing computer system. Figure 4 shows the response of the decomposer and organic matter compartments to normal and perturbed conditions in Lake George, New York, over a period of 827 days. In the normal simulation (Fig. 4A) the annual cycles are evident, and the model is seen to be stable with a large but realistic fluctuation in the freely suspended decomposers.

When the decomposers are removed from the system the response is significantly different (Fig. 4B). Labile DOM increases rapidly, while refractory DOM increases more slowly. POM exhibits a stable seasonal fluctuation; but, as will be shown later, it does not reach the peak concentrations that are attained with normal seasonal contributions from algal production. In the absence of heterotrophic uptake, sorbed DOM exhibits slight annual peaks that do not occur under normal conditions.

In Figure 4C a simulation without influence of phytoplankton is shown. In this detritus based system the decomposer and organic matter compartments maintain stable annual patterns of

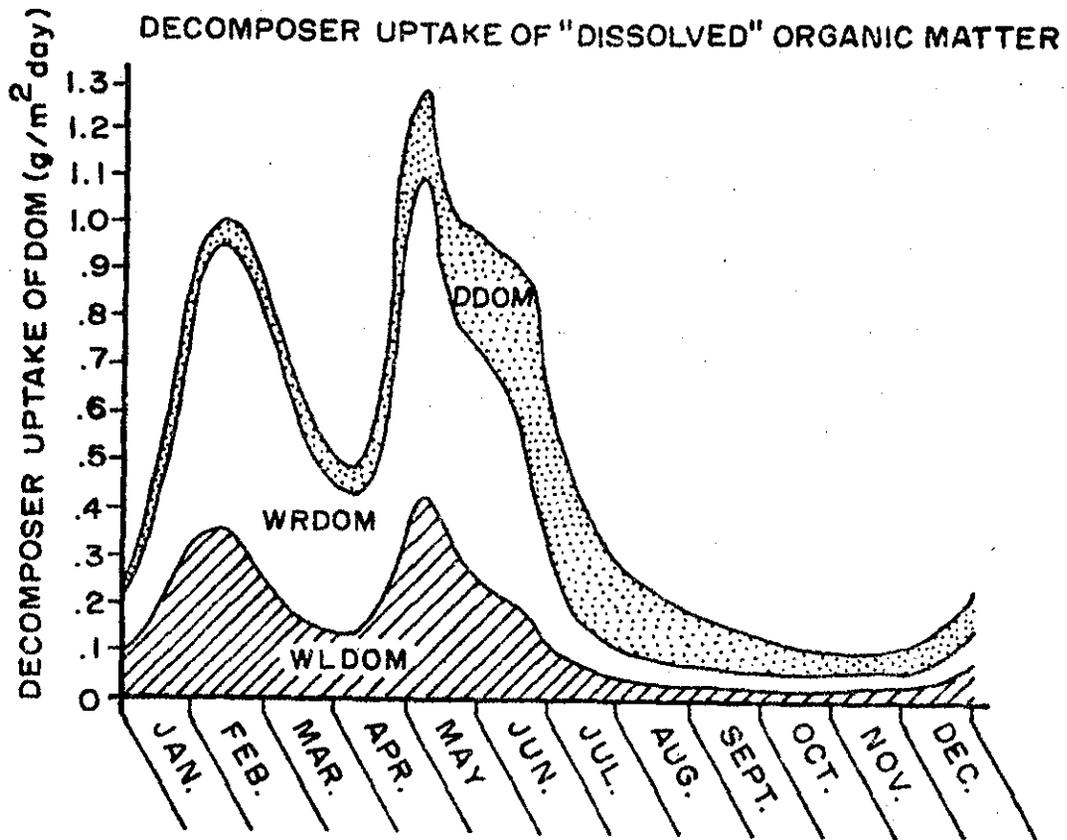


Figure 3. Uptake of DOM classes as predicted by a one-year simulation.

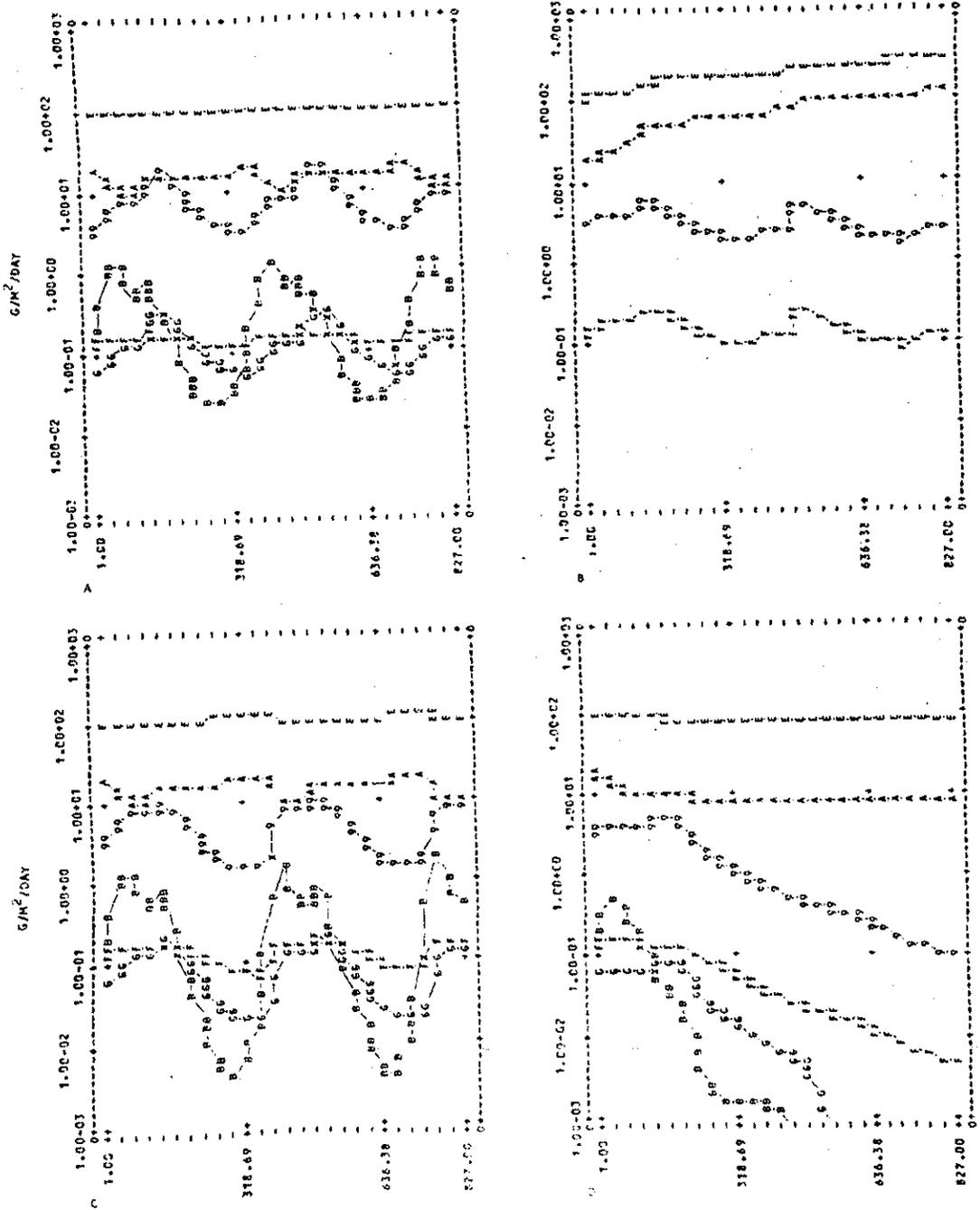


Figure 4. Response of decomposer and organic matter compartments to three perturbations. 4A, non-perturbed; 4B, in the absence of decomposers; 4C, in the absence of phytoplankton; 4D, in the absence of allochthonous organic loading. A = WDOM, B = WDEC, E = WRODM, F = DDOM, G = DDEC, 9 = POM.

oscillations. However, the patterns reflect the seasonal loadings of organic matter; without autotrophic production in the late spring and summer the freely suspended decomposers and, to a lesser extent, the POM and attached decomposers exhibit pronounced troughs. The abnormally low microbial activity, in turn, results in a slight seasonal rise in refractory DOM that is not seen in a normal simulation.

The complete absence of allochthonous organic loadings, as shown in Figure 4D, leads to an entirely different series of patterns of declining concentration. This suggests that with the present calibration the decomposition submodel is quite sensitive to external loadings. This sensitivity is questionable considering the ecology of the basin and lake, and is therefore the subject of continuing analysis. Interestingly, the DOM compartments show little change; they are receiving some input from autochthonous sources, but are not subject to the solubilization and sedimentation that affect the POM pool.

Figure 5 demonstrates the control that remineralization and autotrophic uptake exercise over the nutrient pools. In Lake George the dissolved oxygen and CO_2 levels are rather uninteresting. However, in a normal simulation (Fig. 5A) phosphate exhibits the effects of remineralization followed by severe depletion as a result of phytoplankton growth. Nitrogen has a less marked seasonal fluctuation.

In Figure 5B there is no remineralization by decomposers, and phosphate disappears as soon as the growing season begins. Soluble inorganic nitrogen is remineralized more readily by

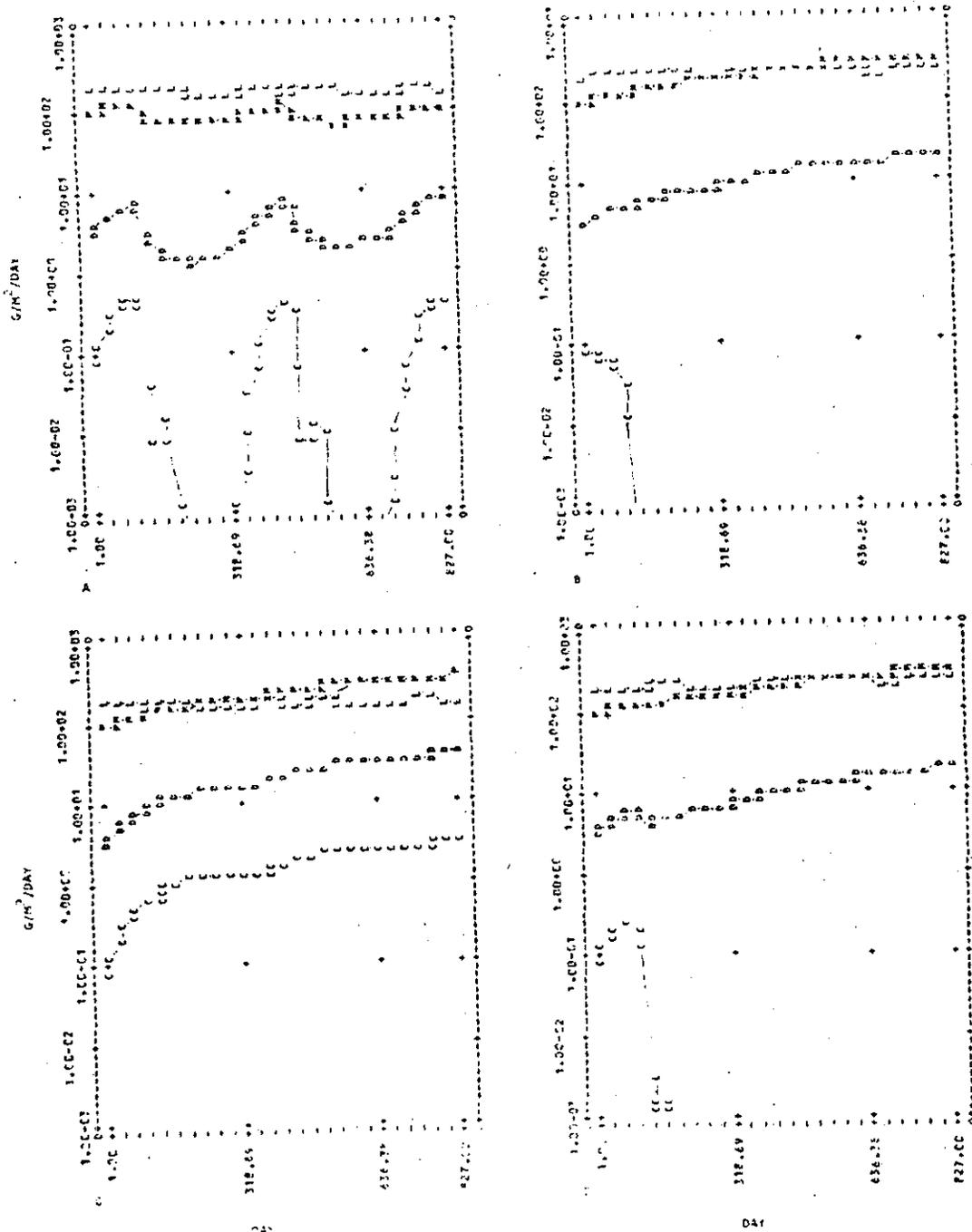


Figure 5. Response of nutrient pools to three perturbations. 5A, non-perturbed; 5B, in the absence of decomposers; 5C, in the absence of phytoplankton; 5D, in the absence of allochthonous organic loading. C = soluble reactive phosphate, D = soluble inorganic nitrogen, L = dissolved oxygen, m = carbon dioxide.

higher organisms and is also brought in through precipitation and runoff so that it gradually increases in concentration.

In the absence of uptake by phytoplankton (Fig. 5C), nitrogen, phosphorous, and carbon increase in concentration. Without organic loadings (Fig. 5D), there is an initial remineralization of phosphate by decomposers; but otherwise the effects of decomposition are limited, and the result is similar to that of no decomposers (Fig. 5B).

The biomass and relative importance of the phytoplankton (Fig. 6) are controlled by the levels of available nutrients. Under low nutrient conditions the relatively efficient nanrophytoplankton can take advantage of the rapid turnover of phosphate and consequently outcompete the larger net phytoplankton

The net phytoplankton are more sensitive and gradually disappear when decomposer remineralization fails to maintain a suitable level of phosphate (Fig. 6B). Likewise a similar pattern is seen in the absence of an allochthonous supply of phosphate (Fig. 6D). In this version of the model the blue-green algae have been parameterized as being virtually non-contributory to the POM pool and unimportant as a food source. Hence they are virtually immortal, although the phosphate level is unfavorable. This shortcoming of the model is being remedied with a construct for mortality that considers osmotic fragility as a function of nutrient concentrations.

Although beyond the scope of this paper, we have included simulation of the higher consumers (Fig. 7) to provide insight into the overall dynamics of the ecosystem. Obviously, the

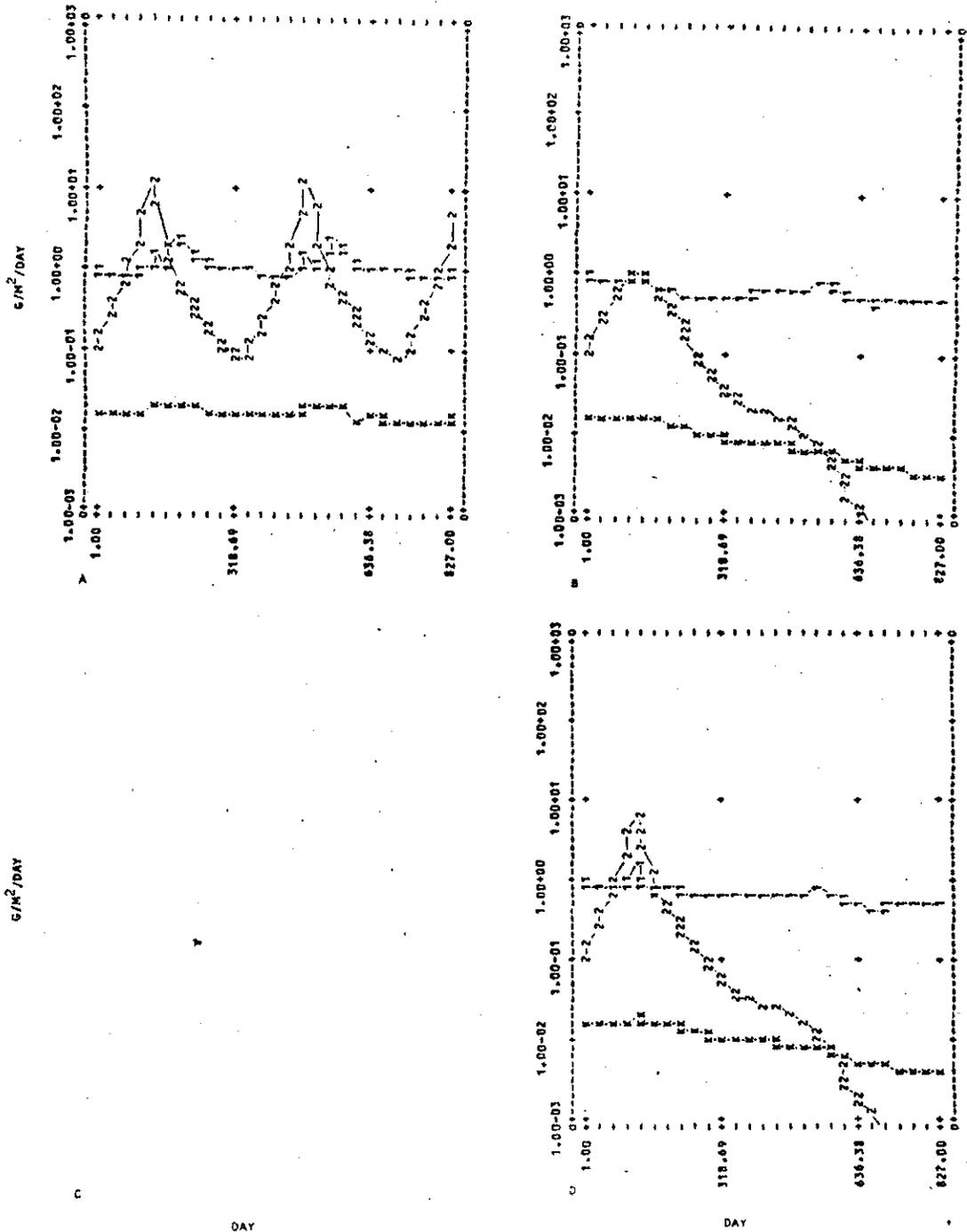


Figure 6. Response of phytoplankton to two perturbations. 6A, non-perturbed; 6B, in the absence of decomposers; 6C, not applicable (no phytoplankton); 6D, in the absence of allochthonous organic loading. 1 = nannophytoplankton, 2 = net phytoplankton, k = blue-green algae.

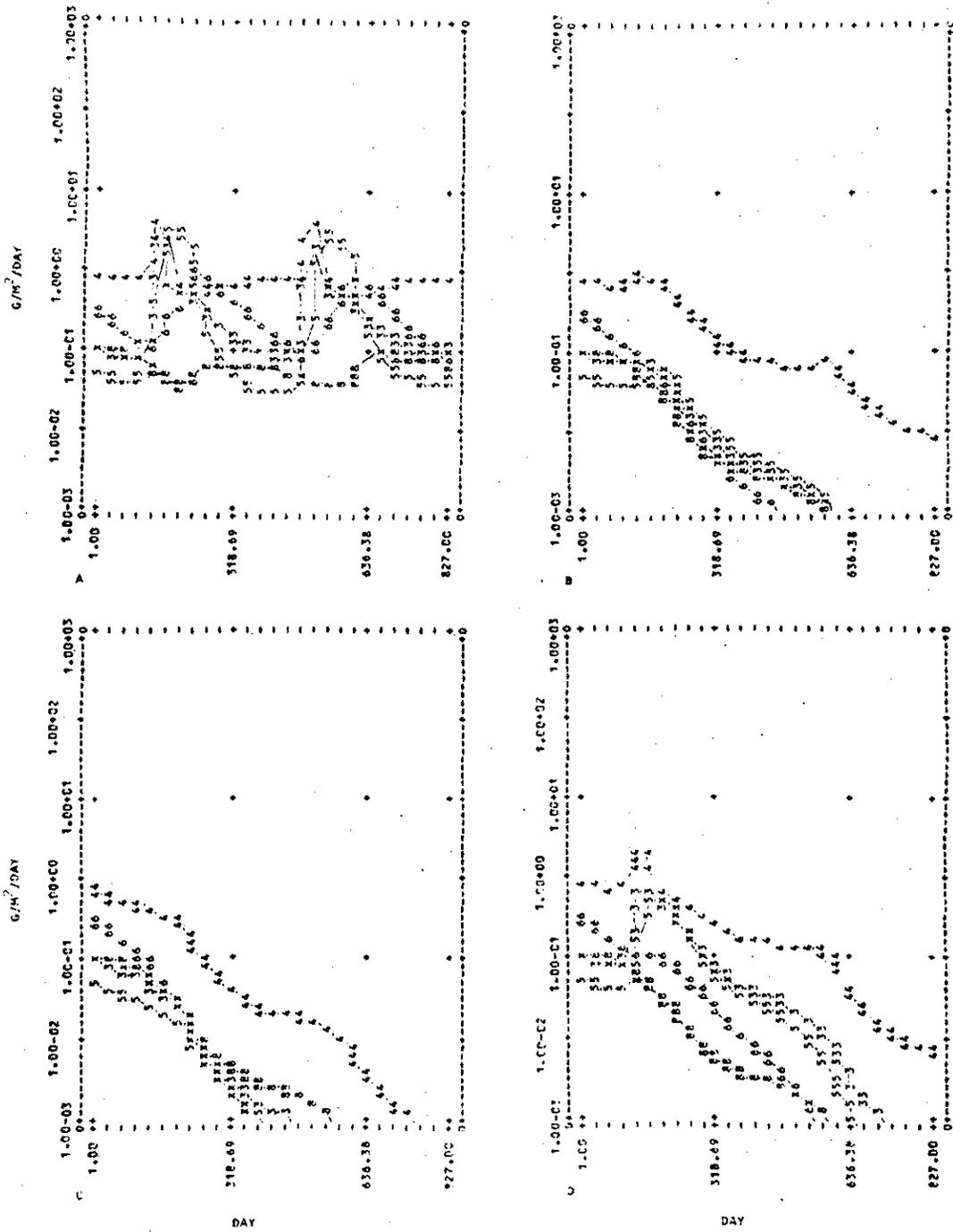


Figure 7. Response of higher consumers to three perturbations. 7A, non-perturbed; 7B, in the absence of decomposers; 7C, in the absence of phytoplankton; 7D, in the absence of allochthonous organic loading. 3 = cladocerans, 4 = copepods, 5 = predatory zooplankton, 6 = perch, 8 = trout.

higher levels of the food chain are dependent on the dynamics of the phytoplankton and therefore are sensitive to remineralization rates.

SUMMARY

A microbial decomposition model has been developed for use in analyzing natural systems and their response to environmental perturbations. The model represents microbial processes with greater realism than most existing ecosystem models and therefore promises to be of general application under varying environmental conditions. The model is coupled to the ecosystem model CLEANER. Its use in determining the sensitivity of the aquatic ecosystem to decomposer, phytoplankton and organic compartments has been demonstrated.

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Table 1. Decomposer Submodel

$$\frac{dB_i}{dt} = \left[\sum_j V_{ij} - \left(\sum_j R_{ij} + M_i + U_i + S_i + D_i + C_i \right) \right] \cdot B_i \quad \text{Eq. 1.0}$$

where

- B_i = concentration of biomass of the i^{th} decomposer group (g-m⁻²)
- V_{ij} = Uptake of j^{th} DOM by i^{th} decomposer group (g-m⁻²-day⁻¹)
- R_{ij} = remineralization of DOM by decomposers (g-m⁻²-day⁻¹)
- M_i = mortality of decomposers (g-m⁻²-day⁻¹)
- U_i = release by decomposers of dissolved organic matter as a result of metabolism (g-m⁻²-day⁻¹)
- S_i = sedimentation of decomposer cells (g-m⁻²-day⁻¹)
- C_i = consumption of decomposers by higher organisms (g-m⁻²-day⁻¹)
- D_i = transfer of decomposers between water and detritus as function of scouring and colonization sites on detritus (g-m⁻²-day⁻¹)

$$V_{ij} = V_{MAX_i} \cdot \frac{q_{ij} \cdot B_j}{\sum_j q_{ij} \cdot B_j + K_{DOM_i}} \quad \text{Eq. 1.1}$$

where

- V_{MAX}_i = Maximum uptake rate by decomposers as a function of water temperature (day⁻¹)
 B_j = Concentration of the jth dissolved organic matter group (DOM) (g-m⁻²)
 q_{ij} = Degradability weighting factor. A constant with range 0 to 1 indicating the relative degradability of the jth dissolved organic matter group by the ith decomposer group (unitless)
 K_{DOM}_i = The concentration of DOM that results in the decomposers taking up DOM at a rate equal to one-half V_{MAX}_i (g-m⁻²)

- R_{ij} = $U_{REM}_{ij} \cdot V_{ij} + R_{MIN}$ Eq. 1.2
 U_{REM}_{ij} = Fraction of DOM taken up that is re-mineralized (unitless)
 R_{MIN} = Endogenous remineralization rate necessary for maintenance metabolism as a function of temperature (g-m⁻²-day⁻¹)

$M_i = K_{MORT}_i \cdot 2^A$ Eq. 1.3

where

$$A = \begin{cases} T - T_{CRIT}, & T > T_{CRIT} \\ 0 & T < T_{CRIT} \end{cases}$$

- K_{MORT}_i = Mortality rate as a function of temperature (day⁻¹)
 T = temperature (°C)
 T_{CRIT} = Critically high temperature (°C)

$$S_i = (KSED_i + KDV_i \cdot T) \quad \text{Eq. 1.4}$$

where

$$KSED_i = \text{Sedimentation rate of decomposers at} \\ \text{depth-averaged water temperature of} \\ 0^\circ\text{C} \quad (\text{day}^{-1})$$

$$KDV_i = \text{Coefficient determining the effect of} \\ \text{water temperature on sedimentation} \quad (^\circ\text{C}^{-1}\text{-day}^{-1})$$

$$D_i = \begin{cases} KSHED_i + B_i \cdot b_i & b_i < 0, B_i = \text{DDEC} \\ KTRANS_i \cdot B_i \cdot b_i & b_i > 0, B_i = \text{WDEC} \\ 0 & b_i = 0 \end{cases} \quad \text{Eq. 1.5}$$

where

$$b_i = 1 - \frac{B_i}{KSV_k \cdot B_k} \quad B_i = \text{DDEC} \quad \text{Eq. 1.51}$$

$$KSHED_i = \text{Endogenous shedding rate} \quad (\text{days}^{-1})$$

$$KTRANS_i = \text{Maximum colonization rate} \quad (\text{m}^2\text{g}^{-1}\text{ days}^{-1})$$

$$KSV_k = \text{Surface area coefficient} \quad (\text{unitless})$$

$$B_k = \text{Concentration of POM} \quad (\text{g-m}^{-2})$$

Table 2. Particulate Organic Matter Submodel

$$\frac{dB_k}{dt} = [(E_k + M_k + I_k) - (S_k + \sum_j H_{jk} + C_k)] \cdot B_k \quad \text{Eq. 2.0}$$

where

- B_k = Concentration of the k^{th} POM group (g-m⁻²)
- E_k = Contribution of POM through egestion (g-m⁻²-day⁻¹)
- M_k = Contribution of POM through mortality (g-m⁻²-day⁻¹)
- I_k = Observed loading of allochthonous POM
into water column (g-m⁻²-day⁻¹)
- S_k = Sedimentation of POM (g-m⁻²-day⁻¹)
- H_{ik} = Solubilization of POM by i^{th} attached
decomposer (g-m⁻²-day⁻¹)
- C_k = Consumption of POM by higher organisms (g-m⁻²-day⁻¹)

$$H_{ik} = HMAX_{ik} \cdot \frac{KSV_k \cdot B_k \cdot B_i}{KPOM_k + KSV_k \cdot B_k + B_i} \quad \text{Eq. 2.1}$$

where

- $HMAX_{ik}$ = Maximum solubilization rate as a function
of temperature (day⁻¹)
- $KPOM_k$ = Saturation coefficient of k^{th} POM (g-m⁻²-day⁻¹)
- KSV_k = Surface area coefficient (unitless)
- B_i = Biomass of attached i^{th} decomposer (g-m⁻²-day⁻¹)

Table 3. Dissolved Organic Submodel

$$\frac{dB_j}{dt} = [(U_j + M_j + I_j + D_j + \sum_k H_{jk}) - \sum_j V_{ij}] \cdot B_j \quad \text{Eq. 3.0}$$

where

- B_j = Concentration of j^{th} dissolved organic group (DOM) ($g \cdot m^{-2}$)
- U_j = Contribution of DOM by excretion ($g \cdot m^{-2} \cdot \text{day}^{-1}$)
- M_j = Contribution of DOM through mortality ($g \cdot m^{-2} \cdot \text{day}^{-1}$)
- I_j = Observed loading of allochthonous DOM into the lake ($g \cdot m^{-2} \cdot \text{day}^{-1}$)
- D_j = Transfer between sorbed and dissolved phase ($g \cdot m^{-2} \cdot \text{day}^{-1}$)
- H_{jk} = Solubilization of k^{th} POM to form j^{th} DOM (see Eq. 2.1) ($g \cdot m^{-2} \cdot \text{day}^{-1}$)
- V_{ij} = Uptake of DOM by i^{th} decomposer (See Eq. 1.1) ($g \cdot m^{-2} \cdot \text{day}^{-1}$)

$$D_j = \begin{cases} KTRANS_j \cdot a_j & a_j \leq 0 \\ KTRANS_j \cdot a_j \cdot b_j & a_j > 0, b_j \geq 0 \\ 0 & b_j < 0 \end{cases} \quad \text{Eq. 3.1}$$

where

- $KTRANS_j$ = maximum sorption rate ($m^2 \cdot g^{-1} \cdot \text{day}^{-1}$)
- $a_j = B_\ell - (KE \cdot B_m)$ Eq. 3.11
- B_ℓ = Concentration of DOM in water (WLDOM or WRDOM) ($g \cdot m^{-2}$)

- B_m = Concentration of organic material sorbed
to POM (DDOM) (g-m⁻²)
- b_j = $1 - \frac{B_l}{KSV_k \cdot B_k}$ Eq. 3.12
- B_k = Concentration of POM (see Eq. 1.51) (g-m⁻²)
- KE = Partition coefficient (unitless)

Table 4. Nutrient Submodel

$$\frac{dB_n}{dt} = [I_n + \sum_j KU_{nj} R_j + D_n - \sum_j KU_{mn} P_m] \cdot B_n \quad \text{Eq. 4.0}$$

where

- B_n = Concentration of the n^{th} nutrient (g-m⁻²)
- I_n = Observed loading of the n^{th} nutrient into the lake (g-m⁻²-day)
- KU_{nj} = Remineralization constant representing the proportion of the nutrient available through remineralization (R_j) of the j^{th} organic material (unitless)
- D_n = Inputs or losses of the nutrient due to insolubilization or turbulent diffusion (g-m⁻²-day)
- KU_{mn} = Constant for the removal of the nutrient due to gross primary production by the m^{th} phytoplankton (unitless)
- P_m = Gross primary production by phytoplankton (g-m⁻²-day⁻¹)