

DOCUMENTATION OF SELECTED CONSTRUCTS AND PARAMETER VALUES IN THE AQUATIC MODEL CLEANER †

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ABSTRACT

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Process representations critical to the phytoplankton and zooplankton submodels are described. These include constructs for: light- and nutrient-limitations and their interaction, temperature, consumption, and population-age structure. Values for key parameters are documented with reference to the literature on aquatic ecology and ecological modelling. Time-course relationships of the processes affecting the phytoplankton, zooplankton, phosphorus and nitrogen compartments are presented and discussed. These serve as additional documentation and are an important result of modelling synthesis.

INTRODUCTION

The aquatic model CLEAN was formulated by approximately 25 investigators in the Eastern Deciduous Forest Biome, U.S. International Biological Program (Park et al., 1974). It incorporates a number of submodels for ecologic and physiologic processes (Bloomfield et al., 1973) based on detailed studies by Biome participants at the Lake Wingra, Wisconsin, and Lake George, New York sites. Implementation of the generalized Biome version was effected at Rensselaer Polytechnic Institute (Scavia et al., 1974).

More recently the basic model has been improved with the incorporation of phosphorus and nitrogen cycling, the addition of compartments for blue-green algae and dissolved oxygen, the reformulation of the decomposition

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submodels, and refinement of various process terms. A subroutine has also been included to transform biomass values into environmental-perception characteristics such as predicted secchi disc readings, fish catch, algal ratios, and concentrations of noxious algae. The result is CLEANER, the Comprehensive Lake Ecosystem ANalyzer for Environmental Resources (Scavia, 1974; Park et al., 1975; Bloomfield et al., 1975).

Development of CLEAN and CLEANER has been guided by a concern for biologic realism at the process level balanced against the realization that simplifications are necessary if all the principal elements of the aquatic food web are to be modelled simultaneously. Nowhere is this illustrated better than in the phytoplankton, zooplankton, decomposer, and nutrient submodels (Tables I–IV). The objectives of this paper are (1) to describe the mathematical constructs (process representations) critical to the phytoplankton and zooplankton submodels in CLEANER, (2) to document the parameterizations of the phytoplankton, zooplankton, and nutrient submodels, and (3) to illustrate the behavior of these through simulation of a typical year.

TABLE I
Phytoplankton

1.0	$\frac{dB_i}{dt} = PPROD - RES - SED - MORT - GRZ - EXC$
1.1	$PPROD = \text{photosynthesis}$ $= PMAX * U_T * TEMP * B$
1.2.0	$U_T = N / \sum_i^n \left(\frac{1}{U_i} \right)$
1.2.1	$U_i = \frac{S_i}{K_i + S_i}$
1.2.2	$U_I = \frac{2.718 * FP}{\epsilon' * Z} * \left[\exp\left(-\frac{I_o}{I_s * FP} \exp[-\epsilon' * Z] \right) - \exp\left(-\frac{I_o}{I_s * FP} \right) \right]$
	$PMAX = \text{maximum photosynthetic rate (day}^{-1}\text{)}$ $S_i = \text{nutrient concentration}$ $K_i = \text{half-saturation constant (mg/l)}$ $FP = \text{photoperiod}$ $I_s = \text{saturating light intensity (langley/day)}$ $I_o = \text{incident solar radiation}$ $Z = \text{depth (m)}$
1.2.3.	$\epsilon' = \epsilon + PHYTEX * \sum_i B_i$
	$\epsilon = \text{extinction coefficient of water}$ $PHYTEX = \text{extinction coefficient for biomass}$ $B = \text{phytoplankton biomass (g/m}^2\text{)}$

TABLE 1 (continued)

1.3	$TEMP = V^x e^{x(1-V)}$ $V = \frac{TMAX - T}{TMAX - TOPT}$ $X = \left[W \left(1 + \sqrt{1 + \frac{40}{w}} \right) \right]^2 / 20$ $W = \ln(Q_{10}) * (TMAX - TOPT)$ <p> <i>T</i> = temperature (°C) <i>TMAX</i> = maximum temperature for biologic process <i>TOPT</i> = optimum temperature </p>
1.4	$RES = \text{respiration}$ $= KRESP * PMAX * TEMP * B$ <p> <i>KRESP</i> = relationship constant between maximum respiration and maximum photosynthesis </p>
1.5	$SED = \text{sedimentation}$ $= KSED * (1 + KSLOPE * T) * B/Z$ <p> <i>KSED</i> = basal sedimentation rate at about $T = 0^\circ\text{C}$ (m/sec) <i>KSLOPE</i> = slope of sedimentation - temperature curve ($^\circ\text{C}^{-1}$) </p>
1.6	$MORT = \text{non-predatory mortality}$ $= KMORT * BEHAVE * POPUL * \left(\frac{CROWD * B}{KCAP} + 1 \right) * B * 2^A$ $A = \begin{cases} T - TCRIT, & T > TCRIT \\ 0 & T < TCRIT \end{cases}$ <p> <i>KMORT</i> = natural mortality rate (day^{-1}) <i>BEHAVE</i> = function available for behavioral effects <i>POPUL</i> = function available for population-age effects <i>CROWD</i> = coefficient for crowding effects <i>KCAP</i> = carrying capacity for population (g/m^2) <i>TCRIT</i> = critically high temperature ($^\circ\text{C}$) </p>
1.7	$EXC = \text{excretion}$ $= KEXCR * RES$ <p> <i>KEXCR</i> = constant relating excretory products to respiration </p>
1.8	$GRZ = \text{predation} = \sum_j C_j$ $C_j = CMAX_j * TEMP * POPUL * BEHAVE * PREF$
1.8.1	$PREF = \frac{W_{ij} * (B_i - BMIN_{ij})}{Q * Z + R * B_j + \sum_i W_{ij} * (B_i - BMIN_{ij})}$ <p> <i>CMAX_j</i> = maximum consumption rate of consumer <i>j</i> (day^{-1}) <i>W_{ij}</i> = preference of prey <i>i</i> by consumer <i>j</i> <i>B_i</i> = biomass of prey (g/m^3) <i>BMIN_{ij}</i> = minimum feeding level of prey <i>i</i> for consumer <i>j</i> (g/m^2) <i>Q</i> = feeding area coefficient (g/m^3) <i>R</i> = intracompartement competition or interference <i>B_j</i> = biomass of consumer <i>j</i> (g/m^2) </p>

TABLE II
Zooplankton

2.0	$\frac{dB_j}{dT} = CON - RES - EXC - MORT - DEF - GRZ$
2.1	$CON = \sum_i C_i$ (see Eq. 1.8)
2.2	$RES = (RMIN * B + KRESP * CON) * \left(1 + \frac{CROWD * B}{KCAP}\right) * POPUL * TEMP$ $* BEHAVE$ <i>RMIN</i> = endogenous respiration rate at starvation (day ⁻¹) <i>KRESP</i> = respiration rate (day ⁻¹)
2.3	<i>MORT</i> = (see Eq. 1.6)
2.4	<i>EXC</i> = (see Eq. 1.7)
2.5	$DEF = \sum_i E_i * C_i$ <i>E_i</i> = fraction of food <i>i</i> not assimilated <i>C_i</i> = (see Eq. 1.8)
2.6	$GRZ = \sum_k C_k$ (see Eq. 1.8)

TABLE III
Decomposers

3.0	$\frac{dB}{dt} = UPT - RES - DECEXC - MORT - GRZ - SED$
3.1	$UPT = \text{uptake of organics}$ $= \frac{VMAX * (DOM - DOMMIN)}{KDOM + (DOM - DOMMIN)} * TEMP * B$ <i>VMAX</i> = maximum uptake rate (day ⁻¹) <i>DOM</i> = dissolved organic matter (g/m ²) <i>DOMMIN</i> = refractory or otherwise unavailable <i>DOM</i> (g/m ²) <i>KDOM</i> = half-saturation constant for uptake (g/m ²)
3.2	$RES = \text{respiration}$ $= (RMIN * B + URES * UPT) * TEMP$ (see Eq. 3.3)
3.3	<i>DECEXC</i> = (see Eq. 1.7)
3.4	<i>MORT</i> = (see Eq. 1.6)
3.5	$GRZ = \sum_j C_j$ (see Eq. 1.8)
3.6	$SED = PSI (1 + KSED * T)B/Z$ <i>PSI</i> = basal sedimentation rate at 0°C (m/day) <i>KSED</i> = slope of sedimentation — temperature curve (°C ⁻¹) <i>T</i> = temperature (°C) <i>B</i> = decomposer biomass (g/m ²) <i>Z</i> = depth (m)

TABLE IV

Nutrients

4.0	$\frac{dB_p}{dt} = P\phi 4IN + DECIN + OTHRIN - PHYUPT$
4.1	$\frac{dB_n}{dt} = NLOAD + DECIN + OTHRIN - PHYUPT$
4.2	$P\phi 4IN$ = allochthalous loading of phosphorus (g/m ² /day) $NLOAD$ = allochthalous loading of nitrogen (g/m ² /day)
4.3	$DECIN$ = decomposer remineralization $= KU * DECEXC$ KU = % of decomposer release as P (or as N) $DECEXC$ = (see Eq. 1.7)
4.4	$OTHRIN$ = excretion of P (or N) by other organisms $= \sum_j ALPHA_j + EXC_j$ $ALPHA$ = % of excretory release as P (or N)
4.5	$PHYUPT$ = uptake of P (or N) by phytoplankton $= \sum_j KU * PPROD_j$ KU = % of $PPROD$ as P (or N) $PPROD$ = (see Eq. 1.1)

CONSTRUCT DESCRIPTION

Photosynthesis limitation

The effect of resource limitation (U) on primary production is basic to the functioning of the normal aquatic ecosystem and is very important in the model. The two major controls on photosynthesis are nutrient availability and light intensity. Equation 1.2.1. is the construct used for limitation due to nutrient depletion, based on Monod kinetics and supported by many investigators (Dugdale, 1967; Epply et al., 1969; MacIsaac and Dugdale, 1969). This construct can be used for as many nutrients as deemed necessary.

The light-limitation construct takes into account reduction of the photosynthetic rate for light intensities both above and below the saturation level (Steele, 1965):

$$U_i = \frac{I_o}{I_s} \exp\left(1 - \frac{I_o}{I_s}\right)$$

where I_o is the incident solar radiation and I_s is the saturating light intensity. Using Beer's law for light extinction:

$$I_z = I_o e^{-\epsilon Z}$$

where I_z is the light intensity at depth z and ϵ is the extinction coefficient, and integrating over depth and time, the average light limitation for the given time and depth is obtained as shown in Eq. 1.2.2. (Steele, 1965).

One of the subtle but important differences in existing phytoplankton models is the way in which the interaction of these limitation factors is treated. Two constructs that have been used are:

$$(U_1 * U_2 * U_3 \dots)$$

(Chen, 1970; DiToro et al., 1971; and Goodall, 1975),

and

$$\min (U_1, U_2, U_3, \dots)$$

(Larsen et al., 1973).

The first construct has as its biologic basis the multiplicative effects of the enzymatic processes involved in photosynthesis (D. Botkin, personal communication, 1974). However, Bloomfield et al. (1973) and Lassiter and Kearns (1973) point out that this construct becomes extremely limiting for even slightly non-optimal conditions due to the reduction effect of multiplying fractions. This severe limitation is probably not found in natural systems, where adaptive shifts can occur in the algal assemblage. The second construct, which mimics Liebig's law of the minimum, can be expected to produce reasonable results when dealing with pure cultures. When natural assemblages are considered, however, the adaptive ability of the assemblage precludes the use of this construct as well (Steele, 1974).

An alternate construct was developed for CLEAN (Bloomfield et al., 1973). This construct is Eq. 1.2.0, where n is the number of limiting functions and is used to normalize the total limitation term, U_t . U_i are the normalized individual limitation functions described above. If no nutrient is limiting, U_t shows no limitation, and if any one function is absolutely limiting, the function is totally limiting (Table V). Our reason for preferring this new construct is intuitive. We believe it is reasonable to assume that adaptation and species

TABLE V

Variation of total limitation function (U_t) with respect to individual limitation terms

U_1	U_2	U_3	U_t
0.00	1.00	1.00	1.00
1.00	1.00	0.50	0.75
1.00	0.50	0.50	0.60
0.50	0.50	0.50	0.50
1.00	0.50	0.25	0.43
1.00	0.25	0.25	0.33
0.50	0.25	0.25	0.30
0.25	0.25	0.25	0.25
0.50	0.50	~0.00	~0.00
~0.00	0.50	~0.00	~0.00
~0.00	~0.00	~0.00	~0.00

replacement in a natural assemblage will moderate the limiting effect of any particular nutrient or combination of nutrients. Therefore, this construct, which is mathematically analogous to resistors in series, may better represent the actual limitation process at the ecosystem level. However, the half-saturation constants and maximum-photosynthetic rate take on slightly different meaning; and, where these parameters have been adjusted through calibration, they may need to be readjusted to compensate for the decreased limitation. Clearly more experimental data on the limitation of mixed assemblages is needed in order to suggest the best construct and parameter values.

Temperature

The temperature function, $TEMP$ (Eq. 1.3), is a complex empiricism for the nonlinear response often exhibited by biologic processes (Fig. 1). It was slightly modified from one developed to represent the temperature dependencies of respiration and feeding rates in poikilotherms (Shugart et al., 1974). It is incorporated in almost all the process formulations in the model and therefore is very important.

The evaluation of this process—temperature relationship is shown in Figs 2a—c. As the maximum temperature, $TMAX$, approaches the optimum tem-

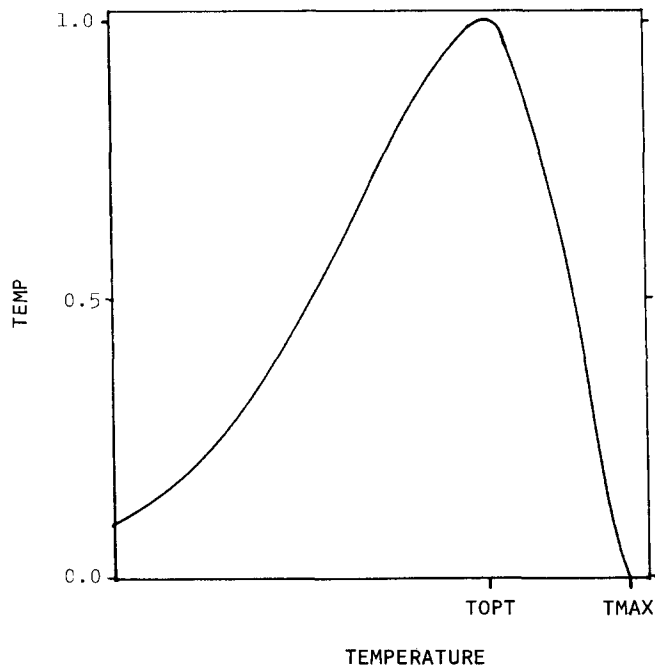


Fig. 1. Relationship between temperature and $TEMP$, the function for non-optimal temperature correction.

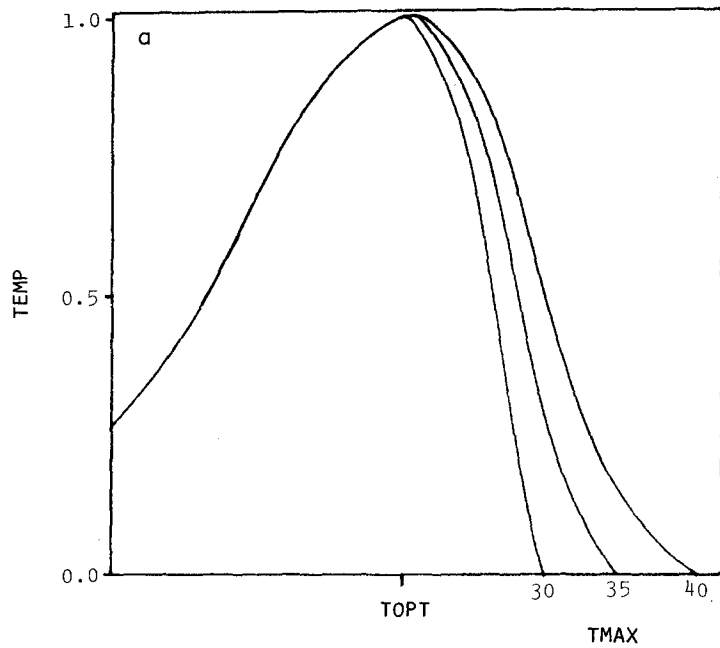


Fig. 2a. Effect of the parameter $TMAX$ ($^{\circ}C$) on $TEMP$, the function for non-optimal temperature correction.

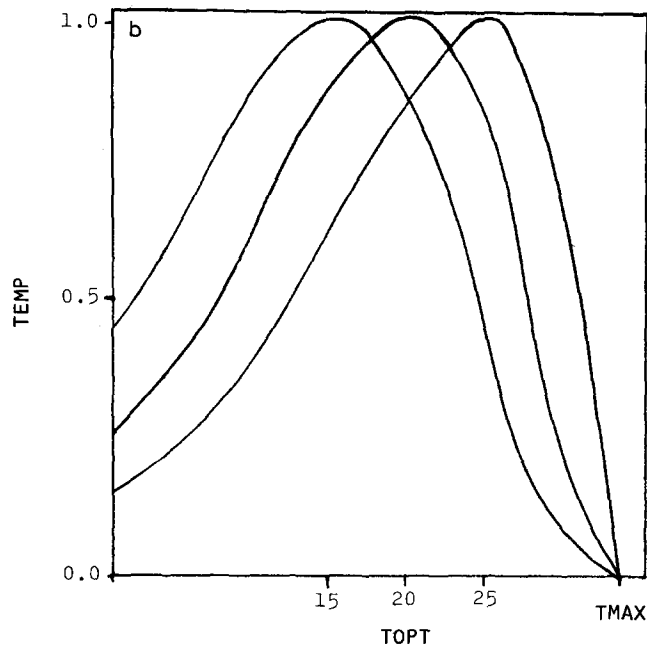


Fig. 2b. Effect of the parameter $TOPT$ ($^{\circ}C$) on $TEMP$, the function for non-optimal temperature correction.

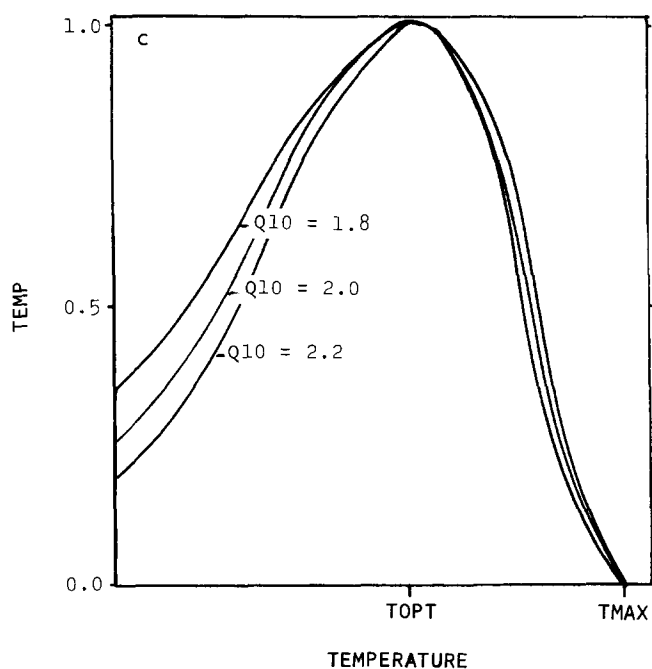


Fig. 2c. Effect of the parameter Q_{10} ($^{\circ}\text{C}^{-1}$) on $TEMP$, the function for non-optimal temperature correction.

perature, $TOPT$, the reduction rate of a process due to higher temperatures is increased (Fig. 2a). Changing $TOPT$ merely translates the curve (Fig. 2b). The Q_{10} (rate of change per 10°C) value has considerable effect on the response of the model (Fig. 2c). As the Q_{10} value increases, the slope of the suboptimal temperature curve increases, and thus the process is more sensitive to temperature. The parameter values used during calibration for Lake George, New York, are listed in Table VI.

Consumption

The general consumption term (Eq. 1.8) is critical because it is the strongest compartment-linking term in the model. C_{MAX} is the maximum adult feeding rate, $TEMP$ is the temperature correction term previously discussed and $POPUL$ is the correction term for the population age structure (discussed in the next section). $PREF$ represents both food preference and the relationship between consumption and total available food. The construct was developed by O'Neill et al. (1972) and modified by Bloomfield et al. (1973). In this factor, $W(i, j)$ is the food preference or capturability index (O'Neill, 1969) and $W(i, j) * (B(i) - B_{MIN})$ is, therefore, the weighted biomass on which the consumer can feed. That is, B_{MIN} is the minimum level of food that will stimulate consumption (Steele, 1974). Evidence of a minimum food level for

TABLE VI
Documentation of parameter values

Parameter	Units	Value used	Literature values ^a	Reference	Comment
PMAX					
nano	day ⁻¹	1.6	1.38-1.6	Epply et al. (1969)	Size-dependency <i>Thalassiosira fluviatilis</i>
net	day ⁻¹	1.4		Fuhs et al. (1972)	
blue-green	day ⁻¹	1.1	1.48 1.3-2.7	Rhee (1972)	<i>Scenedesmus</i> sp. Blue-green
				Sorokin and Krauss (1962) Fogg (1950)	
ISAT					
phytoplankton	langleys/day	350		Canale et al. (1974)	Grand Traverse Bay, Michigan
		300		DiToro et al. (1971)	Used in Mossdale Model
KN					
nano	mg-N/l	0.005	0.001-0.009	Pasciak and Gavis (1974)	<i>Cyclotella nana</i>
net	mg-N/l	0.008	0.014-0.018	MacIsaac and Dugdale (1969)	Natural eutrophic association Nitrogen fixation
blue-green	mg-N/l	0.0001			
KPO4					
nano	mg-P/l	0.005	0.005-0.007, 0.024	Halman and Stiller (1974)	Lake Kinneret natural assemblages
net	mg-P/l	0.015	0.015	Fuhs et al. (1972)	<i>C. nana</i>
			0.015	Halman and Stiller (1974)	Lake Kinneret natural assemblages
blue-green	mg-P/l	0.015	0.053	Fuhs et al. (1972)	<i>T. fluviatilis</i>
			0.01	DiToro et al. (1971)	<i>Microcystis aeruginosa</i>
TOPT					
nano	°C	25		Patrick and Reimer (1966)	b
net	°C	20	20-25	Ryther and Gullard (1962)	General algae
blue-green zooplankton	°C	33	35	Fogg (1965)	Non-thermophylic <i>Daphnia galatae</i>
			20	Fogg (1950) Hall (1962)	

TMAX									
nano	°C	35	32, 34, 37	Patrick and Reimer (1966)	Diatoms				
net	°C	35	35	Canale and Vogel (1974)	Diatoms				
blue-green	°C	45	41	Fogg (1950)	Non-thermophilic				
zooplankton	°C	35	35-50	Brown (1924)	Natural assemblage				
decomposers	°C	50	50	Boylen and Brock (1973)					
Q₁₀									
nano		2.2	2.19	Goldman and Carpenter (1974)	<i>Cyclotella nana</i> and <i>Monochrysis</i> <i>lutheri</i>				
net		1.9	2.0	Canale and Vogel (1974)	Diatoms				
blue-green		2.0	1.8	Epply (1972)	Marine and fresh- water algae				
zooplankton	1.7	1.7	1.7	LaRow (1973)	<i>Diaptomus</i>				
		1.8	1.8	LaRow (1973)	<i>Daphnia</i>				
		1.7	1.7	LaRow (1973)	<i>Cyclops</i>				
decomposers		1.7	1.7	Boylen and Brock (1973)	Natural assemblage				
CMAX									
zooplankton	g/g/day	0.8	0.85	Frederov and Sorokin (1967)	<i>Daphnia longispina</i>				
BMIN									
zooplankton	g/m ³	0.028 ^c	0.028	McAllister (1970)	Marine copepod				
Q									
zooplankton	g/m ³	0.2							

^a Most literature values are determined for particular species. Since the model is disaggregated only to functional groups many parameters had to be adjusted to fit the group rather than the particular species. Also, many parameters are not directly reported in the literature. Deduction may have been necessary.

^b Suggest that *Cyclotella nana* is a warm water species. Ryther and Gullard (1962) also report that *C. nana* will not grow below 15°C.

^c The actual value used for the Lake George simulation is 0.028 g/m³ × 20 m = 0.57 g/m².

consumption was demonstrated in the experiments of Parson et al. (1969). This minimum level was measured by McAllister (1970); he found that feeding response stops below approximately $15 \mu\text{g-C/l}$ in marine zooplankton.

When the term is summed over all food, consumption follows a hyperbolic relationship similar to that used to describe saturation kinetics (Fig. 3). In essence, this classical curve is displaced by the minimum food level, B_{MIN} ; and the half-saturation constant is replaced by a compound variable, $QZ + R(j)B(j)$. QZ represents the minimum feeding area necessary, and $R(j)B(j)$ represents intra-compartment competition.

Figs 4a–c show predictions for various combinations of the controlling parameters C_{MAX} , B_{MIN} , QZ , and R for one food source. Fig. 4a shows the variation in predictions with changes in C_{MAX} . Each curve asymptotically approaches subsequent values of C_{MAX} . In Fig. 4b, the same predictions are shown for various values of QZ . Increases in QZ produce increases in the half-saturation value, and thus delay the approach to C_{MAX} . This means that higher food levels are necessary to achieve the maximum consumption rate. In these evaluations, as in most of our simulations, R has been set equal to zero; an increase in R , however, would produce the same result as an increase in QZ . This would then mimic the real situation where R is constant and the biomass of the consumer is increasing. Fig. 4c shows various displacements of the curve produced through increasing values for the minimum food level, B_{MIN} . Documentation of the parameter values used for zooplankton during calibration is given in Table VI.

Population-age structure

Included in many of the submodels is a correction for population-age structure. This correction term, $POPUL$, is based on the simplifying assumption that populations at very low densities consist primarily of immature individuals, while populations approaching their carrying capacity are primarily composed of adults. It is formulated such that, as the population approaches its all adult population size, $KCAP$, the process approaches the maximum adult rate (Fig. 5). For consumption, the rate for immature organisms is assumed to be higher than for adults while for gametal loss in fish the rate is assumed to be highest when the population is all adults (Shugart et al., 1974).

The construct is:

$$POPUL = \begin{cases} 1 + KPOP \left(\frac{KCAP - B}{KCAP} \right), & B \leq KCAP \\ 1, & B > KCAP \end{cases}$$

where B is the population biomass. When this factor is used for general consumption, $KPOP$ (the percent change due to age structure) is positive, and when used in the term for gametal loss it is negative.

The construct is most realistic for top predators that have inherently stable population-age structures. It is not very satisfactory for populations subject

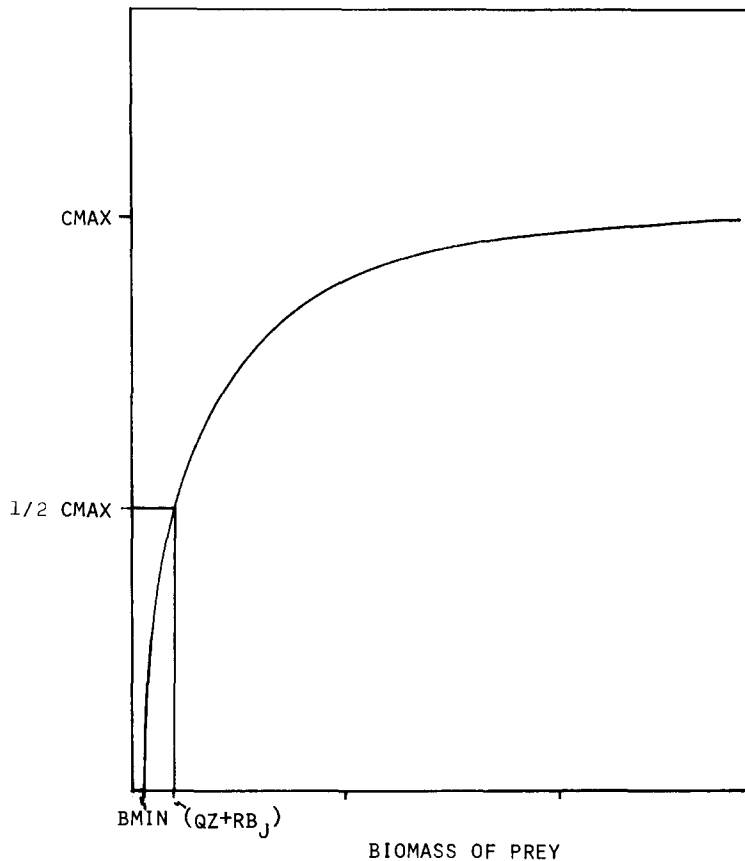


Fig. 3. Relationship between prey biomass and predator consumption term.

to age-dependent predation or migration. A more complex, realistic formulation that considers the effect of mean weight on various processes has been proposed by Zahorcak (1974) for inclusion in CLEANER.

PROCESS RATES

The time-course relationships of the processes controlling the state variables of the model are highly informative. They serve as a means for documentation of parameter values and are an important result of modelling synthesis that is not readily available from traditional laboratory and field studies. By plotting the values of each rate in the differential equation during a full year simulation, one can evaluate the relationships and relative importance of the terms and the processes they represent, especially when the rates are compared with the predicted standing crops during the year (Fig. 6).

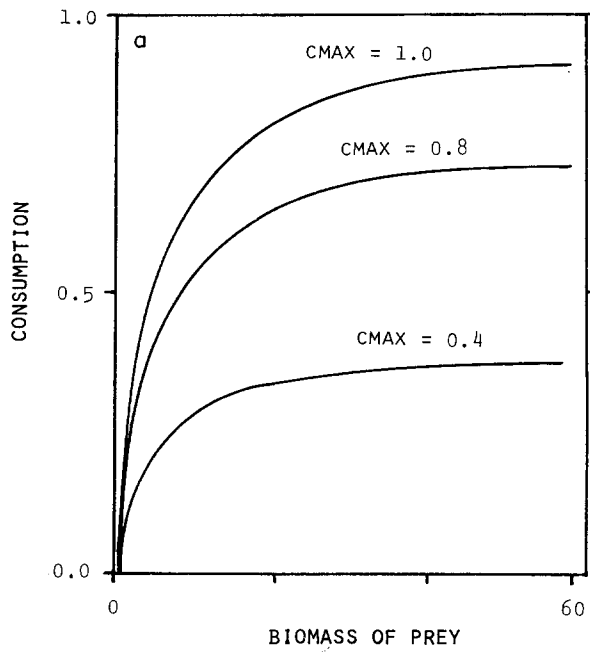


Fig. 4a. Effect of the parameter C_{MAX} (g/g/day) on the consumption term.

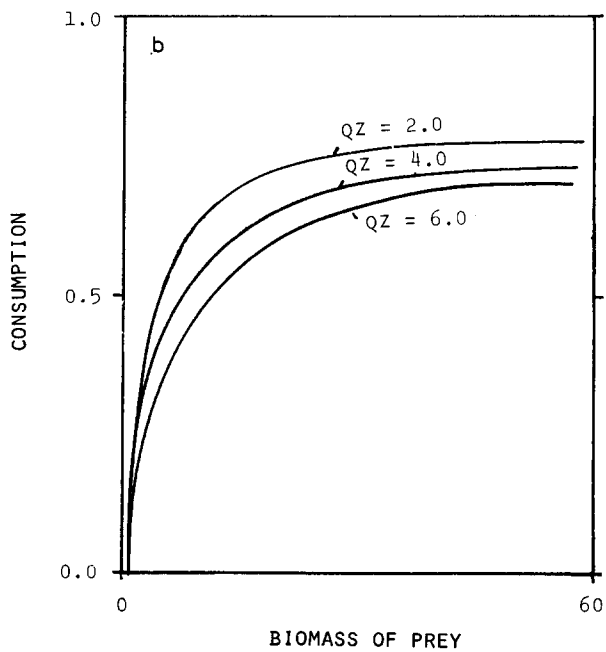


Fig. 4b. Effect of the parameter QZ (g/m²) on the consumption term.

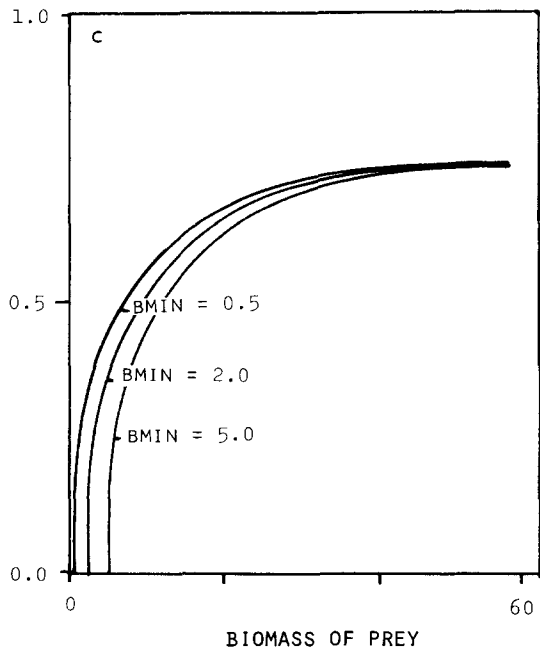


Fig. 4c. Effect of the parameter $BMIN$ (g/m^2) on the consumption term.

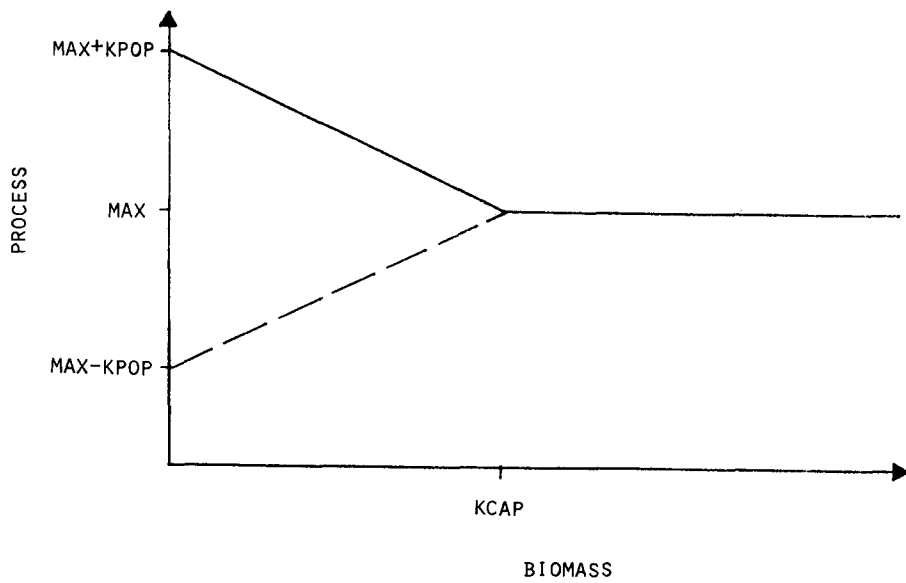


Fig. 5. Relationship between population biomass and $POPUL$, the population-age structure correction term.

Phytoplankton

As shown in Fig. 7, gross primary production in nannophytoplankton follows the sinusoidal pattern of light and temperature, with nutrient limitation strongly superimposed (See Fig. 6). Respiration (Eq. 1.4) is basically a function of temperature, and grazing pressure (Eq. 1.7) is controlled by temperature and zooplankton biomass (Park et al., 1974); both processes are important, with grazing being episodic and respiration having less impact during much of the growing season. These functions, along with sedimentary effects, are accounted for in most phytoplankton models. Sedimentation is contrived as a basal rate (0.2 m/day from Smayda, 1974), modified as a linear function of temperature (Eq. 1.5). The constants of proportionality (0.004 $l/^{\circ}C$ for nannophytoplankton and 0.008 $l/^{\circ}C$ for net phytoplankton) were calculated from data based on the work of Fritz (1935) and presented by Hutchinson (1967).

Nonpredatory mortality and excretion have some effect in the simulations; however, they are not as important as has been suggested by the findings of Jassby and Goldman (1974). In particular, the instantaneous mortality rate

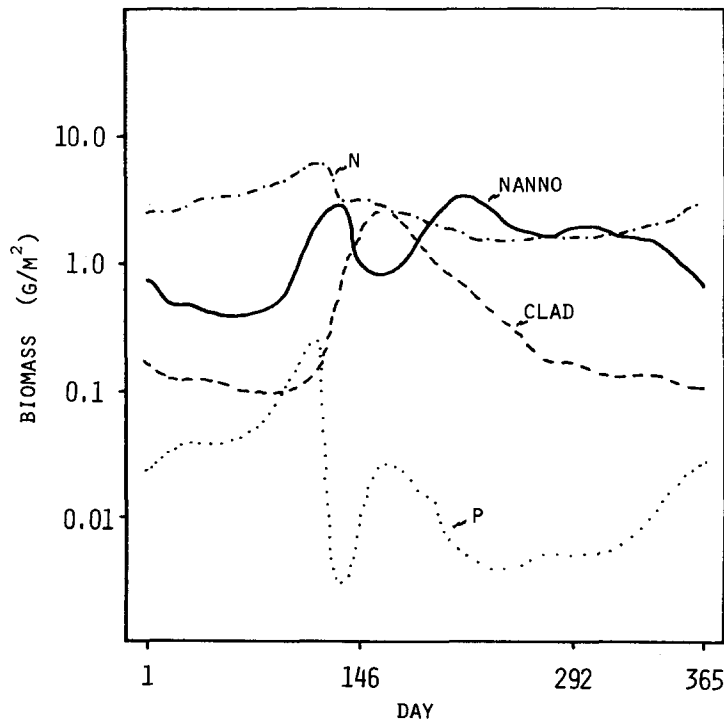


Fig. 6. Predicted biomass levels of nannophytoplankton, cladocera, nitrogen and phosphorus for 1 year.

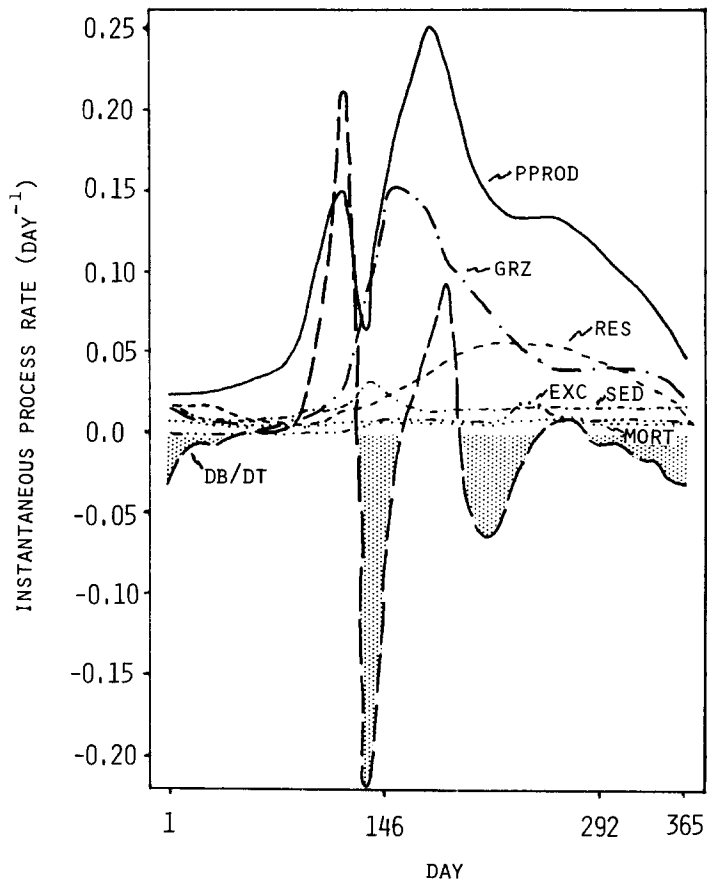


Fig. 7. Predicted instantaneous process rates for nannophytoplankton for 1 year; gross primary production (*PPROD*), grazing pressure (*GRZ*), respiration (*RES*), excretion (*EXC*), sedimentation (*SED*), nonpredatory mortality (*MORT*), and the overall growth rate (*DB/DT*).

should probably be much higher than the 0.01 day^{-1} that has been used in these simulations.

It is also interesting to notice that the rate of change is negative three times during the simulated year. The spring and summer decreases seem to be functions of the relationship between net production and grazing, whereas the winter decrease seems to be dominated more by the net production — natural mortality relationship.

ZOOPLANKTON

The dominant processes in the cladoceran compartment, shown in Fig. 8, are consumption, defecation, predation, and respiration. Consumption rate is in response to phytoplankton biomass and predation rate is stimulated by high zooplankton biomass (Figs 6 and 7). Defecation is a major loss term; in this

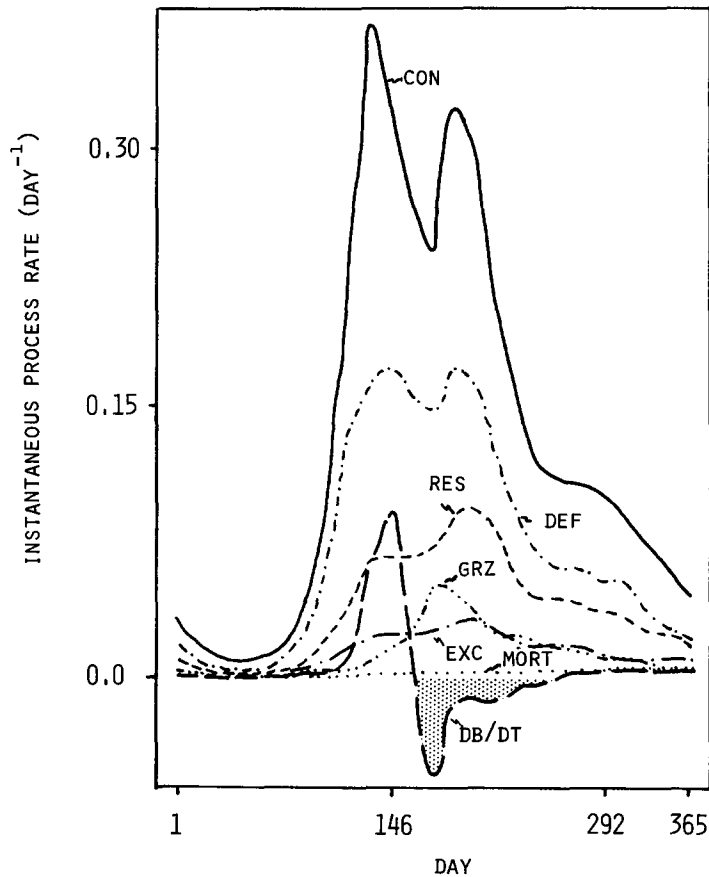


Fig. 8. Predicted instantaneous rates for cladocerans for 1 year; consumption (*CON*), defecation (*DEF*), respiration (*RES*), predation (*GRZ*), excretion (*EXC*), nonpredatory mortality (*MORT*), and the overall growth rate (*DB/DT*).

simulation it is based on a 60% assimilation efficiency — a value that is commonly used in food-chain models (e.g., DiToro et al., 1971; Hinemann, 1973). Assimilation efficiency has been reported by Edmondson (1957) to be between 53 and 78%, by Waterman (1960) and Mullin and Brooks (1970) to be between 63 and 90%, and by Sushchenya (1970) to be between 60 and 80–90%.

Respiration is modelled primarily as a function of consumption and secondarily as a function of zooplankton biomass, representing an endogenous rate during starvation (Eq. 1.2.2). We used a proportionality constant, *KRESP*, of 0.3. When *KRESP* is multiplied by the maximum consumption rate, 0.8 g/g/day (calculated from data of Federov and Sorokin, 1967), the result is 0.24 g/g/day. The respiration rate of a mixed marine population has been reported as about 0.125 mg-C/mg dry weight/day (Menzel and Ryther, 1960),

for an instantaneous rate of 0.22 g/g/day. Thus a value of 0.3 for *KRESP* seems to be reasonable.

Ganf and Blažka (1974) report that nitrogen and phosphorus remineralization through zooplankton excretion is very important in Lake George, Uganda. We converted their data to our units (relating excretion to respiration) and used that value (approximately 0.3 or 30% of the loss due to respiration). Although excretion may be important in remineralization, it seems unimportant as a loss term in this particular formulation.

Population losses due to nonpredatory mortality, or physiological mortality as Hall (1964) refers to it, are relatively small. Hall reports it to be less than 3% of the population per day in his work with *Daphnia galeata mendotae*. In his work with *Daphnia rosea*, Dodson (1972) attributes 93.5% of the total mortality to predation, thus leaving only 6.5% to be explained by all other

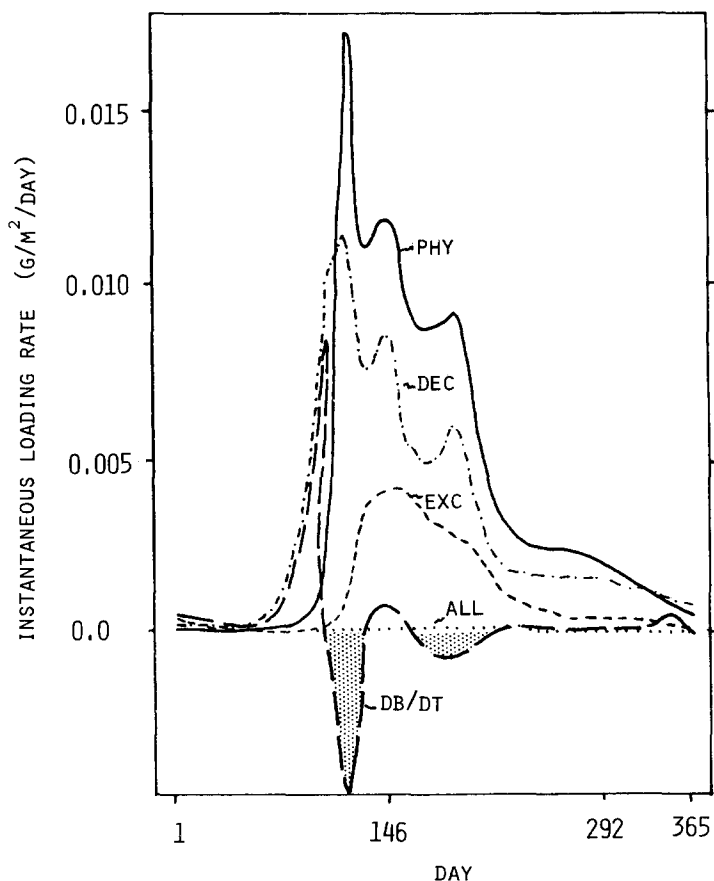


Fig. 9. Predicted instantaneous loading rates for phosphorus for 1 year; phytoplankton uptake (*PHY*), decomposer remineralization (*DEC*), remineralization through excretion (*EXC*), allochthonous loading (*ALL*), and the overall loading rates (*DB/DT*).

causes. Other investigators have also found that physiological mortality accounts for only a small percentage of the total mortality. The model also mimics this phenomenon quite well (Fig. 8). Mortality (Eq. 1.6) is modeled as a constant, intrinsic rate ($KMORT = 0.001 \text{ day}^{-1}$) modified only at extreme temperatures ($TCRIT$ is 35°C).

The time course of the overall rate of biomass change has a positive maximum in late spring, followed closely by a negative maximum, indicating the “oscillating populations and depressions” described by Hutchinson (1967). This particular zooplankton group shows very little activity during the cold, winter months — as one might expect (Hutchinson, 1967).

Nutrients

The dynamics of reactive orthophosphate and nitrogen cycling are shown in Figs 9 and 10. The rates of change of these nutrients are modelled as functions of phytoplankton uptake, decomposer remineralization, plant and animal excretion, and allochthonous loadings.

Loss from the nutrient pools by phytoplankton uptake is assumed to be proportional to primary production. The constants of proportionality, (KU of Eq. 4.3) are based on a stoichiometric ratio of $C_{106}N_{16}P$ (Strumm and Tenney, 1963) and a carbon to dry-weight biomass ratio of 0.53 (Winberg, 1971); for purposes of the model it is assumed that the phytoplankters maintain this stoichiometry. KU for nitrogen is 0.095 and for phosphorus, 0.01.

In modelling decomposer remineralization we have assumed that under aerobic conditions nitrogen and phosphorus are the principal mineral by-products of respiration. If the chemical composition of the organic matter assimilated by the decomposers is similar to their stoichiometry, remineralization of phosphorus and nitrogen is a function of the amount of carbon respired. That is, since respiration of carbon will result in excess N and P in the cell, the release of these nutrients is necessary to maintain a constant chemical balance.

Respiration (Eq. 3.2) is modelled as described above for zooplankton. $URES$, the proportionality term between uptake of organics and respiration, is 0.5, based on the observation of a 5% efficiency in carbon uptake (Bloomfield, 1975), corresponding to a 50% efficiency in biomass flow. $RMIN$, the term relating respiration to decomposer biomass, is used to account for endogenous respiration during starvation and is very low (0.01). $KEXCR$, the constant relating total mineral release to respiration, is 0.2, based on the 5% efficiency, the given stoichiometry, and the requirement of maintaining that stoichiometry after respiratory loss of carbon. The relative-composition coefficients of the remineralization products, 0.88 for nitrogen and 0.120 for phosphorus, are also based on these assumptions.

Direct recycling of these nutrients through plant and animal excretion (Eq. 4.4) is also based on the stoichiometry of the organisms involved. The contribution to each nutrient pool is modelled as a fraction of the total ex-

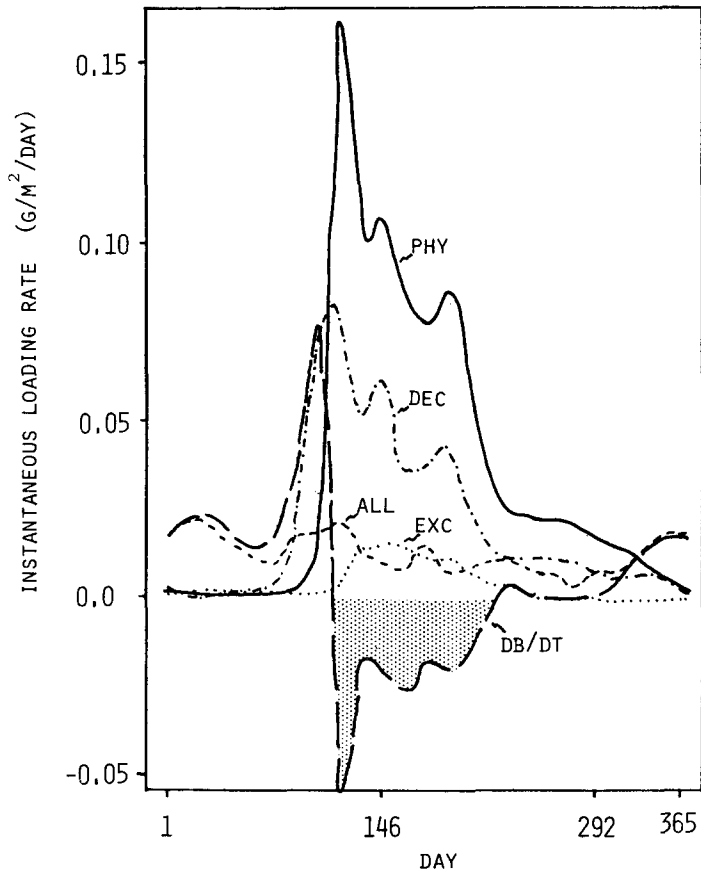


Fig. 10. Predicted instantaneous loading rates for nitrogen for 1 year; phytoplankton uptake (*PHY*), decomposer remineralization (*DEC*), remineralization through excretion (*EXC*), allochthonous loading (*ALL*), and the overall loading rate (*DB/DT*).

cretion. Remineralization constants for zooplankton are based on a carbon to nitrogen ratio of 6.5, nitrogen to phosphorus ratio of 4.3 (Ganf and Blažka, 1974), and a carbon to dry-weight biomass ratio of 0.53 (Winberg, 1971). The coefficients representing the inorganic nitrogen and phosphorus content of zooplankton excreta are 0.08 and 0.02 respectively. The coefficients for phytoplankton excretion are 0.02 for phosphorus and 0.09 for nitrogen. These are based on a carbon to phosphorus ratio of 21.3 and a carbon to nitrogen ratio of 5.5 (Canale et al., 1974), and a carbon to dry-weight biomass ratio of 0.53 (Winberg, 1971).

It can be seen in the simulations that internal cycling is very important in describing the nutrient dynamics in Lake George (Figs 9 and 10). The relationship between phytoplankton uptake and decomposer remineralization controls the size of the nutrient pools. The inputs from excretion by zooplank-

ton, fish, and phytoplankton are significant but less important than decomposer remineralization. Probably the most interesting result of this analysis is that the allochthonous loadings to these nutrient pools (from data of Fuhs, 1972) are far less important than the recycling dynamics of the biotic system in Lake George. This is most dramatic in the phosphorus simulation (Fig. 9).

SUMMARY AND CONCLUSIONS

Detailed justifications for the constructs and parameterizations used in CLEANER are based on the extensive literature on aquatic ecology and ecological modelling. The response of many of these constructs and the sensitivity of selected parameters have been examined by varying the parameter values. In particular, the following points are made:

(1) Limitation of photosynthesis due to nutrient depletion utilizes the well established construct for Monod kinetics.

(2) Limitation of photosynthesis due to light is based on the construct of Steele (1965), which assumes reduction at intensities both above and below the saturation level; light extinction is based on Beer's law, with provision for self-shading due to suspended biomass.

(3) Interaction of light- and nutrient-limitation factors is modelled differently from representations in other models in order to account for adaptive shifts in algal assemblages.

(4) The temperature function is a complex nonlinear representation incorporating the commonly measured Q_{10} parameter (which has considerable effect on the response).

(5) The consumption term includes a construct to represent food preference and the relationship to total available food; there are parameters for food preference, minimum level of food necessary to stimulate consumption, minimum feeding area, and intracompartiment competition; consumption exhibits a hyperbolic relationship and changes in these parameter values, as well as changes in the maximum consumption rate, displace the curve and hasten or delay its approach to the asymptote.

(6) A correction for population-age structure is based on the simplifying assumption that populations at very low densities consist primarily of immature individuals, while populations approaching their carrying capacity are primarily composed of adults.

The time-course relationships of the constituent processes provide a means for evaluation of the model and represent an important modelling result that is not readily available from laboratory and field studies.

Simulation of gross primary production in nannophytoplankton demonstrates an overall response to light and temperature, with nutrient limitation being variable but evidently very important. Loss due to grazing is important as is respiration during most of the growing season. The other terms are only of minor effect, although sedimentation and excretion exhibit some seasonal variation.

In the cladoceran submodel, consumption is dependent on levels of phytoplankton biomass, with defecation being the major loss term. Respiration is also important. Predatory mortality and excretion are both significant; non-predatory mortality is negligible.

According to the assumptions incorporated in the nutrient submodels, internal cycling is very important to the nutrient dynamics of Lake George. Uptake by phytoplankton and remineralization by decomposers are dominant processes; remineralization through excretion is also important. Allochthonous nutrient loadings are of little consequence based on the calibration to observed Lake George conditions.

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