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PERIPHYTON DYNAMICS IN LOTIC ENVIRONMENTS: A SIMULATION MODEL

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In flowing water (lotic) environmetns, microscopic producer organisms and associated heterotrophic microorganisms are organized into complex assemblages that grow attached to rubble, gravel, and other suitable surfaces. Except where mosses, liverworts, aquatic vascular plants, or phytoplankton are prominent, these complex assemblages of microorganisms, often called periphyton communities or aufwuchs, are responsible for most of the primary production that occurs within the lotic system, although large quantities of allochthonous organic matter are frequently introduced from the surrounding terrestrial environment.

The results of 7 years of research with periphyton communities in laboratory streams indicate that viewing these communities as single, functional units or quasi-organisms is somewhat justified. Furthermore, experimental data have suggested that a periphyton community as a unit has a characteristic growth form and responds metabolically to external environmental factors in a predictable way. The simulation model described below is based on the assumption that the periphyton community can be treated as a unit, without a quantitative concern for the dynamics of its many constituent populations. The function statements and parameter estimates incorporated into the model are based on experimental work with laboratory streams and some observational data from Berry Creek Experimental Stream.

The approach used here to model the dynamics of periphyton communities in streams is essentially the same approach employed by Jay W. Forrester[1] to model industrial and urban systems. A particular system is identified by establishing a boundary within which the system interactions take place. Level (state) variables and rate (flow) variables are linked together by a complex system of feedback loops and various intermediate concepts (modules), and these components represent the basic structural elements within the boundary. Function statements that represent relation between structural components of the system are written and programmed in some suitable simulation language (for example, MIMIC or DYNAMO). The computer output usually provides numerical values of particular variables and a plot of these values against time.

A SIMPLE MODEL OF PERIPHYTON DYNAMICS

A simple model of periphyton dynamics (Figure 1) includes one level variable, the biomass of the assemblage, and four rate variables: primary production (PROD), community respiration (RESP), and two export fractions (EXPN and EXPF). Each rate variable can be considered as a subsystem of a larger system and the interrelation between modules that control a particular rate variable can be examined. In this model, we assume that the import of organic matter from outside the system is negligible and that the rate of primary production by the periphyton controls the

[1]FORRESTER, J. W. 1969. Urban dynamics. MIT Press, Cambridge, Mass. 285 p.

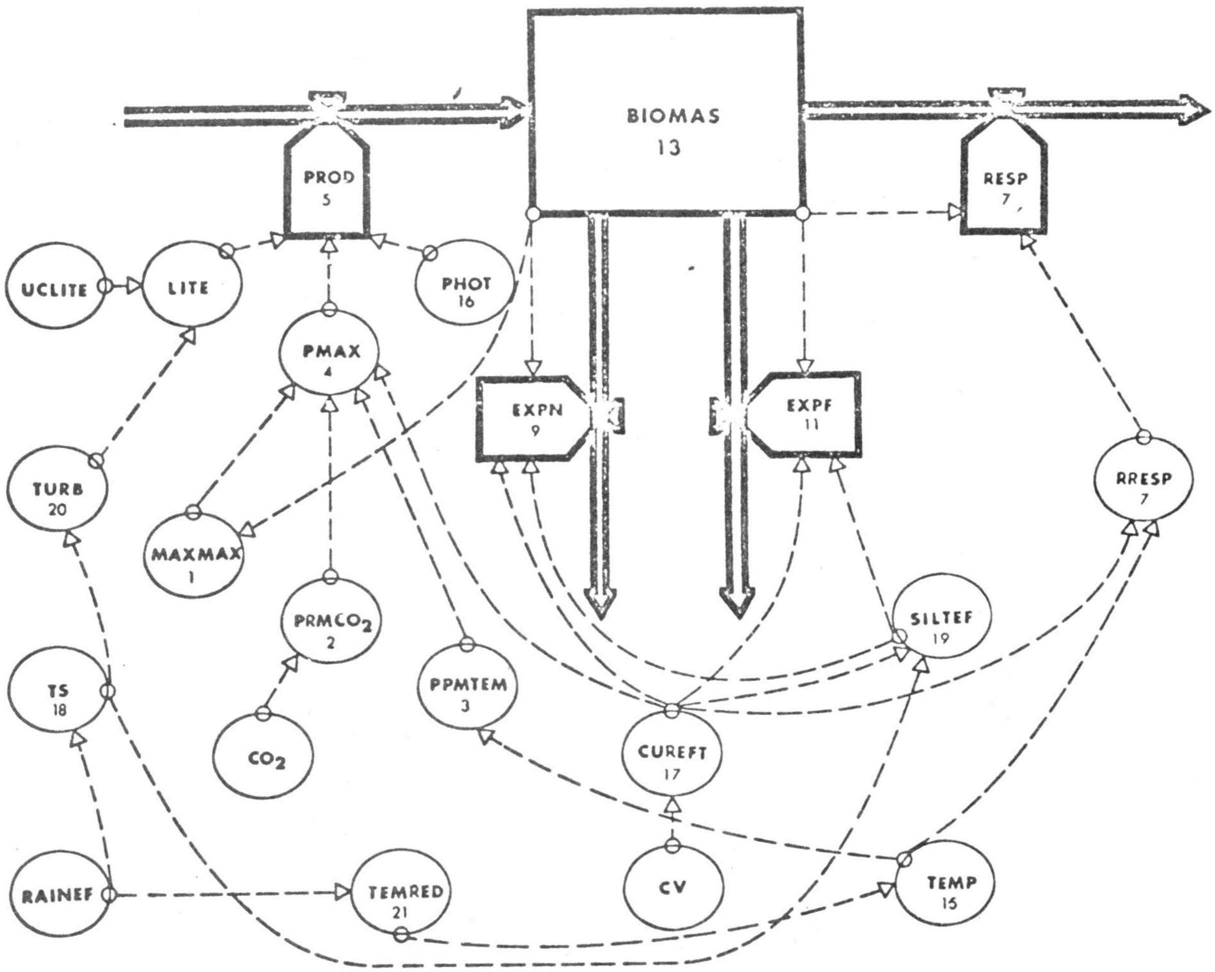


Figure 1. The basic model

addition of organic matter within the system. The losses of organic matter are controlled by the rate of community respiration and the rate at which particles of material are dislodged from the assemblage and exported from the system. Export is divided into two fractions, the material retained by a 20-mesh, silk bolting cloth net (EXPN) and the smaller particles that pass through the net but are retained by a HA millipore filter.

In the simple periphyton model, the rate of primary production is determined by the light intensity reaching the assemblage (LITE), the day length (PHOT), and an asymptotic maximum rate (PMAX). The maximum attainable rate of primary production (MAXMAX) at an optimum temperature, current velocity, and nutrient supply is a function of the periphyton biomass. The effects of temperature (PRMTEM), current velocity (CUREFT), and nutrient or CO_2 concentration (PRMCO2) are expressed as multipliers between 0 and 1, and PMAX at any particular time is the product of MAXMAX, PRMTEM, CUREFT, and PRMCO2. The rate of community respiration per gram of organic matter (RRESP) is a function of temperature (TEMP) and CUREFT; RESP at a particular time is the product of RRESP and BIOMAS. EXPN and EXPF are both controlled by BIOMAS, an interaction between BIOMAS and current velocity (CV), and a multiplier that expresses the effect of silt load (SILTEF). The effect of rainfall on the system is imposed by introducing the rainfall schedule as a table function. The rainfall effect (RAINEF) derived from the tabulated values determines the concentration of total solids (TS) and a temperature reduction factor (TEMRED), TS determines SILTEF and TURB, multipliers ranging from 1 to 4 and 0 to 1, respectively. LITE is the product of TURB and an uncorrected light intensity (UCLITE), and PHOT and TEMP are introduced as trigonometric (sine) functions of time.

To initiate a simulation sequence, UCLITE, CO2, and CV are entered in the program as parameters or as table functions, if desired. The rainfall schedule also is introduced as a table function along with the necessary function statement, constants, and output statements. Moreover, an initial periphyton biomass must be specified because feedback loops occur from BIOMAS to the four rate variables. To simplify matters, the simulation sequence can be based conveniently on a 360-day year (twelve 30-day months). The time interval can vary, depending on the kind of information that is desired. When the total time period was less than 4 years, the output usually was based on a time interval (DT) of 5 days. For periods exceeding 10 years, however, intervals as long as 30 days sometimes were satisfactory.

AN EXPANDED MODEL OF PERIPHYTON DYNAMICS

The simple model of periphyton dynamics can be expanded to include the effects of a grazing organism and an introduction of allochthonous organic material (Figure 2). In the expanded model, the effects of grazing by the aquatic snail Oxytrema silicula are based on studies of food consumption by the animal and its growth in aquaria at different food densities. Large populations of this snail are common in the Willamette Valley, and it is frequently the most conspicuous organism grazing on periphyton communities in the small woodland streams of the area. The snail population

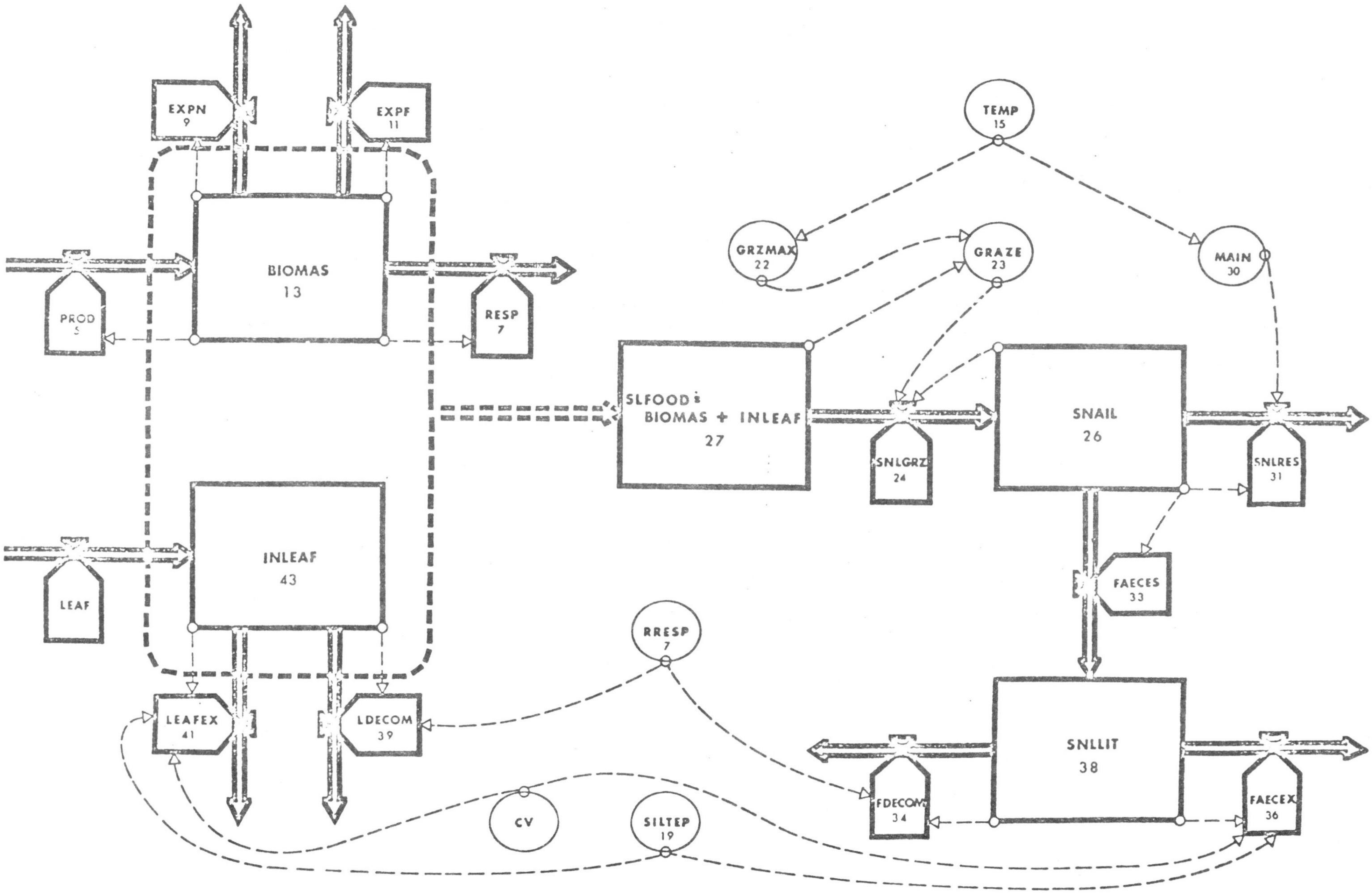


Figure 2. The expanded model.

is treated in the model as a quasi-organism, and no attempt is made to partition age classes or to take into account the bioenergetics of the animal's reproductive behavior. The introduction of allochthonous organic material to the system is based on measurements of the quantity of leaves falling from the forest canopy into the controlled sections of the Berry Creek Experimental Stream. In the model, the total input of this material (500 gm^{-2}) follows a normal distribution over a three-month period, beginning 1 September and ending 30 November.

The expanded model has 4 level-variables (BIOMAS, INLEAF, SNAIL, and SNLLIT) and 12 rate-variables (PROD, RESP, EXPN, EXPF, LEAF, FEAFEX, LDECOM, SNLGRZ, SNLRES, FAECES, FAECEX, and FDECOM). The food (SLFOOD) available to the snail biomass (SNAIL) for consumption at any particular time is the summation of the periphyton biomass (BIOMAS) and the biomass of allochthonous organic material (INLEAF). Food consumption per gram of snails (GRAZE) is assumed to be a function of SLFOOD and the consumption rate by the entire population is the product of GRAZE and SNAIL; the maximum asymtotic consumption rate per gram (GRZMAX) is a nonlinear function of temperature. Losses of organic matter from the snail population are channelled through the rates of respiration (SNLRES) and deposition of faecal material (FAECES). The rate of snail respiration per gram (MAIN) is an exponential function of temperature, and SNLRES is the product of SNAIL and MAIN. Because no experimental data are available on the decomposition and export rates of the faecal and allochthonous organic material, the model temporarily assumes that such rates are the same per unit of biomass as corresponding rates of community respiration and export for the periphyton community. In particular, the decomposition rate of snail faeces (FDECOM) is the product of RRESP and the biomass of the faecal material (SNLLIT), and the export rate of this material is a function of SNLLIT, SILTEF, and an interaction between SNLLIT and CV. Likewise, the decomposition rate of allochthonous organic matter is the product of RRESP and the biomass of the material (INLEAF), and the export rate (LDECOM) is a function of INLEAF, SILTEF, and CV. Parameters in the function statements for FDECOM and LDECOM are the same as those for EXPF and EXPN, respectively. All other details of the expanded model are the same as those described for the simple model.

OUTLINE OF MATHEMATICAL DETAILS

The mathematical details of the periphyton simulation model are outlined below. Equation numbers correspond to the numbers associated with the variables in Figures 1 and 2.

I. Primary production

$$P_{(max|A)} = P_{max}\left(\frac{a_1A}{1+a_1A}\right) \quad (1)$$

$$P_{(rmax|N)} = \frac{a_2N}{1+a_2N} \quad (2)$$

$$P_{(rmax|T)} = \frac{a_3T}{1+a_3T} \quad (3)$$

$$P_{(max|A,N,T,V,)} = P_{(max|A)} \text{ X } P_{(rmax|N)} \text{ X } P_{(rmax|T)} \text{ X } C_{mult} \quad (4)$$

$$\frac{dP}{dt} = P_{(max|A,N,T,V)}\left(\frac{a_4L}{1+a_4L}\right) \quad (5)$$

$$P = \int_{t_o}^{t} P_{(max|A,N,T,V)}\left(\frac{a_4L}{1+a_4L}\right) dt \quad (6)$$

II. Aufwuchs respiration

$$\frac{dR_a}{dt} = C_{mult}A\left(\frac{R_{aspmax}}{1+e^{(b_1-b_2T)}}\right) \quad (7)$$

$$R_a = \int_{t_o}^{t} C_{mult}A\left(\frac{R_{aspmax}}{1+e^{(b_1-b_2T)}}\right) dt \quad (8)$$

III. Aufwuchs export

$$\frac{dE_{an}}{dt} = M_{mult}A(c_1 + c_2V) \quad (9)$$

$$E_{an} = \int_{t_o}^{t} M_{mult} A(c_1+c_2V)dt \qquad (10)$$

$$\frac{dE_{af}}{dt} = M_{mult} A(c_3+c_4V) \qquad (11)$$

$$E_{af} = \int_{t_o}^{t} M_{mult} A(c_3+c_4V)dt \qquad (12)$$

IV. Aufwuchs biomass

$$A = A_I + P - R_a - E_{an} - E_{af} - G_a \qquad (13)$$

V. Temperature, photoperiod, and effect of current velocity

$$D = D_1 + t \qquad (14)$$

$$T = 12 + 6\sin(-e_1 + e_2D) - T_{red} \qquad (15)$$

$$H_L = 12 + 4\sin(-e_1 + e_2D) \qquad (16)$$

$$C_{mult} = e_3 + \frac{e_4V}{1+e_4V} \qquad (17)$$

VI. Total solids, silt effect, and turbidity effect

$$M = M_{max} \left(f_1 + \frac{f_2(W-1)}{1+f_2(W-1)} \right) \qquad (18)$$

$$M_{mult} = 1 + C_{mult} \left(\frac{f_3}{1+e^{(f_4-f_5M)}} \right) \qquad (19)$$

$$I_{mult} = \exp(f_6 - 0.001M) \qquad (20)$$

$$T_{red} = 3 \left(\frac{f_7 W}{1+f_7 W} \right) \quad (21)$$

VII. Snail food consumption, growth, and biomass

$$Z_{spmax} = \frac{g_1 T}{1+g_2 T} \quad (22)$$

$$Z_{sp} = Z_{spmax}\left(1-e^{-g_3(F-1)} \right) \quad (23)$$

$$\frac{dZ}{dt} = SZ_{sp} \quad (24)$$

$$\frac{dS}{dt} = S(g_4 Z_{sp} - R_{ssp}) \quad (25)$$

$$S = S_I + \int_{t_o}^{t} S(g_4 Z_{sp} - R_{ssp})dt \quad (26)$$

$$F = A + B \quad (27)$$

$$\frac{dG_a}{dt} = \frac{A}{F} \cdot \frac{dZ}{dt} \quad (28)$$

$$\frac{dG_b}{dt} = \frac{B}{F} \cdot \frac{dZ}{dt} \quad (29)$$

VIII. Energy losses from snail respiration, decomposition of snail faeces, and export of snail faeces

$$R_{ssp} = k_1 e^{k_2 T} \quad (30)$$

$$\frac{dR_s}{dt} = SR_{ssp} \quad (31)$$

$$R_s = \int_{t_o}^{t} SR_{ssp}\,dt \quad (32)$$

$$\frac{dJ}{dt} = \frac{dZ}{dt} - \frac{dS}{dt} - \frac{dR_s}{dt} \quad (33)$$

$$\frac{dJ_{dec}}{dt} = C_{mult} S_{lit} \left(\frac{R_{aspmax}}{1 + e^{(b_1 - b_2 T)}} \right) \quad (34)$$

$$J_{dec} = \int_{t_o}^{t} C_{mult} S_{lit} \left(\frac{R_{aspmax}}{1+e^{(b_1 - b_2 T)}} \right) dt \quad (35)$$

$$\frac{dJ_{exp}}{dt} = M_{mult} S_{lit} (c_3 + c_4 V) \quad (36)$$

$$J_{exp} = \int_{t_o}^{t} M_{mult} S_{lit} (c_3 + c_4 V)\,dt \quad (37)$$

$$S_{lit} = S_{litI} + J - J_{dec} - J_{exp} \quad (38)$$

IX. Introduction, decomposition, and export of allochthonous organic matter

$$\frac{dB_{dec}}{dt} = C_{mult} B \left(\frac{R_{aspmax}}{1 + e^{(b_1 - b_2 T)}} \right) \quad (39)$$

$$B_{dec} = \int_{t_o}^{t} C_{mult} B \left(\frac{R_{aspmax}}{1+e^{(b_1-b_2T)}} \right) dt \qquad (40)$$

$$\frac{dB_{exp}}{dt} = M_{mult} B(c_1+c_2V) \qquad (41)$$

$$B_{exp} = \int_{t_o}^{t} M_{mult} B(c_1+c_2V)dt \qquad (42)$$

$$B = B_{imp} - B_{dec} - B_{exp} - G_b \qquad (43)$$

X. Definition of symbols and units used in the model

A = aufwuchs biomass ($g\ m^{-2}$);

A_I = initial aufwuchs biomass ($g\ m^{-2}$);

B = biomass of allochthonous organic matter ($g\ m^{-2}$);

B_{dec} = decomposition of allochthonous organic matter integrated over a time interval of interest ($g\ m^{-2}$);

B_{exp} = export of allochthonous organic matter integrated over a time interval of interest ($g\ m^{-2}$);

B_{imp} = introduced allochthonous organic matter integrated over a time interval of interest ($g\ m^{-2}$);

C_{mult} = current velocity multiplier expressed as a proportion of a process of interest attainable at a particular current velocity;

D = day number;

D_1 = day number of the first day of a particular simulation sequence;

E_{af} = aufwuchs export fraction collected by an HA Millipore filter integrated over a time interval of interest ($g\ day^{-1}\ m^{-2}$);

E_{an} = aufwuchs export fraction collected by a 20-mesh silk bolting cloth net integrated over a time interval of interest ($g\ day^{-1}\ m^{-2}$);

F = biomass of food available to snails ($g\ m^{-2}$);

G_a = consumption of aufwuchs by snails integrated over a time interval of interest ($g\ m^{-2}$);

G_b = consumption of allochthonous organic matter by snails integrated over a time interval of interest ($g\ m^{-2}$);

H_L = number of hours per day that the community is exposed to light ($hr\ day^{-1}$);

I_{mult} = turbidity multiplier expressed as a proportion that reduces the effective light intensity;

J = introduction of faecal material by snails integrated over a time interval of interest ($g\ m^{-2}$);

J_{dec} = decomposition of snail faecal material integrated over a time interval of interest ($g\ m^{-2}$);

J_{exp} = export of snail faecal material integrated over a time interval of interest ($g\ m^{-2}$);

L = light intensity (ft-c);

M = concentration of total solids ($mg\ l^{-1}$);

M_{mult} = silt load multiplier expressed as an export enhancement factor ranging from 1 to 4;

N = nutrient concentration ($mg\ l^{-1}$);

P = primary production integrated over a time interval of interest ($g\ m^{-2}$);

P_{max} = maximum rate of primary production at an optimum biomass, nutrient supply, temperature, light intensity, and current velocity ($g\ hr^{-1}\ m^{-2}$);

$P_{(max|A)}$ = maximum rate of primary production given a particular biomass at an optimum nutrient supply, temperature, light intensity, and current velocity ($g\ hr^{-1}\ m^{-2}$);

$P_{(max|A,N,T,V)}$ = maximum rate of primary production attainable given a particular biomass, nutrient contentration, temperature, and current velocity ($g\ hr^{-1}\ m^{-2}$);

$P_{(rmax|N)}$ = the proportion of $P_{(max|A)}$ attainable given a particular nutrient level;

$P_{(rmax|T)}$ = the proportion of $P_{(max|A)}$ attainable given a particular temperature;

R_a = aufwuchs respiration integrated over a time interval of interest ($g\ m^{-2}$);

R_{aspmax} = maximum specific rate of respiration by aufwuchs ($g\ hr^{-1}\ m^{-2}\ g^{-1}$);

R_s = respiration by the entire snail population integrated over a time interval of interest ($g\ m^{-2}$);

R_{ssp} = specific rate of respiration by snails at a particular temperature ($g\ m^{-2}\ g^{-1}$);

S = snail biomass ($g\ m^{-2}$);

S_I = initial snail biomass ($g\ m^{-2}$);

S_{lit} = biomass of snail faecal material (g m^{-2});

S_{litI} = initial biomass of snail faecal material (g m^{-2});

T = temperature (°C);

T_{red} = temperature reduction resulting from a particular rainfall schedule (°C);

t = time (days);

V = current velocity (cm sec^{-1});

W = rainfall effect expressed as the difference between the integrated rainfall at time t and the integrated rainfall with a 10-day lag effect (inches);

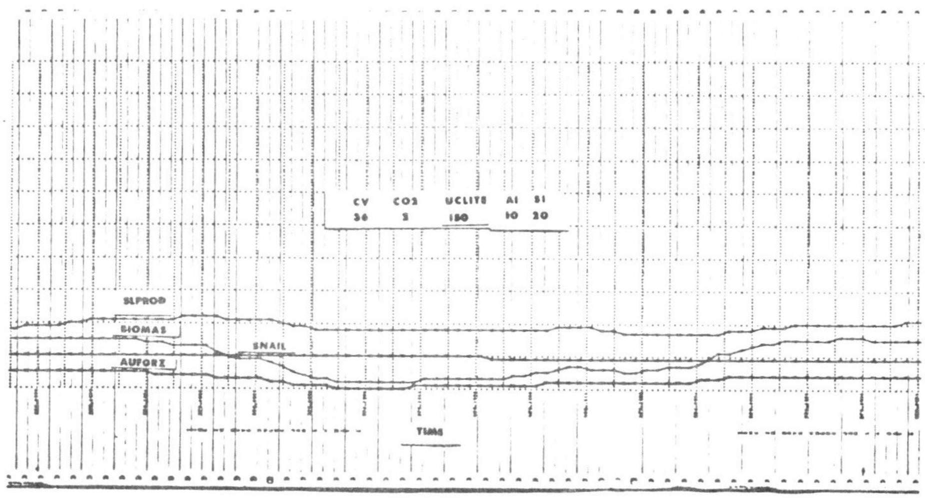
Z = food consumption by the entire snail population integrated over a time interval of interest (g m^{-2});

Z_{sp} = specific rate of food consumption by snails at a particular temperature and food density (g day^{-1} g^{-1});

Z_{spmax} = maximum specific rate of food consumption by snails given a particular temperature at an optimum food density (g day^{-1} g^{-1}).

XI. Values for constants

a_1	= 0.1	D_1	= 1	f_7	= 1
a_2	= 0.8778	e_1	= 1.5708	g_1	= 0.0139
a_3	= 0.4	e_2	= 0.01745	g_2	= 0.5
a_4	= 0.0021	e_3	= 0.2	g_3	= 0.05
P_{max}	= 1000	e_4	= 0.1	g_4	= 0.1667
P_{aspmax}	= 2.6	M_{max}	= 2500	k_1	= 0.5
b_1	= 1.7	f_1	= 0.04	k_2	= 0.09
b_2	= 0.187	f_2	= 0.2		
c_1	= 0.6188	f_3	= 4		
c_2	= 0.0556	f_4	= 1.1		
c_3	= 3.744	f_5	= 0.002		
c_4	= 0.1238	f_6	= 0.1		



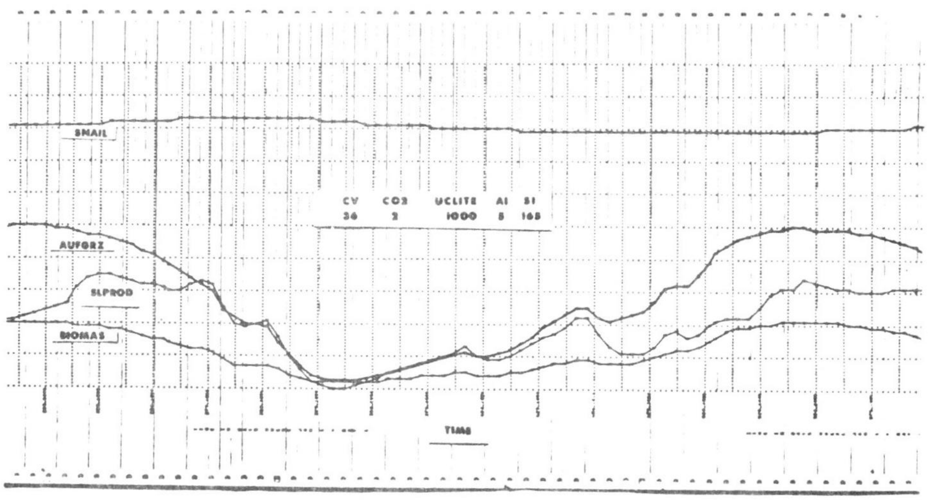


Figure 3. Representative output from the expanded model under two different light regimes and with different initial biomass of aufwuchs and snails.

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