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A HIERARCHICAL MODEL OF LOTIC ECOSYSTEMS[1]

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Abstract. This paper presents the structure and properties of a total stream model that simulates the dynamics of small, flowing-water ecosystems in the northwestern United States. Conceptually, the model is hierarchically structured, consisting of 7 basic processes: periphyton dynamics, grazing, shredding, collecting, invertebrate predation, vertebrate predation, and detrital conditioning. These processes are subprocesses of 3 echelons of higher level processes: detritivory; herbivory; primary consumption; predation; and the total ecosystem. The model has 14 state variables in the 7 basic processes, and is conceptualized in discrete time with a basic time step corresponding to 1 day.

Behavior of the stream model relative to different schedules of energy inputs and to the practice of clear-cut logging was investigated and related to contemporary theory of lotic ecosystems. In general, model behavior indicated that the regulation of biological processes in streams is complex, the mechanisms of which vary seasonally and from process to process. If a process is regulated by food supply, its annual production tends to increase as predation increases, while mean biomass may or may not be affected appreciably. In contrast, an increase in predation tends to decrease both mean biomass and annual production in processes regulated primarily by predation and such life history phenomena as insect emergence. The stream model provided the stimulus that led to a mathematical expression for the rate of production at the level of the entire ecosystem, and model behavior suggests that this rate tends to remain constant along a continuum from small, first-order streams with no tributaries to larger rivers which eventually drain into the sea.

Key words: Collecting; detrital processes; ecosystem; grazing; lotic processes; mathematical model; Oregon; periphyton processes; predation; shredding; streams.

INTRODUCTION

Overview and objectives

Within the past 2 decades, research activity in the field of stream ecology has gradually expanded from pollution-oriented projects to programs with more fundamental objectives, namely the development of a general theory of lotic ecosystems. Basic research related to flowing water ecosystems has been concerned with both community structure (e.g., Patrick 1967, 1968; Patrick et al. 1967; McIntire 1968*a*) and trophic ecology (e.g., Odum 1957; Warren et al. 1964), and research approaches have varied from experiments in laboratory streams to the collection of experimental and observational data in the field. An overview of lotic ecology in considerable detail is now available to interested readers in 2 recent books (Hynes 1970; Whitton 1975).

This paper presents the structure and properties of a total stream model that simulates the dynamics of small flowing-water ecosystems in the northwestern United States. Model structure is based primarily on current concepts of functional groups in stream ecology (McIntire 1968*b*, 1973; Cummins 1974) and on the ecosystem modeling approach in the Coniferous Forest Biome, U.S. International Biological Program (IBP) (Overton 1975). Update and forcing functions as well as parameter estimates, for the most part, were derived from experimental or observational data found in the literature or data made available through the courtesy of an interdisciplinary group of stream ecologists from Oregon State University, Idaho State University, Michigan State University, and the Stroud Water Research Center.

The preliminary results of our initial attempt to develop a total stream model were reported at the 19th Congress of the International Association of Limnology in 1974 (McIntire et al. 1975). At that time, we concluded that the stream model (1) provided the opportunity to synthesize the results of numerous field and laboratory studies of lotic processes; (2) stimulated the evaluation of the existing data base; (3) helped establish priorities for future research; and (4) examined the compatibility of selected sets of process measurements. During the past 2 yr, we have altered the structure of the model and improved the representation of certain hydrologic and biological processes. Furthermore, the behavior of the model in relationship to different schedules of energy inputs (i.e., light energy and allochthonous organic matter) has been investigated and related to some theoretical concepts of lotic ecosystems. Before presenting the details of the current version of the stream model, we further elaborate our goal and objectives.

Broadly stated, our goal of building a stream model is to increase understanding of the behavior of fundamental biological processes in lotic ecosystems and to generate meaningful hypotheses related to lotic dynamics at relatively coarse levels of resolution, i.e., the ecosystem and some of its subsystems. This goal is consistent with the critical evaluation of some of the current theory of lotic ecosystems and, if realized, can

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contribute to theory by providing a hypothetical view of such systems from an integrated perspective. Our goal is being realized through fulfillment of a series of specific objectives during the 2 phases of model development: model building, and the investigation of model properties. A series of specific objectives have been identified to help provide answers to the following questions:

1) What stream processes are relevant to concepts associated with current theory of lotic dynamics?
2) Have we considered all classes of biological processes necessary to manifest lotic dynamics observed under the broad range of environmental conditions encountered in the "real world"? In other words, do we really have a general theory of lotic ecosystems?
3) What are the resolution levels of relevant processes necessary for adequate representation of the behavior of lotic ecosystems relative to specific environmental problems and management strategies?
4) Are such stream processes as collecting, shredding, and grazing controlled by the physical environment, food resources, predation, or by behavioral adaptations at the population level?
5) Are estimates of process rates obtained in the field or laboratory compatible?
6) How do changes in system inputs affect the relative importance of biological processes in streams? In particular, how are stream dynamics affected by changes in energy inputs and properties of the physical environment?

Here, we deal with a subset of specific objectives that relate primarily to questions 1, 4, and 6, although the current model also provides some insights into questions 3 and 5 for specific cases.

The FLEX paradigm

Preoccupation with too much detail is the bane of the ecosystem modeler's struggle for a meaningful representation of the system variables. Yet, many ecologists are, in fact, intuitively more comfortable with population interactions or interactions at the level of the individual organism. Overton (1975) has examined the problem of detail in the mechanistic model and concluded that large ecosystem models should be hierarchically modular. Such an approach involves the identification of systems and subsystems, each of which can be studied in isolation as long as the coupling structure is identified and its integrity maintained. These concepts have been incorporated by Overton (1972, 1975) into a general ecosystem model paradigm called FLEX, based on the general systems theory of Klir (1969). One module of the stream model was originally programmed in MIMIC (McIntire 1973) but was later translated into a form compatible with the FLEX paradigm. The latter served as the basis for expansion to a total stream model.

The FLEX paradigm is implemented by the program FLEX 2, a general model processor that accommodates both holistic (FLEX mode) and mechanistic (REFLEX mode) representations (White and Overton 1974). Complete technical documentation for the nonhierarchical version of the stream model is expressed in the FLEXFORM, the working document of the FLEX paradigm. The stream model FLEXFORM is available as Internal Report No. 165, Coniferous Forest biome, Oregon State University, or can be obtained from the General Systems Depository[1]. This FLEXFORM documentation provides a complete report of the conceptual model and specifies all variables, functions, and parameters according to the FLEX convention. Simulation runs reported here were performed by the FLEX 2 processor on a CDC 3300 computer operating under OS-3 at Oregon State University.

MODEL STRUCTURE

Process modeling

The stream model is conceptualized as a hierarchical system of biological processes (Figs. 1 and 2). For our purpose, a process is a systematic series of actions relevant to the dynamics of the system as it is modeled. Theoretically, any process can be decomposed into a system of coupled subprocesses if model objectives justify the examination of system dynamics at a finer level of resolution. Alternatively, a process also can be considered a component of some supraprocess, the behavior of which can be investigated either holistically or mechanistically. At each particular level of resolution, the details of each process can be elaborated in terms of the corresponding variables, functions, and parameters.

The FLEX paradigm uses the state variable designation for a representation of the instantaneous values of the system outputs. However, in large ecosystem models, there is some question as to just what the state variables associated with each process should represent. This difficulty, the so-called "aggregation" problem, was considered by Overton (1977). In an early version of the stream model, McIntire et al. (1975) selected state variables on the basis of the various functional activities of organisms recognized by current concepts of energy transfer in lotic ecosystems (Cummins 1975*b*). This approach, here, referred to as the quasi-organism viewpoint, designates each state variable as the biomass at any instant of time involved in a particular process. This convention ignores taxonomic position and is different from the paraspecies approach (Boling et al. 1975) which combines taxo-

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[1] General Systems Depository, c/o Professor G. J. Klir, School of Advanced Technology, State University of New York, Binghamton, New York 13900 USA.

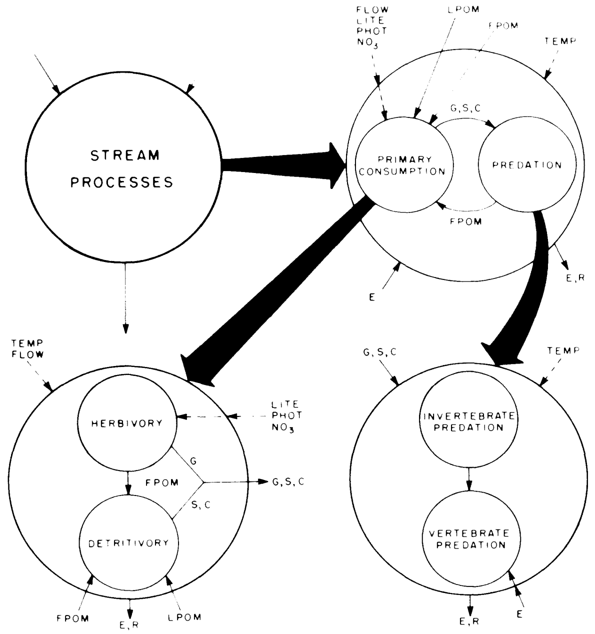

FIG. 1. Schematic representation of a lotic ecosystem showing the hierarchical decomposition of the primary consumption and predation subsystems. The symbols refer to flows of biomass from processes of grazing (G), shredding (S), and collecting (C); large particle (LPOM) and small particle (FPOM) detritus; export or emergence (E); respiration (R); temperature (TEMP); stream discharge (FLOW); photoperiod (PHOT); and nutrient concentration (NO_3).

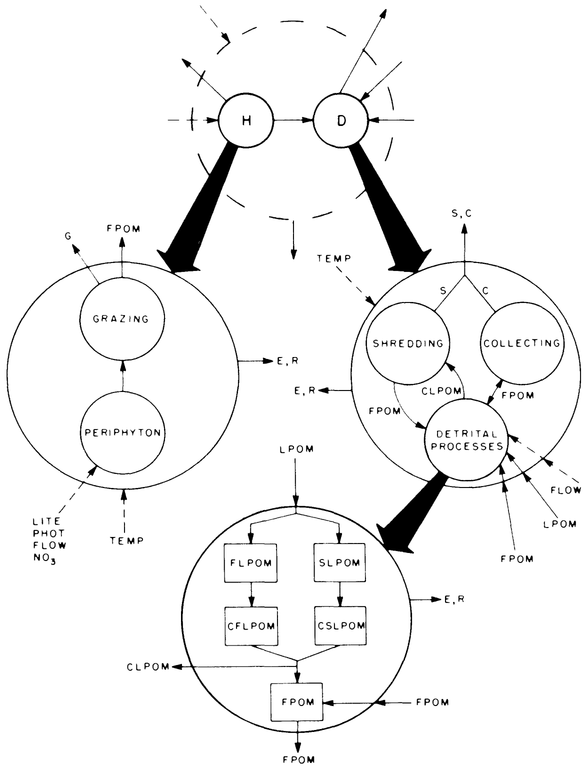

FIG. 2. Schematic representation of the mechanistic structure of the herbivory and detritivory subsystems in a lotic ecosystem. CLPOM represents conditioned large particle detritus; FLPOM, quickly decomposing material; SLPOM, slowly decomposing material; CFLPOM, quickly decomposing material suitable for consumption by macroconsumers; and CSLPOM, slowly decomposing material suitable for consumption by macroconsumers; and the other symbols are the same as given in Fig. 1.

nomic entities into ecologically similar groups. One of the conceptual advantages of process modeling is that it avoids the troublesome problem of dealing with taxa or individual organisms involved in >1 process. However, process modeling can generate serious practical problems of parameter estimation, particularly when field data correspond to dynamics at the population level of organization.

A refinement of the quasi-organism viewpoint is to regard each state variable as the capacity to perform the corresponding process. For example, if the species composition of organisms involved in the process of grazing changes seasonally, the rate of food consumption per gram of biomass could exhibit corresponding changes. Under these circumstances, it makes sense to consider the state variable as the capacity for grazing which is some function of biomass and other properties of the community that changes with community composition (i.e., the genetic information in the system). Relative to process potential, a unit of capacity is time invariant, while a unit of biomass can change over physiological, ecological, or evolutionary time. Therefore, the concept of capacity provides a theoretical basis for representing both qualitative and quantitative changes within each process in an ecosystem model.

Unfortunately, ecosystem research in the field has not provided data necessary to express process capacity as a function of biomass and other community properties. Furthermore, field measurements of process rates in lotic ecosystems are lacking, although leaf-pack studies that examine the shredding capacity in streams (e.g., Sedell et al. 1975) are notable exceptions. In this paper, we consider state variables as biomass and retain the quasi-organism point of view, the viewpoint most compatible with the data sets available to us for parameter estimation.

A hierarchical structure of stream processes

In an earlier publication (McIntire et al. 1975), we described a stream ecosystem mechanistically in terms of 3 subsystems: autotrophic, heterotrophic, and nutrient processes. While such a decomposition has a certain intuitive appeal to ecologists, we later found that an alternative structure had some distinct practical advantages and was more compatible with the investigation of coarse-level resolution dynamics. Now, stream processes are considered as 2 coupled subsystems representing the processes of primary consumption and predation (Fig. 1). Primary consumption represents all processes associated with direct consumption and decomposition of both autotrophic organisms and detritus, including the internal production dynamics of the autotrophic organisms collectively. Predation includes processes related to the transfer of energy from primary to secondary consumers or from secondary to tertiary consumers. Behavior of each of these subsystems can be examined in terms of some arbitrary set of output variables, or each can be decomposed further and investigated in terms of their subsystems. It should be noted that, in the current version of the model, the nutrient processes subsystem has been eliminated, as it was more convenient for our purposes to treat nutrients as an input variable, i.e., a coupling variable with an adjacent terrestrial system.

Figure 1 also illustrates a further decomposition of the primary consumption and predation subsystems. The small, solid arrows represent energy flows, while the dotted arrows emphasize the influence of certain control variables. Predation includes the processes of invertebrate and vertebrate predation, and primary consumption is represented by processes of herbivory and detritivory. Herbivory consists of all processes associated with the production and consumption of autotrophic organisms within the system, whereas detritivory represents the consumption and decomposition of detrital inputs.

Figure 2 depicts the structure of the herbivory and detritivory subsystems in terms of each of their coupled subsystems. Herbivory decomposes into grazing and periphyton subsystems. The structure of the periphyton subsystem and its behavior in isolation were described in detail by McIntire (1973). The grazing subsystem includes processes associated with the flow of energy from periphyton to macroconsumers. Detritivory decomposes into shredding, collecting, and detrital processes. Shredding and collecting are processes associated with flows of energy from large particle detritus (>1 mm) and fine particle detritus (<1 mm) to macroconsumers, the shredders and collectors, respectively. Detrital processes include 5 state variables, each representing the biomass of an arbitrarily designated fraction of the total detrital biomass (Fig. 2). Large particulate organic matter (LPOM) is introduced by a table function as an input variable. This variable is fractionated into material that decomposes quickly (FLPOM) and material that has a relatively slow rate of decomposition (SLPOM). LPOM remains in the system as either FLPOM or SLPOM for periods representing the time it takes for microorganisms to convert these fractions into states (CFLPOM and CSLPOM) suitable for consumption by macroconsumers. Mechanically, the model introduces mean lag periods of 28 and 130 days for transfer of material between FLPOM and CFLPOM and between SLPOM and CSLPOM, respectively. These lag periods are based on data of Sedell et al. (1975). Sources of material for the fine particle detritus state variable (FPOM) include mechanical (nonbiological) transfers from CFLPOM and CSLPOM and from fecal materials associated with the processes of grazing, shredding, collecting, invertebrate predation, and vertebrate predation. This approach to detrital processing was considered adequate for modeling at the ecosystem level. Boling et al. (1975) presented a more detailed representation (39 state variables) in a model of detrital processing for a woodland stream.

Mathematical representation of stream processes

Mathematical representations of the periphyton subsystem and aspects of the primary consumption subsystem were reported by McIntire (1973) and McIntire et al. (1975). In this section, we discuss the mathematical representation of hydrologic control variables and further elaborate the derivation of function statements associated with primary consumption and predation. The letter k is used as the time index in the system equations, and the model is conceptualized in discrete time with a basic time step corresponding to 1 day.

Hydrology.—The stream model permits the introduction of hydrologic driving variables that correspond to any particular natural stream. To represent the hydrology of a particular stream of interest, it is necessary to obtain field data corresponding to stream discharge (Q), channel depth (Z), width (W), cross sectional area (A), slope (S), current velocity (V), and suspended load (SL). These data are used to estimate parameters that relate stream discharge to current velocity, shear stress (τ), and suspended load, the hydrologic variables that couple to the biological processes of the system. Suspended load affects the availability of light for photosynthesis on and near the stream bottom, and current velocity and shear stress relate to biological processes through functions affecting metabolic rates and rates of export, respectively. The biological basis for the effect of current velocity on primary production and periphyton export was given by McIntire (1973, Eqs. 7, 8, and 12), and the relationship between shear stress and export rate was derived from these relationships. Parameter estimates for simulation runs reported in the later sections of this paper are based on data obtained for Oak Creek, a small stream near Corvallis, Oregon (Milhous 1973).

Stream discharge is introduced by the table function

$$Q(k) = t_q(k), \tag{1}$$

where Q(k) is the discharge at time k, and t_q is a table function of values representing a flow schedule for the particular stream of interest. Suspended load is obtained during simulation from the cubic equation

$$SL\ (k) = [b_{11} + b_{10}Q(k) + b_9Q^2(k) + Q^3(k)]\ (1/b_8), \tag{2}$$

where the b values are parameters estimated by multiple regression from field data corresponding to $t_o(k)$. Stream depth, width, and cross sectional area are expressed as power functions of discharge (Leopold et al. 1964):

$$Z(k) = b_6 Q^{b_7}(k), \tag{3}$$

$$W(k) = b_{14} Q^{b_{15}}(k), \tag{4}$$

$$A(k) = b_{16} Q^{b_{17}}(k); \tag{5}$$

where the b values are parameters also estimated from the field data. Assuming broad, U-shaped channels, the equation for the hydraulic radius (R) is

$$R(k) = [A(k)]/[2Z(k) + W(k)]. \tag{6}$$

The roughness coefficient (n) is a power function of flow and reflects the damping effect of the channel on stream velocity. Therefore,

$$n(k) = b_{12} Q^{b_{13}}(k). \tag{7}$$

The b parameters are estimated by curve fitting after n values are obtained for a wide range of Q values from the Manning equation (Leopold et al. 1964). Solving for n,

$$n = V^{-1} R^{2/3} S^{1/2}, \tag{8}$$

where V, R, and S are field measurements corresponding to the Q values. Mean current velocity during a simulation run also is obtained from the Manning equation:

$$V(k) = n^{-1}(k) R^{2/3}(k) S^{1/2}, \tag{9}$$

and shear stress is found from

$$\tau(k) = \gamma R(k) S, \tag{10}$$

where γ is the specific weight of water (Leopold et al. 1964).

The light extinction coefficient (η) at time k is estimated from

$$\eta(k) = 0.207 + 0.03SL(k), \tag{11}$$

and the light intensity reaching the autotrophic organisms (I_z) at time k and depth Z(k) is

$$I_z(k) = I_o(k) \exp[\eta(k) Z(k)], \tag{12}$$

where I_o is the intensity at the surface. Equation 11 was derived from data reported by Ruttner (1952), and Eq. 12 is the common expression for light extinction (Hutchinson 1957).

Primary consumption and predation.—The general equation form that updates biomass for each primary consumer and predator group is given by

$$X(k + 1) = X(k) + \Delta_x(k) \tag{13}$$

and

$$\Delta_x(k) = \Delta_{xa}(k) - \Delta_{xr}(k) - \Delta_{xe}(k) - \Delta_{xm}(k) - \Delta_{xp}(k), \tag{14}$$

where X(k) is the biomass associated with the process of interest at time k; $\Delta_{xa}(k)$ is the assimilation increment for the time period from k to k+1; and $\Delta_{xr}(k)$, $\Delta_{xe}(k)$, $\Delta_{xp}(k)$, and $\Delta_{xm}(k)$ are corresponding incremental losses from respiration, emergence, predation, and mortality, respectively. In practice, the FLEX algorithm calculates $\Delta_x(k)$ values from a flux matrix (F functions) which is derived from a series of equations (G functions) expressing various rate variables and intermediate concepts (White and Overton 1974).

The rate of respiration at time k for each consumer process is

$$R_x(k) = X(k)[b_{1x} + b_{2x} T(k)], \tag{15}$$

where T is the temperature, and b_{1x} and b_{2x} are parameters estimated for each process from laboratory data. The linear relationship expressed in Eq. 15 was derived from studies of the caddisfly *Glossosoma nigrior* (K. W. Cummins, *personal communication*) and from work with *Lepidostoma quercina*, *Lepidostoma unicolor*, and *Clistoronia magnifica* (Grafius 1977). For processes of grazing, shredding, collecting, and invertebrate predation, natural mortality is conceptualized as part of the incremental respiratory loss, i.e., $\Delta_{xr}(k)$, and $\Delta_{xm}(k)$ is omitted from Eq. 14.

The expression representing insect emergence which applies to the processes of grazing, shredding, collecting, and invertebrate predation is

$$EM_x(k) = X(k) b_{8x} t_{ex}(k), \tag{16}$$

where t_{ex} is a table function representing the pattern of emergence loss for each process x, and b_{8x} is a scaling parameter. Table functions were derived from the data of Anderson and Wold (1972) and Speir (1975) and from unpublished emergence-trap data obtained during studies in the H. J. Andrews Experimental Forest in western Oregon.

For the process of vertebrate predation, the mortality rate (M_v) at time k is given by

$$M_v(k) = b_6 X_v(k), \tag{17}$$

where X_v is the biomass associated with the process, and b_6 is the corresponding specific mortality rate, 0.0025 $g \cdot day^{-1} \cdot g^{-1}$ in the simulation runs reported here.

For the process of invertebrate predation, the rate of biomass loss to vertebrate predation (P_i) at time k is found from

$$P_i(k) = C_{v2i}(k), \tag{18}$$

where C_{v2i} is the corresponding consumption rate (define below) by the process of vertebrate predation. Losses to predation at time k for grazing, shredding, and collecting, the primary consumer processes, are given by

$$P_x(k) = [F_x(k)/F_{pe}(k)]\,[C_i(k) + C_{v2pe}(k)], \tag{19}$$

where C_i and C_{v2pe} (defined below) are rates of consumption of biomass associated with grazing, shredding, and collecting by processes of invertebrate predation and vertebrate predation, respectively; F_x is the biomass available for consumption related to primary consumer process x; and F_{pc} is the total biomass available for consumption related to the 3 primary consumer processes.

The assimilation rate A_x at time k is assumed to be a constant proportion of food consumption, that is

$$A_x(k) = b_{3x}C_x(k), \tag{20}$$

where b_{3x} is the assimilation efficiency for process x, and $C_x(k)$ is the rate of food consumption for the process at time k (defined below). In the examples presented in subsequent sections, assimilation efficiencies are 0.55 (grazing), 0.18 (shredding), 0.21 (collecting), 0.82 (invertebrate predation), and 0.86 (vertebrate predation). These values are within the range of values reported in the literature for individual species with known feeding habits (e.g., Trama 1957; Brocksen et al. 1968; McDiffett 1970; Lawton 1971; Sedell 1971; Stockner 1971; Otto 1974; Grafius 1974, 1977). However, model behavior can be examined for any set of b_{3x} values, or model form can be changed slightly to express assimilation efficiency as a function of some other variable (e.g., temperature).

Mathematical representation of food consumption for each consumer process is similar in form to that discussed by McIntire et al. (1975). Food-consumption rate $C_x(k)$ is calculated by adjusting the demand for food with a function expressing the limiting effect of food density. Theoretically, the demand for food $D_x(k)$ is the consumption rate by process x at time k if the food resource is in unlimited supply. For primary consumer processes,

$$C_x(k) = D_x(k)f_{1x}[F(k)], \tag{21}$$

where f_{1x} is a function of food density F(k) with values ranging from 0 to 1. The function f_{1x} is a hyperbolic curve with parameters estimated for each process (see FLEXFORM for details). The demand for each process is found from

$$D_x(k) = X(k)b_{2x}f_{2x}[T(k)], \tag{22}$$

where X(k) is the biomass; b_{2x} is the maximum food consumption rate per unit biomass under optimal conditions of supply and temperature; and f_{2x} is a function of temperature T(k) ranging from 0 to 1. The limiting effect of temperature is expressed as either a hyperbolic curve or a set of linear functions (see FLEXFORM for details).

The concept of demand in the modeling of consumer processes provides a useful way of partitioning the limiting effects of density independent and density dependent factors. For example, demand per unit biomass, $D_x(k)/X(k)$, is a function of density-independent factors, temperature in this model, while food density as well as demand regulate the food consumption rate. The parameter b_{2x} therefore represents maximum potential per unit biomass to process a given resource. This approach to modeling consumer processes provides a convenient mathematical form that aids in the biological interpretation of state variable dynamics. For simulation runs presented here, b_{2x} values expressed as $g \cdot day^{-1} \cdot g^{-1}$ were 0.52 (grazing), 0.70 (shredding), 0.48 (collecting), 0.05 (invertebrate predation), and 0.026 (vertebrate predation). These values were derived from the data of Brocksen et al. (1968), Anderson (1972), Gregory (1972), MacKay (1972), Cummins et al. (1973), and Grafius (1977).

The model permits partitioning of vertebrate predation into benthic and drift feeding. For example, such partitioning would be desirable for the simulation of a system in which both sculpins and trout occur. The rate of food consumption $C_v{}^*$ for the process of vertebrate predation at time k in the absence of competition from invertebrate predation is given by a set of 3 equations:

$$C^*_v(k) = C_{v1}(k) + C^*_{v2}(k); \tag{23}$$

$$C_{v1}(k) = \min\{b_5D_v(k),\ b_{23}\ \Sigma\ EM_x(k)\};\ \text{and} \tag{24}$$

$$C^*_{v2}(k) = D_v(k)\,(1 - b_5)f_{1v}[F(k)]; \tag{25}$$

where

C_{v1} = the consumption rate of drifting organic material for vertebrate predation;

C^*_{v2} = the consumption rate of benthos for vertebrate predation in the absence of competition from invertebrate predation;

b_5 = the fraction of vertebrate predation demand D_v that must be satisfied from drift feeding, or left unsatisfied; and

$b_{23}\ \Sigma\ EM_x$ = the drifting food supply.

In the current version of the model, the sum of emergence increments for processes of grazing, shredding, collecting, and invertebrate predation (ΣEM_x) is used as an index to the drifting food supply, and the scaling parameter b_{23} equals 1. The parameter b_5 is set equal to 0.5, a value based on the trout-sculpin system investigated by Brocksen et al. (1968). Again, f_{1v} is a density dependent limiting function, in this case for vertebrate predation, based on available food supply F.

Consumption rate of invertebrate predator biomass by the process of vertebrate predation $C_{v2i}(k)$ is proportional to total benthic food supply:

$$C_{v2i}(k) = C^*_{v2}(k)\,[F_i(k)]/[F_i(k) + F_{pc}(k)], \tag{26}$$

where F_i is the biomass available for consumption associated with the process of invertebrate predation, and F_{pc} is the corresponding biomass for primary consumer processes (grazing, shredding, and collecting). Invertebrate predation is represented as benthic feeding only, and the rate of food consumption for this

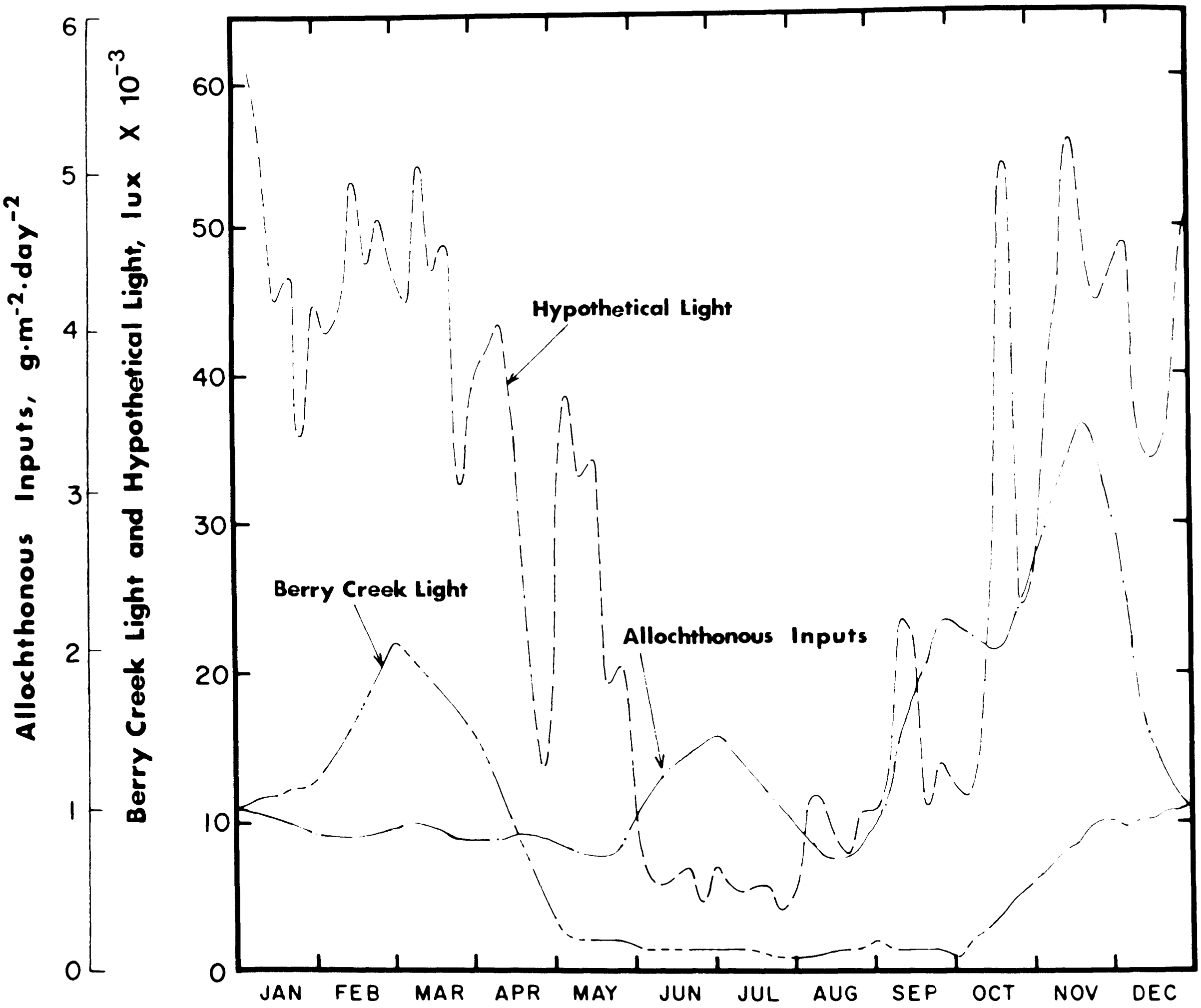

FIG. 3. Annual energy inputs of light and allochthonous organic materials for the standard runs.

process in the absence of competition from vertebrate predation C^*_i is found from

$$C^*_i(k) = D_i(k) f_{li}[F(k)], \tag{27}$$

where D_i and f_{li} are corresponding values for demand and the food density limiting function, respectively.

When the benthic food supply $[F_i(k) + F_{pc}(k)]$ is less than $[D_i(k) + (1 - b_5)D_v(k)]$ multiplied by the time step, i.e., the increment consumed by invertebrate and vertebrate predation between k and k + 1 if demand is satisfied, competition between the processes of invertebrate and vertebrate predation occurs; and food is allotted to each predator process according to C^*_i and C^*_{v2pc}, the consumption rates of biomass associated with primary consumer processes in the absence of competition. Analogous to Eq. 26,

$$C^*_{v2pc}(k) = C^*_{v2}(k)\,[F_{pc}(k)]/[F_i(k) + F_{pc}(k)]. \tag{28}$$

The actual consumption rates of primary consumer biomass by invertebrate predation (C_i) and vertebrate predation (C_{v2pc}) are given by

$$C_i(k) = \min\left\{C^*_i(k),\ b_4\left[\frac{C^*_i(k)}{C^*_i(k) + C^*_{v2pc}(k)}\right] F_{pc}(k)\right\}, \tag{29}$$

and

$$C_{v2pc}(k) = \min\left\{C^*_{v2pc}(k),\ (1 - b_4)\left[\frac{C^*_{v2pc}(k)}{C^*_i(k) + C^*_{v2pc}(k)}\right] F_{pc}(k)\right\}, \tag{30}$$

where b_4 is a competition weighting factor, a value arbitrarily set at 0.8 for simulation runs reported here. The total food consumption rate (C_v) at time k for the process of vertebrate predation is calculated from

$$C_v(k) = C_{v1}(k) + C_{v2i}(k) + C_{v2pc}(k). \tag{31}$$

TABLE 1. Hydrologic properties associated with both versions of the standard run. Maximum, minimum, and mean values correspond to output from Eqs. 1, 2, 3, 4, 5, 8, and 9 during a 1-yr simulation run at a time resolution of one day. Parameters for the equations and the mean channel slope are based on data for Oak Creek, near Corvallis, Oregon (Milhous 1973)

Property	Units	Maximum	Minimum	$\bar{x}$
Flow (Q)	litres/s	3,540	22	221
Current velocity (V)	centimetres/s	231	20	50
Suspended load (SL)	milligram/litre	330	1	14
Roughness coefficient (n)	. . .	0.075	0.048	0.054
Channel width (W)	metres	3.17	3.12	3.13
Channel depth (D)	metres	0.58	0.03	0.09
Cross-sectional area (A)	square metres	6.95	0.28	0.94
Channel slope (S)	metres/metre	. . .	. . .	0.014

ANALYSIS OF MODEL PROPERTIES

Standard runs

Contemporary theory of lotic ecosystems (Cummins 1975*b*; R. L. Vannote, *personal communication*) conceptualizes such systems as continua that run from small, first-order streams with no tributaries to large rivers (orders 7 to 12) which drain into the sea. The model structure described in the previous section is most compatible with the upper segment of the continuum, i.e., stream orders 1 to 4. Leopold et al. (1964) estimate that these lower-order streams represent ≈93% of the total length of flowing water in the United States (≈4,860,200 kilometres). Because the model in its present form emphasizes benthic processes, its structure will need expansion and possibly modification before water column processes of larger rivers are represented adequately. However, with appropriate inputs, the model does provide some insights into benthic processes in larger rivers.

Here, we establish "standard runs" that can serve as a basis for comparisons with other runs based on different sets of assumptions. Our standards are presented as selected output from 2 versions of the stream model, versions that differ only with respect to the input schedule of illumination intensity. In Version I, a table function introduces a schedule of illumination intensities (Fig. 3) derived from light measurements at a location on Berry Creek, a small stream in the Willamette Valley near Corvallis, Oregon (Reese 1966). In Fig. 3, the mean intensity varies from ≈1,000 to 22,000 lux, and the fluctuations reflect the seasonal effect of shading by riparian vegetation. In Version II of the standard run, a table function introduces a hypothetical light schedule that provides the system with considerably more solar energy than the Berry Creek schedule, while retaining the effects of some shading during late spring, summer, and early fall (Fig. 3). Therefore, Version II simulates conditions after a stream is wide enough to allow relatively high illumination intensities to reach the water surface. From the continuum point of view, Version II theoretically represents a stream of higher order than Version I relative to solar energy inputs.

Hydrologic properties introduced for the standard runs are summarized in Table 1. In general, the hydrology reflects the annual climatic cycle typical of western Oregon. Stream discharge is relatively low during late spring, summer, and early fall; it then increases significantly during the first few weeks of the rainy season in November, reaching a maximum by mid-January. Changes in current velocity, suspended load, and channel dimensions exhibit essentially the same seasonal pattern of discharge, with minimum values in September and maximum values in January.

Other variables controlling biological processes in the model include temperature, photoperiod, and input of allochthonous organic matter (LPOM). Temperature and photoperiod are represented as trigonometric functions of time (McIntire 1973). Temperature ranges from 6°C in January to 18°C in July, and photoperiod varies between an 8-h and 16-h light period per day in January and July, respectively. The schedule of allochthonous inputs for the standard runs was derived from direct measurements at a small stream draining Watershed 10, a research area at the H. J. Andrews Experimental Forest. The total annual input of allochthonous organic material is ≈480 g/m^2, a value that includes both litterfall and lateral movement. The daily rate of detrital input ranges from a minimum of 0.70 g·m^{-2}·day^{-1} in April to 3.42 g·m^{-2}·day^{-1} in November (Fig. 3).

Behavior.—Selected output for the 2 versions of the standard run is presented in Tables 2–4. Numerical values in each table represent annual dynamics after system variables reach a steady state for a given set of inputs. For our purposes, production is defined as total net elaboration of new, living tissue in a unit of time (assimilation minus respiration or gross primary production minus periphyton respiration in the case of periphyton processes), irrespective of whether or not that tissue survives to the end of that time (Ricker 1958).

Total production of macroconsumers involved in primary consumption (processes of grazing, shredding, and collecting) is actually slightly greater for the Berry Creek light schedule (Version I) than the hypothetical light schedule (Version II); the correspond-

TABLE 2. Selected output from the stream model representing processes of grazing (GRAZE), shredding (SHRED), collecting (COLLECT), invertebrate predation (I-PRED), vertebrate predation (V-PRED), and autochthonous plant production (ALGAE) for the 2 versions of the standard run

Property	GRAZE	SHRED	COLLECT	I-PRED	V-PRED	ALGAE
			Version I (low light)			
Biomass (g/m^2):						
$\bar{x}$	1.08	1.23	2.57	0.41	6.03	0.94
Max	3.09	2.78	5.79	1.02	9.77	1.90
Min	0.25	0.34	1.13	0.07	3.80	0.55
Production ($g \cdot m^{-2} \cdot yr^{-1}$)	3.40	6.36	12.05	0.84	5.48	**61.10
Turnover (times/yr)	3.16	5.17	4.69	2.07	0.91	65.00
Assimilation ($g \cdot m^{-2} \cdot yr^{-1}$)	27.05	41.83	70.31	3.60	15.45	*71.14
Losses ($g \cdot m^{-2} \cdot yr^{-1}$):						
Respiration or post-mortum decomposition	23.66 (87%)	35.48 (85%)	58.26 (83%)	2.77 (76%)	9.97 (65%)	10.04 (14%)
Vertebrate predation	1.97 (7%)	2.70 (6%)	5.56 (7%)	0.60 (16%)	. . .	. . .
Invertebrate predation or grazing	0.77 (3%)	1.25 (3%)	2.39 (4%)	. . .	. . .	49.19 (69%)
Emergence or mortality	0.66 (2%)	2.37 (6%)	4.08 (6%)	0.26 (7%)	5.43 (35%)	. . .
Export	. . .	. . .	. . .	. . .	. . .	11.90 (17%)
			Version II (high light)			
Biomass ($g \cdot m^{-2}$):						
$\bar{x}$	2.26	0.86	0.93	0.95	4.16	1.03
Max	3.06	1.90	2.06	2.19	6.21	1.31
Min	1.23	0.28	0.42	0.24	2.79	0.68
Production ($g \cdot m^{-2} \cdot yr^{-1}$)	10.66	4.93	4.61	2.14	3.54	**129.89
Turnover (times/yr)	4.71	5.79	4.98	2.26	0.85	126.11
Assimilation ($g \cdot m^{-2} \cdot yr^{-1}$)	63.80	29.00	24.87	8.53	10.36	*141.09
Losses ($g \cdot m^{-2} \cdot yr^{-1}$):						
Respiration or post-mortum decomposition	53.14 (83%)	24.07 (83%)	20.26 (81%)	6.40 (74%)	6.82 (65%)	11.20 (8%)
Vertebrate predation	3.23 (5%)	1.15 (4%)	1.19 (5%)	1.57 (18%)	. . .	. . .
Invertebrate predation or grazing	5.99 (9%)	2.20 (8%)	2.21 (9%)	. . .	. . .	116.01 (82%)
Emergence or mortality	1.43 (2%)	1.61 (6%)	1.24 (5%)	0.63 (7%)	3.75 (35%)	. . .
Export	. . .	. . .	. . .	. . .	. . .	13.88 (10%)

* Gross primary production.

** Net community production for periphyton assemblage.

ing values are 21.8 and 20.2 $g \cdot m^{-2} \cdot yr^{-1}$, respectively (Table 2). Likewise, total production for the process of predation is higher for Version I (5.80 $g \cdot m^{-2} \cdot yr^{-1}$) than Version II (4.33 $g \cdot m^{-2} \cdot yr^{-1}$). It is important to note that production associated with the total process of predation (see Eq. 40 in a later section) is not the summation of production for vertebrate and invertebrate predation processes, as some energy is transferred from the latter to the former. The principal differences between the outputs for the 2 versions of the

TABLE 3. Selected output from the stream model representing processes associated with fine particle detritus (FPOM) and large particle detritus (LPOM) for the 2 versions of the standard run

	Version I (low light)		Version II (high light)	
Property	FPOM	LPOM	FPOM	LPOM
Biomass (g/m^2):				
$\bar{x}$	10.48	60.35	10.70	97.85
Max	23.22	150.43	16.82	175.23
Min	4.15	0.58	5.31	54.02
Inputs ($g \cdot m^{-2} \cdot yr^{-1}$):				
Terrestrial	. . .	473.63	. . .	473.63
Aquatic (feces)	480.49	. . .	281.40	. . .
Mechanical from LPOM	55.08	. . .	35.18	. . .
Losses ($g \cdot m^{-2} \cdot yr^{-1}$):				
Microbial decomposition	120.52 (23%)	114.01 (24%)	120.30 (38%)	176.45 (37%)
Primary consumption	334.79 (63%)	234.40 (49%)	118.41 (37%)	161.09 (34%)
Export	79.95 (15%)	73.93 (16%)	81.16 (25%)	93.02 (20%)
Mechanical to FPOM	. . .	55.08 (12%)	. . .	38.18 (8%)

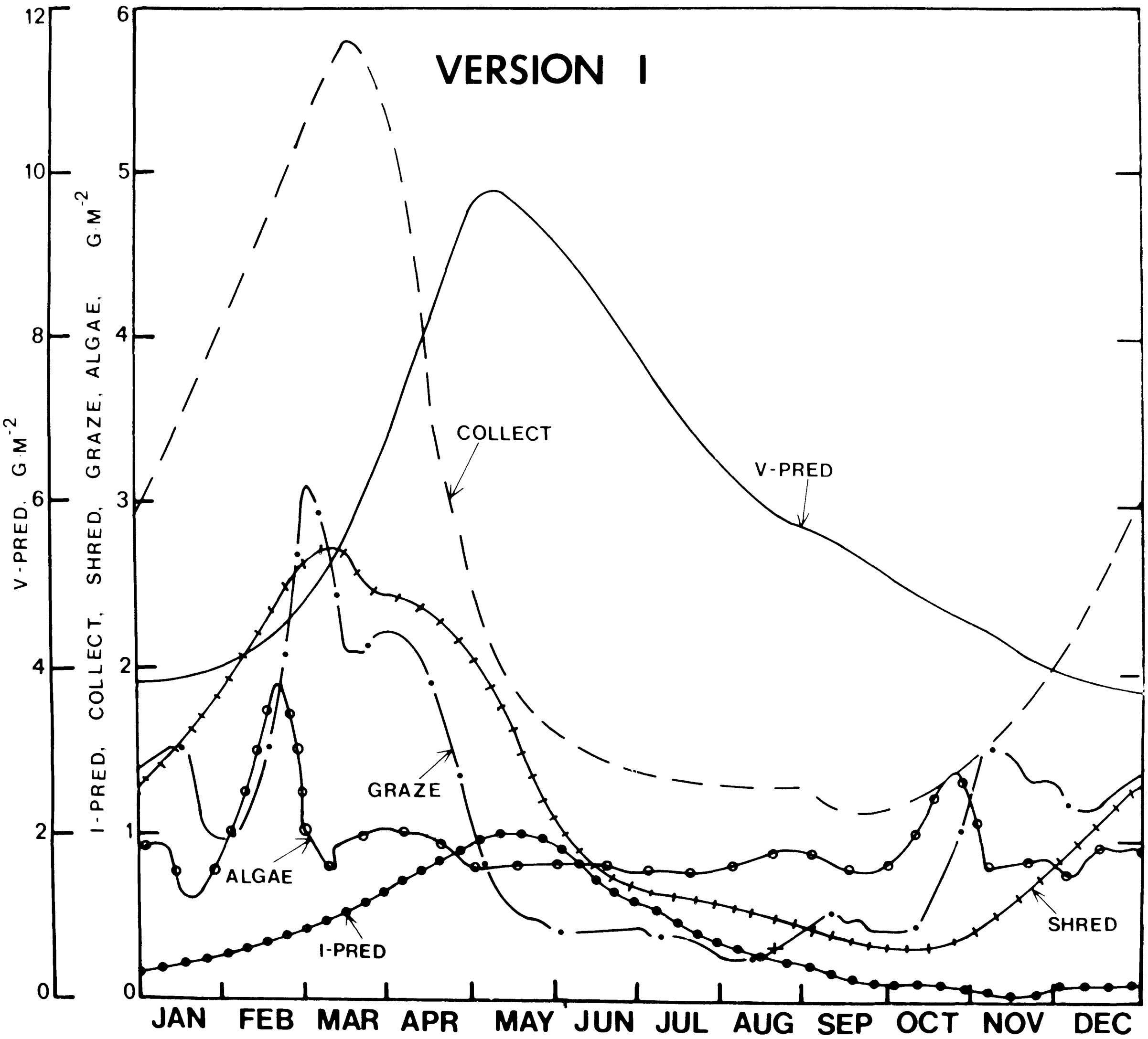

FIG. 4. Seasonal dynamics of the principal state variables for Version I (Berry Creek light schedule) of the standard run. Acronyms refer to periphyton processes (ALGAE) and processes of grazing (GRAZE), collecting (COLLECT), shredding (SHRED), invertebrate predation (I-PRED), and vertebrate predation (V-PRED).

standard runs are manifested by rates of primary production and relative production rates associated with consumer processes. In Version I, production related to primary macroconsumer processes is partitioned as 15.6% grazing and 84.4% shredding and collecting, whereas the corresponding values for Version II are 52.8% and 47.2%. Furthermore, the hypothetical light schedule (Version II) generates an annual rate of gross primary production 98.3% higher than the Berry Creek schedule (Version I). Although autotrophic activity is relatively low in Version I, we emphasize that a small mean biomass (0.94 $g \cdot m^{-2}$) turns over 65 times per year, and that the net periphyton community production rate (61.10 $g \cdot m^{-2} \cdot yr^{-1}$) is still $\approx 3\times$ larger than total production for grazing, shredding, and collecting. Hence, effects of an increase in solar input under conditions of the standard runs are (1) an increase in biomass and production related to grazing and corresponding decreases for the process of collecting; (2) an increase in biomass and production related to invertebrate predation; and (3) an increase in autotrophy.

Seasonal dynamics of the standard runs are illustrated in Figs. 4 and 5. In general, process biomasses exhibit more distinct maxima in Version I than in Version II, illustrating the seasonal effect of shading by a dense canopy of terrestrial vegetation in the former version. The process of collecting is particularly conspicuous during the spring in Version I, whereas grazing is important most of the year in Version II. In either case, the figures illustrate the type of seasonal dynamics generated by the model that can be checked

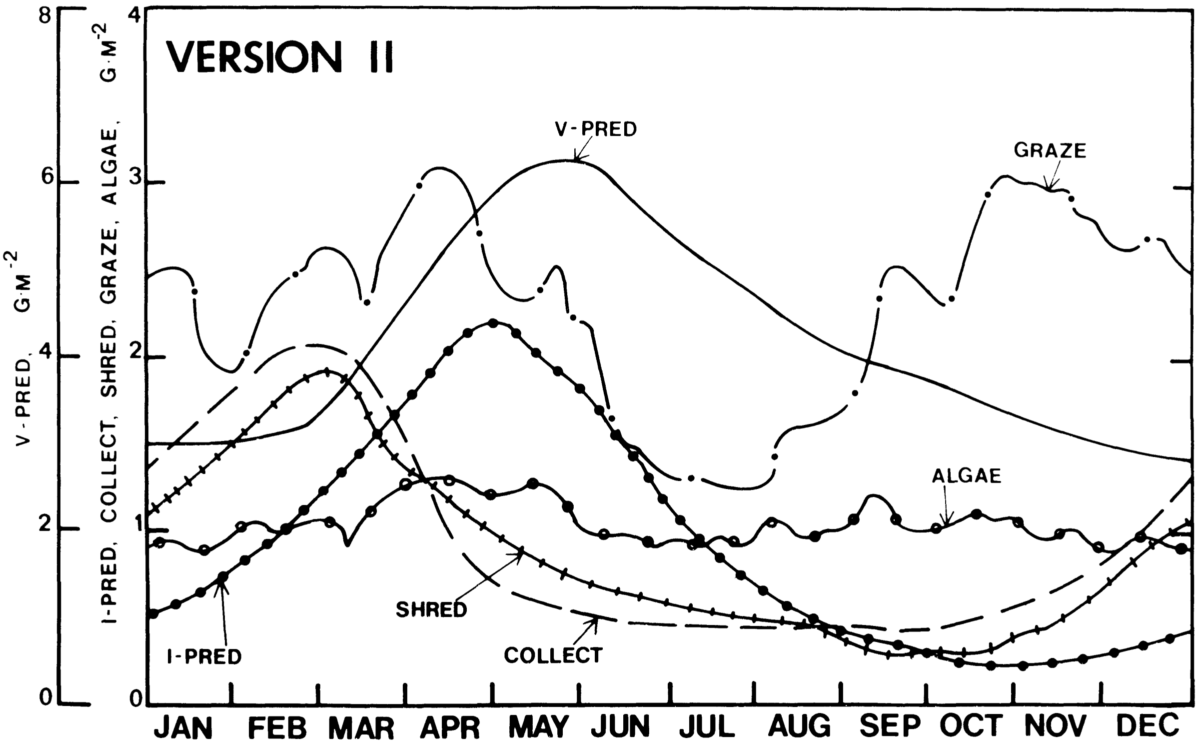

FIG. 5. Seasonal dynamics of the principal state variables for Version II (Hypothetical light schedule) of the standard run. Acronyms are the same as given in Fig. 4.

against field observations for validation or used for predictive purposes.

Validation.—Overton (1977) discussed problems of model validation and acknowledged that internal variables in large ecosystem models are often not represented by data sets and that many of these variables cannot be measured directly. Because we are primarily interested in mechanisms regulating processes in streams, not in the simulation of a particular natural ecosystem, model validation is based in part on comparisons of output from the standard runs with ranges of biomass and production values reported in the literature. Unfortunately, there is a paucity of such values, as many of the coarse-resolution processes represented in the model have not been measured in the field. Therefore, we must rely on indirect estimates of process dynamics for selected natural lotic systems, estimates based primarily on field and laboratory measurements of population parameters. Furthermore, these estimates are more compatible with validation at an annual time resolution, although some published and unpublished data relating to seasonal dynamics are available for comparisons with model output.

Validation of the periphyton module of the stream model has been discussed relative to laboratory stream data and data obtained for a riffle section in Berry Creek (McIntire 1973). Moreover, annual rates of gross primary production for the 2 versions of the standard run (Table 4) are remarkably similar to values measured by S. V. Gregory (*personal communication*)

TABLE 4. Energy budget representing the behavior of the stream model at the ecosystem level for the 2 versions of the standard run

	Version I (low light)		Version II (high light)	
Property	Additions ($g \cdot m^{-2} \cdot yr^{-1}$)	Losses ($g \cdot m^{-2} \cdot yr^{-1}$)	Additions ($g \cdot m^{-2} \cdot yr^{-1}$)	Losses ($g \cdot m^{-2} \cdot yr^{-1}$)
Gross primary production	71.14	. . .	141.09	. . .
Allochthonous input	480.78	. . .	478.54	. . .
Community respiration	. . .	374.69	. . .	418.64
Export and emergence	. . .	178.58	. . .	196.73
Total	551.92	553.27	619.63	615.37
P:R	0.19		0.34	

for experimental sections of Mack Creek (75 $g \cdot m^{-2} \cdot yr^{-1}$) and Lookout Creek (150 $g \cdot m^{-2} \cdot yr^{-1}$) in the H. J. Andrews Experimental Forest. The mean periphyton biomass in a forested section of Mack Creek was 1.6 $g \cdot m^{-2}$ (Lyford and Gregory 1975) which is comparable to values of 0.94 and 1.03 $g \cdot m^{-2}$ for the standard runs (Table 2).

Most of the field or laboratory data available for comparisons with behavior of primary consumer processes (Tables 2 and 3) are for individual species populations. Data presented by Anderson (1972) and Cummins (1975*a*) for grazing caddisflies (*Glossosoma nigrior* and *Agapetus bifidus*) are roughly comparable with grazing behavior generated by the standard runs. Cummins et al. (1973) reported a biomass of 1.43 g/m^2 (Augusta Creek, Michigan) for taxonomic entities designated as shredders (*Tipula* sp. and *Pycnopsyche* sp.). Mean biomasses associated with shredding for the standard runs are 1.23 g/m^2 (Version I) and 0.85 g/m^2 (Version II) with a seasonal range for both versions from 0.28 to 2.78 g/m^2. Indirect estimates of shredder biomass from the leaf pack data of Sedell et al. (1975) yielded maxima of ≈1.62 (Mack Creek) and 0.24 g/m^2 (Watershed-10), assuming that conifer needles are the principal food resource. The estimated mean biomass of taxa classified as collectors during an 11-mo study in Mack Creek was 1.15 g/m^2 (Grafius 1974), corresponding to 2.57 and 0.93 g/m^2 in Table 2 for the process of collecting.

Seasonal dynamics of a group of taxa classified as grazers in Watershed-10, a first-order stream with a mean slope of 45% (F. J. Triska and J. R. Sedell, *personal communication*), closely resembled the pattern of changes exhibited by Version I (Fig. 4), although the mean biomass was considerably less in the natural system. The pattern in the riffle areas in Watershed-10 indicated a maximum grazer biomass during the spring months and a decline during early summer when the system is shaded by riparian vegetation. Grafius (1977) examined the seasonal dynamics of 3 species of *Lepidostoma*, all classified as shredders, and found that the biomass of *Lepidostoma quercina* gradually increased during the fall in Berry Creek, reaching a maximum in January; *Lepidostoma cascadense* and *Lepidostoma unicolor* showed maxima during late spring and early summer in Mack Creek. The pattern exhibited for the process of shredding by the standard runs (Figs. 4 and 5) indicates maximum biomasses in March, 3 mo earlier than the seasonal patterns of *L. cascadense* and *L. unicolor*. This discrepancy is related to the fact that emergence schedules in the model attempt to represent a total process and do not correspond exactly to the dynamics of these particular species. In any case, model form allows for the examination of any emergence schedule of interest.

Some additional comparisons provide further evidence that the stream model is an acceptable representation of biological processes in lotic ecosystems relative to our objectives. Production, biomass, and turnover ratios associated with the process of vertebrate predation for the standard runs (Table 2) are within the range of values given by Chapman (1968), Petrosky and Waters (1975), and Krohn (1968) for individual species of fish. Furthermore, turnover ratios for processes of grazing, shredding, and collecting are similar to those reported for aquatic insects (Waters 1969), and the dynamics of detrital processing simulated in Version I (Table 3) closely resemble the general scheme proposed by Petersen and Cummins (1974) for small woodland streams.

Modifications.—At this point we examine the behavior of Version I in the absence of the processes of predation, primary macroconsumption, and export of LPOM. In general, model behavior is realistic in the absence of such processes, i.e., state variables do not assume unrealistically high values or go to 0. With the deletion of predation, mean biomasses associated with grazing, shredding, and collecting increase to 1.13, 1.64, and 8.21 $g \cdot m^{-2}$, respectively; while corresponding annual production rates actually decrease by 77.1%, 44.5%, and 2.8%. In the absence of predation, food supply becomes more important in the regulation of these processes, and there is a pronounced decrease in the production to biomass ratio, particularly noticeable in the process of grazing. Mechanisms accounting for these changes are discussed in another section. In any case, the annual production and mean biomass values still remain within the range of values recorded for natural streams (e.g., Hynes 1970). If macroconsumer processes (grazing, shredding, collecting, and vertebrate and invertebrate predation) are deleted, 69% of the LPOM is processed by microbial activity, 31% is exported, and gross primary production increases to 534 $g \cdot m^{-2} \cdot yr^{-1}$. The latter value is ≈60% of the annual production measured for a periphyton assemblage grown in isolation in a laboratory stream at a mean illumination intensity of 2,260 lux (McIntire and Phinney 1965). Moreover, there is a remarkable similarity between the mean biomass of periphyton predicted by the model in the absence of macroconsumer processes (20.1 g/m^2) and that actually measured (17.2 g/m^2) for an assemblage grown in a laboratory stream for 8 mo (McIntire 1968*a*). If we assume all LPOM is processed (no export), production related to processes of grazing, shredding, invertebrate predation and vertebrate predation increases by 15%, 35%, 49%, and 12%, respectively; production for collecting is unaffected, while microbial decomposition and losses to shredding increase by 9% and 24%, respectively. The effect of LPOM export on model behavior is of particular interest because of the lack of field data from which to derive parameter estimates.

We also have examined changes in Version II (high light) in the absence of shredding. This change was initiated by introducing all allochthonous material in the form of FPOM. Version II was selected for this manipulation because larger streams and rivers with open water are more likely to receive allochthonous inputs as FPOM than smaller, shaded streams. With the same total quantity of allochthonous material as Version II (474 $g \cdot m^{-2} \cdot yr^{-1}$), the input in the form of FPOM increases collector production by 67% and decreases grazer production by ≈3%; the total production associated with primary consumer processes decreases by 11%. In other words, the increase in collector production does not compensate for the lack of shredding, and macroconsumer processes are less efficient in processing energy inputs without shredding. Correspondingly, the relative amounts of FPOM lost through microbial respiration, consumption by collecting, and export in the absence of shredding are 42%, 27%, and 31%, respectively, as compared to 38%, 37%, and 25% for Version II with shredding. Moreover, gross primary production is 141 $g \cdot m^{-2} \cdot yr^{-1}$ in both cases, and production related to predation as a total process decreases by 15% without shredding. Obviously, such changes may not necessarily take place along the continuum from small streams to larger rivers, as water column processes assume more importance as stream order increases and the stream bed may become less suitable for periphyton growth.

Analysis of mechanisms.—Although Figs. 4 and 5 indicate seasonal dynamics for the standard runs, mechanisms accounting for such dynamics are not obvious from plots of state variables. In particular, we are interested in mechanisms controlling (or limiting) biological processes in streams. For example, processes of grazing, shredding, and collecting in natural streams may be constrained by the genetic constitution of the organisms involved in the process and associated life history phenomena (e.g., the emergence pattern), by physical properties of the system (e.g., temperature and current velocity), and by food supply and the process of predation. To understand lotic ecosystem dynamics, we must be able to evaluate the relative importance of such controlling factors in time and in space along the continuum. In this respect, modeling can help by generating output in a form that partitions out limiting effects of various control variables on the specific growth rate of biomass related to a particular process. This approach is demonstrated now for Version I of the standard run.

The specific growth rate at time k of the biomass associated with a process when food is present in unlimited supply is given by

$$g_0(k) = [X(k)]^{-1} [b_3D(k) - R(k)], \qquad (32)$$

assuming no losses from predation or emergence (export). As indicated above, X is the total biomass, D is the demand for food (Eq. 22), b_3 is the fraction of the demand that is assimilated (i.e., the assimilation efficiency), and R is the rate of respiration. It is interesting to note that g_0 is analogous to the intrinsic rate of natural increase as defined by Birch (1948). In other words, g_0 is a growth rate per unit biomass in an environment with unlimited resources and free from negative effects from other processes; it is a function of density-independent factors only, temperature in the case of the standard runs (Eqs. 15 and 22). If food supply is not unlimited, the specific growth rate, in the absence of emergence and predation, is

$$g_1(k) = [X(k)]^{-1} [b_3C(k) - R(k)], \qquad (33)$$

where C is the actual consumption rate from Eq. 21. If we add the negative effects of emergence, vertebrate predation, and invertebrate predation, in that order, the equations become

$$g_2(k) = [X(k)]^{-1} [b_3C(k) - R(k) - EM(k)], \qquad (34)$$

$$g_3(k) = [X(k)]^{-1} [b_3C(k) - R(k) - EM(k) - PV(k)], \qquad (35)$$

and

$$g_4(k) = [X(k)]^{-1} [b_3C(k) - R(k) - EM(k) - PV(k) - PI(k)], \qquad (36)$$

where EM, PV, and PI are derived from Eqs. 16, 18, and 19. Therefore, limiting effects of food resources, emergence or export, vertebrate predation, and invertebrate predation are $g_0 - g_1$, $g_1 - g_2$, $g_2 - g_3$, and $g_3 - g_4$, respectively.

Next, we define g_r as the actual or realized specific growth rate associated with a particular process. In the stream model, $g_r = g_4$ for grazing, shredding, and collecting; $g_r = g_3$ for invertebrate predation; and $g_r = g_1$ for vertebrate predation after $M_v(k)$ is included within the parentheses. To analyze state variable dynamics, we simply plot g_0, g_r, and all relevant $g_i \mid i=1, 2, \ldots, g_{r-1}$ against time and examine the areas between the curves relative to a plot of the corresponding state variable.

An analysis of state variable dynamics for Version I is illustrated in Fig. 6 and 7. The process of grazing is clearly food limited throughout the year, though not as strongly so in early spring and mid-fall when periphyton production is relatively high (Figs. 4 and 6). Limiting effects of emergence and predation are minor and apparent only during the spring months. In contrast, food is virtually unlimited (demand is satisfied and $g_0 = g_1$) with respect to shredding, except for a short period in early summer. Emergence limits the process in the spring, late summer, and early fall; whereas predation exerts some control from December through May. Food resources also have relatively little controlling influence on collecting as compared to emergence and predation (Fig. 7); emergence is important during spring and fall, while predation has its maximum effect during the first half of the year. Biomasses related to vertebrate and invertebrate predation tend to grow exponentially from January through April, but then become strongly food limited during

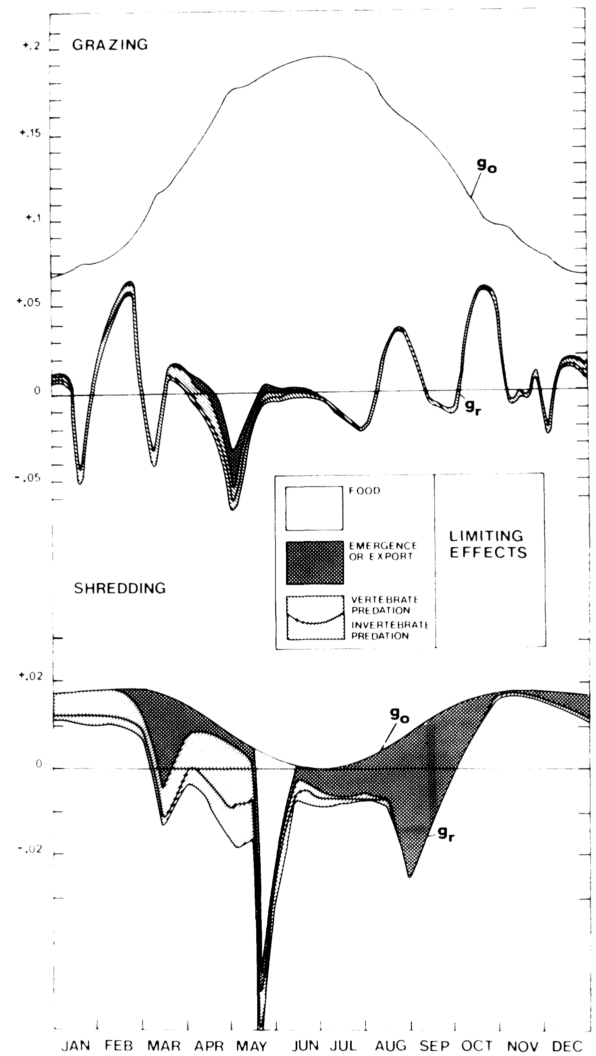

FIG. 6. A family of specific growth rates representing processes of grazing and shredding for Version I of the Standard run. g_0 is the rate in an environment with unlimited resources (food), and g_r is the actual or realized rate.

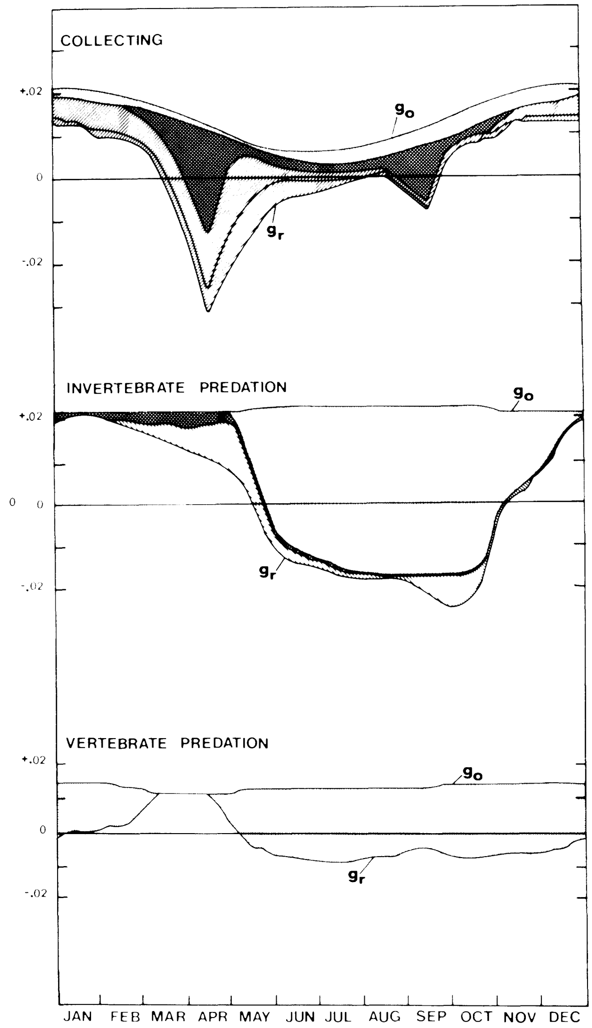

FIG. 7. A family of specific growth rates representing processes of collecting, invertebrate predation, and vertebrate predation. g_0, g_r and the limiting effects are the same as given in Fig. 6.

the rest of the year. Invertebrate predation is inhibited to some degree by vertebrate predation during the spring.

Summarizing, analysis of state variable dynamics in Version I suggests that regulation of biological processes in streams is complex and the mechanisms vary in time and from process to process. Figures 6 and 7 simply indicate mechanisms for 1 particular case, however, we have found it useful to generate plots of specific growth rates from Eqs. 32–36 as part of the regular output for each simulation run. Obviously, in any natural ecosystem, biological processes are ultimately constrained by the genetic constitution of organisms involved in each process, a constraint expressed in the model by aspects of the mathematical structure and the parameter values considered appropriate.

Stream dynamics relative to energy inputs

Inputs of energy into lotic ecosystems include solar radiation and allochthonous organic matter. The latter can be represented by large particulate organic matter resistant to decay (logs, branches, twigs, and bark), whole leaves, leaf fragments, fine particulate organic matter (0.0005 mm < diameter < 1 mm), and dissolved organic matter (Boling et al. 1975; Cummins 1974). Such materials are introduced either directly as litterfall or by lateral movement across the land surface. Moreover, allochthonous materials vary considerably with respect to their relative availability as food for macroconsumers and the time required for microorganism conditioning (Petersen and Cummins 1974; Sedell et al. 1975). As streams gradually change along a continuum from relatively small, shaded streams to larger, more-exposed channels, the ratios of various

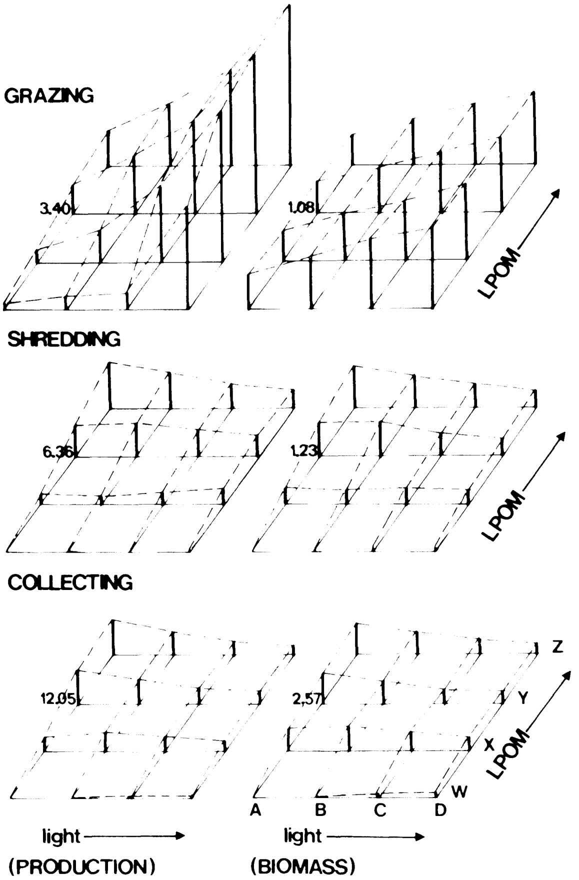

FIG. 8. Three-dimensional histograms representing grazing, shredding, and collecting process dynamics in terms of production ($g \cdot m^{-2} \cdot yr^{-1}$) and mean biomass ($g/m^2$) in response to energy inputs. Scaling is relative to Version I of the standard run, i.e., coordinates (A, Y). Dotted lines are for visual aid only. LPOM represents large particle detritus.

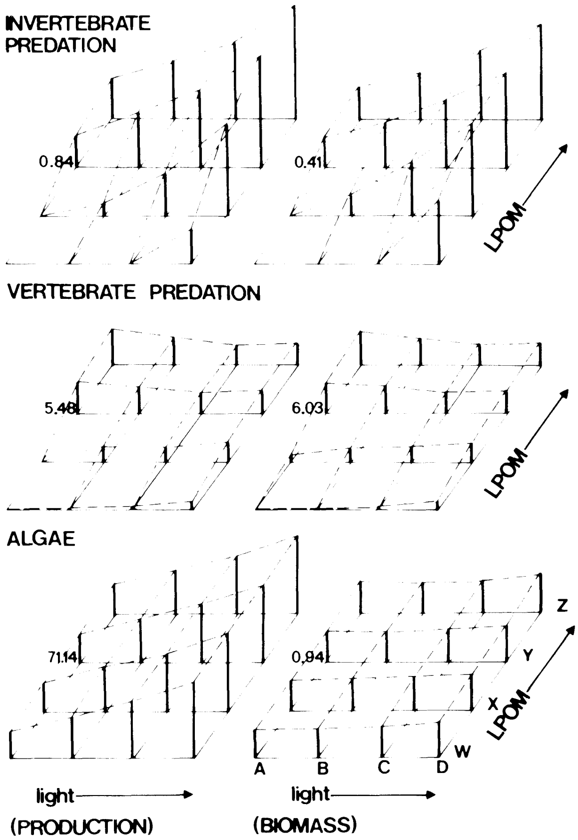

FIG. 9. Three-dimensional histograms representing invertebrate predation, vertebrate predation, and periphyton (ALGAE) process dynamics in terms of production ($g \cdot m^{-2} \cdot yr^{-1}$) and mean biomass ($g/m^2$) in response to energy inputs. Scaling format is the same as given in Fig. 8.

allochthonous inputs to the input of solar energy tend to change in a predictable way characteristic of geographical location. Therefore, we are interested in identifying general hypotheses that relate lotic dynamics to energy inputs within the context of the current continuum theory. For this purpose, the stream model can help by examining the behavior of biological processes relative to energy inputs.

Figures 8 and 9 illustrate fine-resolution behavior of the stream model relative to selected schedules of solar radiation and allochthonous organic matter (LPOM). Model behavior is summarized in terms of annual production and mean biomass, and the values were derived from Table 2 and similar tables of output. Each illustration is presented as a 3-dimensional histogram with the extremities connected by dotted lines to aid in interpretation. Inputs of solar radiation include the Berry Creek schedule (A), the hypothetical schedule (C), one half the daily intensity of the hypothetical schedule (B), and full sunlight (D); relative to total annual radiation, A < B < C < D. In this case, full sunlight is a constant intensity above which there is no effect on rates of primary production (>26,000 lux). Inputs of LPOM include the Watershed-10 schedule of the standard runs (Y), one third the Watershed-10 schedule (X), double the Watershed-10 schedule (Z), and no allochthonous material (W); therefore, W < X < Y < Z. Values in each graph are scaled relative to Version I of the standard run, i.e., coordinates (A, Y); Version II is represented by coordinates (C, Y).

Mean biomass involved in the process of grazing increases with an increase in light energy, but is unaffected by the different LPOM schedules (Fig. 8). However, the corresponding annual production increases with increasing LPOM, the mechanism of which is not intuitively obvious. An analysis of families of growth curves similar to those illustrated in Figs. 6 and 7 indicates that an increase in grazer production channels into predation rather than into the maintenance of a larger biomass. An increase in biomass associated with predation is stimulated through the effect of LPOM on the processes of shredding and collecting (Figs. 8 and 9). In the absence of predation, the energy involved in the maintenance of a primary macroconsumer process is relatively high, i.e., the proportion of energy lost through respiration is high. Therefore, grazer production (assimilation minus respiration) tends to increase with an increase in predator pressure because a smaller proportion of energy goes for maintenance. The conspicuous difference between grazer production for schedules C and D at 0 LPOM is primarily related to food resource (periphyton production) during the period of the year when daylengths are relatively long and shading by riparian vegetation is most pronounced. The relatively high periphyton production channels into predator production and biomass through the process of grazing, an effect that feeds back to the grazing process by increasing the production to biomass ratio.

Several other aspects of Figs. 8 and 9 require discussion. First, model behavior indicates that an increase in light energy enhances periphyton production, but has relatively little effect on periphyton biomass. In this case, the increase in production is simply consumed by the process of grazing, a response discussed in an earlier paper (McIntire 1973). This behavior suggests that periphyton biomass is a relatively poor index to a lotic system's ability to support grazing. Second, the response of shredding and collecting to increasing light energy at a relatively high input of LPOM requires explanation. The processes of shredding and collecting are regulated primarily by predation and life history phenomena (emergence) with the Y and Z detritus schedules. At maximum light (schedule D), grazer production is relatively high as noted above, and this production supports a relatively high production and biomass for the process of invertebrate predation (Fig. 9). Since shredding and collecting are regulated by predation rather than food resources, biomasses and annual production rates associated with these processes decrease with increasing pressure from predation as the input of solar energy increases.

In general, model behavior indicates that the response of a biological process to different energy inputs depends on the mechanisms that regulate that process. If a process is regulated by food supply (resource limitation), its annual production tends to increase as pressure from predation increases, while mean biomass may or may not be affected appreciably. In contrast, an increase in predation tends to decrease both mean biomass and annual production in processes regulated primarily by predation and life history phenomena.

Changes in energy inputs along a continuum from shaded, headwater streams to larger, more-exposed streams can be conceptualized roughly as a trajectory from coordinates (A, Y) or (A, Z) to say, (D, W) or (D, X) of the grids in Figs. 8 and 9. Other coordinates on the grid represent energy inputs of an unusual nature or perhaps inputs more characteristic of man-related perturbations. For example, the vicinity of (A, W) or (A, X) could represent a clear-cut watershed in which a narrow strip of vegetation was allowed to remain intact along the stream channel, and (D, Z) could represent an exposed channel receiving organic effluents from domestic or industrial activities. In any case, relative to the annual production rate, model behavior indicates that shredding, collecting, and vertebrate predation decrease slightly and grazing and invertebrate predation increase along the hypothetical trajectory; primary production also increases, but mean periphyton biomass changes very little.

Coarse-resolution dynamics

The hierarchical structure of the stream model (Figs. 1 and 2) provides an excellent opportunity to explore ecosystem dynamics at different levels of organization. In the previous sections, we were concerned primarily with the fine-resolution dynamics of the biological processes represented in the model. With appropriate changes in model structure, processes of grazing, shredding, collecting, invertebrate predation, and vertebrate predation theoretically can be decomposed even further into subsystems which may be examined relative to their level behavior or mechanistically in terms of their subsystems. In fact, most ecologists feel more comfortable with levels of resolution finer than those represented in the stream model. However, we have carefully avoided preoccupation with such detail by design, and prefer, instead, to investigate model behavior at levels of resolution coarser than those mentioned above, i.e., at the levels of herbivory, detritivory, primary consumption, predation, and the entire ecosystem. This approach is pursued because of our contention that ecosystem theory can be developed more rapidly at this time by the generation and examination of hypotheses relative to biological organization above the population level.

An example of coarse-level resolution model behavior is given in the form of responses to the grid of energy inputs (Figs. 10 and 11). Again, production represents the total, net elaboration of tissue per unit time, 1 yr in this case, regardless of the fate of that tissue. Production equations in terms of herbivory (h), detritivory (d), primary consumption (pc), and predation (p) are:

$$\mathrm{Prod(h)} = \mathrm{GPP} - R_a - R_g; \tag{37}$$

$$\mathrm{Prod(d)} = A_s + A_{c\text{-}a} - R_s - R_c; \tag{38}$$

$$\mathrm{Prod(pc)} = \mathrm{GPP} + A_s + A_{c-a} - R_a - R_g - R_s - R_c; \tag{39}$$

$$\mathrm{Prod(p)} = A_i + A_{v-pc} + A_{v-dft} - R_i - R_v. \tag{40}$$

In these expressions, the symbols refer to gross primary production (GPP); assimilation associated with processes of shredding (A_s), and invertebrate predation (A_i); and respiration associated with periphyton

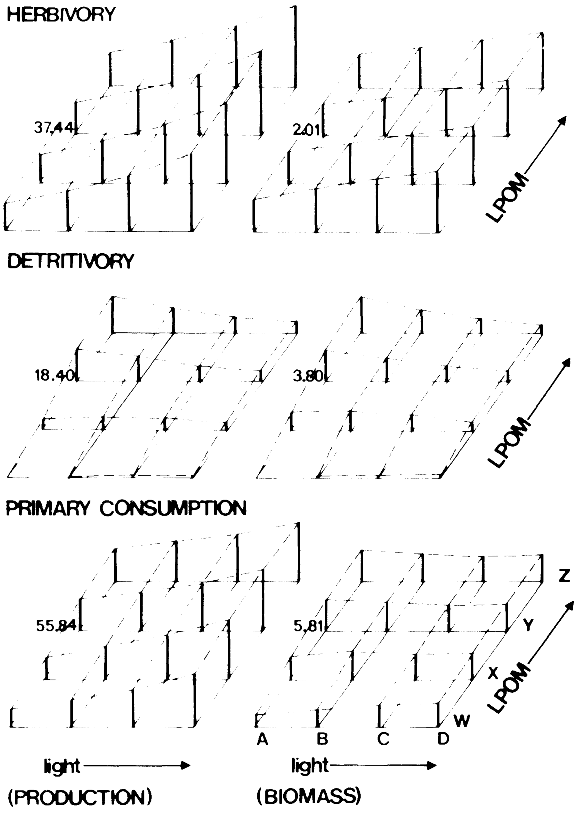

FIG. 10. Three-dimensional histograms representing herbivory, detritivory, and primary consumption process dynamics in terms of production (g · m^{-2} · yr^{-1}) and mean biomass (g/m^2) in response to energy inputs. Scaling format is the same as given in Fig. 8.

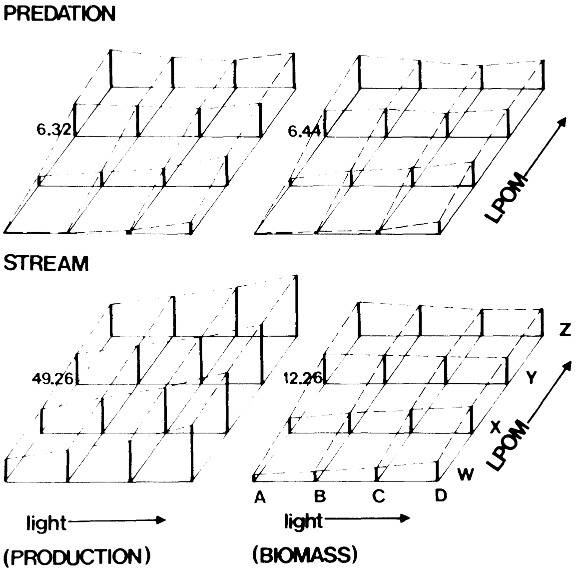

FIG. 11. Three-dimensional histograms representing predation and total stream process dynamics in terms of production (g · m^{-2} · yr^{-1}) and mean biomass (g/m^2) in response to energy inputs. Values for total stream do not include nonperiphytic microbial production (*$A_b - R_b$) or biomass. Scaling format is the same as given in Fig. 8.

processes (R_a) and processes of grazing (R_g), shredding (R_s), collecting (R_c), invertebrate predation (R_i), and vertebrate predation (R_v). Assimilation by collecting (A_{c-a}) includes only allochthonous organic material that does not originate from tissue elaborated within the system. For example, while the assimilation of shredder feces (allochthonous origin) is included in the term A_{c-a}, assimilation of grazer feces (periphyton origin) is excluded. The amount of total collector assimilation that is additive in Eqs. 38 and 39 is derived from only a part (F_{c-a}) of the available food supply. Here,

$$F_{c-a} = \text{Mech-FPOM} + S_f + [(S_f + \text{Mech-FPOM})/(\text{Total FPOM})](1 - b_{3c})C_c, \qquad (41)$$

where Mech-FPOM is mechanical transfer from LPOM, S_f is FPOM (feces) generated by shredding, and the other term represents that proportion of collector feces originally derived from shredder feces and Mech-FPOM. The latter is calculated from the consumption rate (C_c) and assimilation efficiency (b_{3c}) for the process of collecting. These complications arise from the fact that the process of collecting can reconsume its own feces. Assimilation by vertebrate predation is restricted to the assimilation resulting from consumption of primary consumer biomass (A_{v-pc}) and drifting material (A_{v-dft}). In its present form, the model treats drift as an input from outside the system; the emergence rates of grazing, shredding, collecting, and invertebrate predation are used as an index to this input (Eq. 24).

In the model, microbial decomposition of allochthonous material is expressed by rates of respiration associated with the various detrital components. Therefore, Eqs. 38 and 39 are theoretically incomplete, relative to natural streams, as the model does not monitor this microbial production and biomass. However, model behavior for detritivory and primary consumption is reported here in terms of these equations (Fig. 10), and problems associated with estimates of microbial production and biomass are discussed relative to total ecosystem behavior (Eqs. 42–46).

The process of herbivory responds to changes in the light schedule but is relatively unaffected by the LPOM schedule (Fig. 10). The model predicts that biomass for herbivory (periphyton biomass plus grazer biomass) and production associated with herbivory both increase with an increase in light energy. Interestingly, the patterns of production and biomass are similar to corresponding patterns for periphyton and grazing, respectively (Figs. 8 and 9). In other words, periphyton processes dominate the production pattern and grazing dominates the pattern of biomass. An analysis of growth curves analogous to Eqs. 32–36 indicates that herbivory is regulated primarily by light and nutrient resources.

Pattern in the process of detritivory as expressed by Eq. 38 is simply the summation of corresponding patterns in shredding and collecting, as the latter processes are additive (Figs. 8 and 10). In the absence of LPOM, detritivory is identical to collecting. At relatively low inputs of light energy and LPOM, e.g., coordinates (A, X) and (B, X), the process is mostly regulated by mechanisms that control collecting: food limitation, life history phenomena (emergence), and predation. However, at LPOM schedules Y and Z and at coordinates (D, X), detritivory is regulated about equally by mechanisms controlling shredding and collecting, i.e., predation and emergence. As noted earlier, an increase in light energy generates additional predator pressure on shredding and collecting. At LPOM schedule X, the relative importance of predation increases more rapidly in the regulation of collecting than shredding as the input of solar energy increases from schedules A through D. As a result, production associated with shredding actually increases slightly with increasing light energy while the process is still regulated primarily by food limitation and emergence. In contrast, the degree of predator regulation is sufficient to cause a decrease in production associated with collecting as the input of light energy increases from schedules B through D. Consequently, there are corresponding changes in the relative importance of shredding and collecting in relation to the regulation of detritivory.

Production dynamics of primary consumption as expressed by Eq. 39 are regulated primarily by mechanisms that control periphyton dynamics. In this respect, primary consumption is similar to herbivory. Relative to annual production and mean biomass, the summation of herbivory and detritivory generate the patterns of primary consumption (Fig. 10). The values are additive because there is an absence of energy exchange between herbivory and detritivory in the form of macroconsumption of living tissue. Annual production associated with primary consumption increases with an increase in total solar radiation, whereas the mean biomass involved in the process is relatively unaffected by either the light or LPOM schedules.

While production dynamics of primary consumption are related to the input of solar energy, the process of predation (Eq. 40) is more closely associated with the LPOM schedules (Fig. 11). Also, the dynamics of predation depends in part on the competition weighting factor (b_4 of Eqs. 29 and 30), a parameter that needs further investigation. Relative to annual production, processes of invertebrate and vertebrate predation are not additive. At a low input of solar energy (schedules A and B) and b_4 value of 0.8, predation is regulated mostly by mechanisms controlling vertebrate predation, but at high levels of solar energy (schedules C and D), the relative importance of mechanisms controlling invertebrate predation increases to about one third of those regulating vertebrate predation. At 0 or low LPOM inputs (schedules W and X), annual production and mean biomass increase with increasing solar energy, but at schedules Y and Z values are not affected appreciably by the different light schedules. At the higher LPOM and light schedules, the relatively high production associated with grazing channels into invertebrate predation which effectively competes with vertebrate predation for food resources. Hence, production associated with invertebrate predation increases, while corresponding production for vertebrate predation decreases. The process of predation therefore exhibits relatively little variation at LPOM schedules Y and Z.

The concept of stream productivity is ambiguous and usually means the capacity of a body of water to produce organic matter in some particular form, a product of interest (Ivlev 1945), or is used as a synonym for "rate of production" of an arbitrarily selected group of organisms of special interest to the investigator (Odum 1971). For our purpose, we define the rate of production for the total stream ecosystem as

$$\mathrm{Prod(S)} = \mathrm{GPP} + A_d - \mathrm{CR}, \tag{42}$$

where GPP represents the rate of gross primary production, A_d is the rate of assimilation for the biomass involved in the processing of allochthonous organic materials, and CR is the rate of community respiration. In terms related to the stream model,

$$A_d = A_s + A_{c-a} + A_{v-dft} + {}^*A_b, \tag{43}$$

and

$$\mathrm{CR} = R_a + R_g + R_s + R_c + R_i + R_v + R_b. \tag{44}$$

Here, ${}^*A_b$ represents the assimilation rate for microbes processing allochthonous detritus, R_b is the rate of respiration for microbes not associated with the periphyton, and the other terms are defined above. In the model, A_s and A_{c-a} are conceptualized as direct assimilation of LPOM and FPOM, respectively, and it is assumed that the assimilation of microbial biomass by shredding and collecting is negligible. In reality, insects involved in processing LPOM and FPOM often derive a significant amount of energy from microbial populations associated with detritus. Therefore, it is important to emphasize that the application of Eq. 43 to a field problem requires a partitioning of shredder and collector assimilation into direct detrital assimilation and microbial assimilation, as the latter is not additive to ${}^*A_b$.

If the system is in a steady state (i.e., no net change in mean biomass), Prod(S) also is equal to the summation of losses resulting from emergence and export of living tissue elaborated within the system. That is,

$$\mathrm{Prod(S)} = \mathrm{EM}_g + \mathrm{EM}_s + \mathrm{EM}_c + \mathrm{EM}_i + \mathrm{E}_a + \mathrm{M}_v + \mathrm{E}_f, \tag{45}$$

where EM_g, EM_s, EM_c, and EM_i are emergence and export for processes of grazing, shredding, collecting, and invertebrate predation; E_a is export of periphyton; M_v is the natural mortality associated with vertebrate predation, treated by the model as export; and E_f represents the export of feces derived from tissue elaborated within the system. If we assume that collecting is confined to the consumption of F_{c-a} only, this process is treated the same as shredding; and

$$\mathrm{E}_f = \mathrm{G}_t + \mathrm{I}_f + \mathrm{V}_f, \tag{46}$$

where G_t, I_f, and V_f are equal to the fecal losses from grazing, invertebrate predation, and vertebrate predation, respectively. However, if some of the FPOM consumed by collecting is assumed to originate from material elaborated within the system, then G_f, I_f, and V_f represent only feces not consumed by collecting, and an additional term must be included to represent elaborated material ultimately lost as feces by collecting. Actually, GPP and $^*\mathrm{A}_b$ account for most of the total stream production, and model behavior indicates that collector production derived from living tissue elaborated within the system (total FPOM $-$ F_{c-a}) is usually $<2\%$ of this total.

There are probably no reliable estimates of the rate of production for a total stream ecosystem receiving sizeable inputs of allochthonous organic materials. The principal difficulty comes with field measurements of microbial production resulting from decomposition of allochthonous detritus. The stream model accounts for all terms of Eqs. 42–46 except $^*\mathrm{A}_b$. Therefore, the grids representing the total stream as an ecosystem in Fig. 11 do not include the part of microbial production and biomass associated with the processing of allochthonous organic material. This deficiency obviously affects the pattern of annual stream production, but probably has relatively little effect on the corresponding pattern of mean biomass. The latter is affected relatively little by energy inputs when the LPOM input is either the Y or Z schedules (Fig. 11). The pattern of annual stream production calculated from Eq. 42 minus microbial production from the processing of allochthonous material ($^*\mathrm{A}_b - \mathrm{R}_b$) is similar to the corresponding pattern of periphyton production (Fig. 9), as the turnover ratio of the periphyton greatly exceeds that of the macroconsumers involved in detritivory. Consequently, it is of considerable interest to know the effect of ($^*\mathrm{A}_b - \mathrm{R}_b$) on the annual pattern of stream production, particularly since the dynamics of organisms with relatively short generation times and a small biomass essentially determine the rate of production at the ecosystem level.

Odum (1957) assumed that the average production:assimilation ratio for bacteria is 9%. Jones (1975) suggested that this efficiency could be an underestimate for bacteria, but it may be a reasonable estimate for the entire heterotrophic microbial assemblage. We have recalculated stream production for the grid using Eq. 42 while assuming efficiencies (production:assimilation) of 9% and 18% (Fig. 12). In general, inclusion of the assumed values for $^*\mathrm{A}_b$ simply increases total stream production and demonstrates an intuitively obvious relationship between total energy inputs and the rate of production at the ecosystem level. Of more interest, however, is the pattern of production along a hypothetical trajectory from the neighborhood of (A, Y) or (A, Z) to (D, W) or (D, Z), the trajectory corresponding to energy inputs along the river continuum. Values in both grids of Fig. 12 change relatively little along the hypothetical trajectory. Therefore, the model predicts that total stream production per unit area, as defined in Eq. 42, remains essentially the same along a continuum of energy inputs corresponding to gradual changes from low light–high allochthonous inputs (stream order 1 or 2) to high light–low allochthonous inputs (ca. stream order 4). If we accept the hypothesis that annual stream production changes relatively little along the continuum, large local deviations from the mean rate of production in natural streams may represent a system's response to an unusual perturbation (e.g., introductions of toxic substances, nutrients, or organic wastes, canopy removal by logging activities, channelization). Unfortunately, the constant-production hypothesis is difficult to test in the field because of the problem of measuring heterotrophic microbial production.

Dynamics relative to canopy removal

Systems analysis is sometimes used to predict ecosystem dynamics in relation to alternative management strategies and man-caused perturbations (e.g., Watt 1968). Although the stream model was not developed specifically for such simulations, its structure is sufficient to provide some interesting hypotheses concerning the effects of logging practices on lotic ecosystems in the Pacific Northwest. In this section, we present the simulation of stream dynamics following the management practice of clear-cut logging and slash burning.

In western Oregon, streams draining undisturbed, forested watersheds often contain very low concentrations of nitrogen, a nutrient that tends to limit the process of primary production at relatively high illumination intensities (>25,000 lux). In the example presented here, we assume that nitrate is the limiting nutrient and base parameter estimation on recent experiments of S. V. Gregory (*personal communication*). More specifically, we have changed Eq. 2 of McIntire (1973) to the form

$$\mathrm{P}_{\max \mathrm{N}} = \begin{cases} 1.0 \text{ if } \mathrm{N} \geqslant 0.5 \\ \mathrm{c}_1 + \mathrm{c}_2\mathrm{N} \text{ if } 0.001 \leqslant \mathrm{N} \leqslant 0.5 \\ \dfrac{\mathrm{c}_3\mathrm{N}}{1 + \mathrm{c}_3\mathrm{N}} \text{ if } \mathrm{N} < 0.001 \end{cases} \tag{47}$$

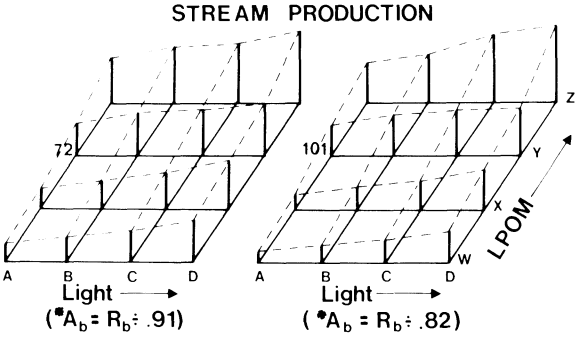

FIG. 12. Three dimensional histograms representing total stream production ($g \cdot m^{-2} \cdot yr^{-1}$) in response to energy inputs, assuming production-assimilation ratios of 9% ($*A_b = R_b \div 0.91$) and 18% ($*A_b = R_b \div 0.82$) for nonperiphytic microorganisms. Scaling format is the same as given in Fig. 8.

where N is the nitrate concentration (mg/litre) and c_1, c_2, and c_3 are parameters estimated from Gregory's data. In our present representation, c_1, c_2, and c_3 assume values of 0.21, 1.58, and 268.36, respectively; and U_{max} of Eq. 1 in McIntire (1973) is rescaled to a value of 2.945 $O_2 \cdot m^{-2} \cdot h^{-1}$. The nitrate schedule used for the standard runs and for runs illustrated by the grid (Figs. 8–12) was obtained from the data of Fredriksen (1971) for a small stream draining an undisturbed watershed in the H. J. Andrews Experimental Forest. Mean nitrate concentration for this schedule is 0.004 mg/litre.

The practice of clear-cut deforestation usually accelerates the addition of nutrients to streams (Likens and Bormann 1972), while canopy removal along a stream channel tends to increase the quantity of solar energy absorbed by the stream. Other effects of timber harvest on lotic ecosystems can include deposition of inorganic and organic materials as well as mechanical damage to the channel and its biota. The simulation presented in this section reflects the effects of nitrate enrichment and canopy removal, but does not include possible effects of mechanical damage or changes in suspended load. The nitrate schedule during logging and slash burning also was obtained from Fredriksen (1971) and represents measurements during a 3-yr period for a stream subjected to the effects of clear-cut logging. Input of solar energy is represented by light schedule D of the grid (full sunlight). Initial conditions for the simulation are state variable values derived from the Berry Creek light schedule and the Watershed-10 detritus schedule, coordinates (A, Y) of the grid (Version I of the standard run).

The simulation represents a period of 6 yr beginning ≈6 mo after logging is initiated and end ≈5 yr after slash burning is completed; it is assumed that burning occurs near the end of year 1. At the beginning of the run, light schedule D is introduced, and the input of LPOM is reduced to one fourth of the Watershed-10 schedule (schedule Y). These inputs remain the same during the simulation of a 3-yr period, while the nitrate concentration varies according to the data of Fredriksen (1971). The nitrate schedule corresponds to changes in concentration that occurred in a natural stream during 10 mo of logging and for 2 yr after slash burning. The last 3 yr are assumed to be a recovery period with a nitrate schedule the same as that used in the standard runs. During the so-called recovery period, the light schedule remains the same (full sunlight), but the schedule of allochthonous inputs is altered to reflect the upstream dynamics of an undisturbed area. For the last 3 yr of simulation, LPOM and FPOM are introduced in the amounts equivalent to corresponding exports in Version I of the standard run. LPOM input follows the relative values of the Y schedule, while FPOM is introduced at a constant daily rate.

Following slash burning in the fall of year 1, nitrate concentration increases from a mean of 0.004 mg/litre to ≈0.06 mg/litre for 4 mo during year 2. During the 2nd year after burning, an even larger introduction of nitrate occurs, reaching a maximum of ≈0.4 mg/litre in October of year 2 and continuing until June of year 3. The 2 input pulses of nitrate following slash burning roughly correspond to the seasonal pattern of rainfall and discharge rate.

Annual system dynamics for Version I of the standard run are compared with the dynamics for the log and burn simulation in Table 5. The combination of high nutrient concentration along with a saturating illumination intensity generates conspicuous changes in state variable dynamics during years 1, 2, and 3. Gross primary production and periphyton biomass increases sharply following nitrate enrichment, the latter reaching maxima of 5.8 and 41.3 g/m^2 during September of year 2 and February of year 3, respectively. A 9-mo period of relatively high primary production from September of year 2 through May of year 3 begins ≈1 yr after slash burning and represents the time of greatest perturbation to the principal state variables of the system. However, the model also predicts that annual gross primary production in year 1, before the period of greatest nitrate input, is 3× higher than the annual value for Version I. Biomasses associated with periphyton processes, grazing, and invertebrate predation are relatively high and exhibit strong oscillations in years 2 and 3. Biomass related to vertebrate predation gradually increases to a maximum of 31.0 g/m^2 in May of year 3. Assuming $*A_b = *R_b/0.91$, total stream production (PROD [S] − 9%) increases from ≈72 to 362 $g \cdot m^{-2} \cdot yr^{-1}$ during logging and burning. This 5-fold increase obviously represents a significant deviation from the predicted production along our hypothetical continuum trajectory discussed in the previous section. Furthermore, there is a conspicuous loss of detrital biomass during year 1, and the system as a whole becomes temporarily autotrophic during years 2 and 3.

TABLE 5. Comparison of the annual dynamics of selected variables for Version I of the standard run with corresponding dynamics for the log and burn simulation. The acronyms refer to gross primary production (GPP), large particulate organic material (LPOM), fine particulate organic material (FPOM), community respiration (CR), emergence and export (EM & E), periphyton processes (ALGAE), grazing (GRAZE), shredding (SHRED), collecting (COLLECT), invertebrate predation (I-PRED), vertebrate predation (V-PRED), and total stream production assuming production:assimilation efficiencies of 9% and 18% for heterotrophic microorganisms, PROD (S) – 9% and PROD (S) – 18%, respectively. Mean biomass is expressed as g/m^2 and all other variables (except GPP/CR) as $g \cdot m^{-2} \cdot yr^{-1}$

Variables	Standard Run Version I	Log and burn simulation					
		Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Inputs:							
GPP	71.1	219.5	599.4	567.0	186.7	186.5	187.1
LPOM	480.8	126.1	123.9	125.7	79.5	80.1	80.1
FPOM	. . .	. . .	. . .	. . .	79.9	79.9	79.9
Losses:							
CR	374.7	329.2	477.3	430.4	249.3	245.9	245.5
EM & E	178.6	152.3	212.5	297.9	106.5	101.3	101.7
GPP/CR	0.19	0.67	1.26	1.32	0.75	0.76	0.76
Biomass change	−1.4	−135.9	+33.5	−35.7	−9.7	−0.7	−0.1
Mean biomass:							
ALGAE	0.94	1.26	2.12	4.59	1.15	1.15	1.15
GRAZE	1.08	3.17	10.33	5.54	2.89	2.82	2.80
SHRED	1.23	0.81	0.33	0.34	0.30	0.27	0.26
COLLECT	2.57	2.09	0.55	0.43	0.69	0.83	0.76
I-PRED	0.41	0.84	1.59	2.68	0.59	1.04	1.20
V-PRED	6.03	8.32	9.62	21.19	8.41	4.42	3.70
Consumer production:							
GRAZE	3.40	23.73	61.51	69.08	13.87	15.85	16.44
SHRED	6.36	2.83	1.52	1.85	0.81	0.89	0.92
COLLECT	12.05	9.96	2.64	2.08	3.11	3.81	3.50
I-PRED	0.84	3.89	9.30	17.00	1.30	2.38	2.40
V-PRED	5.48	11.17	15.61	18.03	1.29	2.78	3.04
PROD(S) – 9%	72.45	140.38	358.98	361.76	103.63	108.86	109.54
PROD(S) – 18%	100.74	158.12	381.65	383.23	118.50	123.50	124.42

After nutrient enrichment is terminated, the system requires ≈2 yr to assume new steady-state dynamics. However, the new steady-state dynamics are different than the corresponding dynamics of Version I (Table 5), as the new energy inputs are full sunlight and one third the Y schedule of allochthonous material. These inputs are similar to expected inputs for a stream section flowing through a meadow. The annual rate of gross primary production for year 6 is only ≈30% of that during the period of maximum perturbation, but is still ≈2.6× greater than the annual rate for Version I. During the recovery period, the system again becomes heterotrophic, but GPP/CR at the new steady state (0.76) is 4× greater than that for Version I (0.19). Immediately after enrichment (year 4), biomass for vertebrate predation begins to decrease, and by year 6 it is only ≈60% of the mean biomass in Version I. Total stream production also decreases during the recovery years, but the new steady-state value for PROD(S) – 9% in year 6 is ≈110 $g \cdot m^{-2} \cdot yr^{-1}$, 51% higher than that for Version I.

In summary, the principal effects of logging and burning predicted by the model include: (1) an increase in the rate gross primary production; (2) an increase in the rate of production for the entire ecosystem; (3) an increase in stream autotrophy; (4) a temporary increase in biomass associated with vertebrate predation followed by a decline to a biomass lower than that exhibited before perturbation; (5) an increase in biomasses related to processes of grazing and invertebrate predation; and (6) a decrease in biomasses for shredding and collecting. Whether or not vertebrate predator biomass will eventually decrease in a natural stream to the relatively low level predicted by the model is uncertain. One field study concerned with the effect of logging practices on fish populations (Aho 1976) reported a significant increase in production after clear-cut logging, an increase that roughly corresponds to model behavior during years 1 through 3. However, long-term follow-up studies after logging and burning have not been reported in the literature. In the model, biomass for vertebrate predation at the new steady state after logging is related to the competitive interaction with invertebrate predation, and this interaction can be adjusted by the b_4 parameter (Eqs. 29 and 30). In the real world, the interaction obviously depends on the genetic information in the system, a property that can be investigated with the model by examining effects of parameter changes and possibly, alternative model structures. Actually, biomass associated with predation as a total process is only slightly less in year 6 than in Version I, and if invertebrate predation is eliminated, production associated with vertebrate predation is 15% higher in year 6 than in Version I.

DISCUSSION

We have used output from the stream model to illustrate one way of viewing lotic ecosystems at different levels of organization. Whether or not such theoretical constructs as herbivory, detritivory, primary consumption, and predation provide a significant contribution to the theory of lotic ecosystems is uncertain without debate and further consideration of alternative concepts. In particular, we have found some of our colleagues uncomfortable with the concept of herbivory as a total process, while the process of detritivory was intuitively more acceptable. Yet, at this level of resolution, these processes are analogous, the only important difference being related to whether the energy resource is generated within the system (autochthonous production) or outside the system (allochthonous input). Notwithstanding such difficulties, output from the stream model indicates that some kind of hierarchical structure can provide a valuable theoretical basis for generation and testing hypotheses in ecosystem research.

Examples of hypotheses generated by the stream model in its present form include:

1) The annual rate of production per unit area for the entire lotic ecosystem does not change appreciably along the continuum from small, headwater streams to larger rivers.
2) In shaded sections of lotic systems receiving high LPOM inputs, the process of grazing is limited primarily by food resources, whereas shredding and collecting are regulated by export or emergence patterns and predation; the process of predation is food-resource limited under these conditions.
3) If a process is limited by food resources, its annual production tends to increase as pressure from predation increases, whereas the mean biomass associated with the process may change very little or actually decrease.
4) If a process is regulated primarily by predation and export or emergence, an increase in pressure from predation tends to decrease both annual production and mean biomass.
5) Periphyton biomass is a poor predictor of both primary production and the ability of a stream ecosystem to support grazing.
6) If macroconsumers are removed from a stream section, microbial activity will process most allochthonous inputs, and the rate of detrital export will not exhibit a large increase.

Much of the benefit that comes with ecosystem modeling unfortunately cannot easily be put into publishable form. In our experience, the stream model stimulated new kinds of questions that, while fundamental to the understanding of system dynamics, were completely obscured before modeling by preoccupation with detail. The model also provided a conceptual basis for specialists to relate their knowledge to the dynamics of the entire ecosystem, a benefit that was derived long before the model was programmed on a computer. Another important benefit was, paradoxically, the occasional failure of the model to generate output even remotely related to reality. These failures, in the absence of programming errors, represented explicit expressions of our lack of understanding of natural streams. Bizarre model behavior therefore forced us to consider alternative parameters and model forms, as such monuments to ignorance were difficult to ignore or rationalize.

The stream model provided the stimulus that led to a mathematical expression for total stream production (Eq. 42). Even if this expression eventually is replaced by something more useful, the model will have accomplished our purpose by suggesting that the concept of production at the ecosystem level be clarified and put into explicit form. Moreover, the need for reliable field measurements of microbial production is reemphasized by the relative importance of $^*A_b$ in Eq. 43. In this paper, we have only speculated on the effect of $(^*A_b - R_b)$ in relationship to total stream production. If our general model form is adopted as a conceptual framework for field research, this expression must be included in production equations representing processes of detritivory and primary consumption to complete the theoretical production dynamics of our hierarchical structure.

The change in genetic information in a system with perturbation is a serious problem associated with process modeling. What are the constraints within which input variables must remain in order to induce realistic behavior with a given model structure? In other words, at what point does model structure break down and no longer provide adequate representation? In its present form, the stream model provides reasonable representation, relative to our objectives, of processes in small, undisturbed and some disturbed streams without vascular hydrophytes. However, we attempted to simulate the dynamics of processes in the outdoor artificial streams located on the Weyerhaeuser Company's tree farm (near Couger, Washington) and ran into difficulties. In these systems, temperature and flow are constant, periphyton biomasses are relatively high, the process of grazing is not (apparently) food limited, and processes of shredding and vertebrate predation are absent. Adequate representation was obtained only after the inclusion of a "self-crowding," density-dependent function for grazing, whose biological basis was uncertain. This experience emphasized the importance of considering alternative model forms as well as different sets of parameters.

In conclusion, it should be emphasized that we did not develop the stream model to optimize the prediction of process dynamics in a particular stream. Instead, we preferred to use the model to help understand fundamental dynamic interrelationships and dependencies among biological processes in lotic ecosystems. From our perspective, the hierarchial model, at least to some degree, has served this purpose, and to this extent, it provided us with more than just a fascinating academic exercise.

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