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The dynamics of small lotic ecosystems: a modeling approach[1]

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With 8 figures and 3 tables in the text

Introduction

> "The whole subject of rivers, now ordinarily though not philologically subsumed in limnology, appears to him as a marvelous foreign territory explored by workers whose audacity is admirable in view of the difficulty of getting a theoretical grasp of the subject."
>
> G. E. Hutchinson 1963.

Since the above quotation was written, much progress has been made toward the understanding of fundamental physical and biological processes that regulate the dynamics of relatively small, flowing-water ecosystems. Contributions in the general area of detrital processing by micro-organisms and macro-invertebrates have been particularly impressive (e.g., Minshall 1967; Kaushik & Hynes 1968; Triska 1970; Cummins 1973; Lush & Hynes 1973). Moreover, the recent application of general systems theory in ecology has provided a stimulus for holistic conceptualizations of lotic ecosystems and for the translation of certain biological and physical concepts into the mathematical domain (e.g., McIntire 1973; Boling et al. 1974 b).

In January 1973, an interdisciplinary group of scientists at Oregon State University (U.S.A.) initiated discussion sessions that were primarily concerned with the development of a general conceptual model of small lotic ecosystems. This group included specialists interested in insect ecology and physiology, fisheries biology, primary production and phycology, detrital processing, data synthesis, and model development. After a series of meetings that extended through the summer of 1973, the group adopted a strategy for modeling streams of the Coniferous Forest Biome (U.S. Analysis of Ecosystems, I.B.P.). Briefly, the stream model was: (1) to develop as an expansion of an earlier model of periphyton dynamics (McItire 1973); (2) to emphasize the total stream subsystem and its couplings with the terrestrial and hydrologic subsystems of the coniferous forest ecosystem; (3) to be concerned primarily with the major processes and functional groups in lotic systems rather than the dynamics of individual species populations; (4) to have a Universe-Coupling structure (Klir 1969) that consists of a hierarchical, modular system of stream processes; and (5) to be programmed in FLEX 2, a general model processor patterned after Klir's General Sequential Systems Paradigm (Overton 1972).

This paper reports the preliminary results of an attempt to construct a total stream model that mathematically simulates the dynamics of small flowing-water systems in northwestern United States. The simulation runs were performed by the FLEX 2 processor implemented on a CDC 3300 computer operating under OS-3 at Oregon State University. The processor algorithm is a standard discrete time algorithm:

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$$\begin{cases} \mathbf{y}(k) = \mathbf{h}(\mathbf{x}(k)) \\ \mathbf{x}(k+1) = \mathbf{x}(k) + \Delta(k), \end{cases}$$

where k is a discrete time index; $\mathbf{x}(k)$ is a vector of state variables, $\mathbf{h}$ is an arbitrary functional vector of $\mathbf{x}$; $\mathbf{y}(k)$ is a vector of outputs at time k; and $\Delta(k)$ is a vector whose p-th element is defined as

$$\Delta p\,(k) = \sum_{i=1}^{n} f_{ip}\,(k) - \sum_{\substack{j=1 \\ j\neq 1}}^{n} f_{pj}(k).$$

Here,

$$f_{ij}(k) = f_{i,j}\,[k,\mathbf{x}(k),\mathbf{z}(k),\mathbf{M}(k),\mathbf{g}(k),\mathbf{s},\mathbf{b},\mathbf{r}],$$

where $\mathbf{z}(k)$ is a vector of input variables; $\mathbf{M}(k)$ is a matrix of required past values of $\mathbf{x}$ and $\mathbf{z}$; $\mathbf{g}(k)$ is a vector of intermediate functions; $\mathbf{s}$ is a vector of special, user-defined functions; and $\mathbf{b}$ and $\mathbf{r}$ are vectors of model parameters. This form provides for the automatic identity of Δ from a matrix of fluxes (f equations) representing the flows of a compartment model. The FLEX 2 model processor was developed under the direction of Dr. W. S. Overton, Oregon State University (Overton et al. 1973).

Model structure

Conceptually, we can view lotic ecosystems either holistically, as processors of inputs, or mechanistically, according to some Universe-Coupling structure (Overton 1972). Figs. 1 and 2 represent one possible hierarchical decomposition of a set of recognized lotic processes. This particular scheme is compatible with the set of processes composing the model currently under investigation. The small solid arrows indicate flows of materials into the system or subsystem, or between various processes within the system or subsystem, while the small dashed arrows represent couplings other than flows. For example, the dashed arrow external to the primary consumption subsystem (Fig. 2) could depict the effect of temperature on the behavior of that subsystem, and the internal dashed arrows from snail processes to the other processes could indicate competitive interactions for food resources.

The total stream system is composed of three subsystems, the autotrophic, heterotrophic, and nutrient processes. The autotrophic subsystem includes all processes, both autotrophic and heterotrophic, that are tightly coupled to the aquatic primary producers. In this subsystem, the principal state variable is the periphyton biomass. The structure of the autotrophic subsystem, its behavior in isolation, and its couplings with other subsystems were described in detail by McIntire (1973) and are not repeated here The nutrient subsystem eventually will contain state variables representing concentrations of various nutrients of interest. In our present version of the total stream model this subsystem is not elaborated, i.e., couplings with the nutrient subsystem are handled either as exports to or inputs from the environment. The heterotrophic subsystem consists of the primary consumption, predation, and detrital processes.

The primary consumption subsystem is composed of subsystems that represent processes associated with functional groups of organisms that feed on either periphyton or detritus or both. The process of grazing involves a flow of energy from the periphyton to a functional group of insects (grazers), the transfer of fecal material to the detrital subsystem, and energy losses to the environment through emergence and respiration (Fig. 2). The shredding and collecting processes include flows of energy from large particle detritus (LPOM) and from fine particulate organic matter (FPOM) to other functional groups of insects, the shredders and collectors, respectively. The transfer of fecal material to FPOM and the emergence and respiratory losses also are part of these processes. Snail processes are not part of the present version of the stream model, but will eventually include flows of energy from LPOM, FPOM, and periphyton to another functional group, an omnivorous snail. It should be emphasized that the couplings between the grazing, shredding, and collecting processes are indirect, representing the influence of nonselective predation.

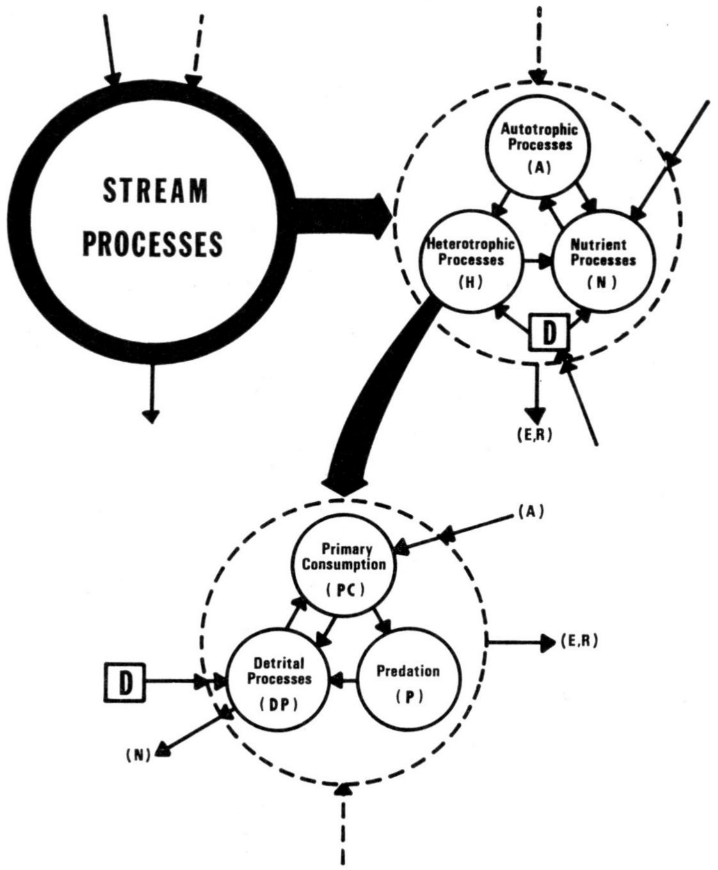

Fig. 1. The major subsystems of a stream ecosystem and the partitioning of the heterotrophic processes subsystem. Specification of the coupling variables among the subsystems allows independent development of their internal structure. Solid arrows represent flows of material, while dotted arrows indicate couplings other than flows. Symbols D, E, and R refer to allochthonous detritus, export (or emergence), and respiration, respectively.

The predation subsystem can be decomposed into vertebrate and invertebrate processes. Both functional groups of predators feed non-selectively on the grazers, shredders, and collectors; vertebrate predators also eat invertebrate predators. Both processes include flows of fecal material to FPOM, respiratory losses, and either mortality (vertebrate predator) or emergence (invertebrate predator). Natural mortality in the invertebrate predator as well as the grazer, shredder, and collector functional groups is considered as part of respiration (post-mortum decomposition). Invertebrate predation is not yet part of the working version of the total stream model.

The detrital subsystem includes FPOM (< 1 mm) processes and LPOM (> 1 mm) processes. Allochthonous organic matter is introduced as a table function (D) and is transferred to LPOM processes. A lag is introduced to represent the time it takes for micro-organisms to render this material suitable for animal (shredder) consumption.

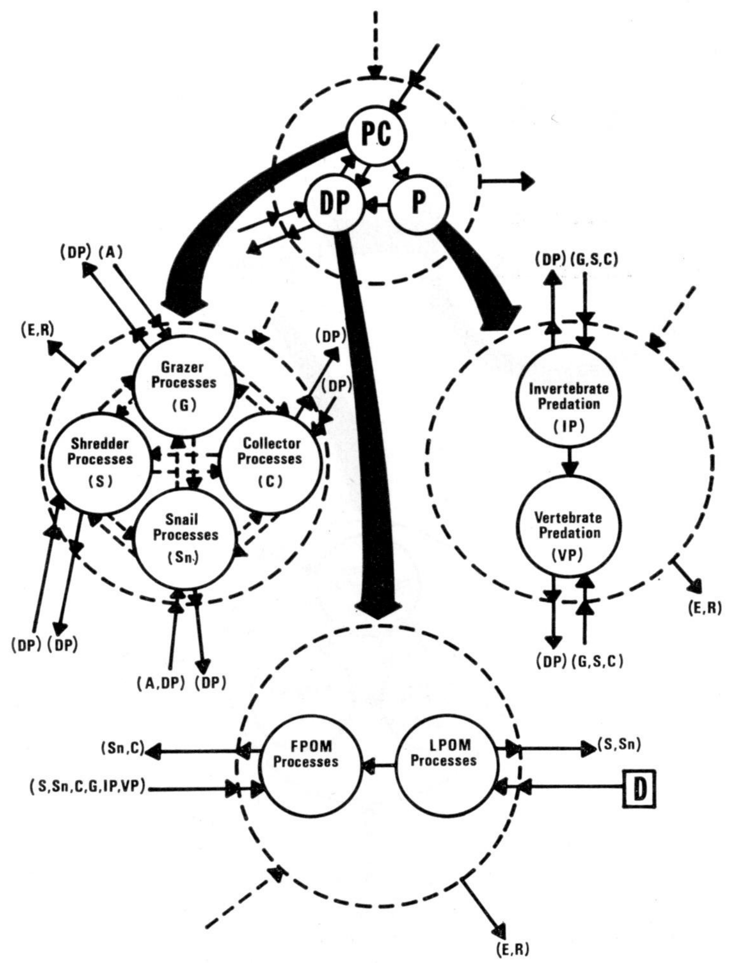

Fig. 2. Further elaboration of the heterotrophic processes subsystem. Solid arrows represent flows of material, while dotted arrows indicate couplings other than flows. Symbols D, E, and R refer to allochthonous detritus, export (or emergence), and respiration, respectively.

Losses of LPOM include transfer to shredding processes, respiration (decomposition), and mechanical transfer to FPOM processes. FPOM processes also receive inputs as fecal material and lose energy to collector and respiratory (decomposition) processes.

The present working version of the model also includes physical variables whose relationships to the system were described by McIntire (1973). More specifically, temperature and photoperiod vary seasonally as trigonometric functions of time, and light intensity and rainfall schedules characteristic of local conditions in western Oregon are introduced as table functions.

Process modeling

The biological basis for selection of the functional groups mentioned above has been discussed by McIntire (1968, 1973) and Cummins (1974). Grazers, shredders, and collectors each represent the total biomass of organisms at any instant of time involved in the consumption and processing of periphyton, LPOM, and FPOM, respectively. This approach is based entirely on an organism's activities, while taxonomic position is essentially ignored. If a particular species population consumes more than one food type during its life history, it is partitioned conceptually into the corresponding functional groups, depending on the instantaneous proportions of the population that are functionally distinct. These proportions each represent a biomass supported by a particular category of food resource — not fractions of the numerical abundance of the population. This convention gets around the problem of individual organisms feeding on several food categories simultaneously.

The broad, functional group approach adopted here represents a coarser resolution than the concept of paraspecies (Boling et al. 1974 a), which combines taxonomic species into groups that are similar to each other with respect to the system as it is modeled. The principal difficulty with our approach, aside from the usual problems of parameter estimation, is related to the evolutionary history of the real world system under consideration. As input variables are changed in the mathematical system (the model), the system will respond according to the set of rules (assumptions) governing the behavior of the processes involved, while in the real world, the system must posses the genetic capability or diversity to respond in the predicted manner. The limitations imposed by this constraint are not yet clear, while the analytical advantages of dealing with general processes instead of individual species populations in complex ecosystem models are substantial.

Process modeling requires a slightly different approach than modeling dynamics of individual species populations and paraspecies. If we consider the process of shredding, functional relationships and parameter estimates must be based on a synthesis of field and experimental data for an arbitrary number of species that engage in the processing of LPOM during all or part of their life history. Therefore, the representation of the process in the model can improve as the data base expands with additional field and laboratory observations. We are essentially after some mean representation of the total process at a level of resolution relevant to our particular model. For example, in the stream model we assume that the maximum relative rate of food consumption for shredders (C_{srmax}) at optimal food density and temperature is 0.7 g g^{-1} day^{-1}. This value is corrected for a particular food density and temperature at time k by the expression

$$C_{F,T}(k) = \left[\min\left(\frac{4.1F(k)}{1+3.4F(k)}, 1\right]\cdot\left[\min\left(\frac{0.20T}{1+0.17T}\right), 1\right]$$

where $C_{F,T}(k)$ is a value ranging from 0 to 1, F(k) is the food density (g m^{-2}) at time k, and T is the temperature (°C). Therefore, the food consumption rate for shredders at time k ($C_s(k)$) is the product of S(k), C_{srmax}, and $C_{F,T}(k)$, where S(k) is the shredder biomass (g m^{-2}) at time k. The rates of respiration ($R_s(k)$) and emergence ($E_s(k)$) for the shredder biomass at time k are

$$R_s(k) = S(k)\,[0.0296 + 0.00446T]$$

and

$$E_s(k) = S(k) \cdot P_{se} \cdot T_{fun}(k), \text{ where}$$

$T_{fun}(k)$ is a table function of values ranging from 0 to 0.03 day^{-1}, P_{se} is a scaling parameter, and the rates are expressed as g m^{-2} day^{-1}. The assimilation rate ($A_s(k)$) at time k (g m^{-2} day^{-1}) is the product of $C_s(k)$ and a parameter (P_{sa}) representing the proportion of consumption that is assimilated. An update on the shredder biomass at time k + 1 is therefore

$$S(k+1) = S(k) + \Delta_s(k), \text{ where}$$
$$\Delta_s(k) = \Delta A_s(k) - \Delta R_s(k) - \Delta E_s(k).$$

The processes of grazing and collecting are modeled in the same way with different parameter values. The process of vertebrate predation also is modeled in a similar manner with the exception that a mortality function is used instead of an emergence table function. Parameters were estimated from published and unpublished data evaluated during interdisciplinary group conferences at Oregon State University.

Analysis of model properties

An analysis of properties of the stream model is still in a preliminary stage. In this section, we present output from five simulation runs. These examples represent responses resulting from the manipulation of selected internal parameters, namely constants controlling the assimilation and emergence rates of the shredders, grazers, and collectors and the mortality and food consumption rates of the vertebrate predator (Tab. 1). In these cases, forcing functions and input parameters are identical. Functions expressing seasonal changes in light intensity, temperature, and photoperiod and the rainfall schedule are the same as those used in the model of periphyton dynamics (McIntire 1973). Input of allochthonous organic matter corresponds to data obtained for Watershed 10 at the H. J. Andrews Experimental Forest in the Oregon Cascade Mountains; current velocity is assumed to be 35 cm sec^{-1}.

Tab. 1. A list of parameter values for five different simulation runs. P_{sa} and P_{se} are the shredder assimilation and emergence parameters (see text), and P_{ga}, P_{ge}, P_{ca}, and P_{ce} are the corresponding values for the grazers and collectors. The mortality rate and maximum possible rate of food consumption for the vertebrate predator are designated by P_{pm} and P_{pc}, respectively.

Simulation run	P_{sa}	P_{se}	P_{ga}	P_{ge}	P_{ca}	P_{ce}	P_{pm}	P_{pc}
1	0.18	1.5	0.55	0.8	0.20	0.80	—	—
2	0.19	1.5	0.55	0.8	0.23	0.80	0.0025	0.030
3	0.19	1.5	0.40	0.8	0.23	0.80	0.0025	0.030
4	0.19	1.5	0.55	0.8	0.23	0.80	0.0050	0.028
5	0.18	0.8	0.55	0.8	0.20	0.35	0.0025	0.026

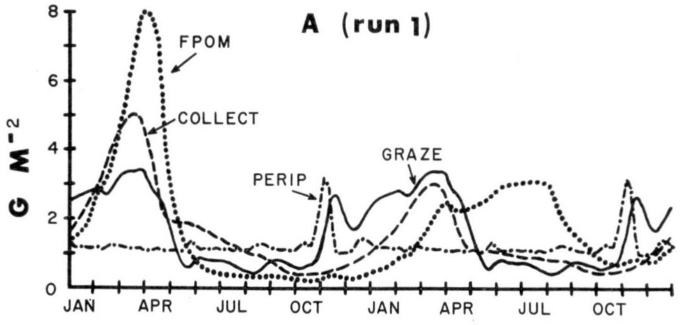

Fig. 3. Dynamics of the shredder (SHRED), collector (COLLECT), and grazer (GRAZE) and their food supplies (i.e., LPOM, FPOM, and PERIP, respectively) in the absence of predation (simulation run 1). Shredder emergence (EMERGE) and food (LPOM) in Fig. 4 are rescaled. Emergence rate expressed as g m^{-2} day^{-1} is equal to the ordinate value multiplied by 4 × 10^{-2}, and LPOM biomass is the ordinate value multiplied by 10^{2}.

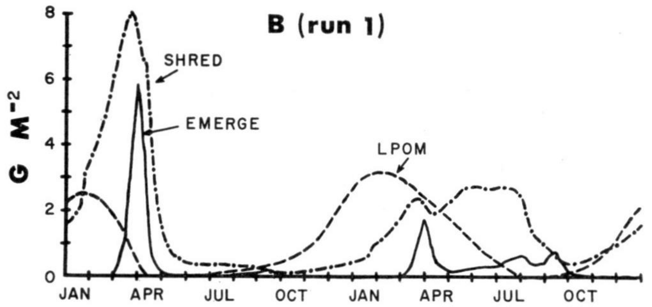

Fig. 4. Continuation of Fig. 3.

Simulation run 1 (Figs. 3 and 4) represents the response of the system without predation processes. Assimilation percentages of consumed food (Tab. 1) were 18 % (shredder), 55 % (grazer), and 20 % (collector). In this case, the grazer and its food source, the periphyton, each have the same annual dynamics, while the shredder and collector exhibit a stable behavior on a 2-year cycle. The 2-year cycles apparently result from a repeating, alternating change in the ratio of the shredder biomass to its food supply (conditioned LPOM) interacting with the pattern of shredder emergence. Since the dynamics of the collector are related to FPOM, collecting processes are coupled to shredder dynamics through the transfer of fecal material to FPOM.

In simulation run 2 (Fig. 5) assimilation percentages of the shredder and collector were increased slightly to 19 % and 23 %, respectively, and a vertebrate predator was introduced. In this case, the 2-year cycles do not occur. The predator is supported primarily by the grazing process, while the shredder and collector biomasses vary at relatively low levels. Run 3 (Fig. 6) represents an attempt to reduce the importance of the grazer in the system by decreasing the grazer assimilation percentage from 55 % to 40 % (Tab. 1). The results of this run were counter-intuitive. Instead of decreasing the prominence of the grazer in the system, the periphyton biomass increased to a high value which eventually generates a grazer biomass approximately four times higher than the maximum value obtained in run 2.

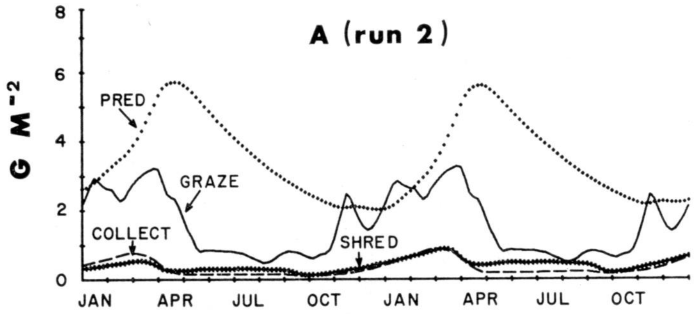

Fig. 5. Dynamics of the predator (PRED), grazer (GRAZE), shredder (SHRED), and collector (COLECT) in simulation run 2 and simulation run 3 (Fig. 6). Relevant parameter values are listed in Tab. 1.

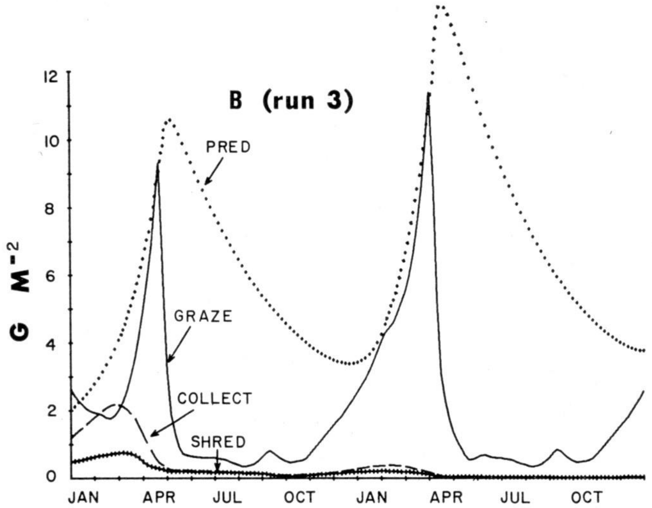

Fig. 6. Continuation of Fig. 5.

Simulation runs 4 and 5 (Figs. 7 and 8) demonstrate the effect of other changes in parameters on the relative importance of the shredding, grazing, and collecting processes. Parameters for run 4 are the same as those in run 2, with the exception that the predator mortality rate (P_{pm}) is increased to 0.005 g g^{-1} day^{-1} and its maximum allowable rate of food consumption (P_{pe}) is decreased slightly to 0.028 g g^{-1} day^{-1} (Tab. 1). With these changes, collector and grazer production and biomass values fluctuate within similar ranges, whereas such values for the shredder are relatively low. Also, the predator exhibits greater seasonal fluctuations in run 4 than in run 2. In run 5 shredder and collector emergence parameters (P_{se} and P_{ce}) are decreased, and P_{pc} is decreased to 0.026 g g^{-1} day^{-1}. These changes produce an increase in the production and biomass of the shredder (Fig. 8) and less seasonal variation in the predator.

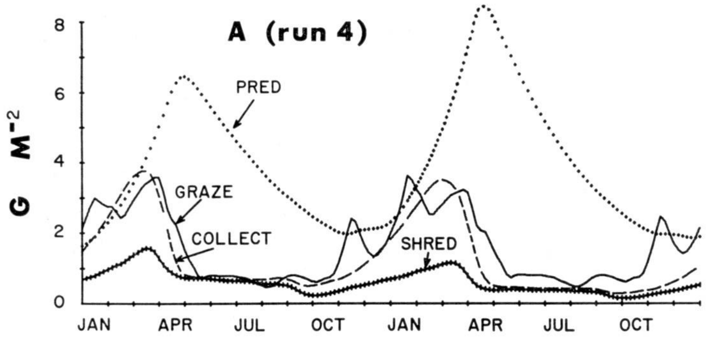

Fig. 7. Dynamics of the predator (PRED), grazer (GRAZE), shredder (SHRED), and collector (COLLECT) in simulation run 4 and simulation run 5 (Fig. 8). Relevant parameter values are listed in Tab. 1.

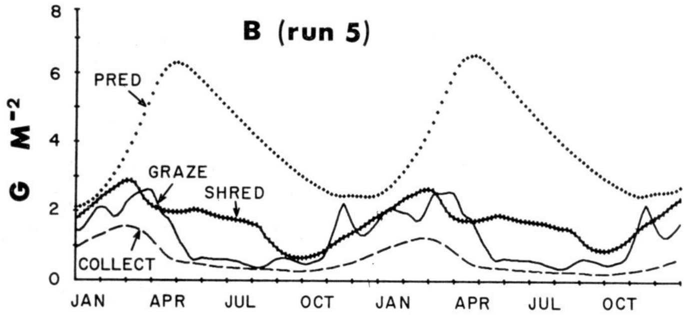

Fig. 8. Continuation of Fig. 7.

Output from runs 1, 2, 4, and 5 generates values for production and biomass of the different functional groups that are more or less similar to such values measured for natural streams with the same inputs. Selected aspects of the holistic behavior of the system for run 5 are summarized in Tab. 2. The model simulates the processing of about 496 g organic matter m^{-2} yr^{-1} while exporting 143 g m^{-2} yr^{-1}. Because of the relatively high input of allochthonous material, the system manifests heterotrophic properties, e.g., the mean ratio of gross primary production to community respiration is 0.14. A more detailed look at dynamics of individual functional groups (Tab. 3) reveals annual turnover rates of 5.25 (Shredder), 4.27 (Grazer), 4.80 (Collector), and 0.98 (Predator). In this particular case, the shredder consumes the most food and loses the most energy through

Tab. 2. Energy budget representing the holistic behavior of the stream model for simulation run 5.

Property	Additions (g m^{-2} yr^{-1})	Losses (g m^{-2} yr^{-1})
Gross primary production	72	
Allochthonous inputs	559	
Community respiration		496
Export and emergence		143
Total	631	639

Tab. 3. Selected output from the stream model obtained for simulation run 5 (see Tab. 1 for relevant parameter values). Sources of food consumed by shredders, grazers, and collectors were LPOM, periphyton, and FPOM, respectively.

Property	Shredder	Grazer	Collector	Predator
Production (g m^{-2} yr^{-1})	9.15	5.33	2.93	3.93
Mean biomass (g m^{-2})	1.74	1.25	0.61	4.00
Turnover (times yr^{-1})	5.25	4.27	4.80	0.98
Emergence (g m^{-2} yr^{-1})	3.49	0.73	0.83	—
Food consumption (g m^{-2} yr^{-1})	314.79	53.97	75.27	11.93
Biomass consumed by predator (g m^{-2} yr^{-1})	5.29	4.45	2.19	—

the process of emergence, while the predator receives over twice as much energy from the shredding and grazing processes as it does from the collecting process.

Future work with the stream model will include: (1) the addition of the snail and invertebrate predator processes, (2) an attempt to improve the representation of certain physical variables, (3) the elaboration of the nutrient processes subsystem, and (4) a more complete analysis of model properties. The snail and invertebrate predator processes will introduce competitive interactions, while the nutrient processes subsystem and physical variables will establish couplings with the terrestrial subsystem of the Coniferous Forest Biome. In particular, the representation of stream flow can be improved to reflect seasonal changes characteristic of the Pacific Northwest. In this region, heavy rainfall during late fall and the winter months often results in freshets that greatly increase the transport of both inorganic and organic materials. Such catastrophic impacts have a devastating effect on biological processes in small streams and tend to reset these systems to relatively low biomass levels. Therefore, the behavior of the model with the manipulation of forcing functions which introduce seasonal changes in flow is of considerable interest. Furthermore, the sensitivity and stability of the system with different sources and quantities of energy inputs needs to be investigated and related to various physical and biological processes in natural streams.

Conclusions

The construction of the stream model has provided the opportunity to synthesize the results of numerous field and laboratory studies of lotic processes and to evaluate the existing data base while establishing priorities for future research. The model also allows us to test the compatibility of selected sets of process measurements. Preliminary analysis of model behavior indicates that insights into stream processes can be gained by examining system dynamics after various parameter changes. We therefore conclude that further expansions and analysis of the model are warranted. The hierarchical, modular structure of the model (i.e., the Universe-Coupling structure) is particularly suited to accommodate additional complexity imposed by such expansions, as properties of subsystems can be investigated in isolation as long as the integrity of the couplings is maintained.

Acknowledgements

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