

Modeling Benthic Algal Communities: An Example from Stream Ecology

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I. INTRODUCTION

A. Modeling and Models

From a scientific perspective, modeling is the process of putting structure on knowledge, and a model is some kind of statement of relationships. Therefore, all research scientists are modelers in the sense that they are involved in generating and updating conceptual models that evolve from field and laboratory studies. In some cases, it is useful to transform conceptual models into integrated numerical systems by mathematical formalization. In ecology, mathematical modeling is the translation of an ecological system into mathematical form and the subsequent investigation of the mathematical system, usually by computer simulation.

The overall goals of model building are description and prediction. In particular, mathematical models can be used for simple forecasting (e.g., the weather) or for scientific purposes: (1) for hypothesis generation; (2) to synthesize the results of field and laboratory studies; (3) to evaluate a data base; and (4) to set priorities for future research. The process of model building usually includes the selection and classification of variables, equation writing and parameterization, simulation, and the comparison of model output with the behavior of the natural system under consideration (model testing). In this chapter, we discuss the use of mathematical modeling for the scientific investigation of benthic algal assemblages and related variables in lotic ecosystems.

B. Examples of Benthic Algal Models from Stream Ecology

Most mathematical models that include algae as a biological component focus on the water column of marine or freshwater ecosystems and simulate patterns of primary production rather than successional trajectories of individual taxa. However, models that represent benthic algae in some way often are similar in mathematical form to models that simulate the production dynamics of planktonic algae (Straškraba and Gnauck, 1985).

One of the first models related to the production dynamics of benthic algae was based on experimental data from laboratory streams (McIntire, 1973). This model represented benthic algae and associated heterotrophic microorganisms as a quasi-species, and there was no attempt to partition the assemblage into individual algal taxa. Later, the model became the primary production module of a stream ecosystem model (McIntire *et al.*, 1975; McIntire and Colby, 1978). In 1974, the Desert Biome (I.B.P.) issued a progress report (Wlosinski, 1974) that described the mathematical details of another stream ecosystem model. In this model, the benthic plant assemblage was divided into four taxonomic groups: two algal species [*Cladophora glomerata* (L.) Kütz. and *Chara vulgaris* L.], all diatom

species collectively, and a vascular plant (*Potamogeton pectinatis* L.). The desert stream model was eventually used to examine compatibility between model behavior and changes in a natural stream at different levels of taxonomic resolution (Wlosinski and Minshall, 1983). Another modeling approach to the study of benthic algae in streams partitioned the dynamics of attached diatom assemblages into the processes of immigration, reproduction, growth, and emigration (Stevenson, 1986; Stevenson and Peterson, 1991). In this case, models were used to examine alternative mechanisms that could account for changes in cell density.

C. Objectives

In small streams, benthic algae may provide the only significant source of autochthonous organic material, particularly when conditions are unsuitable for the establishment of bryophytes or aquatic vascular plants. Experimental work with benthic algae in lotic ecosystems usually has involved the isolation of periphyton assemblages from other components of the ecosystem and the subsequent manipulation of selected environmental variables in some kind of controlled system (see Lamberti and Steinman, 1993, for review). Although such assemblages consist of complex aggregations of microorganisms, the research approach is frequently aut-ecological in the sense that the periphyton assemblage is the focus of the study and is viewed as a single unit or quasi-species, while all other variables are treated as part of the environment. Individual experiments of this design are more meaningful when they are an integral part of a sequence of related studies that systematically examine relationships between benthic algae and other components of the ecosystem. This chapter is primarily concerned with the role of mathematical modeling in the design, evaluation, interpretation, and synthesis of such studies during an ongoing research program.

Specifically, the objectives of this chapter are (1) to describe a modeling approach for the integration of experimental and observational studies of benthic algae in flowing water; (2) to illustrate the approach by examples of output from an existing model; (3) to present some hypotheses that correspond to the model output; and (4) to summarize the kinds of insights and research directions that models of benthic algal assemblages can provide.

II. A MODELING APPROACH

Benthic algae, in their natural surroundings, do not live in isolation. Individual taxa are subjected to complex interactions with abiotic and biotic components within an algal assemblage, and the assemblage as a whole changes its structural and functional attributes in response to direct

and indirect relationships with components outside the boundaries of the assemblage. In the field or laboratory, an individual, replicated experiment is usually designed to examine effects of only one or at most a few variables in systems that maintain the same environment with respect to the variables not under investigation. The role of modeling, as presented in this chapter, is to provide a conceptual and structural basis for a series of experiments that couple together in a way that will help optimize the relevancy of each individual experiment to the objective questions under consideration.

First, we propose a research approach that includes: (1) identification of research goals and specific objectives; (2) system conceptualization, a process that involves the definition of system variables and their coupling structure, and the determination of appropriate levels of resolution relative to time, space, and biological organization; (3) translation of the biological concepts into mathematical form and the subsequent investigation of the mathematical model in relation to the objective questions under consideration; (4) model testing by comparisons of model behavior with observational data from the field; (5) generation of new hypotheses that are based on priorities revealed by modeling and field observations; (6) the design and performance of experiments to examine new hypotheses; (7) modification of the mathematical model and system conceptualization based on the latest experimental results; and (8) reevaluation of specific objectives and research progress in relation to the level of understanding generated by the most recent round of experimental work and modeling. In summary, this approach is iterative and synthetic, and involves the careful interplay between modeling, field observations, experimentation, and a periodic update of specific objectives in relation to an overall research goal.

In the following sections, we emphasize steps (5) and (7) by presenting an example of an ongoing study of plant-herbivore interactions in lotic ecosystems. In the example, an existing model of biological processes in small streams is updated (step 7) to represent and synthesize the results of recent experiments with benthic algal assemblages. Next, behavior of the modified stream model is used to generate new hypotheses (*i.e.*, step 5 in the next iteration of studies) that relate to direct and indirect relationships between benthic algae and other components of lotic ecosystems.

III. THE MCINTIRE AND COLBY STREAM MODEL

Results of experimental studies at Oregon State University provided the basis for an updated version of an existing lotic ecosystem model (McIntire and Colby, 1978; McIntire, 1983). The original version of the model, referred to here as the McIntire and Colby stream model or M & C model, was developed to generate hypotheses, to synthesize the

results of field and laboratory research, and to set priorities for future research. The model has also been used for the integration and evaluation of our latest laboratory stream research with benthic algae and selected herbivores (Steinman and McIntire, 1986, 1987; Steinman *et al.*, 1987a; Lamberti *et al.*, 1987, 1989; DeNicola and McIntire, 1990a,b, 1991; DeNicola *et al.*, 1990) and for the generation of new hypotheses related to the processes of primary production, grazing, shredding, collecting, and predation in lotic ecosystems.

The M & C model is an expansion of the lotic periphyton model described by McIntire (1973). Briefly, the M & C model represents biological processes that are usually active in most streams. From this perspective, stream ecosystems are conceptualized as two coupled subsystems, the processes of primary consumption and predation (Fig. 1). The Primary Consumption subsystem is composed of all processes associated with the direct consumption and decomposition of both autotrophic organisms and detritus, including the production dynamics of the autotrophic organisms collectively. Primary Consumption has two subsystems that represent the processes of herbivory and detritivory. The Herbivory subsystem consists of all processes associated with the production and consumption of benthic algae within the system, that is, the processes of primary production and grazing; whereas Detritivory includes processes related to the consumption and decomposition of detrital inputs, namely, shredding, collecting, and microbial decomposition. The Predation subsystem is composed of the processes of invertebrate and vertebrate predation, processes concerned with the transfer of energy among primary, secondary, and tertiary macroconsumers. In this chapter, we focus on the dynamics of benthic algal assemblages, a component of the Herbivory subsystem, and model output is investigated in relation to changes in parameters, inputs, and the internal structure of the Primary Production and Grazing subsystems.

IV. AN UPDATED HERBIVORY SUBSYSTEM MODEL

A new Herbivory subsystem model was developed by the isolation and modification of the Herbivory subsystem of the M & C model. The structure of the isolated subsystem model was changed and expanded to help synthesize and interpret the results of some recent experiments with benthic algae in laboratory streams.

In the first version of the M & C model, the Herbivory subsystem contains subsystems that represent the processes of primary production and grazing (Fig. 1). The state variable in each of these subsystems represents the biomass that is involved in the corresponding process at any time. New data from the experimental work (Steinman and McIntire, 1986, 1987; Steinman *et al.*, 1987a; Lamberti *et al.*, 1987, 1989) allow the state vari-

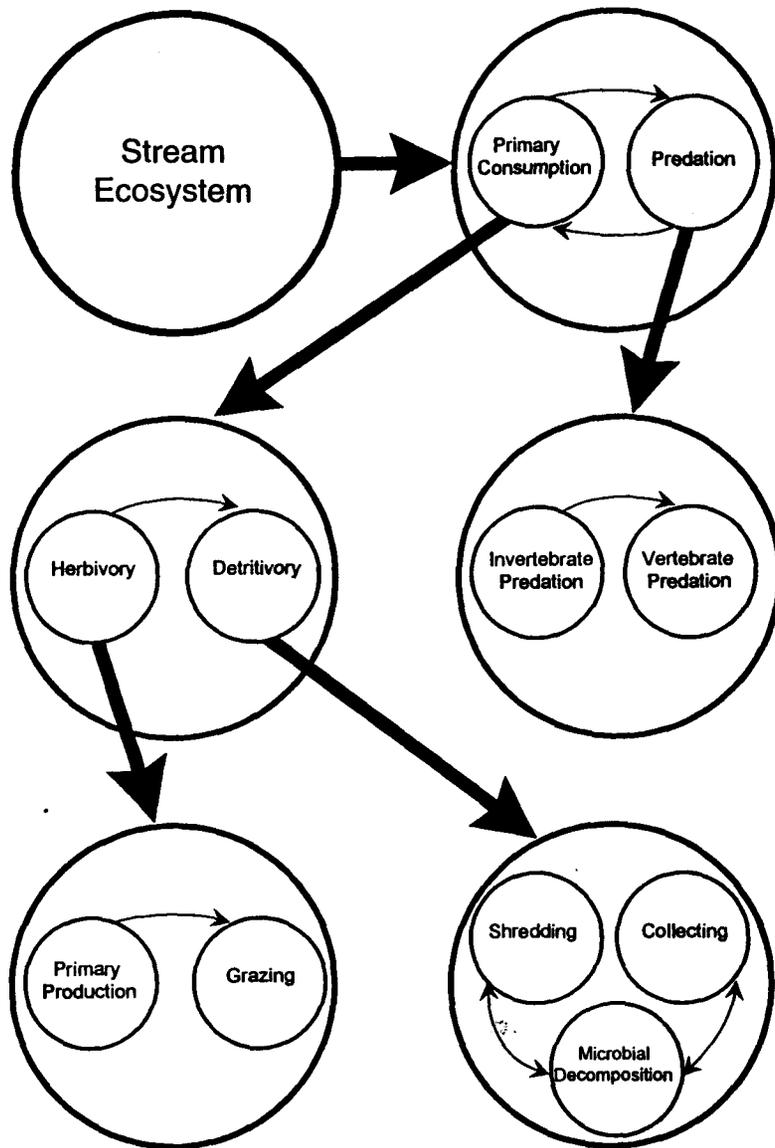


FIGURE 1 Schematic representation of a lotic ecosystem showing the hierarchical decomposition of the Primary Consumption and Predation subsystems and the structure of the Herbivory and Detritivory subsystems. Circles represent biological processes, and small arrows between processes indicate directions of energy flow.

able inside the Primary Production subsystem to be partitioned into three new state variables that are related to the taxonomic composition and successional stage of the algal assemblage. In this case, the state variables represent the collective biomass of filamentous and coenobitic chlorophytes, diatoms, and cyanobacteria, with each functional group including associated heterotrophic microorganisms. In addition, feeding experiments by Lamberti *et al.* (1989, and unpublished data) provide a preliminary basis for establishing a mathematical relationship between the relative abundance of the three algal functional groups and the food consumption rates and assimilation efficiencies associated with the process of grazing.

In the updated Herbivory subsystem model, primary production is modeled according to the mathematical relationships described by McIntire and Colby (1978). This means that calculations of photosynthetic rates, respiratory expenditures, and export losses are based on the total periphyton biomass (i.e., rates are not calculated separately for individual algal functional groups). The algorithm that incorporates the new information into the Herbivory subsystem model has the following characteristics:

1. The new primary production calculated for each day is partitioned among the algal functional groups according to these rules:
 - (a) If the irradiance is $<30 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ or the periphyton biomass (ash-free dry weight) is $<2 \text{ g m}^{-2}$, the new production is 100% diatoms (Fig. 2A);
 - (b) If irradiance is >30 and $<150 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, the new production is partitioned by a linear relationship between light energy and the proportions of diatoms and cyanobacteria, reaching a maximum of 19% cyanobacteria at $50 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ when the algal biomass is $>2 \text{ g m}^{-2}$ (Figs. 2A and 2B);
 - (c) If the irradiance is $>150 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, chlorophytes, diatoms, and cyanobacteria are all part of the new production in proportions that are determined by linear relationships with irradiance and algal biomass (Figs. 2A, 2B and 2C); and
 - (d) If irradiance is $>300 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, the algal assemblage eventually will assume a composition of 48% diatoms, 48% chlorophytes, and 4% cyanobacteria when the algal biomass is $>25 \text{ g m}^{-2}$ (Figs. 2A, 2B and 2C).
2. The assimilation efficiency and a food quality limiting factor associated with the process of grazing are a function of the proportion of diatoms in the algal assemblage according to these rules:
 - (a) Assimilation efficiency is a linear function of the proportion of diatoms in the assemblage, varying between 0.53 (48% diatoms) and 0.73 (100% diatoms); and

- (b) A food quality limiting factor expressed as a proportional adjustment of the food demand (i.e., the food consumption rate with an optimum diet and unlimited food supply) is a linear function of the proportion of diatoms in the assemblage, varying between 0.28 (48% diatoms) and 1.00 (100% diatoms). The rate of grazing is adjusted to the composition of the algal assemblage by multiplying the food demand by the food quality limiting factor (for more detail, see Section V,C).

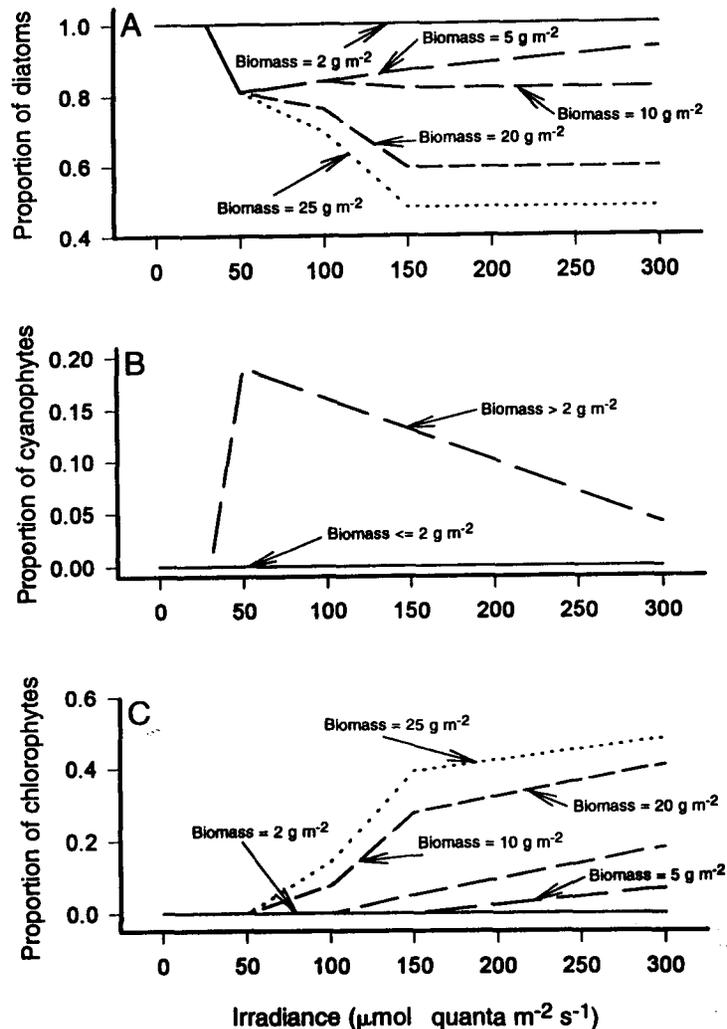


FIGURE 2 Relationships between irradiance and the proportions of diatoms (A), cyanophytes (B), and chlorophytes (C) in the daily increment of biomass generated by pri-

In summary, the new version of the Herbivory subsystem model tracks the successional trajectory and production dynamics of the algal assemblage, as well as the response of grazers to corresponding changes in food quality and quantity. This representation also expresses the feedback control that the process of grazing has on successional changes within the algal assemblage.

V. BEHAVIOR OF THE HERBIVORY SUBSYSTEM MODEL

Behavior of the Herbivory subsystem model in isolation was examined first by obtaining output from a standard run, with and without the process of grazing. This output then was compared to runs designed to investigate the sensitivity of selected variables to changes in the light energy input schedule and to parameters that control the rate of food consumption. Input tables for a standard run were the same as input for the standard run of the M & C model, that is, the Berry Creek light schedule and allochthonous inputs in Fig. 3 of McIntire and Colby (1978). Such tables provide for the simulation of a small, low-order stream receiving annual allochthonous organic inputs of 473 g m^{-2} . The corresponding light schedule generates maximum energy inputs in the spring, with very low inputs during the summer months when the stream is assumed to be shaded by a dense canopy of riparian vegetation. The parameters under investigation, explained in the following section, are a multiplier that controls the light input schedule, a parameter that provides the algal assemblage with varying degrees of protection from the effects of grazing, and five parameters that control the food consumption rates for the process of grazing. For each change in parameters or input tables, the model is allowed to run at a daily time resolution until it exhibits a new steady-state behavior. The simulation period required for the system to reach a steady state may vary between a few years to as long as 40 years, depending on how the changes affect system dynamics. Since input tables correspond to a period of one year, a steady state usually means that state variables have repeatable annual trajectories. However, in some cases the system exhibits repeatable cycles of 2, 3, or even 4 years. Output from each simulation run is usually displayed as a plot of state variables for a 1-year period or is reported as values that are part of an annual energy budget (e.g., an annual production rate or annual mean biomass for functional groups of organisms).

A. Standard Run

Output from a standard run indicates that diatoms dominate the algal assemblage when the system is in a steady state and the process of grazing is in equilibrium with available food resources (Fig. 3). In this case, the model predicts that the algal biomass turns over about 63 times each year,

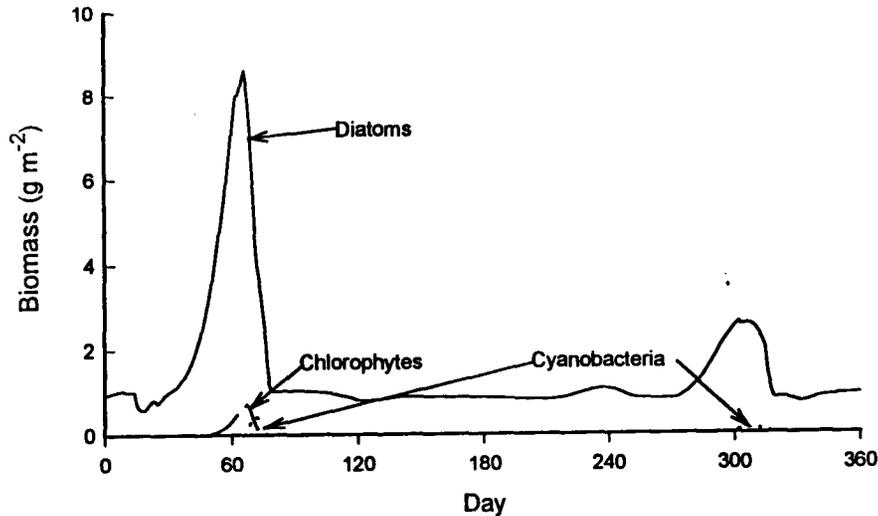


FIGURE 3 Steady-state, seasonal dynamics of state variables representing algal functional groups of the updated version of the Herbivory subsystem model. The graph depicts a run with standard input tables (see text) with grazing. Model is based on 360-day years and 30-day months with the beginning of January as Day 1 and the end of December as Day 360.

and that annual gross primary production, expressed as organic matter, is 106 g m^{-2} , of which green algae and cyanobacteria contribute only 3%. With the standard set of inputs, annual production of herbivore biomass is 6.6 g m^{-2} (organic matter), with a corresponding turnover of 3.4 times per year. If light energy inputs are increased from shaded conditions to full sunlight, the annual mean biomass of grazers increases, whereas annual mean periphyton biomass decreases slightly (Fig. 4A). Also, annual primary production, annual turnover of periphyton biomass, and annual grazer production increase with corresponding increases in light energy (Figs. 4B and 4C), whereas annual turnover of grazer biomass exhibits relatively little change (Fig. 4C). Although the algorithm allows the green algae to reach high biomasses at high inputs of light energy, this does not happen in the presence of grazing, as high rates of algal consumption restrict the flora to a diatom assemblage that is more characteristic of an early stage of succession.

In the absence of grazing (i.e., grazer biomass remains zero), the standard run predicts that the annual mean algal biomass is 20 g m^{-2} , and that all three algal groups are prominent in the spring and fall of the year (Fig. 5). Without grazing, annual gross primary production is 530 g m^{-2} , of which the diatoms, chlorophytes, and cyanobacteria account for 73.3%, 19.3%, and 7.4% of this total, respectively. Corresponding annual turnover

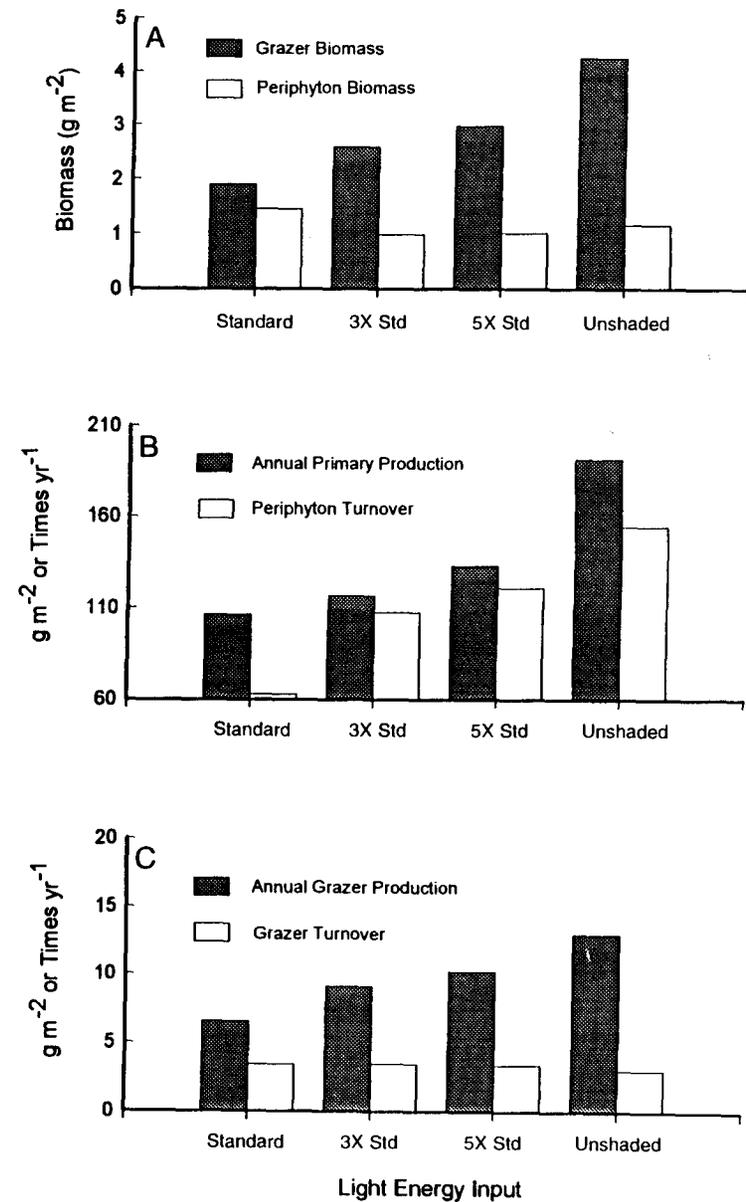


FIGURE 4 Mean grazer and periphyton biomass (A), annual gross primary production and periphyton turnover (B), and annual grazer production and turnover (C) associated with the updated Herbivory subsystem at four levels of light energy input. Levels of irradiance are a standard table of inputs (see text), 3 \times each value in the standard table, 5 \times each value in the standard table, and a constant value above the light saturation intensity for photosynthesis (unshaded).

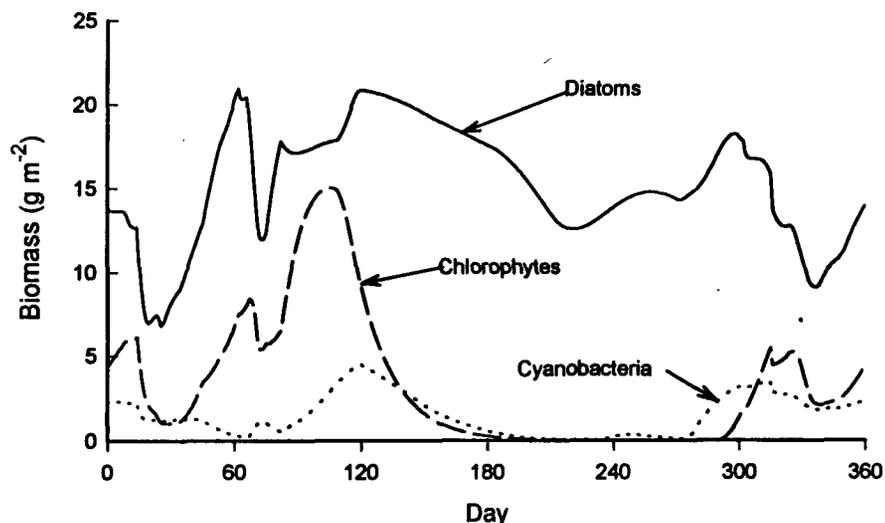


FIGURE 5 Steady-state, seasonal dynamics of state variables representing algal functional groups of the updated version of the Herbivory subsystem model. The graph depicts a run with standard input tables (see text) without grazing. The time scale is the same as in Fig. 3.

numbers for these groups are 14.4, 16.1, and 19.4 times per year. Furthermore, annual energy losses from the algal assemblage, without grazing, partition into 41.8% respiration, 41.9% particulate export, and 16.3% dissolved organic matter (DOM) leakage. In contrast, the standard run with grazing indicates that 62.6% of annual gross primary production and 73.1% of annual net primary production are consumed by herbivores; corresponding losses from respiration, particulate export, and DOM leakage are 14.4%, 20.4%, and 2.6% of gross primary production, respectively. In the latter case, diatoms lose 62.8% to grazing, whereas chlorophytes lose only 49.5%, a manifestation of the effects of the food quality limiting factor on consumption rates.

B. Algal Refuge

Definition: The algal refuge is the algal biomass, expressed as g m^{-2} organic matter, below which the consumption rate by the process of grazing is equal to zero.

A parameter controls the algal refuge level for the Herbivory subsystem. The ecological justification for this parameter is related to (1) differences in feeding efficiencies among consumers with different patterns of behavior and mouthpart morphologies (Steinman *et al.*, 1987a); (2) differences in food availability that result from substrate heterogeneity (DeNi-

cola and McIntire, 1991); and (3) different susceptibilities of algal growth forms to grazing (Steinman *et al.*, 1992). For the standard run, the refuge parameter is set at 0.7 g m^{-2} , a value roughly compatible with algal biomasses observed on flat tile substrata subjected to heavy grazing pressure by snails (*Juga silicula*).

Relationships between the algal refuge parameter and the production dynamics of the Herbivory subsystem were investigated by a series of 11 simulation runs. With the standard set of inputs, annual grazer production and annual mean biomass of grazers are greatest at an algal refuge between 5 and 7 g m^{-2} after the system reaches steady-state behavior (Fig. 6A). These results suggest that secondary production can be limited by

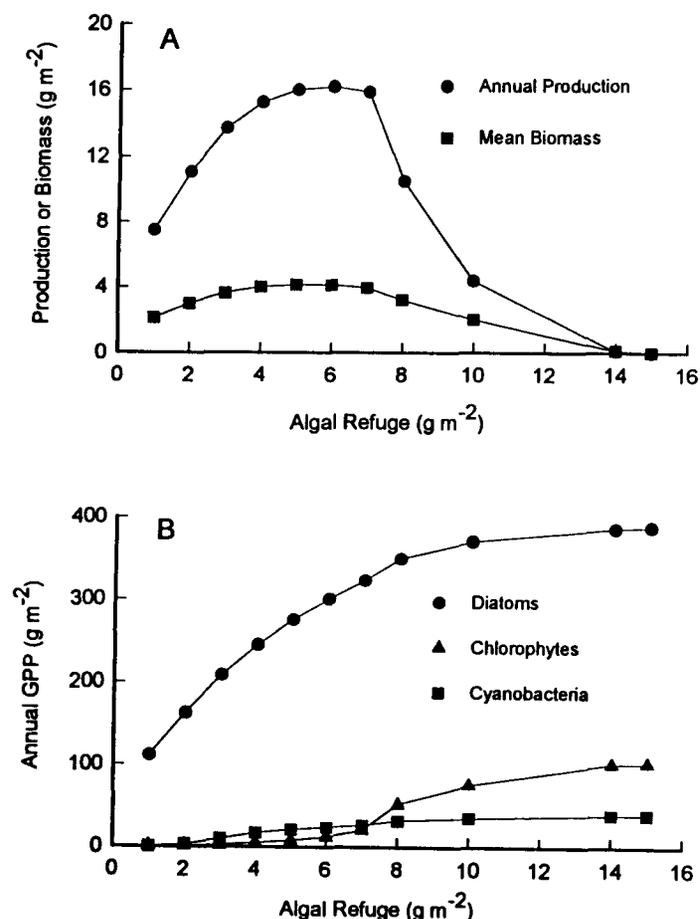


FIGURE 6 Relationships between algal refuge and annual mean grazer biomass and production (A) and between algal refuge and annual gross primary production partitioned by algal functional group (B), as indicated by the updated version of the Herbivory subsystem

overexploitation of food resources under some circumstances. The model also predicts that at refuge values above 7 g m^{-2} , green algae account for a larger proportion of gross primary production (Fig. 6B), a factor that lowers food quality and further contributes to a decline in secondary production (Fig. 6A). As the algal refuge approaches 15 g m^{-2} , secondary production in the Herbivory subsystem goes to zero and algal production reaches its maximum annual rate because grazer losses to emergence and predation exceed the gains through assimilation of algal biomass at this refuge level.

C. Food Consumption and Demand

Model behavior was also investigated in relation to the interaction between the rate of food consumption and inputs of light energy. Food consumption for the process of grazing is a function of food demand and food density (i.e., the biomass of benthic algae and associated microorganisms).

Definition: Food demand is the consumption rate when food is in unlimited supply and the quality of the resource is optimal.

In the model, food demand is a function of temperature and the biomass of the consumer functional group, grazers in this case. Food demand has a maximum value at 18°C and goes to zero as the temperature approaches a low of 0°C and a high of 30°C . In natural streams, food demand also would be expected to vary with the physiological state, life-history stage, and genetic composition of the functional group of grazers. After food demand is calculated, the model determines the realized food consumption rate by multiplying the demand by food quality and food density limiting factors.

Definition: The food quality limiting factor is the proportion of the demand that is allowed by the quality of the food resource.

If the quality of the food resource is optimal, the food quality limiting factor is equal to 1, whereas if the food resource is inedible, the value is zero. The food density limiting factor also ranges from 0 to 1, and is a nonlinear function of the biomass of the food resource [see Eq. (21) in McIntire and Colby, 1978].

The simulation runs generated output for the standard demand (i.e., the demand set up for the standard run), and for a series that included 90%, 80%, 70%, 60%, and 50% of the standard demand. Annual patterns of light energy input were controlled by a multiplier that adjusted the standard table of inputs to the desired level. For the simulation runs reported here, the light schedules included the standard table of

inputs, $3\times$ each value in the standard table, $5\times$ each value in the standard table, and a constant input above the saturation intensity for photosynthesis. Irradiance values in all tables were less than $2000 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$.

At the standard demand and 90% of the standard demand, the model predicts that increases in the inputs of light energy are accompanied by corresponding increases in gross primary production and the biomass and production associated with the process of grazing (Figs. 7A, 7B and 8B); annual mean algal biomass remains low and virtually constant under these conditions, between 1.0 and 1.8 g m^{-2} (Fig. 8A). When demand is reduced to 80% of the standard or below, there is a pronounced increase

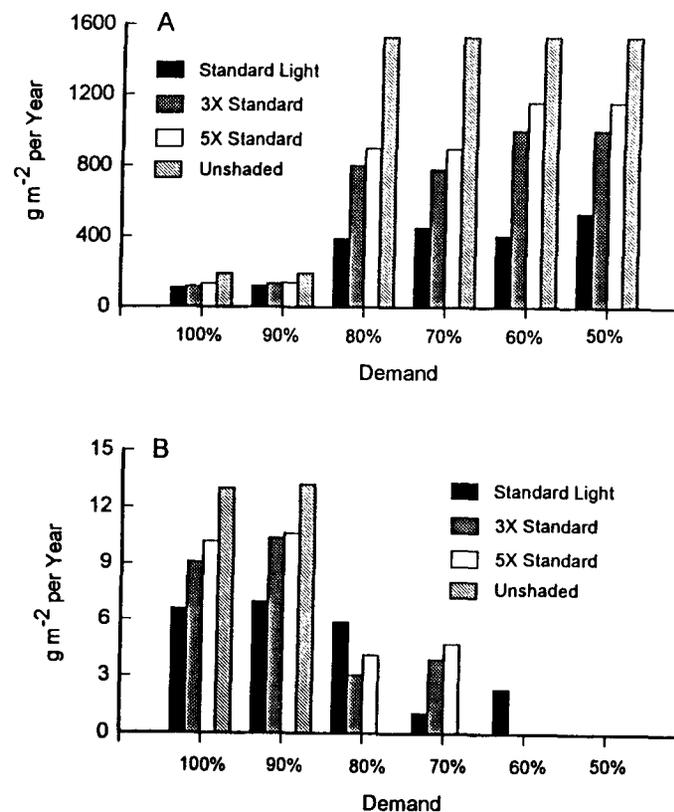


FIGURE 7 Relationships between annual gross primary production and grazer food demand (A) and between annual grazer production and grazer food demand (B) at different levels of light energy input, as indicated by the updated version of the Herbivory subsystem model. Levels of irradiance are the same as in Fig. 4. The concept of food demand is defined in the text.

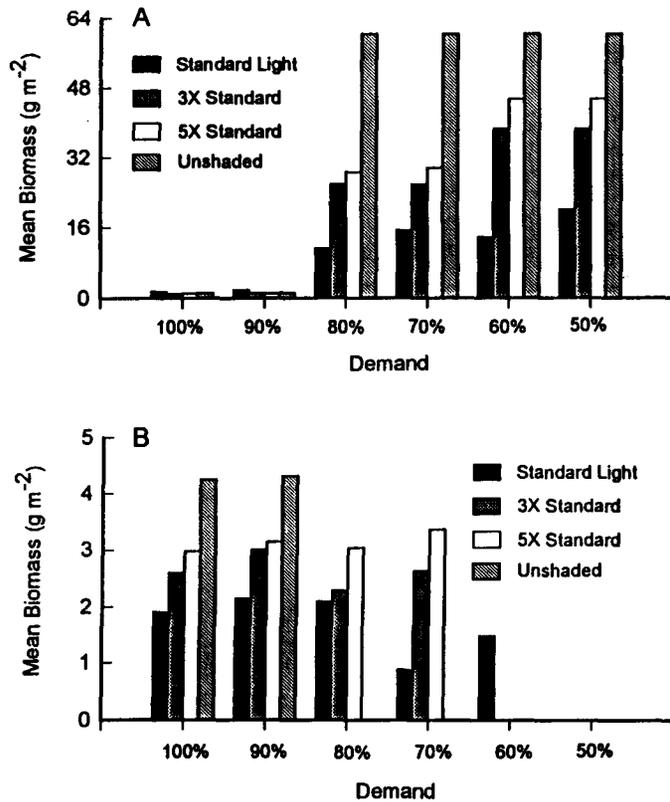


FIGURE 8 Relationship between annual mean periphyton biomass and grazer food demand (A) and between annual mean grazer biomass and grazer food demand (B) at different levels of light energy input, as indicated by the updated version of the Herbivory subsystem model. Levels of irradiance are the same as in Fig. 4. The concept of food demand is defined in the text.

in algal primary production and annual mean algal biomass, and increases in light energy inputs bring about corresponding increases in both of these variables. At 80% demand or below, the system does not support the process of grazing at the highest level of light energy inputs (5× the standard table). On the basis of strictly bioenergetic considerations, these predictions are counterintuitive, as the lowest level of light energy (1× the standard table) supports some grazing at 60% of the standard demand. The explanation for this behavior is related to a model structure that can generate changes in the taxonomic composition of the algal assemblage (Fig. 9). At the highest light energy input and a consumption rate of 80% of the standard demand or below, the model pre-

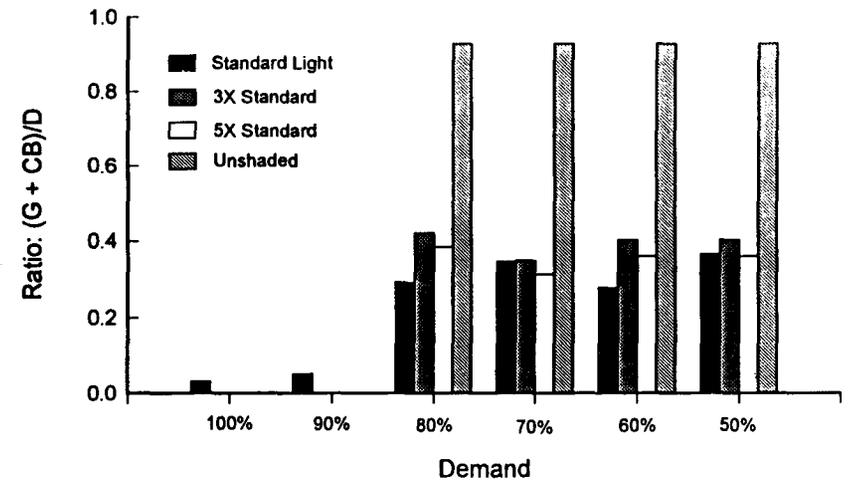


FIGURE 9 Relationship between the taxonomic structure of the algal assemblage and grazer food demand at different levels of light energy input, as indicated by the updated version of the Herbivory subsystem model. Taxonomic structure is defined as the ratio of chlorophyte and cyanobacteria production to diatom production. Levels of irradiance are the same as in Fig. 4. The concept of food demand is defined in the text.

assemblage, a change that has a negative effect on food quality. When consumption is reduced to 50% of the standard demand, the process of grazing is not supported at any of the light energy levels. Although these predictions have not been examined or tested in the field by experimentation, they do suggest that the impact of food quality on trophic relations between benthic algae and grazers may be significant enough to affect patterns of energy flow in streams.

VI. BEHAVIOR OF THE UPDATED M & C MODEL

A. Irradiance and Algal Refuge

After the investigation of the updated Herbivory subsystem in isolation, the new subsystem model was reinserted into the M & C ecosystem model as a replacement for the original representation of the Herbivory subsystem. Behavior of the updated M & C model was examined by manipulating parameters controlling light energy inputs and algal refuge. For these simulations, the corresponding output was structured to demonstrate hypothetical relationships between the process of herbivory in streams and associated consumer processes of shredding, collecting, invertebrate predation, and vertebrate predation. Particular emphasis was

processes when model behavior indicated that analogous dynamics in natural streams may be misinterpreted or remain unexplained. Results from the simulations are presented in six graphs that illustrate the relationship between annual production associated with a particular process and algal refuge at four levels of light energy (Figs. 10A–10C and 11A–11C). For these runs the light schedules included the standard table of inputs (1×) and 2×, 2.5×, and 3× the values in the standard table; algal refuge varied between 0.7 g m^{-2} , the value for the standard run, and 30 g m^{-2} , a value above which the grazer biomass remained zero regardless of the level of irradiance.

The updated M & C model predicts that secondary production associated with the process of grazing increases from $11 \text{ g m}^{-2} \text{ yr}^{-1}$ at an algal refuge of 0.7 g m^{-2} to a maximum of $53 \text{ g m}^{-2} \text{ yr}^{-1}$ at a refuge of 3 g m^{-2} when the light level is 2.5× the standard schedule (Fig. 10A). With the unaltered standard light schedule (1×), production also is maximized at a refuge level of 3 g m^{-2} , but at a value of about $18 \text{ g m}^{-2} \text{ yr}^{-1}$. In comparison, grazer production is maximized at an algal refuge of 6 g m^{-2} when the Herbivory subsystem model is run in isolation without processes associated with the Predation and Detritivory subsystems (Fig. 6A), a pattern that indicates regulatory effects of other consumer processes, particularly invertebrate and vertebrate predation. At 3× the standard schedule, grazer production is relatively low ($<4 \text{ g m}^{-2} \text{ yr}^{-1}$) and annual gross primary production is at a maximum at all algal refuge levels (Fig. 11A). In the latter case, the model predicts a release from the regulatory effects of grazing on the algal assemblage when light energy inputs are increased from 2.5× to 3× the standard schedule, a change that generates a pronounced increase in the production and biomass of chlorophytes and a corresponding decrease in food quality. Therefore, model behavior suggests that the combination of low food quality and predation, which is supported by resources generated by shredding and collecting, can account for relatively low grazer production at a high level of irradiance.

Model simulations also indicate that input variables that directly affect the Herbivory subsystem (e.g., the algal refuge parameter and the schedule of light energy inputs) have indirect effects on the production dynamics of shredding and collecting, the primary consumer processes that utilize detrital materials as a food resource (Figs. 10B and 10C). At algal refuge levels from 3 to 10 g m^{-2} , both shredder and collector production are maximized at 3× the standard light schedule and are minimum at the intermediate light levels (2× and 2.5×), a pattern that is indirectly related to low grazer production with the 3× schedule and the corresponding decreases in the production of vertebrate and invertebrate predators. In other words, the Herbivory subsystem indirectly controls the process of shredding, in part, by its direct effects on invertebrate and vertebrate predation. At algal refuges greater than 10 g m^{-2} , the light schedule has relatively little effect

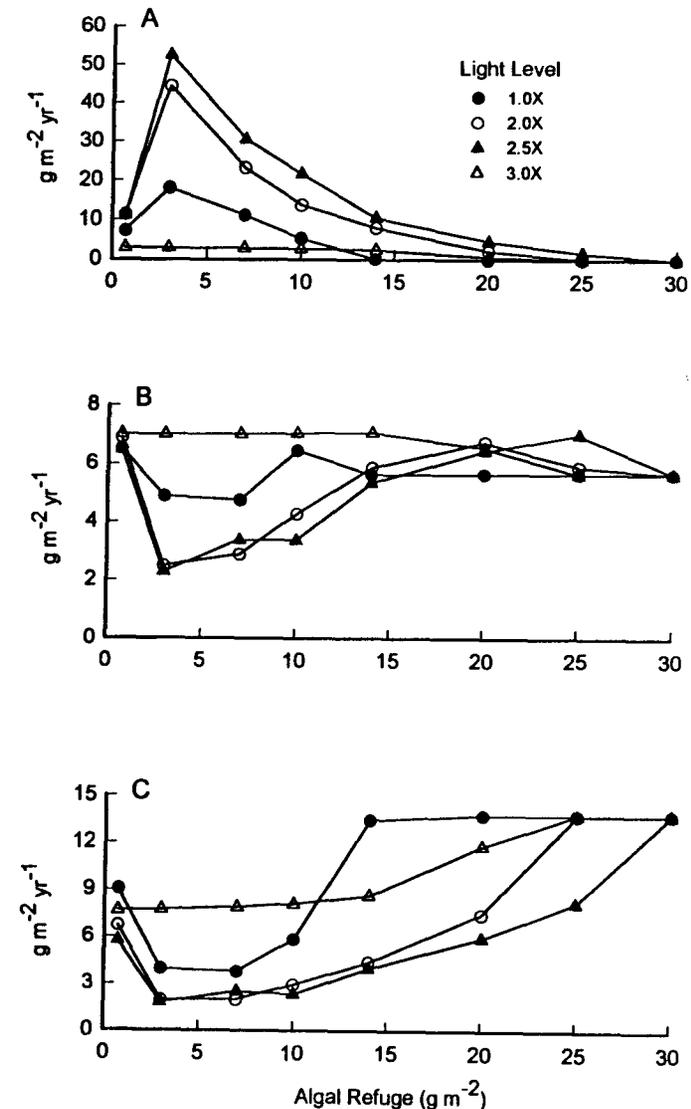


FIGURE 10 Relationships between annual grazer production (A), annual shredder production (B), and annual collector production (C) and algal refuge at different levels of light energy input, as indicated by the updated version of the M & C stream ecosystem model. Levels of irradiance are the standard table of inputs (1×), and 2×, 2.5×, and 3× each value in the standard table.

(i.e., allochthonous particulate organic matter) is independent of the other biological processes and the production of vertebrate and invertebrate predators is relatively low. In contrast, collector production exhibits pronounced light-related differences at algal refuges of 14, 20, and 25 g m^{-2} (Fig. 10C), differences that represent indirect responses to the mechanisms

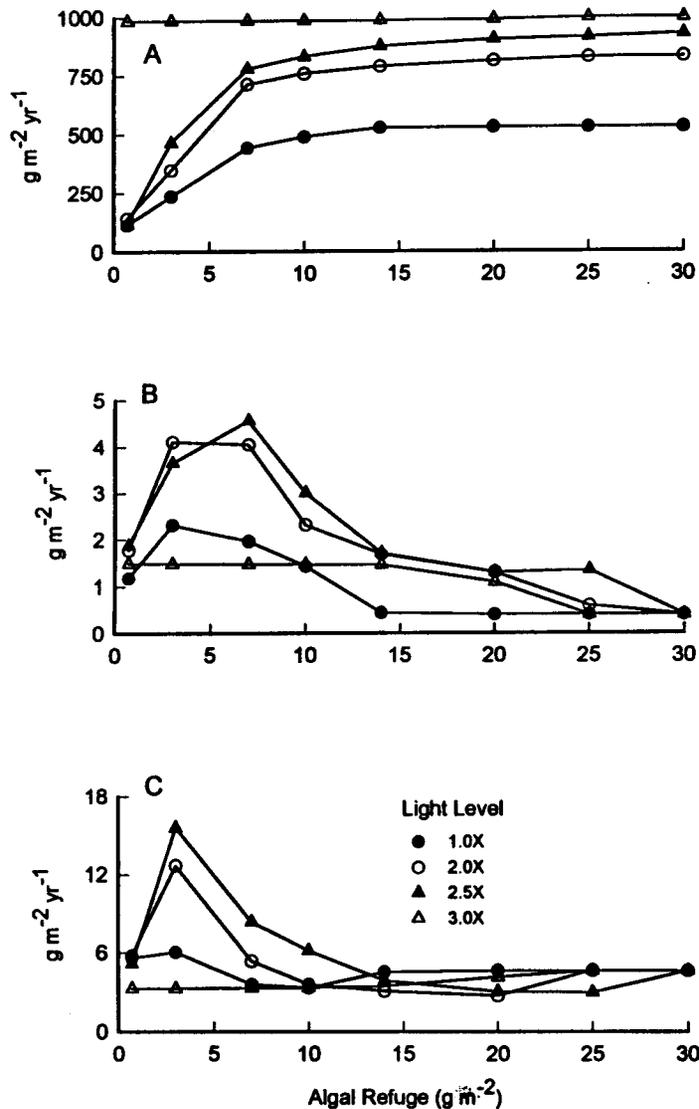


FIGURE 11 Relationships between annual gross primary production (A), annual invertebrate predator production (B), and annual vertebrate predator production (C) and algal refuge at different levels of light energy input, as indicated by the updated version of the M & C stream ecosystem model. Levels of irradiance are the same as in Fig. 10.

that limit shredder production. For most of the selected combinations of inputs, the model predicts that the process of shredding is limited by predation and emergence losses, and that resources are in unlimited supply during most seasons of the year. However, with the standard schedule of allochthonous inputs (Fig. 3 of McIntire and Colby, 1978) shredding

becomes food resource limited for a short period in the late spring and early summer in certain cases (e.g., at an algal refuge of 14 g m⁻² and the 1× light schedule). When this occurs, production and biomass of the functional groups of predators decrease, a change that allows a concurrent increase in collector production. At an algal refuge of 30 g m⁻², the system does not support grazing, and the processes of shredding and collecting become independent of the light input schedule because invertebrate and vertebrate predation are no longer affected by changes in the production and biomass of grazers.

Output from the updated M & C model indicates that the processes of vertebrate and invertebrate predation are tightly coupled to the dynamics of the Herbivory subsystem. In its present form this version of the model allows the assimilation efficiency for grazing to vary between 53 and 73%, and food demand to vary between 28 and 100% of maximum (G. A. Lamberti, unpublished data), depending on the composition of the algal assemblage. Corresponding assimilation efficiencies for shredding and collecting are 18 and 21%, respectively. As a result of this representation, manipulation of variables that affect algal production and composition have a pronounced effect on the production dynamics of the Predation subsystem of the model. Although direct relationships between algae, grazers, and predators are relatively easy to interpret, indirect relationships between the Herbivory subsystem and the processes of shredding and collecting are much less intuitive. Moreover, mechanisms accounting for differences in patterns exhibited by the processes of vertebrate and invertebrate predation are not obvious. In the model, invertebrate predators also serve as a food resource for vertebrate predators. Consequently, the model predicts that the processes of vertebrate and invertebrate predation reach a production maximum at different algal refuge levels: 3 and 7 g m⁻² at the 2.5× light level, respectively (Figs. 11B and 11C).

B. Allochthonous Inputs

Most model simulations were run with an annual input of allochthonous organic matter of 473 g m⁻², a value derived from measured litterfall and lateral movement into a small stream at the H. J. Andrews Experimental Forest in western Oregon (McIntire and Colby, 1978). During the standard run, that is, with an algal refuge of 0.7 g m⁻² and the 1× light schedule, the model predicts that losses of this material to microbial decomposition, the process of shredding, export, and mechanical conversion to fine particulate organic matter are 112 (23.7%), 233 (49.3%), 73 (15.4%), and 55 g m⁻² (11.6%), respectively. To examine the sensitivity of the Predation subsystem to an increase in detrital inputs, the annual allochthonous input was doubled to 946 g m⁻², an input that is higher than values usually reported for natural streams. With this increase, losses

the additional inputs is microbial decomposition (41.6%) and export (21.6%). Patterns of grazer and collector production with all light schedules and at all algal refuge levels were relatively unaffected by the increase in allochthonous inputs. However, with the input of 946 g m^{-2} , the process of shredding was never limited by food resources and its corresponding pattern of production was similar to that found for the collectors (i.e., similar to patterns in Fig. 9C). The increase in allochthonous material had relatively little impact on the general patterns of invertebrate and vertebrate predation because the process of shredding was limited much more by predation and emergence losses than by food resources, and the dynamics of both functional groups of predators were more tightly coupled to the Herbivory subsystem than to the processes of shredding and collecting. The model also predicts that doubling allochthonous inputs has very little or no effect on annual primary production or mean algal biomass. At low algal refuge levels ($<10 \text{ g m}^{-2}$), the process of shredding is not limited by food resources, and therefore the dynamics of this process are not affected by the addition of more allochthonous material. As the algal refuge increases to values above 10 g m^{-2} , effects of grazing on the algal assemblage are minimal because of a decrease in food quality, and therefore indirect relationships between grazing and shredding, through the process of predation, have no significant effects on primary production.

C. Food Quality and Nutrients

The behavior of the updated M & C ecosystem model indicates that the system is sensitive to changes in taxonomic composition of the benthic algal assemblage. This sensitivity is related to direct effects of species composition on food consumption by grazers and indirect effects of grazer production on the processes of vertebrate predation, invertebrate predation, shredding, and collecting. Moreover, in the simulations presented in the foregoing, it is assumed that grazer food demand varies between 28% of the maximum, when the algal assemblage is 48% diatoms, 48% chlorophytes, and 4% cyanobacteria, to maximum demand when the assemblage is 100% diatoms. Because the representation of food quality effects is based on limited experimental data, there is a possibility that such effects are overstated in the model when the productive capacity of the system is relatively high (i.e., when high irradiance and nutrient concentrations generate algal assemblages with high proportions of chlorophytes and cyanophytes).

To investigate algal composition and food quality in more detail, the model was modified to allow control over the effects of food quality on grazer food demand. This was accomplished by introducing a new parameter that sets the minimum value for the food quality limiting factor (see Section V,C for definition). For example, when the value of this param-

eter is 0.28, food demand is 28% of its maximum when the algal assemblage has its lowest percentage of diatoms (48%) and highest percentage of chlorophytes (48%); when the value is 0.75, demand is 75% of the maximum with this taxonomic composition. Therefore, as the parameter increases in value, the effect of food quality on grazer demand decreases, and at a value of 1.0, food quality has no effect on demand. At a value of 0.28, model behavior is identical to patterns illustrated in Figs. 10 and 11.

Simulations that were set for a study of the new parameter also were designed to investigate effects of a limiting nutrient at high inputs of irradiance (i.e., when light energy is not limiting). Such conditions are more typical of larger rivers than of smaller, lower-order streams. It was assumed that the limiting nutrient was nitrate nitrogen and that the range of concentrations of interest was between 0.01 and $0.5 \text{ mg liter}^{-1}$. Annual allochthonous input for these simulations was 210 g m^{-2} , whereas irradiance varied only in relation to daylength and was set at a constant value greater than the saturation intensity for photosynthesis. The schedule of allochthonous inputs was derived from data for the Willamette River (Oregon). In this case, approximately 75% of the detrital inputs were introduced at a time corresponding to a period from the beginning of September to the end of December.

If irradiance is not limiting photosynthesis, the model predicts that the dynamics of the algal assemblage are particularly sensitive to the availability of a limiting nutrient, and that primary and secondary consumers are indirectly affected by nutrient changes, in this case, especially when the nitrate concentration is below $0.1 \text{ mg liter}^{-1}$ (Figs. 12A–12C, 13A, and 13B). At a nitrate concentration of $0.03 \text{ mg liter}^{-1}$ or less, grazers are able to persist in the system when the food quality parameter is low (<0.6) because the algal biomass and primary production are never high enough to allow the growth of chlorophytes (Fig. 13C). In other words, when nutrient supply is low, food quality remains high regardless of the value of the parameter, because diatoms dominate the assemblage at low biomasses. At nitrate concentrations of $0.07 \text{ mg liter}^{-1}$ or greater, grazer production is much more sensitive to changes in the food quality limiting factor. A threshold response value for the food quality parameter is between 0.7 and 0.8. From an ecological perspective, this means that when grazer food demand can be reduced to 70% of the maximum or below by changes in food quality, grazer production actually decreases when increases in nutrient supply and primary production bring about corresponding increases in the proportional abundances of taxa that decrease food quality. Although these taxa are chlorophytes and cyanophytes in the current version of the model, the model can be reparameterized for other relevant functional groups of benthic algae when research dictates a change in mathematical structure. When the effect of food quality is minimal (i.e., the food quality

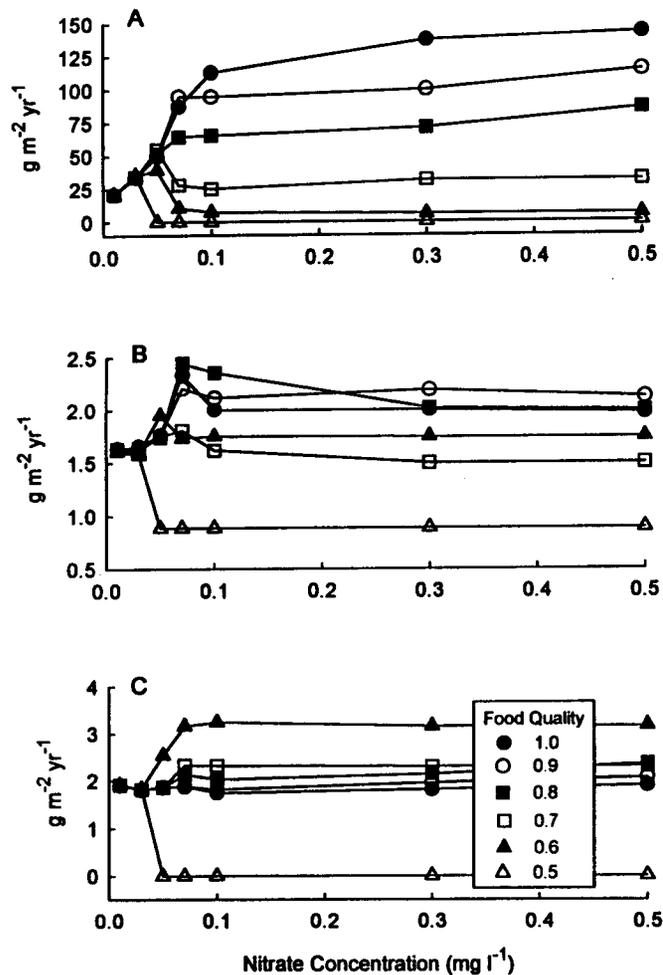


FIGURE 12 Relationships between nitrate concentration (mg liter^{-1}) and annual grazer production (A), annual shredder production (B), and annual collector production (C) at different levels of food quality (see text for explanation), as indicated by the updated version of the M & C stream ecosystem model. In these simulations, irradiance is always above the light saturation value for photosynthesis.

parameter is 0.8 or greater), grazer production increases or is relatively unaffected when nitrate concentration increases to values above $0.07 \text{ mg liter}^{-1}$.

The model predicts that shredders, collectors, and predators have different responses to changes in nitrate concentration and the food quality limiting factor. The response of vertebrate predators is similar to the pattern exhibited by the grazers, indicating that these functional groups are tightly coupled bioenergetically (Figs. 12A and 13A). With a relatively high

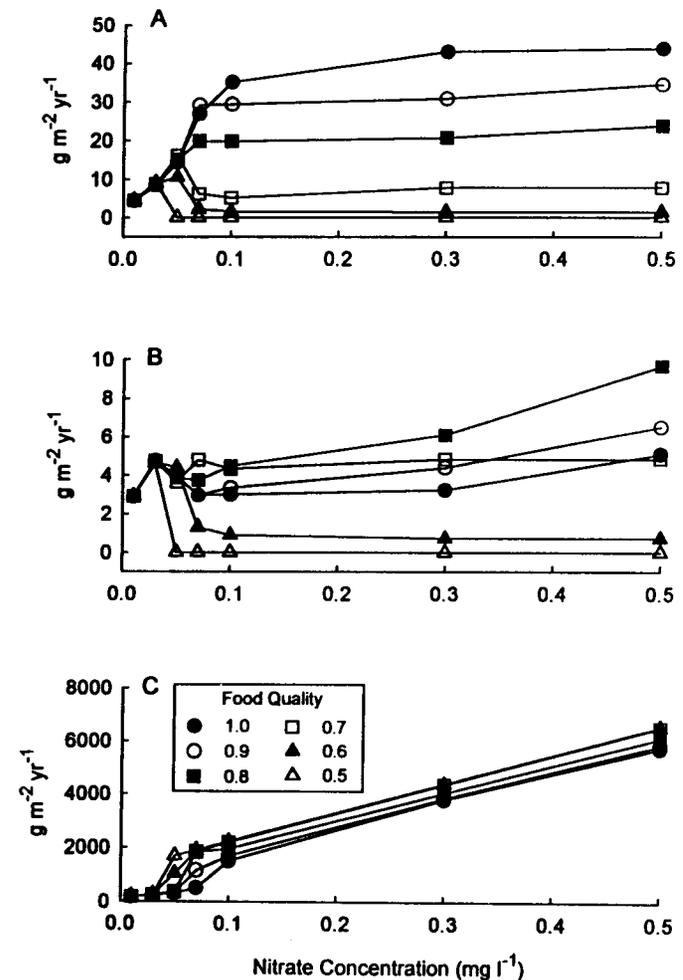


FIGURE 13 Relationships between nitrate concentration (mg liter^{-1}) and annual vertebrate predator production (A), annual invertebrate predator production (B), and annual gross primary production (C) at different levels of food quality (see text for explanation), as indicated by the updated version of the M & C stream ecosystem model. In these simulations, irradiance is always above the light saturation value for photosynthesis.

nitrate concentration ($0.1 \text{ mg liter}^{-1}$ or greater), invertebrate predators reach maximum production when the food quality parameter is 0.8 (Fig. 13B), a pattern that is a manifestation of the trade-offs between availability of food resources (grazer, shredder, and collector biomasses) and biomass losses to vertebrate predators. At nitrate concentrations of $0.07 \text{ mg liter}^{-1}$ and greater, collector production is inversely related to the food quality parameter except when grazer production is zero (parameter =

0.5). This pattern suggests that the process of collecting is controlled by vertebrate predation and becomes resource-limited only when the process of grazing fails to produce enough detrital particles. In reality, there are other sources of fine particulate organic matter in natural streams, and the process of collecting is probably not as tightly coupled to the processes of grazing and shredding as the model suggests. The relationship between shredder production and the food quality limiting factor is complex (Fig. 12B) and is directly related to the seasonal pattern of allochthonous inputs and indirectly related to the response of the functional groups of predators to changes in grazer biomass. However, for any given value of the food quality parameter, shredder production and collector production are relatively unaffected by changes in nitrate supply when concentrations are above $0.07 \text{ mg liter}^{-1}$.

VII. HYPOTHESIS GENERATION

Ongoing laboratory and field studies can provide the basis for a periodic update of the mathematical representation of stream ecosystem dynamics. The end product is a new or modified version of an existing model that is used for synthesis and hypothesis generation. Therefore, modeling can make valuable contributions to a research program by providing new questions and directions for experimental studies. If modeling is used as an iterative approach to the synthesis of past and present research, new hypotheses that emerge from the study of model behavior tend to be highly relevant to the goals of the research program and to the understanding of the corresponding system under investigation. Moreover, hypotheses generated by modeling often are related to questions that are not obvious from the results of individual laboratory or field studies. Examples of hypotheses that follow from some of the simulations described earlier in the chapter are presented in this section.

Hypothesis I: The process of grazing can affect succession in benthic algal assemblages by preventing the development of seral stages with relatively high biomasses of filamentous and colonial chlorophytes.

The structure and parameterization of the updated Herbivory subsystem model was based on experimental work by Steinman *et al.* (1987a) and Lamberti *et al.* (1989). In the study by Steinman *et al.* (1987a), successional trajectories of benthic algal assemblages in laboratory streams depended on the degree of grazing pressure and the kind of grazer (snail or caddis fly) introduced into the system. In addition, results of other studies suggest that grazers can prevent the dominance of filamentous and large, erect unicellular or colonial taxa in benthic algal assemblages, because

such taxa are more easily removed during feeding than the smaller, prostrate taxa (Eichenberger and Schlatter, 1978; Sumner and McIntire, 1982; Gregory, 1983; Perrin *et al.*, 1987; DeNicola *et al.*, 1990; Steinman, 1992). Hypothesis I is worded in terms of taxonomic classes when, in fact, it may be more appropriate to classify according to growth form (e.g., filamentous, colonial, large erect unicellular, and small prostrate growth forms). Moreover, some chlorophytes are heterotrichous (e.g., *Stigeoclonium*) and have the potential to expand from an assemblage of basal cells, under heavy grazing, to a filamentous form, in the absence of grazing. In any case, the current version of the model presents a crude representation of relationships between grazing and algal community structure, and simulates direct and indirect effects that these relationships can have on other components of lotic ecosystems.

Hypothesis II: If the productive capacity of a stream ecosystem is increased by inputs that enhance benthic algal production (e.g., an increase in irradiance or nutrient supply), there is a corresponding increase in the annual mean biomass of primary and secondary consumers while the mean algal biomass may change very little or actually decrease slightly.

The relative importance of allochthonous detrital inputs and autochthonous primary production to the bioenergetics of lotic ecosystems is controversial and has been the subject of considerable research for the past 30 years. Hypothesis II implies that the biomass of benthic algae at any particular time may be a poor indicator of the relative contribution of benthic autotrophs to the food resources of macroconsumers in streams; or stated more specifically, benthic algal biomass may be a poor predictor of the capacity of a stream to support grazing. Model simulations indicate that an increase in primary production can be expressed as an increase in grazer production and biomass rather than a conspicuous increase in algal biomass, because of an increase in the number of times that the algal biomass will turn over during a given period of time.

Most field and laboratory experiments have not been run for a long enough period of time or have concurrent measurements of the necessary variables to provide a satisfactory test for Hypothesis II. Lamberti *et al.* (1989) found that a herbivorous snail (*Juga silicula*) in laboratory streams exhibited a relatively low growth rate at a photon flux density of $20 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ and relatively high growth rates at irradiances of 100 and $400 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$. In this experiment, the snails were able to delay the accumulation of algal biomass, but animal densities were not high enough to prevent algal biomass from reaching levels comparable to those in streams without grazers. However, Steinman *et al.* (1987a) clearly demonstrated that in laboratory streams stocked with high densities of either snails or caddis flies, algal biomasses were less than 3 g m^{-2} when

irradiance was $400 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. In a field experiment, Steinman (1992) also found that biomass-specific algal photosynthesis was enhanced by an increase in irradiance, whereas algal biomass was controlled by grazing pressure. Unfortunately, grazer production was not measured during that experiment.

Hypothesis III: When inputs into a stream ecosystem remain unchanged (i.e., the productive capacity does not change), secondary production is maximized when benthic algal assemblages are protected by mechanisms that prevent overgrazing.

In this chapter, the concept of algal refuge is used in a broad sense to mean any mechanism that prevents harvest of an algal food resource by a consumer when the algal biomass falls below a lower threshold level. Mechanisms associated with such a threshold may relate to substrate heterogeneity (DeNicola and McIntire, 1990a,b, 1991) or to morphological and behavioral characteristics of the consumer organisms (Wiley and Kohler, 1981, 1984; Hart and Resh, 1980; Hart, 1981; Lamberti and Moore, 1984). In the M & C model, the focus is on a spatial scale of one square meter, and it is assumed that the distribution of the algal biomass in relation to the degree of substrate heterogeneity within that area can affect the rate of food consumption by grazers. Steinman *et al.* (1987a) found that in laboratory streams with a smooth, uniform substrate and stocked with high densities of snails (500 m^{-2}) or caddis flies (200 m^{-2}), grazers still were not able to consume all of their algal food resources, and with heavy grazing pressure, algal assemblages consisted of a monolayer of diatoms and *Stigeoclonium* basal cells. As the attachment substrate becomes more irregular, access to an algal food supply presumably becomes more difficult, and the algal biomass below which consumption is zero increases to a level that is determined by complex interactions between the morphological and behavioral characteristics of the grazer and the spatial distribution and microhabitat of individual algal taxa. Therefore, tests of Hypothesis III require measurements of primary production, secondary production, and algal biomass in experimental systems within which resource accessibility can be controlled.

Hypothesis IV: An increase in the productive capacity of a stream ecosystem concurrent with a decrease in the quality of the algal food resource may have a negative effect on grazer production even though algal biomass and primary productivity of the system increase.

Very little information is available concerning effects of the quality of algal food resources on secondary production. In the M & C stream model, food quality is conceptualized as any property of the algal food resource that affects rates of consumption and assimilation by consumers

when the resource is in unlimited supply. Examples of properties that could affect food quality are community physiognomy, the size and shape of individual taxa, and the biochemical composition of the algal food resource.

McIntire *et al.* (1969) demonstrated differences in the fatty acid composition of algal assemblages subjected to different irradiance levels and current velocities in laboratory streams, and Steinman *et al.* (1987b) found that the introduction of herbivores (snails and caddis flies) into laboratory streams altered the fatty acid and species composition of benthic algae, but had less effect on the relative concentrations of amino acids. However, relationships between biochemical composition of algae and grazer production are less clear because secondary production usually is not measured concurrently with studies of algal chemical composition. Lamberti and Moore (1984) suggested that, because of their thick cellulose cells walls and mucous coating, chlorophytes and cyanophytes are digested less easily by grazers than are diatoms. Also, feeding preference studies (Cargill *et al.*, 1985) revealed that the caddis fly *Clistoronia magnifica* preferentially ingested lipid-coated detritus during the last larval instar, indicating that at least some aquatic insects are sensitive to changes in the biochemical components of the food resource during certain periods of their life cycle.

Hypothesis V: When environmental conditions are favorable for the production of benthic algae in streams, predator production is more tightly coupled to the dynamics of grazer populations than to the production of shredders and collectors, even in the presence of relatively high inputs of allochthonous detritus.

Indirect effects of the composition and production of benthic algae on the production of secondary consumers have received relatively little attention from stream ecologists. Some studies of the effects of artificial fertilization on stream communities indicate that nutrient enrichment often is accompanied by an increase in fish production, suggesting that secondary consumers are sensitive to changes in the food supply of insects that feed on benthic algae (Perrin *et al.*, 1987; Deegan and Peterson, 1992; Peterson *et al.*, 1993). Warren *et al.* (1964) found that trout production in Berry Creek, near Corvallis, Oregon, was 21 times greater in riffles enriched with sucrose than in unenriched riffles. In this case, enrichment stimulated the production of *Sphaerotilus natans*, a filamentous bacterium that blanketed the streambed in the enriched section, and both herbivorous and carnivorous insects, the primary food resources for the trout population.

Model simulations suggest that mechanisms accounting for the close association between vertebrate predation and the process of grazing are related to the short generation times for algal assemblages (McIntire and

Colby, 1978) and relatively high assimilation efficiencies found for organisms that consume living algae (Lamberti *et al.*, 1989; McCullough and Minshall, 1979). Consequently, when allochthonous inputs of organic matter are relatively high, the process of grazing tends to be food resource limited, whereas processes of shredding and collecting are limited primarily by predation (see Figs. 6 and 7 in McIntire and Colby, 1978). Therefore, the model implies that when algal food resources are abundant, the capacity of the grazer functional group to support predator production is greater than the capacity of functional groups of detrital feeders, irrespective of the abundance of the detrital food supply. This conclusion is based entirely on bioenergetic considerations and does not consider differences in the behavioral ecology of the different functional groups or negative effects of changes in algal food quality.

Hypothesis VI: When the production of benthic algae in streams is limited by nutrient supply, changes in the nutrient concentration directly affect the quantity and quality of the algal food resource and indirectly affect shredder, collector, and predator production.

Corollary: If an increase in a limiting nutrient generates a decrease in algal food quality below a threshold value, grazer production decreases with an increase in algal productivity, a response that has indirect effects on the processes of shredding, collecting, and predation.

Indirect effects of nutrient enrichment on detritivores and functional groups of predators have received little attention from stream ecologists. Hypothesis VI is similar to Hypothesis IV in that it focuses on indirect relationships between variables that control productive capacity, nutrients in this case, and macroconsumer processes. The proposed mechanisms of interaction relate to trade-offs between algal quantity and quality in relation to associated effects on grazers and indirect effects on shredders, collectors, and predators. The model predicts that indirect effects on shredders and collectors operate through the process of predation, which is tightly coupled to changes in grazer production and biomass.

VIII. DISCUSSION AND CONCLUSIONS

Simulations and hypotheses presented in earlier sections of this chapter are examples of the kinds of insights and research directions that modeling can provide. It is interesting to note that we often learn more when model output is inconsistent with reality than when trajectories of state

variables are similar to what we observe in nature. In some cases, nothing succeeds like failure, because when the model does not exhibit the expected or desired behavior, its current structure represents an explicit expression of ignorance that can be analyzed and evaluated for the purpose of setting priorities for future research. Often, reevaluation of model structure in relation to its current behavior generates new ways of thinking about the system under investigation. In the examples presented for benthic algae in streams, model behavior suggested that we can learn a great deal from studies that examine direct, and particularly the indirect, relationships between the algal assemblage and the primary and secondary consumers in the system. These kinds of studies are much more difficult to design than studies that focus on individual algal taxa or assemblages of taxa in isolation.

Modeling also provides a basis for partitioning ecological processes into their component parts. Simulation runs from the M & C stream model are performed by the FLEX model processor (Overton, 1972, 1975) and are based on a discrete time increment of one day. The update algorithm is a simple difference equation,

$$\mathbf{x}(k+1) = \mathbf{x}(k) + \Delta(k) \quad (1)$$

where \mathbf{x} is a vector of state variable values at time k , $\mathbf{x}(k+1)$ is a vector of values for the same variables one day later, and $\Delta(k)$ is a vector of the net changes in \mathbf{x} between time k and $k+1$ estimated at time k . In the case of primary consumers (grazers, shredders, and collectors),

$$\Delta_i = a_i C_i - R_i - E_i - M_i - P_i \quad (2)$$

where C is the food consumed between k and $k+1$; R , E , M , and P are corresponding losses to respiration, emergence and export, natural mortality, and predation, respectively; and a is the assimilation efficiency. To understand how the system works, each of the components of Δ_i must be investigated. Moreover, components at this level are functions of other variables and can be partitioned into sets of subcomponents. In the examples presented earlier in the chapter, consumption of algal biomass by grazers is a function of food demand and a food density limiting factor, which itself is a function of the algal biomass minus the algal refuge level. Food demand is a function of temperature and is adjusted by the food quality limiting factor.

The value of partitioning ecological processes into their component parts goes beyond the exercise of creating a mathematical model. The identification of process components requires a fundamental understanding of the process and provides an explicit set of variables for research purposes and review. Furthermore, the definition of process components can lead to useful ecological concepts that can serve as a basis for experimental design and hypothesis testing. Examples of such concepts from the M & C stream model include (1) food demand, the function of food quality limiting factor

the supply is unlimited; (2) algal refuge, the algal biomass below which consumption by macroconsumers is zero; and (3) the food quality limiting factor, a value that adjusts the food demand to the quality of the food resource. All three of these concepts can be incorporated into hypotheses and the design of future experiments with benthic algal assemblages.

Output from the M & C stream model clearly demonstrates that links between resource production and consumption are altered by access to the resource. Availability of algal resources in the model is controlled by both physical and biological factors. Substrate heterogeneity and elevation of algal growth forms above the substrate surface are physical characteristics that modify the outcome of grazer-periphyton interactions, whereas biological features that alter the access of herbivores to food resources include food quality, morphology of mouthparts and food-gathering structures, and behavioral patterns. In the M & C model, the algal refuge parameter and a parameter that controls the food quality limiting factor affect food availability, consumption, and assimilation. Both of these parameters have a strong effect on the behavior of the Herbivory subsystem of the model and, as a result, have the capacity to change the production of other components of the system that are indirectly linked to the process of herbivory. Studies of herbivory in streams usually are based on an unstated assumption that 100% of the plant biomass is available to herbivores. However, it is unlikely that this assumption is consistent with the structural and functional attributes of most natural streams. The stream model predicts that biological components in natural streams are sensitive to resource availability and indicates that different patterns of herbivory could be observed in seemingly similar systems.

One of the more interesting hypotheses presented in the previous section indicates that dynamics of vertebrate predator populations may be tightly coupled to patterns of benthic primary production when conditions are favorable for the growth of attached algae (Hypothesis V). If this is really true, indirect relationships between vertebrate predators and benthic algae have management implications in fisheries. If the hypothesis is false, or when it is false, it would be interesting to know why the natural system exhibits behavior that is counter to the outcome predicted by bioenergetic considerations. In streams, periodic dominance of physical factors in interaction with peculiarities of the life-history characteristics of individual taxa may cause deviations from patterns predicted by models in which such details are not represented at the process level of organization. Therefore, model output can sometimes indicate when it is appropriate to do the research necessary to elaborate the structure of the model subsystems in greater detail. The expansion of the Herbivory subsystem of the M & C stream model illustrated how a new set of research objectives required the development of new model structures and concepts at a finer level of resolution.

Mathematical modeling also can be used to address some of the broader, more theoretical aspects of benthic algal ecology. As an example, we consider the question of whether stream ecosystems are controlled by "bottom-up" or "top-down" processes and how the dynamics of benthic algal assemblages relate to this question. In stream ecology, "top-down" control usually refers to a case when an increase in a resource that limits primary production (e.g., light energy or nutrients) has no effect on algal biomass, because autotrophic biomass is controlled by grazers (Steinman, 1992; Rosemond *et al.*, 1993). In contrast, "bottom-up" control means that algal biomass increases significantly with an increase in the input of some limiting factor. Some of the ambiguities about "top-down" and "bottom-up" mechanisms relate to what is actually meant by control and whether the focus is on an individual population, a functional group, or the ecosystem as a whole. For example, the M & C stream model predicts that under some conditions, an increase in the level of a limiting factor can enhance primary production without a conspicuous change in algal biomass, because the biomass turns over more rapidly in response to the increase in resources and concurrent increases in macroconsumer production and biomass. Consequently, "bottom-up" control is achieved without much change in the mean algal biomass. This indicates that it might be less ambiguous to define limitation or control in terms of production instead of biomass. However, in the case of streams, which often obtain their resources from both autochthonous and allochthonous sources, an increase in detrital inputs from the surrounding terrestrial environment will always result in an increase in energy flux through the ecosystem ("bottom-up" control) regardless of the effects of predators on primary consumers. In other words, if shredders and collectors do not process the new material, it will ultimately be processed by the microbial flora. The pronounced seasonality of allochthonous and autochthonous inputs and the frequent disturbance regimes in stream ecosystems make it unlikely that simple "top-down" or "bottom-up" effects would occur throughout a food web. Instead, controls are likely to be transient, and the complex array of life histories and generation times characteristic of lotic ecosystems tends to obscure mechanisms of control and patterns of resource limitation and exploitation.

Experience with the M & C stream model suggests a more direct approach to the understanding of process limitation and control. Modeling for research purposes often requires that each process be partitioned into its component parts [see Eqs. (1) and (2)], each part of which represents either a gain or loss to the associated state variable. Therefore, mechanisms of regulation and control are revealed by the relative importance of the positive or negative effects of each part on the process. McIntire and Colby (1978) and McIntire (1983) defined a new set of variables that allow a graphic display of the factors that prevent a state variable from reaching

its maximum potential specific growth rate. For example, model output predicted that in a shaded stream receiving relatively high allochthonous inputs ($473 \text{ g m}^{-2} \text{ yr}^{-1}$), the process of grazing is controlled by the algal food resource, whereas the processes of shredding and collecting are affected more by predation than by resource limitation (see Figs. 5 and 6 in McIntire, 1983). Model output also indicated that it is possible for such control to vary seasonally and that at certain times physical processes or losses relating to life-history characteristics (e.g., emergence) may have much greater effects on process dynamics than trophic interactions.

In summary, theoretical generalizations can evolve from a systematic investigation of different model structures, while varying inputs and parameters. Experimental and observational studies of benthic algae in streams provide the data base necessary for a modeling approach to the synthesis of existing information and concepts into an integrated theory of how the structure and function of benthic algal assemblages relate to physical processes and to other biological components of ecological systems. In particular, modeling is a powerful research tool when it is used in close association with related laboratory and field studies.

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