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Author(s): Myron P. Zalucki

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MODELING AND SIMULATION OF THE ENERGY FLOW THROUGH ROOT SPRING, MASSACHUSETTS¹

MYRON P. ZALUCKI²

Department of Zoology, Australian National University, Canberra, Australia

Abstract. Four compartment models, each postulating distinct forms of interactions among the organisms in Root Spring, Massachusetts were developed and compared. None were adequate to simulate the dynamics of energy flux in the spring. A model of the spring which adapted a detritus-processing matrix developed for stream systems, together with a more precise statement of feeding relationships, reproduced the observed data more faithfully. This model suggested that certain further information on the biology of the spring would improve understanding of its dynamics.

Key words: *Compartment; decomposers; detritus; energy flow; Massachusetts; modeling; simulation.*

INTRODUCTION

In recent years, modeling and simulation have been applied more and more to whole ecosystems (Patten 1971, 1972, 1975). These methods are useful tools in studying the involved relationships which characterize such complex systems. A sensible approach is to study relatively simple systems, as this enables the testing of different model structures and ideas on interactions within ecosystems. With this point in mind, the broad aim and objective of this study was to model and simulate the energy flow in a well-defined simple ecosystem, Root Spring, Massachusetts, using the compartment approach.

Energy flow through the major biotic components in the spring over a 1-yr period was described by Teal (1957 *a,b*). In a chemically and thermally constant spring, the dynamics of energy flux will depend on external inputs together with the interactions occurring among the inhabitants. The success or failure of a compartment model as a description of such a system, will depend on how adequately the interactions among the species occurring in the spring can be represented in mathematical terms. During the course of the work, 4 distinct network models were developed, each containing different forms of interaction among the spring's species. These 4 models will be described and compared briefly. Finally, a detritus-processing model, developed for stream ecosystems, was adapted to the Root Spring situation. This model provided new insights into the functioning of the ecosystem.

THE NETWORK MODELS OF ENERGY FLOW IN ROOT SPRING

The system is described in the flow diagram in Fig. 1. The compartments shown correspond to the species of organism in the spring for which Teal (1957*a*) de-

rived an energy budget, except for the "ooze" compartment. Ooze was considered to be the top 4 centimetres of the mud which covers the bottom of the spring. This mud contained organic detritus on which the organisms fed. Changes in each compartment were described by the general differential equation:

$$dX_i/dt = S_i + \sum_{j=1}^m I_{ij} - \sum_{k=1}^n O_{ki}, \quad (1)$$

where S_i is input to X_i from a source outside the system, $\sum_{j=1}^m I_{ij}$ is the sum of inputs to X_i from other compartments, and $\sum_{k=1}^n O_{ki}$ is the sum of loss terms to other parts of the system. Inputs to the system (POM in Fig. 1) were added to the ooze compartment. These consisted of net primary production and the whole apple leaves which fell into the spring. It was reasoned that these leaves would not be available for immediate consumption. Whole leaves are colonized and broken down by microorganisms before becoming available to small particle feeders (Cummins and Petersen 1973). This process was modeled by delaying leaf input for 60 days. A time lag of this order would have major effects on the phase behavior of the model. Therefore, an experiment was carried out on apple leaves to determine at what rate leaves are broken down in conditions similar to those in the spring (pH 6.5, 9°C). These observations yielded a decomposition rate of 0.006/day (Zalucki 1976). Using Petersen and Cummins (1974) classification of leaf decomposition, this puts apple leaves into the slow-medium category, with a half-life between 46 and 138 days. The 60-day delay incorporated in the model, therefore, falls within these limits.

The mathematical forms given to the interactions between compartments in the 4 different network models are given in Table 1. In the linear model all feeding flows were donor dependent. The part-linear model considered predatory feeding flows to be de-

¹ Manuscript received 7 February 1977; accepted 21 September 1977.

² Present address: School of Australian Environmental Studies, Griffith University, Nathan, Queensland 4111 Australia.

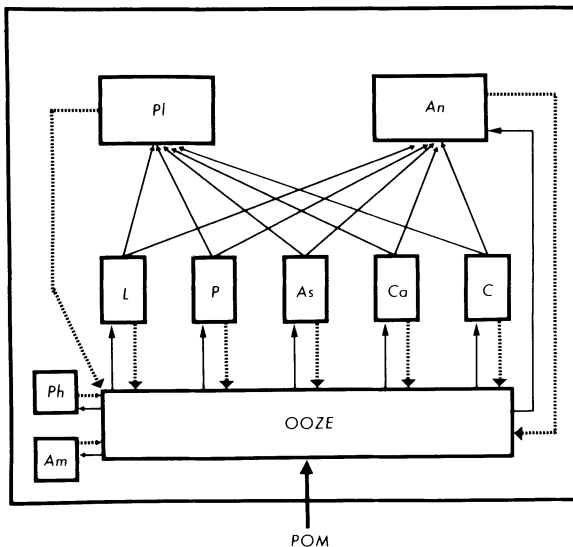


FIG. 1. Flow diagram for network description of Root Spring, respiration and other losses to outside the system not shown. L = *Limnodrilus*; P = *Pisidium*; As = *Asellus*; Ca = *Calopsectra*; C = *Caddis*; An = *Anatopynia*; Ph = *Physsa*; Am = *Amphipods*; Pl = *Planarians* (—) feeding flows; (----) losses to ooze. POM—Particulate organic matter (delayed debris + plant matter).

pendent on donor and recipient compartments, while in the nonlinear model, all feeding flows were in this form. The controlled nonlinear model had self-inhibition terms on all nonlinear flows.

The biological interpretation of the linear model is that feeders are controlled by competition for a limited food supply, the biomass of feeders having no effect on the amount eaten (Kowal 1971). In the part-linear and nonlinear models, food supply and feeders control each other mutually. Many authors (Holling 1966, Kowal 1971, Williams 1971) consider such a formulation a reasonable description of predator-prey interactions. The controlled nonlinear model introduces a negative feedback term to represent intraspecific competition. Williams (1971) used a similar approach when modeling the energy flow through Cedar Bog, Minnesota. There are many other compartment interaction terms that could have been used (e.g., Park 1975, Wiegert 1975) however these formulations require a large amount of information in order to estimate appropriate parameters. The terms used in this study are among the more common and simple of those used in similar models of ecosystems. In addition, the parameters could be estimated from Teal's (1975a) data, as the F_{ij} , X_i and X_j are known. All noninteraction losses from compartments were made donor dependent.

Given the inputs and having specified loss and interaction terms, a model's behavior over time could be simulated and the output compared with observed fluctuations in the spring. Simulations were made using an International mathematical and statistical libraries (IMSL) package called DVOGER which solves

TABLE 1. Summary of models developed and interaction terms used

Model name	Form of interaction term (solid lines in Fig. 1)***
Linear**	$F_{ij} = \phi_{ij}X_i$
Part-linear*	$F_{ij} = \phi_{ij}X_iX_j$
Nonlinear**	$F_{ij} = \phi_{ij}X_iX_j$
Controlled nonlinear**	$F_{ij} = \phi_{ij}X_iX_j(1 - \alpha X_j)$
Matrix**	$F_{ij} = \phi_{ij}X_i$

* Only predator-prey interactions.

** All interactions.

*** Where F_{ij} = the flow from i to j; X_i and X_j are the average biomass levels of compartments i and j; ϕ_{ij} is the flow rate and α is the degree of inhibition.

differential equations using Gear's method (Gear 1971). Stability was tested by simulating the dynamics of the system over 5 yr. Any error in a parameter may cause an error in calculation of the value of a state variable. As this erroneous value is then used to calculate the magnitude of the next variable, the iterative solution of the equations can cause significant accumulation of these errors. A continuous decline, increase or irregular oscillation in the size of a compartment would suggest that the model is unstable. In deterministic models such as these, stability is achieved when each year's output is identical. Stability was tested, therefore, by comparing the 5th year's output with that of previous years.

Where a model was found to be stable using this criterion, the third year of simulation was compared with Teal's (1957a) observed values using the following 3 methods: (1) visual correspondence of predicted and observed maximum and minimum values over the year; (2) the average predicted biomass of each compartment was computed and compared to the observed average using the *t*-statistic; and (3) the observed variance in compartment size was compared with the predicted value using the variance ratio test F_{max} procedure (Sokal and Rohlf 1969). These 3 comparisons are summarized for the models and 7 selected compartments in Table 2.

Both linear and part-linear models are stable. Neither reproduced the dynamics of energy flow through the spring (Table 2). The full nonlinear model failed to achieve cyclical behavior. As Wiegert (1974) points out, models employing such relationships frequently exhibit biologically unrealistic instabilities and sensitivities. By adding self-inhibition terms to all feeding flows, the nonlinear model was stabilized. Because of the method employed in estimating the ϕ and α terms (Table 1; the method used 1 equation where F_{ij} , X_i and X_j were set to their average value and the other using values from that month for which F_{ij} and X_i were at a maximum) compartment predictions were overly large. Minor (60–100%) adjustments to the ϕ and α terms produced a reasonable fit to the observed compartment changes over the year (Table 2). No doubt

TABLE 2. Comparison between predicted and observed values 4 models and 7 compartments*

Compartment	Visual correspondence of maximum and minimum**				Comparison of mean biomass over the year using <i>t</i> test***				Comparison of variance over the year using F_{\max} test***			
	L	P-L	C-NL	M	L	P-L	C-NL	M	L	P-L	C-NL	M
<i>Limnodrilus</i>	No	Yes	No	No	No	Same	Same	Diff.	Diff.	Diff.	Diff.	Same
<i>Pisidium</i>	No	No	Yes	Yes	Same	Same	Diff.	Diff.	Diff.	Same	Same	Same
<i>Asellus</i>	No	No	Yes	Yes	Same	Same	Same	Same	Diff.	Diff.	Same	Same
<i>Calopsectra</i>	No	No	No	No	Same	Same	Same	Same	Diff.	Diff.	Same	Diff.
<i>Caddis</i>	No	No	No	No	Same	Same	Same	Same	Diff.	Diff.	Same	Same
Planarians	No	No	No	Yes	Same	Diff.	Same	Same	Diff.	Same	Same	Diff.
<i>Anatopynia</i>	No	No	Yes	Yes	Same	Same	Same	Same	Diff.	Same	Same	Same

* L = Linear model, P-L = Part-linear, C-NL = controlled Nonlinear, M = Matrix.

** Yes = correspondence, No = no correspondence.

*** Tested at the 5% level.

more tuning would further improve the correspondence. This procedure neither validates nor invalidates the model, nor does it suggest that the dynamics of interaction in the spring are correctly represented by the controlled nonlinear formulation. To validate the model would require further time-series data on energy flow through the spring components, and this is not available. Even though none of the feeding formulations presented above were sufficient to describe the spring, this does not necessarily imply that they are inadequate descriptions of the interactions. Another possibility is that the systems description (Fig. 1) is incorrect. In fact, a major criticism of these models is that all debris is equally available for consumption after the specified time delay. Consequently, a filter-feeding clam, *Pisidium*, is represented as feeding on the same material as an active particle-feeding chironomid larva, *Calopsectra*. The models have not taken into account niche differentiation based on food resource partitioning. It was for these reasons that an attempt was made to develop a model with more biological realism. The basis of this model was a more precise statement of the feeding relationships of the organisms in the spring.

A DETRITUS-PROCESSING MODEL FOR ROOT SPRING

Cummins (1973), Cummins and Petersen (1973), Petersen and Cummins (1974), Kaushik and Hynes (1968) and Boling et al. (1975a) have shown that detritivores show a high degree of preference in the type and size of food particle they will consume. The assumption that predators show no food preferences is also simplistic. Reynoldson (1966), for example, demonstrated that lake-dwelling triclads have distinct prey preferences.

To include the feeding relationships of detritivores in greater detail required a better description of the breakdown of debris into small particles. A model which simulates these processes was developed by Boling et al. (1975a), for a woodland stream. In this model, nonliving particulate organic matter was clas-

sified according to particle size and extent of microbial colonization (conditioning), as reflected by community respiration. There were 6 size and 6 conditioning categories recognized in this model. The size and conditioning categories form a 6×6 matrix which described the detritus pool at any time (Fig. 2). The entries into this descriptive matrix are biomass of debris in kilojoules per square metre. Changes in this biomass can occur by both vertical and horizontal transitions through this matrix. The direction of the horizontal transitions are primarily from left to right. These transitions are a function of fragmentation or flaking of particles due to abrasion and animal feeding. However, right to left transitions are also possible through flocculation and aggregation. Vertical transitions occur due to microbial activity and small amounts of energy are converted to heat by microbial respiration. Movement of organic matter from one bin of the matrix to another represents a transition function, f_{ij} , where f_{ij} is that fraction of bin_i leaving bin_i and entering bin_j in 1 time step. The updating of the descriptive matrix is achieved by matrix algebra using Eqs. 2, 3 and 4 and the f_{ij} values from Boling et al. (1975a).

The detritus matrix replaces the ooze compartment used in previous models. Detritivores remove organic matter from the elements of this matrix via feeding, and return matter in the form of nonpredatory mortality, exuviae, mucus, feces and the leftovers of predation. All feeding flows were considered linear and donor controlled in this model.

The central problem in coupling the energy flow model through organisms to the detritus-processing model was in determining on which particular size and conditioning category of particles the detritivores are feeding. Teal's (1957a) statements on the feeding habits of the spring organisms are very general, and not specific enough to assign organisms unequivocally as feeding on any particular size/conditioning category of detrital particle. The feeding classifications shown in Fig. 2 are hypothetical, rather than being experimentally determined observations. They are based on in-

	AWOM	SWOM	LPOM	MPOM	SPOM	FPOM
Resistant	D	D				
Slow	D	D	D			D
Medium	C	C	Eg,As	P,Eg As,Am	P,Eg Am	
Fast	C,Ca	C,Ca,Ph	Eg Ph,As,Ca	Eg Ca As,Am,An	Eg Am,An,Ca	Pi
Fully Conditioned	C,Ca	C,Ca,Ph	Ph,As,Ca	Ca As,Am,An	Am,An,Ca	Pi,Ca
Post Conditioned	L	L	L	L	L	L

FIG. 2. Size/conditioning categories on which detritivores fed in the matrix model. Bins into which debris, algae and egesta were added are also shown. Inputs: D = debris; P = plant net production; Eg = egesta. Losses to: L = *Limnodrilus*; Pi = *Pisidium*; As = *Asellus*; Ca = *Calopsectra*; C = *Caddis*; Ph = *Physa*; Am = Amphipods; An = *Anatopynia*. AWOM = aggregate whole organic matter; SWOM = small whole organic matter; LPOM = large particulate organic matter; MPOM = medium particulate organic matter; SPOM = small particulate organic matter; FPOM = fine particulate organic matter.

formation in the literature (e.g., Pennak 1953, Minckley 1963), Teal's (1957a) observations and educated guesses. Factors considered included the size of the organism, its mouthparts and methods of feeding: scraping, collecting, filtering, biting or chewing. In general, organisms give preference to particles heavily colonized by bacteria and fungi. Figure 2 also shows into which elements of the detritus matrix net production of plants and egesta from animals were added. Egesta was apportioned equally among its bins. According to the description of Boling et al. (1975a) of the constituents of detritus, benthic algae fall into the medium and small particulate organic matter cate-

gories (MPOM and SPOM, respectively; Fig. 2). The plant input was divided equally among these 2. As the bulk of input consisted of whole leaves, 75% of the debris was added to the slow small whole organic matter (SWOM) category. The remaining 25% was apportioned among other bins so as to take account of twigs, branches, leaf veins and midribs.

The predators, planarians and *Anatopynia* (Chironomidae) were assigned prey preferenda. The planarians were given a preference for *Calopsectra* and *Asellus*. *Anatopynia* was given a preference for *Limnodrilus* (Tubificidae). Both predators took *Pisidium* and *Caddis* larvae equally. The preferences were based on the cor-

response of maximum biomass values for prey and predators, e.g., planarians show a biomass peak soon after *Calopsectra*, etc.

Initial estimates of feeding rates of detritivores were based on the following assumption: at steady state, the average biomass of detritus in each element of the matrix was set to 280 kilojoules/m². This assumed that the average biomass of the ooze used in previous models was distributed evenly amongst elements of the matrix. This gave the average biomass of the bins on which an organism fed. As the flows into all compartments are known, the transfer rates can be estimated.

Initial simulations obtained using the model employing these parameter values were stable but showed poor correspondence with observed values. However, the model was found to be sensitive to the value assigned to the feeding rates of the detritivores and minor adjustments (20–100%) to these produced a much-improved fit (Table 2). While acknowledging this to be an empirically based fitting procedure, it is nevertheless felt that such a procedure has heuristic value. It serves to indicate information required to improve understanding of this system.

At this stage, the matrix model may be viewed as a useful research tool. It suggests information that is required on the biology of the organisms in the spring. Such information would improve the simulation process and, as a result, indicate more clearly the functional roles of particular organisms in the spring ecosystem. Analysis of the present model indicates, specifically, that more information is required on: (1) the feeding habits of the organisms; (2) the rates at which organisms ingest materials; (3) the size and rate of turnover of the organic food available to *Limnodrilus*; (4) the horizontal transition rates of detritus particles in the spring situation; and (5) input data for debris, especially the amount and size spectrum of the debris input and the time taken for leaves to sink to the bottom mud.

The model provides a detailed, if incomplete, description of detritus-processing and feeding relationships of organisms in the spring. If, as Bates (1958) points out, trophic relationships constitute the cement holding biological communities together, then coexistence of, and competition between, species is a function of partitioning of available food resources through various adaptive mechanisms. The model suggests that a better understanding of the functioning and relationships within an ecosystem can be achieved if the feeding relationships and food resources of organisms are more clearly delineated. Classification of organisms into herbivores or carnivores is too superficial a level of abstraction. Conceptually, a better classification system would use feeding mechanisms and/or sizes and types of food ingested. (Compare with Boling et al. [1975b] "paraspecies" concept).

The picture that ecosystem dynamics may be ex-

plained solely by describing food resource partitioning among the component species, is perhaps most applicable to relatively simple systems, such as a spring. Clearly organisms divide a large set of resources, which are themselves discontinuously distributed in time and space. If the interactions between organisms and their environments are to be understood, then ecosystem models will have to include better descriptions of how various resources (other than food) are partitioned.

CONCLUSIONS

The present study has demonstrated that simple compartment models of the Root Spring ecosystem provide inadequate simulation of the system, regardless of the precise formulation of the interactions involved. A more biologically realistic model incorporating detail on feeding habits of the organisms concerned provides a much more promising approach, resulting in a tool which can suggest relatively simple information required on the biology of the spring to improve understanding. Ideally, model building of this type should occur in the preliminary stages of a piece of research with constant feedback between experiment and model allowing the time wasting task of collecting masses of irrelevant observations to be avoided.

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Details of equations, output for all models and a copy of the programs used are in a honors thesis deposited in the Zoology Department Library, Australian National University.

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