Interaction in Ecosystems:

A Queuing Approach to Modeling

Joseph E. Powers and Robert T. Lackey*

**Department of Fisheries and Wildlife*
Oregon State University
Corvallis, Oregon 97331

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Email: Robert.Lackey@oregonstate.edu
Phone: (541) 737-0569
Web: http://fw.oregonstate.edu/content/robert-lackey

Interaction in Ecosystems: A Queueing Approach to Modeling

JOSEPH E. POWERS

AND

ROBERT T. LACKEY

Department of Fisheries and Wildlife Sciences,
Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

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ABSTRACT

A mathematical model is described for calculating the effects of several different types of interaction in an ecosystem. The model is based on queueing theory where the service discipline is governed by preemptive priorities. Graphical results of this approach are presented, as well as an example of the model integrated into an ecosystem dynamics simulator as a subroutine.

INTRODUCTION

Models of ecosystem dynamics depict interaction among ecosystem components and exhibit some degree of realism, generality, and precision. Modelers have decomposed the dynamics of ecosystems into individual ecological processes in a manner similar to that of Holling [2] with his model of predator attack. Timin [4] extended Holling's approach by modeling a multispecies consumption system which can be integrated as a subprogram into a generalized ecosystem simulator. Similarly to Holling's work, interaction has been incorporated into reproduction models [1].

A mathematical model efficiently describing interaction between ecosystem components could be very useful in modeling. Such a model should (at a minimum) include effects of predator-prey relationships, reproduction, and aggressive behavior, as well as the flexibility to include other important interaction processes. Our approach, based on queueing theory, expands on Timin's work to include several types of intra- and interspecific interaction.

MODEL DEVELOPMENT

Consider an animal of the qth type moving through its environment. When another animal of the rth type enters q's sphere of influence, q must react in one of three ways: (1) recognize and react toward r; (2) recognize and avoid r; or (3) recognize and totally ignore r.

Let us further consider the state in which q is reacting toward (chasing) animal r. If another animal (s) enters q's sphere of influence while q is chasing r, the presence of s might change q's strategy. If s is unpalatable, it may be ignored. But, if s is a potential predator, its presence will take preemptive priority over that of q and q will attempt to avoid (escape) s.

Generally, an animal has a more complex priority set than simply chasing, escaping, or ignoring. A more complex priority set may include, for example, escaping a predator, escaping an aggressive dominant, spawning (reproducing), chasing a subdominant, and chasing a prey. An animal's actions may always be characterized with preemptive priorities (arrival of an item of a higher priority will stop service of any item of lower priority). In essence then animal q is the single server in a queueing system in which the service discipline is governed by preemptive priorities and the maximum number allowed in the system is 1 (maximum queue length equals zero). Assuming Poisson arrival and service rates, this can be expressed succinctly in the Kendall-Lee notation as $M/M/1$: PRPR/1 [3].

Let n be the number of response priorities for a particular animal with the highest priority being 1. Associated with each priority i there is an arrival rate λ_i and a service rate μ_i. These rates are the expected number of trespassers of priority i into q's sphere of influence per unit time and the expected number of services of priority i that q can perform per unit time, respectively.

Animal q at any time t can be in one of $2n+1$ mutually exclusive and exhaustive states with a certain probability $P(t)$. Animal q can be in the process of servicing an animal of priority i $[P_i(t)]$; it can be idle having just completed service of priority type i $[P_{0i}(t)]$, or it can be idle having not interacted with any other animal in the ecosystem $[P_{00}(t)]$.

Let Δt be an arbitrarily small time increment in which the probability of more than one arrival or service occurring is extremely small. Then the following equation can be developed:

$$P_{0i}(t+\Delta t)=P_i(t)[\mu_i\Delta t+o(\Delta t)]+P_{0i}(t)\left[1-\sum_{j=1}^{n}\lambda_j\Delta t-o(\Delta t)\right],$$

$$i=1,2,\ldots,n, \tag{1}$$

where $o(\Delta t)$ is an arbitrary function of Δt, many orders of magnitude less than $\lambda_i \Delta t$ [as $\Delta t \to 0$, $o(\Delta t)/\Delta t \to 0$]. Equation (1) formalizes the relationship that the probability of q being idle in the interval Δt, having just completed a service of priority i, is equal to the probability that a service of the ith priority was completed plus the probability that there were no arrivals plus the probability that not more than one arrival or service occurred.

Since

$$\lim_{\Delta t \to 0} \frac{P_{0i}(t+\Delta t) - P_{0i}(t)}{\Delta t} = P'_{0i}(t),$$

Eq. (1) can be manipulated to produce

$$P'_{0i}(t) = \mu_i P_i(t) - \left(\sum_{j=1}^{n} \lambda_j \right) P_{0i}(t). \tag{2}$$

As t approaches infinity, $P'_{0i}(t)$ approaches zero, and $P_{0i}(t)$ approaches P_{0i} (steady state conditions). Therefore,

$$P_{0i} = \frac{\mu_i P_i}{\sum_{j=1}^{n} \lambda_j} \tag{3}$$

In a similar manner,

$$\begin{aligned} P_i(t+\Delta t) = {} & \left[\sum_{j=0}^{n} P_{0j}(t) \right] [\lambda_i \Delta t + o(\Delta t)] \\ & + P_i(t) \left[1 - \mu_i \Delta t - \sum_{j=i+1}^{n} \lambda_j \Delta t - o(\Delta t) \right] \\ & + \left[\sum_{j=1}^{i-1} P_j(t) \right] [\lambda_i \Delta t + o(\Delta t)]. \end{aligned} \tag{4}$$

If we define $\sum_{m=v}^{w} a_m = 0$ when $v > w$, then in the steady state,

$$P_i = \frac{\lambda_i}{\mu_i + \sum_{j=1}^{i-1} \lambda_j} \left(\sum_{j=0}^{n} P_{0j} + \sum_{j=i+1}^{n} P_j \right). \tag{5}$$

Let γ_i $(i=1,2,\ldots,n)$ be new variables such that

$$\gamma_n = \frac{\lambda_n}{\mu_n + \sum_{j=1}^{n-1} \lambda_j}. \tag{6}$$

Substituting (6) into (5) gives

$$\mathrm{P}_n = \gamma_n \sum_{j=0}^{n} \mathrm{P}_{0j}. \tag{7}$$

Then using (7) and (5) and back substituting,

$$\mathrm{P}_{n-1} = \frac{\lambda_{n-1}}{\mu_{n-1} + \sum_{j=1}^{n-2} \lambda_j} \left(\gamma_n \sum_{j=0}^{n} \mathrm{P}_{0j} + \sum_{j=0}^{n} \mathrm{P}_{0j} \right) \tag{8}$$

or

$$\mathrm{P}_{n-1} = \gamma_{n-1} \left(\sum_{j=0}^{n} \mathrm{P}_{0j} \right)$$

where

$$\gamma_{n-1} = \frac{\lambda_{n-1}}{\mu_{n-1} \sum_{j=1}^{n-2} \lambda_j} (1+\gamma_n). \tag{9}$$

By continuing to back substitute, we obtain the general result

$$\mathrm{P}_i = \gamma_i \sum_{j=0}^{n} \mathrm{P}_{0j} \qquad (i=1,2,\ldots,n), \tag{10}$$

where

$$\gamma_i = \frac{\lambda_i}{\mu_i + \sum_{j=1}^{i-1} \lambda_j} \left(1 + \sum_{j=i+1}^{n} \gamma_j \right). \tag{11}$$

Since the $2n+1$ states are mutually exclusive and exhaustive,

$$\sum_{i=0}^{n} \mathrm{P}_{0i} + \sum_{i=1}^{n} \mathrm{P}_i = 1.$$

Note that $P_{00}=0$ for any non-zero arrival rate. Using (10),

$$\sum_{i=0}^{n} \mathrm{P}_{0i} + \sum_{i=1}^{n} \left(\gamma_i \sum_{j=0}^{n} \mathrm{P}_{0j} \right) = 1,$$

and

$$\sum_{i=0}^{n} \mathrm{P}_{0i} = \frac{1}{1+\sum_{i=1}^{n} \gamma_i}. \tag{12}$$

Substituting (12) into (10) produces

$$\mathrm{P}_i = \frac{\gamma_i}{1+\sum_{j=1}^{n} \gamma_j} \tag{13}$$

and using (3),

$$\mathrm{P}_{0i} = \frac{\mu_i \gamma_i}{\left(\sum_{j=1}^{n} \lambda_j\right)\left(1+\sum_{j=1}^{n} \gamma_j\right)}. \tag{14}$$

P_{0i} is the probability the animal is in the idle state having completed a service of priority i. This does not mean, however, that the service was completed successfully. The probability of success given completion would be $\mu_i/(\mu_i+\mu_i^{\sim})$, where $\mu_i^{\sim}$ is the service rate of the other animal performing the complementary service; e.g., if μ_i were the rate of prey capture, then $\mu_i^{\sim}$ would be the rate of escape by that prey.

P_i and P_{0i} are steady state probabilities of an imbedded Markov chain in which the expected recurrence time of a state is the reciprocal of the steady state probability. Therefore, the number of completed services of priority i (X_i) is the product of P_{0i} (the probability of success) and T (the total time being considered). If we assume the P_{0i} calculated for the individual are an adequate representation of those of its species or age class, then this approach may be incorporated into an ecosystem model.

In such a model the arrival rate may be calculated using an analogy from statistical mechanics [4].

$$\lambda_i = 2\mathrm{D}\mathrm{R}_i\mathrm{N}_r(\mathrm{S}_q^2+\mathrm{S}_r^2)^{1/2}, \tag{15}$$

where

D = perception distance,

N_r = density of species r,

$\mathrm{S}_{q,r}$ = searching speed of the server (q) and of species r,

R_i = proportion of species r which are in the ith priority.

It is expected that R will depend on factors such as time of year, preferences for food items and the species. Given that μ_i is known, the P_{0i} may be calculated for each animal type q (Eq. 14).

Example 1. In order to examine some effects of competition using the model, let us consider two consumers (consumer 1 and consumer 2) which compete for a single prey item and are themselves the prey of a single predator. Let us assume the prey item is immobile ($S=0$, $\mu=0$), that $R_i=\frac{1}{4}$ for all species and all i and that consumer 2 displays dominant aggressive behavior toward consumer 1. The priority sequences for the two consumers is as follows:

Consumer 1	*Consumer* 2
(1) Escape predator	(1) Escape predator
(2) Escape dominant	(2) Chase prey
(3) Chase prey	(3) Chase subdominant

TABLE 1

Parameter Values for Four-Species System

Parameter	Prey	Consumer 1	Consumer 2	Predator
N (m^{-2})	10.0	0.5	0.5	0.1
S (m/sec)	0.0	0.02	0.02	0.04
D (m)		0.30	0.30	
μ_i (sec^{-1})				
$i=1$		0.20	0.20	
2		0.25	0.30	
3		0.30	0.25	
		$P_{03}=0.815$	$P_{02}=0.829$	

Table 1 presents the parameter values for this example. Note that the parameters for the two consumers are identical except that the priorities are realigned. The probability of being idle having completed a capture is also given in Table 1. Due to the dominant behavior of consumer 2, consumer 1 is less likely to have completed the capture process. To further investigate this phenomena, P_{03} for consumer 1 is plotted against the service rate of chasing prey and the speed of search (Fig. 1). This is compared to the same service (P_{02}) for consumer 2 (horizontal line in Fig. 1). In order for consumer 1 to increase its capture probability, it must increase its speed or service rate or both. But if the speed is increased too greatly, the chance of encountering a predator or a dominant will increase, and the gains in capture probability are nullified. Hence, the dominant behavior of consumer 2 leads to an advantage in capture of prey.

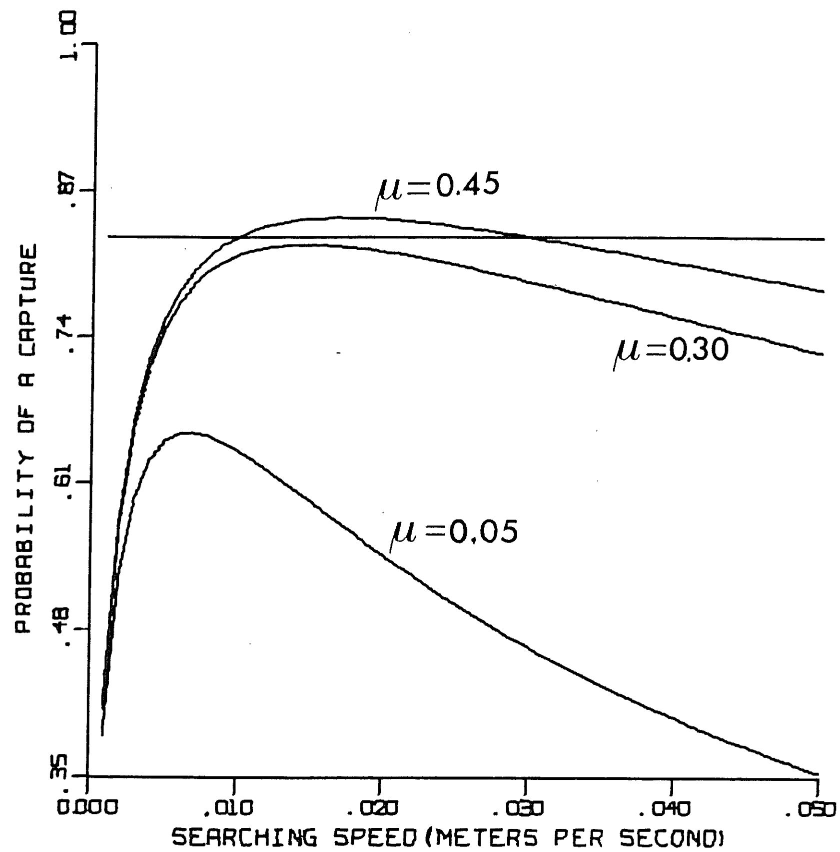

FIG. 1. Probability of capture of a food item by consumer 1, given searching speed and capture rate (μ) in $\sec^{-1}$. The horizontal line is the probability of capture of a food item for consumer 2.

Example 2. The following example shows some results of the queueing approach with a reasonably complete priority sequence incorporated into an ecosystem simulation model currently in use by the authors. This example describes the dynamics of a stream ecosystem composed of species of fish and crayfish, particulate organic matter, and macroinvertebrates. The priority sequence being employed for the fish and crayfish is as follows:

(1) Escape from predator.
(2) Escape from aggressive dominant.
(3) Spawn with receptive mate.
(4) If server in spawning condition, chase of subdominant.
(5) Chase of food item.
(6) If server not in spawning condition, chase of subdominant.

Priorities 4, 5, and 6 imply that when an animal is in spawning condition, aggressive social behavior takes precedence over chasing a food item.

The queueing process (Eq. 14 and 15) is iterated for each species and age class, and the number of successful completions of each priority (X_i) is computed for each time period (T). When X_5 is multiplied by the average weight of the prey, the product is ration size. The number of eggs spawned would be X_4 times the number of eggs per female times the number of

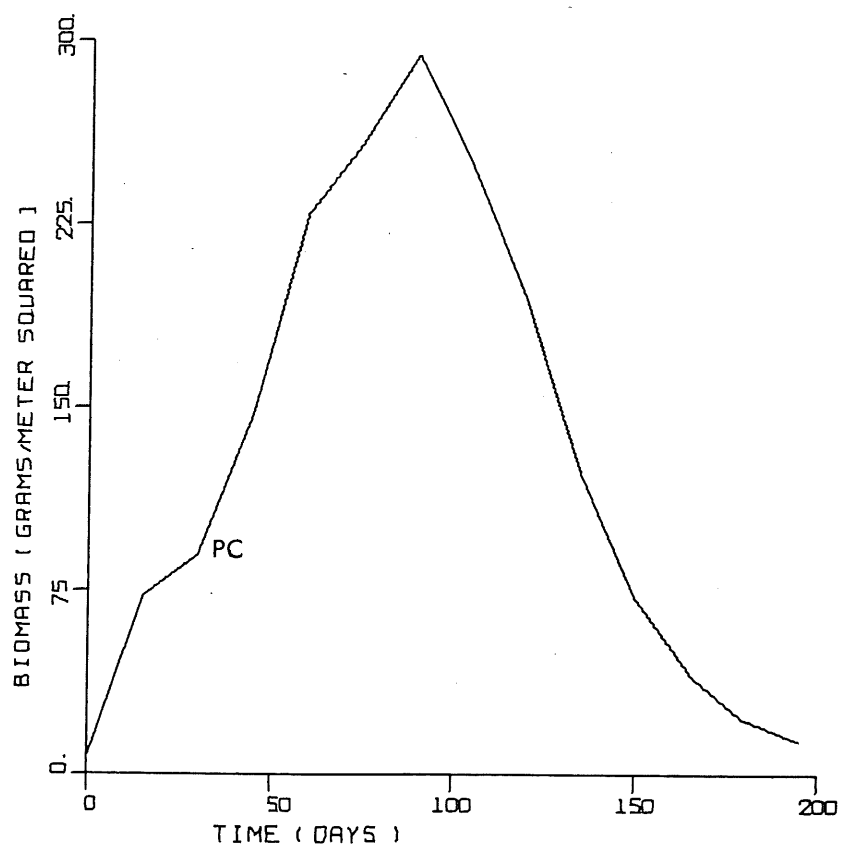

FIG. 2(a) Biomass density from simulation model. POM = particulate organic matter and macroinvertebrates; PC = primary consumers; PR = predators.

females, and the mortality is the product of the number of unsuccessful escapes and the number in the age class.

The above statistics are then inputs to a growth-metabolism routine in which ration is converted to calories and net caloric intake is calculated, and also to a population density routine where births are added and mortality subtracted. Two other subroutines define the fecundity and searching speed as functions of relevant variables such as body weight, ambient temperature, and the time of the year. In this way the queueing process maintains a dynamic nature from one time period to the next.

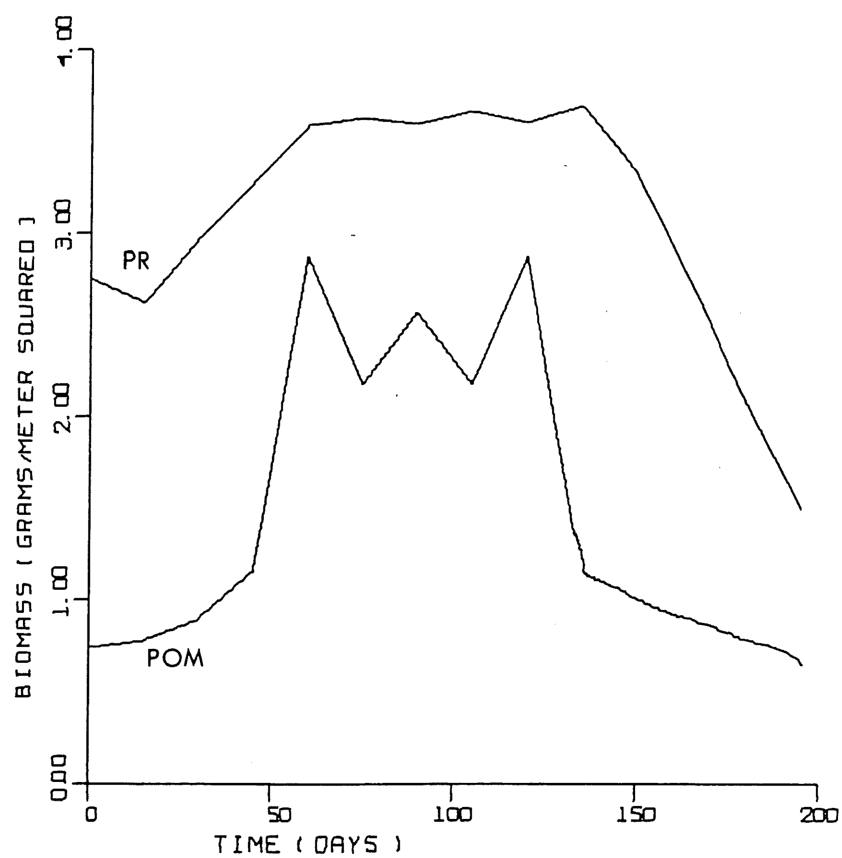

FIG. 2(b) Biomass density from simulation model. POM = particulate organic matter and macroinvertebrates; PC = primary consumers; PR = predators.

Table 2 gives an explanation of the queueing parameters relevant to this table. Simulation results in which the animals are grouped into particulate organic matter and macroinvertebrates (POM), primary consumers (PC), and predators (PR) are shown in Fig. 2(a, b). The PC biomass increases initially due to reproduction and to an increase in POM. The intense competition resulting from the high density causes a subsequent fall in PC biomass. The predator biomass follows the trend of the consumers after a lag period.

TABLE 2

Queueing Parameters for Fig. 2

μ_i $(i \neq 3)$	Service rates for all services other than spawning, 0.25/sec.
μ_3	Spawning rate, $\frac{1}{300}$ sec.
D	Perception distance, ranges from 0.5 to 2.0 m for the predators. It is 0.2 m for all primary consumers.
S	Searching speed, approximately 0.01 m/sec, but this varies with temperature and body weight.
R_i	Proportion of animals in the *i*th priority; these vary with species, time, and priority.
T	Total time of interaction per day, 8 hours.

REFERENCES

1 H. Fujita, An interpretation of the changes in type of the population density effect on the oviposition rate, *Ecology* **35**, 253 (1954).
2 C. S. Holling, The functional response of predators to prey density and its role in mimicry and population regulation, *Mem. Canad. Entomol. Soc.* No. 45 (1965).
3 A. Lee, *Applied Queueing Theory*, MacMillan, Toronto, Can., 1966.
4 M. Timin, A multispecies consumption model, *Math. Biosci.* **16**, 59 (1973).