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Edited by

Ovide Arino

*University of Pau  
Pau, France*

David E. Axelrod

*Rutgers University  
Piscataway, New Jersey*

Marek Kimmel

*Rice University  
Houston, Texas*

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## Competing Size-Structured Species

J. M. CUSHING

*University of Arizona, Tucson, AZ 85721*

### I. INTRODUCTION

Body size is one of the most important attributes of an individual organism. It is significant in determining an organism's energetic requirements and ability to exploit resources for growth and reproduction and its interaction with its physical and biological environment, including predators, prey, and competitors. Despite these obvious and recognized facts, relatively little mathematical theory of size-structured population interactions exists and virtually no dynamical models of competing size-structured species can be found in the literature. For a discussion of the importance of size structure in population dynamics and ecological interactions, particularly competitive interactions, see Werner and Gilliam (1984).

Zooplankton communities provide one important example in which size structure has been of primary significance in the study of multispecies interactions. The observation that species of zooplankton tend to occur in associations characterized by body size and that large size species tend to predominate in zooplankton communities, at least in the absence of planktivorous fish, led Brooks and Dodson (1965) to propose the *size efficiency hypothesis* (SEH). The two basic elements of this hypothesis are that large zooplankton species are more efficient at exploiting resources, which provides the potential for the competitive exclusion of smaller species, and that size-selective predation by large-bodied (vertebrate) predators, which falls more heavily on the larger zooplankton species, can allow for the survival of smaller species or even in some cases result in the elimination of larger species. This hypothesis has been the main theoretical framework of much zooplankton research since its formulation, and many experimental studies have attempted to test its assumptions and verify its implications (see Hall et al., 1976). Although the principle that predator-mediated competition plays an important role in shaping zooplankton community structure seems to be widely accepted, attempts to verify the assumption that larger species are more "efficient" competitors have been equivocal. It appears that this notion is more complicated than first

thought. Furthermore, other factors, such as invertebrate predation and "juvenile bottlenecks," have led to modifications of the original SEH (Dodson, 1974; Hall et al., 1976; Neill, 1975; Lynch, 1978; DeMott and Kerfoot, 1982; Gerritsen, 1984).

The purpose of this paper is to derive and analyze some competition models for the dynamics of  $n$  size-structured species competing for a single limiting resource and to see what implications they have with regard to the relationship between body size and competitive success. In Section II a discrete model is proposed and its dynamics studied. This model is for an "interference" competitive interaction for a single limiting resource that is supplied at a constant rate. In Section III a continuous model for an "exploitative" competition for a single limiting and dynamically varying resource is studied. The model is based on the single-species model of Diekmann et al. (1984). Both models are built on the basic assumption that resource uptake rates are proportional to body surface area. They are therefore particularly relevant to many simple (invertebrate) animals such as made up zooplankton communities (e.g., filter-feeding species of *Daphnia*). The continuous model is more general in that it includes several features neglected in the discrete model: namely, metabolic demands, a model-determined maximal adult size, and resource dynamics. The discrete model, however, is mathematically more tractable.

One major point that emerges from the analyses is that one must be very careful about relating crucial body size measurements (e.g., adult size, juvenile size, or size at birth) to competitive success. Among species that are very similar in all other regards, a large body size is an advantage. However, there are many other factors that can compensate for a competitive disadvantage due to small body size.

## II. DISCRETE SIZE-STRUCTURED COMPETITION MODEL

We begin with the description of a general discrete model for the dynamics of a structured population whose individual members are categorized by means of and are allowed to move between a finite number  $m \geq 1$  of specified classes. Let  $x_i(t)$  denote the number or density of individuals in class  $i$ ,  $1 \leq i \leq m$ , at times  $t = 0, 1, 2, \dots$ , and let  $x(t) = \text{col}(x_i(t))_{i=1}^m$  be the column vector of these densities.

The transitions among all classes that occur between time  $t$  and  $t + 1$  yields a new class distribution vector given by  $Tx(t)$ , where  $T$  is the  $m \times m$  transition matrix

$$T = \begin{bmatrix} \Pi_1(1 - f_1) & \Pi_2 f_{12} f_2 & \cdots & \Pi_m f_{1m} f_m \\ \Pi_1 f_{21} f_1 & \Pi_2(1 - f_2) & \cdots & \Pi_m f_{2m} f_m \\ \Pi_1 f_{31} f_1 & \Pi_2 f_{32} f_2 & \cdots & \Pi_m f_{3m} f_m \\ \vdots & \vdots & \ddots & \vdots \\ \Pi_1 f_{m1} f_1 & \Pi_2 f_{m2} f_2 & \cdots & \Pi_m(1 - f_m) \end{bmatrix}$$

Here  $\Pi_j$  is the probability that a  $j$ -class individual survives one unit of time. After one unit of time, a fraction  $f_j$  of the surviving individuals leave class  $j$ , with a fraction  $f_{ij}$  of this group moving into class  $i \neq j$ . In addition to these transitions, classes may obtain new members due to births. (Immigrations and emigrations will be ignored.) After one unit of time, a surviving  $j$ -class individual gives birth

to  $b_{ij}$   $i$ -class offspring, and consequently, the class distribution vector of offspring at time  $t + 1$  is given by  $Bx(t)$ , where  $B = (\Pi_i b_{ij})$ . [Here the census is assumed taken immediately following reproduction by surviving individuals. If, on the other hand, the census were taken immediately before reproduction, then  $B$  would be  $(\Pi_i b_{ij})$ .] If both births and class transitions are taken into account, the class distribution vector at time  $t + 1$  is the sum  $Tx(t) + Bx(t)$  and the dynamics of the class distribution vector are determined by the matrix difference equation

$$x(t + 1) = Px(t), \quad P = T + B \tag{1}$$

In the event that some parameters are dependent on time  $t$  [either explicitly or implicitly through a dependence upon the density vector  $x(t)$ ] the projection matrix  $P$  is dependent on  $t$  [i.e.,  $P = P(t, x(t))$ ]. Thus (1) can be nonlinear.

This general model includes the famous matrix model for age-structured populations of Leslie (1945). In this case the classes are age classes one time unit in length, so that  $f_j = 1$ ,  $f_{ij} = 0$  if  $j \neq i - 1$ , and  $f_{i, i-1} = 1$ , (i.e., all surviving individuals must advance one age class in one unit of time).  $P$  then becomes a Leslie matrix. Another special case occurs when  $0 < f_j = \text{constant}$ ,  $f_{ij} = 0$  if  $j \neq i - 1$ , and  $f_{i, i-1} = 1$  (i.e., individuals either remain in their class or move to the next class in one unit of time). In this case  $P$  is an Usher matrix. Usher matrix models have found extensive use in size-structured models of tree forest dynamics (see, e.g., Ek and Monserud, 1979; Usher, 1972).

We now make two modeling assumptions. First, we assume that the fractions  $f_{ij}$  are constant, but that the fractions  $f_j$  of  $j$ -class individuals who leave class  $j$  and the birth rates  $b_{ij}$  are proportional to a "resource uptake function"  $u$  which can depend (explicitly or implicitly) on time,  $u = u(t, x(t))$ . Thus we write

$$b_{ij} = \phi_{ij}u, \phi_{ij} \geq 0 \quad \text{and} \quad f_j = \phi_ju, \phi_j \geq 0$$

Here the focus is on the effects of differences in growth and fertility rates between individual organisms in different classes, as opposed to differences in survival rates. Consequently, our second assumption will be that the probability of surviving a unit of time is the same for all classes [i.e.,  $\Pi_j = \Pi(t, x(t))$ ]. This admittedly simplistic assumption is undoubtedly biologically unreasonable in many cases. However, this assumption will permit a considerable amount of analysis to be performed on what are otherwise quite complicated model equations (in particular, on the multispecies competition model in Section IV). Despite this concession in the interest of analytical tractability, it is hoped that by focusing on class-dependent transitions and birthrates alone, at least some understanding will be gained of the effects of the dynamics of competing populations that are due to individual differences in these vital rates.

Under these two assumptions equation (1) can be written in the general form

$$x(t + 1) = P(t)x(t), \quad P(t) = a(t)I + b(t)L \tag{2}$$

This can be done by setting  $a(t) = \Pi(1 - \phi_q u)$ ,  $b(t) = \Pi u$ , and

$$L = \begin{bmatrix} \phi_q - \phi_1 + \phi_{11} f_{12}\phi_2 + \phi_{12} & \cdots & f_{1q}\phi_q + \phi_{1q} & \cdots & f_{1m}\phi_m + \phi_{1m} \\ f_{21}\phi_1 + \phi_{21} & \phi_q - \phi_2 + \phi_{22} & \cdots & f_{2q}\phi_q + \phi_{2q} & \cdots & f_{2m}\phi_m + \phi_{2m} \\ \vdots & \vdots & & \vdots & & \vdots \\ f_{q1}\phi_1 + \phi_{q1} & f_{q2}\phi_2 + \phi_{q2} & \cdots & \phi_{qq} & \cdots & f_{qm}\phi_m + \phi_{qm} \\ \vdots & \vdots & & \vdots & & \vdots \\ f_{m1}\phi_1 + \phi_{m1} & f_{m2}\phi_2 + \phi_{m2} & \cdots & f_{mq}\phi_q + \phi_{mq} & \cdots & \phi_q - \phi_m + \phi_{mm} \end{bmatrix}$$

where  $\phi_q$  is the largest  $\phi_i$  (i.e.,  $\phi_q \geq \phi_i$  for all  $i$ ). Note that  $L$  is a constant, nonnegative matrix.

Let  $w \geq 0$ ,  $w \neq 0$ , be a given vector and let  $w^T$  denote its transpose. Then  $w^T x$  is the usual inner product.  $w$  defines a "weighted population" size  $p(t) = w^T x(t)$ . For example, if all components of  $w$  are 1, then  $p(t)$  is the total population numbers at time  $t$ . Let  $\eta(t) = x(t)/p(t)$  denote the "normalized class distribution." A proof of the following result is sketched in the Appendix to this chapter.

*Theorem 1.* Assume that the following two hypotheses hold.

- (H1) There exist constants  $a_0$  and  $b_0$  such that  $0 < b_0 \leq b(t)$ ,  $0 \leq a(t) \leq a_0$  for all  $t = 0, 1, 2, \dots$
- (H2)  $L$  has a strictly dominant, simple eigenvalue  $\lambda^+ > 0$  with an associated positive eigenvector  $v^+ > 0$ , which is normalized so that  $w^T v^+ = 1$ .

Also assume that  $x(t) \geq 0$  is a solution of (2) for which  $x(0) \geq 0$  ( $\neq 0$ ) and  $p(t) > 0$  for  $t \geq 0$ . Then  $\eta(t) \rightarrow v^+ > 0$  as  $t \rightarrow +\infty$ .

This is a generalization of a nonlinear ergodic result of Cushing (1989b) (see Caswell, 1989). The dynamics of total weighted population size  $p(t)$  are governed by the equation

$$p(t+1) = (a(t) + b(t)w^T L \eta(t))p(t) \quad (3)$$

which can be obtained by forming the inner product of (2) with  $w^T$  and noting that  $w^T L x(t) = w^T L \eta(t)p(t)$ . By Theorem 1,  $w^T L \eta(t) \rightarrow w^T L v^+ = \lambda^+ w^T v^+ = \lambda^+$ . Thus (3) is "asymptotic" to the "limit equation"

$$p(t+1) = (a(t) + \lambda^+ b(t))p(t) \quad (4)$$

and one might expect that the long-time asymptotic dynamics of  $p(t)$  can be deduced from this equation in place of (3). These ideas can be made mathematically rigorous (LaSalle, 1976), but these technicalities will not detain us here. We will use (4) to study the dynamics of the total weighted population sizes in the competition models below.

Let us now briefly consider a specific model of "interference" competition based on size classes. [More details and further analysis of this model will appear elsewhere (Cushing, 1990).] Let  $x_i(t)$  denote the number or density of individuals of length  $s$  lying in the size class interval  $[\bar{s}_{i-1}, \bar{s}_i]$ ,  $0 < \bar{s}_0 < \bar{s}_1 < \dots < \bar{s}_m$ . Let  $s_i$  be a representative length of an individual from size class  $i$  [e.g., the average  $s_i = (\bar{s}_i + \bar{s}_{i-1})/2$ ]. An individual of size  $s_i$  will be an individual of size class  $i$ . If  $r_i$  is the "inherent" resource uptake rate per unit time per unit body area of an individual of size class  $i$  (i.e., the uptake rate at low population densities in the absence of intraspecific or interspecific competitive effects) and  $e^{-d}$  denotes the fractional decrease in resource uptake of an individual (per unit of body surface area per unit time) due to a unit surface area of competitor, the resource uptake rate of an individual of size  $s_i$  is approximately  $r_i \sigma_i s_i^2 \exp(-dp(t))$ . Here  $p(t) = w^T x(t)$  is the total surface area of all individuals at time  $t$  and the weighting vector  $w$  consists of the (average) body surface areas  $w = \text{col}(\sigma_i s_i^2)$ . The constant  $\sigma_i > 0$  is a constant of proportionality that relates surface area to the square of body length (it clearly depends on body geometry). In this model the resource is supplied at a constant rate and is not dynamically modeled.

If all individual organisms of size  $s_i$  have uniform density and body volume scales cubically to length, then an individual's body weight is given by  $W_i = \mu_i s_i^3$ .

The weight change  $\Delta_i W$  of an individual of size  $i$  over a unit of time is approximately  $3\mu_i s_i^2 \Delta_i s$ , where  $\Delta_i s$  is its change in length over one unit of time. On the other hand, weight change can be related to the resource uptake rate by the formula  $\Delta_i W = \kappa_i r_i \sigma_i s_i^2 \exp[-dp(t)]/\eta_i$ , where  $\kappa_i > 0$  is the fraction of consumed resource that individuals of size  $s_i$  allocate to growth and  $\eta_i > 0$  is a conversion factor of resource units to body weight. It follows that the growth rate per unit time of an individual of size  $i$  is  $\Delta_i s = \kappa_i \sigma_i r_i \exp[-dp(t)]/3\mu_i v_i$ .

We will assume that no individual can shrink in size and for simplicity that the size class interval lengths  $\delta_i = \bar{s}_{i+1} - \bar{s}_i$  are chosen so that in one unit of time an individual can grow no more in length than into the next size class. The transition matrix  $T \geq 0$  is given by the bidiagonal matrix

$$T = \Pi \begin{bmatrix} 1 - \beta_1 e^{-dp(t)} & 0 & \dots & 0 & 0 \\ \beta_1 e^{-dp(t)} & 1 - \beta_2 e^{-dp(t)} & \dots & 0 & 0 \\ 0 & \beta_2 e^{-dp(t)} & \dots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & \dots & 1 - \beta_{m-1} e^{-dp(t)} & 0 \\ 0 & 0 & \dots & \beta_{m-1} e^{-dp(t)} & 1 \end{bmatrix} \quad (5)$$

Here  $\beta_i = \kappa_i r_i \sigma_i / 3\mu_i \eta_i \delta_i$  is defined to be the "growth coefficient." The reason for the 1 in the lower right-hand corner of  $T$  is that no individual can grow larger than  $\bar{s}_m$ .

Consider now the fertility matrix  $B$ . It will be assumed that all newborns lie in the smallest size class,  $[\bar{s}_0, \bar{s}_1)$ . If the remaining fraction  $1 - \kappa_i$  of consumed resource is allocated to reproduction and if  $\omega_i > 0$  is a conversion factor of resource units to offspring body weight, the birth rate for an individual of size  $i$  is  $\alpha_i \exp[-dp(t)]$ , where

$$\alpha_i = \frac{(1 - \kappa_i) r_i \sigma_i s_i^2}{\omega_i w_1}$$

is defined to be the "reproductive coefficient" and where  $w_1 = \mu_1 \bar{s}_1^3$  is the weight at birth. Then

$$B = \Pi e^{-dp(t)} \begin{bmatrix} \alpha_1 & \alpha_2 & \dots & \alpha_m \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix} \quad (6)$$

The dynamics of the population density vector  $x(t)$  are governed by equation (2) with

$$a(t) = \Pi(1 - \beta_q e^{-dp(t)}), \quad b(t) = \Pi e^{-dp(t)}$$

and with  $L$  given by the nonnegative Usher matrix

$$L = \begin{bmatrix} \beta_q - \beta_1 + \alpha_1 & \alpha_2 & \dots & \alpha_q & \dots & \alpha_{m-1} & \alpha_m \\ \beta_1 & \beta_q - \beta_1 & \dots & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & \dots & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & \dots & 0 & \dots & \beta_q - \beta_{m-1} & 0 \\ 0 & 0 & \dots & 0 & \dots & \beta_{m-1} & \beta_q \end{bmatrix}$$

where  $\beta_q$  is the largest  $\beta_i$ . Clearly,  $L > 0$ ,  $0 \leq a(t) \leq a_0 = \Pi$ , and  $b(t) \geq 0$ . In fact,  $b(t)$  is bounded away from 0, as is required by (H1), because it can be shown that  $p(t)$  is bounded (see Lemma 2 of the Appendix). Also, if  $L$  satisfies (H2) (the Perron-Frobenius theory applies to this question), the dynamics of  $p(t)$  are determined by the scalar equation (4), that is, by the scalar difference equation

$$p(t+1) = \Pi(1 + \theta e^{-dp(t)})p(t) \quad (7)$$

with  $p(0) = w^T x(0) > 0$ , where  $\theta = \lambda^+ - \beta_q$ . Since  $\lambda^+ > 0$  is the dominant eigenvalue of  $L$ ,  $\theta$  is that eigenvalue of the matrix

$$M = L - \beta_q I = \begin{bmatrix} -\beta_1 + \alpha_1 & \alpha_2 & \cdots & \alpha_{m-1} & \alpha_m \\ \beta_1 & -\beta_2 & \cdots & 0 & 0 \\ 0 & \beta_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & -\beta_{m-1} & 0 \\ 0 & 0 & \cdots & \beta_{m-1} & 0 \end{bmatrix} \quad (8)$$

with the largest real part.

The dynamics of (7) can be summarized as follows. There exists a unique positive equilibrium  $p(t) \equiv e = d^{-1} \ln(\theta/\theta')$ ,  $\theta' = (1 - \Pi)/\Pi$ , provided that  $\theta/\theta' > 1$ . If  $\theta/\theta' > 1$ , then  $p(t) \rightarrow 0$  as  $t \rightarrow +\infty$ . If  $1 < \theta/\theta' < \theta_0 = \exp[1/(1 - \Pi)]$ , then  $e > 0$  is globally attracting and solutions  $p(t)$  are nonoscillatory. If  $\theta_0 < \theta/\theta' < \theta_0^2$ , then  $e > 0$  is globally attracting and solutions  $p(t)$  are oscillatory, but damped. If  $\theta/\theta' > \theta_0^2$ , then  $e > 0$  is repelling and there occurs the familiar cascade of periodic doubling bifurcations of stable limit cycles and ultimately "chaos" as  $\theta/\theta'$  is increased.

Consider now the interaction of  $n$  size-structured species  $j = 1, 2, \dots, n$ , each of whose dynamics is described by a model of the type described above, all of whom utilize a common limiting resource that is supplied to species  $j$  at a constant rate  $r_j$ . Each species is described by an  $m_j$ -vector  $x_j(t) = \text{col}(x_{ij}(t))$  of size class densities. It is assumed that the same length scale is used for each species, but not necessarily the same size classes or number of size classes. All model parameters above are now subscripted by  $j$  to indicate species as well as size dependence. We then obtain a system of  $n$  coupled nonlinear matrix equations for the  $n$  class density vectors  $x_j(t)$ . Just as in the single species case considered above, we find that the normalized size distribution of each species asymptotically approaches the normalized positive eigenvector of  $L_j$ , regardless of the asymptotic dynamics of  $x_j(t)$  or  $p_j(t)$  and that the dynamics of the total population surface areas  $p_j(t)$  are governed by the system of limiting equations

$$p_j(t+1) = \Pi_j(1 + \theta_j e^{-\sum_k d_k p_k(t)})p_j(t) \quad (9)$$

Here  $\theta_j$  is the eigenvalue of  $M_j$  with largest real part.  $M_j$  has the form (8) with additional subscripts  $j$  on its entries to indicate species dependence.

It is easy to see that (9) possesses no equilibria for which all species are positive (except in the infinitely unlikely case when two or more nonlinear equations have identical solutions). The only nonnegative equilibria are the zero equilibrium and the  $n$  axis equilibria for which exactly one species is present, namely  $p_j = 0$  for  $j \neq k$  and



$$p_k = e_k \quad \text{where} \quad e_k = d_k^{-1} \ln \frac{\theta_k}{\theta'_k} \quad (10)$$

provided that  $\theta_k/\theta'_k > 1$  (i.e., provided that the  $k$ th species has a positive equilibrium in the absence of the other species). In fact, any species for which  $\theta_k/\theta'_k < 1$  will be eliminated, that is, any species that has no positive equilibrium in the absence of competition cannot survive in the presence of competition. This is easily seen from the inequality  $0 \leq p_k(t+1) \leq \Pi_k(1 + \theta_k)p_k(t)$ , which follows from (9). Accordingly, we assume that

$$\frac{\theta_j}{\theta'_j} > 1 \quad \text{for all } j$$

(i.e., each species has a positive equilibrium in the absence of competition). A simple linearization argument shows that this assumption implies that the zero equilibrium of (9) is a repeller. Thus all species will not be eliminated.

The axis equilibrium (10) will be referred to as the "inherent equilibrium of the  $k$ th species." An inherent equilibrium will be called "inherently stable" if that species is stable in the absence of competition [i.e., if  $e_k$  is a stable equilibrium of (7) with subscripts  $k$ ]. This occurs if  $\theta_k/\theta'_k < \theta_{0k}^2 = \exp[-2/(1 - \Pi_k)]$ . An inherent equilibrium will be called "competitively stable" if it is stable in the presence of competition, [i.e., if it is stable as an equilibrium of (9)]. A competitively stable axis equilibrium implies that the  $k$ th species is immune to competitive exclusion from invasion by small populations of the other species.

The eigenvalues of the linearization of (9) at the  $k$ th equilibrium (10) are  $1 - (1 - \Pi_k)d_k e_k$  and  $\Pi_j(1 + \theta_j \exp(-d_k e_k))$ ,  $j \neq k$ . The first lies in the interval  $(-1, +1)$  provided that  $\theta_k/\theta'_k < \theta_{0k}^2$ , (i.e., the  $k$ th species is inherently stable). All the remaining positive eigenvalues lie in  $(-1, +1)$  provided that

$$\frac{\theta_k}{\theta'_k} > \frac{\theta_j}{\theta'_j} \quad \text{for all } j \neq k$$

We conclude that the inherent equilibrium (10) for species  $k$  is locally competitively stable provided that it is inherently locally stable and provided that it has the largest ratio  $\theta_j/\theta'_j$ . In particular, the competition equations (9) can have at most one locally stable equilibrium. Under some further parameter restrictions this local stability result can be shown to be global (Cushing, 1990).

This stability result is of course consistent with the basic principle in ecology that no more than one species can survive on a single limiting resource. Whereas this "competitive exclusion principle" holds here as far as equilibrium dynamics is concerned, it does not necessarily hold for model (9) if nonequilibrium dynamics are considered. When one species has nonequilibrium inherent dynamics, it is possible for more than one species to coexist on a single resource. This coexistence is by means of a nonequilibrium state and can be in the form of limit cycles or even "chaos." [This phenomenon has been observed before in nonstructured models for exploitative competition models by McGehee and Armstrong (1977), Butler et al. (1983), and others.] Such cases will not be discussed further here, as only equilibrium dynamics will be considered.

The surviving species is determined by the aggregate parameters  $\theta_j$ , which contain the size-specific parameters of the model, and by  $\theta'_j = (1 - \Pi_j)/\Pi_j$ . With

regard to the size-specific model parameters, this model implies (insofar as equilibrium dynamics are concerned) that it is to a species' advantage in a competitive situation to have a large  $\theta_j$  value. To relate competitive success to species body size it is required to explore the relationship between the eigenvalue  $\theta_j$  and the entries  $\alpha_j, \beta_j$  of the matrix  $M_j$ .

It can be shown, under the reasonable assumptions that  $\alpha_1 = 0$  (the smallest size class is infertile) and  $\alpha_m > \alpha_i$  for all  $i \neq m$ , that the eigenvalue  $\theta$  of a matrix  $M$  with form (8) is an increasing function of each of the size-class-specific reproductive coefficients  $\alpha_i$  (Cushing, 1990). Thus an increase in any of these coefficients can be viewed as advantageous to a species insofar as potential competitive situations are concerned.

For example, consider a competitive interaction between species that are similar, or more precisely model identical, except for maximal adult size. In this case all  $\theta_j$  are equal and the winning species has the largest eigenvalue  $\theta_j$ . The matrices  $M_j$  differ only in the reproductive coefficient of the largest size class  $m$ . As a result the  $\theta_j$  are eigenvalues of matrices (8) differing only in the entry  $\alpha_m$ . It follows that the surviving species (i.e., the only locally stable species) is the one with the largest  $m$  class reproductive coefficient  $\alpha_m$ , which, if all other model parameters are identical, is the species with the largest adult size  $s_m$ . Thus, under these circumstances, our model supports the first tenet of the SEH, at least for competitive interactions between "similar" species.

However, if suitable differences exist between the species (i.e., between other model parameters), it is easily possible for the largest species to be a competitive loser. For example, a smaller species can have a larger ratio  $\theta/\theta'$  by possessing higher survivability factors, smaller resource conversion factors, different resource allocation factors, smaller weight at birth, or smaller maturation size. A simple case will illustrate this point.

Suppose that there are no significant differences in the growth coefficients of all juvenile classes or the reproductive coefficients of all adult classes and suppose that once an individual reaches a maturation size it remains fertile. In such a case all juvenile size classes and all adult size classes can be grouped and a model consisting of only two size classes considered. In this case the matrix

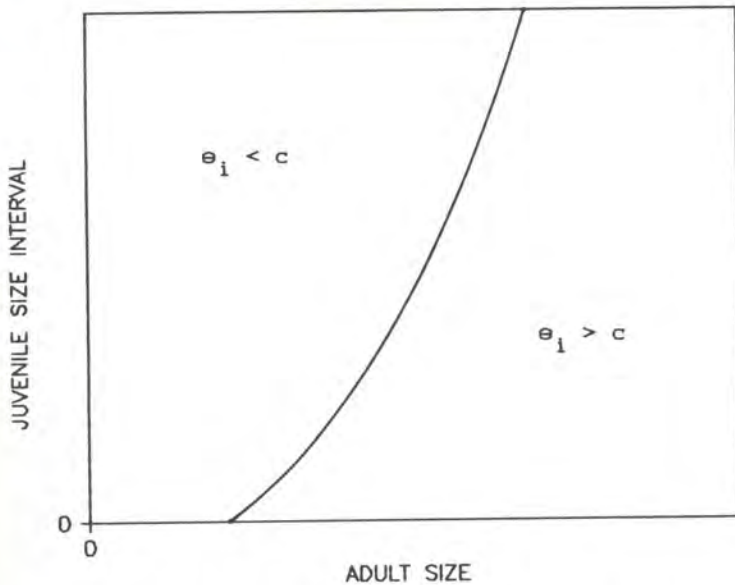
$$M_j = \begin{pmatrix} -\beta_j & \alpha_j \\ \beta_j & 0 \end{pmatrix}$$

is  $2 \times 2$  and a study of the parameter dependence of its eigenvalue

$$\theta_j = \frac{1}{2}(-\beta_j + (\beta_j^2 + 4\beta_j\alpha_j)^{1/2})$$

is relatively straightforward. (For simplicity the unnecessary size class index has been suppressed:  $\beta_j = \beta_{1j}$ ,  $\alpha_j = \alpha_{2j}$  and  $s_j = s_{2j}$ ,  $\kappa_j = \kappa_{1j}$ , etc.)

Consider  $\theta_j = \theta_j(s_j, \delta_j)$  as a function of  $s_j$  (adult size) and  $\delta_j$  (the length of the juvenile size class or simply the "maturation size"). A typical level curve  $C_j$ :  $\theta_j(s_j, \delta_j) = c$  is drawn in Fig. 1. From this graph one sees that a change in  $s_j$  or  $\delta_j$  that moves the point  $(s_j, \delta_j)$  to the right (left) of  $C_j$  will result in an increase (decrease) in  $\theta_j$ . With regard to competitive interactions, this observation can be interpreted in the following way. If another species  $x_k$  with identical parameters, except for  $s_k$  and  $\delta_k$ , is put in competition with species  $x_j$ , then it will competitively exclude this species if the point  $(s_k, \delta_k)$  lies to the right of the curve  $C_j$  in Fig. 1.



**Figure 1** The level curves of the eigenvalue  $\theta_1(s_j, \delta_j) = c$  of  $M_j$  in the  $2 \times 2$  case are parabolic in the  $s_j, \delta_j$ -plane.  $s_j$  is the (average) adult size and  $\delta_j$  is the length of the juvenile size class.

Thus, once again, we find that if two species are otherwise identical, the one with the smaller adult size will suffer competitive exclusion. We also see that if two species are otherwise identical, the species with the larger size at maturation will suffer competitive exclusion.

Notice, however, that if both adult and juvenile sizes are changed, a decrease in adult size need not result in competitive exclusion. It is clear from Fig. 1 that an increase in adult size accompanied by an increase in maturation size could possibly result in parameter values to the left of the curve  $C_j$  and hence a decrease in  $\theta_j$ . Consequently, a species with larger adult size could competitively lose out to a species with a smaller adult size if its maturation size is too much larger than that of the smaller species.

Further studies of this discrete model can be found in Cushing (1990). We turn now to some models of competing size-structured species in which time and size are continuous variables.

### III. CONTINUOUS SIZE-STRUCTURED COMPETITION MODEL

We begin with a capsule summary of the model for the dynamics of a single size-structured species given by Diekmann et al. (1984). A full treatment can be found in Metz and Diekmann (1986, Chap. I.3). The models in Section II are discrete analogs of these continuous models, although there will be some differences (e.g., the inclusion of metabolic demands in the continuous model).

The basic assumption is again that food ingestion is proportional to body surface area. If  $s$  denotes length and  $R$  denotes resource or food density, then

resource uptake rate is  $f(R)s^2$ , where the resource uptake rate (per unit area)  $f(R)$  is dependent on resource density  $R$ . It is assumed that this rate is continuously differentiable and positive whenever the resource density is nonzero:

$$f(0) = 0, \quad f(R) > 0 \quad \text{for } R > 0$$

Although it is not necessary for much of the analysis below, for simplicity only the case of monotonically increasing rates  $f(R)$  will be considered. A typical such relationship is the Michaelis–Menten or Holling type II expression  $f(R) = cR/(a + R)$ ,  $c > 0$ ,  $a > 0$ .

It is further assumed that ingested food is allocated between metabolic maintenance, individual growth, and reproduction. Energy reserves are ignored. If metabolic maintenance needs are assumed proportional to weight (or, up to a scaling factor, to volume), if a fraction  $\kappa$  of ingested food is available for individual growth and metabolic demands, and if  $\eta$  is a conversion factor relating weight to food units, then one obtains a growth equation  $ds/dt = g(R, s)$  with  $g(R, s) = [\kappa f(R) - \zeta s]_+/3\eta$ , where  $\zeta$  is the metabolic rate [i.e., the rate (per unit volume) of food units needed for metabolic maintenance]. Here  $[x]_+ = x$  for  $x > 0$ , and 0 otherwise.

It is assumed that the remaining fraction  $1 - \kappa$  of ingested food is channeled to reproduction. If  $s_b$  and  $s_j$  denote the length at birth of all individuals and the length at which reproduction starts, respectively, and if reproduction ceases when the growth rate drops to zero, the individual birthrate is given by

$$m(R, s) = \begin{cases} 0, & s_b \leq s < s_j \\ \frac{(1 - \kappa)f(R)s^2}{\omega w_b}, & s_j \leq s \leq \underline{s}(R) \\ \frac{f(R)s^2 - \zeta s^3}{\omega w_b}, & \max\{s_j, \underline{s}(R)\} \leq s \leq \bar{s}(R) \end{cases}$$

Here  $\omega$  is a reproduction conversion factor relating food units to offspring weight; that is,  $\omega w_b$  is the amount of food needed to produce one offspring, where  $w_b$  is the weight at birth (if individuals are assumed to have a uniform density, then with an appropriate choice of units,  $w_b = s_b^3$ ).  $\underline{s}(R)$  is the size at which growth stops at resource density  $R$  and  $\bar{s}(R)$  is the size at which all food is needed just for maintenance,

$$\underline{s}(R) = \zeta^{-1} \kappa f(R) \leq \zeta^{-1} f(R) = \bar{s}(R)$$

Finally, it is assumed that the individual death rate  $d > 0$  is a constant independent of size, time, and resource density  $R$ .

The foregoing submodels for growth, birth, and death rates can be incorporated into dynamical equations for population level dynamics by using the modeling methodology of Metz and Diekmann (1986) (see also Sinko and Streifer, 1967). If  $\rho(t, s)$  denotes population density as a function of time  $t$  and length  $s$ , then for  $t > 0$ ,

$$\frac{\partial}{\partial t} \rho(t, s) + \frac{\partial}{\partial s} (g(R, s) \rho(t, s)) = -d\rho(t, s) \quad \text{for } s_b < s < \bar{s}(R)$$

$$g(R, s_b)\rho(t, s_b) = \int_{s_j}^{s(R)} m(R, s)\rho(t, s) ds$$

$$\rho(t, s) = 0, \quad s > \bar{s}(R)$$

To complete the formulation of the model, the dynamics of the resource must be specified. The simplest assumption is that the food resource density  $R$  is somehow held constant over time. This case is investigated in some detail by Metz and Diekmann (1986). The more realistic case when resource density can change due to the feeding activity of the population and to other external causes is considered here. If  $k(R)$  denotes the inherent density dependent growth rate of the resource  $R = R(t)$  in the absence of feeding by the population  $\rho$ , then

$$\frac{dR}{dt} = k(R) - f(R) \int_{s_b}^{s(R)} \rho(t, s)s^2 ds$$

A typical resource growth law is  $k(R) = (R_0 - R)d$ ,  $R_0 > 0$ ,  $d > 0$ , which corresponds to a constant replenishing of nonreproducing food particles and a constant system washout (by, for example, dilution in a continuous-flow culture such as in a chemostat). Another would be the classical logistic law for a self-renewing resource.

We are interested in the dynamics of several competing species of the type meeting the assumptions described above, all of which attempt to utilize the same limiting resource  $R$ . It will be assumed that the  $n$  interacting species, whose densities will be denoted by  $\rho_i$ ,  $1 \leq i \leq n$ , interact with each other by means of this common limited food resource and in no other way so that the competition is of the type usually referred to as "exploitative," as opposed to "interference." Thus, for  $i = 1, \dots, n$  and  $t > 0$ ,

$$\frac{\partial}{\partial t} \rho_i(t, s) + \frac{\partial}{\partial s} (g_i(R, s)\rho_i(t, s)) = -d_i \rho_i(t, s), \quad s_{b_i} < s < \bar{s}_i(R)$$

$$g_i(R, s_{b_i})\rho_i(t, s_{b_i}) = \int_{s_{j_i}}^{s_i(R)} m_i(R, s)\rho_i(t, s) ds \tag{11}$$

$$\frac{dR}{dt} = k(R) - \sum_{i=1}^n f_i(R) \int_{s_{b_i}}^{s_i(R)} \rho_i(t, s)s^2 ds$$

together with  $\rho_i(t, s) = 0$ ,  $s > \bar{s}_i(R)$ . All quantities  $\kappa$ ,  $\zeta$ ,  $\omega$ , and so on, are species specific and are consequently subscripted.

In the absence of the other competitors the dynamics of the species  $\rho_i$  are governed for  $t \geq 0$  by the equations

$$(a) \quad \frac{\partial}{\partial t} \rho_i(t, s) + \frac{\partial}{\partial s} (g_i(R, s)\rho_i(t, s)) = -d_i \rho_i(t, s), \quad s_{b_i} < s < \bar{s}_i(R)$$

$$(b) \quad g_i(R, s_{b_i})\rho_i(t, s_{b_i}) = \int_{s_{j_i}}^{s_i(R)} m_i(R, s)\rho_i(t, s) ds \tag{12}_i$$

$$(c) \quad \frac{dR}{dt} = k(R) - f_i(R) \int_{s_{b_i}}^{s_i(R)} \rho_i(t, s)s^2 ds$$

together with  $\rho_i(t, s) = 0$ ,  $s > \bar{s}_i(R)$ .

We are concerned with both the existence and stability of equilibrium solutions of these equations. A positive equilibrium solution  $(R(t), \rho_i(t, s)) = (\lambda_i, \rho_i^\circ(s)) > 0$  of  $(12)_i$ , is feasible only if  $s_j < \underline{s}_i(\lambda_i)$ . [It is not difficult to show that otherwise the only equilibrium is  $(\lambda, 0)$ , where  $\lambda > 0$  satisfies  $k(\lambda) = 0$ .] If the equilibrium equation  $(12a)_i$ , for  $\rho_i^\circ(s)$  is solved and the general solution

$$\rho_i^\circ(s) = \begin{cases} \rho_i^\circ(s_{b_i}) \left( \frac{\underline{s}_i(\lambda_i) - s}{\underline{s}_i(\lambda_i) - s_{b_i}} \right)^{d_i/\gamma_i - 1} & \text{for } s_{b_i} \leq s < \underline{s}_i(\lambda_i) \\ 0 & \text{for } s \geq \underline{s}_i(\lambda_i) \end{cases}$$

where  $\gamma_i = \zeta_i/\eta_i$ , is substituted into  $(12b)_i$  and  $(12c)_i$ , one finds that  $\lambda_i > 0$  must satisfy

$$\Pi_i(\underline{s}_i(\lambda_i), 0) = 1 \quad (13)_i$$

in which case

$$\rho_i(s_{b_i}) = k(\lambda_i) \left( f_i(\lambda_i) \int_{s_{b_i}}^{\underline{s}_i(\lambda_i)} \left( \frac{\underline{s}_i(\lambda_i) - s_j}{\underline{s}_i(\lambda_i) - s_{b_i}} \right)^{d_i/\gamma_i - 1} s^2 ds \right)^{-1}$$

The expression  $\Pi_i$  in  $(13)_i$  is defined by

$$\Pi_i(\sigma, z) = \frac{(1 - \kappa_i)\zeta_i}{\kappa_i \omega_i W_{b_i} \gamma_i} \frac{\sigma}{\sigma - s_{b_i}} \int_{s_j}^{\sigma} \left( \frac{\sigma - s}{\sigma - s_{b_i}} \right)^{(d_i+z)/\gamma_i - 1} s^2 ds$$

$\Pi_i(\underline{s}_i(\lambda_i), 0)$  is the net reproductive rate at resource level  $\lambda_i$  (i.e., the expected number of offspring per individual per lifetime). There exists a positive equilibrium of  $(13)_i$  if and only if equation  $(13)_i$  has a positive solution  $\lambda_i > 0$  for which  $k(\lambda_i) > 0$ . It can be shown that because  $f_i(\lambda)$  is monotonically increasing in  $\lambda$ , so is  $\Pi_i(\underline{s}_i(\lambda), 0)$ . Inasmuch as  $\Pi_i(0, 0) = 0$ ,  $(13)_i$  has a unique positive solution if  $\Pi_i(\underline{s}_i(\lambda), 0) > 1$  for large  $\lambda > 0$ .

A similar analysis of the equilibrium equations associated with the competition equations (11) shows that in order to have an equilibrium in which two or more  $\rho_i^\circ$  are positive, two or more of the equations  $\Pi_i(\underline{s}_i(\lambda), 0) = 1$  must have a common solution  $\lambda > 0$ . The improbability of this occurrence is commensurate with the principle of competitive exclusion, which says that it is impossible for two or more species to coexist on a single resource. Thus we will restrict our investigation of stability to "axis" equilibria of the form  $(R, \rho_1, \rho_2, \dots, \rho_n) = (\lambda_i, 0, \dots, 0, \rho_i^\circ, 0, \dots, 0)$ ,  $\lambda_i > 0$ ,  $\rho_i^\circ > 0$ , where  $(\lambda_i, \rho_i^\circ)$  is an equilibrium of  $(12)$ .

We are interested in whether or not a species  $\rho_i$ , which can successfully exist on the resource  $R$ , can be invaded by a competitor  $\rho_k$ ,  $k \neq i$ . For simplicity let  $i = 1$ . Thus we will assume the existence of a stable positive equilibrium  $(\lambda_1, \rho_1^\circ) > 0$  of  $(12)_i$  and consider the stability of  $(\lambda_1, \rho_1^\circ, 0, \dots, 0)$  as an equilibrium of (11). Because the competition model (11) is exploitative (i.e., the coupling of the equations is through and only through the resource equation), the linearization at  $(\lambda_i, \rho_i^\circ, 0, \dots, 0)$  is such that given the assumed stability of  $(\lambda_i, \rho_i^\circ)$  as a solution of  $(12)_i$ , stability is determined by the linearization of the  $\rho_i$  equations at  $(\lambda_i, \rho_i^\circ)$  for  $i \neq 1$ . These equations are

$$\frac{\partial}{\partial t} \rho_i + \frac{\partial}{\partial s} (g_i(\lambda_i, s) \rho_i) = -d_i \rho_i$$

$$g_i(\lambda_i, s_{b_i}) \rho_i(t, s_{b_i}) = \int_{s_{j_i}}^{s_i(\lambda_i)} m_i(\lambda_i, s) \rho_i(t, s) ds$$

If we look for nontrivial solutions of the form  $\rho_i = \phi_i(s)e^{zt}$ , the equations for  $\phi_i$  are

$$\frac{d}{ds} (g_i(\lambda_i, s) \phi_i(s)) = -(d_i + z) \phi_i(s)$$

$$g_i(\lambda_i, s_{b_i}) \phi_i(s_{b_i}) = \int_{s_{j_i}}^{s_i(\lambda_i)} m_i(\lambda_i, s) \phi_i(s) ds$$

These equations have a nontrivial solution  $\phi_i$  if and only if  $z$  satisfies the equation  $\Pi_i(\underline{s}_i(\lambda_i), z) = 1$ . If these ‘‘characteristic equations’’ have, for  $i \neq 1$ , only complex roots with  $\text{Re } z < 0$ , the equilibrium is stable. If for some  $i \neq 1$  there exists a root with  $\text{Re } z > 0$ , the equilibrium is unstable. [We have proceeded in a formal fashion in this stability analysis. A rigorous justification of linearized stability for a quite general single-species size-structured model, but without dynamical resource, is given by Tucker and Zimmerman (1988). Their treatment could probably be extended to a system of model equations such as (11) to give rigorous mathematical justification of our results here.]

It can be shown that  $\Pi_i$  has the following properties for  $\sigma > 0$ :

$$\Pi_i(\sigma, z) \rightarrow 0 \quad \text{as } z = \text{real} \rightarrow +\infty$$

$$|\Pi_i(\sigma, z)| \leq \Pi_i(\sigma, 0) \quad \text{for } \text{Re } z \geq 0$$

The following theorem easily follows from these facts.

*Theorem 2.* Assume that equations (12)<sub>*i*</sub> have a stable positive equilibrium  $(\lambda_i, \rho_i^0)$ . If  $\Pi_i(\underline{s}_i(\lambda_i), 0) < 1$  for all  $i \neq 2$ , then the axis equilibrium  $(\lambda_1, \rho_1^0, 0, \dots, 0)$  of equations (11) is stable. If  $\Pi_i(\underline{s}_i(\lambda_i), 0) > 1$  for some  $i \neq 2$ , this equilibrium is unstable.

In the absence of a global analysis of a competition model, questions concerning the competitive outcome are usually investigated by means of the local linearized stability of the ‘‘axis’’ equilibria such as  $(\lambda_1, \rho_1^0, 0, \dots, 0)$ . If such an equilibrium is stable, then the species  $\rho_1$  is invulnerable to competitive exclusion by at least small densities of the remaining species. The criterion for this is, by Theorem 2, that the net reproductive rates of the invading species are all less than replacement level at the resource equilibrium  $\lambda_1$ . If, on the other hand, at least one invading species has a net reproductive rate at resource level  $\lambda_1$  greater than 1, species  $\rho_1$  is vulnerable to exclusion by this species.

The expression

$$\Pi_i(\sigma, 0) = \frac{(1 - \kappa_i) \zeta_i}{\kappa_i \omega_i w_{b_i} \gamma_i} \frac{\sigma}{\sigma - s_{b_i}} \int_{s_{j_i}}^{\sigma} \left( \frac{\sigma - s}{\sigma - s_{b_i}} \right)^{d_i/\gamma_i - 1} s^2 ds \tag{14}$$

can be integrated to obtain

$$\begin{aligned}\Pi_i(\sigma, 0) &= \frac{(1 - \kappa_i)\zeta_i}{\kappa_i \omega_i w_{b_i} d_i} \sigma p_i(\sigma) q_i(\sigma) \\ p_i(\sigma) &= s_{j_i}^2 + \frac{2\gamma_i}{d_i + \gamma_i} s_{j_i}(\sigma - s_{j_i}) + \frac{2\gamma_i^2}{(d_i + \gamma_i)(d_i + 2\gamma_i)} (\sigma - s_{j_i})^2 \\ q_i(\sigma) &= \left( \frac{\sigma - s_{j_i}}{\sigma - s_{b_i}} \right)^{d_i/\gamma_i}\end{aligned}$$

Both  $p_i$  and  $q_i$  are increasing functions of their arguments  $\sigma$ . Thus  $\Pi_i(\sigma, 0)$  is increasing in  $\sigma$ . On the other hand, for fixed  $\sigma$ ,  $\Pi_i(\sigma, 0)$  is decreasing in  $s_{j_i}$  [see (14)].

The stability criteria in Theorem 2 depend on most model parameters in a rather complicated way and we will not attempt here to study this dependence in any detail. Instead, only one question will be asked: For otherwise similar species, how does the stability of the axis equilibria depend on the relative adult and juvenile sizes of the competing species? By "otherwise similar" is meant the identity of all the model parameters

$$\kappa_i = \kappa, \quad \omega_i = \omega, \quad \eta_i = \eta, \quad \zeta_i = \zeta, \quad d_i = d, \quad s_{b_i} = s_b \quad (15)$$

(hence  $\gamma_i = \gamma$ ,  $w_{b_i} = w_b$ ).

Suppose that species  $\rho_1$  has the largest adult size at the resource level  $\lambda_1$  so that  $\underline{s}_1(\lambda_1) < \underline{s}_i(\lambda_1)$ . This will occur if species  $\rho_1$  has a larger resource uptake rate:  $f_1(\lambda_1) < f_i(\lambda_1)$ . Furthermore, if the species have the same maturation length (or slightly more generally, if no species has a smaller maturation length than that of species  $\rho_1$  (i.e.,  $\underline{s}_{j_i} \geq \underline{s}_{j_1}$  for  $i \neq 1$ ]), the monotonicity properties of the  $\Pi_i(\sigma, 0)$  imply the inequalities

$$\Pi_i(\underline{s}_i(\lambda_1), 0) \leq \Pi_1(\underline{s}_i(\lambda_1), 0) < \Pi_1(\underline{s}_1(\lambda_1), 0) = 1$$

Theorem 2 now implies that species  $\rho_1$  is locally invulnerable to invasion. Notice that in the case considered here the largest species wins the competition (at least near equilibrium and against invasion by small densities of smaller species), in keeping with the basic tenet of the SEH.

A species  $\rho_1$  that is largest at the equilibrium resource level  $\lambda_1$  may not be, however, the largest species at another resource level  $\lambda_i$  associated with the axis equilibrium corresponding to another species  $\rho_i$ . That is,  $\underline{s}_1(\lambda_1) > \underline{s}_i(\lambda_1)$  does not necessarily imply that  $\underline{s}_1(\lambda_i) > \underline{s}_i(\lambda_i)$ . If, however,  $\rho_1$  is the largest species at all axis equilibria resource levels  $\lambda_i$ , a similar local stability analysis shows that the other axis equilibria are unstable. This, and the absence of any other positive or nonnegative equilibria, would suggest that the axis equilibrium for species  $\rho_1$  might be globally attracting. This is the case in many exploitative competition models without structure (Butler and Wolkowicz, 1985). On the other hand, if species  $\rho_1$  is the largest species at resource level  $\lambda_1$  while species  $\rho_i$  is the largest species at resource level  $\lambda_i$ , the competitive outcome for initial states far from equilibria will presumably depend on initial densities. These questions need investigation.

A larger species may not be invulnerable to invasion by smaller species if the smaller species has other model parameter that are significantly different from those of the larger species. For example, suppose that we retain the conditions



(15) (so that the species still differ only in adult and juvenile sizes) and still assume that species  $\rho_1$  is the largest species at resource level  $\lambda_1$ . However, unlike the case just considered, suppose that a smaller species  $\rho_i$  has a smaller maturation length  $s_{ji} < s_{j1}$ . As noted above, the net reproductive rate  $\Pi_i(\underline{s}_i(\lambda_1), 0)$  is a decreasing function of  $s_{ji}$ . Consequently, this quantity increases as  $s_{ji}$  decreases and there is the possibility that it will exceed 1 for sufficiently small  $s_{ji}$  (but, of course,  $s_{ji} \geq s_b$ ). If this happens, species  $\rho_1$  would be vulnerable to invasion and exclusion by this smaller (adult size) species. For example, this will definitely occur if  $\zeta(1 - \kappa)/\omega\kappa d > 1$ . This could be interpreted as a simple example of a juvenile bottleneck-like phenomenon, although a more appropriate model of the juvenile bottleneck would incorporate strong competitive effects on the growth of the juveniles of the larger species from the adults of the smaller species.

For a further study of a special case of (11), see Cushing (1989a).

#### IV. CONCLUSION

We have briefly looked at two models for the dynamics of  $n$  size-structured species competing for a single resource, one discrete and one continuous in time and length scales. These models are based on the fundamental assumption that resource uptake scales to the square of body length. Both models are consistent with the basic competitive exclusion principle as far as equilibrium dynamics are concerned (i.e., that at most one species can survive at equilibrium on a single limiting resource). Parameter relationships were derived which determine the surviving species, and as an application the question of how competitive success depends on adult and juvenile body size was considered. It was seen that in general the connection between competitive success and body size in both models is a complicated one involving a large number of the model parameters and that without further restrictions on parameter ranges, body size is not a predictor of competitive success. However, under the assumption that all species are otherwise "similar," it was indeed found that the surviving species has the largest adult body size. However, species with smaller adult sizes can eliminate species with larger adult sizes in a number of different ways, including earlier maturation, smaller weight at birth, higher survivability, more efficient resource conversion factors, or different reproduction-to-growth resource allocation patterns.

#### APPENDIX

*Part of Theorem 1:* From (2) it follows

$$p(t+1) = w^T((a(t)I + b(t)L)x(t))$$

which when divided into (2) yields the equation

$$\eta(t+1) = \frac{(\rho(t)I + L)\eta(t)}{w^T((\rho(t)I + L)\eta(t))}, \quad t = 0, 1, 2, \dots$$

for  $\eta(t)$ , where  $\rho(t) = a(t)/b(t)$ . It is not difficult to show that the solution of this equation is given by  $\eta(t) = \psi(t)/w^T\psi(t)$ , where  $\psi$  is the solution of

$$\psi(t+1) = (\rho(t)I + L)\psi(t), \quad \psi(0) = \eta(0) \tag{A.1}$$

For simplicity we give a proof when  $L$  has a basis of eigenvectors  $v_1 = v^+$ ,  $v_2, \dots, v_m$ . In the more general case a similar proof can be constructed using generalized eigenvectors. [See Impagliazzo (1985) for an analogous proof in the age-structured case.]

The coefficient matrix  $\rho(t)I + L$  in (A.1) has eigenvalues  $\lambda_i + \rho(t)$  with eigenvectors  $v_i$ . Expand  $\eta(0) = \sum_{i=1}^m c_i v_i$ . The solution of (A.1) is given by

$$\psi(t) = \sum_{i=1}^m c_i \prod_{k=0}^{t-1} (\lambda_i + \rho(k)) v_i$$

and  $\eta(t)$  is given by

$$\eta(t) = \frac{\sum_{i=1}^m c_i \prod_{k=0}^{t-1} (\lambda_i + \rho(k)) v_i}{\sum_{i=1}^m c_i \prod_{k=0}^{t-1} (\lambda_i + \rho(k)) w^T v_i}$$

If we divide numerator and denominator by  $\prod_{k=0}^{t-1} (\lambda_i + \rho(k))$  and define

$$\Pi_i(t) = \prod_{k=0}^{t-1} \left( \frac{\lambda_i + \rho(k)}{\lambda_i + \rho(k)} \right)$$

then

$$\eta(t) = \frac{c_1 v_1 + \sum_{i=2}^m c_i \Pi_i(t) v_i}{c_1 w^T v_1 + \sum_{i=2}^m c_i \Pi_i(t) w^T v_i}$$

By Lemma 1 below, we have that  $\Pi_i(t) \rightarrow 0$  as  $t \rightarrow +\infty$  for  $i \geq 2$  and thus  $\eta(t) \rightarrow c_1 v_1 / c_1 w^T v_1 = v_1 = v^+$ . Note:  $c_1$  is positive because  $c_1 = u_1^T \psi(0)$  where  $u_1$  is the left eigenvector of  $L$  associated with  $\lambda_1 = \lambda^+$ , which is known to be a positive vector (Gantmacher, 1960).

*Lemma 1.* If  $\lambda_1 > |\lambda_i|$  for  $i = 2, \dots, m$  and  $0 \leq \rho(t) \leq \rho_0 < +\infty$  for all  $t = 0, 1, 2, \dots$ , then  $\Pi_i(t) \rightarrow 0$  as  $t \rightarrow +\infty$  for each  $i = 2, \dots, m$ .

*Proof:* It is easy to see geometrically in the complex plane that  $\lambda_1 > |\lambda_i|$  implies that  $|\lambda_i + x| / (\lambda_1 + x) < 1$  for all  $x > 0$ . Since this ratio is continuous in  $x$ , it is bounded away from 1 on bounded  $x$  intervals, that is,  $0 < |\lambda_i + x| / (\lambda_1 + x) < m_i$  for some  $m_i < 1$  and all  $x$  on the interval  $[0, \rho_0]$ . Thus  $|\Pi_i(t)| < m_i^t$  and the result follows.

*Lemma 2.* If  $x(t)$  is a solution of (1) with  $T$  and  $B$  given by (4)–(5) with  $x(0) \geq 0$  ( $\neq 0$ ), then  $x(t) \geq 0$ ,  $p(t) > 0$  and both sequences are bounded for all  $t > 0$ .

*Proof:* Assume that  $0 \leq x(t) \neq 0$ . By (H1),  $p(t) \geq 0$  for all  $t$  and from (1) follows  $x(t+1) \geq 0$ . An easy investigation of the components of  $P(t)x(t)$  in reverse order shows that  $x(t+1) = 0$  implies the contradiction  $x(t) = 0$ . Thus  $x(t+1) \neq 0$ . By induction  $0 \leq x(t) \neq 0$  for all  $t$ . This in turn implies that  $p(t) > 0$  for all  $t \geq 0$ .

Clearly,  $p(t)$  is bounded if  $x(t)$  is bounded for  $t \geq 0$ . To show that  $x(t)$  is bounded, we consider  $0 \leq s(t) = \sum_{i=1}^m x_i(t)$ . From (1) and the definitions of  $T$  and  $T$  in (4) and (5), we obtain  $s(t+1) = \Pi s(t) + \Pi r e^{-d p(t)} \sum_{i=1}^m \gamma_i x_i(t)$ , from which follows for  $t \geq 0$

$$0 \leq s(t+1) \leq F(s(t)) \tag{A.2}$$

with  $s(0) = \sum x_i(0) > 0$ , where  $F(s) = \Pi(1 + \gamma^* e^{-s^* s})s$  and  $s^* = \min d \mu_i s_i^2 > 0$ ,  $\gamma^* = \max r \gamma_i \geq 0$ .  $F(s) \geq 0$  has the following property: There exists a real  $s' \geq 0$

such that  $F(s)$  is monotonically increasing and satisfies  $F(s) < s$  for  $s > s'$  and  $\max_{[0, s']} F(s) = F(s')$ .

If it happens that  $s(t) > s'$  for all  $t \geq 0$ , then by (A.2) we have  $s(1) \leq F(s(0)) < s(0)$  and by induction  $s(t+1) \leq F(s(t)) < s(t) \leq s(0)$ . On the other hand, if  $s(t') \leq s'$  for some  $t' \geq 0$ , then by (A.2),  $s(t'+1) \leq F(s(t')) \leq F(s') \leq s'$ . By induction  $s(t) \leq s'$  for all  $t \geq t'$ . In either case  $s(t)$  is bounded and hence so is  $x(t)$ .

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