

## A Discrete Model for Competing Stage-Structured Species

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This paper deals with the problem of relating physiological properties of individual organisms to the dynamics at the total population level. A general nonlinear matrix difference equation is described which accounts for the dynamics of stage-structured populations under the assumption that individuals in the populations can be placed into well defined descriptive stages. Density feedback is modeled through an assumption that (stage-specific) fertilities and transitions are proportional to a resource uptake functional which is dependent upon a total weighted population size. It is shown how, if stage-specific differences in mortality are insignificant compared to stage-specific differences in fertility and inter-stage transitions, a nonlinear version of the strong ergodic theorem of demography mathematically separates the population level dynamics from the dynamics of the stage distribution vector, which is shown to stabilize independently of the population level dynamics. The nonlinear dynamics at the population level are governed by a key parameter  $\theta$  that encapsulates the stage-specific parameters and thereby affords a means by which population level dynamics can be linked to properties of individual organisms. The method is applied to a community of stage-structured populations competing for a common limiting resource, and it is seen how the parameter  $\theta$  determines the competitively superior species. An example of size structured competitors illustrates how the method can relate the competitive success of a species to such size-specific properties as resource conversion efficiencies and allocation fractions for individual growth and reproduction, largest adult body size, and size at birth and maturation. © 1992 Academic Press, Inc.

### 1. INTRODUCTION

The majority of mathematical models for the dynamics of interacting species ignore differences between individual members of each species. They attempt to describe only highly aggregate variables on the scale of total

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population numbers (densities, biomass, dry weight, etc.) as functions of time. In reality, of course, individual organisms of the same species can differ significantly in any number of ways which affect their interactions with their physical and biological environment. Indeed, intra-specific variations in physiological traits such as body size, weight, age, etc., can be greater than inter-specific variations (Werner and Gilliam, 1984). These physiological traits often determine an individual organism's vital rates (e.g., resource consumption, metabolic, fertility, and mortality rates) and as a result play a crucial role in determining the dynamics at the population level.

Important questions thereby arise for the modeler and theoretician. How can one determine what effects physiological traits at the level of the individual have on the dynamics at the population level? What attributes of individual organisms are crucial in determining a population's dynamics? What changes in the population level dynamics result from a change in a physiological trait of the individual members of the species? What will be the effects of such a change on the species's interactions with another species? At an even higher scale, how does community structure depend upon the physiological traits of the individual organisms of the member species?

The current widespread interest in so-called "structured population dynamics" is a recognition of the necessity of taking the differences between individuals into account in order to gain an adequate understanding of the population level dynamics of many populations and multi-species interactions (Metz and Diekmann, 1986). A great deal of biological research concerns the measurement of physiological characteristics of organisms, most of which cannot be used in conjunction with the majority of existing models attempting to describe population or community dynamics because of the phenomenological nature of these models. The inclusion of such lower scale measurements would be a significant improvement in the relevance of these models. Not only would this lead to an improved theory of population and community dynamics, but to improvements in those theories from other disciplines whose models are based upon these models, e.g., epidemiology, cell dynamics, natural resource management, etc. (Gross, 1986).

In Section 2 we present a general discrete time model for the dynamics of a stage-structured population in which rates of transitions between different stages, e.g., individual development and growth and fertility rates, are determined by resource uptake rates. The resource uptake rates are stage and population density dependent. It is shown how, under the simplifying assumption that mortality rates are not significantly stage dependent, a nonlinear ergodic theorem can be used to separate the asymptotics of the stage demographics from that of the population level

dynamics. Population dynamics are governed by a derived equation in which there appears a composite parameter which encapsulates all of the individual level parameters and thereby affords a tractable means by which population dynamics can be analytically linked to physiological properties on the scale of the individual. It is shown, for example, how the winning species in a community of species of this type all competing for a common limiting resource can be easily determined by these composite parameters.

In Section 3 a structured model based on body size is analyzed by this method. Body size is one of the most important attributes on an individual organism in so far as its vital rates (metabolism, growth, fertility, and mortality) and its interaction with its physical and biological environment are concerned. It is more often than not more important, for example, than chronological age (Werner and Gilliam, 1984; Lomnicki, 1988; Ebenman and Persson, 1988; Caswell, 1989). An example of the importance of body size with regard to competitive interactions is provided by zooplankton communities. In order to account for observations concerning zooplankton found in freshwater lakes, Brooks and Dodson (1965) formulated the so-called Size Efficiency Hypothesis. This hypothesis guided research on zooplankton community structure for several decades after its formulation and, although some of its tenets have been subsequently modified, it is still an important theoretical framework in aquatic ecology (Werner and Gilliam, 1984; Hall *et al.*, 1976; Gerritsen, 1984). The fundamental premise of this hypothesis states that larger bodied species of planktonic herbivores are more efficient competitors (for a variety of incompletely understood reasons (Hall *et al.*, 1976)). In the absence of mediating factors, such as predation, seasonal fluctuations or "juvenile bottlenecks," similar but smaller bodied zooplanktors should be competitively eliminated. The model in Section 3 is used to relate adult body size to competitive efficiency, where it is found that all other factors being identical the species with the larger adult size will indeed out compete smaller species. The results also show how a smaller species can adjust size specific, physiological parameters in order to overcome its competitive disadvantage.

## 2. A GENERAL STAGE-STRUCTURED MODEL

A general model describing 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 stages or classes (stage and class will be used interchangeably) is given by the matrix difference equation

$$\begin{aligned} x(t+1) &= Px(t), x(0) \geq 0 \\ P &= T + B, \end{aligned} \tag{1}$$

where the "projection" matrix  $P$  has been additively decomposed into a stage transition matrix  $T$  and a fertility matrix  $B$ . The column vector  $x(t) = \text{col}(x_i(t))_{i=1}^m$  contains the number or density  $x_i(t)$  of individuals in stage  $i$ ,  $1 \leq i \leq m$ , at times  $t = 0, 1, 2, \dots$ . The unit of time is usually taken to be a significant unit in the life cycle of the population, e.g., the length of a growing season, maturation period, etc.

A general form for the transition matrix  $T$  is

$$T = \begin{pmatrix} \pi_1(1-f_1) & \pi_2 f_{12} f_2 & \cdots & \pi_m f_{1m} f_m \\ \pi_1 f_{21} f_1 & \pi_2(1-f_2) & \cdots & \pi_m f_{2m} f_m \\ \vdots & \vdots & \ddots & \vdots \\ \pi_1 f_{m1} f_1 & \pi_2 f_{m2} f_2 & \cdots & \pi_m(1-f_m) \end{pmatrix}, \quad (2)$$

where  $\pi_k$  is the probability that a  $k$ -stage individual survives one unit of time,  $f_k$  is the fraction of the surviving individuals who leave stage  $k$ , and  $f_{ik}$  is the fraction of this group that moves into stage  $i$  in one unit of time. The fraction of  $k$ -stage individuals who survive and remain in stage  $k$  over one unit of time is then  $\pi_k(1-f_k)$ , and the fraction that moves into stage  $i \neq k$  is  $\pi_k f_{ik} f_k$ . The transitions among all stages occurring between time  $t$  and  $t+1$  yields a new stage distribution vector  $Tx(t)$ .

Classes may also obtain new members due to births. Immigrations and emigrations will be ignored here. Let  $b_{ik}$  be the number of  $i$ -stage births per  $k$ -stage individual in one unit of time. Stage-specific surviving offspring at time  $t+1$  are given by  $Bx(t)$ , where

$$B = \begin{pmatrix} \pi_1 b_{11} & \pi_2 b_{12} & \cdots & \pi_m b_{1m} \\ \pi_1 b_{21} & \pi_2 b_{22} & \cdots & \pi_m b_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ \pi_1 b_{m1} & \pi_2 b_{m2} & \cdots & \pi_m b_{mm} \end{pmatrix}. \quad (3)$$

In the event that some of the entities above are dependent on time  $t$  (either explicitly or implicitly through a dependence upon the density vector  $x(t)$ ) the projection matrix  $P$  will be dependent upon  $t$ , i.e.,  $P = P(t)$  or  $P(x(t))$ .

This general model includes the model for age-structured populations of Leslie (1945). In this case the stages are age classes of one time unit in length so that  $f_k = 0$  and  $f_{ik} = 0$  if  $i \neq k+1$  in (2); i.e., all surviving individuals must advance one age class in one unit of time. Since newborns have age 0,  $b_{ij} = 0$  for all  $j$  and all  $i \neq 1$  in (3).  $P$  then becomes a so-called Leslie matrix. A generalization of this age-structure model of Leslie occurs if instead  $f_k > 0$ ; i.e., individuals either remain in their class or move to the next class in one unit of time. In this case, the projection matrix is an

“Usher” or a “standard size classified” matrix (Caswell, 1989). This kind of matrix model has found extensive use, for example, in size-structured models of tree forest dynamics (e.g., see Ek and Monserud, 1979; Usher, 1972). For other applications, see Caswell (1989).

We are interested in the dynamics of structured populations of species competing for a common limiting resource in the case when the ability to obtain this resource is stage dependent and when both fertility and life cycle development (that is to say, transitions between stages) is dependent upon resource consumption. Accordingly, the birth rates  $b_{ik}$  and the fraction  $f_k$  of  $k$ -stage individuals who leave stage  $k$  in one unit of time are assumed to depend upon the amount of resource taken up during that unit of time, which in turn is assumed proportional to a “resource uptake functional”  $u = u(t)$ . The dependence of  $u(t)$  on time can be explicit or implicit through, for example, a dependence upon the population density of the species or of competing species. Thus we write

$$b_{ik} = \phi_{ik} u(t), \phi_{ik} \geq 0, \quad \text{and} \quad f_k = \phi_k u(t), \phi_k \geq 0. \quad (4)$$

An example of what we have in mind is a population structured by size classes for which resource consumption and hence growth and fertility rates of individual organisms are dependent upon body size and on time-dependent resource availability. This is made more explicit in the size-structured models studied below.

In this paper the focus is on the effects of differences in growth, developmental, and fertility rates between individual organisms in different stages, as opposed to differences in survival rates. Consequently, our second assumption is that the probability of surviving a unit of time is the same for all stages, i.e.,  $\pi_k = \pi(t) \in (0, 1]$ . This simplistic assumption is admittedly often biologically unreasonable. For example, survivability often correlates strongly with body size. However, under biological circumstances when this assumption is approximately correct, or at least when stage differences in mortality are considered less significant than those in fertility and development, then the resulting model equations will submit to a considerable amount of tractable analysis which, amongst other things, will allow properties of population level dynamics to be related to the stage specific physiological properties of individual organisms in a rather simple way. Despite this concession in the interest of analytical tractability, it is hoped that by focusing on stage-dependent transition and birth rates alone some understanding will be gained of the effects on the dynamics of competing populations that are due to differences in individual organisms, at least with respect to these vital rates.

Let  $p(t) = \sum_1^m w_k x_k(t)$ ,  $w_k > 0$ , be a specified weighted total population size. Under the assumptions made above it can be shown, provide  $u(t) > 0$

is bounded away from 0 for  $t > 0$ , that the solutions of (1)–(4) have a “stable normalized stage distribution,” i.e.,  $x(t)/p(t) \rightarrow v > 0$  as  $t \rightarrow +\infty$ , and that the population level dynamics are governed by the “limiting” equation

$$p(t+1) = \pi(t)(1 + \theta u(t)) p(t), \quad (5)$$

where  $\theta$  is a real, simple eigenvalue of the matrix

$$M = \begin{pmatrix} -\phi_1 + \phi_{11} & f_{12}\phi_2 + \phi_{12} & \cdots & f_{1m}\phi_m + \phi_{1m} \\ f_{21}\phi_1 + \phi_{21} & -\phi_2 + \phi_{22} & \cdots & f_{2m}\phi_m + \phi_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ f_{m1}\phi_1 + \phi_{m1} & f_{m2}\phi_2 + \phi_{m2} & \cdots & -\phi_m + \phi_{mm} \end{pmatrix} \quad (6)$$

and is larger than the real parts of all other eigenvalues, and  $v > 0$  is the corresponding eigenvector (Cushing, 1990; Crowe, 1991). We assume such an eigenvalue/eigenvector pair exists; see, however, the discussion of this point with regard to the size-structured example below. Since the resource uptake rate  $u$  and the survival probability  $\pi$  are allowed to depend on population density, this result represents a nonlinear generalization of the “strong ergodic theorem of demography” (Impagliazzo, 1985; Caswell, 1989). Asymptotically the demographics of the stage structured population, given by the eigenvector  $v$ , have been separated from the population level dynamics governed by Eq. (5). The population level dynamics do, nonetheless, depend on the stage-specific parameters contained in the parameter matrix  $M$  through the dependence of Eq. (5) on the eigenvalue  $\theta$ . If the dynamics of (5) are understood as a function of  $\theta$ , then how a particular stage specific parameter in  $M$  affects population level dynamics can be determined by studying how the eigenvalue  $\theta$  depends upon this parameter. This affords a means for bridging the gap between the physiological characteristics of individual organisms and the dynamics at the total population level.

In the case of several species competing for a common limiting resource, the strong ergodic theorem can be applied to each species separately to obtain a coupled system of population level difference equations of the form

$$p_j(t+1) = \pi_j(t)(1 + \theta_j u(t)) p_j(t), \quad j = 1, 2, \dots, n,$$

where it is assumed that each species satisfies the assumptions discussed above. The coupling is through the dependence of the per unit resource uptake functional  $u$  on the densities of all species.

In this paper we assume that density effects due to competition are

expressed through a dependence of the resource uptake function  $u$  on the weighted total population sizes of all species,

$$u(t) = u(p_1(t), \dots, p_n(t)) > 0. \quad (7)$$

Here  $u(p_1, \dots, p_n)$  is decreasing in each argument  $p_j$  (approaching 0 as  $p_j \rightarrow +\infty$ ) and, without loss of generality,  $u(0, 0, \dots, 0) = 1$ . Thus increases in the weighted population size of any species has a deleterious effect on the resource uptake rate of every species. For simplicity we assume that survival  $\pi_j$  is not density dependent and write

$$p_j(t+1) = \pi_j(1 + \theta_j u(p_1(t), \dots, p_n(t))) p_j(t), \quad j = 1, 2, \dots, n, \quad (8)$$

where  $\theta_j$  is the eigenvalue with largest real part of a species specific matrix  $M_j$  of the form (6). Before considering a more specific competition model based on body size stages, we first describe some results concerning this general model.

First we remark that the application of the strong ergodic theorem of Cushing (1990) and Crowe (1991), which derives the population level dynamical equations (8) from the structured model (1)–(4) with (7), requires that  $u(t)$  be bounded away from zero, i.e., that solutions of (1)–(4) be bounded above for all time  $t$ . This can be shown to be true by means of a simply extension of an argument given by Cushing (1990) for the size-structure example below.

Consider first the dynamics of one species alone  $n = j = 1$ , in which case we have

$$p_1(t+1) = \pi_1(1 + \theta_1 u(p_1(t))) p_1(t). \quad (9)$$

Define the critical number

$$\theta_1^{\text{cr}} = (1 - \pi_1)/\pi_1.$$

Since  $0 \leq p_1(t+1) \leq \pi_1(1 + \theta_1) p_1(t)$ , it immediately follows that  $p_1(t) \rightarrow 0$  if  $\theta_1 < \theta_1^{\text{cr}}$ . If, on the other hand  $\theta_1 > \theta_1^{\text{cr}}$ ,  $p_1 = 0$  is repelling and there exists a unique positive equilibrium  $e_1 = u^{-1}(\theta_1^{\text{cr}}/\theta_1)$ . An investigation of the derivative of the right hand side of (9) shows that  $e_1$  is stable at least for  $\theta_1 - \theta_1^{\text{cr}}$  small. For large values of  $\theta_1$  Eq. (9) can exhibit now familiar period doubling bifurcations and chaotic dynamics, depending upon the particular nonlinearity introduced by  $u$ ; for example, see Cushing (1990) for the case  $u = \exp(-dp)$ . Another typical nonlinear functional used in density-dependent discrete models is  $u = 1/(1 + dp)$ , in which case  $e_1$  is stable for all  $\theta_1 > \theta_1^{\text{cr}}$ .

The multi-species competition model (8) has no positive equilibrium states (except possibly in the nongeneric case when all critical  $\theta_j^{\text{cr}}$  are

identical). In fact, the only nontrivial equilibria are the “axis equilibria” in which only one species is present

$$p_j = \begin{cases} 0 & \text{for } j \neq q \\ e_q & \text{for } j = q \end{cases}$$

provided  $\theta_q > \theta_q^{cr}$ . If  $\theta_q < \theta_q^{cr}$  it is easy to show that  $p_q(t) \rightarrow 0$ ; that is to say, a species that cannot survive in the absence of competition cannot survive in the presence of competition. Consequently, we assume without loss of generality that

$$\theta_j > \theta_j^{cr} \quad \text{for all } j = 1, \dots, n.$$

A linearization of (8) at the axis equilibrium of species  $j = q$ , yields a triangular matrix whose  $n$  eigenvalues are easily seen to be

$$\pi_j(1 + \theta_j u(0, \dots, e_q, \dots, 0)), \quad j \neq q \tag{10}$$

$$1 + \pi_q \theta_q \frac{\partial}{\partial p_q} u(0, \dots, e_q, \dots, 0). \tag{11}$$

If species  $j = q$  is “inherently stable,” i.e. has a stable equilibrium in the absence of the other species, then eigenvalue (11) lies in the unit interval  $(-1, 1)$ , and the stability of the “competitive” axis equilibrium is determined by the remaining eigenvalues (10) (all of which are positive). The inherently stable  $q$ th species is competitively stable if all the numbers (10) are less than one, a criterion which is easily seen to be equivalent to

$$\theta_q / \theta_q^{cr} > \theta_j / \theta_j^{cr}, \quad j \neq q. \tag{12}$$

This model is consistent with the competitive exclusion principle in that there is only one stable equilibrium and this equilibrium has present in it only one species, namely, the one with the largest ratio  $\theta_j / \theta_j^{cr}$ . (The competitive exclusion principle can be violated, however, with regard to non-equilibrium dynamics in that positive non-equilibrium attractors containing all species can exist. See Crowe, 1991.)

This stability result is a local (linearized) result. A useful global result can easily be obtained from the equation

$$\frac{p_j(t+1)}{p_q(t+1)} = \frac{\pi_j}{\pi_q} \frac{1 + \theta_j r_j u(p_1(t), \dots, p_n(t))}{1 + \theta_q r_q u(p_1(t), \dots, p_n(t))} \frac{p_j(t)}{p_q(t)}.$$

If

$$\pi_q \geq \pi_j \quad \text{and} \quad \theta_q > \theta_j \text{ for } j \neq q \tag{13}$$



(conditions that imply (12)), then the coefficient of the ratio  $p_j(t)/p_q(t)$  on the right hand side is less than, and bounded away from 1 for all  $t$ . Thus, this ratio and hence  $p_j(t)$  tend to 0 as  $t \rightarrow +\infty$ . Note that this global result, namely, that all species other than species  $p_q$  go to extinction, holds regardless of the inherent dynamics of species  $p_q$ . (It would be interesting to know whether the somewhat weaker, local stability conditions (12) imply global stability.)

The stability conditions (12) and (13) utilize the eigenvalue  $\theta_j$  of the species specific matrix  $M_j$  and thereby supply the means by which one can relate the competitive success of a species to the physiological parameters contained in the  $M_j$ . These stability criteria imply, roughly speaking, that *it is to a species' advantage to have a large eigenvalue  $\theta_j$* . This is true with regard to local equilibrium dynamics and criterion (12), and it is true under the global extinction criteria (13) regardless of the nature of the dynamics, i.e., whether species  $p_q$  inherently equilibrates or not.

### 3. SIZE-STRUCTURED MODELS

We now illustrate the application of the methods and results in Sections 2 to a class of size-structured models of the type derived by Cushing (1990) in which an individual's ability to obtain and consume the limiting resource is dependent upon body surface area. In these models the populations are structured by size stages or classes according to body length  $s$ . It has been found that for many species resource uptake scales to body length  $s$  by a power law  $s^\tau$  (Werner and Gilliam, 1984; Calder, 1984), generally with  $\tau$  lying between 2 and 3. That is to say, an individual's ability to gain food resources is generally proportional to its body surface area or volume (weight). For example, this is the case for many zooplankton species (Hall *et al.*, 1976). In the model below,  $\tau = 2$ .

Let  $s_0 < s_1 < \dots < s_m$  define  $m$  size classes  $[\bar{s}_i, \bar{s}_{i+1})$ ,  $i = 0, 1, \dots, m$ . Assume that all newborns lie in the smallest size class  $[\bar{s}_0, \bar{s}_1)$  and that no individual in any size class can grow more than to the next size class in one unit of time. This leads, for one species, to the matrix (Cushing, 1990)

$$T = \pi \begin{pmatrix} 1 - \beta_1 ru(p) & 0 & \dots & 0 & 0 \\ \beta_1 ru(p) & 1 - \beta_2 ru(p) & \dots & 0 & 0 \\ 0 & \beta_2 ru(p) & \dots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & \dots & 1 - \beta_{m-1} ru(p) & 0 \\ 0 & 0 & \dots & \beta_{m-1} ru(p) & 1 \end{pmatrix},$$

$$\beta_i = \kappa_i \sigma_i / 3\mu_i \eta_i \delta_i,$$

where  $p = p(t) = \sum_{i=1}^m w_i x_i(t)$ ,  $w_i = \sigma_i s_i^2$  is total surface area of the species,  $r$  is the "inherent" resource uptake rate per unit time per unit body area of any individual (i.e., the uptake rate at low population densities in the absence of intra-species or inter-species competitive effects), and  $\beta_i > 0$  is defined to be the "growth coefficient" (it has the units of area/unit resource). Here  $\delta_i = \bar{s}_i - \bar{s}_{i-1}$  is the length of the  $i$ th size class and  $s_i \in [\bar{s}_i, \bar{s}_{i+1})$  is a representative size of individuals in the  $i$ th size interval, e.g., the average size, if it assumed that the sizes of  $i$ th class individuals are uniformly distributed throughout the interval at any point in time. By an individual of size  $s_i$  we mean an individual from the  $i$ th size interval. Also we have

$$B = r\pi u(p) \begin{pmatrix} \gamma_1 & \gamma_2 & \cdots & \gamma_m \\ 0 & 0 & & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix}, \quad \gamma_i = \xi_i \sigma_i s_i^2 / \omega_i \mu_1 s_1^3,$$

where  $\gamma_i \geq 0$  is defined to be the "reproductive coefficient" (it also has the units of area/unit resource). It is assumed that at least the largest size class is fertile:  $\gamma_m > 0$ . The matrix  $M$  is given by

$$M = r \begin{pmatrix} -\beta_1 + \gamma_1 & \gamma_2 & \cdots & \gamma_{m-1} & \gamma_m \\ \beta_1 & -\beta_2 & \cdots & 0 & 0 \\ 0 & \beta_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & -\beta_{m-1} & 0 \\ 0 & 0 & \cdots & \beta_{m-1} & 0 \end{pmatrix}. \quad (14)$$

A few technical remarks about this matrix are needed here. If  $k$  is a number larger than all the  $\beta_i$ , then  $M + kI$  is a non-negative matrix to which the famous Perron-Frobenius Theory applies. The eigenvalues of  $M + kI$  are simply those of  $M$  shifted by  $k$ . Because  $\beta_i > 0$  and  $\gamma_m > 0$ , it is not difficult to see that this Usher matrix  $M + kI$  is irreducible (i.e., each class is reachable from any other) and primitive (i.e., some power, in this case the  $(m-2)$ nd power, is strictly positive). It follows from the Perron-Frobenius Theorem that  $M + kI$  has a positive, simple, strictly dominant eigenvalue. Consequently,  $M$  has a simple, real eigenvalue whose real part is larger than those of all the other eigenvalues of  $M$ . This is the eigenvalue  $\theta$ . We see below that in fact  $\theta$  is positive. (This result can be obtained for the more general case (6) using a similar argument.)

The size-specific growth and reproductive coefficients  $\beta_i$  and  $\gamma_i$  are built out of the following *size-specific*, physiological parameters:

$0 \leq \kappa_i =$  fraction of consumed resource allocated to growth and metabolism

$0 \leq \xi_i =$  fraction of consumed resource allocated to reproduction

$0 < \omega_i =$  conversion fraction of resource units to offspring body weight

$0 < \eta_i =$  conversion factor of resource units to body weight

$0 < \mu_i =$  body density (assumed uniform so that body weight is  $\mu_i s_i^3$ )

$0 < \sigma_i =$  the constant of proportionality relating surface area to  $s_i^2$   
(it clearly depends upon body geometry)

$0 < \delta_i =$  the length of the  $i$ th size class.

As we have seen, this model population has a stable size distribution and its population level (total surface area  $p(t)$ ) dynamics is governed by Eq. (9), where  $\theta$  is the eigenvalue with largest real part of the matrix (14).

For several interaction species of this same type, all of the above quantities would have an added subscript  $j$  to indicate their species dependence. Their population level dynamics (for total species surface area  $p_j(t)$ ) is governed by Eq. (8) and the stability criteria (12) and (13) apply. These dynamics and hence the competitive outcome are determined by the eigenvalues  $\theta_j$  of matrices  $M_j$  which have the form (14) for each species, consequently by the growth and reproductive coefficients  $\beta_i$  and  $\gamma_i$ , and ultimately by the physiological parameters  $\kappa_i, \xi_i, \dots$ , listed above, for each species. As noted earlier, criterion (12) or (13) implies that it is to a species' advantage to increase its eigenvalue  $\theta_j$ .

A question that arises then is: what changes in the reproductive and growth coefficients  $\gamma_i, \beta_i$  result in an increase in the eigenvalue  $\theta_i$  of  $M$  given by (14)? Let  $p_m(\theta) = p_m(\theta; \gamma_1, \dots, \gamma_m, \beta_1, \dots, \beta_{m-1})$  denote the  $m$ th-degree monic characteristic polynomial of the  $m \times m$  matrix  $M$ . Since we have seen that  $\theta$  is a simple eigenvalue, we know that  $\partial p_m / \partial \theta > 0$  at the eigenvalue  $\phi$ . A straightforward induction argument establishes the recursive formulas

$$p_2(\theta) = \theta(\theta + r\beta_1 - r\gamma_1) - r^2\gamma_2\beta_1$$

$$p_m(\theta) = (\theta + r\beta_{m-1})p_{m-1}(\theta) + r^m(\gamma_{m-1} - \gamma_m) \prod_{k=1}^{m-1} \beta_k, \quad m \geq 3.$$

Further induction arguments show that  $p_m(0) = -r^m\gamma_m \prod_{k=1}^{m-1} \beta_k < 0$  (which implies that  $\theta > 0$ ) and that  $\partial p_m / \partial \gamma_m = -r^m \prod_{k=1}^{m-1} \beta_k < 0$ ,  $\partial p_m / \partial \gamma_i < 0$  for  $i < m$ . Thus,  $\partial \theta / \partial \gamma_i = -(\partial p_m / \partial \gamma_i) / (\partial p_m / \partial \theta) > 0$ .

This calculation shows that an increase in any reproductive coefficient  $\gamma_i$  results in an increase in the eigenvalue  $\theta$  and hence in increased competitive effectiveness.

The result of an increase in a growth coefficient on  $\theta$  is not, however, as simple. Whether it is advantageous to grow more quickly through a size class or not depends upon the reproductive efficiencies of the larger size classes. It would be interesting to ascertain exactly when an increase or decrease in  $\beta_i$  results in an increase in  $\theta$  in the size-structured model. We do not attempt to do this here, but instead consider only a simple special case for which this is easily done. Suppose that several non-reproductive growing seasons are needed to reach a minimum size needed for reproductive maturation, i.e.,  $\gamma_i = 0$  for all  $i \neq m$ . At the eigenvalue, in this case,  $\partial p_m / \partial \beta_{m-1} = -r p_{m-1} - r^m \gamma_m \prod_{k \neq m-1} \beta_k = -\theta r^m \gamma_m \prod_{k \neq m-1} \beta_k / (\theta + r \beta_{m-1}) < 0$ , and by induction  $\partial p_m / \partial \beta_i < 0$  for  $i < m-2$ . As a result  $\partial \theta / \partial \beta_i = -(\partial p / \partial \beta_i) / (\partial p / \partial \theta) > 0$ , and  $\theta$  increases with each  $\beta_i$ . Thus, in this case, it is to a species' competitive advantage, not surprisingly, to grow as quickly as possible through the infertile size masses in order to reach minimum maturation size.

The coefficients  $\beta_i, \gamma_i$  are themselves composites of the lower level body-size-specific, physiological parameters listed above. An understanding of how  $\theta$  depends on  $\beta_i$  can help in the analysis of the effect on population level dynamics that any one of these parameters has.

For example, with regard to the competitive success of a species and body-size characteristics of its individuals, some conclusions that can be drawn from these results and from (13) are the following. Note that  $\gamma_m$  is proportional to adult size  $s_m$  and inversely proportional to size at birth  $s_1$ , and that  $\beta_i$  is inversely proportional to  $\delta_i$ . If two or more size-structured species of the type modeled above are (model parameter) identical with the sole exception of their maximal adult sizes, then in competition for a common resource the only surviving species will be the one with the largest adult size. The results here show how, on the other hand, a species with smaller adult size can overcome its competitive disadvantage, i.e., gain the largest  $\theta$  while still having the smallest adult size. For example, if this species were to decrease its minimal size at reproductive maturity, or its size at birth, it could gain the upper hand.

These conclusions assume that the species have identical resource conversion factors  $\omega_i, \eta_i$ , allocation fractions  $\kappa_i, \xi_i$ , etc. Significant differences in these parameters can, of course, make any general correlation between body-size characteristics and competitive success impossible. It is obvious how changes in some of these parameters will result in increases in the coefficients  $\gamma_i = \xi_i \sigma_i s_i^2 / \omega_i \mu_1 s_1^3$  and  $\beta_i = \kappa_i \sigma_i / 3 \mu_i \eta_i \delta_i$  and hence in  $\theta$ . For example, a decrease in the conversion factors  $\omega_i$  or  $\eta_i$  will increase the reproductive coefficient  $\beta_i$  or growth coefficient  $\gamma_i$ , respectively. Biologically

some of these parameters may not, however, be reasonably changed independently of others. In such cases, the effects on  $\theta$  due to changes in such parameters is not immediately clear.

For example, an increase in the growth/metabolism allocation fraction  $\kappa_i$  for any particular size class would most likely be made at the expense of a decrease in the reproductive allocation fraction  $\xi_i$ , and vice versa. Suppose that any resource not utilized for growth and metabolism is utilized for reproduction (i.e., storage of consumed resource is neglected). Then we might reasonably set  $\xi_i = 1 - \kappa_i$ . How then does  $\theta$  depend upon  $\kappa_i$ ? Under what circumstances would it be competitively advantageous for individuals of a certain body size to increase their resource allocation to growth and decrease their allocation to reproduction. In other words, when is  $\theta$  an increasing function of  $\kappa_i$ ?

Consider the simple case of just two size categories ( $m=2$ ), both of which are fertile. Then  $\theta$  is the positive root of the second-degree polynomial  $\theta^2 + r(\beta_1 - \gamma_1)\theta - r^2\beta_1\gamma_2$ . Here  $\beta_1 = \kappa_1\sigma_1/3\mu_1\eta_1\delta_1$  and  $\gamma_1 = (1 - \kappa_1)\gamma_{\max}$ , where  $\gamma_{\max} = \sigma_1s_1^2/\omega_1\mu_1s_1^3$  is the maximal obtainable value of the reproductive coefficient  $\gamma_1$  (obtainable when  $\kappa_1 = 0$ , i.e., when no resource is allocated to growth). It is not difficult to compute the derivative  $\partial\theta/\partial\kappa$  and show that it is positive if and only if  $\gamma_2 > \gamma_{\max}(1 + 3\eta_1\delta_1\omega_1^{-1}s_1^{-1})$ . Thus, for this simple case of  $m=2$  size classes, we see that it is competitively advantageous for a smaller individual to increase its resource allocation to growth, decreasing that allocated to reproduction, provided the reproductive coefficient of the larger class is large enough (in particular, if the sufficiently exceeds the maximal reproductive coefficient obtainable at the smaller size).

#### 4. CONCLUDING REMARKS

The main concern of this paper was with the problem of relating physiological properties of individual organisms to the dynamics of the total population. The focus was on the effects that intra- and inter-specific competition between individuals has on those physiological characteristics of individuals that determine fertility and development through like cycle stages or classifications. A general nonlinear, matrix difference equation was described which accounts for the dynamics of stage-distribution vectors under the assumption that individuals in the population are placed into well defined descriptive stages amongst which transition rates over discrete time intervals are known. It was shown how, if stage differences in mortality are insignificant compared to differences in fertility and stage transitions, and hence can be ignored in the model, a nonlinear version of

the strong ergodic theorem of demography mathematically separates the population level dynamics from the dynamics of the stage-distribution vector. The nonlinear equation that governs the population level dynamics contains a key parameter  $\theta$  that encapsulates the individual or stage-level parameters. By understanding how the dynamics of this equation depend upon  $\theta$  and how  $\theta$  is affected by the stage level parameters, one can link the population level dynamics with properties of individual organisms.

This procedure was applied in Section 3 to a model utilizing body-length classes under the assumption that resource consumption is proportional to body surface area. It was shown how the surviving species in a competition interaction could be determined from these  $\theta$  parameters for each species, and how this could in turn be determined from such size-specific properties as adult size, at maturation, size-specific growth and reproduction resource allocation fractions, etc. One of the conclusions reached was that, all other things equal, the species with the largest adult body size has a competitive advantage. Our results also provide a means to determine precise criteria by which a smaller species could overcome its disadvantage, for example by maturing and being born at a sufficiently smaller size or by appropriately increasing or decreasing resource allocation to growth/metabolism vs reproduction at different sizes.

The nonlinear matrix model that was used here could be modified in several ways in order to include features ignored in this study. One example is the fact that populations often significantly affect the dynamics of their resource (prey) which in turn, of course, affects the dynamics of the population. See Crowe (1991). Another example is that structure within the resource population can be significant. For example, the means by which a larger species is competitively more efficient is often attributed to the ability to harvest larger food particles, in addition to the smaller particles utilized by smaller species. Thus, it can be important to dynamically model the resource as a structured population (Hall *et al.*, 1976; Neill, 1975; Fenchel and Kofored, 1976; Wilson, 1975; Hamrin and Persson, 1986; Persson, 1988). This can be done using the types of model introduced here by introducing dynamical equations for a resource population whose state variables determine the resource availability  $r$ . Another example involves seasonality and other factors that cause environmental fluctuations which can significantly affect the dynamics of population growth and competitive interactions (Hutchinson, 1961; Koch, 1974; Oster and Takahashi, 1974; Hall *et al.*, 1976; Levins, 1979; Boyce, 1979; Prout and McChesney, 1985; Hamrin and Persson, 1986; Lomnicki, 1988). Such oscillations lead to periodic fluctuations of model parameters, such as resource availability, allocation fractions, resource availability and uptake rates, etc.

All of these features could easily be incorporated into the model of Section 2, and the methodology there applied to the resulting modifications. In

particular, the nonlinear strong ergodic theorem could still be applied to reduce the population level dynamics to a system of difference equations.

It was assumed in this paper that mortality was independent of body size. It would be of interest to relax this assumption. This would be the case, for example, in using the model to study the effects of predation on the outcome of competition (e.g., predator-mediated competition) between size-structured species, since such predation is often size dependent. In this case, however, the strong ergodic theorem used in this paper would not in general be valid, and an analysis based upon methods different from those utilizing the population-level equations derived above would be required.

#### REFERENCES

- BOYCE, M. S. 1979. Seasonality and patterns of natural selection for life histories, *Am. Nat.* **114**, No. 4, 569–583.
- BROOKS, J. L., AND DODSON, S. I. 1965. Predation, body size, and composition of plankton, *Science* **150**, 28–35.
- CALDER, W. A. 1984. "Size, Function, and Life History," Harvard Univ. Press, Cambridge, MA.
- CASWELL, H. 1989. "Matrix Population Models," Sinauer Assoc. Inc., Sunderland, MA.
- CROWE, K. M. 1991. A discrete size-structured competition model, Ph.D. dissertation, Interdisciplinary Program on Applied Mathematics, University of Arizona, Tucson.
- CUSHING, J. M. 1990. Competing size structured species, in "Mathematical Population Dynamics" (Arino, Axelrod and Kimmel, Eds.), Dekker, New York.
- EBENMAN, B., AND PERSSON, L. 1988. "Size-Structured Populations: Ecology and Evolution," Springer, New York.
- EK, A. R., AND MONSERUD, R. A. 1979. Performance and comparison of stand growth models based on individual tree and diameter class growth, *Can. J. For. Res.* **9**, 231–244.
- FENCHEL, T., AND KOFORED, L. H. 1976. Evidence for exploitative interspecific competition in mud snails (*Hydrobiidae*), *Oikos* **27**, 367–376.
- GERRITSEN, J. 1984. Size efficiency reconsidered: A general foraging model for free-swimming aquatic animals, *Am. Nat.* **123**, No. 4, 450–467.
- GROSS, L. J. 1986. Biophysical ecology: An introduction to organism response to environment, in "Mathematical Ecology" (T. G. Hallam and S. A. Levin, Eds.), Springer, Berlin.
- HALL, D. J., THRELKELD, S. T., BURNS, C. W., AND CROWLEY, P. H. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities, *Ann. Rev. Ecol. Syst.* **7**, 177–208.
- HAMRIN, S. F., AND PERSSON, L. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species, *Oikos* **47**, 223–232.
- HUTCHINSON, G. E. 1961. The paradox of the plankton, *Am. Nat.* **95**, 137–145.
- IMPAGLIAZZO, J. 1985. "Deterministic Aspects of Mathematical Demography," Springer, Berlin.
- KOCH, A. L. 1974. Coexistence resulting from an alternation of density dependent and density independent growth, *J. Theor. Biol.* **44**, 373–386.
- LESLIE, P. H. 1945. On the use of matrices in certain population mathematics, *Biometrika* **33**, 183–212.
- LEVINS, R. 1979. Coexistence in a variable environment, *Am. Nat.* **114**, No. 6, 765–783.

- LOMNICKI, A. 1988. "Population Ecology of Individuals," Monographs in Population Biology, Vol. 25, Princeton Univ. Press, Princeton, NJ.
- METZ, J. A. J., AND DIEKMANN, O. 1986. "The Dynamics of Physiologically Structured Populations," Lecture Notes in Biomathematics, Vol. 68, Springer, Berlin.
- NEILL, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization, *Ecology* **56**, 809-826.
- OSTER, G., AND TAKAHASHI, Y. 1974. Models for age-specific interactions in a periodic environment, *Ecol. Monogr.* **44**, No. 4, 483-501.
- PERSSON, L. 1988. Asymmetries in competitive and predatory interactions in fish populations, in "Size-Structured Populations: Ecology and Evolution" (B. Ebenman and L. Persson, Eds.), Springer, New York.
- PROUT, T., AND MCCHESENEY, F. 1985. Competition among immatures affects their adult fertility: Population dynamics, *Am. Nat.* **126**, No. 4, 521-558.
- USHER, M. B. 1972. Developments in the Leslie matrix model, in "Mathematical Models in Ecology" (J. M. R. Jeffers, Ed.), pp. 29-60, Blackwell Scientific Publishers, London.
- WERNER, E. E., AND GILLIAM, J. F. 1984. The ontogenetic niche and species interaction in size-structured populations, *Annu. Rev. Ecol. Syst.* **15**, 393-425.
- WILSON, D. S. 1975. The adequacy of body size as a niche difference, *Am. Nat.* **109**, No. 970, 769-784.