

## PARAMETER DEPENDENCE, SIZE AND SURVIVABILITY

KATHLEEN M. CROWE

**1. Introduction.** The goal of this paper is to use the available mathematical theory for discrete size-structured models to provide an alternative perspective from which to consider some issues arising from the study of interactions among size-structured species, namely the Size-Efficiency Hypothesis of Brooks and Dodson [1], and some types of life-history strategies and trade-offs.

The Size-Efficiency Hypothesis, which was formulated based upon observations of planktivore-plankton systems, states in part that, "... when predation is of low intensity the small planktonic herbivores will be competitively eliminated by large forms ... ." This hypothesis has been tested on a variety of ecological systems, with varying results. In cases in which the hypothesis failed, many factors, such as the presence of a top predator, asymmetric competition, etc., have been pointed to as contributing to this failure. For the model presented here, we show conditions under which the Size-Efficiency Hypothesis holds and fails and discuss the dependence of these results upon the individual physiological parameters of the model.

We then turn to the study of life-history strategies using this model. One of the most typical life-history trade-offs is between growth and reproduction. Such a trade-off has been documented in a variety of ecological systems (see, for example, Inglesfield and Begon [9] and Eis et al. [8]). We use the size-structured model given here to study some aspects of life-history strategies and trade-offs for a population with density-dependent growth.

---

Received by the editors on October 2, 1992, and in revised form on June 9, 1993. Supported in the Program in Applied Mathematics at the University of Arizona by the Applied Mathematics and Population Biology/Ecology Divisions of the National Science Foundation under grant No. DMS-8902508. Supported at Cornell University by the U.S. Army Research Office through the Mathematical Sciences Institute, Contract DAAL03-91-C-0027.

This work comprises part of the author's dissertation at the University of Arizona, directed by J.M. Cushing.

Copyright ©1995 Rocky Mountain Mathematics Consortium

**2. Model and dynamics.** We consider a population which is divided into four size classes,  $[\bar{s}_{i-1}, \bar{s}_i)$ ,  $i = 1, \dots, 4$ , with at least one juvenile (nonreproducing) class, and assume that individuals can grow no more than one class in a unit of time. We let  $P(t)$  denote the total surface area of the population, i.e.,

$$(1) \quad P(t) = \sum_{i=1}^m s_i^2 x_i(t),$$

and let  $\pi$  represent the survival probability. Then the dynamical equations for this system are given by

$$(2) \quad \begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ x_4(t+1) \end{bmatrix} = \pi \left( \begin{bmatrix} 1 - \beta_1 u(P) & 0 & 0 & 0 \\ \beta_1 u(P) & 1 - \beta_2 u(P) & 0 & 0 \\ 0 & \beta_2 u(P) & 1 - \beta_3 u(P) & 0 \\ 0 & 0 & \beta_3 u(P) & 1 \end{bmatrix} + u(P) \begin{bmatrix} 0 & \gamma_2 & \gamma_3 & \gamma_4 \\ 0 & & & \\ 0 & \mathcal{O} & & \\ 0 & & & \end{bmatrix} \right) \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ x_4(t) \end{bmatrix},$$

where  $u(P)$  is the per-unit resource uptake, and  $\beta_i$  and  $\gamma_i$  are (respectively) the growth and reproduction coefficients for the  $i$ th size class. These coefficients, which depend on various physiological parameters, are given explicitly by:

$$(3) \quad \beta_i = \frac{\kappa_i \sigma_i}{3\mu_i \eta_i \delta_i}, \quad \text{and} \quad \gamma_i = \frac{(1 - \kappa_i) \sigma_i s_i^2}{\omega_i W_1},$$

where the size-specific parameters are contained in Table 1.

TABLE 1. Individual size-specific parameters for species  $i$ .

$s_i$	representative length of $i$ -class individual
$\delta_i$	length of the $i$ th size class ( $\bar{s}_i - \bar{s}_{i-1}$ )
$\mu_i$	body density (assume uniform so that body weight is $W_i = \mu_i s_i^3$ )
$\sigma_i$	constant of proportionality relating surface area to $s_i^2$
$\kappa_i$	fraction of consumed resource allocated to growth
$\eta_i$	conversion factor of resource units to body weight
$\omega_i$	conversion factor of resource units to offspring body weight

Equation (2) belongs to a class of equations for which it has been shown that the normalized size-class distribution vector  $\vec{\eta}(t) \triangleq \vec{x}(t)/P(t)$  will approach a constant vector  $\vec{v}$  (see [3, 5, 6]). Hence, we can study the dynamics of a limiting scalar equation for  $P(t)$  without losing any information about the structure of the species.

For the model under consideration here, we find that  $\vec{\eta}(t) \rightarrow \vec{v}$  as  $t \rightarrow \infty$ , where

$$(4) \quad \vec{v} = \begin{bmatrix} \theta(\theta + \beta_2)(\theta + \beta_3) \\ \theta\beta_1(\theta + \beta_3) \\ \theta\beta_1\beta_2 \\ \beta_1\beta_2\beta_3 \end{bmatrix}$$

is the right eigenvector associated with the maximal eigenvalue  $\theta$  of the matrix

$$(5) \quad \mathcal{M} = \begin{bmatrix} -\beta_1 & \gamma_2 & \gamma_3 & \gamma_4 \\ \beta_1 & -\beta_2 & 0 & 0 \\ 0 & \beta_2 & -\beta_3 & 0 \\ 0 & 0 & \beta_3 & 0 \end{bmatrix},$$

and from this we obtain the limiting equation for  $P(t)$ :

$$(6) \quad P(t+1) = \pi[1 + \theta u(P(t))]P(t).$$

The dynamics of this equation, both with and without a dynamically modeled resource, have been widely studied by Cushing [7] and Crowe [5, 4]. There is a critical value  $\theta^{cr}$  of the parameter  $\theta$  such that for  $\theta < \theta^{cr}$  the trivial equilibrium is globally attracting, and for  $\theta > \theta^{cr}$  there is a unique nontrivial equilibrium that is attracting for small  $\theta$ . As the parameter  $\theta$  is increased, the equilibrium undergoes a typical sequence of period doubling bifurcations. In general, we can characterize the effect of increasing  $\theta$  as a positive one; i.e., increasing  $\theta$  first allows the species to exist on the given amount of resource and then increases away from extinction the population level of the species.

Similar modeling techniques applied in the case of several species yield the equations

$$(7) \quad P_j(t+1) = \pi_j[1 + \theta_j u_j(\vec{P}(t))]P_j(t), \quad j = 1, \dots, n.$$

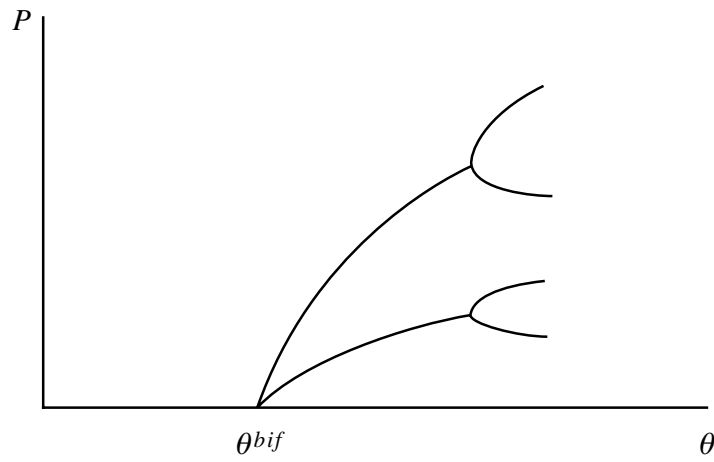


FIGURE 1a. Lift-off of an asymptotically stable 2-cycle in  $n + 1$  species from an asymptotically stable 2-cycle in  $n$  species.

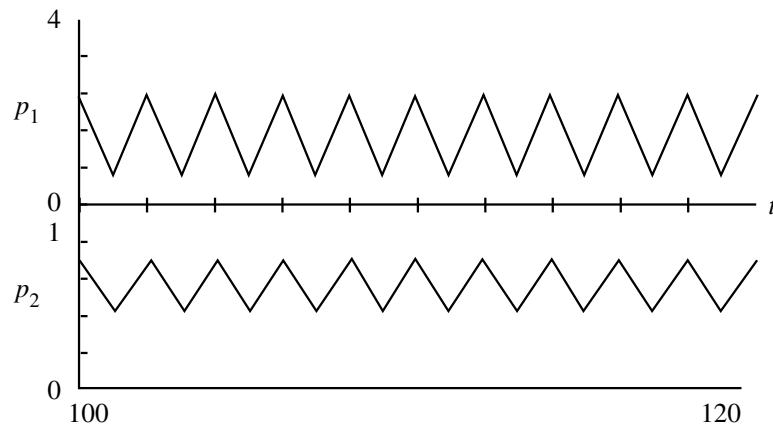


FIGURE 1b. Time series for two species displaying oscillatory coexistence. Here  $\pi_1 = .2$ ,  $\pi_2 = .6$ ,  $u_1(P) = e^{-2P}$ ,  $u_2(P) = e^{-P}$ ,  $\theta_1 = 100.0$ , and  $\theta_2 = 10.0$ .

For this model it has been shown that equilibrium coexistence cannot occur for generic choices of parameters, but oscillatory coexistence can occur (see Crowe, [4, 5]). This is illustrated in Figure 1. Again, the conclusion may be drawn that increasing  $\theta_j$  will benefit the  $j$ th species, allowing it to coexist rather than experience extinction.

**3. Parameter dependence.** As has been shown here, an increase in the parameter  $\theta$  results in general in an increase in the ability of the species to survive. In addition, it can be shown that there is a monotonically increasing relationship between  $\theta$  and the net reproductive number of the population, so increases in  $\theta$  also increase the net reproductive number. However,  $\theta$  is really an aggregate parameter depending upon the entries of the matrix  $\mathcal{M}$ , the  $\beta_i$  and  $\gamma_i$ , which in turn depend upon individual physiological parameters such as  $\eta_i$ ,  $\kappa_i$  and  $\omega_i$ . Thus we may explore the effects that changes in these lowest level parameters may have on the species by seeing how these changes affect  $\theta$ .

In order to study the relationship between species' sizes and survivability, we need a measure of species size. Several different such measures are commonly used, but we will focus on just one of these, that of average adult size. Because the vector  $\vec{v}$  contains the normalized size-class distribution, the average adult size of a species,  $\mathcal{S}$ , may be expressed as

$$\mathcal{S} = \sum_{i=j}^m s_i^2 v_i$$

where  $j$  is the number of the first reproducing class. This allows us to write

$$(8) \quad \mathcal{S} = s_2^2 \theta \beta_1 (\theta + \beta_3) + s_3^2 \theta \beta_1 \beta_2 + s_4^2 \theta \beta_1 \beta_2 \beta_3.$$

From (8) we see the explicit dependence of  $\mathcal{S}$  upon individual physiological parameters.

We observe that the left eigenvector of  $\mathcal{M}$  corresponding to  $\theta$  can be interpreted as the vector of size-class reproductive values; i.e.,  $w_i$  is "the value of an ( $i$ -class) individual as a seed for future population growth" (Caswell [2]).

We now summarize the effects of changes in the parameters  $\omega_i$ ,  $\eta_i$  and  $\kappa_i$  on  $\theta$  and  $\mathcal{S}$ .

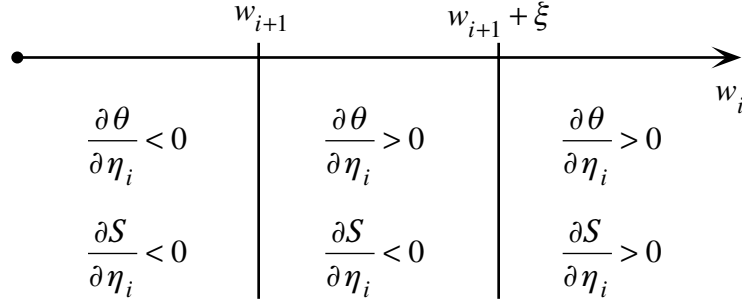


FIGURE 2. Changes in  $\theta$  and  $\mathcal{S}$  with changes in  $\eta_i$  over various ranges of  $w_i$  (reproductive value of class  $i$ ).

$\omega_i$ : By direct calculation we see that

$$\frac{\partial \theta}{\partial \omega_i} < 0 \quad \text{and} \quad \frac{\partial \mathcal{S}}{\partial \omega_i} < 0$$

for all choices of parameter values. Thus, in this case, an increase in  $\omega_i$  (conversion factor of resource units to offspring body weight) results in decreases in both  $\theta$  and  $\mathcal{S}$ .

$\eta_i$ : We have

$$\frac{\partial \theta}{\partial \eta_i} \text{ is } \begin{cases} > 0 & \text{if } w_i > w_{i+1} \\ < 0 & \text{if } w_i < w_{i+1} \end{cases}$$

while

$$\frac{\partial \mathcal{S}}{\partial \eta_i} \text{ is } \begin{cases} > 0 & \text{if } w_i > w_{i+1} + \xi \\ < 0 & \text{if } w_i < w_{i+1} + \xi \end{cases}$$

where  $\vec{w}$  is the left eigenvector of  $\mathcal{M}$  and  $\xi$  is a positive constant which depends on the individual physiological parameters. We may summarize these results in Figure 2.

Here we see that for choices of parameters giving a “low” value of  $w_i$  (i.e.,  $w_i < w_{i+1}$ ), an increase in  $\eta_i$  (conversion factor of resource units to body weight) reduces species size and is harmful to the species, while for parameters giving a “high” value of  $w_i$  ( $w_i > w_{i+1} + \xi$ ), increases in  $\eta_i$  increase size and are beneficial. In addition, for an intermediate

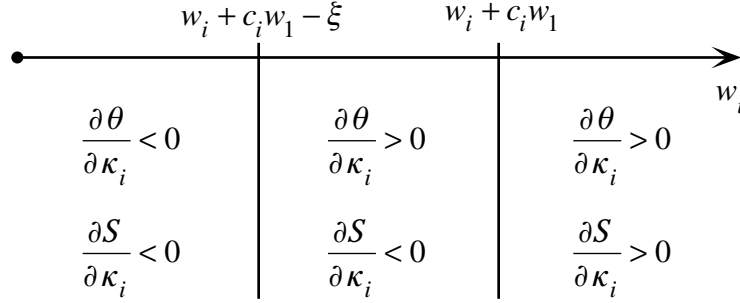


FIGURE 3. Changes in  $\theta$  and  $S$  with changes in  $\kappa_i$  over various ranges of  $w_{i+1}$  (fraction of consumed resource allocated to growth for a class  $i$  individual).

range of  $w_i$  ( $w_{i+1} < w_i < w_{i+1} + \xi$ ) an increase in  $\eta_i$  leads to a decrease in species size and is beneficial to the species.

$\kappa_i$ : We have that

$$\frac{\partial \theta}{\partial \kappa_i} \text{ is } \begin{cases} > 0 & \text{if } w_{i+1} > w_i + c_i w_1 \\ < 0 & \text{if } w_{i+1} < w_i + c_i w_1 \end{cases}$$

while

$$\frac{\partial S}{\partial \kappa_i} \text{ is } \begin{cases} > 0 & \text{if } w_{i+1} > w_i + c_i w_1 + \xi \\ < 0 & \text{if } w_{i+1} < w_i + c_i w_1 + \xi \end{cases}$$

where again  $\xi$ , as well as  $c_i$ , are positive constants. These results may then be summarized by Figure 3.

In this case we see that, for choices of parameters giving a “low” value of  $w_{i+1}$  (i.e.,  $w_{i+1} < w_i + c_i w_1$ ), an increase in  $\kappa_i$  (fraction of consumed resource allocated to growth) reduces species size and is harmful to the species, while for parameters giving a “high” value of  $w_{i+1}$  ( $w_{i+1} > w_i + c_i w_1 + \xi$ ), increases in  $\kappa_i$  increase size and are beneficial. Finally, for an intermediate range of  $w_{i+1}$  ( $w_i + c_i w_1 + \xi < w_{i+1} < w_i + c_i w_1$ ) an increase in  $\kappa_i$  leads to an increase in species size but is harmful to the species.

**4. Conclusion.** We consider these results first in light of the Size Efficiency Hypothesis. An immediate conclusion to be drawn is

that it is not enough to simply consider changes in species' size and survivability; the underlying mechanism(s) of such changes must be studied as well. Indeed, the examples above illustrate the wide range of possible changes in  $\mathcal{S}$  and  $\theta$ , and it is only in the first example, in which changes in  $\mathcal{S}$  and  $\theta$  are caused by changes in  $\omega_i$ , that we see a monotonic relationship between  $\mathcal{S}$  and  $\theta$ . The second and third examples both display ranges of parameters in which  $\mathcal{S}$  and  $\theta$  increase (or decrease) together with changes in  $\kappa_i$  or  $\eta_i$ ; but these examples also display regions in which  $\mathcal{S}$  increases and  $\theta$  decreases (with increasing  $\kappa_i$ ) and  $\mathcal{S}$  decreases while  $\theta$  increases (with increasing  $\eta_i$ ).

We now turn to the issue of life-history strategies and trade-offs. The study of such phenomena comprises a significant part of the study of ecological systems, and these phenomena provide the basis for many studies in evolutionary theory, population genetics, etc.

In the model considered here (as in many models and ecological systems) the most significant trade-off occurs between growth and reproduction. This is due to the terms  $\kappa_i$  and  $1 - \kappa_i$  which occur in  $\beta_i$  and  $\gamma_i$ , respectively (see (3)). Clearly, a change in  $\kappa_i$  affects  $\beta_i$  and  $\gamma_i$  in opposite ways, i.e.,

$$\frac{\partial \beta_i}{\partial \kappa_i} = \frac{\sigma_i}{3\mu_i \eta_i \delta_i} > 0, \quad \text{and} \quad \frac{\partial \gamma_i}{\partial \kappa_i} = -\frac{\sigma_i s_i^2}{\omega_i W_1} < 0,$$

providing a simple illustration of the trade-off between growth and reproduction. Of course, as illustrated in Figures 2 and 3, the significance of this trade-off is best seen in its effect on  $\mathcal{S}$  and  $\theta$ .

Finally we look at the results of Section 3 as statements about general life-history strategies, ignoring the trade-offs that underlie them. Consider first the effects on  $\theta$  of changes in  $\omega_i$ . It was shown that  $\theta$  always increases with decreases in  $\omega_i$ . This merely says that the less resource needed to produce a unit of offspring, the better for the species.

Next consider the effects of  $\eta_i$  on  $\theta$ . Whether  $\theta$  increases or decreases with increasing  $\eta_i$  depends upon the relative values of  $w_i$  and  $w_{i+1}$ , the reproductive values of individuals in classes  $i$  and  $i + 1$ , respectively. Since an increase in  $\eta_i$  increases the amount of resource that an  $i$ -class individual must consume to grow to class  $i + 1$ , we may interpret  $\partial \theta / \partial \eta_i$  as follows:



It is to a species' benefit to slow the growth from class  $i$  to class  $i + 1$  (i.e.,  $\partial\theta/\partial\eta_i > 0$ ) if the reproductive value of an individual in class  $i$  is greater than that of an individual in class  $i + 1$  ( $w_i > w_{i+1}$ ) and, similarly, it is to a species' benefit to grow more quickly to class  $i + 1$  if the reproductive value of a class  $i + 1$  individual is greater than that of a class  $i$  individual.

Finally, we consider the effects of  $\kappa_i$  on  $\theta$ , recalling that an increase in  $\kappa_i$  corresponds to an increase in growth and decrease in reproduction of  $i$ -class individuals. We then see that:

It is to a species' benefit for its  $i$ -class individuals to grow more quickly to class  $i + 1$  ( $\partial\theta/\partial\kappa_i > 0$ ) if the reproductive value of an  $i + 1$ -class individual exceeds the sum of the reproductive value in class  $i$  and a multiple of the 1-class reproductive value ( $w_{i+1} > w_i + c_i w_1$ ), and it is beneficial to the species to grow more slowly if the reproductive value in the next size class ( $i + 1$ ) is not sufficiently large.

These results demonstrate the significance of individual physiological parameters on everything from the population-level dynamics of a species to the life-history strategies employed at the size-class level. In some cases these results confirm what biological intuition already tells us, and in others they show the levels of complexity lacking in some theoretical formulations at the population level.

## REFERENCES

1. J.L. Brooks and S.I. Dodson, *Predation, body size, and composition of plankton*, Science **150** (1965), 28–35.
2. H. Caswell, *Matrix population models*, Sinauer Associates, Inc., Sunderland, MA, 1989.
3. K.M. Crowe, *A nonlinear ergodic theorem for discrete systems*, J. Math. Biol. **32** (1994), 179–191.
4. ———, *Size-structured competitive coexistence in discrete time*, in preparation.
5. ———, *A discrete size-structured competition model*, Ph.D. thesis, University of Arizona, Tucson, Arizona, 1991.
6. J.M. Cushing, *Nonlinear matrix models and population dynamics*, Natur. Resource Modeling **2** (1988), 539–580.
7. ———, *Some competition models for size-structured populations*, Rocky Mountain J. Math. **20** (1990), 879–897.

8. S. Eis, E.H. Garman and L.F. Ebel, *Relationship between cone production and diameter increment of Douglas fir*, (*pseudotsuga menziesii* (Mirb.) France), *Grand fir* (*abies grandus Dougl.*), and *western white pine* (*pinus monticola Dougl.*), Canad. J. Bot. **45** (1965), 1553–1559.

9. C. Inglesfield and M. Begon, *The ontogeny and cost of migration in drosophila subobscura Collin.*, Bio. J. Linnean Soc. **19** (1983), 9–15.

CENTER FOR APPLIED MATHEMATICS, 657 ENGINEERING AND THEORY CENTER,  
CORNELL UNIVERSITY, ITHACA, NY 14853

*Current address:* DEPARTMENT OF MATHEMATICS, HUMBOLDT STATE UNIVERSITY,  
ARCATA, CA 95571