

# **INDIVIDUAL-BASED MODELS AND APPROACHES IN ECOLOGY**

Populations, Communities and Ecosystems

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Louis J. Gross, Editors

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## 6

# The Dynamics of a Size-Structured Intraspecific Competition Model with Density Dependent Juvenile Growth Rates

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**ABSTRACT.** The dynamics of a size-structured population in which adult fertility correlates with body size, and in which adult body size at maturation is dependent (through competitive effects) upon population density during juvenile growth, are studied. A simple discrete model for a population with one juvenile size class and two adult size classes, one consisting of larger and more fertile individuals than the other, is derived and analyzed. The competitive effects on juvenile growth are separated into those due to competition from other juveniles and those due to adults. Parameter regions are determined in which the dynamics equilibrate, approach 2-cycles, or result in chaotic oscillations. The results suggest that intra-specific competition of this kind between juveniles and adults is destabilizing for either small or very large inherent net reproductive rates, strong competitive effects tending to result in a synchronous 2-cycle in which juveniles and adults avoid competition. For intermediate values of the inherent net reproductive rate, however, intra-specific competition has a stabilizing influence, promoting equilibration where there would otherwise be chaotic oscillations.

### Introduction

Biological populations have a natural propensity for exponential growth which in the long run, of course, must be held in check. Nonlinear models of population growth do this by incorporating "density effects" which serve to decrease either fertility or survival. The majority of models for population growth describe highly aggregate population level variables, such as total population size or biomass, and as a result can account for intraspecific competition due to increased population density in only a very qualitative manner. In order to better account for the mechanisms causing intraspecific competition, it is necessary to use a structured population model in which

relevant physiological or behavioral characteristics of individual organisms are distinguished.

There are many means by which individuals of a species might compete for common resources, and by which such competition might express itself. One type of intraspecific competition which has received recent attention is that which can occur between juvenile and adult members of the population (May et al. 1974, Bellows 1982, Tschumy 1982, Ebenman 1987, Ebenman 1988a, Cushing and Li 1989, Cushing and Li 1991, Cushing 1991). The possibility of niche overlap between juveniles and adults exists for species with relatively "simple" life cycles, as opposed to those that undergo significant metamorphosis or otherwise experience radical ontogenetic niche shifts during their development. This includes most reptiles, fish, mammals, and hemimetabolous insects.

The dynamical consequences of juvenile and adult competition has been investigated by means of simple age-structured models by several authors with the conclusion that such competition is usually destabilizing (May et al. 1974, Bellows 1982, Tschumy 1982), but that under certain circumstances can be stabilizing (Ebenman 1987, Ebenman 1988a, Cushing and Li 1989, Cushing and Li 1991, Cushing 1991). In these age-structured models the effects of juvenile vs. adult competition result in either reduced juvenile survival or adult fertility.

Another important effect of competition experienced by juveniles, which is not included in any of these age-structured models, is that of slowed growth. Body size is often a more important physical attribute than is chronological age (Werner and Gilliam 1984, Ebenman and Persson 1988). Body size, not age, is often the key factor in determining vital rates such as fertility, survival, and individual growth rates as well as susceptibility to environmental hazards (such as predation and cannibalism), metabolic demands, etc. Thus, intraspecific competition can slow juvenile growth, reduce size at maturation, and consequently affect population growth by reducing fertility (Wilbur 1980, Botsford 1981, Prout and McChesney 1985, Ebenman and Persson 1988).

In an attempt to study the consequences of slowed juvenile growth due to intraspecific competition, Ebenman (1988b) placed, in a rather *ad hoc* manner, a time delay in his age-structure difference equation model and concluded that strong competition of this sort has a destabilizing effect on the population dynamics. As pointed out by Ebenman, however, it would be more appropriate to analyze this phenomenon by means of a size-structured model. In a later paper, Ebenman (1988b) extended his model to include variable adult size. This extension, however, is sufficiently complicated that virtually no analytical results are attainable and it must be analyzed numerically.

In this paper we consider a model of size-structured, intraspecific com-

petition in which increased competition during juvenile growth reduces size at adulthood and thereby reduces adult fertility. Our goal here is to derive a model which is simple enough to be as analytically tractable as possible, and yet still capture these essential features. We wish to understand the asymptotic dynamics of the model and to draw some conclusions about the stabilizing or destabilizing effects of this kind of intraspecific competitive interaction.

### Model Equations

We wish to write down a model for the dynamics of a population in which an adult individual's fertility is correlated with its body size, which in turn is dependent upon the amount of competition experienced during juvenile growth. In this paper we will consider only the simplest version of the kind of discrete model we have in mind, which nonetheless captures these basic features. We will ignore density dependent fertility and survival rates and focus on the effects of density on growth rates. Such extensions of the model will be studied in a future paper.

Imagine a population in which (surviving) juveniles mature at one of two possible adult sizes after a fixed unit of time  $t = 1$ . The fraction  $\phi(W)$  of surviving juveniles that mature at the larger adult size is dependent upon the amount of competitive pressure experienced during juvenile growth, which is measured here by a weighted total population size  $W = J + \beta_1 A_1 + \beta_2 A_2$ . Here  $J$  is the number or density of juveniles,  $A_1$  is the number of smaller adults, and  $A_2$  is the number of larger adults. Thus the competition coefficients  $\beta_i \geq 0$  measure the effect that an adult individual of size  $i$  has on juvenile growth, relative to the effect of a juvenile individual. If we consider a semelparous population in which there is no adult survival after one unit of time, then the numbers present in each size category after the elapse of one unit of time are given by

$$\begin{aligned} \text{(a)} \quad J(t+1) &= nf_1 A_1(t) + nf_2 A_2(t) \\ \text{(b)} \quad A_1(t+1) &= \pi(1 - \phi(W(t)))J(t) \\ \text{(c)} \quad A_2(t+1) &= \pi\phi(W(t))J(t). \end{aligned} \tag{2.1}$$

for  $t = 1, 2, 3, \dots$ . Of course we are only interested in non-negative solutions of Eqs. (2.1), and in particular for initial conditions

$$J(0) \geq 0, A_1(0) \geq 0, A_2(0) \geq 0. \tag{2.2}$$

In Eqs. (2.1),  $\pi$  is the probability that a juvenile survives to adulthood and  $nf_i$  is the number of offspring produced by an adult of size  $i$  during one unit

of time. The coefficient  $n$  is used here to introduce the inherent net reproductive rate (expected number of offspring per individual per life time at low densities, taking survival into account) explicitly into the model and its analysis. The inherent net reproductive rate is given by  $nf_1\pi(1 - \phi(0)) + nf_2\pi\phi(0)$  and will equal  $n$  if, without loss in generality,  $f_1$  and  $f_2$  satisfy the normalization

$$f_1\pi(1 - \phi(0)) + f_2\pi\phi(0) = 1. \quad (2.3)$$

These parameters are assumed here to be constants, i.e. not density dependent.

The effects of increased population density on juvenile growth will be assumed to be deleterious, and therefore  $\phi$  is a decreasing function of  $W$ . For analytic simplicity only, we will assume here that in the absence of competitive effects, a juvenile will always grow to the larger adult size and that, in the other extreme, at very high (infinitely large) densities all individuals grow to the smaller size. We then have the following condition on the fraction  $\phi(W)$ :

$$\phi \in C^1(\mathbb{R}^+, [0, 1]), \phi(0) = 1, \phi(+\infty) = 0, \phi'(W) < 0.$$

In this case, Eq. (2.3) implies

$$f_2 = 1/\pi.$$

Furthermore, we are interested in the case when larger adults are more fertile so that

$$f_1 < f_2 = 1/\pi.$$

### Properties of the Model

Equations (2.1) have the trivial equilibrium  $(J, A_1, A_2) = (0, 0, 0)$ . It is shown in the Appendix (Theorem 1) that if  $n < 1$  then  $(0, 0, 0)$  is globally attracting. This makes biological sense in that if an individual cannot at least replace itself at low population densities then the population will go to extinction.

On the other hand, for  $n > n_0 = f_2/f_1 = 1/f_1\pi > 1$  it follows from Theorem 2 of the Appendix that the population will increase without bound. This is an artifact of the simplifying assumptions made here. Namely, if the smaller adult class can sustain the population even at arbitrarily large population

densities then the population will grow without bound because no controlling density effects on fertility or survival are present in this simple model.

Consequently, we focus our attention on values of the inherent net reproductive rate between 1 and  $n_0 > 1$ . From the equilibrium equations

$$\begin{aligned} J &= nf_1A_1 + nf_2A_2 \\ A_1 &= \pi(1 - \phi(W))J \\ A_2 &= \pi\phi(W)J \end{aligned}$$

where  $W = J + \beta_1A_1 + \beta_2A_2$  follows

$$J = nf_1\pi(1 - \phi(W))J + nf_2\pi\phi(W)J.$$

If  $J = 0$ , then clearly  $A_1 = A_2 = 0$ , i.e. the only equilibrium with no juveniles present is the trivial equilibrium. A nontrivial equilibrium must have  $J > 0$ , in which case we obtain

$$nN(W) = 1, N(W) = f_1\pi(1 - \phi(W)) + f_2\pi\phi(W),$$

an equation which states the biologically obvious fact that at any nontrivial equilibrium the (density dependent) net reproductive rate  $nN(W)$  must be 1. We can now derive a formula for the equilibrium states by noting that:

$$N(0) = 1, N(+\infty) = 1/n_0, N'(W) < 0.$$

Thus for  $n \in (1, n_0)$  the equilibrium weighted population size is given by:

$$W = W(n) = N^{-1}(1/n).$$

From this and the equilibrium equations above we obtain the equilibria

$$\begin{aligned} J &= \frac{W(n)}{1 + \beta_1\pi + (\beta_2 - \beta_1)\pi\phi(W(n))} \\ A_1 &= \pi(1 - \phi(W(n)))J, A_2 = \pi\phi(W(n))J. \end{aligned} \quad (3.1)$$

We have arrived at the result that there exists a unique, positive equilibrium for all values of the inherent net reproductive rate  $n$  between 1 and  $n_0$ . By a positive equilibrium is meant an equilibrium in which all three classes are present.

Note that the branch of positive equilibrium given by (3.1) bifurcates from the trivial equilibrium at the critical value  $n = 1$  and becomes unbounded as  $n$  approaches  $n_0$ . (See Cushing 1988 for a discussion of the generality of

such global continuum branches of equilibria in discrete population models.) We will study the stability of these equilibria below, but first we note that the Jacobian of Eq. (2) at the trivial solution

$$\begin{pmatrix} 0 & nf_1 & nf_2 \\ 0 & 0 & 0 \\ \pi & 0 & 0 \end{pmatrix} \quad (3.2)$$

has an eigenvalue  $\lambda = +1$  when  $n = 1$ , as is to be expected from the bifurcation of the nontrivial equilibria. Note, however, that when  $n = 1$  this Jacobian also has an eigenvalue  $\lambda = -1$ . This indicates that perhaps there is also present a bifurcating branch of 2-cycles. This borne out by Theorem 3 of the Appendix from which we find that for  $1 < n < n_0$  there exists, in addition to a unique positive equilibrium, a unique synchronous 2-cycle. By a synchronous 2-cycle is meant a period two solution of (2.1) in which the juveniles are synchronized to appear all together at alternating time periods, i.e. a 2-cycle in which  $J(t)$  alternates between 0 and a positive value. Specifically, the bifurcating 2-cycles are given by

$$\begin{aligned} &(J(t), A_1(t), A_2(t)) \\ &= \begin{cases} (W(n), 0, 0), & t = 0, 2, 4, \dots \\ (0, \pi(1 - \phi(W(n)))W(n), \pi\phi(W(n))W(n)) & t = 1, 3, 5, \dots \end{cases} \quad (3.3) \end{aligned}$$

for  $1 < n < n_0$ .

Of interest now are the stability properties of the equilibria and 2-cycles. Analytically, we can determine local asymptotic stability for  $n$  near 1.

First, consider the stability of the trivial equilibrium  $(0, 0, 0)$ . We have seen that this equilibrium is stable for  $n < 1$ . For  $n > 1$ , the eigenvalues of the Jacobian (3.2), which are  $\lambda = 0, \pm\sqrt{n}$ , show that  $(0, 0, 0)$  is unstable. Thus, for  $n > 1$  we expect a viable population, although it is not yet clear what the asymptotic dynamics are.

To determine the local stability of the equilibria (3.1) we need to determine the eigenvalues  $\lambda$  of the Jacobian

$$M = \begin{pmatrix} 0 & nf_1 & nf_2 \\ \pi(1 - \phi(W)) - \pi\phi'(W)J & -\pi\phi'(W)\beta_1J & -\pi\phi'(W)\beta_2J \\ \pi\phi(W) + \pi\phi'(W)J & \pi\phi'(W)\beta_1J & \pi\phi'(W)\beta_2J \end{pmatrix} \quad (3.4)$$

of equations (2.1) evaluated at the equilibrium (3.1). If  $M = M(n)$  is treated



as a function of  $n$ , then near  $n = 1$  we can write  $M = M(1) + M'(1)(n - 1) + O((n - 1)^2)$  and

$$\lambda = \lambda(n) = \lambda(1) + \lambda'(1)(n - 1) + O((n - 1)^2).$$

If we denote the right and left (row) eigenvectors by

$$\begin{aligned} v(n) &= v(1) + v'(1)(n - 1) + O((n - 1)^2), \\ w(n) &= w(1) + w'(1)(n - 1) + O((n - 1)^2) \end{aligned}$$

respectively, then a substitution of these expansions into  $Mv^T = \lambda v^T$  yields the formula (see Caswell 1989)

$$\lambda'(1) = w(1)M'(1)v^T(1)/w(1)v^T(1). \quad (3.5)$$

( $w^T$  denotes the transpose of  $w$ .) We are interested in the two cases  $\lambda(1) = \pm 1$ , the eigenvalues of  $M(1)$ , which is given by (3.2) with  $n = 1$ . The eigenvectors  $v_{\pm}(1)$ ,  $w_{\pm}(1)$  of  $M(1)$  corresponding to these two eigenvalues are

$$\begin{aligned} v_+(1) &= [1, 0, \pi], \quad w_+(1) = [\pi, \pi f_1, \pi f_2] \\ v_-(1) &= [1, 0, -\pi], \quad w_-(1) = [\pi f_2, 0, -\pi] \end{aligned}$$

respectively. The derivative  $M'(1)$  is straightforwardly calculated from (3.4). These calculations and formula (3.5) lead finally to

$$\begin{aligned} \lambda_+ &= 1 - \frac{1}{2}(n - 1) + O((n - 1)^2), \\ \lambda_- &= -1 + \frac{1 - \beta_2 \pi}{2(1 + \beta_2 \pi)}(n - 1) + O((n - 1)^2). \end{aligned}$$

We conclude that for  $n > 1$  sufficiently close to 1, the bifurcating positive equilibria (3.1) are stable if  $\beta_2 < 1/\pi = f_2$  and unstable if  $\beta_2 > 1/\pi = f_2$ .

Each of the triplets in the 2-cycle (3.3) is an equilibrium of the first composite of the equations (2.1). The 2-cycle is stable if the eigenvalues of the Jacobian matrix of this first composite evaluated at one of the triplets (say the first one  $(W(n), 0, 0)$ ) are inside the complex unit circle. This Jacobian turns out, amazingly enough, to be easier to analyze than that of the equilibria (3.1). This is because the first column has 0 as its second and third entries, which means the entry in the upper right hand corner is one eigenvalue while the other two can be found from the lower right hand  $2 \times 2$

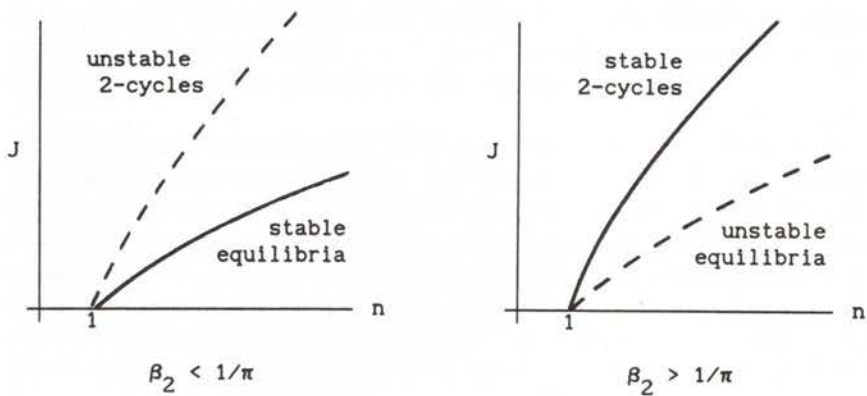


Figure 6.1. Two branches bifurcate from the trivial equilibrium  $(J, A_1, A_2 = (0, 0, 0))$  at the critical value  $n = 1$ , one consisting of equilibria and the other of synchronous 2-cycles. These branches are schematically represented in these graphs of the maximum of the  $J$  component of the attractor against  $n$ . The solutions on the branches have opposite stability properties, depending upon the magnitude of the competition coefficient  $\beta_2$ .

corner matrix. Skipping the straightforward calculation of the Jacobian, it turns out that one eigenvalue is  $\lambda = 0$  and that the other two are

$$\begin{aligned} \lambda_1 &= 1 + n(f_2 - f_1)\pi\phi'(J(n))J(n) \\ \lambda_2 &= \pi n f_1 + n(f_2 - f_1)\pi\phi(W_1(n)) \end{aligned}$$

where

$$\begin{aligned} W_1(n) &= n f_1 A_1(n) + n f_2 A_2(n) \\ &+ \beta_1 \pi (1 - \phi(W(n)))J(n) + \beta_2 \pi \phi(W(N))J(n) \end{aligned}$$

from which we find

$$\begin{aligned} \lambda_1 &= 1 - (n - 1) + O((n - 1)^2) \\ \lambda_2 &= 1 + (1 - \pi\beta_2)(n - 1) + O((n - 1)^2). \end{aligned}$$

Thus for  $n > 1$  sufficiently close to 1, the bifurcating synchronous 2-cycles (3.3) have the opposite stability of the equilibria (3.1), namely they are stable if  $\beta_2 > 1/\pi$  and unstable if  $\beta_2 < 1/\pi$ .

The two possible bifurcation diagrams are schematically represented in Fig. 6.1. These results indicate that, at least for populations with small in-

herent net reproductive rates, strong adult competition affecting juvenile growth and size at maturation is destabilizing. This is implied by the destabilization of the equilibrium and the change from equilibrium to oscillatory dynamics as  $\beta_2$  is increased.

Whether these stability conclusions concerning the equilibria and the 2-cycles remain intact, and also whether other asymptotic dynamics are possible, for larger values of the inherent net reproductive rate  $n$  can be investigated numerically. Fig. 6.2 shows typical bifurcation diagrams, using  $n$  as a bifurcation parameter, for the two cases  $\beta_2 < 1/\pi$  and  $\beta_2 > 1/\pi$ . Notable from these diagrams are the facts that an equilibrium branch originally stable ( $\beta_2 < 1/\pi$ ) can lose its stability through a "Hopf" bifurcation to an invariant circle in which the attractors are aperiodic, and then regain it again for larger  $n$ . In the case where the bifurcating 2-cycle is stable ( $\beta_2 > 1/\pi$ ), the 2-cycle ultimately loses its stability, sometimes to a restabilized equilibrium and sometimes to a period doubled 4-cycle (not shown). It can also happen that for certain  $n$  values there exist both a stable equilibrium and a stable 2-cycle. Thus, equations (2.1) can exhibit exotic dynamics.

Fig. 6.3 shows bifurcation diagrams using the competition coefficient  $\beta_2$  as a parameter. Typically, with increasing  $\beta_2$  one sees the loss of equilibrium stability to a stable 2-cycle for either  $n$  near 1 (as proved above) or for very large  $n$ . For intermediate values of  $n$  (where one can find "chaotic" aperiodic dynamics; see Fig. 6.1), one typically observes an opposite scenario, where the dynamics are unstable and "chaotic" for smaller values of  $\beta_2$ , but are stabilized to equilibrium dynamics for large values of  $\beta_2$ . In the latter case, increased intraspecific competition can be said to be stabilizing.

### Concluding Remarks

Model equations (2.1) describe in a relatively simple way the dynamics of a size-structured population whose juveniles mature to either a small or a large adult size depending upon the intensity of competition due to population density, and in particular due to competition from the larger sized adults as measured by the competition coefficients  $\beta_1$  and  $\beta_2$ . Direct density effects on adult fertility have been ignored, as have density effects on juvenile survival. By investigating the asymptotic dynamics of this model, both numerically and analytically, we have seen that strong intraspecific competition from adults of this kind can result in either equilibrium, oscillatory, or aperiodic "chaotic" dynamics, depending upon relative parameter values in the model. The results suggest that for populations with either very low or very high inherent net reproductive rates, this kind of intraspecific competition is destabilizing. In these cases the dynamics of the model change with increased competition coefficient from equilibration to periodic 2-cycles in which juveniles and adults appear in alternate time intervals. That is to

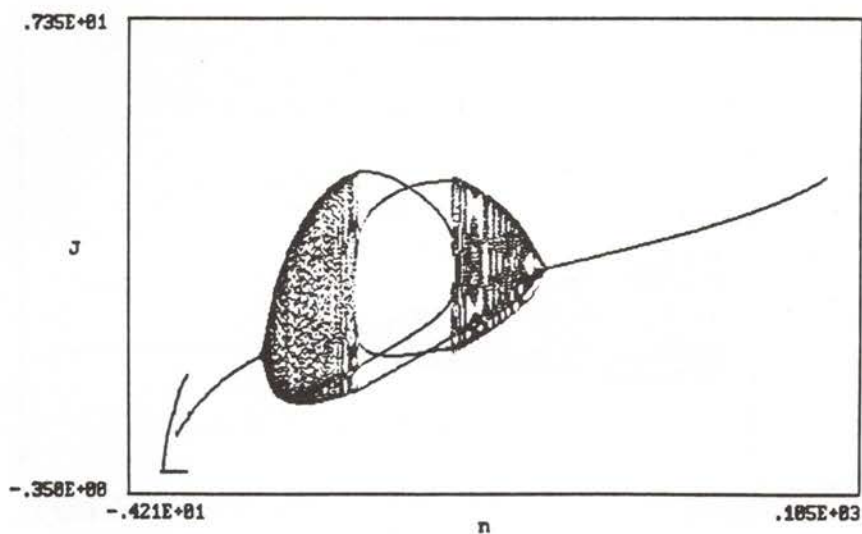
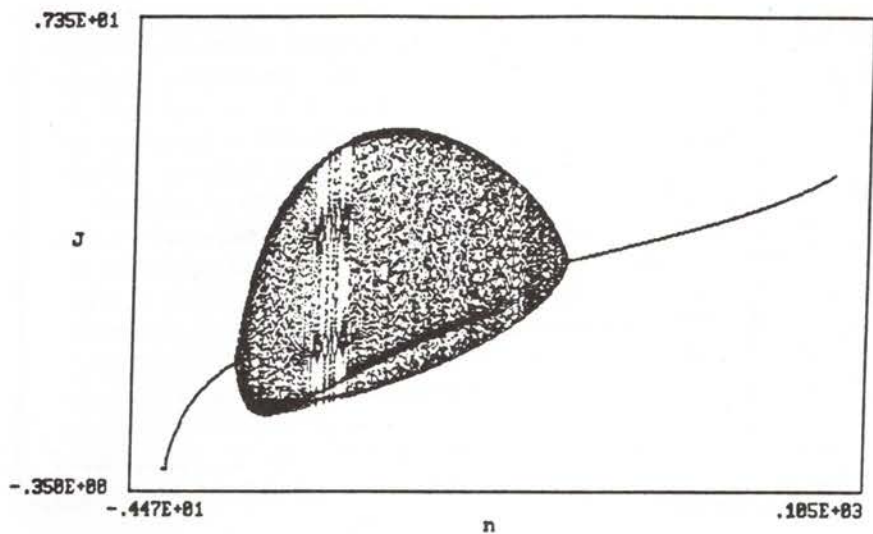


Figure 6.2. The juvenile component of the attractor with  $\phi(W) = \exp(-W)$  in (2.1) is plotted against the inherent net reproductive rate  $n$ .  $\pi = 0.9$ ,  $f_1 = 0.01$ ,  $f_2 = 1.11$ ,  $\beta_1 = 0.5$ ,  $\beta_2 = 0.9$  (top), 1.5 (bottom)

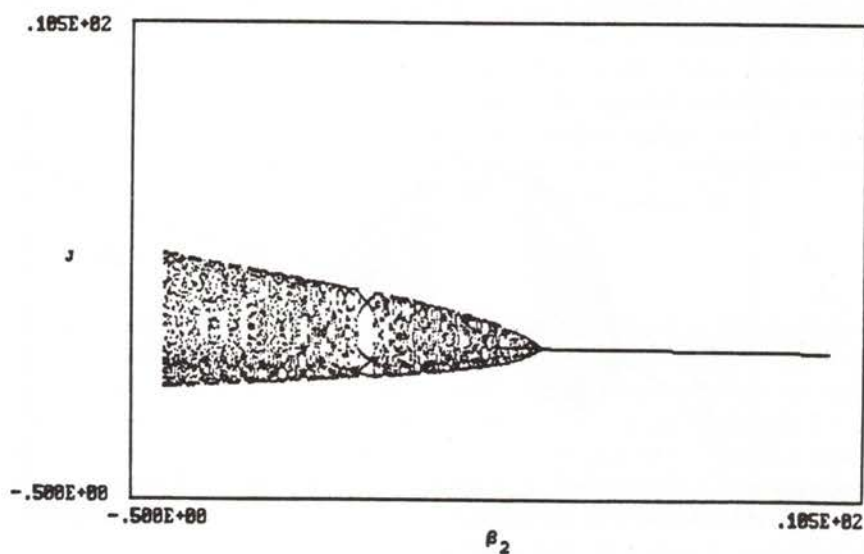
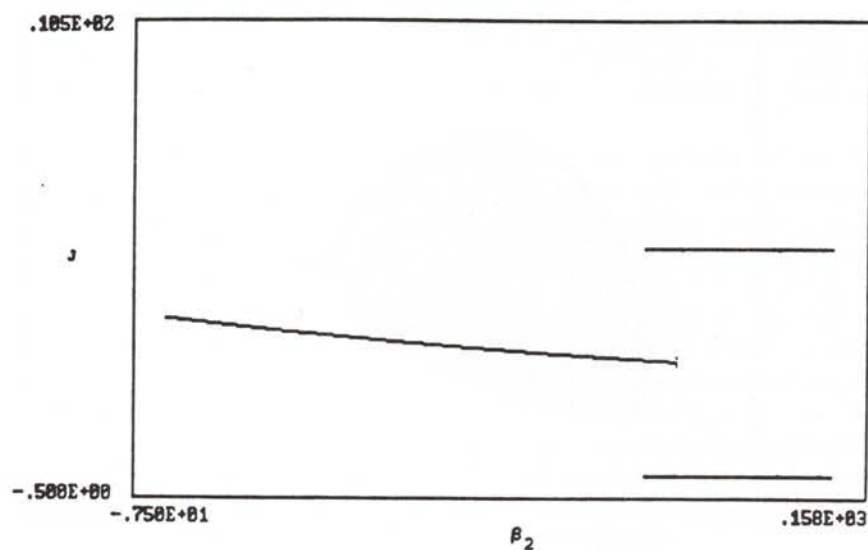


Figure 6.3. The juvenile component of the attractor with  $\phi(W) = \exp(-W)$  in (2.1) is plotted against the competitive coefficient  $\beta_2$ .  $\pi = 0.9$ ,  $f_1 = 0.01$ ,  $f_2 = 1.11$ ,  $\beta_1 = 0.5$ ,  $n = 50$  (top),  $70$  (bottom).

say, increased competition results in the populations adjusting so as to avoid juvenile and adult competition. On the other hand, the model also implies that for populations with "intermediate" values of the inherent net reproductive rate, strong intraspecific competition between adults and juveniles is stabilizing in that increases in the competition coefficient cause the dynamics to equilibrate from otherwise chaotic aperiodic motion.

It would be interesting to see how robust these conclusions would be if some of the simplifying assumptions were dropped. In particular, it would be of interest to assume that juvenile survival is density dependent. This is done in Ebenman (1988b) under the assumption that juvenile survival and individual growth are inversely related to competition through a concept of "plasticity." Fertility in general is also density dependent. Model (2.1) assumes that adults reproduce only once (semelparity) and die. How are these conclusions affected by possible adult survival and repeated reproduction (iteroparity)? We plan to study extensions of model equations (2.1) that include these phenomena in future research.

## Appendix

**THEOREM 1.** If  $n < 1$  then any solution of (2.1)–(2.2) tends geometrically to  $(J, A_1, A_2) = (0, 0, 0)$ .

**Proof:** From (2.1b, c) follows  $A_1(t) + A_2(t) = \pi J(t)$  and from (2.1a)

$$\begin{aligned} J(t+1) &= nf_1\pi J(t) + n(f_2 - f_1)A_2(t) \\ &= nf_1\pi J(t) + n(f_2 - f_1)\pi\phi(W(t-s))J(t-1). \end{aligned}$$

Thus

$$0 \leq J(t+1) \leq n\pi f_1 J(t) + n(1 - \pi f_1)J(t-1)$$

and consequently  $0 \leq J(t) \leq x(t)$  where  $x(t)$  satisfies  $x(0) = J(0)$ ,  $x(1) = J(1)$  and

$$x(t+1) = n\pi f_1 x(t) + n(1 - \pi f_1)x(t-1).$$

The quadratic characteristic equation associated with this second order linear difference equation can easily be shown to have two real roots whose magnitudes are less than one when  $n < 1$ . Thus, in this case,  $x(t)$  and hence  $J(t)$  tend geometrically to zero. Equations (2.1b, c) then imply both  $A_1(t)$  also tend geometrically to zero.

**THEOREM 2.** If  $n > n_0 = f_2/f_1$ , then  $J(t) \rightarrow +\infty$ .

Proof: This follows immediately from the inequality

$$J(t+1) = nf_1 \left[ A_1(t) + \frac{f_2}{f_1} A_2(t) \right] \geq nf_1 [A_1(t) + A_2(t)] = \frac{n}{n_0} J(t-1).$$

**THEOREM 3.** For  $n \in (1, n_0)$  there exists a unique synchronous 2-cycle given by (3.3).

Proof: The first composites of equations (2.1) are

$$\begin{aligned} J(t+2) &= nf_1 \pi (1 - \phi(W(t))) J(t) + nf_2 \pi \phi(W(t)) J(t) \\ A_1(t+2) &= \pi (1 - \phi(W_1(t))) (nf_1 A_1(t) + nf_2 A_2(t)) \\ A_2(t+2) &= \pi \phi(W_1(t)) (nf_1 A_1(t) + nf_2 A_2(t)) \end{aligned}$$

where

$$W_1(t) = nf_1 A_1(t) + nf_2 A_2(t) + \beta_1 \pi (1 - \phi(W(t))) J(t) + \beta_2 \pi \phi(W(t)) J(t)$$

whose equilibrium equations are

$$\begin{aligned} J &= nf_1 \pi (1 - \phi(W)) J + nf_2 \pi \phi(W) J \\ A_1 &= \pi (1 - \phi(W_1)) (nf_1 A_1 + nf_2 A_2) \\ A_2 &= \pi \phi(W_1) (nf_1 A_1 + nf_2 A_2). \end{aligned}$$

It is easy to see that  $(J, A_1, A_2) = (W(n), 0, 0)$  solves these equations and that this is the only solution in which  $J \neq 0$  and  $A_1 = 0$ .

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