

## ON EBENMAN'S MODEL FOR THE DYNAMICS OF A POPULATION WITH COMPETING JUVENILES AND ADULTS

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A general version of a model of Ebenman for the dynamics of a population consisting of competing juveniles and adults is analyzed using methods of bifurcation theory. A very general existence result is obtained for non-trivial equilibria and non-negative synchronous two-cycles that bifurcate simultaneously at the critical value  $r=1$  of the inherent net reproductive rate  $r$ . Stability is studied in this general setting near the bifurcation point and conditions are derived that determine which of these two bifurcating branches is the stable branch. These general results are supplemented by numerical studies of the asymptotic dynamics over wider parameter ranges where various other bifurcations and stable attractors are found. The implications of these results are discussed with respect to the effects on stability that age class competition within a population can have and whether such competition is stabilizing or destabilizing.

*1. Introduction.* One aspect of the important role played by competition in determining the dynamics of a population that until recently has received little attention is that played by competition between different age (or size) classes within the population. This type of competition occurs when two different age classes consume a common resource. Organisms with complex life histories, such as those involving metamorphoses in which larval and adult morphologies are radically different, generally undergo significant resource niche shifts during their development. For such organisms joint use of resources by the different stages or age classes is unlikely (examples include many marine invertebrates, amphibians, and holometabolous insects such as beetles, flies, butterflies and moths). On the other hand, organisms which do not undergo such radical changes during their life cycles (e.g. birds, mammals, most reptiles, fishes, and hemimetabolous insects such as aphids, true bugs and grasshoppers) can experience considerable competition between juveniles and adults for common resources. See Ebenman (1988) for more discussion of this phenomenon and for specific biological examples (as well as further references).

While models for age structured population growth abound in the literature, relatively little literature to date has specifically addressed this type of intraspecific competition. May *et al.* (1974) seem to have been the first to

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consider the effects of age class competition on the dynamics of a population. Using the same differential equation model, Tschumy (1982) extended and elaborated on their results. One of the principal conclusions of these authors was that competition between age classes is destabilizing. Ebenman (1987, 1988) studied age class competition by means of a discrete model involving a system of non-linear difference equations. He argues, amongst other things, that the dynamics implied by this type of competition can be quite diverse and that several of the conclusions drawn by May *et al.* and Tschumy may not hold up over all parameter ranges. In particular, he concludes that competition between juveniles and adults can be, under certain circumstances, a stabilizing influence.

Our primary goal here is to give a more complete analysis of Ebenman's model than is given in his papers, and to do so in a more general setting, with the hope of contributing to the further understanding of this particular type of intraspecific competition. This model in its general setting takes the form:

$$\begin{cases} N_0(t+1) = N_1(t)F(N_1(t) + \alpha N_0(t)) \\ N_1(t+1) = N_0(t)G(N_0(t) + \beta N_1(t)), \end{cases}$$

where  $N_0(t)$  and  $N_1(t)$  denote the densities of juveniles and adults at time  $t$  respectively.  $F$  denotes the per capita number of births per unit time (surviving to time  $t$ ) and  $G$  denotes the fraction of juveniles which survive one unit of time. We are interested in the case when both  $F$  and  $G$  are dependent upon weighted total population sizes. Specifically, we assume (Ebenman, 1988) that  $F$  is a function of  $N_1(t) + \alpha N_0(t)$  and  $G$  is a function of  $N_0(t) + \beta N_1(t)$  where  $\alpha \geq 0$  measures the relatively "competitive" effects that juveniles have on adult fertility while  $\beta \geq 0$  measures that of adults on juvenile survival.

Although it is not necessary for much of our mathematical analysis we will assume (Ebenman, 1987, 1988; Tschumy, 1982) that  $F$  and  $G$  are non-increasing functions of their arguments, i.e. density effects are only deleterious. Introducing the "inherent" (i.e. low density) adult per capita, per unit time birth rate  $B = F(0) > 0$  and the juvenile per unit time survival fraction  $S = G(0) \in (0, 1)$ , we write  $f = F/B$  and  $g = G/S$  and assume:

$$\begin{cases} f, g \in C^1(R \rightarrow R^+) \\ f', g' \leq 0, f(0) = g(0) = 1. \end{cases} \quad (1)$$

Here  $R = (-\infty, +\infty)$  and  $R^+ = [0, +\infty)$ . The model equations above become:

$$\begin{cases} N_0(t+1) = N_1(t)Bf(N_1(t) + \alpha N_0(t)) \\ N_1(t+1) = N_0(t)Sg(N_0(t) + \beta N_1(t)). \end{cases}$$

For our analysis, which uses bifurcation theory techniques, it is convenient to introduce the *inherent net reproductive rate*  $r$ , i.e. the expected number of offspring per individual per lifetime, in place of the birth rate  $B$ . Because of the normalization of  $f$  and  $g$  at 0, this parameter is given by  $r = BS$  and we write the model equations as:

$$\begin{cases} N_0(t+1) = N_1(t)rf(N_1(t) + \alpha N_0(t))/S \\ N_1(t+1) = N_0(t)Sg(N_0(t) + \beta N_1(t)). \end{cases} \quad (2)$$

Our mathematical goal is to explore the asymptotic dynamics implied by equations (2) as they depend upon the system parameters, in particular the inherent net reproductive rate  $r$  and the competition coefficients  $\alpha$  and  $\beta$ . Using the bifurcation theory approach of Cushing (1988), we investigate in Section 2 the existence and stability of positive equilibria as a function of  $r$ . Given the monotonicity assumptions in hypothesis (1), the most common occurrence in non-linear systems of difference equations modeling population growth is the bifurcation from the trivial solution  $(N_0, N_1) = (0, 0)$  of a global continuum of (at least locally) stable positive equilibria (one-cycles) as  $r$  is increased through the critical value  $r = 1$  (cf. Cushing, 1988). Equations (2), however, have the unusual property that at  $r = 1$  there bifurcates, in addition, a continuum of positive two-cycles and furthermore the bifurcating branch of equilibria may not be stable. In Section 2 the existence and stability of these bifurcating one- and two-cycle branches are studied as functions of  $\alpha$  and  $\beta$ . It is also proved that stability cannot persist globally (i.e. for all  $r > 1$ ) along these bifurcating branches and that consequently further bifurcations result. In Section 3 system (2) is further explored numerically in the case of exponential nonlinearities and different types of possible asymptotic dynamics are identified, including multiple attractors, various types of oscillations, period doublings, and different paths to chaos. Some of the biological conclusions of Ebenman, Tschumy and May *et al.* are discussed in Section 4 in light of the findings in Sections 2 and 3.

*2. Analysis.* Our first task is to focus on the existence and stability of equilibria of equations (2) as a function of the inherent net reproductive rate  $r$ . Given the competition coefficients  $\alpha$  and  $\beta$ , the survivability  $S$ , and the density functionals  $f$  and  $g$ , we ask for what values of  $r$  do equilibrium solutions of equation (2) exist? Our analysis of this question will uncover the fact that two-cycles play just as fundamental a role as do equilibria for the model equation (2), at least from our bifurcation theory point-of-view.

A non-negative equilibrium solution of equations (2) is a constant solution  $(N_0(t), N_1(t)) \equiv (N_0, N_1) \geq 0$ . A *positive* equilibrium satisfies  $(N_0, N_1) > 0$ . The equilibrium  $(N_0, N_1) = (0, 0)$  will be referred to as the *trivial* equilibrium.

Obviously for equations (2) a non-trivial, non-negative equilibrium must be positive. A *non-negative* two-cycle satisfies  $(N_0(t+2), N_1(t+2)) \equiv (N_0(t), N_1(t)) \geq 0$ , but is not an equilibrium. A two-cycle is positive if  $(N_0(t), N_1(t)) > 0$  for all  $t$ . A two-cycle can be non-negative and non-positive, provided one component is zero and the other positive for each  $t$ . An equilibrium or a two-cycle pair consists of an  $r$  value and a corresponding equilibrium or two-cycle.

*2.1. Existence.* A very general class of matrix equations, which includes equation (2) as a special case, was studied by Cushing (1988). From Theorem 2 of this paper follows the existence of an unbounded continuum  $C \subset R \times R^2$  of positive equilibrium pairs  $(r, (N_0, N_1))$  which bifurcates from and only from  $(1, (0, 0))$ . That is,  $(1, (0, 0)) \in C$  and  $(r, (N_0, N_1)) \in C \setminus (1, (0, 0))$  implies that  $(r, (N_0, N_1))$  is a positive equilibrium pair.

Let  $\sigma$  denote the *r-spectrum* of  $C$ , i.e. the projection of  $C \setminus (1, (0, 0))$  onto  $R$ . Then for each  $r \in \sigma$  there is at least one positive equilibrium. Because  $C$  is a continuum,  $\sigma$  is an interval. Clearly 1 lies in the closure of  $\sigma$ . From the equilibrium equations:

$$\begin{cases} N_0 = N_1 r f(N_1 + \alpha N_0) / S \\ N_1 = N_0 S g(N_0 + \beta N_1), \end{cases} \quad (3)$$

for any positive equilibria  $(N_0, N_1) > 0$ , including those from  $C$  for  $r \in \sigma$ , one finds

$$r f(N_1 + \alpha N_0) g(N_0 + \beta N_1) = 1. \quad (4)$$

This “invariant” which holds along the continuum  $C$  expresses the biologically reasonable fact that the net reproductive rate (not to be confused with the inherent net reproductive rate  $r$ ) must be 1 at equilibrium.

Note that the monotonicity assumptions on  $f$  and  $g$  in equation (1) are not needed for any of the results so far. However, given these monotonicity assumptions, it follows immediately from equation (4) that no positive equilibrium can exist for  $r < 1$ . Thus, in this case,  $\sigma \subseteq (1, +\infty)$ . Under the added assumption that:

$$\lim_{x \rightarrow \infty} f(x) = \lim_{x \rightarrow \infty} g(x) = 0 \quad (5)$$

(i.e. both fertility and survivability drop to zero as the population density increases without bound) it further follows from equation (4) that  $\sigma$  must be unbounded. This is because if  $\sigma$  were bounded then, since  $C$  is unbounded, it must be the case that the set of positive equilibria  $(N_0, N_1)$  from  $C$  is

unbounded. Thus  $\inf_c \{f(N_1 + \alpha N_0)g(N_0 + \beta N_1)\} = 0$  which, if  $\sigma$  is bounded, contradicts equation (4).

We summarize these conclusions in the following theorem.

**THEOREM 1.** *Under the first hypothesis (1), equations (2) have no positive equilibria for  $r < 1$ . Furthermore, there exists an unbounded continuum of equilibrium pairs  $(r, (N_0, N_1))$  that, except for the trivial solution  $(N_0, N_1) = (0, 0)$ , consists of positive equilibria  $(N_0, N_1) > 0$  for  $r$  from an interval  $(1, r^*)$ ,  $r^* \leq +\infty$ . If hypothesis (5) holds then  $r^* = +\infty$ , i.e. equations (2) have a positive equilibrium for every  $r > 1$ .*

This theorem implies that in order for a population to survive in the sense of equilibration it is necessary that the inherent net reproductive rate be greater than 1, i.e. that at low population densities each individual at least replace itself. Mathematically the phenomenon described by the results above is referred to as “supercritical” bifurcation and is generally associated with a stability of the bifurcating branch. We will see, however, that for the model equations (2) this is *not necessarily the case*.

Before considering this peculiarity of these equations, as well as other stability considerations, another bifurcation property of the critical value  $r = 1$  will be investigated.

In order to take a closer look at those positive equilibria near the bifurcation point we perform a standard parameterization of the branch (Liapunov-Schmidt expansion):

$$\begin{aligned} r &= 1 + r_1 \varepsilon + o(|\varepsilon|) \\ N_i &= x_i \varepsilon + y_i \varepsilon^2 + o(|\varepsilon|^2), \end{aligned} \tag{6}$$

for small  $\varepsilon > 0$ . A substitution of these expansions into the equilibrium equations (3) and an equating of coefficients of resulting like powers of  $\varepsilon$  results in the linear system  $(A - I)x = 0$ , hence  $x = \text{col}(1, S)$  and  $(A - I)y = -b$  for  $y = \text{col}(y_i)$  where:

$$\begin{aligned} A &= \begin{pmatrix} 0 & \frac{1}{S} \\ S & 0 \end{pmatrix}, \quad b = \begin{pmatrix} k(\alpha + S) + r_1 \\ Sk'(1 + \beta S) \end{pmatrix}, \\ & k = f'(0), \quad k' = g'(0). \end{aligned}$$

In order to solve the equation for  $y$  it is necessary that the vector  $b$  be orthogonal the nullspace of the adjoint (transpose) of  $A - I$ . This leads to:

$$r_1 = -(1 + \beta S)k' - (\alpha + S)k.$$

Under hypothesis (1),  $r_1 \geq 0$  as is commensurate with Theorem 1.

That the linearization  $A$  of the equilibrium equations at the trivial solution for  $r=1$  has eigenvalue  $-1$  (in addition to  $+1$ ) suggests the possibility of bifurcating two-cycles. Two-cycles are equilibrium solutions of the first self composition of equations (2) (which are not also equilibria of equations (2)). The equilibrium equations of this composition are given by:

$$\begin{aligned} N_0 &= h_0(r, N_0, N_1)N_0 \\ N_1 &= h_1(r, N_0, N_1)N_1 \end{aligned} \tag{7}$$

where:

$$\begin{aligned} h_0 &= rf \left( r \frac{\alpha}{S} f(N_1 + \alpha N_0)N_1 + Sg(N_0 + \beta N_1)N_0 \right) g(N_0 + \beta N_1) \\ h_1 &= rg \left( r \frac{1}{S} f(N_1 + \alpha N_0)N_1 + \beta Sg(N_0 + \beta N_1)N_0 \right) f(N_1 + \alpha N_0). \end{aligned}$$

If we look for *positive* two-cycles of equations (2), then equations (7) can be written:

$$\begin{cases} h_0(r, N_0, N_1) - 1 = 0 \\ h_1(r, N_0, N_1) - 1 = 0. \end{cases} \tag{8}$$

The Jacobian of this system at  $r=1$ ,  $(N_0, N_1) = (0, 0)$  turns out to be  $-4\lambda_1^+ \lambda_1^- / S$  where:

$$\begin{aligned} \lambda_1^+ &= -\frac{1}{2}r_1 = \left( \frac{\alpha + S}{2} \right)k + \left( \frac{\beta S + 1}{2} \right)k' \\ \lambda_1^- &= \left( \frac{\alpha - S}{2} \right)k + \left( \frac{\beta S - 1}{2} \right)k'. \end{aligned} \tag{9}$$

Under the (“generic”) assumptions that:

$$\lambda_1^- \neq 0 \text{ and in hypothesis (1) either } k, \text{ or } k' \text{ is non-zero} \tag{10}$$

this Jacobian is non-zero and equations (8) have a unique branch of solutions  $(N_0, N_1)$  for  $r$  near 1, which in fact must be the positive equilibria of Theorem 1. Thus there can be no positive two-cycles near this point.

On the other hand, equations (2) can have cycles which are *not* strictly positive, but are non-negative with alternating zero and positive components. We will refer to solution sequences with alternating zero and positive components as *synchronous*, since in such a solution the age classes are synchronized in such a way as to appear and vanish alternately in one time unit.

Synchronous two-cycles of equations (2) can be found by looking for non-trivial equilibria of the composite equations (7) which have one component equal to zero, say without loss in generality  $N_1=0$ . Then the composite equations (7) reduce to the single equation:

$$N_0 = rf(Sg(N_0)N_0)g(N_0)N_0, \tag{11}$$

for  $N_0 > 0$ , a solution of which yields a synchronous two-cycle which alternates between  $(N_0, 0)$  and  $(0, SN_1)$ . Treating this equation by exactly the same methods as used above on equations (3), with the role played by equation (4) now played by:

$$rf(Sg(N_0)N_0)g(N_0) = 1,$$

we obtain a global, unbounded branch of non-negative synchronous two-cycle pairs which bifurcates from  $(0, 0)$  at  $r=1$ . This yields the following result.

**THEOREM 2.** *Under hypothesis (1), equations (2) have no non-negative two-cycles for  $r < 1$ . Furthermore, there exists an unbounded continuum of pairs  $(r, (N_0, N_1))$  that, except for  $(1, (0, 0))$ , consists of non-negative synchronous two-cycles for  $r$  on an interval  $(1, r^*)$ ,  $r^* \leq +\infty$ . If hypothesis (5) holds then  $r^* = +\infty$ , i.e. equations (2) have a non-negative synchronous two-cycle for every  $r > 1$ .*

By Theorems 1 and 2 there are two branches of cycles that simultaneously bifurcate from the trivial solution of equations (2) at the critical value  $r=1$ .

**2.2. Stability.** The linearization of equations (2) at an equilibrium  $(N_0, N_1)$  yields a linear  $2 \times 2$  matrix system with coefficient matrix:

$$A = \begin{pmatrix} \frac{r}{S} \alpha f'(N_1 + \alpha N_0)N_1 & \frac{r}{S} f'(N_1 + \alpha N_0)N_1 + \frac{r}{S} f(N_1 + \alpha N_0) \\ Sg'(N_0 + \beta N_1)N_0 + Sg(N_0 + \beta N_1) & S\beta g'(N_0 + \beta N_1)N_0 \end{pmatrix}.$$

The equilibrium is stable if the eigenvalues  $\lambda^+, \lambda^-$  of  $A$  lie inside the complex unit circle and unstable if at least one lies outside.

If the linearization is carried out for the trivial equilibrium  $(0, 0)$ , it is not difficult to show that this equilibrium loses stability at  $r=1$ . That is, for  $r < 1$ ,  $(0, 0)$  is stable while for  $r > 1$  it is unstable. (Also see Theorem 3 in Cushing (1988) from which this follows.)

Next we turn our attention to the positive bifurcating equilibria near the bifurcation point. Upon substitution of the expansions (6) the matrix  $A$

becomes a function of  $\varepsilon$ . Its eigenvalues and eigenvectors have  $\varepsilon$ -expansions of the form:

$$\begin{aligned}\lambda^\pm &= \lambda_0^\pm + \lambda_1^\pm \varepsilon + o(|\varepsilon|), \\ v^\pm &= v_0^\pm + v_1^\pm \varepsilon + o(|\varepsilon|)\end{aligned}$$

whose coefficients can be found by the usual procedure of substituting these expansions into the equation  $(A - \lambda I)v = 0$  and equating the resulting coefficients of like powers of  $\varepsilon$ . This procedure yields:

$$\begin{aligned}\lambda_0^+ &= 1 & \text{and} & & v_0^+ &= \begin{pmatrix} 1 \\ S \end{pmatrix}, \\ \lambda_0^- &= -1 & \text{and} & & v_0^- &= \begin{pmatrix} 1 \\ -S \end{pmatrix},\end{aligned}$$

and  $\lambda_1^\pm$  given by equations (9).

Under the monotonicity assumption of hypothesis (1) and under hypothesis (10) the coefficients  $\lambda_1^\pm$  are non-zero and hence determine whether the eigenvalues  $\lambda^\pm$  are within or outside the unit circle for  $\varepsilon > 0$  small. Moreover these hypotheses imply  $\lambda_1^+ < 0$  so that  $|\lambda^+| < 1$  for small  $\varepsilon$ . Stability is consequently determined by the sign of  $\lambda_1^-$ . If  $\lambda_1^- > 0$  then the positive equilibrium near bifurcation are locally stable, whereas if  $\lambda_1^- < 0$  then these equilibria are unstable.

The boundary region in the  $\alpha, \beta$  parameter plane determined by  $\lambda_1^- = 0$  is a straight line which divides the positive quadrant into a bounded triangular region I and an unbounded region II (cf. Fig. 1). For parameter values  $\alpha, \beta$  lying in region I the local supercritical bifurcation of positive equilibria described in (a) above gives rise to stable equilibria for  $r$  greater than, but near 1. For  $\alpha, \beta$  lying in region II, however, these supercritically bifurcating equilibria are locally unstable. As we shall see below, in region II it is the bifurcating continuum of two-cycles which is stable.

To investigate the local stability of a synchronous two-cycle, we consider the linearization of equations (7) at  $(N_0, 0)$ . The  $2 \times 2$  matrix of the resulting linear matrix equation has eigenvalues:

$$\begin{aligned}\mu_1 &= h_1(r, N_0, 0) \\ \mu_2 &= h_0(r, N_0, 0) + N_0 \frac{\partial h_0}{\partial N_0}(r, N_0, 0).\end{aligned}$$

We analyze these eigenvalues near bifurcation in exactly the same manner as



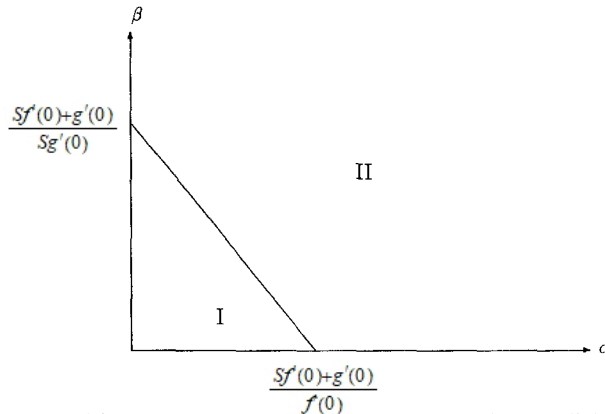


Figure 1. The positive quadrant of the  $(\alpha, \beta)$  parameter plane is divided into two regions of differing local bifurcation properties at the primary bifurcation point  $r=1$ . In the bounded, triangular region I the bifurcating equilibria are stable while in region II the bifurcating two-cycles are stable. See Figs 2a and b, respectively.

we did those for the bifurcating equilibria above. The Liapunov–Schmidt expansion of the bifurcating two-cycle has the form:

$$r = 1 - (Sk + k')\varepsilon + o(|\varepsilon|),$$

$$N_0 = \varepsilon + o(|\varepsilon|),$$

which yields the expansions:

$$\mu_1 = 1 + 2\lambda_1^- \varepsilon + o(|\varepsilon|),$$

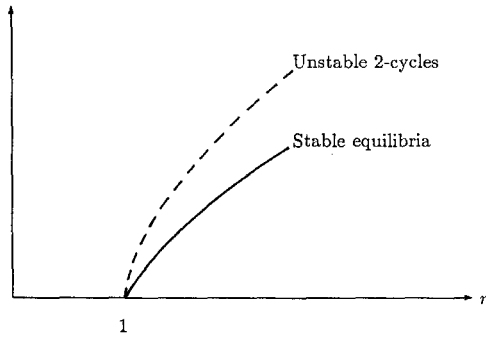
$$\mu_2 = 1 + (k' + Sk)\varepsilon + o(|\varepsilon|).$$

Hypotheses (1) and (10) imply  $\mu_2 < 1$  for  $\varepsilon > 0$  small. Thus stability is determined by  $\mu_1$ , which is less than one in region II and greater than one in region I.

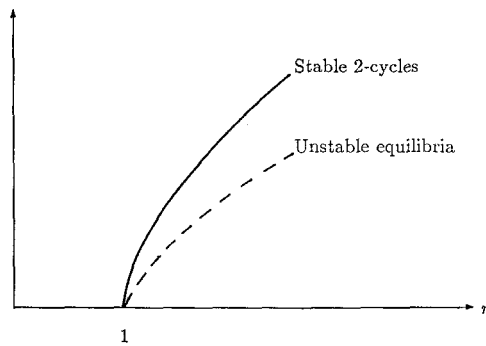
**THEOREM 3.** *Under hypotheses (1) and (10) the bifurcating branches of equilibria and synchronous two-cycles have opposite stability properties in a neighborhood of the bifurcation point  $(1, (0, 0))$ . More specifically, in region I of the  $(\alpha, \beta)$  parameter plane the bifurcating branch of positive equilibria are stable and the branch of two-cycles is unstable while in region II the opposite occurs.*

These results are illustrated in the bifurcation diagrams of Fig. 2.

The stability properties described in Theorem 3 for  $r$  near 1 may not, of course, persist globally along the unbounded branch, i.e. for all  $r > 1$ . One often expects further losses of stability and Hopf-type bifurcations to other oscillatory solutions as  $r$  is increased. The results of some numerical investigations which illustrate the richness of such dynamics for equations (2) will be given in Section 3.



(a)



(b)

Figure 2. Two continua of solutions of equations (2) bifurcate from the trivial solution at the primary critical value  $r=1$ , one consisting of positive equilibria and the other of non-negative synchronous two-cycles. (a) In region I of Fig. 1 the branch of positive equilibria is stable while the branch of non-negative synchronous two-cycles is unstable. (b) In region II of Fig. 1 the branch of non-negative synchronous two-cycles is stable while the branch of positive equilibria is unstable.

Analytically, under the assumption:

$$\begin{cases} (1) \text{ holds and there is a constant } \delta > 0 \text{ such that} \\ |f'(x)/f(x)| \geq \delta \text{ and } |g'(x)/g(x)| \geq \delta \text{ for all } x \in R^+, \end{cases} \quad (12)$$

we can offer the general loss of stability results contained in Theorem 4 below.

From hypothesis (12) and equations (4) we can conclude that the equilibria  $(N_0, N_1)$  on the bifurcating branch  $C$  are unbounded. This follows because the  $r$ -spectrum  $\sigma$  is unbounded and equation (4) implies that along  $C$  either  $f(N_1 + \alpha N_0)$  or  $g(N_0 + \beta N_1)$  is unbounded. This implies that one of the components  $N_0$  or  $N_1$  is unbounded along  $C$ .

The linearized matrix  $A$  can be rewritten using the equilibrium equations (3):

$$A = \begin{pmatrix} \alpha N_0 \frac{f'}{f} & \frac{N_0}{N_1} + N_0 \frac{f'}{f} \\ \frac{N_1}{N_0} + N_1 \frac{g'}{g} & \beta N_1 \frac{g'}{g} \end{pmatrix},$$

where  $f'/f$  and  $g'/g$  are evaluated at  $N_1 + \alpha N_0$  and  $N_0 + \beta N_1$ . The eigenvalues of  $A$  lie inside the complex unit circle if and only if the inequalities  $|\text{tr}A| < 1 + \det A < 2$  hold (cf. May *et al.*, 1974). Now:

$$1 + \det A = (\alpha\beta - 1) \frac{f'}{f} \frac{g'}{g} N_0 N_1 - \frac{f'}{f} N_1 - \frac{g'}{g} N_0. \tag{13}$$

From hypothesis (12)  $g(x) \leq \exp(-\delta x)$  and hence  $0 \leq x^2 g(x) \leq M$  for some  $M$  and all  $x \geq 0$ . From this follows  $N_0 N_1 = S N_0^2 g(N_0 + \beta N_1) \leq S N_0^2 g(N_0) \leq S M$  along the continuum  $C$ . Also from hypothesis (12) follows:

$$-\left( N_1 \frac{f'}{f} + N_0 \frac{g'}{g} \right) \geq \delta(N_0 + N_1),$$

and hence by equation (13),  $1 + \det A$  is unbounded from above along the continuum  $C$ , implying that  $1 + \det A < 2$  cannot hold globally along  $C$ .

A similar argument can be made for the two-cycles and we arrive at the following result.

**THEOREM 4.** *Under hypotheses (1) and (12) the stable bifurcating continuum of equilibria in region I and the stable bifurcating continuum of two-cycles in region II lose stability at some values of  $r > 1$ .*

It will be seen in Section 3 that these losses of stability result in new asymptotic states via secondary bifurcations, but that these new states can be of different types.

In passing we note that it is easily seen from the model equations (2) that if the initial population is seeded with one age class absent, then the age classes are alternately zero for each unit of time. The dynamics of a non-trivial population trajectory, say for:

$$N_0(0) > 0, \quad N_1(0) = 0, \tag{14}$$

are determined by the single scalar difference equation (11). Equilibria of equation (11) yield synchronous two-cycles of equations (2), two-cycles yield synchronous four-cycles of equations (2), etc.

Typically a difference equation like equation (11) possesses the now familiar sequence of stable period doubling bifurcations. This yields stable cycles for equations (2) with respect to the restricted initial conditions (14) (or the

symmetric case  $N_1(0) > 0$ ,  $N_0(0) = 0$ ). However, as we have seen, these cycles may or may not be stable cycles of equations (2) with respect to the more general case of positive initial conditions for *both* age classes. Thus a population seeded with juveniles (or adults) only could exhibit stable cycles whereas the same population seeded with both age classes represented could, for example, equilibrate.

*3. Numerical Results.* The difference equations (2) lend themselves well to numerical solution by computer. In order to corroborate the analytical results of Section 2 and to further study the dynamics implied by the model equations we investigated the prototype equations obtained by setting:

$$f(x) = \exp(-kx), \quad g(x) = \exp(-k'x), \quad k > 0, \quad k' > 0. \quad (15)$$

The resulting difference equations satisfy all the hypotheses of Section 2.

For any fixed  $S > 0$ , the nature of the local bifurcation of equilibria and two-cycles as a function of  $r$  at the *primary* bifurcation point  $r = 1$  depends, as described in Section 2, upon the location of the parameter pair  $\alpha, \beta$  in Fig. 1. By Theorem 4 both the stable equilibrium branch (when  $\alpha, \beta$  lies in region I) and the stable synchronous two-cycle branch (when  $\alpha, \beta$  lies in region II) lose stability if  $r$  is sufficiently increased. We numerically studied the nature of this *secondary* bifurcation at a point  $r = r' > 1$  by calculating linearized eigenvalues and by studying many computed solutions of equations (2) and (15) for appropriate parameter values. Interestingly, these studies show that region I can be subdivided into two subregions according to the properties of this secondary bifurcation (see Fig. 3).

In region Ia the loss of equilibrium stability with increasing  $r$  occurs because the linearized eigenvalues leave the complex unit circle at complex conjugate points with polar argument  $\theta \neq \pi$  (i.e. not at  $-1$ ), but in all cases considered between about 1.6 and  $\pi$ . In region Ib, on the other hand, stability is lost because a real eigenvalue leaves the unit circle through  $-1$ . This means that in region Ib the secondary bifurcation produces a *non-synchronous* two-cycle (via a Hopf bifurcation) while in region Ia this bifurcation leads to non-synchronous periodic cycles of other periods or to aperiodic oscillations with "period" roughly between 2 and 4, depending upon the angle  $\theta$ . These two different bifurcations are illustrated in the sequence of diagrams in Figs 4 and 5.

In region Ib, further increases in  $r > r'$  lead to the familiar cascade of periodic doubling bifurcations. In region Ia, however, further increases in  $r$  lead to more complicated oscillations. In both cases "chaotic" solutions result for large enough values of  $r$ .

Numerical studies carried out for  $\alpha, \beta$  in region II also show that there are two sub-regions of qualitatively different behavior. In region IIb, the stable branch of synchronous two-cycles bifurcating from the primary bifurcation

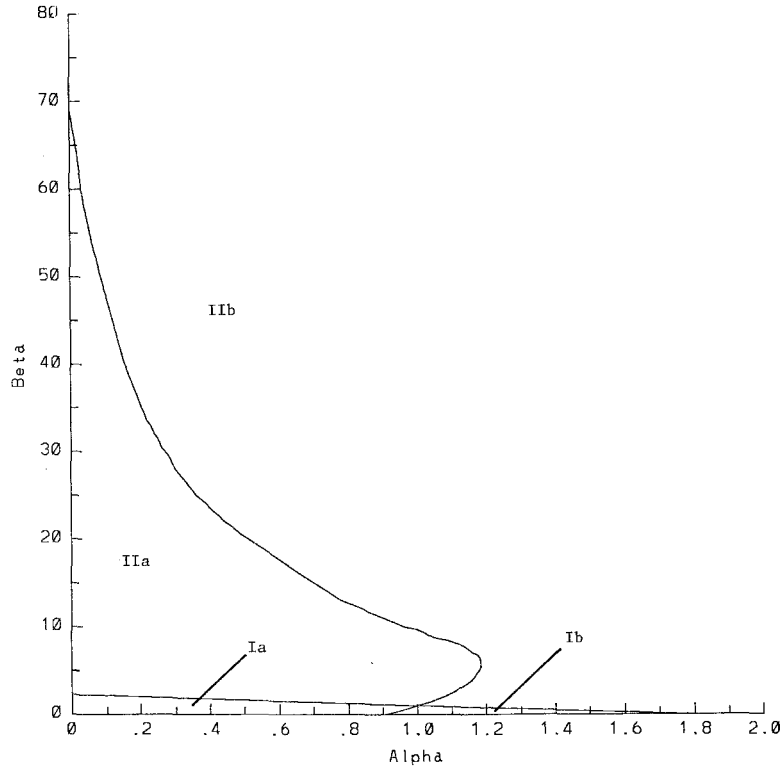


Figure 3. The parameter regions I and II of Fig. 1 can each be sub-divided into two sub-regions according to the nature of the bifurcation at the secondary critical point  $r'$  (Theorem 4). In region Ib the positive equilibria lose stability as a linearized eigenvalue passes through  $-1$ . In Ia an eigenvalue leaves the unit circle through a point other than  $-1$ . In region IIb the equilibrium branch remains unstable while the two-cycle branch undergoes a period doubling cascade of bifurcations to chaos. In region IIa the two-cycles branch repeats this behavior, but the equilibrium branch acquires and again loses stability as an eigenvalue moves into the unit circle through  $-1$  and out again at a point different from  $-1$ . The diagram shown is for equations (2) and (15) with  $S=0.8$ ,  $k=1$ ,  $k'=1$ .

point  $r=1$  undergoes a typical cascade of period doubling, synchronous cycles followed ultimately by "chaos", as  $r > r'$  is increased.

In region IIa the bifurcating branch of synchronous two-cycles again undergoes these same bifurcations. In this region however, the equilibrium branch (which at primary bifurcation is unstable) *acquires stability* as  $r$  is increased passed a critical point  $r'' > 1$ . Thus there are parameter regions in which equations (2) and (15) has simultaneously a locally stable equilibrium and locally attracting synchronous cycles. Upon further increases in  $r$ , this equilibrium stability is lost, this time resulting in a bifurcation to locally stable non-synchronous oscillations (of period not equal to a power of 2), similar to

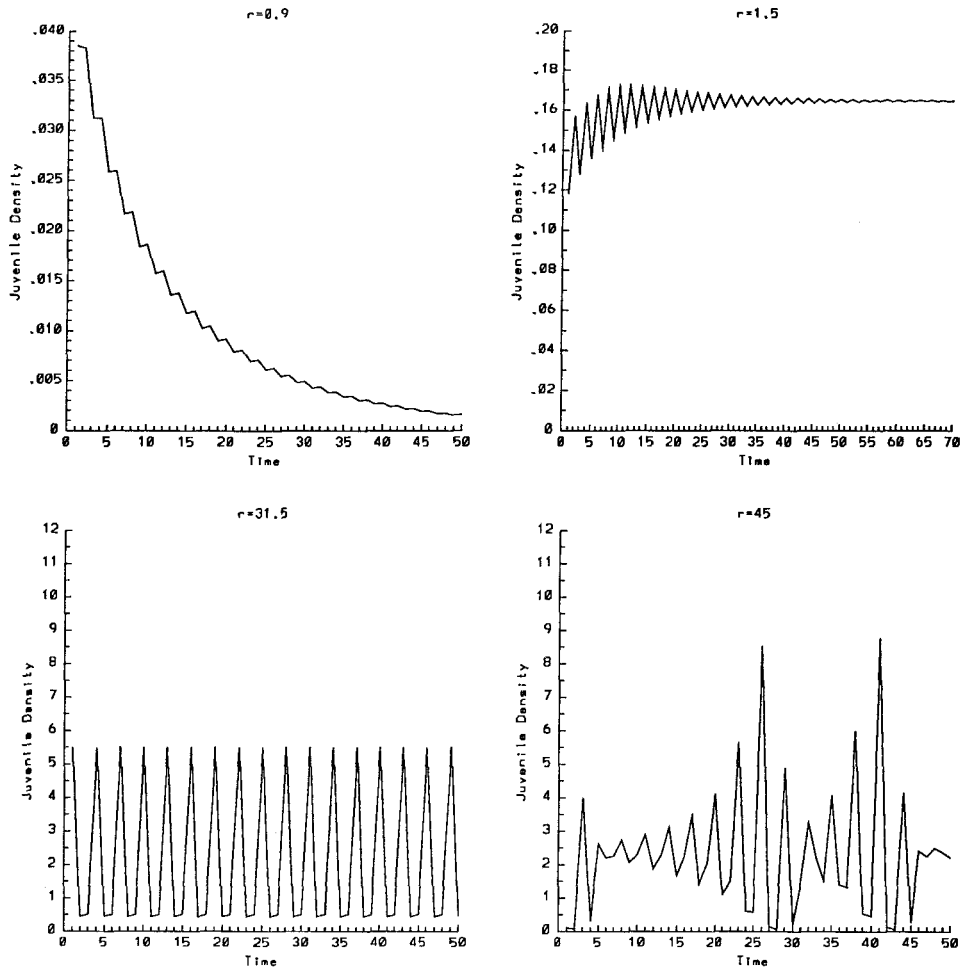


Figure 4. The sequence of bifurcations that occur in region Ia are illustrated by these graphs of juvenile density against time obtained from solutions from equations (2) and (15) with  $S=0.8$ ,  $k=1$ ,  $k'=1$  and with  $(\alpha, \beta)=(0.5, 0.5)$ . (a) Prior to primary bifurcation at  $r=0.9$  the density tends to zero. For  $r=1.5 > 1$ , but prior to secondary bifurcation the juvenile density equilibrates. For  $r=31.5$  secondary bifurcation to an aperiodic solutions has arisen. Chaos is observed for  $r=45$ .

that which occurs in region Ia as described above. Figures 6 and 7 illustrate these features.

**4. Destabilization vs Stabilization.** One of the primary issues in the literature concerning intraspecific competition between age classes is whether such interactions are destabilizing or not and how stability is affected by changes in various model parameters. May *et al.* (1974) and Tschumy (1982) conclude from their studies that strong intraspecific competition between age classes

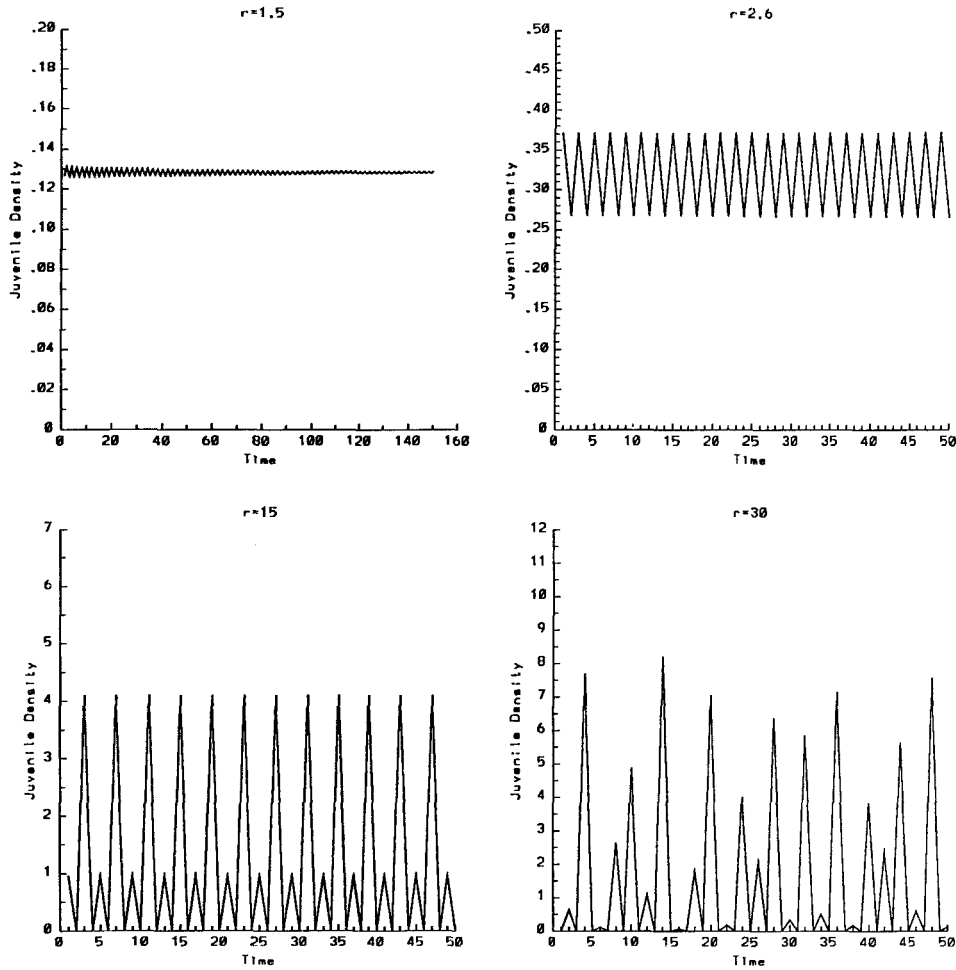


Figure 5. The sequence of bifurcations that occur in region Ib are illustrated by these graphs of juvenile density against time obtained from solutions from equations (2) and (15) with  $S=0.8$ ,  $k=1$ ,  $k'=1$  and with  $(\alpha, \beta)=(1.3, 0.25)$ . For  $r=1.5 > 1$ , but prior to secondary bifurcation the juvenile density equilibrates. At  $r=2.6$  secondary bifurcation positive non-synchronous two-cycles has occurred. A further increase to  $r=15$  shows a period doubling and ultimately chaos at  $r=30$ .

tends to destabilize a population's equilibrium. Using the model equations in Section 1, Ebenman (1987, 1988), on the other hand, concludes that increases (or decreases) in competition between age classes can be either destabilizing or stabilizing depending upon the values of other parameters in the model. The answers to these questions depend on how "destabilization" is defined, i.e. how the stability of two different equations are to be compared. Different definitions are used in different papers (and sometimes different meanings are used within the same paper) and as a result opposing conclusions can be drawn.

It is clear from the results above summarized in Fig. 1 that, in a broad sense, large magnitude competitive effects between juveniles and adults are destabilizing. This is because increases in either  $\alpha$  or  $\beta$  ultimately place the pair parameter  $(\alpha, \beta)$  in region II of Fig. 1 where the primary bifurcation at  $r=1$  results in unstable equilibria. As was seen, in region II there are either no stable equilibria at all (region IIb) or there is a restricted range of  $r$  values corresponding to stable equilibria (region IIa), but even in this case the dynamics tend to be dominated by oscillations of one kind or another. This general conclusion is in agreement with that of May *et al.* (1974) and Tschumy (1982).

Another observation that can be made from Fig. 1 concerns the limiting

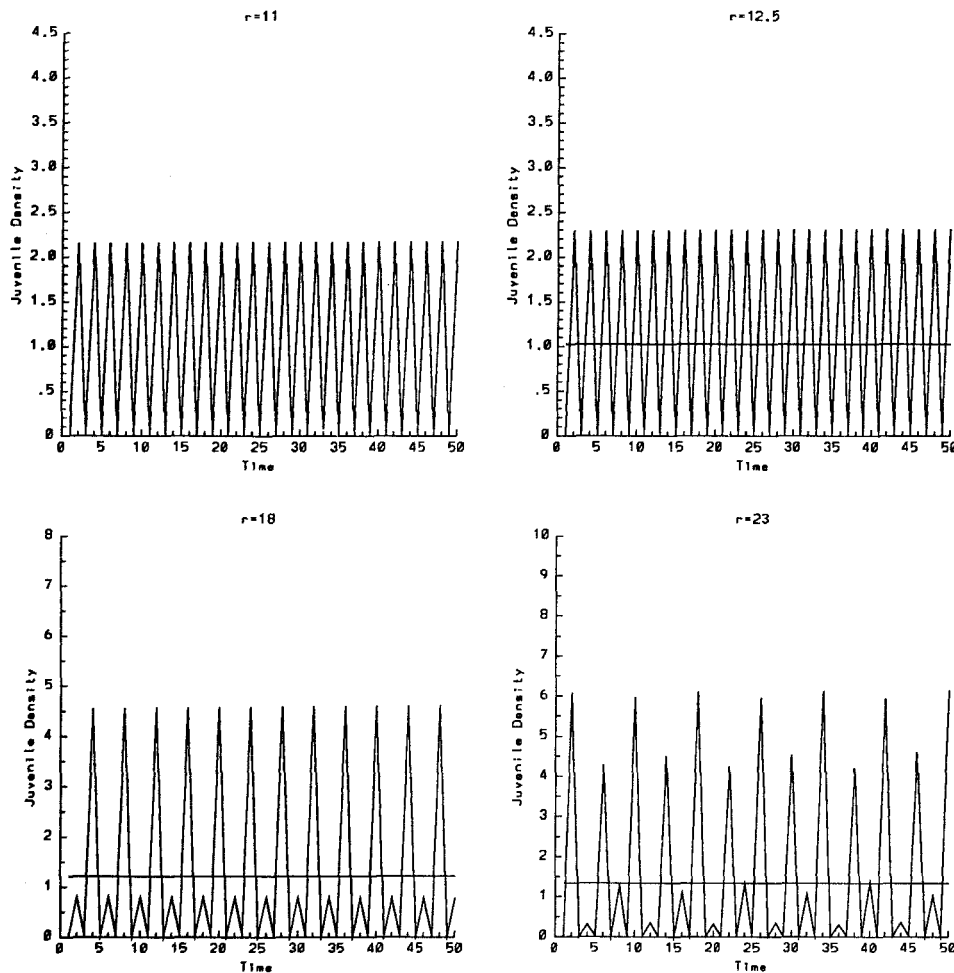


Figure 6. →



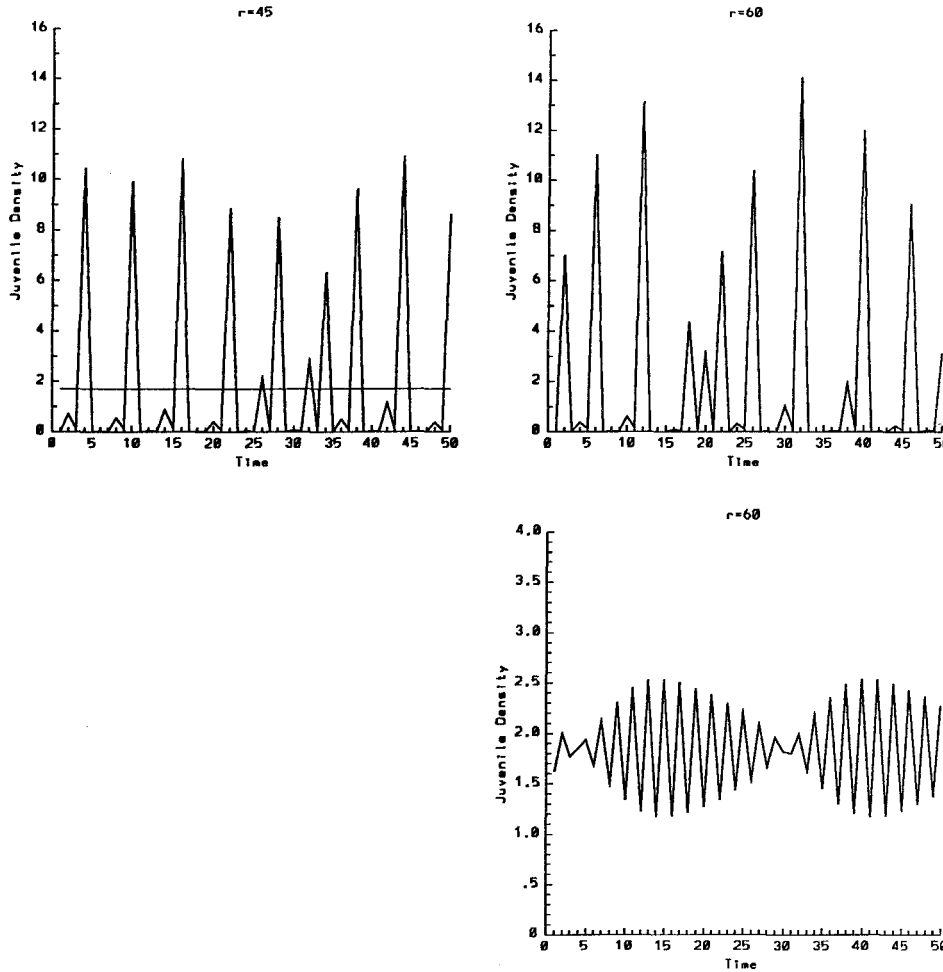


Figure 6. The sequence of bifurcations that occur in region IIa are illustrated by these graphs of juvenile density against time obtained from solutions from equations (2) and (15) with  $S=0.8$ ,  $k=1$ ,  $k'=1$  and with  $(\alpha, \beta)=(0.6, 0.2)$ . The primary bifurcation yields a stable non-negative synchronous two-cycle, shown here for  $r=11$ . At  $r=12.5$  the positive equilibrium branch acquires stability, in the presence of stable synchronous two-cycle. This stable equilibrium persists as the synchronous two-cycle goes through period doublings for  $r=18$  and  $23$  and finally passes to chaos at  $r=45$ . Equilibrium stability is lost at  $r=60$  and gives rise to stable aperiodic oscillations in the presence of other chaotic solutions.

cases as  $k \rightarrow \infty$  or  $k' \rightarrow \infty$  when the triangular region I approaches the semi-infinite rectangular regions in Fig. 8.

From Fig. 8a we see that for  $k \gg k'$  stability is determined by  $\alpha$ . That is, if the density dependence is strongest on adult fertility then stability is determined by the competitive effects of juveniles on adults. This conclusion is in agreement

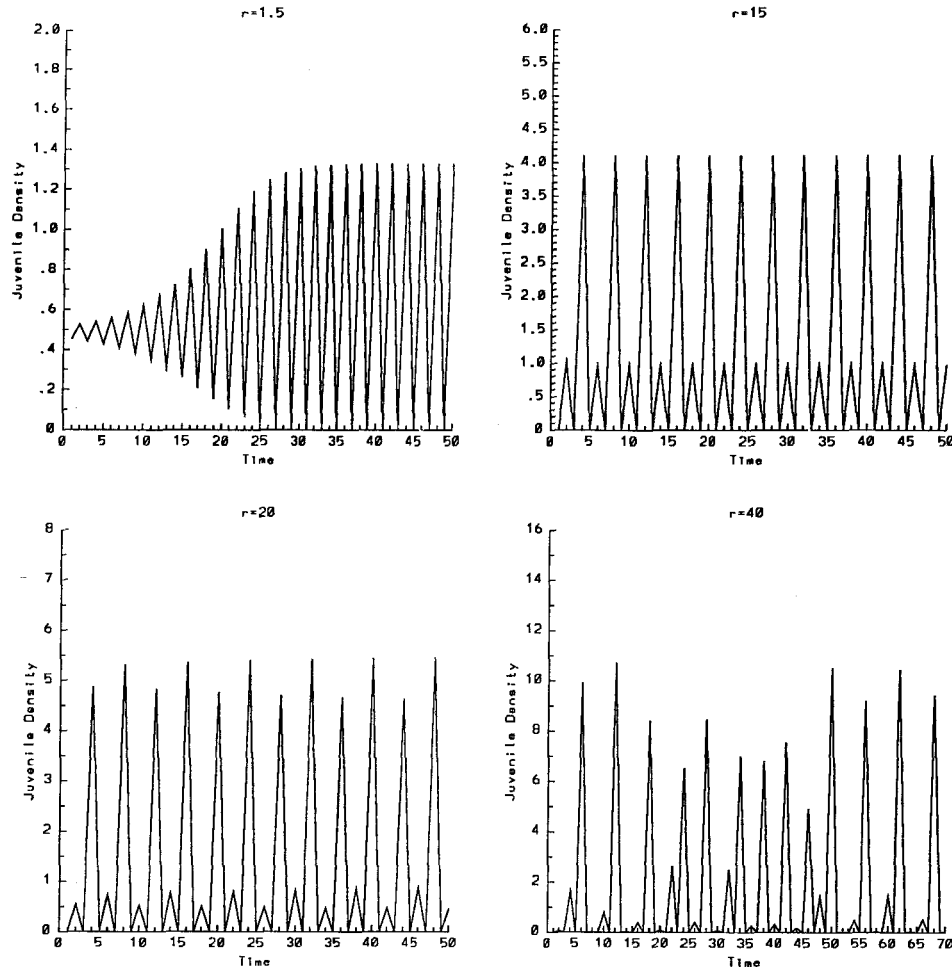


Figure 7. The sequence of bifurcations that occur in region IIb are illustrated by these graphs of juvenile density against time obtained from solutions from equations (2) and (15) with  $S=0.8$ ,  $k=1$ ,  $k'=1$  and with  $(\alpha, \beta)=(1.5, 1.0)$ . The primary bifurcation consists of stable synchronous two-cycles, as illustrated by  $r=1.5$ . These undergo period doublings for  $r=15$  and  $20$ . Chaos is found for  $r=48$ .

with Ebenman (1987). From Fig. 8b it is seen that for the opposite case  $k' \gg k$  stability is determined by  $\beta$ .

For smaller parameter values for  $\alpha$  and  $\beta$  (i.e. within or near region I), Ebenman (1987, 1988) uses the size of stable parameter regions to measure the "stability" of a model, a model with a larger stable parameter region being considered the more stable. In our terminology, a model with a smaller secondary bifurcation value  $r' > 1$  is less stable than one with a larger value of  $r'$ . In general an analytic expression for  $r'$  as a function of  $\alpha$  and  $\beta$  is impossible to

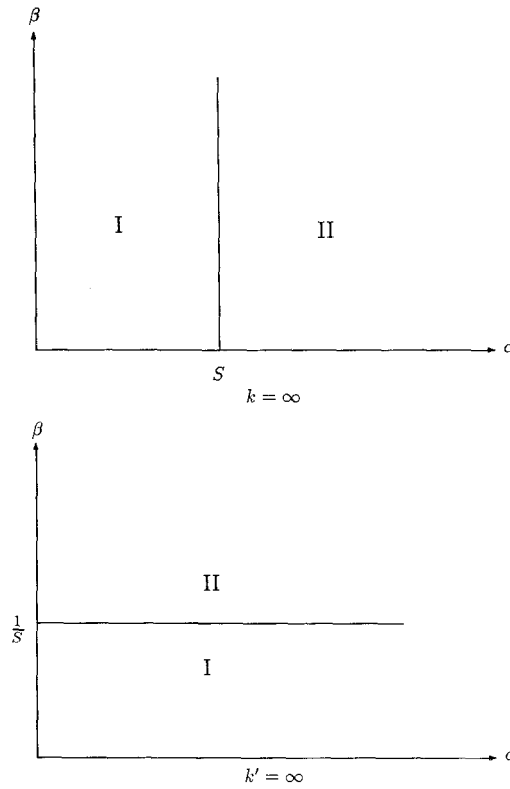


Figure 8. The parameter regions I and II in Fig. 1 are shown in the two limiting cases as the density effects  $k$  on adult fertility and  $k'$  on juvenile survival get arbitrarily large.

obtain, although Ebenman (1988) gives formulas which describe the stability regions for several special cases with either  $f \equiv 1$  or  $g \equiv 1$ .

For models with specified  $f$  and  $g$ , however, stability regions can easily be explored numerically. Some examples for the case (15) can be found in Ebenman (1987, 1988) and in Figs 9 and 10. Given the diversity of the stability regions in these Figures, one must be careful about making general assertions relating the size of the stability interval for  $r$  and increases in the parameters  $\alpha$  and  $\beta$ .

On the whole, our numerical studies show that increases in  $\alpha$  or  $\beta$  (age class competition) are destabilizing by this "stability region size" criterion. There are some notable exceptions, however. In region Ia increases in  $\alpha$  were generally found to be stabilizing, in agreement with Ebenman (1987, 1988); in region Ib however, the opposite is generally true (Fig. 9). Figures 10a-d show cases of destabilization with increasing  $\beta$ , in agreement with Ebenman (1987) (who takes  $\alpha = \beta$ ), but in contrast to the opposite relationship that can be found for different  $k, k'$  values (Ebenman, 1988).

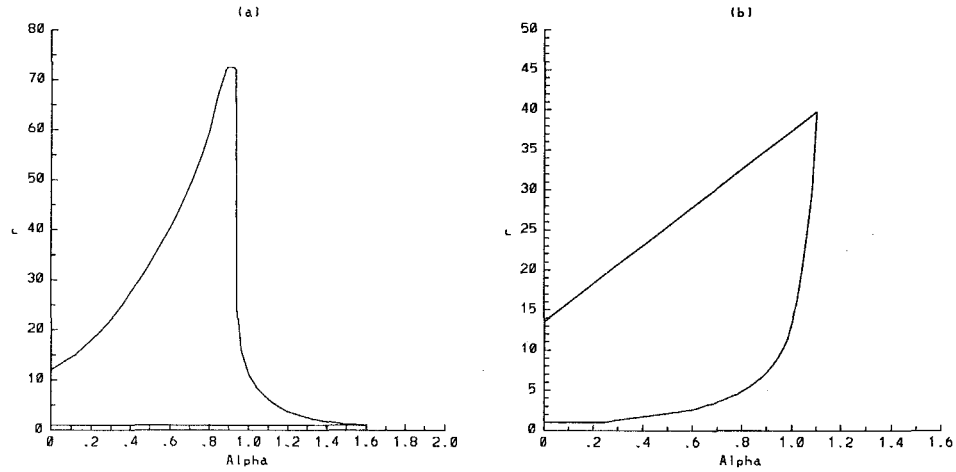


Figure 9. Equilibrium stability regions are shown as a function of  $\alpha$  for equations (2) and (15) with  $S=0.8, k=1, k'=1$ . (a) For  $\beta=0.25$  one crosses region Ia through region Ib into IIb as  $\alpha$  increases. (b) For  $\beta=2.0$  one crosses region Ia into IIa as  $\alpha$  increases.

The measure of model stability based upon sizes of stability parameter regions discussed above distinguishes only between the presence of equilibrium stability and instability and does not take into account relative strengths of stability between two models. A common measure of model stability uses the location of the linearized eigenvalues of a stable equilibrium inside the complex unit circle. Any changes in model parameters which increase the magnitude of the dominant eigenvalue are considered destabilizing while those which decrease the magnitude are considered stabilizing. This measure of stability does not necessarily correlated well with the size of the stable parameter region.

The linearized eigenvalues near the primary bifurcation point  $r=1$  are real and given by  $\lambda^\pm = \lambda_0^\pm + \lambda_1^\pm \varepsilon + o(|\varepsilon|)$  where  $\lambda_0^+ = +1, \lambda_0^- = -1$  and  $\lambda_1^\pm$  are given by formulae (9). First we note that by equations (1) and (10) it is easy to show that  $-\lambda_1^- > \lambda_1^+$  and hence  $|\lambda_1^-| > |\lambda_1^+|$  for small  $\varepsilon > 0$ . The strength of the stability of the bifurcating equilibrium near  $r=1$  is determined by the magnitude of the eigenvalue  $\lambda^- = -1 + \lambda_1^- \varepsilon + o(|\varepsilon|)$ .

We are interested in how  $\lambda^-$  depends on the competition coefficients  $\alpha$  and  $\beta$ , i.e. in the derivatives  $d\lambda^-/d\alpha$  and  $d\lambda^-/d\beta$ . Noting from equations (6) that  $\varepsilon \approx (r-1)/r_1$  for  $r \approx 1$  we write  $\lambda^- \approx -1 + \lambda_1^- (r-1)/r_1$  and hence:

$$\frac{d\lambda^-}{d\alpha} \approx \frac{d(\lambda_1^-/r_1)}{d\alpha} (r-1),$$

and:

$$\frac{d\lambda^-}{d\beta} \approx \frac{d(\lambda_1^-/r_1)}{d\beta} (r-1).$$

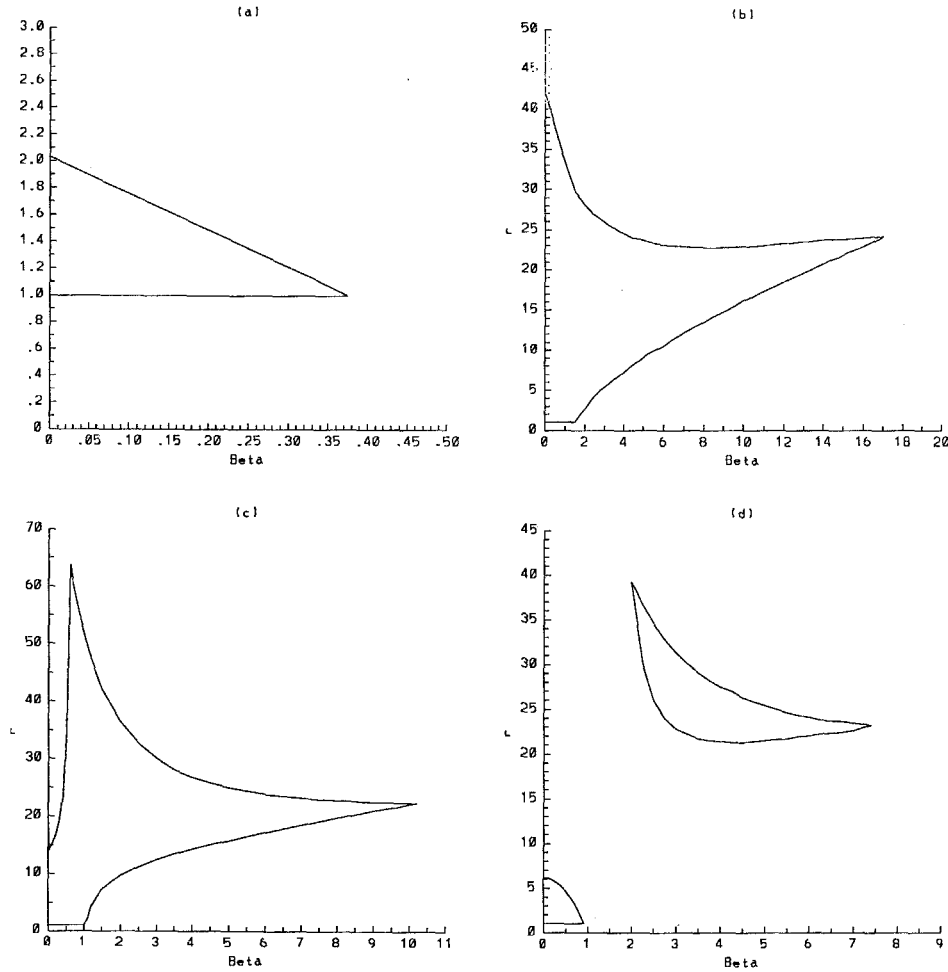


Figure 10. Equilibrium stability regions are shown as a function of  $\beta$  for equations (2) and (15) with  $S=0.8, k=1, k'=1$ . (a) For  $\alpha=1.5$  one crosses region Ib into IIb as  $\beta$  increases. (b) For  $\alpha=0.6$  one crosses region Ia through region IIa into IIb as  $\beta$  increases. (c) For  $\alpha=0.95$  one crosses region Ib through Ia into IIa and finally into IIb as  $\beta$  increases. (d) For  $\alpha=1.1$  one crosses Ib into IIb, then into IIa and back in IIb as  $\beta$  increases. Refer to Fig. 3.

A straightforward calculation yields:

$$\frac{d\lambda^-}{d\alpha} \approx -k(Sk + k')(r-1)/r_1^2,$$

$$\frac{d\lambda^-}{d\beta} \approx -Sk'(Sk + k')(r-1)/r_1^2,$$

$$\frac{d\lambda^-}{d\alpha} - \frac{d\lambda^-}{d\beta} \approx (Sk' - k)(Sk + k')(r-1)/r_1^2.$$

Since both  $d\lambda^-/d\alpha$  and  $d\lambda^-/d\beta$  are negative for  $r > 1$ ,  $r \approx 1$ , it follows that for fixed  $r$  near 1 increases in either  $\alpha$  or  $\beta$  are destabilizing. Consequently, near primary bifurcation we have the opposite conclusion from that of Ebenman, namely that increases in age class competition are destabilizing (again in agreement with Tschumy and May *et al.*).

We also note that:

$$0 > Sk' > k \quad \text{implies} \quad \frac{d\lambda^-}{d\alpha} < \frac{d\lambda^-}{d\beta} < 0;$$

$$0 > k > Sk' \quad \text{implies} \quad \frac{d\lambda^-}{d\beta} < \frac{d\lambda^-}{d\alpha} < 0.$$

From the first inequality we conclude that if the density effects on adult fertility are large in magnitude relative to those on juvenile survivability then stability is more sensitive to increases in  $\alpha$  than in  $\beta$ . This is in agreement with the conclusions of Tschumy (1982) and Ebenman (1987) using parameter region size measures of stability.

Our analysis shows that, on the other hand, if the density effects on adult fertility are weaker than on juvenile survivability, stability is more sensitive to changes in  $\beta$  than to changes in  $\alpha$ . Here our eigenvalue sensitivity measure of system stability leads to the opposite conclusion of Ebenman (1987).

The analysis above is valid only near  $r = 1$ . Any or all of these conclusions can be false for larger values of  $r$ . In Figs 11 and 12 are shown some surfaces that result from plots of the magnitude of the dominant linearized eigenvalue against  $\alpha$  and  $\beta$  and  $r$ . One can see from the complicated topography of these examples that the stabilizing or destabilizing effects caused by changes in these parameters is complicated and not uniform throughout parameter space.

**5. Concluding Remarks.** Using methods of bifurcation theory, supplemented by numerical investigations, we have obtained some fairly complete overviews of the dynamics associated with the model equations (2). This model has the unusual property that two continua, one consisting of equilibria and the other of synchronous two-cycles, simultaneously bifurcate from the trivial solution as the inherent net reproduction rate  $r$  passes through the primary critical point  $r = 1$ . It was shown that when competition is weak (i.e. in region I of Fig. 1) the branch of positive equilibria, near the critical point  $r = 1$ , is stable and the branch of two-cycles is unstable, but that the opposite is true when competition is strong (i.e. in region II). This fact supports the conclusion of Tschumy (1982) and May *et al.* (1974) that competition between age classes tends to be destabilizing.

This conclusion was further supported again near the primary bifurcation point) by a linearized eigenvalue analysis that showed weakened stability, as

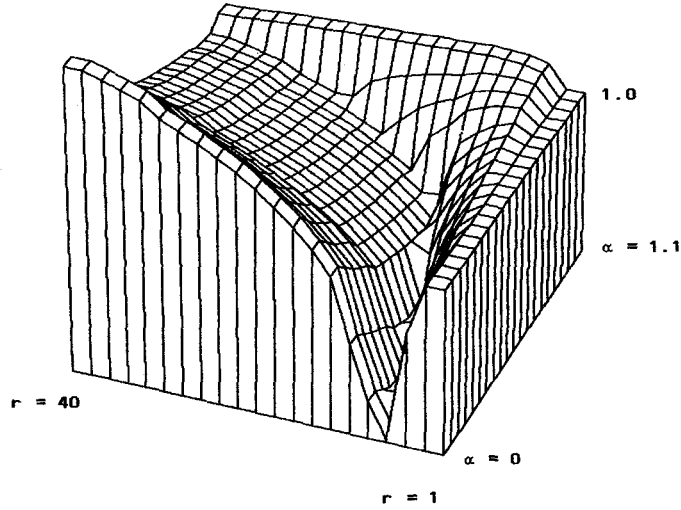


Figure 11. The magnitude of the largest linearized eigenvalue of equations (2) and (15) with  $S=0.8$ ,  $k=1$ ,  $k'=1$ , and  $\beta=2$  is plotted above the  $(\alpha, r)$  parameter plane for  $0 < \alpha < 1.1$  and  $1 < r < 40$ . The lower the surface the more stable is the equilibrium. This surface corresponds to Fig. 9b.

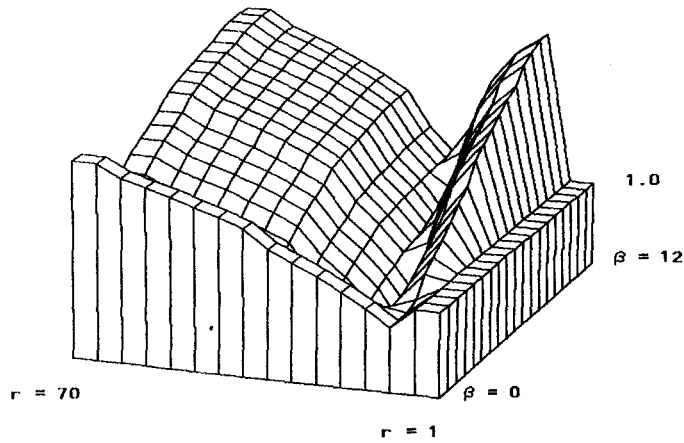


Figure 12. The magnitude of the largest linearized eigenvalue of equations (2) and (15) with  $S=0.8$ ,  $k=1$ ,  $k'=1$ , and  $\alpha=0.95$  is plotted above the  $(\beta, r)$  parameter plane for  $0 < \beta < 12$  and  $1 < r < 70$ . The lower the surface the more stable is the equilibrium. This surface corresponds to Fig. 10c.

measured by the magnitude of the dominant eigenvalue, with increasing competition coefficients (for fixed  $r$ ).

Using a different measure of system stabilization, namely the size of the  $r$  parameter interval for which stable equilibria exist, this conclusion is again confirmed, with some notable exceptions pointed out by Ebenman. Increases in juvenile competitive effects on adult fertility (the  $\alpha$  coefficient) generally results in larger stability regions *provided one remains in region I*, i.e. provided these competition effects are not too great. Also for strong density effects on juvenile survivability (e.g. for  $k \ll k'$ ) increases in competition from adults (i.e. in  $\beta$  in region I) can be stabilizing.

In all parameter regions, destabilization via further bifurcations was found for large inherent net reproductive rate  $r$ . Loss of stability for large  $r$  is, of course, commonly found in simple scalar difference equation models of population growth (May *et al.*, 1974). The explicit incorporation of age structure in model equations (2), however, is seen here to promote more diverse dynamics, including not only the familiar period doubling cascade of bifurcations (of either synchronous or non-synchronous cycles) leading to "chaos", but bifurcations to other periodic and aperiodic oscillations with various properties, equilibrium restabilizations, and the presence of multiple stable attracting states.

The conclusion that stability is more sensitive to the competitive effects of juveniles on adult fertility than to the competitive effects of adults on juvenile survival (Ebenman, 1987; Tschumy, 1982) is borne out by the stability region diagrams in Figs 9–12. It is also corroborated by the local eigenvalue analysis near primary bifurcation, at least when the density effects on adult fertility are relatively stronger than the density effects on juvenile survivability. The eigenvalue sensitivity test of system stability, however, leads to the opposite conclusion when density effects are stronger on juvenile survivability, namely that in this case stability is more sensitive to the competitive effects of adults on juvenile survival.

Another conclusion which follows from our investigations is that age specific properties of vital rates can significantly alter the dynamics of the population trajectory and models which do not take these properties into account can be misleading. For example, the simple model:

$$N(t+1) = rN(t)/(1+N(t)), \quad N(0) > 0,$$

possesses only equilibrium dynamics:  $N(t) \rightarrow 0$  if  $0 < r < 1$  and  $N(t) \rightarrow r-1$  for  $r > 1$ . This equation could be taken as a non-age-structured analog of model equations (2) with the density terms  $f = g = 1/(1+N)$ . The results of Section 2 imply, however, that this age class competition model does not possess only equilibrium dynamics.



Another point along this same line is that the initial age distribution can affect the asymptotic state of the population. Thus a small perturbation in total population size from a stable total population size equilibrium can unexpectedly cause a divergence from this stable equilibrium because of the manner in which the densities of the individual age classes were perturbed. For example, as was pointed out at the end of Section 2, an initial population seeded with only juveniles or only adults can have very different dynamics predicted by equations (2) than does one seeded with all age classes represented, regardless of the total population numbers. Models without age structure cannot account for such occurrences.

Is there any experimental or observational evidence to support these theoretically drawn conclusions? Estimates of only some of the relevant parameters in the models considered here are readily available in the literature. Inherent (density independent) reproductive and survival rates, i.e.  $B$  and  $S$  or equivalently  $r$  and  $S$ , are often estimated (e.g. see Hassell *et al.*, 1976). Estimates for the parameters determining the model non-linearities (density dependent effects) are, on the other hand, less readily available. Therefore, following Ebenman (1987, 1988), we will confine ourselves to some of the more qualitative predictions of the theory above. For populations with weak to moderate juvenile-adult competition (Region I in Fig. 1) the theory here predicts the familiar scenario of stable equilibrium dynamics for small net reproductive rates  $r$  and oscillatory dynamics for large  $r$ . Moreover, the oscillations need not have periods equal to powers of two (in units of developmental time), as is typically the case with simpler non-age structured models (May *et al.*, 1974), but can arise with longer periods or even as aperiodic (but almost periodic) oscillations. A striking example of this is provided by the dynamics of three strains of the beetle *Callosobruchus* (Fujii, 1968). These particular beetles exhibit little juvenile-adult competition and have different net reproductive rates. Corresponding to increasing reproductive rates, their dynamics range from monotonic equilibration to damped oscillatory to sustained oscillations (see Hassell *et al.*, 1976). The sustained oscillations of *C. maculatus* have roughly a period equal to two generations (55–60 days) or 4–5 developmental periods (developmental time is 10–14 days). The well-known experimental results of Nicholson (1954) on the blowfly *Lucilia cuprina* provide another example of a species that exhibits little juvenile-adult competition yet persistent oscillations of roughly 3–4 developmental periods (the oscillations are of period 35–40 days and developmental time is about 10 days). These periods are consistent with the numerical studies reported in Section 3 above where the base “period” of the bifurcating oscillations was roughly between 2 and 4. The waterflea *Daphnia magna* affords an example of a species whose juveniles and adults are potential competitors (Slobodkin, 1961) and whose dynamics also fall within the same scenario, ranging from equilibration to

irregular sustained oscillations (Krebs, 1972) as the reproductive rate is increased (by temperature regulation). According to the theory above species with strong juvenile-adult competition should show a marked propensity to oscillate. Cases in point include the flour beetle *Tribolium castaneum* whose larva suffer a mortality rate due to adult cannibalism of 90% are characterized by fluctuations and non-equilibrium states (Park, 1933). Populations of the Colorado potato beetle *Leptinotarsa decemlineata*, for which there is strong competition affecting adult fertility, show marked oscillations (Harcourt, 1971). Hamrin and Persson (1986) suggest that the 2 year cycles in the planktivorous fish *Coregonus albula* is due to competition between juveniles and older age classes. It is interesting to consider (as does May, 1976) the widely recognized 3–4 year cycles among small mammals in boreal regions. Given the obvious potential for resource competition between juveniles and adults and the often high values of inherent net reproductive rates found in such populations, a 3–4 year oscillation is strikingly commensurate with the periods found in the numerical study in Section 3. The 3–4 period range at bifurcation was found numerically to vary little with changes in the strengths of the nonlinearities as measured by  $k$  and  $k'$ , although as found by Ebenman the critical bifurcation value  $r'$  was significantly affected. Larger values of  $k'$ , corresponding to populations in which adult fertility is more affected by competition than is juvenile survivability, lowered  $r'$  and hence enhanced the probability of population cycles. Density effects in fact heavily affect fertility of small mammal populations (as opposed for example to the case of most birds for which effects on fertility are weak; Lack, 1954). Biological examples that illustrate the theoretical effects predicted by the model due to differences in the competitive effects on adult reproduction vs juvenile survival are discussed in Ebenman (1988). An interesting implication of our study here is that populations with extraordinarily strong juvenile-adult competition (region II in Fig. 1), particularly those in which adult fertility is greatly affected by this competition (large  $\alpha$ ), should have a tendency to exhibit what we called synchronous oscillations, regardless of the magnitude of the inherent net reproductive rate. Consequently these populations tend asymptotically to oscillatory states in which competition is avoided because of the synchronized, out-of-phase appearance of juveniles and adults. It would be interesting to survey the voluminous literature on (mainly insect) species with discrete non-overlapping generations to see which have potentially competing juveniles and adults should these stages coexist. While the examples cited above provide possible support for some of our theoretical conclusions, it must be pointed out that the mechanisms that determine the dynamics of populations, particularly natural populations, are generally multifarious and involve many complicating factors. It is usually too much to hope that the details of the dynamics can be accounted for by simple models such as equations (2). Nonetheless, theoretical investiga-

tions based upon simple models can serve the very important role of focusing attention on specific mechanisms and their implications in order to suggest possible explanations of observed phenomena. In this spirit it is hoped that the results in this paper will serve to provoke further biological study into the effects of competition between age classes.

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