

S. Busenberg M. Martelli (Eds.)

Differential Equations Models in Biology, Epidemiology and Ecology

Proceedings of a Conference held in Claremont
California, January 13-16, 1990

Springer-Verlag

Berlin Heidelberg New York
London Paris Tokyo
Hong Kong Barcelona
Budapest



Some Delay Models for Juvenile vs. Adult Competition

J. M. Cushing

Department of Mathematics, University of Arizona, Tucson, Arizona 85721

1 Introduction

Models of competition have played a central role in theoretical population dynamics and ecology. The vast majority of mathematical models of competitive interactions that have been formulated have been done so with regard to highly aggregate state variables at the total population level and have ignored differences between individual organisms, in effect treating all individuals of a species as identical. Biological populations generally consist, however, of individuals with diverse physiological characteristics, such as age, body size or weight, life cycle stages, etc., (with intra-species variances that in fact can exceed inter-specific variances amongst competing species) and it has become widely recognized that this diversity can have a significant influence upon population level dynamics (Werner and Gilliam (1984), Ebenman and Persson (1988), Metz and Diekmann (1986)). Models that ignore individual level physiological variances cannot, except in the simplest of cases, adequately account for the mechanisms that result in competition between individual organisms for limited resources. In particular, intra-specific competition can be accounted for in such models only in highly qualitative ways at best.

One common type of intra-specific competition found in species with overlapping generations occurs between different age or size classes within the population, in particular between (younger or smaller) juveniles and (older or larger) adults. In species with complex life cycles during which individuals undergo radical changes in morphology, physiology, or behavior (e.g. holometabolous insects, amphibians, and many marine invertebrates), there are often significant changes in resource utilization during the life cycle. For such species, these ontogenetic niche shifts lessen or even exclude possibility of competition between adults and juveniles. However, the potential for juvenile vs. adult competition is increased in species that have simpler life cycles, during which individuals undergo fewer changes during their life history. This is the case for most fishes, birds, mammals, many plants, and for hemimetabolous insects (Ebenman (1987, 1988)). Some questions that arise concerning such species included: what effects do strong competitive interactions between juveniles and adults have on the dynamics of

the population? Do such interactions stabilize or destabilize the population and in what sense?

In an early paper, May et al. (1974) use a simple two-age class difference equation model to conclude that juvenile vs. adult competition has a destabilizing effect on population equilibria. This conclusion was also reached by Tschumy (1982) using a simple differential equation model. Ebenman (1987), however, uses a simple two-age difference model to argue that destabilization was not the only possible effect of strong juvenile vs. adult competition (also see Ebenman (1988), Ebenman and Persson (1988), Cushing and Li (1989)). Ebenman distinguishes between suppressed adult fertility due to strong competition from juveniles and increased juvenile mortality due to competition with adults and he tabulates "all the studies known to (him), where even crude estimates of relevant parameters can be made" and demonstrates two opposing trends (Table 2, Ebenman (1988)). First, in species that possess adult density dependent juvenile survival, population level dynamics progress from "unstable" oscillatory dynamics to stable equilibrium dynamics as one passes from species with weak to species with strong juvenile vs. adult competition. Conversely, in species that possess juvenile density dependent adult fertility, the opposite is true, i.e. population dynamics is destabilized from equilibration to oscillations as one passes from weak to strong juvenile vs. adult competition. These observations were commensurate with the conclusions drawn from his simple model.

Cushing and Li (1989) study Eberman's model in more mathematical detail and argue, in agreement with Eberman, that strong juvenile vs. adult competition can be either stabilizing or destabilizing. They point out, however, that it is difficult to make sweeping conclusions over wide parameter ranges and that any conclusions drawn depend very much upon what is meant by "stabilization" or "destabilization". Different criteria can lead to contradictory conclusions. May et al. and Eberman study the stabilization/destabilization question with regard to the relative sizes of stability regions in certain parameter spaces. Tschumy (1982), on the other hand, uses a criterion based upon linearized eigenvalue sensitivity or changes in equilibrium levels. Loreau (1990) criticizes Eberman's analysis (and implicitly that of May, et al.) and, amongst other things, points out that if the linearized eigenvalues are analyzed for his model one finds that increased competition is always destabilizing (also see Cushing and Li (1989)). We will see here, however, that for more sophisticated continuous time-age variable models, stabilization can indeed occur under the eigenvalue sensitivity criterion.

In this paper we will study the stabilization/destabilization question by models derived using the now standard modeling methodology for age-structured population dynamics (Metz and Diekmann (1986)). In Sect. 2 we will derive, under certain simplifying assumptions, differential delay equations for the dynamics of populations exhibiting the two types of juvenile vs. adult competition distinguished by Eberman. These two cases, namely juvenile density dependent adult fertility and adult density dependent juvenile survivability, will be considered independently in Sect. 3. The existence and stability of positive equilibrium states will be studied and eigenvalue sensitivity to changes in competition coefficients will be used to investigate the stabilization/destabilization question.

2 Model derivation

Using what is now standard methodology for modeling age-structured populations (Hoppensteadt (1975), Gurtin and MacCamy (1974), Metz and Diekmann (1986)), we consider a population described by an age specific density $\rho = \rho(t, a)$ whose dynamics are governed by the equations

$$\partial_t \rho + \partial_a \rho + \mu \rho = 0, \quad (2.1a)$$

$$\rho(t, 0) = \int_0^\infty f \rho da, \quad (2.1b)$$

$$\rho(0, a) = \phi(a) \quad (2.1c)$$

where $t > 0$ is time, $a > 0$ is age, $\mu \geq 0$ and $f \geq 0$ are the unit density mortality and fertility rates respectively, and $\phi \geq 0$ is the initial age distribution. To model the density dependent dynamics of a population one must prescribe how the vital rates μ and f depend on ρ .

In this paper we are interested in populations which consist of immature juveniles and mature adults. It will be assumed that maturity is determined strictly by age, i.e. there exists an age $m > 0$ such that individuals of age $a < m$ are immature and individuals of age $a > m$ are mature. We can then structure the population into two subgroups, namely juveniles and adults whose total numbers are given by the integrals

$$J(t) = \int_0^m \rho(t, a) da, \quad A(t) = \int_m^\infty \rho(t, a) da,$$

respectively. As discussed in Sect. 1, we are interested in the case when competition between these two subgroups is expressed through either increased juvenile mortality and/or decreased adult fertility. Therefore we assume

$$\begin{aligned} 0 \leq \mu &= \mu(a, W(t)), \quad W(t) = J(t) + \gamma A(t) \\ 0 \leq f &= r\beta(a, V(t)), \quad V(t) = \alpha J(t) + A(t) \end{aligned} \quad (2.2)$$

$$\partial_W \mu(a, W) \geq 0, \quad \partial_V \beta(a, V) \leq 0, \quad \beta(a, V) = 0 \quad \text{for } 0 \leq a \leq m.$$

It is also assumed that the normalization

$$\int_0^\infty \beta(a, 0) \exp\left(-\int_0^a \mu(s, 0) ds\right) da = 1 \quad (2.3)$$

is satisfied so that the constant $r \geq 0$ is the "inherent net reproductive rate", i.e. the expected number of offspring per individual per lifetime in the absence of density effects (Cushing (1985)). Here the competition coefficient γ measures the relative effect that an adult individual has on juvenile survival as compared to that of a juvenile. Similarly the coefficient α measures the relative effect that a juvenile individual has on adult fertility as compared to that of an adult individual. The last line in (2.2) expresses the fact that the death rate increases

and the fertility rate decreases with increases in population numbers and that no individual of age less than m is fertile.

In this paper we will be interested in the existence and stability of (non-negative) equilibrium solutions of equations (2.1) and how equilibrium stability depends upon the competition coefficients γ and α . Obviously these equations possess the trivial equilibrium $\rho = 0$ ($J = A = 0$). It follows from general results of Cushing (1985) that there exists an unbounded continuum of equilibrium pairs (ρ, r) that bifurcates from the trivial solution pair $(0, 1)$ and consists of positive equilibria (except for $(0, 1)$). Moreover, because of conditions (2.2), these positive equilibria are locally asymptotically stable at least for r greater than, but close to the critical value 1. In a forthcoming paper, Cushing and Li (1990) study the sensitivity of the stability of these positive equilibria on the competition coefficients γ and α . Here we will study this question for some specializations of equations (2.1) from which can be derived differential delay equations for A and J , or more precisely for A and the total population size $P = J + A = \int_0^\infty \rho(t, a) da$.

We will study the effects of density on juvenile mortality and on adult fertility separately by considering the following two models. For the case of density dependent adult fertility we set

$$\mu = \left\{ \begin{array}{l} \mu_J, 0 < a < m \\ \mu_A, m < a \end{array} \right\}, \beta = \left\{ \begin{array}{l} 0, 0 < a < m \\ \beta_A(V), m < a \end{array} \right\}, V = \alpha J + A \quad (2.4)$$

where $\mu_A > 0$, $\mu_J > 0$ are constants and $\beta_A(V) \geq 0$, $\partial_V \beta_A(V) \leq 0$ for all $V \geq 0$. (For technical reasons we define $\beta_A(V) = \beta_A(0)$ for $V < 0$.) Thus, in this case, the death rate is assumed independent of weighted population size V . Moreover the death rates of juveniles and of adults are assumed constant (independent of an individual juvenile's or adult's age), although these two death rates need not necessarily be the same. The normalization (2.3) requires that

$$\beta_A(0) = \mu_A \exp(\mu_J m). \quad (2.5)$$

For the second case of density dependent juvenile mortality we set

$$\mu = \left\{ \begin{array}{l} \mu_J(W), 0 < a < m \\ \mu_A, m < a \end{array} \right\}, \beta = \left\{ \begin{array}{l} 0, 0 < a < m \\ \beta_A, m < a \end{array} \right\}, W = J + \gamma A \quad (2.6)$$

where $\mu_A > 0$, $\beta_A > 0$ are constants and $\partial_W \mu_J(W) \geq 0$ for all $W \geq 0$, $\mu_J(0) > 0$. (For technical reasons we define $\mu_J(W) = \mu_J(0)$ for $W < 0$.) In this case the juvenile death rate is independent of age, but dependent on population size W . The adult fertility rate is a constant, independent of both age and population size. The normalization (2.3) requires

$$\beta_A = \mu_A \exp(\mu_J(0)m). \quad (2.7)$$

Under these assumptions we can derive differential equations for the rates of change of $J(t)$ and $P(t)$ by integrating (2.1a) with respect to a from 0 to m and 0 to ∞ respectively. Before doing this we point out that an integration of (2.1a) along characteristics, when $\mu = \mu(t, a)$ and $\beta = \beta(t, a)$ yields

$$\rho(t, a) = \left\{ \begin{array}{l} \phi(a-t) \exp(-\int_0^t \mu(s, a-t+s) ds), 0 \leq t \leq a \\ \rho(t-a, 0) \exp(-\int_0^a \mu(a-t+s, s) ds), a < t \end{array} \right\}$$

which implies for the adult fertility problem (2.4) that

$$\rho(t, m) = \left\{ \begin{array}{l} \phi(m-t) \exp(-\mu_J t), 0 \leq t \leq m \\ r\beta_A(V(t-m))A(t-m) \exp(-\mu_J m), m < t \end{array} \right\} \quad (2.8)$$

and for the juvenile mortality problem (2.6) that

$$\rho(t, m) = \left\{ \begin{array}{l} \phi(m-t) \exp(-\int_0^t \mu_J(W(s)) ds), 0 \leq t \leq m \\ r\beta_A A(t-m) \exp(-\int_0^m \mu_J(W(t-m+s)) ds), m < t \end{array} \right\} \quad (2.9)$$

These formulas describe maturation rates for the two problems, i.e. the rate at which juveniles reach age m . For example, in (2.8) the maturation rate during the interval $0 \leq t \leq m$ is simply the initial density $\phi(m-t)$ of individuals of age $m-t$ times the probability $\exp(-\mu_J t)$ of surviving t units of time. Afterwards, for $t > m$, the maturation rate is the birth rate $r\beta_A(V(t-m))A(t-m)$ at time $t-m$ multiplied by the probability $\exp(-\mu_J m)$ of surviving to maturation age m . (2.9) has a similar interpretation.

Under the assumption that ρ vanishes at $a = \infty$, integrations of (2.1a) with respect to a from 0 to ∞ and from m to ∞ yield

$$P' - \rho(t, 0) + \int_0^\infty \mu \rho da = 0, \quad A' - \rho(t, m) + \mu_a A = 0.$$

These equations together with (2.1b) and (2.8)-(2.9) in turn yield the following system of delay equations

$$P' = -\mu_J P + \mu_d A + r\beta_A(V)A \text{ for } t > 0 \text{ where } \mu_d = \mu_J - \mu_A \quad (2.10a)$$

$$A' = -\mu_A A + \phi(m-t) \exp(-\mu_J t) \text{ for } 0 \leq t \leq m \quad (2.10b)$$

$$A' = -\mu_A A + r\beta_A(V(t-m))A(t-m) \exp(-\mu_J m) \text{ for } t > m \quad (2.10c)$$

for the density dependent adult fertility problem and

$$P' = -\mu_J(W)P + (r\beta_A - \mu_A + \mu_J(W))A \text{ for } t > 0 \quad (2.11a)$$

$$A' = -\mu_A A + \phi(m-t) \exp(-\int_0^t \mu_J(W(s)) ds) \text{ for } 0 \leq t \leq m \quad (2.11b)$$

$$A' = -\mu_A A + r\beta_A A(t-m) \exp(-\int_0^m \mu_J(W(t-m+s)) ds) \text{ for } t > m \quad (2.11c)$$

for the density dependent juvenile mortality problem. Note that

$$V(t) = \alpha P(t) + (1-\alpha)A(t) \quad \text{and} \quad W(t) = P(t) + (\gamma-1)A(t).$$

Both problems have the initial conditions (see (2.1c))

$$P(0) = \int_0^{\infty} \phi(a) da \geq 0 \quad \text{and} \quad A(0) = \int_m^{\infty} \phi(a) da \geq 0. \quad (2.12)$$

Equations (b) and (c) in (2.10) and (2.11) have straightforward interpretations. (b) They state that the rate of change of the adult population is determined by the loss $-\mu_A A$ due to deaths plus the gain due to maturation of juveniles. On the interval $0 \leq t \leq m$ this maturation rate is given simply by the survivors, over t units of time, from the initial density $\phi(m-t)$ of juvenile individuals of age $m-t$. For times $t > m$ this maturation rate is given by the birth rate at time $t-m$ multiplied by the probability of surviving the m time units to maturation. Equations (a) express the net change in population size due to deaths and births. For example, the right hand side of (2.10a) can be rewritten as $-\mu_J J - \mu_A A + r\beta_A(V)A$ whereby the change in population size P' is seen to be given by the loss of both juveniles and adults due to death plus the gain due to births from the adult class. A similar interpretation holds for (2.11a).

The problems (2.10)-(2.12) are somewhat nonstandard in that the initial conditions for the delay equations (a) and (c) for $t > m$, rather than being given over the "initial" interval $0 \leq t \leq m$ as is usually the case for delay equations, are determined by the initial conditions (2.12) at $t = 0$ and the equations in parts (a) and (b) over the interval $0 \leq t \leq m$. We will not dwell on this point here, but instead turn to the asymptotic dynamics by restricting our attention to $t > m$.

3 Equilibria and stability

In this section we will analyze the equilibrium solutions of equations (2.10a,c) and (2.11a,c) and their stability properties, including the trivial zero state solution $P = A = 0$. Four theorems will be proved. Theorem 1 shows that if the inherent net reproductive rate r is less than one then the trivial equilibrium is globally attracting and consequently the population asymptotically dies out. The condition $r < 1$ means that at low population densities, when the adverse effects on survival and fertility are minimal, individuals do not on average replace themselves. This "reasonable" result is a consequence of the monotonicity assumptions in (2.2) on the death and fertility rates as functions of population size, assumptions which rule out depensation or Allee effects that in nonlinear problems can lead to viable populations with $r < 1$.

Theorems 2-4 deal with the case when $r > 1$. In this case, the trivial solution is unstable and there exists, for both problems, a unique positive equilibrium which at least for r sufficiently close to 1 is locally asymptotically stable (Theorem 2). It is frequently the case in population dynamical models that equilibria destabilize (usually through a Hopf-type bifurcation to a limit cycle) as r or some other measure of reproductive output is increased sufficiently. We cannot expect, in the generality assumed, that the positive equilibria of equations (2.10a,c) and (2.11a,c) remain stable for all $r > 1$. We do not study this question here, however, and turn instead in Theorems 3 and 4 to the question of the dependence of the equilibria and their stability properties on the competition coefficients α

and γ when r is close to 1 (when we are assured by Theorem 2 that they are indeed stable).

Theorem 3 indicates that increased juvenile vs. adult competition is destabilizing in both models in the sense that equilibrium levels for both the juvenile and adult classes decreases with increased competition. As Theorem 4 indicates, however, this is not always the case if the strength of the equilibrium stability is measured by the effect of the competition on the magnitude of the linearized, stability-determining eigenvalue λ (often referred to as a measure of the "resilience" of the equilibrium). Theorem 4 deals with the change in this eigenvalue caused by changes in α and γ by computing the sign of the derivative $\partial_\alpha \lambda$ for (2.10) and $\partial \lambda_\gamma$ for (2.11). Theorem 2 guarantees that $\lambda < 0$ for $r > 1$ sufficiently close to 1. If the sign of one of these derivatives is positive then an increase in the strength of the intra-specific competition is represented by an increase in the corresponding competitive coefficient is destabilizing since the negative eigenvalue is thereby increased (causing decreased resilience). Similarly a negative derivative implies a stabilizing effect due to increased competition (due to an increase in resilience). Theorem 4 shows that the two problems (2.10) and (2.11) have opposite effects on equilibrium stability. Specifically, in the first case when adult fertility is dependent on population size, increased competition from juveniles is destabilizing. On the other hand, in the second case when juvenile survival is dependent on population size, increased competition is stabilizing.

It is not difficult to see from the equations (2.1)-(2.2) that non-negativity of the initial age distribution $\phi(a) \geq 0$ implies that the density $\rho(t, a) \geq 0$ is non-negative for all time t . Thus the solutions $P(t)$ and $A(t)$ of (2.10) and (2.11) are non-negative for all time t . (A direct proof from equations (2.10) and (2.11) that non-negative initial conditions imply non-negative solutions for all time doesn't appear to be trivial.) Both systems have the trivial zero equilibrium $(P, A) = (0, 0)$ (corresponding to $\phi \equiv 0$).

Theorem 1 *If $r < 1$ and $P(0) \geq 0$, $A(0) \geq 0$, then $(P(t), A(t)) \rightarrow (0, 0)$ as $t \rightarrow +\infty$ for solutions of (2.10) and (2.11).*

Proof. For both problems (2.10) and (2.11) it is easy to see that

$$A'(t) \leq -\mu_A(t) + r\mu_A A(t-m), \quad t > m$$

from which follows that $0 \leq A(t) \leq x(t)$ where $x(t)$ is the solution of

$$x'(t) = -\mu_A x(t) + r\mu_A x(t-m), \quad t > m \quad (3.1)$$

$$x(t) = A(t), \quad 0 \leq t \leq m.$$

Since $r \leq 1$ it follows from a result of Hayes (Theorem 13.8, Chapter 13, of Bellman and Cooke (1963)) that $x(t) \rightarrow 0$ and hence $A(t) \rightarrow 0$ as $t \rightarrow +\infty$.

For (2.10) we note that $P' = -\mu_J P + \psi(t)$ where

$$\psi(t) = (\mu_d + r\beta_A(V(t)))A(t) \rightarrow 0 \quad \text{as } t \rightarrow +\infty.$$

Thus $P(t) \rightarrow 0$ as $t \rightarrow +\infty$.

For (2.11) we define $Q(t)$ as the solution of

$$Q' = -\mu_J(W)Q + (r\beta_A - \mu_A)A, \quad Q(0) = P(0) \geq 0$$

and let $R(t) = P(t) - Q(t)$ so that

$$R' = -\mu_J(W)R + \mu_J(W)A, \quad R(0) = 0.$$

Since $\mu_J(W) \geq \mu_J(0) > 0$ and $A(t) \rightarrow 0$ we see that $Q(t) \rightarrow 0$ as $t \rightarrow +\infty$. Using an integrating factor we find from an integration by parts that

$$R(t) = A(t) - A(0) \exp\left(-\int_0^t \mu_J(W)d\sigma\right) - \exp\left(-\int_0^t \mu_J(W)d\sigma\right) \int_0^t \exp\left(\int_0^s \mu_J(W)d\sigma\right) A'(s) ds.$$

The first two terms tend to 0 as $t \rightarrow +\infty$ as does the last term since from (2.11c) we see that $A'(t) \rightarrow 0$. Thus $R(t)$ and hence $P(t)$ tend to 0 as $t \rightarrow +\infty$. \square

Theorem 2 Suppose $r > 1$. Then $(0,0)$ is unstable for both (2.10) and (2.11) and both systems have a unique positive equilibrium (P_e, A_e) which is asymptotically stable for at least r close to 1.

Proof. The linearization of part (c) of both (2.10) and (2.11) at the trivial equilibrium $(0,0)$ yields the scalar delay equation (3.1), all of whose nontrivial solutions are unbounded (again see Theorem 13.8, Chapter 13, of Bellman and Cooke (1963)) since $r > 1$. Thus $(0,0)$ is unstable for $r > 1$.

Next we look at solutions $(P_e, A_e) \neq (0,0)$ of (2.10) and (2.11) that are constant for $t > m$ by looking for nonzero equilibrium solutions of (a) and (c). (Parts (b) then serve to define the initial equilibrium age distribution ϕ .) For (2.10) this leads to the equations

$$\begin{aligned} 0 &= -\mu_J P_e + (r\beta_A(V_e) + \mu_d)A_e \\ 0 &= -\mu_A + r\beta_A(V_e) \end{aligned}$$

where $V_e = \alpha P_e + (1 - \alpha)A_e$. Using $r > 1$, the normalization (2.5) and the monotonicity of β_A we can rewrite these two equations as

$$\begin{aligned} \mu_J P_e - (\beta_A(0) + \mu_d)A_e &= 0 \\ \alpha P_e + (1 - \alpha)A_e &= \beta_A^{-1}(\beta_A(0)/r) \end{aligned}$$

from which follows the existence of the positive equilibria

$$P_e = V_e(r) \frac{\beta_A(0) - \mu_A + \mu_J}{\alpha(\beta_A(0) - \mu_A) + \mu_J}, \quad A_e = V_e(r) \frac{\mu_J}{\alpha(\beta_A(0) - \mu_A) + \mu_J} \quad (3.2)$$

for $r > 1$ where $V_e(r) = \beta_A^{-1}(\beta_A(0)/r)$.

Similar manipulations with (2.11) lead to the positive equilibria

$$P_e = W_e(r) \frac{r\beta_A - \mu_A + \mu_J(W_e)}{r\beta_A - \mu_A + \gamma\mu_J(W_e)}, \quad A_e = W_e(r) \frac{\mu_J(W_e)}{r\beta_A - \mu_A + \gamma\mu_J(W_e)} \quad (3.3)$$

for $r > 1$ where $W_e(r) = \mu_J^{-1}(\frac{1}{m} \ln r + \mu_J(0))$.

The calculation of the characteristic functions for (2.10) and (2.11) at these two respective equilibria is straightforward. This exercise yields equations

$$p(\lambda; \alpha, r) = 0 \quad \text{and} \quad q(\lambda; \gamma, r) = 0$$

for complex λ where

$$p(\lambda; \alpha, r) = (\lambda + \mu_J)(\lambda + \mu_A - \mu_A e^{-\lambda m}) - rV_e(r)\mu_J\beta'_A(V_e(r)) \frac{a(\lambda)\alpha + b(\lambda)}{c\alpha + d} \quad (3.4)$$

$$a(\lambda) = (\lambda + \mu_A)(1 - \exp(-\mu_J m - \lambda m)), \quad b(\lambda) = (\lambda + \mu_J) \exp(-\mu_J m - \lambda m) \\ c = \beta_A(0) - \mu_A, \quad d = \mu_J$$

and where

$$q(\lambda; \gamma, r) = (\lambda + \mu_J(W_e(r)))(\lambda + \mu_A - \mu_A e^{-\lambda m}) + \mu'_J(W_e(r))W_e(r) \frac{r\beta_A - \mu_A}{r\beta_A - \mu_A + \gamma\mu_J(W_e)} (\lambda + \mu_A - \mu_A e^{-\lambda m}) + \mu'_J(W_e(r))W_e(r)\mu_A \frac{1 - e^{-\lambda m}}{\lambda} c(r) \frac{a(\lambda, r)\gamma + b(\lambda, r)}{c(r)\gamma + d(r)} \quad (3.5)$$

$$a(\lambda, r) = \lambda + \mu_J(W_e(r)), \quad b(\lambda, r) = -\lambda + r\beta_A - \mu_A$$

$$c(r) = \frac{1}{m} \ln r + \mu_J(W_e(r)), \quad d(r) = r\beta_A - \mu_A.$$

Here we have indicated the dependence of p and q on r and the competition coefficients α and γ .

The following partial derivatives evaluated at the critical values $r = 1$ and $\lambda = V_e = W_e = 0$ are easily computed:

$$\partial_\lambda p(0; \alpha, 1) = \mu_J(1 + m\mu_A) > 0 \\ \partial_\lambda q(0; \gamma, 1) = \mu_J(0)(1 + \mu_A) > 0 \quad (3.6)$$

More tedious calculations show that

$$\partial_r p(0; \alpha, 1) > 0, \quad \partial_r q(0; \gamma, 1) > 0$$

and hence in both cases $\partial_r \lambda < 0$ at $r = 1$. It follows that $\lambda < 0$ for r greater than, but close to 1. \square

The effect of increased juvenile vs. adult competition on the positive total and adult reproductive levels P_e and A_e is clear from (3.2) and (3.3). Moreover from the formulas

$$J_e = P_e - A_e = V_e(r) \frac{\beta_A(0) - \mu_A}{\alpha(\beta_A(0) - \mu_A) + \mu_J}$$

$$J_e = P_e - A_e = W_e(r) \frac{r\beta_A - \mu_A}{r\beta_A - \mu_A + \gamma\mu_J(W_e)}$$

for the juvenile equilibrium levels in the two cases respectively, we obtain, with a reference to (2.5) and (2.7), the following result.

Theorem 3 *The unique, positive equilibrium levels for total population size P_e , adult population size A_e , and juvenile population size J_e , all decrease with increased competition coefficients α or γ . The relative proportions A_e/P_e and J_e/P_e , however, remain unaffected.*

Finally we consider the stability sensitivity of the positive equilibria guaranteed by Theorem 2 for r greater than, but close to 1. This we do by computing the change in the stability-determining eigenvalue λ near 0, or more specifically by determining the sign of the derivatives

$$\partial_\alpha \lambda = -\partial_\alpha p(\lambda; \alpha, r) / \partial_\lambda p(\lambda; \alpha, r)$$

$$\partial_\gamma \lambda = -\partial_\gamma q(\lambda; \gamma, r) / \partial_\lambda q(\lambda; \gamma, r)$$

for r greater than, but close to 1. By (3.6) these signs are the opposites of those of the derivatives $\partial_\alpha p(\lambda; \alpha, r)$, $\partial_\gamma q(\lambda; \gamma, r)$ for r greater than, but close to 1.

Theorem 4 *For r greater than, but close to 1, $\partial_\alpha \lambda > 0$ for (2.10) and $\partial_\gamma \lambda < 0$ for (2.11).*

Proof. Consider first (2.10) with the characteristic equation (3.4). It is not difficult to see that $\partial_\alpha p(0; \alpha, 1) = 0$ and therefore we must consider p for r close to but not equal to 1, i.e. for $\lambda < 0$, but close to 0. To determine the monotonicity of p in the variable α we need to determine that of the linear fractional expression in (3.4). Because $\beta'_A < 0$, this linear fractional expression and p have the same monotonicity, which is determined by the sign of the determinant-like expression $\Delta(\lambda) = a(\lambda)d - b(\lambda)c$ for $\lambda < 0$, but near 0. Since $\Delta(0) = 0$ and

$$\partial_\lambda \Delta(0) = \mu_J(1 - \exp(-\mu_J m)) + \mu_A(-1 + m\mu_J + \exp(-\mu_J m)) > 0$$

we find that $\Delta(\lambda) < 0$ for $\lambda < 0$, but near 0, and hence $r > 1$, but near 1. This implies that the linear fractional expression in p and hence p itself is decreasing in α , i.e. $\partial_\alpha p(\lambda; \alpha, r) < 0$, for $r > 1$ near 1.

A similar analysis must be carried out on q defined by (3.5) with respect to γ in order to determine the sign of $\partial_\gamma q(\lambda; \gamma, r)$ for $r > 1$, but near 1. The first term in q is independent of γ and the second term clearly increases as a function of γ . The monotonicity of the third term is the opposite of that of the linear fractional expression appearing there, which is determined by

$$\begin{aligned} \Delta(\lambda) &= a(\lambda, r)d(r) - b(\lambda, r)c(r) \\ &= \left(\frac{1}{m} \ln r + \mu_J - \mu_A(1 - r \exp(\mu_J m)) \right) \lambda + \mu_A(1 - r \exp(\mu_J m)) \frac{1}{m} \ln r. \end{aligned}$$

For $r > 1$, but near 1, and $\lambda < 0$, but near 0, we see that $\Delta(\lambda) < 0$ and hence the third term in q is also increasing in γ . \square

4 Concluding remarks

From the general model equations (2.1) for age-structured population dynamics, we derived the two model systems of differential delay equations (2.10) and (2.11) to describe the dynamics of a population whose intra-specific competition between juveniles and adults leads to juvenile density dependent adult fertility and adult density dependent juvenile survival respectively. Under the assumption that the density dependencies are monotonic functions of weighted total population sizes (and that within the juvenile and adult age classes survival and fertility rates are age independent), it is shown that these model equations possess a positive equilibria if and only if the inherent net reproductive rate r is greater than 1, that these positive equilibria are locally asymptotically stable at least for r near 1, and that all solutions tend to 0 if $r < 1$.

With regard to the stabilization/destabilization question we reached conclusions that in one case disagree and in another agree with those of Ebenman(1988). First of all, the effect on equilibrium levels of increased juvenile vs. adult competition is always adverse (Theorem 3) and in this sense such competition is always destabilizing, in agreement with May et al.(1974) and Tschumy(1982) and in disagreement with Ebenman. However, the effect of increased competition on the linearized eigenvalue leads us to the same conclusion as Ebenman, although for different reasons. Namely, Theorem 4 implies that increases in the strength of competition (as measured by the coefficient α) in the juvenile density dependent adult fertility problem is a destabilizing influence, while increases in the strength of competition (as measured by the coefficient γ) in the adult dependent juvenile survival problem is a stabilizing influence. Ebenman reached these same conclusions using stability region arguments, a procedure criticized by Loreau(1990). To further confuse matters, Ebenman's model predicts destabilization in both cases if linearized eigenvalue sensitivity is used as the criteria. This contradiction between the eigenvalue analysis of Ebenman's model and ours here can be explained by the fact that Ebenman's model is a 2×2 matrix model which is degenerate in the sense that it is not "primitive", i.e. does not have a strictly dominant linearized eigenvalue. (In fact, an unusual double bifurcation of both equilibria and 2-cycles occurs at $r = 1$ because both $+1$ and -1 are linearized eigenvalues; see Cushing and Li (1989).) This peculiarity is purely a mathematical artifact that occurs because Ebenman's discrete time and age matrix equation has exactly two age categories, only one of which is adult, and disallows adult survival after reproduction. The number of age categories and the time scale is arbitrary as far as the modeling is concerned and even a similar model that utilizes just two adult age classes eliminates this degeneracy with the result that an eigenvalue analysis is then in agreement with those in Theorem 4. Loreau's conclusion that stabilization is an unlikely result of juvenile vs. adult competition should perhaps be re-evaluated,

both in view of our result here and because his arguments are also based upon Ebenman's highly simplified model.

Aknowledgment

The author gratefully acknowledges the support of the Applied Mathematics Division and the Population/Ecology Division of the National Science Foundation under grant No. DMS-8902508.

References

1. Bellman, R., Cooke, K. (1963): *Differential-Difference Equations*. Academic Press, New York
2. Cushing, J.M. (1985): Equilibria in structured populations. *J. Math. Biology* **23**, 15-39
3. Cushing, J.M., Li, J.(1989): On Ebenman's model for the dynamics of a population with competing juveniles and adults. *Bull. Math. Biol.* **6**, 687-713
4. Cushing, J.M., Li, J.(1990): Juvenile vs. adult competition. To appear in *J. Math. Biol.*
5. Ebenman, B.(1987): Niche differences between age classes and intraspecific competition in age-structured populations. *J. Theor. Biol.* **124**, 25-33
6. Ebenman, B.(1988): Competition between age classes and population dynamics. *J. Theor. Biol.* **131**, 389-400
7. Ebenman, B., Persson, L.(1988): *Size-Structured Populations: Ecology and Evolution*. Springer-Verlag, Berlin-Heidelberg-New York
8. Gurtin, M.E., MacCamy, R.C.(1974): Nonlinear age-dependent population dynamics. *Arch. Rat. Mech. Anal.* **54**, 281-300
9. Hoppensteadt, F.C.(1975): *Mathematical Theories of Populations: Demographics, Genetics, and Epidemics*. Regional Conference Series in Applied Mathematics, **20**, SIAM, Philadelphia
10. Loreau, M.(1990): Competition between age classes, and the stability of stage-structured populations: a re-examination of Ebenman's model. *J. Theor. Biol.* **144**, 567-571
11. May, R.M., Conway, G.R., Hassell, M.P., Southwood, T.R.E. (1974): Time delays, density-dependence and single-species oscillations. *J. Animal Ecol.* **43**, 747-770
12. Metz, J.A.J., Diekmann, O.(1986): *The Dynamics of Physiologically Structured Populations*. *Lec. Notes in Biomath.* **68**, Springer-Verlag, Berlin-Heidelberg-New York
13. Tschumy, W. (1982): Competition between juveniles and adults in age-structured populations. *Theor. Pop. Biol.* **21**, 255-268
14. Werner, E., Gilliam, J.(1984): The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* **15**, 393-425