

Juvenile versus adult competition

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Abstract. A general class of age-structured models based upon the McKendrick/von Foerster equations are used to study intraspecific competition between juveniles and adults. Criteria for the existence and stability of equilibria are obtained and the dependence of equilibrium stability (i.e. equilibrium resilience) on competition coefficients is analyzed for low inherent net reproductive numbers. The results are applied to the question of whether juvenile vs. adult intraspecific competition is stabilizing or destabilizing. Two types of competition are studied. The first, involving suppressed adult fertility due to competition from juveniles, was found to be destabilizing in that equilibrium levels are lowered and equilibrium resilience weakened by increased competition. The second, involving increased juvenile mortality due to competition from adults, was found to be considerably more complicated. While equilibrium levels were again reduced by increased competition, equilibrium resilience can either be weakened or strengthened. A criterion for determining the effects on resilience is derived and several examples are given to illustrate various possibilities in this case.

Key words: Intraspecific competition – Age-structure – Stability – Resilience – Destabilization

1. Introduction

Biological populations generally consist of a wide diversity of age and size groups. It has become widely recognized that this diversity can have a significant influence upon dynamics at the population level and that in order to understand the dynamics of most populations it is necessary to take this diversity adequately

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into account (Werner and Gilliam 1984; Ebenman and Persson 1989; Metz and Diekmann 1986). Individuals of some species have complex life cycles during which they undergo radical changes in morphology, physiology, or behavior (e.g. holometabolous insects, amphibians, and many marine invertebrates). As they develop such individuals can dramatically alter the nature of their interactions with their physical and biological environments and consequently often significantly change their resource niches. One result of such ontogenetic niche shifts is that intraspecific competition between individuals is lessened, at least between individuals of different age or size classes. Other species, however, have simpler life cycles during which individuals undergo fewer changes and as a result the potential for intraspecific competition by differing age or size groups is increased, either exploitatively through the sharing of a common limiting resource or by direct interference. This is the case for most fishes, birds, mammals, many plants, and for hemimetabolous insects (Ebenman 1987, 1988).

One common type of intraspecific competition found in species with overlapping generations occurs between age and/or size classes and in particular between (younger or smaller) juveniles and (older or larger) adults. A question that arises is: what effects do strong competitive interactions between juveniles and adults have on the dynamics of the population? Specifically, do such interactions stabilize or destabilize the population and in what sense?

Mathematical models of competition have played a central role in theoretical population dynamics and ecology. The majority of these models have been formulated in terms of highly aggregated statistics such as total population size, biomass, dry weight, etc. and have ignored differences between individual organisms, in effect treating all individuals of a species as identical for all time. Such models cannot adequately account for mechanisms causing competition between individual organisms. This is particularly true for intraspecific competition, which in such models can be accounted for only in highly qualitative ways. Appropriate mathematical models can be built, however, using the modeling methodology of "structured" population dynamics (Metz and Diekmann 1986).

In recent years several theoretical studies of intraspecific competition and in particular of juvenile vs. adult competition have appeared in the literature (May et al. 1974; Tschumy 1982; Ebenman 1987, 1988; Ebenman and Persson 1988; Cushing and Li 1989; Loreau 1990). May et al. (1974) conclude that juvenile vs. adult competition has a destabilizing effect while Ebenman (1987, 1988) concludes that under certain circumstances (namely, when juvenile survival is more affected by population size than is adult fecundity) the competition can be stabilizing. These authors use simple discrete difference equation models and use the size of stability regions in certain parameter spaces as a criterion for destabilization. The pitfalls in using this (very model dependent) criterion are pointed out by Loreau (1990). Tschumy (1982), on the other hand, uses the sensitivity of linearized equilibrium eigenvalues to changes in competition coefficients as a criterion (also see Cushing and Li 1989 and Loreau 1990). Unfortunately, Tschumy's simplistic ordinary differential equation model is seriously flawed in that it mistakenly fails to take into account juvenile maturation (which not only changes the structure of his equations, but adds a time delay) and consequently throws his conclusion that juvenile vs. adult competition is always destabilizing into question. Moreover, these simple models that have been studied in the literature also make, either implicitly or explicitly, other stringent biological assumptions that raise further questions concerning the

robustness of the conclusions. For example, models of May et al. and Ebenman assume semelparity and no post-reproductive adult survival and no within class age dependence of vital parameters (as does Tschumy's model).

Thus, the credibility of the answers that have been offered to the stabilization/destabilization question with regard to juvenile vs. adult competition is plagued by the use of over simplistic or incorrect models, of different and often conflicting and questionable stabilization/destabilization criteria, and of model dependent phenomena and conclusions.

A rigorous modeling methodology for structured, and in particular of age-structured, population dynamics has been developed in recent years (see Sinko and Streifer 1967; Gurtin and MacCamy 1974; Metz and Diekmann 1986). Our purpose here is to study juvenile vs. adult competition by means of a very general class of models, based upon the so-called McKendrick/von Foerster equations, which is derived using this methodology. We will thereby gain a considerable amount of generality and robustness in our conclusions. Our focus will be on equilibrium stability. Following Tschumy (1982), Cushing and Li (1989), and Loreau (1990), we will consider the stabilization/destabilization question by means of the sensitivity of a population's "resilience" to model parameters that measure the strength of the competitive interactions. Resilience is measured by the magnitude of the negative real part of the stability determining linearized eigenvalue.

Existence and stability properties of equilibria of the McKendrick/von Foerster equations are known in a very general setting. Using bifurcation theoretic methods Cushing (1984, 1985) has proved the global existence of equilibria and has proved their stability, at least if the inherent net reproductive number (i.e. the expected number of offspring per adult per lifetime at low densities when competition effects are negligible, here denoted by r) is not too large. For large values of r equilibrium stability can be, but is not necessarily lost, usually through a Hopf-type bifurcation to periodic oscillations. Whether this occurs or not and for what value of r is extremely model dependent. In order to confine attention to a more robust analysis of equilibrium stability in a general setting, one must therefore assume that r is not "too large". In spite of the analytic difficulties associated with the McKendrick/von Foerster equations (which are nonlinear, hyperbolic integro-partial differential equations subject to a nonlinear boundary condition) it is possible to carry out a mathematical analysis of the dependence of equilibrium resilience on model competition parameters in a very general setting, at least for r close to the primary bifurcation value of 1.

The model equations are derived in Sect. 2. Following May et al. (1974) and Ebenman (1987, 1988) we will focus in Sect. 3 and Sect. 4, respectively, on two types of juvenile vs. adult competition: suppressed adult fertility caused by competition from juveniles and decreased juvenile survival caused by competition from adults. The exact form of the dependence of mortality and fertility on population size will be otherwise left as general as possible. Our conclusions are summarized in Sect. 5. Proofs appear in the Appendix.

2. The model equations

We will utilize the McKendrick/von Foerster equations for the density $g(t, a)$ of an age-structured population (see Sinko and Streifer 1967; Gurtin and MacCamy

1974; Metz and Diekmann 1986)

$$\begin{aligned} \frac{\partial \varrho}{\partial t} + \frac{\partial \varrho}{\partial a} + \mu \varrho &= 0 \\ \varrho(t, 0) &= \int_0^\infty \phi \varrho \, da. \end{aligned} \tag{2.1}$$

Here t is time and $a \geq 0$ is age so that the integral $\int_{a_2}^{a_1} \varrho(t, a) \, da$ gives the number of individuals between ages a_1 and a_2 at time t . The mortality and fertility rates $\mu \geq 0$ and $\phi \geq 0$ are assumed to be age specific and dependent on population size, i.e. μ and ϕ will be non-negative functions of age a and certain weighted population sizes (not necessarily the same one) of the form $\int_0^\infty w(a)\varrho(t, a) \, da$.

Since we are interested in two distinct classes of individuals, namely non-reproducing juveniles and fertile adults, we distinguish a maximal juvenile age (or a maturation age) $a_j > 0$ before which an individual is infertile. Thus ϕ vanishes for $a < a_j$. In this paper we will not explicitly model the nature of the competitive interaction between juveniles and adults. Instead we will consider the general case when μ and ϕ are general functions of juvenile and adult (weighted) population sizes, the only proviso being that as these population levels increase, their effect is to increase mortality and decrease fertility.

Specifically, let $\alpha > 0$ measure (as in Ebenman 1987, 1988) the relative depressive effect on adult fertility due to an individual juvenile compared to an individual adult, and let $\gamma > 0$ measure the relative depressive effect on juvenile mortality due to an individual adult compared to an individual juvenile. We then assume that the fertility rate ϕ is a non-increasing function of the weighted population size $\alpha J(t) + A(t)$ while the mortality rate μ is an non-decreasing function of the weighted population size $J(t) + \gamma A(t)$ where

$$J(t) = \int_0^{a_j} w_1(a)\varrho(t, a) \, da, \quad A(t) = \int_{a_j}^\infty w_2(a)\varrho(t, a) \, da \tag{2.2}$$

are weighted juvenile and adult population sizes respectively (here $w_i(a) \geq 0$). If both weight functions $w_i(a) \equiv 1$ then J and A reduce to total population numbers of juveniles and adults respectively. With more general weight functions we allow for the modeling of a greater diversity of age-specific effects (or size-specific effects, if size correlates closely to age) by permitting the population density different aged (or sized) juveniles and adults to have different effects on mortality and fertility.

Accordingly we take

$$\phi = \phi(a, \alpha J + A) \geq 0, \quad \mu = \mu(a, J + \gamma A) \geq 0$$

in Eqs. (2.1) where J and A are given by (2.2) and where $\mu(a, W)$ and $\phi(a, W)$ are non-negative, real valued functions of $a \geq 0$ and $W \geq 0$ that satisfy

$$\mu_W(a, W) \geq 0, \quad \phi_W(a, W) \leq 0, \quad \phi(a, W) = 0 \quad \text{for } 0 \leq a < a_j.$$

(Note: $\mu_W = \partial\mu/\partial W$, etc.) Under these assumptions, an increase in α means that the effect that juvenile population size has on adult fertility is increased, while an increase in γ means that the effect that adult population size has on juvenile survival is increased.

Finally, we introduce the inherent net reproductive number r into the model by normalizing ϕ , i.e. we write $\phi(a, W) = r\beta(a, W)$ where β has the same

properties as ϕ in addition to satisfying the normalization

$$\int_{a_j}^{\infty} \beta(a, 0)\Pi(a, 0) da = 1, \tag{2.3}$$

where

$$\Pi(a, x) = \exp\left(-\int_0^a \mu(s, x) ds\right)$$

is the probability of living to age a when the weighted population size is held at level x . With this normalization, r is the expected number of offspring per lifetime per adult at low population levels (technically at $W=0$ or zero population level); see Cushing (1985).

In summary the models to be considered have the form

$$\frac{\partial \varrho}{\partial t}(t, a) + \frac{\partial \varrho}{\partial a}(t, a) + \mu(a, J(t) + \gamma A(t))\varrho(t, a) = 0 \tag{2.4}$$

$$\varrho(t, 0) = r \int_{a_j}^{\infty} \beta(a, \alpha J(t) + A(t))\varrho(t, a) da, \tag{2.5}$$

where the birth rate β satisfies

$$\beta_w(a, W) \leq 0 \text{ for } a_j \leq a \text{ and } \beta(a, W) \equiv 0 \text{ for } 0 \leq a < a_j \tag{2.6}$$

and, because we are interested in the case when only juvenile survival is adversely affected by population size, where the death rate μ satisfies

$$\mu_w(a, W) \equiv 0 \text{ for } a \geq a_j \text{ and } \mu_w(a, W) \geq 0 \text{ for } 0 \leq a < a_j, \tag{2.7}$$

where the normalization (2.3) holds, where $\alpha \geq 0$, $\gamma \geq 0$, and where J and A are weighted juvenile and adult population sizes given by (2.2).

We are interested in equilibrium solutions of these equations and in the dependence of equilibrium resilience upon the competitive coefficients α and γ .

With regard to the existence of equilibria the results of Cushing (1985) imply that there is an unbounded continuum of positive equilibria pairs (r, ϱ) of (2.4)–(2.5) which bifurcates from the trivial equilibrium pair $(r, \varrho) = (1, 0)$. Also if

$$\text{either } \mu_w(a, 0) \neq 0 \text{ or } \beta_w(a, 0) \neq 0, \tag{2.8}$$

on an age interval of positive measure (i.e. if the effects of population size are definitely present at least in some age categories), then the equilibrium bifurcation is “supercritical” and hence locally stable. That is to say, there exist stable positive equilibria for r greater than, but near 1. Moreover, there exist no positive equilibria for $r < 1$ in which case $\varrho \equiv 0$ is stable. For the two distinct cases considered in Sects. 3 and 4, explicit formulas for the equilibria will be found and stability properties will be studied for r greater than, but near the critical value 1.

3. Juvenile competitive effects on adult fertility

Consider the case when juvenile vs. adult competition is only by means of juvenile depression of adult fertility. That is, assume that μ and β satisfy the

conditions in (2.6)–(2.8), but that μ is independent of population size

$$\mu = \mu(a), \quad \beta = \beta(a, \alpha J + A) \tag{3.1}$$

with $0 \leq w_1(a) \neq 0$. This model involves only the weighted population size $W = \alpha J + A$. The resulting partial differential equation (2.4) is linear and has equilibrium solutions

$$\varrho_e(a) = \varrho_e(0)\Pi(a)$$

$$\Pi(a) = \Pi(a, 0) = \exp\left(-\int_0^a \mu(s) ds\right),$$

which when substituted into the birth equation (2.5) yields the equation

$$rf(W_e) = 1 \tag{3.2}$$

for the equilibrium weighted population size W_e where

$$f(x) = \int_{a_j}^\infty \beta(a, x)\Pi(a) da.$$

The assumptions on β imply that $f(0) = 1, f'(0) < 0$ so that, at least for r greater than but close to 1, we have

$$W_e = f^{-1}(1/r). \tag{3.3}$$

However

$$W_e = \alpha J_e + A_e = \varrho_e(0)\left(\alpha \int_0^{a_j} w_1 \Pi da + \int_{a_j}^\infty w_2 \Pi da\right),$$

which leads to the equilibrium solutions

$$\varrho_e(a) = f^{-1}(1/r)\Pi(a)\left(\alpha \int_0^{a_j} w_1 \Pi da + \int_{a_j}^\infty w_2 \Pi da\right)^{-1} \tag{3.4}$$

valid at least for r greater than, but close to 1.

In order to study the resilience of the equilibrium ϱ_e as a function of the competition coefficient α we need to ascertain the dependence on α of the stability determining eigenvalue λ of the linearization of (2.4)–(2.5) at ϱ_e . λ vanishes for $r = 1$ and is known to be real and negative for r greater than, but close to 1 (Cushing 1984). Specifically we wish to determine the sign of the derivative $\partial\lambda/\partial\alpha$. The eigenvalue λ satisfies a characteristic equation associated with the linearized equations which can be obtained from the general formulas developed by Cushing (1984, 1985) or, in the case being considered here, by a straightforward linearization procedure as described in the Appendix; see (A.1). The following theorem is proved in the Appendix.

Theorem 1. *In addition to (2.6)–(2.8), assume that μ and β satisfy (3.1). For r greater than, but close to 1*

$$(a) \quad \frac{\partial\lambda}{\partial\alpha} > 0 \tag{3.5}$$

$$(b) \quad \frac{\partial}{\partial\alpha} \varrho_e(a) < 0 \quad \text{and} \quad \frac{\partial}{\partial\alpha} \left(\frac{\varrho_e(a)}{P}\right) \equiv 0 \quad \text{for all } a \geq 0, \tag{3.6}$$

where $P = \int_0^\infty \varrho_e(a) da$ is the total population size at equilibrium.

This theorem implies that equilibrium resilience is decreased by an increase in the intra-specific competition coefficient α . Moreover, equilibrium levels of all age classes are also decreased (although the proportion of any age class within the total population remains unaffected). Thus, for this case when adult fertility is adversely affected by competition from juveniles, our model implies that this kind of juvenile vs. adult competition is a destabilizing influence, in agreement with the conclusion reached by Ebenman (1987, 1988).

4. Adult competitive effects on juvenile survival

In this section we consider the case complementary to that studied in Sect. 3, namely, the case when the death rate μ is dependent on population size while the fertility rate β is not. Thus we write

$$\mu = \mu(a, J + \gamma A), \quad \beta = \beta(a), \tag{4.1}$$

where $0 \leq w_2(a) \neq 0$ and where (2.6)–(2.8) are satisfied.

The equilibrium equation associated with the nonlinear partial differential equation (2.4) can be equivalently written

$$\varrho_e(a) = \varrho_e(0)\Pi(a, W_e),$$

where W_e is the equilibrium weighted population size $J + \gamma A$. Substitution of this expression for ϱ_e into the birth equation (2.5) yields again an equation of the form (3.2) for W_e where in this case

$$f(x) = \int_{a_j}^{\infty} \beta(a)\Pi(a, x) da.$$

The assumptions on μ imply that $f(0) = 1, f'(0) < 0$ so that at least for r greater than but close to 1 there exists a positive solution of (3.2) given by (3.3). This leads to the equilibrium solution for this case given by

$$\varrho_e(a) = W_e \Pi(a, W_e) \left(\int_0^{a_j} w_1(a)\Pi(a, W_e) da + \gamma \int_{a_j}^{\infty} w_2(a)\Pi(a, W_e) da \right)^{-1}$$

$$W_e = f^{-1}(1/r), \tag{4.2}$$

which is valid at least for r greater than, but close to 1.

The linearized stability analysis of the equilibrium (4.2) is more complicated in this case and the result is not as clear cut as that in Theorem 1. The following theorem is proved in the Appendix. Define the quantity

$$\Delta = \int_{a=0}^{a_j} \int_{s=a_j}^{\infty} w_1(a)w_2(s)\Pi(a, 0)\Pi(s, 0)K(a, s) ds da, \tag{4.3}$$

where the kernel K is given by

$$K(a, s) = \int_{t=a_j}^{\infty} \beta(t)\Pi(t, 0)t dt \int_{t=a}^{a_j} \mu_w(t, 0) dt - (s - a) \int_{t=0}^{a_j} \mu_w(t, 0) dt.$$

Theorem 2. *In addition to (2.6)–(2.8), assume that μ and β satisfy (4.1). Assume also that $\Delta \neq 0$. For r greater than, but close to 1, (3.6) holds and the sign of the derivative $\partial\lambda/\partial\gamma$ is the same as that of Δ .*

In the case when adult fertility depends on juvenile population size considered in Sect. 3 only *decreased* equilibrium resilience resulted from the competition. The situation with regard to equilibrium resilience in the opposing case when juvenile survival depends on adult population size being considered in this section, however, is not so simple. Both decreased ($\partial\lambda/\partial\gamma > 0$) or increased ($\partial\lambda/\partial\gamma < 0$) equilibrium resilience are possibilities in this case, depending upon the sign of the quantity Δ . Note that the kernel K is not of one sign over the specified variable ranges and consequently Δ has no obvious sign. The following examples illustrate that Δ can in fact be either positive or negative and provide, hopefully, some insights into this more complicated case. All conclusions in these examples are for r greater than, but close to 1. The implications of these examples will be discussed in Sect. 5.

Example 1 (concentrated fertility window). Consider a birth-pulse semelparous population which reproduces only once and does so at the age $a = a_j$. Assume also that the effects of adult population size on juvenile mortality are independent of juvenile age (at least at low population levels). To model this situation we take

$$\beta(a) = \beta_0\delta(a - a_j), \quad \mu_w(a, 0) \equiv \mu_w^0, \tag{4.4}$$

where δ is the Dirac function concentrated at 0 and β_0, μ_w^0 are positive constants. The normalization (2.3) in fact requires that $\beta_0 = 1/\Pi(a_j, 0)$. Since $K(a, s) = a_j(a_j - s)\mu_w^0 < 0$ for $s > a_j$ we find that $\Delta < 0$.

It follows from Theorem 2 that equilibrium resilience is *increased* by competition in this case.

Example 2 (age independent fertility over a finite age interval with no post-reproductive survival). We consider next an example that constitutes one possible continuous analog of the discrete model of Ebenman (1988). It is assumed that an individual becomes fertile upon reaching age $a_j > 0$ after which it remains fertile until its death at, or before, a maximum age $a_m > a_j$. Thus there is no post-reproductive adult survival following an age interval of reproduction. It is further assumed that during this reproductive period fertility is independent of age. Finally, it is assumed, as in Example 1, that effects of adult population size on juvenile survivability are independent of juvenile age. To simulate this set of circumstances we take

$$\beta = \begin{cases} \beta_0 & \text{for } a_j \leq a \leq a_m \\ 0 & \text{otherwise} \end{cases} \quad \mu = \begin{cases} \mu_j(W) & \text{for } 0 \leq a \leq a_j \\ (a_m - a)^{-1} & \text{for } a_j < a < a_m \end{cases}, \tag{4.5}$$

where $\mu'_j(0) > 0$. We also choose the weights $w_i(a) \equiv 1$, so that J and A represent total juvenile and adult population sizes, and we assume that inherent juvenile mortality is relatively insignificant, so that $\mu_j(0) = 0$. Under these conditions (as well as the normalization (2.3), which implies that $\beta_0 = 2/(a_m - a_j)$), we find that $\Delta = -a_j^2(a_m - a_j)^2\mu'_j(0)/12 < 0$.

As a result we draw the same conclusion for this case as we did for the case in Example 1, namely that equilibrium resilience is increased by competition.

Example 3 (post-reproductive survival). If in Example 2 we wish to allow for adult survival after fertility then we can replace β in (4.5) by

$$\beta = \begin{cases} \beta_0 & \text{for } a_j \leq a \leq a'_j \\ 0 & \text{otherwise} \end{cases},$$

where the maximal age of fertility a'_j satisfies $a_j < a'_j < a_m$. A straightforward, but rather tedious calculation now yields

$$\Delta = \frac{\mu'_j(0)a_j^2(a_m - a_j)(a' - a_j)}{12((a_m - a_j)^2 - (a_m - a'_j)^2)} Q(a_m),$$

where the quadratic $Q(a_m) = -4a_m^2 + (5a'_j + 3a_j)a_m + (a_j^2 + a'_ja_j + 2a_j'^2)$ is easily shown to be negative for $a_m \geq a'_j$.

Thus post-reproductive survival does not change the conclusions drawn in Examples 1 and 2.

In these three examples juvenile survivability is independent of age and adults are “semelparous” (in the sense that reproduction occurs over a continuous, uninterrupted age window). In all cases the common conclusion was reached that the competitive effects of adults on juvenile survival increase equilibrium resilience. This is in agreement with the conclusion of Ebenman (1987, 1988). If this assumption is modified, however, (the case of iteroparity would be a case in point) this conclusion can be reversed. The next three examples illustrate this point.

Example 4 (iteroparity). Consider the following modification of Example 1 which includes two pulses of reproductive activity at different ages a_j and $a'_j > a_j$. In place of (4.4) we assume

$$\beta(a) = \beta_0\delta(a - a_j) + \beta'_0\delta(a - a'_j), \quad \mu_w(a, 0) \equiv \mu_w^0,$$

where the coefficients β_0 and β'_0 must satisfy the normalization

$$\beta_0\Pi(a_j, 0) + \beta'_0\Pi(a'_j, 0) = 1.$$

Then it turns out that

$$\Delta = (a_j + (a'_j - a_j)(1 - \beta_0\Pi(a_j, 0)))I_1 - I_2,$$

where the integrals

$$I_1 = \mu_w^0 \int_{a=0}^{a_j} \int_{s=a_j}^{\infty} w_1(a)w_2(s)\Pi(a, 0)\Pi(s, 0)(a_j - a) ds da$$

$$I_2 = a_j\mu_w^0 \int_{a=0}^{a_j} \int_{s=a_j}^{\infty} w_1(a)w_2(s)\Pi(a, 0)\Pi(s, 0)(s - a) ds da$$

are positive. Thus Δ is positive for a'_j large. On the other hand, for $a'_j = a_j$ this model reduces to the one in Example 1 for which $\Delta < 0$. Hence for a'_j sufficiently close to a_j , Δ is negative.

In this example we see that if the adult population is iteroparous, possessing two distinct reproductive ages which are spaced sufficiently far apart, then the effect of increased competition is to decrease equilibrium resilience. On the other hand, if the two ages of reproduction do not differ greatly, then the effect is to increase equilibrium resilience.

Example 5 (age dependent juvenile survival). This example is a modification of Example 2. We assume, as in Example 2, that adult fertility is age independent over a finite reproductive window as described by β in (4.5). The effects of adult competition on juvenile survival, however, will be assumed not to be juvenile age independent as in (4.5), but instead will be assumed to fall more heavily either on young juveniles or older juveniles. The death rate in (4.5) is accordingly

replaced by

$$\mu = \begin{cases} \zeta(a)\mu_j(W) & \text{for } 0 \leq a \leq a_j \\ (a_m - a)^{-1} & \text{for } a_j < a < a_m \end{cases}$$

As in Example 2, $\mu_j(0) = 0$ and $\mu'_j(0) > 0$. The function $\zeta(a)$ determines the age-specific effects of adult population size on juvenile survival. We will consider two extreme cases: when these effects fall only upon young juveniles and when they fall only upon older juveniles.

Suppose all adult population size effects are concentrated on juveniles of age $a^* < a_j$ so that $\zeta(a) = \delta(t - a^*)$. Then

$$\begin{aligned} \Delta &= \frac{\mu_W(0)}{a_m - a_j} \int_{a=0}^{a^*} \int_{s=a_j}^{a_m} (a_m - s) \left[\frac{1}{3} (a_m + 2a_j) - (s - a) \right] ds da \\ &\quad - \frac{1}{a_m - a_j} \int_{a=a^*}^{a_j} \int_{s=a_j}^{a_m} (a_m - s)(s - a) ds da. \end{aligned}$$

Since $\Delta \rightarrow -a_j(2a_m + a_j)(a_m - a_j)/12 < 0$ as $a^* \rightarrow 0$, it follows that $\Delta < 0$ for a^* sufficiently small.

On the other hand, $\Delta \rightarrow a_j^2(a_m - a_j)/4 > 0$ as $a^* \rightarrow a_j$ and hence $\Delta > 0$ for a^* sufficiently close to the maximal juvenile age a_j .

Thus, the effects of adult vs. juvenile competition in this case again increase equilibrium resilience provided the effects that adult population size has on juvenile survival fall only on very young juveniles. However, these effects decrease equilibrium resilience if they fall only on older juveniles.

Example 6 (adult age specific density effects on juvenile survival). As a final example we consider a case when the effects of adult competition on juvenile survival are not adult independent. We do this by returning to Example 2 and allowing for the possibility that different aged adults have different effects on juvenile survival. Specifically, we assume that only adults between the two ages $a_j + \delta_1$ and $a_j + \delta_2$ (where $0 \leq \delta_1 < \delta_2 \leq a_m - a_j$) affect juvenile survival which we do by taking

$$w_2(a) = \begin{cases} 1 & \text{for } a_j + \delta_1 \leq a \leq a_j + \delta_2 \\ 0 & \text{otherwise} \end{cases}$$

with $w_1(a) \equiv 1$. μ and β are as in Example 2. The calculation of Δ is tedious, but straightforward. The result is simplified by defining the fractions $\sigma_1 = \delta_1/(a_m - a_j)$, $0 \leq \sigma_1 < \sigma_2 \leq 1$. Then

$$\Delta = \frac{1}{12} a_j^2 \mu'_j(0) (a_m - a_j)^2 (\sigma_2 - \sigma_1) q(\sigma_1, \sigma_2),$$

the sign of which depends upon the sign of the quadratic expression

$$q(\sigma_1, \sigma_2) = 2 - 7(\sigma_1 + \sigma_2) + 4(\sigma_1^2 + \sigma_1\sigma_2 + \sigma_2^2).$$

Within the required range $0 \leq \sigma_1 < \sigma_2 \leq 1$, q can be either positive or negative. It is easy to show, however, that in order for q to be positive both σ_1 and σ_2 must be sufficiently small; see Fig. 1.

We conclude that in this case when juvenile survival is adult population size dependent increased competition results in increased resilience, except when the

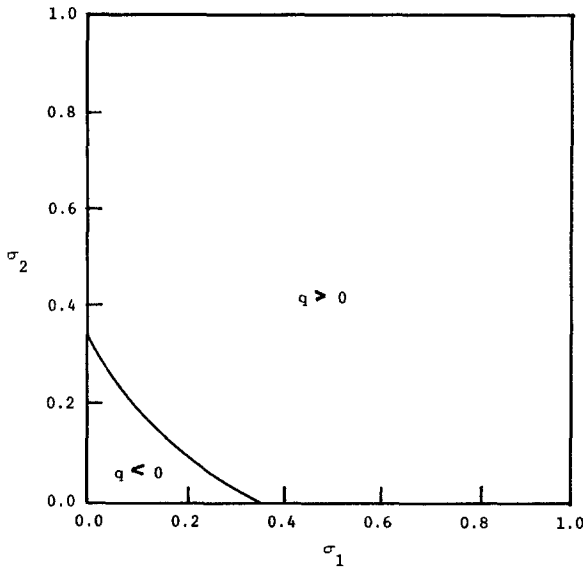


Fig. 1. The regions in the unit square of the (σ_1, σ_2) -plane are shown in which the quadratic q and hence the quantity Δ are positive and negative. The small region in the lower left hand corner where both are negative corresponds to juvenile survival being affected by only young adults, in which case the competition decreases equilibrium resilience. In the remainder of the square, equilibrium resilience is increased

competition is exclusively from younger adults in which case the competition decreases resilience.

5. Concluding remarks

We have considered a general class of model equations describing the dynamics of a population in which there is intraspecific competition between individuals of the population. The focus was on competition between juveniles and fertile adults and how this affects equilibrium resilience, which in order to obtain generality and robustness in our conclusions requires that the inherent net reproductive number not be large. The competition between adults and juveniles was expressed through one of two ways: either the competitive effects of juveniles on adults reduces adult fertility or the competitive effects of adults on juveniles reduces juvenile survivability to maturation. In this paper these two interactions were decoupled and studied separately. Our results are summarized in Theorems 1 and 2 where first of all it is seen that in both cases increased juvenile vs. adult competition results in a decrease in the equilibrium densities in all age classes (although proportional age class densities are unaffected). Moreover, equilibrium resilience is also decreased in the case of reduced fecundity due to increased competition from juveniles. This destabilization result is in agreement with virtually all other authors (May et al. 1974; Tschumy 1984; Ebenman 1987, 1988; Cushing and Li 1989; Loreau 1990).

We found the case when juvenile survivability is adversely affected by adult competition to be more complicated, however (cf. Theorem 2). In this case the effect on equilibrium resilience of increased adult competition depends upon the sign of Δ defined by (4.3). This quantity, which appears to have no simple biological interpretation, depends not only on the nature of dependence of the juvenile death rate on population size, but crucially on the age-specific properties of the vital birth and death rates. This can be seen from the examples following Theorem 2.

In the first three examples in which the effects of population size are independent of juvenile age and the population possesses either a single birth-pulse or continuous birth-flow over a fertility age interval in which birth rates are otherwise age independent, it was found that increased competition had the effect of increasing equilibrium resilience. This stabilization result is in agreement with Ebenman (1987, 1988), but it is based on an entirely different argument, since Ebenman's conclusion is based upon a stability region argument and not equilibrium resilience (see the criticism of Loreau 1990). In fact, Ebenman's simple discrete matrix model implies that equilibrium resilience is decreased in this case, in opposition to our result here (see Cushing and Li 1989; Loreau 1990). The explanation of this discrepancy lies in a mathematical artificiality due to the simplicity of Ebenman's model. This model has the peculiar property that at the primary bifurcation point $r = 1$ there occurs a "non-generic" double bifurcation due to the fact that an eigenvalue leaves the unit circle at -1 as well as $+1$ (cf. Cushing and Li 1989). This lack of "primitivity" of the matrix model is a purely mathematical artifact of having chosen only two discrete age classes, one of which is non-reproducing; it disappears if a finer discretation is taken so that at least two adjacent discretized age intervals are fertile. Then it can be shown that the matrix model also implies increased resilience, in argument with our (more robust) result here.

Example 4 addresses a point raised by Ebenman (1988) in criticism of his own model, namely that it assumes semelparity. For populations possessing two pulses of reproduction at two different ages we found that the competitive effects on equilibrium resilience depends crucially on the length of the time between the reproductive ages. If this length is small, then the effect is stabilizing while it is destabilizing if the length is sufficiently large. Thus, in answer to Ebenman's question concerning the robustness of his conclusions when applied to iteroparous populations, we find that the effect that juvenile vs. adult competition has on equilibrium resilience depends heavily on the reproductive schedule of the adults.

Examples 5 and 6 further illustrate the complexity introduced by the age dependence of the competitive effects on juvenile survival. Juveniles may differ considerably in their vulnerability to competition and adults may vary considerably in their competitive interactions with juveniles. For example, competitive vulnerability very often correlates strongly with body size, which for many species correlates in turn with age (Werner and Gilliam 1984; Ebenman and Persson 1988). If the survivability of the youngest rather than the oldest juveniles is more strongly adversely affected by competition, the result in Example 5 indicates that increased competition would have a stabilizing effect. On the other hand, there is a destabilizing effect if it is the oldest juveniles who are more adversely affected. Example 6 shows that the age of the adults can also be a determining factor. Adults of all age classes may not have the same competitive interaction and effect on juvenile survivability as might be the case, for example, if adults may vary considerably in size or in resource consumption rates at different ages. The result in Example 6 indicates that unless competition is felt only from a narrow age range of the youngest adults, increased competition again increases equilibrium resilience.

In summary, these examples seem to indicate roughly that this kind of intraspecific competition, when juvenile survival is adversely affected by competition with adults, generally increases equilibrium resilience unless the juvenile death rate has a significant within-class age dependence, in which case it is possible that resilience is decreased.

Our conclusions were derived from the analysis of the stability determining eigenvalue for inherent net reproductive numbers r near the critical value 1 and may not be valid for larger values of r . Indeed, stable equilibria may not even exist for large r , in which case equilibrium resilience is irrelevant. For example, the results of Cushing and Li (1989) show that this is indeed the case for Ebenman's discrete, two age class model. This issue is very model dependent. However, despite this parameter range restriction, Ebenman (1988) cites biological evidence that roughly supports the two basic conclusions reached here: namely, that when adult fertility is adversely affected by population size equilibrium resilience is weakened as competition from juveniles is increased and that when juvenile survival is adversely affected by population size equilibrium resilience can increase as competition from adults is increased. Loreau (1990) criticizes Ebenman's conclusion of the possibility of stabilization and the cited biological evidence. While Loreau's points of criticism of Ebenman's conclusions are well taken, his own conclusions that stabilization is not biologically feasible and that increased equilibrium resilience is theoretically not possible, which are also based upon Ebenman's model, might need re-evaluation in view of the over-simplicity of that model.

Appendix

Proof of Theorem 1. Setting $y = \varrho - \varrho_e$ in Eqs. (2.4)–(2.5) and ignoring terms of order higher than linear in y , we obtain the linearized equations

$$\begin{aligned} \frac{\partial y}{\partial t}(t, a) + \frac{\partial y}{\partial a}(t, a) + \mu(a)y(t, a) &= 0 \\ y(t, 0) &= r \int_{a_j}^{\infty} \beta(a, W_e)y(t, a) da + r \int_{a_j}^{\infty} \beta_w(a, W_e)\varrho_e(a) da Y(t) \\ Y(t) &= \alpha \int_0^{a_j} w_1(a)y(t, a) da + \int_{a_j}^{\infty} w_2(a)y(t, a) da, \end{aligned}$$

into which we substitute $y = \psi(a) \exp(\lambda t)$ to obtain the equations

$$\begin{aligned} \psi'(a) + (\lambda + \mu(a))\psi(a) &= 0 \\ \psi(0) &= r \int_{a_j}^{\infty} \beta(a, W_e)\psi(a) da + r \int_{a_j}^{\infty} \beta_w(a, W_e)\varrho_e(a) da \Psi \\ \Psi &= \alpha \int_0^{a_j} w_1(a)\psi(a) da + \int_{a_j}^{\infty} w_2(a)\psi(a) da, \end{aligned}$$

of which we want a nontrivial solution $\psi \neq 0$. Solving the first equation for $\psi = \exp(-\lambda a)\Pi(a)$ and placing this expression into the latter two equations we obtain the characteristic equation

$$c(\lambda, \alpha) = 0 \tag{A.1}$$

for λ where

$$c(\lambda, \alpha) = 1 - r \int_{a_j}^{\infty} \beta_w(a, W_e) \varrho_e(a) da \left(\alpha \int_0^{a_j} w_1(a) e^{-\lambda a} \Pi(a) da + \int_{a_j}^{\infty} w_2(a) e^{-\lambda a} \Pi(a) da \right) - r \int_{a_j}^{\infty} \beta(a, W_e) \Pi(a) e^{-\lambda a} da.$$

(Note: $\beta_w = \partial\beta/\partial W$.) In order to see more explicitly the appearance of α in (A.1) we substitute (3.4) for ϱ_e to obtain

$$c(\lambda, \alpha) = 1 - rf^{-1}(1/r) \int_{a_j}^{\infty} \beta_w(a, W_e) \Pi(a) da \frac{I_1(\lambda)\alpha + I_2(\lambda)}{I_1(0)\alpha + I_2(0)} - r \int_{a_j}^{\infty} \beta(a, W_e) \Pi(a) e^{-\lambda a} da,$$

where

$$I_1(\lambda) = \int_0^{a_j} w_1(a) e^{-\lambda a} \Pi(a) da, \quad I_2(\lambda) = \int_{a_j}^{\infty} w_2(a) e^{-\lambda a} \Pi(a) da.$$

By an implicit differentiation of the characteristic equation (A.1) and using

$$\frac{\partial c}{\partial \lambda}(\lambda, \alpha) \Big|_{r=1} = \int_{a_j}^{\infty} \beta(a, 0) \Pi(a) a da > 0, \tag{A.2}$$

we find that

$$\frac{\partial \lambda}{\partial r} \Big|_{r=1} = - \left(\int_{a_j}^{\infty} \beta(a, 0) \Pi(a) a da \right)^{-1} < 0.$$

(This is consistent with the general exchange of stability result of Cushing (1984) since the conditions (2.6)–(2.8) insure a transcritical bifurcation.) The linear fractional expression appearing in $c(\lambda, \alpha)$ is decreasing in α if and only if $D = I_1(\lambda)I_2(0) - I_1(0)I_2(\lambda) < 0$, which in fact is the case for r greater than, but near 1, since in this case $\lambda < 0$ and

$$D = \int_{a=0}^{a_j} \int_{s=a_j}^{\infty} w_1(a)w_2(s)\Pi(a)\Pi(s)(e^{-\lambda a} - e^{-\lambda s}) ds da.$$

By the assumptions on β it follows that $\partial c/\partial \alpha < 0$, from (A.2) that $\partial c/\partial \lambda > 0$, and from (A.1) that $\partial \lambda/\partial \alpha = -(\partial c/\partial \alpha)/(\partial c/\partial \lambda) > 0$ for r greater than, but near 1. This proves (3.5). The remaining inequalities (3.6) follow easily from (3.4).

Proof of Theorem 2. That (3.6) holds is easily seen from (4.2). Applying procedures similar to those used in the preceding proof of Theorem 1 to the

linearization

$$\frac{\partial y}{\partial t}(t, a) + \frac{\partial y}{\partial a}(t, a) + \mu(a, W_e)y(t, a) + \varrho_e(a)\mu_w(a, W_e)Y(t) = 0$$

$$y(t, 0) = r \int_{a_j}^{\infty} \beta(a)y(t, a) da$$

$$Y(t) = \int_0^{a_j} w_1(a)y(t, a) da + \gamma \int_{a_j}^{\infty} w_2(a)y(t, a) da$$

of (2.4)–(2.5), we obtain the equations

$$\psi'(a) + (\lambda + \mu(a, W_e))\psi(a) + \varrho_e(a)\mu_w(a, W_e)\Psi = 0$$

$$\psi(0) = r \int_{a_j}^{\infty} \beta(a)\psi(a) da$$

$$\Psi = \int_0^{a_j} w_1(a)\psi(a) da + \gamma \int_{a_j}^{\infty} w_2(a)\psi(a) da$$

for the solution $y(t, a) = \psi(a) \exp(\lambda t)$. The first equation is equivalent to

$$\psi(a) = e^{-\lambda a} \Pi(a, W_e) \left(\psi(0) - \Psi \int_{s=0}^a \varrho_e(s)\mu_w(s, W_e) e^{\lambda s} / \Pi(s, W_e) ds \right),$$

which when substituted into the latter two equations yields a linear homogeneous system of equations for the pair $\psi(0)$, Ψ of which we require a nontrivial solution. Setting the determinant of this system to zero, we obtain the characteristic equation

$$c(\lambda, \gamma) = 0, \tag{A.3}$$

where in this case

$$\begin{aligned} c(\lambda, \gamma) = & W_e \left(1 - r \int_{a_j}^{\infty} \beta e^{-\lambda a} \Pi da \right) \left(1 + \int_{a=0}^{\infty} w e^{-\lambda a} \Pi \int_{s=0}^a \varrho_e \mu_w e^{\lambda s} / \Pi ds da \right) \\ & + r \int_0^{a_j} w e^{-\lambda a} \Pi da \int_{a=a_j}^{\infty} \beta e^{-\lambda a} \Pi \int_{s=0}^a \varrho_e \mu_w e^{\lambda s} / \Pi ds da. \end{aligned}$$

Here $\beta = \beta(a)$, $\Pi = \Pi(a, W_e)$, $\varrho = \varrho_e(a)$, and $\mu_w = \mu_w(s, W_e)$ where ϱ_e and W_e are given by (4.2) and where $w = w(a)$ is defined (for notational simplicity) by

$$w(a) = \begin{cases} w_1(a) & \text{for } 0 \leq a < a_j \\ \gamma w_2(a) & \text{for } a_j \leq a \end{cases}.$$

Thus, for example, $W = J + \gamma A = \int_0^{\infty} w(a)\varrho(t, a) da$.

From an implicit differentiation of the characteristic equation (A.3) follows

$$\left. \frac{\partial \lambda}{\partial r} \right|_{r=1} = - \left(\int_{a_j}^{\infty} \beta(a) \Pi(a, 0) a \, da \right)^{-1} < 0.$$

(Once again this result is consistent with the general result of Cushing (1984) that, according to the exchange of stability principle, the positive equilibria (4.2) are stable for r greater than, but close to 1.)

We are interested in computing the sign of $\partial \lambda / \partial \alpha = -(\partial c / \partial \alpha) / (\partial c / \partial \lambda)$ for r greater than, but close to 1. At $r = 1$ where $\lambda = 0$, $q_e \equiv 0$, and $W_e = 0$, it is easy to see that

$$\frac{\partial c}{\partial \lambda}(0, \gamma) = \int_{a_j}^{\infty} \beta(a) \Pi(a, 0) a \, da > 0.$$

The calculation of the sign of the partial derivative $\partial c / \partial \gamma$ is more complicated. First we rewrite $c(\lambda, \gamma)$ in the form

$$c(\lambda, \gamma) = \frac{I_1(\lambda) + I_2(\lambda)\gamma}{I_3 + I_4\gamma} - r \int_{a_j}^{\infty} \beta(a) \Pi(a, W_e) e^{-\lambda a} \, da + 1, \tag{A.4}$$

where

$$\begin{aligned} I_1(\lambda) &= \left(1 - r \int_{a_j}^{\infty} \beta \Pi e^{-\lambda a} \, da \right) \int_{a=0}^{a_j} w_1 \Pi e^{-\lambda a} \int_{s=0}^a \mu_W e^{\lambda s} \, ds \, da \\ &\quad + r \int_0^{a_j} w_1 \Pi e^{-\lambda a} \, da \int_{a=a_j}^{\infty} \beta \Pi e^{-\lambda a} \int_{s=0}^a \mu_W e^{\lambda s} \, ds \, da \\ I_2(\lambda) &= \left(1 - r \int_{a_j}^{\infty} \beta \Pi e^{-\lambda a} \, da \right) \int_{a=a_j}^{\infty} w_2 \Pi e^{-\lambda a} \int_{s=0}^a \mu_W e^{\lambda s} \, ds \, da \\ &\quad + r \int_{a_j}^{\infty} w_2 \Pi e^{-\lambda a} \, da \int_{a=a_j}^{\infty} \beta \Pi e^{-\lambda a} \int_{s=0}^a \mu_W e^{\lambda s} \, ds \, da \\ I_3 &= \int_0^{a_j} w_1 \Pi \, da, \quad I_4 = \int_{a_j}^{\infty} w_2 \Pi \, da. \end{aligned}$$

In these expressions $\beta = \beta(a)$, $\Pi = \Pi(a, W_e)$, $w_i = w_i(a)$, and $\mu_W = \mu_W(a, W_e)$. As a function of γ , $c(\lambda, \gamma)$ is increasing or decreasing according to the monotonicity of the linear fractional expression appearing in (A.4), i.e. according to whether $D = I_2(\lambda)I_3 - I_1(\lambda)I_4$ is positive or negative respectively. For r greater than, but close to 1 a calculation shows that

$$D = -\Delta \left(\int_{a_j}^{\infty} \beta(a) \Pi(a, 0) a \, da \right)^{-1} (r - 1) + O(r - 1)^2,$$

where Δ is given by (4.3). Here (2.6)–(2.8) and the normalization (2.3) are used. This establishes Theorem 2.

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