

INTRA-SPECIFIC COMPETITION AND DENSITY DEPENDENT JUVENILE GROWTH

- J. M. CUSHING*
Interdisciplinary Program in Applied Mathematics,
University of Arizona,
Tucson, AZ 85721, U.S.A.
(*E.mail: CUSHING@ARIZONA.MATH.EDU*)
- JIA LI†
Center for Nonlinear Studies,
Theoretical Division, MS-B258,
Los Alamos National Laboratory,
Los Alamos, NM 87545, U.S.A.

A difference equation model for the dynamics of a semelparous size-structured species consisting of juvenile and adult individuals is derived and studied. The adult population consists of two size classes, a smaller class and a larger more fertile class. Negative feedback occurs through slowed juvenile growth due to increased total population levels during the developmental period and consequently a smaller adult size at maturation. Intra-specific competition coefficients are size dependent and measure the strength of intra-specific competition between juveniles and adults. It is shown that equilibrium states in which adults and juveniles occur together at all times are in general destabilized by significantly increased juvenile *vs* adults competition with the result that stable periodic cycles appear, in which the generations alternate in time and hence avoid competition. This result supports the tenet that intra-specific competition between juveniles and adults is destabilizing. Exceptions to this destabilization principle are found, however, in which populations exhibiting non-equilibrium, aperiodic dynamics can be equilibrated by increase competition between juveniles and adults. This occurs, for example, when adult fertility and competition coefficients are significantly size class dependent.

1. Introduction. Biological populations have a natural propensity for exponential growth. Such growth cannot, of course, be indefinitely sustained and the effects of population density must, by some mechanism or another, serve to curtail unlimited growth. Mathematical models of population growth most often do this by incorporating so-called “density effects” that decrease fertility and/or survival as population density increases. The majority of these (generally nonlinear) models describe highly aggregate population level variables, such as total population size or biomass, and as a result can account for these density effects in only a very qualitative and highly phenomenological

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manner. One cause of adverse effects due to high population density is intra-specific competition between individual organisms of the population for food resources, habitat space, mates, etc. In order to account for such mechanisms causing intra-specific competition between individuals, it is necessary to use so-called "structured population models" in which differences in relevant physiological or behavioral characteristics between individual organisms are distinguished and taken into account.

There are many means by which individuals of a species might compete for resources and by which intra-specific competition might express itself. One type of intra-specific competition which has received recent attention is that which can occur between juvenile and adult individuals. The potential for competition between juveniles and adults, or more generally between individuals from different life cycle stages, exists particularly for species with relatively "simple" life cycles whose resource niches do not undergo significant changes during individual development (Ebenman, 1987, 1988a, 1988b). This includes most reptiles, fish, mammals and hemimetabolous insects. Intra-specific competition is not necessarily limited to organisms with simple life cycles, however. Although species can, for example, avoid competition between individuals from different life cycle stages by undergoing radical metamorphosis during their life cycle, this may also not be the case in that there may not be a corresponding ontogenetic niche shift. The well studied flour beetles of genus *Tribolium* whose adult and larval stages utilize food resources in common provide a case in point. *Tribolium* also illustrate another kind of "intra-specific" competition that is common, namely cannibalism, which in the case of *Tribolium* the adult beetles inflict upon eggs and pupae.

The dynamical consequences of juvenile *vs* adult competition has been investigated by several authors using simple mathematical models. The primary conclusion of earlier studies was that such competition has a destabilizing influence on the dynamics (May *et al.*, 1974; Bellows, 1982; Tschumy, 1982). More recent studies have shown, however, that under certain circumstances juvenile *vs* adult competition can be stabilizing (Ebenman, 1987, 1988a; Cushing and Li, 1989, 1992; Cushing, 1992). These studies were based upon age-structured models in which juvenile *vs* adult competition results in reduced juvenile survival and/or reduced adult fecundity.

Another important effect that competition can have on juveniles, not included (at least explicitly) in age-structured models, is that of slowed juvenile growth and smaller adult size. Body size is often a more important physical attribute than is chronological age (Calder, 1984; Werner and Gilliam, 1984; Ebenman and Persson, 1988; Caswell, 1989). Size, not age, is often the key factor in determining vital rates such as fertility, survival and individual growth rates as well as susceptibility to environmental hazards (such as predation and cannibalism), metabolic demands, etc. Intra-specific competition that slows

juvenile growth can reduce body size at maturation and consequently reduce fertility (Wilbur, 1980; Botsford, 1981; Prout and McChesney, 1985; Weiner, 1985; Ebenman and Persson, 1988; Mueller, 1988). Slowed growth of juveniles can be the result of competition from other juveniles (e.g. see Prout and McChesney, 1985) or from adults. In the latter case, competition may be due to the larger body size of adults (Ebenman, 1988b).

In an attempt to study the consequences of slowed juvenile growth and reduced adult size and fecundity due to intra-specific competition, Ebenman (1988a) placed, in a rather *ad hoc* manner, a time delay in an age-structure difference equation model. As pointed out by Ebenman it would be more appropriate, however, to analyse this phenomenon by a model that is based explicitly on size as opposed to age. In a later paper, Ebenman (1988b) extended his age-structured model to include variable adult size, although this extension proved to be analytically intractable.

In this paper we introduce and study a simple size-structured model for a semelparous population whose juvenile growth and development is slowed, and consequently whose fertility at maturation is decreased, by intra-specific competition. This model will focus on reduced adult size caused by population density and in particular by competition between juveniles and adults and will ignore the effects of population density on juvenile survival and adult fecundity. These simplifying assumptions will make the model amenable to a considerable amount of mathematical analysis. The model is derived in Section 2 and analysed in Section 3. The results are discussed in Section 4.

2. The Model Equations. Let $J(t)$ denote the number or density of juveniles at times $t = 0, 1, 2, \dots$, where the unit of time is taken to be the maturation period. With probability Π a juvenile will survive to maturation at which time it produces offspring. At the end of the time period $[t, t + 1]$ surviving juveniles, which are $\Pi J(t)$ in number, will have grown into one of two adult size classes with numbers or densities $A_i(t)$, $i = 1$ and 2 . Those adult individuals in the i th size class will be said to have size i . We assume that the reproductive period is no longer than the maturation period, after which adult individuals die or otherwise leave the population. Let F_i denote the per individual fecundity of an adult of size i (i.e. the expected number of surviving offspring at the end of one time period). Then the number of juveniles at time $t + 1$ is:

$$J(t + 1) = F_1 A_1(t) + F_2 A_2(t). \tag{1}$$

It is assumed that the two size classes are ordered according to increasing size and that the smaller adult class also has the lower fertility, i.e. $F_1 < F_2$. Suppose that the fraction of surviving juveniles who grow to size i is ϕ_i so that:

$$A_i(t + 1) = \Pi \phi_i J(t). \tag{2}$$

In equations (1) and (2) any of the vital rates, viz. and adult fecundity rates, F_i , the juvenile survival rate, Π , or the growth rates, ϕ_i , could be density dependent. In this paper we are focusing on density dependent juvenile growth and consequently we will assume for simplicity (as does Ebenman, 1988a) that the parameters F_i and Π are constant while only the fractions, ϕ_i , are dependent upon population density. The dependence of growth on population density will be through a dependence upon a weighted total population size:

$$W(t) = J(t) + \gamma_1 A_1(t) + \gamma_2 A_2(t), \quad \gamma_i \geq 0. \quad (3)$$

The size specific competition coefficients, γ_i , measure the effect on juvenile growth due to the presence of an individual adult of size i compared to that of an individual juvenile. Large values of γ_i imply strong intra-specific competition between the larger adult individuals and smaller juvenile individuals. The growth fractions $\phi_i = \phi_i(W(t))$ are assumed dependent on W where:

$$\phi_i: R^+ \rightarrow [0, 1] \text{ is continuously differentiable.} \quad (4)$$

As a result, equations (2) become nonlinear. All surviving juveniles are assumed to be present in the adult classes and consequently:

$$\phi_1(W) + \phi_2(W) \equiv 1. \quad (5)$$

We are interested in the case when competition adversely affects juvenile growth. Thus it is reasonable to assume that:

$$\phi'_1 > 0, \quad \phi'_2 < 0. \quad (6)$$

In addition we assume that:

$$\phi_1(+\infty) = 1 \quad (7)$$

i.e. in the limit, for infinitely large population densities, juveniles can only grow to the smaller adult size.

Finally we introduce the population's inherent (i.e. density independent) net reproductive number or rate, n . This is the expected number of offspring per lifetime per individual and is given by the formula:

$$n = F_1 \Pi \phi_1(0) + F_2 \Pi \phi_2(0).$$

It is introduced explicitly into the dynamical equation (1) by letting f_i denote the ratio of size specific fecundity to the inherent net reproductive number: $F_i = n f_i$ where the f_i satisfy the normalization $f_1 \Pi \phi_1(0) + f_2 \Pi \phi_2(0) = 1$.

For our analysis we introduce, by means of a weighted average of the coefficients γ_i , a "competition coefficient" $\sigma = \gamma_1 \phi_1(0) + \gamma_2 \phi_2(0)$ as a composite

measure of the adult *vs* juvenile competition. This is done by setting $\gamma_i = \sigma\beta_i$ in (3) where the $\beta_i \geq 0$ satisfy $\beta_1\phi_1(0) + \beta_2\phi_2(0) = 1$.

Finally, if the unit used to measure the adult population sizes is taken to be the number of juveniles needed to produce one adult (of either size) at low densities, then Π can effectively be set equal to one. Mathematically, A_i , n , and σ are replaced by A_i/Π , $n\Pi$, and $\sigma\Pi$.

In summary, we have the equations:

$$J(t+1) = n(f_1A_1(t) + f_2A_2(t)) \tag{8}$$

$$A_i(t+1) = \phi_i(W(t))J(t), \quad i = 1 \quad \text{and} \quad 2 \tag{9}$$

$$W(t) = J(t) + \sigma(\beta_1A_1(t) + \beta_2A_2(t)) \tag{10}$$

where:

$$\begin{aligned} n > 0, \quad \sigma > 0, \quad \beta_i \geq 0, \quad f_2 > f_1 > 0 \\ \beta_1\phi_1(0) + \beta_2\phi_2(0) = 1, \quad f_1\phi_1(0) + f_2\phi_2(0) = 1 \end{aligned} \tag{11}$$

and the ϕ_i satisfy (4)–(7). For technical reasons we will also assume that:

$$|W\phi'_i(W)| \quad \text{is bounded for} \quad W > 0. \tag{12}$$

Clearly any solution of (8)–(10) with non-negative initial values $J(0) \geq 0$, $A_i(0) \geq 0$ remains non-negative for all $t = 1, 2, \dots$. By a solution, equilibrium, 2-cycle etc. of (8)–(10) we will always mean non-negative solutions. The trivial solution is the zero state equilibrium, $J \equiv A_i \equiv 0$, for all t and i .

3. Analysis. We wish to study the behavior of solutions of (8)–(10) as $t \rightarrow +\infty$ and we start by considering the equilibrium states in which J and A_i are constant over time.

First of all, it is proved in Section 1 of the Appendix that if $n < 1$ then all solutions tend to the trivial equilibrium $(J, A_1, A_2) = (0, 0, 0)$. That is to say, if the population is incapable of surviving in the absence of intra-specific competition, then it will not be able to survive in the presence of competition.

Consider then the case $n > 1$. From the equilibrium equations:

$$J = n(f_1A_1 + f_2A_2), \quad A_i = \phi_i(W)J, \quad W = J + \sigma(\beta_1A_1 + \sigma_2A_2)$$

we see immediately that only the trivial equilibrium has $J = 0$ and if $J > 0$ then:

$$nN(W) = 1 \tag{13}$$

where $N(W) = f_1\phi_1(W) + f_2\phi_2(W)$. Equation (13) implies that the net reproduc-

tive number at any equilibrium value of $W > 0$ (not to be confused with the *inherent* net reproductive number at $W = 0$) must be one. That is, at equilibrium each individual must exactly replace itself. The continuously differentiable function $N(W)$ has the properties:

$$N: \mathbb{R}^+ \rightarrow (0, 1], \quad N(0) = 1, \quad N(+\infty) = f_1, \quad N' < 0.$$

The monotonicity of N can be seen by using (5) to obtain $N(W) = f_1 + (f_2 - f_1)\phi_2(W)$ and hence $N'(W) = (f_2 - f_1)\phi_2'(W)$. This monotonicity implies that (13) can be solved for the total population equilibrium $W = W(n)$ where:

$$W(n) = N^{-1}(1/n), \quad 1 < n < n_{\max} = \begin{cases} 1/f_1 & \text{if } f_1 \neq 0 \\ +\infty & \text{if } f_1 = 0 \end{cases}$$

which in turn leads to the size class equilibria $J = J(n)$, $A_i = A_i(n)$ where:

$$\begin{aligned} J(n) &= \frac{W(n)}{1 + \sigma(\beta_1\phi_1(W(n)) + \beta_2\phi_2(W(n)))} \\ A_i(n) &= \phi_i(W(n))J(n) \end{aligned} \quad (14)$$

for $1 < n < n_{\max}$. These positive equilibria are unique.

It is also shown in Section 1 of the Appendix that solutions are unbounded if $f_1 \neq 0$ and $n > n_{\max}$. This fact is a consequence of the model assumptions that the only density control is through suppressed juvenile growth. If the smaller adult size class alone has a sufficiently large fecundity, nf_1 , to avoid extinction even at large (infinite) population densities, i.e. if the linear equations $J(t+1) = nf_1A_1(t)$, $A_1(t+1) = J(t)$ have an eigenvalue $(nf_1)^{1/2}$ larger than one, then in the lack of density dependent mortality or fertility controlling factors the population will experience unrestricted geometric growth. We will refer to values of n from the interval $1 < n < n_{\max}$ as “viable”. Only for viable values of n do density dependent growth rates control population growth in our model.

As a function of the inherent net reproductive number n on the interval $1 < n < n_{\max}$ the equilibria (14) constitute an unbounded continuum that bifurcates from the trivial equilibrium at the critical value $n = 1$. Before looking at the stability of these equilibria we note that the Jacobian of (8)–(9) at the trivial equilibrium with $n = 1$

$$\begin{pmatrix} 0 & f_1 & f_2 \\ \phi_1(0) & 0 & 0 \\ \phi_2(0) & 0 & 0 \end{pmatrix}$$

has simple eigenvalues 0 and ± 1 . The eigenvalue -1 suggests the possibility

that also bifurcating from the trivial solution is a branch of 2-cycles [i.e. periodic solutions of (8)–(10) of minimal period 2]. This turns out to be the case. It is easy to check that for viable n values the formulae:

$$\begin{aligned}
 J &= \begin{cases} W(n) & \text{for } t=0, 2, 4, \dots \\ 0 & \text{for } t=1, 3, 5, \dots \end{cases} \\
 A_i &= \begin{cases} 0 & \text{for } t=0, 2, 4, \dots \\ \phi_i(W(n))W(n) & \text{for } t=1, 3, 5, \dots \end{cases} \quad (15)
 \end{aligned}$$

define a continuum of 2-cycles which also bifurcates from the trivial equilibrium at $n=1$. Note that these 2-cycles have the property that all juveniles appear together in synchronism at the times $t=0, 2, 4, \dots$ (or $t=1, 3, 5, \dots$ in the shifted 2-cycle). We will refer to such cycles as “synchronous 2-cycles”. It is not difficult to show that (15) are the only possible synchronous 2-cycles.

In summary, for all viable values of the inherent net reproductive number $1 < n < n_{max}$ there exist both a unique positive equilibrium and a unique non-negative synchronous 2-cycle.

In Section 2 of the Appendix it is shown that “generically” there exist no strictly positive 2-cycles. There can, however, exist positive cycles of longer periods as well as aperiodic attractors (see for example the orbit diagram Fig. 4b). There can also exist synchronous cycles of longer periods as well as other synchronous attractors. These are solutions which are alternately zero (with juveniles and adults out of synchronization). They are given by the positive attractors of the equation $J(\tau + 1) = nN(J(\tau))J(\tau)$ where $\tau = 2t$. The equilibria of this equation are the synchronous 2-cycles (15) of (8)–(10) while the 2-cycles yield synchronous 4-cycles of (8)–(10), the 4-cycles yield synchronous 8-cycles of (8)–(10) and so on. As is well known, a scalar equation like this can, depending on the nonlinearity, $N(J)$, exhibit the familiar period doubling cascade of bifurcations to chaos. Any attractor yields a synchronous attractor of (8)–(10).

The next question we address concerns the stability properties of the positive equilibria (14) and the synchronous 2-cycles (15). One might expect the bifurcating equilibria (14) to be stable, at least for n near 1, since at $n=1$ the trivial equilibrium loses stability and generally there is an exchange of stability associated with transcritical bifurcations (Cushing, 1988). This is not necessarily true for (8)–(10), however, due to the occurrence of the eigenvalue -1 at critical point, $n=1$, associated with the 2-cycles (15). The local stability properties of the equilibrium (14) are determined by the eigenvalues of the 3×3 Jacobian matrix:

$$\begin{pmatrix} 0 & nf_1 & nf_2 \\ \phi_1(W(n)) & 0 & 0 \\ \phi_2(W(n)) & 0 & 0 \end{pmatrix} + J(n) \begin{pmatrix} 0 & 0 & 0 \\ \phi'_1(W(n)) & \beta_1\phi'_1(W(n)) & \beta_2\phi'_1(W(n)) \\ \phi'_2(W(n)) & \beta_1\phi'_2(W(n)) & \beta_2\phi'_2(W(n)) \end{pmatrix}$$

which a simple calculation shows are the roots of the cubic $p(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$ with coefficients:

$$\begin{aligned} a_1 &= \sigma(\beta_1 - \beta_2)\phi'_2(W(n))J(n), & a_2 &= n(f_1 - f_2)\phi'_2(W(n))J(n) - 1 \\ a_3 &= \sigma n(f_1\beta_2 - f_2\beta_1)\phi'_2(W(n))J(n). \end{aligned}$$

The equilibrium is stable if all roots of $p(\lambda)$ lie inside the unit circle of the complex plane. Necessary and sufficient for this are the Jury conditions (Murray, 1989):

- (a) $p(1) = 1 + a_1 + a_2 + a_3 > 0$
- (b) $p(-1) = -1 + a_1 - a_2 + a_3 < 0$
- (c) $|a_3| < 1$
- (d) $|1 - a_3^2| > |a_2 - a_3a_1|$.

From (11) we find that $f_1 + (f_2 - f_1)\phi_2(0) = f_2 + (f_1 - f_2)\phi_1(0) = 1$ and consequently $f_1 \leq 1$ and $1 \leq f_2$. From this we see for $1 < n < n_{\max}$ that $n > 1/f_2$ and:

$$p(1) = (\sigma\beta_1(1 - nf_2) + \sigma\beta_2(nf_1 - 1) + n(f_1 - f_2))\phi'_2(W)J > 0$$

and as a result Jury condition (a) always holds.

Jury condition (b) defines a region I above a curve in the n, σ -parameter plane defined by $\sigma > \sigma(n)$ where:

$$\sigma(n) = \frac{n(f_1 - f_2)}{\beta_1(1 - nf_2) + \beta_2(nf_1 - 1)}, \quad 1 < n < n_{\max} \tag{16}$$

in which the equilibria are unstable. See Figs 1–3. In the region II below this curve the equilibria may or may not be stable. It is shown in Section 3 of the Appendix that in this region II below the curve (16) equilibria will be stable if f_1 and f_2 and if β_1 and β_2 are nearly equal, i.e. if the two adult size classes do not greatly differ in their fertility rates and their relative competitive effects upon juveniles. On the other hand if, for example, the adult size classes do differ significantly in their fertility rates then there can be a subregion of region II in which equilibria are unstable. See Figs 2 and 3 for an illustration. The boundary of this region of instability is defined by equalities in the Jury conditions (c) and (d). Crossing this boundary results in a pair of complex conjugate eigenvalues crossing the unit circle and hence in general there occurs

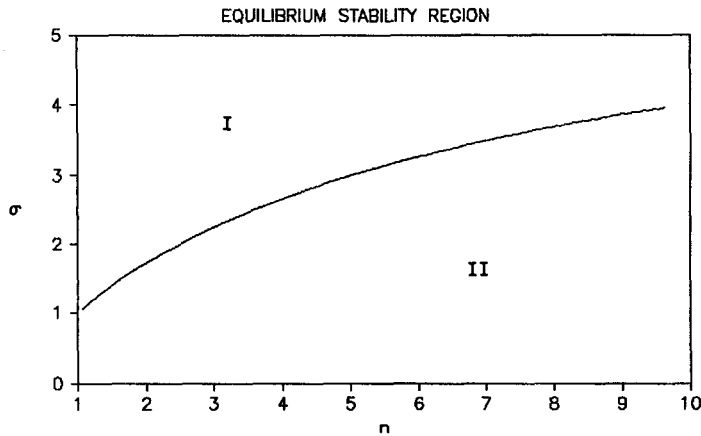


Figure 1. The stability region in the n, σ -plane for the equilibria (14) is shown for equations (8)–(10) with nonlinearity (17) and parameter values $f_1 = 0.1$, $\beta_1 = 0.25$ and $f_2 = \beta_2 = 1$. The equilibria are stable in region II and unstable in region I. In this case the synchronous 2-cycles (15) are stable in I and unstable in II. This example illustrates the destabilization that occurs with increasing adult competition pressure on juvenile growth.

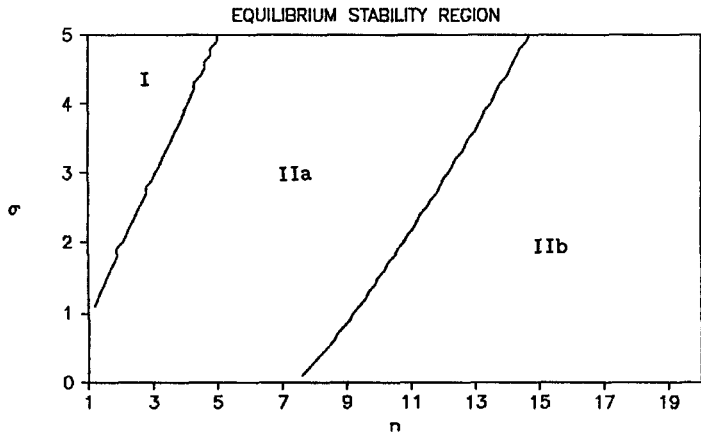


Figure 2. The stability region for the equilibria (14) is shown as in Fig. 1, but with decreased parameter values $f_1 = 0$, $\beta_1 = 0.1$. A subregion IIb of equilibrium instability has intruded in region II. Equilibria are stable in region IIa, but suffer a Hopf bifurcation to an invariant circle when the boundary between IIa and IIb is crossed. Equilibria are also unstable in region I where either the synchronous 2-cycles (15) other synchronous cycles or aperiodic solutions are stable. While there is still an equilibrium destabilization with sufficiently increased competition coefficient σ , crossing the boundary between subregions IIa and IIb by increasing σ results in a stabilization of the equilibrium. See Fig. 4 for orbit diagrams taken along vertical paths in this graph.

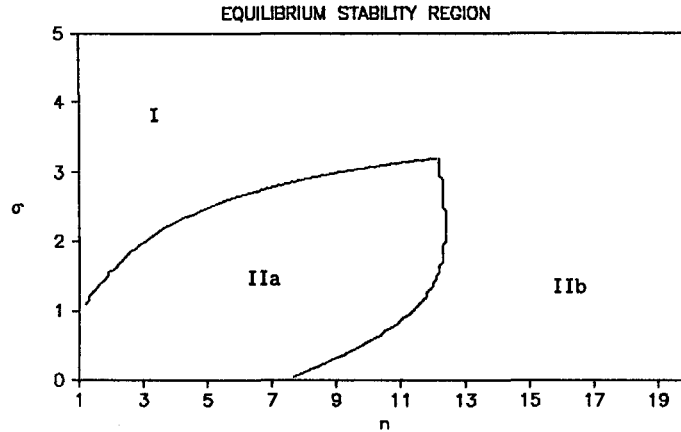


Figure 3. With increased importance of smaller adult competition by increasing β_1 from 0.1 to 0.25 in Fig. 2, the equilibrium instability region IIb has expanded and merged with the instability region I. To see how the dynamics change in moving between these subregions see Fig. 5.

a Hopf bifurcation to an invariant circle (Guckenheimer and Holmes, 1983). In any case it can be shown (see Section 4 of the Appendix) that in region II the equilibria will always be stable for n close to 1.

In order to study the stability properties of the 2-cycles (15), one needs to calculate the Jacobian of the first composite map of (8)–(9). This turns out to be a 3×3 block diagonal matrix of the form:

$$\begin{pmatrix} \lambda_1 & p \\ 0 & Q \end{pmatrix}$$

where $\lambda_1 < 1$ is a scalar and Q is a 2×2 matrix given by:

$$\lambda_1 = 1 + nW(n) (f_1\phi_1'(W(n)) + f_2\phi_2'(W(n))) = 1 + nW(n) (f_2 - f_1)\phi_2'(W(n))$$

$$Q = n \begin{pmatrix} f_1\phi_1(W_1(n)) & f_2\phi_1(W_1(n)) \\ f_1\phi_2(W_1(n)) & f_2\phi_2(W_1(n)) \end{pmatrix}, \quad W_1(n) = W(n)\sigma(\beta_1\phi_1(W(n)) + \beta_2\phi_2(W(n)))$$

and where p is a row vector whose elements need not concern us here. Clearly λ_1 is an eigenvalue and the remaining eigenvalues are those of Q , namely 0 and $\lambda_2 = nN(W_1(n)) > 0$. The 2-cycles (15) are stable if these two real eigenvalues lie inside the unit interval and are unstable if at least one exceeds one in magnitude.

It is shown in Section 5 of the Appendix that the synchronous 2-cycle stability boundary in the n, σ -plane defined by $\lambda_2 = 1$ is identical to that of the equilibrium instability region I defined by (16) and that the synchronous 2-cycles (15) are unstable in region II below this curve. In region I above this

curve these 2-cycles may or may not be stable, depending upon λ_1 being greater than -1 . In any case it is shown in Section 4 of the Appendix that the synchronous 2-cycles will always be stable in region I for n near the critical value of one.

In summary, the positive equilibria (14) and the synchronous 2-cycles (15) are never both stable. For all viable n the equilibria are unstable for $\sigma > \sigma(n)$ while the synchronous 2-cycles are unstable for $\sigma < \sigma(n)$. For $\sigma < \sigma(n)$ equilibria are either stable or lose stability via a Hopf bifurcation to an invariant circle. One case for which the equilibria are stable when $\sigma < \sigma(n)$ is the case when $f_1 \neq 0$ and β_1 do not greatly differ from f_2 and β_2 , respectively. For $\sigma > \sigma(n)$ the synchronous 2-cycles are either stable or lose stability (through period doublings) to other synchronous cycles. In any case, for $n \approx 1$ the equilibria are stable if $\sigma < 1$ and the synchronous 2-cycles are stable if $\sigma > 1$.

Some of the bifurcations described above are illustrated in Figs 4–5 in which orbit diagrams are drawn along paths which cross stability boundaries. These orbit diagrams, as well as the equilibrium stability regions in Figs 1–3, were computed for equations (8)–(10) with:

$$\phi_1(W) = 1 - \exp(-W), \quad \phi_2(W) = \exp(-W). \tag{17}$$

In this case (11) implies $f_2 = \beta_2 = 1$.

Our analysis has shown that at the boundary of σ, n parameter region I determined by (16) the unique positive equilibria are neutrally stable because a linearized eigenvalue equals -1 . Our analysis has also shown that at this same boundary (amazingly enough!) the unique synchronous 2-cycles are also neutrally stable because a linearized eigenvalue of the composite equals $+1$. The usual expectation, upon crossing this boundary from below in the σ, n -plane, would be that a 2-cycle bifurcation of small amplitude (and hence positive and non-synchronous) would occur from the positive equilibria. However, the fact that there are no non-synchronous 2-cycles, as is proved in the Appendix, implies that this bifurcation does not occur in this model. Why this is so, and what the nature of the bifurcation phenomena at both the equilibria and the synchronous 2-cycles is, are interesting mathematical questions which we leave unexplored.

4. Discussion. We have investigated a simple difference equation model (8)–(10) for the dynamics of a semelparous population whose life cycle consists of a juvenile growth stage followed by a reproductive stage at either of two different adult sizes. In this model adult size attained by juveniles at the end of a fixed maturation period depends upon population density during the juvenile period in that increased density results in a smaller fraction of juveniles growing to the larger adult size and a larger fraction to the smaller adult size. Reduced size at maturation due to density effects in turn adversely affects population

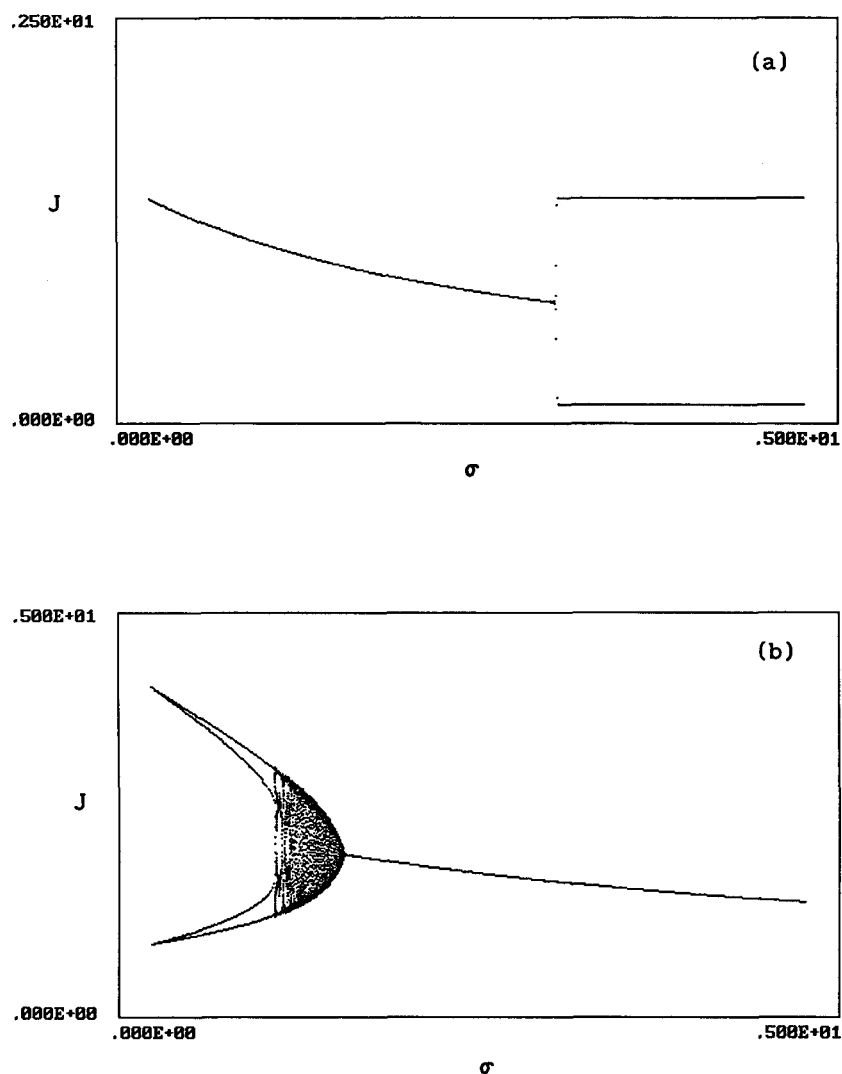


Figure 4. Using the competition coefficient σ as a parameter, orbit diagrams (for the juvenile population, J) are shown for (8)–(10) with parameter values as in Fig. 2 and with n fixed at: (a) $n = 4$; and (b) $n = 12$. In (a), as σ increases from 0 to 5, one moves vertically from region IIa into region I in Fig. 2 and the resulting destabilization of the equilibrium and simultaneous stabilization of the synchronous 2-cycles are clearly seen. In (b), one moves vertically from region IIb into region IIa and the stabilization of the equilibrium is seen.

growth since it is assumed that fecundity correlates with adult body size. In focusing on the effects of density dependent juvenile growth rate, the model ignores density dependent death and fertility rates. Of particular interest are the effects of density dependent juvenile growth on the population's asymptotic

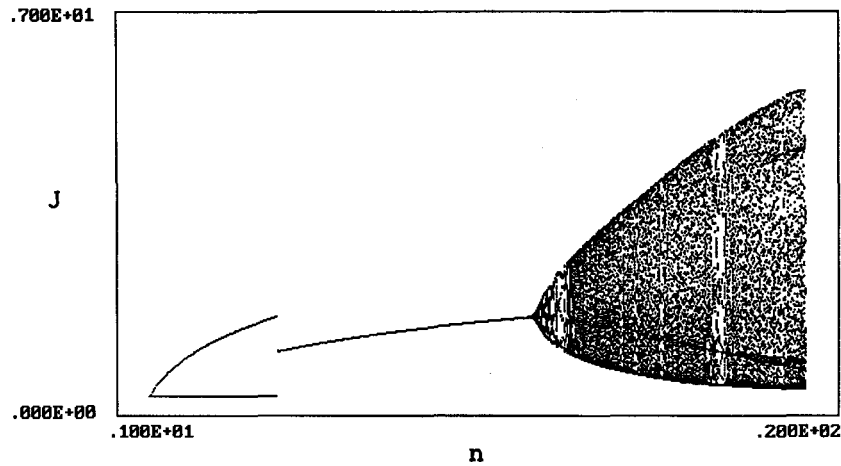


Figure 5. Using the inherent net reproductive rate, n , as a parameter, an orbit diagram (for the juvenile population, J) is shown for (8)–(10) with (17) with parameter values as in Fig. 3 and with $\sigma = 2$. This path crosses regions I, IIa and IIb. The resulting passage from a stable synchronous 2-cycle, to a stable equilibrium, and ultimately to aperiodic motion via a Hopf-type bifurcation is seen.

dynamics and to what extent reduced juvenile growth due to competition from adults is destabilizing.

Our analysis of the model showed that there is an interval of “viable” values of the inherent net reproductive rate, n , in which the population neither dies out nor experiences unbounded growth, i.e. in which density controls on population growth are effective. Within this interval (which is determined by the relative fertility of the smaller adult size) there are two fundamental states for the population, an equilibrium state in which both juveniles and adults are present at all times and a “synchronous” 2-cycle in which the juvenile and adult generations alternately appear and disappear, but are never simultaneously present.

A linearized stability analysis showed that the equilibrium state is unstable if the adult competitive effects on juvenile growth are sufficiently strong, as is measured by the competitive coefficient, σ , in the model. That is, if σ is larger than a critical value, $\sigma(n)$, then the equilibrium state is unstable and the synchronous 2-cycle (or possibly a synchronous cycle of a longer period or even an aperiodic synchronous state) is stable. This result can be viewed as support for the tenet that juvenile *vs* adult competition is destabilizing. It is interesting to note that this result implies that the population’s dynamics asymptotically adjust to strong inter-generational competition by providing a life cycle in which competition is avoided altogether. This is an example of how life cycle intricacies can provide an extra dimension to “ecological niche space” and afford the means by which the population can be sustained despite strong intra-

specific competitive pressures. This idea goes back at least to Hutchinson (1959) for inter-specific competition.

There are, however, exceptions in our model to this “destabilization principle”. For $\sigma < \sigma(n)$, when the synchronous cycles are unstable, the equilibrium state with both generations present is shown to be stable when either inherent net reproductive rates, n , are low or, for any n , when fertility and adult competitive effects on juvenile growth are not strongly adult size dependent. However, when fertility and adult competitive effects on juvenile growth do depend significantly on adult size, equilibrium stability can be lost at larger values of n through a Hopf bifurcation to an invariant circle, which results in aperiodic or even chaotic dynamics in which both juveniles and adults are present. In this case our study shows that increased juvenile *vs* adult competition can have a stabilizing effect in that aperiodic or chaotic dynamics can be equilibrated by an increase in the competition coefficient $\sigma < \sigma(n)$.

We have restricted our attention here to the effects on population level dynamics that are due only to slowed juvenile growth and reduced size at maturation and to the resulting decreased adult fertility that are caused by intra-specific competition experienced by juveniles during their growth and developmental stage. Many important phenomena have been ignored in our model and await further study. For example, we have ignored density effects on juvenile mortality and on adult mortality and fertility. These can be incorporated straightforwardly into the model by making Π and f_i density dependent in some appropriate manner. In this regard, a point made by Ebenman (1988b) should be taken into account, namely that density dependent feedbacks on juvenile growth and mortality are not, in general, independent of one another, but are related to “plasticity of growth” in opposite ways. As another example, our model is suitable only for semelparous species (as indeed are the age-structure models of Ebenman). For iteroparous species when adult survival and fertility (and further growth) are allowed after one unit of time, transitions between the adult size classes might occur and must be incorporated into equations (10). Also the length of the maturation period is known to have a strong influence on a population’s stability (e.g. see McNair, 1989, and the references cited therein). We have assumed a fixed maturation period in our model and therefore could not directly explore the relationship between stability and the length of a variable maturation period. It would be of interest to test the robustness our conclusions for model cases with extended features such as these.

APPENDIX

1. Consider (8) and (10) for $0 < n < 1$. For $t \geq 1$ we have:

$$0 \leq J(t+1) = n \sum_{i=1}^2 f_i \phi_i(W(t-1))J(t-1) = nN(W(t-1))J(t-1) \leq nJ(t-1)$$

since $N(W) \leq 1$. An easy induction shows that $0 \leq J(t) \leq x(t)$ for $t \geq 2$ where $x(t)$ solves the second order linear difference equation $x(t+1) = nx(t-1)$ and the side conditions $x(0) = J(0)$, $x(1) = J(1)$. The characteristic polynomial associated with this difference equation is $\lambda^2 = n$ whose roots lie inside the unit complex disk and consequently $x(t) \rightarrow 0$. Thus, if $0 < n < 1$ then $J(t) \rightarrow 0$ and as a result $A_i(t) \rightarrow 0$.

On the other hand, if $f_1 \neq 0$ and $n > n_{\max} = 1/f_1$ then the inequality:

$$J(t+1) \geq nf_1 \sum_{i=1}^2 \phi_i(W(t-1))J(t-1) = nf_1 J(t-1)$$

and a similar comparison argument implies $J(t) \rightarrow +\infty$.

2. Suppose that equations (8)–(10) have a strictly positive 2-cycle. Then:

$$J(t) = J(t+2) = \sum_{i=1}^2 nf_i A_i(t+1) = \sum_{i=1}^2 nf_i \phi_i(W(t))J(t), \quad t = 0, 1, 2, \dots$$

which implies that $1 = nN(W(t))$, for all t . Thus $W(t)$ is constant: $W(t) \equiv W_0 > 0$ for all t where W_0 satisfies the equations:

$$f_1 \phi_1(W_0) + f_2 \phi_2(W_0) = \frac{1}{n}. \tag{A1}$$

Then $W(t+1) = W(t+2)$ implies:

$$\left(1 - \sigma \sum_{i=1}^2 \beta_i \phi_i(W_0)\right) J(t+1) = \left(1 - \sigma \sum_{i=1}^2 \beta_i \phi_i(W_0)\right) J(t), \quad t = 0, 1, 2, \dots$$

Since $J(t+1) \neq J(t)$ [otherwise (10) implies $A_i(t+1) = A_i(t)$ and the solution is an equilibrium, in contradiction to the definition of a 2-cycle], it follows that W_0 is also a root of the equation:

$$\beta_1 \phi_1(W_0) + \beta_2 \phi_2(W_0) = \frac{1}{\sigma}.$$

This equation together with (A1) and (5) imply that n can only equal one value, namely $\sigma(\beta_2 - \beta_1)/(f_2 - f_1 + \sigma(f_1\beta_2 - f_2\beta_1))$.

3. Note that $n\phi_2'(W(n))W(n)$ is independent of β_1 and β_2 . If $f_1 \neq 0$ then the interval of viable n is finite. This, in addition to (12), implies that $n\phi_2'(W(n))W(n)$ is bounded (uniformly in f_1 and f_2). Thus for $\Delta f = f_1 - f_2$ sufficiently small the inequalities:

$$|n \Delta f \phi_2'(W(n))W(n)| < 1, \quad 1 - (n \Delta f \phi_2'(W(n))W(n))^2 > n \Delta f \phi_2'(W(n))W(n) > 0$$

hold. Since $\sigma(n) \equiv 1$ and $J(n) \equiv W(n)$ when $\Delta\beta = \beta_1 - \beta_2 = 0$, these inequalities imply, respectively, that the Jury conditions (c) and (d) hold for Δf sufficiently small when $\Delta\beta = 0$ and hence by continuity when $\Delta\beta$ is sufficiently small. Since Jury condition (a) always holds and Jury condition (b) holds if $\sigma < \sigma(n)$, we see that all four Jury conditions hold and hence the equilibrium is stable if $\sigma < \sigma(n)$, $f_1 \neq 0$, and both Δf and $\Delta\beta$ are sufficiently small.

4. First consider the stability of the equilibria (14) in Region I for $n \approx 1$. Fix f_i, β_i , and $\sigma < 1$ and consider the four Jury conditions (a)–(d). We have seen that Jury conditions (a) always holds.

Since $\sigma(1) = 1$, we have that $\sigma < \sigma(n)$ and hence Jury condition (b) holds for $n \approx 1$. Since $\phi'_2(W)$ is bounded for $W > 0$ and $J(1) = 0$, we see from:

$$\begin{aligned} a_3 &= 0(J), \quad 1 - a_3^2 = 1 + 0(J^2) \\ a_2 - a_3 a_1 &= -1 + n \Delta f \phi'_2 J + 0(J^2) \end{aligned}$$

that the remaining Jury conditions (c) and (d) hold for $n \approx 1$.

Consider now the stability of the synchronous 2-cycles (15) for $\sigma > \sigma(n)$ and $n \approx 1$. Fix f_i, β_i , and $\sigma > 1$ and consider the eigenvalues:

$$\lambda_1 = 1 + nW(n)(f_2 - f_1)\phi'_2(W(n)) < 1 \quad \text{and} \quad \lambda_2 = nN(W_1(n)) > 0.$$

The 2-cycles are stable if $\lambda_1 > -1$ and $\lambda_2 < 1$. For $n = 1$, $\lambda_1 = 1$ and hence $\lambda_1 > -1$ holds for $n \approx 1$. Since $\sigma > 1$ it follows from (11) that:

$$\sigma(\beta_1 \phi_1(W(n)) + \beta_2 \phi_2(W(n))) > 1$$

and hence $W_1(n) > W(n)$ holds for $n \approx 1$. By the monotonicity of N we find that $\lambda_2 = nN(W_1(n)) < nN(W(n)) = 1$ for $n \approx 1$.

5. In this section we investigate the relationship between the boundary of the equilibrium instability region determined by the Jury condition (b), namely $p(-1) = 0$, and the boundary of the 2-cycle instability region determined by $\lambda_2 = 1$. This relationship is stated in the Lemma below. First note that from (13) and (5) follows:

$$\phi_2(W(n)) = (1 - nf_1)/n(f_2 - f_1). \quad (\text{A2})$$

LEMMA. $p(-1) > 0$ if and only if $\lambda_2 < 1$. Also $p(-1) < 0$ if and only if $\lambda_2 > 1$.

Proof. Since:

$$p(-1) = \phi'_2(W(n))J(n) (\sigma(\beta_1 - \beta_2) - n(f_1 - f_2) + \sigma n(f_1 \beta_2 - f_2 \beta_1))$$

we see that $p(-1) > 0$ if and only if:

$$\begin{aligned} \sigma(\beta_1 - \beta_2) + \sigma n(f_1 \beta_2 - f_2 \beta_1) &< n(f_1 - f_2) \\ \sigma \frac{(\beta_1 - \beta_2) + n(f_1 \beta_2 - f_2 \beta_1)}{n(f_2 - f_1)} &> 1 \\ \sigma \left(\beta_1 + (\beta_2 - \beta_1) \frac{1 - nf_1}{n(f_2 - f_1)} \right) &> 1 \end{aligned}$$

or, by (A2) and (5), if and only if:

$$\sigma(\beta_1 \phi_1(W(n)) + \beta_2 \phi_2(W(n))) > 1$$

that is, upon multiplication by $W(n)$, if and only if $W_1(n) > W(n)$. So, by the monotonicity of $N(W)$ we conclude that $p(-1) > 0$ if and only if $nN(W_1(n)) < nN(W(n)) = 1$.

The second assertion of the Lemma is proved by reversing the inequalities in the above argument.

It follows from this lemma that $p(-1) = 0$ if and only if $\lambda_2 = 1$. ■

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