**Mathematical Biology**

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# A juvenile-adult model with periodic vital rates

**Abstract.** A global branch of positive cycles is shown to exist for a general discrete time, juvenile-adult model with periodically varying coefficients. The branch bifurcates from the extinction state at a critical value of the mean, inherent fertility rate. In comparison to the autonomous system with the same mean fertility rate, the critical bifurcation value can either increase or decrease with the introduction of periodicities. Thus, periodic oscillations in vital parameter can be either advantageous or deleterious. A determining factor is the phase relationship among the oscillations in the inherent fertility and survival rates.

## 1. Introduction

Although most principles in theoretical ecology and population dynamics are formulated using (time) autonomous dynamical systems, the vital rates of many, if not most, biological populations are subject to temporal fluctuations. Many of these fluctuations, rather than being stochastic, are regular. For this reason there is a growing literature on non-autonomous ecological models in which coefficients are periodic functions of time. One question of interest concerns the effects of such periodicities. How, and in what sense, do solutions of periodically forced ecological models compare to those of associated autonomous models? Do basic tenets in theoretical ecology hold up when parameters oscillate, or do they need modification? For some background literature see [2], [4], [5], [6], [7], [8], [12], [31], [32], [33], [35], [37], [38].

For example, one tenet is that oscillations in carrying capacity are deleterious to a population, in the sense that they cause a lower mean population number [31]. The result of an experiment involving laboratory insect populations reported in [26], however, contradicts this tenet. An explanation for this experimental observation, that utilizes a periodically forced, stage structured model, appears in [3], [25]. Subsequently, many authors have investigated similar kinds of periodically forced models and have studied the effects of habitat periodicities (as reflected in periodically fluctuating coefficients in the models) on the dynamics of a population [10], [16], [14], [15], [18], [19], [20], [21], [22], [23], [24], [28], [29], [30], [36].

My purpose in this paper is to consider a general class of periodically forced models for a stage structured population that includes not only environmental

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(carrying capacity) periodicities, but periodic fluctuations in inherent fertility and survival rates. The former appear as periodic oscillations in those model parameters involved with population density effects. The latter involve oscillations in those parameters describing inherent ferility and survival rates. The first goal (the subject of Section 2 ) is a mathematical one, namely, to establish the existence and stability properties of periodic solutions of the model. This will be done using the bifurcation theory provided in the Appendix. That theory is a generalization of an analogous theory for equilibria of autonomous, stage structured models (see [9]). This application will establish a global branch of periodic solutions that bifurcates from a critical value of a model parameter (namely, the mean fertility rate) and provides the threshold below which population extinction is inevitable and above which survival occurs. The second goal of the paper (Section 3) is to investigate in more detail the critical bifurcation value when the period is two or three and how it relates to the critical value when periodicities are absent. The critical bifurcation value is determined by the oscillatory properties of the inherent fertility and survival rates only, and not those of the density regulation terms. A periodicity that results in a lower critical value is interpreted as an advantageous effect, while one that raises the critical value is interpreted as a deleterious effect.

I will focus on discrete time models structured according to reproductive maturity. The lowest dimensional model of this kind is one in which only two state variables are identified, namely, the number (or density) $J$ of juvenile (non-reproducing) individuals and the number (or density) $A$ of adult (reproducing) individuals. Using the matrix modeling methodology in [9] (also see [1]), a general juvenile-adult model has the form

$$J(t+1) = fA(t)$$
$$A(t+1) = \tau_1 J(t) + \tau_2 A(t)$$

where the time unit is the juvenile period. The vital rates $f$, $\tau_1$ and $\tau_2$ are allowed to be functions of $J$ and $A$ (density dependent) and time $t$ (non-autonomous).

Let $Z \triangleq \{0, 1, 2, \cdots\}$ denote the non-negative integers, $R$ the real numbers, $R_+$ the positive real numbers, $\bar{R}_+$ the non-negative real numbers, $R^2 = R \times R$ the Euclidean plane, and $R_+^2 = R_+ \times R_+$ the positive cone in $R^2$. Let $H_{2,p}$ denote the (finite dimensional vector space) of $p$-periodic sequences in $R^2$ ($1 \le p \in Z$). $H_{2,p}$ is a Hilbert space when endowed with the inner product $\langle x, y \rangle \triangleq \Sigma_{t=0}^{p-1} x^*(t) y(t)$ ("*" denotes transpose). Let $H_{2,p}^+$ denote the cone of positive $p$-periodic sequences in $R^2$ and $\bar{H}_{2,p}^+$ the closure of $H_{2,p}^+$. Let $\Omega$ be an open interval in $R$ that contains the closed interval $[0, +\infty[$.

In this paper the vital rates have the form

$$f \triangleq b\phi\left(c_1 J, c_2 A\right), \quad \tau_1 \triangleq s_1 \sigma_1\left(c_{11} J, c_{12} A\right), \quad \tau_2 \triangleq s_2 \sigma_2\left(c_{12} J, c_{22} A\right)$$

where, for some integer $k \ge 1$

$$\phi, \sigma_i \in C^k\left(\Omega \times \Omega \to ]0, 1]\right), \quad \phi(0, 0) = \sigma_i(0, 0) = 1 \tag{1}$$
$$b \in R_+, \quad s_i \in ]0, 1[, \text{ and } c_i, c_{ij} \in \bar{R}_+. \tag{2}$$

The constants $b$ and $s_i$ are the inherent (low density) fertility and survival rates, while the functions $\phi$ and $\sigma_i$ account for the effects of stage specific population densities on these rates. Note that the ranges of $\phi$ and $\sigma_i$ lie in the interval $]0, 1]$ and, therefore, in this model population density cannot increase fertility and survival rates (i.e., there are no Allee effects). The constant intra-specific competition coefficients $c_i$ and $c_{ij}$ measure the effects of the juvenile and adults class densities on the birth and survival rates respectively.

The resulting matrix model

$$J(t+1) = b\phi\left(c_1 J(t), c_2 A(t)\right) A(t)$$

$$\tag{3}$$

$$
\begin{aligned}
A(t+1) = {}& s_1 \sigma_1 \left(c_{11} J(t), c_{12} A(t)\right) J(t) \\
& + s_2 \sigma_2 \left(c_{12} J(t), c_{22} A(t)\right) A(t)
\end{aligned}
$$

is nonlinear and autonomous. An application of the theory in Chapter 1 of [9] implies the existence of a global continuum of positive equilibrium pairs $(b, x)$, $x = \mathrm{col}(J, A)$, that bifurcates from the extinction equilibrium $x = 0$ at the critical value $b_c = (1 - s_2)/s_1$ of the inherent fertility rate. Moreover, the bifurcation is supercritical and stable, i.e., for $b$ near $b_c$ and positive equilibria near 0, $b > b_c$ and the positive equilibria are (locally asymptotically) stable. In the next section, this result is extended to the case when the parameters $b$, $s_i$, $c_i$, and $c_{ij}$ are periodic functions of $t$ (with a common period).

## 2. A Periodically Forced Juvenile-Adult Model

Consider the juvenile-adult model (3) when the coefficients – the vital rates $b$, $s_i$ and the competition coefficients $c_i$, $c_{ij}$ – vary periodically with a common period $p \geq 1$. In place of (2) assume

$$b, s_i \in H_{1,p}^+, \ 0 < s_i(t) < 1 \quad \text{for } t \in Z, \text{ and } c_i, c_{ij} \in \bar{H}_{1,p}^+. \tag{4}$$

The resulting matrix model

$$J(t+1) = b(t)\phi\left(c_1(t) J(t), c_2(t) A(t)\right) A(t)$$

$$\tag{5}$$

$$
\begin{aligned}
A(t+1) = {}& s_1(t)\sigma_1 \left(c_{11}(t) J(t), c_{12}(t) A(t)\right) J(t) \\
& + s_2(t)\sigma_2 \left(c_{12}(t) J(t), c_{22}(t) A(t)\right) A(t)
\end{aligned}
$$

is nonlinear and non-autonomous ($p$-periodically forced). In this section the concern is with the existence and stability of (non-negative) $p$-periodic solutions of system (5), including the stability of the extinction equilibrium

$$\begin{pmatrix} J_e \\ A_e \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \tag{6}$$

Write the periodic fertility rate as

$$b(t) = \mu\left(1 + \beta(t)\right), \quad \mu \geq 0 \tag{7}$$

where $\beta(t)$ is a periodic sequence with mean $0$ and, therefore, $\mu$ is the mean fertility rate. By assumption $b(t)$ remains positive and therefore

$$\beta \in H_{1,p}, \quad \sum_{t=0}^{p-1} \beta(t) = 0, \quad \min \beta(t) > -1.$$

The approach here is to use the mean $\mu > 0$ of the fertility rate as a bifurcation parameter and to study the existence and stability of periodic solutions as a function of this parameter (using the theorems in the Appendix).

The stability properties of the extinction equilibrium (6) relate to the fundamental question of the long term viability of the population. By the linearization principle [13], one can determine the instability and (locally asymptotically) stability of this equilibrium from the stability properties of the linearization of (5) at the equilibrium, namely

$$J(t+1) = \mu \left(1 + \beta(t)\right) A(t)$$

$$\tag{8}$$

$$A(t+1) = s_1(t) J(t) + s_2(t) A(t).$$

This linear system is stable if the spectral radius of the matrix

$$X_\mu(p, 0) = \prod_{i=0}^{p-1} \begin{pmatrix} 0 & \mu \left(1 + \beta(i)\right) \\ s_1(i) & s_2(i) \end{pmatrix}$$

is less than 1 and unstable if it is larger than 1. (Here $X_\mu(t, s)$ is the fundamental solution matrix of the linear system; see the Appendix.) Since the nonzero entries in factors of this product are, by assumption, positive for all $i$, it follows for $p \geq 2$ that $X_\mu(p, 0)$ is a positive matrix. By Perron's theorem it is known that $X_\mu(p, 0)$ has a strictly dominant, positive, simple eigenvalue $\lambda = \lambda(\mu)$ (the spectral radius) and that this eigenvalue has associated positive left and right eigenvectors $l = l(\mu)$, $v = v(\mu)$, which we normalize so that $lv = 1$. Moreover, no other eigenvalue of $X_\mu(p, 0)$ has a non-negative eigenvector.

**Lemma 1.** *Assume (4) and (7). There exists a unique positive number $\mu_c > 0$ such that $\lambda(\mu_c) = 1$ and such that $\lambda(\mu) < 1$ for $\mu < \mu_c$ and $\lambda(\mu) > 1$ for $\mu > \mu_c$.*

*Proof.* By the chain rule it follows that $0 \neq X'_\mu(p, 0) \geq 0$, where the prime denotes differentiation with respect to $\mu$. A differentiation of $X_\mu(p, 0)v = \lambda v$ results in

$$\left(X_\mu(p, 0) - \lambda I\right) v' = \lambda' v - X'_\mu(p, 0)v$$

and

$$l \left(X_\mu(p, 0) - \lambda I\right) v' = \lambda' lv - l X'_\mu(p, 0)v$$

or, since $lv = 1$,

$$\lambda' = l X'_\mu(p, 0)v > 0. \tag{9}$$

It follows that $\lambda = \lambda(\mu)$ is increasing as a function of $\mu \geq 0$. Moreover,

$$\lim_{\mu \to +\infty} \lambda(\mu) = +\infty. \tag{10}$$

This follows from the observation that $\det X_\mu(p, 0)$ is the product of the two (real) eigenvalues of $X_\mu(p, 0)$, hence

$$\left| \det X_\mu(p, 0) \right| < \lambda^2,$$

and the observation that

$$\left| \det X_\mu(p, 0) \right| = \left| \prod_{i=0}^{p-1} \det \begin{pmatrix} 0 & \mu(1 + \beta(i)) \\ s_1(i) & s_2(i) \end{pmatrix} \right| = \mu^p \prod_{i=0}^{p-1} (1 + \beta(i)) s_1(i).$$

Finally, a straightforward induction shows

$$X_0(p, 0) = \prod_{i=0}^{p-1} \begin{pmatrix} 0 & 0 \\ s_1(i) & s_2(i) \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ s_1(0) \prod_{i=1}^{p-1} s_2(i) & \prod_{i=0}^{p-1} s_2(i) \end{pmatrix}$$

and thus

$$\lambda(0) = \prod_{i=0}^{p-1} s_2(i) < 1. \tag{11}$$

The statements in the Lemma follow from (9), (10) and (11). □

By Lemma 1, the linear periodic system (8) is globally asymptotically stable for $\mu < \mu_c$ and unstable for $\mu > \mu_c$.

The extinction equilibrium is $R_+^2$-*globally asymptotically stable* if it is locally asymptotically stable and if all solutions associated with non-negative initial conditions $J_0$ and $A_0$ tend to the extinction equilibrium as $t \to +\infty$.

**Theorem 2.** *Assume (1), (4) and (7). The extinction equilibrium (6) of the juvenile-adult model (5) is $R_+^2$-globally asymptotically stable for $\mu < \mu_c$ and is unstable for $\mu > \mu_c$.*

*Proof.* Lemma 1 and the linearization principle imply the extinction equilibrium is locally asymptotically stable for $\mu < \mu_c$ and unstable for $\mu > \mu_c$ [13]. All that remains to show is that solutions with non-negative initial conditions tend to the extinction equilibrium when $\mu < \mu_c$.

The inequalities

$$0 \leq J(t + 1) \leq \mu(1 + \beta(t))A(t)$$
$$0 \leq A(t + 1) \leq s_1(t)J(t) + s_2(t)A(t)$$

hold for all $t \in Z$. Let $x(t)$ and $y(t)$ denote the solutions of the linear system (8) that satisfies the initial conditions $x(0) = J(0)$ and $y(0) = A(0)$. An induction shows

$$0 \leq J(t) \leq x(t)$$
$$0 \leq A(t) \leq y(t)$$

for $t \in Z$. By Lemma 1, $\mu < \mu_c$ implies $\lim_{t \to +\infty} x(t) = \lim_{t \to +\infty} y(t) = 0$. □

The next problem concerns the existence and stability of positive $p$-periodic solutions of the juvenile-adult system (5). Specifically, the theorems given in the Appendix will aid in showing that a continuum of $p$-periodic solutions bifurcates, as a function of the average fertility rate $\mu$, from the critical value $\mu_c$.

Define $\mathcal{S}$ to be the set of all nontrivial $p$-periodic *solution pairs* $(\mu, x) \in R \times H_{2,p}$, $0 \neq x = \{\mathrm{col}(J(t), A(t))\}$, of (5). If $(\mu_c, 0) \in \bar{\mathcal{S}}$ (the closure of $\mathcal{S}$) then $(\mu_c, 0)$ is a *bifurcation point*. A solution pair $(\mu, x)$ is *positive* if $x \in H_{2,p}^+$ and *stable* if the $p$-periodic solution $x$ is locally asymptotically stable. A *continuum* $\mathcal{C}$ in $R \times H_{2,p}$ is a closed and connected set.

**Theorem 3.** *Assume (1), (4) and (7). The closure of the set of nontrivial p-periodic solution pairs of (5) contains an unbounded continuum $\mathcal{C}^+$ that bifurcates from $(\mu_c, 0)$ and is such that $\mathcal{C}^+ / \{(\mu_c, 0)\}$ contains only positive p-periodic solution pairs with $\mu > 0$.*

*Proof.* This theorem follows from Corollary 7 in the Appendix once the required conditions (1)-(4) appearing in that corollary are shown to hold. In this application of the corollary

$$A(t) = \begin{pmatrix} 0 & 0 \\ s_1(i) & s_2(i) \end{pmatrix}, \quad B(t) = \begin{pmatrix} 0 & 1 + \beta(i) \\ 0 & 0 \end{pmatrix}.$$

(1) It is shown in the proof of Lemma 1, that the linearization (8) has no nontrivial $p$-periodic solutions when $\mu = 0$.

(2) When $\mu = \mu_c$ the linearization (8) has a positive $p$-periodic solution $x(t) = \mathrm{col}(J(t), A(t)) = X_{\mu_c}(t, 0)v_c$.

(3) As indicated prior to Lemma 1, Perron's theorem implies no eigenvalue of $X_\mu(p, 0)$ other than $\lambda$ has a non-negative eigenvector. Thus, for no other value of $\mu$ except $\mu_c$ does the linearization (8) have a non-negative $p$-periodic solution.

(4) Suppose $\mathrm{col}(J(t), A(t))$ is a nontrivial $p$-periodic solution of (5) and suppose for some $t \geq 0$ the component $A(t + 1)$ equals 0. Then from the second equation in (5) it follows that both $J(t)$ and $A(t)$ equal zero. But then $J(t)$ and $A(t)$ both equal 0 for all $t$, a contradiction. Suppose, on the other hand, the component $J(t + 1) = 0$ for some $t \geq 0$. Then from the first equation in (5) it follows $A(t) = 0$ and, as argued above, it follows that $J(t)$ and $A(t)$ both equal 0 for all $t$, a contradiction. All of this is to say, that non-trivial $p$-periodic solutions of (5) are positive. □

An additional technical assumption on the density dependent terms $\phi$, $\sigma_i$ is necessary in order to address the (local asymptotic) stability of the bifurcating positive $p$-periodic solutions. The assumption (1) implies $\phi(x_1, x_2) \leq 1$, $\sigma_i(x_1, x_2) \leq 1$ for $x = (x_1, x_2) \in \Omega \times \Omega \subset R^2$ and hence the gradient vectors $\nabla \phi$ and $\nabla \sigma_i$ are component-wise non-positive at $x = 0$. In the following theorem at least one of these gradients is assumed nonzero. The proof appears in the Appendix.

**Theorem 4.** *Assume $k \geq 2$ in (1) and that at least one of the (non-positive) gradient vectors $\nabla \phi$ and $\nabla \sigma_i$ is nonzero at $x = 0$. There exists a neighborhood $\mathcal{N}$ of the bifurcation point $(\mu_c, 0)$ in $R \times H_{2,p}$ such that solution pairs from $\mathcal{C}^+ \cap \mathcal{N}$ are stable.*

That the continuum in Theorem 3 is unbounded means that either the *range* of $\mathcal{C}^+$ (that is to say, the set of $p$-periodic solutions obtained from solution pairs lying on $\mathcal{C}^+$) is unbounded in $H^+_{2,p}$ or the *spectrum* (the set of $\mu$ values obtained from positive solution pairs lying on $\mathcal{C}^+$) is unbounded in $R$ or both. By Theorems 2 and 3, the spectrum of $\mathcal{C}^+$ is a sub-interval of the half line $\mu > \mu_c$. Under an added condition on the nonlinearities in (5), the spectrum is the entire half line $\mu > \mu_c$.

**Theorem 5.** *Assume (1), (4) and (7). Also assume* $\min(c_2) > 0$, $\max(s_2) < 1$, *and that there exists a constant* $\phi_\infty < +\infty$ *for which*

$$\phi(x_1, x_2)x_2 \le \phi_\infty \quad \text{for all } x = (x_1, x_2) \in \Omega \times \Omega \subset R^2. \tag{12}$$

*Then the spectrum of the continuum* $\mathcal{C}^+$ *of p-periodic solution pairs of (5) given in Theorem 3 is the interval* $]\mu_c, +\infty[$. *In other words, the model system (5) has at least one positive p-periodic solution for each* $\mu > \mu_c$.

*Proof.* For any positive $p$-periodic solution of (5) the inequalities

$$0 < J(t+1) = \mu\,(1 + \beta(t))\,\frac{1}{c_2(t)}\phi\,(c_1(t)J(t), c_2(t)A(t))\,c_2(t)A(t) \le k_1\mu$$

and

$$0 < A(t+1) \le \max(J) + \max(s_2)\max(A)$$

hold for all $t$, where $k_1 \triangleq \phi_\infty\,(1 + \max(\beta))\,/\min(c_2)$. Thus

$$\max(J) \le k_1\mu, \qquad \max(A) \le k_2\max(J)$$

where $k_2 \triangleq 1/(1 - \max(s_2))$. These inequalities imply that if the spectrum of $\mathcal{C}^+$ is bounded then so is the range of $\mathcal{C}^+$. Since $\mathcal{C}^+$ is unbounded, this is a contradiction. Therefore the spectrum must be an unbounded interval. By Theorems 3 and 2 the closure of the spectrum contains $\mu_c$ and no points $\mu < \mu_c$. Thus, the spectrum is the interval $]\mu_c, +\infty[$.                                                                                          □

Under the conditions of Theorems 3 and 2, the periodically forced juvenile-adult model (5) has a branch of positive $p$-periodic solutions that bifurcates from the extinction equilibrium at a critical value of the average fertility rate $\mu$, and the positive $p$-periodic solutions from the continuum are stable at least for $\mu > \mu_c$ near the bifurcation point. Whether stability persists globally along the unbounded continuum $\mathcal{C}^+$ depends on the nature of the nonlinearities in the equations.

## 3. The Critical Mean Fertility Rate $\mu_c$

One of the issues addressed in the literature on periodically forced models for single species growth concerns the effect on population numbers caused by a periodically fluctuating habitat and the resulting oscillation of the carrying capacity. To address this question, authors have studied the properties of periodic solutions of models (whether differential or difference equation models) with periodic density coefficients [3], [8], [11], [14], [15], [20], [21], [24], [25], [28], [29], [30], [31]. One asks

whether such oscillations are advantageous or deleterious in the sense that mean population numbers increase or decrease in a periodic habitat.

Here I will consider a similar, but different question. Are oscillations in inherent vital rates (as opposed to density dependent coefficients) advantageous or deleterious? By advantageous is meant that the critical mean fertility rate $\mu_c$ is smaller when rates oscillate than when they do not. In this case, survival is possible at a smaller mean fertility rate in the oscillatory regime than when vital rates are constant. By deleterious is meant the opposite, that the critical mean fertility rate $\mu_c$ is larger in the presence of oscillations, and accordingly survival requires a higher mean fertility rate when oscillations are present.

Specifically, for period $p = 2$ we write the fertility rate (7) as

$$b(t) = \mu \left(1 + \alpha(-1)^t\right), \quad \mu > 0, \quad 0 \leq \alpha < 1$$

and study the critical mean fertility rate $\mu_c = \mu_c(\alpha)$ for model (5) as a function of the amplitude $\alpha$. We are interested in conditions under which $\mu_c$ increases or decreases as a function of $\alpha$. Note that the phase has been set (without loss in generality) so that the maximum of $b(t)$ occurs at $t = 0$ by requiring $\alpha$ to be positive.

The critical value $\mu_c(\alpha)$ is the value of the mean fertility rate $\mu$ for which the dominant eigenvalue (spectral radius) $\lambda = \lambda(\mu, \alpha)$ of the matrix

$$X_\mu(2, 0) = \prod_{i=0}^{1} \begin{pmatrix} 0 & \mu\left(1 + \alpha(-1)^i\right) \\ s_1(i) & s_2(i) \end{pmatrix}$$

$$= \begin{pmatrix} \mu\left(1 - \alpha\right)s_1(0) & \mu\left(1 - \alpha\right)s_2(0) \\ s_1(0)s_2(1) & s_2(0)s_2(1) + \mu\left(1 + \alpha\right)s_1(1) \end{pmatrix}$$

equals 1. Calculations show

$$\mu_c(\alpha) = \frac{1}{2}\left(\frac{1}{(1+\alpha)\,s_1(1)} + \frac{1}{(1-\alpha)\,s_1(0)} - \Gamma(\alpha)\right) > 0$$

and

$$\mu_c'(\alpha) = \frac{\mu_c(\alpha)}{(1-\alpha^2)\,\Gamma(\alpha)}\left(\frac{s_1(0) - s_1(1)}{s_1(0)s_1(1)} - 2\alpha\mu_c(\alpha)\right) \tag{13}$$

where

$$\Gamma(\alpha) \overset{\circ}{=} \left(\left(\frac{1}{(1+\alpha)\,s_1(1)} - \frac{1}{(1-\alpha)\,s_1(0)}\right)^2 + 4\frac{s_2(0)s_2(1)}{s_1(0)s_1(1)\left(1-\alpha^2\right)}\right)^{1/2} > 0$$

for $0 \leq \alpha < 1$. In the absence of oscillations in the fertility rate $b(t)$ (i.e., when $\alpha = 0$), the critical value is

$$\mu_c(0) = \frac{1}{2}\left(\frac{1}{s_1(1)} + \frac{1}{s_1(0)} - \left(\left(\frac{1}{s_1(1)} - \frac{1}{s_1(0)}\right)^2 + 4\frac{s_2(0)s_2(1)}{s_1(0)s_1(1)}\right)^{1/2}\right).$$

Two cases arise.

Suppose the survival rate $s_1(t)$ is either constant or is out-of-phase with $b(t)$, i.e., $s_1(0) = s_1(1)$ or $s_1(0) < s_1(1)$ respectively. From (13) this case implies $\mu'_c(\alpha) < 0$ for $0 < \alpha < 1$. This means the critical bifurcation value $\mu_c(\alpha)$ is smaller when $b(t)$ is periodic than when it is constant.

The case when $s_1(t)$ oscillates in-phase with $b(t)$, i.e. $s_1(0) > s_1(1)$ is more complicated. From (13) this case implies

$$\mu'_c(0) = \frac{\mu_c(0)}{\Gamma(0)} \left( \frac{s_1(0) - s_1(1)}{s_1(0)s_1(1)} \right) > 0.$$

This means that the critical bifurcation value $\mu_c(\alpha)$ is larger when $b(t)$ is periodic for (at least) small relative amplitude oscillations $\alpha > 0$. However, it can turn out that the reverse is true when $\alpha$ is near 1. For example, a sufficient condition for this is $\mu_c(1) < \mu_c(0)$ where

$$\mu_c(1) \overset{\circ}{=} \lim_{\alpha \to 1-} \mu_c(\alpha) = \frac{1 - s_2(0)s_2(1)}{2s_1(1)}.$$

That is to say, if

$$\frac{s_1(1)}{s_1(0)} > \frac{1 + s_2(0)s_2(1)}{2}$$

then $\mu_c(\alpha) < \mu_c(0)$ for $\alpha$ close to 1. This condition can be interpreted as a constraint on the amplitude of $s_1(t)$. It is possible, when this inequality is violated, that $\mu_c(\alpha) > \mu_c(0)$ for all $0 < \alpha < 1$.

In summary: if the fertility rate $b(t)$ and the juvenile survival rate $s_1(t)$ oscillate out-of-phase, then survival requires a *smaller* critical mean fertility rate $\mu_c(\alpha)$ than if the fertility rate were constant. Moreover, the critical mean fertility rate $\mu_c(\alpha)$ *decreases* as the relative amplitude $\alpha$ of the oscillation increases. If, on the other hand, the oscillations in $b(t)$ and $s_1(t)$ are in-phase, then for small amplitude oscillations survival requires a *larger* critical mean fertility rate than if the fertility rate were constant. However, this can reverse (for example, when the amplitude of the oscillation in $s_1(t)$ is small) for larger relative amplitudes $\alpha$, that is to say, it can happen that for relative amplitudes near $\alpha = 1$ the critical mean fertility rate will decrease and in fact drop below that for a constant fertility rate. These possibilities are illustrated in Fig 1.

As an example, consider the juvenile-adult model

$$J(t + 1) = b(t) \frac{1}{1 + c_2 A(t)} A(t)$$

$$A(t + 1) = s_1(t)J(t) + s_2(t)A(t)$$

(14)

$$b(t) = \mu \left(1 + \alpha(-1)^t\right), \quad s_1(t) = s \left(1 + \alpha_1(-1)^t\right)$$
$$s_2(t) = s_2 = \text{constant}, \quad 0 < s, s_2 < 1.$$

This is a periodically forced, stage structured version of the discrete logistic (Beverton-Holt) equation. Theorem 2 implies global extinction when $\mu < \mu_c(\alpha)$.
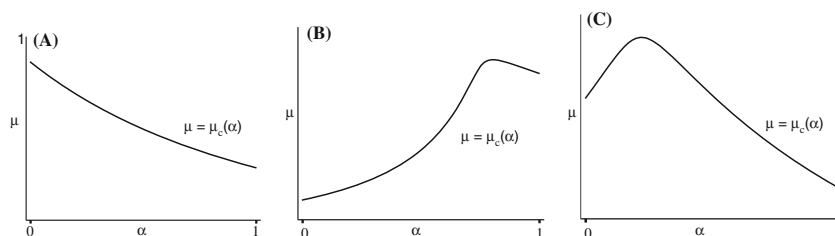
**Fig. 1.** The boundary of the extinction-survival region for model (14) in the $\alpha$, $\mu$-plane is given by the equation $\lambda(\mu, \alpha) = 1$, which serves to define the critical mean value $\mu_c(\alpha)$ of the fertility rate $b(t)$ as a function of the amplitude $\alpha$. Extinction occurs for mean fertility rates $\mu < \mu_c(\alpha)$ and survival occurs for $\mu > \mu_c(\alpha)$. Thus, in the $\alpha$, $\mu$-plane, the extinction region lies under the critical curve defined by $\mu = \mu_c(\alpha)$ shown in plots (A), (B) and (C) and the survival region lies above the curve. (A) When the fertility rate $b(t)$ and the juvenile survival rate $s_1(t)$ oscillate out-of-phase (or if $s_1(t)$ is constant), then the critical mean fertility rate $\mu_c(\alpha)$ decreases as a function of the amplitude $\alpha$. In this case it is advantageous to have an oscillating fertility rate in the sense that survival occurs at a lower critical value $\mu_c(\alpha)$ in the presence of oscillations ($\alpha > 0$) than in their absence ($\alpha = 0$). (B) & (C) When $b(t)$ and $s_1(t)$ oscillate in-phase, then the critical curve increases at least for small amplitudes $\alpha$. The critical curve might or might not lie above the value $\mu_c(0)$ for all amplitudes $\alpha$, however, depending on the amplitude of the oscillation in the survival rate $s_1(t)$. When the survival rate amplitude is large, which is the case in (B), oscillations are deleterious at all fertility rate amplitudes $\alpha$. For smaller survival rate amplitudes, the critical curve can drop below the level $\mu_c(0)$ for $\alpha$ near 1, as illustrated in (C). In this case, oscillating vital rates have a deleterious effect for small fertility rate amplitudes $\alpha$, but an advantageous effect for large amplitudes $\alpha$.

For $\mu > \mu_c(\alpha)$ Theorem 5 implies that there exists at least one positive 2-cycle solution and that it is locally asymptotically stable at least for $\mu$ near $\mu_c(\alpha)$. (If $s_2 = 0$, a case not considered here, it is known that for $\mu > \mu_c(\alpha)$ the positive 2-cycle is unique and is globally asymptotically stable with respect to non-negative, nontrivial initial conditions [18,20]. These global properties of the positive 2-cycles remain open questions when $s_2 > 0$.)

Fig. 2 illustrates the various possibilities concerning the advantageous or deleterious effect of oscillatory $b(t)$ and $s_1(t)$ in (14). In Figure 2A we see how a population that faces extinction can survive, with the same mean fertility rate, if the fertility rate oscillates periodically. If the survival rate $s_1(t)$ also oscillates, and does so out-of-phase with $b(t)$, the population's survivorship is further enhanced. Figure 2B illustrates what can happen, however, when $s_1(t)$ oscillates in-phase with $b(t)$. A population that survives with a constant fertility rate, goes extinct when the fertility rate of the same mean oscillates with small amplitude, but still survives if it oscillates with a large amplitude.

This investigation for period $p = 2$ shows that the phase relationship between oscillations in the fertility rate and the juvenile survival rate are important in determining whether oscillations in inherent vital rates are deleterious or advantageous. For higher periods the situation is more complicated and remains to be investigated. A hint at the important of intricate phase relationships is seen in the period $p = 3$ case.
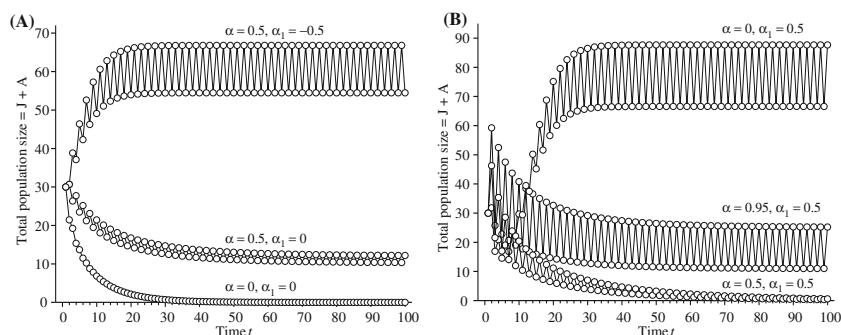
**Fig. 2.** The total population size $J + A$ is displayed for selected solutions of the periodically forced juvenile-adult logistic model (14) for parameter values $c = 0.01$, $s = 0.9$, $s_2 = 0.1$ and initial conditions $J(0) = 0$, $A(0) = 30$. (A) With mean fertility rate $\mu = 0.8$ different asymptotic dynamics occur for different oscillatory properties in the fertility rate $b(t)$ and the survival rate $s_1(t)$. When both rates are constant, the population goes extinct ($\alpha = \alpha_1 = 0$). However, when the fertility rate $b(t)$ oscillates periodically, the population survives ($\alpha = 0.5$, $\alpha_1 = 0$). Survival is enhanced when, in addition, the survival rate $s_1(t)$ oscillates out-of-phase with $b(t)$ ( $\alpha = 0.5$, $\alpha_1 = -0.5$). For these parameter values and this mean fertility rate, oscillations in the adult fertility rate are advantageous. (B) A non-oscillatory fertility rate $b(t)$ with mean $\mu = 1.25$ and an oscillatory survival rate $s_1(t)$ lead to oscillatory survival ($\alpha = 0$, $\alpha_1 = 0.5$). Periodic oscillations in $b(t)$ that are in-phase with those in $s_1(t)$ can lead to either extinction ($\alpha = 0.5$, $\alpha_1 = 0.5$) or survival ($\alpha = 0.95$, $\alpha_1 = 0.5$) depending on the amplitude $\alpha$.

The characteristic polynomial of the $2 \times 2$ matrix $X_\mu(p, 0)$ is $\lambda^2 - T(\mu, \alpha)\lambda + D(\lambda, \alpha)$ where the trace $T(\mu, \alpha)$ and determinant $D(\mu, \alpha)$ of $X_\mu(p, 0)$ depend on the mean and amplitude of the fertility rate $b(t) = \mu(1 + \alpha\beta(t))$. Here $\beta(t)$ is a $p$-periodic sequence of mean 0. The critical mean fertility rate $\mu = \mu_c(\alpha)$ is that value of $\mu$ for which $\lambda = 1$ is a root. An implicit differentiation of $1 - T(\mu_c(\alpha), \alpha) + D(\mu_c(\alpha), \alpha) = 0$ with respect to $\alpha$ followed by an evaluation at $\alpha = 0$ yields the formula

$$\mu_c'(0) = -\left. \frac{\frac{d}{d\alpha}(T - D)}{\frac{d}{d\mu}(T - D)} \right|_{\alpha=0}.$$

In the case $p = 3$ this formula implies

$$\mu_c'(0) = -\frac{1}{\mu_c(0)} \frac{s_1(1)s_2(2) + s_1(2)s_2(0) + s_1(0)s_2(1) + 3s_1(0)s_1(1)s_1(2)\mu_c^2(0)}{s_1(1)s_2(2)\beta(0) + s_1(2)s_2(0)\beta(1) + s_1(0)s_2(1)\beta(2)}.$$

Since the numerator and $\mu_c(0)$ are positive, it follows that

$$\mu_c'(0) > 0 \quad \text{if} \quad \eta < 0$$
$$\mu_c'(0) < 0 \quad \text{if} \quad \eta > 0$$

where

$$\eta \triangleq s_1(1)s_2(2)\beta(0) + s_1(2)s_2(0)\beta(1) + s_1(0)s_2(1)\beta(2).$$

(Note: $\beta(0) + \beta(1) + \beta(2) = 0$.) If $\mu_c'(0) < 0$ then for small amplitudes $\alpha$, the oscillations are advantageous in the sense that survival occurs for a smaller mean fertility rate. If $\mu_c'(0) > 0$ the oscillations are deleterious for small amplitudes $\alpha$ in the sense that survival occurs for a larger mean fertility rate. Which case occurs depends on the sign of $\eta$, that is to say on how the phases of the oscillations in the fertility and survival rates relate.

## 4. Concluding Remarks

The goal of this paper is to consider the effect of modifying the autonomous, discrete juvenile-adult model (3) by permitting the model parameters to be periodic. The autonomous model possesses, under general conditions, a global continuum of positive equilibria that bifurcates from the extinction equilibrium at a critical value of the adult fertility rate $b$. In Section 2 this fact is generalized to the periodically forced version of the model (5). It is shown that there is a unique critical value $\mu_c$ of the mean, adult fertility rate $\mu$ at which a continuum of positive $p$-cycles bifurcate from the extinction equilibrium state. The population goes extinct for mean fertility rates less than the critical value: $\mu < \mu_c$. If $\mu > \mu_c$, there exists a positive (survival) $p$-cycle solution and this cycle is (locally asymptotically) stable at least for $\mu$ near $\mu_c$. In Section 3 the critical fertility rate for the autonomous model is compared to the critical mean fertility rate in the periodic model for the case of period $p = 2$ and 3. It is found that periodic forcing can result in either an increase or a decrease of this critical value, depending on certain phase relationships among the oscillations of the inherent fertility and survival rates (oscillations in density terms are not involved). Thus, for example, when $p = 2$ and the adult fertility and juvenile survival rates oscillate out-of-phase, the critical value decreases with periodic oscillations and in this sense the periodic oscillations are advantageous. If these vital rates oscillate in-phase, the opposite is true for small amplitude oscillations in the fertility rate (although a decrease can occur for large amplitude oscillations). A similar result is shown for $p = 3$, although the phase relationships among the vital rates can be more complicated. In what way these results extend to higher period forcing remains an open question. Also of interest would be to extend these results to structured models with additional life cycle stages.

## Appendix

The set $H_{m,p}$ of $p$-periodic sequences in $R^m$ ($1 \le p \in Z$)

$$H_{m,p} \triangleq \left\{ x : Z \to R^m \text{ and } x(t + p) = x(t), \ t \in Z \right\}$$

is a Hilbert space under the inner product $\langle x, y \rangle \triangleq \Sigma_{t=0}^{p-1} x^*(t) y(t)$ ("*" denotes transpose). Let

$$H_{m,p}^+ = \left\{ x \in H_{m,p} : x(t) > 0 \quad \text{for all } t \in Z \right\}$$

denote the cone of positive $p$-periodic sequences.

Consider the linear matrix equations

$$x(t + 1) = P(t)x(t) \tag{15}$$

$$x(t + 1) = P(t)x(t) + h(t), \quad t \in Z \tag{16}$$

where $h \in H_{m,p}$ and $P(t)$ is a $p$-periodic matrix: $P(t + p) = P(t), t \in Z$. The solution of the homogeneous equation (15) is

$$x(t) = X(t, 0)x(0)$$

where $X(t, s)$ is the fundamental solution matrix

$$X(t, s) \triangleq \begin{cases} P(t-1)P(t-2) \cdots P(s+1)P(s) & \text{for } t = s+1, s+2, \ldots \\ I & \text{for } t = s \end{cases}$$

for $t, s \in Z$. The solution of the homogeneous equation (15) is $p$-periodic if and only if $x(0) = x(p)$, i.e., if and only if $x(0)$ satisfies

$$(X(p, 0) - I) x(0) = 0.$$

Thus, there exists a *nontrivial* $p$-periodic solution if and only if 1 is an eigenvalue of $X(p, 0)$. The solution of the nonhomogeneous equation (16) is given by the discrete variation of constants formula [13]

$$x(t) = \begin{cases} X(t, 0)x(0) + \sum_{i=0}^{t-1} X(t, i+1)h(i) & \text{for } t = 1, 2, \ldots \\ x(0) & \text{for } t = 0. \end{cases} \tag{17}$$

The solution is $p$-periodic if and only if $x(0) = x(p)$, i.e., $x(0)$ solves the equation

$$(I - X(p, 0)) x(0) = \sum_{i=0}^{p-1} X(p, i+1)h(i). \tag{18}$$

If the homogeneous equation has no nontrivial $p$-periodic solution, then $I - X(p, 0)$ is invertible and the nonhomogeneous equation (16) has a unique $p$-periodic solution

$$x(t) = X(t, 0) (I - X(p, 0))^{-1} \sum_{i=0}^{p-1} X(p, i+1)h(i) + \sum_{i=0}^{t-1} X(t, i+1)h(i). \tag{19}$$

The assumption that (15) has no nontrivial $p$-periodic solution is equivalent to the nonsingularity of the matrix $I - X(p, 0)$, i.e., that $\lambda = 1$ is not an eigenvalue of $X(p, 0)$. If the homogeneous equation (15) does have a nontrivial $p$-periodic solution, then the nonhomogeneous equation (18) has a solution if and only if the right hand side is orthogonal to the kernel of the transpose, that is,

$$l \sum_{i=0}^{p-1} X(p, i+1)h(i) = 0 \tag{20}$$

for all left eigenvectors $l$ of $X(p, 0)$ associated with eigenvalue 1.

If 1 is not an eigenvalue of $X(p, 0)$, the unique $p$-periodic solution (19) of the nonhomogeneous equation (16) is

$$x(t) = \sum_{i=0}^{p-1} G(t, i)h(i)$$

where

$$G(t, i) = \begin{cases} X(t, 0)\,(I - X(p, 0))^{-1}\,X(p, i+1) + X(t, i+1) & \text{for } 0 \leq i < t \\ X(t, 0)\,(I - X(p, 0))^{-1}\,X(p, i+1) & \text{for } 0 \leq t \leq i \leq p-1 \end{cases}$$

is the *Green's function* associated with (15). This formula defines a solution operator

$$G : H_{m,p} \to H_{m,p}$$

that is linear and bounded (and therefore compact, since $H_{m,p}$ is finite dimensional). For $h \in H_{m,p}$, $x = Gh$ is the unique $p$-periodic solution of the nonhomogeneous equation (16).

Consider a homogeneous equation whose projection matrix $P$ contains a parameter $\mu \in R$ that appears linearly:

$$x(t+1) = (A(t) + \mu B(t))\,x(t). \tag{21}$$

Denote the fundamental solution matrix by $X_\mu(t, s)$. If (21) has a nontrivial $p$-periodic solution $x \in H_{m,p}$ when $\mu = \mu_c$, then $\mu_c$ is a *characteristic value* $\mu_c$. A characteristic value is *simple* if $\dim \ker \left(I - X_{\mu_c}(p, 0)\right) = 1$, i.e., 1 is an eigenvalue of $X_{\mu_c}(p, 0)$ with (geometric) multiplicity 1.

Consider the periodically forced, nonlinear equation

$$x(t+1) = (A(t) + \mu B(t) + h(t, \mu, x(t)))\,x(t) \tag{22}$$

where $\mu \in R$ is a real parameter. Here $A(t)$ and $B(t)$ are $p$-periodic matrices and the matrix $h = (h_{ij})$ is a higher order term near $x = 0$. Assume[2]

$$h_{ij}(t, \cdot, \cdot) \in C^k \left(R^1 \times H_{1,p} \to H_{1,p}\right), \quad \text{for some } k \in Z \text{ and } \text{ for all } t \in Z \tag{23}$$

$||h(t, \mu, x)x|| = O\left(||x||^2\right)$ near $x = 0$ uniformly on finite $\mu$ intervals and for all $t \in Z$.

Suppose $\mu = 0$ is *not* a characteristic value of (21) and let $G$ be the Green's function of $x(t+1) = A(t)x(t)$. Solving the equation (22) for a $p$-periodic solution $x \in H_{m,p}$ is equivalent to solving the operator equation

$$x = \mu Lx + g(\mu, x) \tag{24}$$

where $L \triangleq GB$ is linear and $g : R^1 \times H_{m,p} \to H_{m,p}$, defined by $g(\mu, x) \triangleq Gh(t, \mu, x)x$, is $O\left(||x||^2\right)$ near $x = 0$ in $H_{m,p}$ uniformly on bounded $\mu$ intervals.

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[2] $||h|| = O\left(||x||^2\right)$ near $x = 0$ means $||h|| \leq c\,||x||^2$ near $x = 0$ for some constant $c$. $||x|| \triangleq \langle x, x \rangle^{1/2}$.

Define $\mathcal{S}$ to be the set of all nontrivial $p$-periodic solution pairs $(\mu, x) \in R \times H_{m,p}$, $x \neq 0$, of (24) (equivalently (22)). If $(\mu_c, 0) \in \bar{\mathcal{S}}$ (the closure of $\mathcal{S}$) then $(\mu_c, 0)$ is a bifurcation point. A solution pair $(\mu, x)$ is *positive* if $x \in H_{m,p}^+$.

A necessary condition that $(\mu_c, 0)$ is a bifurcation point of (24) is that $\mu_c$ be a characteristic value of $L$ (the reciprocal of a nonzero eigenvalue), that is to say, $x = \mu_c L x$ for some $0 \neq x \in H_{m,p}$. By definition, a characteristic value of the linear operator $L$ is a characteristic value of the equation (21).

If $\mu_c$ is a characteristic value of $L$, a *characteristic solution x* is a nontrivial $p$-periodic solution of the linear equation (21), namely, $x = X_{\mu_c}(t, 0)v_c$ where $v_c$ is a right eigenvector of $X_{\mu_c}(p, 0)$ associated with eigenvalue 1.

The following theorem follows from the global bifurcation theorems of Rabinowitz applied to the operator equation (24) [27,34]. For related theorems see [10,22].

**Theorem 6.** *Assume A and B are p-periodic matrices and h satisfies (23) in the nonlinear, periodically forced equation (22). Suppose*

*(1) $\mu = 0$ is not a characteristic value of the linearization (21);*
*(2) $\mu_c$ is a simple characteristic value of (21) for which there is an associated positive characteristic p-periodic solution (i.e., $X_{\mu_c}(p, 0)$ has a positive eigenvector $v_c > 0$ associated with eigenvalue 1).*

*Then there exists a continuum[3] $\mathcal{C}^+$ in $\bar{\mathcal{S}}$ that contains the bifurcation point $(\mu_c, 0)$ and satisfies one of the following alternatives:*

*(a) $\mathcal{C}^+ / \{(\mu_c, 0)\}$ contains only positive p-periodic solution pairs $(\mu, x) \in R \times H_{m,p}^+$ for which $\mu > 0$ and $\mathcal{C}^+$ is unbounded in $R \times H_{m,p}^+$;*
*(b) $\mathcal{C}^+ / \{(\mu_c, 0)\}$ contains a nontrivial, non-negative equilibrium pair $(\mu^*, x^*) \in R \times \partial H_{m,p}^+$;[4]*
*(c) $\mathcal{C}^+ / \{(\mu_c, 0)\}$ contains a point $\left(\mu_c^*, 0\right)$ where $\mu_c^* \neq \mu_c$ is a characteristic value of (21) with $v_c^* \geq 0$.*

Alternative (b) says that the bifurcating continuum of nontrivial equilibria leaves the positive cone. Often in applications one can rule this alternative out by showing that no nontrivial $p$-periodic solution can lie on the boundary $\partial H_{m,p}^+$ of the positive cone; that is to say, in many applications one can show that

$$\text{if } x \in \bar{H}_{m,p}^+ \text{ solves (22) then either } x = 0 \text{ or } x(t) > 0 \quad \text{for } t \in Z. \quad (25)$$

Alternative (c) says that the bifurcating continuum of nontrivial equilibria also bifurcates from another characteristic value of (21). This alternative is ruled out, of course, if no other characteristic value of $L$ is associated with a non-negative solution $x \in \bar{H}_{m,p}^+$.

**Corollary 7.** *[10] Assume A and B are p-periodic matrices and h satisfies (23) in the nonlinear, periodically forced equation (22). Assume*

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[3] A closed connected set.
[4] $\bar{H}_{m,p}^+$ denotes the closure of $H_{m,p}^+$ and $\partial H_{m,p}^+ = \bar{H}_{m,p}^+ / H_{m,p}^+$ denotes the boundary of the positive cone $H_{m,p}^+$.

*(1) $\mu = 0$ is not a characteristic value of the linearization (21);*
*(2) $\mu_c$ is a simple characteristic value of (21) for which there is an associated positive characteristic p-periodic solution;*
*(3) (21) has no other characteristic value with a non-negative solution $x \in \bar{H}_{m,p}^+$;*
*(4) (25) holds.*

*Then there exists an unbounded continuum $C^+$ in $\bar{S}$ such that $C^+ / \{(\mu_c, 0)\}$ contains only positive p-periodic solution pairs $(\mu, x) \in R \times H_{m,p}^+$ with $\mu > 0$.*

That $C^+$ is unbounded means that either the set of positive $p$-cycles associated with $C^+$ is unbounded or the spectrum $\sigma(C^+) \triangleq \{\mu : (\mu, x) \in C^+\}$ is unbounded (or both).

A stability analysis of the equilibrium $x = 0$ of (22) is possible by means of the linearization principle [13]. The Jacobian at $x = 0$ is

$$X_\mu(p, 0) = \prod_{i=1}^p (A(p - i) + \mu B(p - i)). \qquad (26)$$

Define

$$\delta \triangleq l_c \frac{d}{d\mu} X_\mu(p, 0)|_{\mu=\mu_c} v_c \qquad (27)$$

where $l_c$ and $v_c$ are the left and right eigenvalues of $X_{\mu_c}(p, 0)$ normalized so that $l_c v_c = 1$.

**Theorem 8.** *[22] In the nonlinear, periodically forced equation (22) assume A and B are p-periodic matrices and h satisfies (23) with $k \geq 1$. Suppose $\mu_c$ is a simple characteristic value of (21) with the property that 1 is a strictly dominant eigenvalue of $X_{\mu_c}(p, 0)$ and let $l_c$ and $v_c$ denote left and right eigenvectors of $X_{\mu_c}(p, 0)$ normalized so that $l_c v_c = 1$. Further, suppose 0 is not an eigenvalue of $X_{\mu_c}(p, 0)$. If $\delta > 0$ then the trivial solution $x = 0$ loses stability as $\mu$ increases through $\mu_{cr}$. If $\delta < 0$ then $x = 0$ gains stability as $\mu$ increases through $\mu_{cr}$.*

An analysis of the properties of the positive $p$-cycles near the bifurcation point $(\mu_c, 0)$ guaranteed by Theorem 6 is possible by means of a parameterization of the bifurcating branch:

$$x(t) = x_1(t)\varepsilon + O\left(\varepsilon^2\right) \qquad (28)$$

$$\mu = \mu_c + \mu_1 \varepsilon + O\left(\varepsilon^2\right)$$

(under the assumption that $k \geq 2$ in (23)). These expansions provide approximations to the positive $p$-cycles near the bifurcation point and allow us to make approximations to the Jacobian of the composite and its dominant eigenvalue

$$\lambda = 1 + \varepsilon\lambda_1 + O\left(\varepsilon^2\right),$$

which determines the stability of the cycles. Here $x_1(t)$ is the positive $p$-cycle solution of the linearization (21) with $\mu = \mu_{cr}$

$$x_1(t) = X_{\mu_c}(t, 0)v_c$$

and the positive $p$-cycles correspond to $\varepsilon > 0$.

To calculate the coefficients in (28) one substitutes these expansions into the nonlinear equation (22) and equates coefficients of like powers of $\varepsilon$ from both sides of the resulting expressions. This leads to solvable linear equations matrix equations and with the aid of the orthogonality condition (20) one can calculate formulas for $\mu_1$ and $\lambda_1$ [22].

Define $\gamma_{ij}(t)$ to be the gradient of $h_{ij}$ with respect to $x$ evaluated at $(\mu, x) = (\mu_c, 0)$

$$\gamma_{ij}(t) \triangleq \nabla_x h_{ij}(t, \mu, x)\big|_{(\mu,x)=(\mu_c,0)} \tag{29}$$

and let

$$d_{ij}(t) \triangleq \gamma_{ij}^*(t)x_1(t).$$

Form matrix $D(t) = \big(d_{ij}(t)\big)$ and define

$$\kappa \triangleq -l_c\sum_{t=0}^{p-1} X_{\mu_c}(p, t+1)D(t)X_{\mu_c}(t, 0)v_c. \tag{30}$$

Then it turns out

$$\mu_1 = \frac{1}{2}\frac{\kappa}{\delta}, \qquad \lambda_1 = -\frac{1}{2}\kappa. \tag{31}$$

Note that the bifurcation is supercritical if $\mu_1 > 0$ and subcritical if $\mu_1 < 0$. The dominant eigenvalue $\lambda$ is less than 1 (for $\varepsilon > 0$ small) if $\mu_1 > 0$ and greater than 1 if $\mu_1 < 0$.

The bifurcation at $\mu = \mu_c$ described in Theorem 6 is *stable* if the $p$-periodic solutions from the positive solutions pairs near the bifurcation point $(\mu, x) = (\mu_c, 0)$ are (locally asymptotically) stable. If these positive periodic solutions are unstable, then the bifurcation is *unstable*.

The equalities (31) imply the following result.

**Theorem 9.** *[22] In addition to the assumptions in Theorem 8 assume h satisfies (23) with $k \geq 2$ and that $\kappa \neq 0$.*

*Suppose $\delta > 0$, i.e., the trivial (extinction) equilibrium $x = 0$ loses stability as $\mu$ increases through $\mu_c$. Then for $\mu$ sufficiently close to $\mu_c$ the bifurcation of positive p-cycles is supercritical and stable if $\kappa > 0$ and is subcritical and unstable if $\kappa < 0$.*

*Suppose $\delta < 0$, i.e., the trivial (extinction) equilibrium $x = 0$ loses stability as $\mu$ decreases through $\mu_c$. Then for $\mu$ sufficiently close to $\mu_c$ the bifurcation of positive p-cycles is supercritical and stable if $\kappa < 0$ and is subcritical and unstable if $\kappa > 0$.*

Theorems 6, 8 and 9 are generalizations to periodic equations ($p \geq 1$) of theorems known for equilibria of autonomous equations ($p = 1$) [9], [10], [22].

**Proof of Theorem 4.** This theorem follows from Theorem 9 as soon as we show that the quantities $\delta$ and $\kappa$, given by the formulas (27) and (30) are positive.

The quantity $\delta$ is the same as the quantity $\lambda'$ calculated in the proof of Lemma 1. Thus, (9) shows $\delta > 0$.

For the juvenile-adult model (5) the entries in the matrix $h(t, x_1, x_2) = \left(h_{ij}(t, x_1, x_2)\right)$ are

$$h_{11} \equiv 0$$
$$h_{12} = b(t)\left(\phi\left(c_1(t)x_1, c_2(t)x_2\right) - 1\right)$$
$$h_{21} = s_1(t)\left(\sigma_1\left(c_{11}(t)x_1, c_{12}(t)x_2\right) - 1\right)$$
$$h_{22} = s_2(t)\left(\sigma_2\left(c_{21}(t)x_1, c_{22}(t)x_2\right) - 1\right).$$

Thus, the gradient $\gamma_{11} \equiv 0$ and the remaining gradients $\gamma_{ij}$ are, under the assumptions on the gradients of $\phi$ and $\sigma_i$, all non-positive with at least one being nonzero. It follows that the matrix $D(t) = \left(d_{ij}(t)\right)$ has non-positive entries at least one of which is nonzero. Because the fundamental solution matrix has the sign structure

$$X_\mu(2, t) = \begin{pmatrix} 0 & + \\ + & + \end{pmatrix}.$$

both vectors $l_c X_{\mu_c}(p, t + 1)$ and $X_{\mu_c}(t, 0)v_c$ are positive vectors. It follows that each term $l_c X_{\mu_c}(p, t + 1)D(t)X_{\mu_c}(t, 0)v_c$ appearing in the formula (30) for $\kappa$ is positive. As a result $\kappa > 0$.

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