PERIODIC McKENDRICK EQUATIONS FOR AGE-STRUCTURED POPULATION GROWTH

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Abstract—With the averaged net reproductive rate used as a bifurcation parameter, the existence of a local parameterized branch of time-periodic solutions of the McKendrick equations is proved under the assumption that the death and fertility rates suffer small-amplitude time periodicities. The required linear theory is developed and the results are illustrated by means of a simple example in which fertility varies cosinusoidally in time.

INTRODUCTION

The equations

$$\rho_t + \rho_a + D\rho = 0, \quad t > 0, \quad 0 < a < A < +\infty, \tag{1.1}$$

$$\rho(t, 0) = \int_0^A F\rho(t, a)\, da, \quad t > 0, \tag{1.2}$$

for the age-specific density $\rho = \rho(t, a)$ of a single age-structured species at time t describe the death and birth processes respectively in terms of a per unit death rate D and fertility rate F. The real A is a maximum age for any individual in the population and it is required that $\rho(t, A) \equiv 0$ for all $t > 0$. These equations are now usually referred to as the McKendrick equations.

In using the system of Eqs. (1.1)–(1.2) as a model for population growth most studies allow the vital rates D and F to be dependent upon age a and also, in modelling density-dependent growth, upon the density ρ. The vast majority of population growth models are autonomous, i.e. they assume that these vital rates do not depend explicitly on time t. Under such an assumption the important fundamental questions concerning asymptotic states as $t \to +\infty$, around which theoretical population dynamics centers, deal with the existence and stability of equilibrium (i.e. time-independent) solutions and there is a rapidly growing literature on these topics for the general McKendrick Eqs. (1.1)–(1.2) as well as many specialized cases derived from them.

Despite the widely recognized biological fact that death and fertility rates for real populations are rarely constant in time the amount of literature dealing with model equations in which vital rates are explicitly time dependent is comparatively very small. This is true even for the simpler classical models of non-age-structured populations. In recent years considerable attention has been paid to the important and difficult question of the effects due to stochastic fluctuations of model parameters in population-growth models. While it is true that vital rates and other model parameters can be expected to suffer significant stochastic variations in time for some populations under certain conditions, it is also true that some parameters for other populations or for populations under other conditions may well exhibit regular recurring fluctuations in time (e.g., see [1]). For example, physical environmental conditions such as temperature and humidity and the availability of food, water and other resources (just to mention a few) usually vary in time, often fairly regularly, with the yearly seasons (or with daily or monthly periods or even cycles with other periods). Natural birth rates are often markedly seasonal, as are death rates. These can be due to such things as exposure to seasonal weather patterns and resource availabilities, susceptibility to diseases or exposure to predators and competitors, etc.

A natural simplifying mathematical assumption to make in considering such regular fluctuations in model parameters is that they are exactly periodic. This leads to the study of

nonautonomous equations with periodic coefficients. For example. in the general model (1.1)–(1.2) D and F might be assumed to depend explicitly on time t in a periodic manner.

In general. nonautonomous periodic differential equations do not have equilibrium solutions and the familiar techniques available for studying the existence and stability properties of equilibrium solutions are not applicable. Instead one has the more difficult challenge of dealing with the existence and the stability of periodic solutions. as well as the challenge of analysing the properties of these solutions. Such problems have been considered in recent papers for a variety of non-age-structured population-growth models[2–13].

With regard to the autonomous McKendrick equations (1.1)–(1.2) there is a growing body of literature dealing with equilibrium solutions (e.g. [15–19]). but little in the literature concerning periodic solutions of periodic equations[20]. The purpose of this paper is to consider the existence of positive periodic solutions of (1.1)–(1.2) when the vital rates D and F are explicitly periodic in time t. using a bifurcation theory approach analogous to that used in [15,16] for equilibrium solutions of the autonomous case.

The primary assumption will be that the time periodicities in D and F are of small amplitude α. This assumption permits the use of perturbation techniques and the calculation of lower-order approximations to solutions. It is. however. a restrictive assumption and precludes the consideration of large "catastrophic" fluctuations in such things as environmental conditions. availability of resources. population densities. etc. Nonetheless. as is often pointed out with regard to oscillatory phenomena in many kinds of models and applications. small-amplitude parameter oscillations can lead to significant effects and to ignore them in favor of averaged values can be misleading. Moreover. the effects of small-amplitude periodicities often persist in specific models for larger-amplitude periodicities. In any case. the study of small-amplitude time periodicities in the vital rates D and F in (1.1)–(1.2) certainly contributes fundamentally to the general understanding of time-periodic fluctuations in these vital rates.

In order to use a bifurcation-theory approach to Eqs. (1.1)–(1.2) it is necessary to distinguish a bifurcation parameter. In [15,16] this parameter was taken to be the biologically meaningful "inherent net reproductive rate" n defined by

$$n = \int_0^A F_0 \exp\left(-\int_0^a D_0 \, ds \right) \, da.$$

where D_0 and F_0 denote the age-specific vital rates D and F evaluated at $\rho \equiv 0$. Then the fertility rate F is written as $F = nf$, where f is appropriately normalized. When F is periodic in time we will use, more generally, a time-averaged inherent net reproductive rate for the bifurcation parameter.

Suppose $D = D(\rho)(t, a)$ and $F = F(\rho)(t, a)$ depend on the density ρ. age a and periodically on time t. Let $\mathrm{av}[f]$ denote the time t average of f over one period and set

$$n = \mathrm{av}\left[\int_0^A F(0)(t, a) \exp\left(-\int_0^a D(0)(t, s) \, ds \right) \, da \right].$$

If we write $F = nf$, where $f = f(\rho)(t, a)$ is normalized so that

$$\mathrm{av}\left[\int_0^A f(0)(t, a) \exp\left(-\int_0^a D(0)(t, s) \, ds \right) \, da \right] = 1.$$

then Eqs. (1.1)–(1.2) become

$$\rho_t + \rho_a + D(\rho)(t, a)\rho = 0. \quad t > 0. \quad 0 < a < A < -\infty. \tag{1.3}$$

$$\rho(t, 0) = n \int_0^A f(\rho)(t, a)\rho(t, a) \, da. \quad t > 0. \tag{1.4}$$

for $\rho = \rho(t, a) \geq 0$. Of interest here is the existence of nontrivial time t periodic solutions $\rho \geq 0$ ($\not\equiv 0$) satisfying $\rho(t, A) \equiv 0$, or more specifically a determination of those values of n for which such solutions exist.

In [16] it was shown under only mild continuity conditions that when D and f are independent of t a global branch of nontrivial equilibrium solutions $\rho = \rho(a) \geq 0$ exists and bifurcates from (and only from) the critical point $(n, \rho) = (1, 0)$. This continuum branch of equilibria (n, ρ) connects to the boundary of the domain upon which the problem is posed in certain Banach spaces. In [15] this bifurcation phenomenon is studied in more detail locally in a neighborhood of the bifurcation point $(1, 0)$.

In Sec. 3 below a local bifurcation theorem for the existence of nontrivial periodic solutions is proved for (1.3)–(1.4) when D and f are periodic in t, under the assumption that these periodicities have "small amplitude." It establishes the local existence of a parameterized branch of nontrivial periodic solutions which bifurcates from a critical point $(n, \rho) = (n_0, 0)$, where n_0 is an eigenvalue of the linearized problem whose existence is established in Sec. 2. This result extends, indeed generalizes, the existence result of [15], to the case of time-periodic vital rates D and f. The lemmas and theorem of Secs. 2 and 3 allow for the computation of any number of lower-order terms in perturbation expansions for n_0 and the nontrivial solution (n, ρ). These lower-order terms can of course be used as approximations to these solutions in specific applications. A simple example is given in Sec. 4.

The stability of the branch solutions given in the theorem of Sec. 3 is not studied here. For the autonomous case stability was shown in [15] to depend on the "direction of bifurcation," i.e. the branch solutions ρ are stable near bifurcation only if these solutions correspond to $n > n_0 = 1$. Moreover, the trivial solution $\rho \equiv 0$ is stable for $n < 1$ and unstable for $n > 1$. A natural conjecture is that these stability properties remain in force for the periodic, small-amplitude case considered here.

2. THE LINEAR THEORY

Let R and R^- denote the set of reals and the set of nonnegative reals respectively. Denote by Δ the set of continuous functions $\mu: [0, A) \to R$ satisfying

$$\lim_{a \to A^-} M(a) = +\infty, \quad M(a) := \int_0^a \mu(s)\, ds.$$

Set

$$\rho_0(a) = \exp(-M(a)) \quad \text{for } 0 \leq a < A, \; \rho_0(A) = 0.$$

The linear space of continuous functions $h: R \times [0, A] \to R$ for which $h(t, a)/\rho_0(a)$ is continuous and for which h is periodic of period 1 in t is denoted by $P(\mu)$. This space $P(\mu)$ is a Banach space under the norm

$$\|h\|_\mu := \max_{R \times [0, A]} |h(t, a)| / \rho_0(a).$$

The subspace of $h \in P(\mu)$ which are independent of t is the space B_μ used in [15,16] to study equilibrium solutions of autonomous Eqs. (1.3)–(1.4). Note that $\rho_0 \in P(\mu)$ and that $h(t, A) \equiv 0$, $t \in R$, for any $h \in P(\mu)$.

The linear space of functions h for which in addition $h(t, a)/\rho_0(a)$ has continuous first partial derivatives is a Banach space under the norm

$$\|h\|_{\mu, 1} := \|h\|_\mu + \max_{R \times [0, A]} \left| \frac{\partial}{\partial a} (h/\rho_0) \right| + \max_{R \times [0, A]} \left| \frac{\partial}{\partial t} (h/\rho_0) \right|.$$

and is denoted by $P^1(\mu)$. The Banach space of functions h for which $h(t, a)/\rho_0(a)$ has a continuous

first partial in t is denoted by $P^{1-}(\mu)$ and is given the norm

$$\|h\|_{\mu,1-} := \|h\|_\mu + \max_{R \in [0,A]} \left| \frac{\partial}{\partial t}(h \cdot \rho_0) \right|.$$

For $h \in P(\mu)$ define the average $\text{av}[h] := \int_0 h(t, a)\, dt$ and denote by $P_0(\mu)$ the subspace of functions $h \in P(\mu)$ with zero average (for all $a \in [0, A]$); similarly for $P_0^1(\mu)$ and $P_0^{1-}(\mu)$.

Finally, let P^1 be the Banach space of continuously differentiable, periodic functions h: $R \to R$ under the usual supremum norm $\|h\|_1 := \|h\|_0 + \|h'\|_0$, $\|h\|_0 := \max_{0 \le t \le 1} |h(t)|$. P_0^1 is the subspace of functions with zero average. The cross-product space $P^1 \times P^{1-}(\mu)$ is given the norm $\|\cdot\|_1 + \|\cdot\|_{\mu,1-}$. Similar norms are taken for other cross-product spaces.

Consider the nonhomogeneous linear system

$$\rho_t(t, a) + \rho_a(t, a) + \mu(a)\rho(t, a) = h_2 \in P^{1-}(\mu), \quad 0 < a < A < +\infty, \tag{2.1a}$$

$$\rho(t, 0) - \int_0^A \beta(a)\rho(t, a)\, da = h_1 \in P^1. \tag{2.1b}$$

and its associated homogeneous system

$$\rho_t(t, a) + \rho_a(t, a) + \mu(a)\rho(t, a) = 0, \quad 0 < a < A,$$

$$\rho(t, 0) - \int_0^A \beta(a)\rho(t, a)\, da = 0. \tag{2.2}$$

We will also refer to the related systems

$$\rho_a(a) + \mu(a)\rho(a) = h_2 \in B_\mu, \quad 0 < a < A,$$

$$\rho(0) - \int_0^A \beta(a)\rho(a)\, da = h_1 \in R. \tag{2.3}$$

and

$$\rho_a(a) + \mu(a)\rho(a) = 0, \quad 0 < a < A < +\infty,$$

$$\rho(0) - \int_0^A \beta(a)\rho(a)\, da = 0. \tag{2.4}$$

We assume throughout that $\mu \in \Delta$, $\beta \in C^0 = C^0([0, A]; R)$. It is required in all equations that ρ vanish identically when $a = A$, a condition which is met by finding solutions in $P^1(\mu)$.

In [15] a Fredholm-type alternative was proved for (2.3)–(2.4), which formed the basis of the study of equilibrium solutions of nonlinear equations. The goal of this section is to derive a similar result from the t-periodic systems (2.1)–(2.2). First, however, a lemma concerning the integral equation

$$B(t) - \int_0^A \beta(a)\rho_0(a)B(t - a)\, da = h \in P^1. \tag{2.5}$$

and its associated homogeneous equation

$$B(t) - \int_0^A \beta(a)\rho_0(a)B(t - a)\, da = 0 \tag{2.6}$$

is needed. Let Z denote the set of all integers and N denote the subspace of all solutions $B \in P^1$ of (2.6). Also, let $N^\perp = \{h \in P^1: \text{av}[hB] = 0 \ \forall B \in N\}$.

LEMMA 2.1

Assume $\mu \in \Delta$ and $\beta \in C^0$.

(a) dim N is finite.

(b) Equation (2.5) has a solution $B \in P^1$ if and only if $h \in N^-$, in which case (2.5) has a unique solution $B \in N^\perp$ and the operator $L: N^\perp \to N^-$ defined by $B = Lh$ is linear and bounded.

Proof. $B \in P^1$ has a Fourier series $B = \Sigma\, c_m e^{2\pi i m t}$, which when substituted into (2.5) yields the equations

$$\left(1 - \int_0^A \beta(a)\rho_0(a)e^{-2\pi i m a}\, \mathrm{d}a\right)c_m = h_m \qquad (2.7)$$

for the complex coefficients c_m. Here the h_m are the Fourier coefficients of $h \in P^1$.

(a) For the homogeneous Eq. (2.6) all $h_m = 0$ and a nontrivial solution exists in P^1 if and only if

$$\int_0^A \beta(a)\rho_0(a)e^{-2\pi i m a}\, \mathrm{d}a = 1$$

for at least one $m \in Z$. The space N is spanned by the real and imaginary parts of $e^{2\pi i m t}$, $m \in Z_0$, where

$$Z_0 = \left\{m \in Z: \int_0^A \beta(a)\rho_0(a)e^{-2\pi i m a}\, \mathrm{d}a = 1\right\}.$$

By the Riemann–Lebesgue theorem

$$\int_0^A \beta(a)\rho_0(a)e^{-2\pi i m a}\, \mathrm{d}a \to 0 \quad \text{as } |m| \to +\infty, \qquad (2.8)$$

and hence Z_0 is finite.

(b) Clearly it is necessary for the solution of (2.7) that $h_m = 0$ for all $m \in Z_0$. This shows that $h \in N^\perp$ is necessary. Conversely, suppose $h \in N^\perp$. Then (2.7) can be solved to yield the solution

$$B(t) = \sum_{m \notin Z_0} c_m e^{2\pi i m t}, \qquad (2.9)$$

$$c_m = h_m \Big/ \left(1 - \int_0^A \beta(a)\rho_0(a)e^{-2\pi i m a}\, \mathrm{d}a\right), \quad m \notin Z_0.$$

By (2.8) there is a constant k for which

$$\left| 1 \Big/ \left(1 - \int_0^A \beta(a)\rho_0(a)e^{-2\pi i m a}\, \mathrm{d}a\right)\right| \le k, \quad m \notin Z_0.$$

Thus $m^2|c_m|^2 \le k^2 m^2|h_m|^2$. Since $h \in P^1$ it follows that $\Sigma\, m^2|h_m|^2 < +\infty$ and hence $\Sigma\, m^2|c_m|^2 < +\infty$, which means $B(t)$ defined by (2.9) is absolutely continuous and hence differentiable almost everywhere. Since B satisfies (2.5) by construction, it easily follows that in fact $B \in P^1$.

From Eq. (2.5) (k is a generic constant not necessarily the same in different expressions)

$$|B(t)| \leq \left(\int_0^A \beta^2 \rho_0^2 \, da \right)^{1/2} \left(\int_0^A B^2(t-a) \, da \right)^{1/2} + \|h\|_0$$

$$\leq k \left(\int_0^1 B^2(t-a) \, da \right)^{1/2} + \|h\|_0 \leq k \left(\sum_{m \notin Z_0} |c_m|^2 \right)^{1/2} + \|h\|_0,$$

so that

$$\|B\|_0 \leq k \left(\sum_{m \notin Z_0} |h_m|^2 \right)^{1/2} + \|h\|_0 \leq k \left(\int_0^1 h^2 dt \right)^{1/2} + \|h\|_0 \leq k\|h\|_0.$$

Similar inequalities obtained from (2.5) when differentiated show that $\|B'\|_0 \leq k\|h'\|_0$, and consequently $\|B\|_1 = \|Lh\|_1 \leq k\|h\|_1$.   ∎

The general solution of Eq. (2.1a) is

$$\rho(t, a) = \rho_0(a) \left(B(t-a) + \int_0^a h_2(t - a + s, s)/\rho_0(s) \, ds \right), \qquad (2.10)$$

where B is an arbitrary differentiable function. This solution will also solve (2.1b) if and only if B solves the integral Eq. (2.5) with

$$h(t) = h_1(t) + \int_0^A \beta(a)\rho_0(a) \int_0^a h_2(t - a + s, s)/\rho_0(s) \, ds \, da. \qquad (2.11)$$

Note that $(h_1, h_2) \in P^1 \times P^{1-}(\mu)$ implies that $h \in P^1$, and that if $B \in P^1$ solves (2.5) then ρ defined by (2.10) is a solution of (2.1) which lies in $P^1(\mu)$.

Define $N(\mu)$ to be the subspace of all solutions $\rho \in P^1(\mu)$ of (2.2) and let $N^-(\mu) = \{\rho \in P^1(\mu): \Omega[\rho, \tilde{\rho}] = 0 \ \forall \ \tilde{\rho} \in N(\mu)\}$, where

$$\Omega[x, \tilde{x}] := \int_0^A \beta(a) \, \mathrm{av}[x(t, a)\tilde{x}^*(t, a)]/\rho_0(a) \, da.$$

Here "*" denotes complex conjugation. Let $M^-(\mu) \in P^1 \times P^{1-}(\mu)$ be the closed subspace consisting of those (h_1, h_2) for which h defined by (2.11) lies in $N^-(\mu)$.

LEMMA 2.2

Assume $\mu \in \Delta$ and $\beta \in C^0$.

(a) dim $N(\mu)$ is finite.
(b) The system of Eqs. (2.1) has a solution $\rho \in P^1(\mu)$ if and only if $(h_1, h_2) \in M^-(\mu)$, in which case (2.1) has a unique solution $\rho \in N^-(\mu)$ and the operator $S: M^-(\mu) \rightarrow N^-(\mu)$ defined by $\rho = S(h_1, h_2)$ is linear and bounded.

Proof. The space $N(\mu)$ of homogeneous solutions of (2.2) is spanned by the real and imaginary parts of $\tilde{\rho}_m(t, a) = \rho_0(a) \exp(2\pi i m t)$, $m \in Z_0$, and hence is finite dimensional. This proves (a).

Suppose $\rho \in P^1(\mu)$ solves (2.1). Then B in (2.10) solves (2.5) with h given by (2.11). By Lemma 2.1, $h \in N^-$, i.e. $(h_1, h_2) \in M^-(\mu)$.

Conversely, suppose $(h_1, h_2) \in M^-(\mu)$. Then h defined by (2.11) lies in $N^-(\mu)$ and by Lemma 2.1 Eq. (2.5) has a unique solution $Lh \in N^-$. With $B(t) = \sum_{m \in Z_0} c_m \exp(2\pi i m t) - Lh$ for arbitrary coefficients c_m, $m \in Z_0$, $\rho(t, a)$ defined by (2.10) lies in $P^1(\mu)$ and solves (2.1). Now $h \in N^-(\mu)$ if and only if $h_m = 0$, $m \in Z_0$, i.e. if and only if

$$h_{1m} + \int_0^A \beta(a)\rho_0(a) \int_0^a \mathrm{av}[h_2(t - a + s, s)e^{-2\pi i m t}]/\rho_0(s) \, ds \, da = 0, \quad m \in Z_0. \quad (2.12)$$

where h_{1m} are the Fourier coefficients of $h_1(t)$:

$$h_{1m} = \int_0^1 h_1(t)e^{-2\pi imt}\, dt. \tag{2.13}$$

The unique solution ρ of (2.1) which lies in $N^\perp(\mu)$, i.e. which satisfies $\Omega[\rho, \rho_0 \exp(2\pi im(t - a))] = 0$ for all $m \in Z_0$, is obtained by choosing the constants c_m to be equal to h_{1m}. Thus (2.1) has a unique solution $\rho \in N^\perp(\mu)$ given by $\rho = S(h_1, h_2)$, where

$$S := \rho_0(a)\left(\sum_{m \in Z_0} h_{1m}e^{2\pi im(t-a)} + (Lh)(t - a) + \int_0^a h_2(t - a + s, s)/\rho_0(s)\, ds \right), \tag{2.14}$$

with h_{1m} given by (2.13).

Simple inequalities show, using (2.14) and Lemma 2.1, that

$$|S/\rho_0| \le k\|h_1\|_0 + k\|h\|_1 + A\|h_2\|_\mu$$

$$\left|\frac{\partial}{\partial a}(S/\rho_0)\right| \le k\|h_1\|_0 + k\|h\|_1 + \|h_2\|_\mu + A\left\|\frac{\partial}{\partial t}h_2\right\|_\mu,$$

$$\left|\frac{\partial}{\partial t}(S/\rho_0)\right| \le k\|h_1\|_0 + k\|h\|_0 + k\|h\|_1 + A\left\|\frac{\partial}{\partial t}h_2\right\|_\mu,$$

and consequently $\|S(h_1, h_2)\|_{\mu,1} \le k(\|h_1\|_1 + \|h_2\|_{\mu,1-})$.   ∎

We will be interested below in the case when dim $N(\mu) = 1$, that is, when

$$\int_0^A \beta(a)\rho_0(a)\, da = 1, \tag{2.15a}$$

$$\int_0^A \beta(a)\rho_0(a)e^{-2\pi ima}\, da \ne 1, \quad 0 \ne m \in Z. \tag{2.15b}$$

In this case the homogeneous Eqs. (2.2) have exactly one independent solution $\rho \in P^1(\mu)$, namely the time-independent or equilibrium solution $\rho = \rho_0(a)$ of (2.4). Then $N(\mu)$ is spanned by $\rho_0(a)$ and

$$N^\perp(\mu) = \left\{ \rho \in P^1(\mu): \int_0^A \beta(a)\, \mathrm{av}[\rho(t, a)]\, da = 0 \right\}.$$

By (2.12), $(h_1, h_2) \in M^\perp(\mu)$ and the nonhomogeneous Eq. (2.1) have solutions if and only if the single constraint

$$\mathrm{av}[h_1] + \int_0^A \beta(a)\rho_0(a)\int_0^a \mathrm{av}[h_2(t - a + s, s)]/\rho_0(s)\, ds\, da = 0 \tag{2.16}$$

holds. This "orthogonality condition" on (h_1, h_2) is an averaged version of that derived in [15] for $(h_1, h_2) \in R \times B_\mu$ and for equilibrium solutions $\rho \in B_{\mu,1}$ of (2.3).

The condition (2.15a) implies that $n = 1$ is an "eigenvalue" of the problem (2.4) with $\beta(a)$ replaced by $n\beta(a)$. In fact, $n = 1$ is then the only value of n for which this homogeneous problem has a nontrivial solution (namely $\rho = \rho_0$). The next lemma deals with a generalization of this result when μ and β suffer small-amplitude α time-periodic perturbations. Consider the equations

$$\rho_t(t, a) + \rho_a(t, a) + (\mu(a) + r_2(\alpha)(t, a))\rho(t, a) = 0, \tag{2.17a}$$

$$\rho(t, 0) - n_0 \int_0^A (\beta(a) + r_1(\alpha)(t, a))\rho(t, a)\, da = 0, \tag{2.17b}$$

where $n_0 \in R$ and where r_i for each $\alpha \in (-\alpha_0, \alpha_0)$ is a real-valued function of t and a such that

$$r_i(0)(t, a) \equiv 0,$$

and for which the operators defined by

$$l_1(\alpha, \rho) := \int_0^A r_1(\alpha)\rho \, da, \quad l_2(\alpha, \rho) := r_2(\alpha)\rho \qquad (2.18)$$

map

$$l_1 : (-\alpha_0, \alpha_0) \times P^1(\mu) \to P^1 \quad \text{and} \quad l_2 : (-\alpha_0, \alpha_0) \times P^1(\mu) \to P^{1-}(\mu) \qquad (2.19)$$

and are $q \geq 1$ times Fréchet differentiable in (α, ρ).

LEMMA 2.3

Suppose $\mu \in \Delta$ and $\beta \in C^0$ satisfy (2.15) and the r_i are, as described above, real-valued functions for which the operators l_i in (2.18) satisfy (2.19) and are $q \geq 1$ times Fréchet differentiable. Then for sufficiently small $|\alpha| < \tilde{\alpha}_0 \leq \alpha_0$ the homogeneous Eqs. (2.17) have a nontrivial solution

$$\rho(t, a) = \rho_0(a) + z(\alpha)(t, a) \qquad (2.20)$$

for

$$n_0 = 1 + \lambda(\alpha), \qquad (2.21)$$

where $z(\alpha) : (-\tilde{\alpha}_0, \tilde{\alpha}_0) \to N^+(\mu)$ and $\lambda : (-\tilde{\alpha}_0, \tilde{\alpha}_0) \to R$ are $q \geq 1$ times differentiable and where $z(0) = 0$, $\lambda(0) = 0$.

Proof. A substitution of (2.20) and (2.21) into (2.17) results in a system of the form (2.1) for z with

$$h_1 := \int_0^A (r_1(\alpha)(t, a) + \lambda(\beta(a) + r_1(\alpha)(t, a)))(\rho_0(a) + z) \, da,$$
$$h_2 := -r_2(\alpha)(t, a)(\rho_0(a) + z). \qquad (2.22)$$

Because (2.15) holds it is necessary that the "orthogonality" condition (2.16) hold. Thus we reformulate (2.17) with (2.20)–(2.21) as follows. Given $z \in N^-(\mu)$ and $\alpha \in R$ we define λ so that (2.16) holds:

$$\left(1 + \int_0^A \beta(a) \, \text{av}[z(t, a)] \, da + \int_0^A \text{av}[r_1(\alpha)(t, a)(\rho_0(a) + z(t, a))] \, da\right)\lambda$$

$$= -\int_0^A \text{av}[r_1(\alpha)(t, a)(\rho_0(a) + z(t, a))] \, da + \int_0^A \beta(a)\rho_0(a) \int_0^a \text{av}[r_2(\alpha)(t - a + s, s)$$

$$\times (\rho_0(s) + z(t - a + s, s))]/\rho_0(s) \, ds \, da. \qquad (2.23)$$

and then the equation for z is equivalent to the operator equation

$$z - S(h_1(\alpha, z), h_2(\alpha, z)) = 0. \qquad (2.24)$$

where S is the operator of Lemma 2.2 and h_1, h_2 are defined by (2.22) with λ given by (2.23). Clearly, λ is well defined by (2.23) for $|\alpha|$ and $\|z\|_{\mu,1}$ sufficiently small, say in an open neighborhood $\Gamma \subset R \times N^-(\mu)$ of $(\alpha, z) = (0, 0)$.

Under the stated hypotheses the operator $F: \Gamma \to N^{\perp}(\mu)$ defined by $F(\alpha, z) := z - S(h_1(\alpha, z), h_2(\alpha, z))$ is $q \geq 1$ times continuously differentiable and

$$F(0, 0) = 0, \quad F_z(0, 0) = I,$$

where $I : N^{\perp}(\mu) \to N^{\perp}(\mu)$ is the identity operator. The implicit-function theorem implies that (2.24) has a (local) $q \geq 1$ times continuously differentiable solution $z = z(\alpha) \in N^{\perp}(\mu)$, which yields (2.20) and, after a substitution into (2.23), λ in (2.21). ∎

As pointed out above $z \in N^{\perp}(\mu)$ means under (2.15) that

$$\int_0^A \beta(a) \, \mathrm{av}[z(\alpha)(t, a)] \, \mathrm{d}a = 0$$

for each α.

With sufficient differentiability ($q \geq 1$ large enough) lower-order terms of any desired order in the α expansions of ρ and n can be computed by the familiar method of substituting expansions

$$\rho(t, a) = \rho_0(a) + \alpha z_1(t, a) + \alpha^2 z_2(t, a) + \cdots,$$

$$n_0 = 1 + \alpha \lambda_1 + \alpha^2 \lambda_2 + \cdots$$

into (2.17), equating coefficients of like powers of α on both sides of both equations and solving the resulting recursive linear nonhomogeneous systems for z_i. These linear problems have the form (2.1) and are solvable by Lemma 2.2 when the orthogonality condition above is satisfied by an appropriate choice of λ_i.

From (2.23) it is easily seen that

$$\lambda_1 = -\int_0^A \mathrm{av}[r_1'(0)(t, a)]\rho_0(a) \, \mathrm{d}a + \int_0^A \beta(a)\rho_0(a) \int_0^a \mathrm{av}[r_2'(0)(t - a + s, s)] \, \mathrm{d}s \, \mathrm{d}a,$$

where $r_i'(0)$ denotes the partial derivative with respect to α at $\alpha = 0$. This gives a formula for the lowest-order correction to the "eigenvalue" n_0.

A natural way to study time-periodic oscillations in the death and fertility rates is to consider oscillations about (age-specific) averages μ and β, i.e. to assume that

$$\mathrm{av}[r_i(\alpha)(t, a)] \equiv 0, \quad \forall(\alpha, a) \in (-\alpha_0, \alpha_0) \times [0, A]. \tag{2.25}$$

In this case, $\lambda_1 = 0$ and $n_0 = 1 + \alpha^2 \lambda_2 + \cdots$ so that there is a second-order correction to the "eigenvalue" n_0. Moreover, from (2.23) and (2.25),

$$\lambda_2 = -\int_0^A \mathrm{av}[r_1'(0)(t, a)z_1(t, a)] \, \mathrm{d}a$$

$$+ \int_0^A \beta(a)\rho_0(a) \int_0^a \mathrm{av}[r_2'(0)(t - a + s, s)z_1(t - a + s, s)]/\rho_0(s) \, \mathrm{d}s \, \mathrm{d}a,$$

where z_1 is the unique solution of (2.1) in $N^{\perp}(\mu)$ with

$$h_1 = \int_0^A r_1'(0)(t, a)\rho_0(a) \, \mathrm{d}a, \quad h_2 = -r_2'(0)(t, a)\rho_0(a),$$

as guaranteed by Lemma 2.2; that is, z_1 is given by (2.10):

$$z_1(t, a) = \rho_0(a)\left(B(t - a) - \int_0^a r_2'(0)(t - a + s, s) \, \mathrm{d}s\right),$$

where $B(t)$ is the unique solution of the integral Eq. (2.5) satisfying $\mathrm{av}[B] = 0$ with [see (2.11)]

$$h(t) = \int_0^A r_1'(0)(t, a)\rho_0(a)\,\mathrm{d}a - \int_0^A \beta(a)\rho_0(a)\int_0^a r_2'(0)(t - a + s, s)\,\mathrm{d}s\,\mathrm{d}a.$$

Under assumption (2.25) these formulas allow for a study of the effects, to lowest order, on the "eigenvalue" n_0 and "eigensolution" ρ (as determined by λ_2 and z_1) due to periodic oscillations about average death and fertility rates μ and β. An example is given in Sec. 4.

3. A NONLINEAR THEOREM

In [15,16] the autonomous version of the nonlinear Eqs. (1.3)–(1.4) in which the death and fertility rates D and f are general functionals of the population density ρ, but do not depend explicitly on time t, were studied using global and local bifurcation techniques with n as a bifurcation parameter. Under the normalization

$$\int_0^A f(0)(a) \exp\left(-\int_0^a D(0)(s)\,\mathrm{d}s\right)\,\mathrm{d}a = 1$$

and certain minimal smoothness assumptions it was shown in [16] that a global continuum of equilibrium $\rho = \rho(a)$ solution pairs $(n, \rho) \in R \times B_\mu$ exists and bifurcates from the critical point $(1, 0)$. This continuum connects to the boundary of the domain of definition of the functionals D and f. In [15] this bifurcation branch was parameterized and studied locally near the bifurcation point $(1, 0)$.

Here we wish to allow D and f to depend explicitly on time t in a periodic manner as in (1.3)–(1.4). Specifically, let D and f suffer small-amplitude α time-periodic perturbations of the form

$$D = \mu + R_2(\alpha, \rho), \quad f = \beta + R_1(\alpha, \rho), \tag{3.1}$$

where $\mu \in \Delta$ and $\beta \in C^0$ satisfy (2.15) and the terms $R_i = R_i(\alpha, \rho)(t, a)$ are such that $R_i(0, 0)(t, a) \equiv 0$ and the operators defined by

$$n_1(\alpha, \rho) := \int_0^A R_1(\alpha, \rho)(t, a)\rho(t, a)\,\mathrm{d}a, \quad n_2(\alpha, \rho) := R_2(\alpha, \rho)(t, a)\rho(t, a) \tag{3.2}$$

are $q \geq 1$ times Fréchet differentiable as operators mapping

$$n_1 : (-\alpha_0, \alpha_0) \times P^1(\mu) \to P^1, \quad n_2 : (-\alpha_0, \alpha_0) \times P^1(\mu) \to P^1(\mu). \tag{3.3}$$

THEOREM 3.1

Assume that D and f have the form (3.1), where $\mu \in \Delta$ and $\beta \in C^0$ satisfy (2.15) and the perturbation terms R_i are such that $R_i(0, 0) = 0$ and (3.2) defines $q \geq 1$ times Fréchet-differentiable operators which satisfy (3.3). Then for $|\alpha| < \bar{\alpha}_0 \leq \alpha_0$ and for $|\epsilon| < \epsilon_0$ sufficiently small, (1.3)–(1.4) has a (unique) solution of the form

$$\rho = \epsilon\rho_1(\alpha) + \epsilon w(\alpha, \epsilon) \quad \text{with} \quad n = n_0(\alpha) + n_1(\alpha, \epsilon), \tag{3.4}$$

where

$$\rho_1(\alpha) = \rho_0 + z(\alpha), \quad n_0 = 1 + \lambda(\alpha) \tag{3.5}$$

are as in Lemma 2.3 with $r_1 = R_1(\alpha, 0)$ and $r_2 = R_2(\alpha, 0)$ and where

$$w : (-\bar{\alpha}_0, \bar{\alpha}_0) \times (-\epsilon_0, \epsilon_0) \to N^-(\mu), \quad n_1 : (-\bar{\alpha}_0, \bar{\alpha}_0) \times (-\epsilon_0, \epsilon_0) \to R$$

are $q \geq 1$ times Fréchet differentiable and satisfy $w(\alpha, 0) \equiv 0$, $n_1(\alpha, 0) \equiv 0$.

Proof. If (3.1) and (3.4) are substituted into (1.3)–(1.4), then making use of (3.5) we obtain for each α equations of the form (2.1) for w where

$$h_1 = h_1(\alpha, \epsilon, w) := (R_2(\alpha, 0) - R_2(\alpha, \epsilon\rho_1 + \epsilon w))(\rho_1 + w) - R_2(\alpha, 0)w$$

$$h_2 = h_2(\alpha, \epsilon, w) := n_1 \int_0^A (\beta - R_1(\alpha, \epsilon\rho_1 + \epsilon w))(\rho_1 + w)\,da + n_0 \int_0^A R_1(\alpha, 0)w\,da$$

$$+ n_0 \int_0^A (R_1(\alpha, \epsilon\rho_1 + \epsilon w) - R_1(\alpha, 0))(\rho_1 + w)\,da.$$

Choosing n_1 so that $(h_1, h_2) \in M^-(\mu)$, i.e. choosing $n_1 = n_1(\alpha, \epsilon, w)$ so that (2.16) holds, these equations for $w \in N^+(\mu)$ can be equivalently reformulated using Lemma 2.2 as $H(\alpha, \epsilon, w) = 0$, where

$$H(\alpha, \epsilon, w) := w - S(h_1(\alpha, \epsilon, w), h_2(\alpha, \epsilon, w))$$

defines an operator $H: (-\alpha_0, \alpha_0) \times (-\epsilon_0, \epsilon_0) \times N^+(\mu) \to N^+(\mu)$. Note that n_1 so defined is easily seen to be well defined, since the coefficient of n_1 in (2.16) is 1 when $(\alpha, \epsilon, w) = (0, 0, 0)$, and $q \geq 1$ times differentiable for α, ϵ and $\|w\|_{\mu,1}$ sufficiently small. Moreover, a straightforward solution of this linear equation for n_1 shows that $n_1(\alpha, 0, 0) = 0$ for all small $|\alpha|$ and that $\partial n_1(0, 0, 0)/\partial w = 0$.

These facts yield

$$H(0, 0, 0) = 0, \quad \partial H(0, 0, 0)/\partial w = I,$$

and the implicit-function theorem in turn yields a unique solution $w = w(\alpha, \epsilon)$ of $H(\alpha, \epsilon, w) = 0$ satisfying $w(0, 0) = 0$. It is easy to see that $H(\alpha, 0, 0) \equiv 0$, so that $w(\alpha, 0) \equiv 0$, $n(\alpha, 0) \equiv 0$ for all small $|\alpha|$. ∎

For $q \geq 1$ sufficiently large lower-order ϵ coefficients in the expansions (3.4) can be found in the standard manner of deriving and successively solving linear problems of the form (2.1) (for small $|\alpha|$) by the methods in Sec. 2.

4. AN EXAMPLE

Suppose that the age-specific fertility rate oscillates cosinusoidally around an average density-dependent rate with a small-amplitude α (relative to the average):

$$f := \beta(a)(1 + \alpha \cos 2\pi t)g(\rho), \quad 0 \leq \beta \in C^0.$$

Here g is an arbitrary functional of density ρ satisfying $g(0) = 1$, which is sufficiently smooth for an application of the theorem in Sec. 3 ($q \geq 1$ times continuously differentiable). A specific example is the frequently used logistic-type model obtained by setting $g = [1 - \int_0^A k(a)\rho(t, a)\,da]_+$[21].

With regard to the death rate D we assume in this simple example that it is density independent. Specifically, we choose

$$D = \mu := 1/(A - a) \in \Delta$$

so that the death rate is a monotonically increasing function of age $a \in [0, A)$. The system of Eqs. (1.3)–(1.4) then reduces to

$$\rho_t + \rho_a + \frac{1}{A - a}\rho = 0, \quad t > 0, \quad 0 < a < A < +\infty; \tag{4.1}$$

$$\rho(t, 0) = n \int_0^A \beta(a)(1 + \alpha \cos 2\pi t)g(\rho)\rho\,da, \quad t > 0. \tag{4.2}$$

For this example

$$\rho_0(a) = (A - a)/A, \quad 0 \le a \le A, \tag{4.3}$$

and the normalization of β is

$$\int_0^A \beta(a)\rho_0(a) \, da = 1. \tag{4.4}$$

According to the theorem of Sec. 3 (with $R_1 = \beta(a)(-1 + (1 + \alpha \cos 2\pi t)g(\rho))$ and $R_2 \equiv 0$), Eqs. (4.1)–(4.2) have nontrivial periodic solutions of the form (3.4). The lowest-order terms in the expansions (3.4) are given by the solution (3.5) of the linearized equations

$$\rho_t + \rho_a + \frac{1}{A - a} \rho = 0, \tag{4.5}$$

$$\rho(t, 0) = n \int_0^A \beta(a)(1 + \alpha \cos 2\pi t)\rho \, da, \tag{4.6}$$

which can be written

$$\rho_1 = \rho_0(a) + \alpha z_1(t, a) + \alpha^2 z_2(t, a) + \cdots, \quad n_0 = 1 + \lambda_1 \alpha + \lambda_2 \alpha^2 + \cdots. \tag{4.7}$$

From the remarks at the end of Sec. 2 it follows, in fact, that $\lambda_1 = 0$, as will also be seen from the analysis below.

To determine the lower-order coefficients in these α expansions, we substitute (4.7) into (4.5)–(4.6) and equate coefficients of like powers of α. This leads to the following three systems of equations:

$$\rho_{0a} + \frac{1}{A - a} \rho_0 = 0, \quad \rho_0(0) = \int_0^A \beta(a)\rho_0(a) \, da;$$

$$z_{1t} + z_{1a} + \frac{1}{A - a} z_1 = 0, \quad z_1(t, 0) = \int_0^A \beta(a)z_1(t, a) \, da + \lambda_1 + \cos 2\pi t; \tag{4.8}$$

$$z_{2t} + z_{2a} + \frac{1}{A - a} z_2 = 0, \quad z_2(t, 0) = \int_0^A \beta(a)z_2(t, a) \, da + \lambda_2$$

$$+ \int_0^A \beta(a)\rho_1(t, a) \, da \cos 2\pi t. \tag{4.9}$$

to be solved for the first three coefficients in (4.7). The first system is satisfied by the choice (4.3) for $\rho_0(a)$, in view of (4.4).

In order to solve the system (4.8) for z_1 it is necessary by Lemma 2.2 that

$$\mathrm{av}[\lambda_1 + \cos 2\pi t] = 0,$$

i.e. $\lambda_1 = 0$, in which case

$$z_1(t, a) = B(t - a)\rho_0(a), \tag{4.10}$$

where $B(t)$ solves the integral equation

$$B(t) = \int_0^A \beta(a)\rho_0(a)B(t - a) \, da + \cos 2\pi t.$$

The solution of this integral equation is given by

$$B(t) = c_1 \cos 2\pi t + c_2 \sin 2\pi t; \tag{4.11}$$

$$c_1 = \frac{1 - C}{d}, \quad c_2 = \frac{S}{d}, \quad d = (1 - C)^2 + S^2; \tag{4.12}$$

$$C = \int_0^A \beta(a)\rho_0(a) \cos 2\pi a \, da, \quad S = \int_0^A \beta(a)\rho_0(a) \sin 2\pi a \, da. \tag{4.13}$$

Here it is necessary that

$$d > 0$$

in order that (2.15b) holds.

Equations (4.11)–(4.13) define the lowest-order oscillation in ρ_1 of the solution ρ given by (3.4):

$$\rho_1 = \frac{A - a}{A} (1 + \alpha B(t - a) + \cdots).$$

From (4.11) one can determine the age-specific phase and amplitude of this oscillation (relative to that in the fertility rate f) as they depend, through (4.12)–(4.13), on the age-specific inherent fertility rate $\beta(a)$ and the maximum lifespan A. Some general conclusions which can be drawn are as follows. Unless $c_2 = 0$, the "total birth rate" $B(t)$ is not in phase with the oscillation in the fertility rate f. Moreover, since $c_1 \geq 0$, the total birth rate B peaks later than f (with relative phase $\tan^{-1}(S/(1 - C))$ if and only if $S > 0$. The amplitude of B increases without bound as d approaches 0, where (2.15) fails to hold and a resonance occurs.

In order to determine (to lowest order) the effect that the oscillation in f has on the critical value n_0 of the average inherent net reproductive rate n we must (since $\lambda_1 = 0$) calculate λ_2. This is done by means of the required "orthogonality" condition (2.16) for the solution of (4.9). The result is

$$\lambda_2 = (C^2 + S^2 - C)/d.$$

Consequently, in this example there is a second-order adjustment in the critical bifurcation value of the averaged inherent net reproductive rate caused by the oscillation in the fertility rate f. There is an increase in this critical value if $\lambda_2 > 0$ and a decrease otherwise.

A simple example is given by the case when fertility is not age specific: $\beta(a) \equiv \beta_0 = $ const > 0 or, by the normalization (4.4), when $\beta(a) \equiv 2/A$. Then

$$C = (1 - \cos 2\pi A)/2\pi^2 A^2, \quad S = (2\pi A - \sin 2\pi A)/2\pi^2 A^2 \tag{4.14}$$

and $\lambda_2 \geq 0$, i.e. there is an increase in the critical value n_0, since

$$C^2 + S^2 - C = (1 + \pi^2 A^2)(1 + \cos(2\pi A + \phi))/2\pi^4 A^4 \geq 0, \tag{4.15}$$

where $\phi = \tan^{-1}(2\pi A/(\pi^2 A^2 - 1))$. In this example $S > 0$, so that as remarked above the total birth rate $B(t)$ given by (4.11) with (4.14) in the coefficients (4.12) is never exactly in phase with the oscillatory fertility rate f, and in fact peaks after f. Furthermore, in this example, the coefficient of the lowest-order oscillation in the total population size $P = \int_0^A \rho(t, a) \, da$ is easily computed to be

$$\int_0^A z_1(t, a) \, da = \int_0^A B(t - a)\rho_0(a) \, da = -2A((C^2 - S^2 - C) \cos 2\pi t - S \sin 2\pi t)/d.$$

Consequently, by (4.15) and $S > 0$, P oscillates out of phase with the fertility rate f with a phase difference $\tan^{-1}(S/(C^2 + S^2 - C))$ ranging from one-quarter to one-half cycle.

The purpose of this example is simply to illustrate the general results and techniques of Secs. 2 and 3. It is not intended here to study in depth the biological implications of this model or of small-amplitude oscillations in the vital rates in general. It is hoped to do this in a future paper.

5. SUMMARY

The theorem appearing in Sec. 2 establishes a local, parameterized branch of time-periodic solutions of the McKendrick Eqs. (1.3)–(1.4) when the age-specific vital rates D and f suffer small-amplitude α periodicities in time. The branch bifurcates from the trivial solution $\rho \equiv 0$ at a critical value n_0 of the averaged net reproductive rate n, as given by Lemma 2.3. This result is a generalization of the autonomous equilibrium results in [15], which correspond to $\alpha = 0$. This theorem and the lemmas of Sec. 2 permit the use of standard perturbation techniques to calculate lower-order approximations to the time-periodic solutions. A simple example is given in Sec. 4 in which fertility oscillates consinusoidally in time while the death rate is time and density independent. Besides illustrating the general results and techniques, this example shows some interesting biological results that such a model can imply, such as an increased critical bifurcation value for the average net reproductive rate due to the fertility-rate oscillation and certain phase relationships between fertility and the total birth rate and the total population size.

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