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# BIFURCATION OF TIME PERIODIC SOLUTIONS OF THE McKENDRICK EQUATIONS WITH APPLICATIONS TO POPULATION DYNAMICS†

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**Abstract**—A local two parameter bifurcation theorem concerning the bifurcation from steady states of time periodic solutions of a nonlinear system of partial, integro-differential equations is proved. A Hopf bifurcation theorem is derived as a corollary. By means of independent and dependent variable changes this theorem is applicable to the general McKendrick equations governing the growth of an age-structured population (with the added feature here of a possible gestation period). The theorem is based on a Fredholm theory developed in the paper for the associated linear equations. An application is given to an age-structured population whose fecundity is density and age dependent and it is shown that for a sufficiently narrow age-specific "reproductive and resource consumption window" steady state instabilities, accompanied by sustained time periodic oscillations, occur when the birth modulus surpasses a critical value.

## 1. INTRODUCTION

One interesting and important problem in the dynamical theory of population growth concerns the possibility of sustained oscillations of population density in a constant environment. This problem has been addressed by a rather large literature, both mathematical and biological, and many mechanisms have been suggested and studied as causes of such oscillations. With regard to single species growth, the most common explanation of these oscillations mentioned by both biologists and mathematicians is the presence of a time delay in the birth rate and/or the death rate response to changes in population densities. Although the earliest studies of such time delays seem to deal with delayed death rate responses ([18], p. 47–56), more recent research emphasizes delayed birth rate responses as caused by any one of many different biological mechanisms, the most fundamental of which are gestation periods and maturation periods (taken together, the "generation time"), age-specific fertility rates and the nature of the age-specific dependence of fertility on population density[6, 11, 12, 16, 19, 20]. These particular biological, delay causing mechanisms relate to the age structure of the population and hence the mathematical study of these oscillations falls within the purview of the general theory of age-structured population dynamics, which in recent years has been enjoying a rapid growth.

The general theory of age-structured population growth can be based on the McKendrick model equations for the age-specific population density (sometimes called the von Foerster equations) as given by (2.1)–(2.2) below (to which the provision for a gestation period has been added). From these equations virtually all deterministic model equations used in population dynamics and mathematical ecology can be derived by special manipulations and assumptions, be they integral differential, integrodifferential, functional or difference equations. In this way, the study of population stability and oscillations by means of model equations (when it is done carefully, at least) has generally been carried out on equations of one of these types which have been or could be derived from the McKendrick equations by focusing on specific biological mechanisms and phenomena and by making various simplifying assumptions. This is done with the idea in mind of obtaining more tractable equations for which there are available certain mathematical theorems or techniques. As far as nonconstant periodic solutions are concerned, bifurcation techniques such as Liapunov–Schmidt methods and Hopf bifurcation theorems are by in large available for equations of these other "simpler" types. The simplifying assumptions

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necessary for this procedure are not always desirable, however, especially with regard to some of the specific delay causing mechanisms mentioned above. In such cases, unrigorous analysis of the McKendrick equations is sometimes done in order to gain insight into the dynamics[12].

The goal of this paper is to establish a fundamental bifurcation theorem for the existence of nonconstant, time periodic solutions of the McKendrick equations *per se* in as general a form as possible. The main result, a two parameter bifurcation theorem, is given in Section 4 (Theorem 3) after which, as a corollary, a Hopf-type bifurcation result is derived in Section 5 (Theorem 4). These theorems are derived from abstract Liapunov–Schmidt methods and the basic associated linear theory developed in Section 3 (which may be of independent interest and useful for other purposes as well). A sample application is given in Section 6 and formal proofs are given in Section 7.

## 2. PRELIMINARIES

The McKendrick model[9, 10, 21] assumes that a population can be described by a function $\rho(t, a)$ giving the population density of age class $a$ at time $t$. If it is assumed that removal from the population is by death only and that addition to the population is by birth only, the McKendrick equations then consist of the first order partial differential equation

$$\partial\rho/\partial t + \partial\rho/\partial a + d_t(a, \rho)\rho = 0 \tag{2.1}$$

which describes the removal (or death) process in terms of a per unit, age-specific *death rate* $d_t \geq 0$ at time $t$, and the integral equation

$$\rho(t, 0) = \int_{s=0}^{\infty} g(s) \int_{a=0}^{\infty} f_{t-s}(a, \rho)\rho(t-s, a)\, \mathrm{d}a\, \mathrm{d}s, \tag{2.2}$$

which describes the birth process in terms of the per unit, age-specific *fertility rate* $f_t \geq 0$ at time $t$. Here we have included a possible gestation period by means of the *gestation function* $g(s)$ which is assumed to be measurable and to satisfy $g(s) \geq 0$, $\int_0^\infty g(s)\, \mathrm{d}s = 1$. In this paper, the vital parameters $d_t$ and $f_t$ are functions of age class $a$, but are functions of time $t$ only implicitly through a general functional dependence on the population density $\rho$. At this point I am deliberately being vague about the properties of $d_t$ and $f_t$ in order to retain generality. The hypotheses which will be ultimately required are those necessary to allow a reformulation of (2.1)–(2.2) into the form of system (4.1)–(4.3) as described below.

The main interest here is with the bifurcation of time periodic solutions of (2.1)–(2.2) from nontrivial steady state solutions. In order to more directly address this question, I will assume the existence of a nontrivial steady state $\rho = \rho_0(a) \geq 0$. For some general theorems asserting the existence of steady states, see Refs. [14, 15].

Before developing the linear theory associated with systems of the form (2.1)–(2.2) on which the nonlinear bifurcation results will be based, it is necessary to introduce certain technical Banach spaces. Let $R$ denote the set of real numbers and $R^+$ the set of nonnegative reals. Denote by $B^1_{\gamma,p}$ the space of functions $g = g(\tau, a)$: $R \times R^+ \to R$ which are continuous and $p$-periodic in $\tau \in R$, once continuously differentiable in $a > 0$ and satisfy $\|g\|^1_{\gamma,p} < +\infty$. The norm $\|\cdot\|^1_{\gamma,p}$ is defined as follows:

$$\|g\|^1_{\gamma,p} := \|g\|_\gamma + \|\partial g/\partial a\|_\gamma + \|g\|_{\gamma,2} + \|\partial g/\partial a\|_{\gamma,2}$$

$$\|g\|_\gamma := \sup_{-p/2 \leq \tau \leq p/2, a>0} |g(\tau, a)|\, \mathrm{e}^{\gamma a}, \quad \|g\|_{\gamma,2} := \|\{\sup_{a>0} |jg_j(a)|\, \mathrm{e}^{\gamma a}\}\|_2$$

where $\|\{\sigma_j\}\|_2 := (\sum_{j=-\infty}^{+\infty} |\sigma_j|^2)^{1/2}$ and $\gamma$ is a positive real constant. The $g_j$ are the Fourier coefficients $g_j(a) := p^{-1}\int_{-p/2}^{p/2} g(\tau, a)\, \mathrm{e}^{-ij\omega\tau}\, \mathrm{d}\tau$, $j = 0, \pm 1, \pm 2 \ldots$ where $\omega = 2\pi/p$ and $i^2 = -1$.

Next let $B^0_{\gamma,p}$ be the space of functions $g = g(\tau, a)$: $R \times R^+ \to R$ which are continuous and $p$-periodic in $\tau \in R$, continuous in $a \geq 0$ and satisfy $\|g\|^0_{\gamma,p} := \|g\|_\gamma + \|g\|_{\gamma,2} < +\infty$. Finally, $B_p$ denotes the space of functions $h = h(\tau)$: $R \to R$ which are continuous and $p$-periodic in $\tau$ and satisfy $\|h\|_p < +\infty$ where $\|h\|_p := \|h\|_0 + \|h\|_2$ with $\|h\|_2 := \|\{jh_j\}\|_2$ and $\|h\|_0 := \sup_{-p/2 \leq \tau \leq p/2} |h(\tau)|$.

That the spaces $B^0_{\gamma,p}$, $B^1_{\gamma,p}$ and $B_p$ are Banach spaces is established in Section 7.

## 3. THE LINEAR THEORY

This section deals with the existence of solutions in $B^1_{\gamma,p}$ of certain nonhomogeneous and homogeneous linear equations which will ultimately be associated with (2.1)–(2.2), namely

$$\partial z/\partial a + c_1(a)z + c_2(a)\int_0^\infty k_1(\alpha)z(\tau + a - \alpha, \alpha)\,d\alpha = g(\tau, \alpha).$$

$$z(\tau, 0) = \int_{s=0}^\infty \int_{a=0}^\infty k_2(s, a)z(\tau - s - a, a)\,da\,ds + h(\tau) \tag{NH}$$

and the associated homogeneous system

$$\partial y/\partial a + c_1(a)y + c_2(a)\int_0^\infty k_1(\alpha)y(\tau + a - \alpha, \alpha)\,d\alpha = 0$$

$$y(\tau, 0) = \int_{s=0}^\infty \int_{a=0}^\infty k_2(s, a)y(\tau - s - a, a)\,da\,ds \tag{H}$$

where $(g, h) \in B^0_{\gamma,p} \times B_p$. The goal is to obtain a Fredholm-type alternative for (NH) upon which to base the study of nonlinear versions of this system.

The coefficients and kernels appearing in these systems will be assumed to satisfy the following conditions

H1: $c_i$: $R^+ \to R$ is continuous and bounded ($i = 1, 2$), $k_1$: $R^+ \to R$ is measurable and bounded and $k_2$: $R^+ \times R^+ \to R$ is measurable where, for some constants $0 < \gamma < c_0$, we have $0 < c_0 \le c_1(a)$, $\sup_{a \ge 0}|c_2(a)|\,e^{\gamma a} < +\infty$ and $\int_{s=0}^\infty \int_{a=0}^\infty |k_2(s, a)| \exp(-c_0 a)\,da\,ds < +\infty$.

Define for $j = 0, \pm 1, \pm 2, \ldots$ the complex numbers

$$\Delta_j := 1 + \int_0^\infty k_1(a)\,e^{-ij\omega a}\,e^{-C(a)}\int_{\alpha=0}^a e^{C(\alpha)}c_2(\alpha)\,e^{ij\omega\alpha}\,d\alpha\,da$$

where $C(a) := \int_0^a c_1(\alpha)\,d\alpha$. Note that $\bar{\Delta}_j = \Delta_{-j}$, $j \ge 0$, there the bar "—" denotes complex conjugation. Assume that

H2: $\Delta_j \neq 0$ for all $j \ge 0$.

Define $J$ to be the set of integers (positive, negative or zero) for which

$$D_j := 1 - \int_{s=0}^\infty \int_{a=0}^\infty k_2(s, a)\,e^{-ij\omega(s+a)}y_j^0(a)\,da\,ds = 0 \tag{3.1}$$

where

$$y_j^0(a) := e^{-C(a)}\left[1 - w_1{}^j \int_0^a e^{C(\alpha)}c_2(\alpha)\,e^{ij\omega\alpha}\,d\alpha\right] \tag{3.2}$$

$$w_1{}^j := \int_0^\infty k_1(a)\,e^{-ij\omega a}e^{-C(a)}\,da/\Delta_j.$$

Note that $\bar{w}_1{}^j = w_1{}^{-j}$, $\bar{y}_j^0(a) = y^0_{-j}(a)$ and hence $\bar{D}_j = D_{-j}$ for all $j \ge 0$.

It turns out (see Section 7) that (H) has nontrivial solutions in $B^1_{\gamma,p}$ if and only if $J \neq \emptyset$ in which case a set of independent solutions is given by the real and imaginary parts of the solutions $y(\tau, a) = y_j^0(a)\,e^{ij\omega\tau}$, $j \in J$.

Finally, for $(g, h) \in B^0_{\gamma,p} \times B_p$ define

$$x_j^0(a) := e^{-C(a)}\int_{\alpha=0}^a e^{C(\alpha)}[g_j(\alpha) - w_2{}^j c_2(\alpha)\,e^{ij\omega\alpha}]\,d\alpha$$

$$w_2{}^j := \int_{a=0}^\infty k_1(a)\,e^{-ij\omega a}\,e^{-C(a)}\int_{\alpha=0}^a e^{C(\alpha)}g_j(\alpha)\,d\alpha\,da/\Delta_j \tag{3.3}$$

$$\Omega_j[g, h] := \int_{s=0}^\infty \int_{a=0}^\infty k_2(s, a)\,e^{-ij\omega(s+a)}x_j^0(a)\,da\,ds + h_j$$

for $j=0,1,2,\ldots$ where $g_j(a)$ and $h_j:=p^{-1}\int_{-p/2}^{p/2} h(\tau)\,e^{-ij\omega\tau}\,d\tau$ are the Fourier coefficients of $g$ and $h$ respectively. Again, all entities with negative indices are the conjugates of those with the corresponding positive indices.

The following theorem describes a type of Fredholm alternative for (NH).

THEOREM 1. *Assume* H1 *and* H2 *hold*

(a) *The homogeneous system* (H) *has at most a finite number $n \geq 0$ of independent solutions in $B^1_{\gamma,p}$ (i.e. J contains n integers).*

(b) *If $n=0$ (i.e.* (H) *has no nontrivial solutions in $B^1_{\gamma,p}$), then the nonhomogeneous system* (NH) *has a unique solution in $B^1_{\gamma,p}$ for each $(g,h)\in B^0_{\gamma,p}\times B_p$. Moreover, the operator taking $(g,h)$ to the unique solution of* (NH) *is a linear and bounded operator from $B^0_{\gamma,p}\times B_p \to B^1_{\gamma,p}$.*

(c) *If $n>0$ then* (NH) *has a solution in $B^1_{\gamma,p}$ for $(g,h)\in B^0_{\gamma,p}\times B_p$ if and only if $\Omega_j[g,h]=0$ for all $j\in J$. Moreover, the operator taking $(g,h)$ to the unique solution of* (NH) *satisfying*

$$\int_{-p/2}^{p/2} z(\tau,a)y_0^j(a)\,e^{-ij\omega\tau}\,d\tau=0 \text{ for all } j\in J \tag{3.4}$$

*is a linear and bounded operator from $B^0_{\gamma,p}\times B_p\to B^1_{\gamma,p}$.*

The unique solution of (NH) guaranteed when $J=\emptyset$ by Theorem 1(b) is

$$z(\tau,a)=\sum_{j=-\infty}^{+\infty}[\Omega_j[g,h]D_j^{-1}y_j^0(a)+x_j^0(a)]\,e^{ij\omega\tau}.$$

When $J\neq\emptyset$, (NH) has infinitely many solutions given by

$$z(\tau,a)=\sum_{j\in J}[\kappa_j y_j^0(a)+x_j^0(a)]\,e^{ij\omega\tau}+\sum_{j\notin J}[\Omega_j[g,h]D_j^{-1}y_j^0(a)+x_j^0(a)]\,e^{ij\omega\tau}$$

where $\kappa_j$ are arbitrary constants satisfying $\kappa_{-j}=\bar{\kappa}_j$ for $j\in J$, $j\geq 0$. These solutions are in fact continuously differentiable in $\tau$ (as well as in $a$).

The proofs of these results and of the next Theorem 2, which constitute the bulk of the technical analysis of this paper, appear in Section 7 below.

Theorem 1 concerns the nullspace and range of the operator $L$: $B^1_{\gamma,p}\to Y$ defined by

$$Ly:=\Big(\partial y/\partial a+c_1y+c_2\int_0^\infty k_1(\alpha)y(\tau+a-\alpha,\alpha)\,d\alpha,\ y(\tau,0)\\ -\int_{s=0}^\infty\int_{a=0}^\infty k_2(s,a)y(\tau-s-a,a)\,da\,ds\Big) \tag{3.5}$$

where for convenience we denote $Y:=B^0_{\gamma,p}\times B_p$. The basic properties of this operator are more fully described in the next theorem.

THEOREM 2

*The linear operator $L$: $B^1_{\gamma,p}\to Y$ defined by* (3.5) *is bounded. The nullspace $N(L)$ and the range $R(L)$ are closed and admit bounded projections. Moreover,* codim $R(L)=\dim N(L)=n<+\infty$.

In the next section I will be particularly interested in the case $n=2$ when (H) has exactly two independent (nontrivial) solutions in $B^1_{\gamma,p}$. This case occurs when (3.1) holds for $j=1$ and fails for $j\neq 1$ $(j\geq 0)$ in which case

$$y(\tau,a)=y_1{}^0(a)\,e^{i\omega\tau} \tag{3.6}$$

is a complex valued solution of (H). This occurrence is equivalent to the root condition

$$D(i\omega)=0 \text{ and } D(ij\omega)\neq 0 \text{ for } j\neq 1, j\geq 0$$

where $D$ is the "characteristic function" of the complex variable $\zeta$ defined by

$$D(\zeta):=1-\int_{s=0}^{\infty}\int_{a=0}^{\infty}k_2(s,a)\,\mathrm{e}^{-\zeta(s+a)}\,\mathrm{e}^{-C(a)}$$

$$\times\left[1-\frac{1}{\Delta(\zeta)}\int_{\alpha=0}^{\infty}k_1(\sigma)\,\mathrm{e}^{-\zeta\sigma}\,\mathrm{e}^{-C(\sigma)}\,\mathrm{d}\sigma\int_{\alpha=0}^{a}\mathrm{e}^{C(\alpha)}c_2(\alpha)\,\mathrm{e}^{\zeta\alpha}\,\mathrm{d}\alpha\right]\mathrm{d}a\,\mathrm{d}s$$

$$\Delta(\zeta):=1+\int_{a=0}^{\infty}k_1(a)\,\mathrm{e}^{-\zeta a}\,\mathrm{e}^{-C(a)}\int_{\alpha=0}^{a}\mathrm{e}^{C(\alpha)}c_2(\alpha)\,\mathrm{e}^{\zeta\alpha}\,\mathrm{d}\alpha\,\mathrm{d}a.$$

## 4. A BIFURCATION THEOREM

Consider now the nonlinear system

$$\partial x/\partial a+c_1(a)x+c_2(a)\int_0^{\infty}k_1(\alpha)x(\tau+a-\alpha,\alpha)\,\mathrm{d}\alpha=n_1(x,\lambda) \quad (4.1)$$

$$x(\tau,0)=\int_{s=0}^{\infty}\int_{\alpha=0}^{\infty}k_2(s,a)x(\tau-s-\alpha,\alpha)\,\mathrm{d}\alpha\,\mathrm{d}s+n_2(x,\lambda) \quad (4.2)$$

for $x=x(\tau,a)\in B^1_{\gamma,p}$ where the right hand sides depend on two real parameters $\lambda=(\lambda_1,\lambda_2)\in R^2:=R\times R$. More specifically

$$n_1=\lambda_1L_1x+\lambda_2L_2x+g(x,\lambda),\quad n_2=\lambda_1K_1x+\lambda_2K_2x+h(x,\lambda) \quad (4.3)$$

where

H3: $L_i$: $B^1_{\gamma,p}\to B^0_{\gamma,p}$ and $K_i$: $B^1_{\gamma,p}\to B_p$ are linear and bounded operators

and the terms $g$ and $h$ are "higher order" in the sense that

H4: the operator $N$: $\Lambda_1\times\Lambda_2\to B^0_{\gamma,p}\times B_p$ defined by $N=N(x,\lambda):=(g(x,\lambda),h(x,\lambda))$, where $\Lambda_1$ and $\Lambda_2$ are open neighborhoods of $x=0$, $\lambda=0$ in $B^0_{\gamma,p}$ and $R^2$ respectively, has the property that $N(\epsilon x,\lambda)=\epsilon M(x,\lambda,\epsilon)$ where $M$: $\Lambda_1\times\Lambda_2\times(-\epsilon_0,\epsilon_0)\to B^0_{\gamma,p}\times B_p$ is a $q\geq 1$ times continuously (Fréchet) differentiable operator which satisfies $M(x,0,0)=M_x(x,0,0)=0$, $x\in\Lambda_1$.

Under the assumptions H1–H4 it is possible, by making use of Theorem 2, to apply a general abstract bifurcation theorem to obtain nontrivial solutions of (4.1)–(4.3) in $B^1_{\gamma,p}$ as described in the following theorem. The details are given in Section 7.

THEOREM 3

*Assume that* H1–H4 *hold and that the linear, homogeneous system* (H) *has exactly two independent (nontrivial) solutions in* $B^1_{\gamma,p}$. *Also assume that*

$$\delta:=Im[\bar{\Omega}_1(L_1y,K_1y)\Omega_1(L_2y,K_2y)]\neq 0 \quad (4.4)$$

*where* $y$ *is given by* (3.6). *Then* (4.1)–(4.3) *has a solution of the form*

$$x(\tau,a)=\epsilon y(\tau,a)+\epsilon z(\tau,a,\epsilon),\ \lambda=\lambda(\epsilon)$$

*for all* $\epsilon$ *satisfying* $|\epsilon|<\epsilon_1(0<\epsilon_1\leq\epsilon_0)$ *where* $z=z(\cdot,\cdot,\epsilon)$: $(-\epsilon_1,\epsilon_1)\to B^1_{\gamma,p}$, $\lambda$: $(-\epsilon_1,\epsilon_1)\to R^2$ *are* $q\geq 1$ *times continuously differentiable in* $\epsilon$ *with* $\|z(\tau,a,\epsilon)\|^1_{\gamma,p}=0(|\epsilon|)=0(|\epsilon|)$ *as* $\epsilon\to 0$.

In the so-called "nondegeneracy condition" (4.4), *Im* means the "imaginary part of". The function $x(\tau,a)$ is in fact also continuously differentiable in $\tau$ and satisfies (4.1)–(4.2) everywhere.

Theorem 3 can be applied to the general McKendrick model equations (2.1)–(2.2) by setting $x(t,a)=\rho(t,a)-\rho_0(a)$, where $\rho_0(a)\geq 0$ is a steady-state solution of (2.1)–(2.2), changing independent variables from $t$, $a$ to $\tau$, $a$ where $\tau = t - a$ and choosing two parameters $\mu_1$, $\mu_2$ in (2.1)–(2.2) to serve as bifurcation parameters. The resulting equations are then linearized at $x = 0$ and $\mu_i = \mu_i^0$ where $\mu_i^0$ are critical values of the parameters at which the linearization (H) has two independent (nontrivial) solutions in $B^1_{\gamma,p}$. The expressions $n_i$ are the higher order terms in this linearization and the parameters $\lambda_i$ are given by $\lambda_i = \mu_i - \mu_i^0$.† The nondegeneracy condition (4.4) (a "generic" condition in the sense that it is an inequality) then insures the existence of a local, bifurcating branch of periodic solutions of *fixed* period $p$ of the form

$$\rho(t, a) = \rho_0(a) + \epsilon y(t-a, a) + \epsilon z(t-a, a, \epsilon) \tag{4.5}$$

for parameter values

$$\mu_i = \mu_i^0 + \lambda_i(\epsilon) \tag{4.6}$$

as given in Theorem 3.‡ An example of this procedure will be given in Section 6.

In order to carry out this procedure it is necessary to determine for what values $\mu_i^0$ of the parameters $\mu_i$ the homogeneous linearized system (H) has nontrivial solutions $y \in B^1_{\gamma,p}$ (as given by (3.6)). Moreover, if higher order terms are desired in the Liapunov–Schmidt expansions (4.5)–(4.6) then it is necessary, as usual, to be able to solve a sequence of nonhomogeneous systems of the form (NH). Formulas for solutions of (H) and NH) were given in preceding Section 3.

The details of the proofs in Section 7 below show that the above results remain valid for the systems (H), (NH) and (4.1)–(4.3) obtained by formally setting $k_2(s, a) = \delta(s - \sigma_1)k(a)$ in (4.2) and/or $k_1(\alpha) = \delta(\alpha - \sigma_2)$ in (4.1) where $\delta(s)$ is the Dirac function at $s = 0$. In applications to (2.1)–(2.2) this can come about, for example, by choosing the gestation function $g(s) \equiv \delta(s - \sigma_1)$, i.e. by assuming that there is a constant, instantaneous gestation period of fixed length $\sigma_1 \geq 0$ ($\sigma_1 = 0$ corresponding to the assumption of no gestation period which is the most common one made in the literature).

It is also possible to repeat the proofs of Section 7 verbatim for systems of equations of the type (4.1)–(4.3) and obtain Theorem 3. For simplicity, however, I do not treat systems here.

## 5. ONE PARAMETER OF HOPF-TYPE BIFURCATION

In the above described application of Theorem 3 to the equations (2.1)–(2.2) the choice of the two bifurcation parameters $\mu_i$ can, of course, be made in any manner from the available parameters in the equations. On the other hand, it is also possible to choose only one parameter $\mu_1$ which appears explicitly in the equations (as is done for the case of the more familiar Hopf bifurcation phenomenon) while the second parameter $\mu_2 = p$ is the unknown period (if the system is autonomous) and is introduced into the equations by means of a rescaling of the independent variables from $t$, $a$ to $t/p$, $a/p$. Theorem 3 is then applied on the space $B^1_{\gamma,1}$ of fixed period one. In terms of the original variables one then sees a period varying ($p = \mu_2^0 + \lambda_2(\epsilon)$), Hopf-type bifurcation as the explicitly appearing parameter $\mu_1 = \mu_1^0 + \lambda_1(\epsilon)$ passes through its critical value. (This all can be done, of course, only for autonomous equations, i.e. equations for which the operators $n_i$ satisfy H4 for all periods $p$. Theorem 3 can, however, apply to nonautomous, periodic equations (4.1)–(4.3) as well. For an example, see [2].)

This procedure is straightforward and routine, the only analysis involved, as far as deriving such a Hopf bifurcation theorem from the two parameter bifurcation results in Theorem 3 is concerned, is that in showing that the assumptions concerning the existence of nontrivial solutions of the linear system (H) and the nondegeneracy assumption (4.4) can be equivalently statéd, in the familiar manner of Hopf-type bifurcation, as the transversal crossing of a pair of roots of the characteristic equation across the imaginary axis away from the origin.

Thus one parameter Hopf-type bifurcation results can be proved from multiparameter bifurcation theorems such as Theorem 3 and this is in fact often done for various types of

†It is possible that the resulting equations are not quite of the form (4.1)–(4.2). The only constraint required (beyond the necessary smoothness to perform the linearization) is that the integral on the left side of equation (4.1) have a multiplicatively separable kernel. This will be true, for example, if the functional dependence of the death rate $d_t$ on density $\rho$ is by means of an integral with such a kernel.

‡The steady state $\rho_0(a)$ may depend on the parameters $\mu_i$.

equations [3–5, 13, 17]. I will make one such application of Theorem 3 to the McKendrick equations (2.1)–(2.2) in Theorem 4 below.

The relationship between the two parameter bifurcation phenomenon for solutions of a fixed period as described in Theorem 3, and the one parameter, period varying bifurcation obtained from Theorem 3 by the procedure described above is qualitatively that discussed and graphically displayed in [3] for integrodifferential equations. In the $\mu_1$, $\mu_2$ plane there is a "bifurcation curve $C$" of critical values $\mu_1^0(p)$, $\mu_2^0(p)$ parameterized by the period $p = \omega/2\pi$ from which emanates the family of paths $\mu_i = \mu_i^0(p) + \lambda_i(\epsilon, p)$ along which time periodic solutions of fixed period $p$ bifurcate from the steady state. By holding one of the parameters $\mu_i$ fixed, however, and varying only the other, one in general cuts across this family of paths transversally, hence the period varying property of the one parameter bifurcation. As one can see, however, the bifurcation phenomena in both cases are identical when viewed in the $\mu_1$, $\mu_2$ plane. While one may prefer to vary only one explicit parameter in a given system, it is frequently easier to vary two explicit parameters in order to justify and understand the bifurcation phenomenon. For one thing, if only one parameter, say $\mu_1$, is varied there is necessarily the extra concern of being certain that the horizontal lines $\mu_2 = constant$ transversally cross the bifurcation curve $C$ in order to guarantee that bifurcation occurs. (See Fig. 1 in Section 6 below.)

As an example of a one parameter Hopf-type bifurcation result for equations of the form (4.1)–(4.3) as derived by this procedure using Theorem 3 consider the equations

$$\partial x/\partial a + c(a, \mu)x = h(x, \mu) \tag{5.1}$$

$$x(\tau, 0) = \int_0^\infty k(a, \mu)x(\tau - a, a)\,\mathrm{d}a + g(x, \mu) \tag{5.2}$$

where $\mu \in R$. Here a single real parameter $\mu$ appears in the equations and I have taken $k_2(s, a) = \delta(s)k(a, \mu)$, $c_2(a) \equiv 0$. I am not trying for the greatest generality here, but have restricted my attention to a case for which I have been able to demonstrate that the nondegeneracy condition (4.4) is equivalent to the familiar transversality condition in Hopf bifurcation.

Suppose the change of variables from $\tau$ to $\tau/p$ is made in (5.1)–(5.2) and one defines $\lambda_1 = \mu - \mu^0$, $\lambda_2 = p - p^0$ where $\mu^0$, $p^0$ are yet to be determined critical values of the parameter $\mu$ and the period $p$ respectively. Then (5.1)–(5.2) takes the form (4.1)–(4.3) with

$$\begin{aligned} &c_1(a) = p^0c(ap^0, \mu^0),\ \ k_2(s, a) = \delta_0(s)p^0k(ap^0, \mu^0),\ \ k_1(a) \equiv c_2(a) \equiv 0 \\ &L_1x = -p^0c_\mu(ap^0, \mu^0)x,\ \ L_2x = -[c(ap^0, \mu^0) + p^0c_a(ap^0, \mu^0)]x \\ &K_1x = \int_0^\infty p^0k_\mu(ap^0, \mu^0)x(\tau - a, a)\,\mathrm{d}a,\ K_2x = \int_0^\infty [k(ap^0, \mu^0) \\ &\qquad\qquad + p^0ak_a(ap^0, \mu^0)]x(\tau - a, a)\,\mathrm{d}a. \end{aligned} \tag{5.3}$$

Assume that under this change of variable the operators $h$ and $g$ become new operators $\tilde{h}$ and $\tilde{g}$ for which

H5: $\tilde{h}$, $\tilde{g}$ satisfy H4 with $p = 1$ and $c, k$: $R^+ \times R \to R$ are continuously differentiable functions for which the operators, kernels and coefficients defined by (5.3) satisfy H1 and H3 with $p = 1$.

Since $k_1(a) \equiv 0$ implies $\Delta_j = 1$ for all $j$ we see that H2 holds. Hence all hypotheses H1–H4 in Theorem 3 are implied by H5 and as a result Theorem 3 with $p = 1$ can now be applied to the resulting system. One needs only require the existence of nontrivial solutions of the linearization and the validity of the nondegeneracy condition (4.4). These latter two requirements will now be shown to be equivalent to the existence of purely imaginary roots of the characteristic equation with certain properties.

The characteristic equation for the linearization of (5.1)–(5.2) reduces to

$$D(\zeta, \mu) := 1 - \int_{a=0}^\infty k(a, \mu)\,\mathrm{e}^{-\zeta a}\,\mathrm{e}^{-C(a,\mu)}\,\mathrm{d}a = 0 \tag{5.4}$$

where $C(a,\mu) := \int_0^a c(\alpha,\mu)\,d\alpha$. As pointed out above in Section 3 it is sufficient for the linearization to have exactly two independent solutions in $B^1_{\gamma,p}$ that (5.4) has the simple root $\zeta = i\omega_0$, $\omega_0 = 2\pi/p^0$, and no other purely imaginary root when $\mu = \mu_0$. Assuming

$$\text{H6:}\quad D_\zeta(i\omega_0,\mu_0) = \int_0^\infty ak(a,\mu_0)\,e^{i\omega_0 a}\,e^{-C(a,\mu_0)}\,da \neq 0$$

one can deduce, from the implicit function theorem, the existence of a continuously differentiable function $\zeta = \zeta(\mu)$, $\zeta(\mu_0) = i\omega_0$, such that $D(\zeta(\mu),\mu) = 0$ for all $\mu$ near $\mu_0$. The two solutions of period one of (H) with coefficients (5.3) turn out to be the real and imaginary parts of

$$y(\tau,a) = \exp\left(-p^0\int_0^a c(\alpha p^0,\mu_0)\,d\alpha\right)e^{2\pi i\tau}$$

which, together with (5.3), can be used to compute the quantity $\delta$. A straightforward, but lengthy calculation shows that

$$\delta = Im\left\{\frac{d}{d\mu}\int_{a=0}^\infty k(a,\mu)\,e^{-C(a,\mu)}e^{i\omega_0 a}\,da\Big|_{\mu=\mu_0}\frac{1}{p^0}\int_{a=0}^\infty\frac{d}{da}\left[ak(a,\mu_0)\,e^{-C(a,\mu_0)}\right]e^{-i\omega_0 a}\,da\right\}.$$

On the other hand, an implicit differentiation of $D(\zeta(\mu),\mu) = 0$ shows that

$$\zeta'(\mu_0) = -D_\mu(i\omega_0,\mu_0)\overline{D_\zeta(i\omega_0,\mu_0)}/|D_\zeta(i\omega_0,\mu_0)|^2.$$

A calculation of $D_\mu$ and $D_\zeta$ from (5.4) yields

$$D_\mu(i\omega_0,\mu_0) = -p^0\frac{d}{d\mu}\int_{a=0}^\infty k(a,\mu)\,e^{-C(a,\mu)}\,e^{-i\omega_0 a}\,da\Big|_{\mu=\mu_0}$$

and after an integration by parts

$$D_\zeta(i\omega_0,\mu_0) = -\frac{i}{\omega_0}\int_{a=0}^\infty\frac{d}{da}\left[ak(a,\mu_0)\,e^{-C(a,\mu_0)}\right]e^{-i\omega_0 a}\,da$$

provided

$$ak(a,\mu_o)\,e^{-C(a,\mu_0)} \to 0 \quad\text{as}\quad a\to+\infty, \tag{5.5}$$

a condition which holds if $k(a,\mu_0)$ is bounded for $a \geq 0$. These calculations lead to

$$Re\zeta'(\mu_0) = ARe\left\{i\frac{d}{d\mu}\int_0^\infty k(a,\mu)\,e^{-C(a,\mu)}\,e^{-i\omega_0 a}\,da\Big|_{\mu=\mu}\int_0^\infty\frac{d}{da}\left[ak(a,\mu_0)\,e^{-C(a,\mu_0)}\right]e^{-i\omega_0 a}\,da\right\}$$

or $Re\,\zeta'(\mu_0) = A\delta$ where $A := 1/\omega_0|D_\zeta(i\omega_0,\mu_0)|^2 > 0$. Thus, the nondegeneracy condition $\delta \neq 0$ is equivalent to $Re\,\zeta'(\mu_0) \neq 0$ and we have the following one parameter, Hopf-type bifurcation result for (5.1)–(5.2) which now follows from Theorem 3.

THEOREM 4

*Suppose H5 holds and that the characteristic equation* (5.4) *has a complex root* $\zeta = \zeta(\mu)$ *for which* $\zeta(\mu_0) = i\omega_0$, $\omega_0 > 0$, $\mathrm{Re}\,\zeta'(\mu_0) \neq 0$ *and no other purely imaginary root for* $\mu = \mu_0$. *Assume that* $k(a,\mu_0)$ *is bounded for* $a \geq 0$ *(or more generally that* (5.5) *holds). Then* (5.1)–(5.2) *has a solution of the form* $x(\tau,a) = y(\tau/p, a/p) + \epsilon z(\tau/p, a/p,\epsilon)$ *for* $\mu = \mu_0 + \lambda_1(\epsilon)$ *and* $p = p^0 + \lambda_2(\epsilon)$ *for small* $|\epsilon|$ *where* $y, z \in B^1_{\gamma,1}$ *and* $\lambda_i(\epsilon)$ *are as in Theorem* 3.

Note that in Theorem 4 the solution $x(\tau,a)$ is $p(\epsilon)$-periodic in $\tau$. It is in fact also continuously differentiable in $\tau$.

## 6. AN APPLICATION

In order to illustrate the use of the bifurcation results in Theorems 3 and 4 consider the McKendrick equations (2.1)–(2.2) with $d_t \equiv d = constant > 0$, $f_t = b\beta(a)[1 - \int_0^\infty w(\alpha)\rho(t, \alpha)\,d\alpha]_+$ and $g(s) = \delta(s)$; that is, consider

$$\partial\rho/\partial t + \partial\rho/\partial a + d\mu = 0 \tag{6.1}$$

$$\rho(t, 0) = \int_{a=0}^{\infty} b\beta(a)\left[1 - \int_{\alpha=0}^{\infty} w(\alpha)\rho(t, \alpha)\,d\alpha\right]_+ \rho(t, a)\,da. \tag{6.2}$$

Here $b$ is a positive constant, $\beta$ and $w$: $R^+ \to R^+$ are bounded and continuous with $\int_0^\infty \beta(a)\,da = 1$ and $\int_0^\infty w(a)\,da < +\infty$, and $[\nu]_+ = \nu$ if $\nu \geq 0$ and $[\nu]_+ = 0$ if $\nu < 0$. This particular model system is frequently studied as a "first approximation" or a prototype for more complicated cases involving more involved death and fecundity rate dependencies on age $a$ and density $\rho$ [6, 9, 11, 12]. It assumes that age dependence is more important in the fecundity rate than in the death rate (indeed, the death rate is taken independent of age) and that fecundity is a decreasing linear functional of density. There is no gestation period and the dependence of fecundity on age is described by the normalized "maturation function" $\beta(a)$. The weighting function $w(\alpha)$ describes the effect that the density of age class $\alpha$ has on the fecundity of age class $a$ (which is, since $w$ is here taken independent of $a$, the same for all age classes $a$).

The intent here is not to study (6.1)–(6.2) in depth, but only to illustrate a case of the bifurcation of time periodic solutions. For a study of this model (including a gestation period) and the destabilizing effects of the various biological mechanisms represented by $\beta$, $w$ and $g$, see [6].

For simplicity, take

$$w(a) \equiv \beta(a) \text{ and assume } \int_0^\infty a^j\beta(a)\,da < +\infty \text{ for } j = 1, 2, 3. \tag{6.3}$$

(These finite moments guarantee the smoothness condition $q \geq 1$ in H4.) This means that the effect on fecundity caused by the density of age class $a$ is proportional to the fecundity of age class $a$. This is reasonable, for example, if the age of greatest fecundity is also the age of the maximum consumption of resources (used by all age classes), whose consumption in turn affects fertility.

The steady state solution of (6.1)–(6.3) is then found to be

$$\rho^0(a) = (b\beta^*(d) - 1)\,e^{-da}/b\beta^*(d)^2 \tag{6.4}$$

where "*" denotes the Laplace transform. This steady state is positive if and only if $b\beta^*(d) > 1$ (which has the biological interpretation that the net reproductive rate at low densities per individual per lifetime exceeds unity). Let $x = \rho - \rho^0$, $\lambda_1 = d - d_0$ and $\lambda_2 = b - b_0$. Then (6.1)–(6.2) can be put in the form (4.1)–(4.3) with $c_1(a) \equiv d_0$, $c_2(a) \equiv k_1(a) \equiv 0$, $L_1 x = -x$, $g(x, \lambda) \equiv 0$ and

$$k_2(s, a) = \delta(s)[2 - b_0\beta^*(d_0)]\beta(a)/\beta^*(d_0), \; K_1 x \equiv 0, \; K_2 x = -\int_{a=0}^{\infty} w(a)x(t, a)\,da$$

$$h(x, \lambda) = 2\int_{a=0}^{\infty} r_1(\lambda_1)\beta(a)x(t, a)\,da \int_{s=0}^{\infty} \beta(s)x(t, s)\,ds$$

where $r_1(\lambda_1) = 0(\lambda_1^2)$ is the remainder in the Taylor series expansion $1/\beta^*(d) = 1/\beta^*(d_0) - \lambda_1\beta^{*\prime}(d_0)/\beta^*(d_0)^2 + r_1(\lambda_1)$.

If $\gamma$ is any constant $0 < \gamma < d_0$ then it is an easy matter to check that all the hypotheses H1–H4 hold with $q = 1$. Thus, to apply Theorem 3 we need only find those critical values $d_0$, $b_0$ at which the linearization at $\rho^0(a)$:

$$\partial y/\partial a + d_0 y = 0, \; y(\tau, 0) = [(2 - b_0\beta^*(d_0))/\beta^*(d_0)]\int_{a=0}^{\infty} \beta(a)y(\tau - a, a)\,da$$

has exactly two independent solutions in $B^1_{\gamma,p}$ for some period $p$ and then verify the nondegeneracy condition (4.4). This linearized problem has a solution $y(\tau, a) = y_1(a)\,e^{i\omega\tau}$ if and only if $y_1(a)$ is a constant multiple of $\exp(-d_0 a)$ and

$$1 = [(2 - b_0\beta^*(d_0))/\beta^*(d_0)]\beta^*(d_0 + i\omega), \quad \omega = 2\pi/p \tag{6.5}$$

which, from the real and imaginary parts, is equivalent to

$$S(d_0, p) = 0, \quad C(d_0, p) \neq 0, \quad b_0 = [2C(d_0, p) - \beta^*(d_0)]/\beta^*(d_0)C(d_0, p) \tag{6.6}$$

where $S$ and $C$ are the Fourier integrals ($\omega = 2\pi/p$)

$$S(d_0, p) := \int_{a=0}^{\infty} e^{-d_0 a}\beta(a)\sin\omega a\,da, \quad C(d_0, p) := \int_{a=0}^{\infty} e^{-d_0 a}\beta(a)\cos\omega a\,da.$$

The equation (6.6a) constitutes, for a given $p$, an equation to be solved for $d_0 = d_0(p) > 0$, subject to the inequality (6.6b) whose solution defined the critical value $b_0 = b_0(p)$ by means of (6.6c) which in turn must satisfy

$$b_0\beta^*(d_0) > 1 \tag{6.7}$$

in order to define a positive steady state. So that the linearized problem has no other independent solutions in $B^1_{\gamma,p}$ it is necessary to require that (6.6) is not satisfied by $d_0(p)$ and $b_0(p)$ when $p$ is replaced in (6.6) by $p/2$, $p/3, \ldots$.

Finally, a calculation of $\delta$ shows that the nondegeneracy condition (4.4) reduces to

$$\int_{a=0}^{\infty} e^{-d_0 a} a\beta(a)\sin\omega a\,da \neq 0, \quad \omega = 2\pi/p. \tag{6.8}$$

In summary, *Theorem* 3 *implies the bifurcation of p-periodic solutions of* (6.1)–(6.3) *in the space* $B^1_{\gamma,p}$ *(for* $\gamma < d_0$*) from the positive steady state* (6.4) *at the critical values* $d_0$ *and* $b_0$ *of the death and birth modula d and b which satisfy* (6.6)–(6.8).

As an example, consider the frequently used normalized distributions

$$w(a) \equiv \beta(a) = \frac{1}{n!}\left(\frac{n}{m}\right)^{n+1} a^n e^{-na/m}, \quad n = 1, 2, 3, \ldots \tag{6.9}$$

where $m > 0$ is the age of maximum fecundity. For $n = 1$

$$S(d_0, p) = 2\omega m(d_0 m + 1)/[(d_0 m + 1)^2 + \omega^2 m^2]^2 \neq 0, \quad \omega = 2\pi/p$$

for all $p > 0$, $m > 0$, $d_0 > 0$. Thus (6.6a) fails to hold and no bifurcation occurs because the linearization at the steady state possesses no nontrivial solutions in $B^1_{\gamma,p}$.

On the other hand, for the "narrower distribution" (or "maturation window" as it is frequently called), when $n = 2$ one finds $\beta^*(d_0) = 8/(d_0 m + 2)^3$ and

$$S(d_0, p) = 8\omega m[3(d_0 m + 2)^2 - \omega^2 m^2][(d_0 m + 2)^2 + \omega^2 m^2]^{-3}$$

$$C(d_0, p) = 8(d_0 m + 2)[(d_0 m + 2)^2 - 3\omega^2 m^2][d_0 m + 2)^2 + \omega^2 m^2]^{-3}, \quad \omega = 2\pi/p$$

and hence (6.6a) and (6.6c) imply

$$d_0 = (\omega m - 2\sqrt{3})/m\sqrt{3}, \quad b_0 = 5\omega^3 m^3\sqrt{3}/36, \quad \omega = 2\pi/p \tag{6.10}$$

in which case $C(d_0, p) = -3\sqrt{3}/\omega^3 m^3 < 0$ so that (6.6b) holds. (6.7) is easily checked and another computation shows that

$$\int_{a=0}^{\infty} e^{-d_0 a} a\beta(a)\sin\omega a\,da = -9\sqrt{3}/4\omega^4 m^3 \neq 0$$

so that the nondegeneracy condition (6.8) holds. Theorem 3 implies that period $p$ bifurcation occurs along paths $P(\epsilon)$ in the $d$, $b$ parameter plane emanating from the critical point $d_0$, $b_0$. The formulas (6.10) define a bifurcation curve parameterized by the period $p = 2\pi/\omega$. This curve is graphed in Fig. 1.

This same example can be used to illustrate the Hopf-type bifurcation of Theorem 4. If $d$ is held fixed and $\mu = b$ is chosen as the bifurcation parameter, then the characteristic equation (5.4) reduces to

$$(m\zeta + dm + n)^{n+1} = 2(md + n)^{n+1} - \mu n^{n+1}. \tag{6.11}$$

For $n = 1$ the roots $\zeta = [-(dm+1) \pm \sqrt{[2(dm+1)^2 - \mu)}]/2$ never cross the imaginary axis for $\mu > (dm+1)^2$ (which is required by (6.7) for the existence of a positive steady state). On the other hand for $n = 2$ (and, in fact, for $n \geq 3$), the roots of (6.11) do cross the imaginary axis. This occurs at $\zeta = i\omega_0$ for

$$\mu_0 = b_0 = (dm+n)^{n+1} n^{-n-1}[2 + \sec^{n+1}(\pi/(n+1)], \quad \omega_0 = (dm+n)m^{-1}\tan(\pi/(n+1)).$$

Moreover, $Re\zeta'(\mu_0) = (dm+n)m^{-1}\cos^{n+1}(\pi/(n+1)) \neq 0$.

The nature of the surface given by the solution $\rho(t, a)$ of (6.1)–(6.3) as this bifurcation occurs is shown in the sequence of graphs in Figs. 2–5. These solution surfaces were numerically computed for $\beta(a)$ and $w(a)$ given by (6.9) with $n = 2$ and $d = m = 1$.

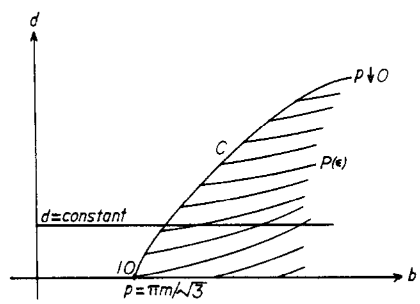



Fig. 1. The bifurcation curve $C$ given by (6.10), parameterized by the period $0 < p < \pi m/\sqrt{3}$, is graphed for the system (6.1)–(6.2) with (6.9) and $n = 2$. Along the paths $P(\epsilon)$ the bifurcation of time periodic solutions in $B^1_{\gamma,p}(\gamma < d_0(p))$ occurs for fixed period $p$. If one moves along a horizontal line $d = constant$ by increasing $b$, then a Hopf-type bifurcation of period varying type occurs as $C$ and the paths $P(\epsilon)$ are transversally crossed.

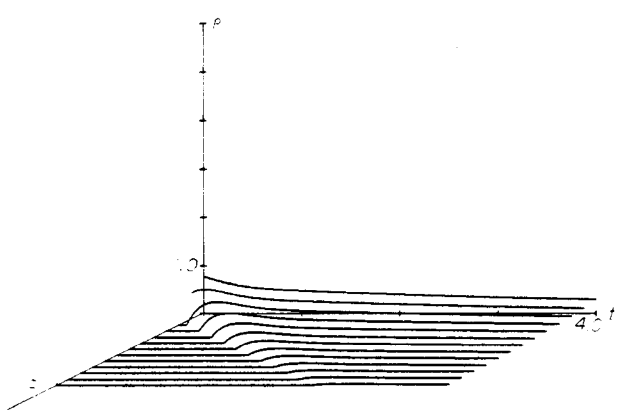
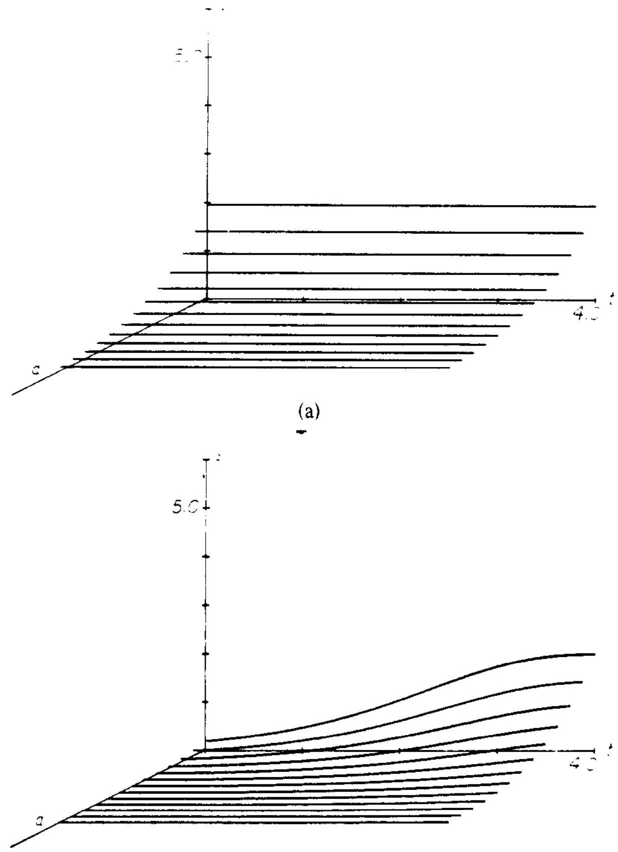


Fig. 2. The birth modulus $b = 3.2$ is less than the critical value 27/8 for which $b\beta^*(d) > 1$ is satisfied and hence no positive steady-state exists. The solution of (6.1)–(6.2) with (6.9) and $n = 2$, $m = d = 1.0$ shown is tending to zero as $t \to +\infty$ in all age classes.



(a)

(b)

Fig. 3. A positive steady state exists for $b = 8.0$ and is shown in (a). In (b) a solution surface is shown monotonically increasing (in a logistic-like manner) to the steady state.

## 7. PROOFS

In this final section proofs are given for Theorems 1–3. Before this is done, however, the assertion that the spaces $B^0_{\gamma,p}$, $B^1_{\gamma,p}$ and $B_p$ are Banach spaces is justified. That these three spaces are linear and that their norms defined in Section 2 are really norms are both easy to verify. It only remains to shown completeness. This will be done for $B^0_{\gamma,p}$ only, the completeness of the other two spaces having similar verifications.

Suppose that $g_n \in B^0_{\gamma,p}$ is a Cauchy sequence. This implies that $g_n$ is also Cauchy with respect to the norm $\|\cdot\|_\gamma$. Thus $g_n$ converges with respect to this norm to a continuous, $p$-periodic function $g$ for which $\|g\|_\gamma < +\infty$[1]. Let $\mathscr{L}^2$ denote the (Hilbert) space of square summable sequences of complex numbers. The sequence of sequences

$$\sigma^n = \{\sup_{a\geq 0} j|c_j(g_n)(a)|\,e^{\gamma a}\}_{j=0}^{\infty},\quad c_j(g_n)(a) := p^{-1}\int_{-p/2}^{p/2} g_n(\tau, a)\,e^{-ij\omega\tau}\,d\tau$$

is Cauchy in the $\|\cdot\|_2$ norm and consequently converges to a sequence $\sigma = \{\sigma_j\} \in \mathscr{L}^2$. It follows that the same is true of the sequence of sequences

$$s^n = \{\sup_{a\geq 0}|c_j(g_n)(a)|\,e^{\gamma a}\}_{j=0}^{\infty}$$

which converges to a sequence $s = \{s_j\} \in \mathscr{L}^2$. It is easy to show that $\sigma_j = js_j$. The conclusion is that

$$\{\sup_{a\geq 0}|c_j(g_n)(a)|\,e^{\gamma a}\}_{j=0}^{\infty} \to \{s_j\}_{j=0}^{\infty} \in \mathscr{L}^2 \text{ as } n \to +\infty \tag{7.1}$$

$$\{\sup_{a\geq 0} j|c_j(g_n)(a)|\,e^{\gamma a}\}_{j=0}^{\infty} \to \{js_j\}_{j=0}^{\infty} \in \mathscr{L}^2 \text{ as } n \to +\infty \tag{7.2}$$

in the $\mathscr{L}^2$ norm $\|\cdot\|_2$.

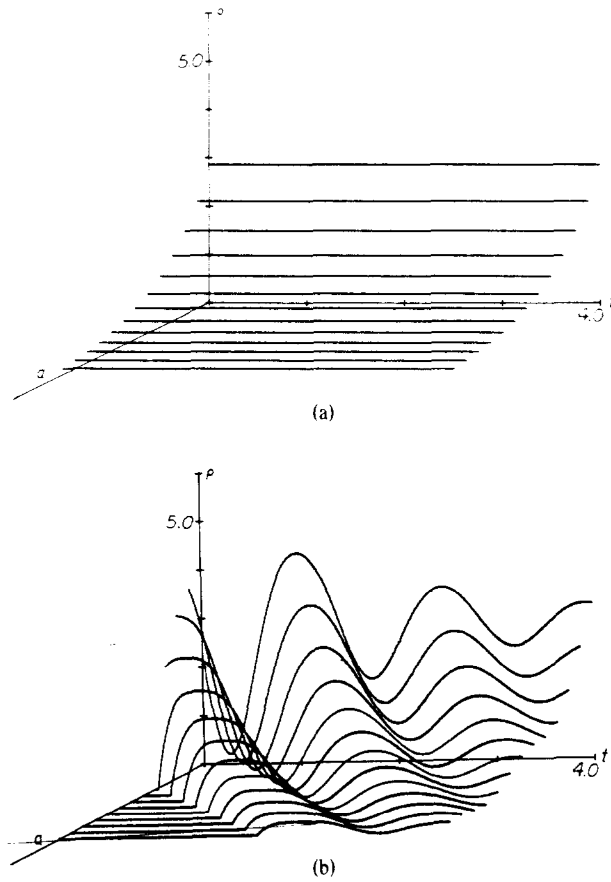



Fig. 4. A positive steady state exists for $b = 22.0$ and is shown in (a). In (b) a damped oscillatory solution surface is shown approaching the steady state.

Next it will be shown that

$$\sup_{a\geq 0}|c_j(g)(a)|\, e^{\gamma a} = s_j \tag{7.3}$$

for all $j$, which will imply that the function $g$ also belongs to the space $B^0_{\gamma,p}$. To do this, note first of all that (7.1) implies

$$\lim_{n\to\infty}\sup_{a\geq 0}|c_j(g_n)(a)|\, e^{\gamma a} = s_j \tag{7.4}$$

for each $j$. Secondly the inequalities

$$\begin{aligned}|\sup_{a\geq 0}|c_j(g_n)(a)|\, e^{\gamma a} - \sup_{a\geq 0}|c_j(g)(a)|\, e^{\gamma a}| &\leq \sup_{a\geq 0}\|c_j(g_n)(a)| - |c_j(g)(a)\|\, e^{\gamma a}\\ \leq \sup_{a\geq 0}|c_j(g_n)(a) - c_j(g)(a)|\, e^{\gamma a} &\leq \sup_{a\geq 0}|c_j(g_n - g)(a)|\, e^{\gamma a} \leq \|g_n - g\|_\gamma\end{aligned}$$

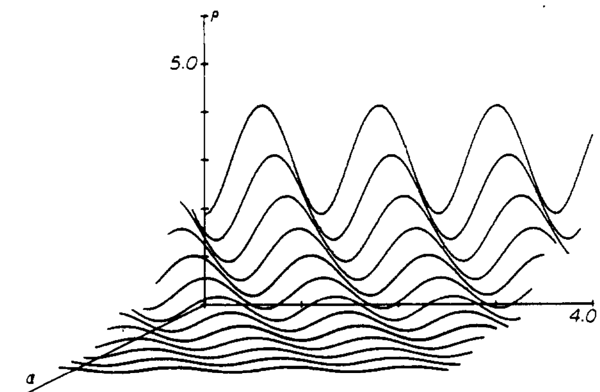
show that

$$\lim_{n\to\infty} \sup_{a\geq 0}|c_j(g_n)(a)|\, e^{\gamma a} = \sup_{a\geq 0}|c_j(g)(a)|\, e^{\gamma a}$$

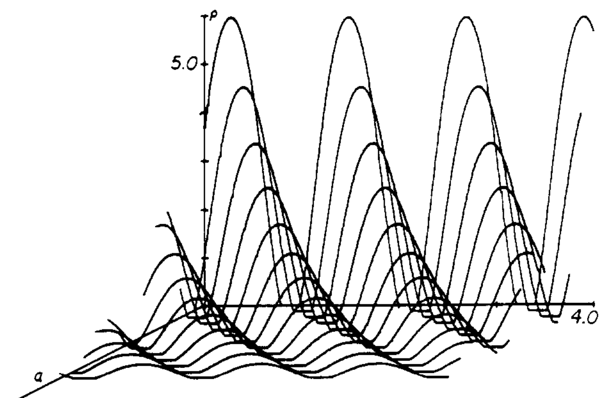
which together with (7.4), verifies (7.3).

At this point it has been shown that corresponding to any Cauchy sequence $g_n \in B^0_{\gamma,p}$ is a function $g \in B^0_{\gamma,p}$ for which $g_n \to g$ in the norm $\|\cdot\|_\gamma$. But (7.2) shows that $g_n \to g$ in the norm $\|\cdot\|_{\gamma,2}$ also. It thus follows that $g_n \to g$ in the norm $\|\cdot\|^0_{\gamma,p}$ and hence that $B^0_{\gamma,p}$ is complete.

Before proving Theorem 1 it is necessary to establish the following preliminary results. Let $Z$ denote the complex numbers.




(a)




(b)

Fig. 5. For $b = 34.0$ and $b = 35.0$ in (a) and (b) respectively, solutions periodic in time have bifurcated from the steady-state.

LEMMA 1

*Suppose that $c_1$: $R^+ \to R$, $\bar{c}_2$: $R^+ \to Z$ are continuous and bounded and satisfy $c_1(a) \geq c_0 > 0$, $\sup_{a\geq 0}|\bar{c}_2(a)|\, e^{\gamma a} < +\infty$, $0 < \gamma < c_0$, and that $\bar{k}_1$: $R^+ \to Z$ is bounded and measurable. The linear homogeneous integrodifferential equation*

$$y'(a) + c_1(a)y(a) + \bar{c}_2(a)\int_{a=0}^{\infty} \bar{k}_1(s)y(s)\,\mathrm{d}s = 0 \tag{7.5}$$

*has a unique solution $y^0(a)$ satisfying $y(0) = 1$ provided*

$$1 + \int_{a=0}^{\infty} \bar{k}_1(a)\,\mathrm{e}^{-C(a)}\int_{\alpha=0}^{a} \mathrm{e}^{C(\alpha)}\bar{c}_2(\alpha)\,\mathrm{d}\alpha\,\mathrm{d}a \neq 0. \tag{7.6}$$

*The general solution of (7.5) is a constant multiple of $y^0(a)$.*

*Proof.* For any complex number $w_1 \in Z$ the equation

$$y'(a) + c_1(a)y(a) + \bar{c}_2(a)w_1 = 0 \tag{7.7}$$

has a unique solution satisfying $y(0) = 1$ given by

$$y^0(a) = \mathrm{e}^{-C(a)} - \mathrm{e}^{-C(a)}\int_{\alpha=0}^{a} \mathrm{e}^{C(\alpha)}\bar{c}_2(\alpha)w_1\,\mathrm{d}\alpha. \tag{7.8}$$

Solving (7.5) is equivalent to choosing $w_1$ such that $w_1 = \int_0^\infty \bar{k}_1(a)y^0(a)\,da$, an equation which has the unique solution

$$w_1 = \int_{a=0}^{\infty} \bar{k}_1(a)\,e^{-C(a)}\,da \Big/ \left[1 + \int_{a=0}^{\infty} \bar{k}_1(a)\,e^{-C(a)} \int_{\alpha=0}^{a} e^{C(\alpha)}\bar{c}_2(\alpha)\,d\alpha\,da\right]. \tag{7.9}$$

Thus the unique solution of (7.5) with $y(0) = 1$ is given by (7.8)–(7.9).

Clearly any constant multiple of $y^0(a)$ solves (7.5). Conversely, let $y(a)$ be an arbitrary solution of (7.5). Then $w(a) := y(0)y^0(a) - y(a)$ solves (7.5) with $w(0) = 0$. Hence $w(a)$ solves (7.7) with $w_1 = \int_0^\infty \bar{k}_1(a)w(a)\,da$ which, together with $w(a) = -e^{-C(a)} \int_0^a e^{C(\alpha)}\bar{c}_2(\alpha)w_1\,d\alpha$, implies that $w_1 = 0$. Thus $w(a) \equiv 0$ or $y(a) \equiv y(0)y^0(a)$.§§

Note that from (7.8)–(7.9) follows

$$\sup_{a\geq 0}|y^0(a)|\,e^{\gamma a} < +\infty. \tag{7.10}$$

The general solution of the nonhomogeneous equation

$$x'(a) + c_1(a)x(a) + \bar{c}_2(a)\int_{a=0}^{\infty} \bar{k}_1(s)x(s)\,ds = g(a) \tag{7.11}$$

is, of course, given by $\kappa y^0(a) + x^0(a)$ where $x^0(a)$ is any particular solution of (7.11). Consider (7.11) with (for simplicity) the initial condition $x^0(0) = 0$, a problem which is equivalent to solving the equations

$$x'(a) + c_1(a)x(a) + \bar{c}_2(a)w_2 = g(a), \quad \int_{a=0}^{\infty} \bar{k}_1(s)x(s)\,ds = w_2, \quad x(0) = 0$$

where $w_2 \in Z$. The first and third equations imply

$$x^0(a) = e^{-C(a)} \int_{\alpha=0}^{a} e^{C(\alpha)}\,[g(\alpha) - w_2\bar{c}_2(\alpha)]\,d\alpha. \tag{7.12}$$

The second equation and (7.12) lead to the unique value of $w_2$ given by

$$w_2 = \int_{s=0}^{\infty} \bar{k}_2(s)\,e^{-C(s)} \int_{\alpha=0}^{s} e^{C(\alpha)}g(\alpha)\,d\alpha\,ds \Big/ \left[1 + \int_{a=0}^{\infty} \bar{k}_1(a)\,e^{-C(a)} \int_{\alpha=0}^{a} e^{C(\alpha)}\bar{c}_2(\alpha)\,d\alpha\,da\right] \tag{7.13}$$

Lemma 2

*Under the same assumptions as in Lemma* 1 *together with* $\sup_{a\geq 0}|g(a)|\,e^{\gamma a} < +\infty$, *the general solution of the nonhomogeneous equation* (7.11) *is given by* $x(a) = \kappa y^0(a) + x^0(a)$ *for an arbitrary constant* $\kappa$, *for* $y^0(a)$ *given by* (7.8)–(7.9) *and* $x^0(a)$ *given by* (7.12)–(7.13).

Note that from (7.12)–(7.13) follows

$$\sup_{a\geq 0}|x^0(a)|\,e^{\gamma a} < +\infty.$$

Using these two lemmas, one can easily obtain a Fredholm alternative for the following linear problem:

$$z'(a) + c_1(a)z(a) + \bar{c}_2(a)\int_{a=0}^{\infty} \bar{k}_1(s)z(s)\,ds = g(a) \tag{7.14}$$

$$z(0) = \int_{s=0}^{\infty}\int_{a=0}^{\infty} \bar{k}_2(s, a)z(a)\,da\,ds + h \tag{7.15}$$

LEMMA 3

*In addition to the assumptions of Lemma 1 assume that* $h \in Z$ *that* $\tilde{k}_2$: $R^+ \times R^+ \to Z$ *is measurable and* $\int_0^\infty \int_0^\infty \tilde{k}_2(s, a)\, e^{-\gamma a}\, da\, ds < +\infty$, *and that* $g$: $R^+ \to Z$ *is continuous and* $\sup_{a \geq 0} |g(a)|\, e^{\gamma a} < +\infty$.

(a) *If*

$$1 - \int_{s=0}^{\infty} \int_{a=0}^{\infty} \tilde{k}_2(s, a) y^0(a)\, da\, ds \neq 0 \tag{7.16}$$

*then* (7.14)–(7.15) *has a unique solution given by* $z(a) = \kappa y^0(a) + x^0(a)$ *where*

$$\kappa = \left[\int_{s=0}^{\infty} \int_{a=0}^{\infty} \tilde{k}_2(s, a) x^0(a)\, da\, ds + h\right] \Big/ \left[1 - \int_{s=0}^{\infty} \int_{a=0}^{\infty} \tilde{k}_2(s, a) y^0(a)\, da\, ds\right]. \tag{7.17}$$

(b) *If*

$$1 - \int_{s=0}^{\infty} \int_{a=0}^{\infty} \tilde{k}_2(s, a) y^0(a)\, da\, ds = 0 \tag{7.18}$$

*then* (7.14)–(7.15) *has a solution if and only if*

$$\int_{s=0}^{\infty} \int_{a=0}^{\infty} \tilde{k}_2(s, a) x^0(a)\, da\, ds + h = 0 \tag{7.19}$$

*in which case* $z(a) = \kappa y^0(a) + x^0(a)$ *is a solution for all* $\kappa$.

This lemma follows by substituting the general solution of (7.14) from Lemma 2 into (7.15) and deriving the equation

$$\kappa = \int_{s=0}^{\infty} \int_{a=0}^{\infty} \tilde{k}_2(s, a)[\kappa y^0(a) + x^0(a)]\, da\, ds + h \tag{7.20}$$

for the constant $\kappa$.

Note that the homogeneous version of (7.14)–(7.15) (obtained by setting $g(s) \equiv 0$, $h = 0$) has no nontrivial solution if and only if (7.16) holds. If, on the other hand, (7.18) holds then this homogeneous problem has the nontrivial solutions $\kappa y^0(a)$, $0 \neq \kappa \in Z$.

*Proof of Theorem* 1. A formal solution of (NH) can be found by substituting the Fourier series

$$z(\tau, a) = \sum_j z_j(a)\, e^{ij\omega\tau}, \quad \omega = 2\pi/p \tag{7.21}$$

into (NH) and obtaining the equations

$$z_j'(a) + c_1(a) z_j(a) + c_2(a)\, e^{ij\omega a} \int_{\alpha=0}^{\infty} k_1(\alpha)\, e^{-ij\omega\alpha}\, z_j(\alpha)\, d\alpha = g_j(\alpha) \tag{7.22}$$

$$z_j(0) = \int_{s=0}^{\infty} \int_{a=0}^{\infty} k_2(s, a)\, e^{-ijw(s+a)} z_j(a)\, da\, ds + h_j \tag{7.23}$$

for the coefficients $z_j(a)$. Here $g(\tau, a) = \sum_j g_j(a)\, e^{ij\omega\tau}$, $h(\tau) = \sum_j h_j\, e^{ij\omega\tau}$. Equations (7.22)–(7.23) have the form (7.14)–(7.15) with

$$\tilde{c}_2(a) = c_2(a)\, e^{ij\omega a}, \quad \tilde{k}_1(a) = k_1(a)\, e^{-ij\omega a}, \quad \tilde{k}_2(s, a) = k_2(s, a)\, e^{-ij\omega(s+a)} \tag{7.24}$$

and thus Lemma 3 can be applied (since H1 and $g \in B^0_{\gamma,p}$ imply the hypotheses of this Lemma).

Let $y_j^0(a)$ and $x_j^0(a)$ be the solutions (7.8) and (7.12) respectively for these coefficients (see (3.2)–(3.3)).

If the Fourier series $y(\tau, a) = \sum_j y_j(a)\,e^{ij\omega\tau}$ is substituted into (H) there results the following equations for the coefficients $y_j(a)$:

$$y_j'(a) + c_1(a)y_j(a) + c_2(a)\,e^{ij\omega a}\int_{\alpha=0}^{\infty} k_1(\alpha)\,e^{-ij\omega\alpha}\,y_j(\alpha)\,d\alpha = 0 \tag{7.25}$$

$$y_j(0) = \int_{s=0}^{\infty}\int_{a=0}^{\infty} k_2(s, a)\,e^{-ij\omega(s+a)}y_j(a)\,da\,ds. \tag{7.26}$$

(a) The homogeneous equation (H) has a nontrivial solution if and only if (7.25)–(7.26) does for at least one $j$. This occurs if and only if (3.1) holds for at least one $j$. The number $n$, $0 \le n \le +\infty$, nontrivial solutions of (H) is identical with the number of integers in $J$. From (7.10), the integrability assumption on $k_2$ in H1 and the Riemann–Lebesgue Lemma ([8], p. 40) it follows that $D_j \to 1$ as $|j| \to +\infty$ and hence $J$ is finite.

(b) Formally, part (b) follows from Lemma 3a since if (H) has no nontrivial solution ($J = \emptyset$) each $z_j(a)$ is then uniquely defined as a solution of (7.22)–(7.23) and (7.21) becomes the unique solution of (NH). Similarly for part (c) which follows from Lemma 3b. In this case a solution $z_j(a)$ of (7.22)–(7.23) for $j \in J$ exists since $\Omega_j[g, h] = 0$ implies the necessary and sufficient condition (7.19) in Lemma 3b. For $j \notin J$, $z_j(a)$ exists uniquely by Lemma 3a. The series (7.21) then formally defines a solution of (NH). What remains to be shown is that (7.21) really defines a function in $B^1_{\gamma,p}$. This is a matter of obtaining estimates on the $z_j(a)$ which guarantee sufficient convergence of the Fourier series. Since the finite number of terms corresponding to $j \in J$ have no effect on the convergence properties, the proof that $z \in B^1_{\gamma,p}$ is the same for both cases (b) and (c).

In the following bounds $K > 0$ denotes a constant independent of the independent variables $\tau$, $a$ and the index $j$, but is not necessarily the same in every case. From (7.10), $|y_j^0(a)| \le K\,e^{-\gamma a}$ for all $j$. Since $g \in B^0_{\gamma,p}$

$$j|g_j(a)|\,e^{\gamma a} \le \sup_{a\ge 0} j|g_j(a)|^{\gamma a} := \eta_j \text{ and } \{\eta_j\} \in \mathscr{L}^2.$$

This, together with the fact that $\Delta_j \to 1$ as $|j| \to +\infty$, (which can be easily seen to follow from the Riemann–Lebesgue Lemma) and hence that $|\Delta_j| \ge K$ for all $j$ (see H2), implies for all $j$ that $j|w_2{}^j| \le K\eta_j$ where $w_2{}^j$ is given by (3.3b). Thus, from (3.3a) and H1 comes the estimate

$$\begin{aligned} j|x_j^0(a)| &\le \int_{\alpha=0}^{a} e^{-c_0(\alpha-a)}[j|g_j(\alpha)| + j|w_2{}^j||c_2(\alpha)|]\,d\alpha \\ &\le [\eta_j + K\eta_j\|c_2\|_\gamma]\int_{\alpha=0}^{a} e^{-c_0(\alpha-a)}\,e^{-\gamma a}\,d\alpha \\ &\le [\eta_j + K\eta_j\|c_2\|_\gamma]\,e^{-\gamma a}/(c_0-\gamma) \le K\eta_j\,e^{-\gamma a} \end{aligned} \tag{7.27}$$

for all $j$. Furthermore, since $|D_j| \ge K^{-1} > 0$ for $j \notin J$, the bound

$$j|\kappa_j| \le \left[\int_{s=0}^{\infty}\int_{a=0}^{\infty} |k_2(s, a)|j|x_j^0(a)|\,da\,ds + j|h_j|\right]K$$

$$\le \left[\int_{s=0}^{\infty}\int_{a=0}^{\infty} |k_2(s, a)|\,e^{-\gamma a}\,da\,ds K\eta_j + j|h_j|\right]K \le K[\eta_j + j|h_j|]$$

follows from H1, (7.17) and (7.27) for $j \notin J$. If one defines $\kappa_j = 0$ for $j \in J$ then this inequality is also valid for $j \in J$. Finally, for $z_j(a) = \kappa_j y_j^0(a) + x_j^0(a)$, the following bounds follow from those above:

$$j|z_j(a)| \le K(\eta_j + j|h_j|)K\,e^{-\gamma a} + K\eta_j\,e^{-\gamma a} \tag{7.28}$$

and $\sup_{a\geq 0} j|z_j(a)|\,e^{\gamma a} \leq K(\eta_j + j|h_j|)$ for all $j$. Since $\{\eta_j\}$ and $\{j|h_j|\} \in \mathscr{L}^2$, it follows that $\{\sup_{a\geq 0} j|z_j(a)|\,e^{\gamma a}\} \in \mathscr{L}^2$. Thus the fourier series (7.21) defines an absolutely continuous, $p$-periodic function of $\tau$ for each $a \geq 0$ ([7], p. 129). It is consequently differentiable almost everywhere and satisfies (7.22)–(7.23) almost everywhere. From this one can deduce that this series is in fact continuously differentiable everywhere.

Next the smoothness of this series in $a$ is established. Each coefficient $z_j(a)$, as a solution of (7.22)–(7.23), is continuously differentiable in $a \geq 0$. The bound

$$|z_j(a)| \leq K(\eta_j/j + |h_j|),\ j \neq 0 \tag{7.29}$$

which follows from (7.28), together with the fact that the series $\sum_{j=0} \eta_j/j$ and $\sum_j |h_j|$ converge shows the uniform and absolute convergenge in $a \geq 0$ and $\tau$ of (7.21). This series thus defines a function continuous in $a \geq 0$. The bound (7.28), the hypothesis H1 and the equation (7.22) for $z_j(a)$ yield immediately that

$$\sup_{a\geq 0} j|z_j'(a)|\,e^{\gamma a} \leq K(\eta_j + j|h_j|) \tag{7.30}$$

and hence the series $\sum_j z_j'(a)\,e^{ij\omega\tau}$ also converges uniformly and absolutely in $a \geq 0$ and $\tau$.

As a result the Fourier series (7.21) defines a function continuous in $a$ and $\tau$, $p$-periodic in $\tau$ and continuously differentiable in $a$.

Now from (7.28)

$$\begin{aligned}|z(\tau, a)|\,e^{\gamma a} &\leq \sum_j |z_j(a)|\,e^{\gamma a} \leq K(\|\{\eta_j\}\|_2 + \|\{j|h_j|\}\|_2)\\ &= K(\|g\|_{\gamma,2} + \|\{j|h_j|\}\|_2)\end{aligned}$$

and hence $\|z\|_\gamma \leq K(\|g\|^0_{\gamma,p} + \|h\|_p)$. Similarly from (7.30) follows $\|\partial z/\partial a\|_\gamma \leq K(\|g\|^0_{\gamma,p} + \|h\|_p)$. Furthermore (7.28) implies

$$\begin{aligned}\|z\|_{\gamma,2} = \|\{\sup_{a\geq 0} j|z_j(a)|\,e^{\gamma a}\}\|_2 &\leq K(\|g\|_{\gamma,2} + \|\{j|h_j|\}\|_2)\\ &\leq K(\|g\|^0_{\gamma,p} + \|h\|_p).\end{aligned}$$

Similarly (7.30) yields $\|\partial z/\partial a\|_{\gamma,2} \leq K(\|g\|^0_{\gamma,p} + \|h\|_p)$. These bounds together imply

$$\|z\|^1_{\gamma,p} \leq K(\|g\|^0_{\gamma,p} + \|h\|_p) < +\infty \tag{7.31}$$

and hence the formal solution defined by the Fourier series (7.21) lies in $B^1_{\gamma,p}$.

This last inequality holds for that solution for which $\kappa_j = 0$, $j \in J$ (i.e. for which (3.4) holds) and hence establishes the boundedness of the linear operators described in Theorem 1.

*Proof of Theorem* 2. Let $z \in B^1_{\gamma,p}$ and $Lz = (L_1 z, L_2 z) \in Y$. Straightforward estimates show that $\|L_1 z\|_\gamma \leq K(\|z\|_\gamma + \|\partial z/\partial a\|_\gamma)$, $\|L_1 z\|_{\gamma,2} \leq K(\|z\|_{\gamma,2} + \|\partial z/\partial a\|_{\gamma,2})$ and $\|L_2 z\|_0 \leq K\|z\|_\gamma$, $\|L_2 z\|_2 \leq K\|z\|_{\gamma,2}$. Thus, $\|Lz\|_Y \leq K\|z\|^1_{\gamma,p}$. Now

$$N(L) = \operatorname{span}\{Re\, y_j^0(a)\,e^{ij\omega\tau}, Im\, y_j^0(a)\,e^{ij\omega\tau}\},\ R(L) = \{(g,h) \in Y\colon \Omega_j[g,h] = 0,\ j \in J\}$$

where without loss in generality the homogeneous solutions $y_j^0(a)$ have been chosen so that $\int_0^\infty y_j^0(a) y_k^0(a)\,da = \delta_{jk}$. If we define the closed linear spaces

$$N^\perp(L) = \{z \in B^1_{\gamma,p}\colon \int_{\alpha=0}^\infty \frac{1}{p}\int_{\tau=-p/2}^{p/2} z(\tau,\alpha) y_j^0(\alpha)\,e^{-ij\omega\tau}\,d\tau\,d\alpha = 0,\ j \in J\}$$

$$R^\perp(L) = \{(0,h) \in Y\colon h = \textstyle\sum_{j\in J} h_j\,e^{ij\omega\tau},\ h_j \in Z \text{ arbitrary},\ \bar{h}_j = h_{-j}\}$$

it follows that $B^1_{\gamma,p} = N(L) \oplus N^\perp(L)$ and $Y = R(L) \oplus R^\perp(L)$. This can be seen by writing

$$z(\tau, a) = \sum_{j\in J} \kappa_j y_j^0(a)\, e^{ij\omega\tau} + \left[\sum_{j\in J} z_j^\perp(a)\, e^{ij\omega\tau} + \sum_{j\notin J} z_j(a)\, e^{ij\omega\tau}\right]$$

$$z_j^\perp(a) := -\kappa_j y_j^0(a) + z_j(a), \quad \kappa_j := \int_{a=0}^{\infty} z_j(a) y_j^0(a)\, da \Big/ \int_{a=0}^{\infty} [y_j^0(a)]^2\, da, \quad j \in J$$

$$(g, h) = \left[\sum_{j\notin J} (g_j(a), h_j)\, e^{ij\omega\tau} + \sum_{j\in J} (g_j(a), h_j - \Omega_j[g, h])\, e^{ij\omega\tau}\right]$$

$$+ \sum_{j\in J} (0, \Omega_j[g, h])\, e^{ij\omega\tau}.$$

The first term in $z(\tau, a)$ lies in $N(L)$ while the last two bracketed terms lie in $N^\perp(L)$. The first two terms in $(g, h)$ lie in $R(L)$ while the last term lies in $R^\perp(L)$. From these two decompositions, the two projections $P_1$: $B^1_{\gamma,p} \to N(L)$ and $P_2: Y \to R(L)$ can be defined by

$$P_1 z = \sum_{j\in J} \kappa_j y_j^0(a)\, e^{ij\omega\tau}$$

$$P_2(g, h) = \sum_{j\notin J} (g_j(a), h_j)\, e^{ij\omega\tau} + \sum_{j\in J} (g_j(a), h_j - \Omega_j[g, h])\, e^{ij\omega\tau}.$$

Lengthy, but straightforward estimates show that $\|P_1 z\|^1_{\gamma,p} \le K\|z\|^1_{\gamma,p}$ and $\|(I - P_2)(g, h)\|_Y \le K(\|h\|_0 + \|g\|_{\gamma,2}) \le K(\|h\|_p + \|g\|^0_{\gamma,p}) = K\|(h, g)\|_Y$. Thus $P_1$ and $I - P_2$ (and hence $P_2$) are bounded projections.§§

*Proof of Theorem* 3. Theorem 3 follows immediately from a direct application of certain abstract, multi-parameter bifurcation results of the Liapunov–Schmidt type. Specifically one can apply Theorem 1 of [3] (also see [4]) with linear operator $L$ given by (3.5) and nonlinear operator $T(x, \lambda) := (n_1(x, \lambda), n_2(x, \lambda))$ by means of which (4.1)–(4.2) is equivalent to the abstract operator equation $Lx = T(x, \lambda)$. The necessary hypotheses H1–H4 in [3] for this application are implied by the hypotheses H1–H4 above, the nondegeneracy condition (4.4) and the results in Theorem 2 above.§§

## 8. SUMMARY

Based on the linear theory for equations (NH) and (H) contained in Theorems 1 and 2 the general two parameter bifurcation result in Theorem 3 for the nonlinear equations (4.1)–(4.3) is derived from abstract Liapunov–Schmidt techniques. Hopf-type one parameter bifurcation results can be derived as a corollary as is shown by Theorem 4 for the one parameter system (5.1)–(5.2). These results are applicable to the general McKendrick equations (2.1)–(2.2) for the growth in density of an age-structured population by means of variable changes as is illustrated by the application in Section 6. In this application it is shown how instabilities in the steady state and accompanying time periodic oscillations can occur for sufficiently large modula under certain modeling assumptions, here including a constant (non-age or -density dependent) death rate and an age-specific and density dependent fecundity rate with a sufficiently narrow age class "window". See [6] for a further study and discussion of instabilities and oscillations and their crucial relationship and dependence on the nature of the age and density dependencies of the fecundity rate.

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