NONLINEAR PHENOMENA IN MATHEMATICAL SCIENCES

Edited by

V. Lakshmikantham

Department of Mathematics
The University of Texas at Arlington
Arlington, Texas

1982

ACADEMIC PRESS
A Subsidiary of Harcourt Brace Jovanovich, Publishers
New York London
Paris San Diego San Francisco São Paulo Sydney Tokyo Toronto

ACADEMIC PRESS, INC.
111 Fifth Avenue, New York, New York 10003

United Kingdom Edition published by
ACADEMIC PRESS, INC. (LONDON) LTD.
24/28 Oval Road, London NW1 7DX

Library of Congress Cataloging in Publication Data
Main entry under title:

Nonlinear phenomena in mathematical sciences.

"Proceedings of an International Conference on Nonlinear Phenomena in Mathematical Sciences, held at the University of Texas at Arlington June 16-20, 1980"--P.
1. Nonlinear theories--Congresses. I. Lakshmikantham, V. II. International Conference of Nonlinear Phenomena in Mathematical Sciences (1980 : University of Texas at Arlington)
QA427.N66 1982 515'.252 82-20734
ISBN 0-12-434170-5

PRINTED IN THE UNITED STATES OF AMERICA

82 83 84 85 9 8 7 6 5 4 3 2 1

BIFURCATION OF PERIODIC SOLUTIONS OF NONLINEAR EQUATIONS IN AGE-STRUCTURED POPULATION DYNAMICS*

J. M. Cushing
University of Arizona

I. 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 biological and mathematical, and many mechanisms have been suggested and studied as causes of such oscillations. Mathematically, a variety of model equations of different types have been investigated with regard to the existence of nontrivial periodic solutions, including differential delay, integral, integro-differential and difference equations. Virtually all of the equations which have appeared in the literature on population dynamics (whether concerned with this problem or not) can be derived from a general model of age-structured populations based upon the McKendrick equation subjected to a nonlinear boundary condition. To make such derivations, however, always necessitates some kind of specialized, simplifying assumptions ... the mathematical purpose of which is in fact to derive a simplified equation of one of the above mentioned types for which there are available analytical techniques and theorems. For example, bifurcation theorems and bifurcation techniques for the existence of nontrivial periodic solutions for such types of equations can be used. These simplifying assumptions, however, often go contrary to biological situations in which one is interested or which the biological literature indicates are of primary importance as far as oscillations are concerned. For example, the most frequently mentioned primary causes of population density oscillations are gestation periods, maturation periods and age differential resource consumption (e.g. see Slobodkin (1961)) all of which are ignored in models which, as is very common, ignore age structure and also assume that vital parameters are functionals of total population size. The famous, overworked delay logistic equation and similar ordinary delay differential equations are examples of equations which are not appropriate model equations as far as these basic biological mechanisms are concerned.

In order to permit a more general study of the question of sustained oscillations in a constant environment of a single species population, I have developed a multi-parameter bifurcation theorem applicable to general model equations based upon the general McKendrick partial differential equation which applies to the equations per se and does not necessitate a reduction, under simplifying assumptions, to some simpler equations. This is given in Section 3. The approach taken is the classical one of Lyapunov-Schmidt for which a Fredholm-type alternative on a suitable space of functions is established. A Hopf-type bifurcation theorem is proved in Section 4 under the one

**This material is based upon work supported by the National Science Foundation under Grant No. MCS-7901307.*

ISBN 0-12-434170-5

simplifying assumption that the age-specific death rate is a function of present age-specific population density. Specific illustrative examples are given in Section 5.

Most details of proofs, being rather involved, are left out for want of space here, but will hopefully appear elsewhere. While attention is restricted to single species dynamics here, the techniques and results are extendable in a straightforward way to systems.

Let $\rho = \rho(t,a)$ be the density of (female) individuals of age a at time t. The McKendrick equation describing the removal of individuals from the population (assumed caused by death only) is

$$\rho_t + \rho_a + d\rho = 0 \tag{1}$$

where $d \geq 0$ is the per capita age-specific death rate. This equation is supplemented by the birth equation

$$\rho(t,0) = \int_{s=0}^{\infty} g(s) \int_{a=0}^{\infty} m\rho(t-s,a)\,da\,ds \tag{2}$$

where $m \geq 0$ is the age-specific fecundity function describing the per capita number of eggs fertilized to individuals of age a (resulting in female births) and $g(s) \geq 0$ is a gestation probability density function. We ignore initial conditions and ask for classical, differentiable solutions of (1) - (2) for $-\infty < t < +\infty$, $a \geq 0$. We assume that the vital parameters d, m are functionals of the density ρ:

$$\begin{aligned} d &= d(a,\delta\rho), \quad \delta\rho := \int_0^{\infty} w_1(a)\rho(t,a)\,da \\ m &= m(a,\mu\rho), \quad \mu\rho := \int_0^{\infty} w_2(a)\rho(t,a)\,da \end{aligned} \tag{3}$$

where the weighting functions $w_i(a) \geq 0$ describe the manner in which the vital parameters d, m depend on age-specific densities (as might be caused, for example, by age-specific differentials in resource consumption). Different model equations modelling different biological situations are obtained by the prescription of d and m in (3).

I am interested in solutions of (1) - (3) which are periodic in t and which bifurcate from an equilibrium $\rho(t,a) = e(a)$ solution (which is assumed to exist).

The results given below remain valid when all hypotheses on $g(s)$ appearing below are dropped and $g(s)$ is formally replaced by the Dirac function $\delta_0(s)$ at $s = 0$, which corresponds to assuming that there is no gestation period (which is done in practically all models considered in the literature).

II. LINEAR EQUATIONS

Let P_p^2 denote the Banach space of twice continuously differentiable, p-periodic functions under the usual norm $|f|_0^2 := \sum_{i=0}^{2} \sup_{0\le\tau\le p} |d^i f/d\tau^i|$ and let B_γ^2, $\gamma > 0$, denote the Banach space of twice continuously differentiable functions under the norm $|f|_\gamma^2 := \sum_{i=0}^{2} \sup_{\alpha\ge 0} e^{\gamma\alpha}|d^i f/d\alpha^i|$. Also $B_{\gamma,p}^2$ will denote the Banach space of functions $f(\tau,\alpha)$ which are twice continuously differentiable in τ and α and are p-periodic in τ under the norm $|f|_{\gamma,p}^2 := \sum_{0\le m+n\le 2} \sup_{0\le\tau\le p,\alpha\ge 0} e^{\gamma\alpha}|\partial^{m+n} f/\partial\tau^m\partial\alpha^n|$. Finally, $B_{\gamma,p}^{2+}$ denotes the Banach space of those functions $f \in B_{\gamma,p}^2$ for which $\partial^3 f/\partial\alpha^3$ is continuous with the norm $|f|_{\gamma,p}^{2+} := |f|_{\gamma,p}^2 + \sup_{0\le\tau\le p,\alpha\ge 0} e^{\gamma\alpha}|\partial^3 f/\partial\alpha^3| < +\infty$.

Consider the nonhomogeneous linear problem for $y = y(\tau,\alpha)$:

$$
\begin{aligned}
&y_\alpha + c_1(\alpha)y + c_2(\alpha)\int_0^\infty k_1(a)y(\tau+\alpha-a,a)da = f(\tau,\alpha) \\
&y(\tau,0) = \int_0^\infty g(s)\int_0^\infty k_2(a)y(\tau-s-a,a)dads = g(\tau)
\end{aligned}
\tag{NH}
$$

and the related homogeneous problem

$$
\begin{aligned}
&y_\alpha + c_1(\alpha)y + c_2(\alpha)\int_0^\infty k_1(a)y(\tau+\alpha-a,a)da = 0 \\
&y(\tau,0) = \int_0^\infty g(s)\int_0^\infty k_2(a)y(\tau-s-a,a)dads = 0
\end{aligned}
\tag{H}
$$

under the assumption

(H1) $c_1(\alpha)$ is bounded and continuously differentiable for $\alpha \ge 0$ and satisfies $0 < c \le c_1(\alpha)$ for some constant $c > 0$; $k_i(a)$ is bounded and measurable; and $c_2(\alpha)$, $g(s) \in B_c^2$.

Of interest are τ-periodic solutions of (NH) and (H) for τ-periodic forcing functions f, g. Lacking sufficient space for a full development of the theory of these linear equations, I will only informally sketch the details. Substitution of $y(\tau,\alpha) = \sum_{m=-\infty}^{+\infty} c_m(\alpha)\exp(im\omega\tau)$, $\omega = 2\pi/p$, into (NH) yields the equations

$$
c_m'(\alpha) + c_1(\alpha)c_m(\alpha) + c_2(\alpha)e^{im\omega\alpha}\int_0^\infty k_1(a)e^{-im\omega a}c_m(a)da = f_m(\alpha) \tag{4}
$$

$$
c_m(0) = \int_0^\infty g(s)e^{im\omega s}\int_0^\infty k_2(a)e^{im\omega a}c_m(a)dads + g_m \tag{5}
$$

to be solved for $c_m(\alpha)$, $\alpha \ge 0$, $-\infty < m < +\infty$. Here $f = \sum f_m(\alpha)\exp(im\omega\tau)$

and $g = \sum g_m \exp(im\omega\tau)$. It can be shown that the general solution of (4) is given by $c_m(\alpha) = c_m(0)y_m(\alpha) + \Omega_m(f)(\alpha)$ where $y_m(\alpha)$ is the fundamental solution of the associated homogeneous equation and is given by

$$y_m(\alpha) := e^{-C(\alpha)} - e^{-C(\alpha)}\int_0^\alpha e^{C(a)}c_2(a)e^{im\omega a}da\int_0^\infty k_1(a)e^{-im\omega a}e^{-C(a)}da\Lambda_m^{-1} \quad (6)$$

$$C(\alpha) := \int_0^\alpha c_1(a)da, \quad \Lambda_m := 1 + \int_0^\infty k_1(\alpha)e^{-m\omega\alpha}e^{-C(\alpha)}\int_0^\alpha e^{C(a)}c_2(a)e^{im\omega a}dad\alpha$$

which satisfies $y_m(0) = 1$ and where $\Omega_m(f)(\alpha)$ is the particular solution of (4) which vanishes at $\alpha = 0$:

$$\Omega_m(f)(\alpha) := e^{-C(\alpha)}\int_0^\alpha e^{C(a)}(f_m(a)-c_2(a)e^{im\omega a}\Gamma_m)da$$

$$\Gamma_m := \int_0^\infty k_1(\alpha)e^{-im\omega\alpha}e^{-C(\alpha)}\int_0^\alpha e^{C(a)}f_m(a)dad\alpha\Lambda_m^{-1}.$$

To solve (5) the initial condition $c_m(0)$ must be chosen so that

$$(1-\int_0^\infty \Phi_m(a)y_m(a)da)c_m(0) = \int_0^\infty \Phi_m(a)\Omega_m(f)(a)da + g_m$$

$$\Phi_m(a) := \int_0^\infty g(s)e^{im\omega s}dsk_2(a)e^{-im\omega a}.$$

These manipulations lead to the following lemma (whose rigorous proof is omitted).

<u>Lemma</u>. Assume $\gamma < c$, H1 and that $\Lambda_m \neq 0$ for all $-\infty < m < +\infty$.

(a) The solution space $S \subset B^{2+}_{\gamma,p}$ of the homogeneous equation (H) is finite dimensional and is spanned by the real and imaginary parts of the set of solutions $\{c_m(\alpha)\exp(im\omega\tau) \mid m \in M\}$ where $M := \{m \mid 1 - \int_0^\infty \Phi_m(a)y_m(a)da = 0\}$.

(b) If the homogeneous equation (H) has no nontrivial solutions in $B^{2+}_{\gamma,p}$ i.e. if $M = \emptyset$, then (NH) has a unique solution in $B^{2+}_{\gamma,p}$ for each $f \in B^2_{\gamma,p}$ and $g \in P^2_p$.

(c) If $M \neq \emptyset$ then (NH) has a solution in $B^{2+}_{\gamma,p}$ if and only if f, g satisfy

$$Q[f,g] := \int_0^\infty \Phi_m(a)\Omega_m(f)(a)da + g_m = 0, \quad m \in M$$

in which case there exists a unique solution y of (NH) lying in the subspace $S^\perp = \{y \in B^{2+}_{\gamma,p} \mid \int_0^p y(\tau,\alpha)\exp(-im\omega\tau)d\tau \equiv 0,\ m \in M\}$ and the linear operator defined by $A(f,g) = y$ mapping $B^2_{\gamma,p} \times P^2_p$ into $S^\perp$ is bounded.

III. A BIFURCATION THEOREM

Consider the nonlinear equations for $x = x(\tau,\alpha)$

$$
\begin{aligned}
&x_\alpha + c_1(\alpha)x + c_2(\alpha)\int_0^\infty k_1(a)x(\tau+\alpha-a,a)da = \sum_{i=1}^{2} \lambda_i L_i x + f(x,\lambda) \\
&x(\tau,0) - \int_0^\infty g(s)\int_0^\infty k_2(a)x(\tau-s-a,a)dads = \sum_{i=1}^{2} \lambda_i K_i x + g(x,\lambda)
\end{aligned}
\qquad (7)
$$

where $\lambda := (\lambda_i) \in R^2$ and

(H2) $L_i : B^{2+}_{\gamma,p} \to B^2_{\gamma,p}$ and $K_i : B^{2+}_{\gamma,p} \to P^2_p$ are bounded linear operators for $\gamma < c$,

The nonlinear operators f and g satisfy the following hypotheses.

(H3) Let $h(x,\lambda) := (f(x,\lambda),g(x,\lambda)) : B^{2+}_{\gamma,p} \times R^2 \to B^2_{\gamma,p} \times P^2_p$, $\gamma < c$. Then $h(\varepsilon x,\lambda) = \varepsilon\bar{h}(x,\lambda,\varepsilon)$ for all $\varepsilon \in R$ where the operator $\bar{h} : B^{2+}_{\gamma,p} \times R^2 \times R \to B^2_{\gamma,p} \times P^2_p$ is $q \geq 1$ times continuously Fréchet differentiable and $\bar{h}(x,0,0) \equiv 0$, $\partial\bar{h}(x,0,0)/\partial x \equiv 0$, $\partial\bar{h}(x,0,0)/\partial\lambda \equiv 0$.

It is now possible to reformulate equations (7) as an operator equation on certain Banach spaces in such a way that established bifurcation theorems apply. Write (7) as $Lx = T(x,\lambda)$ where L is the linear operator $L : B^{2+}_{\gamma,p} \to B^2_{\gamma,p} \times P^2_p$ defined by the left hand sides of (7) and where the nonlinear operator $T : B^{2+}_{\gamma,p} \times R^2 \to B^2_{\gamma,p} \times P^2_p$ is defined by the right hand sides of (7). The linear operator L is bounded and has closed range and nullspace, both of which admit bounded projections. Moreover, the range of L has a finite codimension which equals the dimension of the nullspace of L. It will be assumed that this codimension equals two. The operator T has the property that $T(\varepsilon x,\lambda) = \varepsilon\bar{T}(x,\lambda,\varepsilon)$ where $\bar{T} : B^{2+}_{\gamma,p} \times R^2 \times R \to B^2_{\gamma,p} \times P^2_p$ is $q \geq 1$ times continuously Fréchet differentiable with $\bar{T}(x,0,0) = \bar{T}_x(x,0,0) \equiv 0$.

Established bifurcation results (see e.g. Cushing (1979a,b)) now yield a bifurcation result for (7) provided, as usual, a certain nondegeneracy condition holds. Suppose (H) has exactly two independent, nontrivial solutions in $B^{2+}_{\gamma,p}$ given by the real and imaginary parts of a complex solution

$$y_1(\tau,\alpha) = c_1(\alpha)e^{i\omega\tau}$$

as described in Section 2 above. The nondegeneracy condition is that the Jacobian (at $x = y_1$, $\lambda = 0$, $\varepsilon = 0$) with respect to λ_1, λ_2 of the two real "bifurcation equations" given by the real and imaginary parts of the equation $Q[\bar{T}_1(x,\lambda,\varepsilon),\bar{T}_2(x,\lambda,\varepsilon)] = 0$, $\bar{T} = (\bar{T}_1,\bar{T}_2)$, be nonsingular. This nondegeneracy condition is thus

(H4) $\Delta := \mathrm{Im}\, \hat{Q}[L_1y_1, K_1y_1]Q[L_2y_1, K_2y_1] \neq 0$

where "^" denotes complex conjugation.

While the nondegeneracy condition H4 is rather complicated, it is (to use popular jargon) "generic" in the sense that it is an inequality. It will be shown in the next section 4 that in at least one special, but important case H4 is equivalent to the transversal crossing of the imaginary axis of a pair of nonzero complex roots of a certain characteristic equation associated with (H).

Theorem 1. Assume $\gamma < c$, H1 - H4 and $\Lambda_m \neq 0$ for all integers $-\infty < m < +\infty$. Suppose that (H) has exactly two independent, nontrivial solutions in $B^{2+}_{\gamma,p}$. Let $y(\tau,\alpha) \in B^{2+}_{\gamma,p}$ be a nontrivial solution of (H). Then (7) has nontrivial solutions of the form

$$x(\tau,\alpha) = \varepsilon y(\tau,\alpha) + \varepsilon z(\tau,\alpha,\varepsilon) \in B^{2+}_{\gamma,p}$$

for small $|\varepsilon|$ and $\lambda_i = \lambda_i(\varepsilon) \in R$ where $z(\cdot,\cdot,\varepsilon)$ and $\lambda_i(\varepsilon)$ are $q \geq 1$ times continuously Fréchet differentiable and $|z|^{2+}_{\gamma,p} = O(|\varepsilon|)$, $\lambda_i = O(|\varepsilon|)$ near $\varepsilon = 0$.

This theorem can be applied to the original problem (1) - (3) after setting $x = \rho - e$, changing independent variables to $\tau = t - a$, $\alpha = a$ and identifying two parameters which can be used as the bifurcation parameters λ_i. While these bifurcation parameters can be chosen to be parameters appearing in (3), they can also be implicitly appearing parameters introduced explicitly into the analysis by rescalings. This is the case with "Hopf-type" bifurcation in which the unknown period is one of the bifurcation parameters.

IV. A HOPF-TYPE BIFURCATION THEOREM

Consider the problem

$$\begin{aligned} &x_\alpha + c(\alpha,\mu)x = f_0(x,\mu) \\ &x(\tau,0) - \int_0^\infty k(a,\mu)x(\tau-a,a)da = g_0(x,\mu) \end{aligned} \tag{8}$$

where f_0 and g_0 satisfy H3. Here $\mu \in R$ is a bifurcation parameter. Changing variables form τ, α to τ/p, α/p and setting $\lambda_1 = \mu - \mu_0$, $\lambda_2 = p - p_0$ one finds that (8) takes the form (7) with

$$c_1(\alpha) := p_0c(\alpha p_0,\mu_0),\ g(s) \equiv \delta_0(s),\ k_2(\alpha) := p_0k(p_0\alpha,\mu_0),\ k_1(\alpha) \equiv c_2(\alpha) \equiv 0$$

$$L_1x := -p_0c_\mu(\alpha p_0,\mu_0)x,\quad L_2x := -(c(\alpha p_0,\mu_0)+p_0\alpha c_\alpha(\alpha p_0,\mu_0))x \tag{9}$$

$$K_1x := \int_0^\infty p_0k_\mu(\alpha p_0,\mu_0)x(\tau-a,a)da,\ K_2x := \int_0^\infty (k(\alpha p_0,\mu_0)+p_0\alpha k_\alpha(\alpha p_0,\mu_0))x(\tau-a,a)da.$$

Assume f_0, g_0 become new operators $\tilde{f}_0$, $\tilde{g}_0$ for which

(H5) $\tilde{f}_0$, $\tilde{g}_0$ satisfy H3 with $p = 1$ and c, k are continuously differentiable functions for which the operators, kernels and coefficients defined by (9) satisfy H1 and H2 with $p = 1$.

Theorem 1 now yields a bifurcation result for (8). Before stating this result we first interpret the nondegeneracy condition H4.

Define the <u>characteristic equation</u>

$$F(z,\mu) := 1 - \int_0^\infty k(a,\mu)\exp\left(-\int_0^a c(\alpha,\mu)d\alpha\right)\exp(-za)da = 0. \tag{10}$$

Suppose that for $\mu = \mu_0$ equation (10) has exactly one pair of purely imaginary roots $z = i\omega_0$, $\omega_0 > 0$. Let $p_0 = 2\pi/\omega_0$. If

(H6) $F_z(z_0,\mu_0) = \int_0^\infty ak(a,\mu_0)\exp(-\int_0^a c(\alpha,\mu_0)d\alpha)\exp(-i\omega_0 a)da \neq 0$

then there is a continuously differentiable root $z = z(\mu)$ for μ near μ_0 such that $z(\mu_0) = z_0 = i\omega_0$.

We see from Section 2 that this supposition implies that (H) has exactly two independent nontrivial solutions in $B^{2+}_{\gamma,1}$ given by the real and imaginary parts of $y_1(\tau,\alpha) = \exp(-p_0\int_0^\alpha c(p_0 s,\mu_0)ds)\exp(2\pi i\tau)$. A straightforward, but tedious calculation shows that

$$\Delta = \mathrm{Im}\left[\frac{d}{d\mu}\int_0^\infty p_0 k(p_0 a,\mu)\exp\left(-p_0\int_0^a c(p_0 s,\mu)ds\right)\exp(2\pi i a)da\Big|_{\mu=\mu_0}\right]$$
$$\cdot\left[\int_0^\infty \frac{d}{da}\left\{ak(p_0 a,\mu_0)\exp\left(-p_0\int_0^a c(sp_0,\mu_0)ds\right)\right\}\exp(2\pi i a)da\right]. \tag{11}$$

On the other hand, implicit differentiation of $F(z(\mu),\mu) = 0$ with respect to μ evaluated at $\mu=\mu_0$ implies that $z'(\mu_0) = -F_\mu(i\omega_0,\mu_0)\hat{F}_z(i\omega_0,\mu_0)/|F_z(i\omega_0,\mu_0)|^2$. A calculation of F_μ and F_z from (10) followed by some elementary manipulations shows, upon referring to (11), that

$$\mathrm{Re}\ z'(\mu_0) = K\Delta, \quad K := p_0^2/2\pi|F_z(i\omega_0,\mu_0)|^2 > 0$$

and hence H4 is equivalent to $\mathrm{Re}\ z'(\mu_0) \neq 0$.

<u>Theorem 2</u>. Assume H5, H6 and that $\Lambda_m \neq 0$ for all integers $-\infty < m < +\infty$. If the characteristic equation (10) has a root $z = z(\mu)$ such that $z(\mu_0) = i\omega_0$, $\omega_0 > 0$, $\mathrm{Re}\ z'(\mu_0) \neq 0$ (and $F(z,\mu_0) = 0$ has no other purely imaginary roots) and if H6 holds, then (8) has a solution of the form

$$x(\tau,\alpha) = \varepsilon y(\tau/p,\alpha/p) + \varepsilon z(\tau/p,\alpha/p,\varepsilon)$$

for small $|\varepsilon|$ and for $\mu = \mu_0 + \lambda_1(\varepsilon)$, $p = p_0 + \lambda_2(\varepsilon)$ where $y(\tau,\alpha)$, $z(\tau,\alpha,\varepsilon) \in B^{2+}_{\gamma,1}$ and λ_i, y, z are as in Theorem 2.

Note that $x(\tau,\alpha)$ is p-periodic in τ in Theorem 2.

V. AN APPLICATION

An example of a kind of model equation (1) - (3) to which Theorem 2 applies is (see Hoppensteadt (1975))

$$\rho_t + \rho_a + (d_1 + d_2\rho)\rho = 0$$
$$\rho(t,0) = \int_0^\infty b\beta(a)[1 - w_0\int_0^\infty w(s)\rho(t,s)ds]_+\rho(t,a)da \tag{12}$$

in which $d = d_1 + d_2\rho$, $m = b\beta(a)[1 - w_0\int_0^\infty w(s)\rho(t,s)ds]_+$ for constants $d_i \geq 0$, $b > 0$ and functions $\beta(a)$, $w(a) \geq 0$ lying in $B^2_{\gamma^*}$ for some $\gamma^* > 0$. Here d_1, b are <u>inherent</u> (i.e. low density) <u>death</u> and <u>birth moduli</u> respectively and $b\beta(a)$ is the <u>inherent age-specific fecundity</u>. The constant d_2 measures the magnitude of the effect of increased density of individuals of age a on the death rate of individuals of age a while $w_2(s) = w_0 w(s)$ describes the age-specific effect that individuals of age s have on the birth rate of individuals of age a. Here $[\xi]_+ = \max\{\xi, 0\}$. Assume that $\int_0^\infty \beta(a)da = 1$. Note that there is no gestation period in (12) (i.e. $g(s) = \delta_0(s)$).

We hold all of the parameters fixed except b. If $\rho = e(a;b)$ is an equilibrium solution of (12) as a function of b, define $x = \rho - e$ and change variables from t, a to $\tau = t - a$, $\alpha = a$. Then (12) takes the form of (8) with

$$\mu = b, \quad c(\alpha,\mu) = d_1 + d_2 e(\alpha,\mu), \quad f_0(x,\mu) = -d_2 x^2$$

$$k(\alpha,\mu) = b\left\{\beta(\mu)(1 - w_0\int_0^\infty w(s)e(s;\mu)ds) - w_0 w(\alpha)\int_0^\infty \beta(s)e(s;\mu)ds\right\}$$

$$g_0(x,\mu) = -\int_0^\infty b\beta(\alpha)w_0\int_0^\infty w(s)x(\tau - s,s)ds\,x(\tau-\alpha,\alpha)d\alpha.$$

Several examples will be investigated.

<u>Example 1</u>. Suppose $d_2 = 0$, $d_1 > 0$ so that the death rate is density and age independent. Then

$$e(a;b) = e_0(b)\exp(-d_1 a), \quad e_0(b) := (R-1)/S$$

$$R := b\beta^*(d_1), \quad S := bw_0 w^*(d_1)\beta^*(d_1)$$

where "*" denotes the Laplace transform. It is seen that $R > 1$ is necessary and sufficient for the existence of a positive equilibrium. R is the inherent net reproductive rate. The characteristic equation becomes

$$1 - \frac{\beta^*(z+d_1)}{\beta^*(d_1)} + \frac{b\beta^*(d_1)-1}{w^*(d_1)} w^*(z+d_1) = 0. \tag{13}$$

(a) Suppose that $w(a) \equiv 1$; i.e. fecundity is a function of total population size $\int_0^\infty \rho(t,a)da$. This is a common assumption (Gurtin and MacCamy (1974,1979)). Then (13) reduces to

$$\frac{\beta^*(z+d_1)}{\beta^*(d_1)} - \frac{z+d_1R}{z+d_1} = 0.$$

But because $R > 1$ it is easy to see that this equation cannot be satisfied for $\operatorname{Re} z \geq 0$. See Cushing (1980).

Thus, for this model in which fecundity depends on total population size there is no Hopf bifurcation of sustained oscillations in time regardless of the nature of the maturation function $\beta(a)$ and any maturation delay it might describe.

(b) Suppose on the other hand it is assumed that fecundity is a weighted function of population density in which the density of one age class $T_1 > 0$ affects fecundity more than any other. Furthermore, suppose that there is one age class $T_2 > 0$ of maximum fecundity. To be specific, let

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

Here, for mathematical simplicity, it is assumed that $T_1 = T_2 = T$. These distribution functions are frequently used when it is desired to have a nonnegative function which vanishes at $a = 0$ and $+\infty$ with a unique global maximum at $a = T$ and normalized so that $\int_0^\infty w(a)da = 1$ (Cushing (1979c, 1980), MacDonald (1978), Gurtin and MacCamy (1979)). The reciprocal of the integer n measures the "width" of the distribution.

The characteristic equation is in this case

$$(Tz+d_1T+n)^{n+1} = (2-R)(Td_1+n)^{n+1}$$

where $R = bn^{n+1}/(Td_1+n)^{n+1}$. A simple analysis of the roots shows that a nonzero complex pair transversally crosses the imaginary axis if and only if $n \neq 1$ in which case the root $z = z(b)$ of largest real part satisfies $z(b_0) = i\omega_0$ where

$$b_0 = (d_1T+n)^{n+1}n^{-n-1}(2+\sec^{n+1}(\pi/(n+1))), \quad \omega_0 = (d_1T+n)T^{-1}\tan(\pi/(n+1))$$

and $\operatorname{Re} z'(b_0) = (d_1T+n)T^{-1}\cos^{n+1}(\pi/(n+1))$.

Thus, a Hopf bifurcation occurs and we conclude that if the fecundity of all age classes is a weighted functional of population density sharply enough weighted most towards the age class of maximum fecundity, then sustained oscillations of density in time will occur for birth moduli greater than a critical value.

Example 2. The case when the death rate d depends on density ρ in (1) is typically more difficult to analyse. Suppose now that $d_2 \neq 0$, but $w_0 = 0$ in (12), so that the death rate, but not fecundity, is density dependent. Then the equilibrium is

$$e(a;b) = \delta e_0(b)/\{-e_0(b)+(\delta+e_0(b))\exp(d_1 a)\}, \quad \delta := d_1/d_2$$

where $e_0(b)$ is the unique positive solution of the equation

$$1 - b\int_0^\infty \frac{\delta\beta(a)}{-e_0+(\delta+e_0)\exp(d_1 a)}\, da = 0 \tag{14}$$

under the assumption that $R := b\beta^*(d_1) > 1$. The characteristic equation is $F(z,b) = 0$ where

$$F(z,b) := 1 - \int_0^\infty b\beta(a)\exp\left(-\int_0^a (d_1+2d_2 e(\alpha,b))d\alpha\right)e^{-za}da$$

$$= 1 - \int_0^\infty b\beta(a)\frac{\delta\ \exp(-d_1 a)}{\delta+e_0(b)-e_0(b)\exp(-d_1 a)}e^{-za}da.$$

But then $F(z,b) \neq 0$ for $\operatorname{Re} z > 0$ by (14) so that there is no Hopf bifurcation of sustained oscillations in time in model (12) when $w_0 = 0$.

REFERENCES

[1] Cushing, J. M. (1979a). "Nontrivial periodic solutions of some Volterra integral equations." Proc. Helsinki Symposium on Volterra Equations, *Lec. Notes in Math. 737*, Springer-Verlag, Berlin.

[2] Cushing, J. M. (1979b). "Nontrivial periodic solutions in integrodifferential equations." *J. Integral Eqs. 1*, 165-181.

[3] Cushing, J. M. (1979c). "Lectures on Volterra integrodifferential equations in population dynamics." Proc. of the Centro Internazionale Matematico Estivo Session on "Mathematics in Biology." Florence, Italy.

[4] Cushing, J. M. (1980). "Model stability and instability in age structured populations" (to appear in *J. Theoretical Biology*).

[5] Gurtin, M. E., and MacCamy, R. C. (1974). "Non-linear age-dependent population dynamics." *Arch. Rational Mech. Anal. 54*, 281-300.

[6] Gurtin, M. E., and MacCamy, R. C. (1978). "Some simple models for nonlinear age-dependent population dynamics." *Math. Biosciences 43*, 199-211.

[7] Hoppensteadt, F. (1975). "Mathematical Theories of Populations: Demographics, Genetics and Epidemics." Soc. Ind. Appl. Math., Regional Conf. Series in Applied Math., Philadelphia.

[8] MacDonald, N. (1978). "Time Lags in Biological Models." *Lec. Notes in Biomath. 27*, Springer-Verlag, Berlin.

[9] Slobodkin, L. B. (1961). "Growth and Regulation of Animal Populations." Holt, Rinehart and Winston, New York.