

EQUILIBRIA AND OSCILLATIONS IN AGE-STRUCTURED POPULATION GROWTH MODELS

J.M. CUSHING

Department of Mathematics, University of Arizona, Tucson, Arizona U.S.A.

1 INTRODUCTION

The purpose of this paper is to describe some recent results concerning the dynamics of some quite general age-structured population growth models and hopefully to demonstrate the usefulness of a certain approach to the study of asymptotic states. This approach is based upon bifurcation theory and methods. Its benefits lie not only in the resulting wealth of mathematical techniques which can be brought to bear on the equations, both for the detailed study of specific model equations and for the derivation of very general and generic results for more general models, but also in the conceptual simplification, organization and unification of many phenomena which appear in common to a wide diversity of models and model equations types.

The model equations to be studied here are sufficiently general as to include virtually all equations for single population growth dynamics and for many species interactions which appear in the literature, whether they involve ordinary differential equations, delay or functional differential equations, integrodifferential equations, integral equations, or (by discretization) difference and Leslie matrix-type equations.

The motivation for the approach lies in the observation that if the asymptotic states are studied as a function of a model parameter measuring an "inherent growth" or "birth" rate, here denoted by r , then the following scenario usually occurs: for "small" values of r the population does not survive in that its density tends to zero as $t \rightarrow \infty$ and only if r surpasses a critical value can the population survive in the sense that there exists a stable equilibrium state (not necessarily unique). Furthermore for larger values of r the equilibrium sometimes destabilizes and a sustained time periodic oscillation results. Moreover, further increases in r can sometimes result in repeated destabilizations and even "chaotic" dynamics as is so familiar now with well studied difference equations for populations with nonoverlapping generalizations.

The model assumes that each population can be described by a density $w = w(t, x) \geq 0$ where t is time and x is a characteristic which structures the population (such as age, size, length, weight, amount of some chemical, etc.) whose growth rate is given by $dx/dt = v$. In general v depends on t , x , and w . The dynamics of w are governed by the equation

$$d_t w + d_x(vw) + \delta = 0, \quad t > 0, \quad 0 < x < X \leq +\infty$$

where δ is a growth rate depending in general on t , x , and w (Nisbet and Gurney (1982); Sinko and Streifer (1967)). Side conditions, besides the prescription of an

initial condition $w(0, x)$, include $w(t, x) \equiv 0$ for $x \geq X$ (X is the maximal characteristic value for all members of the population) and a birth law $vw = \beta$ at $x = 0$ where the birth rate β is a function of t and w . Here it is assumed that all newborns have the same characteristic value which has been normalized to $x = 0$.

The mathematical theory of these model equations is not well developed, at least in this generality, and even such fundamental mathematical questions as the existence and uniqueness of solutions await study. One case which in recent years has been well studied is the case when v is independent of the density w and t , i.e. when $v = v(x) > 0$. For this case a change of variables from x and w to the variables

$a = \int_0^x (1/v(s)) ds$ and $u = vw$ reduces the equations to similar equations for the density

$u = u(t, a)$ in which $v \equiv 1$. In this equivalent formulation the population is structured by age a and it is with these equations with which I will deal in this paper.

I will assume here that there is no seeding/harvesting or immigration/emigration so that the vital rates δ, β drop to zero when the density u is zero. Furthermore, I will assume, although it is not mathematically necessary for many of the results to be described below, that δ is a death rate, i.e., $\delta \leq 0$ (which is consistent with the only entries into the population being births). Actually, for simplicity of presentation, I will assume here that the vital birth and death rates β and δ can be expressed in terms of nonnegative per unit density rates F and D . Thus, in summary, I will consider in this paper model equations of the form

$$\begin{aligned} (a) \quad & d_t u + d_a u + uD = 0, \quad t > 0, \quad 0 < a < A \leq +\infty \\ (b) \quad & u(t, 0) = \int_0^A uF da, \quad t > 0 \\ (c) \quad & u(t, a) = 0, \quad t > 0, \quad a \geq A \end{aligned} \tag{1}$$

where A is the maximal possible age and D, F depend in general explicitly on t, a and (in so-called density dependent models) on u . Rather than write $D = D(t, a, u)$, $F = F(t, a, u)$ however, I will for the sake of simplicity write $D = D(u) \geq 0$, $F = F(u) \geq 0$ in which the dependence on the independent variables t, a is notationally suppressed.

These equations can be found in early works of McKendrick (1926) and in later works of several authors (Hoppenstaedt (1975); Sinko and Streifer (1967); von Forester (1959)). A seminal paper on nonlinear versions of (1) which initiated a great deal of research interest during the last ten years is that of Gurtin and MacCamy (1974). A recent modern mathematical treatment can be found in the new book by Webb (1985) (which also has a large bibliography). Also forthcoming is a book by Gurtin (to appear) on age-structured population dynamics.

The modelling of a specific population growth problem is done by assigning specific properties to the vital per unit rates D and F . Often the resulting equations

can be manipulated into other simpler equations. For example if these vital rates are not age specific and if they depend on density u only through total population size

$P = \int_0^A u(t, a) da$ then an integration of (1a) from 0 to A leads to the equation

$d_t P = PG(t, P)$ where $G = F - D$ is a per unit net growth rate. Thus, classical ordinary differential equation models (of so-called Kolmogorov type) for total population size are included in (1) as special cases. Often other special cases also lead to ordinary differential equation models (Gurtin (to appear); Gurtin and Levine (1979)). To see how integrodifferential and delay functional differential equations can be derived from (1) (see Cushing (1980 and 1981)). Renewal Volterra type integral equations and difference equations can also arise from (1) (see (Cushing (1981) and Oster (1977)).

In this paper the emphasis will be on the general model (1) with as few restrictive assumptions as possible. It will be seen that a great deal can be said about some fundamental properties of the long time asymptotic states under only the mildest of assumptions on the vital death and birth rates D and F as they depend on population density in an arbitrary way.

First equilibria for single species models will be considered. Then equilibria for m interacting age-structured populations will be considered using similar techniques. Finally, some brief remarks will be made concerning unforced and forced periodicities in population densities.

2 SINGLE SPECIES GROWTH MODELS

2.1. A Global Existence Result.

If the vital rates D and F do not explicitly depend on time t then the first order hyperbolic partial differential equation (1a) is autonomous and an important role is played by equilibrium solutions $u = u(a) \geq 0$. The equilibrium equations are

$$\begin{aligned} d_a u + uD &= 0, \quad 0 < a < A \\ u(0) &= \int_0^A uF da, \quad u(a) = 0 \text{ for } a \geq A. \end{aligned} \tag{2}$$

First, without loss in generality, write $D = \mu + d(u)$ where $d(0) = 0$. Now suppose that $\mu = \mu(a)$ is a continuous real-valued function on $[0, A)$ which satisfies $M(A^-) = +\infty$ where $M(a) := \int_0^a \mu ds$ and let $u_0(a) := \exp(-M(a))$ for $0 \leq a < A$ and 0 for $a \geq A$.

$u_0(a)$ is the probability of living to age a .

The function u_0 is continuous for $a \geq 0$ and can be used to define a Banach space $B = B(\mu)$ of continuous functions $u: \mathbb{R} \rightarrow \mathbb{R}$, with support on $[0, A]$, for which u/u_0 is continuous on $[0, A]$ under the norm $\sup_{0 \leq a \leq A} |u/u_0|$. A solution of (2) in B is a differentiable function on $(0, A)$. Note that solutions in B automatically satisfy the

condition $u(a) = 0$ for $a \geq A$. A positive solution in B satisfies $u > 0$ on $[0, A)$. Note that (2) has the trivial solution $u \equiv 0$ in B . Also note that $u_0 \in B$ solves $d_a u + \mu u = 0$.

Suppose that $F = nf$ where $n \in \mathbb{R}$ and $f = f(u)$ is normalized so that

$$\int_0^A u_0 f(0) da = 1. \quad (3)$$

Then $n = \int_0^A u_0 F(0) da$ is the inherent net reproductive rate, i.e., the expected number of offspring per individual per lifetime.

Question: for what values of the inherent net reproductive rate n do the equilibrium equations in (2) have a positive solution in B ? and when it is stable as a solution of the dynamical equations (1)?

An equilibrium pair $(n, u) \in \mathbb{R} \times B$ is a pair for which u is a solution of (2) in B with $F = nf$. A positive equilibrium pair is one for which u is a positive equilibrium solution. Equations (2) have the trivial solution pairs $(n, 0)$ for all $n \in \mathbb{R}$.

A fundamental principle of bifurcation theory is that bifurcation from the trivial solution $u \equiv 0$ can occur only at a value of n at which the linearized equations have nontrivial solutions. It is elementary to see that the linear equations

$$d_a u + \mu u = 0, u(0) = n \int_0^A u f(0) da$$

have a nontrivial solution in B if and only if $n = 1$ (cf. (3)) in which case all solutions are constant multiples of u_0 . Thus the only possible bifurcation point is $(n, u) = (1, 0)$. But does bifurcation of positive equilibrium pairs actually occur at $(1, 0)$?

Assume $F = nf$, $f = \phi + r(u)$ where $r(0) \sim 0$ and $\phi = f(0) \in L_1[0, A]$ satisfies the normalization (3). Suppose $A < +\infty$. If the higher order operators

$$\int_0^A ur(u) da, ud(u) \quad (4)$$

are continuous as operators from B into \mathbb{R} and B respectively, then it is possible to show [6], using abstract bifurcation theory methods, that the equilibrium equations (2) possess a continuum C (i.e. a closed and connected set) of equilibrium pairs (n, u) with the following properties:

$$(0, 1) \in C$$

$(n, u) \in C \setminus (1, 0)$ is a positive equilibrium pair

C is unbounded in $\mathbb{R} \times B$.

This fundamental existence result shows that the primary bifurcation in the scenario described in the Introduction is, with regard to the inherent net reproductive rate of the population and positive equilibrium states, a universal property of population

growth models. Note the biological significance of the critical value $n = 1$, namely when $n = 1$ birth and death are balanced so that exact per unit replacement occurs at low (technically zero) density.

It must be kept in mind that for specific model equations it is possible that positive equilibrium pairs exist which do not lie on the bifurcating continuum C . For an example see Cushing (1984).

The higher order terms (4) need not have the form above, i.e. δ, β need not arise from per unit density vital rates D and F , for this general existence result although in the general case only positivity near the bifurcation point $(1, 0)$ can be guaranteed (see Cushing (1985)).

If $A = +\infty$ one loses a crucial compactness property in the proof of the above result and this global result (i.e. the unboundedness of C) remains an open question in this case. Local bifurcation still occurs however (see Cushing (1984)).

2.2. Local Analysis.

One wishes to know not only the existence of positive equilibrium densities, but also about the stability properties of these equilibria as solutions of the dynamical equations (1). In general one cannot expect that the equilibrium pairs on the continuum C are stable. Indeed, as already mentioned in the Introduction, even if the pairs "start out" stable near the bifurcation point $(1, 0)$ they need not globally remain stable. For example, Hopf-type bifurcation from equilibria to nontrivial time periodic solutions of (1) is a possibility. Moreover, the positive equilibria from C need not "start out" stable near $(1, 0)$ as will be seen.

Locally, near the bifurcation point, it is possible to prove some precise and very general results concerning the (linearized) stability of both the trivial equilibrium $u \equiv 0$ and the positive equilibria from the continuum C . First, a refinement of the existence result above can be made near $(1, 0)$ by means of classical implicit function theorem (or Liapunov-Schmidt) methods. Suppose $A \leq +\infty$ and that the operators in (4) are $q \geq 1$ times continuously (Fréchet) differentiable near $u = 0$. Then the (necessarily unique) positive equilibrium pairs near the bifurcation point can be expressed for $\varepsilon > 0$ sufficiently small as

$$n = n(\varepsilon) = 1 + \gamma(\varepsilon), \quad u = u(\varepsilon) = \varepsilon u_0 + \varepsilon u_1(\varepsilon) \quad (5)$$

where γ, u_1 are continuously differentiable as functions of ε for small $|\varepsilon|$ near $\varepsilon = 0$ which map into \mathbb{R} and B_0 (the functions u in B satisfying $\int_0^A uu_0 \, da = 0$) and which satisfy $\gamma(0) = 0, u_1(0) = 0$.

In order to study the stability of both these positive equilibrium solutions and the trivial equilibrium $u \equiv 0$, the dynamical equations can be linearized at the equilibrium in

question and solutions of the resulting linear equations sought in the form $u = y \exp(zt)$ where $0 \neq y \in B$ and z is a complex number. If such a solution can be found with $\operatorname{Re} z > 0$ then the equilibrium will be called unstable. If no such solutions exist for $\operatorname{Re} z \geq 0$ then the equilibrium will be called stable (locally asymptotically stable). For a rigorous justification of this standard procedure for (1) (although in a slightly different setting) see Webb (1985).

The stability of the trivial pairs $(n, u) = (n, 0)$ is easily ascertained by this method, for the linearization of (1) at $u = 0$ with $F = nf$ leads, with $u = y \exp(zt)$, to the equations

$$d_a y + y(\mu + z) = 0, \quad y(0) = n \int_0^A y \phi \, da.$$

This pair of equations is easily seen to have a nontrivial solution $y \in B$ if and only if z satisfies the "characteristic equation"

$$1 = nc(z), \quad c(z) := \int_0^A e^{-za} u_0 \phi \, da.$$

Inasmuch as $|nc(z)| < 1$ for $n < 1$ and $\operatorname{Re} z \geq 0$ while for $n > 1$, $nc(0) > 1$ and $nc(z) \rightarrow 0$ as $z = \operatorname{real} \rightarrow +\infty$ it is seen that $u = 0$ is stable for $n < 1$ and unstable for $n > 1$.

Thus the trivial equilibrium $u = 0$ loses stability as the inherent net reproductive rate n increases through the critical value 1.

The stability of the positive bifurcating equilibria (5) is more difficult to study. The linearization procedure leads to linear homogeneous equations in which the parameter ϵ appears. It is possible to show (Cushing (1985 and 1984)) that these equations possess "eigen-solutions" of the form $u = y(\epsilon) \exp(z(\epsilon)t)$ for $|\epsilon|$ small where $y(\epsilon) = u_0 + v(\epsilon)$, $z = z(\epsilon)$, with $v(0) = 0$, $z(0) = 0$. Moreover

$$z'(0) = -\gamma'(0)/m_1, \quad m_1 := \int_0^A a u_0(a) \phi(a) \, da > 0. \quad (6)$$

Thus $z(\epsilon) > 0$ if $\gamma'(0) < 0$ and $z(\epsilon) < 0$ if $\gamma'(0) > 0$ for $\epsilon > 0$ small.

Since $\gamma'(0) < 0$ means $n < 1$ for $\epsilon > 0$ small this case is called subcritical bifurcation. Similarly the case $\gamma'(0) > 0$ is called supercritical bifurcation and corresponds to $n > 1$. The result (6) implies that the stability of the bifurcating branch depends on the direction of bifurcation.

Thus, locally near bifurcation, the positive equilibrium pairs (5) from C are stable if and only if the bifurcation supercritical or in other words $n > 1$.

The implicit function theorem methods used to obtain this result also yield a formula for $\gamma'(0)$:

$$\gamma(0) = \int_0^A u_0 \phi \int_0^a d'(0)(u_0) ds da - \int_0^A \phi r'(0)(u_0) da \quad (7)$$

where $d'(0)$ and $r'(0)$ are Fréchet derivatives at $u = 0$. Thus the direction of bifurcation is determined by the (age-specific) changes in the vital rates D and f with respect to density u near $u = 0$.

For example, if an increase in density (at low levels) is deleterious in the sense that the death rate cannot decrease and the birth rate cannot increase, i.e. $d'(0)(u_0) \geq 0$, $f'(0)(u_0) \leq 0$ for all age classes (but are not both identically zero) then clearly $\gamma(0) > 0$. Thus in this case, which occurs very frequently in model equation for single species growth, only supercritical stable bifurcation can occur. Not all models of interest have these properties however. Nor do all models of interest display supercritical stable bifurcation. Examples will be given below.

Further examples of the use of formula (7) can be found in Cushing (1984). The expansions (5) are also of use in studying the nonlinear effects of density on the equilibrium age distribution Cushing (1984).

Although formula (7) can be used to determine the direction of bifurcation (in the "generic" case when $\gamma(0) \neq 0$, i.e. when the bifurcation is not locally vertical) it will be seen in the next subsection that there is often a simpler method of determining not only the direction of bifurcation, but other properties of the continuum C as well.

The stability results described here can also be extended to more general vital rates δ, β (Cushing (1985)).

2.3 The spectrum

In Section 2 above a very general existence result for positive equilibrium solutions of (1) with $F = nf$ was given, namely that there exists an unbounded continuum C of positive equilibrium pairs (n, u) . In this section I want to return to the question raised in Section 2 and discuss the problem of describing the spectrum associated with C :

$$\sigma = \{n \in \mathbb{R} | (n, u) \in C / (1, 0) \text{ for some } u \in B\}.$$

For each $n \in \sigma$, (1) has at least one positive equilibrium with $F = nf$. The closure $cl(\sigma)$ of σ is an interval $cl(\sigma) = [\sigma_l, \sigma_s]$, possibly infinite, which contains the critical value 1 .

The problem is to find ways of describing $cl(\sigma)$ from a knowledge of the properties of the vital rates D and f as functions of density u . For each $n \in \sigma$, (1) with $F = nf$ has at least one positive equilibrium. Also of interest is the uniqueness or lack of uniqueness of this bounded equilibrium.

Since C is unbounded, either σ is unbounded or the set of positive equilibria from C

$$\Sigma = \{u \in B \mid (n, u) \in C \text{ for some } n \in \sigma\}$$

is unbounded (or both). A useful tool in studying these sets is a certain invariant on C which derives from the biological fact that in order to be at equilibrium a population's net reproductive rate must equal 1, i.e. each individual (or unit) is ultimately replaced by exactly one individual offspring. Mathematically, this principle is derived by noting that equation (2a) is equivalent to $u(a) = u(0) \exp(-\int_0^a D ds)$ which when substituted into the birth equation (2b) yields, for nontrivial equilibria $u(0) \neq 0$, the invariant

$$1 = nN(u) \tag{8}$$

$$N(u) := \int_0^A f(u) \exp(-\int_0^a D ds) da .$$

In particular the invariant (8) holds for (n, u) from C and hence $\sigma_1 \geq 0$. In general the endpoints σ_i, σ_S of the spectrum can lie anywhere within the range

$$0 \leq \sigma_i \leq 1 \leq \sigma_S \leq +\infty .$$

One can however often derive properties of $N(u)$ from specified properties of the density dependent vital per unit rates D and f which permit one to compute σ_i and σ_S using (8). In fact formulas for these endpoints are rather easily derived in terms of N :

$$\sigma_i = 1/N_S, \quad \sigma_S = 1/N_i \quad (\text{extended sense})$$

where $N_i := \inf_{\Sigma} N(u)$ and $N_S := \sup_{\Sigma} N(u)$.

As a simple example consider the commonly occurring case when density effects cannot increase fertility nor decrease the death rate for all age classes:

$$0 \leq f(u) \leq f(0) = \phi, \quad 0 \leq D(0) = \mu \leq D(u) \quad \text{for positive } u \in B .$$

Then clearly $N(u) \leq 1$ by (3) so that $N_S \leq 1$ and hence $\sigma_i \geq 1$. It follows that $\text{cl}(\sigma) = [1, \sigma_S]$ and hence supercritical stable bifurcation occurs in this case.

Another frequently occurring case is when either the birth rate f drops to zero or the death rate D tends to infinity as the density u increases without bound. Then $N(u)$ drops to zero as n increases without bound. Consequently if Σ is unbounded then $N_i = 0$. But either Σ or σ is unbounded and hence in either case $\sigma_S = +\infty$ or $\text{cl}(\sigma) = [\sigma_i, +\infty)$.

Models often have all of the properties above and hence the spectrum is

precisely $\beta = (1, +\infty)$. In such cases it follows that a positive equilibrium exists for every inherent net reproductive rate n greater than 1 and at least those for n near 1 are stable.

The invariant (8) becomes particularly useful in the important case when the dependence of D and f on density u is through a dependence on a single positive linear functional $p = p(u)$ of density. Suppose $F = nf$ and $D = \mu + d$ where

$$f = f(a, p(u)), \quad d = d(a, p(u))$$

$$f: [0, A] \times \mathbb{R}^+ \rightarrow \mathbb{R}^+, \quad d: [0, A] \times \mathbb{R}^+ \rightarrow \mathbb{R}^+$$

and p is a strictly positive bounded linear functional:

$$p: B \rightarrow \mathbb{R}, \quad p(u) > 0 \text{ for } u \geq 0, \quad u \equiv 0.$$

Examples for p include total population size $p = \int_0^A u da$, weighted integrals $p = \int_0^A k u da$, $k \geq 0$, and point evaluations $p = u(a_0)$, $0 \leq a_0 < A$, all of which appear in the literature of density dependent population dynamics (Cushing (1985)). Here p will be referred to as "population size" for simplicity.

In this case the invariant (8) becomes

$$1 = nN(p(u))$$

$$N(x) := \int_0^A f(a, x) u_0(a) \exp(-\int_0^a d(s, x) ds) da.$$

Thus the graph $P = \{(n, p(u)) \in \mathbb{R}^2 \mid (n, u) \in C\}$ must lie on the planar graph of the relation $nN(x) = 1$. Hence a "bifurcation diagram" of the pairs (n, u) can often easily be drawn by either an explicit calculation of N or by a simple analysis of its graph. A couple of examples are given in the next subsection. More examples can be found in Cushing (1984).

Although not completely obvious it is easily shown that for equilibrium solutions $p(u_1) = p(u_2)$ if and only if $u_1 = u_2$ and that P is unbounded if and only if Σ is unbounded (Cushing (1985)). Thus any uniqueness or boundedness properties derived from this graphical method are in fact valid for solutions of (2).

2.4 Some Examples

A standard procedure in studying bifurcation phenomena is to draw a "bifurcation diagram" in which some measure of the nontrivial solutions is plotted against the bifurcation parameter. For (2) a natural choice is to plot the B-norm

$|u|_\mu := \sup_{0 \leq a \leq A} |u/u_0|$ against n . The general results above concerning positive equilibria of (1) are represented in Figure 1.

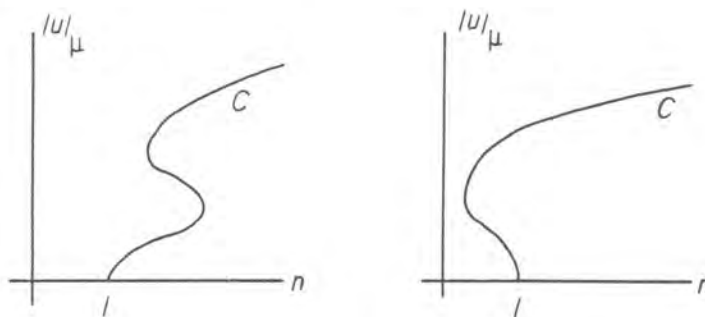


FIGURE 1. Supercritical Stable Bifurcation and Supercritical Unstable Bifurcation

For the case discussed at the end of the last subsection when F and D depend on a single positive linear functional p of density, it is more natural and convenient to construct a bifurcation diagram by plotting $p(u)$ against n as demonstrated in Figure 2.

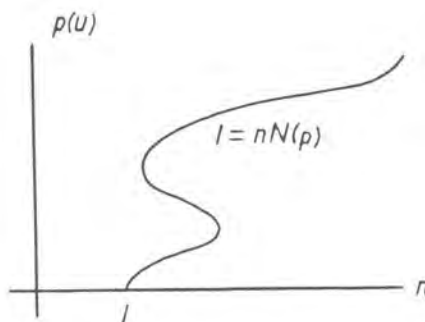


FIGURE 2. A bifurcation diagram in $(n, p(u))$ coordinates.

Two examples illustrating the two cases of supercritical stable bifurcation and subcritical unstable bifurcation will now be given.

Consider the "logistic" type case when the birth rate depends linearly on a functional p of density (Hoppenstaedt (1975)):

$$f = \phi(a)[1 - c(a)x]_+, \int_0^A \phi u_0 da = 1, c(a) > 0, \phi(a) \geq 0$$

where $[x]_+ = x$ for $x \geq 0$ and $= 0$ for $x < 0$. Suppose that the death rate D increases with population size p :

$$d(a, 0) \equiv 0, d_x(a, x) \geq 0, 0 < a < A, x > 0. \quad (9)$$

Then

$$N(x) = \int_0^A \phi[1 - cx]_+ u_0 \exp(-\int_0^a d(s, x) ds) da$$

has the following properties: $N(0) = 1$, $N(x) \equiv 0$ for $x \geq x_0 := \max 1/c$ and $N(x)$ is strictly decreasing on $0 < x < x_0$. Thus the graph of the relation $1 = nN(x)$ and hence the bifurcation diagram for this example appears as in Figure 3.

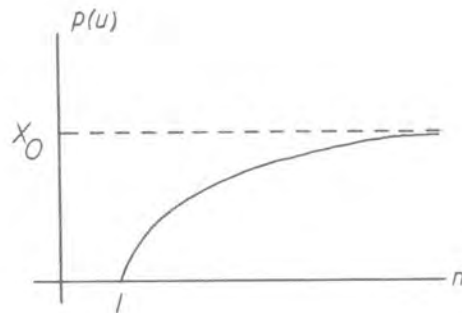


FIGURE 3 Bifurcation diagram for "logistic" model

It follows for this example that a positive equilibrium exists if and only if $n > 1$ in

which case it is unique; that supercritical bifurcation occurs and hence the unique positive equilibrium is stable at least for n close to 1; and that $p(u) \rightarrow x_0$ as $n \rightarrow +\infty$.

As already remarked, stability does not in general persist globally along C . As will be seen below this fact can be illustrated using this particular example. A challenging mathematical problem is to study the global stability properties of examples such as this one ... global stability in both the sense of a global (nonlocal) stability analysis of a given density u for a specified fixed n and in the sense of a global analysis along C , i.e. for all $n \in \sigma$. Some results for special cases of this particular example have been obtained (see Marcati (1982) and Webb (1985)).

Supercritical stable bifurcation does not always occur, even in simple examples. Consider the so-called "depensation" model in which $F = b(e + x)/(c + x^2)$ for positive constants b , e , and c . The normalization (3) is accomplished by setting

$$f = \frac{c}{e} \frac{e + x}{c + x^2}, \quad n := be/c, \quad I := \int_0^A u_0 \, da.$$

Suppose as a special case of (9) that the death rate is also "logistic-like" and linear in p : $d = x\psi(a)$, $\psi(a) > 0$. Then

$$N(x) = \frac{c}{e} \frac{e + x}{c + x^2} \int_0^A u_0 e^{-x\Psi(a)} \, da, \quad \Psi(a) := \int_0^a \psi(\alpha) \, d\alpha.$$

Then $N(0) = 1$ and $N(+\infty) = 0$ so that $\sigma_S = +\infty$. If $N'(0) > 0$ then $N_S > 1$ and $\sigma_i < 1$ so that subcritical unstable bifurcation occurs. The condition $N'(0) > 0$ occurs for example if $1 > e\Psi(A)$.

Since $cl(\sigma) = [\sigma_i, +\infty)$, $0 < \sigma_i < 1$ in this case, there exist at least two positive equilibria for $\sigma_i < n < 1$. Roughly speaking one has a bifurcation diagram as given in Figure 4.

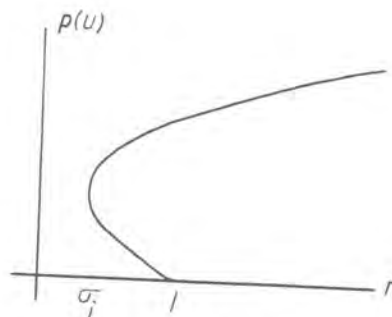


FIGURE 4 Bifurcation diagram for "depensation" model

An interesting problem for subcritical bifurcation cases such as this one is to determine what the asymptotic dynamics of (1) are. One might conjecture that in many circumstances the "upper" branch in this bifurcation diagram consists of stable positive equilibria while the lower branch consists of unstable positive equilibrium (from the local stability analysis above we know this is true near $(1, 0)$). If this is true the population is vulnerable to sudden collapses as n is decreased (below σ_1) and a hysteresis phenomenon is possible. Such phenomena have been suggested as being important in explaining some fishery collapses (see Clark (1976)).

The asymptotic dynamics of age-structured subcritically bifurcating population models such as this one pose challenging mathematical problems in that they can be quite complicated. I have for example investigated a simple depensatory type model in which preliminary investigations show that while it is true that the upper branch is stable and the lower branch is unstable as conjectured above, there also exist uncountably many positive periodic solutions each of which is approached by uncountably many trajectories.

These types of model equations are not without biological interest as they related to the so-called "Allee effect" when density effects on vital rates are not deleterious at low densities (although they might be at high densities) but in fact birth rates might increase with increased low level densities (e.g. due to an increased probability of mating) or death rates might decrease with increased low densities (e.g. due to the increased safety from herding or schooling). The periodic oscillations mentioned above in an age-structured subcritically bifurcating model suggest the possibility of a source of oscillations different from the familiar ones in population dynamics (time lags, predator-prey interactions, environmental periodicities, etc.) which is due to the internal age structure of the population together with an "Allee" or "depensatory" effect.

3 INTERACTING SPECIES

There is a rapidly growing literature on age-structured population interactions in which terms such as predation rates and preferences, competitive interaction coefficients, resource preferences and consumption rates, etc. are age specific (e.g. see Cushing and Seleem (1984, 1983); Diekmann, Nisbet, Gurney, and van den Bosch (1985); Gurtin and Levine (1979); Hastings (1983); Saleem (1984); and Webb (1985) just to cite a few). Such interactions can be modeled by coupling equations of the form (1) for the density of each species by assuming that the per unit birth and death rates depend on the densities of other species.

The approach taken here to the questions of equilibrium existence and stability for a single species as described above can be extended to the case of $m \geq 2$ interacting species in the following way. Suppose that a community of $m - 1 \geq 1$

interacting species with densities u_i , $1 \leq i \leq m-1$, is known to have a positive equilibrium $u_i = u_i^0(a) > 0$, $0 \leq a < A_i$. Under what conditions will the addition of an m^{th} species result in a system with a positive equilibrium and when will this equilibrium be stable?

Let $s = s(a)$ be the density of the m^{th} species and let $u = u(a)$ denote the vector of densities $(u_i) = (u_i)_{i=1}^{m-1}$. Then (u, s) denotes a vector of m densities. The equilibrium equations are

$$d_a u_i + u_i D_i = 0, \quad 0 < a < A_i$$

$$u_i(0) = \int_0^{A_i} u_i F_i \, da, \quad u_i(A_i) = 0 \quad (10)$$

$$d_a s + s D_m = 0, \quad 0 < a < A_m$$

$$s(0) = \int_0^{A_m} s F_m \, da, \quad s(A_m) = 0$$

where the vital rates $D_i = D_i(u, s)$, $F_i = F_i(u, s)$ depend on the densities u_i and s .

Assume that the subcommunity of u_i governed by the "reduced" system

$$d_a u_i + u_i D(u, 0) = 0, \quad 0 < a < A_i$$

$$u_i(0) = \int_0^{A_i} u_i F_i(u, 0) \, da, \quad u_i(A_i) = 0 \quad (11)$$

has a positive equilibrium u^0 in $B^{m-1} := B(\mu_1) \times \dots \times B(\mu_{m-1})$, $\mu_i = D_i(0, 0)$. Here each μ_i satisfies the conditions on μ in the single species model equations above (but not necessarily with the same maximal age A_i).

Assume further that the subcommunity equilibrium u^0 is nonsingular, i.e. that the linearization of (11) at u^0 possesses no nontrivial (i.e. nonidentically zero) solutions in B^{m-1} .

As in the approach for the single species case a parameter n is introduced into (10) by a normalization of the birth rate F_m of the species s and then equilibrium "pairs" $(n, (u, s))$ are sought which bifurcate from the trivial solution $(n, (u^0, 0))$. Specifically, let $F_m = n f_m$ where

$$\int_0^A s_0 f_m(u^0, 0) da = 1$$

$$s_0 := \exp(-\int_0^a D_m(u^0, 0) d\alpha) . \quad (12)$$

Then n has the biological interpretation of an inherent (i.e. low s density) net reproductive rate for species s when the other species u are at the subcommunity equilibrium u^0 .

The linear equations resulting from a linearization of (10) at $(u^0, 0)$ are not as easily studied as in the one species case. This is because the linearized equations for u_i has the form

$$d_a u_i + u_i D_i(u^0, 0) + u_i^0 d_u D_i(u^0, 0) (u) = 0$$

in which there appears (unlike in the single species case linearized at $u = 0$) a "nonlocal" linear operator involving the Fréchet derivative of D_i with respect to u . Nonetheless an adequate linear theory for these and the remaining equations from the linearization of (10) can be established (including a requisite Fredholm theory) which permits the application of the global and local bifurcation theory techniques used in the single species case (see Cushing (to appear)).

The result is the following. Assume $A_i < \infty$ and that the operators

$$u_i D_i(u, s) , \int_0^{A_i} u_i F_i(u, s) da$$

are $q \geq 1$ times continuously Fréchet differentiable at $(u, s) = (u^0, 0)$ as operators from B^m into $B(\mu_i)$ and R respectively. Let $F_m = n f_m$ where f_m satisfies the normalization (12). Then the equilibrium equations (10) with $F_m = n f_m$ possess a continuum C of equilibrium "pairs" $(n, (u, s))$ with the following properties

$$(1, (u^0, 0)) \in C$$

C is unbounded in $R \times B^m(\mu)$

near $(1, (u^0, 0))$ the equilibrium pairs on C are positive and have the form

$$n = 1 + \gamma(\epsilon) , u = u^0 + y(\epsilon) , s = \epsilon s_0 + \epsilon x(\epsilon) \quad (13)$$

for $\epsilon > 0$ small where $\gamma(0) = 0$, $y(0) = 0$, $x(0) = 0$. Thus near the bifurcation point the

equilibria from C are positive.

The only significant difference between this multi-species result and the single species result above is that in general for the case of $m \geq 2$ interacting species the global, unbounded continuum C cannot be expected to consist entirely of positive equilibria, i.e. this continuum can leave the cone of positive functions in B^m . This fact can be seen for example from the classical Lotka-Volterra predator-prey or competition equations. If C does leave the positive cone, it must do so at a point

$(n', (u', s')) \neq (1, (u^0, 0))$ for which at least one u'_i identically vanishes or s' identically

vanishes. This is because solutions of (10) are necessarily of one sign. Such a point corresponds to an equilibrium state for another "reduced" system or subcommunity of (10).

A linearized stability analysis completely analogous to that carried out for the single species case can be applied to (10). If the nonsingular equilibrium u^0 of the reduced system (11) is stable (as a solution of the corresponding dynamical equations for the reduced system), then the trivial equilibrium $(n, (u^0, 0))$ is stable if and only if $n < 1$ and the positive equilibria (13) are stable if and only if the bifurcation is supercritical (see Cushing (to appear)).

The direction of bifurcation can, as in the single species case, be determined from an explicit formula for $\gamma'(0)$:

$$\gamma'(0) = \int_0^A s_0 f_m^0 \int_0^a \nabla D_m^0 d\alpha da - \int_0^A s_0 \nabla f_m^0 da$$

where the superscript "0" denotes evaluation at $(u, s) = (u^0, 0)$ and

$$\nabla D_m^0 := d_u D_m(u^0, 0)(d_e y(0)) + d_s D_m(u^0, 0)(s_0)$$

(a similar formula holding for ∇f_m^0). If $\gamma'(0) > 0$ then the bifurcation is supercritical and stable.

The local stability near the bifurcation point in the case of supercritical bifurcation can be lost along C . Classical examples of predator-prey interactions between unstructured populations which undergo Hopf bifurcations to stable limit cycles illustrate this fact.

Similar to the single species case properties of the continuum C can be deduced from the invariants

$$1 = nN_m(u, s), \quad 1 = N_i(u, s), \quad 1 \leq i \leq m-1 \quad (14)$$

which hold for any equilibrium $(u, s) \neq (0, 0)$ and in particular for the positive equilibria from C .

These are particularly useful when the vital rates D_i, F_i all depend on the densities (u, s) through strictly positive linear functionals (or "population sizes") $p_i: B(\mu_i) \rightarrow \mathbb{R}$ as follows:

$$D_i = \mu_i + d_i(a, p(u), p_m(s)), F_i = F_i(a, p(u), p_m(s))$$

$$p(u) := (p_i(u_i))_{i=1}^{m-1}, d_i(a, 0, 0) \equiv 0$$

where $d_i, F_i: [0, A_i] \times \mathbb{R}^m \rightarrow \mathbb{R}$. Then (14) implies that the graph $\{(n, (p(u), p_m(s)) | (n, (u, s)) \in C\}$ lies on the graph of the relations

$$1 = nN_m(x, x_m), 1 = N_i(x, x_m), 1 \leq i \leq m-1 \quad (15)$$

where $x = (x_i)_{i=1}^{m-1}$ and

$$N_i := \int_0^A F_i(a, x, x_m) \exp(-\int_0^a (\mu_i + d_i(\alpha, x, x_m)) d\alpha) da$$

$$N_m := \int_0^A f_m(a, x, x_m) \exp(-\int_0^a (\mu_m + d_m(\alpha, x, x_m)) d\alpha) da$$

Let $p^0 := (p_i(u_i^0))_{i=1}^{m-1}$. By the normalization (12) and from the invariants for the equilibrium u^0 of the reduced system one has

$$1 = N_i^0, 1 \leq i \leq m.$$

The relations (15) can be used, amongst other things, to determine the direction of bifurcation. Suppose that the last $m-1$ equations in (15) are solved for $x = x(x_m)$, $x(0) = p^0$, and that these solutions are substituted into the first equation. Supercritical and hence stable bifurcation occurs if

$$d_{x_m} N_m(x(x_m), x_m)|_{x_m=0} < 0.$$

Consequently if the Jacobian

$$J := (d_i N_j^0)_{1 \leq i, j \leq m-1}, d_i := d_{x_i}$$

is nonsingular, then supercritical bifurcation occurs if

$$((d_j N_m^0), d_m N_m^0) \cdot (-J^{-1}(d_m N_i^0), 1) < 0$$

where the dot " \cdot " denotes the usual vector inner product.

These existence and stability conditions yield constraints on the density dependence of the net reproductive rates N_i of all species under which the species s can "invade" and coexist (at low densities) with the stable subcommunity of species u_i in the sense that there exists a stable positive equilibrium of the full m species community. This interpretation is valid at least near bifurcation (i.e. for low s densities).

As an example consider the often studied case of $m = 2$ interacting species. The conditions above for supercritical bifurcation reduce to

$$d_1 N_1^0 \neq 0, d_2 N_2^0 - d_1 N_2^0 d_2 N_1^0 / d_1 N_1^0 < 0. \quad (16)$$

Two species interaction models for unstructured populations are usually categorized by the interspecies effects that total population size P_i has on the per capita growth rates P_i'/P_i . For example species i is said to prey on species j if $d_{P_j}(P_i'/P_i) > 0$ and $d_{P_i}(P_j'/P_j) < 0$ or these two species are said to compete if the first inequality is reversed.

For age-structured models appropriate assumptions need to be made on the dependencies of the age-specific death and birth rates of each species on the density of the other (or in the case being considered here on the population sizes $p_i(u_i)$ of the other species) according to the type of interaction being modeled. The conditions (16) suggest, on the other hand, that for age-structured populations an appropriate categorization of the type of interaction might instead be made according to each species' effect on the net reproductive rate of the other.

One might for example distinguish the two fundamental cases

$$d_1 N_2 > 0, d_2 N_1 < 0 \quad (\text{Predator-prey}) \quad (17)$$

$$d_1 N_2 < 0, d_2 N_1 < 0 \quad (\text{Competition}). \quad (18)$$

If the common intraspecific density effect assumptions $d_i N_i < 0$ are made whereby a species' net reproductive rate at equilibrium decreases with increases in population size, then the supercritical stable bifurcation condition (16) is equivalent to the determinant-like condition

$$d_1 N_2^0 d_2 N_1^0 - d_1 N_1^0 d_2 N_2^0 < 0. \quad (19)$$

For the predator-prey case (17) this condition is always met. Thus, a predator s can always survive on a prey u_1 (at least at low predator densities) if its inherent net reproductive rate n when the prey u_1 is at stable equilibrium is larger than one.

For the competition case (18) however stable coexistence is possible only if (19) holds. Condition (19) is very analogous to the classical condition for two species coexistence in unstructured populations which requires that the determinant of the so-called "community matrix" be positive. It is susceptible to the same interpretation as that for the classical unstructured population growth equations, namely that stable coexistence requires intraspecific competition (as measured by the product $d_1 N_1^0 d_2 N_2^0$) to be stronger than interspecific competition (as measured by the product $d_1 N_2^0 d_2 N_1^0$).

4. PERIODIC OSCILLATIONS

4.1. The Autonomous Case.

I have until now considered only the primary bifurcation in the bifurcation scenario described in the Introduction, namely the bifurcation of equilibrium states from zero densities as a function of the inherent net reproductive rate n . But I have repeatedly pointed out that even when this primary bifurcation is supercritical and hence stable and even when the existence of positive equilibria is global it is not necessarily true that stability persists globally. For example it can happen when n reaches a second critical value $n_0 > 1$ that the stable equilibria destabilize and a Hopf-type bifurcation to nonsteady, time periodic densities $u = u(t, a) > 0$ occurs.

This problem was studied for the general age-structured equations (1) in (see Cushing (1983)) (the results there can be extended in a straightforward way to systems (10)). Rather than describe the results in Cushing (1983) here, I will simply illustrate them by an example based on the first example in Section 4 above.

Consider the following case of Hoppensteadt's model studied in Section 4 above:

$$\begin{aligned} d_t u + d_a u + u D &= 0, \quad 0 < a < A = +\infty \\ u(t, 0) &= n \int_0^A \phi(a) [1 - \rho(u)]_+ u(t, a) da \\ \rho(u) &:= \int_0^A \phi(a) u(t, a) da \end{aligned} \quad (20)$$

$$D = \text{constant} > 0, \phi(a) \geq 0, \int_0^A \phi(a) e^{-Da} da = 1.$$

The equilibrium solutions can easily be found by direct calculation:

$$u(a) = (n - 1)e^{-Da/n} \quad (21)$$

and the continuum C consists of these equilibria for $n \geq 1$. Clearly the bifurcation is supercritical and hence stable. Positive equilibria exist and are unique for all $n > 1$.

It was shown in Cushing (1983) that if the "characteristic equation" of the linearization of (20) at the equilibrium (21) possesses a conjugate pair of complex roots which transversally crosses the imaginary axis (at a nonzero point) as n increases through a critical value n_0 then bifurcating from the equilibria (21) will be a continuum of nontrivial time periodic solutions of (20) in the usual Hopf-like manner. The characteristic equation for the example being considered here is

$$C(z) := 1 - (2 - n) \int_0^A \phi(a) e^{-Da} e^{-za} da = 0.$$

Depending on the properties of the age specific birth rate coefficient ϕ , this equation can have a conjugate pair of complex roots which transversally cross the imaginary axis at some critical value of n . This is perhaps best illustrated here by a concrete example.

The function $\phi(a)$ in (20) describes the inherent age-specific birth rate of the species. That $p(u)$ is as defined in (20) means that the adverse effects of population density on fertility are in this model age-specific and caused by the more fertile age classes themselves. A specific type of kernel ϕ which is frequently used in qualitative studies is

$$\phi(a) = \frac{1}{k!} \left(\frac{k}{M} + D \right)^{k+1} a^k e^{-ka/M}, \quad M > 0, k = 1, 2, 3, \dots \quad (22)$$

Such a kernel implies that fertility monotonically increases from zero (at age zero) with age until peaking at the age M of maximum fertility before monotonically decreasing to zero as age continues to increase without bound. The peak is sharper, i.e. maximum fertility is narrowly distributed around age M , for larger k . The constants appearing in ϕ are chosen so that the normalization in (20) holds.

For such a kernel the characteristic equation reduces to

$$1 - (2 - n)(q/(q + z))^{k+1} = 0, \quad q := \frac{k}{M} + D$$

whose roots are $z = q(-1 + (2 - n)^{1/(k+1)})$.

For $1 < n < 3$ all roots lie in the left half plane for all k . For $k = 1$, all roots lie in the left half plane for all $n > 1$. In these cases the equilibrium (20) is stable.

However, if the age-specific fertility function ϕ is sufficiently narrowly peaked at $a = M$, i.e. if $k \geq 2$, then a pair of conjugate roots z transversally crosses into the right half plane at the critical value

$$n_0 := 2 + \sec^{k+1}(\pi/(k+1)) > 3$$

where

$$z = i\theta, \theta = q(n_0 - 2)^{1/(k+1)} \sin(\pi/(k+1)).$$

Thus, by the results in Cushing (1983), a Hopf bifurcation from the equilibria (21) to nontrivial time periodic solutions of (20) occurs as n increases through n_0 for the kernels (22) with $k \geq 2$.

The bifurcation results in Cushing (1983) for equations of the type (1) are purely existence results. A stability analysis awaits future research. Perhaps the semi-group theory developed in Webb (1985) would be useful for this purpose.

4.2 The Nonautonomous Case.

The model equations studied so far have been all time autonomous, i.e. the equations do not depend explicitly on time t . Even though it is widely recognized (even by such early founding fathers of mathematical population dynamics as Volterra, Kostitzin and others) that important modeling parameters can and often do fluctuate significantly in time, there has been relatively speaking little research done on nonautonomous model equations. This is undoubtedly due to a large extent to the difficulties in mathematically analysing nonautonomous equations as compared to autonomous equations.

There are roughly two broad classes of nonautonomous equations which are being studied in an increasing amount of literature: stochastic equations and time periodic equations. With regard to the age-structured model equations (1) and (10) however there seems to have been very little research done on the difficult problems arising when the vital rates D, F are allowed to fluctuate stochastically. See however Witten (1983) for a study of the linear case.

If the vital rates R and D are allowed to oscillate periodically with a common period, a natural question which arises from the approach taken here is whether the bifurcation results for positive equilibria in the autonomous case can be extended to positive time periodic densities in the periodic case. For the unstructured population

case this has been successfully carried out for general systems of interacting populations in Cushing (1982) . For the age-structured case of a single species governed by (1) I have (in a forthcoming paper (Cushing (to appear); also see Cushing (1986)) extended the local bifurcation results described above for the autonomous case to the periodic case. This extension involves much more sophisticated mathematics than needed for the autonomous case (such as the use of results and methods concerning power compact, strictly positive operators on Banach lattices in order to handle the necessary linear equations, which are in this case periodic partial differential equations). A global analysis for periodic versions of (1) and an analysis of periodic versions of systems (10) remains to be carried out.

5 CONCLUDING REMARKS

There are of course many possibilities for further analysis of age-structured population growth models using the approach taken in this paper. For example there is the problem of studying the dynamics of the model equations (1) or (10) when the growth rate v of the physical parameter x depends on t and, as would certainly be the case in many biologically reasonable cases, on the densities u_j . This assumption introduces further nonlinearities into the equations which pose new mathematical difficulties because the characteristics of the resulting hyperbolic equations then depend on the solutions.

Another example of an important and interesting problem is to introduce spatial heterogeneity and allow for spatial diffusion by the populations as well as for age structure within the population. Spatial diffusion by unstructured populations has been extensively studied in recent years.

There are of course also many interesting, challenging, and important mathematical problems involved in modeling and analysing population growth dynamics for specific types of populations and for specific types of multi-species interactions. This is especially true for age-structured populations or for populations structured by other internal variables.

In this paper however I have not discussed in detail any particular type of population or community of populations, but have instead emphasized some very general results which apply to very general dynamical growth models. I have done this with the hope that the approach taken here, which utilizes bifurcation theory and techniques, has not only suggested a way to apply the powerful analytical techniques available from this theory, but has shown how this theory can provide a unification of some fundamental properties shared in common by a very broad class of population dynamical models.

REFERENCES

- Clark, C.W., 1976. Mathematical Bioeconomics, Wiley, New York.
- Cushing, J.M., 1980. Model stability and maturation periods in age structured populations, *J. Theo. Biol.* 86:709-730.
- _____, 1981. Volterra Integrodifferential Equations in Population Dynamics, in Mathematics in Biology (M. Iannelli ed.), Liguori Editore, Naples.
- _____, 1982. Periodic Kolmogorov systems, *SIAM J. Math. Anal.* 13, no. 5, 811-827.
- _____, 1983. Bifurcation of time periodic solutions of the McKendrick equations with applications to population dynamics, *Comp. & Math. Appl.* No. 3, 9: 459-478.
- _____, 1985. Equilibria in structured populations, *J. Math. Biol.* 23: 15-39.
- _____, Existence and stability of equilibria in age-structured population dynamics, 1984. *J. Math. Biol.* 20: 259-276.
- _____, Periodic McKendrick equations for age-structured population growth, 1986. *Comp. & Math. Appl.* 415: 513-526.
- _____, Periodic McKendrick equations, to appear in *Comp. & Math. Appl.*
- _____, Equilibria in systems of interacting structured populations, to appear *J. Math. Biol.*
- _____, and M. Saleem, A competition model with age structure, 1984. In Mathematical Ecology (S.A. Levin and T.G. Hallam, ed.), *Lec. Notes in Biomath.* 54: 178-192.
- _____, Competition and age-structure, 1983. In Population Biology (H.I. Freedman & C. Strobeck ed.), *Lec. Notes in Biomath.* 52: 210-217.
- Diekmann, O., Nisbet, R.M., Gurney, W.S.C., and van den Bosch, F. 1985. Simple mathematical models of cannibalism: a critique and a new approach, Centre for Math. & Comp. Sci., Report no. Am-R8505, Amsterdam.
- Gurtin M. and MacCamy, R.C., 1974. Nonlinear age dependent population dynamics, *Arch. Rat. Mech. Anal.* 54: 281-300.
- Gurtin, M., The Mathematical Theory of Age-Structured Populations, to appear.
- Gurtin, M. and Levine, D.S., 1979. On predator-prey interactions with predation dependent on age of prey, *Math. Biosci.* 47: 207-219.
- Hastings, A. 1983. Age dependent predation is not a simple process I: continuous time models, *Theo. Pop. Biol.* 23: 347-362.
- Hoppensteadt, F. 1975. Mathematical Theories of Populations: Demographics, Genetics, and Epidemics, SIAM Conf. Series on Appl. Math., Philadelphia.
- Marcati, P. On the global stability of the logistic age dependent population equation, 1982. *J. Math. Biol.* 15: 215-226.
- McKendrick, A.G. 1926. Applications of mathematics to medical problems, *Proc. Edin. Math. Soc.* 44: 98-130.
- Nisbet, R.M. and Gurney, W.S.C. 1982. Modelling Fluctuating Populations, Wiley, New York.
- Oster, G., 1977. Lectures in Population Dynamics. In Lectures in Applied Mathematics, AMS, 16: 149-170.
- Saleem, M. 1984. Predator-prey relationships: Indiscriminate predation, *J. Math. Biol.* No. 1, 21: 25-34.
- Sinko, J.W. and Streifer, W. 1967. A new model for the age-size structure of a population, *Ecol.* 48: 910-918.
- von Forester, H. 1959. Some remarks on changing populations. In The Kinetics of Cellular Proliferation (F. Stholman Jr. ed.), 382-407, Grune & Stratton, New York.
- Webb, G.F. 1985. Theory of Nonlinear Age-Dependent Population Dynamics, Monographs in Pure and Applied Mathematics Series, vol. 89, Marcel Dekker, New York.
- _____, Logistic models of structured population growth, 1986. *Comp. & Math. Appl.* 12A, Nos. 4/5: 527-539.
- Witten, Matthew. 1983. On stochasticity in the von Forester hyperbolic partial differential equation system. Further applications to the modeling of an asynchronously dividing cellular system, *Comp. & Math. Appl.* No.3, 9: 447-458.