Lecture Notes in Biomathematics

Managing Editor: S. Levin

54

Mathematical Ecology

Proceedings of the Autumn Course (Research Seminars),
held at the International Centre for Theoretical Physics,
Miramare-Trieste, Italy, 29 November – 10 December 1982

Edited by S. A. Levin and T. G. Hallam

Springer-Verlag
Berlin Heidelberg New York Tokyo 1984

Editors

Simon A. Levin
Ecology & Systematics, E 347 Corson Hall
Cornell University, Ithaca, NY 14853-0239, USA

Thomas G. Hallam
Department of Mathematics, University of Tennessee
Knoxville, TN 37996-1300, USA

TABLE OF CONTENTS

A COMPETITION MODEL WITH AGE STRUCTURE

J. M. Cushing and M. Saleem

The University of Arizona
Department of Mathematics and
Program on Applied Mathematics
Building # 89
Tucson, Arizona 85721
USA

1. Introduction. In recent years there has been a great deal of interest in
modeling and analyzing the growth and interactions of populations with age structure.
A large portion of the recent literature was stimulated by some seminal papers of
Gurtin and MacCamy [7-9] in which the growth of a single age-structured population
was modeled by a first order partial differential equation (which has come to be
called "McKendrick's equation) for the population density. More recently papers
have appeared in which systems of such equations have been used to describe inter-
actions between age-structured populations [2,4-6,11,12,15,16] nearly all of which
have dealt with predator-prey interactions. As pointed out in [2,10] the presence
of age structure within one or more of the interacting populations can significantly
change the dynamics of the interaction and in fact can lead to violations of often
held basic tenets in theoretical population dynamics.

In this paper we will derive and investigate a model for the dynamics of several
competing age-structured populations in order to see to what extent some of the
fundamental notions of the theory of competition (e.g. competitive exclusion,
ecological niche and limiting similarity) can be affected by the presence of age
structure within the populations. The model equations will be derived from the
McKendrick equations and will serve as a generalization of the classical Lotka-
Volterra equations. We will derive the system parameters as is done in the MacArthur-
Levins theory [1,13], but with allowance for dependence of the various parameters
in this theory on age. Although the MacArthur-Levins theory is perhaps naive and a
bit out-dated, we felt that given the influence which it has had on the thinking in
theoretical ecology, it   would be both interesting and reasonable in this, a
preliminary study of age-structure and competition, to model the derivation on (and
in fact generalize) this theory. Regardless of how the "coefficients" in the

equations are derived, however, it will be seen to what extent the usual dynamics and concepts in competition theory generalize to age-structured populations and what new dynamics can possibly result.

2. Derivation of the Model Equations. If it is assumed that n populations are described by age-specific density functions $\rho_i(t,a)$, $i = 1$ to n, (where t is time and a is age) so that $\int_{a_2}^{a_1} \rho_i(t,a)da$ is the total population between ages a_1 and a_2, then the McKendrick equations which describe the growth dynamics are

$$\partial \rho_i/\partial t + \partial \rho_i/\partial a + \mu_i \rho_i = 0 \qquad\qquad (2.1)$$

$$\rho_i(t,0) = \int_{a=0}^{\infty} f_i \rho_i(t,a)\, da , \quad i = 1,2,\ldots n . \qquad (2.2)$$

Here μ_i and f_i are respectively the per unit density death and fecundity rates and hence (2.1) simply accounts for the removals from the ith population by death and (2.2) accounts for the additions to the ith population at age $a = 0$ made by births from all contributing age classes. In general μ_i and f_i are functions of t and a and for populations which exhibit density dependent self-regulation and/or mutual interactions they are functionals of the densities ρ_j, $j = 1$ to n, as well.

In this paper these vital rates μ_i, f_i will be assumed explicitly independent of time t so that (2.1)-(2.2) is an autonomous set of equations. We are interested in competing species so that the functional dependencies of μ_i and f_i on population densities will have the properties that increased densities cannot increase fecundity nor decrease the death rate. In fact, the case when the effect of competition for a common resource is predominantly felt in reduced fecundity (rather than increased death rate) will be considered and hence it will be assumed that μ_i is independent of the densities ρ_j. Finally, it will be assumed throughout that μ_i is also independent of age a. Although the results of this paper remain valid if this assumption is not made and $\mu_i = \mu_i(a)$ is an integrable function of a, there is a great simplification in notation and details if we assume $\mu_i = $ constant ≥ 0. This is a frequently made assumption in age-structured population dynamics and corresponds to an exponentially descreasing survivorship curve.

We consider now, as in the classical MacArthur-Levins theory, the case of competition for a one-dimensional resource as measured by a real parameter r. If

$R_i(r,a)dr$ = the amount of resource of type r to $r + dr$ available to age class a ;

$u_i(r,a)$ = the age-specific per unit density resource consumption rate of resource r by species ρ_i ;

$\beta_i(r,a)$ = the age-specific conversion of per unit resource r to number of off-spring of species ρ_i (per unit density) ;

then

$$f_i = \int_{-\infty}^{+\infty} \beta_i(r,a)u_i(r,a)R_i(r,a)dr . \qquad (2.3)$$

If it assumed that the amount of resource r which would be available to species ρ_i but is instead consumed by species ρ_j is proportional to the total consumption rate of resource r by species ρ_j then

$$R_i(r,a) = A_i(r,a) - \Sigma_{j=1}^n c_{ij}(r,a)\int_{s=0}^{\infty} u_j(r,s)\rho_j(t,s)ds . \qquad (2.4)$$

Here n is the number of competing species and $A_i(r,a)$ is the amount of resource r made available to age class a of species ρ_i in its habitat. If the <u>total</u> <u>birth</u> <u>rate</u> of species ρ_i is denoted by $B_i(t) := \rho_i(t,0)$, then the linear partial differential equation (2.1) implies that $\rho_i(t,a) = B_i(t-a)\exp(-\mu_i a)$. When substituted into the birth equation (2.2) this expression, together with (2.3)-(2.4), results in a system of integral equations to be solved for $B_i(t)$:

$$B_i(t) = \int_0^{\infty}\int_{-\infty}^{+\infty}\beta_i u_i[A_i - \Sigma_{j=1}^n c_{ij}\int_0^{\infty} u_j B_j(t-s)\exp(-\mu_j s)ds]dr\, B_i(t-a)\exp(-\mu_i a)da.$$

$$(2.5)$$

Our primary interest is with the existence and stability of equilibrium solutions of (2.5). A positive equilibrium $B_i(t) \equiv B_i^0 > 0$ is a solution of the algebraic equations

$$\Sigma_{j=1}^n\int_{a=0}^{\infty}\int_{-\infty}^{+\infty}\beta_i u_i c_{ij}\int_{s=0}^{\infty}u_j\exp(-\mu_j s)ds\,\exp(-\mu_i a)da\,B_j^0 =$$

$$\int_{a=0}^{\infty}\int_{-\infty}^{\infty}\beta_i u_i A_i dr\,\exp(-\mu_i a)da - 1. \qquad (2.6)$$

The first term on the right hand side is the <u>inherent</u> <u>per</u> <u>capita</u> <u>net reproductive</u>

rate n_i of species ρ_i and we arrive at the conclusion that (2.5) can have a positive equilibrium only if this inherent net reproductive rate is larger than one, a not too surprising result because $n_i = 1$ means exact replacement.

In order to make this system more tractable, we will make several further simplifying assumptions (using the MacArthur-Levins theory as a guide). First of all it will be assumed that the resource availability A_i is the same for all age classes: $A_i(r,a) = A_i(r)$ and that the constants of proportionality c_{ij} are independent of a and r: $c_{ij}(r,a) = c_{ij} > 0$. Secondly we write

$$u_i(r,a) = n_i w_i(a) p_i(r) \qquad (2.7)$$

where $p_i(r)$ is a probability density function (referred to as the resource "picking" or "preference" function) for which $p_i(r)dr$ represents the probability of choosing resource in the range r to $r + dr$ (or it is the fraction of resource in this interval consumed) and $n_i w_i(a)$ is the <u>age-specific</u> <u>resource</u> <u>consumption</u> <u>rate</u>. Here the age-specific distribution $w_i(a)$ is normalized so that

$$A_i \int_{a=0}^{\infty} \beta_i(a) w_i(a) \exp(-\mu_i a) da = 1 , \quad A_i := \int_{-\infty}^{\infty} p_i(r) A_i(r) dr \qquad (2.8)$$

which has the effect of introducing the inherent net reproductive rates n_i explicitly into the equations and analysis through (2.7). Finally, it will be assumed that a given species' resource consumption rate effects all other species' resource availabilities equally: $c_{ij} = c_j$. By rescaling the units used to measure population densities, one can assume that $c_{ii} = 1$. Thus in (2.5) we will take $c_{ij} = 1$.

With all these assumptions in place, (2.5) reduces to

$$B_i(t) = [A_i - \Sigma_{j=1}^{n} n_j P_{ij} \int_0^{\infty} w_j(a) B_j(t-a) \exp(-\mu_j a) da] \int_0^{\infty} \beta_i(a) n_i w_i(a) B_i(t-a) \exp(-\mu_i a) da$$

$$(2.9)$$

where $P_{ij} := \int_{-\infty}^{\infty} p_i(r) p_j(r) dr$. In the following sections the resource preference functions will be taken to be Gaussian with mean r_i and standard deviation W_i

(the niche "location" and "width" respectively). If it is assumed that the resource niche widths are equal for all species: $W_i = W > 0$ and that the niches are equally spaced: $|r_i - r_j| = d|i-j|$, $d > 0$, then

$$P_{ij} = \gamma \alpha^{(i-j)^2}, \quad \alpha := \exp(-d^2/4W^2), \quad \gamma := (4\pi W^2)^{1/2} \tag{2.10}$$

in (2.9). Note that $0 < \alpha < 1$.

The technical requirements on the functions $w_i(a)$, $A_i(r)$ and $p_i(r)$ needed throughout are that these are continuous, non-negative functions for which the integrals $\int_0^\infty w_i(a)\exp(-\mu_i a)da$, $\int_0^\infty a w_i(a)\exp(-\mu_i a)da$ and $\int_{-\infty}^\infty A_i(r)p_i(r)dr$ are finite.

If all parameters are independent of age a: $\beta_i(a) \equiv$ constant and $w_i(a) \equiv$ constant, then it is possible to show that the above model reduces to the classical Lotka-Volterra system. To see this, integrate (2.1) from $a = 0$ to $a = +\infty$, introduce the total population sizes $P_i(t) := \int_0^\infty \rho_i(t,a)da = \int_0^\infty B_i(t-a)\exp(-\mu_i a)da$ and use (2.9) in the result. This will yield the Lotka-Volterra system of ordinary equations for the P_i.

3. <u>Equilibria</u>. An equilibrium $B_i(t) \equiv B_i^0 =$ constant > 0 of equation (2.9) yields a steady-state population density $\rho_i = B_i^0 \exp(-\mu_i a)$. Such an equilibrium is a positive solution of the algebraic equations (2.6), which under the added assumptions made at the end of Section 2, become

$$\Sigma_{j=1}^n \alpha^{(i-j)^2} \Gamma_j = A_i(n_i-1)/n_i \tag{3.1}$$

where $\Gamma_j := n_j \gamma w_j^*(\mu_j) B_j^0$ and "*" denotes Laplace transform. A conclusion which can be drawn from (3.1) is that the classical principle of "limiting similarity" remains valid for this more general age-structured model. For, if it is assumed that the species are similar in reproductive output $n_i = N > 0$ and are supplied with equal amounts of resource $A_i = A > 0$, then the positive equilibrium equations (3.1) can be written

$$\Sigma_{j=1}^n \alpha^{(i-j)^2} \Omega_j = 1 \tag{3.2}$$

where $\Omega_j := N\Gamma_j/A(N-1)$, which are identical to those for the classical Lotka-Volterra-MacArthur-Levins equations [1,13]. It is known that (3.2) has a positive equilibrium for all niche separation to width ratios d/W if $n = 2$, but that if $n \geq 3$ then there is a positive lower bound for d/W of order of magnitude one below which no positive equilibrium exists and above which one does exist and is stable. Thus, this principle of limiting similarity remains intact (as far as the existence of a positive equilibrium is concerned) for the age-structure model considered here.

Note that complete symmetry is not required for this result. The death rates μ_i and the age-specific resource consumption rates $Nw_i(a)$ are not necessarily identical for all species.

There is, as will be seen in the following sections, a crucial difference, however, between the age-structure model above and the classical Lotka-Volterra model. In the classical model a positive equilibrium, when it exists, is always (asymptotically) stable [1]. Positive equilibria of the equations (2.9) can on the other hand be unstable, even in the case $n_i = N$, $A_i = A$ which is analogous to the classical case.

In the next section the stability of equilibrium solutions of (2.9) is studied under certain restrictions for the case of two species $n = 2$.

4. Stability of Equilibria. The stability (local, asymptotic) of an equilibrium solution of (2.9)-(2.10) can be investigated analytically by the usual procedure of investigating the roots of the characteristic equation of the linearization [14]. If $x_i = B_i - B_i^0$ and all terms higher order in x_i are ignored, then (2.9) takes the (vector) form

$$x(t) = \int_0^\infty K(a)x(t-a)da$$

whose characteristic equation is given by

$$D := \det(I - K^*(z)) = 0 \qquad (4.1)$$

If there are no roots z for which $\operatorname{Re} z \geq 0$, then B_i^0 is (locally, asymptotically) stable while if there exists a root $\operatorname{Re} z > 0$ then B_i^0 is unstable.

In general (4.1) is a transcendental equation in z and an analysis of the roots is very complicated. One case for which we have managed to carry out a rather complete analysis is the case of two species $n = 2$ under the further restrictions

$$\mu_1 = \mu_2 = \mu > 0, \quad \beta_1(a) = \beta_2(a) \equiv \text{constant} > 0, \quad w_1(a) = w_2(a) = w(a)$$

$$A_1 = A_2 = A > 0 .$$

(4.2)

Thus, it is assumed that the two species have identical death rates μ_i, resource-to-offspring conversion factors β_i and age-specific resource rate age distributions $w_i(a)$. We have also assumed here that the β_i are non-age dependent and consequently that the only age-specific parameter in the model is the resource consumption rate $n_i w(a)$. Also the total resource availability A_i is the same for both species. Note that the inherent net reproductive rates n_1, n_2 are not assumed identical, however.

Under these simplifying assumptions, the characteristic equation (4.1) in the case $n = 2$ reduces, for an arbitrary equilibrium (B_1^0, B_2^0), to

$$D := \det \begin{pmatrix} 1 - n_1\beta[A - 2n_1\gamma w^*(\mu)B_1^0 - n_2\gamma\alpha w^*(\mu)B_2^0]w^*(z+\mu) & n_1 n_2 \gamma\alpha\beta w^*(\mu)B_1^0 w^*(z+\mu) \\ \\ n_1 n_2 \gamma\alpha\beta w^*(\mu)B_2^0 w^*(z+\mu) & 1 - n_2\beta[A - n_1\gamma\alpha w^*(\mu)B_1^0 - 2n_2\gamma w^*(\mu)B_2^0]w^*(z+\mu) \end{pmatrix} = 0.$$

The normalization (2.8) of $w(a)$ implies that

$$A\beta w^*(\mu) = 1 .$$

(4.3)

Note that any z for which $w^*(z+\mu) = 0$ cannot be a root of this characteristic equation. Thus we assume throughout that $w^*(z+\mu) \neq 0$.

The equilibria $(B_1^0, B_2^0) = E$ are given by

$$E_0 := (0,0), \quad E_1 := (\beta A^2(n_1-1)/n_1^2\gamma, 0), \quad E_2 := (0, \beta A^2(n_2-1)/n_2^2\gamma)$$

$$E_3 = (\beta A^2 [1-n_1^{-1}-\alpha(1-n_2^{-1})]/\gamma n_1(1-\alpha^2), \; \beta A^2[1\; n_2^{-1}-\alpha(1-n_1^{-1})]/\gamma n_2(1-\alpha^2)) \; .$$

What makes the analysis of (4.1) tractable for any of these equilibria is that although the characteristic equation is transcendental in z, it turns out to be a polynomial (of degree two or less) in the ratio

$$\eta(z) := w^*(\mu)/w^*(z+\mu) \; .$$

This fact, together with $|\eta(z)| \geq 1$ for $\mathrm{Re}\; z \geq 0$, allows us to obtain stability for those parameter values for which all roots of this polynomial in η lie in the unit circle $|\eta| < 1$. We have used this approach to obtain those regions in the n_1,n_2-plane where the individual equilibria E_i above are stable. Instability, at least for n_1,n_2 near the boundaries of these regions, can be proved by an implicit function theorem argument which yields a root with $\mathrm{Re}\; z > 0$. A simple example is detailed below. FIGURE 1 contains a summary of these general results.
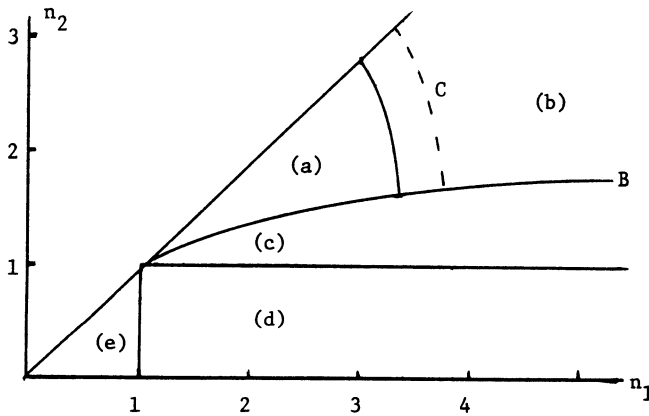

FIGURE 1: A positive equilibrium E_3 of (2.9) exists for $n_1 < n_2$ only in the regions (a) and (b) bounded by the line $n_1 = n_2$ and the curve B which is asymptotic to the line $n_2 = 1/(1-\alpha)$. It is stable in at least region (a) whose boundary is the solid line ($\eta_- = -1$). The dashed line is the actual stability boundary for the example (4.4), $m \geq 2$. In (c), E_1 and E_2 are both nonnegative, but only E_1 is stable (at least for $n_1 < 3$). In (d) only E_1 is nonnegative (it is stable at least for $n_1 < 3$). In (e) only E_0 is nonnegative and it is stable (E_0 is unstable outside (e)).

We give here the details only for the simplest case of E_0. The remaining equilibria are analysed in a similar manner, although the details are in some cases very tedious. For E_0 the characteristic equation reduces to the factorable quadratic equation in η

$$D := (1 - n_1/\eta)(1 - n_2/\eta) = 0$$

whose roots lie inside the unit circle $|\eta| \leq 1$ if and only if n_1 and $n_2 < 1$. Thus E_0 is stable if both $n_i < 1$. This manner of reasoning yields sufficient conditions for stability. It does not follow that the equilibrium is necessarily unstable if an η root lies outside the unit circle. To establish that E_0 is unstable outside the square $0 < n_i < 1$ (at least near the boundaries $n_i = 1$) we treat D as a function of z and one of the n_i, say n_1 (holding n_2 fixed, the opposite case is symmetric):

$$D = D(z, n_1), \quad D(0,1) = 0, \quad D_z(0,1) = \beta A \int_0^\infty aw(a)\exp(-\mu a)da(1-n_2) > 0.$$

The implicit function theorem implies the existence of a root $z = z(n_1)$, $z(1) = 0$, for $n_1 \sim 1$. An implicit differentiation gives further that

$$\text{Re } z'(0) = (1 - n_2)/D_z(0,1) > 0$$

and hence $\text{Re } z(n_1) > 0$ for $n_1 > 1$ near 1.

For the equilibrium E_3 to be positive, n_1 and n_2 must lie in a region R of the shape of (a) plus (b) in FIGURE 1 (plus its reflection through the line $n_1 = n_2$). The characteristic equation associated with E_3 is a quadratic equation $\eta^2 + c_1\eta + c_2 = 0$ in the ratio η where $c_1 := \gamma\beta^{-1}A^{-2}(n_1^2 B_1^0 + n_2^2 B_2^0) - 2$ and $c_2 := 1 - \gamma\beta^{-1}A^{-2}(n_1^2 B_1^0 + n_2^2 B_2^0) + (1-\alpha^2)\gamma^2\beta^{-2}A^{-4}n_1^2 n_2^2 B_1^0 B_2^0$. It is not difficult to show that this quadratic has two real roots $\eta_- < \eta_+ < 1$ and hence the characteristic roots are the roots of the two equations $\eta(z) = \eta_-$, $\eta(z) = \eta_+$. Thus $\eta_- > -1$ implies stability and $\eta_- = -1$ <u>defines the boundary of a region of stability of the positive equilibrium</u> <u>E</u>$_3$. This subregion of R in FIGURE 1 consists of (a) and its reflection through the line $n_1 = n_2$ and contains the point $(n_1, n_2) = (3,3)$ on its boundary. <u>This</u>

stability region is not necessarily maximal as the example below shows, but it is the largest possible in general (i.e. for arbitrary $w(a)$) as the example below also shows.

It is curious to note the importance of the integers $1, 2$ and 3 for this competition system of equations. For all other values of the other system parameters and for all age-specific resource consumption distributions $w(a)$, 1 is the minimal value of the net reproductive rates n_i for the survival of both species, 2 is the value of the n_i which maximizes the equilibrium E_3 (i.e. $\max(|B_1^0| + |B_2^0|)$ occurs at $n_1 = n_2 = 2$) and 3 is the maximum value of n_1, n_2 for which the stability of the positive equilibrium can be guaranteed in general.

As an example set

$$w(a) = La^m \exp(-am/T) \tag{4.4}$$

$T > 0$, $m = 1, 2, \ldots$ and $L = (\mu T + m)^{m+1}/m! A\beta T^{m+1}$ is chosen so that the normalization (4.3) holds. For this case $\eta(z) = (zT + \mu T + m)^{m+1}/(\mu T + m)^{m+1}$. The characteristic roots are $z = (\mu T + m) T^{-1}(-1 + |\eta_\pm|^{1/(m+1)} r_j)$ where r_j are the $(m+1)^{st}$ roots of $+1$ if $\eta_\pm > 0$ and -1 if $\eta_\pm < 0$. Thus, the positive equilibrium is always stable if $m = 1$, but is unstable for $m \geq 2$ when η_- or $\eta_+ < 0$ and $-1 + |\eta_\pm|^{1/(m+1)} \cos(\pi/(m+1)) > 0$. Thus the region of stability is defined by the curve C: $\eta_- = -\sec^{m+1}(\pi/(m+1))$ in the n_1, n_2-plane. Note that this curve approaches the curve $\eta_- = -1$ as $m \to +\infty$ (i.e. as the age distribution of the resource consumption rate narrows around the mean $T > 0$).

5. Oscillations. With the onset of instability occuring as one leaves a region of stability in the n_1, n_2-plane, the possibility of nonconstant oscillations arises. Rigorous theorems and bifurcation techniques for integral equations of the form (2.9) can be used to prove the existence of nonconstant periodic solutions for n_1, n_2 near these boundaries [3]. We will describe this phenonemnon only for the example given in Section 4, our purpose being restricted here to demonstrating clearly the possibility of nonconstant (stable) periodicities in an age-structured competition model (a possibility which does not occur in non-age-structured models) and to illustrate

some interesting features of these oscillations.

Bifurcation of nonconstant periodic solutions from the positive equilibrium E_3 occurs at a parameter point $(n_1, n_2) = (n_1^0, n_2^0)$ at which the characteristic equation has a root $z = i\omega$, $\omega \neq 0$. For $w(a)$ as in the example in Section 4 above, this occurs for (n_1^0, n_2^0) on the boundary line C when $m \geq 2$ in FIGURE 1. Thus $\omega = (\mu T + m)^{-1} \tan(\pi/(m+1))$. The bifurcation theory in [3] implies the existence of a path emanating from (n_1^0, n_2^0) in the n_1, n_2-plane along which there exist nonconstant solutions of (2.9) of fixed period

$$p = 2\pi/\omega = 2\pi(\mu T + m)^{-1} T \cot(\pi/(m+1)) . \tag{5.1}$$

Note that this period p is independent of the critical point (n_1^0, n_2^0) and hence we have an unusual case where all bifurcating periodic solutions near the critical boundary curve C have the same period (usually the period changes with the parameters (n_1, n_2)). This is corroborated by numerically computed solutions of (2.9) which we have carried out.

The solutions graphed in FIGURES 2-5 were computed with $n_1 = n_2 = N$, $m = 17$ and parameter values $\mu = W = \beta = A = 1.0$ and $T = 0.5$. Equal initial data was used so that $B_1(t) \equiv B_2(t)$ in these graphs. FIGURE 6 shows a case with $n_1 \neq n_2$ so that $B_1(t) \not\equiv B_2(t)$. Note that the species oscillate in phase. FIGURE 2 shows both species' birth rates tending to zero for $N < 1$ and approaching an equilibrium for $1 < N < 3$ with the maximum equilibrium occurring at $N = 2$ and damped oscillations occuring for $N = 3$. FIGURE 3 shows a sinusoidal-like periodicity for N above criticality with period $p \sim 1.1$ which is consistent with (5.1). The periodicities in FIGURES 4 and 5 exhibit an interesting period doubling (to approximately 2.2 in FIGURE 4 and to approximately 4.4 in FIGURE 5 for the slowly varying outer harmonic) as N is increased further. This is reminiscent of the same phenomenon which is well-known to occur in difference equations.
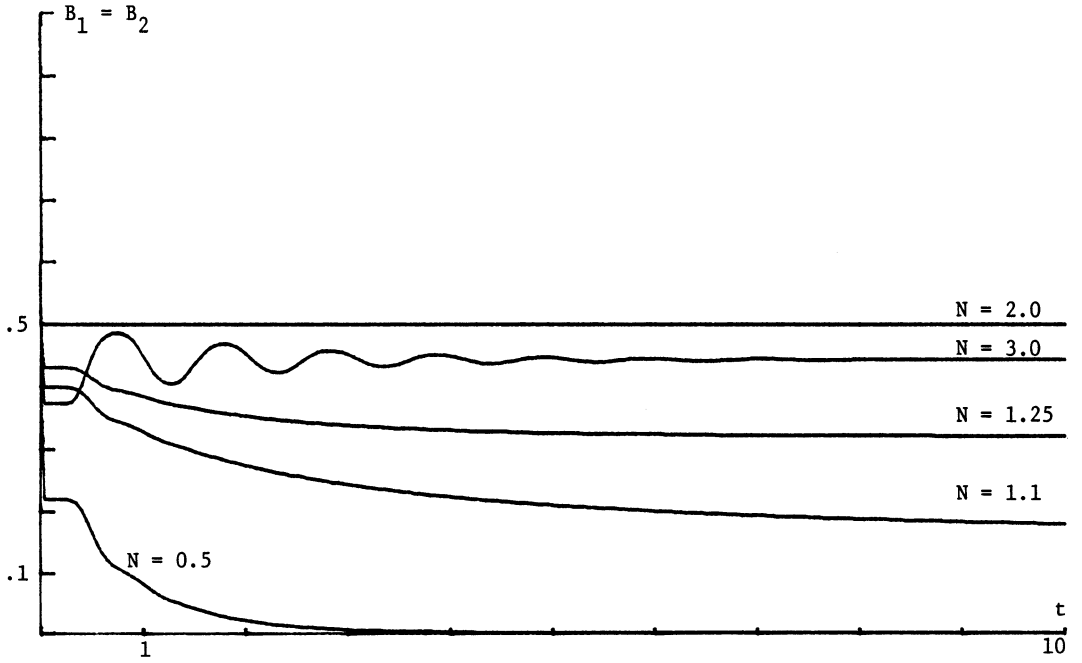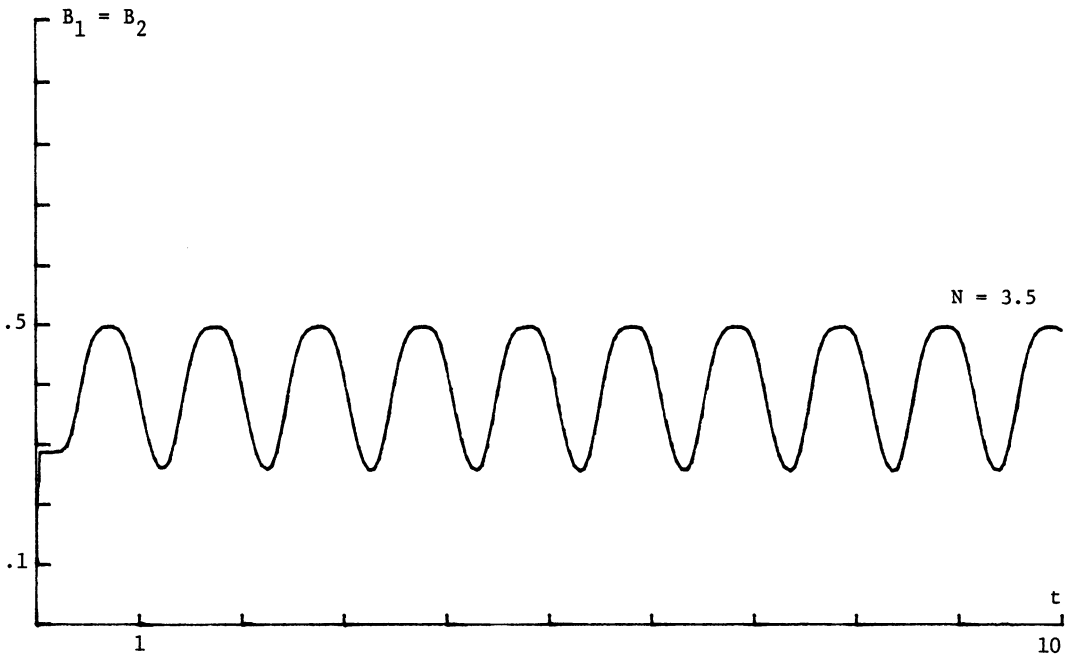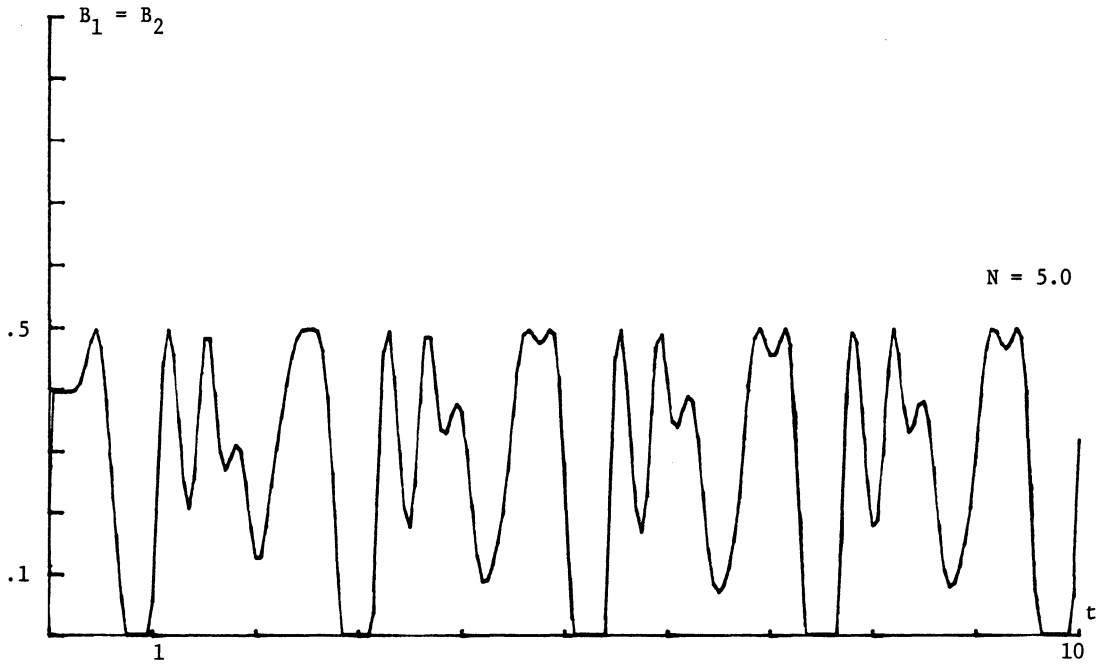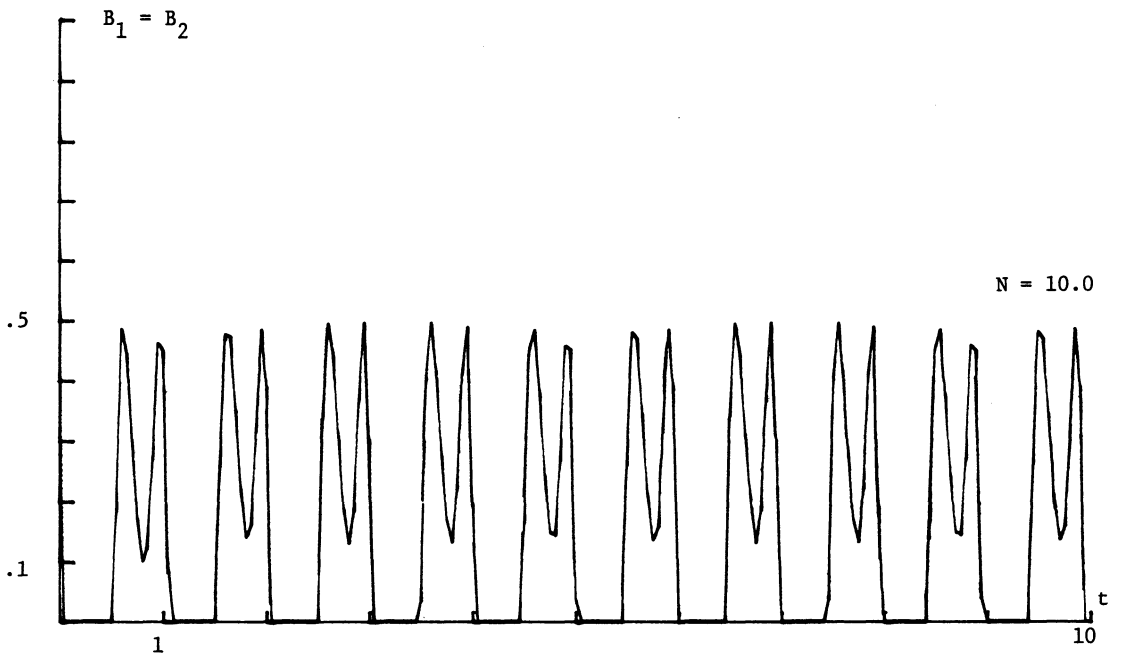
FIGURE 2

FIGURE 3

FIGURE 4

FIGURE 5

A connection to such difference equations can be made by formally passing $m \to +\infty$ in the model equations (in which case $w(a)$ in (4.4) becomes a Dirac function) which then reduce (with $n_1 = n_2 = N$ so that $B_1 \equiv B_2 \equiv B$) to the difference equation

$$B(t) = (A - N(1+\alpha^2)\exp(-\mu T)B(t-T))N\beta\exp(-\mu T)B(t-T).$$

If we let $t = jT$, $j = 0,1,2,\ldots$, $B_j := B(jT)$ and $d_1 := NA\beta\exp(-\mu T)$, $d_2 := N^2\mu(1+\alpha^2)\exp(-2\mu T)(1+\alpha^2)$ then we find that

$$B_{j+1} = B_j(d_1 - d_2 B_j) \ .$$

This is a well studied difference equation which is known to have rich and sometimes exotic dynamical behavior, including cascading period doubling periodicities and "chaos".

It would have been interesting to have found "chaotic" solutions for the integral equations (perhaps to be expected for large m and/or n_i), but as can be seen from FIGURES 4 and 5 the equations become quite "stiff", a fact which prevented us from carrying out further numerical solutions for larger $n_i = N$ or larger m.
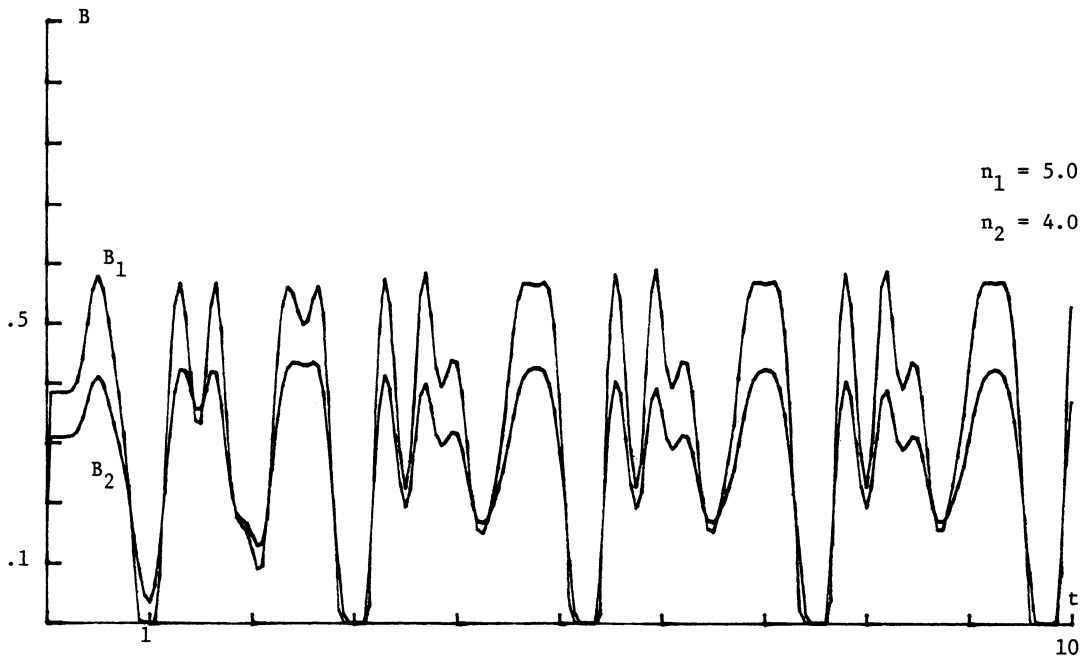

FIGURE 6

REFERENCES

[1] Christiansen, F. B. and Fenchel, T. M. (1977). Theories of Populations in Biological Communities, Ecol. Studies 20, Springer, Berlin.

[2] Cushing, J. M. and Saleem, M. (1982). A predator-prey model with age structure, J. Math. Biol. 14:231-250.

[3] Cushing, J. M. and Simmes, S. D. (1980). Bifurcation of asymptotically periodic solutions of Volterra integral equations, J. Integral Equations 4:339-361.

[4] Gopalsamy, K. (1982). Time lags and density dependence in age dependent two species competition, Bull. Aust. Math. Soc.

[5] Gurtin, M. E. and Levine, D. S. (1979). On predator-prey interactions with predation dependent on age of prey. Math. Biosci. 47:207-219.

[6] _____ (1982). On populations that cannibalize their young, SIAM J. Appl. Math. 42:94-108.

[7] Gurtin, M. E. and MacCamy, R. C. (1974). Non-linear age-dependent population dynamics, Arch. Rat. Mech. 3:281-300.

[8] _____ (1979). Population dynamics with age dependence, in Nonlinear Analysis and Mechanics, Heriot-Watt Symposium Vol. 3 (R. J. Knops, ed.), Pitman, London :1-35.

[9] _____ (1979). Some simple models for nonlinear age-dependent population dynamics, Math. Biosci. 43:199-211.

[10] Hastings, A. (1982). Age dependent predation is not a simple process, Proc. Autumn Course on Math. Ecology, Int. Centre for Theo. Physics, Trieste, Italy.

[11] Levine, D. S. (1982). Bifurcating periodic solutions for a class of age-structured predator-prey systems, preprint.

[12] _____ (1981). On the stability of a predator-prey system with egg-eating predators, Math. Biosci. 56:27-46.

[13] May, R. M. (1974). Stability and Complexity in Model Ecosytems, Monographs in Pop. Biol. 6, Princeton U. Press, Princeton, N. J.

[14] Miller, R. K. (1971). Nonlinear Volterra Integral Equations, W. A. Benjamin, Menlo Park, California.

[15] Saleem, M. (1982). Predator-prey relationships: egg eating predators, preprint.

[16] Thompson, R. W., DiBiasio, D. and Mendis, C. (1982). Predator-prey interactions: egg eating predators, Math. Biosci. 60:109-120.