STABILITY AND MATURATION PERIODS

IN AGE STRUCTURED POPULATIONS*

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I. INTRODUCTION

Any biological or physical mechanism which causes a delay in the growth rate response of a population to changes in its environment is generally considered to be a destabilizing agent. This is a widespread tenet in population biology and it finds theoretical support in a large variety of mathematical models which exhibit a loss of the stability of an equilibrium in the presence of a sufficiently large delay. There are, of course, a great many such delay causing mechanisms, but as pointed out by Ricklefs (1973) the primary ones are concerned with the fecundity of the population. Those specifically detailed by Slobodkin (1961) are gestation and maturation periods (taken together these are often referred to as the "generation time" needed to produce a new generation) and age-specific differentials in resource consumption. Many mathematical model equations in the literature which attempt

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to incorporate delays into the growth dynamics of a population
are very inadequately derived with regard to the exact mecha-
nism causing the delay and very often are inappropriate as far
as these specific, primary delay causing mechanisms are con-
cerned. A good example is the overworked delay-logistic equa-
tion which is certainly inappropriate for any of these parti-
cular delay causing mechanisms.

In a recent paper (Cushing (1980)) the relative effects
on stability and instability caused by delays due to gesta-
tion periods, maturation periods and age-specific resource
consumption as it affects age-specific per capita fecundity
were considered. It was argued there that the effects on the
stability of equilibria caused by these primary delay mecha-
nisms are in general substantially different and distinct.
While instability (and accompanying oscillations and even
"chaotic" behavior of population size) usually does occur
when these delays are sufficiently large...particularly in
the case of gestation period delays and certain types of age-
specific density or self-regulating effects on fecundity...
this was found not always to be the case. In particular,
maturation periods were often found not to be strong desta-
bilizing agents.

My main purpose here is to justify an even stronger state-
ment concerning maturation periods: for a broad class of
model equations, it is short maturation periods which are
destabilizing and longer ones which are stabilizing.

The model equations considered here are based on
McKendrick's equation for age-structured population (Hoppen-
steadt (1975)) under certain simplifying assumptions stated
in §2. Unlike the single equation models considered by

Cushing (1980), the model equations (4) considered below include an equation governing the growth of the population's resources (which are lumped into one resource function). In structure then, the model has the form of a predator-prey system in which the predator population is assumed to have a significant age structure and age-specific fecundity. It is first shown (Theorems 1 and 2) that there is a threshold value of the resource's inherent carrying capacity below which the population cannot survive and above which coexistence is possible (and is assured if the resource carrying capacity is near the threshold value). Then it is shown (Theorem 3) that a positive equilibrium exists and is unstable for short maturation periods. For long maturation periods the model has no positive equilibrium (Theorem 4). Formal proofs of theorems are given in V. A summary of the conclusions appears in VI.

II. THE MODEL EQUATIONS

Let $\rho = \rho(t,a)$ denote the density of (female) individuals of age a at time t and let $P(t) := \int_0^\infty \rho(t,a)\,da$ denote the total population size (of females). If $\mu \geq 0$ is the per capita death rate, taken here to be a constant independent of age and time, then $\rho_t + \rho_a + \mu\rho = 0$ for $a > 0$ and $-\infty < t < +\infty$ (McKendrick's equation) expresses the assumption that removal from the population is by death only. Additions to the population, assumed to occur by birth only, are governed by the equation

$$B(t) = \int_0^\infty f\, B(t-a)\exp(-\mu a)\,da \qquad (1)$$

for the total birth rate $B(t) := \rho(t,0)$ where f is a per

capita fecundity or fertility function which is assumed to be
a function of age a. The fecundity function f will also
be assumed to be a function of time t, not explicitly, but
by means of a dependence of f on the total population size
of both the population P and its resource R. Thus, we
write $f = f(x,P,R)$. Any gestation period has been ignored
(see Cushing (1979, 1980)) as have been initial conditions.

An equation to be satisfied by the total population size
$P(t)$ can be derived from McKendrick's equation and (1). It
is easy to see from McKendrick's equation that $P'(t) + \mu P(t)$
$= B(t)$ from which, together with (1), is obtained the inte-
grodifferential equation

$$P'(t) + P(t) = \int_0^\infty f(a,P,R)\{P'(t-a) + \mu P(t-a)\}exp(-\mu a)da.$$

Under the assumption that $f(a,P,R)$ is continuously differ-
entiable in a and is bounded for $a \geq 0$ and all values
of P,R and that $P(\tau)$ is bounded for all $\tau \leq t$, an
integration by parts yields

$$P'(t) + \mu P(t) = \int_0^\infty f_a(a,P,R)P(t-a)exp(-\mu a)da \qquad (2)$$

where the reasonable assumption that newborns have zero fecun-
dity, i.e, $f(0,P,R) \equiv 0$, has been made.

A more general equation for $P(t)$ when μ depends on t
(explicitly or through a dependence on P,R) and including
a gestation period can be derived in a similar way (see
Cushing (1979)).

Equation (2) constitutes the first equation in the model
to be studied here. To this equation will be added an equa-
tion for the dynamics of the resource's total population size
$R = R(t)$. One can also derive this equation in a similar

manner, but inasmuch as the resource will be assumed to have no significant age structure affecting its growth dynamics these details will be skipped. It will be assumed that the dynamics of the resource population is governed by the differential equation $R' = rR(1-R/K) - Rg(P)$ where $r > 0$ is the inherent growth rate of the resource population, $K > 0$ is its carrying capacity in the absence of the predator population P and $g(P)$ describes the effect of predation by P on the per capita growth rate of R. Assume $g(0) = 0$. This predation equation is general enough to encompass many if not most predation models found in the literature in which the resource (prey) is assumed to obey a logistic growth law in the absence of predators.

Finally it will be assumed that the fecundity function f has the form $f = b\beta(a)h(R)$ where $\beta(a)$ is a bounded, continuously differentiable function which satisfies the conditions

$$\beta(a) \geq 0, \quad \beta(0) = 0, \quad \int_0^\infty \beta(a)da = 1, \quad 0 < \int_0^\infty a\beta(a)da < +\infty. \quad (3)$$

The model equations to be studied are then

$$P'(t) + \mu P(t) = bh(R(t)) \int_0^\infty \beta'(a)P(t-s)exp(-\mu a)da$$

$$(4)$$

$$R' = rR(1 - \frac{R}{K}) - Rg(P).$$

The assumption on f implies, of course, that the fecundity of the population P is independent of its own population size. This assumption (termed "laissez faire interactive" for plant-herbivore systems by Caughley (1976)) is appropriate for predators, such as non-territorial ungulates, who do not interfere significantly with each other's search for food.

It is made here purely for mathematical simplicity. The analysis below can be carried out, at the expense of additional complicating details, for fecundity functions f which depend on P as well as R. The constant $b > 0$ will be called the <u>birth modulus</u> and the normalized function $\beta(a)$, which describes the age-specificity of fecundity, will be called the <u>maturation function</u>. It is this function which describes the nature of any maturation period for the individuals of population P. The function h describes the functional response of fecundity to changes in the resource population size R.

III. AN EXAMPLE

The following simple example illustrates and motivates the general results for (4) in IV and V below. Let $g(P) \equiv \gamma P$, $\gamma > 0$, and $h(R) \equiv R$ in (4). These linear predator-prey response functions are like those used in the classical Volterra-Lotka predator-prey equations (with density regulation) and suffer the same criticisms as are often made of this famous equation. As will be seen in V below, however, many of the important qualitative properties of this simple example are shared by the more general model equations (4).

The maturation function $\beta(a) \equiv T^{-2} a exp(-a/T)$ describes a population for which $T > 0$ is the age of maximum fecundity (the "maturation period"), but which has a rather broad "reproductive window" (i.e. fecundity is rather broadly distributed throughout age classes). With these choices of g, h and β, (4) has three equilibria (P_0, R_0): namely, $(0,0)$ $(0,K)$ and
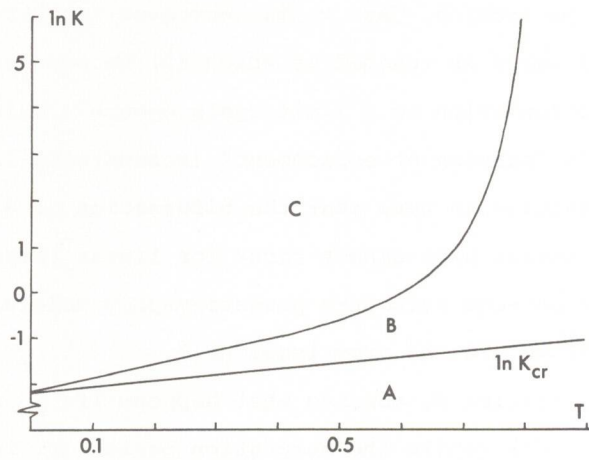
FIGURE 1

$$R_0 = (\mu T + 1)^2/b, \quad P_0 = r(K - R_0)/K\gamma . \tag{5}$$

It is easy to see that *(0,0)* is unstable. A linearized
(local) stability analysis of the two remaining equilibria as
it depends on the two parameters *K* and *T* yields a result
qualitatively the same as that shown in FIGURE 1 in which
μ = 1, *b = r = 10* and *γ = 1/10*. In region *A* the only
positive equilibrium is *(0,K)* and it is stable. In region
B equilibrium (5) is positive and stable while *(0,K)* is
unstable. Both of these positive equilibria are unstable
in *C*.

In FIGURE 1, if *T > 0* is fixed and *K* is increased
from *0*, one observes first a bifurcation of equilibria and
an exchange of stability when *K* passes through the critical
value $K_{cr} = (\mu T+1)^2/b$ as the equilibria *(0,K)* and (5)
intersect. This is a common feature of predator-prey models
and can be interpreted as a threshold phenomenon for the
prey's carrying capacity *K* above which coexistence is pos-
sible and below which the predator cannot be sustained and

and goes to extinction. As K is increased further a second critical value is reached at which (5) becomes unstable and a Hopf bifurcation to a limit cycle occurs. This is Rosenszweig's "paradox of enrichment" (Rosenszweig (1971)). (It is interesting to note that the bifurcation of a limit cycle as it occurs here cannot occur for linear response functions in non-age structure predatory-prey models, but requires a "hump" in the prey isocline.)

More interestingly, observe what happens if K is held fixed $(K > 1/10)$ while the maturation period T is changed in FIGURE 1. The same sequence of bifurcations occurs as described above for fixed T, but in this case for <u>decreasing</u> T. Stable coexistence is possible only for a finite interval of T values determined by the region B in FIGURE 1. In particular, <u>small</u> <u>maturation</u> <u>periods</u> T <u>yield</u> <u>instability</u>. T <u>must</u> <u>be</u> <u>large</u> <u>enough</u> (<u>but</u> <u>not</u> <u>too</u> <u>large</u>) <u>for</u> <u>the</u> <u>population</u> <u>to</u> <u>share</u> <u>a</u> <u>stable</u> <u>equilibrium</u> <u>with</u> <u>its</u> <u>resource</u>.

IV. EQUILIBRIA AND STABILITY

In this section a detailed study of the stability and instability of equilibria will be undertaken for the system (4). It will be shown that the basic features of the equilibrium stability diagram in FIGURE 1 are present for the more general case of system (4). The response functions are assumed throughout to satisfy the conditions

$$g,h \in C^1(R^+,R^+), \quad g(0) = h(0) = 0.$$

The death rate μ, the birth modulus b and the resource inherent growth rate r are fixed positive constants.

It is usually the case for equations of type (4) (i.e.

for predator-prey models which have a self-inhibitory term)
that there is a threshold value K_{cr} of the natural carrying
capacity K of the prey R below which the resource cannot
support the exploiting species P and above which coexistence
is possible. This phenomenon is examined in part (a) of this
section for the general system (4). In part (b) the stabili-
ty of positive equilibria is studied as a function of a
"maturation period" introduced below for the population P.

Note that (4) has at least two equilibria $(P(t),R(t))$
$= (P_0,R_0)$: namely $(0,0)$ and $(0,K)$. The trivial solution
$(0,0)$ is easily seen to be unstable. In order for (P_0,R_0)
to be positive equilibrium the equations

$$g(P_0) = r(1-R_0/K), \quad bh(R_0)\beta*(\mu) = 1 \tag{6}$$

must be satisfied.

(a) Consider now the equilibrium $(0,K)$ and linearize
(4) around this equilibrium by setting $x_1 = P$, $x_2 = R-K$ and
ignoring higher order terms:

$$x_1' = -\mu x_1 + bh(K)\int_0^\infty \beta'(a)x_1(t-a)exp(-\mu a)da,$$

$$x_2' = -Kg'(0)x_1 - rx_2 \ .$$

The asymptotic stability of this linear integrodifferential
system and hence the local asymptotic stability of the equili-
brium $(0,K)$ of (4) is determined by the complex roots z of
the characteristic equation $(z+r)(z+\mu)(1-bh(K)\beta*(z+\mu)) = 0$
where $\beta*(z)$ is the Laplace transform of β. If this equa-
tion has no roots z satisfying $Re\ z \geq 0$ then $(0,K)$ is
locally asymptotically stable whereas if $Re\ z > 0$ it is
unstable (Miller (1972), Cushing (1975)). Since $r,\mu > 0$ we

become concerned with the equation

$$\Delta(z,K) := 1 - bh(K)\beta^*(z+\mu) = 0. \tag{7}$$

Define the constant

$$N = N(K) := b\beta^*(\mu)h(K)$$

which biologically is the <u>net reproductive rate</u> (i.e. the
expected number of (female) offspring per female over her
lifespan) under the assumption that the resource population
is held constant at its inherent carrying capacity: $R(t) \equiv K$.
Since $|\beta^*(z+\mu)| \leq \beta^*(\mu)$ for $Re\ z \geq 0$ one easily gets the
following result.

THEOREM 1. *The equilibrium* $(0,K)$ *of (4)* *is locally*
asymptotically stable if the net reproductive rate $N(K)$ *is*
less than one.

The conclusion of this theorem is to be interpreted as
the inability of the population P to survive if its indivi-
duals cannot at least replace themselves when the resource
population is at its inherent carrying capacity.

In particular, $N(K) < 1$ holds when K is sufficiently
small since $h(0) = 0$ and hence $N(0) = 0$. Suppose now
that as K is increased from zero it reaches a critical
value K_{cr} at which the net reproductive rate equals one.
Specifically assume that

H1   *there exists a positive real* $K_{cr} > 0$
          such $N(K_{cr}) = 1$ *and* $h'(K_{cr}) > 0$.

The question is now: what happens for $K > K_{cr}$?

If $g'(0) > 0$ then (4) has a positive equilibrium given

by

$$P_0 = g^{-1}(r(1-K_{cr}/K)), \quad R_0 = K_{cr} \qquad (8)$$

for $K \gtrsim K_{cr}$. Note that for $K = K_{cr}$ this equilibrium coincides with the equilibrium $(0,K)$ and thus there occurs a bifurcation of equilibria as K increases through K_{cr}. The next theorem states that an exchange of stability takes place between these equilibria.

THEOREM 2. *Assume* H1 *holds. For* $K \gtrsim K_{cr}$ *the equilibrium* $(0,K)$ *is unstable. If* $g'(0) > 0$ *then for* $K \gtrsim K_{cr}$ *the positive equilibrium* (8) *is locally asymptotically stable.*

The conclusion to be drawn from these two theorems is that for populations whose growth dynamics are, together with that of their resource populations, described by the general system (4) there is a threshold phenomenon with respect to the survival of the population and the magnitide of the inherent carrying capacity of the resource population. As was seen in the example of section II it is possible that the stable coexistence of the population with its resource can be lost upon further increase of K (i.e. enrichment of the resource) and a second bifurcation to a limit cycle can occur. This phenomenon will not be studied here. Instead the stability and instability of a positive equilibrium will now be studied as it depends on the maturation function $\beta(a)$.

(<u>b</u>) Let $\beta_0(a)$ be a maturation function which satisfies the conditions in (3) and which has been chosen in such a way that age $a = 1$ is, by some suitable definition, the "maturation period". For example $\beta(a)$ might have a global maximum at $a = 1$ such as is the case with the frequently used func-

tions $(n^{n+1}/n!)a^n exp(-na)$, $n = 1,2,\ldots$. Or one could require that $\int_0^1 \beta(a)da = \int_1^\infty \beta(a)da$. In any case, maturation functions defined by

$$\beta(a) = \frac{1}{T} \beta_0(\frac{a}{T}), \quad T > 0 \tag{9}$$

whose maturation period is $a = T$ will be considered here.

Another way to define "maturation period" would be as the first moment of β. In this case one could take a normalized function $\beta_0(a)$ with first moment equal to one (in place of $\int_0^\infty \beta_0(a)da = 1$) and consider maturation functions $\beta(a) = (1/TL^2)\beta_0(a/TL)$, $L := \int_0^\infty \beta_0(a)da$, which then has first moment equal to T. Only the simpler case (9) will be considered here, although the analysis below can be carried out for this case as well.

Assume that

H2

> *there exists a positive solution* (P_0,R_0) $= (P_0^0,R_0^0)$ *of the equations* $bh(R_0) = 1$, $g(P_0) = r(1-R_0/K)$ *for which* $h'(R_0^0) > 0$, $g'(P_0^0) > 0$.

This assumption means that a positive equilibrium exists (as a solution of (6)) when $T = 0$. Then it is easy to see that (6) with $\beta^*(\mu) = \beta_0^*(\mu T)$ has a positive solution and hence (4) has a positive equilibrium $(P_0,R_0) = (P_0(T),R_0(T))$ for small $T > 0$ which is continuously differentiable in T and satisfies $(P_0(0),R_0(0)) = (P_0^0,R_0^0)$. The next theorem deals with the instability of this equilibrium for small T.

For technical reasons $\beta_0(a)$ is also assumed to have a Laplace transform which is analytic and nonzero for $Re\ z \geq -\delta$ for some constant $\delta > 0$.

THEOREM 3. Assume H2 *and that* $\beta_0(a)$ *is given by* (9).
Then for small T > 0 *the positive equilibrium* $(P_0(T), R_0(T))$
of (4) *is unstable.*

Consider now the case of large maturation periods T. As
$T \to +\infty$, $\beta^*(\mu) = \beta_0^*(\mu T) \to 0$. Thus from the second equation
in (6) either $R_0(T) > 0$ fails to exist for large T or
$R_0 \to +\infty$ as $T \to +\infty$. In the latter case, however, a positive
solution P_0 of the first equation in (6) fails to exist for
large T.

THEOREM 4. If $\beta(a)$ *is given by* (9) *then the system* (4)
has no positive equilibrium for large T.

The four theorems above establish for the general system
(4) the essential features of FIGURE 1 with regard to the
stability properties of equilibria and the parameters K and
T.

V. PROOFS

In this section proofs of Theorems 2 and 3 are given.

By H1 equation (7) has root $z = 0$ when $K = K_{cr}$, i.e.
$\Delta(0, K_{cr}) = 0$. Since $\Delta_z(0, K_{cr}) = bh(K_{cr}) \int_0^\infty a\beta(a)exp(-\mu a)da$
> 0, the implicit function theorem implies that (7) has a
roots $z = z(K)$, $z(K_{cr}) = 0$ for K close to K_{cr}. Now
$\Delta_K(0, K_{cr}) = -bh'(K_{cr})/\Delta_z(0, K_{cr}) < 0$ and an implicit differ-
entiation yields $z'(K_{cr}) = -\Delta_K(0, K_{cr})/\Delta_z(0, K_{cr}) > 0$ so that
$Re\ z(K) > 0$ for $K \gtrsim K_{cr}$. This proves the first conclusion
of Theorem 2.

The final conclusion of Theorem 2 will follow if the
characteristic equation associated with a positive equilibrium

(P_0, R_0) of system (4), which turns out to be the equation

$$D(z, K) := (z + \frac{rR_0}{K})(z + \mu)(1 - \frac{\beta^*(z+\mu)}{\beta^*(\mu)})$$

$$+ \mu b \beta^*(\mu) P_0 R_0 h'(R_0) g'(P_0) = 0, \tag{10}$$

has no roots satisfying $Re\ z \geq 0$ when $K \gtrsim K_{cr}$. This will be shown to be true by a contradiction argument.

Suppose that $D(z_n, K_n) = 0$ for $Re\ z_n \geq 0$ and $K_n > K_{cr}$, $K_n \to K_{cr}$. It is easy to see from the definition of D that since $D(z_n, K_n) = 0$ the sequence z_n must be bounded and hence, by extracting a subsequence if necessary, $z_n \to z_0$. Clearly $Re\ z_0 \geq 0$. From the continuity of $D(z, K)$ and the fact that $P_0 \to 0$ as $K \to K_{cr}$ it follows that $\beta^*(z_0+\mu) = \beta^*(\mu)$ (see (10)). But (3) then implies that $z_0 = 0$ and we have sequences z_n, K_n such that

$$z_n \to 0, \ Re\ z_n \geq 0, \ K_n > K_{cr}, \ K_n \to K_{cr}, \ D(z_n, K_n) = 0. \tag{11}$$

The proof will be completed by showing that (11) contradicts the implicit function theorem.

Since P_0 is a function of K, write $P_0 = P_0(K)$. Then $P_0(K_{cr}) = 0$. From $D(0, K_{cr}) = 0$ and

$$D_z(0, K_{cr}) = r\mu \int_0^\infty a\beta(a) e^{-\mu a} da / \beta^*(\mu) > 0,$$

$$D_K(0, K_{cr}) = \mu b \beta^*(\mu) P_0'(K_{cr}) K_{cr} h'(K_{cr}) g'(0)$$

one finds by the implicit function theorem that (10) has a <u>unique</u> root $z = z(K)$, $z(K_{cr}) = 0$, differentiable in K near K_{cr}. An implicit differentiation yields $z'(K_{cr}) = -D_K(0, K_{cr})/D_z(0, K_{cr})$ and hence $sign\ z'(K_{cr}) = -sign\ P_0'(K_{cr})$. From (8) $P_0'(K_{cr}) = r/K_{cr} g'(0) > 0$. Thus, $sign\ z'(K_{cr}) < 0$

and $Re \; z(K) < 0$ for $K \gtrsim K_{cr}$. Since this is the only root near $z = 0$, $K = K_{cr}$ a contradiction to (11) results. This completes the proof of Theorem 2.

To prove Theorem 3, first note that $\beta^*(z) = \beta_0^*(zT)$ and that the characteristic equation (10) can be written

$$(z + \frac{rR_0(T)}{K})(z+\mu)(1- \frac{\beta_0^*(zT+\mu T)}{\beta_0^*(\mu T)}) + C(T) = 0 \qquad (12)$$

where $C(T): = \mu b \beta_0^*(\mu T) P_0(T) R_0(T) h'(R_0(T)) g'(P_0(T))$. Let $z = \zeta/T^{1/3}$ and rewrite this equation as

$$\Omega(\zeta,T): = \zeta(\zeta + \frac{rT^{1/3}R_0(T)}{K})(\zeta + T^{1/3}\mu) H(\zeta,T) + \frac{C(T)}{\beta_0^*(\zeta T^{2/3}+\mu T)} = 0 \qquad (13)$$

$$H(\zeta,T): = \frac{\beta_0^*(\mu T) - \beta_0^*(\zeta T^{2/3} + \mu T)}{\zeta T^{2/3} \beta_0^*(\mu T) \beta_0^*(\zeta T^{2/3} + \mu T)} \; .$$

LEMMA 1. H(ζ,T) defined by (13) is continuous in ζ,T and continuously differentiable in ζ for Re ζ > 0 for small |T|.

Proof. Write $H(\zeta,T) = G(\zeta,T)/\beta_0^*(\mu T)\beta_0^*(\zeta T^{2/3}+ \mu T)$ where $G(\zeta,T): = [\beta_0^*(\mu T) - \beta_0^*(\zeta T^{2/3}+ \mu T)]/\zeta T^{2/3}$. Clearly the assumptions made on $\beta_0^*(z)$ in section IV imply that the expression $1/\beta_0^*(\mu T)\beta_0^*(\mu T^{2/3}+ \mu T)$ is continuous in ζ,T and continuously differentiable in ζ for $Re \; \zeta > 0$ and for small $|T|$. Consider

$$G(\zeta,T) = \int_0^\infty \beta_0(a) (\frac{1-exp(-a\zeta T^{2/3})}{\zeta T^{2/3}}) exp(-\mu Ta) da \; . \qquad (14)$$

Because the term in parentheses is bounded and continuous in ζ,T and continuously differentiable (in fact analytic) in ζ for $Re \; \zeta > 0$, small $|T|$ and each $a \geq 0$, standard theorems concerning functions defined by integrals imply the

result.

LEMMA 2. $H(\zeta,0) = m := \int_0^\infty a\beta_0(a)da$ *for* $Re\ \zeta > 0$.

Proof. By (3), $\beta_0^*(0) = 1$. This lemma follows from the dominated convergence theorem together with the easily seen fact that the term in parentheses under the integral in (14) approaches a as $T \to 0$ for any $Re\ \zeta > 0$.

LEMMA 3. $H_\zeta(\zeta,0) = 0$ *for* $Re\ \zeta > 0$.

Proof. Differentiation of (13) with respect to ζ yields

$$H_\zeta(\zeta,T) = -\frac{1}{\zeta} H(\zeta,T) - \frac{1}{\zeta} \frac{(d/dz)\beta_0^*(\zeta T^{2/3} + \mu T)}{[\beta_0^*(\zeta T^{2/3} + \mu T)]^2} \ .$$

Now $(d/dz)\beta_0^*(\zeta T^{2/3} + \mu T)\big|_{T=0} = -m$. Thus by Lemma 2, $H_\zeta(\zeta,0)$ $= -\frac{m}{\zeta} - \frac{1}{\zeta}(-m) = 0$.

By means of these lemmas, Theorem 3 will be established by showing that the characteristic equation (12) has roots in the right half plane for $|T|$ small.

By Lemma 1, $\Omega(\zeta,T)$ is continuous in ζ,T and continuously differentiable in ζ, $Re\ \zeta > 0$ for small $|T|$. Furthermore, by Lemma 2 follows $\Omega(\zeta,0) = \zeta^3 m + C(0)$ where $C(0)$ $= \mu b P_0^0 R_0^0 h'(R_0^0) g'(P_0^0) > 0$. Thus the equation $\Omega(\zeta,0) = 0$ has roots

$$\zeta_0 = (C(0)/m)^{1/3}(1 \pm i3^{1/2})/2$$

lying in the right half plane $Re\ \zeta > 0$.

To solve $\Omega(\zeta,T) = 0$ near $\zeta = \zeta_0$, $T = 0$ one can use an early form of the implicit function theorem due to Goursat (1903) which requires, for the existence of a continuous root $\zeta = \zeta(T)$, $\zeta(0) = \zeta_0$, the continuity of Ω in ζ,T, the

continuous differentiability of Ω only in ζ (not in T) and of course that $\Omega_\zeta(\zeta_0,0) \neq 0$. Since H2 and Lemma 1 guarantee these smoothness requirements, only the last inequality needs verification. From Lemma 3 one finds that $\Omega_\zeta(\zeta_0,0) = 3\zeta_0^2 m \neq 0$.

Theorem 3 is now proved, for it has been shown that the characteristic equation (12) has roots of the form $z = \zeta(T)/T^{1/3}$, $\zeta(T)$ continuous and $\zeta(0) = \zeta_0$, which lie in the right half plane $Re\ \zeta > 0$ for $|T|$ small.

VI. CONCLUSIONS

The model equations (4) offer a possible description of the growth dynamics of a population P and its resource R. It is assumed that the population has a constant death rate, but an age-specific fecundity which depends in a general way on the total population size of the resource R. For simplicity, it is also assumed here that members of the population do not significantly interfere with each other's search for the resource R. The resource population grows logistically in the absence of the population P, but in the presence of P has a general growth rate response function $g(P)$.

Under very weak restrictions on the response functions h,g two basic conclusions (which are examplified in FIGURE 1) are drawn concerning the possible coexistence of P and R. (Here coexistence is meant in the sense of the existence of a stable positive equilibrium of (4).) First, there is a threshold value of R's inherent carrying capacity below which P cannot survive and (slightly) above which coexistence occurs. This is a typical phenomenon for predator-prey models.

Secondly, and more interestingly and surprisingly, it is found that with regard to maturation periods coexistence is impossible for short maturation periods. This is in marked contrast to the usual tenet found frequently in the literature that an increase of a maturation period (or "generation time") will result in a destabilization and even oscillations in population sizes. Here the situation is exactly reversed: destabilization of the positive equilibrium occurs as the population's maturation period is <u>decreased</u>. It is also shown above that coexistence is impossible if the maturation period is too long, but this is because of the nonexistence of a positive equilibrium in this case. The phenomenon of destabilization of an equilibrium (and presumably the onset of oscillations and possibly eventually chaos, although these possibilities are not studied here) occurs for decreasing, not for increasing maturation periods in the general model (4) studied here.

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