

A Predator Prey Model with Age Structure

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Abstract. A general predator-prey model is considered in which the predator population is assumed to have an age structure which significantly affects its fecundity. The model equations are derived from the general McKendrick equations for age structured populations. The existence, stability and destabilization of equilibria are studied as they depend on the prey's natural carrying capacity and the maturation period m of the predator. The main result of the paper is that for a broad class of maturation functions positive equilibria are either unstable for small m or are destabilized as m decreases to zero. This is in contrast to the usual rule of thumb that increasing (not decreasing) delays in growth rate responses cause instabilities.

Key words: Predator-prey – Age structure – Stability

1. Introduction

The age-specific fecundity or fertility rate of a population is one of the most fundamental parameters in both the theory and practice of population dynamics and demography. The characteristics of the fecundity rate as a function of age have often been argued (both theoretically and experimentally) to be crucial determining factors in the resulting dynamical growth and age distribution of the population. In particular, the existence of an equilibrium (or stationary) age distribution, its stability properties and the occurrence of regular or even chaotic oscillations in population size all have been related to age-specific fecundity or to other parameters closely connected with it, such as maturation time, mean generation time, age of maximum fecundity or width of the “reproductive window” (e.g. see [4, 5, 12–14, 16, 17, 21, 26]). It has been generally asserted that if reproduction is sufficiently delayed because of age specificity in fecundity then the equilibrium population level is apt to be unstable and oscillations of some sort are likely to occur. This is usually based upon the generally held tenet in population biology that

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a time delay in the growth rate response to environmental changes (including changes in the population's own size) will, if long enough, lead to instabilities or at least to destabilization of equilibrium population levels.

There appears in the literature a great number of mathematical models which support this tenet. These invariably take the form of difference, differential-delay, integrodifferential or integral equations which exhibit the loss of stability of an equilibrium as some parameter measuring the "delay" is increased. Often a bifurcation or repeated bifurcations to limit cycles occur as well as other exotic behavior such as "chaos". Much has been written about these interesting phenomena in recent years even though the equations studied are very often inadequately derived and poorly related (or even irrelevant) to the delay causing mechanisms most frequently mentioned by population biologists, namely those related to age structure, fecundity and gestation periods (i.e. see [23]). Cases in point are the famous, overworked delay logistic (or Hutchinson's) equation and other similar delay equations of Kolmogorov type which, as can be seen from the fundamental McKendrick model equations for age structured populations [10, 11, 25], do not model growth dynamics in which growth rate response delays are caused by mechanisms related to age-specific fecundity or gestation periods. (The delay logistic equation was first introduced and studied by V. Volterra [24] in an attempt to study the case of a delay caused by an entirely different mechanism involving the death rate and the accumulation of toxins over past time.)

In an attempt to study the effects on model stability of several specific biological, delay causing mechanisms related to fecundity, Cushing [4] investigated many equations derived from the McKendrick model for age-structured populations. This study concentrated on the effects of maturation periods (or, more generally, of age related differentials in inherent fecundity), of gestation periods and of age related differentials in the effects of density changes on fecundity (see [23] for a biological discussion of these phenomena). One of the several conclusions reached in [4] was that maturation periods per se, while they can cause instabilities in certain circumstances (in particular in suitable combination with the last two mentioned mechanisms), are not in general strongly destabilizing agents of model equilibria.

The biological motivation for our investigations in the present paper lie in an attempt to understand further the effects on model stability of maturation periods in an age structured population and in particular to further justify the above stated conclusion from [4]. In fact, for the class of model equations considered here, our main result (Theorem 2) allows a stronger statement to be made: namely, in contrast to the generally held tenet mentioned above, destabilization of model equilibria occurs for *decreasing* and not increasing maturation periods.¹

The mathematical goal of this paper is to study the fundamental dynamics of a system of integrodifferential equations ((2.8) below). This system is derived from the McKendrick equations which describe the growth of an age-structured population. Unlike the single equations studied in [4] however, this model system

¹ Although examples of this phenomenon for delay differential equations have been found [3, 9] these have been purely mathematical exercises. Here we have tried to carefully relate our equations to the theory of population dynamics.

contains an equation which describes the growth of a (lumped) resource or prey population and as a result it has the form of a predator-prey system. The derivation of the equations (which is made in Section 2) is made under several basic biological assumptions with certain types of predator and prey populations in mind which we now describe. The more technical mathematical assumptions are stated in detail in the following sections.

To begin with, we assume that the populations of both the predator and its prey are closed to immigration and emigration and that they interact in a constant environment. Since we are primarily concerned here with (predator) populations which have age-specific differentials in reproductive output, we concentrate on age-specific, (predator) fecundity rates at the expense of ignoring age-differentials in the death rate. In particular, we are interested in maturation periods as a delay and instability causing mechanism, delays in death rate responses generally being considered of less importance [20, p. 488, 23]. This assumption that the predator's death rate μ is independent of age a (which is a common one in the literature [7, 8, 10, 16, 17]) is equivalent to the assumption that the survivorship curve is exponentially decreasing ($\exp(-\mu a)$). Survivorship curves are a fundamental tool of population biologists and appear abundantly throughout the literature for many different species (a sampling is given by Pianka [18, p. 101 – 102]). These curves, which are decreasing functions of age a , are roughly categorized by population biologists into three broad types, the so-called Type II being those which are in fact exponential. Type III curves result from species with high juvenile mortality followed by relatively lower mortality at later ages and can also, if not too extreme, be approximated by exponentials. Examples of species with such survivorship curves (and hence for which the assumption that μ is independent of age would seem to be reasonable) include the lizards *Uta stansburiana* and *Eumeces fasciatus*, the warthog and most birds for Type II and most insects and many fish, plants and marine invertebrates for Type III [18, 19].

We also ignore here any age structure in the prey population. That is to say, we assume that either the prey's vital parameters are not age-specific or that their dependence on prey age structure is insignificant as far as their effect on predator fecundity and death rates is concerned and is insignificant in comparison to the predator fecundity dependence on predator age structure. Examples of such predator-prey interactions might include predators which consume primarily inorganic nutrients or dead organic matter or those which graze or browse on plants (such as grasses) whose life cycle is so simple as to render age structure within them insignificant or whose life cycle is significantly longer (or shorter) than that of the predators.

Finally, we assume that the prey grows logistically in the absence of predation and that both the prey's growth rate response to predation and the predator fecundity rate are general functions of the total population sizes of both species. The predator's death rate μ , however, we assume to be constant and independent of these population sizes. This frequently made assumption in models is reasonable for species for which the scarcity of resources has a more profound impact on fecundity than on survivorship.

Under these basic assumptions, model equations governing the growth rates of the predator and prey populations are derived in Section 2. In Section 3 a simple

example is discussed. The two Figs. 1 and 2 in Section 3 serve not only to summarize the fundamental dynamical behavior of the example, but also serve to motivate the general results of the following Sections 4 and 5. In Section 4 the existence and stability of equilibria are studied as they depend on the prey's inherent carrying capacity K while in Section 5 they are studied as functions of the predator's maturation period m . The results (contained in Theorems 1 and 2) serve to establish the essential features of the stability region diagrams in the K, m parameter plane given in Figs. 1 and 2 for the prototype example of Section 3.

On the basis of these results we draw several conclusions concerning predator-prey interactions of the type described above, the most of important of which are as follows. First of all, as is the case with most predator-prey models, if the prey's inherent carrying capacity K is too small there exists no positive equilibrium and hence no possibility of stable coexistence of the two populations and the predator population dies out. "Too small" here means so small that the predator's net reproductive rate at low predator population levels (and hence prey population level near K) is less than one (Theorem 1b). However, if this net reproductive rate of the predators increases with increasing prey population levels (while the predation rate also increases with increasing predator population levels) and if there exists a (minimal) value of the prey's inherent carrying capacity K at which this net reproductive rate equals one, then stable coexistence and the survival of the predator population is possible (see Fig. 3). Under these circumstances, stable coexistence occurs if and only if the prey and predator isoclines bear a certain relationship to one another (see Figs. 4 and 5), a relationship which has the biological interpretation given at the end of Section 4.

Secondly, while holding the prey carrying capacity K fixed at a value for which a positive equilibrium exists, a sufficient decrease in the predator's maturation period m will either result in an unstable equilibrium or a destabilization of the equilibrium.

Thus, we conclude that a predator maturation period of sufficient length coupled with a prey inherent carrying capacity of sufficient size (but not too large) are the means by which predator and prey populations of the kind meeting the description above and modelled by equations (2.8) below can coexist in a stable manner.

Although we are claiming here that increased maturation periods do not lead to model instabilities (to the contrary), we hasten to point out that the opposite conclusion can be drawn under a different set of assumptions concerning the populations. We have assumed, for example, that fecundity is dependent on total population sizes. As was stressed in [4], the assumption concerning how population density affects fecundity is a very crucial one insofar as equilibrium stability is concerned and if fecundity dependence on population density is a more complicated one related to the age structure within the population then increased maturation periods can very well lead to instabilities (and even chaos). This is in fact the case, whether explicitly stated or not, in many model equations studied in the literature [4, 16, 17].

A summary of our results is given in Section 7, while mathematical proofs have been relegated to an Appendix.

2. The Model Equations

We will derive our model equations from the general theory of age structured populations essentially due to McKendrick [11] (also see [10, 25]). In this theory it is assumed that the population of reproducing individuals (here taken as the predator population) can be described by a *density function* $\rho(a, t)$ of *time* t and *age* a , measured on the same scale, whose integral $\int_{a_1}^{a_2} \rho(a, t) da$ yields the total population between ages a_1 and a_2 at time t . Thus, the *total population* (of predators) of all ages at time t is $P(t) = \int_0^\infty \rho(a, t) da$. If initial conditions are ignored, the McKendrick equations are

$$\rho_a + \rho_t = -\mu\rho, \quad a > 0, \tag{2.1}$$

$$\rho(0, t) = \int_0^\infty f(a, t)\rho(a, t) da \tag{2.2}$$

for $-\infty < t < +\infty$ where μ is the (per unit predator density) *death rate* and f is the (per unit predator density) *fecundity rate*.

The first order partial differential equation (2.1) accounts for removals from the predator population, which are assumed to be by death only. As discussed in Section 1, μ is taken to be a positive constant independent of a, t and ρ .

The Eq. (2.2) accounts for births into the predator population (which is assumed to be the only way to enter that population) by means of the age-specific fecundity rate function $f(a, t)$ which is assumed to be a function of time t only implicitly through a dependence on the total population size P of the predators and also that R of a *prey species*. Specifically, we assume that f has the form

$$f = b\beta(a)h(R, P).$$

The positive constant $b > 0$ is called the *birth modulus* and the function $\beta(a)$ is called the *maturation function*. The maturation function β clearly describes the effects of age on fecundity. It will be assumed to be continuously differentiable and bounded for $a \geq 0$ and to satisfy

$$\beta(a) \geq 0, \quad \beta(0) = 0, \quad \beta^*(\mu) := \int_0^\infty \beta(a)e^{-\mu a} da < +\infty. \tag{2.3}$$

The condition (2.3) implies that the *net reproductive rate at equilibrium*

$$\int_0^\infty f(a, t)e^{-\mu a} da = bh(R, P)\beta^*(\mu)$$

is finite. The function h , which will be referred to as the *fecundity response function*, is assumed to be twice continuously differentiable for $R, P \geq 0$ and to satisfy

$$h(R, P) \geq 0, \quad h(0, 0) = 0,$$

i.e. the nonnegative predator fecundity rate drops to zero when both populations disappear.

Before considering the dynamical equations for the resource population R , we will derive an integrodifferential equation for $P = P(t)$. Assume $\rho(+\infty, t) = 0$ for all t , i.e. that the density in age class a drops to zero as $a \rightarrow +\infty$. Integration of

(2.1) yields

$$\rho(a, t) = B(t - a)e^{-\mu a} \tag{2.4}$$

where $B(t) := \rho(0, t)$ which, when substituted into (2.2), yields

$$B(t) = \int_0^\infty f(a, t)B(t - a)e^{-\mu a} da. \tag{2.5}$$

On the other hand, an integration of (2.1) from $a = 0$ to $+\infty$ gives

$$P'(t) + \mu P(t) = B(t) \tag{2.6}$$

which, after substitution into (2.5) and an integration by parts, gives

$$P'(t) + \mu P(t) = \int_0^\infty f_a(a, t)P(t - a)e^{-\mu a} da. \tag{2.7}$$

A solution of (2.7) defines the density ρ by means of (2.6) and (2.4).

Similar equations could be derived for the prey population R . However, since our interest here lies in the case when the age structure of the resource is insignificant in comparison to that of the predator population P , we will avoid doing this by simply writing the differential equation

$$R' = rR \left(1 - \frac{R}{K} \right) - g(R, P)$$

for the growth rate of R where the *predation response function* g is assumed to be twice continuously differentiable for $R, P \geq 0$ and satisfy

$$g(R, P) \geq 0, \quad g(R, 0) \equiv 0$$

(which implies that predation drops to zero in the absence of predators). This equation is sufficiently general to include the prey equation in most predator-prey equations in the literature under the assumption that in the absence of predation by P the resource R grows logistically. The positive constants $r, K > 0$ are the prey's *inherent growth rate* and *natural carrying capacity* respectively.

Thus, the equations to be considered in this paper are

$$P'(t) + \mu P(t) = bh(R(t), P(t)) \int_0^\infty \beta'(a)P(t - a)e^{-\mu a} da,$$

$$R'(t) = rR(t) \left(1 - \frac{R(t)}{K} \right) - g(R(t), P(t)), \tag{2.8}$$

where the above stated conditions on the constants and functions are assumed in force throughout.

We will be interested exclusively in the existence and the stability or instability of nonnegative equilibria solutions $(R(t), P(t)) = (R, P) = \text{constant} \geq 0$ of (2.8). A nonnegative equilibrium must satisfy the equations

$$(bh(R, P)\beta^*(\mu) - 1)P = 0,$$

$$rR \left(1 - \frac{R}{K} \right) - g(R, P) = 0, \tag{2.9}$$

for which there are at least two nonnegative solutions $(R, P) = (0, 0)$ and $(K, 0)$. Positive equilibria lie at the intersection in the R, P plane of the *prey isocline* defined by the second equation and the *predator pseudo-isocline* defined by $bh(R, P)\beta^*(\mu) = 1$. This predator pseudo-isocline defines equilibrium population levels at which the net reproductive rate is equal to one (exact replacement) and is not a true isocline in that it implies zero growth rate only for populations held at equilibrium.

By the *stability* of an equilibrium will be meant the usual (local) asymptotic stability in the theory of integro-differential equations (see e.g. [1, 15]). Necessary and sufficient for this stability is that the characteristic equation of the linearization at equilibrium have no complex roots z which satisfy $\text{Re } z \geq 0$. If (R, P) is an equilibrium of (2.8) then the characteristic equation turns out to be

$$D := \left(z - r + 2r \frac{R}{K} + g_R(R, P) \right) [(z + \mu)(1 - bh(R, P)\beta^*(z + \mu)) - b\beta^*(\mu)\mu P h_P(R, P)] + b\beta^*(\mu)\mu P g_P(R, P) h_R(R, P) = 0, \tag{2.10}$$

where $\beta^*(z) := \int_0^\infty e^{-za} \beta(a) da$ is the Laplace transform of β . If (2.10) has at least one root z with $\text{Re } z > 0$ then (R, P) is unstable.

We wish also to consider the *destabilization* of a stable equilibrium of (2.8). By this we mean that as some parameter in the system approaches a limiting value there is at least one root of (2.10) whose distance from the imaginary axis $\text{Re } z = 0$ tends to zero. This means, of course, that the rate of convergence to the equilibrium as measured by the real part of the smallest (in magnitude) root of (2.10) tends to zero as the parameter approaches its limit.

3. An Example

As a motivating example consider (2.8) with $r = b = 1$ and

$$\beta(a) = \left(\mu + \frac{1}{m} \right)^2 a e^{-a/m}, \quad h = R(cP + 1), \quad g = RP, \tag{3.1}$$

where $m > 0$ and c are constants. This choice of the maturation function β implies that fecundity peaks at age $a = m$ (although it is rather broadly distributed around $a = m$) which might be taken as a measure of a biological maturation period. For simplicity β has been normalized so that $b\beta^*(\mu) = 1$ for $m > 0$, i.e. the net reproductive rate at equilibrium of the predator equals $h(R, P)$ and is independent of m . These particular choices of the fecundity and predation response functions h and g are of “mass action” type familiar in Lotka-Volterra theory and as a result suffer the many often repeated shortcomings of such models. Nonetheless, as the general results in the following sections show, many of the interesting and fundamental features of this simple example are present for very general h, g and β in (2.8).

The trivial equilibrium $(R, P) = (0, 0)$ is unstable since the characteristic equation (2.10) is a quadratic with roots $z = 1$ and $-\mu$. The characteristic equation (2.10) for the equilibrium $(R, P) = (K, 0)$ has four roots $z = -1, -\mu$ and $(-1 \pm \sqrt{K})(\mu m + 1)/m$ and hence $(K, 0)$ is stable if and only if $K < K_{cr} := 1$.

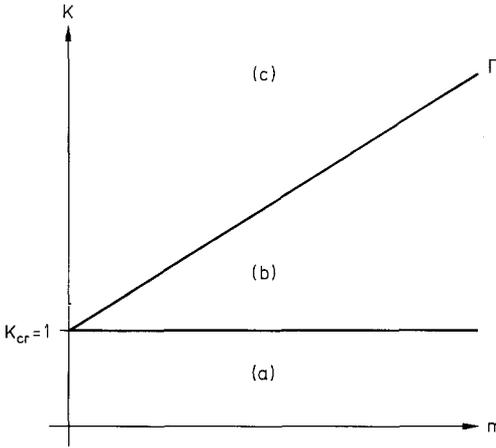


Fig. 1. Stability regions for nontrivial equilibria of (2.8) with (3.1) and $r = b = 1, c = \frac{1}{2}$ and $\mu \approx 0$ are shown. In region (a) no positive equilibria exist and $(R, P) = (K, 0)$ is stable. In (b) and (c), $(K, 0)$ is unstable and there exists a unique positive equilibrium which is stable in (b) and unstable in (c)

From the equilibrium equations (2.9) one finds that a unique positive equilibrium exists if and only if $K > K_{cr}$. If $K < K_{cr}$ then there exists a positive equilibrium if and only if $c > 1$ in which case there are exactly two. These positive equilibria are given by $R = 1/(cP + 1)$ and $P = P^+$ or P^- , P^\pm being roots of the quadratic

$$cKP^2 + K(1 - c)P + 1 - K = 0.$$

To study the stability properties of these positive equilibria we turn to the characteristic equation (2.10), the left-hand side of which is a rational function of z whose numerator is a quartic polynomial in z . The location of the roots can be determined by the Hurwitz criteria. These criteria, however, turn out to be rather formidable inequalities involving m, K and μ . They can be greatly simplified by setting $\mu = 0$, the resulting stability and instability criteria remaining valid for $\mu \approx 0$. When $\mu = 0$, one finds that a positive equilibrium is stable if and only if

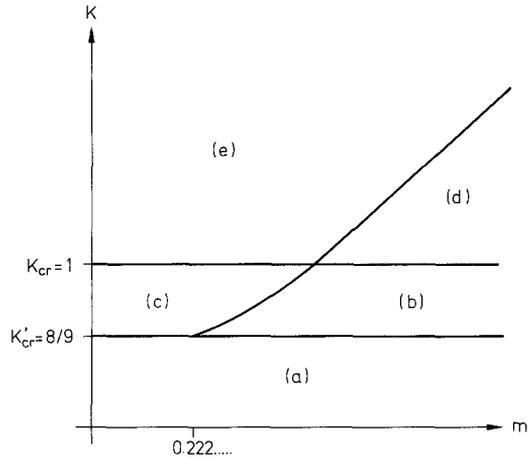
$$P < 1, \quad 2(cP^2 + 1)m > Pc, \quad 2cP + (1 - c) > 0, \\ (1 - P)(2cP^2 + (c - 1)P + 4)m > 2P(cP + 1).$$

It is not our intent here to study this example or these inequalities in depth. Observe, however, that P is a function of K and hence these inequalities determine certain regions in the first quadrant of the m, K parameter plane. These regions are drawn for two cases $c = \frac{1}{2}$ and $c = 2$ in Figs. 1 and 2 which serve to motivate the general results in the following sections. The case $c = 0$, for which a diagram similar to that in Fig. 1 results, was given by Cushing [5].

There are several key features in Figs. 1 and 2 relative to the general considerations in following sections. First, in Fig. 1 note that if the carrying capacity $K > K_{cr}$ is held fixed one finds that *the positive equilibrium is unstable for small m* . Thus, stable coexistence is possible only for sufficiently large maturation periods m . Note that both the equilibrium and the net reproductive rate at equilibrium remain constant as m is varied in this example.

Secondly, for fixed maturation period m , Fig. 1 shows that stable coexistence is impossible until a threshold value $K_{cr} = 1$ of the prey's natural carrying capacity K

Fig. 2. Stability regions for the same parameter values in Fig. 1, except that $c = 2$, are shown. Region (a) is as in Fig. 1. In regions (c) and (b) there exist two positive equilibria (R, P^\pm) , both of which are unstable in (c) and only one of which (R, P^-) is stable in (b). In regions (d) and (e) there is only one positive equilibrium (R, P^+) which is stable in (d) and unstable in (e). The equilibrium $(K, 0)$ is stable in (b) and (c) and is unstable in (d) and (e)



is surpassed (there is a supercritical bifurcation of equilibria and an exchange of stability at $K = K_{cr}$), but the stable equilibrium loses its stability at a second critical value of K determined by the curve Γ (at which point a Hopf bifurcation to a limit cycle occurs). These features are typical of predator-prey models. The destabilization of the positive equilibrium with increasing K is referred to as the “paradox of enrichment” (Rosenzweig [22], Cushing [2]).

A slightly more complicated situation occurs for $c = 2$ as can be seen in Fig. 2. The remarks concerning varying m still remain valid. On the other hand, the bifurcation at $K = K_{cr} = 1$ is now subcritical and unstable. For m sufficiently large ($m > 0.222\dots$) there is still a threshold value $K'_{cr} = \frac{8}{9}$ of K above which stable coexistence is possible, but this is due to the existence in this example of a stable equilibrium (with large P) which does not bifurcate from $(K_{cr}, 0)$.

4. Critical Carrying Capacity

The purpose of this section is to study the existence and stability of equilibria for predator-prey interactions modelled by (2.8) as they depend on the inherent prey carrying capacity K . It will be shown that the alternatives near $K = K_{cr} = 1$ in Figs. 1 and 2 for the prototype example in Section 3 hold for the more general system (2.8). We will also determine those properties of the predation response function g and the fecundity response function h which differentiate between these two alternatives, that is to say between the case of a stable bifurcation (to the “right” as K increases through a critical value K_{cr}) of a stable positive equilibrium as in Fig. 1 and an unstable bifurcation (to the “left” as K decreases through K_{cr}) of an unstable positive equilibrium as in Fig. 2.

It will be assumed throughout this section that

$$g_R(K, 0) \geq 0 \quad \text{for all} \quad K \geq 0. \tag{4.1}$$

This assumption means roughly that for small predator population sizes the predation rate does not decrease with increasing prey populations near carrying capacity.

First of all, the characteristic equation (2.10) associated with the trivial equilibrium $(0, 0)$ has roots $z = -\mu$ and $r - g_R(0, 0)$ so that $(0, 0)$ is stable if and only if $r < g_R(0, 0)$. Thus, small populations of both predator and prey die out if the inherent (per unit) prey growth rate is less than the (per unit) predation rate.

Turning now to the equilibrium $(K, 0)$, $K > 0$ we find that (2.10) has as roots the negative reals $z = -\mu$ and $-r - g_R(K, 0)$ as well as all the roots of the equation

$$bh(K, 0)\beta^*(z + \mu) - 1 = 0. \quad (4.2)$$

Since $|b\beta^*(z + \mu)| \leq b\beta^*(\mu)$ for $\operatorname{Re} z \geq 0$ by (2.3), we see immediately that (4.2) has no roots with $\operatorname{Re} z \geq 0$ if $bh(K, 0)\beta^*(\mu) < 1$, i.e. the net reproductive rate of predators at low population levels is less than one for prey population level near carrying capacity. In this case, which certainly occurs for small K since $h(0, 0) = 0$, the equilibrium $(K, 0)$ is stable and in this sense the population P cannot survive (at least small populations cannot) and the prey population returns to its natural carrying capacity K .

Suppose now that there exists a critical value of $K = K_{cr}$ for which the net reproductive rate of predators is equal to one. Specifically, suppose

$$bh(K_{cr}, 0)\beta^*(\mu) = 1, \quad h_R(K_{cr}, 0) \neq 0. \quad (4.3)$$

The question to be answered is what happens for K near K_{cr} ? The following theorem whose proof appears in the Appendix answers this question and summarizes the results of this section.

Theorem 1. *Assume (4.1).*

(a) *The trivial equilibrium $(0, 0)$ is stable if and only if $r < g_R(0, 0)$. That is to say, small populations of both predator and prey die out if the (per unit) inherent prey growth rate is less than the (per unit) predation rate.*

(b) *If $bh(K, 0)\beta^*(\mu) < 1$, then the equilibrium $(R, P) = (K, 0)$ is stable. That is to say, if the predator net reproductive rate at low population levels is less than one (exact replacement), small populations of predators will die out while the prey population tends to its carrying capacity K .*

Assume that there exists a critical value of the prey inherent carrying capacity $K = K_{cr}$ for which the predator net reproductive rate equals one, i.e. for which (4.3) holds.

(c) *The equilibrium $(R, P) = (K, 0)$, for $K \approx K_{cr}$ is stable when $K < K_{cr}$ ($> K_{cr}$) and unstable for $K > K_{cr}$ ($< K_{cr}$) provided $h_R(K_{cr}, 0) > 0$ (< 0), i.e. provided predator fecundity at low population levels increases (decreases) with increasing prey population levels.*

Assume that

$$J_{cr} := b\beta^*(\mu) \det \begin{pmatrix} h_R(K_{cr}, 0) & h_P(K_{cr}, 0) \\ -r - g_R(K_{cr}, 0) & -g_P(K_{cr}, 0) \end{pmatrix} \neq 0.$$

(d) *There exists a unique equilibrium $(R(K), P(K))$, continuous for K near K_{cr} and satisfying $(R(K_{cr}), P(K_{cr})) = (K_{cr}, 0)$, which is positive for $K > K_{cr}$ ($< K_{cr}$) provided $h_R(K_{cr}, 0)/J_{cr} < 0$ (> 0).*

(e) *This positive equilibrium is stable and the predator and prey populations can stably coexist if $J_{cr} < 0$ and it is unstable if $J_{cr} > 0$.*

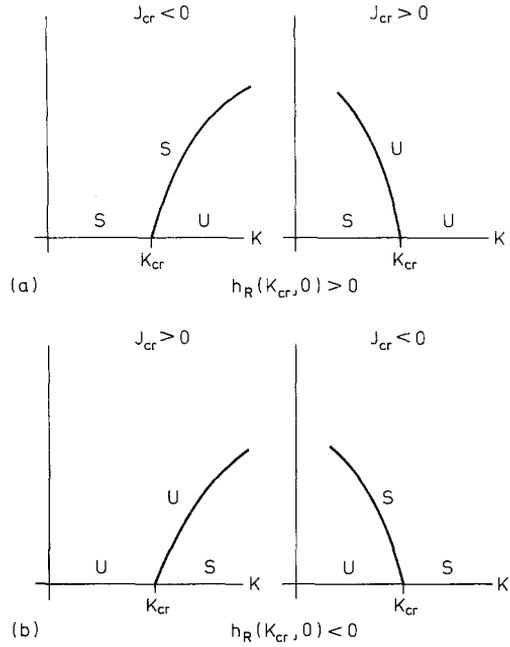


Fig. 3. The distance of the positive, nontrivial equilibria of Theorem 1 from the equilibrium $(K, 0)$ is plotted against the prey carrying capacity K . The horizontal K axis represents $(K, 0)$. An s indicates stability while a u indicates instability

This long list of statements is pictorially summarized by the bifurcation diagrams in Fig. 3.

Since $h(0, 0) = 0$, it follows that if K_{cr} is taken to be the *first* value of K for which the net reproductive rate equals one ($bh(K_{cr}, 0)\beta^*(\mu) = 1$) then it follows that $h_R(K_{cr}, 0) \geq 0$. If we assume that $h_R(K_{cr}, 0) > 0$, then for this first critical value the alternatives in Fig. 3(a) hold. These correspond exactly to the situation near $K_{cr} = 1$ (for fixed m) in Figs. 1 and 2 respectively of the example in Section 3. Notice that it is the sign of the Jacobian J_{cr} which distinguishes between the two alternatives.

The possibility of stable coexistence of the predator and prey populations (of interest here because it implies the survival of the predator) is implied by the existence and stability of a positive equilibrium. Theorem 1(e) shows that this stability is, for prey carrying capacities near criticality where the predator has a net reproductive rate of one, equivalent to the analytical condition $J_{cr} < 0$. We close this section with a discussion of the biological and the phase plane geometrical meaning of this sign condition on the Jacobian J_{cr} . From (2.9) the equations for a positive equilibrium are

$$\begin{aligned} bh(R, P)\beta^*(\mu) - 1 &= 0, \\ rR\left(1 - \frac{R}{K}\right) - g(R, P) &= 0, \end{aligned} \tag{4.4}$$

the Jacobian of whose left-hand side is

$$J := b\beta^*(\mu) \det \begin{pmatrix} h_R & h_P \\ r - 2r\frac{R}{K} - g_R & -g_P \end{pmatrix}.$$

Let $G := dR/dt/R$ denote the *per capita growth rate of the prey* R and note that

$$J = b\beta^*(\mu)R \det \begin{pmatrix} h_R & h_P \\ G_R & G_P \end{pmatrix}.$$

Then J_{cr} equals J evaluated at $K = K_{cr}$ and $(R, P) = (K_{cr}, 0)$.

Let \mathbf{i}, \mathbf{j} denote unit co-ordinate vectors in the (R, P) plane and let \mathbf{k} be a mutually perpendicular unit vector so that \mathbf{i}, \mathbf{j} and \mathbf{k} form a right-handed Cartesian co-ordinate system. Then $J/b\beta^*(\mu)R$ is the \mathbf{k} component of the curl of the vector field (h, G) , that is

$$J = b\beta^*(\mu)R(\nabla h \times \nabla G) \cdot \mathbf{k} \tag{4.5}$$

and $\text{sign } J_{cr} = \text{sign}(\nabla h \times \nabla G)_{cr} \cdot \mathbf{k}$. Suppose $\nabla h(K_{cr}, 0)$ is rotated to $\nabla G(K_{cr}, 0)$ (through the smallest angle between them). *The stability condition $J_{cr} < 0$ is equivalent to this rotation being clockwise.*

The gradients ∇G and ∇h are normal to the prey isocline and the predator pseudo-isocline respectively and point in the direction in the (R, P) plane of maximum increase in prey per unit growth rate and in predator net reproductive rate (or equivalently predator fecundity rate) respectively.

We will now give a biological interpretation of this rotation condition for the case of the smallest critical value K_{cr} and $h_R(K_{cr}, 0) > 0$ (see Fig. 3a) in which case $\nabla h(K_{cr}, 0)$ lies in the right half plane. Now the condition (4.1) implies that $\nabla G(K_{cr}, 0)$ lies in the left half plane. Under the added reasonable assumption that $G_P(K_{cr}, 0) < 0$ (or equivalently $g_P(K_{cr}, 0) > 0$), the gradient ∇G lies in the third

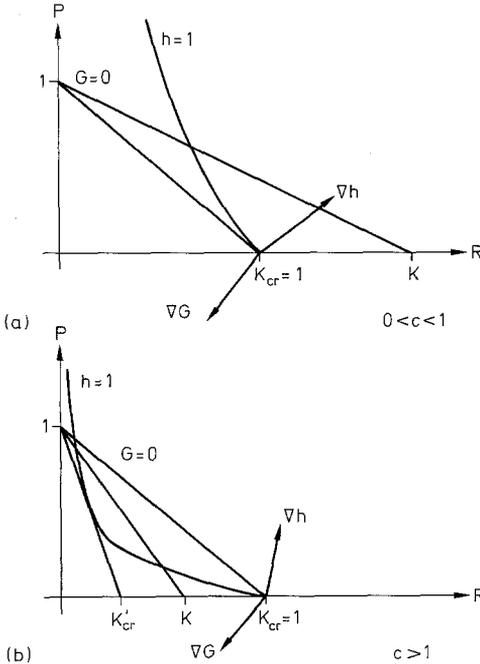


Fig. 4. The isocline $h = 1$ is drawn for (a) $0 < c < 1$ and (b) $c > 1$ for the example of Section 3 as illustrated in Figs. 1 and 2. Several isoclines $G = 0$ are drawn for K values for which positive equilibria exist. In (a) the rotation of ∇h to ∇G is clockwise and the positive equilibrium is stable. The rotation is counterclockwise in (b) and the positive equilibrium is unstable. These correspond to the two cases in Fig. 3a

quadrant. Thus, if prey per unit growth decreases with increased predator population sizes (or equivalently if the predation rate increases with increased predator population sizes), then the clockwise rotation stability condition stated above can be given the following biological interpretation near the smallest critical value K_{cr} : stable coexistence near $(R, P) = (K_{cr}, 0)$ occurs if and only if for a unit increase in the prey population the amount of change in predator necessary to attain maximal increase in predator net reproductive rate is less than the amount of change in predator necessary to attain maximal decrease in prey per capita growth rate.

The example in Section 3 illustrates these results. The isoclines and gradients are drawn for this example in Fig. 4.

5. Maturation Periods

We now turn to the main results of the paper. These results will concern the stability properties of positive equilibria for small maturation periods. The notion of a “maturation period” is, in the theory and model equations of Section 2, necessarily contained in the maturation function $\beta(a)$ which serves to describe the dependence of fecundity on age. In order to introduce a parameter which represents a maturation period we do the following. Without attempting to define “maturation period” per se, we simply assume that an arbitrary maturation function $\beta_0(a)$ is given which satisfies the conditions

$$m_0 := \int_0^\infty \beta_0(a) da < +\infty, \quad m_1 := \int_0^\infty a\beta_0(a) da < +\infty$$

and which has, by some suitable definition of maturation period, a maturation period equal to one. Our results deal with system (2.8) with maturation functions of the form

$$\beta(a) = n(m)m^{-1}\beta_0(am^{-1}) \tag{5.1}$$

for which $m > 0$ is now the maturation period. The constant $n(m)$ is assumed independent of R and P and to satisfy

$$n(m) \rightarrow n_0 \quad \text{as} \quad m \downarrow 0, \quad \text{where} \quad 0 < n_0 < +\infty. \tag{5.2}$$

Condition (5.2) guarantees that the net reproductive rate at equilibrium $bh\beta^*(\mu) = bh n(m)\beta_0^*(\mu m)$ approaches a finite, nonzero limit $bh n_0 m_0$ as $m > 0$ decreases to zero.

The restriction of β to the class of maturation functions described by (5.1) is equivalent to the biological assumption that the ratio $\rho = \rho(m)$ of per unit offspring from age class a to $a + da$ when the maturation period equals m to that from age class a/m to $(a + da)/m$ when the maturation period equals one is independent of a . For a justification of this, see the Appendix below.

In order to study the question of stable coexistence for small predator maturation periods we first assume that a positive equilibrium exists for small m (for if none did, the question would be meaningless). Sufficient for this is the assumption that the equations

$$b n_0 m_0 h(R, P) - 1 = 0, \quad rR \left(1 - \frac{R}{K} \right) - g(R, P) = 0 \tag{5.3}$$

have a positive solution $(R^0, P^0) > 0$ and that the equilibrium equations

$$bn(m)\beta_0^*(\mu m)h(R, P) - 1 = 0, \quad rR\left(1 - \frac{R}{K}\right) - g(R, P) = 0, \quad (5.4)$$

which reduce to (5.3) when $m = 0$, have a smooth solution $(R(m), P(m))$ for $m \approx 0$ such that $(R(0), P(0)) = (R^0, P^0)$. This is guaranteed if the Jacobian J , given in Section 4, evaluated at (R^0, P^0) is nonzero. We denote this equilibrium by $(R, P) = (R(m), P(m))$. Our main result is contained in the following theorem.

Theorem 2. *The positive equilibrium $(R, P) = (R(m), P(m))$ corresponding to a maturation function β given by (5.1) is either unstable for small $m > 0$ or destabilized as $m > 0$ decreases to zero.*

This result implies that in order for a predator-prey interaction of the type being considered here to have a stable positive equilibrium, it is necessary for the predator’s maturation period to be sufficiently long.

We note in passing that one particular class of maturation functions consists of those with $n(m) = 1$ for which $\int_0^\infty \beta(a) da = 1$ for all m . This normalization implies in the biological characterization above that the ratio $\rho(m) \equiv 1$. It is a frequently used one and is satisfied by the often used functions $\beta(a) = (n/m)^{n+1} a^n e^{-na/m}$, $n = 1, 2, 3, \dots$. Another class is given by $n(m) = 1/b\beta_0^*(\mu m)$ which implies that the net reproductive rate at equilibrium of the predator is $h(R, P)$ which is thus independent of the maturation period m . This normalization, which is used in Section 3, has the simplifying feature that the equilibrium equations (5.4) and hence the equilibria themselves are independent of the maturation period m .

If the first alternative in Theorem 2 holds and the equilibrium becomes unstable, then it can happen that a Hopf bifurcation to a stable limit cycle occurs as m decreases through a positive critical value. This is the reverse of the usual case when a Hopf bifurcation occurs for a “delay” which increases through a critical value. We will not study this bifurcation phenomenon here, but we will offer some conditions sufficient to guarantee that the first alternative of Theorem 2 does in fact hold.

Theorem 3. *The positive equilibrium $(R(m), P(m))$ is unstable for small $m > 0$ if any one of the following conditions on the predator’s fecundity response function is satisfied:*

- (a) $h_P(R^0, P^0) > 0$;
- (b) $h_P(R^0, P^0) = 0$ and $h_R(R^0, P^0)g_P(R^0, P^0) \neq 0$;
- (c) $h_P(R^0, P^0) < 0$ and $J_0 > 0$.

In this theorem J_0 denotes the Jacobian J evaluated at the equilibrium (R^0, P^0) . It has the same interpretation as in Section 4 and is given by (4.5).

The special case when h is independent of P was considered by Cushing [5] with $n(m) \equiv 1$. His results are a special case of Theorem 3(b).

We can apply Theorems 2 and 3 to the specific example in Section 3 by way of illustration. In this example the positive equilibrium is independent of m . Since $h_P = cR$ in this example, Theorem 3(a) shows that the positive equilibrium is unstable for small $m > 0$. Since $h_R g_P = (cP + 1)R = R$ for $c = 0$, Theorem 3(b) implies the same conclusion when $c = 0$. Finally, if $c < 0$ the isoclines appear as in

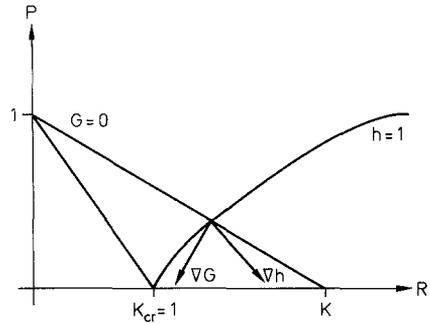


Fig. 5. The isoclines for the example in Section 3 are drawn, as in Fig. 4, but here for $c < 0$

Fig. 5. Since J is given by (4.5) and the rotation of ∇h to ∇G is clockwise it follows that $J < 0$ for $c < 0$. Thus, Theorem 3(c) does not apply when $c < 0$, but Theorem 2 does imply in this case that the positive equilibrium at least destabilizes for m decreasing to zero.

6. Remarks on Maturation Periods

In Section 5 no attempt was made to define a “maturation period”. For the example of Section 3 the parameter m appearing in β defined by (3.1), which was referred to as the “maturation period”, is actually the age at which the fecundity rate is maximum (for fixed population sizes). While this seems to be not necessarily a good definition of what most would consider to be meant by “maturation period”, it nonetheless provides a reasonable measure of the delay in growth rate response to population changes which is caused by age differentials in fecundity. Other measures of this delay (e.g. the first moment of β) could just as well be used.

If one wished to consider the “maturation period” to be the youngest age at which an individual in the population P could reproduce, then one might consider a maturation function β satisfying $\beta(a) \equiv 0$ for $0 \leq a \leq m$ where $m \geq 0$ is now defined to be the “maturation period”. If β is continuously differentiable for $a \geq 0$, then the results of the previous sections of course apply.

On the other hand, it is frequently the case in models involving age specific fecundity that β is taken to have jump discontinuities, in particular at $a = m$. One general form of maturation function with jump discontinuities for which our results above still apply is (5.1) with

$$\beta_0(a) = [u(a) - u(a - \tau)]\gamma(a), \quad 1 < \tau \leq + \infty, \quad (6.1)$$

where $u(a)$ is the unit step function at $a = 1$. The function $\gamma(a)$ is nonnegative and continuously differentiable for $1 \leq a \leq \tau$. In the maturation function $\beta(a)$ given by (5.1) the constant τ is the ratio of the maximal age τm of fecundity to the maturation period m .

The simple and frequently used “block” function is the special case when $\gamma \equiv \text{constant}$.

In the model equations of Section 2 the effect of considering such a maturation function is to replace the integral \int_0^∞ in the birth equation by the integral \int_m^m . If this change is followed through the derivations of Section 2, one finds that Eq. (2.7) has the additional term

$$f(m, t)P(t - m)e^{-\mu m} - f(\tau m, t)P(t - \tau m)e^{-\mu \tau m} \quad (6.2)$$

(which are the boundary terms in the integration by parts) added to the right-hand side. Thus, the first equation in the system (2.8) is replaced by

$$P'(t) + \mu P(t) = bh(R(t), P(t)) \left[\int_m^{\tau m} \beta'(a)P(t - a)e^{-\mu a} da + P(t - m)\beta(m)e^{-\mu m} - P(t - \tau m)\beta(\tau m)e^{-\mu \tau m} \right] \quad (6.3)$$

that is, system (2.8) now has instantaneous time lags in it due to the step discontinuities at $a = m$ and, if $\tau < +\infty$, at $a = \tau m$.

It is a straightforward calculation to show that for β defined by (5.1) with β_0 given by (6.1) the equilibrium and characteristic equations remain unchanged from (2.9) and (2.10). Because the analysis in Sections 4 and 5 and in the Appendix depends only on these equations it follows that *all of our results above apply for this kind of maturation function with step discontinuities.*

7. Summary

The system of integrodifferential equations (2.8) models the growth dynamics of a (predator) population and its (prey) resource under the assumption that the predator population has an age structure which significantly effects its birth rate, but not its death rate, while the resource or prey population has fecundity and death rates which are independent of any age structure. Predator fecundity and the predation rate are general functions of total population sizes and the prey grows logistically in the absence of predation. Under mild assumptions it is shown that unless the natural carrying capacity K of the prey exceeds a critical value determined by the predator net reproductive rate set equal to one then (small) predator populations go to extinction while the prey tends to its carrying capacity K (Theorem 1). At this critical value of the carrying capacity a bifurcation of positive equilibria is shown to occur, either a stable bifurcation (in which an exchange of stability occurs) or an unstable bifurcation. These bifurcations are characterized analytically (Theorem 1) as well as biologically and geometrically with respect to the predator and prey isocline structure (Section 4).

A "maturation period" m is introduced into the model equations (2.8) and into the analysis by means of (5.1). The class of maturation functions defined by (5.1) is characterized by the requirement that the ratio of per capita offspring from any age class a to $a + da$ for maturation period m to that of age group a/m to $(a + da)/m$ for maturation period one is independent of a . It is shown that positive equilibrium of (2.8) are either unstable for *small* m or are destabilized as $m \downarrow 0$ (Theorem 2). This is the reverse of the usual principle that instabilities or destabilization occurs for increasing delays. Some simple conditions on the fecundity and predation response functions are given (Theorem 3) which are sufficient to insure that the first alternative of instability occurs.

These general results for (2.8) are illustrated by an example in Section 3. Figs. 1 and 2 for this example exemplify the fundamental dynamical behavior in K, m parameter space of the general system (2.8) as described above.

Appendix

Formal proofs of Theorems 1 – 3 will be given in this Appendix. We begin with that of Theorem 1. Parts (a) and (b) of Theorem 1 were proved in Section 4. To prove part (c) observe that the characteristic equation (2.10) for the equilibrium $(K, 0)$

$$D(z, K) := (z + r + g_R(K, 0))(z + \mu)(1 - bh(K, 0)\beta^*(z + \mu)) = 0 \tag{A.1}$$

has, by definition of K_{cr} , the root $z = 0$ when $K = K_{cr}$. Since

$$D_z(0, K_{cr}) = (r + g_R(K_{cr}, 0))\mu bh(K_{cr}, 0) \int_0^\infty e^{-\mu a} a\beta(a) da > 0 \tag{A.2}$$

the implicit function theorem implies the existence of a *unique* root $z = z(K)$ of (A.1) for $K \approx K_{cr}$ satisfying $z(K_{cr}) = 0$. An implicit differentiation of (A.1) with $z = z(K)$ shows that $z'(K_{cr}) = -D_K(0, K_{cr})/D_z(0, K_{cr})$ where

$$D_K(0, K_{cr}) = -(r + g_R(K_{cr}, 0))\mu bh_R(K_{cr}, 0)\beta^*(\mu)$$

and hence

$$\text{sign } z'(K_{cr}) = \text{sign } h_R(K_{cr}, 0). \tag{A.3}$$

It follows that $\text{Re } z(K) > 0$ for $K > K_{cr}$ ($< K_{cr}$) provided $h_R(K_{cr}, 0) > 0$ (< 0) which proves the instability assertion in (c).

It also follows from (A.3) that $\text{Re } z(K) < 0$ for $K < K_{cr}$ ($> K_{cr}$) provided $h_R(K_{cr}, 0) > 0$ (< 0). This proves the stability assertion in (c) provided the existence of other roots with $\text{Re } z \geq 0$ can be ruled out for $K \approx K_{cr}$. This we can do by a contradiction argument as follows. Suppose to the contrary that there exist sequences

$$K_n \uparrow K_{cr} \ (\downarrow K_{cr}), \quad \text{Re } z_n \geq 0, \quad D(z_n, K_n) = 0,$$

where $h_R(K_{cr}, 0) > 0$ (< 0). The sequence z_n cannot be unbounded because if this were so then $D(z_n, K_n)$ would be unbounded. The roots z_n are bounded and (by extracting a subsequence if necessary) it can be assumed without loss of generality that $z_n \rightarrow z_0$ for some $z_0, \text{Re } z_0 \geq 0$. By continuity, $D(z_0, K_{cr}) = 0$ which implies

$$1 - bh(K_{cr}, 0)\beta^*(z_0 + \mu) = 0$$

or $\beta^*(z_0 + \mu) = \beta^*(\mu)$. This implies $z_0 = 0$. But the existence of the roots z_n near zero for $K_n < K_{cr}$ ($> K_{cr}$) contradicts the uniqueness of the branch found by the implicit function theorem for which $\text{Re } z < 0$ when $K < K_{cr}$ ($> K_{cr}$).

Part (d) follows from a straightforward application of the implicit function theorem applied at $(K_{cr}, 0)$ to the positive equilibrium equations (4.4) using the assumed Jacobian condition $J_{cr} \neq 0$. An implicit differentiation of (4.4) with $(R, P) = (R(K), P(K))$ yields

$$dP(K_{cr})/dK = -b\beta^*(\mu)rh_R(K_{cr}, 0)/J_{cr} \tag{A.4}$$

which implies the inequalities in (d).

Finally, to prove part (e) of Theorem 1 we turn to the characteristic equation (2.10) with $(R, P) = (R(K), P(K))$:

$$D(z, K) := \left(z - r + 2r\frac{R}{K} + g_R(R, P)\right) \left[(z + \mu) \left(1 - \frac{\beta^*(z + \mu)}{\beta^*(\mu)}\right) - b\beta^*(\mu)\mu P h_P(R, P) \right] + b\beta^*(\mu)\mu P g_P(R, P) h_R(R, P) = 0.$$

Since $D_z(0, K_{cr})$ is as given by (A.2) there exists a unique root $z = z(K)$, $z(K_{cr}) = 0$ for $K \approx K_{cr}$. An implicit differentiation yields $z'(K_{cr}) = -D_K(K_{cr}, 0)/D_z(K_{cr}, 0)$ where

$$D_K(0, K_{cr}) = -\mu J_{cr} dP(K_{cr})/dK = b\beta^*(\mu)r\mu h_R(K_{cr}, 0)$$

by (A.4). Thus

$$\text{sign } z'(K_{cr}) = -\text{sign } h_R(K_{cr}, 0). \tag{A.5}$$

Now suppose $J_{cr} > 0$. By part (d) the positive equilibrium exists for $K > K_{cr}$ ($< K_{cr}$) when $h_R(K_{cr}, 0) < 0$ (> 0). Thus, by (A.5) the root $z(K)$ satisfies $\text{Re } z(K) > 0$ for $K > K_{cr}$ ($< K_{cr}$) and the positive equilibrium is unstable.

Suppose that $J_{cr} < 0$. Then similarly by (A.5) the root $z(K)$ (unique for $K \approx K_{cr}$) satisfies $\text{Re } z(K) < 0$ for $K > K_{cr}$ ($< K_{cr}$) when $h_R(K_{cr}, 0) > 0$ (< 0). This would imply stability, except that we must rule out the possible existence of roots other than on this branch which satisfy $\text{Re } z \geq 0$. Such roots can be ruled out for $K \approx K_{cr}$ by a contradiction argument similar to that in the proof of part (c) given above.

This completes the proof of Theorem 1.

We turn now to the proof of Theorem 2, which is based upon an investigation of the roots of the following characteristic equation associated with the equilibrium $(R, P) = (R(m), P(m))$ when β is given by (5.1):

$$D(z, m) := \left[z - r + 2r \frac{R}{K} + g_R(R, P) \right] \left[(z + \mu) \left(1 - \frac{\beta_0^*(zm + \mu m)}{\beta_0^*(\mu m)} \right) - bn(m)\beta_0^*(\mu m)\mu Ph_P(R, P) \right] + bn(m)\beta_0^*(\mu m)\mu Ph_R(R, P)g_P(R, P) = 0. \tag{A.6}$$

We are interested in the location of the roots of (A.6) for $m > 0$ near zero. If we make the change of variable

$$z = \zeta/|m|^{1/2}$$

in (A.6) then $D = |m|^{-1/2} \Delta(\zeta, m)$, where

$$\Delta(\zeta, m) := \left[\zeta + |m|^{1/2} \left(-r + 2r \frac{R}{K} + g_R \right) \right] \left[(\zeta + \mu|m|^{1/2}) \frac{\beta_0^*(\mu m) - \beta_0^*(\zeta|m|^{1/2} + \mu m)}{|m|^{1/2} \beta_0^*(\mu m)} - bn(m)\beta_0^*(\mu m)\mu Ph_P \right] + |m|^{1/2} bn(m)\beta_0^*(\mu m)\mu Ph_R g_P.$$

Now

$$\frac{\beta_0^*(\mu m) - \beta_0^*(\zeta|m|^{1/2} + \mu m)}{|m|^{1/2} \beta_0^*(\mu m)} = \frac{1}{\beta_0^*(\mu m)} \int_0^\infty e^{-\mu a} \beta_0(a) \frac{1 - \exp(-\zeta|m|^{1/2}a)}{|m|^{1/2}} da \rightarrow \frac{\zeta m_1}{m_0}$$

as $m \rightarrow 0$. Thus

$$\Delta(\zeta, 0) = \zeta \left(\zeta^2 \frac{m_1}{m_0} - bn_0 m_0 \mu P^0 h_P(R^0, P^0) \right).$$

Suppose that $h_P(R^0, P^0) > 0$ and let $\zeta_0 > 0$ be the positive root of $\Delta(\zeta, 0) = 0$, i.e. $\zeta_0 = (bn_0 m_0^2 \mu P^0 h_P(R^0, P^0)/m_1)^{1/2}$. Now $\Delta(\zeta, m)$ is defined and continuous in (ζ, m) near $(\zeta_0, 0)$ and is continuously differentiable in ζ . In fact,

$$\partial \Delta(\zeta_0, 0) / \partial \zeta = 2bn_0 m_0 \mu P^0 h_P(R^0, P^0) > 0$$

and consequently the implicit function theorem (Goursat [6]) implies the existence of a root $\zeta = \zeta(m)$ for $m \sim 0$ satisfying $\zeta(0) = \zeta_0 > 0$. It follows that $\text{Re } \zeta(m) > 0$ for $m \approx 0$. Thus, the characteristic equation has a root

$$z(m) = \zeta(m)/m^{1/2}, \quad \text{Re } \zeta(m) > 0 \quad \text{for } m > 0, \quad m \approx 0 \tag{A.7}$$

lying in the right half plane and the equilibrium is consequently unstable for $m \approx 0$.

Suppose now that $h_P(R^0, P^0) < 0$. Then $\Delta(\zeta, 0) = 0$ has two purely imaginary roots

$$\zeta_0 = \pm i(-bn_0 m_0^2 \mu P^0 h_P(R^0, P^0)/m_1)^{1/2}.$$

Since again $\partial \Delta(\zeta_0, 0) / \partial \zeta = 2bn_0 m_0 \mu P^0 h_P(R^0, P^0) \neq 0$ we find that the implicit function theorem implies the existence of a root of (A.6)

$$z(m) = \zeta(m)/m^{1/2}, \quad \text{Re } \zeta(0) = 0.$$

It follows that the equilibrium is destabilized as $m \downarrow 0$.

A further investigation of the sign of $\text{Re } z(m)$ for $m \approx 0$ would determine when $\text{Re } z(m) > 0$ and hence the equilibrium is genuinely unstable for $m \approx 0$. In principle this is easily done by a calculation of $z'(m)$ for $m \approx 0$, but we found the resulting condition too complicated and awkward to present here. In any case the destabilization in the case when $h_p(R^0, P^0) < 0$ has been established.

Finally, consider the case when $h_p(R^0, P^0) = 0$. In this case we proceed slightly differently by writing $z = \zeta/m^{1/3}$ and

$$D = D(\zeta, m) = \left[\zeta + m^{1/3} \left(-r + 2r \frac{R}{K} + g_R \right) \right] (\zeta + \mu m^{1/3}) \frac{\beta_0^*(\mu m) - \beta_0^*(\zeta m^{2/3} + \mu m)}{m^{2/3} \beta_0^*(\mu m)} + bn(m)\beta_0^*(\mu m)\mu P h_R g_P = 0.$$

Since

$$\frac{\beta_0^*(\mu m) - \beta_0^*(\zeta m^{2/3} + \mu m)}{m^{2/3} \beta_0^*(\mu m)} \rightarrow \zeta \frac{m_1}{m_0}$$

as $m \rightarrow 0$ it follows that

$$D(\zeta, 0) = \zeta^3 \frac{m_1}{m_0} + bn_0 m_0 \mu P^0 h_R(R^0, P^0) g_P(R^0, P^0) = 0$$

has at least one root ζ_0 , $\text{Re } \zeta_0 > 0$, when $h_R(R^0, P^0) g_P(R^0, P^0) \neq 0$. Since $D_\zeta(\zeta_0, 0) = 3\zeta_0^2 m_1/m_0 \neq 0$ the implicit function theorem implies the existence of a root

$$z(m) = \zeta(m)/m^{1/3}, \quad \text{Re } \zeta(m) > 0 \quad \text{for} \quad m \approx 0 \tag{A.8}$$

and the instability of the equilibrium follows.

If $h_R(R^0, P^0) = 0$ then the characteristic equation has root $z = 0$ for all m which meets the definition of the destabilization of the equilibrium. The same is true if $g_P(R^0, P^0) = 0$.

This completes the proof of Theorem 2.

Finally we prove Theorem 3. Part (a) follows from (A.7) while part (b) follows from (A.8). We have only to prove part (c). Putting $m = 0$ in (A.6) we find that

$$D(z, 0) = \left[z - r + 2r \frac{R^0}{K} + g_R(R^0, P^0) \right] [-bn_0 m_0 \mu P^0 h_P(R^0, P^0)] + bn_0 m_0 \mu P^0 h_R(R^0, P^0) g_P(R^0, P^0) = 0$$

which, when solved for z , yields the real root

$$z = z_0 := -J_0/bm_0 n_0 h_P(R^0, P^0) > 0.$$

Since $D_z(z_0, 0) = bn_0 m_0 \mu P^0 h_P(R^0, P^0) \neq 0$ another implicit function theorem application implies the existence of roots $z = z(m)$ for $m \approx 0$ which satisfy $z(0) = z_0$ and hence $\text{Re } z(m) > 0$ for $m \approx 0$. This completes the proof of Theorem 3.

Finally, we verify the characterization of the maturation functions (5.1) given in Section 5. Suppose that the ratio ρ described in this characterization is independent of a . If $\beta = \beta(a, m)$ is an arbitrary maturation function with maturation period m then

$$\frac{bh(R, P)\beta(a, m) da}{bh(R, P)\beta(a/m, 1)d(a/m)} = \rho(m)$$

which implies that β is given by (5.1) with $\beta_0(a) := \beta(a, 1)$ and $n(m) = \rho(m)$. Conversely, suppose that β is given by (5.1). Then

$$\frac{bh(R, P)\beta(a) da}{bh(R, P)\beta(a/m)d(a/m)} = \frac{n(m)}{n(1)}$$

is independent of a .

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