

Proceedings of The Autumn Course Research Seminars

# MATHEMATICAL ECOLOGY

International Centre for Theoretical Physics

Miramare — Trieste, Italy

November 24 — December 12, 1986

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**World Scientific**

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Published by

World Scientific Publishing Co. Pte. Ltd.  
P.O. Box 128, Farrer Road, Singapore 9128

U. S. A. office: World Scientific Publishing Co., Inc.  
687 Hartwell Street, Teaneck NJ 07666, USA

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ISBN 9971-50-556-8

Printed in Singapore by Chong Moh Offset Printing Pte Ltd.

## THE ALLEE EFFECT IN AGE-STRUCTURED POPULATION DYNAMICS

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## ABSTRACT

The existence and stability of positive equilibrium states for general models of age-structured population growth are discussed from a bifurcation theory point of view using the inherent net reproductive rate as a parameter. The subcritical, unstable bifurcation case is shown to correspond to the "Allee" effect and the asymptotic dynamics for this case are considered.

## 1. THE MCKENDRICK EQUATIONS

Assume that a population can be described by a density  $\rho = \rho(t, a) \geq 0$  which depends on time  $t$  and age  $a$  so that the integral  $\int_c^d \rho(t, a) da$  is the total population between ages  $c$  and  $d$  and

$$P(t) = \int_0^A \rho(t, a) da$$

is the total population size. Here  $A \leq +\infty$  is the maximum age of any individual in the population. If it is assumed that the only entries into the population are newborns and that fertility is given by an age specific *per unit rate*  $F$  and if it is further assumed that removals (via deaths or other means) are given by an age specific *per unit rate*  $D$ , then the dynamics of  $\rho$  are determined by

the equations

$$\begin{aligned} \partial_t \rho + \partial_a \rho + D\rho &= 0, \quad t > 0, \quad 0 < a < A \\ \rho(t, 0) &= \int_0^A F\rho \, da, \quad t > 0 \\ \rho(t, a) &= 0, \quad t > 0, \quad a \geq A. \end{aligned} \quad (1)$$

If  $F$  and  $D$  depend on  $a$ , but not on  $t$  or  $\rho$ , then the theory based on the resulting linear equations is equivalent to classical renewal theory (e.g. see Hoppensteadt (1975)). I'll be concerned here with the nonlinear case when these vital rates depend on density  $\rho = \rho(t, a)$  and age  $a$  but not explicitly on time  $t$ .

Let  $F_0$  denote the *inherent per unit fertility rate*, i.e.  $F_0 = F|_{\rho \equiv 0} \geq 0$ . This is the per unit density fertility rate at low population (technically zero) population levels when density effects on fertility are nil. The *inherent net reproductive rate* (i.e. the expected number of offspring per lifetime per unit density) is given by

$$n = \int_0^A F_0 \Pi \, da$$

where  $\Pi = \Pi(a)$  is the "inherent" probability of a newborn living to age  $a$

$$\Pi(a) = \exp\left(-\int_0^a D_0 \, ds\right), \quad D_0 = D|_{\rho \equiv 0}.$$

The inherent net reproductive rate  $n$  can be explicitly introduced into the dynamical equations (1) by defining a *normalized fertility rate*  $f$  in such a way that  $F = nf$  where  $f$  satisfies the normalization

$$\int_0^A f_0 \Pi \, da = 1. \quad (2)$$

where  $f_0 = f|_{\rho \equiv 0}$ .

## 2. EQUILIBRIA

An equilibrium is a time independent solution  $\rho = \rho(a) \geq 0$  of (1). If  $F$  and  $D$  are independent of density  $\rho$  then it is easy to see that there exists an equilibrium if and only if  $n = 1$  (when each unit of density exactly replaces itself in the long run) in which case  $\rho$  is an arbitrary constant multiple of  $\Pi(a)$ . Moreover, classical renewal theory implies that all solutions tend to  $\rho \equiv 0$  as  $t \rightarrow +\infty$  when  $n < 1$  and are unbounded when  $n > 1$ . The trivial equilibrium  $\rho \equiv 0$  is then stable for  $n < 1$  and unstable for  $n > 1$ . The asymptotic dynamics for this linear case are schematically summarized in Fig. 1 where some measure of the equilibria (e.g. some Banach space norm  $\|\rho\|$ ) is plotted against  $n$ .

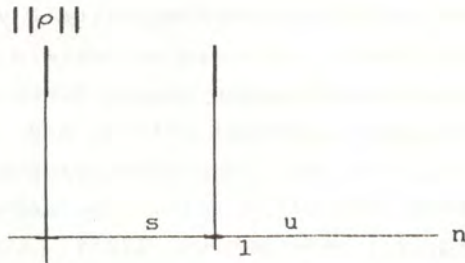


Fig. 1 The linear case

For the nonlinear, density dependent case when the vital rates  $f$  and  $D$  depend on  $\rho$  it can be proved that a similar diagram holds true in that a branch (i.e. continuum) of nontrivial positive equilibria "bifurcates" from the critical value  $n = 1$  as in Fig. 1. However, unlike in the linear case, this branch does not in general have a vertical graph and hence the "spectrum" of  $n$  values corresponding to positive equilibria is not the discrete point  $n = 1$ . Nonlinearities bend the branch

either to the right or left as in Fig. 2 (at least locally near the bifurcation point  $(n, \rho) = (1, 0)$ ). Moreover the stability of the positive branch equilibria near bifurcation depends on which of these two cases occurs.

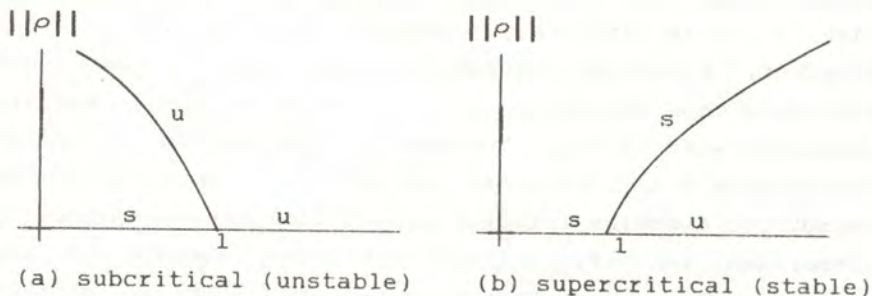


Fig. 2 The nonlinear case

These facts were proved by Cushing (1984) under only very weak smoothness conditions on the per unit vital rates  $f$  and  $D$ , as they depend on  $\rho$  in a certain Banach space setting, by use of bifurcation theory techniques; in fact they hold for more general birth and death rates. Furthermore, if  $A < +\infty$  then the branch of positive equilibria exists globally (i.e. is unbounded in the diagram of Fig. 2); see Cushing (1985).

The existence of stable, positive equilibria is clearly important in population growth models. The case of supercritical stable bifurcation in Fig. 2b for which stable positive equilibria do exist, at least for  $n$  close to 1, is the more commonly occurring of the two alternatives.

It should be remarked here that virtually all model equations which have been used in the literature to describe population growth can be derived using the McKendrick (von Foerster) equations (1) as a starting point (or their generalization when the vital rates are

not necessarily of per unit type). This includes familiar model equations for total population size  $P(t)$  involving ordinary or integrodifferential or delay differential equations, equations for the total birth rate  $B(t) = \rho(t,0)$  involving integral equations (as in classical renewal theory) and even discrete difference and Leslie matrix equations. Thus the equilibrium question for all such models, being a special case of that for (1), can be viewed in the context of Fig. 2. This gives one a feeling for the generality of these results and the ubiquity in theoretical population dynamics of the bifurcation phenomenon as described in Fig. 2.

An illustration is provided by the classical logistic equation for  $P$ , which is usually viewed in elementary introductions to population dynamics as the simplest modification of the exponential growth law. Suppose  $D = d_1 + d_2 P$  and  $f = [f_1 - f_2 P]_+$  where  $f_1 \geq 0$ ,  $d_i \geq 0$  are constants. (Here  $[x]_+ = x$  if  $x \geq 0$  but  $= 0$  if  $x < 0$ .) The normalization condition (2) requires the condition  $f_1 = d_1$ . If the first equation in (1) is integrated with respect to  $a$  from 0 to  $A = +\infty$  and use is made of the remaining equations in (1), then the logistic equation  $dP/dt = r(1 - P/K)$  results with  $r = f_1(n-1)$  and  $K = K(n) = f_1(n-1)/(d_2 + nf_2)$ . This is under the assumption that  $f$  and  $D$  really do depend on total population size  $P$ , i.e.  $d_2^2 + f_2^2 \neq 0$ . If on the other hand  $d_2^2 + f_2^2 = 0$ , then the same manipulations result in the linear exponential equation  $dP/dt = rP$ . These two cases illustrate the passage from Fig. 1 to Fig. 2b as seen in Fig. 3.

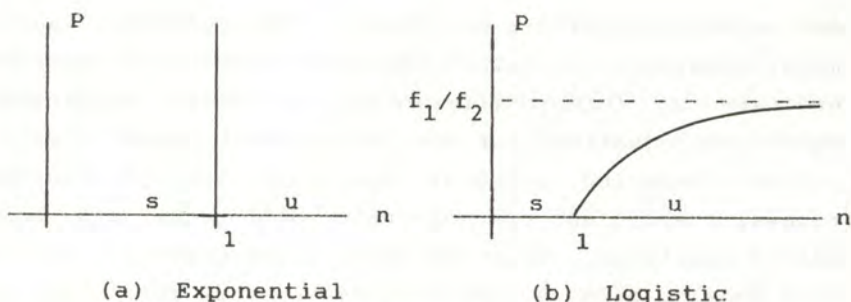


Fig. 3

### 3. THE DIRECTION OF BIFURCATION

Return now to the general McKendrick model (1) as seen from the bifurcation theory point-of-view represented in Fig. 2 and ask the following questions. How does one determine which of the two alternatives in Fig. 2 occurs and in particular what properties of the density dependency in the vital rates result in supercritical, stable bifurcation? Is the subcritical, unstable case biologically important and if so what are the asymptotic dynamics in this case?

The direction of bifurcation can be determined by means of a standard Liapunov-Schmidt expansion near the critical bifurcation point  $(n, \rho) = (1, 0)$ . Using this procedure one parameterizes the bifurcating branch in terms of an auxiliary parameter  $\varepsilon$  and then calculates the coefficients of the lowest order terms in the Taylor expansions of  $\rho$  and  $n$ :

$$\rho(\varepsilon) = \varepsilon \Pi(\varepsilon) + \dots, \quad n = 1 + n_1 \varepsilon + \dots$$

This technique relies on a Fredholm alternative for linear equations of the form (1). It turns out that

$$n_1 = \int_0^A f_0 \Pi \int_0^a \partial_\rho D_0(\Pi) d\alpha da - \int_0^A \Pi \partial_\rho f_0(\Pi) da \quad (6)$$



where  $\partial_{\rho} D(\cdot)$  and  $\partial_{\rho} f_0(\cdot)$  are (Fréchet) derivatives of  $D$  and  $f$  with respect to  $\rho$  at  $\rho \equiv 0$ . Since positive equilibria correspond to  $\epsilon > 0$  the direction of bifurcation is determined by the number  $n_1$  as follows

$$\begin{aligned} n_1 > 0 & \text{ implies supercritical stable bifurcation} \\ n_1 < 0 & \text{ implies subcritical unstable bifurcation.} \end{aligned}$$

In view of formula (3) we see that it is the nature of the density dependence of the vital rates, as expressed by the  $\rho$  derivatives of  $D$  and  $f$ , which determines the direction of bifurcation.

For example, by far the most common modelling assumption is that the effect on the vital rates of an *increase* in population density is to *increase* the death rate and *decrease* fertility. If this is assumed true for all age classes then

$$\partial_{\rho} D(\Pi) \geq 0 \quad \text{and} \quad \partial_{\rho} f_0(\Pi) \leq 0 \quad \text{for all } a. \quad (4)$$

Referring to (3) we see in this case that  $n_1 > 0$  (except in the special case  $n_1 = 0$ , which we ignore). Thus under such common modelling assumptions, supercritical stable bifurcation always occurs.

Another method for studying the (global) properties of the bifurcation diagram in Fig. 2 is based on the invariant

$$nN(\rho) = 1 \quad (5)$$

which holds for any non-identically zero equilibrium  $\rho$  and in particular along the branch of positive equilibria bifurcating from  $(n, \rho) = (1, 0)$ . Here

$$N(\rho) = \int_0^A f(\rho) \exp\left[-\int_0^a D(\rho) ds\right] da. \quad (6)$$

The identity (5) expresses the fact that the net reproductive rate at equilibrium  $nN(\rho)$  must be equal to

one. From a knowledge of the properties of  $f$  and  $D$  as they depend on density  $\rho$  it can be determined how the quantity  $N(\rho)$  (the *normalized net reproductive rate* at equilibrium) depends on  $\rho$  and from the invariant (5), which relates  $n$  and  $\rho$  along the branch, one can often obtain an accurate plot of the bifurcation diagram Fig. 2.

Note that the normalization (2) implies  $N(0) = 1$ . Also note that

$$n_1 = - \frac{\partial N(0)}{\partial \rho} . \quad (7)$$

For example the extent of the nonlinear spectrum and the direction of bifurcation can often be deduced as well as the uniqueness or multiplicity of positive equilibria for a given value of  $n$ ; for examples see Cushing (1985).

This procedure is particularly useful when  $f$  and  $D$ , and hence  $N$ , depend on  $\rho$  through a dependence on a linear functional

$$W = \int_0^A w(a)\rho(a) da, \quad w(a) \geq 0 (\neq 0)$$

which is a *weighted total population size*. In this case  $f = f(a, W)$ ,  $D = D(a, W)$  and  $N = N(W)$  where  $f$ ,  $D$  and  $N$  are real valued functions of real variables and the bifurcation diagram with  $W$  plotted against  $n$  can be obtained by plotting the relation

$$nN(W) = 1 \quad (8)$$

in the  $n, W$ -plane.

For example, for the logistic equation considered above the relation (8) reduces to

$$n \frac{[f_1 - f_2]_+}{d_2 + f_2 W} = 1$$

which gives rise to the diagram in Fig. 3b, but here for the more general case of an arbitrarily weighted total

population size  $W$  (note that  $W = P$  if  $w \equiv 1$ ).

Note that by (7) the bifurcation is supercritical if  $\partial_{\rho} N(0) < 0$  (or in the case of dependence on  $W$  as in the above example if  $N'(0) = dN(0)/dW < 0$ ). As will be discussed below stability of an equilibrium is often closely related to the sign of this derivative at equilibrium.

Even in the case of stable supercritical bifurcation, the stability of the positive equilibria may not persist globally along the branch however (as it does in the classical logistic example with  $W = P$  above). Well known examples involving time lags or difference equation analogs of the logistic can lose equilibrium stability for critical values of  $n$  greater than 1 and suffer Hopf bifurcations to limit cycles and even chaotic dynamics through cascades of further bifurcations. My concern here will not be with such phenomena however, but with the other alternative of subcritical unstable bifurcation.

Before turning to this case I'll pause briefly for a few remarks concerning related models.

#### 4. VARIATIONS, GENERALIZATIONS AND SOME OPEN PROBLEMS

If a population is structured by a dynamic variable  $x$ , not necessarily age, then the differential expression  $\partial_t \rho + \partial_a \rho$  in (1) is replaced by  $\partial_t \rho + \partial_x (v\rho)$  where the coefficient  $v = dx/dt$  is the growth rate of  $x$  (Streifer 1974). Thus the growth dynamics of a population involves specifying the three vital rates  $F$ ,  $D$  and  $v$ . The incorporation of the rate  $v$  into the model is important since the question of how such an individual growth rate (of a variable such as size or weight) affects the dynamics of the population is of biological interest. In general it is expected that  $v$  will depend on  $t$ ,  $x$  and  $\rho$ . Although the theory for the age structured case  $x = a$  when  $v \equiv 1$  is well developed (Metz and Diekmann 1986,

Webb 1985) there is little theory available for the more general case when  $v$  is density dependent or is allowed to be negative. If  $v = v(x) > 0$  then a change of variables reduces the problem to the age structured case.

If time and age are discretized and difference approximations made to the derivatives in (1), the model can be rewritten as a nonlinear Leslie matrix model  $\hat{\rho}(i+1) = M(\hat{\rho}(i))\hat{\rho}(i)$  where  $\hat{\rho} = (\rho_j(i))_{j=1}^k$  is the vector of densities  $\rho_j(i)$  of individuals whose age lies in the interval  $[i, i+1)$  at time  $i$  and  $M$  is a matrix of the "Leslie" form

$$\begin{bmatrix} nf_0 & nf_1 & nf_2 & \dots & nf_{k-1} & nf_k \\ p_1 & 0 & 0 & & 0 & 0 \\ 0 & p_2 & 0 & & 0 & 0 \\ \vdots & \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & 0 & & p_{k-1} & p_k \end{bmatrix} . \quad (9)$$

Here  $p$  is the probability of surviving from age class  $j$  to  $j+1$  and  $nf_j$  is the average number of offspring from class  $j$  which survive the first age class. The quantities  $f_j$  and  $p_j$  are allowed to depend on  $\hat{\rho}(i)$  in some manner (e.g. through a dependence on a weighted total population size  $\sum w_j \rho_j(i)$ ). The general existence and stability results concerning equilibria as summarized in Figs. 1 and 2 can be shown to hold for this discretized model.

In fact these general results are obtainable for a more general matrix model in which some or all of the 0's in the "projection" matrix  $M$  are replaced by nonzero probabilities and thus, in this discrete case at least, the existence and stability results described above hold for structuring variables other than age and for which regressions to former categories is permitted (analogous in the continuous model to allowing  $v$  to be both density dependent and/or to change sign). These results will

appear in a forthcoming paper.

The results obtained via bifurcation theory techniques have been extended to coupled systems of equations of the form (1) and hence to models of interacting structured populations by Cushing (1987).

##### 5. SUBCRITICAL BIFURCATION AND THE ALLEE EFFECT

In view of the fact that the conditions (4) imply supercritical stable bifurcation it follows that subcritical bifurcation can occur only if at least one of these conditions is violated, at least for low population densities for at least some age classes. That is to say, an *increase* in small densities must result in either a *decrease* in mortality or an *increase* in fertility for at least some age classes. If in fact such effects occur for all age classes so that the inequalities in (4) are both reversed then subcritical unstable bifurcation will indeed occur since  $n_1 < 0$  in this case. Are there any compelling biological reasons which could account for these "reversed" density effects on fertility and mortality and is there any evidence of their occurrence?

With regard to stimulating effects of increased density on fertility one of the most frequently mentioned possible causes, at least in sexually reproducing populations, is the increased probability of finding a mate. Indeed increased fertility with increased low level densities has been observed in several species of beetle (Allee 1931) and insects (Watt 1968), although it is not clear what the causal mechanisms are. (In certain beetle species females experiencing a higher incidence of copulation have been noted to produce more eggs per laying.) This effect has also been documented, perhaps surprisingly, in some asexually reproducing species, e.g. in protozoa by Robertson (1929) and in paramecium by Peterson (1929). Also see Parise (1966) for a case

involving rotifers.

Concerning the beneficial effects of crowding on survival rates one immediately thinks of the possible increased chance of survival of young as a result of increased care and nurturing within groups of animals. Indeed herding, flocking, schooling, etc. can provide general protection to individual members from predators and adverse environmental events. Also survival can be enhanced by more efficient harvesting or hunting of prey resources by herds or packs. Indeed survival enhancement in the presence of crowding has been observed in grasshoppers, beetles and *Drosophila*, although the causal mechanisms are not always understood. Allee (1931) describes studies of some specific mechanisms which result in improved survival probabilities due to crowding; these include protection from toxic reagents in starfish, protozoa, shrimp and waterfleas, protection from high temperatures in protozoa and ultraviolet light in worms and lower metabolic rates in starfish. Studies showing enhanced survival for plant species in the presence of increased densities are described by Silvertown (1981) (for *pinus ponderosa*) and by Sarukhan (1974) (for *Ranunculus bulbosa*).

As we have seen it is these effects and mechanisms which can cause a subcritical bifurcation in the model equations discussed in Secs. 1-4 above. A beneficial effect of increased population density is usually referred to as an "Allee effect" (an earlier term used was Robertson's "allelocatalytic effect"). In some literature the same effect is referred to as "strict depensation" (Clark 1976).

## 6. ASYMPTOTIC DYNAMICS IN THE SUBCRITICAL CASE

We are interested here in the subcritical bifurcation case pictured in Fig. 2a and consequently

assume  $n_1 = -\frac{\partial N(0)}{\partial \rho} < 0$ . This means, roughly speaking, that *increases* in *low level* densities results in an *increased* net reproductive rate.

Suppose we also accept the common assumption that an *increase* in *large* densities results in a *decreased* net reproductive rate. This implies that the graph of the bifurcating positive equilibrium in Fig. 2a must "turn around" as in Fig. 4. In fact if  $N$  drops to zero as  $\|\rho\|$  increases without bound (a common property of models) then the "spectrum" must be infinite, i.e. positive branch equilibrium exist for all  $n > n_{cr}$ . This follows from the invariant (5) and the fact that the branch is a continuum which implies that if  $N(\rho) \rightarrow 0$  along the branch then  $n \rightarrow +\infty$ .

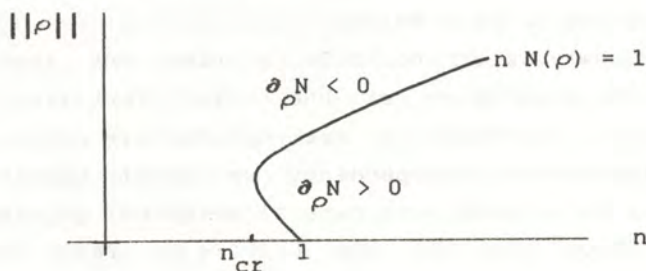


Fig. 4

It follows from these assumptions that at least for some values of the inherent net reproductive rate  $n$  there exist multiple positive equilibrium states (namely for  $n \in (n_{cr}, 1)$ ). Simple models of growth dynamics usually do not have this property, but it is often pointed out in the literature that more realistic models probably should. For example, C. S. Holling (1973) states that "Empirical evidence, therefore, suggests that realistic forms to fecundity and mortality curves will generate .... the possibility of a number of equilibrium states, some

transient and some stable."

With regard to stability properties of the equilibria schematically represented in Fig. 4 we have seen that the trivial equilibrium  $\rho \equiv 0$  loses stability as  $n$  increases through the bifurcation value  $n = 1$  and that the positive equilibria  $\rho$  from the branch are unstable at least for  $(n, \rho)$  close to  $(1, 0)$ . A natural conjecture is that this instability persists along the branch until the turning point is reached and that the upper "rising part" of the branch consists of stable equilibria.

The question then arises about the relationship between stability and the sign of the derivative  $\frac{\partial N}{\partial \rho}$  at equilibrium. Some results concerning this question can be found in the literature, at least in restricted cases, and will be described briefly below.

First, however, it should be pointed out that in most models the dependence of the vital fertility and mortality rates, and hence the net reproductive rate  $N$ , on density is through a dependency on total population size  $P = \int_0^A \rho da$  or some more general weighted population size  $W$  as above. In this case  $N$  is a real valued function of a real variable  $W$  and it is more natural to construct bifurcation diagrams in the  $n, W$ -plane using analytical geometric methods to study the graph of the relation  $1 = n N(W)$ . The Fréchet derivative  $\frac{\partial N}{\partial \rho}$  is then replaced by the derivative  $dN/dW = N'$  and the question above concerns the relationship between stability and the sign of this derivative.

Although results in the literature may not be cast in the bifurcation theory framework set forth here, they can usually be reinterpreted in this context. I will mention results on two "opposite" special cases which appear in the literature and which bear on the question



raised above.

Rorres (1979a,b) considered the case when only fertility is density dependent:  $D = D(a)$ ,  $F = F(a,W)$  (and  $A = +\infty$ ). In this case (1) can easily be reduced to an equivalent nonlinear Volterra integral (or renewal) equation for the *total birth rate*  $B(t) = \rho(t,0)$ . Amongst other things Rorres proves that  $N'(W) > 0$  at equilibrium implies instability. (In Rorres' papers focus is placed on the net reproductive rate at equilibrium  $n_N$  which he denotes by  $R$ .) Thus, in this case, the "falling part" of the branch in Fig. 4 is indeed unstable.

On the other hand one cannot expect in general that the "rising part" of the branch is stable, even in this special case considered by Rorres. Indeed, even for the supercritical stable case Fig. 2b stability can be lost along the rising part of the branch and result in a Hopf bifurcation to limit cycles. Thus  $N'(W) \leq 0$  is only a necessary condition for stability. Some further conditions which are sufficient to insure stability are given by Rorres for the special case he considers.

Consider next an opposite case when only mortality is density dependent. Specifically let  $D = \mu(a) + d(W)$ ,  $d(0) = 0$  and  $F = F(a)$  with  $A = +\infty$ . Here the age specific and density effects on mortality are additive and the density effects affect all age classes equally. The following results due to Simmes (1978) and (independently) to Bussenberg and Iannelli (1985). There is a unique real  $r$  such that

$$\int_0^{\infty} e^{-ra} \Pi(a) F(a) da = 1$$

and

$$\lim_{t \rightarrow \infty} u(t,a) = u_{\infty}(a) = e^{-ra} \Pi(a) \int_0^{\infty} e^{-ra} \Pi(a) da$$

where  $u(t,a) = \rho(t,a)/P(t)$  represents the proportion of

individuals of age  $a$  in the total population. The dynamics of the density  $\rho$  are determined by the differential equation

$$dP/dt = [r - d(\Gamma P)]P \quad (10)$$

for the total population size. If  $P = P_\infty > 0$  is an asymptotically stable equilibrium of (10) then

$$\rho(t, a) = P_\infty e^{-ra} \Pi(a) / \int_0^\infty e^{-ra} \Pi(a) da$$

is a stable equilibrium density.  $P = P_\infty$  is a stable equilibrium of (10) if  $d'(\Gamma P_\infty) > 0$  and is an unstable equilibrium if  $d'(\Gamma P_\infty) < 0$ . Now  $W_\infty = \Gamma P_\infty$  and

$$nN(W) = \int_0^\infty F(a) \Pi(a) \exp(-d(W)a) da .$$

Consequently  $d'(\Gamma P_\infty) > 0$  if and only if  $N'(W_\infty) < 0$ .

This establishes the desired connection between the sign of  $\partial_\rho N = N'$  (i.e. the slope of the graph of the bifurcating branch in Fig. 4) and stability. Namely, in this case considered by Simmes and by Busenberg and Iannelli, the rising portions of this graph are stable and the falling portions are unstable.

Based on these examples we conjecture that a necessary condition for the stability of a positive equilibrium  $\rho$  of (1) is the condition

$$\partial_\rho N(\rho) < 0 .$$

The net reproductive rate  $nN(\rho)$  acts as a kind of restoring force. If  $\partial_\rho N(\rho) < 0$  and  $\rho$  is increased above equilibrium then this net reproductive rate drops below 1 and density decreases (recall  $nN(\rho) = 1$  at equilibrium). Conversely, if  $\rho$  is decreased below equilibrium this net reproductive rate rises above 1 and the density is increased. Consequently the expression (6)

should be useful in the construction of Liapunov functionals for the study of global stability properties of (1). This interesting observation has not been explored.

## 7. EXAMPLES

In this final section two examples of subcritical bifurcation are considered, one continuous in time and age and the other discrete.

(a) In (1) let the maximal age be  $A = 1$  and set  $D = 1/(1-a)$ . Then  $\Pi(a) = 1-a$  and  $\rho(t,a) = B(t-a)\Pi(a)$  where  $B(t) = \rho(t,0)$  is the total birth rate. Assume that the fertility rate  $F$  is density dependent through a dependency on  $B$ . Specifically assume that the fertility of age class  $a$  is a function of the density of its cohort at birth, i.e. of  $B(t-a)$ . This is the well-known Easterlin hypothesis for which there is some evidence in some species (e.g. in human populations; see Rorres 1979a,b). Thus we write

$$F = nf, \quad f = \beta(a)g(B(t-a))$$

where, in order to obtain the normalization (2), the age specific "inherent" fertility factor  $\beta(a) \geq 0$  satisfies

$$\int_0^1 \beta(a) da = 1$$

and the function  $g$  satisfies  $g(0) = 0$ .

Subcritical bifurcation will occur if  $g'(0) > 0$ . We assume for simplicity that  $g$  has a graph as appears in Fig. 5.

The model equations (1) can be rewritten as the nonlinear Volterra integral equation

$$B(t) = h(t) + n \int_0^t \beta(a)(1-a)g(B(t-a))B(t-a) da$$

where  $h(t)$  is the contribution to the birth rate from

the members of the initial population density which we denote by  $\rho^0(a) = \rho(0,a)$ ,  $0 < a < 1$ .

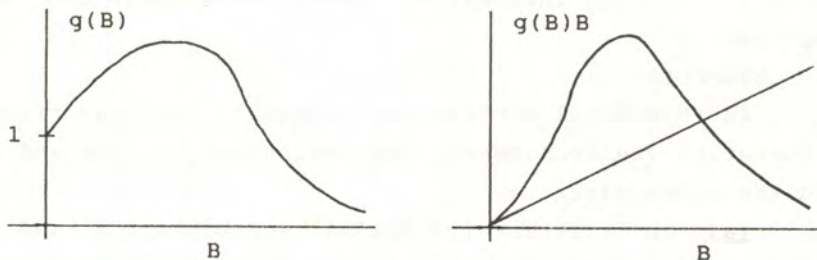


Fig. 5

Suppose it is further assumed that reproduction is concentrated at an age  $a = m$ ,  $0 < m < 1$ . A substitution of a Dirac function centered at  $m$  for  $\beta(a)$  in the integral equation above results in the following continuous difference equation for

$$B(t) = \begin{cases} ng(B(t-m))B(t-m) & \text{for } t > 0 \\ \rho^0(-t)/(1+t) & \text{for } t < 0. \end{cases}$$

This equation can be analyzed by selecting an arbitrary  $t \in (-1,0)$  and considering the sequence  $B_i$  of  $B$  values at subsequent time intervals  $t_i = t + im$ ,  $i = 1,2,3,\dots$ . The familiar "cobwebbing" procedure applied to the simple difference equation

$$B_{i+1} = ng(B_i)B_i, \quad i = 1,2,3,\dots$$

$$B_0 = \rho^0(t)/(1+t)$$

by means of the appropriate graph in Fig. 6 yields the asymptotic behavior of  $B_i$ .

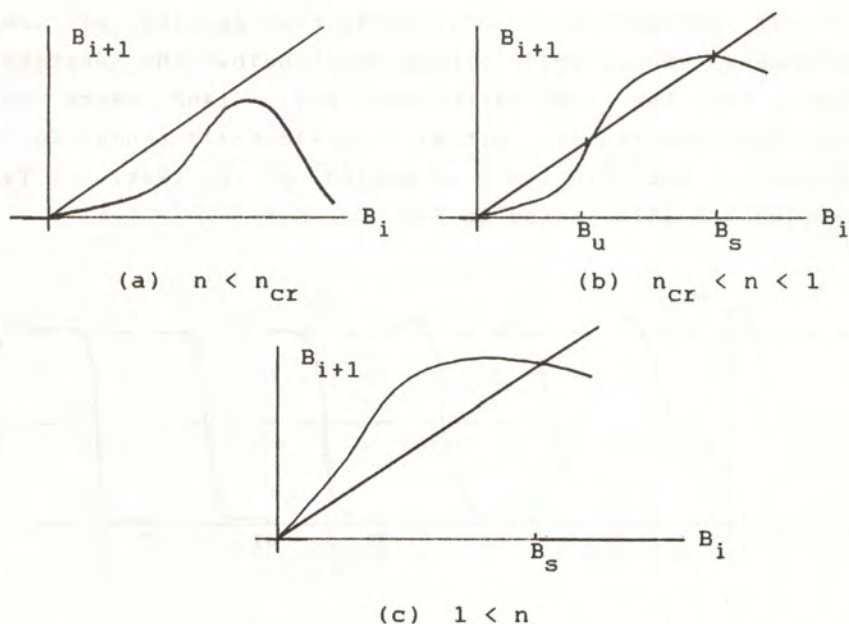


Fig. 6

An interesting situation arises when  $n_{cr} < n < 1$  and there exist two stable equilibria in Fig. 6b. The time sequence  $B_i$  tends to  $B_s$  or to 0 depending on whether  $B_0$  is greater than or less than the threshold value  $B_u$ , i.e. on whether the total birth rate  $B(t) = \rho^0(-t)/(1+t)$  for  $-m < t < 0$  exceeds  $B_u$ . This clearly depends on the initial density distribution  $\rho^0(a)$  on the interval  $0 < a < m$ , namely  $B(t) > B_u$  or  $B(t) < B_u$  holds if and only if  $\rho^0(a) > (1-a)B_u$  or  $< (1-a)B_u$  at  $a = -t$  where  $(1-a)B_u$  is the unstable equilibrium density.

Thus, if the birth rate  $B(t)$  is below  $B_u$  for all  $-m < t < 0$ , i.e. if the initial density  $\rho^0(a)$  is below the unstable density for all age classes prior to maturation, then all time sequences  $B_i \rightarrow 0$ . All  $B_i \rightarrow B_s$  in the opposite case when  $B(t) > B_s$  for all  $-m < t < 0$ .

If, on the other hand, the initial density of some age classes exceed while others fall below the unstable density then the total birth rate  $B(t)$  (and hence the time dependent density  $\rho(t,a) = (1-a)B(t-a)$ ) tends to a nonconstant periodic limit of period  $m$  (or less). Two examples are illustrated in Fig. 7.

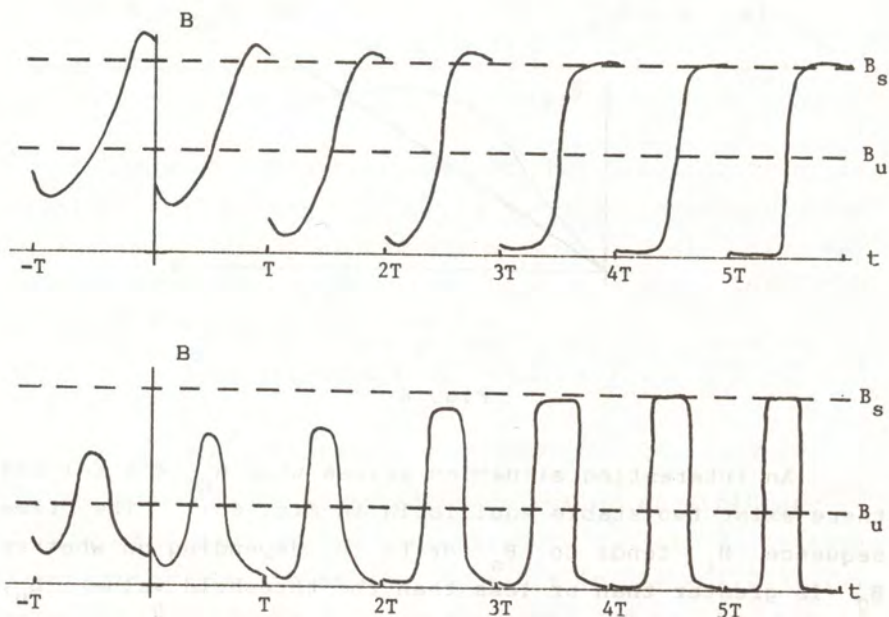


Fig. 7

Clearly there are infinitely many different asymptotic periodic states each of which attracts infinitely many initial age densities. Note that these periodicities, having alternate intervals of zero  $B$  values, imply a synchronization of the age classes.

(b) As a second example consider the  $k = 2$  age class nonlinear Leslie matrix model with a projection matrix (9). Suppose that only the older class (adults) are fertile  $f_0 = 0$  and that no adults survives more than

one time unit  $p_2 = 0$ . Density regulation occurs through fertility which depends on a weighted total population size as follows.

$$0 < p = p_1 < 1 \quad \text{and} \quad f_1 = f(W)$$

$$W = w_0 \rho_0 + w_1 \rho_1, \quad 0 \leq w_i \leq 1, \quad w_0^2 + w_1^2 \neq 0.$$

The normalization (2) requires that  $f(0)p = 1$  and a subcritical bifurcation occurs if

$$f'(0) > 0$$

which we assume true. The model matrix equation becomes

$$\begin{bmatrix} \rho_0(i+1) \\ \rho_1(i+1) \end{bmatrix} = \begin{bmatrix} 0 & nf(W(i)) \\ p & 0 \end{bmatrix} \begin{bmatrix} \rho_0(i) \\ \rho_1(i) \end{bmatrix}.$$

Finding a positive equilibrium  $\rho_0(i) = e_0 > 0$ ,  $\rho_1(i) = e_1 > 0$  is equivalent to solving  $nf(W_0)p = 1$  for  $W_0 > 0$  in which case

$$e_0 = W_0 / (w_0 + pw_1), \quad e_1 = pe_0.$$

The (local) stability of an equilibrium is determined by the eigenvalues  $\lambda$  of the Jacobian at equilibrium of the map  $R^2 \rightarrow R^2$  defined by

$$m(\hat{\rho}) = \begin{bmatrix} F(w_0 \rho_0 + w_1 \rho_1) & \rho_1 \\ p & \rho_0 \end{bmatrix}. \quad (11)$$

$|\lambda| < 1$  implies stability. A calculation of these eigenvalues leads to the following results.

The trivial equilibrium  $\rho \equiv 0$  is stable if  $nf(0)p = n < 1$  and unstable if  $n > 1$ .

For a positive equilibrium,  $|\lambda| < 1$  if and only if

- (i)  $0 < -nf'(W_0)W_0p < 2(w_0 + pw_1)/p^2w_1$   
 (ii)  $w_0 < pw_1$

Note that (i) requires  $f'(W_0)p = N'(W_0) < 0$  as is consistent with the conjecture at the end of Sec. 6. The inequality  $f'(W_0) > 0$  implies that  $W_0$  is unstable. On the other hand  $f'(W_0) < 0$  is not sufficient to guarantee stability, although if in addition to this  $f'(W_0)$  is sufficiently small then (i) will hold. Thus if (ii) holds then there is an exchange of stability at the "turning point"  $(n, W) = (n_{cr}, W_{cr})$  in Fig. 8b. The necessary condition (ii) for stability expresses the important role (in this model) of adult density control of

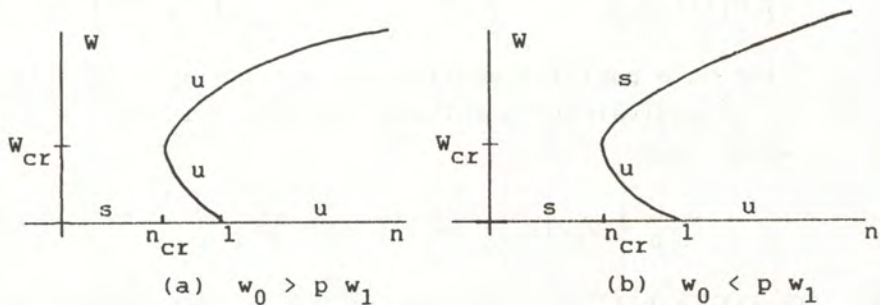


Fig. 8

fertility. In particular if adult density has no effect on (adults) fertility  $w_1 = 0$  then there is no stable positive equilibrium (cf. Fig. 7a).

Taking a hint from the previous example (a) one might naturally consider the possibility of nonconstant periodic solutions for  $n_{cr} < n < 1$  in which the age classes are synchronized. It is not difficult to see in the current example that if  $e_0 > 0$ ,  $e_1 > 0$  is an equilibrium then



$$\begin{aligned} \rho_0(i) &= \rho_0 \quad \text{for } i \text{ odd and } 0 \quad \text{for } i \text{ even} \\ \rho_1(i) &= 0 \quad \text{for } i \text{ odd and } p\rho_0 \quad \text{for } i \text{ even} \end{aligned} \quad (12)$$

where

$$\rho_0 = e_0(w_0 + pw_1)/pw_1. \quad (13)$$

Such 2-cycles are fixed points of the composite map  $m \circ m$  and their stability is determined by the eigenvalues of the Jacobian of  $m \circ m$ . This analysis leads us to the following conclusions. If  $n$  is such that there exists a positive equilibrium then for this  $n$  there exists a positive 2-cycle (12) which is stable if and only if (that is, the eigenvalues  $\lambda$  of the Jacobian of the composition  $m \circ m$  satisfy  $|\lambda| < 1$  if and only if)

$$(iii) \quad 0 < -n f'_0(w_0)w_p < 2$$

$$(iv) \quad f(w_0w_0/pw_1) < f(w_0).$$

Note that (iii) implies (i).

In summary: a positive 2-cycle (12)-(13) exists whenever a positive equilibrium exists and the 2-cycle is stable if (iii)-(iv) hold.

The 2-cycle can be stable if the equilibrium is either stable or unstable. Suppose  $f$  has a graph as in Fig. 9. This gives rise to bifurcation diagrams as in Fig. 8. As an example if  $w_0$

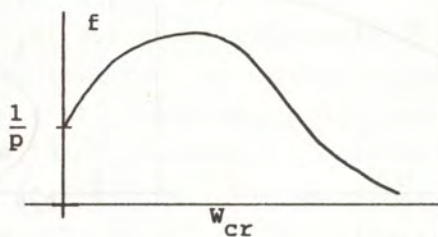


Fig. 9

is close to (but larger than)  $W_{cr}$  then (iii) and hence (i) hold and if  $w_0$  is small then clearly both (ii) and (iv) hold. In this case for  $n$  near (but larger than)  $n_{cr}$  in the bifurcation diagram Fig. 8b there is a stable equilibrium from the upper branch (near the turning point) as well as a stable 2-cycle.

As another example, if again  $W_0$  is close to (but larger than)  $W_{cr}$  but instead  $w_0 > pw_1$  then (ii) fails but (iii) and (iv) hold. In this case the equilibrium from the upper branch near the turning point is unstable while the 2-cycle is stable as in Fig. 8a.

A concrete case is provided by  $f = [1 + W - 2W^2]_+/p$  whose bifurcation diagrams for both equilibria and 2-cycles appear in Fig. 10.

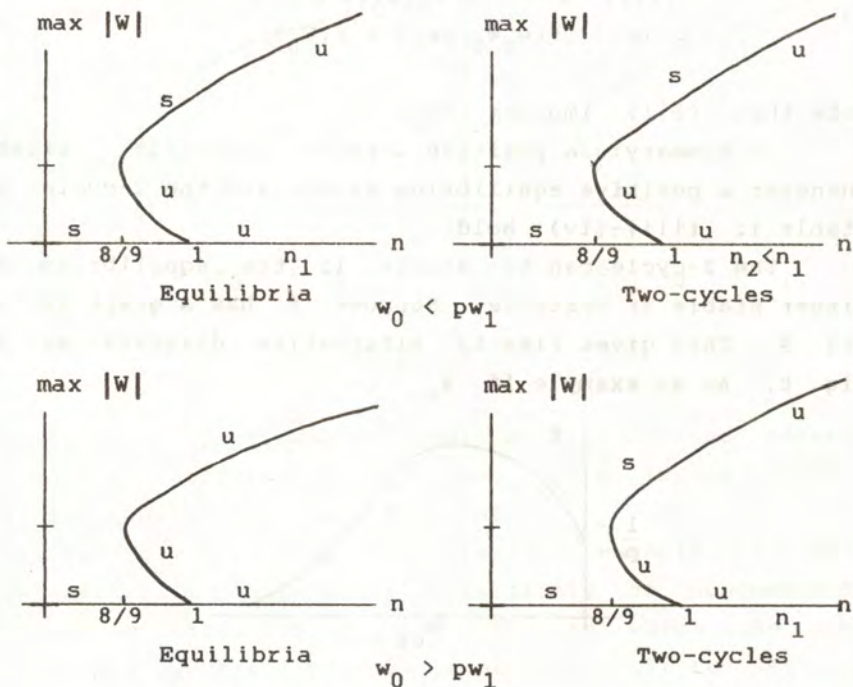


Fig. 10

As in the first example we note that some of the distinctive characteristics of these 2-cycles include their appearance (with increasing inherent net reproductive rate  $n$ ) as large amplitude oscillations with a period equal to the maturation period for "small" values of  $n$  and their synchronization of the age classes.

Nonconstant periodic asymptotic states are not unusual in models of population growth. The mechanisms which lead to such oscillations in the overwhelming majority of cases, however, are relatively few: time delays, periodic forcing or multi-species interactions (such as predator-prey interactions). In the example above one finds asymptotic periodic states which are the result of different mechanisms, namely age structure and subcritical bifurcation (multiple equilibria). Moreover the characteristics of these periodic solutions are different in many fundamental aspects. In the bifurcation diagram Fig. 3 as  $n$  is increased through the critical value  $n_{cr}$  the population passes from one of non-viability ( $\rho \equiv 0$  is globally attracting) to one which possesses not only two stable equilibrium states but which possesses attracting nonconstant periodic states as well. At onset these periodicities are of large amplitude and consequently this phenomenon is quite different from the onset of small amplitude oscillations by means of a familiar stable Hopf bifurcation. Moreover the oscillations exist for "small" parameter values  $n < 1$  unlike the more familiar examples of Hopf bifurcation occurring for a critical value greater than 1 in the supercritical bifurcation case. Also the limit state depends on the initial age distribution, in the first example, unlike the case of limit cycles.

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