

Oscillatory Population Growth in Periodic Environments

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Received September 21, 1984

A general first-order nonlinear differential equation is derived for the dynamics of a population in such a way that the inherent growth rate r and the equilibrium "carrying capacity" K appear explicitly as parameters. By means of standard regular perturbation techniques, properties of the periodic asymptotic state of the population are studied under the assumption that r and K suffer periodic perturbations of small amplitude. Specific examples are studied analytically and numerically.

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1. INTRODUCTION

Most natural populations experience fluctuations in biological and environmental factors which affect their growth rates. Despite this rather obvious and often stated fact the amount of analysis which has been carried out on time-autonomous growth models far exceeds that which has been done on models in which parameters are allowed to fluctuate in time. In recent years an increasing amount of attention has been paid in both the biological and mathematical literature to the effects that such fluctuations have on population growth. A great deal of this attention has concerned the important problem of stochastic fluctuations in the parameters of model growth equations. On the other hand, it is clear that many of the fluctuations with which a population must cope are regular and recurring. Birth and death rates can be seasonal. Despite having stochastic variations, climatic factors which affect birth and death rates (such as temperature, humidity, rainfall, and sunlight) can also vary in a regular manner. The quantity and quality of food and other vital resources, the occurrence of predation and competition, and the susceptibility or exposure to diseases or other hazards are but a few other examples of things which can affect a population's growth and which can vary regularly [for example see Pianca (1978, Chapter 2)]. Cycles can be of different lengths, having yearly, monthly, or even daily periods.

In trying to analyze the effects of such regular and nearly periodic fluctuations it is reasonable as a first approximation to consider them to be exactly periodic. A natural approach might then be to study the effects of periodic oscillations in the appropriate parameters of model equations which have been used to describe population growth in constant environments, beginning perhaps with the simplest classical differential equations of population dynamics and mathematical ecology. Surprisingly, there is comparatively little literature on such periodic differential equations.

In general periodic differential equations do not, of course, possess equilibrium solutions. The study of equilibria and their stability, which plays such an important role in population dynamics, is thus replaced by the more difficult problems of the existence and stability of periodic solutions of periodic differential equations. Consequently most of the fundamental techniques used for the analysis of autonomous equations (such as phase plane analysis and the algebraic methods of linearized stability theory) are no longer available and, although the fundamental theory of periodic differential equations is well developed, it becomes much more difficult to analyze even these basic questions for periodic equations than it is for their autonomous counterparts. Some recent papers have concentrated on these questions and some very general existence and stability results for periodic Kolmogorov type equations have been established (Cushing, 1982). Specific types of interspecies interactions, such as predator-prey (Bardi, 1983; Butler and Freedman, 1981; Cushing, 1977a, 1984) and competition interactions (Cushing, 1980, 1983, 1984; de Mottini and Schiaffino, 1981; Rosenblat, 1980) have been studied in more detail. Single-species growth models have been specifically considered by Badii and Schiaffino (1982), Cohen and Rosenblat (1982), Cushing (1977b), and Rosenblat (1980). These references deal for the most part with the existence and stability of positive periodic solutions and do not study other properties of these solutions (e.g., the amplitude, phase, and average of these solutions).

The classical logistic equation with periodic coefficients has been studied in a good deal more depth. The existence and stability questions in this case are easily handled since the equation is solvable, as a Riccati equation, in closed form (Sanchez, 1982). The properties of the periodic solution have been studied analytically and/or numerically by Boyce and Daley (1980), Coleman (1979), Coleman *et al.* (1979), Mottoni and Schiaffino (1979), Nisbet and Gurney (1976), and Sonneveld and van Kan (1979).

If, in addition to the periodicity of the parameter fluctuations, one assumes that these fluctuations are of small amplitude (relative to an average value), then classical perturbation techniques become available for the analysis of periodic solutions. Such methods were used by Rosenblat (1980) in his study of a modified logistic equation. The assumption of

small amplitudes is of course a restrictive one and precludes the consideration of the effects of large "catastrophic" fluctuations in environmental parameters. Nonetheless, small-amplitude oscillations contribute quantitatively and qualitatively to the solution in significant ways and, as pointed out by Rosenblat, to neglect them in favor of averaged quantities can be misleading. Moreover, numerical studies (such as those in Section 5 below) often show for specific equations that the effects of small-amplitude oscillations in parameters can persist for large-amplitude oscillations. Certainly an understanding of the effects of small-amplitude oscillations constitutes the first step in understanding the effects of periodic fluctuations in general and of fluctuations of larger amplitude in particular.

The purpose of this paper is to study in a fairly thorough way the effects of small-amplitude periodicities on a single population whose growth dynamics are governed by a very general differential equation for total population size or density. In Section 3 a general (per unit) nonlinear growth equation for population density is derived in such a way that the *inherent growth rate* r and the equilibrium state or the environmental *carrying capacity* K appear explicitly as parameters. Under the assumption that $K = K_0$ is stable in the autonomous case, the general regular perturbation formulas given in Section 2 are applied to this equation when r and K are subjected to small-amplitude ε periodicities around averages r_0 and K_0 . By means of the lowest-order terms in an expansion of the periodic solution in powers of the amplitude ε , the properties of this solution are studied as they depend upon those of r and K . In particular the extrema, phase, and average of the population density are analyzed. Of particular interest are questions concerning the extent to which some of the results which have been obtained for the simple classical logistic hold for this more general equation and the extent to which some of these results are model dependent and may not hold for nonlogistic growth equations. It will be found, for example, that to lowest order the basic properties of the amplitude and phase of the oscillation in population density are roughly model independent. The value of the average population density, however, turns out to be very model dependent and of importance for this average is the phase difference between the oscillations in r and K .

The results of numerical studies of several examples which illustrate and corroborate the analytical results in Section 3 are given in Section 4. A short summary appears in Section 5.

In this paper only the problem of analyzing the oscillatory properties of a population density is studied when the parameters r and K in its governing dynamical growth law are subjected to periodic oscillations. The interesting question of the evolution of parameters describing population growth under such periodicity conditions, as was studied by Hastings (1984), is not considered here.

2. SMALL-AMPLITUDE PERIODICITIES

Consider a general growth model equation

$$P' = f(P, \bar{v}) \quad (2.1)$$

in which the time rate of change P' of some measure of population size or density $P = P(t)$ is both a function of population size and of an n -vector \bar{v} of model parameters. Suppose that for parameter values $\bar{v} = \bar{v}_0$ there exists a stable equilibrium $P = P_0$, i.e., suppose that

$$f(P_0, \bar{v}_0) = 0, \quad f_P(P_0, \bar{v}_0) < 0.$$

If the model parameters in the vector \bar{v} are given small amplitude, periodic perturbations of the form

$$\bar{v} = \bar{v}_0 + \varepsilon \bar{v}_1(t) + \varepsilon^2 \bar{v}_2(t) + \cdots \quad (2.2)$$

around the average \bar{v}_0 , then (2.1) becomes a nonautonomous periodic differential equation. Here ε is a small real, $\bar{v}_i(t)$ is a periodic vector valued function of minimal period p and with zero average:

$$\text{av}[\bar{v}_i(t)] := \frac{1}{p} \int_0^p \bar{v}_i(t) dt = 0.$$

Well known theorems (Coddington and Levinson, 1955, Chapters 1 and 14) can be applied to (2.1) to yield the existence of a stable periodic solution, under suitable smoothness assumptions on f , of the form

$$P(t) = P_0 + \varepsilon P_1(t) + \varepsilon^2 P_2(t) + \cdots \quad (2.3)$$

for ε small and for periodic coefficients $P_i(t)$. The coefficients P_i can be calculated by solving certain recursive linear, nonhomogeneous differential equations obtained by substituting the expansions (2.2) and (2.3) into Eq. (2.1) and equating coefficients of like powers of ε on both sides of the resulting equation. The first two of these equations are

$$P'_1 = f_P^0 P_1 + f_{\bar{v}}^0 \cdot \bar{v}_1 \quad (2.4a)$$

$$P'_2 = f_P^0 P_2 + P_1 f_{P\bar{v}}^0 \cdot \bar{v}_1 + f_{\bar{v}}^0 \cdot \bar{v}_2 + \frac{1}{2} f_{PP}^0 P_1^2 + \frac{1}{2} f_{\bar{v}\bar{v}}^0 \bar{v}_1 \cdot \bar{v}_1. \quad (2.4b)$$

Here, as throughout the paper, subscripts denote partial differentiation, $f_{\bar{v}}$ denotes the gradient of f with respect to \bar{v} , $f_{\bar{v}\bar{v}}$ denotes the Jacobian matrix of second partial derivatives, the superscript 0 denotes evaluation at $\varepsilon = 0$ (i.e., at $P = P_0$, $\bar{v} = \bar{v}_0$), and the dot denotes the usual n -vector scalar product.

Equation (2.4a) allows a determination, to lowest order in ε , of various oscillatory properties of the solution (2.3) such as amplitude and phase. An averaging of this equation yields $\text{av}[P_1] = 0$ so that the effects of parameter oscillations on the average population size can be determined only by computing $\text{av}[P_2]$ since

$$\text{av}[P] = P_0 + \varepsilon^2 \text{av}[P_2] + \dots$$

An averaging of Eq. (2.4b) shows that

$$\text{av}[P_2] = -(\text{av}[P_1 f_{p\bar{v}}^0 \cdot \bar{v}_1] + \frac{1}{2} f_{pp}^0 \text{av}[P_1^2] + \frac{1}{2} \text{av}[f_{\bar{v}\bar{v}}^0 \bar{v}_1 \cdot \bar{v}_1]) / f_p^0. \quad (2.5)$$

3. A GENERAL PER UNIT GROWTH RATE EQUATION

We wish to apply the technique of Section 2 to a general model of density-dependent population growth in which two specific biological and environmental parameters have been distinguished. The first assumption of this model is that the population has an inherent exponential growth rate r , i.e., in the absence of density effects (in other words, at low population densities) population growth is described by the equation

$$P'/rP = 1. \quad (3.1)$$

Here r is a constant which can be positive or negative. It is referred to as the *inherent growth rate* and is one of the two fundamental parameters in our model.

The second assumption is that for large population densities the growth dynamics represented by (3.1) must be modified by a term g on the right-hand side which is a function of P and that this modification results in the existence of (at least one) stable positive equilibrium K . We assume that this density term g depends on a parameter p which determines this equilibrium level: $g = g(P, p)$. Thus we replace the right hand side of (3.1) by $1 - g(P, p)$ where $g(0, p) \equiv 0$ and $g(K, p) = 1$. This equation can in general be solved for $p = p(K)$ ($g_p(K, p) \neq 0$ is sufficient) and if we denote $g(P, p(K))$ by $h(P, K)$ we arrive at the equations

$$P' = rP(1 - h(P, K)), \quad h(0, K) \equiv 0 \quad (3.2)$$

$$h(K, K) \equiv 1. \quad (3.3)$$

The stability assumption of $P \equiv K$ means that

$$-rKh_p(K, K) < 0. \quad (3.4)$$

Two differentiations of (3.3) with respect to K yield

$$h_p(K, K) + h_K(K, K) \equiv 0, \quad h_{PP}(K, K) + 2h_{PK}(K, K) + h_{KK}(K, K) \equiv 0. \quad (3.5)$$

The model equation (3.2) depends on the two parameters r, K which, in keeping with the classical logistic equation when $h = P/K$, we have termed the *inherent growth rate* and *environmental carrying capacity*, respectively. Our goal is to study Eq. (3.2) when these two parameters are given small-amplitude periodic oscillations as in Section 2. Periodic fluctuations in the inherent growth rate r could be due for example to seasonal birth or death rates. Fluctuations in K , the equilibrium density supportable by the habitat or environment if conditions are held constant, could be due to a variety of causes such as seasonal availability of food, cycles in other required resources such as light and water, temperature and other climatic changes, and many others. Although not necessarily strictly accurate, we will refer to r as a biological parameter which to some extent might be under the control of the population and to K as an external environmental parameter.

Suppose then that the environmental parameter K is subject to oscillations

$$K = K_0(1 + \varepsilon K_1(t) + \varepsilon^2 K_2(t) + \cdots), \quad K_0 > 0, \quad \text{av}[K_i(t)] = 0 \quad (3.6)$$

about the average K_0 . Here ε is a small (dimensionless) parameter and can be thought of as a measure of the amplitude of the oscillation in K (relative to the average K_0). $K_i(t)$ is a (dimensionless) periodic function of minimal period p and of zero average.

Similarly we assume that r can have periodic oscillations

$$r = r_0(1 + \varepsilon r_1(t) + \varepsilon^2 r_2(t) + \cdots), \quad \text{av}[r_i(t)] = 0 \quad (3.7)$$

where $r_i(t)$ is a periodic function of period p and zero average. The average r_0 can be positive or negative.

It will be assumed that the average $K_0 > 0$ is a stable equilibrium when r and K are held constant (i.e., when $\varepsilon = 0$)

$$h^0 = 1, \quad r_0 \lambda > 0, \quad \lambda := K_0 h_p^0 \quad (3.8)$$

where $h^0 = h(K_0, K_0)$, $h_p^0(K_0, K_0)$, etc.

By the general results and techniques outlined in Section 2 with $f = rP(1 - h(P, K))$, $\bar{v} = \text{col}(r, K)$ Eq. (3.2) with (3.6) and (3.7) has a periodic solution of period p

$$P(t) = K_0(1 + \varepsilon P_1(t) + \varepsilon^2 P_2(t) + \cdots)$$

for small ε . Our goal here is to study the phase, amplitude, and average of P , as they depend on the properties of r and K , by calculating the necessary lower-order terms in this expansion.

Formula (2.4a) together with (3.6) and (3.7), yields the linear differential equation

$$P_1' = -r_0 \lambda P_1 + r_0 \lambda K_1 \tag{3.9}$$

for P_1 . Note that the oscillatory terms r_i in r are absent in this equation.

More specifically, if K_1 is expanded in a trigonometric Fourier series

$$K_1(t) = \sum_{n \geq 1} a_n \cos 2\pi n t/p + b_n \sin 2\pi n t/p$$

then

$$P_1(t) = \sum_{n \geq 1} A_n \cos 2\pi n t/p + B_n \sin 2\pi n t/p$$

$$A_n = \tau \lambda \frac{\tau \lambda a_n - 2\pi n b_n}{\tau^2 \lambda^2 + 4\pi^2 n^2}, \quad B_n = \tau \lambda \frac{2\pi n a_n + \lambda b_n}{\tau^2 \lambda^2 + 4\pi^2 n^2}, \quad \tau := p r_0. \tag{3.10}$$

Consequently

$$\begin{aligned} \text{av}[P_1^2] &= \frac{1}{2} \sum_{n \geq 1} A_n^2 + B_n^2 = \frac{1}{2} \sum_{n \geq 1} \frac{\tau^2 \lambda^2}{\tau^2 \lambda^2 + 4\pi^2 n^2} (a_n^2 + b_n^2) \\ &\leq \frac{1}{2} \sum_{n \geq 1} a_n^2 + b_n^2 = \text{av}[K_1^2]. \end{aligned} \tag{3.11}$$

The magnitude $|\tau|$ of the dimensionless constant τ will play an important role in some of the analysis that follows. It is the ratio of the forcing period p to the so-called (averaged) “characteristic response time” $1/|r_0|$ of the population’s exponential growth at low density.

From these formulas

$$\text{av}[P_1^2] \rightarrow \begin{cases} 0 & \text{as } |\tau| \rightarrow 0 \\ \text{av}[K_1^2] & \text{as } |\tau| \rightarrow +\infty \end{cases} \tag{3.12}$$

and

$$P_1 \sim K_1 \text{ for } |\tau| \sim +\infty, \quad P_1' \sim \tau \lambda K_1 \text{ for } |\tau| \sim 0.$$

These results lead us to the following conclusions concerning the general growth model (3.2) and (3.3) with periodic parameters (3.6) and (3.7). *To lowest order the oscillations in population density P are determined by the*

oscillation in the environmental parameter K only and not that in the inherent growth rate r . The amplitude $\text{av}[P_1^2]$ of the lowest order oscillation in P is always less than that in K and P is never exactly in phase with K . For large values of $|\tau|$ the oscillation in P is close, in phase and in amplitude, to that in K , while for small $|\tau|$ the oscillation in P is small in amplitude and out of phase with K .

These conclusions extend to the general model above many established results known for the periodic logistic $h = P/K$ (May, 1976).

We turn now to the more difficult problem of the average of P . An application of the formula (2.5) yields

$$\begin{aligned} \text{av}[P] &= K_0(1 + \varepsilon^2 \text{av}[P_2] + \cdots) \\ \text{av}[P_2] &= \text{av}[r_1(K_1 - P_1)] + \frac{K_0 h_{KK}^0}{2h_p^0} (\text{av}[P_1^2] - \text{av}[K_1^2]). \end{aligned} \quad (3.13)$$

Consequently the effect of the oscillations in r , K is to decrease the population average below what it would be for r , K held constant at the average values r_0 , K_0 if $\text{av}[P_2] < 0$ or to increase this average if $\text{av}[P_2] > 0$. The formula (3.13) for $\text{av}[P_2]$ shows that *either* is a possibility.

A. That the average population density is decreased by environmental oscillations is a frequently stated tenet in theoretical population dynamics (Boyce and Daley, 1980; May, 1976). It is generally based upon properties of the classical logistic equation with oscillations in K only. Indeed, if $h = P/K$ and if r does not oscillate (i.e., $r_1 \equiv 0$) then

$$\text{av}[P_2] = \text{av}[P_1^2] - \text{av}[K_1^2] < 0$$

by (3.11). This decrease in average density is in fact true for arbitrary periodic oscillations in K in the logistic equation (i.e., it is not restricted to those of small amplitude) (Boyce and Daley, 1980).

Since

$$K_0 h_{KK}^0 / 2h_p^0 = r_0 K_0^2 h_{KK}^0 / 2r_0 K_0 h_p^0$$

we see more generally that if $r_1 \equiv 0$ then $\text{av}[P_2] < 0$ if and only if

$$r_0 h_{KK}^0 > 0. \quad (3.14)$$

Thus, contrary to what happens for the classical logistic equation, an oscillation in K can cause an *increase* in average population density if

$$r_0 h_{KK}^0 < 0. \quad (3.15)$$

That higher-order terms in the density effects h can cause such an increase was observed by Rosenblat (1980) for a generalized logistic equation slightly different from (3.2).

The inequalities (3.14) and (3.15) involve the sign of the average inherent growth rate r_0 as well as the concavity of h as a function of K . The sign of r_0 determines the stability of the trivial solution $P \equiv 0$; i.e., $P \equiv 0$ is unstable if $r_0 > 0$ and stable if $r_0 < 0$. The most common assumption is that $r_0 > 0$, which guarantees that the population increases at low densities and theoretically never goes to extinction. On the other hand, many populations are better described by models in which the zero solution $P \equiv 0$ is stable, i.e., r_0 is negative, so that the model has the property that a minimal initial population size is required before extinction can be avoided and a stable positive equilibrium reached (Beddington and May, 1975). Obviously the sign condition on h''_{KK} required for an increased population average is opposite for these two cases $r_0 > 0$ and $r_0 < 0$.

A simple example of a case when (3.15) holds, together with the resulting increase in population average, can be constructed by choosing $r_0 > 0$ and by choosing the density term h to be, as in the classical logistic equation, a function of the ratio P/K : $h = h(P/K)$ where $h(x)$ as a function of its argument is concave down for large x . This means that the effects of population density level off or saturate for large densities. The function

$$h = \frac{(1 + \beta)(P/K)^m}{(P/K)^m + \beta}, \quad 0 < \beta \tag{3.16}$$

for m a positive integer, is a simple example which meets these requirements and all other requirements of h above. In this case

$$h''_{KK} = m((\beta - 1)m + 1 + \beta)/K_0^2(1 + \beta)^2 \tag{3.17}$$

and Eq. (3.15) holds only if $\beta < (m - 1)/(m + 1)$. Under these condition $av[P_2] > 0$ while the opposite case $av[P_2] < 0$ occurs if this condition fails to be met.

This example shows that the average population density does not always decrease in the presence of environmental periodicities, as it does for the classical logistic, but that it can increase or decrease depending on parameter relationships in the equation. We see then that *it is not possible to assert in general that oscillations in the environmental carrying capacity cause a decrease in average population density, even in the absence of oscillations in the inherent growth rate r .*

B. The effect that an oscillation in r can have on the average population density seems to have been nearly completely overlooked in the

literature. That this effect can be significant is seen by the presence of the first term in the expression (3.13) for $\text{av}[P_2]$.

Suppose that the oscillation in r is decomposed into the sum of a component correlated with the oscillation in K and a component orthogonal to the oscillation in K :

$$r_1 = \kappa K_1(t) + \omega \Omega(t)$$

$$\text{av}[\Omega K_1] = 0, \quad \text{av}[\Omega^2] = 1.$$

Then since $\text{av}[P_1 K_1] = \text{av}[P_1^2]$ (as follows easily from multiplying Eq. (3.9) by P_1 and averaging the result) it follows that

$$\text{av}[r_1(K_1 - P_1)] = \kappa(\text{av}[K_1^2] - \text{av}[P_1^2]) - \omega \text{av}[P_1]$$

and consequently from (3.13) that

$$\text{av}[P_2] = \left(\kappa - \frac{K_0 h_{KK}^0}{2h_p^0} \right) (\text{av}[K_1^2] - \text{av}[P_1^2]) - \omega \text{av}[\Omega P_1]. \quad (3.18)$$

Consider first the case when r and K are strongly positively correlated, i.e.,

$$\kappa > 0, \quad |\omega| \approx 0. \quad (3.19)$$

This case is noteworthy in that varying environmental parameters are likely to affect r and K in similar ways and, in any case, a strongly negative correlation between r and K is not biologically very plausible. Under the assumptions in (3.19), formula (3.18), together with the inequality (3.11), shows that $\text{av}[P_2]$ will be positive if

$$\kappa > \frac{K_0 h_{KK}^0}{2h_p^0} = r_0 h_{KK}^0 \left(\frac{K_0^2}{2r_0 \lambda} \right), \quad (3.20)$$

an inequality valid when (3.15) holds.¹ In the opposite case (3.14) this inequality demands that κ be sufficiently large.

Thus a sufficiently strong positive correlation between the periodicities in r and K together with an oscillation in r of sufficiently large amplitude (this is not required in case (3.15)) will result in an increased average population density.

As will be seen from the examples involving purely sinusoidal oscillations which are studied in the following section, the conditions (3.19) and (3.20) are not the only ways to ensure an increased average population

¹ $\text{av}[P_2]$ will be positive for $|\omega| \approx 0$ whenever this inequality holds regardless of the sign of κ .

density. In particular it may not be necessary that $|\omega|$ be small in order to obtain $\text{av}[P_2] > 0$ from (3.18). Among other possibilities it could happen that κ is large and $\text{av}[\Omega P_1]$ is small (instead of $|\omega|$). For example, it was seen above that if $|\tau|$ is large then $P_1 \approx K_1$ in which case $\text{av}[\Omega P_1] \approx \text{av}[\Omega K_1] = 0$. Consequently an increased average population density can result even when r contains a large-amplitude oscillatory component orthogonal to the oscillation in K (i.e., even when $|\omega|$ is large) provided $|\tau|$ and κ are sufficiently large.

The importance of the phase relationship between r and K was noted by Nisbet and Gurney's (1976) numerical studies of the periodic logistic.

C. In concluding this section we note that $\tau^2 \lambda^2 / (\tau^2 \lambda^2 + 4\pi^2 n^2)$ and hence $\text{av}[P_1^2]$ as functions of increasing τ are decreasing for $\tau < 0$ and increasing for $\tau > 0$. Thus if $r_1 \equiv 0$ and

$$h_{KK}^0 / h_p^0 > 0 \tag{3.21}$$

then the same is true for $\text{av}[P]$. If

$$h_{KK}^0 / h_p^0 < 0 \tag{3.22}$$

then the opposite monotonicity properties for $\text{av}[P]$ hold. For example, in the classical logistic equations, $h_{KK}^0 / h_p^0 = 2/K_0 > 0$ and the average population density is an increasing function of the inherent growth rate r_0 (p fixed). This corroborates the result of Sonneveld and van Kan (1979) when $r_1 \equiv 0$. It is clear here, however, that for nonlogistic growth such a monotonic relationship between the average density and the (constant) growth rate r_0 may not be valid and in fact can be reversed. For example, for h given by (3.16) then $h_p^0 = m\beta/K_0(1 + \beta) > 0$ and h_{KK}^0 is given by (3.17). Thus either (3.21) or (3.22) can hold depending on values of m and β as described above for this example and consequently the average density can either increase or decrease with $r_0 > 0$ for fixed period p .

Another interpretation of these observations can be based on the fact that, for constant parameters, $r_0 \lambda > 0$ in (3.9) measures the strength of the stability of the equilibrium $K = K_0$. Thus for a given value of $K = K_0$ the stability of $P = K_0$ is strengthened with increasing $|r_0|$. When r and K oscillate the stability of the positive periodic solution P is determined by the Floquet exponent which to lowest order is just $-r_0 \lambda$. Consequently it follows, for fixed p , that when r is nonoscillatory and (3.21) holds then increased stability corresponds to increased average population density. On the other hand, if the reverse inequality (3.22) holds then increased stability corresponds to decreased average density.

If r is oscillatory then there is no clear-cut monotonic relationship between the average density and changes in r_0 because of the appearance of the first term in (3.13).

4. SOME EXAMPLES

A. COSINUSOIDAL OSCILLATIONS. Suppose that to lowest order the periodicity in K is simply cosinusoidal $K_1(t) = \cos 2\pi t/p$. Then from the formulas (3.10)

$$P_1(t) = \frac{r\lambda}{(\tau^2\lambda^2 + 4\pi^2)^{1/2}} \cos(2\pi t/p - \psi), \quad \psi = \text{Tan}^{-1}(2\pi/\tau\lambda) \quad (4.1)$$

$$\lambda := K_0 h_p^0, \quad \tau := r_0 p.$$

We see clearly here that P is out of phase with K with the oscillatory properties described in Section 3 as a function of τ . Furthermore, if the periodicity in r is to lowest order cosinusoidal $r_1(t) = R \cos(2\pi t/p + \phi)$, $0 \leq R$, $0 \leq \phi < 2\pi$ then

$$\text{av}[P_2] = \frac{\pi R}{(\tau^2\lambda^2 + 4\pi^2)^{1/2}} \sin(\phi + \psi) - \frac{K_0 h_{\kappa\kappa}^0 \pi^2}{h_p^0 (\tau^2\lambda^2 + 4\pi^2)}$$

or

$$\text{av}[P_2] = \frac{\pi R}{(\tau^2\lambda^2 + 4\pi^2)^{1/2}} \sin(\phi + \psi) - r_0 h_{\kappa\kappa}^0 \frac{K_0^2 \pi^2}{r_0 \lambda (\tau^2\lambda^2 + 4\pi^2)}. \quad (4.2)$$

We see that if the relative amplitude of r_1 vanishes $R=0$, then the sign of $\text{av}[P_2]$ is that of $-r_0 h_{\kappa\kappa}^0$, in keeping with the general results of Section 3.

As far as increasing the average population is concerned $\text{av}[P_2] > 0$ results if $\phi \approx 0$ ($\omega = -R \sin \phi \approx 0$) and $R \approx +\infty$ ($\kappa = R \cos \phi \approx +\infty$), as predicted in the previous section. However, the "optimal" choice of the phase of r , all other parameters held fixed, is determined by

$$\phi + \psi = \pi/2. \quad (4.3)$$

Note that

$$\psi \approx \begin{cases} \pi/2 & \text{for } |\tau| \approx 0 \\ 0 & \text{for } |\tau| \approx +\infty. \end{cases}$$

In the following examples r and K are cosinusoidal

$$K(t) = K_0(1 + \varepsilon \cos 2\pi t/p), \quad r(t) = r_0(1 + \varepsilon R \cos(2\pi t/p + \phi)) \quad (4.4)$$

$$K_0 > 0, \quad 0 \leq R, \quad 0 \leq \phi < 2\pi.$$

B. THE CLASSICAL LOGISTIC. When $h = P/K$ then $\lambda = 1$ in (4.2) and

$$\text{av}[P_2] = \frac{\pi R}{(\tau^2 + 4\pi^2)^{1/2}} \sin(\phi + \psi) - \frac{2\pi^2}{\tau^2 + 4\pi^2}, \quad \psi = \text{Tan}^{-1}(2\pi/\tau).$$

Thus $\text{av}[P_2] > 0$ and the average population density will show an increase if $0 < \phi + \psi < \pi$ and

$$R > \frac{2\pi}{(\tau^2 + 4\pi^2)^{1/2}} \csc(\phi + \psi).$$

The optimal phase ϕ for r is

$$\phi = \frac{\pi}{2} - \text{Tan}^{-1}\left(\frac{2\pi}{\tau}\right) \tag{4.5}$$

in which case the relative amplitude must satisfy

$$R > \frac{2\pi}{(\tau^2 + 4\pi^2)^{1/2}}. \tag{4.6}$$

Figure 1 shows the effect of the phase ϕ on the maximum, minimum, and average of the population density computed and graphed from many numerical solutions of the classical logistic with coefficients (4.4) for selected parameter values. It clearly shows the population average being maximum and greater than both the constant environment average $K_0 = 1$ and the population average if r does not oscillate $R = 0$ at a phase angle ϕ

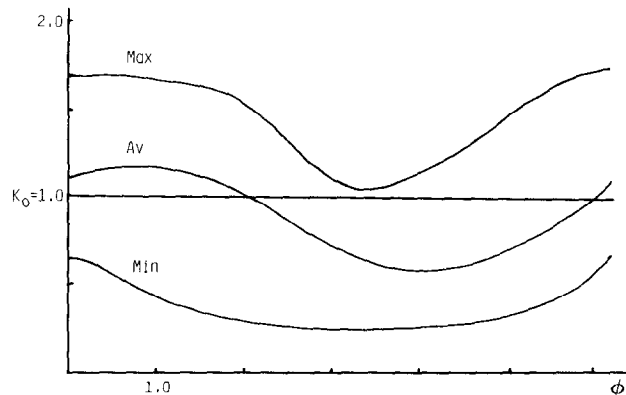


FIG. 1. The maximum, minimum, and average of solutions of the periodic logistic ((3.2) with $h = P/K$) with cosinusoidal coefficients (4.4) are plotted as functions of the phase difference ϕ between r and K . The numerical solutions were computed with $K_0 = 1.0$, $r_0 = 10.0$, $p = 1$, $R = 1.33$, and $\epsilon = 0.75$ in (4.4).

very close to that prescribed by (4.5) when $r_0 = 10$ (namely, $\phi = 1.01$). Note that certain phase angles ϕ result in population averages below both of these averages.

Figure 2 shows the effect of the relative amplitude R in the growth rate oscillation for the same parameter values as in Fig. 1 and at approximately the optimum for the phase angle $\phi = 1$. The average density rises above the constant parameter average $K_0 = 1$ only when R is larger than a value roughly approximated by (4.6) (namely, $R = 0.53$), even though in these graphs $\varepsilon = 0.75$ is not exceptionally small.

Figure 3 is a graph illustrating the monotonic increase of average population density and of the oscillatory amplitude with increased average growth rate r_0 when the growth rate r is nonoscillatory $R = 0$.

C. EXAMPLE (3.16). For h given by (3.16) the oscillation in P_1 is given by (4.1) with $\lambda = m\beta/(1 + \beta)$. Then $\text{av}[P_2]$ is given by (4.2) with h_{KK}^0 as in (3.17).

The point of this example is to demonstrate that it is possible to have an increased average density even in the absence of oscillations in r . Thus take $R = 0$ (ϕ is irrelevant). Then $\text{av}[P_2]$, as pointed out in Section 3, is positive if and only if $\beta < (m - 1)/(m + 1)$.

Figure 4 shows computed averages (and extrema) as a function of β for $m = 2$. It is seen in Fig. 4 that the average density is greater than the constant environmental case $K_0 = 1$ for β smaller than approximately 0.4, which is close to the value $1/3$ obtained from the lowest-order approximation $(m - 1)/(m + 1)$ when $m = 2$.

In Fig. 5 is illustrated the point made in Section 3 that it is possible for the average population density to either increase or decrease with an increase in average growth rate r_0 , depending upon parameter relationships.

D. AN EXAMPLE WITH $r_0 < 0$. Consider the case when

$$h = P(K + K^* - P)/KK^*, \quad 0 < K^* < K \quad (4.7)$$

with $r_0 < 0$ in (3.2). Equation (3.2) then has three equilibria: $P = 0$ which is stable, $P = K^*$ which is unstable, and $P = K$ which is stable. Thus in the autonomous case of constant coefficients, extinction can be avoided and the equilibrium state K attained only if the initial population density is sufficiently large (namely, greater than K^*).

Now let r and K take on the cosinusoidal oscillations (4.4) with $r_0 < 0$, $K_0 > K^*$. Then the lowest-order oscillation coefficient P_1 is given by (4.1) with $\lambda = (K^* - K_0)/K^* > 0$ and $\text{av}[P_2]$ is given by (4.2) with

$$r_0 h_{KK}^0 = 2r_0(K^* - K_0)/K_0^2 K^* > 0.$$

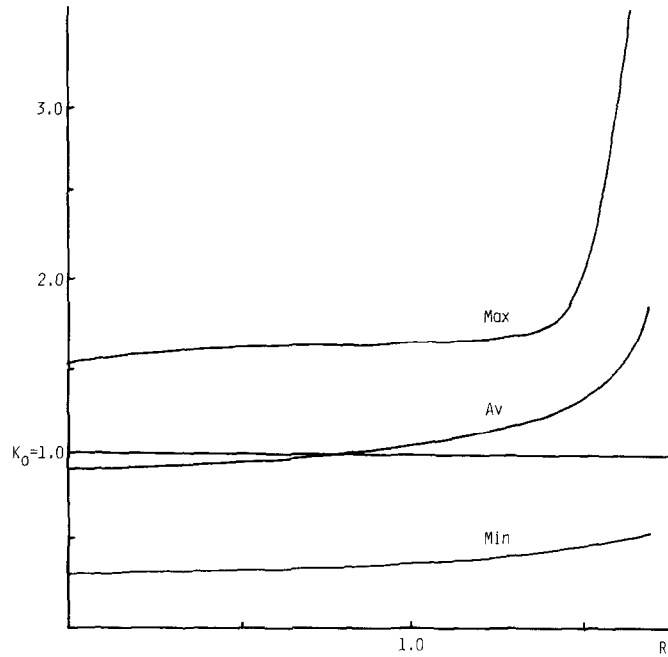


FIG. 2. The maximum, minimum, and average of solutions of the periodic logistic ((3.2) with $h = P/K$) with cosinusoidal coefficient (4.4) are plotted as functions of the relative amplitude R of r . Numerical solutions were computed with $K_0 = 1.0$, $r_0 = 10.0$, $\phi = 1.0$, $p = 1$, and $\epsilon = 0.75$ in (4.4).

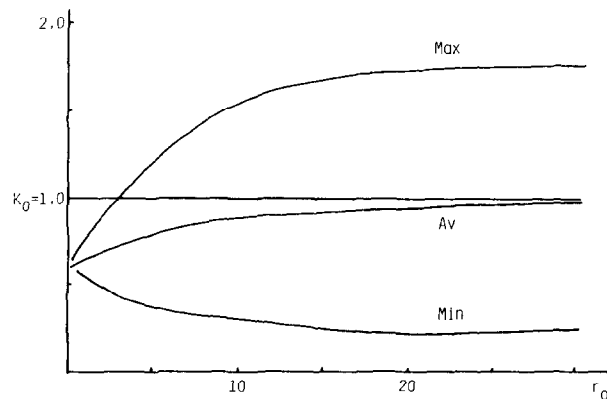


FIG. 3. The maximum, minimum, and average of solutions of the periodic logistic ((3.2) with $h = P/K$) with cosinusoidal coefficients (4.4) are plotted as functions of the average inherent growth rate r_0 . Numerical solutions were computed with $K_0 = 1.0$, $R = 0.0$, $\phi = 0.0$, $p = 1$, and $\epsilon = 0.75$ in (4.4).

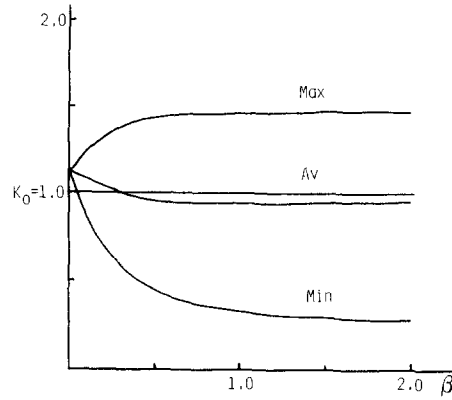


FIG. 4. The maximum, minimum, and average of solutions of (3.2) with h given in (3.16) are plotted against β . Here $m=2$ in (3.16) and other parameter values are $K_0=1.0$, $r_0=10.0$, $R=0.0$, $\phi=0.0$, $p=1$, and $\varepsilon=0.75$.

In the absence of oscillations in r the average population density is decreased below K_0 . The optimal phase ϕ for a cosinusoidal oscillation (4.4) in r is given by (4.3) or

$$\phi = \frac{\pi}{2} - \text{Tan}^{-1} \frac{2\pi K^*}{\tau(K^* - K_0)}. \tag{4.8}$$

In Fig. 6 the extrema and average of P are plotted against the phase difference ϕ for selected values of the parameters. For phase differences ϕ

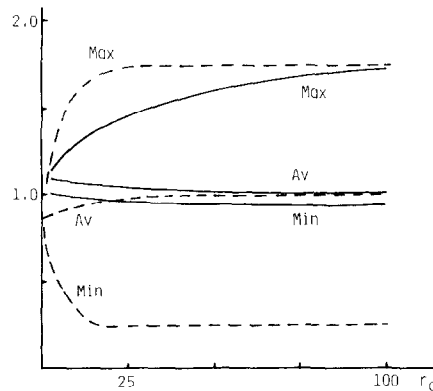


FIG. 5. The maximum, minimum, and average of solutions of (3.2) with h given by (3.16) are plotted as functions of the average inherent growth rate r_0 . The solid lines are for $\beta=0.1$ and the broken lines are for $\beta=1.0$. Here $m=2$ and other parameter values are $K_0=1.0$, $R=0.0$, $\phi=0.0$, $p=1$, and $\varepsilon=0.75$.

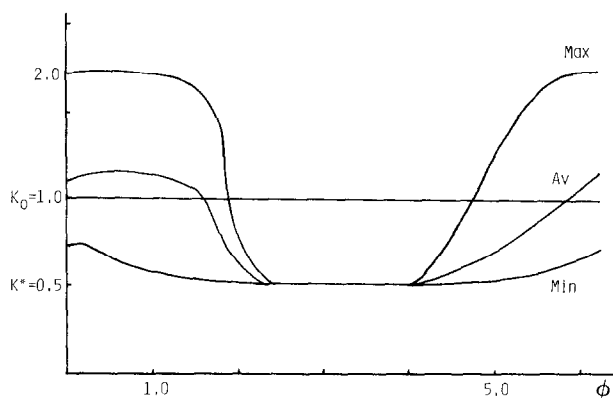


FIG. 6. The maximum, minimum, and average of solutions of (3.2) with h given by (4.7) are plotted as functions of the phase difference ϕ between r and K . Other parameter values are $K_0 = 1.0$, $K^* = 0.5$, $r_0 = -10.0$, $R = 1.33$, $p = 1$, and $\varepsilon = 0.75$.

between about -0.48 and 1.6 the population averages are indeed greater than the nonoscillatory equilibrium K_0 (the optimal ϕ predicted by the lowest-order approximation (4.8) is 1.01).

A very interesting feature of this example illustrated in Fig. 6 is that for r and K out of phase ($\phi \approx \pi$) the population density is forced very near the *unstable* autonomous equilibrium K^* .

Fig. 7 shows an increasing average population density with increasing magnitude $|r_0|$ as predicted by the theory of Section 3.

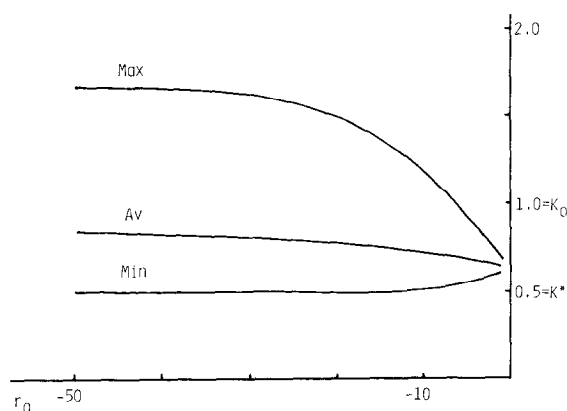


FIG. 7. The maximum, minimum, and average of solutions of (3.2) with h given by (4.7) are plotted as functions of the (negative) average inherent growth rate r_0 . Other parameter values are $K_0 = 1.0$, $K^* = 0.5$, $R = 0.0$, $\phi = 0.0$, $p = 1$, and $\varepsilon = 0.75$.

5. SUMMARY AND CONCLUSIONS

A general nonlinear per unit growth rate model equation (3.2) for population density P was derived in which the inherent growth rate r and an assumed existent (but not necessarily unique) equilibrium K appear as parameters. Under the assumptions that r and K are subjected to small-amplitude p -periodic oscillations around averages r_0 and $K_0 > 0$, where K_0 is assumed stable as a nonoscillatory equilibrium of the averaged equation, the lowest-order terms in the ε expansion of the stable periodic oscillation in the population density P were derived by the standard perturbation techniques given in Section 2. An analysis of these terms leads to several conclusions regarding the properties of P as they depend upon the properties of r and K .

To lowest order the oscillation in P depends only on the oscillation in K and not that in r . The oscillation in P is always less in (relative) amplitude than that in K and is never exactly in phase with K . However, as is well known for the classical logistic, the population in general tends to "track" K for large values of $p|r_0|$ in the sense that both its (relative) amplitude and its phase tend to those of K as $p|r_0| \rightarrow +\infty$. On the other hand, for small $p r_0$, the oscillation in P has a vanishingly small (relative) amplitude and a phase which tends to that of K' as $p r_0 \rightarrow 0$. The population density of populations with small average inherent growth rates r_0 is thus less affected by small-amplitude environmental oscillations of a given fixed period p than that of populations with large average inherent growth rates. These general facts are well known for the case of the classical logistic. It was found here that (for small-amplitude oscillations at least) they hold for general growth models.

With regard to the average population density the situation is a good deal more complicated. A tenet often espoused in the literature is that environmental oscillations cause a decrease in average population density. It is found by the analysis in Section 3 that in general this is not true and that this tenet is a very model-dependent phenomenon.

A drop in average population density will indeed occur if there is no oscillation in the inherent growth rate r and if, as in the classical logistic equation, a certain concavity condition depending on the sign of r_0 holds for the density response term h as a function of the carrying capacity K . Otherwise a drop in average population density may not occur. In fact if the opposite concavity condition holds an *increase* in average population density will result from oscillations in K .

Moreover, if oscillations in r occur in addition to those in K , then the effect on the average population density is even more involved. Depending upon the phase and relative amplitude, an oscillation in r can contribute to either an increase or a decrease in average density and can either enhance

or detract (even reverse) the effect of an oscillation in K . In fact, one result of the analysis is that regardless of the properties of the density term h as a function of K , the oscillatory properties K , or the sign of the average inherent growth rate r_0 , it is always possible to obtain an increase in average population density by an appropriate choice of the phase and amplitude of r (relative to those in K). In particular if r is strongly positively correlated with the oscillation in K and of sufficiently large amplitude then an increase average population density will occur. As the examples in Section 4 show, however, an increased average population density can occur under other circumstances as well.

The importance of the phase relationship between r and K can be seen in the examples of Section 4 where many of the analytical results are illustrated numerically. Of particular interest is example D where it is seen that for an appropriate "optimal" phase difference the average population is increased above the constant (averaged) parameter case while for other phase differences the population average (and maximum and minimum) are extraordinarily close to an unstable equilibrium. Under certain conditions it appears that a population can be forced near an unstable equilibrium by oscillations in r and K .

Another property of the classical logistic which was found to be model dependent is the monotonic increase of average population density which increases in the average inherent growth rate r_0 . When r does not oscillate the monotonic relationship between average population density and r_0 depends on the concavity of the density term h . When r does oscillate there is no clear-cut monotonic relationship at all between these parameters.

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