

Time Delays in Single Species Growth Models

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Summary

A general model is considered for the growth of a single species population which describes the per unit growth rate as a general functional of past population sizes. Solutions near equilibrium are studied as functions of $\varepsilon = 1/b$, the reciprocal of the inherent per unit growth rate b of the population in the absence of any density constraints. Roughly speaking, it is shown that for large ε the equilibrium is asymptotically stable and that for ε small the solutions show divergent oscillations around the equilibrium. In the latter case a first order approximation is obtained by means of singular perturbation methods. The results are illustrated by means of a numerically integrated delay-logistic model.

1. Introduction

One of the most common experiments in population dynamics is that involving the growth of a single species in an isolated laboratory environment with a constant supply of food. Typically, there are a variety of radically different outcomes: the population might become extinct; or it might fluctuate wildly, often about some equilibrium; or it might stabilize at some equilibrium value either monotonically or in an oscillatory manner. After having made these same observations May et al. [5, 6] offer an explanation of these various possibilities in terms of an interplay between what they call "the characteristic return time" inherent in the density-dependence of the species and the time delays present in the response of the population to changes in resources and/or the density effects. (These authors also consider time delays due to age structure or the presence of different generations, all of which we ignore here by making the usual assumption that the age distribution in the population is constant.) Their conclusions are drawn from a variety of specific discrete and differential models which are found in the literature. A discussion of these conclusions centered around the delay-logistic equation may be found in [6, 7]; they are briefly as follows: if the characteristic return time (defined to be the reciprocal $1/b$ of the inherent net, per unit birth rate $b > 0$) is large compared to the "delay time" $T > 0$, then the equilibrium is asymptotically stable while if this return time is decreased until it reaches a critical value then oscillations about the equilibrium occur.

Some of these features of single species growth have been mathematically established for certain models. For example, for the logistic equation with a

single instantaneous time lag T (often called Hutchinson's model) it is known that for $1/(bT)$ large the equilibrium is asymptotically stable. If $1/(bT)$ is decreased then the stability becomes oscillatory and eventually yields to the existence of stable periodic solutions as $1/(bT)$ passes through a critical value (see [3, 4, 6] and the references cited therein). May [6, 7] considers the logistic equation with a more general (and realistic) "continuously distributed" delay of Volterra integral form. His mathematical analysis is, however, strictly linear. Rigorously speaking, the linearization approach for this model is valid (at least locally) as far as the stability or even instability of the equilibrium is concerned [1, 8]; however, a study of oscillatory features and the existence of periodic cycles is more difficult as these are essentially nonlinear phenomena. Asymptotic stability of the equilibrium is studied in [2, 9].

The purpose of this paper is to establish mathematically some of the above described features for a very general single species, density-dependent model with continuously distributed delays. We will show, relative to a fixed delay kernel, that for $1/b$ large the equilibrium is (locally) asymptotically stable and that for $1/b$ small the solutions exhibit divergent oscillations about the equilibrium. The latter case is established by proving the existence of solutions, which, to the first order of approximation in $b^{-1/3}$, are divergent oscillations at least for short time intervals. Most likely it is only relatively short time intervals that would be of interest in this case since small population sizes would be subject to extinction. These solutions are found by means of a singular perturbation analysis. All of our results, which are given in chapter 2, are proved in chapter 4. In chapter 3 the delay-logistic equation is discussed and numerically integrated solutions are displayed in order to illustrate the theorems.

2. Results

We consider the general model

$$N'/N = b g \left(\int_{-\infty}^t k(t-s) N(s) ds \right), \quad ' = d/dt \tag{2.1}$$

where the following hypotheses are assumed to hold:

$$(H 1) \quad \begin{cases} b = \text{constant} > 0, g(0) = 1 \\ 0 \leq k(t) \in C^0(R^+, R^+), \int_0^\infty k(t) dt = 1 \\ g(c) = 0 \text{ for some } c \in R^+, c \neq 0, g'(c) < 0 \\ g(\xi) \text{ is twice continuously differentiable in a neighborhood of } \xi = c. \end{cases}$$

Here R is the set of real numbers and $R^+ = \{r \in R : r \geq 0\}$. In this model g describes of course the per unit growth rate as a function of past population sizes as weighted by the delay kernel k and is accordingly referred to as the *density dependence term*. If g were independent of N , that is if $g \equiv 1$, then we see that b is the per unit growth rate of the population in the absence of such density dependent restraints. The constant c is an equilibrium; if it is asymptotically stable, it is called a *carrying capacity* of the environment. Our analysis will be carried out locally near c and as a result no global assumptions are made on g . In particular, we do not necessarily assume that c is a unique equilibrium.

We wish to study the behavior of the solutions of (2.1) as they are functions of the parameter $\varepsilon = 1/b > 0$. By a *solution* of (2.1) we mean an $N \in C^1(\mathbb{R}^+, \mathbb{R}^+)$, bounded and piece-wise continuous on $t \leq 0$, for which (2.1) is an identity for $t > 0$. Notice that we have restricted our definition to positive functions $N(t) \geq 0$ as is only reasonable for applications to population dynamics. We have chosen (arbitrarily, but without loss in generality) the initial time $t=0$ and we refer to the initial value problem associated with (2.1) as that of finding a solution satisfying $N(t) = N_0(t)$, $t \leq 0$ for a given bounded initial function $N_0(t) \geq 0$, $t \leq 0$. This reduces (2.1) to a standard Volterra integrodifferential equation to which basic existence and uniqueness theorems are applicable [10]. We say that the equilibrium c is (locally) *stable* if given $\gamma > 0$ there exists a $\delta = \delta(\gamma) > 0$ such that $|N_0(t) - c| \leq \delta$ for all $t \leq 0$ implies that $|N(t) - c|_0 = \sup_{t \in \mathbb{R}} |N(t) - c| \leq \gamma$ and we say that c is (locally) *asymptotically stable* if in addition $N(t) \rightarrow c$ as $t \rightarrow +\infty$.

Theorem 1: *If (H 1) holds and if $\int_0^\infty t k(t) dt < +\infty$ then the equilibrium c is (locally) asymptotically stable as a solution of (2.1) for $\varepsilon = 1/b > 0$ sufficiently large.*

For small values of $\varepsilon = 1/b$ we have the following result.

Theorem 2: *Suppose that (H 1) holds and for t small $k \in C^2(\mathbb{R}^+, \mathbb{R}^+)$ can be written $k(t) = \mu t + t^2 m(t)$, $\mu = k'(0) > 0$ for $m \in C^2(\mathbb{R}^+, \mathbb{R}^+)$. Let $x_0(t)$, $t \leq 0$, be piece-wise continuous with compact support. Given any finite number $U > 0$ there exists an $\varepsilon_0 = \varepsilon_0(U) > 0$ such that for all $0 < \varepsilon < \varepsilon_0$, $\varepsilon = 1/b$, the unique solution of (2.1) satisfying the initial condition*

$$N(t) = c \exp(\theta x_0(t)), \quad t \leq 0, \quad \theta = \varepsilon^{1/3}$$

is given by

$$N(t) = c \exp(\theta q(t/\theta) + \theta z(t/\theta, \theta)), \quad 0 \leq t \leq U \theta \tag{2.2}$$

where q is given by (4.6) below and hence exhibits exponentially divergent oscillations and where $z \in C^0[0, U]$ satisfies $|z(u, \theta)| = 0(\theta)$ uniformly for $u \in [0, U]$.

Roughly speaking the above theorems state that as the parameter $\varepsilon = 1/b$ passes from large values to small positive values, the model (2.1) possesses respectively an asymptotically stable equilibrium c and divergent oscillations (at least for small t) exhibited by solutions initially near equilibrium. In the latter case we have the first order (in $\varepsilon^{1/3}$) approximation $N \sim c \exp(\varepsilon^{1/3} q(t/\varepsilon^{1/3}))$ valid near $t=0$.

3. An Example

In order to illustrate the results of chapter 2 and also in order to observe the degree of accuracy of the first-order oscillations obtained in Theorem 2 we numerically integrated the delay-logistic model

$$N'/N = b T \left(1 - c^{-1} \int_{-\infty}^t k(t-s) N(s) ds \right) \tag{3.1}$$

with the delay kernel

$$k(t) = t \exp(-t). \tag{3.2}$$

This model has been studied in several publications [6, 7]. Equation (3.1) can be viewed as a reformulation of the delay-logistic with kernel $k_T(t) = t T^{-2} \exp(-t/T)$ by means of a time rescaling from t to t/T . Since the unique maximum of $k_T(t)$ occurs at $t = T$ it is natural to think of T as “the delay” or at least a reasonable measure of the delay represented by this kernel. Equation (3.1) then results from using the delay T as a unit of time and explicitly exhibits this delay parameter in the analysis. Our three theorems of chapter 2 apply to (3.1) with b replaced in the theorems by $b T$.

Clearly (H 1) holds with $g(\xi) = 1 - c^{-1} \xi$ and as a result Theorem 1 applies: $N = c$ is asymptotically stable for $b T$ small. This is illustrated in Fig. 1.

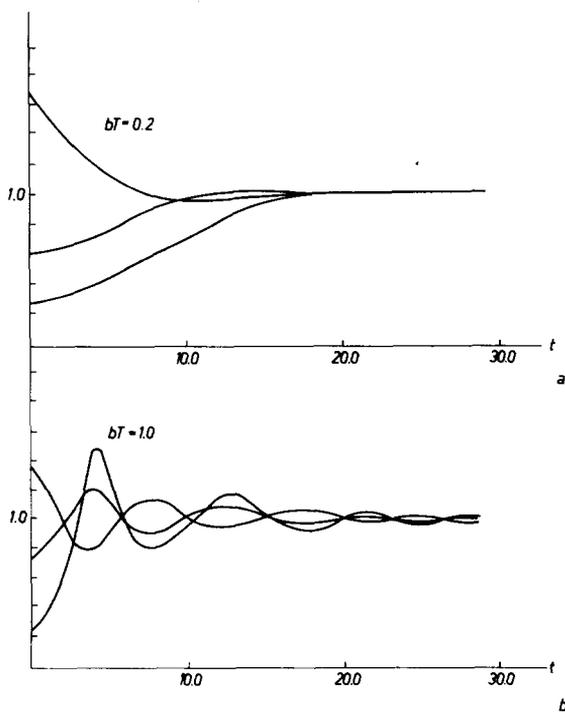


Fig. 1. a) Three solutions of (3.1) are shown for kernel (3.2) and $bT = 0.2$. This illustrates the case of nonoscillatory, asymptotic stability of the equilibrium $N \equiv 1$ for small bT . b) As the value of bT is increased to $bT = 1.0$ the equilibrium is still asymptotically stable, but the solutions are now oscillatory

The critical value of bT is that value at which the linear equation is neutrally stable (e.i. the roots of its characteristic equation are purely imaginary, see the proof of Theorem 2 below). This turns out for this example to be $bT = 2$. For values of bT near 2 the oscillations were numerically found to be sustained as is illustrated in Fig. 2 a.

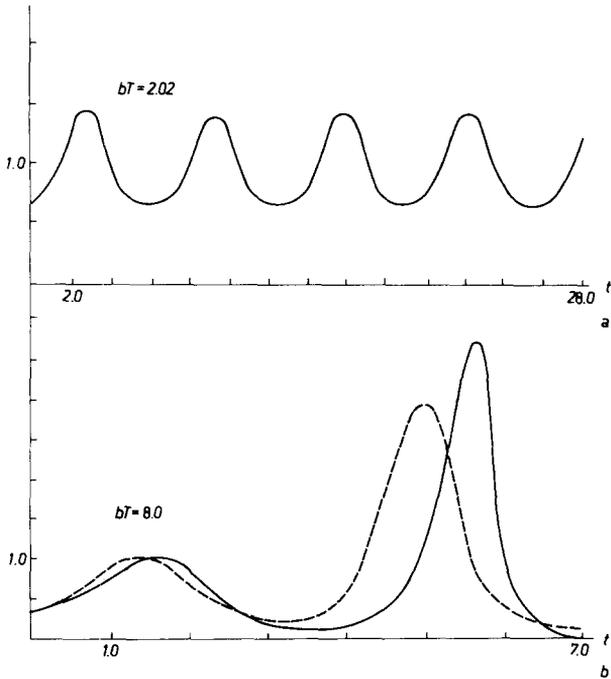


Fig. 2. The solutions of (3.1) with kernel (3.2) for certain initial values are shown (a) for $bT = 2.02$ near the critical value of $bT = 2.0$ and (b) for "large" $bT = 8.0$. The solution in (a) appears to be periodic while the solution in (b) shows a divergent oscillation. The dashed graph in (b) is that of the first order approximation (3.3)

Finally, all the hypotheses on k in Theorem 2 can easily be shown to hold. Hence for bT sufficiently large, solutions $N(t)$ of (3.1) exist which have the asymptotic form (2.2) with $\mu = k'(0) = 1$ and as a result exhibit undamped divergent oscillations. To the first order in $(bT)^{1/3}$

$$N(t) \sim c \exp((bT)^{-1/3} q(t(bT)^{1/3})), \quad t=0((bT)^{-1/3}) \tag{3.3}$$

with q given by (4.6) with $\mu = 1$. This result is illustrated in Fig. 2(b) where a solution is plotted together with the graph of the first order approximation. In this numerical work it was found generally that the first order approximations were qualitatively accurate for at least the first and often for the first two cycles; in particular they seem to predict fairly well the time and magnitude of the first maximum of $N(t)$ and the duration and depth of the first population "crash" or minimum of N . Generally speaking the first order approximation was found to show divergent oscillations whose maxima were slightly smaller (and whose minima were larger) while occurring sooner and with greater frequency than those of the actual solution $N(t)$. For the equations integrated the oscillations of the actual solution quickly became very violent and steep with a period much longer (particularly as t increased) than that of the approximation.

4. Proofs

Proof of Theorem 1: Let $x=N-c$ and write $g(c+\xi)=-a\xi+o(|\xi|)$, $a=-g'(c)>0$. Then (2.1) reduces to

$$x' = -b a c \int_0^t k(t-s)x(s) ds - b a c \int_t^\infty k(s)x_0(t-s) ds + o(|x|_0)$$

where $x_0=N_0-c$. Since $\int_t^\infty k(s)x_0(t-s) ds \rightarrow 0$ as $t \rightarrow +\infty$ for any bounded x_0 we have by means of established linearization principles [1, 8] that $x=0$ (i.e. $N=c$) is locally asymptotically stable if this is true of $x=0$ for the linear equation

$$x' + b a c \int_0^t k(t-s)x(s) ds = 0.$$

This linear equation is asymptotically stable if and only if [8]

$$p(z) \equiv z + b a c k^*(z) \neq 0 \text{ for } \text{Re } z \geq 0$$

$$k^*(z) = \int_0^\infty k(t) \exp(-zt) dt.$$

Thus Theorem 1 will be proved if we can show that the only roots of the characteristic equation $p(z)=0$ lie in the left half plane $\text{Re } z < 0$. Let $\eta = b a c$ and write $p = p(z, \eta)$.

Lemma: *If $k(t)$ satisfies (H 1) as well as $\int_0^\infty t k(t) dt < +\infty$ then there exists a unique solution branch $z = z(\eta)$ of $p(z, \eta) = 0$ defined for η small: $|\eta| < \eta_0$. This branch is such that $z(0) = 0$ and $\text{Re } z(\eta) < 0$ for $\eta > 0$.*

This lemma is an application of the implicit function theorem. We note that $p(0, 0) = 0$, $\partial p(0, 0) / \partial z = 1 \neq 0$ and hence the existence of a unique solution branch as described in the lemma is guaranteed. Implicit differentiation of $p(z(\eta), \eta) = 0$ yields $z'(0) = -1$ so that $\text{Re } z(\eta) < 0$ for $\eta > 0$.

Returning to the proof of Theorem 1, we suppose that the assertion of this theorem is false. Then for some sequence $\eta_n, \eta_n \rightarrow 0$ there exists at least one root z_n of p satisfying $\text{Re } z_n \geq 0$. Thus

$$z_n = -\eta_n \int_0^\infty k(t) \exp(-z_n t) dt$$

from which follows the estimate $|z_n| \leq \eta_n$ and the fact that $z_n \rightarrow 0$ as $n \rightarrow \infty$. Since $\text{Re } z_n \geq 0$ we have a contradiction to the uniqueness assertion in the above lemma and as a result Theorem 1 is proved. ■

Proof of Theorem 2: Let $\bar{N} = \ln(N/c)$ and $\theta = \varepsilon^{1/3}$, $\varepsilon = 1/b$. Letting $u = t/\theta$ and $x(u) = \bar{N}(u, \theta)$ we find that equation (2.1) becomes

$$dx/du = -ac \int_{-\infty}^u \theta^{-1} k(\theta(u-s))x(s) ds + T(x, \theta) \tag{4.1}$$

$$T(x, \theta) = ac \int_{-\infty}^u \theta^{-1} k(\theta(u-s))(1+x-e^x) ds + \theta^{-2} r(c \int_{-\infty}^u \theta k(\theta(u-s))(e^x-1) ds).$$

We attempt to solve (4.1) for small $\theta > 0$, subject to the initial condition

$$x(u) = \theta x_0(u), \quad u \leq 0 \tag{4.2}$$

for $x(u)$ in the form

$$x(u) = \theta q(u) + \theta z(u, \theta) \text{ for } q(u) = x_0(u), z(u, \theta) = 0 \text{ when } u \leq 0 \quad (4.3)$$

where z is higher order in θ : $z = 0(\theta)$.

If (4.3) is substituted into (4.1) and higher order terms in θ are ignored we arrive at the linear equation

$$dq/du + ac\mu \int_{-\infty}^u (u-s)q(s)ds = 0, q(u) = x_0(u) \text{ for } u \leq 0 \quad (4.4)$$

to be solved for $q(u)$, $u > 0$. Here $k(0) = 0$ is used and $\mu = k'(0) > 0$. Now $k(t) = \mu t + t^2 m(t)$, $m \in C^2(\mathbb{R}^+, \mathbb{R}^+)$. The higher order terms in θ yield the following nonlinear equation for z (after a cancellation of a θ)

$$dz/du + ac\mu \int_{-\infty}^u (u-s)z(s)ds = T^*(\theta, z) \quad (4.5)$$

$$T^*(\theta, z) = -ac\theta \int_{-\infty}^u (u-s)^2 m(\theta(u-s))(q+z)ds + \theta^{-1} T(\theta q + \theta z, \theta).$$

First we consider (4.4). This equation can be easily solved by performing two differentiations with respect to u and solving the resulting third order, linear homogeneous ordinary differential equation. This yields q in (2.2):

$$q(u) = A e^{-\lambda u} + e^{2u/2} (B \cos(\lambda u \sqrt{3}/2) + C \sin(\lambda u \sqrt{3}/2))$$

$$3A = x_0(0) - \lambda^2 \left(\int_{-\infty}^0 s x_0(s) ds + \int_{-\infty}^0 x_0(s) ds \right)$$

$$3B = 2x_0(0) + \lambda^2 \left(\int_{-\infty}^0 s x_0(s) ds + \int_{-\infty}^0 x_0(s) ds \right) \quad (4.6)$$

$$3C = \lambda^2 \sqrt{3} \left(\int_{-\infty}^0 s x_0(s) ds - \int_{-\infty}^0 x_0(s) ds \right)$$

$$\lambda = (ac\mu)^{1/3}, \mu = k'(0) > 0, a = -g'(c) > 0.$$

The nonhomogeneous problem

$$dz/du + ac\mu \int_{-\infty}^u (u-s)z(s)ds = f(u), z(u) = 0 \text{ for } u \leq 0$$

has solution $z(u) = \int_0^u G(u, s) f(s) ds$ where the fundamental solution $G(u, s)$ solves

$$\partial G(u, s) / \partial u + ac\mu \int_s^u (u-\sigma)G(\sigma, s) d\sigma = 0, s < u$$

$$G(s, s) = 1, G(u, s) = 0 \text{ for } u < s.$$

Thus

$$G(u, s) = \begin{cases} \frac{1}{3} e^{-\lambda(u-s)} + \frac{2}{3} e^{\lambda(u-s)/2} \cos \lambda \sqrt{3} (u-s)/2, & s \leq u \\ 0, & u < s. \end{cases}$$

Equation (4.5) is accordingly equivalent to

$$z(u) = \int_0^u G(u, s) T^*(\theta, z(s)) ds. \quad (4.7)$$

Consider the Banach space $C^0[0, U]$, $|z|_{0,U} = \max_{0 \leq u \leq U} |z(u)|$ for some arbitrary, but fixed $U > 0$. Let $B_U(r) = \{z \in C^0[0, U] : |z|_{0,U} \leq r\}$. A straightforward investigation of $T^*(\theta, \cdot)$ as an operator from $C^0[0, U]$ into itself (for fixed θ) shows that (a) for fixed small r there exists a $\theta_0 > 0$ such that $|T^*(\theta, z)|_{0,U} \leq r$ for all $0 < \theta < \theta_0$, $z \in B_U(r)$ and that (b) the operator $T^*(\theta, \cdot)$ is Fréchet differentiable at every $z_0 \in B_U(r)$ with $|D_z T^*(\theta, z_0) h|_{0,U} \leq c\theta |h|_{0,U}$ for some constant $c > 0$ and all $h \in C^0[0, U]$. It follows (for θ_0 smaller if necessary) that $T^*(\theta, z)$ is a

contraction from $B_U(r)$ into itself for each θ , $0 < \theta < \theta_0$. Thus, (4.7) has a unique solution $z \in B_U(r)$. Since $|T^*(\theta, z)|_{0, U} = 0(\theta)$ for $z \in B_U(r)$ we see that $|z(u, \theta)|_{0, U} = 0(\theta)$. ■

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