LINEAR CHARACTER-DEPENDENT MODELS WITH CONSTANT TIME DELAY IN POPULATION DYNAMICS

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Abstract—We reduce the extended MacKendrick–Von Foerster formalism of Gurney and Nisbet—an initial boundary value problem—to the solution of a single Volterra integral equation with a constant time lag. We then establish the existence, uniqueness and continuation of solutions for all $t > 0$, and reduce a simplified version of this model to a time-delay version of the classical MacKendrick model, for which the standard stability results for persistent distributions are available.

INTRODUCTION

In 1954 and 1957 Nicholson performed his now classical experiments on laboratory cultures of the sheep blowfly *Lucila cuprina* [1, 2]. Since then, attempts to model this experiment have been made by May [3] and Varley *et al.* [4] among others. According to Blythe *et al.* [5], these attempts have produced at best "generalized insights" and, furthermore, "no theoretical model has yet yielded a truly satisfactory quantitative fit to the time history of even a single culture, still less has it been possible to formulate a comprehensive framework within which the various subtly different experimental results can be systematically interrelated". In a more recent paper, Gurney *et al.* [6] point out that the failure of these models lies in their lack of a mathematically rigorous foundation. Nisbet and Gurney [7] remark that in their 1983 paper with Lawton [6] they "showed that if the life history of an insect involved developmental stages of *arbitrary* duration, then the normal integro-differential equations describing a population with overlapping generations reduced to a set of coupled ordinary delay-differential equations, provided only that all individuals in a particular age class have the same birth and death rates". Their integro-differential equations were derived from the rigorous Lotka–MacKendrick–Von Foerster age-dependent formalism, and when they numerically apply their reduced delay-differential equation formalism to the Nicholson experimental data they obtain close agreement with his experimental results. They further note that "physiologically... for most insect species it is not chronological age but weight gain that triggers the various moults, a doubling of weight during an instar being typical (Dyar's 'law', Chapman [8])", and they mention several well-documented studies "which demonstrate simple linear or nonlinear relationships between growth rate (i.e. weight gained per unit time) and food absorption rate within an instar". Finally, they conclude that "the existence of a well-defined relationship between instar duration and food absorption rate can be expected for many insect species".

The linear formalism of this paper was developed by Nisbet and Gurney [7] in "response to a number of questions raised by the experiments of Lawton *et al.* [1980] on the damselfly *Ischnura elegans* (van der Lind), certain instars of which have the ability to survive for long periods of a 'no food, no growth' state without a high level of deaths through starvation. Instars 10 and 12 could for instance vary in length from under 20 to over 100 days with significant numbers still surviving to the end of the instar". They later used their formalism to construct "a 'strategic model' (in the sense of May [3]) designed to demonstrate the effect on population stability of a high level of elasticity in instar duration".

Although their formalism resembles the MacKendrick–Von Foerster formalism, there is the additional assumption of a time lag corresponding to an egg stage of fixed duration (MacKendrick models with delay have been studied by Cushing [9]). As in their paper with Lawton [6], they reduce their formalism to a set of coupled ordinary delay-differential equations and then they study

them numerically. The resulting model, as they point out, "is not a representation of a damselfly population, but solely a theoretical construct intended to elucidate a regulating mechanism suggested by the damselfly experiments".

In this paper, we first provide a careful new derivation of this model, then we proceed to show that it is well-posed. This is done by reducing the model to the solution of a single Volterra integral equation. Although the possibility of this type of reduction has been mentioned for similar models at least as early as 1967 [10], as far as the author knows, except for the trivial case when the characteristic curves are just lines, nobody has provided a systematic way of doing this reduction. In this paper, the Osgood-Wintner-Conti-Brauer theory of global solutions for ordinary differential equations is used for this purpose [11-17]. This theory is again used by the author in a follow-up paper [24] to analyze a nonlinear version of the Gurney-Nisbet model.

The Gurney-Nisbet Model

In the Gurney-Nisbet (GN) model the dynamics of a one-sex population are described using a density function $f(a, m, t)$, where a denotes age, m denotes size, i.e. mass, and t denotes time. This function describes the size-age structure of the population at time t. We assume that the changes in $f(a, m, t)$ are due to:

- individuals aged between a and $a + \Delta a$ and with size between m and $m + \Delta m$ mature and grow to an older age class and a bigger size class or die;

or, more specifically,

- individuals aged between a and $a + \Delta a$ and with size between m and $m + \Delta m$ who survive enter the age class $a + \Delta a$ to $a + \Delta a + \Delta t$ and enter the size class $m + g(a, m, t)\Delta t$ to $m + \Delta m + g(a, m + \Delta m, t)\Delta t$, where $g(a, m, t)$ denotes the average growth rate of an individual of size m, age a, at time t.

These assumptions provide a basis for the following development of the GN model. We begin by letting:

(a) $f(a, m, t)$ denote the age-size density function so that the number of members of the population at time t with age a between a_0 and a_1 and size m between m_0 and m_1 is given by

$$\int_{m_0}^{m_1} \int_{a_0}^{a} f(a, m, t) \mathrm{d}a \mathrm{d}m;$$

(b) $g(a, m, t)$ be the average growth rate of an individual of age a with size m at time t;

(c) $\theta(a, m, t)$ denote the age-size specific death rate so that $\theta(a, m, t) f(a, m, t) \Delta a \Delta m$ is the number of individuals per unit time dying at time t with age between a and $a + \Delta a$ and size between m and $m + \Delta m$;

(d) $\lambda(a, m', m, t)$ be the age-size specific fertility rate so that

$$\Delta t \int_0^\infty \int_0^\infty \lambda(a, m', m, t) f(a, m', t) \mathrm{d}m' \mathrm{d}a$$

is the total number of offspring of size m in the time interval $(t, t + \Delta t)$;

(e) $f_0(a, m)$ be the initial size-age distribution.

At time $t + \Delta t$ the number of surviving individuals that at time t had sizes between m and $m + \Delta m$ and ages between a and $a + \Delta a$ is given by

$$\int_m^{m+\Delta m} \int_a^{a+\Delta a} f(a', m', t)\mathrm{d}a'\mathrm{d}m' - \theta(a, m, t)f(a, m, t)\Delta a\Delta m\Delta t \simeq f(a, m, t)[1 - \theta(a, m, t)\Delta t]\Delta a\Delta m. \tag{1}$$

Since the size range at time $t + \Delta t$ is between $m + g(a, m, t)\Delta t$ and $m + \Delta m + g(a, m + \Delta m, t)\Delta t$ with age range between $a + \Delta t$ and $a + \Delta a + \Delta t$, we have that the number of individuals at time $t + \Delta t$ with ages between $a + \Delta t$ and $a + \Delta a + \Delta t$ and with sizes between $m + g(a, m, t)\Delta t$ and $m + \Delta m + g(a, m + \Delta m, t)\Delta t$ is therefore given by

$$\int_{m+g(a,m,t)\Delta t}^{m+\Delta m+g(a,m+\Delta m,t)\Delta t} \int_{a+\Delta t}^{a+\Delta a+\Delta t} f(a', m', t + \Delta t)\mathrm{d}a'\,\mathrm{d}m'$$

$$\simeq f(a + \Delta t, m + g(a, m, t)\Delta t, t + \Delta t)\{\Delta m + [g(a, m + \Delta m, t) - g(a, m, t)]\Delta t\}\Delta a.$$

If we approximate $g(a, m + \Delta m, t)$ by $g(a, m, t) + \partial/\partial m[g(a, m, t)]\Delta m$ and equate this expression with equation (1), then after dropping the terms of order higher than 1 we arrive at the following partial differential equation:

$$\frac{\partial}{\partial m}fg + \frac{\partial}{\partial a}f + \frac{\partial}{\partial t}f + \theta f = 0. \tag{2}$$

The "recruitment" of population is given by

$$f(0, m, t) = \int_0^\infty \int_0^\infty \lambda(a, m', m, t)f(a, m', t)\mathrm{d}m'\mathrm{d}a, \qquad t > 0, \tag{3}$$

and the initial size–age distribution is given by

$$f(a, m, 0) = f_0(a, m). \tag{4}$$

The population growth is therefore modelled by the initial boundary value problem (IBVP) described by equations (2)–(4). Observe that equation (3) is not required to hold at $t = 0$. This relation will be satisfied at $t = 0$ iff f_0 satisfies the compatibility condition $f_0(0, 0) = \int_0^\infty \int_0^\infty \lambda(a, m', 0, 0)\mathrm{d}m'\mathrm{d}a$, which simply implies that the initial data be consistent with the renewal process. This kind of construction will not be imposed throughout because our interest is in situations where the initial size–age distribution f_0 is completely arbitrary.

The Age-independent Model

Assume that g, λ, and θ depend on size and time, but not on age; furthermore, let $\rho(m, t)$ be such that $\int_m^{m+\Delta m} \rho(m', t)\mathrm{d}m'$ denotes the number of individuals with sizes in the range m to $m + \Delta m$ irrespective of age, so that $\rho(m, t) = \int_0^\infty f(a, m, t)\mathrm{d}a$. After integrating equation (2) formally from 0 to ∞ on the age variable and under the assumption that $f(\infty, m, t) = 0$, we arrive at the following equation:

$$\frac{\partial}{\partial t}\rho + \frac{\partial}{\partial m}g\rho + \theta\rho = f(0, m, t). \tag{5}$$

Under these circumstances the renewal equation becomes

$$f(0, m, t) = \int_0^\infty \lambda(m, m', t)\rho(m', t)\mathrm{d}m', \qquad t > 0, \tag{6}$$

and the initial condition

$$\rho(m, 0) = \int_0^\infty f_0(a, m) \mathrm{d}a. \tag{7}$$

The size-dependent population growth is then modelled by the IBVP described by equations (5)–(7).

The Renewal Equation

The derivation of the following renewal equation is entirely due to Nisbet and Gurney [7]. For many populations (e.g. insects), the following assumptions are quite reasonable:

(i) all "eggs" have the same size m_1—in other words, all individuals have the same size at birth;

(ii) the egg-stage duration τ_E and the probability of survivorship P_E are constant;

(iii) g, λ and θ depend on size and time.

Hence, if we let $R(t)$ denote the total rate of recruitment at time t from the egg stage and if we let $E(t)$ be the total egg-production rate at time t, then it follows that

$$R(t) = P_E E(t - \tau_E), \tag{8}$$

and since

$$E(t) = \int_{m_1}^\infty \lambda(m', t)\rho(m', t)\mathrm{d}m', \tag{9}$$

then using equation (9), equation (8) can be written as follows:

$$R(t) = P_E \int_{m_1}^\infty \lambda(m', t - \tau_E)\rho(m', t - \tau_E)\mathrm{d}m'. \tag{10}$$

Now, first we observe that $R(t)\Delta t$ gives the total recruitment during the time interval t to $t + \Delta t$ and the recruits will have sizes ranging from m_1 to $m_1 + \Delta m$, where $\Delta m_1 = g(m_1, t)\Delta t$. Secondly, we see that $\rho(m_1, t)\Delta m_1$ also denotes the total number of individuals with sizes in the range m_1 to $m_1 + \Delta m$ at time t. From these observations and equation (10) we obtain

$$\rho(m_1, t) = [P_E/g(m_1, t)] \int_{m_1}^\infty \lambda(m', t - \tau_E)\rho(m', t - \tau_E)\mathrm{d}m', \qquad t > \tau_E, \tag{11}$$

which in conjunction with

$$\frac{\partial}{\partial t}\rho + \frac{\partial}{\partial m}\rho g + \theta\rho = 0, \qquad m > m_1, \tag{12}$$

and an appropriate initial condition, provide us with a description of the dynamics of a population satisfying assumptions (i)–(iii). To prescribe the initial conditions, we could proceed in at least two ways:

(a) we could assume that the birth rate has been prescribed for the time interval $[0, \tau_E]$ by a function $\Psi(t)$, i.e.

$$\rho(m_1, t) = \Psi(t), \qquad 0 \leqslant t \leqslant \tau_E,$$

(b) we could assume an empty system $[\rho(m,t) = 0$ for $t < 0]$ which is then instantaneously "seeded" with an initial size distribution $\rho(m,0) = \rho_0(m)$.

A Delay-differential Equation

If we now assume that g, θ, λ depend only on time and let $F(t) = \int_{m_1}^{\infty} \rho(m',t)\mathrm{d}m'$ be the total population at time t then, under the assumption that $\rho(m,t) \to 0$ as $m \to \infty$, we obtain after integrating equation (12) formally that

$$\frac{\mathrm{d}}{\mathrm{d}t} F(t) + \theta(t)F(t) = g(t)\rho(m_1,t) \tag{13}$$

with a corresponding renewal equation given by

$$g(t)\rho(m_1,t) = P_\mathrm{E}\lambda(t - \tau_\mathrm{E})F(t - \tau_\mathrm{E}). \tag{14}$$

Substituting equation (14) into equation (13) we obtain the following delay-differential equation in terms of the total population at time t, namely:

$$\frac{\mathrm{d}}{\mathrm{d}t} F(t) = P_\mathrm{E}\lambda(t - \tau_\mathrm{E})F(t - \tau_\mathrm{E}) - \theta(t)F(t). \tag{15}$$

We observe that $P_\mathrm{E}\lambda(t - \tau_\mathrm{E})F(t - \tau_\mathrm{E})$ gives the rate of recruitment for a population of size $F(t - \tau_\mathrm{E})$ with maturation period τ_E if we also observe that $\theta(t)F(t)$ represents the rate of death of a population of size $F(t)$. If λ is constant then we see that equation (15) is a delay-differential equation of the form

$$\frac{\mathrm{d}}{\mathrm{d}t} F(t) = R(F(t - \tau_\mathrm{E})) - D(F(t)).$$

For an analysis of this type of delay-differential equations see Blythe et al. [5] and Brauer [18].

MATHEMATICAL ANALYSIS

We assume that g, θ and λ are nonnegative and age independent, and that all individuals have the same size m_1 at birth with egg-stage duration τ_E and probability of survivorship P_E, both assumed constant. Then the population growth is found to be partially modelled by the following IBVP in which $\rho_0(m)$ denotes the initial size distribution:

$$\frac{\partial}{\partial t}\rho(m,t) + g(m,t)\frac{\partial}{\partial m}\rho(m,t) + \left[\frac{\partial}{\partial m}g(m,t) + \theta(m)\right]\rho(m,t) = 0, \qquad m > m_1, \tag{16a}$$

$$\rho(m_1,t) = \frac{P_\mathrm{E}}{g(m_1,t)}\int_{m_1}^{\infty}\lambda(m')\rho(m',t - \tau_\mathrm{E})\mathrm{d}m' \equiv B(t), \qquad t > \tau_\mathrm{E}. \tag{16b}$$

Remark 1

For technical, as well as biological, reasons we make the following assumptions: g, θ, λ are nonnegative and continuously differentiable functions of m and t in $[m_1,\infty) \times [0,\infty)$, λ is assumed to have compact support; moreover, we assume that there exists an $\varepsilon > 0$, s.t. $g(m,t) > 0$ for (m,t) in $(m_1 - \varepsilon,\infty) \times [0,\infty)$ with $g(m_1,t)$ bounded away from zero $\forall t > 0$ by a constant $\delta_0 > 0$, and that $[g(m_1,t)]^{-1}$ has a uniformly bounded derivative $\forall t > 0$.

In order to have a well-posed problem we still have to prescribe an appropriate set of initial

conditions. Promising applications of this model to laboratory insect populations suggest

$$\rho(m, 0) = \rho_0(m) \tag{16c}$$

and

$$\rho(m, t) = 0, \quad \cdot \quad t < 0, \tag{16d}$$

where equation (16d) indicates an empty system and equation (16c) that it has been "seeded" (instantaneously) at $t = 0$ by means of an arbitrary size distribution. A second possibility consists of taking equation (16c) in conjunction with

$$B(t) = \psi(t), \qquad 0 \leqslant t \leqslant \tau_E, \tag{16e}$$

where $\psi(t)$ is an arbitrary function.

We will work with equations (16c, d) as our set of initial conditions. Equations (16a–d) provide us with an IBVP. In order to reduce it to a single integral equation, we proceed to solve equation (16a) by the method of characteristics.

Let $\Gamma = \{(m, t): \geqslant m_1, t = 0\}$ and parametrize Γ as follows: $m = l(u) = u$; $t = p(u) = 0$, $u \geqslant m_1$; with $h(u) = \rho_0(u)$ as the initial data on Γ. It is then clear that Γ is noncharacteristic.

Let $X_u(v) = (M(u, v), T(u, v))^t$ (t denotes the transpose) be the unique characteristic through $(u, 0)$ parametrized by v. If $f(X_u) = (g(X_u), 1)^t$, then $X_u(v)$ will satisfy

$$X_u' = f(X_u) \quad \left(' = \frac{\mathrm{d}}{\mathrm{d}v} \right); X_u(0) = \binom{u}{0}. \tag{17}$$

In order for the system of equations (17) to have global solutions (i.e. for $v \geqslant 0$) for all values $u \geqslant m_1$ we assume the existence of nonnegative continuous functions $\alpha_i(w)$ ($i = 1, 2$) with domain in (m_1, ∞) and, such that for $i = 1, 2$,

$$\frac{\mathrm{d}}{\mathrm{d}v} w = \alpha_i(w), \quad w(0) = |X_u(0)| \equiv |u| + |0| \tag{18}$$

with

$$\alpha_1(|X_u|) \leqslant |f(X_u)| \leqslant \alpha_2(|X_u|), \quad |X| < \infty, \tag{19}$$

and such that $J_{\alpha_i}(w) = \int_{m_1}^{w} \frac{\mathrm{d}s}{\alpha_i(s)}$ diverges at $+\infty$ and at $m_1 - \varepsilon$, where $0 < \varepsilon \ll m_1$. Hence if we have that $\alpha_1(0) \leqslant \alpha_2(0)$ then all solutions satisfying $\alpha_1(0) \leqslant |X_u(0)| \leqslant \alpha_2(0)$ exist on $(m_1 - \varepsilon, \infty)$ and satisfy $J_{\alpha_2}^{-1}(J_{\alpha_2}(\alpha_2(0)) + v - m_1) \geqslant |X_u(v)| \geqslant J_{\alpha_1}^{-1}(J_{\alpha_1}(\alpha_1(0)) + v - m_1)$, and since $J_{\alpha_1}^{-1}$ is an increasing function of v we then have that $|X_u(v)| \to \infty$ as $v \to \infty$. These conclusions follow from the Osgood–Wintner–Conti–Brauer theory of global solutions for ordinary differential equations.

We now let $Y_s(r) = (M(s, r), T(s, r))^t$ and parametrize $\Gamma' = \{(m, t): m = m_1, t \geqslant 0\}$ by taking $m = l(s) = m_1$, $t = p(s) = s$, $s \geqslant 0$. Our assumptions on g guarantee us that Γ' is noncharacteristic, and hence the characteristic curves are the solutions to

$$Y_s' = f(Y_s) \quad \left(' = \frac{\mathrm{d}}{\mathrm{d}r} \right); Y_s(0) = \binom{m_1}{s}. \tag{20}$$

Under analogous conditions to those imposed on the system of equations (17) we have that the system of equations (20) have unique global solutions. If we now let $\alpha(m, t) \equiv (\partial/\partial m)g(m, t) + \theta(m, t)$

we immediately see that along characteristic curves equation (16a) becomes either one of the following differential equations:

$$\frac{dz}{dv} = -\alpha(M, T)z, \qquad z(u, 0) = \rho_0(u) \tag{21a}$$

or

$$\frac{dz}{dr} = -\alpha(M, T)z, \qquad z(s, m_1) = B(s), \tag{21b}$$

which have formal solutions given by

$$z(u, v) = \rho_0(u) \exp\left[-\int_0^v \alpha(M(u, v'), T(u, v'))dv' \right] \tag{22a}$$

and

$$z(s, r) = B(s) \exp\left[-\int_0^r \alpha(M(s, r'), T(s, r'))dr' \right]. \tag{22b}$$

The main characteristic C_M, i.e. the characteristic through $(m_1, 0)$, divides the region of interest to us in the subregions G_i, $i = 1, 2$ clearly depicted in Fig. 1. Moreover, from the previous analysis it follows that the maps $(u, v) \rightarrow (M(u, v), T(u, v))$ and $(s, r) \rightarrow (M(s, r), T(s, r))$ are C' invertible on G_1 and G_2 respectively as they define a semiflow on $[m_1, \infty) \times [0, \infty)$, so that the formal solution to equation (16a) in terms of the original variables is given by

$$\rho(m, t) = z(u(m, t), v(m, t)), \qquad (m, t) \in G_2, \tag{23a}$$

and

$$\rho(m, t) = z(s(m, t), r(m, t)), \qquad (m, t) \in G_1. \tag{23b}$$

If $m = f(t)$ denotes C_M in functional form we can rewrite equations (23a, b) explicitly as follows:

$$\rho(m, t) = \begin{cases} B(s(m, t))\exp\left[-\int_0^{t-s(m,t)} \alpha(M(s(m, t), t'))dt' \right], & \text{for } m_1 < m < f(t), \\[2em] \rho_0(u(m, t))\exp\left[-\int_0^t \alpha(M(u(m, t), t'))dt' \right], & \text{for } m > f(t). \end{cases} \tag{24}$$

Now consider equation (16b) in the following form:

$$B(s) = \frac{P_E}{g(m_1, s)} \int_{m_1}^\infty \lambda(m')\rho(m', s - \tau_E)dm', \qquad s > \tau_E. \tag{25}$$

To simplify the notation we introduce the following terminology:

$$F(l) \equiv \frac{P_E}{g(m_1, l + \tau_E)} \int_{f(l)}^\infty \lambda(m', l)\rho_0(u(m', l)) \cdot \exp\left[-\int_0^l \alpha(m'(u(m', l), t'))dt' \right]dm' \tag{26}$$

and

$$K(l, m') \equiv P_E \lambda(m') \exp\left[- \int_0^{l - s(m', l)} \alpha(m'(s(m', l), t')) dt' \right]. \tag{27}$$

With these, equation (25) becomes

$$B(s(m, t)) = \frac{1}{g(m_1, s(m, t))} \int_{m_1}^{f(s(m,t) - \tau_E)} B(s(m', s(m, t) - \tau_E)) K(m', s(m, t) - \tau_E) dm'$$

$$+ F(s(m, t) - \tau_E), \qquad s(m, t) - \tau_E > 0. \tag{BIE}$$

Therefore if $B(s)$ is the unique continuous function satisfying (BIE) for s in $[\tau_E, \infty)$ then equation (24) gives the unique solution to equations (16a)–(16d or 16e) and conversely.

Hence the determination of the existence of solutions to the initial IBVP (16a–e) has now been reduced to the determination of the existence of solutions to a Volterra integral equation with a time delay that we will refer to as BIE.

At this point, for technical reasons, we again mention that equation (16b) is not required to hold at $t = \tau_E$ but that it will be satisfied at $t = \tau_E$ whenever ρ_0 satisfies the compatibility condition

$$\rho(m_1, \tau_E) = \frac{P_E}{g(m_1, \tau_E)} \int_{m_1}^{\infty} \lambda(m') \rho(m', 0) dm' = \frac{P_E}{g(m_1, \tau_E)} \int_{m_1}^{\infty} \lambda(m') \rho_0(m') dm'. \tag{28}$$

This condition simply implies that the initial data is consistent with the renewal process. We are not assuming this compatibility condition. B, as defined by equation (16b), will exhibit a discontinuity at $t = \tau_E$ and therefore B as defined by equation (16b) at $t = \tau_E$ will not agree with B as defined by BIE as $s = \tau_E$. We therefore define B as in equation (16b) for $t > \tau_E$ and take $B(\tau_E) = B(\tau_E^+)$ [which under equation (16d) equals zero]. The following lemma will be of extreme importance throughout the analysis of BIE.

Lemma 1

If m' satisfies $m_1 < m' < f(s(m, t) - \tau_E)$, then

$$s(m, t) - \tau_E - s(m', s(m, t) - \tau_E) > 0 \qquad \text{for } s(m, t) > \tau_E. \tag{29}$$

Proof. In order to follow the proof, Fig. 2 is necessary. From it we observe that there exists a unique characteristic through A_2. Moreover, it does not intersect C_M; therefore, it starts at a point
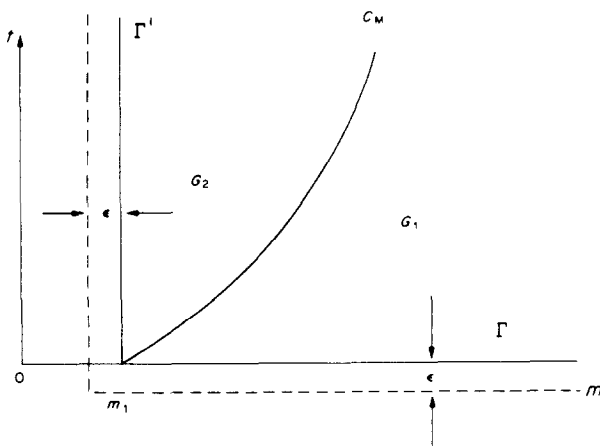

Fig. 1

$A_1 = (m_1, s(m, t) - \tau_E)$
$A_2 = (m'_1, s(m, t) - \tau_E)$
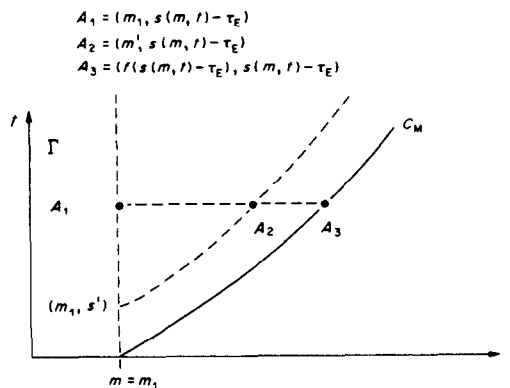$A_3 = (f(s(m, t) - \tau_E), s(m, t) - \tau_E)$

Fig. 2

(m_1, s') with $s' > 0$. The characteristic through (m_1, s') may be denoted by $M(s', r)$, and $T(s', r) = s' + r$ is a solution to equations (20). Therefore we have that $M(s', 0) = m_1$, and more importantly, that $M(s', s(m, t) - \tau_E) = m'$. It is now clear that the definition of s implies that $s(m', s(m, t) - \tau_E) = s'$ and since $s' < s(m, t) - \tau_E$, then it can be concluded that inequality (29) holds. This lemma indicates that "left" values of B are being used to compute its "right" values.

LOCAL EXISTENCE AND UNIQUENESS

Existence of solutions for BIE can be studied by assuming that the initial history is provided by either equations (16c) and (16e) or equations (16c) and (16d). In the first case we can make use of Fig. 2 to observe that $\{s(m', l): m_1 < m' < f(\tau_E)\} = [0, \tau_E]$ and hence if equation (16e) is assumed, B is prescribed on $[0, \tau_E]$. We then observe that the r.h.s. of BIE defines B on $[\tau_E, 2\tau_E]$; as this process can be repeated, it is clear that we obtain global existence and uniqueness.

When equations (16c) and (16d) are assumed, we only know that $B(\tau_E) \equiv B(\tau_E^+) = 0$ and hence a fixed-point argument is needed to establish existence and uniqueness.

We follow the results on Volterra integral equations as found in Miller [19]. A series of technical lemmas will be proved that will lead towards the resolution of the questions of existence and uniqueness for BIE. If we let $s(m, t) - \tau_E = l$ then BIE can be written as follows:

$$B(l + \tau_E) = \frac{1}{g(m_1, l + \tau_E)} \int_{m_1}^{f(l)} B(s(m', l)) K(m', l) dm' + F(l), \qquad l > 0. \tag{BIE}$$

If we set

$$G(l, m', B) \equiv \begin{cases} BK(m', l) & \text{if } m_1 \leqslant m' \leqslant f(l) \\ 0 & \text{otherwise,} \end{cases}$$

then with this notation the following lemma holds.

Lemma 2

F and G satisfy accordingly the following properties:

H1. F is defined and continuous for all $l \geqslant 0$.

H2. G is a Lebesgue measurable function in (l, m', B) for $m_1 \leqslant m' \leqslant f(l)$, $0 \leqslant B < \infty$. Moreover, $G(l, m', B)$ is a continuous function of B for each fixed pair (l, m') and $G(l, m', B) = 0$ if $m' > f(l)$.

H3.   Let $R > m_1$ and S be a bounded subset of the nonnegative reals, then there exists a measurable function N such that $|G(l, m', B)| \leqslant N(l, m')$ whenever $m_1 \leqslant m' \leqslant f(l) \leqslant R$ and $B \in S$ and we also have that

$$\sup \left[\int_{m_1}^{f(l)} N(l, m') dm' : m_1 \leqslant f(l) \leqslant R \right] < \infty.$$

H4.   For each compact subinterval J in $[m_1, \infty)$ and each bounded subset S of the nonnegative reals and each l in $(0, \infty)$ we have that

$$\sup \left[\int_J \left| G(l, m', \phi(s(m', l))) - G(l_0, m', \phi(s(m', l_0))) \right| dm' : \phi \in C(J; S) \right] \to 0 \text{ as } l \to l_0,$$

where $C(J; S)$ denotes the set of all continuous functions ϕ with domain J and range in S.

H5. For each constant $Q > 0$ and each bounded subset S of the nonnegative real numbers, there exists a measurable function $K(l, m')$ such that $|G(l, m', B_1) - G(l, m', B_2)| \leq K(l, m')|B_1 - B_2|$ whenever $m_1 \leq m' \leq f(l) \leq Q$ and both B_1 and B_2 are in S.

Proof. Property H1 follows clearly from the definition of F. Moreover, since $G(l, m', B)$ is a continuous function in (l, m', B) for $m_1 \leq m' \leq f(l)$ and B in $[0, \infty)$ then it satisfies clearly properties H2–H4; property H5 is immediate using the given $K(l, m')$.

Remark

We observe that to fulfill property H3 we could use $k_s K(l, m')$ as $N(l, m')$, where k_s is any bound for the bounded set S. One more lemma is needed before we reach the main theorem of this section.

Lemma 3

For each $R > m_1$ there exists an N, as in property H3, such that $\int_{m_1}^{f(l)} N(l, m')dm' \to 0$ as $l \to 0^+$.

Proof. From the above remark it follows that we may take $N(l, m') \equiv k_s K(l, m')$. Since $\int_{m_1}^{f(l)} K(l, m')dm$ is a continuous function of l and $f(l)$ decreases to m_1 as $l \to 0^+$, then we see that the result follows.

We have finally arrived at the main result of this section.

Theorem 1

Assume that F and G satisfy the conditions specified in Lemmas 2 and 3, then there exists a constant $\beta > 0$ such that BIE has a unique continuous solution on the interval $[0, \beta]$, i.e. $B(l + \tau_E)$ is in $C[0, \beta]$.

Proof. We will set up matters so that we may apply a contracting argument for maps. Let

$$S = \{B \geq 0 : |B - F(l)| \leq 1 \quad \text{for some } l \text{ in } [0, 1]\}.$$

Lemmas 2 and 3 allow us to choose a $\beta > 0$, small enough so that

$$\frac{1}{\delta_0} \int_{m_1}^{f(l)} K(l, m')dm' \leq \frac{1}{2} \text{ and } \frac{1}{\delta_0} \int_{m_1}^{f(l)} k_s K(l, m')dm' \leq 1 \quad \text{for } l \text{ in } [0, \beta].$$

Let $X = C([0, \beta]; S)$, i.e. the set of all continuous functions ϕ with domain $[0, \beta]$ and range in S. If we take the uniform norm on X, i.e. $\|\phi\|_\beta = \sup|\phi(l)|$ where the supremum is taken for l in $[0, \beta]$, then it is easily checked that X becomes a Banach space. A mapping T on X is defined as follows:

$$(T\phi)(l) = F(l) + \frac{1}{g(m_1, l + \tau_E)} \int_{m_1}^{f(l)} G(l, m', \phi(s(m', l)))dm', \quad l \text{ in } [0, \beta].$$

Since

$$|(T\phi)(l) - F(l)| \leq \frac{1}{\delta_0} k_s \int_{m_1}^{f(l)} K(l, m')dm' \leq 1,$$

then $(T\phi)(l)$ is in S. Moreover, if we let $q(t) \equiv \frac{1}{g(m_1, t)}$ and assume that it is a continuously bounded

differentiable function of t so that there exists a constant c_1 such that $|g'(t)| \leqslant c_1 \, \forall \, t > 0$, then we can see that

$$|(T\phi)(l+h) - (T\phi)(l) \leqslant |F(l+h) - F(l)| + \frac{1}{\delta_0} \int_{m_1}^{f(\beta)} \left| G(l+h, m', \phi(s(m', l+h))) \right.$$

$$\left. - G(l, m', \phi(s(m', l))) \right| \mathrm{d}m + c_1 \cdot h \int_{m_1}^{f(\beta)} \left| G(l, m', \phi(s(m', l))) \right| \mathrm{d}m,$$

$$= \frac{1}{\delta_0} \left| \int_{f(l)}^{f(l+h)} G(l+h, m', \phi(s(m', l+h))) \mathrm{d}m' \right| + \frac{1}{\delta_0} \left| \int_{f(l)}^{f(l+h)} G(l, m', \phi(s(m', l))) \mathrm{d}m' \right|$$

$$= I_1 + I_2 + I_3 + I_4 + I_5.$$

The continuity of F and f and property H4 clearly imply that $I_i \to 0$ as $h \to 0$ for $i = 1, 2, 3, 4,$ 5 and therefore $T\phi \in X$. Moreover, T is a contracting map. To see this, let ϕ_1 and ϕ_2 be members of X and let $l \in [0, \beta]$, then

$$|(T\phi_1)(l) - (T\phi_2)(l)| \leqslant \frac{1}{\delta_0} \int_{m_1}^{f(l)} K(l, m') |\phi_1(s(m', l)) - \phi_2(s(m', l))| \mathrm{d}m'.$$

Since $m_1 < m' < f(l)$, Lemma 1 implies that $s(m', l) < l$. But l is in $[0, \beta]$ and $s(m', l) \geqslant 0$, hence $s(m', l)$ is in $[0, \beta] \, \forall \, l$ in $[0, \beta]$, and therefore we have that

$$|(T\phi_1)(l) - (T\phi_2)(l)| \leqslant \frac{1}{\delta_0} \|\phi_1 - \phi_2\|_\beta \int_{m_1}^{f(l)} K(l, m') \mathrm{d}m' \leqslant \frac{1}{2} \|\phi_1 - \phi_2\|_\beta.$$

Hence T is a contracting map on X and therefore it has a unique fixed point, i.e. BIE has a unique continuous solution on $C[0, \beta]$.

CONTINUATION OF SOLUTIONS

The purpose of this section is to show that the unique local solution of Theorem 1 can be continued uniquely to the "right" for all time. We begin with the following theorem.

Theorem 2

Assume that F and G satisfy the conditions of Lemmas 2 and 3. Let $B(l + \tau_E)$ be the bounded solution to BIE for l in $[0, \alpha]$. Then $B(l + \tau_E)$ can be uniquely extended as a continuous solution to BIE to an interval $[0, \alpha_0]$ with $\alpha_0 > \alpha$.

Proof. Let Q be a bound for $|B(l + \tau_E)|$ when $l \in [0, \alpha]$ and let $S_Q = \{B \geqslant 0 : B \leqslant Q\}$. Choose a sequence $\{l_m\}$ in $[0, \alpha]$ and such that $l_m < l_{m+1}$ and $\lim l_m = \alpha$ when $m \to \infty$. For $m > n$, we then have

$$\left| q(l_m + \tau_E) \int_{m_1}^{f(l_m)} G(l_m, m', B(s(m', l_m))) \mathrm{d}m' - q(l_n + \tau_E) \int_{m_1}^{f(l_n)} G(l_n, m', B(s(m', l_n))) \mathrm{d}m' \right|$$

$$\leqslant \frac{1}{\delta_0} \int_{m_1}^{f(l_m)} |G(l_m, m', B(s(m', l_m))) - G(l_m, m', B(s(m', l_n)))| \mathrm{d}m'$$

$$+ c_1(l_m - l_n) \left| \int_{m_1}^{f(\alpha)} G(l_n, m', B(s(m', l_n))) \mathrm{d}m' \right| = I_1 + I_2,$$

since by definition $G(l_n, m', B) = 0$ for $m' > f(l_n)$. Let $X^\alpha_Q = C[[0, \alpha]; S_Q]$ and ϕ in X^α_Q, then

$$\delta_0 I_1 < \sup_{\phi \text{ in } X^\alpha_Q} \int_{m_1}^{f(l_m)} |G(l_m, m', \phi(s(m', l_m))) - G(l_n, m', \phi(s(m', l_n)))| dm' \to 0$$

as $l_n, l_m \to \alpha^-$ by virtue of property H4. Since

$$|(TB)(l_m) - (TB)(l_n)| \leqslant |F(l_m) - F(l_n)| + \left| q(l_m + \tau_E) \int_{m_1}^{f(l_m)} G(l_m, m', B(s(m', l_m))) dm' \right.$$

$$\left. - q(l_n + \tau_E) \int_{m_1}^{f(l_n)} G(l_n, m', B(s(m', l_n))) dm' \right|$$

then using the continuity of F and the above estimates we have that $|(TB)(l_m) - (TB)(l_n)| \to 0$ as $m, n \to \infty$. Since $l_m \to \alpha^-$ as $m \to \infty$, we conclude that $\lim_{m \to \infty} (TB)(l_m)$ exists. So we are able to extend $B(l + \tau_E)$ as a continuous function on $[0, \alpha]$ by taking the preceding limit as the definition of $B(\tau_E + \alpha)$.
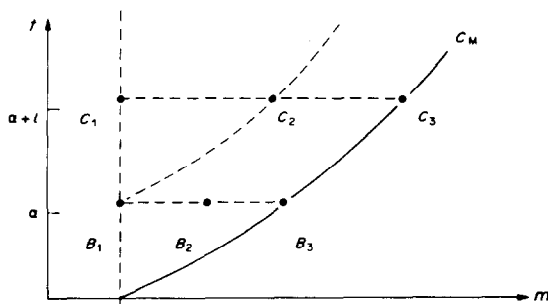
Now let $P(l) \equiv B(\tau_E + l + \alpha)$. We then have that

$$(TP)(l) = (TB)(\tau_E + \alpha + l)$$

$$= F(l + \alpha) + q(l + \tau_E + \alpha) \int_{m_1}^{f(l + \alpha)} G(l + \alpha, m', B(s(m', l + \alpha))) dm'. \tag{30}$$

In order to change this integral to a form suitable to our former analysis we make use of Fig. 3, where appropriate points have been identified. There is a unique characteristic through B_1 which is parametrized by $m(r) = M(\alpha, r)$ and $t(r) = r + \alpha$. This characteristic intersects the line $t = \alpha + l$ at the point $C_2 = (m', \alpha + l)$ and therefore $s(m', \alpha + l) = \alpha$. Hence from Fig. 3 we see that $s(m'', \alpha + l) < s(m', \alpha + l) = \alpha$ whenever $m' < m'' \leqslant f(\alpha + l)$. With this we can rewrite equation (30) as follows:

$$(TP)(l) = F(l + \alpha) + q(l + \tau_E + \alpha) \cdot \int_{m_1}^{M(\alpha, l)} G(l + \alpha, m'', B(s(m'', l + \alpha))) dm''$$

$$+ q(l + \tau_E + \alpha) \int_{M(\alpha, l)}^{f(\alpha + l)} G(l + \alpha, m'', B(s(m'', l + \alpha))) dm''. \tag{31}$$

$B_1 = (m_1, a), \qquad B_2 = (m', a), \qquad B_3 = (f(a), a)$

$C_1 = (m_1, a + l), \qquad C_2 = (m', a + l), \qquad C_3 = (f(a + l), l + a)$

By the above remarks $B(s(m'', l + \alpha))$ is known for values of m'' with $M(\alpha, l) \leqslant m'' \leqslant f(\alpha + l)$. Define

$$F_\alpha(l) \equiv F(l + \alpha) + q(l + \tau_E + \alpha) \int_{M(\alpha, l)}^{f(\alpha + l)} G(l + \alpha, m'', B(s(m'', l + \alpha)))dm''.$$

Then equation (31) can be written as

$$(TP)(l) = F_\alpha(l) + q(l + \tau_E + \alpha) \int_{m_1}^{M(\alpha, l)} G(l + \alpha, m'', B(s(m'', l + \alpha)))dm''$$

or as

$$(TB)(\tau_E + l + \alpha) = F_\alpha(l) + q(l + \tau_E + \alpha) \int_{m_1}^{M(\alpha, l)} G(l + \alpha, m'', B(s(m'', l + \alpha)))dm''. \tag{32}$$

We let

$$G_\alpha(l, m'', B(s(m'', l))) = \begin{cases} G(l + \alpha, m'', B(s(m'', l + \alpha))), & \text{for } m_1 \leqslant m'' \leqslant f(l + \alpha), \\ 0, & \text{otherwise.} \end{cases}$$

Hence we see that F_α and G_α satisfy the conditions of Lemmas 2 and 3 with $K_\alpha(l, m'') \equiv K(m', l + \alpha)$. With the aid of these lemmas we choose $\delta > 0$ small enough so that

$$\frac{1}{\delta_0} \int_{m_1}^{M(\alpha, l)} K_\alpha(l, m'')dm'' \leqslant \frac{1}{2} \quad \text{and} \quad \frac{1}{\delta_0} \int_{m_1}^{M(\alpha, l)} k_s K_\alpha(l, m'')dm'' \leqslant 1,$$

for l in $[0, \delta]$. Then on the Banach space $X_\alpha = C([0, \delta]; S_\alpha)$, the mapping

$$(T_\alpha \phi)(l) = (T\phi)(\tau_E + l + \alpha) = F_\alpha(l) + \int_{m_1}^{M(\alpha, l)} G(l, m'', \phi(s, m'', l)))dm''$$

is a contractive map and hence it has a unique fixed point ϕ_0. Therefore, $\forall l$ in $[0, \delta]$, $(T_\alpha \phi_0)(l) = \phi_0(l)$ and in particular $\phi_0(0) = (T_\alpha \phi_0)(0) = B(\tau_E + \alpha)$. Hence, ϕ_0 is the unique continuation of $B(l + \tau_E)$ to $[0, \alpha + \delta]$.

Corollary 1

Assume F and G in BIE satisfy the conditions of Lemmas 2 and 3. Then there exists a unique continuous solution of BIE that can be extended to the right to obtain a unique maximally defined solution of BIE.

Proof. Let $B(l + \tau_E)$ denote the local solution to BIE, l in $[0, \beta]$ and $B(l + \tau_E)$ in $C[0, \beta]$. We now use Theorem 2 to extend $B(l + \tau_E)$ to the right. Two possibilities arise: either $B(l + \tau_E)$ can be defined for $\forall l \geqslant 0$; or else, $B(l + \tau_E)$ can only be defined on a bounded interval. By Theorem 2, if $B(l + \tau_E)$ can be defined only on a bounded interval then this interval must be of the form $[0, \alpha)$ and $B(l + \tau_E) \to +\infty$ as $l \to \alpha^-$. Uniqueness also follows from Theorem 2.

Theorem 3

$B(l + \tau_E)$ can be uniquely continued for $\forall l \geqslant 0$.

Proof. Let us assume that the unique solution to BIE has been uniquely extended to a maximally defined solution $B(l + \tau_E)$ with l in $[0, \alpha)$. If $\alpha = +\infty$, then there is nothing to prove, therefore we assume that α is in $(0, \infty)$. We will now show that $\lim_{l \to \alpha^-} B(l + \tau_E)$ is finite so that Theorem 2 will

then contradict the maximality of our solution. For our solution $B(l + \tau_E)$ to BIE, we have that

$$B(l + \tau_E) = q(l + \tau_E) \int_{m_1}^{f(l)} K(l, m', B(s(m', l))) dm' + F(l)$$

with $0 \leqslant s(m', l) < l$ whenever $m_1 \leqslant m' \leqslant f(l)$. We choose $\delta > 0$ such that $0 < \delta < \tau_E$ and $0 < \delta < \alpha$ and let l in $[0, \alpha - \delta]$. Since B is in $C[0, \alpha - \delta]$ this implies that there exists a $C > 0$ such that $|B(s(m', l))| \leqslant C$ for l in $[0, \alpha - \delta]$ and m' such that $m_1 \leqslant m' \leqslant f(l)$ and hence $\|B\|_{[0, \alpha - \delta]} \leqslant C$. Hence,

$$B(l + \tau_E) \leqslant \frac{C}{\delta_0} \int_{m_1}^{f(\alpha - \delta)} K(l, m') dm' + \|F\|_{[0, \alpha - \delta]},$$

which in turn implies that there exists $C' > 0$ such that

$$B(l + \tau_E) \leqslant C' \qquad \text{for } l \text{ in } [0, \alpha - \delta] \text{ or equivalently}$$
$$B(l) \leqslant C' \qquad \text{for } l \text{ in } [\tau_E, \alpha - \delta + \tau_E],$$

and since $[\tau_E, \alpha)$ is contained in $[\tau_E, \alpha + \delta + \tau_E]$, we have the desired contradiction.

We summarize all the results of this section in the following theorem:

Theorem 4

Assume that F and G satisfy the conditions specified in Lemmas 2 and 3, then BIE has a unique continuous solution on the interval $[\tau_E, \infty)$.

EQUILIBRIUM SIZE DISTRIBUTION—STABILITY

We will study the problem of stability of solutions for equations (16a–d) in the particular case where g is time independent, $[g(m, t) \equiv g(m)]$. In this case the change of variable provided by

$$J(m) = \int_{m_1}^{m} \frac{ds}{g(s)} \text{ with } \beta(J, t) \equiv [\theta(m(J), t)]/g(m(J)), \ \gamma(J, t) \equiv [P_E/g(m_1)]\lambda(m(J), t) g(m(J)), \ h_0(J) \equiv \rho_0(m(J))$$

and $h(J, t) = g(m(J)) \rho(m(J), t)$ reduces equations (16a–d) to the following model:

$$\frac{\partial}{\partial t} h(J, t) + \frac{\partial}{\partial J} h(J, t) + \beta(J, t) h(J, t) = 0, \qquad J > 0, \tag{33a}$$

$$B_h(t) = \int_0^\infty \gamma(J, t) h(J, t - \tau_E) dJ, \qquad t > \tau_E, \tag{33b}$$

$$h(J, 0) = h_0(J), \tag{33c}$$

$$h(J, t) = 0 \qquad t < 0. \tag{33d}$$

This model, when $\tau_E = 0$, provides us with the familiar set of equations associated with MacKendrick [20] which has the familiar solution

$$h(J, t) = \begin{cases} h_0(J - t) \exp\left[-\int_0^t \beta(J - t + s, s) ds \right], & \text{for } J \geqslant t \\ \\ B_h(t - J) \exp\left[-\int_0^J \beta(s, t - J + s) ds \right], & \text{for } t > J. \end{cases} \tag{34}$$

If this solution is substituted in equation (33b) with

$$K_1(J, l) = \exp\left[-\int_0^J \beta(s, l - J + s)ds\right]\gamma(J, l + \tau_E) \qquad (35)$$

and

$$F_1(l) = \int_{l+\tau_E}^{\infty} \gamma(J, l)h_0(J - l)\exp\left[-\int_0^l \beta(l - t + s, s)ds\right]dJ, \qquad (36)$$

it then reduces the study of equations (33a–d) to the study of

$$B_h(l + \tau_E) = \int_0^l B_h(l - J)K(J, l)dJ + F_1(l). \qquad (37)$$

Moreover, if β and γ are assumed independent of t then equation (37) becomes

$$B_h(l + \tau_E) = \int_0^l K_1(l - J)B_h(J)dJ + F_1(l). \qquad (38)$$

If we let $b(s)$, $k(s)$ and $f(s)$, denote the Laplace transforms of B_h, K_1, and F_1, respectively, it then follows that

$$b(s) = \frac{f(s)}{\exp(\tau_E s) - k(s)} \qquad (39)$$

exists and defines an analytic function of s $\forall s$ with $\mathscr{R}e(s) > s^*$, where s^* is the unique real solution of the corresponding Lotka characteristic equation

$$\exp(-\tau_E s)k(s) = 1. \qquad (40)$$

Moreover, all other roots (complex conjugate pairs) satisfy $\mathscr{R}e(s) < s^*$, and it can be shown that $B_h(t) = 0$ $(\exp(s^*t))$ for s values satisfying $\mathscr{R}e(s) > s^*$ and $B_h(l) = B_0\exp(s^*t) + 0(\exp(s^*t))$ as $t \to \infty$, where B_0 is the residue of $b(s)$ at $s = s^*$. Also,

$$\exp(-s^*t)h(J, t) \to B_0\exp\left[-s^*J - \int_0^J \beta(u)du\right] \qquad (41)$$

uniformly as $t \to \infty$ where the r.h.s. of expression (41) provides the so-called persistent or stable distribution. Finally, we observe that $s^* > 0$, whenever $k(0) > 1$, and $s^* < 0$, whenever $k(0) < 1$. All of the above analysis is well-known; a nice exposition can be found, for example, in [21].

If we let

$$\Pi(m) = [g(m_1)/g(m)]P_E\exp\left\{-\int_{m_1}^m [\theta(w)/g(w)]dw\right\} \qquad (42)$$

denote the probability that an individual will grow to size m, and if we proceed to determine solutions of equation (16a) of the form $M(m)T(t)$. We easily find that a necessary and sufficient

condition for the existence of such solutions is given by the Lotka characteristic equation

$$g(m_1) = \int_{m_1}^{\infty} \Pi(m')\lambda(m')\exp\left[-s\left\{\tau_E + \int_{m_1}^{m'} [1/g(w)]dw\right\}\right]dm', \tag{43}$$

where s denotes the separation constant. A simple calculus argument such as the one found in Pollard [22] shows that equation (43) has a unique real solution s_0 such that

$$\int_{m_1}^{\infty} \lambda(m)\Pi(m)dm > g(m_1) \qquad \text{iff } s_0 > 0 \tag{44a}$$

and

$$\int_{m_1}^{\infty} \lambda(m)\Pi(m)dm < g(m_1) \qquad \text{iff } s_0 < 0. \tag{44b}$$

In addition, complex roots z appear in conjugate pairs with $\mathcal{R}e(z) < s_0$.

Therefore inequality (44b) provides necessary and sufficient conditions (in terms of the original variables) for the existence of persistent or stable size distributions. We finally observe that the delay just modifies the corresponding Lotka characteristic equation (43). A similar effect is produced in the classical MacKendrick–Von Foerster model by a constant rate of harvesting of all individuals older than a fixed age [23].

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