LOGISTIC MODELS OF STRUCTURED POPULATION GROWTH

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Abstract—A general model of structured population dynamics with logistic-type nonlinearity is considered. The model consists of a semilinear hyperbolic partial differential equation with a linear boundary condition and an initial value. The logistic nonlinearity corresponds to increased mortality as the population increases. The problem is treated as an abstract semilinear evolution equation. Sufficient conditions are given for the solutions to converge to an equilibrium solution. Applications are made to age-structured populations, size-structured populations, multispecies-structured populations, and cell populations.

INTRODUCTION

The purpose of this paper is to prove the convergence to equilibrium of solutions of structured population models with logistic nonlinearities. The prototype of such models is an age-structured population described as follows: Let $p(a, t)$ be the density of a population at time t with respect to an age variable a, so that the total population at time t between ages a_1 and a_2 is

$$\int_{a_1}^{a_2} p(a, t) \, da.$$

Let ω be a weight function and let

$$Q(t) = \int_0^\infty p(a, t)\omega(a) \, da$$

be the weighted integral of the density. Consider the logistic model of age-structured population growth given by

$$p_t(a, t) + p_a(a, t) = -[\mu(a) + \eta(Q(t))]p(a, t), \tag{1.1}$$

$$p(0, t) = \int_0^\infty \beta(a)p(a, t) \, da, \tag{1.2}$$

$$p(a, 0) = \phi(a), \tag{1.3}$$

where μ and β are the age-specific mortality and fertility moduli, respectively, $\eta(Q(t))$ is the density-dependent mortality, and ϕ is the known initial age distribution at time 0. The logistic term $\eta(Q(t))$ provides a mechanism for increased mortality as the portion $Q(t)$ of the population increases and the effects of crowding and resource limitation take hold.

The separated form of the right-hand side of (1.1) is essential to our development. This form for the mortality process has been described by M. Gurtin[1] and W. Streifer[2] as a separation into an endogenous part $\mu(a)$, which depends on age, but is not influenced by environmental limitations, and an exogenous part $\eta(Q(t))$, which is independent of age, but arises as resources become limited because of crowding. The form of the birth process (1.2) is also essential to our approach in that it is not effected by crowding. Nonlinear age-dependent population models having the form (1.1)–(1.3) have been studied by a number of researchers, including M. Gurtin and R. MacCamy[3,4], J. Prüss[5–7], M. Gurtin[1], and the author[8]. Recently, P. Marcati[9], S. Busenberg and M. Iannelli[10], and M. Iannelli[11] have treated such models and established the convergence of solutions to equilibrium age distributions. In this paper we will simplify their proofs and extend their results to the general context of a population structured by internal variables.

Our approach to this problem rests upon viewing it as a semilinear evolution equation in a Banach space. The linear part of this equation corresponds to a strongly continuous semigroup of bounded linear operators in this Banach space. The behavior of the solutions of the linear problem is determined by the dominant real eigenvalue of the infinitesimal generator of this semigroup. The nonlinear problem is subsequently analyzed as a simple nonlinear perturbation of the linear semigroup. In this paper we will first prove a general theorem concerning logistic nonlinear structured population dynamics and then apply it to a variety of biological populations.

2. AN ABSTRACT LOGISTIC EQUATION

In this section we investigate the stability of equilibrium solutions to an abstract logistic equation in a Banach space. The formulation of the abstract problem allows applications to diverse models of structured populations. Let X be a Banach lattice with norm $\| \ \|$ and let X_- denote the cone of nonnegative elements of X (see [12], p. 369). We require the following hypotheses:

$T(t)$, $t \geq 0$ is a strongly continuous semigroup of bounded linear operators in X
with infinitesimal generator A and $T(t)x \in X_+$ for $x \in X_+$.   (2.1)

There exist a real number λ_0 and a direct sum decomposition $X = X_0 \oplus X_1$ with
associated projections P_i, $P_iX = X_i$, $i = 0, 1$, such that $P_iT(t) = T(t)P_i$,
$i = 0, 1$, $T(t)P_0 = e^{\lambda_0 t}P_0$, $t \geq 0$, and for some constants $M \geq 1$, $\omega < \lambda_0$.
$|T(t)P_1| \leq Me^{\omega t}|P_1|$, $t \geq 0$.   (2.2)

$\mathcal{F}$ is a bounded linear functional on X such that $\mathcal{F}x > 0$ for $x \in X_+ - \{0\}$.   (2.3)

η is a continuous increasing function from $[0, \infty)$ onto $[0, \infty)$.   (2.4)

Remark 2.1 The hypothesis (2.2) implies that $AP_0x = \lambda_0P_0x$ for any $x \in X$ so that λ_0 is an eigenvalue of A. In a typical case the spectrum of A consists of a finite number of eigenvalues lying to the right of some line parallel to the imaginary axis and nonessential spectrum lying to the left of this line. The eigenvalue λ_0 is dominant in the sense that $\lambda_0 > \mathrm{Re}\, \lambda$ for any λ in the spectrum of A. Furthermore, $\lim_{t \to \infty}|e^{-\lambda_0 t}T(t) - P_0| = \lim_{t \to \infty}|e^{-\lambda_0 t}T(t)P_1| \leq \lim_{t \to \infty}Me^{-(\lambda_0 - \omega)t}|P_1| = 0$.

Consider the abstract logistic equation

$$w'(t) = Aw(t) - \eta(\mathcal{F}w(t))w(t), t \geq 0, \quad w(0) = x. \tag{2.5}$$

Models such as (1.1)–(1.3) can be formulated as in (2.5), where the boundary condition (1.2) is incorporated into the domain in A.

THEOREM 2.1

Let (2.1)–(2.4) hold and let $x \in X_+ \cap D(A)$ such that $P_0x \in X_+ - \{0\}$. There exists a unique continuously differentiable function $w: [0, \infty) \to X_+ - \{0\}$ such that w satisfies (2.5). If $\lambda_0 < 0$, then $\lim_{t \to \infty}w(t) = 0$, and if $\lambda_0 \geq 0$, then $\lim_{t \to \infty}w(t) = \eta^{-1}(\lambda_0)P_0x/\mathcal{F}P_0x$.

Proof. We first claim that

$$T(t)x \in X_+ - \{0\} \quad \text{and} \quad \mathcal{F}(T(t)x) > 0 \quad \text{for } t \geq 0. \tag{2.6}$$

If on the contrary, $T(t_1x) = 0$ for some t_1; then $0 = P_0T(t_1)x = e^{\lambda_0 t_1}P_0x$, which contradicts $P_0x \in X_+ - \{0\}$. We also claim that

$$\lim_{t \to \infty} \mathcal{F}(T(t)Ax)/\mathcal{F}(T(t)x) = \lambda_0, \tag{2.7}$$

since

$$\mathcal{F}(T(t)Ax)/\mathcal{F}(T(t)x) = \mathcal{F}(\lambda_0 e^{\lambda_0 t}P_0x + T(t)P_1Ax)/\mathcal{F}(e^{\lambda_0 t}P_0x + T(t)P_1x)$$
$$= \mathcal{F}(\lambda_0 P_0x + e^{-\lambda_0 t}T(t)P_1Ax)/\mathcal{F}(P_0x + e^{-\lambda_0 t}T(t)P_1x).$$

We next show that for each $t_1 > 0$ there exists a continuous function $F: [0, \infty) \to [0, \infty)$ such that for $0 \le t \le t_1$,

$$F(t) = \exp[- \int_0^t \eta(F(s)) \, ds] \mathscr{F}(T(t)x). \tag{2.8}$$

Let W be the closed convex subset of the Banach space $C([0, t_1], R)$ consisting of functions F such that $\|F\|_{C[0,t_1]} \le |\mathscr{F}|(|P_0| + M \max\{1, e^{\lambda_0 t_1}\}|P_1|)$. Define $K: W \to W$ by

$$(KF)(t) = \exp\left[- \int_0^t \eta(F(s)) \, ds\right] \mathscr{F}(T(t)x), \quad F \in W, 0 \le t \le t_1.$$

By the hypothesis K is a continuous mapping of W into itself. Also, the image of K is compact by the Arzelá–Ascoli Theorem (see [13], p. 266). By the Schauder–Leray Theorem (see [14], p. 50) K has a fixed point F in W.

We claim that this fixed point of K is unique. Notice that F satisfies

$$F'(t) = [G(t) - \eta(F(t))]F(t), \tag{2.9}$$

where $G(t) = \mathscr{F}(T(t)Ax)/\mathscr{F}(T(t)x)$. Suppose that F and $\hat{F}$ are both fixed points of K. Since η is increasing,

$$\begin{aligned}
\tfrac{1}{2} d/dt[F(t) - \hat{F}(t)]^2 &= G(t)[F(t) - \hat{F}(t)]^2 \\
&\quad - [\eta(F(t))F(t) - \eta(\hat{F}(t))\hat{F}(t)][F(t) - \hat{F}(t)] \\
&\le \left(\sup_{0 \le \tau \le t_1} G(\tau)\right)[F(t) - \hat{F}(t)]^2.
\end{aligned}$$

Since $F(0) = \hat{F}(0)$, this last differential inequality implies that $F \equiv \hat{F}$ on $[0, t_1]$. Since t_1 is arbitrary, we conclude that there exists a unique function $F: [0, \infty) \to [0, \infty)$ satisfying (2.8). Define $w: [0, \infty) \to X_+ - \{0\}$ by

$$w(t) = \exp\left[- \int_0^t \eta(F(s)) \, ds\right] T(t)x, \quad t \ge 0.$$

Notice that $w(t) \in D(A)$, since $x \in D(A)$. Also, $\mathscr{F}w(t) = F(t)$ and so w is the unique continuously differentiable function satisfying (2.5).

If $\lambda_0 < 0$, then $T(t)x \to 0$ as $t \to \infty$, so that $w(t) \to 0$ as $t \to \infty$. If $\lambda_0 \ge 0$, then let $\in > 0$ and set $\delta = \eta(\eta^{-1}(\lambda_0) + \in) - \lambda_0$. By (2.7) there exists $t_1 > 0$ such that if $t \ge t_1$ then $|G(t) - \lambda_0| < \delta/2$. Suppose that $t \ge t_1$ and $F(t) \ge \eta^{-1}(\lambda_0) + \in$. Then, $\eta(F(t)) \ge \eta(\eta^{-1}(\lambda_0) + \in) = \lambda_0 + \delta > G(t) + \delta/2$. Thus, $F(t)$ is not $> \eta^{-1}(\lambda_0) + \in$ for all $t > t_1$, since (2.9) would then imply that $F'(t) < -(\delta/2)F(t)$, which in turn implies that $F(t) \le e^{-\delta t/2}F(t_1)$, a contradiction. Thus, there exists $t_2 > t_1$ such that $F(t_2) < \eta^{-1}(\lambda_0) + \in$. Assume that there exists $t > t_2$ such that $F(t) > \eta^{-1}(\lambda_0) + \in$ and let t_3 be the infimum of all such t_2. Then, $t_3 > t_2$, $F(t_3) \ge \eta^{-1}(\lambda_0) + \in > F(t)$ for $t_2 < t < t_3$ and as above, $F'(t_3) < 0$. But then $F(t)$ is decreasing at t_3 and this yields a contradiction. Hence, $F(t) < \eta^{-1}(\lambda_0) + \in$ for all $t > t_2$. A similar argument shows that $F(t) > \eta^{-1}(\lambda_0) - \in$ for all $t >$ some t_2' (unless $\lambda_0 = 0$). Therefore $\lim_{t \to \infty} F(t) = \eta^{-1}(\lambda_0)$. From (2.8) we have that

$$\begin{aligned}
\lim_{t \to \infty} \exp\left[\lambda_0 t - \int_0^t \eta(F(s)) \, ds\right] &= \lim_{t \to \infty} F(t)/\mathscr{F}(e^{-\lambda_0 t}T(t)x) \\
&= \eta^{-1}(\lambda_0)/\mathscr{F}P_0 x,
\end{aligned} \tag{2.10}$$

which implies that $\lim_{t \to \infty} w(t) = \eta^{-1}(\lambda_0)P_0 x/\mathscr{F}P_0 x$. ∎

Remark 2.2. Notice that if $w = \eta^{-1}(\lambda_0)P_0 x/\mathscr{F}P_0 x$, then $Aw = \eta(\mathscr{F}w)w$. Thus $w(t)$ con-

verges to an equilibrium solution of (2.5). Furthermore, if $P_0 x / \bar{\mathscr{F}} P_0 x$ is independent of x, then $w(t)$ converges to a unique equilibrium, as is the case if P_0 has rank one.

3. CHRONOLOGICAL AGE-STRUCTURED POPULATIONS

The classical linear model of age-dependent population dynamics has the formulation

$$l_t(a, t) + l_a(a, t) = -\mu(a)l(a, t), \tag{3.1}$$

$$l(0, t) = \int_0^\infty \beta(a)l(a, t) \, da, \tag{3.2}$$

$$l(a, 0) = \phi(a). \tag{3.3}$$

where μ and β are the age-specific mortality and fertility moduli, respectively (the units of μ and β are 1/time) and ϕ is the known initial age distribution. In [8] it is shown that the solutions of (3.1)–(3.3) correspond to a strongly continuous semigroup of bounded linear operators in the Banach space $L^1(0, \infty)$, satisfying (2.1) and (2.2). We collect these results ([8], Proposition 3.2, Proposition 3.7, and Theorem 4.10) into the following theorem.

THEOREM 3.1
    Let $\mu \in L^\infty(0, \infty)$ and let $\beta \in L^\infty_+(0, \infty) - \{0\}$. Define $A: L^1(0, \infty) \to L^1(0, \infty)$ by

$$A\phi = -\phi' - \mu\phi, \; D(A) = \left\{ \phi \in L^1(0, \infty): \; \phi \text{ is absolutely continuous,} \right.$$

$$\left. \phi' \in L^1(0, \infty), \text{ and } \phi(0) = \int_0^\infty \beta(a)\phi(a) \, da \right\}. \tag{3.4}$$

Then, A is the infinitesimal generator of a strongly continuous semigroup of bounded linear operators $T(t)$, $t \geq 0$ in $L^1(0, \infty)$ satisfying (2.1), and if $\phi \in D(A)$, then $l(a, t) = (T(t)\phi)(a)$ is the unique solution of (3.1)–(3.3). Let $\lambda = \lambda_0$ be the (necessarily) unique real solution of the equation

$$1 = \int_0^\infty e^{-\lambda a}\beta(a)\Pi(a, 0) \, da. \tag{3.5}$$

Let $\lambda_0 > -\underline{\mu}$ where $\underline{\mu} \equiv \sup_{a \to \infty} \text{ess-inf}_{b>a}\mu(b)$, and define $P_0: L^1(0, \infty) \to L^1(0, \infty)$ by

$$(P_0\phi)(a) = e^{-\lambda_0 a}\Pi(a, 0)V_{\lambda_0}(\phi)/M_{\lambda_0}, \; \phi \in L^1(0, \infty), \quad a \geq 0, \tag{3.6}$$

where

$$\Pi(a, b) = \exp\left[-\int_b^a \mu(c) \, dc \right], \quad 0 \leq a \leq b; \tag{3.7}$$

$$V_{\lambda_0}(\phi) = \int_0^\infty \beta(a)e^{-\lambda_0 a}\left[\int_0^a e^{\lambda_0 b}\Pi(a, b)\phi(b) \, db \right] da, \quad \phi \in L^1(0, \infty); \tag{3.8}$$

$$M_{\lambda_0} = \int_0^\infty \beta(a)ae^{-\lambda_0 a}\Pi(a, 0) \, da. \tag{3.9}$$

Then, (2.2) is satisfied for this λ_0, P_0, $P_1 = I - P_0$, and any $\omega < \lambda_0$ sufficiently close to λ_0. Consequently,

$$\lim_{t \to \infty} |e^{-\lambda_0 t}T(t) - P_0| = 0.$$

Remark 3.1. The Equation (3.5) is known as the *characteristic equation* and its unique real solution λ_0 is known as the *intrinsic growth constant*. The quantity $\Pi(a, b)$ is the *survival probability* of an individual from age b to age a. The quantity $V_{\lambda_0}(\phi)$ is called the *natural reproductive value* of the initial age distribution ϕ, and the quantity M_{λ_0} is called the *mean age of childbirth*. The connection of the characteristic equation to the ultimate behavior of the solutions of (3.1)–(3.2) was discovered by F. Sharpe and A. Lotka[15] in 1911, and the first rigorous treatment was given by W. Feller[16] in 1941. Recently, operator-theoretic methods have been used to prove this result in [8,17–20]. In the classical theory of linear age-dependent population dynamics the density $T(t)P_0\phi = e^{\lambda_0 t}P_0\phi$ is called a *stable age distribution*, since it has the property that the proportion of the population in the age range $[a_1, a_2]$

$$\int_{a_1}^{a_2} (T(t)P_0\phi)(a)\,\mathrm{d}a \bigg/ \int_0^{\infty} (T(t)P_0\phi)(a)\,\mathrm{d}a$$

is constant for all time t.

Remark 3.2. In [8] stronger hypotheses are placed on μ and β than stated in Theorem 3.1. In particular μ and β are required to be continuous in [8], but this hypothesis may be weakened to measurable and essentially bounded using the methods in [20]. Also, μ is require to be bounded below above 0 in [8], but this hypothesis may be replaced by the condition $\lambda_0 > -\underline{\mu}$, as is easily seen from the proof given in [8], Theorem 4.6.

Theorem 2.1 now applies immediately to the logistic model of chronological age-structured population dynamics (1.1)–(1.3).

THEOREM 3.2

Let $\mu \in L^{\infty}(0, \infty)$, let $\beta, \omega \in L^{\infty}_+(0, \infty) - \{0\}$, let $\lambda_0 > -\underline{\mu}$, let η satisfy (2.4), and let $\phi \in L^1_+(0, \infty) \cap D(A)$ such that $P_0\phi \in L^1_+(0, \infty) - \{0\}$. The unique solution of (1.1)–(1.3) satisfies $\lim_{t\to\infty}\|p(\cdot, t)\|_{L^1(0,\infty)} = 0$ if $\lambda_0 < 0$, and $\lim_{t\to\infty}\|p(\cdot, t) - \eta^{-1}(\lambda_0)\phi_0/\int_0^{\infty} \phi_0(a)\omega(a)\,\mathrm{d}a\|_{L^1(0,\infty)} = 0$ if $\lambda_0 \geq 0$, where $\phi_0(a) = e^{-\lambda_0 a}\Pi(a, 0)$, $a \geq 0$.

The ideas of Theorems 3.1 and 3.2 can be implemented for systems of hyperbolic partial differential equations with logistic type nonlinearities. As an example of such a system consider two interacting species with density functions $p_1(a, t)$ and $p_2(a, t)$. The densities satisfy the equations

$$p_{1t}(a, t) + p_{1a}(a, t) = -[\mu_1(a) + \mu_{11}(Q_1(t)) + \mu_{12}(Q_2(t))]p_1(a, t), \tag{3.10}$$

$$p_{2t}(a, t) + p_{2a}(a, t) = -[\mu_2(a) + \mu_{21}(Q_1(t)) + \mu_{22}(Q_2(t))]p_2(a, t), \tag{3.11}$$

$$p_1(0, t) = \int_0^{\infty} \beta_1(a)p_1(a, t)\,\mathrm{d}a, \tag{3.12}$$

$$p_2(0, t) = \int_0^{\infty} \beta_2(a)p_2(a, t)\,\mathrm{d}a, \tag{3.13}$$

$$p_1(a, t) = \phi_1(a), \tag{3.14}$$

$$p_2(a, t) = \phi_2(a). \tag{3.15}$$

Here μ_i, β_i are the age-specific mortality and fertility moduli for species $i = 1, 2$:

$$Q_i(t) = \int_0^{\infty} p_i(a, t)\omega_i(a)\,\mathrm{d}a,$$

with ω_i a weight function, μ_{ij}, $i, j = 1, 2$, correspond to intraspecies or interspecies contributions to the mortality processes, and ϕ_i is the known initial age distribution. If μ_{12} and μ_{21} are increasing functions, then this system corresponds to a model of two competing species, and if μ_{12} is decreasing and μ_{21} is increasing, then this system corresponds to a predator–prey model with p_1 the density of the predator and p_2 the density of the prey. Similar models of age-dependent interacting species have been treated in [8,21–25].

We require the following hypothesis:

μ_1, $\mu_2 \in L^\infty_+(0, \infty)$, β_1, β_2, ω_1, $\omega_2 \in L^\infty_+(0, \infty) - \{0\}$, and μ_{11}, μ_{12}, μ_{21}, μ_{22}
are continuously differentiable functions from $[0, \infty)$ to $[0, \infty)$.   (3.16)

For $i = 1, 2$ define

$$A_i \phi = -\phi' - \mu_i \phi, \quad D(A_i) = \left\{ \phi \in L^1(0, \infty): \phi \text{ is absolutely continuous,} \right.$$

$$\left. \phi' \in L^1(0, \infty), \text{ and } \phi_i(0) = \int_0^\infty \beta_i(a)\phi(a) \, da \right\}.$$ (3.17)

By Theorem 3.1 A_i is the infinitesimal generator of a strongly continuous semigroup of bounded linear operators $T_i(t)$, $t \geq 0$ in $L^1(0, \infty)$ satisfying (2.1) and (2.2) with dominant real eigenvalue λ_{0i}, as in (3.5) and associated projection P_{0i} as in (3.6).

THEOREM 3.3

Let (3.16) hold, let $\lambda_{0i} > -\underline{\mu}_i$, $i = 1, 2$, and let $\phi_i \in L^1_+(0, \infty) \cap D(A_i)$ such that $P_{0i}\phi_i \in L^1_+(0, \infty) - \{0\}$, $i = 1, 2$. There exists a unique solution to the problem (3.10)–(3.15). Suppose there exist $\hat{Q}_1$, $\hat{Q}_2 \geq 0$ such that

$$\mu_{11}(\hat{Q}_1) + \mu_{12}(\hat{Q}_2) = \lambda_{01} \quad \text{and} \quad \mu_{21}(\hat{Q}_1) + \mu_{22}(\hat{Q}_2) = \lambda_{02}.$$ (3.18)

If

$$\mu'_{11}(\hat{Q}_1)\hat{Q}_1 + \mu'_{22}(\hat{Q}_2)\hat{Q}_2 > 0 \quad \text{and} \quad \mu'_{11}(\hat{Q}_1)\mu'_{22}(\hat{Q}_2) > \mu'_{12}(\hat{Q}_1)\mu'_{21}(\hat{Q}_2),$$ (3.19)

then

there exists $t_1 > 0$ and $\delta > 0$ such that if $\|p_i(\cdot, t_1) - \hat{\phi}_i\|_{L^1(0,\infty)} < \delta$, $i = 1, 2$,

then $\lim_{t \to \infty} \|p_i(\cdot, t) - \hat{Q}_i\hat{\phi}_i / \int_0^\infty \hat{\phi}_i(a)\omega_i(a) \, da\|_{L^1(0,\infty)} = 0$, where $\hat{\phi}_i(a) =$

$$e^{-\lambda_{0i}a} \exp\left[-\int_0^a \mu_i(c) \, dc \right], \quad a \geq 0, \, i = 1, 2.$$ (3.20)

Proof. Under the hypothesis stated the existence of a unique solution $\{p_1(\cdot, t), p_2(\cdot, t)\}$ from $[0, \infty)$ to $L^1_+(0, \infty) \times L^1_+(0, \infty)$ for the problem (3.10)–(3.15) follows from Theorems 2.1, 2.3, 2.4, 2.5, 2.9, and Proposition 3.6 in [8]. In addition the following formulas hold for $i = 1, 2$:

$$p_i(\cdot, t) = \exp\left[-\int_0^t \{\mu_{i1}(Q_1(s)) + \mu_{i2}(Q_2(s))\} \, ds \right] T_i(t)\phi_i, \quad t \geq 0.$$ (3.21)

$$Q_i(t) = \exp\left[-\int_0^t \{\mu_{i1}(Q_1(s)) + \mu_{i2}(Q_2(s))\} \, ds \right] S_i(t), \quad t \geq 0.$$ (3.22)

$$Q'_i(t) = [S'_i(t)/S_i(t) - \mu_{i1}(Q_1(t)) - \mu_{i2}(Q_2(t))]Q_i(t), \quad t \geq 0.$$ (3.23)

where

$$S_i(t) = \int_0^\infty (T_i(t)\phi_i)(a)\omega_i(a) \, da, \quad t \geq 0,$$

and $S_i(t) > 0$ for all $t \geq 0$ as in (2.6).

As in (2.7) $\lim_{t\to\infty} S_i'(t)/S_i(t) = \lambda_{0i}$, $i = 1, 2$. Thus, the system of ordinary differential equations (3.23) can be written as

$$Q'(t) = LQ(t) + f(Q(t)) + g(t, Q(t)),\qquad(3.24)$$

where

$$Q(t) = \{Q_1(t), Q_2(t)\}, \; LQ(t) = \{\lambda_{01}Q_1(t), \lambda_{02}Q_2(t)\},$$

$$f(Q(t)) = -\{[\mu_{11}(Q_1(t)) + \mu_{12}(Q_2(t))]Q_1(t), [\mu_{21}(Q_1(t)) + \mu_{22}(Q_2(t))]Q_2(t)\},$$

$$g(t, Q(t)) = \{(S_1'(t)/S_1(t) - \lambda_{01})Q_1(t), (S_2'(t)/S_2(t) - \lambda_{02})Q_2(t)\}.$$

If (3.18) holds, then the linearization of the system (3.24) about $\{\hat{Q}_1, \hat{Q}_2\}$ yields

$$R'(t) = [L + f'(\{\hat{Q}_1, \hat{Q}_2\})]R(t) + o(R(t)) + g(t, R(t) + \{\hat{Q}_1, \hat{Q}_2\}),\qquad(3.25)$$

where

$$R(t) = \{Q_1(t) - \hat{Q}_1, Q_2(t) - \hat{Q}_2\},$$

$$f(\{R_1, R_2\} + \{\hat{Q}_1, \hat{Q}_2\}) - f(\{\hat{Q}_1, \hat{Q}_2\}) = f'(\{\hat{Q}_1, \hat{Q}_2\})$$
$$\times \{R_1, R_2\} + o(\{R_1, R_2\}),$$

$$f'(\{\hat{Q}_1, \hat{Q}_2\})\{R_1, R_1\} = -\{[\mu_{11}'(\hat{Q}_1)R_1 + \mu_{12}'(\hat{Q}_2)R_2]\hat{Q}_1$$
$$+ [\mu_{11}(\hat{Q}_1) + \mu_{12}(\hat{Q}_2)]R_1,$$
$$[\mu_{21}'(\hat{Q}_1)R_1 + \mu_{22}'(\hat{Q}_2)R_2]\hat{Q}_2 + [\mu_{21}(\hat{Q}_1) + \mu_{22}(\hat{Q}_2)]R_2\}.$$

The hypothesis (3.18) and (3.19) means that the eigenvalues of $L + f'(\{\hat{Q}_1, \hat{Q}_2\})$ have negative real parts, so that $\lim_{t\to\infty} R(t) = 0$ if $R(t_1)$ is sufficiently small (see [26], p. 327 or [27], p. 89). The conclusion (3.20) now follows as in (2.10). ∎

Remark 3.3. The local asymptotic stability of the nontrivial equilibrium $\{\hat{Q}_1, \hat{Q}_2\}$ [that is, the conclusion (3.20)] is a consequence of the domination of the interspecies mortality by the intraspecies mortality [that is, hypothesis (3.19)]. Results similar to Theorems 3.2 and 3.3 were obtained by J. Prüss in [6].

4. PHYSIOLOGICAL AGE-STRUCTURED POPULATIONS

For some biological populations the chronological age of individuals is not easily monitored. For these populations there may be some other physical characteristic such as size, volume, mass, or protein content which provides a suitable measure of individual differences. Models of populations structured by size or some other indicator of physiological age have been treated in [19,20,28–34].

Consider a population structured by physiological age s (which we will refer to as the size variable), but which is, in general, a physical characteristic of individuals different from chronological age. The total population at time t having sizes between s_1 and s_2 is

$$\int_{s_1}^{s_2} n(s, t) \, ds,$$

where $n(s, t)$ is the density with respect to size s at time t. The linear formulation of physiological age structured population dynamics is

$$n_t(s, t) + (g(s)n(s, t))_s = -\mu(s)n(s, t),\qquad(4.1)$$

$$g(s_0)n(s_0, t) = \int_{s_0}^{\infty} \beta(s)n(s, t) \, ds,\qquad(4.2)$$

$$n(s, 0) = \phi(s).\qquad(4.3)$$

Here μ and β are the size-specific mortality and fertility moduli, respectively, s_0 is the size of all neonates, g is the growth rate of size in individuals (in the sense that

$$\int_{s_1}^{s_2} g(s)^{-1} \, ds$$

is the time required for an individual to grow from size s_1 to size s_2), and ϕ is the initial size distribution of the population at time 0. The units of μ and β are 1/time and the units of g are size/time.

In [19] it is shown that the solutions of (4.1)–(4.3) give rise to a strongly continuous semigroup of bounded linear operators $T(t)$, $t \geq 0$ in $L^1(s_0, \infty)$. We collect the results from [19] into the following.

THEOREM 4.1

Let $\mu \in L^\infty(s_0, \infty)$, let $\beta \in L^\infty(s_0, \infty) - \{0\}$, and let $g: [s_0, \infty) \to [0, \infty)$ be continuously differentiable with g and g' bounded on $[s_0, \infty)$ and g bounded away from 0 on $[s_0, \infty)$. Define $A: L^1(s_0, \infty) \to L^1(s_0, \infty)$ by

$$A\phi = -(g\phi)' - \mu\phi, \quad D(A) = \Big\{ \phi \in L^1(s_0, \infty): \phi \text{ is absolutely continuous,}$$

$$(g\phi)' \in L^1(s_0, \infty), \text{ and } g(s_0)\phi(s_0) = \int_{s_0}^\infty \beta(s)\phi(s) \, ds \Big\}. \tag{4.4}$$

Then A is the infinitesimal generator of a strongly continuous semigroup of bounded linear operators $T(t)$, $t \geq 0$ in $L^1(s_0, \infty)$ satisfying (2.1), and if $\phi \in D(A)$, then $n(s, t) = (T(t)\phi)(s)$ is the unique solution of (4.1)–(4.3). Let $\lambda = \lambda_0$ be the (necessarily) unique real solution of the equation

$$1 = \int_{s_0}^\infty \exp[-\lambda\tau(s)] \frac{\beta(s)}{g(s)} \Lambda(s, s_0) \, ds, \tag{4.5}$$

let $\lambda_0 > -(\underline{\mu + g'})$, where $\underline{\mu + g'} \equiv \sup_{a\to\infty} \text{ess-inf}_{b>a}\mu(b) + g'(b)$, and define $P_0: L^1(s_0, \infty) \to L^1(s_0, \infty)$ by

$$(P_0\phi)(s) = \exp[-\lambda_0\tau(s)] \frac{g(s_0)}{g(s)} \Lambda(s, s_0)W_{\lambda_0}(\phi)/N_{\lambda_0}, \quad \phi \in L^1(s_0, \infty), \quad s \geq s_0, \tag{4.6}$$

where

$$\tau(s) = \int_{s_0}^s g(\sigma)^{-1} \, d\sigma, \quad s \geq s_0, \tag{4.7}$$

$$\Lambda(s, r) = \exp\left[-\int_r^s \mu(\sigma)g(\sigma)^{-1} \, d\sigma \right], \quad s_0 \leq r \leq s, \tag{4.8}$$

$$W_{\lambda_0}(\phi) = \int_{s_0}^\infty \beta(s) \exp[-\lambda_0\tau(s)] \Big\{ \int_{s_0}^s \exp[\lambda_0\tau(r)]\Lambda(s, r)$$

$$\times \phi(r)g(s)^{-1} \, dr \Big\} \, ds, \quad \phi \in L^1(s_0, \infty), \tag{4.9}$$

$$N_{\lambda_0} = \int_{s_0}^\infty \beta(s)\tau(s) \exp[-\lambda_0\tau(s)]\Lambda(s, s_0) \frac{g(s_0)}{g(s)} \, ds. \tag{4.10}$$

Then (2.2) is satisfied for this λ_0, P_0, $P_1 = I - P_0$, and any $\omega < \lambda_0$ sufficiently close to λ_0. Consequently, $\lim_{t\to\infty} |e^{-\lambda_0 t}T(t) - P_0| = 0$.

Remark 4.1. The various quantities in Theorem 4.1 are analogous to those in Theorem 3.1. For example, $\Lambda(s, r)$ is the probability that an individual survives from size r to size s. Notice from (4.6), (4.7), and (4.8) that

$$(P_0\phi)(s) = \exp\left[-\int_{s_0}^{s}\{\lambda_0 + \mu(r) + g'(r)\}g(r)^{-1}\,dr\right]W_{\lambda_0}(\phi)/N_{\lambda_0}.$$

If $\lambda_0 + \mu(s) + g'(s) < 0$ for $s \in [s_1, s_2]$, then the stable size distribution $(T(t)P_0\phi)(s) = e^{\lambda_0 t}(P_0\phi)(s)$ will be increasing for $s \in [s_1, s_2]$. The biological interpretation of this phenomenon is that a "stacking up" occurs in the size range $[s_1, s_2]$ in the sense that more individuals grow into this range than grow or die out of it. In [34] Vansickle discusses such phenomena in fish populations with s corresponding to body size.

Remark 4.2. The proof of Theorem 4.1 given in [19] uses a transformation of the independent variable s to convert the problem to the case of Theorem 3.1. In [19] an additional hypothesis was required, namely that ess-inf$(\mu + g') > 0$. That this hypothesis may be omitted follows from the fact that ess-inf μ need not be positive in Theorem 3.1 (see Remark 3.2).

Theorem 2.1 now applies immediately to the logistic model of physiological age-structured population dynamics:

$$n_t(s, t) + (g(s)n(s, t))_s = -[\mu(s) + \eta(Q(t))]n(s, t), \tag{4.11}$$

$$g(s_0)n(s_0, t) = \int_{s_0}^{\infty}\beta(s)n(s, t)\,ds, \tag{4.12}$$

$$n(s, 0) = \phi(s), \tag{4.13}$$

where $Q(t) = \int_{s_0}^{\infty} n(s, t)\omega(s)\,ds$ for some weight function ω.

THEOREM 4.2

Let $\mu \in L^{\infty}(s_0, \infty)$, let $\beta, \omega \in L_{+}^{\infty}(s_0, \infty) - \{0\}$, let $g: [s_0, \infty) \to [0, \infty)$ be continuously differentiable with g and g' bounded on $[s_0, \infty)$ and g bounded away from 0 on $[s_0, \infty)$, let $\lambda_0 > -(\mu + g')$, let η satisfy (2.4), and let $\phi \in L_{+}^{1}(s_0, \infty) \cap D(A)$ such that $P_0\phi \in L_{+}^{1}(s_0, \infty) - \{0\}$. The unique solution of (4.11)–(4.13) satisfies $\lim_{t\to\infty}\|n(\cdot, t)\|_{L^1(s_0,\infty)} = 0$ if $\lambda_0 < 0$, and $\lim_{t\to\infty}\|n(\cdot, t) - \eta^{-1}(\lambda_0)\phi_0/\int_{s_0}^{\infty}\phi_0(s)\omega(s)\,ds\|_{L^1(s_0,\infty)} = 0$ if $\lambda_0 \geq 0$, where $\phi_0(s) = e^{-\lambda_0\tau(s)}\Lambda(s, s_0)$, $s \geq s_0$.

Remark 4.3. The ideas we have developed can be applied to another type of nonlinear structured population problem. This problem does not have logistic form, but rather models a renewable resource with constant yield harvesting. Similar models of harvested structured populations have been treated in [1,29,35–37]. Suppose the hypothesis and notation of Theorem 4.1 and consider a size-structured population with density $p(s, t)$ subject to a constant-yield size-dependent harvesting $h(s)$ with $h \in L_{+}^{1}(s_0, \infty)$. The equations of the model are

$$p_t(s, t) + (g(s)p(s, t))_s = -\mu(s)p(s, t) - h(s), \tag{4.14}$$

$$g(s_0)p(s_0, t) = \int_{s_0}^{\infty}\beta(s)p(s, t)\,ds, \tag{4.15}$$

$$p(s, 0) = \phi(s). \tag{4.16}$$

The solution of (4.14)–(4.16) is given by

$$p(\cdot, t) = T(t)\phi - \int_{0}^{t}T(\sigma)h\,d\sigma, \quad t \geq 0. \tag{4.17}$$

Let P_0 and P_1 act on (4.17) to yield

$$P_0 p(\cdot, t) = e^{\lambda_0 t} P_0 \phi - \int_0^t e^{\lambda_0 \sigma} P_0 h \, d\sigma, \quad t \geq 0. \tag{4.18}$$

$$P_1 p(\cdot, t) = T(t) P_1 \phi - \int_0^t T(\sigma) P_1 h \, d\sigma, \quad t \geq 0. \tag{4.19}$$

From (4.18) we obtain

$$P_0 p(\cdot, t) = P_0 \phi - t P_0 h, \; \lambda_0 = 0, \quad t \geq 0,$$
$$P_0 p(\cdot, t) = e^{\lambda_0 t}[P_0 \phi - P_0 h/\lambda_0] + P_0 h/\lambda_0, \; \lambda_0 \neq 0, \quad t \geq 0, \tag{4.20}$$

and from (4.19) we obtain

$$\|P_1 p(\cdot, t)\|_{L^1(s_0, \infty)} \leq M e^{\omega t}\|P_1 \phi\|_{L^1(s_0, \infty)} + (e^{\omega t} - 1)M\|P_1 h\|_{L^1(s_0, \infty)}/\omega, \quad t \geq 0. \tag{4.21}$$

Since $\omega < \lambda_0$ and $p(\cdot, t) = P_0 p(\cdot, t) + P_1 p(\cdot, t)$, we conclude from (4.20) and (4.21) the following behavior: If $\lambda_0 = 0$ (that is, the unharvested population is in equilibrium), then constant-yield harvesting extinguishes the population in finite time. If $\lambda_0 > 0$ (that is, the unharvested population has exponential growth), then constant-yield harvesting does not extinguish the population provided that $P_0 \phi > P_0 h/\lambda_0$ (in fact, $\lim_{t \to \infty} e^{-\lambda_0 t} p(\cdot, t) = P_0(\phi - h/\lambda_0)$) so that the population maintains exponential growth).

5. CELL POPULATIONS

Structured population models have been used to model the growth of cell populations by many authors. The earliest such models are found in [28,33,38,39]. Recently, the theory of linear operator semigroups has been applied to a linear model of physiological age-structured cell growth by O. Diekmann et al.[40]. The model in [40] derives from the earlier models of Bell and Anderson[28] and Sinko and Streifer[33], which also involved chronological age as well as physiological age. In this section we will describe the linear model in [40] and apply Theorem 2.1 to a nonlinear variation of it involving a logistic-type nonlinearity.

Consider a population of cells structured by a size variable s in which mother cells divide by fission into two equal-size daughter cells. There is a minimum size $s_1 > 0$ which cells must reach before fission can occur and there is a maximum size $s_2 > s_1$ at which fission must occur. Consequently, newly formed daughter cells must lie in the size range $[s_1/2, s_2/2]$ and all cells must lie in the size range $[s_1/2, s_2]$. It is required that $s_1 \geq s_2/2$, which means that the maximum size of a daughter cell is less than or equal to the minimum size of a mother cell. The following equations (which are derived in [40] and [33]) are satisfied by the density function $n(s, t)$ of the cell population:

$$n_t(s, t) + (g(s)n(s, t))_s = -[\mu(s) + b(s)]n(s, t) + 4b(2s)n(2s, t). \tag{5.1}$$

$$n(s_1/2, t) = 0, \tag{5.2}$$

$$n(s, 0) = \phi(s). \tag{5.3}$$

Here μ, b, and g are the size-specific rates at which cells die, divide, and grow, respectively, and ϕ is the initial size distribution of the population [the last term in (5.1) is interpreted to be 0 whenever $s \geq s_2/2$].

The following hypothesis is required.

μ is a nonnegative continuous function on $[s_1/2, s_2]$. \hfill (5.4)

b is continuous on $[s_1/2, s_2)$, $b(s) = 0$ for $s \in [s_1/2, s_1]$, $b(s) > 0$ for $s \in (s_1, s_2)$,

and $\lim_{s \to s_2} \int_{s_1}^{s} b(\sigma) \, d\sigma = \infty$.

$$\tag{5.5}$$

g is strictly positive and continuous on $[s_1/2, s_2]$ and $g(2s) < 2g(s)$ for $s \in [s_1/2, s_2/2]$ (which means that two daughter cells together gain greater size than the undivided mother would have). (5.6)

Define Λ by

$$\Lambda(s, r) = \exp\left[-\int_r^s (\mu(\sigma) + b(\sigma))g(\sigma)^{-1}\,d\sigma\right], \quad s_1/2 \le r \le s \le s_2. \quad (5.7)$$

Notice that $\Lambda(s, r)$ is the probability that a cell of size r reaches size s without dying or dividing. Define the Banach lattice $X = \{\phi: \phi$ is a continuous function from $[s_1/2, s_2]$ to R, $\phi(s_1/2) = 0$, and $\sup_{s_1/2 \le s < s_2}|\phi(s)|/\Lambda(s, s_1/2) < \infty\}$ with norm $\|\phi\| = \sup_{s_1/2 \le s < s_2}|\phi(s)|/\Lambda(s, s_1/2)$.

The following theorem is proved in [40].

THEOREM 5.1

Let (5.4)–(5.6) hold and define $A: X \to X$ by

$$(A\phi)(s) = -(g(s)\phi(s))' - [\mu(s) + b(s)]\phi(s) + 4b(2s)\phi(2s),$$

$D(A) = \{\phi \in X: g(s)\phi(s)$ is continuously differentiable on

$[s_1/2, s_2/2) \cup (s_2/2, s_2), \lim_{s \to s_2/2^-}\{-(g(s)\phi(s))' - [\mu(s) + b(s)]\phi(s)$

$+ 4b(2s)\phi(2s)\} = \lim_{s \to s_2/2^-}\{-(g(s)\phi(s))' - [\mu(s) + b(s)]\phi(s)\},$

$-(g(s_1/2)\phi(s_1/2))' - (\mu(s_1/2) + b(s_1/2))\phi(s_1/2) + 4b(s_1)\phi(s_1)$

$= 0,$ and $\sup_{s_1/2 \le s \le s_2, s \ne s_2/2}\{[-(g(s)\phi(s))' - [\mu(s) + b(s)]\phi(s)$

$+ 4b(2s)\phi(2s)]/\Lambda(s, s_1/2)\} < \infty\}.$ (5.8)

Then A is the infinitesimal generator of a strongly continuous semigroup of bounded linear operators $T(t)$, $t \ge 0$ in X satisfying (2.1), and if $\phi \in D(A)$, then $n(s, t) = (T(t)\phi)(s)$ is the unique solution of (5.1)–(5.3). Let $\lambda = \lambda_0$ be the (necessarily) unique real solution of the equation

$$1 = 4\int_{s_1/2}^{s_2/2} \exp[-\lambda(\tau(2\sigma) - \tau(\sigma))]b(2\sigma)\Lambda(2\sigma, \sigma)/g(2\sigma)\,d\sigma, \quad (5.9)$$

and define $P_0: X \to X$ by

$$P_0\phi = \phi_0 U_{\lambda_0}(\phi)/Q_{\lambda_0}, \quad (5.10)$$

where

$$\tau(s) = \int_{s_1/2}^s g(\sigma)^{-1}\,d\sigma, \quad s_1/2 \le s \le s_2, \quad (5.11)$$

$$U_{\lambda_0}(\phi) = \int_{s_1/2}^{s_2/2} \exp[-\lambda_0(\tau(s_2/2) - \tau(\sigma))]\{\phi(\sigma)\Lambda(\sigma, s_1/2)^{-1}$$

$$+ 4b(2\sigma)g(2\sigma)^{-1}\Lambda(2\sigma, \sigma)\int_{s_2/2}^{2\sigma} \exp[-\lambda_0(\tau(2\sigma) - \tau(\xi))]$$

$$\times \phi(\xi)\Lambda(\xi, s_1/2)^{-1}\,d\xi\}\,d\sigma, \quad \phi \in X, \quad (5.12)$$

$$Q_{\lambda_0} = \int_{s_1/2}^{s_2/2} (\tau(2\sigma) - \tau(\sigma)) \exp[-\lambda_0(\tau(2\sigma) - \tau(\sigma))]$$

$$\times 4b(2\sigma)\Lambda(2\sigma, \sigma)/g(2\sigma) \, d\tau, \tag{5.13}$$

$$\phi_0(s) = \Lambda(s, s_1/2)g(s)^{-1} \exp[-\lambda_0(\tau(s_1) - \tau(s_1/2))]$$

$$\times \int_{s_1/2}^{\min\{s, s_2/2\}} \exp[-\lambda_0(\tau(2\sigma) - \tau(\sigma))]$$

$$\times 4b(2\sigma)\Lambda(2\sigma, \sigma)/g(2\sigma) \, d\sigma. \tag{5.14}$$

Then (2.2) is satisfied for this λ_0, P_0, $P_1 = I - P_0$, and any $\omega < \lambda_0$ sufficiently close to λ_0. Consequently, $\lim_{t\to\infty}|e^{-\lambda_0 t}T(t) - P_0| = 0$.

If the mortality of cells is dependent upon the total population, or if cells enter a nonproliferating state as the total population increases, then Theorem 2.1 may be applied. The equations of such a nonlinear logistic version of this problem are

$$q_t(s, t) + (g(s)q(s, t))_s = -[\mu(s) + \eta(Q(t)) + b(s)]q(s, t) + 4b(2s)q(2s, t), \tag{5.15}$$

$$q(s_1/2, t) = 0, \tag{5.16}$$

$$q(s, 0) = \phi(s), \tag{5.17}$$

where $Q(t) = \int_{s_1/2}^{s_2} q(s, t)\omega(s) \, ds$ for some weight function ω and the term $\mu(s) + \eta(Q(t))$ accounts for either mortality or passage to a permanent state of nonproliferation. By virtue of Theorem 2.1 we have the following.

THEOREM 5.2

Let (5.4)–(5.6) hold, let $\Lambda(s, s_1/2)\omega(s) \in L_+^1(s_1/2, s_2) - \{0\}$, let η satisfy (2.4), and let $\phi \in X_+ \cap D(A)$ such that $P_0\phi \in X_+ - \{0\}$. The unique solution of (5.15)–(5.17) satisfies $\lim_{t\to\infty}\|q(\cdot, t)\|_X = 0$ if $\lambda_0 < 0$, and $\lim_{t\to\infty}\|q(\cdot, t) - \eta^{-1}(\lambda_0)\phi_0/\int_0^\infty \phi_0(s)\omega(s) \, ds\|_X = 0$ if $\lambda_0 \geq 0$.

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