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Asymptotic Similarity and Malthusian Growth in Autonomous and Nonautonomous Populations

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We consider the dynamics of a multistate age-structured population as a nonautonomous system of partial differential equations. This system generates a positive process on a space of bounded functions. We give sufficient conditions for asymptotic similarity of this process, i.e., we show when the asymptotic behaviour of the process at $t \to \infty$ is independent of the initial distribution. © 1994 Academic Press, Inc.

I. INTRODUCTION

Mathematical models of age-structured populations have had a long history starting with the work of McKendrick [17] on epidemics, the von Foerster [26] considerations of cell kinetics, and Keyfitz's [11] work on demography. Subsequently, considerations of the dynamics of age-structured populations have received substantial and sophisticated treatment in a variety of fields [see 1, 3–8, 13, 19–21, 23–25]. Metz and Diekmann [18] provide an especially thorough and readable survey.

Here we examine the limiting growth characteristics of a multistate age-structured population of the type considered by Inaba [8]. Specifically, we

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consider a population of individuals consisting of n subtypes such that the vector of population numbers at time t and age a is given by

$$p(a, t) =: \begin{pmatrix} p_1(a, t) \\ p_2(a, t) \\ \vdots \\ p_n(a, t) \end{pmatrix}. \tag{1.1a}$$

These n subtypes can be thought of as, e.g., n phenotypes or n demographically distinct populations or with $n = 2$ a two sex population, *etc*. The interpretation is clearly quite flexible.

Under the assumption that units of these subpopulations age with unitary velocity, then the evolution of the vector p through (a, t) space is governed by the first-order partial differential equation (transport equation)

$$\frac{\partial p(a, t)}{\partial t} + \frac{\partial p(a, t)}{\partial a} = Q(a, t)p(a, t), \tag{1.1b}$$

wherein Q is the instantaneous $(n \times n)$ *transition rate matrix*. (We make these specifications more precise in the next section.) To complete the formulation of this problem requires the specification of a boundary condition

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

where M is the $(n \times n)$ *reproductive rate matrix*, and an initial condition

$$p(a, t = 0) = \varphi(a). \tag{1.3}$$

Inaba [8] has exploited a semigroup approach to the study of the asymptotic properties of the system (1.1)–(1.3) in the special case where the death and reproductive matrices Q and M are autonomous, *i.e.*, independent of time t. In this paper Inaba has shown *strong ergodicity* of this system, *i.e.*, the exponential growth of $p(a, t)$ to some distribution which does not depend on the initial condition. This property is also called *exponential stationarity* (see [14, 22]). When the matrices Q and M depend on time, then the phenomenon that the long-run behaviour of the age distribution is independent of the initial date is called *weak ergodicity* (see Lopez [16]). In [9] Inaba has given a sufficient condition for weak ergodicity of $p(a, t)$. His method is based on the Birkhoff [2] lattice-theoretic approach to multiplicative processes. Another method of investigation of nonautonomous populations is given in the recent paper of Inaba [10]. The multiplicative process corresponding to system (1.1)–(1.3) can be obtained by perturbing some semigroup, which allows one to prove the strong ergodic theorem for this system.

In the present paper we prove a theorem on weak ergodicity of nonautonomous populations for a large class of matrices Q and M. This theorem generalizes Inaba's results concerning weak ergodicity [9] and strong ergodicity [8]. The method of proof is based on ideas similar to Inaba [9]. However, we restrict our investigation to a space of real-valued bounded functions with the supremum norm. This allows us to omit the lattice-theoretic apparatus used in [9].

The plan of the paper is as follows. In Section 2 we precisely formulate the problem posed by the system (1.1)–(1.3), while Section 3 introduces the property of asymptotic similarity. The notion of asymptotic similarity describes the same feature of the multiplicative process as weak ergodicity, but in our case it is more convenient. Section 4 presents our main result (Theorem 2) on the growth properties of the system, and this result is proved in Section 5. Finally, Section 6 considers both autonomous and nonautonomous growth properties using Theorem 2. In particular, if the matrices Q and M are periodic with respect to t, we show that the process exhibits behaviour similar to the exponential growth observed in the autonomous case.

2. Formulation of the Problem as an Integral Equation

We consider the following system of equations:

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) p(a, t) = Q(a, t)p(a, t) \tag{2.1}$$

$$p(0, t) = \int_0^{a_r} M(a, t)p(a, t)\, da. \tag{2.2}$$

Remember that Q is the *transition rate matrix* while M is the *reproductive rate matrix*. We assume that

(1) the elements $q_{ij}(a, t)$ and $m_{ij}(a, t)$, $1 \le i, j \le n$, of the matrices Q and M are continuous bounded functions;

(2) $m_{i,j}(a, t) \ge 0$ for $1 \le i, j \le n$, so the average number of progeny of type i produced by individuals of type j at (a, t) is nonnegative;

(3) $q_{ij}(a, t) \ge 0$ for $i \ne j$, so the instantaneous transition from type j to type i at (a, t) is nonnegative; and

(4) $q_{ii}(a, t) = -\mu_i(a, t) - \sum_{j \neq i} q_{ji}(a, t)$, where $\mu_i(a, t) \geq 0$. Therefore, the death rate of type i at (a, t) is nonpositive.

Formally, the matrices Q and M are defined for $a \geq 0$ and $t \geq 0$, but for technical reasons we assume that Q and M are defined and continuous for all real numbers a and t. Moreover, $m_{ij}(a, t) = 0$ for $a \geq a_r$, where a_r denotes the maximum reproductive age. We assume that the function $p(a, t)$ is given for $t = 0$ by (1.3), $p(a, 0) = \varphi(a)$.

Now let a and t be given real numbers. The *survival rate matrix* $L(h; a, t)$ is defined as the solution of the matrix differential equation

$$\frac{d}{dt} L(h; a, t) = Q(a + h, t + h)L(h; a, t), \qquad L(0; a, t) = I, \tag{2.3}$$

where I denotes the $(n \times n)$ identity matrix. From the definition of $L(h; a, t)$ it follows that the elements of the matrix $L(h; a, t)$ are continuous functions of a, t, and h; all elements of $L(h; a, t)$ are nonnegative [8, Lemma 1]; and for all real numbers a, t, h, and h_1 we have

$$L(h_1 + h; a, t) = L(h_1; a + h, t + h)L(h; a, t). \tag{2.4}$$

Integrating Eq. (2.1) along characteristics, the solution of Eq. (2.1) is given by the formula

$$p(a, t) = \begin{cases} L(a; 0, t - a)p(0, t - a) & \text{for } t \geq a \\ L(t; a - t, 0)p(a - t, 0) & \text{for } t < a. \end{cases} \tag{2.5}$$

Substituting (2.5) into (2.2) we obtain

$$p(0, t) = \int_0^t M(a, t)L(a; 0, t - a)p(0, t - a)\, da$$

$$+ \int_t^\infty M(a, t)L(t; a - t, 0)p(a - t, 0)\, da.$$

According to (2.4),

$$L(t; a - t, 0) = L(a; 0, t - a)L(t - a; a - t, 0). \tag{2.6}$$

Further, if we set $K(a, t) = M(a, t)L(a; 0, t - a)$ and $w(r) = L(-r; r, 0)p(r, 0)$, then

$$p(0, t) = \int_0^t K(a, t)p(0, t - a)\, da + \int_t^\infty K(a, t)w(a - t)\, da.$$

The matrix $L(a; 0, t-a)$ is the solution of (2.3) on the finite interval $[0, a_r]$ (remember that a_r is the maximum reproductive age), so all elements of this matrix are bounded and continuous. Hence all elements k_{ij} of the matrix K are bounded continuous nonnegative functions.

The function $p(a, t)$ is given for $t = 0$, and therefore the function $w(r)$ is defined for $r \geq 0$. Now substituting $\Phi(t) = w(-t)$ for $t < 0$ and $\Phi(t) = p(0, t)$ for $t \geq 0$, we obtain

$$\Phi(t) = \int_0^\infty K(a, t)\Phi(t-a)\, da. \tag{2.7}$$

Since $k_{i,j}(a, t) = 0$ for $a \geq a_r$, Eq. (2.7) is equivalent to

$$\Phi(t) = \int_0^{a_r} K(a, t)\Phi(t-a)\, da. \tag{2.8}$$

If we assume that the function Φ is given on the interval $[t_0 - a_r, t_0)$, then Eq. (2.8) has a unique solution $\Phi: [t_0, \infty) \to R^n$ in the class of locally bounded functions. Moreover, if for every $i \in \{1, \ldots, n\}$ and $\omega \in [t_0 - a_r, t_0)$ we have $\Phi_i(\omega) \geq 0$, then $\Phi_i(t) \geq 0$ for every $i \in \{1, \ldots, n\}$ and $t \geq t_0$. In our case the function Φ is given for $t \leq 0$ and all coordinates Φ_i are nonnegative for $t \leq 0$, which implies that Eq. (2.8) has a unique nonnegative solution for $t > 0$.

3. Processes Generated by the Integral Equation (2.8)

Let D be an arbitrary nonempty set and $B(D)$ be the space of all real-valued bounded functions defined on D with the norm $\|f\| = \sup_{x\in D}|f(x)|$. Let X be an arbitrary fixed linear subspace of $B(D)$ and

$$X_+ = \{f \in X : \inf_{x\in D} f(x) > 0\}.$$

We assume that X_+ is a nonempty set.

A linear operator $P: X \to X$ is called *positive* if $P(X_+) \subset X_+$. A family $\{P(t, s)\}_{t\geq s\geq 0}$ of linear operators $P(t, s): X \to X$ is called a *process* if

(i) $P(s, s) = \mathrm{Id}$ (Id = Identity); and

(ii) $P(t, r)P(r, s)f = P(t, s)f$ for $f \in X$ and $t \geq r \geq s \geq 0$.

A process $\{P\}$ will be called *positive* if, for every $t \geq s \geq 0$ the operator $P(t, s)$ is positive. Further, the process $\{P\}$ is said to be *eventually uniformly positive* if $\{P\}$ is a positive process and there is a subset $X_0 \subset X_+$

dense in X_+ as well as a constant $\alpha > 0$ such that for every $f \in X_0$ and $s \geq 0$ the inequality

$$\frac{P(t, s)f}{\|P(t, s)f\|} \geq \alpha \tag{3.1}$$

holds for sufficiently large t (say $t \geq t_0 = t_0(f, s)$).

The process $\{P\}$ is *asymptotically similar* if for every $f \in X$, $g \in X_+$, and $s \geq 0$ there is a constant $c = c(f, g, s)$ such that

$$\lim_{t \to \infty} \left\| \frac{P(t, s)f}{P(t, s)g} - c \right\| = 0. \tag{3.2}$$

The process $\{P\}$ is *weakly ergodic* if for every $f, g \in X_+$ and $s \geq 0$, we have

$$\lim_{t \to \infty} \frac{\sup_{x \in D}(P(t, s)f(x)/P(t, s)g(x))}{\inf_{x \in D}(P(t, s)f(x)/P(t, s)g(x))} = 1.$$

From asymptotic similarity weak ergodicity follows immediately. But in fact, according to [9, Proposition 3.2], both of these notions are equivalent.

In our study of systems described by (2.8), we will use the following theorem.

THEOREM 1. *Every eventually uniformly positive process has the property of asymptotic similarity.*

A simple proof of theorem 1 is given in [15], but this theorem also follows from the results of Inaba [9].

In the case considered here, $D = [-a_r, 0) \times \{1, \ldots, n\}$ and X is the set of all bounded measurable functions f: $D \to R$. The operators $P(t, s)$ on X are defined by

$$(P(t, s)f)(\omega, k) = \Phi_k(t + \omega) \qquad \text{for } \omega \in [-a_r, 0) \text{ and } t \geq 0,$$

where Φ is the solution of (2.8) satisfying

$$\Phi_k(s + \omega) = f(\omega, k) \qquad \text{for } \omega \in [-a_r, 0). \tag{3.3}$$

The semigroup properties (i) and (ii) of $\{P\}$ follow immediately from the uniqueness of the solutions of (2.8).

If we assume that for every $t > 0$ and $i \in \{1, \ldots, n\}$ there exist $a \in$

$(t - a_r, t)$ and $j \in \{1, \ldots, n\}$ such that $k_{ij}(a, t) > 0$, then from Eq. (2.8) it follows that the process $\{P\}$ is positive.

4. Asymptotic Similarity

Now we formulate our main theorem.

THEOREM 2. *Assume that there exist continuous nonnegative bounded functions* b_{ij}: $[0, \infty) \to [0, \infty)$, $1 \le i, j \le n$, *satisfying the following conditions*:

(a) $b_{ij}(a) \le k_{ij}(a, t)$ *for every* $a \in [0, a_r]$ *and* $t \ge 0$,

(b) *the matrix* $[c_{ij}]$, *where* $c_{ij} = \int_0^{a_r} b_{ij}(a)\, da$, *is indecomposable.*

Then the process $\{P\}$ *generated by Eq.* (2.8) *has the property of asymptotic similarity.*

Remark 1. A nonnegative $n \times n$ matrix $C = [c_{ij}]$ is called *decomposable* if there exist two subsets G and H of integers $J = \{1, 2, \ldots, n\}$ such that $G \cap H = \emptyset$, $G \cup H = J$, and $c_{ij} = 0$ for $i \in G, j \in H$. A nonnegative matrix $C = [c_{ij}]$ is called *indecomposable* if it is not decomposable and is not the zero matrix of order one. A matrix C is indecomposable if and only if for every $1 \le i \le n$ and $1 \le j \le n$ there exists a sequence or *chain* of integers $1 \le i_0, \ldots, i_m \le n$ such that $i_0 = i$, $i_m = j$, and

$$c_{i_0 i_1} c_{i_1 i_2} \cdots c_{i_{m-1} i_m} > 0. \tag{4.1}$$

From condition (b) it follows that for every $1 \le i \le n$ and $1 \le j \le n$ there exists a sequence of integers $1 \le i_0, \ldots, i_m \le n$ and a sequence of real numbers $a_0, \ldots, a_m \subset [0, a_r]$ such that $i_0 = i$, $i_m = j$, and

$$b_{i_0 i_1}(a_1) b_{i_1 i_2}(a_2) \cdots b_{i_{m-1} i_m}(a_m) > 0. \tag{4.2}$$

Condition (a) in conjunction with (4.2) implies that the process $\{P\}$ is positive.

Remark 2. The assumptions of (a) and (b) of Theorem 2 can be interpreted biologically in the following way. For each i and j, the individuals born in the subtype i have descendants in the subtype j.

Remark 3. In the paper of Inaba [9] the property of asymptotic similarity was proved under some stronger assumption. Namely, the following two conditions were assumed:

(1) there exist numbers γ_1, γ_2, and a primitive matrix $N \geq 0$ such that

$$K(a, t) \geq N \qquad \text{for all } (a, t) \in [\gamma_1, \gamma_2] \times [0, \infty),$$

(2) the elements of the matrix $S(a, t)$ defined by

$$S(a, t) = \int_0^{a_r} M(a + \rho, t + \rho)L(\rho; a, t)\, d\rho$$

satisfy the condition

$$\max_i s_{ij}(a, t) \leq \omega \min_i s_{ij}(a, t)$$

for $(a, t) \in [0, a_r] \times [0, \infty)$, $1 \leq j \leq n$, and some $\omega > 0$.

We recall that a nonnegative matrix A is primitive if some power of A is strictly positive. It is well known that a primitive matrix is indecomposable, but not vice versa.

5. Proof of Theorem 2

In the proof of Theorem 2 we use the following notation:

(1) if $f: [0, \infty) \to R$ is a locally integrable function then

$$\|f\|_a^b = \int_a^b |f(x)|\, dx \qquad \text{for } 0 \leq a < b < \infty,$$

(2) if $f: [0, \infty) \to R^n$ is a locally integrable function then

$$|||f|||_a^b = \sum_{i=1}^n \int_a^b |f_i(x)|\, dx \qquad \text{for } 0 \leq a < b < \infty.$$

The proof is based on two lemmas.

Lemma 1. *Let Φ be a solution of* (2.8) *satisfying* (3.3), *where $f \in X_+$ and $s > 0$. Then there exist positive constants t_0, p, and Γ independent of f, such that for $t \geq t_0 + s$ and $j = 1, \ldots, n$ we have*

$$\Phi_j(t) \geq \Gamma |||\Phi|||_{t-p-3a_r}^{t-p}. \tag{5.1}$$

Proof. Set $Z = \{(i, j): 1 \le i \le n, 1 \le j \le n\}$ and $Z' = \{(i, j) \in Z : b_{ij} \neq 0\}$. Then there is an $\alpha \in (0, 1)$ and $h \in (0, 1)$ such that for every $(i, j) \in Z'$ there exists an interval

$$\Delta_{ij} = [d_{ij}, d_{ij} + h] \subset [0, a_r]$$

with $b_{ij}(\tau) \ge \alpha$ for $\tau \in \Delta_{ij}$. Let $I = (i_0, i_1, \ldots, i_\vartheta)$ be a chain which connects type i with type j. The letter ϑ will be called the *length* of the chain I.

From the definition of Φ in Eq. 2.8 and from condition (a) it follows immediately that for $t \ge a_r(\vartheta - 1) + s$ we have

$$\Phi_j(t) \le \int_0^{a_r} \cdots \int_0^{a_r} \Phi_i(t - \tau_1 - \cdots - \tau_\vartheta) b_{i_0 i_1}(\tau_1) \cdots b_{i_{\vartheta-1} i_\vartheta}(\tau_\vartheta) d\tau_1 \cdots d\tau_\vartheta$$

$$\ge \alpha^\vartheta \int \underset{\Delta}{\cdots} \int \Phi_i(t - \tau_1 - \cdots - \tau_\vartheta) d\tau_1 \cdots d\tau_\vartheta,$$

where

$$\Delta = \Delta_{i_0 i_1} \times \cdots \times \Delta_{i_{\vartheta-1} i_\vartheta}.$$

By an inductive argument it is easy to verify that

$$\Phi_j(t) \ge \alpha^\vartheta \left(\frac{h}{3}\right)^{\vartheta - 1} \int_{h(\vartheta-1)/3}^{2h(\vartheta-1)/3} \Phi_i(t - d(I) - \tau)\, d\tau, \tag{5.2}$$

where $d(I) = d_{i_0 i_1} + \cdots + d_{i_{\vartheta-1} i_\vartheta}$. Inequality (5.2) can be rewritten in the form

$$\Phi_j(t) \ge \alpha^\vartheta \left(\frac{h}{3}\right)^{\vartheta - 1} \|\Phi_i\|_{t-d(I)-2h(\vartheta-1)/3}^{t-d(I)-h(\vartheta-1)/3}. \tag{5.3}$$

Denote by $I(i)$ a chain which connects type i with type 1 and by $I'(i)$ a chain which connects type 1 with type i. Let ϑ_i be the length of $I(i)$ and ϑ_i' be the length of $I'(i)$. Type i can be connected with type j by means of a long chain $I(i, j)$ which contains the chain $I(i)$, x chains $I(1)$, and the chain $I'(j)$. Then $d(I(i, j)) = d(I(i)) + xd(I(1)) + d(I'(j))$ and the length of $I(i, j)$ is $\vartheta_i + x\vartheta_1 + \vartheta_j'$. We set

$$\xi = \max\{\vartheta_i + \vartheta_j' : 1 \le i, j \le n\}$$

and

$$\eta = \max\{d(I(i)) + d(I'(j)) \colon 1 \leq i, j \leq n\}.$$

Then

$$t - d(I(i,j)) - 2h\frac{(\vartheta_{ij} - 1)}{3} \leq t - xd(I(1)) - 2h\frac{(x\vartheta_1 - 1)}{3}$$

and

$$t - d(I(i,j)) - h\frac{(\vartheta_{ij} - 1)}{3} \geq t - xd(I(1)) - \eta - h\frac{(\xi + x\vartheta_1 - 1)}{3}.$$

Take an x sufficiently large such that

$$h\frac{(x\vartheta_1 - 1)}{3} - h\frac{\xi}{3} - \eta \geq 3a_r$$

and set

$$p = xd(I(1)) + \eta + h\frac{(\xi + x\vartheta_1 - 1)}{3}.$$

Then

$$t - d(I(i,j)) - 2h\frac{(\vartheta_{ij} - 1)}{3} \leq t - p - 3a_r$$

and

$$t - d(I(i,j)) - h\frac{(\vartheta_{ij} - 1)}{3} \geq t - p.$$

From inequality (5.3) it follows that

$$\Phi_j(t) \geq \alpha^{p\vartheta_1 + \xi}\left(\frac{h}{3}\right)^{p\vartheta_1 + \xi - 1} \|\Phi_i\|_{t-p-3a_r}^{t-p} \qquad \text{for } t \geq t_0 + s,$$

where $t_0 = p + 2a_r$. Finally defining

$$\gamma = \frac{1}{n}\left(\frac{\alpha h}{3}\right)^{pm_1 + \xi},$$

we obtain

$$\Phi_j(t) \geq \Gamma \| \, |\Phi| \, \|_{t-p-3a_r}^{t-p} \qquad \text{for } t \geq t_0 + s,$$

and the lemma is proved. ∎

The second lemma required for the proof of Theorem 2 is the following.

LEMMA 2. *Let Φ be a function and p be the constant from Lemma 1. Then there exist positive constants t_1 and L, independent of Φ, such that*

$$|\Phi(t)| \leq L \| \, |\Phi| \, \|_{t-p-2a_r}^{t-p-a_r} \qquad \textit{for } t \geq t_1. \tag{5.4}$$

Proof. Since the functions $k_i(a, t)$ are bounded there exists a positive constant $\mathcal{M}$ such that

$$k_{ij}(a, t) \leq \mathcal{M} \qquad \text{for } 1 \leq i, j \leq n, \, a \in [0, a_r], \text{ and } t \geq 0.$$

This implies that

$$|\Phi(t)| \leq \mathcal{M} n \int_{t-a_r}^{t} |\Phi(\tau)| d\tau \qquad \text{for } t \geq a_r.$$

Let $u \geq s$ be given. Then for $t \geq u$ we have

$$|\Phi(t)| \leq \mathcal{M} n \int_{u-a_r}^{u} |\Phi(\tau)| d\tau + \mathcal{M} n \int_{u}^{t} |\Phi(\tau)| d\tau.$$

From Gronwall's inequality it follows that

$$|\Phi(t)| \leq \mathcal{M} n \int_{u-a_r}^{u} |\Phi(\tau)| d\tau e^{\mathcal{M} n (t-u)} \qquad \text{for } t \geq u.$$

Set $u = t - p - a_r$ and $L = \mathcal{M} n e^{\mathcal{M} n (p + a_r)}$. Then

$$|\Phi(t)| \leq L \int_{t-p-2a_r}^{t-p-a_r} |\Phi(\tau)| d\tau = L \| \, |\Phi| \, \|_{t-p-2a_r}^{t-p-a_r}$$

for $t \geq t_1 = p + a_r + s$. Thus Lemma 2 is proved. ∎

With these two results, we can prove Theorem 2.

Proof of Theorem 2. Since $(P(t, s)f)(\omega, k) = \Phi_k(\omega + t)$, from Lemma 1 it follows that

$$(P(t, s)f)(\omega, k) \geq \Gamma \| \, |\Phi| \, \|_{t+\omega-p-3a_r}^{t+\omega-p} \geq \Gamma \| \, |\Phi| \, \|_{t-p-3a_r}^{t-p-a_r}$$

for sufficiently large t. From Lemma 2 we obtain

$$\|P(t, s)f\| \leq L \max_{\omega \in [-a_r, 0]} \| |\Phi| \|_{t-p-2a_r+\omega}^{t-p-a_r+\omega} \leq L \| |\Phi| \|_{t-p-3a_r}^{t-p-a_r}$$

for $t \geq t_1$. Thus for sufficiently large t we have

$$\frac{(P(t, s)f)(\omega, k)}{\|P(t, s)f\|} \geq \gamma = \frac{\Gamma}{L}, \tag{5.5}$$

and the proof is complete. ∎

6. Asymptotic Similarity in Autonomous and Nonautonomous Situations

In this section we characterize the asymptotic behaviour of the population in two cases:

(1) when the matrices Q and M are independent of t (the autonomous case); and

(2) when these matrices are periodic with respect to t (the nonautonomous case).

Theorems covering these two situations are preceded by the following proposition which has a general character and is, simultaneously, auxiliary to Theorem 2.

PROPOSITION 1. *Assume that the elements of the matrices Q and M satisfy all of the assumptions of Theorem* 1. *Let $p(a, t)$ be a solution of the system* (2.1), (2.2) *such that* $\inf\{p(a, 0): a \in [0, a_r]\} > 0$. *Then for every solution $\bar{p}(a, t)$ of the system* (2.1), (2.2) *there exists $c \in R$ such that*

$$\lim_{t\to\infty} \left\| \frac{\bar{p}_i(a, t)}{p_i(a, t)} - c \right\| = 0 \qquad \text{for } i \in \{1, \ldots, n\}, \tag{6.1}$$

and the process generated by (2.1), (2.2) *is asymptotically similar.*

Proof. Let Φ and $\bar{\Phi}$ be the solutions of (2.8) corresponding to p and $\bar{p}$ and let $g(\omega, k) = \Phi_k(\omega)$ and $f(\omega, k) = \bar{\Phi}_k(\omega)$ for $\omega \in (-a_r, 0)$ and $k \in \{1, \ldots, n\}$. Then $\Phi_k(t + \omega) = (P(t, 0)g)(\omega, k)$ and $\bar{\Phi}_k(t + \omega) = (P(t, 0)f)(\omega, k)$. Thus, according to Theorem 2, there exists $c \in R$ such that

$$\lim_{t\to\infty} \left\| \frac{\bar{\Phi}_i(t + \omega)}{\Phi_i(t + \omega)} - c \right\| = 0 \qquad \text{for } i \in \{1, \ldots, n\}.$$

This and (2.5) implies (6.1). ∎

6.1. *The Autonomous Case*

If the matrices Q and M are independent of time, then a result of [8] follows directly. Namely, we have the following.

PROPOSITION 2. *Let $k_{ij}^* = \int_0^{a_r} k_{ij}(a)da$ and assume that the matrix $K^* = [k_{ij}^*]$ is indecomposable. Then there exist a vector $v \in R^n$ and a real constant λ such that for every solution of* (2.1) *and* (2.2) *we have*

$$\lim_{t\to\infty} \|e^{-\lambda t}p(a, t) - ce^{-\lambda a}L(a)v\| = 0$$

for some positive constant c. The matrix $L(a)$ satisfies the equation $L'(a) = Q(a)L(a)$ with the initial condition $L(0) = I$, and the vector v and the constant λ satisfy the equation

$$v = \int_0^{a_r} e^{-\lambda\tau}K(\tau)v\, d\tau.$$

Proof. If the matrices Q and M do not depend on t, then neither does the matrix K so $K(a) = M(a)L(a)$, where the matrix $L(a)$ is the solution of the equation $L'(a) = Q(a)L(a)$ with the initial condition $L(0) = I$. If K does not depend on t we also have $P(t, s) = P(t - s, 0)$, and setting $P_t = P(t, 0)$ we obtain a semigroup $\{P_t\}$ (i.e., $P_0 = \mathrm{Id}$ and $P_{t+s} = P_t \circ P_s$ for $t \geq 0$ and $s \geq 0$).

Let f be a function from X. Then $P_h f \in X$ for $h > 0$. From Theorem 2 it follows that there is a function $c: [0, \infty) \to R$ such that

$$\frac{P_t(P_h f)}{P_t f} \to c(h)$$

uniformly on D.

Let $\Phi: [-a_r, \infty) \to R^n$ be a function such that $P_t f(\omega) = \Phi(t + \omega)$. Then for every $k = 1, \ldots, n$ we have

$$\lim_{t\to\infty} \frac{\Phi_k(t + h)}{\Phi_k(t)} = c(h).$$

From (5.5) it follows that

$$\gamma \leq c(h) \leq 1/\gamma \qquad \text{for } h \in [0, a_r].$$

This implies that the function

$$z(h) = \log c(h)$$

is bounded at 0. Moreover, if we take $h_1 > 0$ and $h_2 > 0$ then we have

$$c(h_1 + h_2) = c(h_1)c(h_2).$$

This implies that the function z satisfies Cauchy's equation

$$z(h_1 + h_2) = z(h_1) + z(h_2).$$

It is known [12] that all solutions of Cauchy's equation bounded at 0 are of the form $z(t) = \lambda t$ where $\lambda \in R$. From this it follows that

$$\frac{\Phi_k(t + h)}{\Phi_k(t)} \to e^{\lambda h}.$$

Now set $v(t) = \Phi(t)/|\Phi(t)|$. Then $|v(t)| = 1$ and $v_k(t) \geq \gamma/n$ for sufficiently large t. Substituting v into Eq. (2.8) we obtain

$$v(t) = \int_0^{a_r} \frac{|\Phi(t - \tau)|}{|\Phi(t)|} K(\tau)v(t - \tau)d\tau. \tag{6.3}$$

Hence

$$\begin{aligned} v(t) = &\int_0^{a_r} e^{-\lambda\tau}K(\tau)v(t)d\tau \\ &+ \int_0^T \left[\frac{|\Phi(t - \tau)|}{|\Phi(t)|} - e^{-\lambda\tau}\right] K(\tau)v(t)d\tau \\ &+ \int_0^T \frac{|\Phi(t - \tau)|}{|\Phi(t)|} K(\tau)(v(t - \tau) - v(t))d\tau. \end{aligned}$$

Both integrands in the second and third integrals are bounded and tend to 0 when $t \to \infty$ for every $\tau \in [0, a_r]$. Thus Eq. (6.3) can be rewritten in the form

$$v(t) = \left(\int_0^{a_r} e^{-\lambda\tau}K(\tau)d\tau\right) v(t) + w(t),$$

where $w(t) \to 0$ when $t \to \infty$.

Since $|v(t)| = 1$ for $t > 0$, we can choose a sequence $t_n \to \infty$ and a vector $v \in R^n$ such that $v(t_n) \to v$. The vector v is positive ($v_k > 0$ for $k = 1, \ldots, n$), $|v| = 1$, and satisfies the equation

$$v = \int_0^{a_r} e^{-\lambda\tau}K(\tau)v \, d\tau. \tag{6.4}$$

From (6.4) it follows that the function $\Phi(t) = e^{\lambda t}v$ is a solution of (2.8). This and (2.5) imply that the function $e^{\lambda(t-a)}L(a)v$ is a solution of (2.1) and (2.2). Proposition 1 now gives (6.2). ∎

The biological interpretation of this theorem is interesting. From Proposition 2 it follows that if the population growth and transition laws (M and Q) are autonomous, then the population numbers grow almost exponentially with a Malthusian parameter λ which is independent of the initial conditions. Further, in the asymptotic limit the density of the population age and type distribution function does not depend on the initial distribution.

These properties of populations with time-independent growth and death laws are well-known. What is a bit surprising is that a time-dependent (nonautonomous) population can display some of the same features. Thus, from Proposition 1 it follows that the distribution function of the population is asymptotically independent on the initial function. However, in this nonautonomous case the population will, in general, not grow exponentially since we can control the population growth by altering the matrices Q and M.

6.2. *The Nonautonomous Case*

Now we consider the alternative case in which the matrices Q and M are periodic with respect to t. The major result in this instance is given in the following.

PROPOSITION 3. *Assume there exists a $T > 0$ such that for every $a \in [0, a_r]$ and $t \geq 0$ we have*

$$Q(a, t + T) = Q(a, t) \qquad \text{and} \qquad M(a, t + T) = M(a, t).$$

Moreover, we assume that the elements of the matrices Q and M have continuous bounded partial derivatives and that all conditions of Theorem 2 are fulfilled. Then there exists a strictly positive solution of the problem (2.1), (2.2) satisfying the condition

$$p(a, t + T) = \alpha p(a, t) \qquad \text{for } a \in [0, a_r],\ t \geq 0,$$

where α is a positive constant. Moreover, for every solution $\bar{p}(a, t)$ of (2.1), (2.2) there exists $c \in R$ such that

$$\lim_{t\to\infty} \left\| \frac{\bar{p}(a, t)}{p(a, t)} - c \right\| = 0. \tag{6.5}$$

Proof. From the assumption that $Q(a, t + T) = Q(a, t)$ it follows that $L(h; a, t + T) = L(h; a, t)$ for every a, t, h and consequently

$$K(a, t + T) = K(a, t) \qquad \text{for } a \in [0, a_r],\ t \geq 0.$$

This implies that the process P satisfies

$$P(t + T, s + T) = P(t, s) \qquad \text{for } t \geq s \geq 0. \tag{6.6}$$

Let Φ be a strictly positive solution of (2.8). Then from (5.5) it follows that there exists $\gamma \in (0, 1)$ such that for sufficiently large t (say $t \geq t_0$) we have

$$\gamma \leq \frac{\Phi_i(t + \omega_1)}{\Phi_j(t + \omega_2)} \leq \frac{1}{\gamma} \qquad \omega_1, \omega_2 \in [-a_r, 0],\ i, j \in \{1, \ldots, n\}. \tag{6.7}$$

Let

$$|\Phi(t)| = |\Phi_1(t)| + \cdots + |\Phi_n(t)|$$

and

$$v_\nu(t) = \frac{\Phi(t + \nu T)}{|\Phi(\nu T)|} \qquad \text{for } t \in [-a_r, T],\ \nu \geq (a_r + t_0)/T.$$

The relation $K(a, t + T) = K(a, t)$ implies that

$$v_\nu(t) = \int_0^{a_r} K(a, t) v_\nu(t - a) da \qquad \text{for } t \in [0, T]. \tag{6.8}$$

All of the v_ν are continuous functions from $[-a_r, T]$ to R^n and from (6.7) it follows that the sequence $\{v_\nu\}$ is bounded in the space $C([-a_r, T], R^n)$.

We next show that the sequence $\{v_\nu\}$ is equicontinuous. Since

$$\Phi'(t) = K(0, t)\Phi(t) - K(a_r, t)\Phi(t - a_r) + \int_{t-a_r}^{t} \frac{d}{dt} K(t - s, t)\Phi(s) ds,$$

there exists a constant β such that for every $t \geq 0$ we have

$$|\Phi'(t)| \leq \beta \sup\{|\Phi(s)| : s \in [t, t - a_r]\}.$$

This and (6.7) imply that

$$|\Phi'(t)| \leq \frac{\beta}{\gamma} |\Phi(t)| \qquad \text{for } t \geq t_0$$

and consequently

$$|v_\nu'(t)| \le \frac{\beta}{\gamma}|v_\nu(t)|.$$

Hence the sequence $\{v_\nu\}$ is bounded and equicontinuous, and by the Arzeli–Ascoli theorem, the sequence $\{v_\nu\}$ contains a subsequence $\{v_{\nu k}\}$ which converges to some $v \in C([-a_r, T], R^n)$. The function v is strictly positive and satisfies Eq. (6.8) for $t \in [0, T]$.

Next we show there exists $\alpha > 0$ such that for every $t \in [-a_r, 0]$ we have $v(t + T) = \alpha v(t)$. Indeed, let

$$f(\omega, k) = \Phi_k(\omega) \qquad \text{for } \omega \in [-a_r, 0],\ k \in \{1, \dots, n\}.$$

and $g = P(T, 0)f$. Then from (6.6) it follows that

$$P(t + T, 0)f = P(t + T, T)P(T, 0)f = P(t, 0)P(T, 0)f = P(t, 0)g.$$

According to Theorem 2 there exists $\alpha > 0$ such that

$$\frac{P(t, 0)g}{P(t, 0)f} \to \alpha \qquad \text{if } t \to \infty.$$

This implies

$$\frac{\Phi_k(t + T)}{\Phi_k(t)} \to \alpha \qquad \text{if } t \to \infty \text{ for } k \in \{1, \dots, n\}.$$

From this it follows that

$$\frac{\Phi_k(t + \nu T + T)}{\Phi_k(t + \nu T)} \to \alpha \qquad \text{if } \nu \to \infty$$

and consequently

$$\frac{v_{\nu,k}(t + T)}{v_{\nu,k}(t)} \to \alpha \qquad \text{if } \nu \to \infty.$$

The last condition implies that $v(t + T) = \alpha v(t)$ for $t \in [-a_r, 0]$.

Finally we extend the function v on the set $[T, \infty)$ by setting $v(t) = \alpha^n v(t - nT)$ for $t \in [nT, (n + 1)T)$. It is easy to check that v satisfies Eq. (2.8) for $t \ge 0$ and $v(t + T) = \alpha v(t)$ for $t \ge 0$. This implies that

$$p(a, t) = L(a; 0, t - a)v(t - a)$$

satisfies the system (2.1) and (2.2) and $p(a, t + T) = \alpha p(a, T)$ for every $a \in [-a_r, 0]$ and $t \geq 0$. Condition (6.5) follows immediately from Proposition 1. This finishes the proof of the proposition. ∎

The interpretation of this result is surprising. Namely, if the matrices Q and M are periodic then every solution of (2.1), (2.2) asymptotically approaches a solution p which has the property $p(a, t + T) = \alpha P(a, t)$. This result is very similar to the exponential growth found in the autonomous case, because from this it follows that $p(a, t + nT) = \alpha^n p(a, t)$.

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