To the Graduate Council:

I am submitting herewith a dissertation written by Jia Li entitled "Persistence and Extinction of Populations". I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Mathematics.

Thomas G. Hallam, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

PERSISTENCE AND EXTINCTION OF POPULATIONS

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Degree

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DEDICATION

To my mother, Rong Li.

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ABSTRACT

Survival analyses of populations are developed in discrete growth processes and continuous growth processes. Persistence and extinction attributes of age-independent and age-dependent discrete population models are explored on both a finite and infinite time horizon. Conditions for persistence and extinction are found. Decompositions of the initial population size axes into intervals where populations are persistent at time N and intervals leading to extinction at time n, where $n \leq N$, are found for age-independent discrete population models and two age class discrete population models. Persistence criteria of a class of continuous age-structured population models with separable mortality function and fertility function are established by investigation of asymptotic behaviors of solutions of a first order partial differential equation. Continuous population models with several age classes are studied as well by considering sets of ordinary differential equations. Finally, the connection between individual dynamics and population dynamics is discussed briefly.

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CHAPTER 1

INTRODUCTION

The question of persistence and extinction of populations is of importance in ecology. Since the start of the Cambrian 10^8 to 10^9 years ago there have been 10^8 to 10^9 species extinctions (Levins, 1970) . Many existent species still face the risk of extinction because of increase of pollutants, by-products of the development of modern science and technology, in the environment. To maintain the ecological balance in the interest of humanity, it is the task for ecologists and applied mathematicians to describe and predict the ultimate fate of species; that is, to study persistence and extinction of populations quantitatively or qualitatively.

From a mathematical modelling perspective, populations are modelled either by a discrete growth process when generations in a population do not overlap or population size is relatively small, or alternatively by a continuous growth process (May, 1976a; Pielou, 1977; Hallam, 1986). In each case, there is in the formulation in an explicit or implicit way, a measure of the population, for example size or biomass. To study persistence and extinction of populations, we need to find conditions under which this measure is always positive and not arbitrarily small for all time t. Such populations could be described as being persistent. Conditions under which the solutions become zero at a finite time or go to zero as time goes to infinity indicate that the population might go to extinction. The purpose of this dissertation is to explore persistence and extinction of model populations.

When generations of a population do not overlap or the population size is relatively small, discrete models are generally used in modelling processes. If age independence is assumed in a population growth process and one denotes population size or biomass at generation n by x_n, then

$$x_{n+1} - x_n = \text{birth} - \text{death} = b_n x_n - (d_n - f(x_n))\, x_n,$$

or

$$x_{n+1} = x_n\,(r_n - f(x_n))\,. \tag{1.1}$$

Here, $r_n - 1$ represents the time-varying intrinsic growth rate; f represents density dependent mortality.

As is well known, the simplest case of (1.1), where $r_n \equiv r$ is assumed to be time independent and the density dependent mortality function is chosen to be linear, exhibits a remarkable spectrum of dynamical behaviors, from stable equlibria, to stable cyclic oscillations between 2 points, to stable cycles with 4, 8, 16, ... points, through to a chaotic regime in which cycles of any period occur (May, 1974, 1976b; Feigenbaum 1980). This, obviously, impeded the use of difference equations in modelling processes.

However, although it may be unrealistic to seek to describe in detail the qualitative behavior of the model (1.1), it is still feasible and very interesting, due to importance of the model (1.1) from biological perspective, to establish persistence and extinction conditions. In Chapter 2, we discuss dynamical behaviors of populations based on the model (1.1). Persistence and extinction are investigated for autonomous difference equations and nonautonomous difference quations as well. Some necessary conditions and sufficient conditions for survival of model

populations are found. An interesting and important decomposition of the initial population size axis into intervals where populations are persistent at some time N and intervals leading to extinction at time n, where $n \leq N$, is given.

When age structure is introduced into discrete population models, systems of difference equations are used (Leslie, 1945; Pielou, 1977). Obviously, the dynamic analysis, now, becomes more difficult. Most studies consider only the cases where the demographic parameters are time independent, density independent, or time slowly changing, and have focused on the asymptotic behaviors of equilibria (Lopez, 1961; Sykes, 1969; Cooke & Leon, 1976; Geramita & Pullman, 1984; Artzrouni, 1986).

When demographic variation and density dependent effects are employed in the model population, dynamical behavior of the population model is very complicated. In Chapter 3, we consider some special cases of discrete models of age structured populations. We focus on the model of the form

$$\begin{aligned} x_{n+1} &= y_n \left(\alpha_n - f(y_n)\right), \\ y_{n+1} &= x_n \left(\beta_n - g(y_n)\right), \end{aligned} \tag{1.2}$$

where α_n is the birth rate at generation n, and β_n is the death rate at generation n. Persistence and extinction attributes of (1.2) are investigated. Under certain assumptions, a decomposition of the initial population axes is still possible; this is discussed in Chapter 3. It is also pointed out that the decomposition is more complex than that in the one-dimensional case.

If a population has overlapping generations, it is often appropriate to use a continuous growth process to study the dynamics of the population and, hence, differential

equations or integral equations are needed (McKendrick, 1926; von Foerster, 1957; Freedman, 1980; Hoppensteadt, 1974; Cushing, 1986b; Metz & Diekmann, 1986). While there are many studies of persistence in communities (Freedman & Waltman, 1977, 1984, 1985; Gard & Hallam, 1979; Gard, 1984), there are few explicitly on one species. Recently, Hallam and Ma (1986, 1987) studied survival in populations with demographic variations, but the age structure is ignored. In Chapter 4, we consider a class of continuous population models with age structure by using the so-called McKendrick or von-Foerster equation

$$\begin{aligned} &\frac{\partial \rho(a,t)}{\partial a} + \frac{\partial \rho(a,t)}{\partial t} = -D(a,t,P)\rho(a,t) \\ &\rho(0,t) = \int_0^\infty n(a,t,P)\rho(a,t)da, \\ &\rho(a,0) = \phi(a), \end{aligned} \tag{1.3}$$

where $P(t) = \int_0^\infty \rho(a,t)da$ is the total population. We assume that the mortality function has the form $D(a,t,P(t)) = c(t)+\mu(a)+f(P(t))$, and the fertility function has the form $n(a,t,P(t)) = b(t)\beta(a)$. First, the existence and uniqueness of the solution are established. Then, by using a comparison technique, persistence and extinction conditions are found.

Chapter 5 discusses the case where populations have several distinct age classes and are modelled by a continuous growth process. Sets of ordinary differential equations that represent this situation might have the following form

$$\begin{aligned} \frac{dH_0}{dt} &= \sum_{i=1}^{n} \beta_i H_i - \mu_0 H_0 - m_0 H_0, \\ \frac{dH_i}{dt} &= m_{i-1}H_{i-1} - \mu_i H_i - m_i H_i, \quad i = 1,2,\ldots,n-1, \\ \frac{dH_n}{dt} &= m_{n-1}H_{n-1} - \mu_n H_n. \end{aligned} \tag{1.4}$$

Here, H_i represents the number of individuals in age class i; β_i represents the birth rate of the population in age class i; m_i is the transition rate of the population from age class i to age class $i+1$; μ_i is the death rate of the population in age class i. Criteria for persistence and extinction of populations with time independent vital rates, as well as time dependent vital rates, are obtained.

A population consists of individuals. The fate of a population is, therefore, related to dynamics of individuals. We discuss the relationship between dynamics of individuals and dynamics of the population from persistence and extinction perspective in Chapter 6.

CHAPTER 2

DISCRETE AGE-INDEPENDENT MODELS

A population in which generations do not overlap or population size is relatively small is probably best modelled by a discrete growth process. Nonlinear difference equations are often utilized to describe the dynamics of such populations where growth occurs in isolated steps (c.f. Nicholson & Bailey, 1935; Maynard Smith, 1968; Hallam & Levin, 1986).

Extinction of a population, of special concern when population size is small, should probably be investigated by use of a discrete model. However, there are few analytical studies of extinction in nonlinear difference models (Hutson & Moran, 1982). In this chapter, we investigate persistence and extinction in some rudimentary difference equation models of populations. It will be demonstrated that survival analysis in a discrete setting is complicated and that persistence is difficult to predict even if complete demographic variation and density dependent mortality are known. Moreover, a very interesting decomposition of the initial population size axis is found. It demonstrates that, under certain hypotheses, intervals of initial values of populations that are persistent at a given finite time are interspersed with intervals of initial values of populations that go to extinction at various finite times.

§ 2.1 The Autonomous Model.

As a basis, we first develop a survival theory for an autonomous model. The discrete population model

$$x_{n+1} = x_n\,(r - f(x_n))\,, \qquad n = 0, 1, \ldots, \tag{2.1.1}$$

where f satisfies the conditions that $f(0) = 0$, $xf(x) > 0$, and $f'(x) = \frac{f(x)}{dx}$ is positive for x positive, is considered. Here, $r - 1$ represents the initial growth rate of the population. This term reflects fecundity and density independent mortality while f represents density dependent mortality. A prototype of these models is the logistic equation

$$x_{n+1} = (1 + r)\, x_n - rk^{-1}x_n^2, \qquad n = 0, 1, 2, \ldots, \tag{2.1.2}$$

where r and k are positive constants. As is well known, the dynamical behavior of (2.1.2) covers a range from asymptotic extinction to intricate chaos (May et al., 1974; May, 1976b; Guckenheimer et al., 1977; Hallam, 1986). In general, it is difficult to do analytic studies for (2.1.1) when a nonlinear density function $f(x)$ is employed. However, it is possible to discuss and study survival.

DEFINITION 2.1.1.

a) *A population, represented by a solution sequence* $\{x_n\}$ *of (2.1.1), is persistent at time* N *if* $x_n > 0$, $n = 0, 1, \ldots, N$;

b) *A population is persistent if it is persistent at time* N *for each* N, $N = 0, 1, 2, \ldots$, *and* $\limsup_{n\to\infty} x_n > 0$;

c) *A population goes to extinction at time* N *provided* $x_n > 0$, $n = 0, 1, \ldots, N-1$, *and* $x_N \leq 0$;

d) *A population goes to extinction asymptotically provided it is persistent at time* N *for each* $N = 0, 1, 2, \ldots$, *and* $\lim_{n\to\infty} x_n = 0$.

We have, for convenience, defined extinction at time N as $x_N \leq 0$. When extinction at time N occurs, because of the discreteness of the system, there is no

guarantee that the trajectory hits zero exactly. Should this be desired, it may be accomplished by defining (2.1.1) as

$$x_{n+1} = max\left\{x_n\left(r_n - f(x_n)\right), 0\right\}.$$

Some routine properties of (2.1.1) include the following on extinction, persistence, and stability. When $r \leq 1$ the population trajectory is decreasing and extinction at some time results for any initial size; hence, the case of interest in our considerations of survival is $r > 1$. Whenever $r > 1$ the zero solution of (2.1.1) is unstable. This, of course, relates to persistence but does not guarantee it since the possibility of extinction at a finite time has not been eliminated. The initial value interval, $0 < x_0 < f^{-1}(r)$, determines population trajectories of (2.1.1) that persist at time 1; the complementary set $\left[f^{-1}(r), \infty\right)$ consists of initial values of populations that go to extinction at time 1. We therefore concentrate on the behavior of populations with initial sizes in $I \equiv \left(0, f^{-1}(r)\right)$ and, subsequently, we tacitly assume that initial values, x_0, are in I unless otherwise specified.

The following result classifies populations modelled by (2.1.1) that go to extinction at a finite time.

THEOREM 2.1.2. *Let $F(x) \equiv x\left(r - f(x)\right)$. The autonomous model (2.1.1) has populations that go to extinction at time N, for each $N = 1, 2, 3, \ldots$, if and only if*

$$\max_{x \in I} F(x) \geq f^{-1}(r). \tag{2.1.3}$$

PROOF: If $\max_{x \in I} F(x) < f^{-1}(r)$, obviously, each population with $x_0 \in I$ is persistent. Then, it suffices to find a population that goes to extinction for each N as (2.1.3) holds. Note that the maximum of F is attained in I since $F(0) = F\left(f^{-1}(r)\right) = 0$.

We now proceed to find trajectories that go to extinction at time N. As a second step (extinction at time 1 has already been discussed) from (2.1.1) and (2.1.3) it follows that the population with initial size $x_0 \equiv x_*$, where $F(x_*) = \max_{x \in I} F(x)$, has $x_2 \leq 0$ since $x_1 = F(x_0) \geq f^{-1}(r)$ or $r - f(x_1) \leq 0$.

Next, we observe that if x_* satisfies $F(x_*) = \max_{x \in I} F(x)$ then $x_* < f^{-1}(r-1) \equiv x^*$, where x^* is, by definition, an equilibrium of (2.1.1). If this were not true, then $x_* \geq x^*$ or $r - f(x_*) \leq 1$. Hence,

$$F(x_*) = x_*\,(r - f(x_*)) \leq x_* < f^{-1}(r) \tag{2.1.4}$$

which is a contradiction. Since $F(0) = 0$, $F'(0) = r > 1$ and x^* is the unique positive fixed point of F(x), $(F(x^*) = x^*)$, $F(x) > x$ for all x, $0 < x < x^*$; in particular, $F(x_*) > x_*$.

We now define x_0, the initial population, and generate the population dynamical behavior sequence $\{x_i\}$ such that $x_N \leq 0$. First, choose $x_{N-1} = x_*$ and define

$$H_N(x) = F(x) - x_{N-1}. \tag{2.1.5}$$

Since $H_N(x_{N-1})$ is positive and $H_N(0) = -x_* < 0$ there exists an x_{N-2}, $0 < x_{N-2} < x_{N-1} \equiv x_*$, where $H_N(x_{N-2}) = 0$. With this x_{N-2}, $F(x_{N-2}) = x_{N-1}$. Continuing in this manner, for each $i = 1, 2, \ldots, N$, let

$$H_{N-i+1}(x) = F(x) - x_{N-i} \tag{2.1.6}$$

have x_{N-i-1} as a zero, with $x_{N-i-1} < x_{N-i}$. This solution sequence $\{x_i\}_{i=0}^{N}$ has $x_i > 0$, $i = 0, 1, \ldots, N-1$ and $F^N(x_0) = F(F(\ldots(F(X_0)))) = x_N \leq 0$.

A consequence of this classification of extinction is the following persistence result.

COROLLARY 2.1.3. *Let $r > 1$ and*

$$\max_{x \in I} F(x) < f^{-1}(r). \tag{2.1.7}$$

Then, all populations modelled by (2.1.1) with $x_0 \in I$ are persistent.

PROOF: Theorem 2.1.2 implies that all populations with $x_0 \in I$ are persistent at time N for each $N = 1, 2, 3, \ldots$. The persistence follows from the instability of the zero solution of (2.1.1).

§ 2.2 The Nonautonomous Model.

Mortality and fertility of populations are almost never constant (Hutchinson, 1978; Artzrouni, 1986). Both endogenous and exogenous events provide motivation to develop a survival theory for nonautonomous population models:

$$x_{n+1} = x_n (r_n - f(x_n)) \qquad n = 0, 1, \ldots. \tag{2.2.1}$$

Employing the guidance provided by the constant demographic situation discussed in §2.1 and a comparison technique, we investigate persistence and extinction in (2.2.1) where the growth rate sequence is time dependent.

An obvious condition sufficient for extinction, either at time N, $N = 2, 3, \ldots$, or at infinity, is that the growth rate sequence satisfy $r_n \leq 1$, $n = 0, 1, 2, \ldots$.

A sufficient condition for persistence at time n is provided by a procedure analogous to that employed in Theorem 2.1.2. If, for each n, $n = 0, 1, 2, \ldots$,

$$\max_{x \in I_n} \{x (r_n - f(x))\} < f^{-1}(r_{n+1}) \tag{2.2.2}$$

where $I_n = \left(0, f^{-1}(r_n)\right)$, then each population (again $x_0 \in I_0$) is persistent at time N, $N = 1, 2, 3, \ldots$. The task of checking each of these inequalities may be burdensome; it is convenient to develop a simpler, more readily tested condition.

THEOREM 2.2.1. *Suppose* $0 < r \leq r_n \leq R$, $n = 0, 1, 2, \ldots$. *If*

$$\max_{0<x<f^{-1}(R)} \{x\,(R - f(x))\} < f^{-1}(r) \tag{2.2.3}$$

then $x_n > 0$ *for each* $n = 1, 2, \ldots$; *that is, any population of (2.2.1) with* $x_0 \in I_0$ *is persistent at time* N *for each* $N = 1, 2, 3, \ldots$.

PROOF: The proof, similar to the appropriate part of Theorem 2.1.2, is by induction and utilizes the inequalities

$$\begin{aligned} x_m &= x_{m-1}\,(r_{m-1} - f(x_{m-1})) \\ &\leq x_{m-1}\,(R - f(x_{m-1})) < f^{-1}(r) \leq f^{-1}(r_m). \end{aligned} \tag{2.2.4}$$

The inequality (2.2.3) leads to an interesting optimization problem since an increase in R results in an increase in $\max_{0<x<f^{-1}(R)} \{x\,(R - f(x))\}$ and a decrease in r decreases $f^{-1}(r)$. Basically, persistence at time N is guaranteed if the lowest intrinsic growth rate exceeds some threshold determined by f.

The instability of the zero solution of (2.1.1) for $r > 1$ in combination with Theorem 2.2.1 leads to the following result.

COROLLARY 2.2.2. *Let the hypotheses of Theorem 2.2.1 be satisfied and* $\liminf_{n\to\infty} r_n > 1$. *Then, each population is persistent.*

PROOF: Theorem 2.2.1 establishes persistence at time N for each $N = 1, 2, 3, \ldots$ while the ultimate comparison equation (2.1.1) with the coefficient $r = \liminf_{n\to\infty} r_n$ yields $\limsup_{n\to\infty} x_n > 0$.

The persistence criterion allows r_n to be less than one for some values of n and yet the population can survive.

Two rudimentary examples illustrate the above results.

EXAMPLE 1: (Logistic).

Consider the logistic model

$$x_{n+1} = x_n(r_n - x_n), n = 1, 2, \ldots.$$

A sufficient condition for persistence is $1 < r \leq r_n \leq R$ where $R^2 < 4r$. The last inequality is a consequence of

$$\frac{1}{4}R^2 = \max_{0<x<R} x(R-x) < r.$$

When the growth rate sequence satisfies $1 < r \leq r_n \leq 4$ then all populations modelled by the logistic equation are persistent. This range of growth parameters, $r \in (1,4)$, is the one typically studied for the autonomous logistic equation (e.g. Roughgarden, 1979; May, 1976a; Hallam, 1986).

EXAMPLE 2: (Hyperbolic Density Dependent Formulation).

The model

$$x_{n+1} = x_n \left(r_n - \frac{kx_n}{x_n + 1} \right)$$

with $1 < r \leq r_n \leq k < \frac{1}{2}\left(r + (r^2 + 4r)^{1/2}\right)$ is persistent.

The extinction results are now presented. The first result is obtained from the persistence criterion presented in Theorem 2.2.1.

THEOREM 2.2.3. *Let the hypotheses of Theorem 2.2.1 be satisfied and* $\limsup_{n\to\infty} \prod_{k=0}^{n} r_k < 1$. *Then each population goes to extinction asymptotically.*

PROOF: From Theorem 2.2.1 it follows that each population is persistent at each

finite time. Hence,

$$\begin{aligned} x_n &< r_{n-1}x_{n-1} < \dots \\ &< \left(\prod_{k=0}^{n-1} r_k\right) x_0 = \left(\left(\prod_{k=0}^{n-1} r_k\right)^{\frac{1}{n-1}}\right)^{n-1} x_0 \\ &< (1-\epsilon)^{n-1} x_0, \end{aligned} \tag{2.2.5}$$

where ϵ is a small positive number. This leads to $\lim_{n\to\infty} x_n = 0$.

The following results establish extinction of a population at a finite time.

THEOREM 2.2.4. *Assume that there is an N such that*

$$1 < r_N = \min_{0\le k\le N} r_k$$

and

$$\max_{0<x<f^{-1}(r_N-1)} \{x\,(r_N - f(x))\} > f^{-1}(r_{N+1}). \tag{2.2.6}$$

Then, there exists a subinterval $S_0 \subset \left(0, f^{-1}(r_0)\right)$ with the property that if $x_0 \in S_0$ the associated population trajectory has $x_k > 0$, $k = 1, 2, \dots, N+1$ and $x_{N+2} \le 0$.

PROOF: The arguments follow those of the constant growth rate case developed in Theorem 2.1.2. First, define the sequence of functions, $F_k(x) = x\,(r_k - f(x))$, $k = 1, 2, \dots$, and let x_k^* denote the unique fixed point of $F_k(x)$; that is, $F_k(x_k^*) = x_k^*$ or $x_k^* = f^{-1}(r_k - 1)$. The uniqueness of x_k^* is a consequence of the hypothesis that f is increasing. It follows from $r_N = \min_k r_k$ that $x_N^* \le x_k^*$, $0 < k \le N$. Since $r_k > 1$, it follows that $F_k(x) > x$ for all x, $0 < x < x_k^*$. If x_N is defined by the relationship

$$F_N(x_N) = \max_{0<x<f^{-1}(r_N-1)=x_N^*} \{x\,(r_N - f(x))\}, \tag{2.2.7}$$

then $x_N < x_N^*$, $x_{N+1} > f^{-1}(r_{N+1})$, and, hence, $x_{N+2} \leq 0$. It remains to find an $x_0 \in (0, f^{-1}(r_0))$ with the property that the population trajectory has $F_{N-1}(x_{N-1}) = x_N$. To accomplish this, we define

$$H_{N-1}(x) = F_{N-1}(x) - x_N; \tag{2.2.8}$$

then, $H_{N-1}(0) = -x_N < 0$ and

$$H_{N-1}(x_N) = F_{N-1}(x_N) - x_N > 0.$$

Thus, there exists a point x_{N-1} where $F_{N-1}(x_{N-1}) = x_N$. The construction of the sequence proceeds in this manner employing the function $H_{N-i} = F_{N-i}(x) - x_{N-i+1}$ and defining its zero to be x_{N-i}. This leads to an initial position x_0 in $(0, f^{-1}(r_0 - 1))$ and a sequence $\{x_k\}$ with $x_k > 0$, $k = 0, 1, \ldots, N+1$ and $x_{N+2} \leq 0$.

Using analogous techniques the following result may be obtained.

THEOREM 2.2.5. *Let $r_k > 1$, $k = 0, 1, 2, \ldots$ and suppose that there is an N with*

$$\max_{0<x<f^{-1}(r_N-1)} \{x\,(r_N - f(x))\} > f^{-1}(r_{N+1}) \tag{2.2.9}$$

and

$$\max_{0<x<f^{-1}(r_{k-1}-1)} F_{k-1}(x) > \bar{x}_k, \quad k = 1, 2, \ldots, N, \tag{2.2.10}$$

where $\bar{x}_k$ is obtained from

$$F_k(\bar{x}_k) = \max_{0<x<f^{-1}(r_k-1)} F_k(x),$$

with $F_k(x) = x\,(r_k - f(x))$. Then, there exists an initial population $x_0 \in (0, f^{-1}(r_0 - 1))$ whose solution trajectory goes to extinction at time $N + 2$.

The results of Theorem 2.2.4 and Theorem 2.2.5 are qualitative in character. To provide a more quantitative criterion of extinction which illustrates the required inequalities the following theorem is presented.

THEOREM 2.2.6. *Let $f(x) \leq kx$ for some positive constant k and for all x positive. Assume that there exists an integer N, $N \geq 1$, where the intrinsic growth function satisfies $r_{N-1}^2 \geq 4kf^{-1}(r_N)$. Define*

$$\alpha_N = \frac{1}{2k}\left\{r_{N-1} - \left(r_{N-1}^2 - 4kf^{-1}(r_N)\right)^{\frac{1}{2}}\right\}$$

and

$$\alpha_i = \frac{1}{2k}\left\{r_{i-1} - \left(r_{i-1}^2 - 4k\alpha_{i+1}\right)^{\frac{1}{2}}\right\}, \qquad i = 1, 2, \ldots, N-1. \tag{2.2.11}$$

Let

$$\beta_N = \frac{1}{2k}\left\{r_{N-1} + \left(r_{N-1}^2 - 4kf^{-1}(r_N)\right)^{\frac{1}{2}}\right\}$$

and

$$\beta_i = \begin{cases} \min\left\{\dfrac{\beta_{i+1}}{r_{i-1} - f(\alpha_i)}, \dfrac{1}{2k}\left(r_{i-1} + \left(r_{i-1}^2 - 4k\alpha_{i+1}\right)^{\frac{1}{2}}\right)\right\}, \\ \qquad \text{provided } r_{i-1} > f(\alpha_i), \quad i = 1, 2, \ldots, N-1; \\ \dfrac{1}{2k}\left\{r_{i-1} + \left(r_{i-1}^2 - 4k\alpha_{i+1}\right)^{\frac{1}{2}}\right\}, \\ \qquad \text{provided } r_{i-1} \leq f(\alpha_i), \quad i = 1, 2, \ldots, N-1. \end{cases} \tag{2.2.12}$$

Let x_0 satisfy $\alpha_1 \leq x_0 \leq \beta_1$ and $r_{i-1}^2 \geq 4k\alpha_{i+1}$, $i = 1, 2, \ldots, N-1$, then the population trajectory goes to extinction at time $N+1$.

PROOF: The population goes to extinction at time $N+1$ if $x_{N+1} \leq 0$ (by Definition 2.1.1); that is, $r_N \leq f(x_N)$, which is equivalent to

$$f^{-1}(r_N) \leq x_{N-1}\left(r_{N-1} - f(x_{N-1})\right),$$

or

$$x_{N-1}f(x_{N-1}) - r_{N-1}x_{N-1} + f^{-1}(r_N) \leq 0. \tag{2.2.13}$$

Since $f(x) \leq kx$, clearly, whenever

$$kx_{N-1}^2 - r_{N-1}x_{N-1} + f^{-1}(r_N) \leq 0, \tag{2.2.14}$$

(2.2.13) holds and, hence, $x_{N+1} \leq 0$.

From the assumption that $r_{N-1}^2 - 4kf^{-1}(r_N) \geq 0$, it follows that (2.2.14) is satisfied provided $\alpha_N \leq x_{N-1} \leq \beta_N$. However, $x_{N-1} \geq \alpha_N$ if and only if

$$x_{N-2}f(x_{N-2}) - r_{N-2}x_{N-2} + \alpha_N \leq 0.$$

Hence, it follows from

$$\alpha_{N-1} \leq x_{N-2} \leq \frac{1}{2k}\left(r_{N-2} + \sqrt{r_{N-2}^2 - 4k\alpha_N}\right) \tag{2.2.15}$$

that $x_{N-1} \geq \alpha_N$. That is, as $\alpha_{N-1} \leq x_{N-2} \leq \beta_{N-1}$, $x_{N-1} \geq \alpha_N$.

On the other hand,

$$\begin{aligned} x_{N-1} - \beta_N &= x_{N-2}r_{N-2} - x_{N-2}f(x_{N-2}) - \beta_N \\ &\leq x_{N-2}\left(r_{N-2} - f(\alpha_{N-1})\right) - \beta_N, \end{aligned} \tag{2.2.16}$$

provided $x_{N-2} \geq \alpha_{N-1}$, since $f(x)$ is increasing. By the definition (2.2.12), if $x_{N-2} \leq \beta_{N-1}$,

$$x_{N-2}\left(r_{N-2} - f(\alpha_{N-1})\right) - \beta_N \leq 0,$$

which implies $x_{N-1} \leq \beta_N$. Therefore, as $\alpha_{N-1} \leq x_{N-2} \leq \beta_{N-1}$, $\alpha_N \leq x_{N-1} \leq \beta_N$, and, then, $x_{N+1} \leq 0$.

Continuing in this manner, the interval (α_0, β_0) of initial values, which leads to $x_{N+1} \leq 0$, is found.

§ 2.3 Decomposition of Initial population Axis.

Just as the dynamical behavior of discrete models can be complex, extinction behavior can likewise be complicated. The main result of this chapter demonstrates that, for a prescribed generation N, the initial population axis is subdivided into subintervals containing trajectories that go to extinction at finite times less than or equal to N and subintervals containing trajectories that persist at time N. Such a decomposition can result in populations going to extinction at time N while populations with larger or smaller initial sizes can persist at time N.

A lemma that describes a geometrical configuration for F much like the logistic is now given. The model is (2.1.1), $x_{n+1} = F(x_n)$ where $F(x) = x\,(r - f(x))$.

LEMMA 2.3.1. *Assume that*

(i) $f \in C^2[R_+, R_+]$, $f(0) = 0$, $f'(x) = \dfrac{f(x)}{dx} > 0$ *and* $\max\limits_{x>0} f(x) > r$.

(ii) *There exists an* $x^* > 0$ *such that*

$$f''(x) = \frac{d^2 f(x)}{dx^2} \begin{cases} \leq 0 & \text{for } x > x^*, \\ \geq 0 & \text{for } x \leq x^*. \end{cases}$$

(iii) *One of the following holds:*

(a) $f'(x) \geq x|f''(x)|, \quad x \geq x^*$; *or*

(b) *there exists* $\tilde{x} \geq x^*$ *where* $f'(x) < x|f''(x)|$ *for all* $x > \tilde{x}$, *but*

$r - f(\tilde{x}) \leq f^{-1}(r) f'\left(f^{-1}(r)\right)$.

Then, $F'(x) = 0$ *has a unique solution* $\bar{x} \in \left(0, f^{-1}(r)\right)$ *and, hence, for* $y^* < \max\limits_{0<x<f^{-1}(r)} F(x)$, $F(x) = y^*$ *has exactly two solutions.*

PROOF: Two observations that are utilized below are $xf'(x)$ is increasing for $x \leq x^*$ and $r - f(x)$ is decreasing. Since

$$F'(x) = r - f(x) - xf'(x), \text{ and } F'(0) > 0,$$

either (α) there exists exactly one $\bar{x} \leq x^*$ where $F'(\bar{x}) = 0$ or (β) $F'(x) > 0$ for all $x \leq x^*$. When (α) and (iii)(a) are valid, $F'(x) < 0$ for $x > \bar{x}$. If (β) and (iii)(a) hold then there exists an $\bar{x} > x^*$, where $F'(\bar{x}) = 0$ and $F'(x) < 0$ for $x > \bar{x}$.

Whenever (iii)(b) holds, $xf'(x)$ is decreasing on $\left(\tilde{x}, f^{-1}(r)\right)$ and

$$xf'(x) > f^{-1}(r)f'\left(f^{-1}(r)\right) \qquad \text{on} \quad \left(\tilde{x}, f^{-1}(r)\right).$$

When (α) holds, $F'(x)$ is negative for $x > \tilde{x}$ since from (i) and (iii)(b) it follows that

$$r - f(x) < r - f(\tilde{x}) \leq f^{-1}(r)f'\left(f^{-1}(r)\right) < xf'(x), \qquad \text{if} \quad x > \tilde{x}.$$

Thus, the uniqueness of $\bar{x}$ is guaranteed. If (β) holds, we have $F'(x) > 0$ for $x \leq x^*$. The functions $xf'(x)$ and $r - f(x)$ are both decreasing on $\left(\tilde{x}, f^{-1}(r)\right)$ with $xf'(x)$ positive at $f^{-1}(r)$ while the function $r - f(x)$ is zero at $f^{-1}(r)$. Again the uniqueness of $\bar{x}$ with $F'(\bar{x}) = 0$ follows.

An example other than the obvious linear (logistic) function that satisfies the hypotheses of Lemma 2.3.1 is defined by

$$f(x) = \begin{cases} ke^{-\frac{\alpha}{x}}, & x > 0, \\ 0, & x = 0, \end{cases}$$

where k and α are positive constants.

With the configuration of F as prescribed by Lemma 2.3.1, extinction dynamically structures a decomposition of the initial population axis for model (2.2.1).

THEOREM 2.3.2. *Let the assumptions (i) for each n where r is replaced by r_n and (ii) of Lemma 2.3.1 hold. Let there exist an $N > 0$ where*

$$\max_{0<x<f^{-1}(r_k)} \{x\left(r_k - f(x)\right)\} \geq f^{-1}(r_{k+1}), \qquad k = 0, 1, \ldots, N-1, \qquad (2.3.1)$$

and

$$\max_{0<x<f^{-1}(r_N)} \{x\,(r_N - f(x))\} > f^{-1}(r_{N+1}). \tag{2.3.2}$$

In addition suppose that

$$f'(x) \geq x|f''(x)| \qquad \text{for all } x \geq x^*,$$

or, for each $k = 0, 1, \ldots, N$, *suppose there exist* $\tilde{x}_k \geq x^*$ *where*

$$f'(x) \leq x|f''(x)|, \qquad x \geq \tilde{x}_k, \tag{2.3.3}$$

and

$$r_k - f(\tilde{x}_k) \leq f^{-1}(r_k) f'\left(f^{-1}(r_k)\right). \tag{2.3.4}$$

Then in the interval $I_0 = \left(0, f^{-1}(r_0)\right)$ *there exist* 2^{N+1} *disjoint, nonempty, closed subintervals that consist of initial conditions,* x_0, *of solutions of (2.2.1) whose solution sequence* $\{x_k\}$ *goes to extinction at time* $N+2$. *The complement of the union of these subintervals necessarily consists of initial positions of populations that are persistent at time* $N+2$ *together with subintervals of initial positions of populations that go to extinction at times* $1, 2, 3, \ldots, N+1$.

PROOF: By Lemma 2.3.1, $F_N(x) = x\,(r_N - f(x)) = f^{-1}(r_{N+1})$ has exactly two solutions, $x = a_N$ and $x = b_N$, where $0 < a_N < b_N < f^{-1}(r_N)$. Every trajectory of (1.3.1) with x_N in $[a_N, b_N]$ has $x_{N+2} \leq 0$ since $f^{-1}(r_{N+1}) < x_{N+1}$. Traversing the population trajectory in reverse time, we find that because of the configuration of F_{N-1}, there exist $a^1_{N-1}, b^1_{N-1}, a^2_{N-1}, b^2_{N-1}$

where

$$0 < a^1_{N-1} < b^1_{N-1} < a^2_{N-1} < b^2_{N-1} < f^{-1}(r_{N-1})$$

such that for $x_{N-1} \in [a^1_{N-1}, b^1_{N-1}] \cup [a^2_{N-1}, b^2_{N-1}]$, $x_N \in [a_N, b_N]$. On the other hand, for $x_N \notin [a_N, b_N]$, $x_{N+2} > 0$; that is, $\forall x_N \in (0, a_N) \cup \left(b_N, f^{-1}(r_N)\right)$, $x_{N+2} > 0$. By similarly traversing the population trajectory in reverse time, $\forall x_{N-1} \in (0, a^1_{N-1}) \cup \left(b^2_{N-1}, f^{-1}(r_{N-1})\right)$, $x_N \in (0, a_N)$ and hence $x_{N+2} > 0$, but for $x_{N-1} \in (b^1_{N-1}, a^2_{N-1})$, either $x_N \in \left(b_N, f^{-1}(r_N)\right)$, which gives $x_{N+2} > 0$, or $x_N \geq f^{-1}(r_N)$, which gives $x_{N+1} \leq 0$. Continuing this process, we find a decomposition of $\left(0, f^{-1}(r_0)\right)$ into 2^{N+1} subintervals that are composed of initial conditions for population trajectories that go to extinction at time $N+2$. The complement of this set must necessarily consist of initial values of populations that are persistent at time $N+2$ and solutions that have gone to extinction at time prior to $N+2$.

§ 2.4 The Periodic Model.

We end Chapter 2 with a specific case where the demographic variation is periodic. This assumption is based on the fact that most natural populations experience fluctuations in biological and environmental factors which affect their growth rates and many of the fluctuations with which a population must cope are regular and recurring, for example, seasonal (c.f. Harper, 1968; Pianka, 1971; Pielou, 1978; Ricklefs, 1974; Zaret & Rand, 1971).

The results of nonautonomous models, of course, may be applied to the periodic models, and a further qualitative result is obtained in the following theorem.

THEOREM 2.4.1. *Assume that there is an integer T such that $r_{n+T} = r_n$ for all $n = 0, 1, 2, \ldots$ in the model (2.2.1) and*

$$\prod_{i=0}^{T-1} r_i > 1.$$

Then there exists at least one positive periodic solution with the period T.

PROOF: First, it is easy to see that if there exists a periodic solution with a positive initial value, it must be positive at any time. Indeed, otherwise, $x_k \leq 0$ for some $k > 0$, and, then, $x_{n+k} \leq 0$ for all n, a contradiction in the periodicity of the solution.

Since

$$x_T = x_0 \left(r_0 - f(x_0)\right) \prod_{i=1}^{T-1} \left\{ r_i - f\left(x_0 \prod_{k=0}^{i-1} (r_k - f_k) \right) \right\}, \tag{2.4.1}$$

obviously, there exists a periodic solution with the period T if and only if there is a point, x_0, in the initial axis, such that $x_T = x_0$ and, equivalently, if and only if the equation

$$\left(r_0 - f(x_0)\right) \prod_{i=1}^{T-1} \left\{ r_i - f\left(x_0 \prod_{k=0}^{i-1} (r_k - f_k) \right) \right\} = 1 \tag{2.4.2}$$

has a solution x_0, $0 < x_0 < f^{-1}(r_0)$, where $f_k = f(x_k)$.

Let $y = r_0 - x_0$. Then $0 < y < r_0$. Rewrite (2.4.2) as

$$\frac{1}{y} = \prod_{i=1}^{T-1} \left\{ r_i - f\left(x_0 y \prod_{k=1}^{i-1} (r_k - f_k) \right) \right\},$$

and let

$$G(y) = \frac{1}{y} - \prod_{i-1}^{T-1} \left\{ r_i - f\left(x_0 y \prod_{k=1}^{i-1} (r_k - f_k) \right) \right\}. \tag{2.4.3}$$

Clearly, $G(y)$ is continuous for $0 < y < r_0$, and

$$\lim_{y \to 0+} G(y) = \infty,$$

$$\lim_{y \to r_0 - 0} G(y) = \frac{1}{r_0} - \prod_{i=1}^{T-1} r_i = \frac{1}{r_0}(1 - \prod_{i=0}^{T-1} r_i) < 0, \tag{2.4.4}$$

since $x_0 \to 0$ as $y \to r_0 - 0$. Thus, there exists at least one zero y_0 of (2.4.3) with $0 < y_0 < r_0$. That is, the periodic model (2.2.1) has at least one positive periodic solution.

It is also clear that determination of persistence of populations in periodic models is simpler than general nonautonomous models, because there are only T inequalities that need to be checked; that is, if

$$\max_{0<x<f^{-1}(r_i)} (x(r_i - f(x)) > f^{-1}(x_{i+1}), \qquad i = 0, 1, \ldots, T-1$$

then each population persists for $0 < x_0 < r_0$. Furthermore, Theorem 2.4.1 gives the existence of a regularly oscillatory population trajectory with the fixed period T.

It is not a trivial task to find how many positive periodic solutions there are. To illustrate the difficulties that might arise, we discuss a simple example as follows.

Consider the periodic logistic equation

$$x_{n+1} = x_n (r_n - x_n), \tag{2.4.5}$$

where $r_T = r_0$. By induction, it is easy to find the general form of the solution:

$$x_n = \sum_{k=1}^{2^n} (-1)^{k-1} a_k x_0^k, \qquad n \geq 1, \tag{2.4.6}$$

where $a_k > 0$ are combinations of r's and $a_1 = \prod_{j=1}^{n-1} r_j$. By Descarte's rule, we can get a simple proof of existence of at least one positive periodic solution provided $\prod_{j=1}^{T-1} r_j > 1$. Furthermore, if $T = 2$, then the positive periodic solution is unique. Indeed, clearly, it suffices to show that there is only one positive solution satisfying $x_2 = x_0$, that is, to show uniqueness of the positive solution of the equation

$$x_0^3 - 2r_0 x_0^2 + (r_0^2 + r_1)x_0 - (r_0 r_1 - 1) = 0. \tag{2.4.7}$$

Rewrite (2.4.7) as

$$x_0^2 - 2r_0x_0 + (r_0^2 + r_1) = \frac{r_0r_1 - 1}{x_0}.$$

Let

$$g(x_0) = x_0^2 - 2r_0x_0 + (r_0^2 + r_1).$$

Since

$$4r_0^2 - 4(r_0^2 + r_1) = -r_1 < 0,$$

$$g(x_0) > 0, \quad \forall x_0,$$

and $g(x_0)$ has a minimum r_1 at r_0. On the other hand, if we let $\psi(x_0) = \frac{r_0r_1 - 1}{x_0}$, then $\psi(x_0)$ is decreasing and always positive and $\lim_{x_0 \to 0+} \psi(x_0) = +\infty$, $\psi(r_0) = r_1 - \frac{1}{r_0} < r_1$. This shows that there is a unique intersection point between $g(x_0)$ and $\psi(x_0)$; that is, the positive periodic solution is unique.

§ 2.5 Discussion.

Our analysis of one-dimensional discrete population models with demographic variation and density dependence illustrates a feature that one might expect when studying stressed populations from a persistence and extinction perspective. That is, when environmental oscillations are pronounced, there is a possibility that a population goes to extinction at a finite time. The criteria for extinction in this chapter are based on relationships between the quantities $\max\{x(r - f(x))\}$ and $f^{-1}(r)$, or $\max\{x(r_n - f(x))\}$ and $f^{-1}(r_n)$. Theory developed in autonomous cases provided a basis to develop concepts in nonautonomous cases. In general, this theory cannot be applied to situations where species, like daphnia, have the capacity to protect themself from stress by optimizing energy allocation, maturity time and reproduction when the environment is constant or slowly changed (Gabriel, 1982).

However, when the environment is fluctuating, especially when rapid changes occur in environment, some species would lose their capacity to adapt to the changes.

An interpretation in our analysis is that if r_{n+1} at some generation $n+1$ is so small that $\max\{x\,(r_n - f(x))\}$ exceeds $f^{-1}\,(r_{n+1})$ then some populations go to extinction immediately after generation $n+1$. From this result, we see, once again, the effects of time delay in modelling population processes. In the extinction criterion, $\max\{x\,(r_n - f(x))\}$ is evaluated at generation n but $f^{-1}(r_{n+1})$ is evaluated at generation $n+1$. This is additional evidence that although there is no explicit time delay in our models, difference equations have already had a one generation time lag built into them (Levin & May, 1976).

Perhaps the most interesting result in this chapter relates to decomposition of the initial population axis. Subject to certain hypotheses, for each generation time N, the initial population size axis may be decomposed into extinction and persistence components. The dynamic decomposition corresponding to time 1 divides R_+ into two subintervals I_{p_1} and I_{e_1} where if $x_0 \in I_{p_1}$, the population with initial size x_0 is persistent at time 1, while if $x_0 \in I_{e_1}$, the population with initial size x_0 goes to extinction at time 1. The persistent set I_{p_1} is then decomposed into nonempty subintervals associated with persistence at time 2 and extinction at time 2. In general, we have shown that there are 2^{N-1} nondegenerate subintervals where extinction at time N results.

The decomposition occurs when a single inequality is satisfied for autonomous models or when several additional inequalities are valid for nonautonomous models (see Theorem 2.3.2). When the additional inequalities are not valid, for given f, the geometrical configuration of the population growth rate determines whether

extinction or persistence ensues at a given time. For example, the a_N and b_N in the proof of Theorem 2.3.2 might exceed the maximum of F_{N-1}. This would terminate the reverse construction of the population trajectory and there would not exist a solution emanating from time 0 that goes to extinction at time $N+1$. This is a difference between autonomous and nonautonomous models. Autonomous models which have trajectories that go to extinction at time N also have trajectories that go to extinction at time $1, 2, \ldots, N-1$. Nonautonomous models need not have this intermediate extinction property.

It should also be noted that the process employed to decompose the initial population interval is applicable to more general nonlinearities in (2.2.1) than the logistic-like formulation employed in Theorem 2.3.2. This is more complicated than the uniform case considered above because it is possible, for example, to have intersections numbering more than two at reverse time steps. The decomposition method, when it is applicable, will have at least 2^{N+1} subintervals for extinction at time $N+2$ and, depending upon F (where $x_{N+1} = F(x_N)$), could have many more. Hence, it appears to be a nontrivial task to predict extinction in difference equation models, primarily because of the characteristics of the extinction decomposition of the initial population size axis. It seems feasible that given any decomposition of the type described in Theorem 2.3.2, there is a viable density dependent mortality representation, f, and an appropriate growth rate sequence, $\{r_N\}$, which affects that extinction-persistence decomposition in (2.2.1).

The analysis of persistence and extinction for periodic population models is an interesting topic to develop further. In nature, many of the fluctuations with which a population must cope are regular and recurring. Birth and death rates can be

seasonal. Climatic factors which affect birth and death rates can also vary in a regular manner (Cushing, 1986a). All of these phenomena provide motivation to consider periodic models. In this chapter, we just initiated an elementary study on the periodic difference equation model. $\prod_{j=0}^{T-1} > 1$ is a sufficient condition for existence of a positive periodic solution with period T. We have also seen that the periodic solution is unique in a simple case where $T = 2$. When T becomes large, the task to determine the uniqueness of the positive periodic solution or to find the number of positive periodic solutions is complicated.

CHAPTER 3

DISCRETE AGE STRUCTURED MODELS

In Chapter 2, we have studied persistence and extinction of populations for discrete models without age structure; that is, we assumed that individual dynamics are not important for population dynamics. Obviously, this is only an approximation and, more realistically, we need to introduce some physiological or age structure into population models. When an age structure is viewed in a discrete population model setting, higher dimensional difference equations are often used. The well known Leslie matrix model is a typical example, that has been used frequently. However, in most of the literature, it is assumed that mortality and fertility are constant or time independent (c.f. Sykes, 1969; Cull & Vogt, 1973; Green, 1979; Geramita & Pullman, 1984), although there has been some attention devoted to effects of periodic events (Kot & Schaffer, 1984).

In this chapter, we study models with demographic variation and density dependence. The analysis of the dynamical behavior of population trajectories can be very complicated; hence, we focus initially on some special cases where populations are assumed to consist of only two age classes. This is a reasonable approximation for many species of birds (Capildeo & Haldane, 1954), for some species of snails (Wolda, 1970), and for some species of insects (Tschumy, 1982).

§ 3.1 Autonomous Two Age Class Model.

Suppose that a population consists of two age classes. All juveniles become adults and all adults die at the next generation after reproducing offspring. "Intraspecific competition" acts only within the adult class so that the density functions are only

functions of the adult population. The environment is assumed to be constant. Then, we assume that the model has the following form:

$$\begin{cases} x_{n+1} = y_n(\alpha - f(y_n)), \\ y_{n+1} = x_n(\beta - g(y_n))^+, \end{cases} \tag{3.1.1}$$

where x_n and y_n denote numbers or biomass of juveniles and adults respectively at time n; α is the birth rate and β is the survival probability; f and g represent density dependent relationships and satisfy that $f(0) = 0$, $g(0) = 0$; $f(y) \equiv 0$, and $g(y) \equiv 0$ if $y \leq 0$; $f'(y) > 0$ and $g'(y) > 0$ for $y \geq 0$. Here,

$$(\beta - g(y))^+ \equiv \max\{\beta - g(y), 0\}.$$

For simplicity, we omit the superscript "+" afterwards in this chapter.

When $\alpha\beta < 1$, the zero solution $(0,0)$ is stable and the population goes to extinction at some time for any initial size. When $\alpha\beta = 1$, the population trajectories are decreasing and extinction also results. Hence, we are most interested in the case $\alpha\beta > 1$. As we mentioned in Chapter 2, this relates to persistence but does not guarantee it since the possibility of extinction at some finite time has not been eliminated.

DEFINITION 3.1.1.

a) *A population, represented by a solution sequence* $\{(x_n, y_n)\}$ *of (3.1.1) is strongly persistent at time* N *if* $x_n > 0$, *and* $y_n > 0$, *for each* $n = 0, 1, \ldots, N$;

b) *A population is weakly persistent at time* N *if* $x_n > 0$ *and* $y_n > 0$ *for each* $n = 0, 1, \ldots, N-1$, *and* $x_N \geq 0$, $y_N \geq 0$, $x_N + y_N > 0$.

c) *A population is strongly persistent if it is strongly persistent at time* N *for each* $N = 0, 1, \ldots$ *and* $\limsup_{n\to\infty} x_n > 0$, $\limsup_{n\to\infty} y_n > 0$;

d) *A population is weakly persistent if it is persistent at time N for each $N = 0, 1, \ldots$ and* $\limsup_{n\to\infty}(x_n + y_n) > 0$;

e) *A population goes to extinction at time N provided it is persistent at time $N-1$ but $x_N \leq 0$ and $y_N \leq 0$;*

f) *A population goes to extinction asymptotically provided it is persistent at time N for each $N = 0, 1, \ldots$ and* $\lim_{n\to\infty} x_n = 0$, $\lim_{n\to\infty} y_n = 0$.

First, we discuss persistence of the population.

THEOREM 3.1.2. *Let* $l = \min\left\{f^{-1}(\alpha), g^{-1}(\beta)\right\}$ *and assume*

$$\max_{0<y<l}\{y\,(\alpha - f(y))\} \leq \frac{l}{\beta}. \tag{3.1.2}$$

Then each population with

$$\begin{aligned} 0 < x_0 &< \frac{l}{\beta - g(y_0)}, \\ 0 < y_0 &< l \end{aligned}$$

is strongly persistent at time N for each $N = 1, 2, \ldots$. Furthermore,

$$\begin{aligned} 0 < x_n &\leq \frac{l}{\beta}, \\ 0 < y_n &< l, \end{aligned} \tag{3.1.3}$$

for all $n > 1$.

PROOF: Clearly, it is sufficient to show (3.1.3) and this is done by induction on n. (3.1.3) is trivially true for $n = 1$. In fact, obviously, $x_1 > 0$ and $y_1 > 0$. Since $0 < y_0 < l$, and by the assumption (3.1.2)

$$\begin{aligned} x_1 &= y_0\,(\alpha - f(y_0)) \leq \frac{l}{\beta}, \\ y_1 &= x_0\,(\beta - g(y_0)) < l. \end{aligned}$$

Assume $0 < x_k \leq \dfrac{l}{\beta}$ and $0 < y_k < l$. It follows immediately that $x_{k+1} > 0$, $y_{k+1} > 0$, and

$$x_{k+1} = y_k\,(\alpha - f(y_k)) \leq \frac{l}{\beta},$$
$$y_{k+1} = x_k\,(\beta - g(y_k)) < x_k\beta \leq l.$$

COROLLARY 3.1.3. *Assume that the hypotheses of Theorem 3.1.2 hold and* $\alpha\beta > 1$. *Then each population is strongly persistent.*

PROOF: Persistence at time N for each $N = 1, 2, \ldots$ is from Theorem 3.1.2. Since

$$\begin{cases} x_{n+1} &= y_n\,(\alpha - f(y_n)) \approx \alpha y_n, \\ y_{n+1} &= x_n\,(\beta - g(y_n)) \approx \beta x_n, \end{cases} \tag{3.1.4}$$

for small (x_n, y_n), the linearized system

$$\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = \begin{pmatrix} 0 & \alpha \\ \beta & 0 \end{pmatrix} \cdot \begin{pmatrix} x_n \\ y_n \end{pmatrix}$$

has at least one eigenvalue greater than 1 whenever $\alpha\beta > 1$. Hence, the zero solution $(0, 0)$ is unstable and the population is strongly persistent.

THOREM 3.1.4. *Assume*

$$\max_{0<y<f^{-1}(\alpha)} \{y\,(\alpha - f(y))\} < \frac{f^{-1}(\alpha)}{\beta}. \tag{3.1.5}$$

Then each population is weakly persistent at time N *for* $N = 1, 2, \ldots$ *provided*

$$0 < x_0 < \frac{f^{-1}(\alpha)}{\beta - g(y_0)},$$
$$0 < y_0 < \max\left\{f^{-1}(\alpha), g^{-1}(\beta)\right\}.$$

PROOF: Suppose that there is a population which is not weakly persistent. Then, it must go to extinction at some time, say $n+1$, i.e.

$$\begin{cases} x_{n+1} &= y_n\,(\alpha - f(y_n)) \le 0, \\ y_{n+1} &= x_n\,(\beta - g(y_n)) \le 0. \end{cases} \tag{3.1.6}$$

Then, there are three and only three possibilities:

i)
$$\begin{cases} x_n \le 0, \\ y_n \le 0; \end{cases}$$

ii)
$$\begin{cases} x_n \le 0, \\ y_n \ge f^{-1}(\alpha); \end{cases}$$

and

iii)
$$\begin{cases} x_n > 0 \\ y_n \ge f^{-1}(\alpha), \quad \text{and} \quad y_n \ge g^{-1}(\beta). \end{cases}$$

By the definition of weak persistence, case i) cannot happen.

Notice that

$$y_n = x_{n-1}\,(\beta - g(y_{n-1})) \le x_{n-1}\beta < \frac{f^{-1}(\alpha)}{\beta}\beta = f^{-1}(\alpha),$$

this means case ii) and iii) cannot happen either. Hence, $x_{n+1} > 0$, or $y_{n+1} > 0$, for each n.

Similarly, we have the following result.

COROLLARY 3.1.5. *Suppose that the hypotheses of Theorem 3.1.4 are satisfied and* $\alpha\beta > 1$. *Then each population is weakly persistent.*

REMARK 3.1.6: It is clear from the definitions that strong persistence implies weak persistence; however,the converse is not true. For example, suppose that the following inequalities

$$\frac{g^{-1}(\beta)}{\beta} < \max_{0<y<f^{-1}(\alpha)} \{y(\alpha - f(y))\} < \frac{f^{-1}(\alpha)}{\beta}$$

hold. Choose x_0 very small and y_0 so that

$$y_0(\alpha - f(y_0)) > \frac{g^{-1}(\beta)}{\beta}.$$

Then

$$\begin{aligned} y_2 &= y_0(\alpha - f(y_0))(\beta - g(x_0(\beta - g(y_0)))) \\ &\geq \frac{g^{-1}(\beta)}{\beta}\beta = g^{-1}(\beta). \end{aligned}$$

Hence

$$\left.\begin{array}{l} x_{2n+1} > 0, \\ y_{2n+1} = 0; \end{array}\right\} \quad \text{and} \quad \left\{\begin{array}{l} x_{2n+2} = 0, \\ y_{2n+2} > 0; \end{array}\right.$$

$n = 1, 2, \ldots$. The population is therefore only weakly persistent.

The following theorem discusses a sufficient condition for finite time extinction.

THEOREM 3.1.7. *Assume*

$$\max_{0<y<f^{-1}(\alpha)} \{\beta y(\alpha - f(y))\} > L, \tag{3.1.7}$$

where $L = \max\left\{f^{-1}(\alpha), g^{-1}(\beta)\right\}$.

Then the model (3.1.1) has populations that go to extinction at time N, for each $N = 1, 2, \ldots$.

PROOF: To show that a population goes to extinction at time N, i.e. $x_N \leq 0$, and $y_N \leq 0$, it is sufficient to find x_0 and y_0 with

$$0 < x_0 < \frac{l}{\beta - g(y_0)}, \qquad 0 < y_0 < l$$

such that the generated sequence $\{(x_n, y_n)\}$ has $y_{N-1} \geq L$, since $L = \max\left\{f^{-1}(\alpha), g^{-1}(\beta)\right\}$.

From (3.1.7) and

$$\begin{aligned} y_{N-1} &= x_{N-2}\left(\beta - g(y_{N-2})\right) \\ &= y_{N-3}\left(\alpha - f(y_{N-3})\right)\left(\beta - g\left(x_{N-3}\left(\beta - g(y_{N-3})\right)\right)\right), \end{aligned} \tag{3.1.8}$$

it follows that there exist a_{N-3} and b_{N-3} with

$$0 < a_{N-3} < b_{N-3} < f^{-1}(\alpha)$$

such that $\forall y_{N-3} \in (a_{N-3}, b_{N-3})$, $y_{N-3}\left(\alpha - f(y_{N-3})\right)\beta > L$. Hence, $y_{N-1} \geq L$ provided $x_{N-3} \ll 1$, where "$\ll 1$" denotes being a sufficiently small value. Indeed, if $y_{N-3} \geq g^{-1}(\beta)$ then $y_{N-2} = 0$, and $y_{N-1} = y_{N-3}\left(\alpha - f(y_{N-3})\right)\beta > L$. Otherwise,

$$y_{N-2} = x_{N-3}\left(\beta - g(y_{N-3})\right) \ll 1$$

and

$$y_{N-1} = x_{N-2}\left(\beta - g(y_{N-2})\right) \approx x_{N-2}\beta = y_{N-3}\left(\alpha - f(y_{N-3})\right)\beta > L.$$

Next, we consider

$$\begin{cases} x_{N-3} = y_{N-4}\,(\alpha - f(y_{N-4}))\,, \\ y_{N-3} = x_{N-4}\,(\beta - g(y_{N-4}))\,. \end{cases} \tag{3.1.9}$$

Obviously, by choosing $y_{N-4} \ll 1$, $(3.1.9)_1$ is solved. The iterate x_{N-3} and, hence, y_{N-4} can be chosen to be arbitrarily small. If x_{N-4} can be found so that $x_{N-4}\beta \in S_{N-3}$, where $S_{N-3} = (a_{N-3}, b_{N-3})$, then (3.1.9) is solved. But this is trivial from (3.1.7) and the hypothesis that f is increasing. In fact, since

$$\max_{0<y<f^{-1}(\alpha)} \{\beta y\,(\alpha - f(y))\} > L > f^{-1}(\alpha),$$

there exist a_{N-5} and b_{N-5} with $a_{N-5} < b_{N-5} < f^{-1}(\alpha)$ such that $\forall y_{N-5} \in S_{N-5} = (a_{N-5}, b_{N-5})$

$$a_{N-3} < x_{N-4}\beta = \beta y_{N-5}\,(\alpha - f(y_{N-5})) < b_{N-3}.$$

That is, (3.1.9) is satisfied if $y_{N-5} \in S_{N-5}$ and $x_{N-5} \ll 1$. Continuing in this fashion, the proof is completed inductively.

REMARK 3.1.8: It is easy to see from the proof of Theorem 3.1.7 that

(1) If N is an odd integer, then there is a subset $S_0 \subset \left(0, f^{-1}(\alpha - \frac{1}{\beta})\right)$ such that the population with $x_0 \ll 1$ and $y_0 \in S_0$ goes to extinction at time N.

(2) If N is an even integer,then there is a subset $S_1 \subset \left(0, f^{-1}(\alpha - \frac{1}{\beta})\right)$ such that the population with $x_0\beta \in S_1$ and $y_0 \ll 1$ goes to extinction at time N.

§ 3.2 Nonautonomous Two Age Class Model.

In § 3.1, we assumed that the birth rate and the death rate are time independent; that is, a constant environment and physiology are assumed. More realistically, we assume that the birth rate and the death rate are time dependent, and, hence, the

following nonautonomous difference model is needed:

$$\begin{cases} x_{n+1} = y_n\left(\alpha_n - f(y_n)\right), \\ y_{n+1} = x_n\left(\beta_n - g(y_n)\right). \end{cases} \tag{3.2.1}$$

Here, we still assume that density effects only depend upon the numbers of the adults.

Since

$$\begin{cases} x_{n+2} = x_n\left(\beta_n - g(y_n)\right)\left(\alpha_{n+1} - f(y_{n+1})\right), \\ y_{n+2} = y_n\left(\alpha_n - f(y_n)\right)\left(\beta_{n+1} - g(y_{n+1})\right), \end{cases} \tag{3.2.2}$$

if $\beta_n\alpha_{n+1} \leq 1$ and $\alpha_n\beta_{n+1} \leq 1$, the population size becomes smaller and smaller. Hence, an obvious condition for extinction, either at time N, $N = 2, 3, \ldots$, or at infinity, is that $\alpha_n\beta_{n+1} \leq 1$ and $\alpha_n\beta_{n-1} \leq 1$, $n = 1, 2, \ldots$. We are most interested in the case where $\alpha_n\beta_{n+1} > 1$ or $\alpha_n\beta_{n-1} > 1$, $n = 1, 2, \ldots$.

The following results are based on an approach analogous to the one employed in § 3.1.

THEOREM 3.2.1. *Let*

$$0 < a \leq \alpha_n \leq A,$$

$$0 < b \leq \beta_n \leq B,$$

$n = 0, 1, \ldots$, *and* $\bar{l} = \min\left\{f^{-1}(a), g^{-1}(b)\right\}$. *Assume that*

$$\max_{0<y<\bar{l}} \left\{y\left(A - f(y)\right)\right\} < \frac{\bar{l}}{B}. \tag{3.2.3}$$

Then,

$$0 < x_n < \frac{\bar{l}}{B},$$

$$0 < y_n < \bar{l},$$

$n = 1, 2, \ldots$, *provided*

$$\begin{cases} 0 < x_0 < \dfrac{\bar{l}}{\beta_0 - g(y_0)}, \\ 0 < y_0 < \bar{l}. \end{cases} \tag{3.2.4}$$

That is, each population with initial sizes satisfying the inequality (3.2.4) *is strongly persistent at time* N *for each* $N = 1, 2, \ldots$.

The proof is straightforward from induction as that in the proof of Theorem 3.1.2.

COROLLARY 3.2.2. *Let the hypotheses of Theorem 3.2.1 be satisfied and* $\liminf_{n\to\infty} \alpha_n\beta_{n-1} > 1$, $\liminf_{n\to\infty} \alpha_n\beta_{n+1} > 1$. *Then each population with initial sizes satisfying* (3.2.4) *is strongly persistent.*

PROOF: Theorem 3.2.1 established persistence at time N for each $N = 1, 2, \ldots$. From (3.2.2), it follows that $\limsup_{n\to\infty} x_n > 0$ and $\limsup_{n\to\infty} y_n > 0$.

THEOREM 3.2.3. *Suppose that*

$$0 < a \leq \alpha_n \leq A,$$

$$0 < b \leq \beta_n \leq B,$$

$n = 0, 1, 2, \ldots$, *and*

$$\max_{0<y<f^{-1}(A)} \{y\,(A - f(y))\} < \frac{f^{-1}(a)}{B}. \tag{3.2.5}$$

Then, each population with the initial values (3.2.4) is weakly persistent at each time N *for* $N = 1, 2, \ldots$.

PROOF: Assume, for purpose of contradiction, that the conclusion is false. Then there is an N such that the population is persistent at time N but $x_{N+1} \leq 0$ and

$y_{N+1} \leq 0$. Hence,

$$\begin{cases} y_N\,(a - f(y_N)) \leq y_N\,(\alpha_N - f(y_N)) \leq 0, \\ x_N\,(b - g(y_N)) \leq x_N\,(\beta_N - g(y_N)) \leq 0. \end{cases} \tag{3.2.6}$$

To satisfy (3.2.6), clearly, it is necessary that one of the following is satisfied:

$$\begin{cases} x_N \leq 0, \\ y_N \leq 0; \end{cases} \tag{3.2.7}$$

$$\begin{cases} x_N \leq 0, \\ y_N \geq f^{-1}(a); \end{cases} \tag{3.2.8}$$

$$\begin{cases} x_N > 0, \\ y_N \geq f^{-1}(a), \quad \text{and} \quad y_N \geq g^{-1}(b). \end{cases} \tag{3.2.9}$$

Since

$$\begin{aligned} y_N &= x_{N-1}\,(\beta_{N-1} - g(y_{N-1})) \\ &\leq \beta_{N-1} x_{N-1} \leq B x_{N-1} < f^{-1}(a), \end{aligned}$$

(3.2.7) must be satisfied. This contradicts to persistence of the population at time N.

EXAMPLE: Consider a simple case:

$$\begin{cases} x_{n+1} = y_n(\alpha_n - y_n), \\ y_{n+1} = x_n(\beta_n - y_n). \end{cases}$$

Assume

$$a \leq \alpha_n \leq A,$$

$$b \leq \beta_n \leq B.$$

Then, if $4b < AB < 4a$, each population with the initial sizes

$$\begin{aligned} 0 < x_0 &< \frac{\min\{a, b\}}{\beta_0 - y_0}, \\ 0 < y_0 &< \min\{a, b\}, \end{aligned} \tag{3.2.10}$$

is weakly persistent; and if

$$AB < 4\min\{a, b\},$$

each population with the initial sizes (3.2.10) is strongly persistent.

Similarly, we have the following result.

COROLLARY 3.2.4. *Suppose that the hypotheses of Theorem 3.2.3 are satisfied and* $\liminf_{n\to\infty} \alpha_n\beta_{n+1} > 1$, $\liminf_{n\to\infty} \alpha_n\beta_{n-1} > 1$, $n = 1, 2, \ldots$. *Then each population with the initial values (3.2.4) is weakly persistent.*

Now, we consider extinction of populations. The following theorem is obtained by procedure analogous to that employed in § 3.1.

THEOREM 3.2.5. *Assume that there is an* N *such that*

$$\max_{0<y<f^{-1}(\alpha_{N-2k})} \{\beta_{N-2k+1} y\,(\alpha_{N-2k} - f(y))\} \geq f^{-1}(\alpha_{N-2k+2}) \tag{3.2.11}$$

for $k = 1, 2, \ldots, [\frac{N}{2}]$, *and*

$$\max_{0<y<f^{-1}(\alpha_N)} \{\beta_{N+1} y\,(\alpha_N - f(y))\} > L_{N+2} \equiv \max\left\{f^{-1}(\alpha_{N+2}), g^{-1}(\beta_{N+2})\right\}. \tag{3.2.12}$$

Then, there is a population with the initial values (3.2.4) that goes to extinction at time $N + 3$.

PROOF: First, we assume that N is an even integer and let it be written as $2n$.

Since

$$x_{2n+3} = y_{2n+2}\,(\alpha_{2n+2} - f(y_{2n+2})),$$

$$y_{2n+3} = x_{2n+2}\,(\beta_{2n+2} - g(y_{2n+2})),$$

and

$$\begin{aligned} y_{2n+2} &= x_{2n+1}\left(\beta_{2n+1} - g(y_{2n+1})\right) \\ &= y_{2n}\left(\alpha_{2n} - f(y_{2n})\right)\left(\beta_{2n+1} - g(y_{2n+1})\right), \end{aligned}$$

if $y_{2n+1} = 0$ or $0 < y_{2n+1} \ll 1$, by employing (3.2.12), we find that there exist a_{2n} and b_{2n} with

$$0 < a_{2n} < b_{2n} < f^{-1}(\alpha_{2n})$$

such that

$$y_{2n+2} > L_{2n+2}, \tag{3.2.13}$$

for $y_{2n} \in S_{2n}$, where S_{2n} is the set defined by (a_{2n}, b_{2n}). Hence, the inequalities $x_{2n+3} \leq 0$, $y_{2n+3} \leq 0$ are valid provided $y_{2n} \in S_{2n}$. Recall that $y_{2n+1} = x_{2n}\left(\beta_{2n} - g(y_{2n})\right)$. If $y_{2n} \geq g^{-1}(\beta_{2n})$, then $y_{2n+1} = 0$; otherwise,

$$x_{2n} = \frac{y_{2n+1}}{\beta_{2n} - g(y_{2n})}.$$

Choosing x_{2n} very small we can get $0 < y_{2n+1} \ll 1$. Assume $0 < y_{2n+1} \ll 1$.

As the next step, we need to satisfy

$$\begin{cases} x_{2n} = y_{2n-1}\left(\alpha_{2n-1} - f(y_{2n-1})\right), \\ y_{2n} = x_{2n-1}\left(\beta_{2n-1} - g(y_{2n-1})\right), \end{cases} \tag{3.2.14}$$

for x_{2n-1} and y_{2n-1}, where $x_{2n} \ll 1$ and $y_{2n} \in S_{2n}$. Without loss of generality, y_{2n+1} and x_{2n} may be taken arbitrarily small, hence if we can show that there is a x_{2n-1} such that $x_{2n-1}\beta_{2n-1} \in S_{2n}$, by choosing y_{2n-1} very small, (3.2.14) and, subsequently, (3.2.13) can be satisfied.

Since $b_{2n} < f^{-1}(\alpha_{2n})$, it follows from (3.2.11) that there exist a_{2n-2} and b_{2n-2} with

$$a_{2n-2} < b_{2n-2} < f^{-1}(\alpha_{2n-2})$$

such that

$$\beta_{2n-1}x_{2n-1} = \beta_{2n-1}y_{2n-2}\left(\alpha_{2n-2} - f(y_{2n-2})\right) \in S_{2n}$$

for $y_{2n-2} \in S_{2n-2}$, where $S_{2n-2} = (a_{2n-2}, b_{2n-2})$. Thus, $x_{2n-2} \ll 1$ and $y_{2n-2} \in S_{2n-2}$ satisfy (3.2.14). Continuing in this manner, we can find the initial values $x_0 \in \left(0, \dfrac{\min\{\alpha_1, \beta_1\}}{\beta_0 - g(y_0)}\right)$ and $y_0 \in (0, \min\{\alpha_0, \beta_0\})$ such that $x_{2n+3} \leq 0$ and $y_{2n+3} \leq 0$. (More precisely, $x_0 \ll 1$, and $y_0 \in S_0 = (a_0, b_0)$, where $0 < a_0 < b_0 < f^{-1}(\alpha_0)$).

If N is odd, by the procedure described above, we find the set S_1 such that $\forall y_1 \in S_1$ and $0 < x_1 \ll 1$, $x_{N+3} \leq 0$, $y_{N+3} \leq 0$. Then, choosing $0 < y_0 \ll 1$ and x_0 such that $x_0\beta_0 \in S_1$ leads to $x_{N+3} \leq 0$ and $y_{N+3} \leq 0$.

§ 3.3 Decomposition of Initial Population Axes.

By discussing decomposition of initial population axis in § 2.3 for one dimensional difference models, we have indicated that extinction behaviors of populations are complex. When age structures are involved in population models, complexity increases and the decomposition becomes more complicated. However, in the two age class models when the population size is small in one age class, the population model behaves like an age independent model in the sense that it is still possible, for a prescribed generation N, to subdivide the initial population axes into subintervals containing trajectories that go to extinction at finite times less than or equal to N and subintervals containing trajectories that strongly or weakly persist at time N.

THEOREM 3.3.1. *Assume that $f(y)$ satisfies the assumptions of Lemma 2.3.1 and Theorem 3.1.7. Let $f^{-1}(\alpha) \leq g^{-1}(\beta)$. Then, for N an odd integer, there exist 2^{N-1} disjoint, nonempty subintervals that consist of initial positions, y_0, of solutions of (3.1.1), in the interval $\left(0, f^{-1}(\alpha)\right)$, with x_0 small, whose solution sequence $\{(x_n, y_n)\}$ goes to extinction at time N. The complement of the union of these subintervals*

contains initial positions, y_0, of populations with the same x_0 that are persistent at time N together with subintervals of the initial positions of populations that go to extinction at times $1, 2, \ldots, N-1$. For N an even integer, the decomposition process can happen in the x_0 axis with y_0 small.

PROOF: In the proof of Theorem 3.1.7, we have shown that $\forall y_{N-3} \in S_{N-3}$ and for $0 < x_{N-3} \ll 1$, it holds that $y_{N-1} \geq L$ and, hence, the population goes to extinction at time N. Since, now, $f^{-1}(\alpha) \leq g^{-1}(\beta)$, $y_{N-3} < f^{-1}(\alpha) \leq g^{-1}(\beta)$, $y_{N-2} \ll 1$ is positive and so is x_{N-1}. It follows from the configuration of $\beta y\,(\alpha - f(y))$ that there exist two nonempty open subintervals $(0, a'_{N-3})$ and $\left(b'_{N-3}, f^{-1}(\alpha)\right)$, where $a'_{N-3} < a_{N-3}$ and $b_{N-3} < b'_{N-3}$, in the complement of the closure of S_{N-3} in $\left(0, f^{-1}(\alpha)\right)$, such that $\forall y_{N-3} \in (0, a'_{N-3}) \cup \left(b'_{N-3}, f^{-1}(\alpha)\right)$ with the same x_{N-3}, $y_{N-1} < L$ and, hence, at least $y_N > 0$. Traversing the population trajectory in reverse time, we find that there exist b^1_{N-5}, a^2_{N-5}, b^2_{N-5}, a^3_{N-5}, b^3_{N-5}, a^4_{N-5}, b^4_{N-5}, a^5_{N-5}, b^5_{N-5}, a^6_{N-5} with

$$\begin{aligned} 0 < b^1_{N-5} < a^2_{N-5} < b^2_{N-5} < a^3_{N-5} < b^3_{N-5} \\ < a^4_{N-5} < b^4_{N-5} < a^5_{N-5} < b^5_{N-5} < a^6_{N-5} < f^{-1}(\alpha) \end{aligned}$$

such that for

$$y_{N-5} \in (0, b^1_{N-5}) \cup (a^3_{N-5}, b^3_{N-5}) \cup (a^4_{N-5}, b^4_{N-5}) \cup \left(a^6_{N-5}, f^{-1}(\alpha)\right)$$

with $x_{N-5} \ll 1$

$$y_{N-3} \in (0, a'_{N-3}) \cup (b'_{N-3}, f^{-1}(\alpha)),$$

and for

$$y_{N-5} \in (a^2_{N-5}, b^2_{N-5}) \cup (a^5_{N-5}, b^5_{N-5})$$

with $x_{N-5} \ll 1$, $y_{N-3} \in (a_{N-3}, b_{N-3})$. Continuing this process, when N is odd, we find a decomposition of $\left(0, f^{-1}(\alpha)\right)$ into 2^{N-1} subintervals that are composed of initial conditions for population trajectories that go to extinction at time N. The complement of this set contains a union of nonempty subintervals that composed of initial values of populations that are persistent at time N or have gone to extinction at time prior to N, and these two sets of subintervals are nested. When N is even, the decomposition of the population size at time 1 is found. Denote the set containing the subintervals for populations that go to extinction by S_1. Then, by choosing $0 < y_0 \ll 1$ and $\forall x_0$ so that $\beta_0 x_0 \in S_1$, the population trajectories go to extinction at time N. Similarly, we can find the union of initial values corresponding to population trajectories which are persistent at time N or have gone to extinction at a time prior to N.

Likewise, we have the following result for the nonautonomous model.

THEOREM 3.3.2. *Let the assumption (i) where r is replaced by r_n for each n hold and (ii) of Lemma 2.3.1 hold. Let there be an N such that (3.2.10) and (3.2.11) in Theorem 3.2.5 hold. In addition, suppose that*

$$f'(x) \geq x|f''(x)| \qquad \forall x \geq x^*,$$

or, for each $k = 1, 2, \ldots, [\frac{N}{2}]$, suppose there exist $\tilde{x}_{2k} \geq x^*$ where

$$f'(x) \leq x|f''(x)|, \quad x \geq \tilde{x}_{2k} \tag{3.3.1}$$

and

$$r_{2k} - f(\tilde{x}_{2k}) \leq f^{-1}(\alpha_{2k}) f'\left(f^{-1}(\alpha_{2k})\right). \tag{3.3.2}$$

Morever, assume that $f^{-1}(\alpha_{N+1}) \leq g^{-1}(\beta_{N+1})$. *Then, for* N *an odd integer, there exist* 2^{N+2} *disjoint, nonempty subintervals composed of initial positions,* y_0, *of solutions of (3.2.1), in the interval* $\left(0, f^{-1}(\alpha_0)\right)$, *with* x_0 *small, whose solution sequence* $\{(x_n, y_n)\}$ *goes to extinction at time* $N+3$. *The complement of the union of these subintervals contains initial positions,* y_0, *of populations with the same* x_0 *that are persistent at time* $N+3$ *together with subintervals of the initial positions of populations that go to extinction at times* $1, 2, \ldots, N+2$. *For* N *an even integer, the decomposition process can happen in the* x_0 *axis with* y_0 *small.*

§ 3.4 Discussion.

As is well known, even the simplest one-dimensional nonlinear difference equation model can exhibit a remarkable spectrum of dynamical behaviors. It is not surprising that dynamical behaviors of discrete nonlinear population models become very complicated when age structure is employed. While the analysis in this chapter only focused on some rudimentary models, some differences between age-independent models and age-specific models already exist. One essential difference is that some age subclasses in an age structured model can go to extinction at a finite time but the total population is still persistent at that time and after one or more generations, the extinct age class could appear again. From this viewpoint, as the number of age classes increases, a population with age structure might have more opportunities to survive.

One assumption for the models in this chapter is that individuals change their stages completely from one generation to another generation. That is, after contributing offspring to the next generation, all adults die and progeny mature into a fertile adult stage with a certain survival probability. The main dominant factor

is the quantity $\beta_{n+1}\{y_n(\alpha_n - f(y_n))\}$ which describes the maximum number of individuals that might become adults at generation $n+1$. Since only "intraspecific competition" within the adult class is concerned, when this amount exceeds $f^{-1}(\alpha_{n+1})$, reproduction is stopped, and when it exceeds $g^{-1}(\beta_{n+1})$, no offspring survives to the next generation. If only one of these above cases occurs, weak persistence might occur. If both happen, there are some populations that go to extinction at time $n+2$.

Decomposition of the initial population axis is an interesting phenomenon in one-dimensional nonlinear difference equation models. This game can also be played in two-dimensional models, but the situation is more complicated. When the initial population size in one age class is small, the population model behaves like an age-independent model. Hence, it is still possible to decompose the initial population size axes; however, the complement of the union of the subintervals that consist of initial positions whose solution sequence goes to extinction no longer necessarily consists only of initial positions of populations that are persistent at that time together with subintervals of initial positions of populations that go to extinction at prior times. In other words, the union of the subintervals consisting of initial positions of populations that are persistent at that time together with subintervals of initial positions of populations that go to extinction at prior times is only a nonempty subset of the complement but not the complement itself. The rest of the two unions consists of subintervals of initial positions whose solution sequence behavior is not readily determined.

When the initial population size is not small in either age class, it is very difficult to decompose initial population size axes into any definitive structure.

For simplicity, we assumed that "intraspecific competition" acts only within the adult class. It is more realistic to consider that this competition acts in the offspring class as well; that is, it is reasonable to consider the following model:

$$\begin{cases} x_{n+1} = y_n \left(\alpha_n - f_1(x_n) - f_2(y_n)\right), \\ y_{n+1} = x_n \left(\beta_n - g_1(x_n) - g_2(y_n)\right). \end{cases}$$

The dynamic behavior of this system is not known but it is expected to be more complicated than the previously studied situations.

CHAPTER 4

CONTINUOUS MODEL WITH AGE STRUCTURE

In the previous two chapters, we have discussed persistence and extinction of populations by employing models of discrete growth processes. Discrete models are probably suited to describe the survival patterns of species because of small population sizes associated with extinction. However, when generations in a population overlap, it is realistic to use a continuous growth process to study the dynamics of populations. Then, ordinary differential equation models or partial differential equation models are used. The theory of differential equations has been generally well developed. This provides a solid foundation for initial analysis of continuous population models.

In this chapter, we consider certain special population models with age structure modelled by partial differential equations. The existence and uniqueness of the solution are established first. By using a transformation and a comparison technique, some basic results for persistence and extinction are presented.

§ 4.1 Formulation of the Problem.

Since the beginning of this century, the importance of age dependence in a population modelling process has been recognized. The theory of age-dependent population dynamics has been extensively developed (c.f. Sharpe & Lotka, 1911; McKendrick, 1926; Hoppensteadt, 1974; Gurtin & MacCamy, 1974; Cushing, 1977, 1985b; Nisbet & Gurney, 1982; Webb, 1985; Metz & Diekmann, 1986) with the basic continuous age structured population model described by the McKendrick

equation or von Foerster equation:

$$\frac{\partial \rho(a,t)}{\partial a} + \frac{\partial \rho(a,t)}{\partial t} = D(a,t,P)\rho(a,t), \tag{4.1.1}$$

$$\rho(0,t) = \int_0^\infty n(a,t,P)\rho(a,t)da, \tag{4.1.2}$$

$$\rho(a,0) = \phi(a). \tag{4.1.3}$$

Here, $\rho(a,t)$ is the density distribution of a population so that $\int_\alpha^\gamma \rho(a,t)da$ gives the number of individuals with age between α and γ at time t; $D(a,t,P)$ is the age specific mortality function; $n(a,t,P)$ is the age specific fertility function; $P(t) = \int_0^\infty \rho(a,t)da$ is the total population size; and $\phi(a)$ is the initial age distribution.

This is a first order hyperbolic partial differential equation and it can be solved theoretically by using the method of characteristics. However, when this method is applied, the unknown function is still involved implicitly in the expression for the solution. Hence, the solution is not explicitly found, and, in general, the analytic study of the model is very difficult, especially, when time variation in demographic parameters and density dependence are included in the formulation.

In order to obtain certain theoretical results several studies have assumed that the mortality function μ and the fertility function β are time independent or density independent (e.g. Sinko & Streifer, 1967; Gurtin & MacCamy, 1974, 1979; Cushing 1980, 1984, 1985; Wang, 1980; Pruss, 1983; Busenberg & Iannelli, 1985; Valad & Popa, 1985; Swart, 1986). Clearly, when food limitations and environmental effects are considered, it is more realistic to assume that the mortality and the fertility are time dependent and density dependent. Swick (1977) studied persistence and extinction under the assumptions that $\underline{D}(a) \leq D(a,t,P) \leq \bar{D}(a)$, $\underline{n}(a)P^r \leq n(a,t,P)$, or $n(a,t,P) \leq \bar{n}(a)P^r$. The persistence and extinction results

are determined by $\underline{n}(a)$, $\bar{n}(a)$, $\underline{D}(a)$, and $\bar{D}(a)$. Hence, in fact, time variation is ignored. Haimovici (1979) studied dynamics of populations involving resources and pollution, but persistence and extinction of populations were not considered.

Here, we assume that the population is subjected to a fluctuating environment so that the mortality function and the fertility function are time varying, and that a limited food supply only affects the mortality representation. Furthermore, we assume that the mortality function is separable in the variables a, t and P. These assumptions, together with some others, are collected as follows.

$$D = c(t) + \mu(a) + f\left(P(t)\right) \tag{4.1.4}$$

where

$c(t)$ represents an exogenous factor that increases the death rate of the population (Hallam & Ma, 1986) and satisfies

$$0 \leq c(t) \leq \bar{c} < \infty; \tag{4.1.5}$$

$\mu(a)$ represents the age dependent factor, such that

$$0 < \mu(a) \leq \bar{\mu} < \infty; \tag{4.1.6}$$

$f(P)$ is the density function which satisfies $f(0) = 0$, and

$$f(P) \leq \bar{f} < \infty, \quad 0 < f'(P) \leq k, \quad \forall P \geq 0.$$

The fertility function is assumed to be of the separable form

$$n = b(t)\beta(a),$$

where $0 < b_* \leq b(t) \leq b^*$, and $\beta(a) \geq 0$ has compact support on $[0, \infty)$ because no individuals would survive beyond some maximum age; that is, $\exists A > 0$, such that $\beta(a) = 0$, $\forall a \geq A$. Denote $\sup_{0 \leq a \leq A} \beta(a)$ by $\bar{\beta}$.

To have solutions which are continuous, we also assume that

$$\phi(0) = b(0) \int_0^\infty \beta(a)\phi(a)da \tag{4.1.7}$$

§ 4.2 Existence and Uniqueness of Solutions.

In this section, we will use the method in Gurtin and MacCamy (1974) to show existence and uniqueness.

By employing the characteristics curves, it is easy to get the solution representation

$$\rho(a,t) = \begin{cases} \phi(a-t)e^{-\int_0^t (c(\tau)+\mu(a-t+\tau)+f(P(\tau)))d\tau} & a \geq t, \\ B(t-a)e^{-\int_0^a (c(t-a+\tau)+\mu(\tau)+f(P(t-a+\tau)))d\tau} & a < t, \end{cases} \tag{4.2.1}$$

where

$$B(t) = \rho(0,t) \tag{4.2.2}$$

is the birth rate. Substituting (4.2.1) into (4.1.2) and changing several variables of integration yields

$$\begin{aligned} B(t) = &\int_0^t b(t)\beta(t-a)e^{-\int_0^{t-a}(c(a+\tau)+\mu(\tau)+f(P(a+\tau)))d\tau} B(a)da \\ &+ \int_0^\infty b(t)\beta(a+t)\phi(a)e^{-\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau)))d\tau} da, \end{aligned} \tag{4.2.3}$$

and

$$\begin{aligned} P(t) = &\int_0^t B(a)e^{-\int_0^{t-a}(c(a+\tau)+\mu(\tau)+f(P(a+\tau)))d\tau} da \\ &+ \int_0^\infty \phi(a)e^{-\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau)))a\tau} da. \end{aligned} \tag{4.2.4}$$

Let

$$K(a,t,P) = e^{-\int_0^{t-a}(c(a+\tau)+\mu(\tau)+f(P(a+\tau)))d\tau}, \tag{4.2.5}$$

$$M(a,t,P) = e^{-\int_0^{t}(c(\tau)+\mu(a+\tau)+f(P(\tau)))d\tau}. \tag{4.2.6}$$

Then

$$\begin{aligned} B(t) &= \int_0^t b(t)\beta(t-a)K(a,t,P)B(a)da + \int_0^\infty b(t)\beta(a+t)\phi(a)M(a,t,P)da, \\ P(t) &= \int_0^t K(a,t,P)B(a)da + \int_0^\infty \phi(a)M(a,t,P)da. \end{aligned} \tag{4.2.7}$$

The process described above shows that if ρ is a solution of (4.1.1) – (4.1.3), then B and P satisfy the coupled integral equations (4.2.7). Conversely, if B and P are nonnegative continuous solutions of (4.2.7), then by (4.2.1), ρ is the solution of (4.1.1) – (4.1.3). Hence, we note the equivalence between the partial differential equation (4.1.1) – (4.1.3) and the integral equations (4.2.7) in the sense that existence and uniqueness of (4.1.1) – (4.1.3) can be obtained in terms of those of (4.2.7).

THEOREM 4.2.1. *Let ρ be a solution of* (4.1.1) – (4.1.3) *on* $[0,T]$. *Then the total population P and the birth rate B satisfy the integral equations* (4.2.7). *Conversely, if P and B are nonnegative continuous solutions of* (4.2.7), *then the function defined by* (4.2.1) *on* $\Re^+ \times [0,T]$ *is a solution of* (4.1.1) – (4.1.3).

For fixed $P \in C^+[0,T]$, equation $(4.2.7)_1$ is a linear Volterra integral equation for B. Hence, it has a unique solution on $[0,T]$, which is denoted by

$$B(t) = \mathcal{B}_T(P)(t). \tag{4.2.8}$$

Using this solution, we define an operator $\mathcal{P}_T$ on $C^+[0,T]$ by

$$\mathcal{P}_T(P)(t) = \int_0^T K(a,t,P)\mathcal{B}_T(P)(a)da + \int_0^\infty \phi(a)M(a,t,P)da. \tag{4.2.9}$$

Obviously,

$$\mathcal{B}_T, \quad \mathcal{P}_T \ : \ C^+[0,T] \to C^+[0,T].$$

Then, to prove existence and uniqueness of solutions of (4.1.1)–(4.1.3) on $\Re^+ \times [0,T]$, it is sufficient to show the existence and uniqueness of a fixed point of the operator $\mathcal{P}_T$.

LEMMA 4.2.2. *There exists a $T > 0$ such that the operator $\mathcal{P}_T : C^+[0,T] \to C^+[0,T]$ defined by (4.2.9) has a unique fixed point.*

PROOF: Let $\Phi = \int_0^\infty \phi(a)da$ and

$$R_T = \left\{ g \mid g \in C^+[0,T], \ \ ||g - \Phi||_T \le d \right\},$$

where $||\cdot||_T$ is a supremum norm in $C^+[0,T]$ and $d > 0$ is a constant.

First, we show that $\mathcal{P}_T(P)$ maps R_T into itself.

From the assumptions,

$$\begin{aligned}\mathcal{B}_T(P)(t) = &\int_0^t b(t)\beta(t-a)K(a,t,P)\mathcal{B}_T(P)(a)da \\ &+ \int_0^\infty b(t)\beta(a+t)\phi(a)M(a,t,P)da \\ \le &b^*\bar{\beta}\int_0^t \mathcal{B}_T(P)(a)da + b^*\bar{\beta}\Phi.\end{aligned}$$

By Gronwall's inequality,

$$\mathcal{B}_T(P)(t) \le b^*\bar{\beta}\Phi e^{b^*\bar{\beta}t}. \tag{4.2.10}$$

Hence,

$$|\mathcal{P}_T(P)(t) - \Phi| \leq b^*\bar{\beta}\Phi \int_0^t e^{b^*\bar{\beta}a} da + \int_0^\infty \phi(a)\,|M(a,t,P) - 1|\,da$$
$$\leq \Phi\left(e^{b^*\bar{\beta}T} - 1\right) + \Phi(\bar{c} + \bar{\mu} + \bar{f})Te^{(\bar{c}+\bar{\mu}+\bar{f})T},$$

since

$$|M(a,t,P) - 1| = \left|e^{-\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau)))d\tau} - 1\right|$$
$$\leq \left|\int_0^t \left(c(\tau) + \mu(a+\tau) + f\left(P(\tau)\right)\right) d\tau\right| e^{\int_0^t |c(\tau)+\mu(a+\tau)+f(P(\tau))|d\tau}$$
$$\leq (\bar{c} + \bar{\mu} + \bar{f})Te^{(\bar{c}+\bar{\mu}+\bar{f})T},$$

for $0 \leq t \leq T$. It follows that $\mathcal{P}_T(P) \in R_T$ for T small.

As the next step, if we can show that $\mathcal{P}_T(P)$ is attractive, then by the contraction mapping principle, $\mathcal{P}_T(P)$ has a unique fixed point.

$$\|\mathcal{P}_T(P) - \mathcal{P}_T(Q)\| \leq \int_0^t |K(a,t,P) - K(a,t,Q)|\,\mathcal{B}_T(P)(a)da$$
$$+ \int_0^t K(a,t,Q)\,|\mathcal{B}_T(P)(a) - \mathcal{B}_T(Q)(a)|\,da$$
$$+ \int_0^t |M(a,t,P) - M(a,t,Q)|\,\phi(a)da. \tag{4.2.11}$$

We, then, estimate the three parts on the right of (4.2.11).

$$|K(a,t,P) - K(a,t,Q)| = e^{-\int_0^{t-a}(c(a+\tau)+\mu(\tau))d\tau}$$
$$\cdot \left|e^{-\int_0^{t-a} f(P(a+\tau))d\tau} - e^{-\int_0^{t-a}(f(Q(a+\tau))d\tau}\right|$$
$$\leq \left|1 - e^{\int_0^{t-a}(f(P(a+\tau))-f(Q(a+\tau)))d\tau}\right|$$
$$\leq kTe^{2\bar{f}T}\|P - Q\|_T, \tag{4.2.12}$$

where $k = \sup f'(P)$. Similarly,

$$|M(a,t,P) - M(a,t,Q)| \leq kTe^{2\bar{f}T}\|P - Q\|_T. \tag{4.2.13}$$

Let $\eta(t) = \mathcal{B}_T(P)(t) - \mathcal{B}_T(Q)(t)$.

$$\begin{aligned}\eta(t) = &\int_0^t b(t)\beta(t-a)K(a,t,P)\eta(a)da \\ &+ \int_0^t b(t)\beta(t-a)\left(K(a,t,P) - K(a,t,Q)\right)\mathcal{B}_T(Q)(a)da \\ &+ \int_0^\infty b(t)\beta(a+t)\phi(a)\left(M(a,t,P) - M(a,t,Q)\right)da,\end{aligned}$$

Via (4.2.10) and (4.2.12),

$$\left|\int_0^t b(t)\beta(t-a)\left(K(a,t,P) - K(a,t,Q)\right)\mathcal{B}_T(Q)(a)da\right| \leq C_1\|P - Q\|_T,$$

$$\left|\int_0^\infty b(t)\beta(a+t)\phi(a)\left(M(a,t,P) - M(a,t,Q)\right)da\right| \leq C_2\|P - Q\|_T.$$

Thus,

$$|\eta(t)| \leq \tilde{C}\|P - Q\|_T + b^*\bar{\beta}\int_0^t \eta(a)da,$$

and by Gronwall's inequality again,

$$\|\eta(t)\| \leq \tilde{C}e^{b^*\bar{\beta}T}\|P - Q\|_T. \tag{4.2.14}$$

Substituting (4.2.12) – (4.2.14) into (4.2.11),

$$||\mathcal{P}_T(P) - \mathcal{P}_T(Q)|| \leq \bar{k}||P - Q||_T, \tag{4.2.15}$$

where $\bar{k} < 1$ for T small. This completes the proof.

Lemma 4.2.2 gives local existence and uniqueness. We can also easily get global existence and uniqueness. In fact, from the proof of Lemma 4.2.2, the time T is a

continuous function of Φ, which is the initial population size at time 0. On the other hand, from (4.1.7), $\rho(a,t)$ is continuous as long as it exists and so is $P(t)$. Hence, $P(t)$ is bounded on $[0,T]$. Using $P(T)$ as an initial size at time T and following the same procedure in Lemma 4.2.2, we can get another time interval $[T,T_1]$ on which the solution exists and is unique and continuous. Continuing in this process, we get existence and uniqueness on $[T,T_\infty)$. Now we claim $T_\infty = \infty$. From $(4.2.7)_1$,

$$B(t) \leq b^*\bar{\beta}\int_0^t B(a)da + b^*\bar{\beta}\Phi.$$

By virtue of Gronwall's inequality,

$$B(t) \leq b^*\bar{\beta}\Phi e^{b^*\bar{\beta}t}. \tag{4.2.16}$$

Substituting (4.2.16) into equation $(4.2.7)_2$,

$$\begin{aligned} P(t) &\leq b^*\bar{\beta}\Phi\int_0^t e^{b^*\bar{\beta}\tau}d\tau + \Phi \\ &= e^{b^*\bar{\beta}t}. \end{aligned} \tag{4.2.17}$$

If $T_\infty < \infty$, then $\rho(a,t)$ has to be unbounded as $t \to T_\infty$. By viewing (4.2.17), clearly, it is impossible. Therefore, $T_\infty = \infty$. This gives global existence and uniqueness. Hence we have

THEOREM 4.2.3. *Under the hypotheses (4.1.5)–(4.1.7), the system (4.1.1)–(4.1.3) has a unique solution defined on* $[0,\infty)$.

§ 4.3 Asymptotic Behaviors of Population Solutions.

In this section, we investigate persistence and extinction of populations modelled by the system (4.1.1) – (4.1.3). Persistence and extinction of populations relates to

the positivity of the total population size $P(t) = \int_0^\infty \rho(a,t)da$. There does not exist any finite time t such that $P(t) = 0$ because this leads to $\rho(a,t) \equiv 0$, which is not a solution of the system (4.1.1) – (4.1.3). On the other hand, no individuals will survive beyond some maximum age. Hence, $\lim_{t\to\infty} P(t) = 0$ if only if $\lim_{t\to\infty} \rho(a,t) = 0$, for all a. This motivates the following definition of persistence.

DEFINITION 4.3.1.

(1) *A population, represented by a solution* $\rho(a,t)$ *of* (4.1.1)–(4.1.3), *is persistent if* $\liminf_{t\to\infty} \rho(a,t) > 0$;

(2) *A population goes to extinction if* $\lim_{t\to\infty} \rho(a,t) = 0$.

We have shown the global existence and uniqueness of the system (4.1.1)–(4.1.3). Thus, the following change of variables is well defined:

$$m(a,t) = e^{\int_0^t (c(\tau)+f(P(\tau)))d\tau} \rho(a,t). \tag{4.3.1}$$

Now, we make this change of variables to simplify the system.

$$\frac{\partial m(a,t)}{\partial a} = e^{\int_0^t (c(\tau)+f(P(\tau)))d\tau} \frac{\partial \rho(a,t)}{\partial a}, \tag{4.3.2}$$

$$\begin{aligned}\frac{\partial m(a,t)}{\partial t} &= (c(t) + f(P(t)))\, e^{\int_0^t (c(\tau)+f(P(\tau)))d\tau} \rho(a,t) \\ &\quad + e^{\int_0^t (c(\tau)+f(P(\tau)))d\tau} \frac{\partial \rho(a,t)}{\partial t}.\end{aligned} \tag{4.3.3}$$

Hence,

$$\begin{aligned}\frac{\partial m(a,t)}{\partial a} + \frac{\partial m(a,t)}{\partial t} &= -\mu(a) e^{\int_0^t (c(\tau)+f(P(\tau)))d\tau} \rho(a,t) \\ &= -\mu(a) m(a,t).\end{aligned}$$

The renewal equation becomes

$$m(0,t) = e^{\int_0^t (c(\tau)+f(P(\tau)))d\tau}\rho(0,t) = \int_0^\infty b(t)\beta(a)m(a,t)da.$$

Obviously,

$$m(a,0) = \rho(a,0).$$

Collecting these changes, we arrive a new system

$$\begin{aligned} &\frac{\partial m(a,t)}{\partial a} + \frac{\partial m(a,t)}{\partial t} = -\mu(a)m(a,t), \\ &m(0,t) = \int_0^t b(t)\beta(a)m(a,t)da, \\ &m(a,0) = \phi(a). \end{aligned} \tag{4.3.4}$$

Time variation and density dependence no longer appear in the mortality function. This simplifies the analysis and stable age distribution theory can be applied, as will be seen later.

Although the fertility function still involves time variation it is bounded by the assumption $b_* \leq b(t) \leq b^*$. This provides motivation to consider a comparison technique.

We need the following lemmas.

LEMMA 4.3.2. (Hochstadt, 1973; Pogorzelski, 1966)
Let $f(x) \in L_2[a,b]$ and $N(x,y)$ be continuous for $x, y \in [a,b]$. Then the equation

$$u(x) = f(x) + \lambda \int_a^x N(x,y)u(y)dy$$

has a unique bounded solution, given by

$$u(x) = f(x) + \lambda \int_a^x \Gamma(x,y,\lambda)f(y)dy,$$

where the resolvent kernel

$$\Gamma(x, y, \lambda) = \sum \lambda^n N_{n+1}(x, y),$$

and the iterated kernel

$$N_{n+1}(x, y) = \int_y^x N(x, z) N_n(z, y) dz,$$

where $N_1(x, y) = N(x, y)$.

Using Lemma 4.3.2, the following is a straightforward result.

LEMMA 4.3.3. *Assume*

$$f_i(x) \geq 0, \qquad N_i(x, y) \geq 0, \quad i = 1, 2, \quad \forall x, y \in [a, b].$$

Let $u_i(x)$ *be solutions of*

$$u_i(x) = f_i(x) + \int_a^x N_i(x, y) u_i(y) dy, \quad i = 1, 2,$$

respectively. Then

$$u_1(x) \leq u_2(x)$$

if either $f_1(x) \leq f_2(x)$, *and* $N_1(x, y) \equiv N_2(x, y)$

or $f_1(x) \equiv f_2(x)$, *and* $N_1(x, y) \leq N_2(x, y)$.

To set up appropriate boundary conditions for the population model, the next lemma is usefull.

LEMMA 4.3.4. *Let $\beta(a)$ and $u(a)$ be nonnegative continuous functions satisfying*

$$u(0) = \lambda \int_0^\infty \beta(a)u(a)da$$

where $\lambda > 0$. Then, for any $\theta \geq \lambda$, there exists a continuous function $v(a)$ such that

$$v(0) = \theta \int_0^\infty \beta(a)v(a)da$$

and $v(a) \geq u(a)$, $\forall a \geq 0$.

PROOF: Let

$$v(a) = u(a) + Ce^{\delta a}, \tag{4.3.5}$$

where, $C > 0$ and δ are to be determined. Then,

$$v(0) = u(0) + C = \lambda \int_0^\infty \beta(a)u(a)da + C.$$

To satisfy

$$\begin{aligned} v(0) &= \theta \int_0^\infty \beta(a)v(a)da \\ &= \theta \int_0^\infty \beta(a)u(a)da + C\theta \int_0^\infty \beta(a)e^{\delta a}da, \end{aligned}$$

we need

$$C - (\theta - \lambda) \int_0^\infty \beta(a)u(a)da = C\theta \int_0^\infty \beta(a)e^{\delta a}da. \tag{4.3.6}$$

Denote

$$(\theta - \lambda) \int_0^\infty \beta(a)u(a)da = W.$$

Then

$$C - W = C\theta \int_0^\infty \beta(a)e^{\delta a}da;$$

i.e.

$$C = \frac{W}{1 - \theta \int_0^\infty \beta(a) e^{\delta a} da}. \tag{4.3.7}$$

By choosing a proper δ, C is positive. This gives desirable $v(a)$.

Consider two comparison systems:

$$\begin{aligned} &\frac{\partial m^*(a,t)}{\partial a} + \frac{\partial m^*(a,t)}{\partial t} = -\mu(a) m^*(a,t), \\ &m^*(0,t) = b^* \int_0^\infty \beta(a) m^*(a,t) da, \\ &m^*(a,0) = \phi^*(a), \end{aligned} \tag{4.3.8}$$

where $\phi^*(a)$ is an arbitrary continuous function satisfying $\phi(a) \leq \phi^*(a)$, $\forall a \geq 0$, and

$$\phi^*(0) = b^* \int_0^\infty \beta(a) \phi^*(a) da.$$

$$\begin{aligned} &\frac{\partial m_*(a,t)}{\partial a} + \frac{\partial m_*(a,t)}{\partial t} = -\mu(a) m_*(a,t), \\ &m_*(0,t) = b_* \int_0^\infty \beta(a) m_*(a,t) da, \\ &m_*(a,0) = \phi_*(a), \end{aligned} \tag{4.3.9}$$

where $\phi_*(a)$ is an arbitrary continuous function satisfying $\phi_*(a) \leq \phi(a)$, $\forall a \geq 0$, and

$$\phi_*(0) = b_* \int_0^\infty \beta(a) \phi_*(a) da.$$

By Lemma 4.3.4, $\phi^*(a)$ and $\phi_*(a)$ exist.

THEOREM 4.3.5. *Let* $m(a,t)$, $m^*(a,t)$, *and* $m_*(a,t)$ *be solutions of* (4.3.4), (4.3.8), *and* (4.3.9) *respectively. Then*

$$m_*(a,t) \le m(a,t) \le m^*(a,t) \tag{4.3.10}$$

for all $a \ge 0$, $t \ge 0$.

PROOF: Along characteristics,

$$m_*(a,t) = \begin{cases} B_*(t-a)e^{-\int_0^a \mu(\tau)d\tau} & a \le t, \\ \phi_*(a-t)e^{-\int_0^t \mu(a-t+\tau)d\tau} & a \ge t, \end{cases} \tag{4.3.11}$$

where

$$\begin{aligned} B_*(t) = m_*(0,t) = &\int_0^\infty b_*\phi_*(a)\beta(a+t)\hat{M}(a,t)da \\ &+ \int_0^t b_*\beta(t-a)\hat{K}(a,t)B_*(a)da; \end{aligned} \tag{4.3.12}$$

$$m(a,t) = \begin{cases} B(t-a)e^{-\int_0^a \mu(\tau)d\tau} & a \le t, \\ \phi(a-t)e^{-\int_0^t \mu(a-t+\tau)d\tau} & a \ge t, \end{cases} \tag{4.3.13}$$

where

$$\begin{aligned} B(t) = m(0,t) = &\int_0^\infty b(t)\phi(a)\beta(a+t)\hat{M}(a,t)da \\ &+ \int_0^t b(t)\beta(t-a)\hat{K}(a,t)B(a)da; \end{aligned} \tag{4.3.14}$$

and

$$m^*(a,t) = \begin{cases} B^*(t-a)e^{-\int_0^a \mu(\tau)d\tau} & a \le t, \\ \phi^*(a-t)e^{-\int_0^t \mu(a-t+\tau)d\tau} & a \ge t, \end{cases} \tag{4.3.15}$$

where

$$B^*(t) = m^*(0,t) = \int_0^\infty b^*\phi^*(a)\beta(a+t)\hat{M}(a,t)da + \int_0^t b^*\beta(t-a)\hat{K}(a,t)B^*(a)da. \tag{4.3.16}$$

Here

$$\begin{cases} \hat{K}(a,t) = e^{-\int_0^{t-a}\mu(\tau)d\tau}, \\ \hat{M}(a,t) = e^{-\int_0^t \mu(a+\tau)d\tau}. \end{cases} \tag{4.3.17}$$

By Lemma 4.3.4,

$$B_*(t) \le B(t) \le B^*(t),$$

and from the expressions (4.3.11), (4.3.13), and (4.3.15), the proof is completed.

Now, we focus on the system (4.3.8) and observe the following. By a well known result (Hoppensteadt, 1975) the system (4.3.8) has a separable solution

$$m^*(a,t) = A(a)T(t)$$

if and only if the equation

$$b^* \int_0^\infty \beta(a)e^{-ra}e^{-\int_0^a \mu(s)ds}da = 1 \tag{4.3.18}$$

has a real solution $r = r^*$ in which case the solution has the form

$$m^*(a,t) = C^*e^{r^*(t-a)}e^{-\int_0^a \mu(s)ds},$$

where C^* is a positive constant.

Define

$$R^*(r) = b^* \int_0^\infty \beta(a)e^{-ra}e^{-\int_0^a \mu(s)ds}da.$$

Since $\beta(a)$ has compact support on $[0,\infty)$,

$$\lim_{r\to-\infty} R^*(r) = +\infty,$$
$$\lim_{r\to+\infty} R^*(r) = 0.$$

Notice that

$$R'^*(r) = -b^* \int_0^\infty a\beta(a)e^{-ra}e^{-\int_0^a \mu(s)ds}da < 0.$$

It follows that the equation (4.3.18) has a unique real solution r^*. We can analogously discuss the system (4.3.9). With these lemmas the following main result can be obtained.

THOREM 4.3.6. *The population, described by the system* (4.1.1) – (4.1.3), *is persistent if*

$$\int_0^\infty (r_* - c(\tau))\,d\tau > -\infty, \tag{4.3.19}$$

where r_* is the real solution of

$$\int_0^\infty \beta(a)e^{-ra}e^{-\int_0^a \mu(s)ds}da = \frac{1}{b_*}; \tag{4.3.20}$$

the population goes to extinction if

$$\int_0^\infty (r^* - c(\tau))\,d\tau = -\infty, \tag{4.3.21}$$

where r^* is the real solution of

$$\int_0^\infty \beta(a)e^{-ra}e^{-\int_0^a \mu(s)ds}da = \frac{1}{b^*}. \tag{4.3.22}$$

PROOF: As we discussed above,

$$m^*(a,t) = C^* e^{r^* t} e^{-\left(r^* a + \int_0^a \mu(s)ds\right)} \equiv e^{r^* t} E^*(a),$$

and

$$m_*(a,t) = C_* e^{r_* t} e^{-\left(r_* a + \int_0^a \mu(s)ds\right)} \equiv e^{r_* t} E_*(a).$$

By Theorem 4.3.5,

$$E_*(a)e^{r_* t} \leq m(a,t) \leq E^*(a)e^{r^* t}. \tag{4.3.23}$$

Hence

$$\begin{aligned} &E_*(a)e^{\int_0^t (r_* - c(\tau))d\tau} e^{-\int_0^t f(P(\tau))d\tau} \\ &\quad \leq \rho(a,t) \leq E^*(a)e^{\int_0^t (r^* - c(\tau))d\tau} e^{-\int_0^t f(P(\tau))d\tau}. \end{aligned} \tag{4.3.24}$$

Let the hypothesis (4.3.19) hold and let

$$\int_0^\infty (r_* - c(\tau))\, d\tau \geq -H > -\infty.$$

Then

$$\begin{aligned} \rho(a,t) &\geq E_*(a)e^{\int_0^t (r_* - c(\tau))d\tau} e^{-\int_0^t f(P(\tau))d\tau} \\ &\geq E_*(a)e^{-H} e^{-\int_0^t f(P(\tau))d\tau}. \end{aligned} \tag{4.3.25}$$

Suppose that the population goes to extinction. Then $P(t) \to 0$, as $t \to \infty$ and there exists a positive number δ such that $P(t) \leq \delta < \infty$, $\forall t \geq 0$. Since $f(0) = 0$ and $f(P)$ is increasing and nonnegative,

$$\int_0^t f\left(P(\tau)\right) d\tau \leq \int_0^\delta f(y)dy \equiv \widehat{N}.$$

It follows that

$$\rho(a,t) \geq E_*(a)e^{-(H+\widehat{N})} > 0,$$

uniformly for all $t \geq 0$, a contradiction. This completes the first part of the proof.

Next, it is clear that

$$\begin{aligned}\rho(a,t) &\leq E^*(a)e^{\int_0^t (r^*-c(\tau))d\tau}e^{-\int_0^t f(P(\tau))d\tau} \\ &\leq E^*(a)e^{\int_0^t (r^*-c(\tau))d\tau} \to 0, \qquad \text{as } t \to \infty,\end{aligned}$$

if the hypothesis (4.3.21) is satisfied. This completes the proof.

COROLLARY 4.3.7. *Assume* $\int_0^\infty c(t)dt < \infty$. *Then, the population is persistent if*

$$\int_0^\infty \beta(a)e^{-\int_0^a \mu(s)ds}da \geq \frac{1}{b_*}, \tag{4.3.26}$$

and the population goes to extinction if

$$\int_0^\infty \beta(a)e^{-\int_0^a \mu(s)ds}da < \frac{1}{b^*}. \tag{4.3.27}$$

If $\int_0^\infty c(t)dt = \infty$, *then the population goes to extinction provided*

$$\int_0^\infty \beta(a)e^{-\int_0^a \mu(s)ds}da \leq \frac{1}{b^*}. \tag{4.3.28}$$

PROOF: Suppose $\int_0^\infty c(t)dt < \infty$. From (4.3.26), it follows that $r_* \geq 0$ which leads to (4.3.19). Consequently, the population is persistent. From (4.3.27) it follows $r^* < 0$ and (4.3.21) holds; this leads to the conclusion that the population goes to extinction.

When $\int_0^\infty c(t)dt = \infty$, (4.3.28) implies $r^* \leq 0$ and, consequently, that (4.3.21) holds. This gives extinction for the population.

REMARK 4.3.8: If the mortality is time independent, $c(t) = 0$. Then, (4.3.26) leads to persistence and (4.3.27) gives extinction for the population.

The following is a direct consequence of Theorem 4.3.6.

COROLLARY 4.3.9. *Assume that the fertility is time independent; that is,* $b(t) \equiv b =$ *constant. Then the population goes to extinction if and only if*

$$\int_0^\infty (r - c(\tau))\, d\tau = -\infty,$$

where r *is the real solution of the equation*

$$b \int_0^\infty \beta(a) e^{-ra} e^{-\int_0^a \mu(s)ds} da = 1.$$

§ 4.4 Discussion.

The classical McKendrick or von Foerster equation is used in this chapter to study persistence and extinction of the continuous population model with age structure.

When vital parameters are time independent, which means that a constant environment is assumed, persistence and extinction are simply determined by positivity of the root r of the equation

$$\int_0^\infty e^{-ra} \beta(a) e^{-\int_0^a \mu(s)ds} da = 1$$

or, equivalently, by checking whether the quantity $\int_0^\infty \beta(a) e^{-\int_0^a \mu(s)ds} da$ is less than or greater than one. When time variation in the death rate and birth rate is considered, persistence and extinction are determined by the integral $\int_0^\infty (r^* - c(\tau))\, d\tau$ or the integral $\int_0^\infty (r_* - c(\tau))\, d\tau$. If we regard the root r as an "intrinsic value" or "intrinsic growth rate" of the population, which determines persistence and extinction of the population in a constant enviornment, the integral $\int_0^\infty (r - c(\tau))\, d\tau$ can be regarded as a measure of the capacity of the population to protect itself against stress or perturbation.

As $\beta(a)$ increases or $\mu(a)$ decreases, r_* and r^* are increasing. The integral $\int_0^\infty (r_* - c(\tau))\, d\tau$ might be bounded below and the population might be persistent. As $\beta(a)$ decreases or $\mu(a)$ increases, the integral $\int_0^\infty (r^* - c(\tau))\, d\tau$ might be decreasing and the population might go to extinction.

The main result in this chapter also shows that the density dependence in a continuous population model is not significant when extinction is the main concern because studies of extinction focus on the case where population size is very small.

Density dependence in the birth rate is ignored in this chapter. If we consider

$$\rho(0,t) = \int_0^\infty b(t)\,(\beta(a) - g\,(P(t)))\,\rho(a,t)da,$$

there is no difficulty in proving existence and uniqueness. Using a similar comparison technique, criteria for persistence and extinction might be obtained as well.

CHAPTER 5

CONTINUOUS MODEL WITH SEVERAL AGE CLASSES

Since in any real situation, demographic parameters are age dependent and age structure is important in a population modelling process, the theory of age-dependent population dynamics has been extensively developed. Leslie matrix transition models have been frequently used to model discrete time growth processes while the McKendrick or von Forester equation has been used in continuous population models as a main tool. When a population has several distinct age classes and continuous time is considered, ordinary differential equation models can be used to describe the population dynamics as well. Gazis et. al. (1973), Smith and Mead (1974), and Hastings (1983) have used ordinary differential equation models with age structure in prey-predator systems and Acevedo (1987) discussed the ordinary differential equation models from an ecological perspective.

In this chapter, we consider population models by using ordinary differential equations and focus on conditions for persistence and extinction.

§ 5.1 Model.

Assume a population has $n+1$ age (or stage) classes. Age class 0 represents newborn individuals who do not reproduce. The rest of the age classes are fertile and contribute newborns to age class 0 with birth rate β. The oldest age class is class n so that no transition occurs from age class n. The length of age intervals can be different. As time elapses, individuals in each age class die with the death rate μ and survivors move to an older age class with transition rate m. Summarizing these, a set of ordinary differential equations is used as follows:

$$\begin{cases} \dfrac{dH_0}{dt} = \sum\limits_{j=1}^{n} \beta_j H_j - m_0 H_0 - \mu_0 H_0, \\ \dfrac{dH_1}{dt} = m_0 H_0 - m_1 H_1 - \mu_1 H_1, \\ \quad \vdots \\ \dfrac{dH_{n-1}}{dt} = m_{n-2} H_{n-2} - m_{n-1} H_{n-1} - \mu_{n-1} H_{n-1}, \\ \dfrac{dH_n}{dt} = m_{n-1} H_{n-1} - \mu_n H_n. \end{cases} \tag{5.1.1}$$

Here, H_j represents the number of individuals in the j-th age class, and it is always assumed that $H_j(0) \geq 0$, $\sum\limits_{j=0}^{n} H_j(0) > 0$, and $\mu_j > 0$, $j = 0, 1, \ldots, n$. The birth rates β_j, the transition rates m_j, and the death rates μ_j can be time dependent and density dependent. We discuss these cases in the following sections.

If we write this system in matrix form, then

$$\frac{d\mathbf{H}}{dt} = \begin{pmatrix} -m_0 - \mu_0 & \beta_1 & \beta_2 & \ldots & \beta_{n-1} & \beta_n \\ m_0 & -m_1 - \mu_1 & 0 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & -m_{n-1} - \mu_{n-1} & 0 \\ 0 & 0 & 0 & \ldots & m_{n-1} & -\mu_n \end{pmatrix} \cdot \mathbf{H} \equiv \mathbf{M}\mathbf{H}, \tag{5.1.2}$$

where $\mathbf{H} = (H_0, H_1, \ldots, H_n)^T$.

To make biological sense, population size cannot be negative; that is, H_j must be always nonnegative. For the model (5.1.1), we have the following.

LEMMA 5.1.1. *The set* $\bar{S}$: $\{0 \leq H_j < \infty; j = 0, 1, \ldots, n\}$ *is time invariant. That is, the trajectories of* (5.1.1) *are always nonnegative for all* t *provided* $H_j(0) \geq 0$.

PROOF: First, assume that there is a time $t > 0$, such that $H_k(t) < 0$, for some k,

but $H_j(t) \geq 0$, for all $j \neq k$. Then, since $H_j(0) \geq 0$, there is $T \geq 0$ such that

$$H_k(T) = 0, \qquad \frac{dH_k(T)}{dt} < 0,$$

and $H_j(T) \geq 0$, $j \neq k$.

If $k = 0$,

$$\frac{dH_0(T)}{dt} = \sum_{j=1}^{n} \beta_j(T) H_j(T) \geq 0;$$

if $k > 0$,

$$\begin{aligned} \frac{dH_k(T)}{dt} &= m_{k-1}(T) H_{k-1}(T) - (m_k(T) + \mu_k(T)) H_k(T) \\ &= m_{k-1}(T) H_{k-1}(T) \geq 0. \end{aligned}$$

Either case leads to a contradiction. Hence, $H_j(t) \geq 0$, $\forall t \geq 0$, $j = 0, 1, \ldots, n$.

Next, we assume that there is $t > 0$ such that $H_k(t) < 0$, $H_p(t) < 0$, for some k and p, but $H_j(t) \geq 0$, for all $j \neq k, p$.

Suppose $k = 0$ and $p = 1$. Then $\exists T \geq 0$ such that

$$\begin{aligned} &\text{either} \quad H_0(T) = 0, \quad \frac{dH_0(T)}{dt} < 0, \quad \text{but} \quad H_1(T) \geq 0, \\ &\text{or} \quad H_1(T) = 0, \quad \frac{dH_1(T)}{dt} < 0, \quad \text{but} \quad H_0(T) \geq 0. \end{aligned}$$

It is easy to see that it is impossible in either case. Similarly, we can prove that it leads to a contradiction for $k = 0$, $p > 1$ and $k > 0$, $p > 1$.

Continuing in this manner inductively, it can be shown that the following can not happen:

$$H_{k_1}(t) < 0, \; H_{k_2}(t) < 0, \; H_{k_3}(t) < 0;$$

$$H_{k_1}(t) < 0, \; \ldots, \; H_{k_4}(t) < 0;$$

until

$$H_0(t) < 0, \ \ldots, \ H_n(t) < 0.$$

Hence, the set $\bar{S}$ is time invariant.

Now, we define persistence and extinction of populations.

DEFINITION 5.1.2.

(1) *A population is persistent provided*

$$\limsup_{t\to\infty} \sum_{j=0}^{n} H_j(t) > 0;$$

(2) *A population goes to extinction if it is not persistent; that is*

$$\lim_{t\to\infty} \sum_{j=0}^{n} H_j(t) = 0,$$

which is, clearly, equivalent to $\lim_{t\to\infty} H_j(t) = 0$, *for all* j.

Since $H_j(t) \equiv 0$, $j = 0, 1, \ldots, n$ is a solution of (5.1.1), by Lemma 5.1.1, the population modelled by (5.1.1) goes to extinction if and only if the trivial solution $\mathbf{H} \equiv \mathbf{0}$ is asymptotically stable.

§ 5.2 Autonomous Case.

As a basis for our development, we first consider the autonomous case; that is, we assume that all parameters m_j, μ_j, and β_j are constant. Now, the dynamical behavior of the model (5.1.1) is essentially governed by the matrix M. We investigate properties of the matrix M as follows.

LEMMA 5.2.1. *Define*

$$D_k = \begin{vmatrix} -m_0 - \mu_0 & \beta_1 & \ldots & \beta_k \\ m_0 & -m_1 - \mu_1 & \ldots & 0 \\ \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & \ldots & -m_k - \mu_k \end{vmatrix},$$

$k = 1, 2, \ldots, n$, *where* $m_n = 0$.

Then

$$D_k = (-1)^{k-1} \left\{ \prod_{j=0}^{k} (m_j + \mu_j) - \sum_{l=1}^{k} \beta_l \prod_{j=0}^{l-1} m_j \prod_{i=l+1}^{k} (m_i + \mu_i) \right\}, \qquad (5.2.1)$$

where

$$\prod_{i=l+1}^{k} (m_i + \mu_i) = 1, \qquad \text{if} \quad l \geq k.$$

PROOF: We prove this by induction. When $k = 1$,

$$\begin{aligned} D_1 &= (m_0 + \mu_0)(m_1 + \mu_1) - \beta_1 m_0 \\ &= (-1)^0 \prod_{j=0}^{1} (m_j + \mu_j) - \sum_{l=1}^{1} \beta_l \prod_{j=0}^{l-1} m_j. \end{aligned}$$

(5.2.1) holds. Suppose that (5.2.1) is true for $k = p$. Then

$$\begin{aligned} D_{p+1} &= -(m_{p+1} + \mu_{p+1}) D_p + (-1)^{p+3} \beta_{p+1} \prod_{j=0}^{p} m_j \\ &= -(m_{p+1} + \mu_{p+1})(-1)^{p-1} \\ &\quad \cdot \left\{ \prod_{j=0}^{p} (m_j + \mu_j) - \sum_{l=1}^{p} \beta_l \prod_{j=0}^{l-1} m_j \prod_{i=l+1}^{p} (m_i + \mu_i) \right\} \\ &\quad + (-1)^{p+3} \beta_{p+1} \prod_{j=0}^{p} m_j \prod_{i=p+2}^{p+1} (m_i + \mu_i) \\ &= (-1)^p \left\{ \prod_{j=0}^{p+1} (m_j + \mu_j) - \sum_{l=1}^{p} \beta_l \prod_{j=0}^{l-1} m_j \prod_{i=l+1}^{p+1} (m_i + \mu_i) \right\} \\ &\quad + (-1)^p \beta_{p+1} \prod_{j=0}^{p} m_j \prod_{i=p+2}^{p+1} (m_i + \mu_i) \\ &= (-1)^p \left\{ \prod_{j=0}^{p+1} (m_j + \mu_j) - \sum_{l=1}^{p+1} \beta_l \prod_{j=0}^{l-1} m_j \prod_{i=l+1}^{p+1} (m_i + \mu_i) \right\}. \end{aligned}$$

Thus, (5.2.1) is true for all k.

We will have need of the concept of an M-matrix.

LEMMA 5.2.2 (Plemmons, 1977). *An $n \times n$ matrix $M = (m_{ij})$ is an M-matrix if and only if $m_{ij} \leq 0$ for $i \neq j$ and any one of the following is true:*

(1) *all principle minors of M are positive;*

(2) *all eigenvalues of M have positive real parts;*

(3) *there exists a vector $w > 0$ such that $M^T w > 0$.*

Now, we establish the main result.

THEOREM 5.2.3. *The population modelled by* (5.1.1) *with constant demographic parameters goes to extinction if and only if*

$$\sum_{l=1}^{n} \beta_l \prod_{j=0}^{l-1} m_j \prod_{i=l+1}^{n} (m_i + \mu_i) < \prod_{j=0}^{n} (m_j + \mu_j), \tag{5.2.2}$$

where

$$\prod_{i=l+1}^{k} (m_i + \mu_i) = 1, \qquad \text{if } l \geq k.$$

PROOF: First, we prove that the inequality (5.2.2) is sufficient for extinction of the population. By Lemma 5.2.1, it is clear that (5.2.2) is equivalent to $(-1)^{n+1} D_n > 0$. Now, we claim that

$$(-1)^{n+1} D_n > 0 \text{ implies } (-1)^{k+1} D_k > 0, \quad k = 1, 2, \ldots, n-1.$$

Indeed, since

$$D_k = -(m_k + \mu_k) D_{k-1} + (-1)^{k+2} \beta_k \prod_{j=0}^{k-1} m_j,$$

$$(-1)^{n+1}D_n = (-1)^n \mu_n D_{n-1} - \beta_n \prod_{j=0}^{n-1} m_j.$$

Whenever $(-1)^{n+1}D_n > 0$,

$$(-1)^n D_{n-1} > \frac{\beta_n}{\mu_n} \prod_{j=0}^{n-1} m_j \geq 0.$$

Going to the next step,

$$(-1)^n D_{n-1} = (-1)^{n-1}(m_{n-1} + \mu_{n-1})D_{n-2} - \beta_{n-1} \prod_{j=0}^{n-2} m_j > 0,$$

which implies that

$$(-1)^{n-1} D_{n-2} > 0.$$

Continuing with this process,

$$(-1)^{k+1} D_k > 0, \qquad k = 1, 2, \ldots, n.$$

By Lemma 5.2.2, -**M** is an M-matrix and hence, all eigenvalues of the matrix **M** have negative real parts. It follows that the zero solution of the system is asymptotically stable (Coddington & Levinson, 1955). Hence, the population goes to extinction.

Next, we prove that the inequality (5.2.2) is necessary for extinction of populations by showing that if the inequality (5.2.2) does not hold the population is persistent.

Assume

$$\sum_{l=1}^{n} \beta_l \prod_{j=0}^{l-1} m_j \prod_{i=l+1}^{n} (m_j + \mu_j) > \prod_{j=0}^{n} (m_j + \mu_j) \tag{5.2.3}$$

That is, $(-1)^{n+1}D_n < 0$, or $(-1)^n D_n > 0$. Since $\prod_{j=0}^{n} \lambda_j = D_n$, where λ_j are eigenvalues of **M**, the inequality (5.2.3) implies $(-1)^n \prod_{j=0}^{n} \lambda_j > 0$.

It is easy to see that if n is odd and $\prod_{j=0}^{n} \lambda_j < 0$, at least one λ is positive, and if n is even and $\prod_{j=0}^{n} \lambda_j > 0$ at least one λ is positive. Thus, when $(-1)^n \prod_{j=0}^{n} \lambda_j > 0$, the matrix M has at least one positive eigenvalue. It shows that the population is persistent whenever (5.2.3) holds.

It remains to show that if

$$\sum_{l=1}^{n} \beta_l \prod_{j=0}^{l-1} m_j \prod_{i=l+1}^{n} (m_i + \mu_i) = \prod_{j=0}^{n} (m_j + \mu_j), \tag{5.2.4}$$

the population is persistent.

From (5.2.4), the matrix M has at least one zero eigenvalue. The associated eigenvector is $\mathbf{H}^* = (H_j^*)$,

where

$$H_0^* = \left\{ \frac{1}{m_0 + \mu_0} \sum_{j=1}^{n} \beta_j \prod_{l=j}^{n-1} \left(\frac{m_{l+1} + \mu_{l+1}}{m_l} \right) \right\} c,$$

$$H_j^* = \prod_{k=j}^{n-1} \frac{m_{k+1} + \mu_{k+1}}{m_k} c, \qquad j = 1, 2, \ldots n-1,$$

$$H_n^* = c > 0.$$

The general solutions of the system are

$$H_j(t) = \sum_k \alpha_k^{(j)} e^{\lambda_k t} + H_j^*, \tag{5.2.5}$$

where $\alpha_k^{(j)}$ might be polynomials of t.

Observe that if we let $\mathrm{Re}\lambda_l = \max_k \mathrm{Re}\lambda_k$ and $\mathrm{Re}\lambda_l \geq 0$, α_l must be nonnegative for t large because, otherwise, $H_j(t) < 0$ for t large, a contradiction to Lemma 5.1.1.

It follows that

$$\text{if} \quad \mathrm{Re}\lambda_l < 0, \qquad \sum_k \alpha_k^{(j)} e^{\lambda_k t} \to 0;$$

$$\text{if} \quad \mathrm{Re}\lambda_l > 0, \qquad \sum_k \alpha_k^{(j)} e^{\lambda_k t} \to \infty,$$

Hence $\lim_{t\to\infty} \mathbf{H} = \mathbf{H}^*$, if $\mathrm{Re}\lambda_l < 0$; $\lim_{t\to\infty} \mathbf{H} = \infty$, if $\mathrm{Re}\lambda_l > 0$. When $\mathrm{Re}\lambda_l = 0$, obviously, $\mathbf{H} \geq \mathbf{H}^*$. That is, the population is persistent.

We now examine the necessary and sufficient condition (5.2.2) in the simple cases of two and three age classes.

EXAMPLE 1: n=1.

$$\begin{cases} \dfrac{dH_0}{dt} = \beta_1 H_1 - m_0 H_0 - \mu_0 H_0, \\ \dfrac{dH_1}{dt} = m_0 H_0 - \mu_1 H_1. \end{cases}$$

The population goes to extinction if and only if

$$m_0\beta_1 < (m_0 + \mu_0)\mu_1,$$

or, equivalently,

$$\beta_1 < \left(1 + \frac{\mu_0}{m_0}\right)\mu_1,$$

if $m_0 \neq 0$.

EXAMPLE 2: n=2.

$$\begin{cases} \dfrac{dH_0}{dt} = \beta_1 H_1 + \beta_2 H_2 - m_0 H_0 - \mu_0 H_0, \\ \dfrac{dH_1}{dt} = m_0 H_0 - m_1 H_1 - \mu_1 H_1, \\ \dfrac{dH_2}{dt} = m_1 H_1 - \mu_2 H_2. \end{cases}$$

The population goes to extinction if and only if

$$m_0(\mu_2\beta_1 + m_1\beta_2) < (m_0 + \mu_0)\mu_1\mu_2 + (m_0 + \mu_0)m_1\mu_2,$$

or, equivalently,

$$\mu_2\beta_1 + m_1\beta_2 < \left(1 + \frac{\mu_0}{m_0}\right)\mu_1\mu_2 + \left(1 + \frac{\mu_0}{m_0}\right)m_1\mu_2,$$

if $m_0 \neq 0$.

We now consider the effects of density dependent regulation. We assume that the transition rates are $m_j - \phi_j(P)$; the death rates are $\mu_j + \psi_j(P)$; and the birth rates are $\beta_j - b_j(P)$. Here, $P(t) = \sum_{j=0}^{n} H_j(t)$ is the total population. The population model, now, is

$$\frac{d\mathbf{H(t)}}{dt} = \begin{pmatrix} -m_0 - \mu_0 & \beta_1 & \dots & \beta_{n-1} & \beta_n \\ m_0 & -m_1 - \mu_1 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & -m_{n-1} - \mu_{n-1} & 0 \\ 0 & 0 & \dots & m_{n-1} & -\mu_n \end{pmatrix}$$

$$\cdot \mathbf{H(t)}$$

$$+ \begin{pmatrix} \phi_0(P) - \psi_0(P) & -b_1(P) & \dots & -b_{n-1}(P) & -b_n(P) \\ -\phi_0(P) & \phi_1(P) - \psi_1(P) & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & \phi_{n-1}(P) - \psi_{n-1}(P) & 0 \\ 0 & 0 & \dots & -\phi_{n-1}(P) & -\psi_n(P) \end{pmatrix}$$

$$\cdot \mathbf{H(t)}. \tag{5.2.6}$$

When population size is very small the density effects are negligible from an extinction viewpoint. Hence, we assume the density functions are higher order terms as the total population size becomes very small.

THEOREM 5.2.4. *Assume that*

$$\begin{cases} \phi_j(P) = O(P), \\ \psi_j(P) = O(P), \\ b_j(P) = O(P), \end{cases} \tag{5.2.7}$$

as $P \to 0$. *Then the population goes to extinction if and only if* (5.2.2) *is satisfied.*

PROOF: This is trivial by noticing that the zero solution of the linearized system is asymptotically stable if and only if (5.2.2) holds from Theorem 5.2.3.

§ 5.3 Nonautonomous Case.

In this section, we consider nonautonomous differential equation models; that is we assume the demographic parameters are time varying. First we ignore density dependent effects. The model is assumed to have the following form:

$$\begin{cases} \dfrac{dH_0(t)}{dt} = \sum\limits_{j=1}^{n} \beta_j(t)H_j(t) - m_0(t)H_0(t) + \mu_0(t)H_0(t), \\ \dfrac{dH_1(t)}{dt} = m_0(t)H_0(t) - m_1(t)H_1(t) - \mu_1(t)H_1(t), \\ \quad \vdots \\ \dfrac{dH_{n-1}(t)}{dt} = m_{n-2}(t)H_{n-2}(t) - m_{n-1}(t)H_{n-1}(t) - \mu_{n-1}(t)H_{n-1}(t), \\ \dfrac{dH_n(t)}{dt} = m_{n-1}(t)H_{n-1}(t) - \mu_n(t)H_n(t). \end{cases} \tag{5.3.1}$$

Since all demographic parameters are nonnegative and the set $\bar{S}$ in Lemma 5.1.1 is time invariant, the next result can be applied to the system (5.3.1).

LEMMA 5.3.1. (see Lakshmikantham & Leela, 1969) *Let* $\mathbf{F} : \Re \times \Re^n \to \Re^n$ *be quasimonotone in* $\mathbf{X}$; *i.e. each component* $f_j(t, x_1, \ldots x_n)$ *is nondecreasing in* x_i *for* $i = 1, \ldots j-1, j+1, \ldots n$. *Assume that*

$$\begin{cases} \dfrac{d\mathbf{X}}{dt} = \mathbf{F}(t, \mathbf{X}), \qquad t \geq 0, \\ \mathbf{X}(0) = \mathbf{X}_0 > \mathbf{0}, \end{cases}$$

has a unique continuously differentiable solution for $t \geq 0$. *If*

$$\frac{dy_j(t)}{dt} \leq (\geq)\ f_j(t, \mathbf{Y}), \qquad \forall t \geq 0, \qquad j = 1, 2, \ldots n,$$

and

$$y_j(0) \leq (\geq)\ x_j(0),$$

then

$$y_j(t) \leq (\geq)\ x_j(t), \qquad \forall t \geq 0, \qquad j = 1, 2, \ldots n.$$

From an ecological perspective, all demographic parameters are finite. Hence, we assume that they are bounded:

$$0 \leq \beta_{j*} \leq \beta_j(t) \leq \beta_j^*,$$

$$0 \leq m_{j*} \leq m_j(t) \leq m_j^*,$$

$$0 \leq \mu_{j*} \leq \mu_j(t) \leq \mu_j^*.$$

From these hypotheses, we consider two comparison systems

$$\begin{cases} \dfrac{dH_0}{dt} = \displaystyle\sum_{j=1}^{n} \beta_{j*} H_j - m_0^* H_0 - \mu_0^* H_0, \\ \dfrac{dH_1}{dt} = m_{0*} H_0 - m_1^* H_1 - \mu_1^* H_1, \\ \qquad \vdots \\ \dfrac{dH_{n-1}}{dt} = m_{n-2*} H_{n-2} - m_{n-1}^* H_{n-1} - \mu_{n-1}^* H_{n-1}, \\ \dfrac{dH_n}{dt} = m_{n-1*} H_{n-1} - \mu_n^* H_n; \end{cases} \tag{5.3.2}$$

and

$$\begin{cases} \dfrac{dH_0}{dt} = \sum\limits_{j=1}^{n} \beta_j^* H_j - m_{0*} H_0 - \mu_{0*} H_0, \\ \dfrac{dH_1}{dt} = m_0^* H_0 - m_{1*} H_1 - \mu_{1*} H_1, \\ \qquad \vdots \\ \dfrac{dH_{n-1}}{dt} = m_{n-2}^* H_{n-2} - m_{n-1*} H_{n-1} - \mu_{n-1*} H_{n-1}, \\ \dfrac{dH_n}{dt} = m_{n-1}^* H_{n-1} - \mu_{n*} H_n. \end{cases} \tag{5.3.3}$$

Based on the two comparison systems and from stability of the zero solutions, it is easy to obtain the following results.

THEOREM 5.3.2. *The population modelled by* (5.3.1) *goes to extinction if*

$$\sum_{l=1}^{n} \beta_l^* \prod_{j=0}^{l-1} m_j^* \prod_{i=l+1}^{n} (m_{i*} + \mu_{i*}) < \prod_{j=0}^{n} (m_{j*} + \mu_{j*}). \tag{5.3.4}$$

The population is persistent if

$$\sum_{l=1}^{n} \beta_{l*} \prod_{j=0}^{l-1} m_{j*} \prod_{i=l+1}^{n} (m_i^* + \mu_i^*) \geq \prod_{j=0}^{n} (m_j^* + \mu_j^*). \tag{5.3.5}$$

If density dependence is hypothesized, the population model takes the form

$$\frac{d\mathbf{H(t)}}{dt} =$$

$$\begin{pmatrix} -m_0(t)-\mu_0(t) & \beta_1(t) & \dots & \beta_{n-1}(t) & \beta_n(t) \\ m_0(t) & -m_1(t)-\mu_1(t) & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & -m_{n-1}(t)-\mu_{n-1}(t) & 0 \\ 0 & 0 & \dots & m_{n-1}(t) & -\mu_n(t) \end{pmatrix} \cdot \mathbf{H(t)}$$

$$+ \begin{pmatrix} \phi_0(P)-\psi_0(P) & -b_1(P) & \dots & -b_{n-1}(P) & -b_n(P) \\ -\phi_0(P) & \phi_1(P)-\psi_1(P) & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & \phi_{n-1}(P)-\psi_{n-1}(P) & 0 \\ 0 & 0 & \dots & -\phi_{n-1}(P) & -\psi_n(P) \end{pmatrix} \cdot \mathbf{H(t)}. \tag{5.3.6}$$

Analogous to Theorem 5.2.4, it is a trivial task to prove the next theorem.

THEOREM 5.3.3. *Assume that the hypothesis* (5.2.6) *holds. Then, the population modelled by* (5.3.6) *goes to extinction if the inequality* (5.3.4) *is satisfied and the population is persistent if* (5.3.5) *is satisfied.*

§ 5.4 Discussion.

When an age structure is introduced into a population model, the survival behavior of the population is no longer simply determined by birth rates and death rates only. They are affected by "intraspecies relations" as well; that is, transitions between different age classes also play a role. The simplest example is Example 1 in § 5.2 which models a population with two age classes. Obviously, if $\beta_1 \leq \mu_1$, the population goes to extinction, but persistence of the population is not guaranteed if

$\beta_1 > \mu_1$. To have persistence, the stronger inequality $\beta_1 \geq \left(1 + \frac{\mu_0}{m_0}\right)\mu_1$ is needed. For fixed μ_0, μ_1, and β_1, the larger the transition rate m_0, the more chance of survival the population has. As the number of age classes increases, the survival relation is messy in the sense that it is not easy to obtain a interpretation by analyzing the relation between parameters from (5.2.2). This difficulty of interpretation translates to the dynamics of a population with complex age structure.

There is another interesting phenomenon in the models discussed in this chapter. By viewing the inequality (5.2.2), it can be seen that the ratio $\frac{\mu_0}{m_0}$ is an important factor for all models with different numbers of age classes. For example, a population with two age classes is persistent if

$$\beta_1 \geq \left(1 + \frac{\mu_0}{m_0}\right)\mu_1;$$

a population with three age classes is persistent if

$$\mu_2\beta_1 + m_1\beta_2 \geq \left(1 + \frac{\mu_0}{m_0}\right)\mu_1\mu_2 + \left(1 + \frac{\mu_0}{m_0}\right)m_1\mu_2;$$

a population with four age classes is persistent if

$$\mu_3\beta_1 + \frac{m_1\mu_3}{m_2 + \mu_2}\beta_2 + \frac{m_1m_2}{m_2 + \mu_2}\beta_3 \geq \left(1 + \frac{\mu_0}{m_0}\right)(m_1 + \mu_1)\mu_3.$$

When all parameters are fixed except the ratio $\frac{\mu_0}{m_0}$, the population with a smaller ratio has more chance to survive than that with a larger ratio because the above inequalities are easier to be satisfied when the ratio is smaller. If we define the ratio $\frac{\mu_j}{m_j}$ to be the survival ratio in the j-th age class, the survival ratio in the newborn class is the only one which has such an important effect on extinction; that is, if all parameters are fixed except the survival ratio in the j-th age class where $j > 0$

we cannot conclude that it is easier to satisfy the above inequalities as the survival ratio in j-th age class increases. This means that to some extent the survival ratio in the newborn class has a dominant effect on survival of populations.

The theorems involving density dependence once again show that, from the extinction viewpoint, density dependence is negligible in a continuous population model because when population size becomes small the density effects become small as well and the effect on the rate of change of population size can be ignored.

CHAPTER 6

COMMENTS

§ 6.1 Comparison Between Discrete Models and Continuous Models.

The important question of persistence and extinction of populations has been studied in the previous chapters. Discrete models as well as continuous models are used. From the persistence and extinction viewpoint, the relevant case is where the population size is relatively small. Hence, discrete models are generally more appropriate in studies of population survival. A feature which advocates the use of discrete models is that finite time extinction might occur. In a real situation, when environmental fluctuations are pronounced, there should be a possibility that a population goes to extinction at a finite time. Ecotoxicology provides many examples, such as when the effects of a chemical reach certain levels in a region, all individuals in a population are killed by the chemical and then the population becomes extinct in a finite time.

Another feature of the use of discrete models is that density dependence affects the fate of populations and this might be what we expect. That is, as number of individuals in a population sharply increases, food limitation can become a crucial factor so that there might be a possibility of sudden extinction of the population.

Hallam and Ma (1987) demonstrated finite time extinction in an ordinary differential equation model with nonuniqueness of solutions. However, in general, these features are not present in most continuous population models.

From a mathematical perspective, the difference between discrete models and continuous models is caused by time discreteness or definite time delay. As time

continuously elapses, the change of population size is relatively smooth in a continuous model and there is, in most cases, uniqueness of the zero solution which excludes finite time extinction. On the other hand, density dependence only affects the rate of change of population size in a continuous model. Whenever population size becomes very small the density dependence would be negligible. Contrarily, it is assumed that the change of population size is discontinuous in discrete models. Hence, there might be a big jump of population size between two generations and this might lead to the case where population is large at a generation but then goes to extinction at the next generation. There is no uniqueness of the zero solution in discrete models in the sense that a solution sequence of a discrete model with positive initial value might be less than or equal to zero at a finite time. The population size of a given generation affects the population size of the next generation in addition to the rate of change. These actions let density dependence become an effective regulator.

These comments indicate that it is important to pursue further analytical study in discrete models as difficult as they may be.

Nevertheless, the importance of the use of discrete population models in the study of persistence and extinction of populations does not contradict development of the theory of population survival by using continuous models. To address finite time extinction and the action of density dependence on dynamics of the population, a modification of the traditional definition of extinction at zero population level might be useful.

The Allee principle states that undercrowding can be an important factor limiting population growth. Limitations at low population densities might occur if the

population is so widely dispersed that reproductive contacts are restricted and infrequent (Hallam, 1986). This motivates introduction of the concept of β-extinction, that is, extinction at a nonzero threshold level β (Hallam & Ma, 1987). It might be difficult to study β-extinction of populations when age structure is employed in a continuous population model; however, undoubtedly, this is a very interesting and promising area.

§ 6.2 Connection Between Individual Dynamics and Population Dynamics.

When persistence and extinction of one population are investigated, environmental effects, such as food limitation, temperature and toxicants, are major factors, on the fate of a population. These factors actually affect individual physiology directly and, then, the effects are transfered from individuals to the population (Hallam et al., 1987). From this viewpoint, it would be more appropriate to combine the dynamics of individuals and the dynamics of a population. A way to handle this is to formulate a population model with physiological structure (Auslander et al. 1974; Metz & Diekmann, 1986; Nisbet & Gurney, 1982; VanSickle, 1977). The following generalized McKendrick-von Foerster model is used in a continuous population growth process.

$$\frac{\partial \rho(\Xi,t)}{\partial t} + \sum_{j=1}^{n} \frac{\partial g_j(\Xi,t)\rho(\Xi,t)}{\partial \xi_j} = -D(\Xi,t)\rho(\Xi,t), \tag{6.2.1}$$

where

$\Xi = (\xi_1\ \xi_2\ \ldots\ \xi_n)$ is a vector of physiological properties (such as body weight, length, lipid component and protein component);

$g_j(\Xi,t) = \dfrac{d\xi_j}{dt}$ is the rate of change of the j-th property.

Now, connection between individual dynamics and population dynamics has been set up because $\frac{d\xi_j}{dt}$ is, indeed, the rate of change of the j-th property of an individual. The environmental effects on individuals can be delineated by an exogenous factor $c(t)$ which leads to

$$\frac{d\Xi}{dt} = \mathbf{G}(\Xi, c(t)). \tag{6.2.2}$$

As the exogenous factor $c(t)$ changes, individual dynamics changes and these effects will be transfered to the population model (6.2.1) by affecting the death rate or the birth rate.

A typical instance can be found in Hallam et al. (1987) for the daphnia model. Affected by levels of a chemical in environment, lipid component and protein component of an individual daphnia are fluctuating. When amounts of these components are below certain levels, the individual dies. If we consider the population dynamics, toxicity changes the lipid and protein distribution in the population, which affects the fate of the population.

Analytical analyses of such models become very difficult now. Besides the difficulty in analysis of the individual model (6.2.2), since the equation (6.2.1) with proper boundary conditions (which are not discussed here), is a boundary problem of a hyperbolic partial differential equation in an $n + 1$ dimensional space, more difficulties are created.

Although numerical analysis of the population model (6.2.1) is still feasible, as the dimension of the space increases, the amount of computing work goes up rapidly. To overcome this difficulty, we make a change of variables which we anticipate to reduce computational work significantly. For simplicity, we use the daphnia model as an example.

The population model of daphnia has the form

$$\rho_a + \rho_t + (\rho L)_{m_l} + (\rho P)_{m_p} = -\mu(a, t, m_l, m_p)\rho, \tag{6.2.3}$$

where the subscripts denote partial derivatives; $\rho = \rho(a, t, m_l, m_p)$ is the population density distribution; m_l represents the lipid component; m_p represents the protein component; and $L = \dfrac{dm_l}{dt}$, $P = \dfrac{dm_p}{dt}$ represent the growth rates of m_l and m_p respectively.

Since m_l and m_p are the physiological components of an individual of age a at time t,

$$m_l = m_l(a, t), \qquad m_p = m_p(a, t).$$

Let

$$n(a, t) = \rho(a, t, m_l(a, t), m_p(a, t))h(a, t), \tag{6.2.4}$$

where $h(a, t)$ satisfies

$$h_a + h_t = \left(L_{m_l}\left(t, m_l(a, t), m_p(a, t)\right) + P_{m_p}\left(t, m_l(a, t), m_p(a, t)\right)\right) h. \tag{6.2.5}$$

Then

$$n_a = (\rho_a + \rho_{m_l} m_{l_a} + \rho_{m_p} m_{p_a})h + \rho h_a,$$

$$n_t = (\rho_t + \rho_{m_l} m_{l_t} + \rho_{m_p} m_{p_t})h + \rho h_t.$$

On the characteristics

$$m_{l_a}(a, t) + m_{l_t}(a, t) = L,$$

$$m_{p_a}(a, t) + m_{p_t}(a, t) = P.$$

By simplifying, we find n satisfies the equation

$$n_a + n_t = -\mu n.$$

Thus, the equation (6.2.3) is changed to coupled equations

$$\begin{aligned} &n_a(a,t) + n_t(a,t) = -\mu(a,t,m_l,m_p)n(a,t), \\ &m_{l_a}(a,t) + m_{l_t}(a,t) = L(a,t,m_l,m_p), \\ &m_{p_a}(a,t) + m_{p_t}(a,t) = P(a,t,m_l,m_p), \\ &h_a(a,t) + h_t(a,t) = (L_{m_l} + P_{m_p})h(a,t). \end{aligned} \tag{6.2.6}$$

All these equations are in only a two-dimensional space. This obviously simplifies the numerical analysis and gives hope for success in analytical analysis. We intend to pursue this problem soon.

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