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Graham Kenneth Winley
University of Wollongong

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GRAHAM KENNETH WINLEY, B.A., MACQUARIE, M.Sc.(O.R), N.S.W.

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This thesis is primarily concerned with age dependent population models and in particular with the integral equation initially described by Lotka, A.J. Relationships are developed between this integral equation and various other formulations such as partial differential equations and difference equations. As an example of such relationships the set of differential difference equations representing a multi stage population is reduced to a single integral equation.

Many models are systems of autonomous differential equations such as the logistic. For these to be valid population models they must represent the mean behaviour of some associated stochastic model. It is shown that if this stochastic model is to be a birth and death system then the transition probabilities for a single individual must be entirely dependent on the mean and not the actual numbers in the population. In the situation where the transition probabilities are functions of the actual numbers the single autonomous equation for the mean becomes a coupled system of differential equations involving second and higher moments. Techniques are developed that enable the solution of these coupled equations.

The original integral equation is now modified to account for a fissioning population in which not all the products of fission continue to fission. The case where the production rate of fissioning cells is constant is extended to include time dependence in the production rate and various forms of time dependence are analysed where the generation time for the fissioning cells has an Erlangian distribution. Consideration is also given to the use of empirical forms of the generation time distribution and numerical difference equation schemes are developed for analysing the total birth rate and mean numbers for such processes.
This model is then extended to describe the growth of a column of cells where fissioning parameters depend on both age and position. Such a model may be used to represent the growth of a root or a maize leaf. It appears that this is the first description of a model where both age and position dependence are described.

It should be noted that part of chapter three is to be published as the article "Stochastic Growth Models with Logistic Mean Population" in the Journal of Theoretical Biology and also most of chapter five is to be published as the article "The Growth of a Column of Age and Position Dependent Cells" in Mathematical Biosciences.
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1. THE INTEGRAL EQUATION OF POPULATION DYNAMICS

1.1 The Historical Development

The complete age dependent analysis of the transient behaviour of a population can be formulated in both discrete and continuous forms. The discrete form has been analysed using matrices (Bernardelli, H. (1941), Lewis, E.G. (1942), Leslie P.H. (1945)) and difference equation (Thompson, W.R. (1931), Dobbernack, W., Tietz, G. (1940)). The continuous form has been analysed using integral equation (Sharpe, F.R., Lotka, A.J. (1911)) and various types of differential equations, which will be discussed in chapter two.

In principle, any property of the population process can be found from any of the formulations with numerical differences between the discrete and continuous type models disappearing as the intervals of time and age become sufficiently small. However, the matrix formulation has been found the simplest for obtaining long term population projections. It is closest to actuarial practice and is most convenient when age specific birth and death rates are given as empirical data rather than in the form of analytical formulae. The difference equation has been shown by Cole, L.C. (1954) to be particularly useful in some biological applications while the partial differential equation formulation (Von Foerster, H.) (1959)) has appeared in a wide range of applications being particularly useful in the study of two-sex population models, including marriage (Fredrickson, A.G. (1971)). The integral equation gives a superior approximation for the intrinsic rate of natural increase and provides a simple basis for perturbation analysis (Keyfitz, N. (1977), page 141).
Our concern is with the analysis of population growth as formulated by the integral equation of Sharpe and Lotka in 1911, often described as the renewal equation. Historically the earliest of the four formulations this paper is considered to mark the beginning of the subject of Population Mathematics. The same type of integral equation had also been studied in connection with the movement of electrons by Hertz, P. (1908) and the form of solution proposed by Hertz was adopted by Sharpe and Lotka in their 1911 paper. Hertz's method of solution is very clearly explained by Rhodes, E.C. (1940). The investigation of an actuarial problem had also led Herbelot, L. (1909) to use a renewal equation, the solution this time being obtained by the method of successive differentiations. This method of solution was adopted by several other researchers including Risser, R. (1912) and Preinreich, G.A.D. (1938). The relative merits of these methods are discussed in papers by Lotka, A.J. (1939(a)), (1940) and Preinreich, G.A.D. (1939). The solution of the renewal equation by Laplace transforms, as presented in a paper by Feller, W. (1941), lays down a rigorous presentation of the theory of the renewal equation and sets straight many of the difficulties and controversies that had arisen due to the heuristic nature of the literature on the subject up to that time. An examination of the references cited by Feller, W. (1941) and Lotka, A.J. (1939(a)), (1939(b)) indicates the large volume of literature on the renewal equation up to 1941. Ninety papers were listed and this list was by no means exhaustive. Since then renewal theory has provided the most powerful mathematical analysis of the age structure of populations which are varying with time. Its importance in the study of a great many biological and physical phenomena is stressed by Hoppensteadt, F. (1975) where he shows that the formulation using a partial differential equation, referred to above as the Von

1.2 Formulation of the Integral Model

We assume that the population consists entirely of females such that a female is capable of giving instantaneous birth to other females, but only single births can occur. Using $x$ to represent an individual's age at time $t$ we note that $x = c + t$. If $x \geq t$ then $c$ represents the individual's age at $t = 0$ while if $x < t$ then $-c$ represents the time at which the individual was born. This obvious relationship between $x$ and $t$ also appears as an integral for the subsidiary equations of (1.1).

Let $M(t) =$ the mean number of individuals in the population at time $t$ ; $B(t) =$ the total birth rate at time $t$ due to all mothers; $\ell(x,t) =$ the survivor function; $\beta(x,t) =$ the age specific birth rate; $f(x,t) =$ the death density so that, $F(x,t) =$ the death function; $\mu(x,t) =$ the age specific mortality and $a(x,t) =$ the age density function.

We see that,

$\mu(x,t)\Delta x + o(\Delta x) = Pr$ (an individual of age $x$ at time $t$ will die in the next time interval $\Delta x$), where $o(y)$ is any function such that $\lim_{y \to 0} \frac{o(y)}{y} = 0$. 
So that,

\[ l(x + \Delta x, t) = \Pr \text{ (an individual born at } t - x - \Delta x \text{ is alive at time } t), \]

\[ = \Pr \text{ (individual born at } t - x - \Delta x \text{ survives to age } x ) \times [1 - \Pr \text{ (an individual of age } x \text{ at time } t - \Delta x \text{ dies in the next time interval } \Delta x)]. \]

Hence,

\[ l(x + \Delta x, t) = l(x, t - \Delta x)[1 - \mu(x, t - \Delta x)\Delta x] + o(\Delta x) \]

and this gives,

\[
\frac{l(x + \Delta x, t) - l(x, t)}{\Delta x} + \frac{l(x, t + (-\Delta x)) - l(x, t)}{(-\Delta x)}
\]

\[ = -l(x, t - \Delta x)\mu(x, t - \Delta x) + \frac{o(\Delta x)}{\Delta x}. \]

Taking limits as \( \Delta x \) approaches zero we have,

\[
\frac{\partial l(x, t)}{\partial x} + \frac{\partial l(x, t)}{\partial t} = -l(x, t)\mu(x, t),
\]

(1.1)

with \( l(0, t) = 1. \)

This partial differential equation does not seem to appear in the literature. It has the solution:

\[ l(x, t) = \exp \left[ - \int_0^x \mu(s, s + t - x)ds \right], \]

(1.2)

and so,

\[ l(x, t) = \frac{f(x, t)}{\mu(x, t)}, \quad 1 - \int_0^x f(s, s + t - x)ds = l(x, t). \]

(1.3)

We note that only one of the \( f(x, t), \mu(x, t), l(x, t) \) is independent. The relationships between these are given by (1.1), (1.2) and (1.3).
Mothers alive at \( t \) of age \( x \) to \( x + \Delta x \) must have been born between \( t - x \) and \( t - x - \Delta x \) and survived a period of at least \( x \). Thus, \( B(t - x)\Delta x \ell(x,t) = M(t)a(x,t)\Delta x \) and summing over all ages,

\[
M(t) = \int_0^\infty B(t - x)\ell(x,t)dx. \tag{1.4}
\]

Now the birth rate at time \( t \) of the mothers we have just been considering is \( B(t - x)\Delta x \ell(x,t) \beta(x,t) \) and consequently,

\[
B(t) = \int_0^\infty B(t - x)\ell(x,t)\beta(x,t)dx. \tag{1.5}
\]

The equations (1.4) and (1.5) require a full history of the remote past. To overcome this difficulty we suppose that we know the number of individuals \( M(0) \) at some origin and that we also know \( a(x,0) \) at this origin. Then the birth rate at time \( t \) due to these original mothers is given by:

\[
M(0) \int_0^\infty a(x,0)\frac{\ell(x + t,t)}{\ell(x,0)} \beta(x + t,t)dx,
\]

and the number of survivors at time \( t \) from this original population is given by,

\[
M(0) \int_0^\infty a(x,0)\frac{\ell(x + t,t)}{\ell(x,0)} dx.
\]

Consequently (1.5) and (1.4) can be written as:

\[
B(t) = B_0(t) + \int_0^t B(t - x)g(x,t)dx,
\]

where,

\[
B_0(t) = M(0) \int_0^\infty a(x,0)\frac{g(x + t,t)}{\ell(x,0)} dx, \tag{1.6}
\]

\[
g(x,t) = \ell(x,t)\beta(x,t),
\]

= the maternity function.
and

\[
M(t) = M_0(t) + \int_0^t B(t - x) \ell(x,t) \, dx
\]

where,

\[
M_0(t) = M(0) \int_0^\infty a(x,0) \frac{\ell(x + t,t)}{\ell(x,0)} \, dx.
\]

Consider, \( M(t)a(x,t)dx \), the number of individuals alive at time \( t \) of age \( x \) to \( x + \Delta x \) then,

\[
M(t)a(x,t) = \begin{cases} 
M(0)a(x - t,0) \frac{\ell(x,t)}{\ell(x - t,0)} , & x \geq t, \\
B(t - x) \ell(x,t) , & 0 \leq x < t.
\end{cases}
\]

If we define, \( D(t) \) = the total death rate of all mothers at time \( t \), then we have,

\[
D(t) = D_0(t) + M(t) \int_0^t a(x,t) \mu(x,t) \, dx,
\]

where,

\[
D_0(t) = M(0) \int_0^\infty a(x,0) \frac{\ell(x + t,t)}{\ell(x,0)} \, dx.
\]

In the development presented above the time parameter is expressed through \( t \), the time now. Consequently the model involving \( \ell(x,t), \mu(x,t), \beta(x,t) \) could be regarded as reflecting the individual's environment to a greater extent than the model developed using a time parameter \( t - x \), the time at which the individual was born. This latter model would emphasise genetic factors to a greater extent than the present environmental model. If we express the time parameter through \( t - x \) we have instead of (1.1), (1.2) and (1.3) the corresponding equations,

\[
\frac{\partial \ell(x,t - x)}{\partial x} + \frac{\partial \ell(x,t - x)}{\partial t} = -\ell(x,t - x) \mu(x,t - x); \ell(0,t) = 1,
\]

giving,

\[
\ell(x,t - x) = \exp \left[ -\int_0^x \mu(s,t - x) \, ds \right],
\]
and so,
\[ \ell(x,t-x) = f(x,t-x)/\mu(x,t-x), \quad 1 - \int_0^x f(s,t-x)ds = \ell(x,t-x). \]

Equations (1.6), (1.7), (1.8) and (1.9) become,

\[
\begin{align*}
B(t) &= B_0(t) + \int_0^t B(t-x)g(x,t-x)dx, \\
M(t) &= M_0(t) + \int_0^t B(t-x)\ell(x,t-x)dx,
\end{align*}
\]

where,

\[
\begin{align*}
B_0(t) &= M(0) \int_0^\infty a(x,0) g(x + t,-x) \frac{\ell(x,-x)}{\ell(x,-x)} dx, \\
g(x,t-x) &= \ell(x,t-x) \beta(x,t-x), \\
M_0(t) &= M(0) \int_0^\infty a(x,0) \frac{\ell(x + t,-x)}{\ell(x,-x)} dx.
\end{align*}
\]

and

\[
\begin{align*}
M(t) &= M_0(t) + \int_0^t B(t-x) \ell(x,t-x)dx, \\
\end{align*}
\]

where,

\[
\begin{align*}
M_0(t) &= M(0) \int_0^\infty a(x,0) \frac{\ell(x + t,-x)}{\ell(x,-x)} dx.
\end{align*}
\]

We also have,

\[
\begin{align*}
M(t)a(x,t) &= \begin{cases} 
M(0)a(x-t,0) \frac{\ell(x,t-x)}{\ell(x-t,t-x)}, & x \geq t, \\
B(t-x)\ell(x,t-x), & 0 \leq x < t.
\end{cases}
\end{align*}
\]

In equations (1.1) through to (1.13) we have formulated both the environmental and genetic models. For example, once the solution for \( B(t) \) is known from (1.6) we can find \( M(t) \) from (1.7) then \( a(x,t) \) and \( D(t) \) follow from (1.8) and (1.9) respectively. The alternative approach of regarding \( B(t) \) as the unknown in (1.7), thus solving for \( B(t) \) to give \( a(x,t) \) and \( D(t) \) from (1.8) and (1.9), has been considered by Lotka, A.J. (1939(b), pp 44-48), (1939(c)) and more recently by Keyfitz, N. (1968, chapter 9).
1.3 The Solution of the Integral Equation

We recognise equation (1.6) as a Volterra linear equation of the second kind with a difference kernel. Following Corduneanu, C. (1977, chapter 6) we have,

Theorem 1.

Let the kernel \( g(t - x, t) = k(x, t) \) and \( B_0(t) \) of (1.6) be continuous (real) functions on \( [0, a] \), \( a > 0 \); and \( \Delta: 0 \leq x \leq t \leq a \), respectively. Then there exists a unique, continuous solution \( B(t) \) of (1.6) defined for \( t \in [0, a] \) and given by,

\[
B(t) = B_0(t) + \int_0^t B_0(x)k(x,t)dx, \tag{1.14}
\]

with \( k(x,t) \), the resolvent kernel of (1.6), continuous on \( \Delta \) given by,

\[
k(x,t) = \sum_{j=1}^\infty k_j(x,t),
\]

where,

\[
k_j(x,t) = \begin{cases} 
\int_x^t k(s,t)k_{j-1}(s,x)ds, & j \geq 2, \\
k(x,t), & j = 1.
\end{cases}
\tag{1.15}
\]

We see that construction of the resolvent kernel allows the integral representation of the solution for any free term \( B_0(t) \). Equation (1.14) holds also for piecewise continuous \( B_0(t) \) or even more general functions. Also, from (1.15) we have,

\[
k(x,t) = k(x,t) + \int_0^t k(s,t)k(x,s)ds,
\]

which is the integral equation satisfied by the resolvent kernel of (1.6).

The usual derivation of the integral (renewal) equation (1.6), as given for example by Lotka, A.J. (1939(a)), assumes that \( f, \ell \) and \( \beta \) depend only on \( x \), the individual's age. Using this
assumption, and writing \( f(x,t) = f(x), \ell(x,t) = \ell(x), \beta(x,t) = \beta(x) \) and \( \mu(x,t) = \mu(x) \), we find that (1.1) becomes an ordinary differential equation with the solution \( \ell(x) = \exp \left[ -\int_0^x \mu(s) \, ds \right] \) and so (1.6) becomes,

\[
B(t) = B_0(t) + \int_0^t B(t-x)g(x) \, dx,
\]

with

\[
g(x) = \ell(x)\beta(x), \text{ called the net maternity function,}
\]

and

\[
B_0(t) = M(0) \int_0^\infty a(x,0)\frac{g(x + t)}{\ell(x)} \, dx.
\]

Similar simplifications occur in equations (1.7) through to (1.13) and of course under these conditions there is no difference between the environmental and genetic models.

The Hertz form of the solution of (1.16), adopted by Sharpe, F.R., Lotka, A.J. (1911), states that,

\[
B(t) = \sum_{i=1}^\infty A_i e^{r_i t},
\]

where the \( r_i \) are the solutions for \( s \) of,

\[
\int_0^\infty e^{-st} g(t) \, dt = 1,
\]

called the characteristic equation. It is easily shown that \( \int_0^\infty e^{-st} g(t) \, dt \) decreases monotonically as \( r \) increases, since, from its nature \( g(t) > 0 \) for all \( t \). Hence, (1.18) can have only one real root, \( r_1 \), and \( r_1 > 0 \) according as \( R_0 = \int_0^\infty g(t) \, dt \), called the net reproduction rate, \( > 1 \). The other roots of the characteristic equation occur in complex conjugate pairs and have real parts less than \( r_1 \).

Lotka, A.J. (1939(a)) finds the \( A_i \) by a method resembling that by which the constants in a Fourier series are determined and,
\[ A_i = \frac{\int_0^\infty e^{-r_i t} B_0(t) \, dt}{\int_0^\infty e^{-r_i x} g(x) \, dx}, \quad i = 1, 2, 3, \ldots \] (1.19)

Herglotz, G. (1908) gives a discussion of the convergence of the series in (1.17).

An alternative argument uses Laplace transforms in (1.16).

So that if \( F^*(s) = \int_0^\infty e^{-st} F(t) \, dt \) is the Laplace transform of \( F(t) \), then recognising the convolution in (1.16) we have,

\[ B^*(s) = B_0^*(s) + B^*(s)g^*(s) \]

\[ B^*(s) = \frac{B_0^*(s)}{1 - g^*(s)} = \sum_{i=1}^{\infty} \frac{A_i}{s - r_i}, \]

where the \( r_i \) are the roots of \( 1 - g^*(s) = 0 \), which is the characteristic equation (1.18). The \( A_i \) are given by,

\[ A_i = \lim_{s \to r_i} \left[ \frac{(s - r_i)B_0^*(s)}{1 - g^*(s)} \right] = \frac{-B_0^*(s)}{\frac{dg^*(s)}{ds}} \bigg|_{s=r_i} \]

which is identical to (1.19). Inversion of \( B^*(s) \) then gives (1.17).

Another way of applying the Laplace transform to the integral equation is by calculating offspring generation by generation. The births due to the original population of \( M(0) \) individuals or of the zero-th generation are \( B_0(t) \), of the first generation

\[ B_1(t) = \int_0^\infty B_0(t - x) g(x) \, dx \]

and of the \( n \)-th generation

\[ B_n(t) = \int_0^\infty B_{n-1}(t - x) g(x) \, dx. \]

Taking transforms of the \( B_n(t) \) we have,

\[ B_0^*(s), \text{ for the zero-th generation}, \]

\[ B_1^*(s) = B_0^*(s)g^*(s), \text{ for the first generation}, \]

\[ B_2^*(s) = B_1^*(s)g^*(s) = B_0^*(s)[g^*(s)]^2, \text{ for the second generation}, \]

\[ \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \]
$B_n(s) = B_0(s)[g(s)]^n$, for the n-th generation.

Now, $B(t) = \sum_{j=0}^{\infty} B_j(t)$ so that,

$$B^*(s) = \sum_{j=0}^{\infty} B_j^*(s) = B_0^*(s) \sum_{j=0}^{\infty} [g^*(s)]^j = \frac{B_0^*(s)}{1 - g^*(s)},$$

which is the same as before.

It was remarked earlier that Feller, W. (1941) laid down a rigorous presentation of the theory for the methods of solution of (1.16) that have just been outlined. The following two theorems stated and proved by Feller, W. (1941) cover the situations of practical concern.

**Theorem 2.**

Suppose $g(t)$ and $B_0(t)$ are measurable, non-negative and bounded in every finite interval $0 \leq t \leq T$. Let the integrals,

$$g^*(s) = \int_0^\infty e^{-st}g(t)dt, \quad B_0^*(s) = \int_0^\infty e^{-st}B_0(t)dt$$

converge for $s > r$. Then there exists a unique non-negative solution $B(t)$ of (1.16) which is bounded in every finite interval. With this function the integral,

$$B^*(s) = \int_0^\infty e^{-st}B(t)dt,$$

converges at least for $s > r_1$, where $r_1 = r$ if $\lim_{s \to r} g^*(s) \leq 1$, and otherwise $r_1 > r$ is defined as the root for $s$ of the characteristic equation $g^*(s) = 1$. For $s > r_1$, we have

$$B^*(s) = \frac{B_0^*(s)}{1 - g^*(s)}.$$ If $g(t)$ is continuous except, perhaps, at a finite number of points then $B(t) - B_0(t)$ is continuous.
Theorem 3.

In order that the solution $B(t)$ of Theorem 2 may be expressed in the form (1.17) where the series converges absolutely for $t \geq 0$ and where $r_i$ denote the roots for $s$ of the characteristic equation $g^*(s) = 1$, it is necessary and sufficient that the Laplace transform $B^*(s)$ admit an expansion,

$$B^*(s) = \frac{B_0^*(s)}{1 - g^*(s)} = \sum_{i=1}^{\infty} \frac{A_i}{s - r_i},$$

and that $\sum_{i=1}^{\infty} |A_i|$ converges absolutely. The coefficients $A_i$ are determined by, $A_i = \lim_{s \to r_i} \left[ \frac{-B_0^*(s)}{dg^*(s)/ds} \right]$. In particular, it is necessary that $B^*(s)$ be a one-valued function.

If the characteristic equation has multiple roots the expression for $B^*(s)$ takes the form,

$$B^*(s) = \sum_{i=1}^{\infty} \left[ \frac{A_i^{(1)}}{s - r_i} + \frac{A_i^{(2)}}{(s - r_i)^2} + \ldots + \frac{A_i^{(n_i)}}{(s - r_i)^{n_i}} \right],$$

where $n_i$ is the multiplicity of the root $r_i$. This gives an expansion,

$$B(t) = \sum_{i=1}^{\infty} \left[ A_i^{(1)} + A_i^{(2)} t + A_i^{(3)} t^2 + \ldots + \frac{A_i^{(n_i) t^{n_i-1}}}{(n_i - 1)!} \right],$$

instead of (1.17).

The behaviour of $B(t)$, for large values of $t$, is shown to be dominated by the first term of the series (1.17). Consequently, for large values of $t$,

$$B(t) = A_1 e^{r_1 t} \quad (1.20)$$

where,

$$A_1 = \frac{B_0^*(r_1)}{\sum_{i=1}^{\infty} \frac{t^i}{r_1}} \int_0^1 xe^{ix} g(x)dx \quad , \text{from (1.19).}$$
Hence, from (1.7), for large values of $t$,

$$M(t) = A_1 \ell^*(r_1) e^{r_1 t}$$  \hfill (1.21)

and from (1.8) we see that,

$$\lim_{t \to \infty} a(x,t) = \frac{\ell(x)e^{-r_1 x}}{\ell^*(r_1)},$$

called the stable age density, is independent of $a(x,0)$. This is the ergodic property which has the demographic interpretation that a population tends to forget its initial age distribution. Lotka, A.J. (1907), Sharpe, F.R., Lotka, A.J. (1911) describe this age density as being both "fixed" and "stable". "Fixed" refers to the result that substitution of (1.20) and (1.21) in (1.8), together with the assumption that the original population, $M(0)$, have all died out, gives $a(x,t)$ independent of $t$. "Stable" refers to the fact that since $a(x,t)$ is independent of $a(x,0)$ then this is the age density to which the population would tend to return if it was given a small displacement. It is usual to describe the process as being in the transient stage when $t$ is not large enough to assume that $B(t)$ and $M(t)$ have the forms given in (1.20), (1.21) respectively. Once $t$ has become large enough to be approximated by (1.20) and (1.21) the process is described as being in the stable stage.

The following theorems provide the theoretical background for the description of the stable population given above. The first two are due to Feller, W. (1941) and the other is due to Lotka, A.J. (1937).

**Theorem 4.**

For $g(t), B_0(t)$ as in Theorem 2 suppose

$$\int_0^\infty g(t)dt = R_0 < \infty, \quad \int_0^\infty B_0(t)dt = b < \infty.$$  

Then,
Theorem 4. describes the asymptotic behaviour of the mean value \( \frac{1}{t} \int_0^t B(s)ds \). The proof, as shown by Feller, requires the simplest Tauberian theorems for Laplace integrals. Theorem 5. deals more explicitly with the asymptotic behaviour of \( B(t) \) under assumptions met in practical situations.

Theorem 5. 

For \( g(t), B_0(t) \) as in Theorem 2. suppose \( R_0 = \int_0^\infty g(t)dt = 1, \int_0^\infty B_0(t)dt = b < \infty \) and there exists an integer \( n \geq 2 \) such that 

\[ R_k = \int_0^\infty s^k g(s)ds, \quad k = 1, 2, 3, \ldots, n, \]

are finite and the functions \( g(t), tg(t), t^2 g(t), \ldots, t^{n-2} g(t) \) are of bounded total variation over \((0, \infty)\). Further suppose that 

\[ \lim_{t \to \infty} \left[ t^{n-2} B_0(t) \right] = 0 \quad \text{and} \quad \lim_{t \to \infty} \left[ t^{n-2} \int_0^t B_0(s)ds \right] = 0. \]

Then, 

\[ \lim_{t \to \infty} t^{n-2} \left[ \frac{B(t) - \frac{b}{R_1}}{R_1} \right] = 0 \quad \text{for} \quad n \geq 2. \]

If \( R_0 > 1 \) and we suppose that \( e^{-r_1 t} g(t) \) is of bounded total variation and 

\[ \lim_{t \to \infty} e^{-r_1 t} B_0(t) = 0 \]

then for large values of \( t \) \( B(t) = \frac{b}{Z} e^{r_1 t} \), where, \( r_1 \), is the positive root of \( g^*(s) = 1 \), \( b = B_0^*(r_1) \) and 

\[ Z = \int_0^\infty s e^{-r_1 s} g(s)ds. \]
If \( R_0 < 1 \) \( B(t) \) will in general not show an exponential character. However, if \( g(t) \) is of bounded variation and has a finite moment of second order and \( \lim_{t \to \infty} g(t) = 0 \) then \( \lim_{t \to \infty} B(t) = 0 \).

In the stable population \( \bar{Z} = \int_0^\infty xe^{-r_1 x} g(x)dx \) is the average age of childbearing. If \( r_1 = 0 \) the population is said to be stationary and so for the stationary population \( \bar{Z} = \int_0^\infty xg(x)dx = R_1 \). The zero-th moment about zero of the maternity function is \( R_0 = \int_0^\infty g(x)dx \) and is the average number of offspring a newborn mother will produce in her lifetime. The length of generation \( T \) is defined as the interval of time over which births increase in the ratio \( R_0 \). Hence, \( T \) satisfies \( R_0 = \frac{B(t)}{B(t - T)} \) and if \( B(t) = A_1 e^{r_1 t} \) then \( T = \frac{\ln R_0}{r_1} \). Lotka, A.J. (1939(b)) shows that \( T \) is approximately the arithmetic mean of \( \bar{Z} \) for the stable population and \( \bar{Z} \) for the stationary population. We also see the doubling time \( t_d \) is given by \( t_d = \frac{\ln 2}{r_1} \). The variance of age at childbearing in the stable population is \( \frac{R_2}{R_0^2} - \left( \frac{R_1}{R_0} \right)^2 \) and these moments, \( R_0, R_1, R_2 \), of the maternity function play an important role in efforts to fit curves to the maternity function. Keyfitz, N. (1967) describes Lotka's graduation of \( g(x) \) by a normal density function (Lotka, A.J. (1939(b)), Wicksell's graduation by a Pearson Type III density (Wicksell, S.D. (1931)) and Hadwiger's graduation by consideration of the probability of a newborn mother having a daughter, a granddaughter, a great-granddaughter, and so on, by age \( x \) (Hadwiger, H. (1940)).

**Theorem 6.**

A closed population which is increasing at a constant rate \( r_1 \) per head, under the regime of a constant age schedule of mortality and fertility, can have no other than the stable age distribution. That is, it can not be merely approaching that distribution. The stable
age distribution must be actually established.

Here Lotka is describing conditions under which the solutions to the equations describing the process will be the same in both the transient and stable stages.

We now define $\bar{Z}_i = \int_0^\infty xe^{-r_i x} g(x)dx$, $a_i(x) = \frac{\ell(x)e^{-r_i x}}{\ell^*(r_i)}$ and $v_i(x) = \frac{1}{\ell(x)} \int_0^\infty e^{-r_i t} g(x + t)dt$. $\bar{Z}_i$ and $a_i(x)$ can be seen as being generalised from $\bar{Z}$, the mean age at childbearing in the stable population, and $a(x)$ the stable age density, respectively. $v_i(x)$ will be seen later to be generalised from Fisher's reproductive value of a woman.

Suppose we have an initial population of $M(0)$ individuals with age density $a(x,0)$ we see from (1.19) that,

$$A_i = \left( \int_0^\infty e^{-r_i t} \int_0^\infty M(0)a(x,0)\frac{g(x + t)}{\ell(x)} dx dt \right) \bar{Z}_i$$

$$= M(0) \int_0^\infty a(x,0)\frac{v_i(x)}{\bar{Z}_i} dx$$

(1.22)

Consequently, $\frac{v_i(y)}{\bar{Z}_i}$ can be interpreted as the contribution to $A_i$, in (1.17), due to an individual of age $y$ at the time $t = 0$.

If the initial population consisted of just one individual of age $y$ then $A_i$ for this population would be given by, $A_i = \frac{v_i(y)}{\bar{Z}_i}$ and if this individual happened to be newborn then $A_i = \frac{1}{\bar{Z}_i}$.

Considering the stable population developing from a single individual of age $y$ at $t = 0$ we have,

$$A_i = \frac{v_i(y)}{\bar{Z}_i}$$

(1.23)
where,
\[ \bar{Z}_1 = \bar{Z}, \] the mean age at childbearing in the stable population, and from (1.19) \[ v_1(y) = B_0^*(r_1), \] called the reproductive value of a woman of age \( y \).

Fisher, R.A. (1930) introduced the idea of reproductive value and describes it as a measure of the discounted future births to a female aged \( y \), the discount rate corresponding to the intrinsic rate of increase per annum of the population. The total reproductive value, \( V \), of a population of \( M(0) \) individuals with age density \( a(x,0) \) is given by,

\[
V = \int_0^\infty M(0)a(x,0)v_1(x)dx.
\]

Hence, from (1.23)

\[
V = A_1 \bar{Z}_1 = B_0^*(r_1).
\]

These remarks suggest the following experiment. We note that if the initial population consisted of exactly one newborn individual then from (1.23),

\[
A_1 = \frac{1}{\bar{Z}_1}. \tag{1.24}
\]

Suppose that we start our population with just one newborn and after a time long enough for us to consider the population stable we could solve for \( A_1 \) in (1.24) and hence obtain \( \bar{Z}_1 \). We now repeat this experiment by considering populations developing from single individuals of various ages \( y \). Hence with measures of \( A_1 \), corresponding to a range of values of \( y \) we could obtain a plot of \( v_1(y) \) from (1.23). This then enables us to estimate \( A_1 \), from (1.22), for a population which initially had \( M(0) \) individuals.
with any arbitrary age density \( a(x,0) \).

It is possible to obtain an expansion for \( M(0)a(x,0) \) in terms of \( a_1(x) \). If we write,

\[
M(0)a(x,0) = \sum_{i=1}^{\infty} Q_i a_i(x),
\]

where the \( Q_i \) are to be determined, and use the result that,

\[
\int_0^\infty v_i(x) a_j(x) \, dx = \begin{cases} 0, & i \neq j, \\
\frac{z_i}{\ell^*(r_i)}, & i = j,
\end{cases}
\]

then we have,

\[
\int_0^\infty v_i(x) a(x,0) M(0) \, dx = \int_0^\infty Q_i v_i(x) a_i(x) \, dx,
\]

\[
= Q_i \frac{z_i}{\ell^*(r_i)}.
\]

Hence,

\[
Q_i = \ell^*(r_i) \int_0^\infty \frac{M(0)a(x,0)v_i(x)}{z_i} \, dx,
\]

\[
= \ell^*(r_i) A_i, \quad \text{from (1.22)}.
\]

Now considering this same population at time \( t \) we have from (1.12),

\[
M(t)a(x,t) = \begin{cases} M(0)a(x-t,0) \frac{\ell(x)}{\ell(x-t)}, & x \geq t, \\
B(t-x) \ell(x), & 0 \leq x < t,
\end{cases}
\]

(1.26)

and using the expansion we have just obtained for \( M(0)a(x,0) \) together with the expansion (1.17) for \( B(t) \) we can find a series expansion for \( M(t)a(x,t) \) from (1.26),

\[
M(t)a(x,t) = \sum_{i=1}^{\infty} Q_i a_i(x) e^{r_i t}.
\]
In addition to providing the above insights the definitions for \( z_i \), \( a_i \) and \( v_i \) enable us to relate the integral formulation to the discrete, matrix formulation of Leslie, P.H. (1945). This is done under the heading of "Spectral Decomposition" by Keyfitz, N. (1968, page 107).

1.4 An Example

Many of the preceding remarks can be illustrated by considering a population where,

\[ M(0)a(x,0) = \delta(x)M(0), \]

which means the population at time \( t = 0 \) consists entirely of \( M(0) \) newborn individuals. \( \delta(x) \) is the Dirac delta function,

\[ \beta(x) = \beta, \text{ constant}. \]

We see from (1.4) and (1.5) that

\[ B(t) = \beta M(t) \]

and so the crude birth rate, \( \frac{B(t)}{M(t)} \), is \( \beta \)

\[ f(x) = \frac{(\lambda k)^k}{(k-1)!} \frac{e^{-\lambda k x}}{x^k}, \]

Also, \( 0 \leq x < \infty, \lambda > 0 \) and \( k \) is a positive integer. This Erlangian or Pearson type III density is a biologically plausible choice for \( f(x) \), as shown by Kendall, D.G. (1948) and others. Thus, from (1.3),

\[ \ell(x) = \sum_{j=0}^{k-1} \frac{(\lambda k)^j}{j!} e^{-\lambda k x}. \]

By taking Laplace transforms we have,

\[ \ell^*(s) = \frac{1}{s} \left[ 1 - f^*(s) \right], \quad (1.27) \]

\[ f^*(s) = \left( \frac{\lambda k}{s + \lambda k} \right)^k, \quad (1.28) \]

and from (1.16),

\[ B^*(s) = \frac{BM(0)\ell^*(s)}{1 - \beta \ell^*(s)}, \quad (1.29) \]
On substituting (1.27) and (1.28) in (1.29) we have,

$$B^*(s) = \frac{P(s)}{Q(s)}$$  \hspace{1cm} (1.30)

where,

- $P(s)$ is a monic polynomial of degree $k - 1$,
- $Q(s)$ is a monic polynomial of degree $k$.

In general we can factorise $Q(s)$ over the complex field giving

$$Q(s) = (s - s_1)(s - s_2) \ldots (s - s_k).$$

If $s_i \neq s_j$ for $i \neq j$ we can obtain a partial fraction expansion for $B^*(s)$ of the form,

$$B^*(s) = \frac{k}{\ell} \sum_{i=1}^{\ell} \frac{A_i}{(s - s_i)} ,$$

where,

$$A_i = \lim_{s \to s_i} \left[ (s - s_i)B^*(s) \right] .$$

$B(t)$ can then be found by inverting term by term to give,

$$B(t) = \sum_{i=1}^{k} A_i e^{s_i t} .$$

If any zero of $Q(s)$ is repeated, for example, suppose $s_2$ is a zero of multiplicity $1 \leq m \leq k$, then when obtaining the partial fraction expansion of $B^*(s)$ we will need to consider terms of the type

$$\frac{m}{j=1} \frac{A_j}{(s - s_2)^j} .$$

For the case where $k = 1$ (Malthusian model or simple exponential) we have from (1.30),

$$\frac{B^*(s)}{\beta M(0)} = \frac{1}{s + (\lambda - \beta)} .$$

The solutions for $B(t)$ and $M(t)$ during the transient stage of growth are,
\[ B(t) = BM(0)e^{(\beta - \lambda)t}, \]
\[ M(t) = M(0)e^{(\beta - \lambda)t}, \]

and
\[ M(t)a(x,t) = \begin{cases} M(0)\delta(x-t)e^{-\lambda t}, & x \geq t, \\ BM(0)e^{(\beta - \lambda)t-Bx}, & 0 \leq x < t. \end{cases} \]

The solutions for \( B(t) \) and \( M(t) \) in the stable stage of growth are the same as during the transient stage.

For the case \( k = 2 \) we have,
\[ B^*(s) = \frac{BM(0)(s + 4\lambda)}{s^2 + (4\lambda - \beta)s + 4\lambda(\lambda - \beta)}. \]

So during the transient stage we have,
\[ B(t) = \begin{cases} \frac{4}{3}BM(0) \left[ 1 - \frac{e^{-3\beta t}}{4} \right], & \lambda = \beta, \\ \frac{BM(0)}{(r_1 - r_2)} \left[ (r_1 + 4\lambda)e^{r_1 t} - (r_2 + 4\lambda)e^{r_2 t} \right], & \lambda \neq \beta, \end{cases} \]

where,
\[ r_1 = \frac{-4\lambda + \beta + \sqrt{\beta(\beta + 8\lambda)}}{2}, \quad r_2 = \frac{-4\lambda + \beta - \sqrt{\beta(\beta + 8\lambda)}}{2}. \]

\[ M(t) = \begin{cases} \frac{4}{3}M(0) \left[ 1 - \frac{e^{-3\beta t}}{4} \right], & \lambda = \beta, \\ \frac{M(0)}{(r_1 - r_2)} \left[ (r_1 + 4\lambda)e^{r_1 t} - (r_2 + 4\lambda)e^{r_2 t} \right], & \lambda \neq \beta. \end{cases} \]

For the stable stage of growth we have,
\[ B(t) = \begin{cases} \frac{4}{3}BM(0), & \lambda = \beta, \\ \frac{BM(0)}{(r_1 - r_2)}(r_1 + 4\lambda)e^{r_1 t}, & \lambda \neq \beta, \end{cases} \]
and,

\[ M(t) = \begin{cases} 
\frac{4}{3}M(0), & \lambda = \beta, \\
\frac{M(0)}{(r_1 - r_2)(r_1 + 4\lambda)}r_1^t, & \lambda \neq \beta.
\end{cases} \]

Expressions can be developed for several other quantities of interest. If we let \( r_1 \) be the largest real root of the characteristic equation, \( g^*(s) = 1 \), we see that the average number of offspring a newborn mother will produce in her lifetime is \( R_0 = \beta \int_0^{\infty} \ell(x)dx = \beta/\lambda \) and the mean age of childbearing in the stable population is:

\[ \frac{1}{r_1} \left\{ \left( 1 - \left( \frac{\lambda k}{r_1 + \lambda k} \right)^k \right) - \frac{r_1 k}{r_1 + \lambda k} \left( \frac{\lambda k}{r_1 + \lambda k} \right)^k \right\}. \]

In the stationary population this becomes \( \frac{\beta(1 + k)}{2k\lambda^2} \). The generation length is \( T = \frac{\ln(\beta/\lambda)}{r_1} \) and the life expectancy of a newborn individual is \( \frac{1}{\lambda} \).
2. THE DIFFERENTIAL AND DIFFERENCE EQUATIONS OF POPULATION DYNAMICS

2.1 The Von Foerster Partial Differential Equation

Let \( N(x,t)\Delta x = M(t)a(x,t)\Delta x \) be the number of individuals in the age range \( x \) to \( x + \Delta x \) at time \( t \). Considering the number of these individuals remaining in the population after a further time \( \Delta t \) we see that \( N(x + \Delta t, t + \Delta t)\Delta x - N(x,t)\Delta x \) represents the change in this part of the population during the time interval \( \Delta t \). Assuming this change to be directly proportional to \( N(x,t)\Delta x \) and \( \Delta t \) we can write the conservation equation,

\[
N(x + \Delta t, t + \Delta t)\Delta x - N(x,t)\Delta x = -\left[ \mu(x,t)\Delta x + o(\Delta x) \right] N(x,t)\Delta t, \tag{2.1}
\]

where,

\[
\mu(x,t) = \text{the age specific mortality and } o(y) \text{ is any function such that } \lim_{y \to 0} \frac{o(y)}{y} = 0.
\]

Hence,

\[
\frac{N(x + \Delta t, t + \Delta t) - N(x,t + \Delta t) + N(x,t + \Delta t) - N(x,t)}{\Delta t} = -\mu(x,t)N(x,t) + N(x,t)\frac{o(\Delta x)}{\Delta x}
\]

and on taking limits as \( \Delta t \) approaches zero we have,

\[
\frac{\partial N(x,t)}{\partial x} + \frac{\partial N(x,t)}{\partial t} = -\mu(x,t)N(x,t). \tag{2.2}
\]

We can also proceed from (2.1) to (2.2) by expanding the first term on the left hand side of (2.1) in powers of \( \Delta t \),

\[
N(x + \Delta t, t + \Delta t) = N(x,t) + \frac{\partial N(x,t)}{\partial t} \Delta t + \frac{\partial N(x,t)}{\partial x} \Delta t + \ldots + O(\Delta t^2)
\]
After substituting this series in (2.1), \( N(x,t)A\Delta x \) is eliminated from the left hand side and division by \( A\Delta t \) followed by taking the limit as \( A\Delta t \) approaches zero gives (2.2).

Equation (2.2) is referred to as the Von Foerster equation (Von Foerster, H. (1959)). It was first proposed to describe the growth of cell populations and has not received as much attention in demography as many of the formulations described below, although, as noted by Hoppensteadt, F. (1975) and Trucco, E. (1965), it is implicit in the work of McKendrick, A.G. (1910, 1926), Fredrickson, A.G. et al., (1963, 1967) and Scherbaum, O., Rasch, G. (1957).

Auslander, D.M., Oster, G.F. and Huffaker, C.B. (1974) give an interesting derivation of (2.2) by considering a problem in mechanical engineering which is analogous to the study of a fully age-structured population model. It is assumed that grains of sand, each representing an individual, are carried on a conveyor belt so that age, \( x \), is represented by the distance travelled by the grain of sand since it was first deposited on the belt, at age zero, from a hopper. The belt has velocity \( \frac{dx}{dt} = 1 \). The age specific mortality, \( \mu(x,t) \), is accounted for by a leakage of sand particles through the belt. The rate at which births occur is determined by the number of individuals on the belt who have reached the breeding age and their fecundity. Consequently, the hopper is controlled by a distributed feedback loop.

By considering the equation of motion for the sand density, \( N(x,t) \), Auslander, D.M., et al., show that the Von Foerster equation (2.2) is just a particular example of the equation of convective transport.

\( N(x,t) \) in (2.2) can be determined only if \( N(0,t) \) and \( N(x,0) \) or an equivalent set of boundary values are given. It is
usually assumed that the number of individuals introduced into the population in the time interval \( t \) to \( t + \Delta t \) is
\[
\int_0^\infty \beta(x,t)N(x,t)dx,
\]
where \( \beta(x,t)\Delta t \) is the number of births due to an individual of age \( x \) at time \( t \) over the next time interval \( \Delta t \).

This means that we know \( N(o,t) \) where,
\[
N(o,t) = M(t)a(o,t),
\]
\[
= B(t), \quad \text{from (1.8)},
\]
\[
= \int_0^\infty B(t - x)\ell(x,t)\beta(x,t)dx, \quad \text{from (1.5)},
\]
\[
= \int_0^\infty M(t)a(x,t)\beta(x,t)dx, \quad \text{from (1.8)},
\]
\[
= \int_0^\infty N(x,t)\beta(x,t)dx.
\]

We also assume that \( N(x,o) \), the initial age distribution, is a known smooth function. Typically this function is zero for large values of \( x \). If this is so for \( x \geq A \) then \( N(x,t) = 0 \) for \( x \geq A + t \) and consequently the integral in (2.3) is generally over a finite interval.

Using these assumptions (2.2) can be solved (see Trucco, E. (1965)) to give,
\[
N(x,t) = \begin{cases} 
N(x - t,o)\exp\left[-\int_0^t \mu(x - t + s,s)ds\right], & x \geq t, \\
N(o,t - x)\exp\left[-\int_0^x \mu(s,s + t - x)ds\right], & 0 \leq x < t,
\end{cases}
\]

and since, \( B(t) = N(o,t) = \int_0^\infty \beta(x,t)N(x,t)dx \) we have,
\[
B(t) = \int_0^t \beta(x,t)B(t - x)\exp\left[-\int_0^x \mu(s,s + t - x)ds\right]dx
\]
\[
+ \int_t^\infty \beta(x,t)N(x - t,o)\exp\left[-\int_0^t \mu(s + x - t,s)ds\right]dx.
\]
We recognise, from (1.2), that,
\[
l(x,t) = \exp \left[ -\int_0^x \mu(s, s + t - x) \, ds \right].
\]
So we can write,
\[
\int_0^\infty \beta(x,t)N(x - t, o) \exp \left[ -\int_0^t \mu(s + x - t, s) \, ds \right] \, dx
\]
\[
= \int_0^\infty a(x, o) \beta(x + t, t) \frac{\ell(x + t, t)}{\ell(x, o)} \, dx = B_0(t), \text{ from (1.6)}.
\]

Consequently, \( B(t) = B_0(t) + \int_0^t B(t - x) g(x, t) \, dx \). This means that starting with the formulation represented by the Von Foerster partial differential equation (2.2) and the boundary conditions described above we can reproduce the integral formulation studied in chapter 1.

Starting with the integral formulation for \( B(t) \) and \( M(t) \) in (1.5), (1.4) respectively we see that we can obtain (1.8),
\[
M(t)a(x,t) = \begin{cases} 
M(0)a(x - t, o) \frac{\ell(x, t)}{\ell(x - t, o)}, & x \geq t; \\
B(t - x) \ell(x, t), & 0 \leq x < t. 
\end{cases}
\]

Differentiating partially with respect to \( t \) and then with respect to \( x \) and adding the results we have,
\[
\frac{\partial [M(t)a(x,t)]}{\partial x} + \frac{\partial [M(t)a(x,t)]}{\partial t} = \begin{cases} 
-M(0)a(x - t, o) \frac{\ell(x, t) \mu(x, t)}{\ell(x - t, o)}, & x \geq t; \\
-\mu(x, t) B(t - x) \ell(x, t), & 0 \leq x < t. 
\end{cases}
\]

So using (1.8) and \( M(t)a(x,t) = N(x,t) \) we have,
\[
\frac{\partial N(x,t)}{\partial x} + \frac{\partial N(x,t)}{\partial t} = -\mu(x,t)N(x,t), \text{ which is the Von Foerster}
equation. This means that we may start with the integral formulation and obtain the Von Foerster equation. Combining these remarks with those of the preceding paragraph we see that the integral formulation and the formulation represented by the Von Foerster partial differential equation are equivalent.

Frequently we wish to characterize individuals by physiological properties other than just chronological age. For example, we may wish to take account of volume, mass, length or other chemical variables which play an important role in an individual's development. If we let \( x_i(t) \) be a measure of the \( i \)th characteristic under consideration then, following Ausländer, D.M., et al., (1974) we can generalise the Von Foerster equation (2.2) to account for all these characteristics. The generalisation of (2.2) is,

\[
\frac{\partial N(x_1, x_2, \ldots, t)}{\partial t} + \sum_{i} \left[ \frac{dx_i}{\partial x_i} \right] N(x_1, x_2, \ldots, t) = -\mu(x_1, x_2, \ldots, t)N(x_1, x_2, \ldots, t),
\] (2.5)

where,

\[
\frac{dx_j}{dt} = 1, \text{ if } x_j \text{ is the measure of chronological age.}
\] (2.5)

can be generalised further to take account of the fact that all individuals may not be influenced to the same degree by the factor \( x_1 \). Hence, the effects of genetic and environmental differences on the maturation rate of an individual can be accounted for. Let \( \sigma_i(x_1, x_2, \ldots, t) \) be the dispersion rate of the characteristic \( x_i \) then (2.5) becomes,

\[
\frac{\partial N(x_1, x_2, \ldots, t)}{\partial t} + \sum_{i} \left[ \frac{dx_i}{\partial x_i} \right] N(x_1, x_2, \ldots, t) + \sum_{i} \left[ \frac{\sigma_i^2}{\partial x_i^2} \right] \left( \sigma_i(x_1, x_2, \ldots, t)N(x_1, x_2, \ldots, t) \right) = -\mu(x_1, x_2, \ldots, t)N(x_1, x_2, \ldots, t),
\] (2.6)
If \( u(x_1, x_2, \ldots, t) = 0 \) in (2.6) we recognise the forward Kolmogoroff or Fokker-Planck diffusion equation which has been extensively studied in relation to stochastic population models (Astrom, K.J. (1970), Saaty, T.L. (1967)). We discuss this equation and its use in population modelling in section 3.1.

2.2 Ordinary Differential Equations

Realistically the population size at time \( t, M(t), \) is represented by an integer-valued function of time. The discrete changes in the population size correspond to a single birth or death in the population. The rates at which births and deaths occur may depend on the population size, the individual's age and the length of time the process has been running. However, it is common to consider models where \( M(t) \) is a continuous real-valued function of time and the rate at which the population is changing, \( \frac{dM(t)}{dt} \), is related to \( M(t) \) in the form of an ordinary differential equation. Such models are in fact models of the mean behaviour of the more realistic integer-valued process and assuming the coefficient of variation of the integer-valued process is small the continuous model is taken to represent the actual population.

Hence, we consider equations of the form,

\[
\frac{dM(t)}{dt} = F(M(t)).
\]  

(2.7)

When the right hand side of (2.7) does not depend on \( t \) explicitly it is usual to call (2.7) an autonomous differential equation. If the per capita growth rate, \( \frac{1}{M(t)} \frac{dM(t)}{dt} \), is a constant we classify the growth as being density independent. For any other function the growth is density dependent.
In cases where the population consists of more than one type of individual it is usual to analyse the population growth by using a coupled set of equations, each of the form (2.7), one for each type of individual. However, as pointed out by Trucco, E. (1965), such a set of equations neglects one very important feature of the system, namely the age distribution within each group. This lack of attention to age structure is typical of models represented by equations of the form (2.7).

Equations of the form (2.7) can be obtained from the Von Foerster equation (2.2). Since \( M(t) = \int_0^\infty N(x,t)dx \) and \( \lim_{x \to \infty} N(x,t) = 0 \) we can integrate (2.2) over all ages to

\[
\frac{dM(t)}{dt} = N(o,t) - \int_0^\infty \mu(x,t)N(x,t)dx,
\]

\[
= \int_0^\infty [\beta(x,t) - \mu(x,t)]N(x,t)dx, \quad (2.8(a))
\]

\[
= B(t) - D(t), \quad (2.8(b))
\]

\[
= \frac{B(t)}{M(t)} - \frac{D(t)}{M(t)} M(t),
\]

where,

\( D(t) \) = the total death rate, from (1.9), and \( \frac{B(t)}{M(t)} \), \( \frac{D(t)}{M(t)} \) are the crude birth and death rates respectively.

We see from (2.8(b)) that often the differential equation (2.7) is expressing the rate of increase of population size as a balance between the rate at which individuals are entering the population (births) at time \( t \) and the rate at which they are leaving the population (deaths). In particular, if \( \beta(x,t) - \mu(x,t) = r \), constant, then from (2.8(a)) we have the simplest density independent Malthusian model. Lotka, A.J. (1956) and May, R.M. (1976) point out that attempts to account for all the biological (e.g. the ageing process) and physical...
(e.g. food supply) aspects that affect individuals in the population can lead to balance equations of the type (2.8(b)) where parameters such as these are summarized in terms of some overall intrinsic growth rate or carrying capacity. The logistic model is a particular example of this approach where in (2.7) we have,

\[ F(M(t)) = r M(t) \left[ 1 - \frac{M(t)}{K} \right], \quad (2.9) \]

where,

\[ K \] is the carrying capacity (i.e. the maximum population the environment will support) and \( r \) is the intrinsic rate of increase (i.e. the difference between the mean birth and death rates per individual measured at low population level). A further example due to Smith, F.E. (1963) modifies the logistic model to account for availability of food by using,

\[ F(M(t)) = r M(t) \left[ 1 - \frac{f(t)}{s(t)} \right], \]

where,

\[ s(t) = \text{the rate at which food is used when the population reaches saturation level } K, \]
\[ f(t) = \text{the rate at which food is used before the population becomes saturated}. \]

It has been common to select \( F(M(t)) \) in (2.7) so that the solution \( M(t) \) has an S-shaped graphical representation. Several of the theories underlying these choices are discussed in the collection of papers by Hazen, W.E. (1975). The main support for these S-shaped curves comes from the observation that many biological populations exhibit sigmoid growth curves. The logistic equation is certainly one of the most popular choices, although, as we shall see in chapter 3, this may be justified in terms of its simplicity and not its realism.
Turner, M.E., Bradley, E.L., Kirk, K.A. and Pruitt, K.M. (1976) develop an expression for \( F(M(t)) \) which under certain limiting conditions produces most of the commonly used growth equations of the form (2.7) thus unifying the theories which previously led separately to these particular forms for \( F(M(t)) \). In addition some new growth equations are developed and the most general of these, (2.10), is shown to match empirical data quite successfully. The development begins with three postulates:

The first asserts that the rate of growth is jointly proportional to (a) a monotonic function of the generalised distance between the origin and the present population size \( M(t) \), and (b) a monotonic function of the generalised distance between the present population size and the saturation level \( K \). The generalised distance between \( M(t) \) and \( K \) being defined as,

\[
(K^n - M^n(t))^{1/n}, \quad K \geq M(t) > 0, \quad n > 0.
\]

The second postulate restricts the monotonic functions to being power functions while the third postulate restricts the indices in the power functions to be of the form, \( 1 - np \) and \( n + np \), where \(-1 < p < 1/n\).

Using these assumptions the growth equation,

\[
\frac{dM(t)}{dt} = \frac{r}{K^n} M^{1-np}(t) \left[ K^n - M^n(t) \right]^{1+p}, \quad (2.10)
\]

is developed where \( r \) enters as a constant of proportionality. If \( p \to 0 \) in (2.10) we have,

\[
\frac{dM(t)}{dt} = \frac{r}{K^n} M(t) \left[ K^n - M^n(t) \right], \quad (2.11)
\]
which is the generalised logistic model of Bertalanffy, L. (1941) and
gives the logistic model (2.9) if we let \( n = 1 \). Also from (2.11) as
\( n \to 0 \) and \( rn \to r^1 \) we have,

\[
\frac{dM(t)}{dt} = r^1 M(t) \log \left( \frac{K}{M(t)} \right),
\]

(2.12)

which is the familiar Gompertz growth curve. Finally, as \( K \to \infty \) in
(2.11) or (2.9), and \( r^1 \log K + r \) in (2.12), we have,

\[
\frac{dM(t)}{dt} = r M(t),
\]

which is the Malthusian model.

2.3 Difference Equations

Many populations are effectively made up of a single generation.
Examples are found in many of the temperate zone arthropod species
with one short-lived adult generation each year. One generation breeds
at the end of its lifespan, \( \tau \), and is completely replaced by the
subsequent generation. So the population growth occurs in discrete
steps. For these populations the appropriate models are difference
equations of the form,

\[
M(t + \tau) = G(M(t)),
\]

(2.13)

where \( M(t) \) is the population size at time \( t \). If the right hand
side of (2.13) is a nonlinear function of \( M(t) \) we describe the growth
as density dependent. Otherwise we have simpler but less realistic
density independent models.

May 1974(b) discusses models of the form (2.13) which are
homologous to the differential equations of section 2.2 in the sense
that all the biological features of both models are the same except
that the population growth in (2.13) takes place at discrete intervals rather than as a continuous process, as in (2.7). For example, corresponding to the differential equation model \( \frac{dM(t)}{dt} = r M(t) \), which is the simple Malthusian model, we have the homologous difference equation model \( M(t + \tau) = (1 + r\tau)M(t) \) where \( \tau \) is the time between changes in the population size. We discuss the relationship between difference and differential equation models in more detail below.

According to rigorous usage difference equations, while defined as known relations between the values of an unknown function at a discrete pattern of values of the argument, such as \( t - \tau, t - 2\tau, \ldots \), where \( \tau \) is a fixed known number, allow the argument \( t \) to vary continuously. Recurrence relations, on the other hand, while defined in the same way, do not allow \( t \) to vary continuously and in fact \( t \) will take on only equally spaced discrete values which are multiples of \( \tau \). However, in accordance with common usage (Miller, K.S. (1968)) we will use the terms difference equation and recurrence relation interchangeably. Hence, if \( t \) is being measured in units of \( \tau \) then \( M(t) \), in (2.13), represents the size of the \( t/\tau \)th generation.

There is a considerable literature on the relationship between differential equations and difference equations as used in population modelling (May, R.M. (1974(a)), (1974(b)), Van Der Vaart, H.R. (1973)). Two fundamental questions arise. Starting with a differential equation how do we find the difference equation with the "same" solutions as the differential equation? In what sense do we want the solutions to be the "same"?

If we begin with the differential equation,

\[
\frac{dM(t)}{dt} = F(t,M(t))
\]  

(2.14)
and solve for \( M(t) \) we have found a function \( \phi(t; t_0, M(t_0)) \) such that for all \( t_0, M(t_0), t \) we have,

\[
\phi(t_0; t_0, M(t_0)) = M(t_0)
\]

(2.15)

and

\[
\frac{\partial}{\partial t} \phi(t; t_0, M(t_0)) = F(t, \phi(t; t_0, M(t_0))).
\]

In fact \( \phi(t; t_0, M(t_0)) \) gives the value at \( t \) of the solution function \( M(t) \) whose graph passes through the initial point \( (t_0, M(t_0)) \). Hence the value of \( M(t) \) at \( t + \tau \) is given by,

\[
M(t + \tau) = \phi(t + \tau; t, M(t)).
\]

(2.16)

This is the difference equation whose solutions are the same as the solutions of (2.14) in the sense that there is a one to one correspondence between the collection of solution sequences of (2.16) and the collection of solution functions of (2.14) so that all points of the graph of any one solution sequence belong to the graph of the corresponding solution function. Consequently, once the solution, \( \phi(t; t_0, M(t_0)) \) of the differential equation (2.14) has been found we can write down the difference equation (2.16) by eliminating \( t_0 \) and \( M(t_0) \) from the simultaneous equations,

\[
\begin{align*}
M(t) &= \phi(t; t_0, M(t_0)), \\
M(t + \tau) &= \phi(t + \tau; t_0, M(t_0)).
\end{align*}
\]

(2.17)

Van Der Vaart, H.R. (1973) points out that the validity of this approach rests on the use of the group property of \( \phi(t; t_0, M(t_0)) \) which states that,

\[
\phi(t_2; t_0, M(t_0)) = \phi(t_2; t_1, M(t_1)) = \phi(t_2; t_1, \phi(t_1; t_0, M(t_0)))
\]

where,

\[
M(t_1) = \phi(t_1; t_0, M(t_0)).
\]

(2.18)
If we apply (2.18) to (2.17) with \( t_1 = t, t_2 = t + \tau \) we have,

\[
M(t + \tau) = \phi(t + \tau; t_0, M(t_0)),
\]
\[
= \phi(t + \tau; t, \phi(t; t_0, M(t_0))),
\]
\[
= \phi(t + \tau; t, M(t)),
\]
which is the difference equation (2.16).

As an example, suppose we have the logistic differential equation,

\[
\frac{dM(t)}{dt} = r M(t) \left[ 1 - \frac{M(t)}{K} \right].
\]  
(2.19)

The solution passing through \((0, M(0))\) is given by,

\[
M(t) = \frac{M(0) e^{rt}}{1 + A e^{-rt}},
\]
where,

\[
A = \frac{K - M(0)}{M(0)}, \quad 0 < M(0) < K
\]
(2.20)

The difference equation whose solutions are the same as those of (2.19), in the sense described above, is given by (2.16) as,

\[
M(t + \tau) = \frac{K}{1 + A e^{-r(t+\tau)}} = \frac{e^{r\tau} M(t)}{1 + \left( \frac{e^{r\tau} - 1}{K} \right) M(t)}
\]
which has the solution,

\[
M(n\tau) = \frac{M(0) e^{r\tau(n+1)}}{1 - \frac{M(0) e^{r\tau(n+1)}}{K}}; \quad n = 1, 2, 3, \ldots
\]
(2.21)

We note that if we make the substitution \( n = t/\tau \) in (2.21) and consider \( \lim_{\tau \to 0} M(n\tau) \) then we reproduce (2.20).

May, R.M. (1974(b)) proceeds from a differential equation model to an homologous difference equation model by a different technique. Starting with (2.14) he uses,

\[
\frac{dM(t)}{dt} = \lim_{\tau \to 0} \frac{M(t + \tau) - M(t)}{\tau}
\]
and consequently obtains the difference equation

\[
M(t + \tau) = \tau F(t, M(t)) + M(t)
\]
(2.22)
Applying this to our example, from (2.19) we have,

\[ M(t + \tau) = \left[ 1 + r\tau - \frac{rt}{K} M(t) \right] M(t) \]  

(2.23)

In (2.23) we note that if \( 0 < rt < 1 \) and \( 0 < M(t) < K \) then \( M(t + \tau) < K \). If \( r\tau > 1 \) and \( 0 < M(t) < K \) then \( M(t + \tau) > K \) whenever \( \frac{K}{r\tau} < M(t) < K \). Analysing the case \( r\tau > 1 \) further we see that if \( K > M(0) > \frac{K}{r\tau} \) then \( M(\tau) > K \) while if \( 0 < M(0) < \frac{K}{r\tau} \) then \( M(\tau) > r\tau M(0) \). After a finite number, say \( n \), of steps we find \( M(n\tau) > (r\tau)^n M(0) > \frac{K}{r\tau} \). Now \( M(n\tau) \) may be greater than \( K \) after these \( n \) steps or if not \( M(n\tau + \tau) \) will be greater than \( K \) by the preceding argument. Also whenever \( M(t) > K \) and \( r\tau > 1 \) we have \( M(t + \tau) < K \). So if \( r\tau > 1 \) we find that \( M(t) \) is oscillating around the saturation level \( K \). This is not the same behaviour as that exhibited by the solution (2.20) of the differential equation.

Consequently, difference equations formed from differential equations using (2.22) will not generally exhibit solutions which are the "same" as the solutions of the differential equation in the sense that led us to (2.16).

We now consider finding the differential equation with the same solution as a given difference equation ("same" in the sense that gave (2.16)). Suppose we have a function \( \phi(t; t_o, M(t_o)) \) in (2.17) which satisfies (2.15) and the group property (2.18) then,

\[
\frac{\phi(t + \tau; t_o, M(t_o)) - \phi(t; t_o, M(t_o))}{\tau} = \left[ \phi(t + \tau; t_o, M(t_o)) - \phi(t; t_o, M(t_o)) \right] / \tau
\]

So,

\[
\frac{\partial}{\partial \tau} \phi(t; t_o, M(t_o)) = \frac{\partial}{\partial \tau} \phi(t; t_o, M(t_o))
\]
which means that \( \phi(t; t_0, M(t_0)) \) is a solution of the differential equation,

\[
\frac{dM(t)}{dt} = \sum_{t_0} \phi(t; t, M(t)) = F(t, M(t)),
\]

and satisfies the initial conditions.

If we apply this to the difference equation (2.23) we have,

\[
\phi(t, t_0, M(t_0)) = \left[ 1 - r(t - t_0) - \frac{r(t - t_0)M(t_0)}{K} \right] M(t_0),
\]

and we see that the group property is not satisfied. This means that there is no differential equation of the form (2.14) with the same solutions as the difference equation (2.23).

We can form a huge collection of difference equations of the form (2.13), all of which, upon division by \( \tau \) and application of the operation, \( \lim_{\tau \to 0} \), will yield the differential equation (2.14). This means that the development of realistic difference equation models requires considerable information about the physical and biological factors influencing the population growth. A comprehensive list of the widely used choices for \( G(M(t)) \) is provided by May, R.M. (1974(a), table22, 1976) together with detailed discussion of the behaviour of the resulting models.

Since the use of numerical methods in solving differential equations usually results in replacing the given differential equation by an appropriate difference equation it is reasonable to assume that formulating the problem from the start with a difference equation may avoid the doubly approximative process which results from working with a differential equation and solving it numerically. The same comment also applies to formulations which require the numerical solution of an integral equation. A difference equation model has been used by Thompson, W.R. (1931), Dobbernack, W., Tietz, G. (1940) and
Lotka, A.J. (1948) to approximate the model represented by the integral equation (1.5),

\[ B(t) = \int_0^\infty B(t - x)\ell(x)\beta(x)dx. \]

The \( B(t - \tau) \) individuals born in the calendar year \( t - \tau \), that is, between the times \( (t - \frac{1}{2} - \tau) \) and \( (t + \frac{1}{2} - \tau) \), will be \( \tau \) years old some time during the calendar year \( t \), that is, between times \( (t - \frac{1}{2}) \) and \( (t + \frac{1}{2}) \). If their births were evenly distributed over the year \( (t - \tau) \) so their birthdays will be evenly distributed over the year \( t \), their average age during year \( t \) being \( \tau \). The average number of survivors to that age \( \tau \) during the year \( t \) will be approximately \( B(t - \tau)\ell(\tau) \), where \( \ell(\tau) \) is the probability at birth of surviving to age \( \tau \). If the annual reproduction rate is \( \beta(\tau) \), at age \( \tau \), then the \( B(t - \tau)\ell(\tau) \) survivors will give birth to \( B(t - \tau)\ell(\tau)\beta(\tau) \) individuals during the year \( t \). If \( B(t) \) is the total number of births in the calendar year \( t \) then for positive values of \( t \) we have the difference equation,

\[ B(t) = \sum_{\tau=1}^{T} B(t - \tau)\ell(\tau)\beta(\tau), \quad (2.24) \]

where \( T \) is the upper limit of the reproductive period. The detailed solution of the difference equation (2.24) is given by Lotka, A.J., (1948) and Keyfitz, N. (1968) where a wealth of numerical data is used to show the close relationship between results obtained from (2.24) and the integral formulation.

### 2.4 Differential Delay Equations

The use of differential delay equations in population dynamics comes from the idea that the growth rate of a species will often not respond immediately to changes in its own population or that of an
interacting species but rather will do so after a time delay. This phenomenon is not peculiar to population growth. The idea of feedback loops is evident in systems studied in engineering and economics and it is well known that if the delay in the feedback loop is substantial then oscillations of large amplitude are likely to result. For example, if the growth of a species in the absence of delayed regulation is represented by \[ \frac{1}{M(t)} \frac{dM(t)}{dt} = r, \] as with the simple Malthusian model, then it is usual to refer to \( 1/r \) as the natural period of the system and a delay, \( T \), in the feedback loop greater than this natural period will produce large amplitude oscillations in the value of \( M(t) \).

Maynard Smith, J. (1974) identifies three causes of delayed regulation in ecosystems. The first is related to changes that occur in the environment such as increases in resources which may produce an immediate change in the age specific birth rate that will have an effect on the number of adults in subsequent generations. He notes that the appropriate model would then be represented by

\[ \frac{dM(t)}{dt} = F(M(t - T)) \]

where \( M(t) \) is the present population size and \( T \) is the time taken for newborn, at time \( t - T \), to reach adult status.

Secondly, the fact that some species breed only at a specific time each year has an important effect on the dynamics of the population. If the breeding pattern is such that individuals can survive to breed in successive seasons then some delayed effect is still evident in the dynamics of the system. For species surviving for a number of years producing relatively few newborn each year, the delay time of one year, due to the discrete breeding seasons, is likely to be less than the natural period of the species and consequently the oscillations produced by the delay will converge. In cases where adults breeding in one season rarely survive to breed in subsequent
seasons the effect on the age specific mortality rate has important delayed effects on the population size. It is suggested that in such cases the appropriate model is a difference equation of the form

\[ M(n + 1) = G(M(n)) \]

where \( M(n) \) is the population size in year \( n \).

The third cause of delayed regulation is due to delayed responses occurring in factors which limit the species' development. Typically such effects are due to delayed regulation occurring in other species which may be predators of the species being considered. Delays in the regulatory systems of vital limiting resources, such as the characteristic regeneration time of vegetation, also produce delayed effects on the species - as May, R.M. (1974(b), page 94) says "... one has to wait until the next generation is confronted with the havoc its predecessors wrought".

May, R.M. (1974(a)) discusses the relationship between difference equation models, of the form (2.13), and those represented by differential delay equations. We start with a population whose dynamics are represented by a density dependent form of the difference equation (2.13) where discrete population changes occur at intervals of \( \tau \), starting at \( t = 0 \). Now we feed into the system further populations whose generations overlap those of the original system having discrete population changes \( \tau \) apart occurring initially anywhere in the time interval \((0,\tau)\) but definitely not at \( t = 0 \). May shows that the neighbourhood stability properties of the total population are given by a delayed differential equation of the form,

\[
\frac{dM(t)}{dt} = M(t) \left[ H(M(t - \tau)) \right].
\]

(2.25)

Greater realism is achieved in the nature of the time delay in (2.25) if it is replaced by \( T \), called the lag time, rather than \( \tau \) the
generation time. In discussing specific choices of the function \( H \) in (2.25) May gives details of the nature of the oscillations produced for different values of \( T \).

A rigorous discussion of the methods for solving differential difference equations, the conditions under which these solutions are unique and the stability properties of the solutions is presented by Bellman, R., Cooke, K.L. (1963, chapters 3, 4, 9, 10). Mazanov, A., Tognetti, K.P. (1974) present a clear warning on a method of solution, first proposed by Cunningham, W.J. (1954), which uses a truncated Taylor series expansion of the delay term \( M(t - T) \) to obtain a new differential equation which in some way is characteristic of the original solution. They illustrate that in particular this method is not valid in solving (2.26).

One of the most widely discussed equations of the form (2.25) is the time-delayed logistic,

\[
\frac{dM(t)}{dt} = r M(t) \left[ 1 - \frac{M(t - T)}{K} \right]. \tag{2.26}
\]

This equation was first proposed by Hutchinson, G.E. (1948). The reasoning behind the equation develops from the idea that as the size of a population increases the resources available to it decrease. So starting with the logistic equation (2.9) we build in the assumption that because resources are self-renewing the actual level of resources available at any time will depend on the regulated density of the population at a time \( T \) in the past. Details of the stability properties of (2.26) are given by May, R.M. (1974(b)) and Maynard Smith, J. (1974). In particular May successfully uses (2.26) to fit the data obtained from Nicholson's experiment (Nicholson, A.J. (1957)) where blowfly larvae depleted a constant food supply to the extent
that, due to starvation, the reduced adult section of the population produced a greatly reduced birth feedback thus permitting the food supply to replenish.

The relationship between models represented by delayed differential equations and the fully age-structured model represented by the Von Foerster equation (2.2) has been considered by Ausländer, D.M., et al., (1974). They show that (2.26) represents a model which is an approximation to the fully age-structured model. Starting with the Von Foerster equation (2.2) we integrate over all ages to obtain (2.8(a)). We assume that the age specific mortality \( \mu(x,t) \) of a cohort depends on its nutritional history and consequently depends on the number of individuals in the population at an earlier time \( t - \tau \). So we write,

\[
\mu(x,t) = \mu + c M(t - \tau); \quad \mu, c, \text{ constants.}
\]

If we also assume that \( \beta(x,t) = \beta, \text{ constant} \), then in (2.8(a)) we have,

\[
\frac{dM(t)}{dt} = M(t)\left[\beta - \mu - c M(t - \tau)\right].
\]  

(2.27)

If we let \( c = \frac{\beta - \mu}{K} \) in (2.27), where \( K \) is the maximum population sustainable by the environment then,

\[
\frac{dM(t)}{dt} = (\beta - \mu) M(t)\left[1 - \frac{M(t - \tau)}{K}\right],
\]

which is the time-delayed logistic (2.26), with \( r = \beta - \mu \).

Wangersky, D.J., Cunningham, W.J. (1956) extend (2.26) by introducing a lag time into the term \( r M(t) \). May, R.M. (1974(b)) generalises (2.26) by suggesting that it is more realistic to introduce the time delay into (2.26) so that it will not depend on
the population size at some particular instant in the past but rather on a weighted average of past population sizes. This means that (2.26) is replaced by,

\[ \frac{dM(t)}{dt} = r M(t) \left( 1 - \frac{1}{K} \int_0^\infty w(s)M(t - s)ds \right) , \quad (2.28) \]

We note that if \( w(s) = \delta(s - T) \) then we recover (2.26). Also from (2.28) we see that integro-differential equations may arise in the study of population dynamics. The stability properties of models represented by equations of the form (2.28) are discussed by May, R.M. (1973) and it is noted that the analysis of (2.28) using Laplace transform techniques is usually easier than the analysis required to study (2.26).

We now consider the way in which differential delay equations and integro-differential equations arise when the model is formulated using the integral formulation of chapter 1.

Suppose the age specific mortality \( \mu(x) = \mu \), constant, and the age specific birth rate \( \beta(x) = \beta \), constant, throughout the individual's reproductive age range \( a \) to \( \gamma \). Then,

\[ \begin{align*}
\mu(x) &= \mu H(x), \\
\beta(x) &= \beta H(x - a)H(\gamma - x),
\end{align*} \quad (2.29) \]

where,

\[ H(y) = \begin{cases} 
1, & y \geq 0, \\
0, & y < 0,
\end{cases} \]

and from (1.2)

\[ \ell(x) = e^{-\mu x}, \quad x \geq 0. \]
Considering the integral equation (1.16) for the total birth rate, \( B(t) \), we have,

\[
B_0(t) = \begin{cases} 
\beta M(0) e^{-\mu t} \int_0^{\gamma-t} a(x,0) \, dx, & 0 \leq t \leq \alpha, \\
\beta M(0) e^{-\mu t} \int_0^{\gamma-t} a(x,0) \, dx, & \alpha \leq t \leq \gamma, \\
0 & t \geq \gamma
\end{cases}
\]

and so,

\[
B(t) = \begin{cases} 
\beta M(0) e^{-\mu t} \int_0^{\gamma-t} a(x,0) \, dx, & 0 \leq t \leq \alpha \\
\beta M(0) e^{-\mu t} \int_0^{\gamma-t} a(x,0) \, dx + \int_\alpha^t \beta e^{-\mu x} B(t-x) \, dx, & \alpha \leq t \leq \gamma, \\
\beta \int_\alpha^{\gamma-t} e^{-\mu x} B(t-x) \, dx & t \geq \gamma
\end{cases}
\]

Differentiating with respect to \( t \) in (2.30) we have,

\[
\frac{dB(t)}{dt} = \begin{cases} 
-\mu B(t) + \beta M(0) e^{-\mu t} [a(\alpha - t,0) - a(\gamma - t,0)], & 0 \leq t \leq \alpha, \\
-\mu B(t) - \beta M(0) e^{-\mu t} a(\gamma - t,0) + \beta e^{-\mu t} B(t - \alpha), & \alpha \leq t \leq \gamma, \\
-\mu B(t) + \beta [e^{-\alpha t} B(t - \alpha) - e^{-\gamma t} B(t - \gamma)], & t \geq \gamma
\end{cases}
\]

and so the long term behaviour of \( B(t) \), \( t > \gamma \), is described by the differential delay equation,

\[
\frac{dB(t)}{dt} = -\mu B(t) + \beta [\ell(\alpha) B(t - \alpha) - \ell(\gamma) B(t - \gamma)] .
\]

We note that this equation can also be obtained by considering the change, \( B(t + \Delta t) - B(t) \), in \( B(t) \) over the next time interval \( \Delta t \), dividing throughout by \( \Delta t \) and then passing to the limit as \( \Delta t \) approaches zero.
We see from (2.31) that the behaviour of $B(t)$ is described by a system of differential delay equations. However, if $\mu(x)$ and $\beta(x)$ do not take on constant values for the reproductive period, $\alpha \leq x \leq \gamma$, then from the integrals in (2.30) we see that differentiating (2.30) with respect to $t$ gives a system of integro-differential equations.

As a particular example we now consider the population where,

$$\beta(x) = \beta H(x - \alpha) H(\gamma - x),$$

as in (2.29),

and

$$\ell(x) = \begin{cases} 1 & \text{if } x = 0 \\ \ell & \text{if } 0 < x \leq \gamma \\ 0 & \text{otherwise} \end{cases},$$

where,

$$\ell$$

is a constant, $0 < \ell \leq 1$, which means that we take account of the fact that some newborn individuals may die very soon after birth.

From the integral equation for $B(t)$ in (1.16) we have,

$$B_0(t) = \begin{cases} \int_0^\gamma a(x,o) dx & , 0 \leq t \leq \alpha \\ \int_0^\gamma a(x,o) dx & , \alpha \leq t \leq \gamma \\ 0 & , t \geq \gamma \end{cases}$$

If we assume that the initial age density $a(x,o)$ is a uniform age density on $(0,\gamma)$ then,

$$a(x,o) = \begin{cases} \frac{1}{\gamma} & , 0 < x < \gamma \\ 0 & , \text{otherwise} \end{cases}$$
and so,

\[
B(t) = \begin{cases} 
\frac{\beta M(0)}{\gamma} (\gamma - t), & 0 \leq t \leq \alpha, \\
\beta \int_{\alpha}^{t} B(t - x)dx + \frac{\beta M(0)}{\gamma} (\gamma - t), & \alpha \leq t \leq \gamma, \\
\beta \int_{\alpha}^{\gamma} B(t - x)dx, & t \geq \gamma.
\end{cases}
\]

Hence, differentiating with respect to \( t \) we have,

\[
\frac{dB(t)}{dt} = \begin{cases} 
0, & 0 \leq t \leq \alpha, \\
-\frac{\beta M(0)}{\gamma} + \beta B(t - \alpha), & \alpha \leq t \leq \gamma, \\
\beta [B(t - \alpha) - B(t - \gamma)], & t \geq \gamma.
\end{cases}
\]

and so for \( t \geq 0 \) we have,

\[
\frac{dB(t)}{dt} = -\frac{\beta M(0)}{\gamma} H(t - \alpha)H(\gamma - t) - \beta B(t - \gamma)H(t - \gamma) + \beta B(t - \alpha)H(t - \alpha).
\]

Taking Laplace transforms we have,

\[
B^*(s) = \frac{M(0)}{\ell \gamma s} + \frac{B(0) \ell \gamma - M(0)}{\ell \gamma [s + \beta \ell[e^{-\gamma s} - e^{-\gamma s}]]},
\]

which on inversion gives,

\[
B(t) = \frac{B(0)}{\beta \ell (\gamma - \alpha)} \left\{ 1 + \left[ \beta \ell (\gamma - \alpha) - 1 \right] \sum_{n=0}^{\infty} (\beta \ell)^n \right. \\
\left. \times \left[ \sum_{j=0}^{n} (-1)^j \binom{n}{j} H(t - K_{n,j}) (t - K_{n,j})^n \right] \right\},
\]

where,

\[K_{n,j} = (\gamma - \alpha)j + n \alpha,\]
and we have used $B(0) = B_0(0)$ to express $M(0)$ as $\frac{\gamma B(0)}{\beta(\gamma - \alpha)}$.

2.5 A Two Stage Population Model

Consider an organism that becomes an adult if it survives an initial stage that we will call an egg stage. It is assumed the mortality of the eggs and adults is age and density independent and that adults procreate at a constant rate throughout their lifetime; that is, the egg production rate per adult is constant. At time $t$ let,

- $M_A(t) = \text{the number of adults},$
- $B(t) = \text{the egg production rate},$
- $\alpha_A(x,t) = \text{the age density for adults of age } x,$
- $\tau, \text{ constant} = \text{the duration of the egg stage},$
- $d = \text{the death rate per egg},$
- $\mu = \text{the death rate per adult},$
- $\beta = \text{the rate of egg production per adult}.$

Tognetti, K.P., Mazanov, A. (1970) show that the behaviour of the adult population can be analysed using,

$$B(t) = \beta M_A(t),$$

$$\frac{dM_A(t)}{dt} = \beta e^{-d\tau} M_A(t - \tau) - \mu M_A(t), \quad (2.32)$$

with the initial conditions, $M_A(t) = \begin{cases} M(0), & t = 0, \\ 0, & t < 0. \end{cases}$

They show that although a solution for $M_A(t)$ can be built up by analytic continuation for any $(n - 1)\tau \leq t < n\tau$, $n = 1, 2, 3, \ldots$, a more general solution can be obtained by taking Laplace transforms in (2.32) to give,
They also give a complete description of the asymptotic behaviour of the adult population showing that the long term behaviour is Malthusian with \( \tau \beta e^{-\mu t} \) and \( \tau \mu \) corresponding to the Malthusian birth and death rates respectively.

Tognetti, K.P. (1975(a)) extends the model so that an organism may exist for a random period as an egg before it becomes an adult. Also the egg and adult mortality, as well as the adult fecundity, are age dependent. It is shown that the population of eggs and adults as well as their birth rates may be represented in terms of four coupled Volterra integral equations. The model in which the organism may exist for a constant period as an egg before becoming an adult is extended to a stochastic model by Tognetti, K.P. (1975(b)) and in the case where birth and mortality rates are age independent constants expressions are developed for the distribution function for the population size at time \( t \), the variance and the extinction probabilities.

We now show that for the population where an egg has to survive a fixed period \( \tau \) before becoming an adult, with constant birth and mortality rates for eggs and adults, it is possible to analyse both the egg and adult subpopulations by using an integral formulation which considers the total population of adults plus eggs. This represents an extension of the model used by Tognetti, K.P., Mazaňov, A. (1970), which only considered the adults, and is simpler than the formulation using four coupled integral equations proposed by Tognetti, K.P. (1975(a)).
Consider a population where at time $t$,

$B(t) = \text{the total birth rate},$

$M(t) = \text{the mean number in the population},$

$a(x,t) = \text{the age density for individuals of age } x,$

$\beta(x) = \text{the age specific birth rate},$

$\ell(x) = \text{the survivor function},$

$s = \beta H(x - \tau),$

$\ell(x) = \left\{\begin{array}{ll}
 e^{-\mu x}, & 0 \leq x < \tau, \\
 Le^{-\mu x}, & x \geq \tau \\
 0, & \text{otherwise,}
\end{array}\right.$

where,

$L = e^{\tau(\mu - d)}.$

Assuming the population at $t = 0$ consists entirely of $M(0)$ individuals all age $\tau$ then $a(x,0) = \delta(x - \tau)$ and from (1.16) we have,

$B(t) = \begin{cases}
 \beta M(0)e^{-\mu t}, & 0 \leq t < \tau \\
 \beta M(0)e^{-\mu t} + \int_{\tau}^{t} B(t - x)\ell e^{-\mu x}dx, & t \geq \tau,
\end{cases}$ (2.33)

and from (1.7),

$M(t) = \begin{cases}
 M(0)e^{-\mu t} + \int_{0}^{t} B(t - x)e^{-\mu x}dx, & 0 \leq t < \tau, \\
 M(0)e^{-\mu t} + \int_{0}^{t} B(x)\left[ e^{-d(t-x)}H(t - t + x) + Le^{-\mu(t-x)} \right]x H(t - x - \tau)dx, & t \geq \tau
\end{cases}$ (2.34)

From (1.12) we have,
\[ M(t) = M(0) \delta(x - t - \tau) e^{-\mu t} H(x) \Pi(x - t) + B(t - x) H(t - x) H(x) \times \left[ e^{-dx} H(t - x) + Le^{-\mu x} H(x - \tau) \right]. \quad (2.35) \]

If we suppose that a newborn individual becomes an adult after surviving a period of \( \tau \) then the number of adults in the population, \( M_A(t) \), is given by (2.35) as,

\[
M_A(t) = \int_0^\infty M(t) a(x, t) dx ,
\]

\[
= \int_0^\infty M(0) \delta(x - t - \tau) e^{-\mu t} dx + \int_0^t B(t - x) Le^{-\mu x} dx ,\]

\[
= M(0) e^{-\mu t} + Le^{-\mu t} \int_0^{t-\tau} B(x) e^{\mu x} dx. \quad (2.36)
\]

Differentiating (2.36) with respect to \( t \) and substituting for \( L \) gives,

\[
\frac{dM_A(t)}{dt} = e^{-d\tau} B(t - \tau) - \mu M_A(t) , \quad (2.37)
\]

and, for \( t \geq \tau \), we see from (2.33) and (2.36) that,

\[
B(t) = \beta M_A(t) . \quad (2.38)
\]

Substituting (2.38) in (2.37) gives,

\[
\frac{dM_A(t)}{dt} = \beta e^{-dt} M_A(t - \tau) - \mu M_A(t),
\]

which is the same differential delay equation, (2.32), used by Tognetti, K.P., Mazanov, A. (1970) in their analysis of the adult population. We see that any information about either the subpopulation of eggs (individuals of age less than \( \tau \)) or the subpopulation of adults is given by considering (2.33), (2.34) and (2.35). For example, the expected number of eggs produced by an individual in its lifetime
is
\[ \int_{0}^{\infty} \ell(x) \beta(x) \, dx = \int_{1}^{\infty} \beta e^{-\mu x} \, dx = \frac{\beta e^{-\tau \mu}}{\mu} \]
and it follows that if this expected number of progeny is greater than one, which means \( \beta e^{-\tau \mu} > \mu \),
then an increase in population is assured.
3. **STOCHASTIC POPULATION MODELLING**

3.1 **Introduction**

Early studies in the mathematics of population growth were mainly concerned with deterministic models. Typically these models are represented by differential or difference equations of the type discussed in chapter two where the population size is determined by solving a functional equation given some initial conditions such as the population size at time $t = 0$. There are at least two objections to this approach:

Firstly, these models assume that the population size is a real-valued continuous function of time, whereas realistically it must be an integer-valued function of time.

Secondly, these models predict that at time $t$ the population size will always be the same if the initial conditions are not altered. This ignores the large number of random or chance factors that can influence the population growth.

Attempts to overcome these objections led to the development of stochastic (probabilistic) models of population growth. The early work being done by McKendrick, A.G. (1926) and Yule, G.J. (1924). Feller, W. (1939) was the first to treat systematically stochastic models of population growth within the framework of the theory of stochastic processes and significant contributions have been made since by Kendall, D.G. (1948(a), 1949), Bartlett, M.S. (1960, 1973) and Pollard, J.H. (1966, 1973).
May, R.M. (1974(b), page 33) notes that stochastic features, arising from the fact that the population size is fundamentally discrete, have come to be christened "demographic stochasticity". These features are built into the model by considering the probabilities that an individual will give birth or die in the next time interval $\Delta t$. By considering the resulting birth and death process we are either able to make a probability statement about the population size at time $t$ or at least determine the mean population size and the variance at that time.

Stochastic elements related to a fluctuating environment can also be included in our models. For example, Levins, R. (1969) studies the effects of introducing stochasticity into the parameters $r$ (intrinsic rate of increase) and $K$ (saturation level) in the logistic model of population growth. In such cases the analysis of the probability distribution of population size is often done using the Fokker-Planck (Kolmogroff) diffusion equation where it is assumed that the variability in the environmental parameter is "white noise" (May, R.M. (1974(b), pages 116-117)). It is important to realise that the use of the diffusion equation in this way is an approximative procedure where the probability density function of a discrete random variable is being approximated by the probability density function of a continuous random variable. In choosing the appropriate diffusion model we have to be careful and adopt the proper limiting procedures for the scales being used to measure population size and time. A clear discussion of the use of diffusion models is given by Bailey, N.T.J. (1964, chapter 14) and Feller, W. (1951).

Before considering particular stochastic models we point out that our concern is with stochastic forms of deterministic models.
where the actual population size satisfies an autonomous differential equation. In particular we require that the mean behaviour of the stochastic process also satisfies the same differential equation. We are not concerned with the analysis of random fluctuations in the environmental parameters, of the type studied by Levins, R. (1969), which, as mentioned above, leads to the use of diffusion approximations.

Suppose that the population level at time \( t \) is represented by the random variable \( N(t) \). Then if the mean \( M(t) = E[N(t)] \), our autonomous differential equation can be expressed in the form

\[
\frac{1}{M(t)} \frac{dM(t)}{dt} = F[M(t)] ,
\]

where the term on the left side represents the average rate of increase per individual.

Associated with such a relationship is a system of differential equations which describes the transition probabilities. Let \( P_k(t) = P[N(t) = k | N(0) = N_0] \), then using the standard techniques for birth and death processes (see Bharucha-Reid, A.T. (1969, page 87)) we can represent this system by

\[
\begin{align*}
\frac{dP_k(t)}{dt} & = U_k P_{k-1}(t) + D_{k+1} P_{k+1}(t) - (U_k + D_k) P_k(t), \\
\frac{dP_0(t)}{dt} & = D_1 P_1(t),
\end{align*}
\]

where, \( U_k \) and \( D_k \) are called, respectively, the infinitesimal birth and death rates. \( U_k \Delta t + o(\Delta t) \) is the probability at time \( t \) that in a population of size \( k \) there will be a single birth in the next time interval \( \Delta t \). Similarly \( D_k \Delta t + o(\Delta t) \) represents the probability of a death in the next time interval \( \Delta t \) and \( o(\gamma) \) is any function such
that $\lim_{y \to 0} \frac{o(y)}{y} = 0$. It should be noted that $U_k$, $D_k$ may be functions of time in which case the process is time inhomogeneous otherwise the process is homogeneous.

We also have,

$$M(t) = \sum_{k=1}^{\infty} k P_k(t)$$  \hspace{1cm} (3.3)

The first part of our problem is to identify functions $P_k(t)$ together with transition functions $U_k$ and $D_k$ that satisfy (3.2) and (3.3) for a given $M(t)$ expressed in the form (3.1). We will consider in detail the particular case where (3.1) is logistic. In general we might not be able to evaluate the $P_k(t)$ explicitly but we might hope to at least obtain expressions for the variance.

It is immediately obvious that such solutions would be non unique but it could be hoped that we can identify a class of functions which is at least plausible.

For the second part of our problem we consider, from section 1.2, the following integral formulation,

$$B(t) = B_0(t) + \int_0^t B(t - x)\ell(x, t)\beta(x, t)dx,$$  \hspace{1cm} (3.4)

$$M(t) = M_0(t) + \int_0^t B(t - x)\ell(x, t)dx,$$  \hspace{1cm} (3.5)

$$M(t)a(x, t) = \begin{cases} M(0)a(x - t, 0) \frac{\ell(x, t)}{\ell(x - t, 0)}, & x > t, \\ B(t - x)\ell(x, t), & x \leq t, \end{cases}$$  \hspace{1cm} (3.6)

where $B(t) = \text{total birth rate}$, $\ell(x, t) = \text{survivor function}$, $\beta(x, t) = \text{age specific birth rate}$, $a(x, t) = \text{age density function}$, where in each case $x$ refers to age and $t$ to time and $M(0) = N_0$. 

Our second problem is to obtain expressions for the demographic parameters \( \ell(x,t) \) and \( \beta(x,t) \) such that the solution of (3.5) is in agreement with (3.1). A by-product of this investigation will give expressions for \( B(t) \) and \( a(x,t) \).

For the simple Malthusian (exponential) model we find the mean \( M(t) = M(0)e^{(\beta-\mu)t} \) can be obtained by choosing \( U_k = U^{(1)} + U^{(2)}M(t) \), \( D_k = D^{(1)} + D^{(2)}M(t) \), where \( U^{(1)} + U^{(2)} = \beta \), \( D^{(1)} + D^{(2)} = \mu \). Consequently, there are an infinite number of stochastic models that have a Malthusian mean. The variance for these processes is given by

\[
\frac{\beta + \mu}{2(D^{(1)} - U^{(1)}) + (\beta-\mu)} \left[ M(t) - M(0)e^{2(U^{(1)} - D^{(1)})t} \right].
\]

The most popular transition functions are \( U^{(1)} = \beta \), \( D^{(1)} = \mu \) giving a process with variance \( \frac{\beta+\mu}{\beta-\mu}M(t)[\exp((\beta-\mu)t) - 1] \).

When considering processes where (3.1) is logistic we find in general that \( \frac{U_k}{K} \) and \( \frac{D_k}{K} \) must be functions of \( M(t) \) only and thus they are time dependent and so (3.2) describes a time inhomogeneous system.

### 3.2 The Logistic Relationship

The logistic relationship is defined by (2.19) as

\[
\frac{dM(t)}{dt} = rM(t)\left[1 - \frac{M(t)}{K}\right],
\]

where \( r \) is the intrinsic rate of increase (difference between mean birth and death rates per individual for low population level).

The solution of (3.7) is,

\[
M(t) = \frac{K}{1 + A \exp(-rt)}.
\]
where,

\[ A = \frac{K - M(0)}{M(0)}. \]

The plot of \( M(t) \) against \( t \) has the following features. Starting with an initial value of \( M(0) \) less than \( K \), \( M(t) \) at first increases (roughly exponentially if \( M(0) \) is small). The initial rate for small \( M(0) \) is roughly \( rM(t) \) which increases until at \( M(t) = K/2 \) (where the slope is \( rK/4 \)) there is a point of inflexion. After this, it decreases asymptotically to zero and \( M(t) \) approaches \( K \). For \( M(0) \) greater than \( K \) the plot is no longer \( S \) shaped.

Feller, W. (1940) warned against blind faith in the use of the logistic. He considered the usual \( S \) shaped data from some experiment. He then selected several \( S \) shaped distribution functions at random from the back of a statistics book. One of these was in fact the cumulative normal distribution function. Applying the usual criteria of best fit he then ranked the various functions. The results were that the logistic fitted the data worse than the other arbitrary functions (although a better technique for fitting the data resulted in an improvement for the logistic).

His message was that "the recorded agreement between the logistic and actually observed phenomena of growth does not produce any significant new evidence in support of the logistic beyond the great plausibility of its deduction."

3.3 **Stochastic Models of the Logistic**

Stochastic models will now be considered that have a mean behaviour described by (3.7)."
individual at low population level and \( m = \text{mean mortality (death rate)} \) per individual at low population level.

We now make the following plausible assumptions: The probability of a single individual dying in the next time interval \( \Delta t \) is \( m(t)\Delta t + o(\Delta t) \); the probability of a single individual producing a single birth in the next time interval \( \Delta t \) is \( b(t)\Delta t + o(\Delta t) \); births and deaths of individuals are independent: So the system (3.2) becomes with \( U_k = k b(t) \), \( D_k = k m(t) \),

\[
\begin{align*}
\frac{dP_k(t)}{dt} &= (k - 1)b(t)P_{k-1}(t) + (k + 1)m(t)P_{k+1}(t) \\
&\quad - k(b(t) + m(t))P_{k}(t); \quad k \geq 1,
\end{align*}
\]

(3.9)

Consider,

\[
\begin{align*}
b(t) &= b \left[ 1 - \frac{\gamma_1 M(t)}{bk} \right], \\
m(t) &= m \left[ \frac{\gamma_2 M(t)}{mk} + 1 \right].
\end{align*}
\]

(3.10)

Now it is required that the model should satisfy the following conditions: The mean, \( M(t) \), behaves according to (3.7); \( b(t) \) decreases with \( t \); \( m(t) \) increases with \( t \) to the limiting value of \( b(t) \).

The first condition is satisfied if \( \gamma_1 + \gamma_2 = 1 \) and the desired behaviour for \( b(t) \) and \( m(t) \) follows if \( 0 \leq \gamma_1 \leq 1 \). The limiting value of both \( b(t) \) and \( m(t) \) is then \( b\gamma_2 + m\gamma_1 \).
Following results established by Kendall, D.G. (1948(a)) we can obtain the probability generating function as

\[
\phi(z,t) = \left[ \frac{\zeta + (1 - \zeta - \eta)z}{1 - \eta z} \right]^{M(0)},
\]

where,

\[
\zeta = \frac{mA(l - e^{-rt}) + r(b - r\gamma_1)t}{mA(l - e^{-rt}) + r(b - r\gamma_1)t + r(1 + A)},
\]

\[
\eta = \frac{bA(l - e^{-rt}) + r(b - r\gamma_1)t}{bA(l - e^{-rt}) + r(b - r\gamma_1)t + r(1 + Ae^{-rt})},
\]

\[A = \frac{K - M(0)}{M(0)}.\]

From Bailey, N.T.J. (1964, page 112) we have,

\[
P_k(t) = \sum_{j=0}^{\text{min}} \binom{M(0)}{j} \binom{M(0) + k - j - 1}{M(0) - 1} \zeta^n \left[ 1 - \zeta - \eta \right]^j,
\]

where,

\[\text{min} = \text{min}(M(0), k)\]

If we take \(\gamma_1 = \frac{b}{r}\) and \(\gamma_2 = \frac{m}{r}\) then \(\gamma_1 + \gamma_2 = 1\) and so the process has mean logistic behaviour but in this case both \(b(t)\) and \(m(t)\) asymptotically decrease to zero. Since this requires the individual to be ultimately endowed with eternal life it is of perhaps more use to the theologian rather than the demographer. Actually those individuals that reached this state would necessarily be in a state of eternal bliss as they would also be endowed with eternal sterility.

The stochastic model usually regarded as the analogue of the logistic relationship is described by Pielou, E.C. (1969). This model has,
\[ U_k = ck - dk^2 \]
\[ D_k = ek + fk^2 \]

where,
\[ c - e = r, \quad d + f = \frac{r}{k}. \]

This means that the probabilities of birth and death for a single individual in the time interval \( t \) to \( t + \Delta t \), in a population of size \( k \), depend on the actual population size \( k \) rather than the mean population size \( M(t) \), as in our model (3.10). This is a more plausible assumption. However, substituting (3.11) in (3.9), multiplying by \( k \) and summing over \( k \) gives,
\[
\frac{dM(t)}{dt} = r M(t) \left[ 1 - \frac{S(t)}{KM(t)} \right], \quad (3.12)
\]

where \( S(t) = \mathbb{E}[N^2(t)] \) and since \( S(t) > M^2(t) \) we see that,
\[
\frac{dM(t)}{dt} < r M(t) \left[ 1 - \frac{M(t)}{K} \right],
\]

which means that although the assumptions concerning individual birth and death rates are more plausible the mean behaviour of the process is no longer logistic. We note from (3.11) that the model being considered in (3.10), with the conditions \( \gamma_1 + \gamma_2 = 1, \quad 0 \leq \gamma_1 \leq 1 \), corresponds to replacing the actual population size \( k \) in (3.11) by the mean \( M(t) \) and introducing the condition that \( d \) and \( f \) are positive to ensure that the birth and death rates decrease and increase respectively to the same limiting value.

We see from (3.12) that the differential equation for the mean involves the second moment \( S(t) \). This is a particular case of the more general problem where the differential equation for the \( j \)th moment of the process involves moments higher than the \( j \)th. We
examine this problem in later sections of this chapter and propose a new technique for "decoupling" the resulting set of coupled moment equations.

We now consider the variance and age structure of the process given by (3.9) where $b(t)$ and $m(t)$ are as in (3.10).

Multiplying the $k^{th}$ differential equation of (3.9) by $k^2$ and summing over $k$ we obtain,

$$ \frac{dS}{dt} = 2Sr \left(1 - \frac{M}{K}\right) + M \left(g + \frac{rM}{K} - \frac{2r\gamma_1 M}{K}\right) $$

where,

$$ g = b + m, \quad M = M(t), \quad S = E\left[N(t)^2\right]. $$

From which,

$$ \text{VAR}(N(t)) = \left[ \frac{gt}{K} - \frac{gAe^{-rt}}{r} + \frac{r}{K} (1-2\gamma_1) t + \frac{gA}{r} \right] M^2, \quad (\text{VAR} \equiv \text{Variance}). $$

Hence, for large $t$,

$$ \text{VAR}(N(t)) \sim 2Kt(b\gamma_2 + m\gamma_1) $$

and the coefficient of variation is proportional to $\sqrt{t}$.

If $\mu(x,t)\Delta t + o(\Delta t) = \text{Probability that an individual of age $x$ at time $t$ will die in the next time interval $\Delta t$}$, then from (1.1) we have,

$$ \frac{\partial \ell(x,t)}{\partial x} + \frac{\partial \ell(x,t)}{\partial t} = -\ell(x,t)\mu(x,t); \quad \ell(0,t) = 1. \quad (3.13) $$

So provided $\int_0^X \mu(s, s+t-x) ds$ exists we have, from (1.2),

$$ \ell(x,t) = \exp\left[-\int_0^X \mu(s, s+t-x) ds\right]. \quad (3.14) $$

If we consider models where $\beta(x,t) = \beta(t)$, $\mu(x,t) = \mu$ we can solve the integral equation (3.4) by substituting $B(t)e^{\mu t} = \phi(t)$ to obtain
\[ \beta(t) \phi'(t) - [\beta'(t) + \beta(t)^2] \phi(t) = 0 . \]

Hence,

\[ B(t) = M(0) \beta(t) \exp \left[ -\mu t + \int_0^t \beta(s) ds \right] , \]

\[ M(t) = M(t) e^{-\mu t} \left[ 1 + \int_0^t \psi(x,t) dx \right] , \]

\[ a(x,t) = \begin{cases} \frac{a(x-t,0)}{1 + \int_0^t \psi(x,t) dx} , & x > t , \\ \frac{\psi(x,t)}{1 + \int_0^t \psi(x,t) dx} , & x \leq t , \end{cases} \]

where,

\[ \psi(x,t) = \beta(t-x) \exp \left[ \int_0^{t-x} \beta(s) ds \right] . \]

These results apply to our model given by (3.10), only in the case \( \gamma_1 = 1 , \gamma_2 = 0 . \)

Let us now make the assumption that the initial population consists entirely of \( M(0) \) newborn and that \( \beta(x,t) = \beta(t) \).

Then from (3.4) and (3.5),

\[ B(t) = M(0) \ell(t,t) \beta(t) + \beta(t) \int_0^t B(t-x) \ell(x,t) dx , \]

\[ M(t) = M(0) \ell(t,t) + \int_0^t B(t-x) \ell(x,t) dx . \]

It follows immediately from (3.15) and (3.16) that

\[ B(t) = M(t) \beta(t) , \]

and hence \( \beta(t) \) is always the crude birth rate. Also
a(x, t) = \begin{cases} \frac{B(t-x)\ell(x, t)}{M(t)}, & \text{for } 0 \leq x < t, \\ 0, & \text{otherwise}. \end{cases}

Now for the models we are concerned with \( \mu(x, t) = m(t) \) as in (3.10). Before proceeding we note that if \( \mu(x, t) = \mu(t) \) then (3.14) becomes

\[ \ell(x, t) = \exp\left(-\int_0^x \mu(s+t-x)ds\right). \]

So for \( \beta(t) = b(t) \) and \( \mu(t) = m(t) \) as in (3.10), we have,

\[ \ell(x, t) = \left[\frac{M(t)}{M(t-x)}\right]^{\gamma_2} \exp[-x(my_1 + by_2)], \]

\[ B(t) = M(t)b(t) = bM(t)\left[1 - \frac{ry_1M(t)}{bK}\right], \]

and

\[ a(x, t) = \begin{cases} b\left[1 - \frac{ry_1M(t-x)}{bK}\right]\left[\frac{M(t-x)}{M(t)}\right]^{\gamma_1} \exp[-x(my_1 + by_2)], & \text{for } 0 \leq x < t, \\ 0, & \text{otherwise}. \end{cases} \]

Thus asymptotically \( B(t) \) approaches \( K(my_1 + by_2) \) and \( a(x, t) \) approaches \( (by_2 + my_1)\exp[-x(by_2 + my_1)] \).

3.4 Conclusions Regarding Stochastic Models of the Logistic

Stochastic models have been described that have mean behaviour corresponding to the logistic. Superficially these appear to be reasonable models since they require that the individual birth rate be initially greater than the death rate and that the birth rate decreases while the death rate increases with time to the same value. At this stage the process becomes a symmetric random walk.
However, there is a serious defect in these models which makes their use for simulation suspect. The models assume that the density dependent effect is based on the mean population rather than the actual population level. Unfortunately any attempt to take account of the actual population level in determining the transition probabilities results in the introduction of higher moments and the loss of the logistic relationship.

This means that one cannot simulate these processes on a computer relying only on information contained in the simulated population level; one must also evaluate independently the expression for the mean value.

The demographic implications follow immediately from this simulation model. The density dependence is not directly in terms of the actual numbers in the population but in terms of the expected numbers. Thus although the probability of the population increasing from $N(t)$ to $N(t) + 1$ during a small time interval $\Delta t$ is proportional to $N(t)$, the probability of an individual giving birth is not a function of $N(t)$ but a function of the expected numbers.

The same implications apply for deaths. Consider the following experiment to illustrate this. We place some people, say 100, in a closed environment with some food. After a given time, say 20 years, we single out a person and try to guess the probability of this person dying during the next small time interval. We are able to observe the number of people at this time.

Surely the most demographically plausible assumption would be that this probability should be proportional to the actual number of people. Thus, if there were 1000 people present there would be a high probability of any individual dying whilst if there were 3 people
there should be only a small probability.

Unfortunately the insistence that the mean behaviour must be logistic casts out this plausible assumption and denies that the actual number of people is significant. In its place it assumes that the mean number in the population determines the probability. In other words the logistic behaviour tells us that instead of counting the number of people present, we must ignore this information and look at a clock to see how long it is since the beginning of the experiment, this time then allows us to compute the mean numbers from the logistic equation and only on this basis are we to calculate our probability. So whether we have 3 or 1000 people present, logistic behaviour tells us that the probability of one of these dying is exactly the same. Surely any demographer knows better.

The conclusion is that the logistic and perhaps all other autonomous equations (and sets of such equations) require individual behaviour that is just not demographically acceptable.

On this basis such relationships have no special claim which better suit them to describe demographic populations than other arbitrary functions that have been selected on statistical best fit criteria. The "plausibility" that Feller ascribed to the logistic in our earlier reference disappears once we attempt to look at an individual in the population.

3.5 The Moment Equations of a Stochastic Process

In studying birth and death processes, where the population level at time $t$ is given by the random variable $N(t)$, we consider the system of equations (3.2). The differential equation for the $j^{th}$
moment, \( M_j(t) = E(N^j(t)) \), is obtained from (3.2) by multiplying by \( k^j \) and summing over \( k \) to give,

\[
\frac{dM_j(t)}{dt} = \sum_k [U_k((k+1)^j-k^j) - D_k(k^j-(k-1)^j)]P_k(t), \quad j \geq 1 . \quad (3.17)
\]

If \( U_k = \sum_{i=0}^{n} \alpha_i k^i \) and \( D_k = \sum_{i=0}^{n} \beta_i k^i \) we have, from (3.17), that the differential equation for \( M_j(t) \) will be free of moments higher than the \( j \)th provided \( \alpha_2 = \beta_2 \) and \( \alpha_i = \beta_i = 0 \) for \( 3 \leq i \leq n \).

In this case the system of differential equations (3.17) can be solved successively. If this condition is violated we find that the differential equation for \( M_j(t) \) involves moments higher than the \( j \)th and consequently the system of differential equations, an open coupled set, cannot be solved successively. Various methods of decoupling this set of equations have been proposed.

If we are concerned only with obtaining estimates of the first \( \ell \) moments Goel, N.S., Richter-Dyn, N. (1974) suggest expressing all the moments higher than the \( \ell \)-th moment, appearing in the first \( \ell \) equations, in terms of the first \( \ell \) moments. This is done by using,

\[
M_j(t) = M_\ell(t) M_{j-\ell}(t), \quad j > \ell .
\]

Wang, Y.K. (1971) assumes that \( M_j(t) \equiv \xi_j \) is a smooth function of \( j \) and uses this to express \( \xi_j , j > \ell , \) in terms of \( \xi_1, \xi_2, \ldots, \xi_\ell \) by polynomial extrapolation where in general,

\[
\xi_j = \sum_{i=1}^{\ell} (-1)^{\ell-i} \binom{\ell-i}{i} \binom{j-i-1}{\ell-1} \xi_i , \quad j > \ell .
\]

Bailey, N.T.J. (1964) suggests setting the \((\ell+1)\)th cumulant of the process to zero. This is equivalent to expressing the \((\ell+1)\)th moment in terms of lower moments and as with the previous two suggestions
results in a set of \( \ell \) nonlinear differential equations which may be solved by numerical methods. Truncation of the set of equations (3.17) at a higher order results in an improvement of the estimates of the moments but is achieved at the expense of more difficult computation.

If only estimates of \( M_1(t) \) and \( M_2(t) \) are required then McQuarrie, D.A. (1968) suggests two techniques. Each of these avoids the numerical solution of a pair of nonlinear differential equations as required by any of the previous methods. McQuarrie presents these two approaches in discussing a stochastic model of an irreversible biomolecular chemical reaction for which results obtained from the exact equations of the process are available for comparison.

We describe a new technique for estimating \( M_1(t) \) and \( M_2(t) \) which compares favourably with the two techniques proposed by McQuarrie and produces estimates in closer agreement with the exact solutions. We also consider a biologically plausible model of population growth for which Kendall, D.G. (1949) has shown that the moments can not be found explicitly by the use of the moment generating function. Applying our technique, as well as McQuarrie's, to the estimation of the first two moments of this growth process illustrates a serious defect in one of the techniques suggested by McQuarrie.

3.6 Estimating the First and Second Moments

We are particularly concerned with estimates of \( M_1(t) \) and \( M_2(t) \) when \( U_k = \alpha_o + \alpha_1 k + \alpha_2 k^2 \), \( D_k = \beta_o + \beta_1 k + \beta_2 k^2 \) and \( \alpha_2 \neq \beta_2 \). In (3.17) this gives,

\[
\frac{dM_1(t)}{dt} = c_o + c_1 M_1(t) + c_2 M_2(t),
\]

(3.18)
\[
\frac{dM_2(t)}{dt} = c_0 + (2c_0 + d_1)M_1(t) + (2c_1 + d_2)M_2(t) + 2c_2M_3(t), \quad (3.19)
\]

where,

\[c_i = \alpha_i - \beta_i, \quad d_i = \alpha_i + \beta_i, \quad \text{for } i = 0, 1, 2.\]

Following Goel, N.S., et al., we would replace \(M_3(t)\) in (3.19) by \(M_1(t)M_2(t)\). Wang's technique would replace \(M_3(t)\) by \(\left(2\sqrt{M_2(t)} - M_1(t)\right)^3\) and Bailey's suggestion amounts to using \(M_3(t) = 3M_1(t)M_2(t) - 2M_1^3(t)\). Any of these approaches will produce a pair of simultaneous nonlinear differential equations which could be integrated by a numerical method.

McQuarrie offers two techniques for avoiding the often expensive task of solving these nonlinear differential equations. The first technique introduces the simplifying assumption that \(M_2(t) = M_1^2(t)\) in (3.18). It is important to realise that this is equivalent to assuming that the variance of the stochastic process is zero. In this case, the solution is the same as that obtained from the deterministic model of the process. In this case, from (3.18) we have,

\[
M_1(t) = \begin{cases} 
\frac{Ae^{at} - B}{2c_2[1-Ce^{at}]}, & c_1 > 4c_o c_2, \\
\frac{2N_0 + (N_1c_1 + 2c_2)t}{2 -(2c_2N_0 + c_1)t}, & c_1 = 4c_o c_2,
\end{cases} \quad (3.20)
\]

where,

\[a = \sqrt{c_1^2 - 4c_o c_2}, \quad B = c_1 - a, \quad D = c_1 + a. \quad C = \frac{2c_2N_0 + B}{2c_2N_0 + D}, \quad A = DC.\]

Substituting (3.20) into (3.19) gives an equation of the form,
\[
\frac{dM_2(t)}{dt} + P(t)M_2(t) = Q(t), \text{ which can be solved, using the integrating factor } \exp\left[\int P(t)dt\right], \text{ to give an estimate of } M_2(t). \text{ Equation (3.20) is a more general result than that proposed by McQuarrie since he considered the use of this technique in relation to (3.24) and (3.25), which are special cases of (3.18) and (3.19).}
\]

To gain insight into the second technique used by McQuarrie we make the simplifying assumption that \( M_2(t) = f(t)M_1(t) \). Differentiating and using (3.18) gives

\[
\frac{dM_2(t)}{dt} = f^1(t)M_1^2(t) + 2f(t)M_1(t) \frac{dM_1(t)}{dt},
\]

\( (3.21) \)

If we insist that (3.21) is identical to (3.19) at \( t = 0 \), using \( M_2(0) = M_1^2(0) = N_o^2 \), we have,

\[
f(0) = 1 \text{ and } f^1(0) = \frac{d_o + d_1N_o + d_2N_2^2}{N_o^2}.
\]

Consequently, we see why McQuarrie assumes that,

\[
M_2(t) = M_1^2(t)e^{pt},
\]

where,

\[
p = \frac{d_o + d_1N_o + d_2N_2^2}{N_o^2}.
\]

By using (3.22) in (3.18) together with the substitution,

\[
M_1(t) = -\frac{du(t)}{dt}/c_2u(t)e^{pt},
\]

we can obtain the series solution,

\[
M_1(t) = \frac{c_2N_o - \sum_{n=2}^{\infty} nu^{n-1}}{c_2[1 - c_2N_o t + \sum_{n=0}^{\infty} u^n t^n]e^{pt}},
\]

\( (3.23) \)
where,
\[ n(n-1)u_n - (c_1 + p)(n-1)u_{n-1} + c_0 c_2^m \sum_{m=0}^{n-2} \frac{u_p^{n-2-m}}{(n-2-m)!} = 0, \quad n \geq 2, \]
\[ u_0 = 1, \quad u_1 = -c_2 N_0. \]

Using (3.23) in (3.22) gives our estimates for \( M_2(t) \). It should be noted that the assumption expressed in (3.22) is equivalent to assuming the process has a coefficient of variation (c.v.) given by,
\[ (c.v.)^2 = \frac{M_2(t) - M_1^2(t)}{M_1^2(t)} = e^{pt} - 1. \]

For the chemical reaction considered by McQuarrie in (3.24) and (3.25) this assumption seems reasonable. However, as we see in discussing a population process represented by (3.27) and (3.28) this assumption can not be made for all processes. Again the estimates given by (3.23) and (3.22) are more general than those used by McQuarrie who was considering (3.24) and (3.25). As we shall see closed form expressions can often be obtained for \( M_1(t) \) and \( M_2(t) \) in (3.23) and (3.22).

The technique we wish to describe assumes that \( M_2(t) = M_1^2(t) \) in (3.18) and consequently we would arrive at the same estimate of \( M_1(t) \) as obtained by McQuarrie in (3.20). This estimate is then used in (3.19) together with the substitution, \( M_3(t) = 3M_1(t)M_2(t) - 2M_1^3(t) \). The result is that (3.19) becomes a differential equation in \( M_2(t) \) only. It is different in general from that obtained by McQuarrie's first technique, described above, but is still of a form that can be readily solved analytically by the use of an appropriate integrating factor. McQuarrie's first technique could be described as being based on Goel's suggestion for decoupling (3.18) and (3.19) while the present technique is based on Bailey's suggestion where, in both cases, the solution of a pair of nonlinear simultaneous differential
equations has been avoided by assuming $M_1(t) = M_2(t)$ in (3.18).

### 3.7 A Stochastic Model of a Chemical Process

In studying a stochastic model of an irreversible bimolecular reaction McQuarrie considered the differential equations for the moments of the process as given by,

\[
\frac{dM_1(t)}{dt} = rM_1(t) - rM_2(t), \quad (3.24)
\]

\[
\frac{dM_2(t)}{dt} = -2rM_1(t) + 4rM_2(t) - 2rM_3(t), \quad (3.25)
\]

which are a particular case of (3.18) and (3.19).

Using McQuarrie's first technique to decouple (3.24) and (3.25) we have, from (3.20),

\[
M_1(t) = \frac{N_0}{N_0 + (1-N_0)e^{-rt}},
\]

which when used in (3.25), gives,

\[
M_2(t) = M_1^2(t) \left[ \frac{2}{3} \left( \frac{N_0-1}{N_0} \right) (e^{2rt}e^{-rt}) + 1 \right],
\]

and

\[
(c.v.)^2 = \frac{2}{3} \left( \frac{N_0}{N_0} \right) (e^{2rt}e^{-rt}).
\]

Numerical values based on these estimates are shown in Table 1 under the column headed "Method 1". The results compare favourably with values obtained from considering the exact equations for the reaction as shown in the same table under the heading "Exact Solutions".
<table>
<thead>
<tr>
<th>$n_{rt}$</th>
<th>Method 1 $M_1(t)/n_0$ c.v.</th>
<th>Method 2 $M_1(t)/n_0$ c.v.</th>
<th>Method 3 $M_1(t)/n_0$ c.v.</th>
<th>Exact Solutions $M_1(t)/n_0$ c.v.</th>
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TABLE 2
THE NUMERICAL SOLUTIONS OF THE NONLINEAR PAIR OF EQUATIONS (3.24) AND (3.25)

<table>
<thead>
<tr>
<th>( M_3(t) ) in (3.24) replaced by ( M_1(t)M_2(t) )</th>
<th>Goel Wang Bailey</th>
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<tr>
<td>( 2\sqrt{M_2(t)} - M_1(t) )^3 ( 3M_1(t)M_2(t) - 2M_1^3(t) )</td>
<td>( M_1(t)/N_0 ) c.v.</td>
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<tr>
<td>1.50</td>
<td>0.397</td>
<td>0.279</td>
<td>0.492</td>
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If McQuarrie's second technique, which led to the estimates (3.23) and (3.22), is applied to (3.24) and (3.25) we have,

\[ M_1(t) = \frac{N_0(p+r)}{N_0 e^{pt} - (rN_o - p - r)e^{-rt}}, \]

\[ M_2(t) = M_1^2(t)e^{pt}, \]

where,

\[ p = 2r \left( \frac{N_o - 1}{N_o} \right), \]

and,

\[ (c.v.)^2 = e^{pt} - 1. \]

These estimates have been used to arrive at the numerical values in the column headed "Method 2" of table 1. They can be seen to be in reasonable agreement with those headed "Method 1" and also those under the heading "Exact Solutions".

Following our technique we find that,

\[ M_1(t) = \frac{N_o}{N_o + (1-N_o)e^{-rt}}, \]

\[ M_2(t) = \sum_{n=1}^{6} Q_n e^{nt} / (e^{rt} + A)^6, \]

\[ (c.v.)^2 = \sum_{n=1}^{6} Q_n e^{rt(n-2)} \left( \frac{e^{rt} + A}{(e^{rt} + A)^4} \right) - 1, \]

where,

\[ A = \frac{1-N_o}{N_o}, \quad Q_1 = \frac{2A^5}{3}, \quad Q_2 = 5A^4, \quad Q_3 = 16A^3, \]

\[ Q_4 = (N_o^{-4} - 1 - 2A - 16A^3 - 5A^4 - 2A^5 - 8A^{2rt}), \quad Q_5 = 2A, \]

\[ Q_6 = 1. \]
Numerical values based on these estimates appear in table 1 under the heading "Method 3". They show much closer agreement with the values under "Exact Solutions" than those obtained by either of the previous two techniques and are still readily calculated on a desk calculator.

Table 2 shows the numerical solutions of the nonlinear pair of equations (3.24) and (3.25), obtained by replacing \( M_3(t) \) in (3.25) by the expressions suggested by Goel, N.S., et al., Wang and Bailey. A fourth order Runge-Kutta method was used to obtain the solutions which compare favourably with the solutions shown in table 1.

### 3.8 A Stochastic Population Process

For the population we define:

- \( b \) = the mean birth rate per individual at low population level,
- \( m \) = mean mortality (death rate) per individual at low population level,
- \( r = b - m \).

Now consider the model described by (3.2) where,

\[
U_k = kb \left[ 1 - \frac{r \gamma_1 k}{bK} \right], \\
D_k = km \left[ 1 + \frac{r \gamma_2 k}{mK} \right],
\]

with,

\( r > 0, \ K > N_0 \geq 1 \).

Hence, if the population is of size \( k \) at time \( t \) then \( U_k \Delta t + o(\Delta t) \) and \( D_k \Delta t + o(\Delta t) \) represent the probabilities of a birth and death respectively in the next time interval \( \Delta t \). Realistically these probabilities should depend on \( k \), the present population size, and
should decrease and increase respectively to the same limiting value as $k$ approaches $K$. Such is the case if we use $U_k$, $D_k$ as in (3.26) with the condition that $\gamma_1 + \gamma_2 = 1$, $0 \leq \gamma_1 \leq 1$.

Using (3.26) in (3.18) and (3.19) we have,

$$\frac{dM_1(t)}{dt} = rM_1(t) - \frac{r}{K}M_2(t), \quad (3.27)$$

$$\frac{dM_2(t)}{dt} = d_1M_1(t) + (2r+d_2)M_2(t) - \frac{2r}{K}M_3(t), \quad (3.28)$$

where,

$$d_1 = b + m, \quad d_2 = \frac{r}{K}(1-2\gamma_1).$$

Decoupling (3.27) and (3.28) by McQuarrie's first technique we have,

$$M_1(t) = \frac{K}{1 + \left(\frac{K-N_o}{N_o}\right)e^{-rt}}, \quad (3.29)$$

$$M_2(t) = \left\{ \begin{array}{l}
\frac{M_2(t)}{K^2} \left[ K^2 + \frac{d_1K}{d_2} + \frac{K(L-N_o)d_1}{N_o(r+d_2)} \right] e^{d_2t} - \left[ \frac{d_1K}{d_2} + \frac{Kd_1(K-N_o)e^{-rt}}{N_o(r+d_2)} \right] \\
M_2(t) \left[ 1 + \frac{d_1t}{K} + \frac{d_1(K-N_o)}{N_oKr} (1-e^{-rt}) \right], \quad d_2\neq 0,
\end{array} \right.$$

For large values of $t$, these estimates become,

$$M_1(t) = K, \quad M_2(t) = -\frac{Kd_1}{d_2}, \quad d_2 > 0,$$

$$M_1(t) = K, \quad M_2(t) = \left\{ \begin{array}{l}
\frac{d_1K}{d_2} + \frac{Kd_1(K-N_o)}{N_o(r+d_2)} e^{d_2t} - \frac{d_1K}{d_2}, \quad d_2 = 0,
\end{array} \right.$$
\[ (c.v.)^2 = \begin{cases} \frac{-d_1}{\kappa d_2} - 1, & d_2 < 0, \\
\frac{d_1 t}{K} + \frac{d_1 (K-N_o)}{r KN_o}, & d_2 = 0. \end{cases} \]

The approximate solution for \( M_1(t) \) in (3.29) is recognised as the familiar logistic equation. Since it was obtained by using \( M_2(t) = M_1^2(t) \) in (3.27) we conclude that the stochastic population model has mean behaviour which is approximated by the deterministic logistic relationship,

\[ \frac{dN(t)}{dt} = rN(t) - \frac{r}{K} N^2(t), \]

and in this sense could be described as a stochastic version of the logistic population model.

Using our technique for obtaining estimates of \( M_1(t) \) and \( M_2(t) \) we have, \( M_1(t) \) as in (3.29),

\[ M_2(t) = \begin{cases} \frac{M_1^2(t)}{K(e^{rt}+A)} \left\{ \sum_{n=-1}^{4} Q_0 e^{nrt} + \left[ K N_o - \sum_{n=-1}^{4} Q_n \right] e^{2t} \right\}, & d_2 \neq 0, \\
\frac{M_1^2(t)}{K(e^{rt}+A)} \left\{ \sum_{n=-1}^{4} R e^{nrt} + \left[ K N_o - \sum_{n=1}^{4} R_n - \frac{A^5 d_{1/2}}{r} \right] \right\}, & d_2 = 0, \end{cases} \]

where,

\[ A = \frac{K-N_o}{N_o}, \quad Q_0 = -\frac{A^5 d_1}{r+d_2}, \quad Q_1 = -\frac{5A^4 d_1}{d_2}, \quad Q_2 = \frac{2A^3(5d_1+2rK)}{2r-d_2}, \quad Q_3 = \frac{A(5d_1+12rK)}{3r-d_2}, \quad Q_4 = \frac{d_1+4rK}{4r-d_2}. \]
\( R_n = Q_n \), with \( d_2 = 0 \), for \( n = -1,1,2,3,4 \), \( R_0 = 5A^4d_1t \).

For large values of \( t \) we have,

\[
M_1(t) = K, \quad M_2(t) = \frac{K(d_1+4rK)}{4r-d_2},
\]

\[
(c.v.)^2 = \frac{d_1Kd_2}{K(4r-d_2)}.
\]

Both techniques assume a mean population size which is approximately logistic. However, our technique leads to a smaller estimate for \( M_2(t) \) than that obtained by McQuarrie's method.

Turning to the second technique proposed by McQuarrie we assume \( M_2(t) = M_1^2(t)e^{pt} \) in (3.27). Solving for \( M_1(t) \) we have,

\[
M_1(t) = \frac{N_0K(r+p)}{[(K(r+p)-rN_0)e^{-rt}+rN_0e^{pt}]}
\]

where, from (3.22),

\[
p = d_1 + d_2N_0,
\]

\[
M_2(t) = M_1^2(t)e^{d_1+d_2N_0},
\]

and,

\[
(c.v.)^2 = e^{d_1+d_2N_0} - 1.
\]

For \( 0 \leq \gamma_1 < 1 \), \( p > 0 \). As \( t \) increases \( M_1(t) \) increases to a maximum value of \( \frac{pN_0}{K(r+p)-rN_0} \), at \( t = \frac{1}{(r+p)}ln\left(\frac{K(r+p)-rN_0}{pN_0}\right) \), then decreases asymptotically to zero. In view of our assumptions about the transition probabilities for the model the approximate solution we have obtained for \( M_1(t) \), by this technique, seems quite unrealistic. This would indicate that care will need to be taken in assuming that
\( M_1^2(t)e^{pt} = M_2(t) \) as a basis for decoupling moment equations of the type in (3.18), (3.19). On the other hand, both our technique and McQuarrie's first method provide estimates which seem plausible.
4. A BINARY FISSION PROCESS

4.1 Introduction

We consider the population of a mixture of cells, some of which are fissioning (viable cells) and the remainder are vegetative (non-viable cells). The fissioning cells have a random life-time (generation time). When a fission occurs exactly two new cells are produced. On average, at time $t$, $\alpha(t)$ of these two new cells are fissioning cells, capable of further division, while the remaining $2 - \alpha(t)$ are vegetative cells.

By modifying the integral formulation presented in chapter 1 expressions are obtained for determining the total birth rate, the mean number of cells and the age structure for both classes of cells for both transient and stable growth, where the terms "transient" and "stable" are taken to have the meanings defined in section 1.3.

Thornley, J.M. (1976) gives expressions for the mean numbers and the age structures by assuming the fissioning process is initially stable with a constant generation time for all the fissioning cells. Powell, E.O. (1956) also assumes a stable fissioning population and working with a variable generation time considers the age structure and growth rate of the viable cells. He suggests, on the basis of extensive empirical evidence, that the generation time distribution is adequately represented by the Pearson type III distribution. This assumption is supported by Kendall, D.G. (1948) who deals with the particular case where $\alpha(t) = 2$, that is, no vegetative cells are produced. We consider plausible choices for the generation time distribution and analyse the model with particular forms of time dependence in $\alpha(t)$. The transient solutions are emphasized since we
feel that the preoccupation in the literature with the stable solutions may not be justified in terms of the variability of environmental and other factors which influence the process.

Let $q_i$ (i=0,1,2) be the probability of a fission producing i viable cells. Then we can compare our integral model with the formulation of the problem as an age-dependent Bellman-Harris process. Processes of this type form part of the study of branching process and have their background in the physical and biological (cells, bacteria) sciences. They developed separately from the models favoured by demographers, such as the integral model of Lotka and the stochastic models of Kendall, the major developments being due to the work of Bellman, R., Harris, T.E. (1948, 1952). A detailed discussion of branching processes and their relationship to the other lines of development in population dynamics is given by Jagers, P. (1975) and Bharucha-Reid, A.T. (1960, pages 94-98).

4.2 A modification of the Integral Formulation

For the fissioning cell population we define:

$f(x) = \text{generation time density function.}$

$F(x) = \text{probability that a newborn cell will have fissioned before age } x.$

$l(x) = \text{probability that a newborn cell will not have fissioned before age } x.$

$\mu(x) = \text{age specific fission rate.}$

$c(x) = \text{density function for the age of fissioning cells in the stable population (Powell's "carrier distribution" Powell, E.D. (1956)).}$

$Y = \text{the mean age of these cells.}$
Only one of these is independent and they are connected by the relationships: \( F(x) = \int_0^x f(u) \, du \), \( f(x) = \mu(x) \ell(x) \), \( \ell(x) = \exp\left[-\int_0^x \mu(s) \, ds\right] \), see (1.1), (1.2), (1.3).

At time \( t \) for the viable cells let,

- \( D(t) = \) total death rate,
- \( M(t) = \) mean number,
- \( B(t) = \) total birth rate,
- \( a(x,t) = \) age density function,
- \( \beta(x,t) = \) age specific fecundity.

Viable cells alive at \( t \) of age \( x \) to \( x + \Delta x \) must have been produced between \( t - x \) and \( t - (x + \Delta x) \) and not fissioned before reaching age \( x \). Thus,

\[
B(t - x)\Delta x \ell(x) = M(t)a(x,t)\Delta x ,
\]

and summing over all ages we have,

\[
M(t) = \int_0^\infty B(t - x)\ell(x) \, dx .
\]

The birth rate of viable cells at time \( t \) of age \( x \) to \( x + \Delta x \) is \( B(t) \Delta x \ell(x)\beta(x,t) \). Hence,

\[
B(t) = \int_0^\infty B(t - x)\ell(x)\beta(x,t) \, dx .
\]

Similarly,

\[
D(t) = \int_0^\infty B(t - x)\ell(x)\mu(x) \, dx .
\]

\( M(t)a(x,t)\Delta x \) is the number of fissioning cells at time \( t \) in the age range \( x \) to \( x + \Delta x \) and \( \mu(x)\Delta t \) is the fraction that will fission in the next \( \Delta t \). Each fission produces \( a(t) \) viable cells. \( \beta(x,t)\Delta t \) is the fraction of newly fissioned cells due to mothers of
age \( x \) to \( x + \Delta x \). Hence, \( \beta(x,t) = \alpha(t)\mu(x) \). Using this result and our relationship between \( f(x) \), \( \ell(x) \) and \( \mu(x) \) we have,

\[
M(t) = \int_0^\infty B(t - x)\ell(x) \, dx ,
\]

\[
B(t) = \alpha(t) \int_0^\infty B(t - x)f(x) \, dx ,
\]

\[
D(t) = \int_0^\infty B(t - x)f(x) \, dx .
\]

(4.1)

Since \( \frac{dM(t)}{dt} = B(t) - D(t) \) and \( B(t) = \alpha(t)D(t) \) we have

\[
\frac{dM(t)}{dt} = \frac{B(t)}{\gamma(t)} , \text{ where } \gamma(t) = \frac{\alpha(t)}{\alpha(t) - 1} .
\]

If there are \( M(0) \) viable cells initially then

\[
M(t) = M(0) + \int_0^t B(u) \gamma(u) \, du .
\]

(4.2)

The intrinsic rate of increase \( r(t) = \frac{dM(t)}{dt} / M(t) \). Hence,

\[
r(t) = \frac{B(t)}{\gamma(t)M(t)} = \frac{a(o,t)}{\gamma(t)} ,
\]

(4.3)

where \( a(o,t) \) is the crude birth rate \( (B(t)/M(t)) \).

The set of equations (4.1) requires a full history of the remote past. To overcome this difficulty suppose that we know the number of viable cells \( M(o) \) at some origin and that we also know the age density \( a(x,o) \) at this origin. Then the birth rate at time \( t \) due to viable cells alive at the origin is given by

\[
M(0) \int_0^\infty a(x,o)\frac{\ell(x + t)}{\ell(x)} \beta(x + t,t) \, dx = M(0) \int_0^\infty a(t)a(x,o)\frac{f(x + t)}{\ell(x)} \, dx
\]

and the birth rate due to viable cells produced since the origin is

\[
\int_0^t B(t - x)\ell(x)\beta(x,t) \, dx = \int_0^t \alpha(t)B(t - x)f(x) \, dx .
\]
Hence,
\[ B(t) = a(t)M(0)\psi_1(t) + a(t) \int_0^t B(t - x)f(x) \, dx , \]
where,
\[ \psi_1(t) = \int_0^t a(x,0)\frac{f(x + t)\,dx}{\ell(x)} . \]  

In a similar way we can show that,
\[ M(t) = M(0)\psi_2(t) + \int_0^t B(t - x)\ell(x) \, dx , \]
where,
\[ \psi_2(t) = \int_0^\infty a(x,0)\frac{\ell(x + t)\,dx}{\ell(x)} . \]  

By considering the number of fissioning cells alive at time \( t \) of age \( x \) to \( x + \Delta x \) we have
\[ M(t)a(x,t) = \begin{cases} M(0)a(x - t,0)\frac{\ell(x)}{\ell(x - t)} , & \text{for } x \geq t , \\ B(t - x)\ell(x) , & \text{for } 0 \leq x < t . \end{cases} \]  

Taking the Laplace transform of \( M(t) \) in (4.2) and (4.5) it is easy to show that both expressions for \( M(t) \) are the same.

Equations (4.2) through to (4.6) provide a full description of the viable cell population.

The subscripts \( V \) and \( T \) will be used to describe the vegetative cell population and total population respectively. The following equations can be derived by arguments similar to those used in describing the viable cell population.
\[ B_V(t) = \left[ \frac{2 - \alpha(t)}{\alpha(t)} \right] B(t) \quad (4.7) \]
\[ M_V(t) = M_V(o) + \int_0^t B_V(u) \, du \quad (4.7) \]

where \( M_V(o) \) is the initial number of vegetative cells.

\[ r_V(t) = a_V(o, t) \]
\[ M_V(t)a_V(x,t) = \begin{cases} M_V(o)a_V(x - t, o), & \text{for } x \geq t, \\ B_V(t - x), & \text{for } o \leq x < t. \end{cases} \quad (4.8) \]

Hence,
\[ B_T(t) = B(t) + B_V(t) = \frac{2B(t)}{\alpha(t)}, \quad (4.9) \]
\[ M_T(t) = M_T(o) + \int_0^t \frac{B(u)}{\alpha(u)} \, du \quad (4.9) \]

where,
\[ M_T(o) = M_V(o) + M(o). \]
\[ r_T(t) = \lambda a_T(o, t), \]
\[ M_T(t)a_T(x,t) = \begin{cases} M(o)a(x - t, o)\frac{\ell(x)}{\ell(x - t)} + M_V(o)a_V(x - t, o), & \text{for } x \geq t, \\ B(t - x)\ell(x) + B_V(t - x), & \text{for } o \leq x < t. \end{cases} \quad (4.10) \]

\[ \alpha(t) = \text{constant}. \]

We now assume that \( \alpha(t) = \alpha(\text{constant}) \). Powell, E.O. (1956) claims that for well-nourished cells we can expect \( \alpha = 2 \). Then taking Laplace transforms in (4.4) we have,
\[ B^*(s) = \frac{\alpha M(o) \ell^*(s)}{1 - \alpha \ell^*(s)}. \]

This enables us to express \( B(t) \) as \( \sum_{j=0}^{\infty} \lambda_j e^{r_j t} \), where \( s = r_o \) is the largest real root of \( 1 - \alpha \ell^*(s) = 0 \). Complex roots occur in conjugate pairs with real parts less than \( r_o \) and \( \lambda_j \) is given by
This completes the set of equations necessary to analyse the process during the transient stage of growth.

**The Stable Population**

To analyse the process during the stable stage of growth we see that if $A = A_o$ and $r = r_o$ then in the stable population,

$$B(t) = A e^{rt}.$$  

By considering, $\int_0^{\infty} af(x) \, dx = \alpha$, we note that $\alpha$ greater than, equal to, less than unity implies $r$ is positive, zero, negative respectively. Hence,

$$M(t) = \begin{cases} \frac{A e^{rt}}{\gamma r}, & \alpha \neq 1, \, \gamma = \frac{\alpha}{\alpha - 1}, \\ M(0), & \alpha = 1, \end{cases}$$

$$M(t) a(x,t) = A e^{r(t-x)} \ell(x), \text{ for } 0 \leq x < t.$$ 

For the vegetative cells,

$$B_v(t) = \left[ \frac{2 - \alpha}{\alpha} \right] A e^{rt}, \quad M_v(t) = \left[ \frac{\alpha - 2}{\alpha - 1} \right] M(0) + M_v(0) + \left[ \frac{2 - \alpha}{ar} \right] A e^{rt},$$

for $\alpha \neq 1$.

We note that,

$$\frac{dM_v(t)}{dt} = A, \text{ for } \alpha = 1.$$ 

$$M_v(t) \cdot a_v(x,t) = \begin{cases} \left[ \frac{2 - \alpha}{\alpha} \right] A e^{r(t-x)}, & \text{for } 0 \leq x < t, \\ M_v(0) \cdot a_v(x-t,0), & \text{for } x \geq t. \end{cases}$$
Considering the total population we have:

\[ B_T(t) = \frac{2A}{\alpha} e^{\alpha t}, \quad M_T(t) = \left( \frac{\alpha - 2}{\alpha - 1} \right) M(o) + \frac{A e^{\alpha t}}{\alpha r} , \]

for \( \alpha \neq 1 \) and \( \frac{dM_T(t)}{dt} = A \), for \( \alpha = 1 \).

\[ M_T(t) a_T(x,t) = \begin{cases} Ae^{r(t-x)} \left( l(x) + \frac{2 - \alpha}{\alpha} \right), & \text{for } 0 \leq x < t , \\ M_V(o) a_V(x-t,o), & \text{for } x \geq t . \end{cases} \]

The crude birth rate for the viable cells = \( a(o,t) = \begin{cases} \gamma r, & \text{for } \alpha \neq 1 , \\ \frac{A}{M(o)}, & \text{for } \alpha = 1 . \end{cases} \)

For the non-viable cells,

\[ r_V(t) = a_V(o,t) = \frac{2 - \alpha}{\alpha} Ae^{rt} \left[ M_V(o) + \left( \frac{\alpha - 2}{\alpha - 1} \right) M(o) + \frac{2 - \alpha}{\alpha r} \right], \]

for \( \alpha \neq 1 \), while \( M_V(t) a_V(o,t) = A \), for \( \alpha = 1 \).

For the total cell population,

\[ 2r_T(t) = a_T(o,t) = \frac{2}{\alpha} Ae^{rt} \left[ M_V(o) + \left( \frac{\alpha - 2}{1 - \alpha} \right) M(o) + \frac{A e^{\alpha t}}{\alpha r} \right], \]

for \( \alpha \neq 1 \), while \( M_T(t) a_T(o,t) = 2A \), for \( \alpha = 1 \).

From these results the following observations can be made.

The viable cell population is stationary at \( M(o) \) when \( \alpha = 1 \). Otherwise, as \( t \) increases it decreases to a limiting value of zero, when \( 0 < \alpha < 1 \) and increases without bound, for \( 1 < \alpha \leq 2 \).

If \( 1 < \alpha \leq 2 \) the youngest viable cells are present in the greatest proportion. As \( t \) increases the number of young viable cells increases.
for $1 < \alpha \leq 2$, decreases for $0 < \alpha < 1$ and is constant for $\alpha = 1$.

The viable cell population has a stable age distribution (independent of $t$) for $1 < \alpha \leq 2$.

The vegetative cell population is constant at $M_v(o)$ for $\alpha = 2$.

Otherwise, as $t$ increases, it increases to a limiting value of

$$\left[\frac{2 - \alpha}{1 - \alpha}\right] M(o) + M_v(o),$$

for $0 < \alpha < 1$, and increases without bound for $1 < \alpha < 2$. If $\alpha = 1$ the vegetative cells are being produced at a constant rate, $A$, for large values of $t$. As $t$ increases, the number of young vegetative cells increases for $1 < \alpha < 2$, decreases to a limit of zero for $0 < \alpha < 1$ and remains constant for $\alpha = 1$.

Although $a(x,t)$ is independent of $t$ for large values of $t$ this is not generally true for $a_v(x,t)$. As $t \to \infty$ we see that

$$a_v(x,t) \to \begin{cases} re^{-rx}, & \text{for } 1 < \alpha < 2, \\ 0, & \text{for } 0 < \alpha < 1. \end{cases}$$

It is interesting to note that if $M_v(o) = \left[\frac{2 - \alpha}{\alpha - 1}\right] M(o)$, which is only possible for $1 < \alpha \leq 2$, then the age distribution for the vegetative cells produced since the origin is stable at

$$\begin{cases} re^{-rx}, & \text{for } 1 < \alpha < 2, \\ 0, & \text{for } \alpha = 2. \end{cases}$$

Under these conditions the age distribution for all cells, viable and non-viable, produced since the origin is stable at

$$a_r \left[\ell(x) + \frac{2 - \alpha}{\alpha}\right], \text{ for } 1 < \alpha \leq 2.$$

The total cell population increases to a limiting value of

$$\left[\frac{2 - \alpha}{1 - \alpha}\right] M(o) + M_v(o),$$

for $0 < \alpha < 1$ and increases without bound for all other values of $\alpha$. As $t$ increases the number of young cells in the total population increases for $1 < \alpha \leq 2$, decreases to a limit of zero for $0 < \alpha < 1$ and is constant for $\alpha = 1$. 
The average age of a cell producing fission in the stable population, \( Y \), is determined by Powell's carrier distribution which has a density function \( c(x) = ae^{-rx} f(x) \) (see Powell, E.O. (1956)). Hence,

\[
Y = a \int_{0}^{\infty} xe^{-rx} f(x) \, dx . \tag{4.11}
\]

### 4.3 The Generation Time Distribution Starting with Newborn Cells.

The simplest approach to modelling the generation (interdivision) time distribution is to assume that each fissioning (viable) cell has a constant lifetime of say \( \tau \). This means that the generation time density function \( f(x) = \delta(\tau - x) \) and \( \ell(x) = H(\tau - x) \), where \( \delta \) and \( H \) are the Dirac delta and Heaviside functions respectively. This is the model used by Thornley, J.M. (1976) who further assumes the process is in a stable state. We now consider the process in both the transient and stable states making the assumptions that the initial population consists entirely of \( M(0) \) newborn fissioning cells and \( a(t) = \alpha \), constant. This implies that,

\[
\begin{align*}
\psi_1(t) &= f(t) , \\
\psi_2(t) &= \ell(t) , \\
M_V(0) &= 0 , \\
\text{and, } a_v(x,t) &= 0 , \text{ for all } x \text{ and } t , \text{ when } \alpha = 2 .
\end{align*}
\tag{4.12}
\]

Substituting in (4.4) and taking Laplace transforms we have,

\[
B^*(s) = \frac{\alpha M(0)}{s} , \text{ which when inverted gives,}
\]

\[
B(t) = M(0) \sum_{j=1}^{\infty} \alpha^j \delta(j\tau - t) .
\]

Using (4.2) and taking Laplace transforms we have,

\[
M^*(s) = \frac{M(0)}{s} + \left( \frac{\alpha - 1}{\alpha s} \right) B^*(s) , \text{ which on inversion gives,}
\]


\[ M(t) = \alpha^n M(0), \text{ for } n\tau \leq t < (n + 1)\tau, \ n = 0, 1, 2, \ldots \]

From (4.6) we have,

\[
M(t) a(x, t) = \begin{cases} 
H(\tau - x) M(0) \sum_{j=1}^{\infty} \alpha^j \delta(j\tau - t + x), & \text{for } 0 \leq x < t, \\
0, & \text{otherwise.}
\end{cases}
\]

For the vegetative cells (4.7) gives, for \( n\tau \leq t < (n + 1)\tau, \ n = 0, 1, 2, \ldots \)

\[
M_v(t) = \begin{cases} 
\left( \frac{2 - \alpha}{1 - \alpha} \right) M(0) (1 - \alpha^n), & \text{for } \alpha \neq 1, \\
n M(0), & \text{for } \alpha = 1,
\end{cases}
\]

\[
B_v(t) = \left( \frac{2 - \alpha}{\alpha} \right) M(0) \sum_{j=1}^{\infty} \alpha^j \delta(j\tau - t).
\]

From (4.8) we have,

\[
M_v(t) a_v(x, t) = \begin{cases} 
\left( \frac{2 - \alpha}{\alpha} \right) M(0) \sum_{j=1}^{\infty} \alpha^j \delta(j\tau + x - t), & \text{for } 0 \leq x < t, \\
0, & \text{otherwise.}
\end{cases}
\]

Using these results, describing the transient stage of growth for the viable and non-viable cells, we can easily describe the total population with (4.9) and (4.10).

When the fissioning cell population is stable we may apply the equations previously derived with \( \alpha = \frac{M(0)}{\tau} \) and \( \tau = \frac{\ln \alpha}{\tau} \). This gives,

\[
B(t) = \frac{M(0)}{\tau} \alpha^{t/\tau}, \quad M(t) = \begin{cases} 
\frac{(\alpha - 1)}{\ln \alpha} \alpha^{t/\tau - 1} M(0), & \text{for } \alpha \neq 1, \\
M(0), & \text{for } \alpha = 1,
\end{cases}
\]

\[
M(t) a(x, t) = H(\tau - x) \frac{M(0)}{\tau} \alpha^x, \text{ for } 0 \leq x < t.
\]  \hspace{1cm} (4.13)
For the vegetative cells we have,

\[ B_V(t) = \left( \frac{2 - \alpha}{\tau} \right) M(0) \frac{a t}{\tau - 1}, \quad M_V(t) = \frac{a - 2}{a - 1} \frac{M(0)}{\ln \alpha} \left[ \ln \alpha + (1 - \alpha) \frac{t}{\tau - 1} \right], \]

for \( \alpha \neq 1 \) and \( \frac{dM_V(t)}{dt} = \frac{M(0)}{\tau} \), for \( \alpha = 1 \).

These equations include those derived by Thornley, J.M. (1976) but provide a more complete description of the process, particularly for the transient stage of growth. In dealing with the case \( \alpha = 2 \) Thornley, J.M. (1976) stresses that at time \( t \) in the stable population, there are twice as many newborn fission cells as cells about to fission. From (4.13) it is easy to see that the corresponding ratio is \( \alpha \) for the process where non-viable cell production is possible. Since \( Y = \tau \), this means the crude birth \( a(o,\infty) = a\alpha(Y,\infty) \), where \( a(Y,\infty) \) represents the crude death rate for the viable cells. The doubling time, \( t_d \), for the stable fissioning population is given by,

\[ t_d = \tau \left( \frac{\ln 2}{\ln \alpha} \right). \]

Extensive measurements of generation times of individual cells were first published by Kelly, C., Rahn, O. (1932). Working with a small isolated sample of seven or eight cells they measured the generation times of three generations of these cells. Their method of sampling could have biased their results since a correct sample of \( f(x) \) relies on the measurement of the generation times of all cells formed during a chosen time interval. Subsequent to this work Rahn, O. (1932) proposed a model for the distribution of generation times which is backed by empirical evidence from other investigations (Powell, E.O. (1955)). However, it is not generally as popular as other models. He assumes that a cell divides as soon as some fixed number \( g \) of events have all occurred inside the cell. The events occur independently of one another; but each
has the same exponential frequency function of occurrence at age $x$, $\beta e^{-\beta x}$. The probability that any given event has occurred by age $x$ is $1 - e^{-\beta x}$, and the probability that all $g$ events have occurred is $(1 - e^{-\beta x})^g$, which is Yule's distribution. Consequently,

$$f(x) = (1 - e^{-\beta x})^{g-1} \beta e^{-\beta x}.$$  \hspace{1cm} (4.14)

Using the assumption (4.12) and substituting (4.14) in (4.4) we have, on taking Laplace transforms,

$$B^*(s) = \frac{\alpha M(o) g! \beta^g}{g} \prod_{j=1}^g (s + j\beta) - g! \alpha \beta^g \hspace{1cm} (4.15)$$

The inversion of (4.15) is in general a difficult procedure, the result being dependent on the value of $\alpha$. However, for the particular cases $g = 1$, $g = 2$ the expressions for $B(t)$ and $M(t)$, in both the transient and stable stages of growth, are reasonable.

(a) $g = 1$ (Simple exponential or Malthusian Model).

For the transient stage of growth,

$$B(t) = \alpha \beta M(o) \exp \left[ \beta(\alpha - 1)t \right], \quad M(t) = M(o) \exp \left[ \beta(\alpha - 1)t \right],$$

and for the stable stage of growth we have exactly the same results.

(b) $g = 2$.

The transient solutions are,

$$B(t) = \frac{2\alpha \beta N(o)}{\sqrt{1 + 8\alpha}} \left[ \frac{\beta}{2} \left( \sqrt{1 + 8\alpha} - 3 \right) t - \frac{\beta}{2} \left( \sqrt{1 + 8\alpha} + 3 \right) t \right] - e^{\frac{-\beta}{2} \left( \sqrt{1 + 8\alpha} + 3 \right) t},$$

$$M(t) = \frac{4(\alpha-1)M(o)}{\sqrt{1 + 8\alpha}} \left[ \frac{\beta}{2} \left( \sqrt{1 + 8\alpha} - 3 \right) t + \frac{\beta}{2} \left( \sqrt{1 + 8\alpha} + 3 \right) t \right] + e^{\frac{\beta}{2} \left( \sqrt{1 + 8\alpha} + 3 \right) t},$$
and for the stable stage of growth,

\[ B(t) = \frac{2\alpha \beta M(0)}{\sqrt{1 + 8\alpha}} e^{\frac{\beta}{2} (\sqrt{1 + 8\alpha} - 3) t} \]

\[ M(t) = \frac{4(\alpha - 1)M(0)}{\sqrt{1 + 8\alpha}} e^{\frac{\beta}{2} (\sqrt{1 + 8\alpha} - 3) t} \]

An alternative model for the generation time distribution is proposed by Kendall, D.G. (1948). He also assumes that division takes place as soon as a fixed number \( g \) of events have occurred in the cell, but he assumes that these events must occur in a specific order so that the expected rate of occurrence of the next event is the constant \( \beta \). Defining \( p_k(x) \) to be the probability that exactly \( k \) events have occurred within a cell by age \( x \) we see from Kendall's assumptions that,

\[ \frac{dp_0(x)}{dx} = -\beta p_0(x) , \]

\[ \frac{dp_k(x)}{dx} = \beta p_{k-1}(x) - \beta p_k(x) . \]

It is not difficult to show that the solution of these equations is the Poisson distribution (Karlin, S. (1969, pp 13-16),

\[ p_k(x) = e^{-\beta x} (\beta x)^k / k! . \]

The expected rate at which the \( g \)th event occurs at age \( x \) is therefore \( \beta p_{g-1}(x) \). So Kendall's model predicts that \( f(x) \) will be a Pearson type III frequency function given by,

\[ f(x) = \frac{\beta^g e^{-\beta x} g!}{(g-1)!} , \quad 0 < x < \infty , \quad g(\text{integral}) \geq 1. \]
Powell, E.O. (1955) shows that a Pearson type III distribution can usually be fitted satisfactorily to his data and that the best fit of the Yule distribution (Rahn's model) is usually less satisfactory. Also, as we see below, the mathematical analysis of the process using (4.16) can be carried much further than was the case with Rahn's model (4.14).

Using (4.12) and (4.16) in (4.4) and taking Laplace transforms we have,

\[ B^*(s) = a M(o)(\beta)^j \sum_{j=1}^{\infty} \frac{\alpha^{-1}(\beta)(j-1)g}{(s + \beta)^{jg}}, \text{ which on inversion gives,} \]

\[ B(t) = M(o) e^{-\beta t} \sum_{j=1}^{\infty} \frac{[\alpha(\beta)^j]^j t^{jg-1}}{(jg - 1)!}. \]

This result in (4.2) gives,

\[ M(t) = M(o) \left\{ 1 + (\alpha - 1) \sum_{j=1}^{\infty} \alpha^{-1} \left[ 1 - e^{-\beta t} \left( 1 + \beta t + \frac{(\beta t)^2}{2!} + ... \right) + \frac{(\beta t)^{jg-1}}{(jg - 1)!} \right] \right\} \]  

(4.17)

and with \( \ell(x) = 1 + \beta x + \frac{(\beta x)^2}{2!} + ... + \frac{(\beta x)^{g-1}}{(g-1)!} \) we have,

on substituting in (4.6),

\[ M(t) a(x,t) = \begin{cases} 
M(o) e^{\beta(x-t)} \ell(x) \sum_{j=1}^{\infty} \frac{[\alpha(\beta)^j]^j}{(jg - 1)!} (t - x)^{jg-1}, & \text{for } 0 \leq x < t, \\
0, & \text{otherwise.} 
\end{cases} \]

Combining these results with (4.7) and (4.8) we have, for the vegetative cells,

\[ B_V(t) = \frac{(2 - \alpha)}{\alpha} M(o) e^{-\beta t} \sum_{j=1}^{\infty} \frac{[\alpha(\beta)^j]^j t^{jg-1}}{(jg - 1)!}, \]
\[ M_v(t) = \frac{(2 - \alpha)}{\alpha} M(o) \sum_{j=1}^{\infty} a_j \left[ 1 - e^{-\beta_j} (1 + \beta_j \frac{(\beta_j)^2}{2!} + \ldots \right] \]

and

\[ M_v(t) a_v(x,t) = \left[ \frac{(2 - \alpha)}{\alpha} M(o) e^{-\beta_j (t-x)} \sum_{j=1}^{\infty} \frac{a_j (\beta_j)^j}{j!} (t-x)^j \right], \text{ for } 0 \leq x < t,
\]

\[ 0, \text{ otherwise.} \]

From (4.9) and (4.10) it is possible to obtain expressions describing the total population. Reasonable closed form expressions can be obtained when:

(a) \( g = 1 \) (Simple exponential or Malthusian Model).

\[ B(t) = \alpha \beta M(o) e^{\beta (a-1)t}, \quad M(t) = M(o) e^{\beta (a-1)t} \]

and

\[ M(t) a(x,t) = \left[ \alpha M(o) e^{\beta (at-\alpha x-t)} \right], \text{ for } 0 \leq x < t,
\]

\[ 0, \text{ otherwise.} \]

\[ B_v(t) = (2 - \alpha) \beta M(o) e^{\beta (a-1)t}, \quad M_v(t) = \left[ \frac{2 - \alpha}{\alpha - 1} \right] M(o) e^{\beta (a-1)t - 1} \]

and

\[ M_v(t) a_v(x,t) = \left[ (2 - \alpha) \beta M(o) e^{\beta (a-1)(t-x)} \right], \text{ for } 0 \leq x < t,
\]

\[ 0, \text{ otherwise.} \]

(b) \( g = 2 \).

\[ B(t) = \frac{\beta \sqrt{\alpha}}{2} M(o) \left( e^{\beta \sqrt{\alpha} t} - e^{-\beta \sqrt{\alpha} t} \right) e^{-\beta t}, \]

\[ M(t) = \frac{M(o)}{2\sqrt{\alpha}} \left[ (\sqrt{\alpha} + 1) e^{\beta (\sqrt{\alpha} - 1)t} + (\sqrt{\alpha} - 1) e^{-\beta (\sqrt{\alpha}+1)t} \right] \]
and,

\[
M(t) a(x,t) = \begin{cases} 
\frac{\sqrt{a}}{2} M(o) \left( 1 + \beta x \right) \left( e^{\beta \sqrt{a} (t-x)} - e^{-\beta \sqrt{a} (t-x)} \right) e^{-\beta(t-x)}, & \text{for } 0 \leq x < t, \\
o, & \text{otherwise}.
\end{cases}
\]

For the vegetative cells,

\[
B_v(t) = \left( \frac{2 - \alpha}{2 \sqrt{\alpha}} \right) M(o) \left( e^{\beta \sqrt{a} t} - e^{-\beta \sqrt{a} t} \right) e^{-\beta t},
\]

\[
M_v(t) = \left( \frac{2 - \alpha}{\alpha - 1} \right) M(o) \left( (\sqrt{\alpha} + 1)e^{\beta(\sqrt{\alpha} - 1)t} + (\sqrt{\alpha} - 1)e^{-\beta(\sqrt{\alpha} + 1)t} - 2\sqrt{\alpha} \right),
\]

\[
M_v(t)a_v(x,t) = \left[ \frac{2 - \alpha}{2 \sqrt{\alpha}} \right] M(o) \left( e^{\beta \sqrt{a} (t-x)} - e^{-\beta \sqrt{a} (t-x)} \right) e^{-\beta(t-2x)},
\]

\[
\frac{1}{2 - \alpha} M(o) \left( \frac{1}{2} e^{-\beta \sqrt{a} (t-x)} - e^{-\beta \sqrt{a} (t-x)} \right) e^{-\beta(t-2x)},
\]

\[
0, \text{ otherwise}.
\]

Kendall's paper (1948) deals with the particular case where \( \alpha = 2 \) which means no vegetative cell production occurs. He assumes that the initial population consists of one cell which is experiencing the first of the \( g \) sequential events it must complete before dividing. For the population of cells at time \( t \) he defines \( P_{n_2,t}^{n_1} \) as the probability that there are \( n_1 \) cells undergoing the \( i \)-th of the \( g \) sequential events, \( i = 1,2, \ldots, g \). The probability generating function \( \phi \left( \begin{array}{c} z_1 \cr z_2 \cr \vdots \cr z_g \end{array} \right) t \) for the distribution of cells undergoing the events \( 1,2,3, \ldots, g \) is given by,

\[
\phi \left( \begin{array}{c} z_1 \cr \vdots \cr z_g \end{array} \right) t = \sum_{n_1}^{n_g} \frac{n_1}{n_2} \frac{n_2}{n_3} \ldots \frac{n_{g-1}}{n_g} \left( \begin{array}{c} n_g \\ n_1 \end{array} \right) \left( \begin{array}{c} \frac{z_1}{z_2} \cr \vdots \cr \frac{z_{g-1}}{z_g} \end{array} \right) t.
\]
and is shown to be \( e^{-\beta t} Z(\beta t) \) where \( Z(u) \) satisfies \( \frac{d^g Z(u)}{du^g} = e^{-u} Z(u) \)

with the boundary conditions \( \frac{d^i Z(u)}{du^i} \bigg|_{u=0} = z_{i+1}, \quad 0 \leq i \leq g-1 \). Kendall notes that this differential equation is intractable for values of \( g \geq 2 \).

Kendall also shows that if \( v_i \) is the expected value of \( n_i = E(n_i) \) then,

\[
\frac{dv_i}{d\theta} = 2v_g - v_1,
\]

\[
\frac{dv_i}{d\theta} = v_{i-1} - v_i, \quad 1 < i \leq g,
\]

where, \( \theta = \beta t \). This system is solved using the substitution \( \rho_i = v_i e^\theta \) to finally give,

\[
E(n_i) = \frac{2}{g} \sum_{r=0}^{g-1} w^{(1-i)r} \exp \left[ \begin{array}{c} 1 \\ (2^g w^r - 1) \beta t \end{array} \right]
\]

where \( w \) is the primitive \( g^{th} \) root of unity given as \( \exp \left[ \frac{2\pi i}{g} \right] \).

Hence, the expected population size at time \( t \) is given by,

\[
M(t) = \sum_{i=1}^{g} E(n_i),
\]

\[
e^{-\beta t} \sum_{m=0}^{\infty} \left\{ 2^m \sum_{r=0}^{g-1} \frac{(\beta t)^{mg+r}}{(mg+r)!} \right\}.
\]

Our result for \( M(t) \) in (4.17) reduces to that obtained by Kendall when we substitute \( M(0) = 1 \) and \( \alpha = 2 \). We note that the development which led to (4.17) is easier than Kendall's approach and certainly gives a more general result because we have accounted for the possibility of non-viable cell production in (4.17) as well as allowing for an initial population size \( M(0) \geq 1 \).
The following description of the stable population carries
our generalisation of Kendall's results further.

\[ f^*(s) = \frac{1}{\alpha} \]
Solving \[ f^*(s) = - \] we obtain \[ r = \beta(a^g - 1) \] and hence,
\[ A = \frac{\beta a^{1/g}}{g} M(o) \]. So the stable population equations become,
\[ B(t) = \frac{\beta}{g} M(o) a^{1/g} e^{\beta(a^g - 1)t} \]
\[ M(t) = \frac{a^{1/g} M(o)}{a^{1/g} - 1} e^{\beta(a^g - 1)t} \]
and,
\[ M(t) a(x,t) = \begin{cases} \frac{a^{1/g} M(o)}{g} e^{\beta(t-x)(a^g - 1) \ell(x)} , & \text{for } 0 \leq x < t , \\ 0 , & \text{otherwise.} \end{cases} \]  

From (4.11) we see that the average age of a cell producing
fission in the stable population is \[ Y = \frac{g}{\beta a^{1/g}} \], whereas, the expected
time to fission for a newborn individual is \[ \frac{g}{\beta} \].

The stable population equations for the vegetative population
are most easily expressed in terms of (4.18) and (4.19).
\[ B_v(t) = \left[ 2 - \alpha \right] B(t) , \quad M_v(t) = \left[ \frac{2 - \alpha}{a - 1} \right] [M(t) - M(o)] \]
and
\[ M_v(t) a_v(x,t) = \begin{cases} \left[ \frac{2 - \alpha}{a \ell(x)} \right] M(t) a(x,t) , & \text{for } 0 \leq x < t , \\ 0 , & \text{otherwise.} \end{cases} \]  

In particular, for \( g = 1 \), we have \( B(t), M(t), B_v(t), M_v(t) \) the
same as during the transient stage of growth,
and for \( g = 2 \), \[ B(t) = \frac{\beta \sqrt{a}}{2} M(o) e^{\beta(v\sqrt{a} - 1)t} , \quad M(t) = \left\{ \frac{\sqrt{a} + 1}{2\sqrt{a}} \right\} M(o) e^{\beta(v\sqrt{a} - 1)t} , \]
\[ B_v(t) = \frac{(2 - \alpha)}{2\sqrt{a}} \beta M(o) e^{\beta(v\sqrt{a} - 1)t} \quad \text{and} \quad M_v(t) = \frac{2 - \alpha}{a - 1} \frac{M(o)}{2\sqrt{a}} (e^{\beta(v\sqrt{a} - 1)t} - 2\sqrt{a}) . \]
From (4.18) we see the doubling time for the viable cell population is given by \( t_d = \frac{\ln 2}{\beta (\alpha^{1/g} - 1)} \).

In order to formulate the problem as a Bellman-Harris process (Bellman, R., Harris, T.E. (1952)) we need to be able to specify, \( q_i \) \((i=0,1,2)\), the probability that when a fission occurs \( i \) fission cells will be produced. Since in a well-nourished culture \( \alpha = 2 \) it seems reasonable to use \( q_0 = 0 \), \( q_1 = 2 - \alpha \) and \( q_2 = \alpha - 1 \), where we have used the fact that \( \sum_{i=0}^{2} iq_i = \alpha \). Let \( N(t) \) = number of fissioning cells in the population at time \( t \).

If \( P_j(t) \) = Probability there are \( j \) fission cells in the population at time \( t \), and \( F(s,t) = \sum_{j=0}^{\infty} P_j(t) s^j \), \(|s| < 1\) is the probability generating function then from Bharucha-Reid, A.T. (1960, pp 94-98), we have,

\[
F(s,t) = \int_0^t h[F(s,t-x)] f(x) \, dx + s \ell(t),
\]

where,

\[
h(s) = (2 - \alpha)s + (\alpha - 1)s^2.
\]

Hence, using \( f(x) \) as in (4.16) we obtain,

\[
F(s,t) e^{\beta t} = (2 - \alpha) \frac{(\beta)g}{(g-1)!} \int_0^t F(s,x) e^{\beta x} (t - x)^{g-1} \, dx + (\alpha - 1) \frac{(\beta)g}{(g-1)!} \int_0^t F^2(s,x) e^{\beta x} (t - x)^{g-1} \, dx + [1 + \beta t + \frac{(\beta t)^2}{2} + \ldots + \frac{(\beta t)^{g-1}}{(g-1)!}] s
\]

By differentiation,

\[
\frac{\partial}{\partial t} e^{\beta t} F(s,t) = e^{\beta t} (\beta)g F(s,t)[(\alpha - 1)F(s,t) + (2 - \alpha)]
\]

In particular, for \( g = 1 \) (Malthusian) this partial differential equation becomes
\[ \frac{\partial^2 F}{\partial t^2} = (\alpha - 1) \beta F(F - 1) \], with the initial condition

\[ M(o) = 1 \], that is, \( F(s,o) = s \). The solution is easily found to be,

\[
F(s,t) = \begin{cases} 
  s & \text{for } \alpha = 1, \\
  s e^{-(\alpha-1)\beta t} & \text{for } 1 < \alpha \leq 2 , \\
  1 - (1 - e^{-(\alpha-1)\beta t}) s & \text{for } 1 < \alpha \leq 2 ,
\end{cases}
\]

and hence, for \( t > 0 \), we have,

\[
P_j(t) = \begin{cases} 
  e^{-(\alpha-1)t}[1 - e^{-(\alpha-1)t}](j-1) & \text{for } j \geq 1 , \\
  0 & \text{for } j = 0 , \\
  1 & \text{for } j = 1 , \\
  0 & \text{otherwise,}
\end{cases} \quad \alpha = 1.
\]

With \( M_2(t) = 2(\alpha - 1) \int_0^t M^2(t-x) f(x) \, dx + \alpha \int_0^t M_2(t-x) f(x) \, dx \)

it can be shown (Bharucha-Reid, A.T. (1960, pp 94-98)) that

\[ \text{VAR}(N(t)) = M_2(t) + M^2(t) + M(t). \]

So for our choice of \( f(x) \) we find that \( M_2(t) \) satisfies,

\[
\frac{\partial^2 [e^{\beta t} M_2(t)]}{\partial t^2} = (\beta)^2 e^{\beta t} [2(\alpha - 1) M_2(t) + \alpha M_2(t)] ,
\]

where \( M(t) \) is given by (4.17) and \( M_2(o) = 0 \).

If \( g = 1 \) we have,

\[
\frac{\partial M_2(t)}{\partial t} + \beta(1 - \alpha) M_2(t) = 2\beta(\alpha - 1) e^{2\beta(\alpha - 1)t} 
\]

which gives \( M_2(t) = \begin{cases} 
  2 e^{\beta(\alpha - 1)t} [e^{\beta(\alpha - 1)t} - 1] & \text{for } 1 < \alpha \leq 2 , \\
  0 & \text{for } \alpha = 1,
\end{cases} \)

and so,
VAR \{ N(t) \} = \begin{cases} 
\beta (\alpha - 1) t [e^{\beta (\alpha - 1) t} - 1], & \text{for } 1 < \alpha < 2, \\
0, & \text{for } \alpha = 1.
\end{cases}

The coefficient of variation = \sqrt{1 - e^{-\beta (\alpha - 1) t}}, \text{ for } 1 < \alpha < 2,

which approaches 1 for large values of \( t \).

We see that with appropriate values for \( q_i \) we are able to determine the distribution for the size of the fissioning cell population and obtain the variance of this population size for the Malthusian case \( (g = 1) \). The \( g \)th order differential equations for \( F(s,t) \) and \( M_2(t) \) indicate the difficulties of obtaining similar results for \( g \geq 2 \) by analytic methods. In practice, it seems reasonable to assume that an estimate of \( \alpha \) would be easier to obtain than values for \( q_i \).

From an estimate of \( \alpha \) our modified integral formulation provides extensive information about the process without requiring any knowledge of the \( q_i \).

Kendall, D.G. (1952) has generalised the model given by the Pearson type III density function (4.16) by assuming that the \( g \) sequential events, which each cell must complete before dividing, take place at different rates \( \beta_1, \beta_2, \beta_3, \ldots, \beta_g \). If \( p_k(x) \) is the probability that exactly \( k \) events have occurred in a cell by age \( x \) then,

\[
\frac{dp_0(x)}{dx} = -\beta_1 p_0(x),
\]

\[
\frac{dp_k(x)}{dx} = \beta_k p_{k-1}(x) - \beta_{k+1} p_k(x).
\]

This system can be solved using Laplace transforms to give,
\[ p^*(s) = \frac{\prod_{j=1}^{g} \beta_j}{s(s + \beta_1)(s + \beta_2) \ldots (s + \beta_g)}. \]

So if \( f^*(s) \) is the Laplace transform of the generation time density \( f(x) \) then,

\[
f^*(s) = \left\{ \prod_{j=1}^{g} \beta_j \right\} \frac{\sum_{j=1}^{g} A_j}{s + \beta_j}.
\]

where,

\[
A_j = \lim_{s \to -\beta_j} \frac{(s + \beta_j)}{\prod_{i=1}^{g} (s + \beta_i)}; \quad j = 1,2, \ldots, g.
\]

Consequently, on inversion, we have,

\[
f(x) = \left\{ \prod_{j=1}^{g} \beta_j \right\} \frac{\sum_{j=1}^{g} A_j e^{-\beta_j x}}{s + \beta_j}.
\]

where,

\[
A_j = \lim_{s \to -\beta_j} \left[ \frac{s + \beta_j}{\prod_{i=1}^{g} (s + \beta_i)} \right].
\]

We note that (4.20) reduces to (4.16) if \( \beta_j = \beta, \quad j=1,2, \ldots, g \)
and more importantly we find (4.20) reduces to the density function in
(4.14), which is the Yule density, if we have \( \beta_1 = \beta, \beta_2 = 2\beta, \beta_3 = 3\beta, \ldots, \beta_g = g\beta \). This result is important because the model which led to (4.14),
Rahn’s model, and the model which led to (4.20) are fundamentally
different and yet if we took measurements of \( f(x) \), as evidence for
or against the adoption of either model, we would not be able to
distinguish between the two. From this we conclude that agreement
between a model for \( f(x) \) and actual measures of \( f(x) \) should never
be interpreted as substantial evidence for the truth of the model. If
the predictions of a model are in satisfactory agreement with
experimental data on \( f(x) \), then sound physiological evidence must be
found if the model is to be accepted.

As might be expected the analysis of the process using (4.20) is difficult. For comparison purposes we again present the results for \( B(t) \) and \( M(t) \) in the particular cases \( g = 1 \) and \( g = 2 \).

(a) \( g = 1 \) (The Simple Exponential or Malthusian Model).

The transient solutions and stable solutions are exactly those given for the process where \( f(x) \) is represented by (4.14) or (4.16).

(b) \( g = 2 \).

The transient solutions are,

\[
B(t) = \frac{aM(0)\beta_1\beta_2}{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2}} \left[ \exp \left\{ \frac{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2} - (\beta_1 + \beta_2)}{2} \right\} \right. \\
- \left. \exp \left\{ -\frac{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2} - (\beta_1 + \beta_2)}{2} \right\} \right],
\]

\[
M(t) = \frac{2(a - 1)M(0)\beta_1\beta_2}{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2}} \left[ \exp \left\{ \frac{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2} - (\beta_1 + \beta_2)}{2} \right\} \right. \\
- \left. \exp \left\{ -\frac{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2} - (\beta_1 + \beta_2)}{2} \right\} \right].
\]

The stable solutions are,

\[
B(t) = \frac{aM(0)\beta_1\beta_2}{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2}} \exp \left\{ \frac{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2} - (\beta_1 + \beta_2)}{2} \right\} \right),
\]

\[
M(t) = \frac{2(a - 1)M(0)\beta_1\beta_2}{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2}} \exp \left\{ \frac{\sqrt{(\beta_1 - \beta_2)^2 + 4\alpha_1\beta_2} - (\beta_1 + \beta_2)}{2} \right\} \right).
Often the data collected in experiments on the measurement of generation time distributions is represented in graphical form (see Kendall, D.G. (1948), Powell, E.O. (1956)). We consider such forms as part of the material presented in section 4.5 of this chapter.

4.4 The Consideration of Various Forms of Time Dependence in \( a(t) \).

So far we have used \( a(t) = \alpha \), constant, where \( \alpha \approx 2 \) in a well-nourished culture (Powell, E.O. (1956). It would seem more realistic to suppose that factors in the cell's environment or within the cell itself will cause the production rate of viable cells to vary with time.

We consider various forms of time dependence in \( a(t) \) and, working with a generation time density \( f(x) \) represented by the Pearson type III density in (4.16), we examine the transient and stable solutions for \( B(t) \). Once \( B(t) \) is determined the other quantities of interest such as \( M(t) \), \( a(x,t) \) can be obtained from the equations presented in section 4.2 of this chapter.

We assume that the initial population consists entirely of \( M(o) \) newborn viable cells and hence we substitute (4.12) in the integral equation (4.4) to give,

\[
B(t) = \alpha(t)M(o)f(t) + \alpha(t) \int_0^t B(t - x)f(x)dx , \tag{4.21}
\]

where, \( f(x) \) is the Pearson type III density function (4.16). Unfortunately (4.21) is no longer readily amenable to the Laplace transform method of solution as it is when \( \alpha(t) = \alpha \), constant.

We now make the substitution \( B(t) = e^{-\beta t} \alpha(t)v(t) \) in (4.21) to give,
Differentiating (4.22) \( g \) times with respect to \( t \) gives,

\[
\frac{d^g v(t)}{dt^g} - \beta^g \alpha(t)v(t) = 0
\]

(4.23)

Assuming that \( \alpha(t) \) is analytic for \( t \geq 0 \) and working in the usual way (Brauer, F. Nohe, J.A. (1967), chapter 4) we obtain the series solution for (4.23) as,

\[
v(t) = \beta^g M(o)t^{g-1} + \sum_{n=g}^{\infty} a_n t^n
\]

where,

\[
a_o = a_1 = a_2 = \ldots = a_{g-2} = 0, \ a_{g-1} = \beta^g M(o), \]

\[
a_{g+k} = \frac{\beta^g k!}{(g + k)!} \sum_{j=0}^{k} a_j ; \ k=0,1,2, \ldots ,
\]

and \( a_j \) are the coefficients in the series expansion of

\[
\alpha(t) = \sum_{j=0}^{\infty} a_j t^j.
\]

(4.25)

Hence, we have the series solution for \( B(t) \) in (4.21) as,

\[
B(t) = e^{-\beta t} \alpha(t)v(t), \text{ where } v(t) \text{ and } \alpha(t) \text{ have the series expansions (4.24) and (4.25), respectively.}
\]

We can also find a series expansion for \( M(t) \). Using,

\[
M(t) = M(o) + \int_{0}^{t} \frac{a(u) - 1}{a(u)} B(u) du,
\]

we find that substituting the series expansion for \( B(t) \) gives,
\[ M(t) = M(o) + \sum_{n=0}^{\infty} b_n t^{n+1} \frac{n}{(n+1)}, \]

where,

\[ b_n = \sum_{j=0}^{n} \alpha_j \left[ \sum_{i=0}^{n-j} \frac{(-\beta)^{n-j-i} a_i}{(n-j-i)!} \right] - \sum_{i=0}^{n} \frac{a_i (-\beta)^{n-i}}{(n-i)!}, \quad n \geq 0, \]

and the \( a_i, \alpha_i \) are given by (4.24) and (4.25) respectively.

In the particular case where \( g = 1 \) we obtain simpler expressions for \( B(t) \) and \( M(t) \). These solutions are,

\[
\begin{align*}
B(t) &= \beta M(o) \alpha(t) \exp \left[ \beta \int_{0}^{t} (\alpha(u) - 1) \, du \right], \\
M(t) &= M(o) \exp \left[ \beta \int_{0}^{t} (\alpha(u) - 1) \, du \right].
\end{align*}
\]

Consequently, closed form expressions for \( B(t) \) and \( M(t) \) are usually obtainable for the case \( g = 1 \) whereas for \( g \geq 2 \) series expansions for \( B(t) \) and \( M(t) \) are given by (4.24), (4.25) and (4.26). Furthermore, for \( g = 1 \) we can write reasonable expressions for \( B(t) \) and \( M(t) \) for the stable stage of growth.

Table 3 gives the transient solution for \( B(t) \) for various choices of \( \alpha(t) \). This has been done for the case where \( f(x) \) has a Pearson type III density of order \( g \) and the particular case \( g = 1 \) is considered. The stable solution for \( B(t) \) for the case \( g = 1 \) is also shown.

4.5 Empirical Forms of the Generation Time Distribution

We now consider the solutions of the integral equation (4.21) where time dependence is retained in \( \alpha(t) \) and the generation time density function, \( f(x) \), is in either histogram or concentrated form.
### TABLE 3

**SOLUTIONS TO (4.21) FOR VARIOUS CHOICES OF \( a(t) \) WITH A PEARSON TYPE III GENERATION TIME DENSITY**

<table>
<thead>
<tr>
<th>( a(t) )</th>
<th><strong>TRANSIENT SOLUTIONS FOR B(t)</strong></th>
<th><strong>STABLE B(t)</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>( g \geq 2 )</td>
<td>( g = 1 )</td>
</tr>
<tr>
<td>( \alpha(t) )</td>
<td>( B(t) = \beta M(o) \left[ \frac{L}{1 + \left( \frac{L-C}{C} \right) e^{-\lambda t}} \right] v(t), )</td>
<td>( B(t) = \beta M(o) \left[ \frac{L}{1 + \left( \frac{L-C}{C} \right) e^{-\lambda t}} \right] )</td>
</tr>
<tr>
<td>2 ( L+c )</td>
<td>( v(t) = \beta^g M(o) t^{g-1} + \sum_{n=g}^{\infty} a_n t^n, )</td>
<td>( \times \exp \left{ \frac{\beta}{\lambda} \left[ \frac{L}{1 + (c-1)t} e^{-\lambda t} \right] \right} )</td>
</tr>
<tr>
<td>( \lambda &gt; 0, )</td>
<td>( a_0 = a_1 = \ldots = a_{g-2} = 0, )</td>
<td>( \frac{\beta L}{\lambda} \frac{\beta (c-1) t}{\lambda} )</td>
</tr>
<tr>
<td>( 0 &lt; c &lt; L+c \leq 2 )</td>
<td>( a_{g-1} = \beta^g M(o), )</td>
<td>( \beta M(o) c e^{-\lambda t} )</td>
</tr>
<tr>
<td>1</td>
<td>( a_g = \frac{\beta^g k!}{(g+k)!} \sum_{j=0}^{k} \alpha_j a_{k-j}, k=0,1,2, \ldots, )</td>
<td></td>
</tr>
<tr>
<td>( \alpha_0 = c + L, \alpha_j = \frac{L(-)^j}{j!}, j=1,2,3, \ldots )</td>
<td>( B(t) = \beta c M(o) \left[ \frac{c + (L-c)e^{-\lambda t}}{L} \right] \beta - \lambda )</td>
<td>( \beta M(o) L \left( \frac{c}{L} \right) \frac{\beta}{\lambda} )</td>
</tr>
<tr>
<td>(b)</td>
<td>( B(t) = e^{-\beta t} \left[ \frac{L}{1 + \left( \frac{L-c}{c} \right) e^{-\lambda t}} \right] v(t), )</td>
<td>( \beta M(o) L \left( \frac{c}{L} \right) \frac{\beta}{\lambda} )</td>
</tr>
<tr>
<td>( \alpha(t) )</td>
<td>( v(t) = \sum_{n=0}^{\infty} a_n t^n, a_0 = a_1 = \ldots = a_{g-2} = a_g = 0, )</td>
<td></td>
</tr>
<tr>
<td>( 2 ) ( L )</td>
<td>( a_{g-1} = \beta^g M(o), )</td>
<td></td>
</tr>
<tr>
<td>( \lambda &gt; 0, )</td>
<td>( a_g = \frac{c \beta^g k! a_k}{(g+k)!} + \frac{(c-L) k!}{L(g+k)!} \sum_{j=1}^{k} \frac{(-)^j (g+k-j)!}{(k-j)!} )</td>
<td></td>
</tr>
<tr>
<td>( 1 &lt; c &lt; L \leq 2 )</td>
<td>( a_{g+k} = \frac{c \beta^g k! a_k}{(g+k)!} + \frac{(c-L) k!}{L(g+k)!} \sum_{j=1}^{k} \frac{(-)^j (g+k-j)!}{(k-j)!} \times a_{g+k-j}, )</td>
<td></td>
</tr>
<tr>
<td>( \alpha_0 = c + L, \alpha_j = \frac{L(-)^j}{j!}, j=1,2,3, \ldots )</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3 (CONTINUED)

<table>
<thead>
<tr>
<th>$\alpha(t)$</th>
<th>TRANSIENT SOLUTIONS FOR $B(t)$</th>
<th>STABLE $B(t)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha(t)$</td>
<td>$B(t) = e^{-\beta t} \left[ L + (c-L)e^{-\lambda t} \right] v(t),$</td>
<td>$B(t) = \beta M(o) \left[ L + (c-L)e^{-\lambda t} \right]$</td>
</tr>
<tr>
<td>$L + (c-L)e^{-\lambda t},$</td>
<td>$v(t) = \sum_{n=0}^{\infty} a_n t^n,$ $a_0 = a_1 = a_2 = \ldots,$</td>
<td>$\times \exp \left{ \beta \left[ t(L-1) + \frac{c-L}{\lambda} (1-e^{-\lambda t}) \right] \right} \times e^{\frac{\beta}{\lambda}}$</td>
</tr>
<tr>
<td>$\lambda &gt; 0,$</td>
<td>$a_{g-1} = \beta^g M(o),$</td>
<td>$\beta M(o) e^{\frac{\beta (L-1) t}{\lambda}} \frac{\beta}{\lambda} \frac{\beta (c-L)}{\lambda} \frac{1}{\lambda}$</td>
</tr>
<tr>
<td>$0 &lt; c &lt; L \leq 2.$</td>
<td>$a_{g+k} = \frac{\beta^g k!}{(g+k)!} \sum_{j=0}^{k} a_j a_{k-j},$ $k=0,1,2,\ldots,$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\alpha_0 = c,$ $\alpha_j = \frac{(c-L)(-\lambda)^j}{j!},$ $j=1,2,3,\ldots$</td>
<td></td>
</tr>
</tbody>
</table>
### TABLE 3 (CONTINUED)

<table>
<thead>
<tr>
<th>( \alpha(t) )</th>
<th>( g \geq 2 )</th>
<th>( g = 1 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( (L+c) - \frac{L}{1 + \left(\frac{L-c}{c}\right)e^{-\lambda t}} )</td>
<td>( B(t) = e^{-\beta t} \left[ \frac{(L+c) - \frac{L}{1 + \left(\frac{L-c}{c}\right)e^{-\lambda t}}}{(L+c)} \right] v(t) ), ( v(t) = \sum_{n=0}^{\infty} a_n t^n ), ( a_0 = a_1 = \ldots = a_{g-2} = 0 ), ( a_{g-1} = \beta^g M(0) ), ( a_{g+k} = \frac{\beta^g Lk!}{(g+k)!} a_k + \frac{\beta^g (L-c)^2 k!}{L(g+k)!} \sum_{j=1}^{k} \frac{(-\lambda)^j}{j!} a_{k-j} )</td>
<td>( B(t) = \beta M(0) e^{\beta (L+c-1) t} \times \left[ \frac{(L+c) - \frac{L}{1 + \left(\frac{L-c}{c}\right)e^{-\lambda t}}}{(L+c)} \right] ), ( c \beta M(0) \left( \frac{\beta L}{\lambda} \right) e^{\beta (c-1) t} )</td>
</tr>
<tr>
<td>( L )</td>
<td>( (L+c) - \frac{L}{1 + \left(\frac{L-c}{c}\right)e^{-\lambda t}} )</td>
<td>( \lambda &gt; 0 ), ( 2 \geq L &gt; c &gt; 1 )</td>
</tr>
</tbody>
</table>
TABLE 3 (CONTINUED)

<table>
<thead>
<tr>
<th>( \alpha(t) )</th>
<th>TRANSIENT SOLUTIONS FOR ( B(t) )</th>
<th>STABLE ( B(t) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g \geq 2 )</td>
<td>( \text{DAMPED OSCILLATIONS (0 &lt; } \eta &lt; 1 )</td>
<td>( g = 1 )</td>
</tr>
<tr>
<td>( B(t) = e^{-\beta t} \left[ L + \frac{c}{\sqrt{1-\eta^2}} \sin(\lambda \sqrt{1-\eta^2} t) \right] v(t) )</td>
<td>( \text{DAMPED OSCILLATIONS} )</td>
<td>( \text{DAMPED OSCILLATIONS} )</td>
</tr>
<tr>
<td>( v(t) = \sum_{n=0}^{\infty} a_n t^n, \ a_0 = a_1 = \ldots = a_{g-2} = 0, \ a_{g-1} = g \beta M(o) )</td>
<td>( B(t) = \beta M(o) \left[ L + \frac{c}{\sqrt{1-\eta^2}} \right] )</td>
<td>( \beta \left[ (L-1) t + \frac{c}{\lambda} \right] )</td>
</tr>
<tr>
<td>( a_{g+k} = \frac{\beta^g k!}{(g+k)!} \sum_{j=0}^{g} a_j a_{k-j}, \ k = 0, 1, 2, \ldots )</td>
<td>( \text{UDAMPED OSCILLATIONS} )</td>
<td>( \text{UDAMPED OSCILLATIONS} )</td>
</tr>
<tr>
<td>( \lambda &gt; 0, )</td>
<td>( L, c ) can be any of the</td>
<td>( \beta M(o) \left[ L + c \sin \lambda t \right] \times )</td>
</tr>
<tr>
<td>( (L, c) \text{ can be any of the} )</td>
<td>points in the shaded</td>
<td>( \exp \left{ \beta \left[ (L-1) t + \frac{c}{\lambda} \right] \right} )</td>
</tr>
<tr>
<td>( \eta = 0 ) we have undamped</td>
<td>otherwise ( 0 &lt; \eta &lt; 1 )</td>
<td>( \text{UDAMPED OSCILLATIONS} )</td>
</tr>
<tr>
<td>( \text{oscillations in} \ \alpha(t). )</td>
<td>gives damped</td>
<td>( B(t) = \beta M(o) \left[ L + c \sin \lambda t \right] \times )</td>
</tr>
<tr>
<td>( \text{oscillations in} \ \alpha(t). )</td>
<td>Otherwise ( 0 &lt; \eta &lt; 1 )</td>
<td>( \exp \left{ \beta \left[ (L-1) t + \frac{c}{\lambda} \right] \right} )</td>
</tr>
</tbody>
</table>
TABLE 3 (CONTINUED)

<table>
<thead>
<tr>
<th>α(t)</th>
<th>TRANSIENT SOLUTIONS FOR B(t)</th>
<th>STABLE B(t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>α(t) (f)</td>
<td>g ≥ 2</td>
<td>g = 1</td>
</tr>
<tr>
<td>2L</td>
<td>( B(t) = e^{-\beta t} L \left( \frac{c}{L} \right) \exp(-\lambda t) )</td>
<td>( B(t) = \beta M(o) L \left( \frac{c}{L} \right) \exp(-\lambda t) \times \exp \left[ \beta \left( t(L-1) \right) - \frac{L}{\lambda} \sum_{n=1}^{\infty} \frac{\left[ \ln \left( \frac{c}{L} \right) \right]^n}{n \cdot n!} \right] )</td>
</tr>
<tr>
<td>c</td>
<td>( v(t) = \sum_{n=0}^{\infty} a_n t^n, \quad a_0 = a_1 = a_2 = \ldots = a_{g-2} = 0, )</td>
<td>( + \frac{\beta L}{\lambda} \sum_{n=1}^{\infty} \frac{\left[ \ln \left( \frac{c}{L} \right) \right]^n}{n \cdot n!} )</td>
</tr>
<tr>
<td>Gompertz ( \exp(-\lambda t) )</td>
<td>( L \left( \frac{c}{L} \right) ), ( \lambda &gt; 0 ), ( 2 \geq L &gt; c &gt; 0 )</td>
<td>( \beta M(o) L \times )</td>
</tr>
</tbody>
</table>

\[
\alpha_j = \frac{1}{j! \lambda^j} \left[ (-1)^j \ln \left( \frac{c}{L} \right) + \frac{(-2)^j \left[ \ln \left( \frac{c}{L} \right) \right]^2}{2!} + \frac{(-3)^j \left[ \ln \left( \frac{c}{L} \right) \right]^3}{3!} + \ldots \right], \\
\quad j = 0, 1, 2, \ldots
\]
In practice, values of the function \( f(x) \) are obtained from experimental data and are most naturally represented in either histogram or concentrated form. We have have seen, in section 4.3, one approach is to fit theoretical forms (e.g. Pearson type III curves) of \( f(x) \) to the empirical data. One of the difficulties of this approach is discussed in the remarks following (4.20) in section 4.3. Also, Feller, W. (1941) notes that unless the curve fitting is done by the method of moments then the asymptotic values of \( B(t) \) in (4.21) will depend on the method used and consequently, it is often an advantage to use the empirical data as it is.

If \( f(x) \) is in histogram form (see Figure 1) then,

\[
f(x) = \begin{cases} f_i, & \beta_i < x \leq \beta_{i+1}, \quad i = 1, 2, \ldots, N-1, \\ 0, & \text{otherwise,} \end{cases}
\]

(4.28)

where,

\[0 < \beta_1 < \beta_2 < \ldots < \beta_N .\]

We note that \((\beta_{i+1} - \beta_i)f_i = \text{Probability that a newborn viable cell will fission between ages } \beta_i \text{ and } \beta_{i+1} .\]

![Figure 1](image)

If we can move in steps of length \( \beta_i \) for \( t \), without straddling any of the \( \beta_i \) then it is possible to build up the solutions to

\[
\frac{B(t)}{\alpha(t)} = M(o)f(t) + \int_0^t B(t - x)f(x)dx \quad \text{in the form of a system of}
\]
integro-difference equations given by,

\[
\begin{aligned}
B(t) &= 0 , \quad 0 < t \leq \beta_1 , \\
\frac{B(t)}{a(t)} &= \begin{cases} 
M(0)f_1 + \int_0^{t-\beta_1} B(u) du , & \beta_1 < t \leq \beta_2 , \\
M(0)f_n + \int_0^{t-\beta_n} B(u) du + \sum_{m=1}^{n-1} \left[ f_m \int_0^{t-\beta_m} B(u) du \right] , & \beta_n < t \leq \beta_{n+1} , \\
\sum_{m=1}^{N-1} \left[ f_m \int_0^{t-\beta_m} B(u) du \right] , & t > \beta_N .
\end{cases}
\end{aligned}
\]

However, in practice it is more likely that the data in the histogram is equally spaced at widths \( \gamma \) which will almost certainly not be the same width as the interval \([0, \beta_1]\). Consequently, we will need to further subdivide the step length \( \beta_1 \). This is done by using,

\[
\beta_1 = k\gamma , \quad \beta_2 = (k+1)\gamma , \quad \beta_3 = (k+2)\gamma , \ldots , \quad \beta_N = (k+N-1)\gamma , \quad (4.29)
\]

where \( k \) is some integer \( \geq 1 \) and we note the probability of a newborn viable cell fissioning between ages \( \beta_i \) and \( \beta_{i+1} \) is now given by \( \gamma f_i \).

Using the new step length \( \gamma \) we build up the solution to the integral equation for \( B(t) \) in the form,

\[
\begin{aligned}
B_n(t) &= 0 , \quad (n-1)\gamma < t \leq n\gamma , \quad n = 1, 2, 3, \ldots , k , \quad k \geq 1 . \\
\frac{B_{k+1}(t)}{a(t)} &= f_1 \left[ M(0) + \int_0^{t-k\gamma} B_1(u) du \right] , \quad k\gamma < t \leq (k+1)\gamma , \\
\frac{B_{k+n}(t)}{a(t)} &= f_n \left[ M(0) + \int_0^{t-(k+n-1)\gamma} B_1(u) du \right] + \sum_{m=1}^{n-1} \left[ f_m \int_0^{t-(k+m)\gamma} B(u) du + \int_{n-m}^{n-m+1} B(u) du \right] , \quad [k + (n-1)\gamma < t \leq [k + n]\gamma ; \quad n=2, 3, \ldots , N-1 ,
\end{aligned}
\]
From (4.2) we can build up a system of integro-difference
equations for $M(t)$,

$$
M_n(t) = M(0), \quad (n-1)\gamma < t \leq n\gamma; \quad n=1,2,3, \ldots, k; \quad k \geq 1,
$$

$$
M_{k+1}(t) = M(0) + \int_{k\gamma}^{t} \left[ \frac{\alpha(u) - 1}{\alpha(u)} \right] B_{k+1}(u) du, \quad k\gamma < t \leq (k+1)\gamma,
$$

$$
M_{k+n+1}(t) = M(0) + \int_{(k+n)\gamma}^{t} \left[ \frac{(k+m+1)\gamma}{(k+m)\gamma} \right] B_{k+m+1}(u) du + \sum_{m=0}^{n-1} \left[ \frac{(k+m+1)\gamma}{(k+m)\gamma} \right] B_{k+m+1}(u) du,
$$

(k + n)\gamma < t \leq (k + n + 1)\gamma; \quad n=1,2,3, \ldots

As an example, we consider the histogram for $f(x)$ with $N = 4$
in (4.28) and $k = 2$ in (4.29). We also choose $\alpha(t) = Le^{-\lambda t} + c$, $\lambda > 0$, $0 < c < L+c \leq 2$, which is (a) in table 3. From (4.30) and (4.31) we find,

$$
B_1(t) = B_2(t) = 0,
$$

$$
B_3(t) = f_1 M(0) \left[ (c-L)e^{-\lambda t} + L \right]
$$

$$
B_4(t) = f_2 M(0) \left[ (c-L)e^{-\lambda t} + L \right]
$$

$$
B_5(t) = M(0) \left[ f_3 + \frac{f_2^2 (c-L)}{\lambda} \left( e^{-2\lambda \gamma} - e^{-\lambda (t-2\gamma)} \right) + f_1^2 L(t - 4\gamma) \right] \left[ (c-L)e^{-\lambda t} + L \right],
$$
\begin{align*}
B_6(t) &= f_1 M(o) \left\{ 2L \gamma (3f_1 - 5f_2) + \frac{(c-L)}{\lambda} (f_2 - f_1) e^{-3\lambda \gamma} \\
&+ f_2 (c-L) e^{-2\lambda \gamma} + L(2f_2 - f_1) t + \frac{(c-L)}{\lambda} (f_1 - f_2) e^{-\lambda (t-3\gamma)} \\
&- \frac{f_2 (c-L)}{\lambda} e^{-\lambda (t-2\gamma)} \right\} \left[ (c-L) e^{-\lambda t} + L \right],
\end{align*}

and

\begin{align*}
M_1(t) &= M_2(t) = 0, \\
M_3(t) &= M(o) + f_1 M(o) \left[ (c-1)t - \frac{Le^{-\lambda t}}{\lambda} + \frac{Le^{-2\lambda \gamma}}{\lambda} - 2\gamma (c-1) \right], \\
M_4(t) &= M(o) \left\{ 1 + 3\gamma (c-1) (f_1 - f_2) + \frac{Le^{-3\lambda \gamma}}{\lambda} (f_2 - f_1) \\
&+ \frac{L e^{-2\lambda \gamma}}{\lambda} - 2\gamma f_1 (c-1) + f_2 \left[ (c-1)t - \frac{Le^{-\lambda t}}{\lambda} \right] \right\}, \\
M_5(t) &= M(o) \left\{ 1 + f_1 \left[ 3\gamma (c-1) - \frac{Le^{-3\lambda \gamma}}{\lambda} + \frac{Le^{-2\lambda \gamma}}{\lambda} - 2\gamma (c-1) \right] \\
&+ f_2 \left[ 4\gamma (c-1) - \frac{Le^{-4\lambda \gamma}}{\lambda} + \frac{Le^{-3\lambda \gamma}}{\lambda} - 3\gamma (c-1) \right] \\
&+ \left[ f_3 + f_1 \left. \frac{2Le^{-2\lambda \gamma}}{\lambda} - 4\gamma f_1^2 \right] \right\} (c-1)t - \frac{Le^{-\lambda t}}{\lambda} \\
&+ \frac{Le^{-4\lambda \gamma}}{\lambda} - 4\gamma (c-1) \right] + f_1^2 c (c-1) \left[ \frac{t^2}{2} - 8\gamma^2 \right] \\
&- \frac{f_1^2 L^2}{2\lambda^2} \left[ e^{-6\lambda \gamma} - e^{-2\lambda (t-\gamma)} \right] \\
&- \frac{f_1^2 L (c-1)}{\lambda^2} \left[ e^{-2\lambda \gamma} - e^{-\lambda (t-2\gamma)} \right] \\
&+ \frac{f_1^2 cL}{\lambda} \left[ e^{-4\lambda \gamma} \left( 4\gamma + \frac{1}{\lambda} \right) - e^{-\lambda t} \left( t + \frac{1}{\lambda} \right) \right] \right\}.
\end{align*}
If \( f(x) \) is presented in concentrated form then,

\[
f(x) = \sum_{n=1}^{N} F_n \delta(x - \beta_n) = F_1 \delta(x - \beta_1) + F_2 \delta(x - \beta_2) + \ldots + F_N \delta(x - \beta_N), \tag{4.32}
\]

where,

\( \delta(x - \beta_n) \) is the Dirac delta function defined as zero everywhere except at \( \beta_n \) and having the property \( \int F_n \delta(x - \beta_n) = F_n \), provided \( \beta_n \) is in the interval of integration. Consequently, we see that,

\[
\int_{0}^{\beta_i+1} f(x)\,dx = F_i = \text{Probability that a newborn viable cell will fission between age } \beta_i \text{ and } \beta_{i+1}; i=1,2, \ldots, N.
\]

The graphical form of \( f(x) \) would be as in Figure 1 except that the rectangular areas would be replaced by spikes of infinite height above each of the \( N \) divisions of the \( x \) axis.

As with the analysis of the histogram, provided we can move in steps of length \( \beta_1 \), without straddling any \( \beta_i \), we can build up the solution for \( B(t) \) in the form of a system of difference equations given by,

\[
B(t) = \begin{cases} 
0 & , 0 \leq t < \beta_1, \\
M(o)F_n \delta(t - \beta_n) + \sum_{m=1}^{N} F_m B(t - \beta_m), & \beta_n \leq t < \beta_{n+1}, n=1,2, \ldots, N-1, \\
M(o)F_N \delta(t - \beta_N) + \sum_{m=1}^{N} F_m B(t - \beta_m), & t \geq \beta_N.
\end{cases}
\]

However, this situation is again unlikely and almost certainly we will have to subdivide the step length as we did in (4.29). Hence substituting (4.29) and (4.32) in (4.4) we have solutions for \( B(t) \).
and \( M(t) \) given by,

\[
\frac{B_n(t)}{\alpha(t)} = 0, \quad (n-1)\gamma < t < n\gamma; \quad n = 1, 2, 3, \ldots, k,
\]

\[
\frac{B_{k+n}(t)}{\alpha(t)} = \int_0^t \frac{a(u) - 1}{\alpha(u)} B_{k+1}(u) \, du,
\]

\[\text{for } k\gamma < t < (k+1)\gamma,\]

\[
\frac{B_{k+N+n}(t)}{\alpha(t)} = \sum_{m=1}^{N} \int_0^t \frac{a(u) - 1}{\alpha(u)} B_{k+n+1}(u) \, du,
\]

\[\text{for } (k+N+n-1)\gamma < t < (k+N+n)\gamma; \quad n = 1, 2, 3, \ldots, k,
\]

and

\[
M_n(t) = M(0), \quad n = 1, 2, \ldots, k,
\]

\[
M_{k+1}(t) = M(0) + \int_0^t \frac{a(u) - 1}{\alpha(u)} B_{k+1}(u) \, du, \quad k\gamma < t < (k+1)\gamma,
\]

\[
M_{k+N+1}(t) = M(0) + \int_0^t \frac{a(u) - 1}{\alpha(u)} B_{k+n+1}(u) \, du + \sum_{m=0}^{n-1} \int_0^t \frac{a(u) - 1}{\alpha(u)} B_{k+m+1}(u) \, du,
\]

\[\text{for } (k+n)\gamma < t < (k+n+1)\gamma; \quad n = 1, 2, 3, \ldots,
\]

The simpler form of (4.33) and (4.34) in comparison with (4.30), (4.31) is essentially due to the introduction of the Dirac delta function in (4.32). It is also noted that the simple generation time model considered in section 4.3 and proposed by Thornley, J.M. (1976), where \( f(x) = \delta(t - x) \), is a particular case of the more general form (4.32), where \( \beta_1 = \tau, \quad N = 1 \) and \( F_1 = 1 \).
As an example, we will consider the solutions given by (4.33), (4.34) where \( \alpha(t) = e^{-\lambda t} + c; \lambda > 0, 0 < c < L + c \leq 2 \) and \( k = 2, N = 4 \) in (4.29) and (4.32) respectively. Making these substitutions in (4.33) and (4.34) we have,

\[
\begin{align*}
B_1(t) &= B_2(t) = 0, \\
B_3(t) &= F_1 M(o) \delta(t - 2\gamma) \left[ e^{-\lambda t} + c \right], \\
B_4(t) &= F_2 M(o) \delta(t - 3\gamma) \left[ e^{-\lambda t} + c \right], \\
B_5(t) &= M(o) \delta(t - 4\gamma) \left[ F_3 + F_1^2 (e^{-\lambda(t-2\gamma)} + c) \right] \left[ e^{-\lambda t} + c \right], \\
B_6(t) &= M(o) \delta(t - 5\gamma) \left[ F_4 + F_1 F_2 (e^{-\lambda(t-2\gamma)} + c) + F_1 F_2 (e^{-\lambda(t-3\gamma)} + c) \right] \times \left[ e^{-\lambda t} + c \right], \\
B_7(t) &= F_1 M(o) \delta(t - 6\gamma) \left[ F_3 + F_1^2 (e^{-\lambda(t-4\gamma)} + c) \right] \times \left[ e^{-\lambda(t-2\gamma)} + c \right] + F_2^2 M(o) \delta(t - 6\gamma) \times \left[ e^{-\lambda(t-3\gamma)} + c \right] + F_1 F_3 M(o) \delta(t - 6\gamma) \times \left[ e^{-\lambda(t-4\gamma)} + c \right],
\end{align*}
\]

and

\[
\begin{align*}
M_1(t) &= M_2(t) = M(o), \quad 0 \leq t < 2\gamma, \\
M_3(t) &= M(o) + F_1 M(o) \left[ e^{-2\lambda t} + c - 1 \right], \quad 2\gamma \leq t < 3\gamma, \\
M_4(t) &= M(o) \left\{ 1 + F_2 \left[ e^{-3\lambda t} + c - 1 \right] + F_1 \left[ e^{-2\lambda t} + c - 1 \right] \right\}, \quad 3\gamma \leq t < 4\gamma, \\
M_5(t) &= M(o) \left\{ 1 + F_2 \left[ e^{-3\lambda t} + c - 1 \right] + F_1 \left[ e^{-2\lambda t} + c - 1 \right] \right. \\
&\quad + \left. \left[ F_3 + F_1^2 (e^{-2\lambda t} + c) \right] \left[ e^{-4\lambda t} + c - 1 \right] \right\}, \quad 4\gamma \leq t < 5\gamma.
\end{align*}
\]
\[ M_6(t) = M(o) \left\{ 1 + F_2 \left[ L e^{-3\lambda t} + c - 1 \right] + F_1 \left[ L e^{-2\lambda t} + c - 1 \right] \right. \\
+ \left. \left[ F_3 + F_1^2 (L e^{-2\lambda t} + c) \right] \left[ L e^{-4\lambda t} + c - 1 \right] \right. \\
+ \left. \left[ F_4 + F_1 F_2 (L e^{-3\lambda t} + c) + F_1 F_2 (L e^{-2\lambda t} + c) \right] \right. \\
\times \left. \left[ L e^{-5\lambda t} + c - 1 \right] \right\}, \quad 5 \leq t < 6 \gamma \\
\]

\[ M_7(t) = M_6(t) + M(o) \left\{ F_1 \left[ F_3 + F_1^2 (L e^{-2\lambda t} + c) \right] \left[ L e^{-4\lambda t} + c \right] \right. \\
+ \left. F_2^2 (L e^{-3\lambda t} + c) + F_1 F_3 (L e^{-2\lambda t} + c) \right\} \\
\times \left. \left[ L e^{-6\lambda t} + c - 1 \right] \right\}, \quad 6 \gamma \leq t < 7 \gamma . \\
\]

Although the analysis is less tedious than with the histogram form of \( f(x) \) it is obvious that analytic solutions are not easy to obtain. However, as with (4.30), (4.31), the systems (4.33), (4.34) have merit as a basis for numerical computation.
5. THE GROWTH OF A COLUMN OF AGE AND POSITION DEPENDENT CELLS

5.1 Introduction

If we were to place a pin at some point in a column of cells then the movement of this pin in time would trace out a curve, which on a very small time scale and with very high magnification, would consist of a polygonal arc with the vertices representing the instants of fission of any cell in the column below the point. If we could repeat this experiment many times the mean of these polygonal arcs could be represented by a curve, which we will call the trajectory, with a continuous derivative which would have an S shape.

Supposing that we now placed many pins on our column such that initially they were at equidistant centres. Then our problem reduces to describing simultaneously in time the set of trajectories traced out by these pins. There are two methods which can be used in this problem.

The first method we consider will be referred to as the logistic approach. Here a typical trajectory is fitted by a logistic or one of the many other standard S shaped functions. It should be noted from section 3.4 that the logistic approach throws away all the age dependent properties of the cells and considers only some artificial average cell that is experiencing fission at a particular time dependent rate.

The second method represents a new approach. Here the integral formulation of chapter 1, which considers the age specific characteristics of an individual cell, is extended to account for position dependency. Hence a model is developed which can account for a fissioning process, of the type discussed in chapter 4, so that in a column of cells the
rates depend on the position of the cells in the column as well as their ages.

We introduce the following definitions and notation,

\[ L \] = Total height of column initially.

\[ y(t, p) \] = Height of point from base at time \( t \) which was initially positioned at height \( p \) at time zero,

\[ \sigma(t, p) \] = Stretch ratio \( \frac{3y(t, p)}{3p} \)

For fissioning cells (viable) in position \( p \) at time \( t \),

\[ M(t, p)dp \] = Mean number of cells in element \( dp \),

\[ B(t, p)dp \frac{dt}{dt} \] = Number of births of \( M(t, p)dp \) cells in time \( t \) to \( t+dt \),

\[ B(t) \] = Total birth rate in the column,

\[ a(x, t, p) \] = Density function of cells of age \( x \),

\[ g(x, t, p) \] = The length of cells of age \( x \),

\[ f(x, t-x, p) \] = Density function of the generation time, \( X \), for cells of age \( x \),

\[ \mu(x, t-x, p) \] = Age specific fission rate of cells of age \( x \),

\[ \ell(x, t-x, p) \] = Survivor function for fissioning cells. The probability that fission has not occurred by age \( x \) for cell born at \( t-x \),

\[ D(t, p) \] = Fission rate of cells.

Similar definitions hold where subscripts \( V \) and \( T \) have been used to describe the vegetative and total cell populations respectively.
5.2 The Logistic Approach

Following Salamon, P., List, A., Grenetz, P.S. (1973) we define the following. \( y(t,p) \) is a variable which can describe the mean growth of all parts of the stem simultaneously, and is the distance from the base of the stem at time \( t \) of a point that was originally positioned at \( p \) at time zero. Hence it immediately follows that \( y(0,p) = p \).

Thus we can characterise points in terms of their initial position and refer to \( y(t,p) \) as "the position of the point \( p \) at time \( t \)". It follows that \( y(t,p) \) for growth in the stem is a non-decreasing function in \( t \). If \( \frac{\partial y(t,p)}{\partial t} > 0 \), then there is growth at some point in the stem below \( p \). If \( L \) is the initial length of the stem then obviously \( \frac{\partial y(t,L)}{\partial t} = 0 \) implies that all growth has ceased. It is plausible to consider a model such that once growth has stopped there will be no further growth. The stretch ratio is a measure of how much the initial element \( dp \) has stretched in time \( t \). Thus the stretch ratio \( \sigma(t,p) \) is defined as \( \frac{\partial y(t,p)}{\partial p} \) and \( \frac{\partial y(t,p)}{\partial t} \) is of course the velocity of the point \( p \) and \( \frac{\partial^2 y(t,p)}{\partial t^2} \) is its acceleration.

It is immediately apparent that \( \sigma(t,p) \) is a non-decreasing function in \( t \) and that as \( \sigma(0,p) = 1, \sigma(t,p) \geq 1 \). (Because of this the Salamon, P. et al. (1973) paper is in error. Part F of Fig. 8 incorrectly indicates that \( \sigma(0,p) > 1 \)). As soon as \( \sigma(t,p) \) becomes constant in time, growth has finished for element \( dp \).

If it is asked what point in the stem is moving fastest in relation to a given point \( p \) at time \( t \) then perhaps one might consider the gradient of \( y(t,p) \) at \( p \), \( \nabla y(t,p) = \left( \sigma(t,p), \frac{\partial y(t,p)}{\partial t} \right) = (\text{stretch, velocity}) \). If we move in the direction of the gradient we will find such a point.
The following table (table 4) defines all these different variables and shows the relationship between them. The literature fails to emphasise that only one of these variables is independent.

To give some idea of the logistic approach we consider a logistic approximation to the stretch ratio:

As \( a(0,p) = 1 \), we have,

\[
\sigma(t, p) = \frac{K_p}{1 + (K - 1)e^{-r_pt}}, \quad r_p \geq 0.
\]

We will restrict ourselves in what follows to \( r_p = r \) and note that if \( K_p = K \) we reproduce the simple logistic formula,

\[
\sigma(t, p) = \sigma_1(t) = \frac{K}{1 + (K-1)e^{-rt}}, \quad \text{for which } y(t, p) = \sigma_1(t)p \]

and \( y(\infty, p) = pK \).

If we try \( K_p = pk \), which is a crude approximation to root growth, we obtain,

\[
y(t, p) = e^{rt} \left[ p - \frac{e^{rt} - 1}{K} \ln \left( 1 + \frac{pK}{e^{rt} - 1} \right) \right]
\]

and note that \( y(\infty, p) = kp^2K \).

Modifying this to \( K_p = (1-p)K \), which is more applicable to leaf growth, we have

\[
y(t, p) = e^{rt} \left[ p + \frac{e^{rt} - 1}{K} \ln \left( 1 - \frac{pK}{e^{rt} + K - 1} \right) \right].
\]

Again it is noted that \( y(\infty, p) = Kp - \frac{p^2K}{2} \).

As \( p \geq 0 \) it follows that for \( \sigma(\infty, p) = (1-p)K \geq 1 \), then \( K > 0 \), and \( p \leq 1 - \frac{1}{K} \). So this would be a reasonable model if the length of the stem \( \leq 1 - \frac{1}{K} \) and \( K > 1 \) (to ensure that this length is positive).
Hence, the growth of any point \( p \) is \( \frac{p(2(K-1) - pK)}{2} \) and, in particular, when \( p = 1 - \frac{1}{K} \), the growth of the leaf is \( \frac{(K-1)^2}{2K} \).

Finally, if \( K_p = Ke^{-\lambda p} \)

\[
y(t,p) = \frac{e^{rt}}{\lambda} \ln \left[ 1 + \frac{K(t - e^{-\lambda p})}{Ke^{-\lambda p} + e^{rt} - 1} \right] \text{ and } y(\infty,p) = \frac{K}{\lambda} (1 - e^{-\lambda p}).
\]

This model is reasonable if the length of the stem \( \leq \frac{\ln K}{\lambda} \), where \( K > 1 \). The growth of point \( p \) is \( \frac{K}{\lambda} (1 - e^{-\lambda p}) - p \) and in particular for \( p = \frac{\ln K}{\lambda} \) the growth is \( \frac{(K-1) - \ln K}{\lambda} \).

5.3 The Age specific Model

Our column consists of a mixture of cells, some of which are fissioning (viable) cells and the remainder are vegetative (non-viable) cells. Both types of cells are capable of growth but only the viable cells can fission and when a fission occurs exactly two new cells are produced. Of these two new cells on average \( \alpha(t,p) \) are viable cells and \( 2 - \alpha(t,p) \) are vegetative cells. The subscripts \( V \) and \( T \) will be used to describe the vegetative cell population and the total population respectively.

We represent each cell by a point and thus we are able to consider the age specific random point process within the element \( dp \). The initial mean number of these point cells is \( M_T(o,p)dp \) and the number of these, after time \( t \), is \( M_T(t,p)dp \). Thus as long as we consider only the population of points, we do not have to concern ourselves as to whether the element \( dp \) has been stretched by elongation of the cells to \( dy \).
**TABLE 4**  
**GROWTH PARAMETERS**

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>ONE DIMENSION</th>
<th>TWO DIMENSIONS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>$y(t)$</td>
<td>$y(t,p)$</td>
</tr>
<tr>
<td>Growth rate (velocity)</td>
<td>$v(t) = \frac{dy}{dt}$,</td>
<td>$v(t,p) = \frac{3y}{3t}$,</td>
</tr>
<tr>
<td></td>
<td>$y(t) = y(0) + \int_{0}^{t} v(u)du.$</td>
<td>$y(t,p) = \int_{0}^{t} v(z,p)dz + p.$</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>$p(t) = \frac{1}{y} \frac{dy}{dt} = \frac{v}{y} = \frac{d\ln y}{dt}$,</td>
<td>$p(t,p) = \frac{1}{y} \frac{3y}{3t} = \frac{v}{y}$,</td>
</tr>
<tr>
<td></td>
<td>$y(t) = y(0) \exp \int_{0}^{t} p(z)dz.$</td>
<td>$y(t,p) = y(0) \exp \int_{0}^{t} p(z,p)dz.$</td>
</tr>
<tr>
<td>Stretch ratio</td>
<td>-</td>
<td>$\sigma(t,p) = \frac{3y}{3p}$,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$y(t,p) = \int_{0}^{\sigma} \sigma(t,z)dz.$</td>
</tr>
<tr>
<td>Divergence</td>
<td>-</td>
<td>$\delta(t,p) = \frac{3\sigma}{3t} = \frac{3v}{3p} = \frac{3^2y}{3p3t}$,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$y(t,p) = \int_{0}^{t} \sigma(u,z)dz du.$</td>
</tr>
<tr>
<td>Relative Elemental Growth Rate (RELEG)</td>
<td>$g = \frac{dv}{dy} = \frac{1}{v} \frac{dv}{dt} = \frac{d\ln v}{dt}$,</td>
<td>$g = \frac{\delta}{\sigma} = \frac{3\sigma}{3t}/\sigma = \frac{3\ln \sigma}{3t}$,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$g = \frac{\text{acceleration}}{\text{velocity}}$.</td>
</tr>
<tr>
<td></td>
<td>$y(t) = y(0) + v(0) \int_{0}^{t} \exp \int_{0}^{u} g(z)dz du.$</td>
<td>$y(t,p) = \int_{0}^{p} \exp \int_{0}^{t} g(z,u)dz du.$</td>
</tr>
</tbody>
</table>
Hence, considering the population of fissioning cells, we may apply the age specific integral formulation of chapter 1 to this point process to obtain \( M(t,p) \) and \( a(x,t,p) \) the age density function, where \( x \) refers to the age of the cell and \( a(x,t,p)dx \) is the fraction of those cells of age \( x \) to \( x+dx \) at position \( p \) at time \( t \). At this stage we can then grow each cell according to some length function \( g(x,t,p) \).

To calculate \( M \) and \( a \) it is also necessary to determine \( B(t,p) \) which is the birth rate density. \( B(t,p)dp \) is the production rate of new fissioning cells within the element.

Another byproduct of the calculation is, \( D(t,p) \), the death rate of the cells. \( D(t,p)dp \) is thus the fission rate of those cells within \( p \) to \( p+dp \).

We now modify the integral formulation of chapter 1 to account for fissioning. The fissioning process is characterised as follows. Let \( X \) be the random variable representing the generation time for a cell which is timed from the instant when it was born from the fission of its mother cell until it fissions (or dies). Let \( f(x,t-x,p) \) be the density function associated with \( X \). Then \( f(x,t-x,p)dx \) is the probability that a newly fissioned cell will die between age \( x \) to \( x+dx \). The time parameter is best indicated through \( t-x \), the instant at which the cell was born. Also we define \( \mu(x,t-x,p)dx = \) Prob \( (x < X \leq x+dx \mid X > x) \) which is the age specific fission rate, or the probability that a cell will die in the next time instant \( dx = dt \), given that it is alive now and of age \( x \). Only one of these variables characterising death (or fissioning) is independent as,
\[ \mu(x, t-x, p) = \frac{f(x, t-x, p)}{g(x, t-x, p)} . \]

From the above definitions it follows that the number of cells of age \( x \) to \( x + dx \) within our element \( dp \) is,

\[ M(t, p) a(x, t, p) dx \; dp = B(t-x, p) \frac{\bar{z}(x, t-x, p)}{\bar{g}(x-t, t-x, p)} \; dx \; dp . \]

Knowing the initial mean density of the cells and the initial age density at time \( t \) this becomes,

\[ M(t, p) a(x, t, p) = \begin{cases} 
B(t-x, p) \bar{z}(x, t-x, p), & 0 < x < t, \\
M(0, p) a(x, t, 0, p) \bar{z}(x-t, 0, p), & x \geq t. 
\end{cases} \quad (5.1) \]

To proceed with our formulation we repeatedly convolve (5.1). For example, integration with respect to \( x \) gives directly,

\[ M(t, p) = M_0(t, p) + \int_0^t B(t-x, p) \bar{z}(x, t-x, p) dx , \quad (5.2) \]

where

\[ M_0(t, p) = M(0, p) \int_t^\infty a(x-t, 0, p) \frac{\bar{z}(x, t-x, p)}{\bar{g}(x-t, t-x, p)} \; dx , \]

\[ = M(0, p) \int_0^\infty a(x, 0, p) \frac{\bar{z}(x+t, -x, p)}{\bar{g}(x, -x, p)} \; dx , \quad (5.3) \]

\[ = \int_t^\infty B(t-x, p) \bar{z}(x, t-x, p) \; dx . \]

\( M_0(t, p) \; dp \) thus represents the survivors from our initial (mother) cells and the integral term in (5.2) represents cells that have been created since the origin. Similarly, the death rate density is,

\[ D(t, p) = D_0(t, p) + \int_0^t B(t-x, p) f(x, t-x, p) dx , \]

where,

\[ D_0(t, p) = M(0, p) \int_0^\infty a(x, 0, p) \frac{f(x+t, -x, p)}{\bar{g}(x, -x, p)} \; dx , \]
\( D(t,p) \, dp \) gives the rate of fission within the element \( dp \) at time \( t \).

Now we can consider the birth rate. To do this we refer again to our fission process. At the instant of fission the viable cell divides into two. Let us assume that of these two cells only \( \alpha(t,p) \) continue to fission. Then we can describe the fissioning cell population in terms of,

\[
B(t,p) = G(t,p) + \alpha(t,p) \int_0^t B(t-x,p) f(x,t-x,p) \, dx , \quad (5.4)
\]

where,

\[
G(t,p) = \alpha(t,p) \int_t^\infty B(t-x,p) f(x,t-x,p) \, dx ,
\]

\[
= \alpha(t,p) M(0,p) \int_0^\infty a(x,0,p) \frac{f(x+t,-x,p)}{l(x,-x,p)} \, dx . \quad (5.5)
\]

Thus, \( G(t,p) \, dp \) is the birth rate of cells due to mothers who were alive at the origin, whilst the integral term in (5.4) relates to mothers that have been born since the origin.

It is seen that \( B(t,p), M(t,p) \) and \( D(t,p) \) have a similar structure. In fact if we had knowledge of \( B(t,p) \) for \( t < 0 \) we could write,

\[
B(t,p) = \alpha(t,p) \int_0^\infty B(t-x,p) f(x,t-x,p) \, dx = \alpha(t,p) D(t,p)
\]

\[
M(t,p) = \int_0^\infty B(t-x,p) l(x,-x,p) \, dx , \quad (5.6)
\]

\[
D(t,p) = \int_0^\infty B(t-x,p) f(x,t-x,p) \, dx .
\]

From this it is seen that,

\[
\frac{dM(t,p)}{dt} = B(t,p) - D(t,p) .
\]
But it immediately follows from (5.6) that,

\[ D(t,p) = \frac{1}{\alpha(t,p)} B(t,p) . \]  

(5.7)

Hence,

\[ \frac{dM(t,p)}{dt} = \frac{1}{\gamma(t,p)} B(t,p) , \]

where,

\[ \gamma(t,p) = \frac{\alpha(t,p)}{\alpha(t,p) - 1} . \]

Consequently,

\[ M(t,p) = M(0,p) + \int_0^t \frac{B(u,p)}{\gamma(u,p)} \, du , \]  

(5.8)

It can be shown that (5.8) and (5.2) are equivalent but as (5.8) is the simpler we will use it in future.

The following equations for the vegetative (V) and total cell (T) populations can be derived by arguments similar to those used in describing the viable cell population, noting that

\[ B_v(t) = [2 - \alpha(t,p)] D(t) , \]

\[ B_v(t,p) = \left[ \frac{2 - \alpha(t,p)}{\alpha(t,p)} \right] B(t,p) , \]

\[ M_v(t,p) = M_v(0,p) + \int_0^t B_v(u,p) \, du , \]  

(5.9)

\[ M_v(t,p) a_v(x,t,p) = \begin{cases} M_v(0,p) a_v(x-t,0,p), & x \geq t, \\ B_v(t-x,p), & 0 \leq x < t, \end{cases} \]  

(5.10)

and,

\[ B_T(t,p) = 2B(t,p)/\alpha(t,p) , \]

\[ M_T(t,p) = M_T(0,p) + \int_0^t \frac{B(u,p)}{\alpha(u,p)} \, du , \]  

(5.11)
\[ M_T(t,p)a_T(x,t,p) = \begin{cases} M(0,p)a(x-t,0,p) \frac{L(x,t-x,p)}{L(x-t,t-x,p)} \\ + M_V(0,p)a_V(x-t,0,p) \\ B(t-x,p)Z(x,t-x,p) + B_V(t-x,p), \quad 0 \leq x < t. \end{cases} \] (5.12)

Now our problem has been formulated. It is hoped that we can now calculate \( B(t,p) \) from (5.4) and hence we have as a by-product, \( D(t,p) \) from (5.7). Then we calculate \( M(t,p) \) from (5.8) and finally we are in a position to attempt to calculate \( a(x,t,p) \) from (5.1). Equations (5.9) through to (5.12) complete the analysis of the point process.

Having described the point process we are now in a position to consider the length of the cells in our element \( dp \). A viable cell of age \( x \) to \( x+dx \) in the element \( dp \) has length \( g(x,t,p) \) and a vegetative cell of the same age has length \( g_V(x,t,p) \). The total number of viable cells, in our element \( dp \), of age \( x \) to \( x+dx \) is \( M(t,p)a(x,t,p)dx \) and the total number of vegetative cells, of the same age, is \( M_V(t,p)a_V(x,t,p)dx \). Consequently, the total length of those cells of age \( x \) to \( x+dx \) in our element must then be,

\[ [M(t,p)a(x,t,p)g(x,t,p) + M_V(t,p)a_V(x,t,p)g_V(x,t,p)]dx dp . \]

Hence, considering cells of all ages in our element we see that the stretched element, \( dy(t,p) \), is given by,

\[ dy(t,p) = \int_0^\infty [M(t,p)a(x,t,p)g(x,t,p) + M_V(t,p)a_V(x,t,p)g_V(x,t,p)]dx dp . \]

It follows that the stretch ratio can be written as,

\[ \sigma(t,p) = \frac{3y(t,p)}{3p} = M(t,p)h(t,p) + M_V(t,p)h_V(t,p) , \] (5.13)

where,
\[ h(t,p) = \int_0^\infty a(x,t,p)g(x,t,p)\,dx , \]
\[ h_V(t,p) = \int_0^\infty a_V(x,t,p)g_V(x,t,p)\,dx . \]

We note that \( h(t,p) \) is the mean length of viable cells and \( h_V(t,p) \) is the mean length of vegetative cells.

After growth we have \( M_T(t,p)\,dp \) cells spread over \( dy \). Hence, the density of cells in the stretched stem is \( \frac{M_T(t,p)}{\sigma(t,p)} \) and the mean cell length in the stretched stem is \( h_T(t,p) = \frac{h(t,p)}{M_T(t,p)} \). Hence from (5.13), \( h_T(t,p) = \frac{M_T(t,p)}{M_V(t,p)} h(t,p) + \frac{M_V(t,p)}{M_T(t,p)} h_V(t,p) \) and since \( \sigma(o,p) = 1 \) we have,

\[ 1 = M(0,p)h(0,p) + M_V(0,p)h_V(0,p) . \] (5.15)

Growing the whole column at time \( t \), we have from (5.13),

\[ y(t,p) = \int_0^p \sigma(t,z)\,dz = \int_0^p [M(t,z)h(t,z) + M_V(t,z)h_V(t,z)]\,dz . \] (5.16)

This, of course, satisfies the initial condition \( y(0,p) = p \). In particular, the length of the whole column after time \( t \) is

\[ y(t,L) = \int_0^L \sigma(t,z)\,dz . \]

It should also be noted that the actual displacement of the point \( p \) is \( y(t,p) - p \).

5.4 The Length Functions \( g(x,t,p), g_V(x,t,p) \)

At time \( t-x \) there are \( M(t-x,p)a(s,t-x,p)\,dp \,ds \) viable cells, in our element \( dp \), of age \( s \) to \( s+ds \). \( u(s,t-x-s,p)\,ds \) is the fraction of these cells that will fission in the next time interval \( ds \) and each of these cells has length \( g(s,t-x,p) \). Hence, at time \( t-x \),
the total number of viable cells that will fission in the next time interval \( ds \), to produce exactly two new cells, is

\[
\left[ \int_0^\infty M(t-x,p)a(s,t-x,p)\mu(s,t-x-s,p)ds \right]dp \, ds
\]

and the total length of these cells is given by,

\[
\left[ \int_0^\infty M(t-x,p)a(s,t-x,p)\mu(s,t-x-s,p)g(s,t-x,p)ds \right]dp \, ds.
\]

So at time \( t-x \) the mean length of a viable cell that will fission in the next time interval \( ds \) is given by,

\[
\left[ \int_0^\infty M(t-x,p)a(s,t-x,p)\mu(s,t-x-s,p)g(s,t-x,p)ds \right]dp \, ds
\]

\[
\left[ \int_0^\infty M(t-x,p)a(s,t-x,p)\mu(s,t-x-s,p)ds \right]dp \, ds
\]

\[
\int_0^\infty a(s,t-x,p)\mu(s,t-x-s,p)g(s,t-x,p)ds
\]

\[
\int_0^\infty a(s,t-x,p)\mu(s,t-x-s,p)ds
\]

If we are considering a cell in our element \( dp \) at time \( t \) of age \( x \) to \( x+dx \) then regardless of whether it is a viable cell or a vegetative cell it must be the offspring of one of the viable cells considered above. When a fission occurs exactly two new cells are produced and it is reasonable to suppose that each cell will have a length exactly half that of the cell which fissioned to produce it. If we also assume that the increase in the length of a cell since its birth is a linear function of its present age then it is reasonable to have,

\[
g(x,t,p) = g_v(x,t,p)
\]

\[
= x + \frac{\int_0^\infty a(S,t-x,p)\mu(s,t-x-s,p)g(s,t-x,p)ds}{2\int_0^\infty a(s,t-x,p)\mu(s,t-x-s,p)ds}, \quad (5.17)
\]
which expresses the idea that, in our element $dp$, at time $t$ the
length of a cell (viable or vegetative) in the age range $x$ to $x+dx$
is half the average length of the viable cell which fissioned to
produce it plus its present age.

We note that (5.17) requires a complete knowledge of the
remote past. To overcome this difficulty suppose that at $t=0$ the
entire population consists of $K$ newborn viable cells. Then from
(5.17) we have,

$$g(x,t,p) = \begin{cases} 
x + \frac{1}{K}, & x = t \geq 0, \\
\frac{t-x}{a(s,t-x,p)\mu(s,t-x-s,p)g(s,t-x,p)ds} & 0 < x < t, \\
0, & \text{otherwise}
\end{cases}$$

(5.18)

and

$$g_v(x,t,p) = \begin{cases} 
g(x,t,p), & 0 \leq x < t, \\
0, & \text{otherwise}
\end{cases}$$

(5.19)

We note that (5.18), (5.19) enable us to determine $g(x,t,p)$
and $g_v(x,t,p)$ since $\mu(s,t-x-s,p)$ is known and $a(s,t-x,p)$ is
given by (5.1).

5.5 Time Independent Fission Density

We now consider the case where $f(x,t,p) = f(x,p)$ and hence
$z(x,t-x,p) = z(x,p)$ with $a(t,p) = a_p$. 
Then (5.4) becomes,
\[ B(t,p) = G(t,p) + \alpha_p \int_0^t B(t-x,p)f(x,p)dx, \quad (5.20) \]
\[ G(t,p) = \alpha_p M(0,p)\psi(t,p), \]
where,
\[ \psi(t,p) = \int_0^\infty a(x,0,p) \frac{f(x+t,p)}{L(x,p)} dx. \]

Let \( F^*(s) \) be the Laplace transform of the function \( F(x) \) such that
\[ F^*(s) = \int_0^\infty e^{-sx} F(x)dx. \]

We can now take Laplace transforms of (5.20) and apply the convolution theorem to the integral to obtain,
\[ B^*(s,p) = G^*(s,p) + \alpha_p B^*(s,p)f^*(s,p), \]
from which,
\[ B^*(s,p) = \frac{\alpha_p M(0,p)\psi^*(s,p)}{1 - \alpha_p f^*(s,p)}, \quad (5.21) \]
and,
\[ \psi^*(s,p) = \int_0^\infty e^{-st} \int_0^\infty a(x,0,p) \frac{f(x+t,p)}{L(x,p)} dx dt. \]

From the theory of the position independent age specific model (see section 1.3) the solution of (5.20) is,
\[ B(t,p) = \sum_{j=1}^{\infty} A_{j,p} r_{j,p}^t + A_p e^{rt}, \]
where \( r_p \) is the real and \( r_{j,p} \) are the complex zeros of the denominator of (5.21) or the root of \( s \) of,
\[ \alpha_p f^*(s,p) = 1 \quad (5.22) \]

It can be readily shown that \( r_p \) is greater than the real part of any \( r_{j,p} \), and it follows that for large \( t \) (the stable
B(t,p) = A_p e^{r_p t}.

From (5.8) it is seen that,

$$\frac{1}{M} \frac{dM}{dt} = B - D = \frac{1}{M} \frac{B(t,p)}{\gamma(t,p) M(t,p)}.$$  \hspace{1cm} (5.23)

Now from (5.6) it is seen that,

$$M(t,p) = \int_0^\infty A_p e^{r_p (t-x)} l(x,p) dx,$$

$$= B(t,p) \int_0^\infty e^{-r_p x} l(x,p) dx.

Hence, with the stable population the rate $B(t,p)/M(t,p)$, which we will now call the crude birth rate density $b_p$, is independent of $t$.

Similarly, $D(t,p)/M(t,p)$, the crude death rate density $d_p$, is independent of time.

It follows from (5.23) that in the stable population,

$$\frac{1}{M} \frac{dM}{dt} = b_p - d_p = \frac{b_p}{\gamma_p} = r_p.$$  \hspace{1cm}

Thus for large $t$,

$$M(t,p) = \frac{A_p e^{r_p t}}{\gamma_p r_p}.$$  \hspace{1cm}

Again from (5.1) the asymptotic age density becomes,

$$a(x,\infty,p) = \gamma_p r_p e^{r_p x} l(x,p).$$

Thus,

$$b_p = \frac{1}{\gamma_p} \int_0^\infty e^{-r_p x} l(x,p) dx = r_p \gamma_p.$$
\[
\frac{d_p}{p} = \frac{\int_0^\infty e^{-\frac{r_p}{p} x} f(x, p) dx}{\int_0^\infty e^{-\frac{r_p}{p} x} \lambda(x, p) dx} = \frac{\frac{b_p}{\alpha_p} \frac{r_p}{p}}{\alpha_p - 1}.
\]

The \( A_j, p \) are complex and obtained from,
\[
A_{j, p} = \frac{\frac{M(0, p) \psi^* (r_j, p, p)}{\int_0^\infty xe^{-\frac{j}{p} x} f(x, p) dx}}{\int_0^\infty xe^{-\frac{j}{p} x} f(x, p) dx}.
\]

\( A_p \) is real and obtained from,
\[
A_p = \frac{\frac{M(0, p) \psi^* (r_p, p)}{\int_0^\infty xe^{-\frac{r_p}{p} x} f(x, p) dx}}{\int_0^\infty xe^{-\frac{r_p}{p} x} f(x, p) dx},
\]
where,
\[
\overline{Z}_p = \alpha_p \int_0^\infty xe^{-\frac{r_p}{p} x} f(x, p) dx.
\]

\( \overline{Z}_p \) is the mean of a random variable, \( Z_p \), which has the following significance. From (5.22), \( \alpha_p \psi^* (r_p, p) = \alpha_p \int_0^\infty e^{-\frac{r_p}{p} x} f(x, p) dx = 1 \) and hence, if we have \( f_Z(x, p) = \alpha_p e^{-\frac{r_p}{p} x} f(x, p) \) then \( f_Z(x, p) \) is a density function. \( Z_p \) can be regarded as the age at which a fission occurs in the stable population (i.e. we take out a cell about to fission and ask how old it is) assuming that there are \( b_p M(t, p) \) in the population.

For a stable population of fissioning cells the following equations, obtained from (5.9) through to (5.12), describe the vegetative cells and the total population of cells.
\[
\begin{align*}
B_V(t, p) &= \left(\frac{2^\alpha - \alpha_p}{\alpha_p}\right) \Lambda_p e^{r_p t}, \\
M_V(t, p) &= \left(\frac{\alpha - 2}{\alpha - 1}\right) M(0, p) + M_V(0, p) + \left(\frac{2^\alpha}{r_p p}\right) \Lambda_p e^{r_p t},
\end{align*}
\]
137.

\[ M_V(t,p) a_V(x,t,p) = \begin{cases} M_V(0,p) a_V(x-t,0,p) & , \quad x \geq t, \\ \frac{2-\alpha}{\alpha} \frac{\Delta}{p} e^p(t-x) & , \quad 0 \leq x < t, \end{cases} \] 

(5.25)

\[ B_T(t,p) = \frac{2A}{\alpha} e^p t, \]

(5.26)

\[ M_T(t,p) = \left[ \frac{\alpha-2}{\alpha-1} \right] M(0,p) + M_V(0,p) + \frac{A}{\alpha} e^p t, \]

(5.27)

\[ M_T(t,p) a_T(x,t,p) = \begin{cases} M_V(0,p) a_V(x-t,0,p) + M(0,p) a(x-t,0,p) \frac{\beta(x,p)}{\beta(x-t,p)} & , \quad x \geq t, \\ \frac{\alpha}{\alpha-1} e^p(t-x) ( \frac{\beta(x,p)}{\alpha} + \frac{2-\alpha}{p} ) & , \quad 0 \leq x < t. \end{cases} \]

If we assume that

\[ g(x,t,p) = g_V(x,t,p) \] then equation (5.13) can be written as,

\[ \sigma(t,p) = M_T(t,p) h_T(t,p), \]

(5.28)

where,

\[ h_T(t,p) = \int_0^\infty a_T(x,t,p) g(x,t,p) dx. \]

(5.29)

From (5.15) this means that \( h_T(0,p) \) is the initial mean length of the cells and \( h_T(t,p) \) is the mean length of cells in the stretched stem. From (5.16) we have,

\[ y(t,p) = \int_0^p M_T(t,z) h_T(t,z) dz. \]

5.6 Examples

In selecting a suitable \( \beta(x,p) \) we must have \( \beta(0,p) = 1 \) and \( \beta(x_2,p) \leq \beta(x_1,p) \) for \( x_2 \geq x_1 \). \( \beta(x,p) = e^{-px} \) satisfies these criteria and has the corresponding density function \( f(x,p) = pe^{-px} \).
This fission process is such that no fission occurs at the base and the mean time between fissions is \( \frac{1}{p} \) which decreases with \( p \) until it is least at \( L \) which corresponds roughly to the growth of a root.

We also assume that at \( t = 0 \) the column of cells is made up entirely of \( M(0,p) = K \), (constant), newborn viable cells. So \( M_V(0,p) = 0 \) and \( a(x,0,p) = \delta(x) \) for all \( p \).

If \( p = \alpha \), (constant), we have,

\[
f^*(s,p) = \frac{p}{p+s} \quad \text{and thus} \quad B^*(s,p) = \frac{apK}{s-p(a-l)}
\]

from which,

\[
B(t,p) = pK\alpha e^{p(a-l)t} = B(0,p) e^{p(a-l)t}
\]

\[
M(t,p) = K e^{p(a-l)t}.
\]

The transient solution is the same as the stable solution in this case as (5.22) has only a single root \( p(a-l) \) and this root is real.

From equations (5.24) to (5.27) we have,

\[
B_V(t,p) = p(2-\alpha)Ke^{p(a-l)t},
\]

\[
M_V(t,p) = \left[ \frac{2-\alpha}{\alpha-1} \right] K (e^{p(a-l)t}-1),
\]

\[
M_V(t,p)a_V(x,t,p) =
\begin{cases} 
0 & , x \geq t, \\
(2-\alpha)pKe^{p(a-l)(t-x)} & , 0 \leq x < t,
\end{cases}
\]

and,

\[
B_T(t,p) = 2pKe^{p(a-l)t},
\]

\[
M_T(t,p) = \frac{K}{(a-1)} [a - 2 + e^{p(a-l)t}], \quad (5.30)
\]
\[ M(t,p,aT(x,t,p)) = Ke^{-pt} \Phi(Xrt) \], \( X > t \),

\[ 0 < x < t. \]

If we have linear length functions independent of time and position, then,

\[ g(x,t,p) = g(x,t,p) = g(x) = c + x. \]

With \( t = 0 \) in (5.29) we have,

\[ g(x,0,p) = g(x,0,p) = g(x) = c + x. \]

Thus, \( a + A = \frac{1}{K} \),

where, \( A \) is the average initial cell age. Hence, if all cells are initially newborn \( A = 0 \) and \( g(x) = x + 1 \). Each newborn cell is now of the same length, \( \frac{1}{K} \), which is in contrast with the length functions discussed in section 5.4.

From (5.28),

\[ \dot{g}(t,p) = \frac{K - p(g-1)t}{K - p(g-1)t} - \frac{aT(x,t,p)}{aT(x,t,p)} + \frac{p(g-1)t}{p(g-1)t}. \]

\[ c + A = \frac{1}{K}. \]

Thus, \[ g(x,t,p) = g(x,t,p) = g(x) = c + x. \]

With \( t = 0 \) in (5.29) we have,

\[ g(x,0,p) = g(x,0,p) = g(x) = c + x. \]

If we have linear length functions independent of time and position, then,

\[ M(t,p,aT(x,t,p)) = Ke^{-pt} \Phi(Xrt) \], \( X > t \),

\[ 0 < x < t. \]
Then,

$$y(t, p) = \int_0^P \sigma(t, z) \, dz ,$$

$$= \frac{1}{t(t-1)^2} \left[ e^{t(a-1)p} - 1 \right] + \frac{a-2}{(a-1)^2} (1+Kt)p$$

$$+ \frac{K}{a(a-1)^2} \sum_{j=1}^{\infty} \frac{(tp)^j [(a-1)^j - (-1)^j(a-1)^2]}{j(j!)}$$

From (5.30) and (5.32) we have, for large values of $t$,

$$h_T(t, p) = \frac{\sigma(t, p)}{M_T(t, p)} = \begin{cases} \frac{K-ap+ap^2}{Kap(a-1)}, & a > 1, \\ \frac{t}{K}, & a < 1. \end{cases}$$

We also have a total birth rate,

$$B(t) = \int_0^L B(t, u) \, du = \frac{ak}{t^2(a-1)^2} \left[ 1 - e^{(a-1)tL(1-(a-1)tL)} \right].$$

Hence, for large values of $t$,

$$B(t) = \begin{cases} \frac{aKe^{(a-1)tL}}{t^2(a-1)^2} [L(a-1)t - 1], & a > 1, \\ 0, & a < 1. \end{cases}$$

If instead of (5.31) we have length functions given by,

$$g(x, t, p) = g_T(x, t, p) = x + h_T(t-x, p),$$

then substituting in (5.29) we have,

$$h_T(t, p) \left[ a-2 + p(a-1)t \right] = \frac{(a-1)(ap-K)e^{-pt}}{akp} + \frac{e^{p(a-1)t}}{ap(a-1)} + (a-2)t$$

$$+ \frac{(a-2)}{p(a-1)} + p(a-1)e^{p(a-1)t}$$

$$\times \int_0^t [(2-a)e^{p(1-a)x} + aae^{-px}] h_T(t-x, p) \, dx ,$$

(5.34)
which is not amenable to the use of Laplace transform methods. However, if we assume that \( \alpha = 2 \) then (5.34) becomes,

\[
h_T(t,p) = \frac{1}{2p} + \frac{e^{-pt}}{K} - \frac{e^{-2pt}}{2p} + \frac{t}{2} \int_0^t e^{-2px} h_T(t-x,p) \, dx
\]

which, on taking Laplace transforms, gives,

\[
h_T^*(s,p) = \frac{1}{2s} + \frac{2}{ks} - \frac{1}{K(s+p)}.
\]

Inverting we have,

\[
h_T(t,p) = \frac{2}{K} - \frac{e^{-pt}}{K} + t,
\]

(5.35)

and for large values of \( t \),

\[
h_T(t,p) = \frac{2}{K} + t.
\]

From \( y(t,p) = \int_0^p M_T(t,z) h_T(t,z) \, dz \) we have,

\[
y(t,p) = \frac{e^{pt}}{t} (2 + Kt) - p - K - \frac{2}{t},
\]

(5.36)

which for large values of \( t \) becomes \( \frac{e^{pt}}{t} (2 + Kt) \). We also have

\[
\sigma(t,p) = \frac{\partial y(t,p)}{\partial p} \quad \text{and so,}
\]

\[
\sigma(t,p) = e^{pt} (2 + Kt) - 1
\]

(5.37)

which for large values of \( t \) becomes \( e^{pt} (2 + Kt) \). We see that the quantities of interest in table 4 are readily obtained using (5.35), (5.36) and (5.37). We also note that the length functions (5.33) reduce to the length functions in (5.31) if we assume that \( h_T(t-x,p) \) is \( \frac{1}{K} \) and, since \( h_T(0,p) = \frac{1}{K} \), this amounts to assuming that all newborn viable cells have a length of \( \frac{1}{K} \).

If we assume that the length functions are given by,
\[ g(x,t,p) = g_V(x,t,p) = L + \left( \frac{1}{K} - L \right) e^{-xpt}, \quad 0 < \frac{1}{K} < L, \quad (5.38) \]

then from (5.28) we have,

\[ \sigma(t,p) = A_1(t)e^{p(a-1)t} + A_2(t)e^{-pt(1+t)} + A_3(t)e^{pt(a-2-2t)} \]
\[ + A_4(t)e^{-t^2p} + KLe^{-pt} + \frac{KL(2-a)}{1-a}, \]

where,

\[ A_1(t) = \frac{a(a+t+KLt)}{(a+2t)(a+t)} - \frac{(a-2)(a-1+KLt)}{(1-t-a)(1-a)}, \]
\[ A_2(t) = 1 - \frac{KL(2a+t)}{(a+t)}, \]
\[ A_3(t) = \frac{a(KL-1)}{(a+2t)}, \]
\[ A_4(t) = \frac{(2-a)(1-KL)}{(1-t-a)}. \]

We see that for large values of \( t \),

\[ \sigma(t,p) = \begin{cases} 
A_1(t)e^{p(a-1)t}, & \alpha > 1, \\
\frac{KL(2-a)}{1-a}, & \alpha < 1.
\end{cases} \]

We then have,

\[ y(t,p) = \frac{A_1(t)}{(a-1)t} \left[ e^{t(a-1)p} \right] + \frac{A_2(t)}{t(1+t)} \left[ 1 - e^{-t(1+t)p} \right] \]
\[ + \frac{A_3(t)}{t(a-2-2t)} \left[ e^{t(a-2-2t)p} \right] + \frac{A_4(t)}{t^2} \left[ 1 - e^{-t^2p} \right] \]
\[ + \frac{KL}{t} \left[ 1 - e^{-tp} \right] + \frac{KL(2-a)p}{1-a}, \]

and for large values of \( t \),

\[ y(t,p) = \begin{cases} 
\frac{A_1(t)}{(a-1)t} e^{p(a-1)t}, & \alpha > 1, \\
\frac{KL(2-a)}{(1-a)}, & \alpha < 1.
\end{cases} \]
As a final example we consider the length functions discussed in section 5.4. Using \( \mu(x,p) = \frac{f(x,p)}{l(x,p)} \), we have \( \mu(x,p) = p \) and so from (5.18) and (5.19) we have,

\[
g(x,t,p) = \begin{cases} 
  x + \frac{1}{K}, & x = t \geq 0, \\
  t-x, & 0 \leq x < t,
\end{cases}
\]

and,

\[
g_v(x,t,p) = \begin{cases} 
  g(x,t,p), & 0 \leq x < t \\
  0, & \text{otherwise},
\end{cases}
\]

Hence from (5.14) we have,

\[
h(t,p) = e^{-apt} \left( t + \frac{1}{K} \right) + \int_0^t a(x,t,p)g(x,t,p)dx,
\]

and so from (5.39) we have,

\[
g(x,t,p) = x - \frac{1}{4}e^{-ap(t-x)}(t-x+\frac{1}{K}) + \frac{1}{2}h(t-x,p),
\]

which when substituted in (5.41) gives,

\[
h(t,p) = e^{-apt} \left[ 2t - \frac{ap}{2K} - \frac{ap^2}{4} + \frac{1}{K} - \frac{1}{ap} \right] + \frac{1}{ap}
\]

\[
+ \frac{1}{2}ap \int_0^t e^{-apx}h(t-x,p)dx.
\]

Taking Laplace transforms and applying the convolution theorem gives,

\[
h^*(s,p) = \frac{(4K - ap)}{2K} \cdot \frac{1}{(s+ap)(s+\frac{ap}{2})} - \frac{ap}{2(s+ap)^2(s+\frac{ap}{2})}
\]

\[
+ \frac{(ap-K)}{apK} \cdot \frac{1}{(s+\frac{ap}{2})} + \frac{(s+ap)}{aps(s+\frac{ap}{2})}
\]
On inversion we have,

\[ h(t,p) = e^{-apt} \left( \frac{ap - 2K}{apK} + \frac{apt}{2} \right) + \frac{2}{ap} . \]  

(5.43)

Now using (5.14) we have,

\[ h_V(t,p) = \int_0^t a_V(x,t,p) g_V(x,t,p) dx , \]

and substituting for \( a_V(x,t,p) \) and \( g_V(x,t,p) \), from (5.40), we have,

\[ h_V(t,p) = \frac{(a-l)}{4[1 - e^{-p(a-l)t}]} \int_0^t e^{px} a(x,t,p) g_V(x,t,p) dx , \]

\[ = \frac{(a-l)}{4[1 - e^{-p(a-l)t}]} \int_0^t e^{px} a(x,t,p) g(x,t,p) dx . \]  

(5.44)

Using (5.42) and (5.43) in (5.44) we have,

\[ h_V(t,p) = \frac{1}{e^{p(a-l)t}} \left[ \frac{2a-1}{p(1-a)} - t - \frac{(a-1)(4+2a-a^2)}{4ap} \right] \]

\[ + \frac{(a-l)e^{-pt}}{4[e^{p(a-l)t} - 1]} \left[ 2(2a) - \frac{4ap}{ap} \right] \]

\[ + \frac{e^{p(a-l)t}[2(2a) - a(a-1)]}{2ap(1-a)[e^{p(a-l)t} - 1]} . \]  

(5.45)

Using (5.43) and (5.45) in (5.13) we have,

\[ \sigma(t,p) = \frac{K e^{-pt}}{4} \left[ \frac{4(p-k) + apK(a-2)}{pk} + (16 - 2a + a^2 p) t \right] \]

\[ + \frac{K e^{p(a-l)t}}{2(a-1)^2} \left[ 2 + (2-a)(a-1)^2 \right] \]

\[ + \frac{(2-a)K(4(2a-1) + (1-a)^2(4+2a-a^2) - t)}{(a-1)} . \]  

(5.46)
For large values of \( t \) we see from (5.46) that,

\[
\sigma(t, p) = \begin{cases} 
\frac{a Ke^{p(a-1)t}}{2(a-1)^2} \left[ 2 + (2-a)(a-1)^2 \right] - \frac{(2-a)Kt}{(a-1)}, & a > 1, \\
\frac{(2-a)Kt}{(1-a)}, & a < 1,
\end{cases}
\]

and from (5.46) we can determine other parameters of interest in table 4.
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