Population Dynamics based on the McKendrick-von Foerster Model

by

Robyn Seillier

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Abstract

The current state of information concerning the classical model of deterministic, age-dependent population dynamics - the McKendrick von Foerster equation - is overviewed.

This model and the related Renewal equation are derived and the parameters involved in both are elaborated upon. Fundamental theorems concerning existence, uniqueness and boundedness of solutions are outlined. A necessary and sufficient condition concerning the stability of equilibrium age-distributions is rederived along different lines.

Attention is then given to generalizations of the McKendrick-von Foerster model that have arisen from the inclusion of density- dependence into the parameters of the system; the inclusion of harvesting terms; and the extension of the model to describe the dynamics of a two-sex population.

A technique which reduces the model, under certain conditions on the mortality and fertility functions, to a system of ordinary differential equations is discussed and applied to specific biochemical population models. Emphasis here is on the possible existence of stable limit cycles.

The Kolmogorov system of ordinary differential equations and its use in describing the dynamics of predator-prey systems is examined. The Kolmogorov theorem is applied as a simple alternative to a lengthy algorithm for determining whether limit cycles are stable. Age-dependence is incorporated into this system by means of a McKendrick - von Foerster equation and the effects on the system of different patterns of age-selective predation are demonstrated. Finally, brief mention is made of recent work concerning the use of the McKendrick - von Foerster equation to describe the dynamics of both predator and prey.

A synthesis of the theory and results of a large number of papers is sought and areas valuable to further research are pointed out.

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Preface

The research described in this thesis was carried out in the Department of Mathematics and Applied Mathematics, University of Natal, Durban, from January 1986 to December 1988, under the supervision of Professor John H. Swart.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

Acknowledgements

Contents

Chapter 1

Introduction

The use of mathematical models to describe the growth and development of populations, be they human, animal, or otherwise, dates back at least as far as the late eighteenth century, when the English demographer T.R. Malthus [1] proposed that human populations have a constant, natural growth rate by means of the model

$$\frac{dP(t)}{dt} = rP(t), \; r = \text{ constant}, \tag{1.1}$$

$P(t)$ being the total population size at time t and r the constant growth rate.

Since for $r > 0$, Mathus' model predicts unlimited population growth, it was modified by P.F. Verhulst [2], who, in 1832, offered the alternative

$$\frac{dP(t)}{dt} = (r - sP(t))P(t), \; r, s = \text{ constants}, \tag{1.2}$$

a choice which involves the growth rate being a function of the population size. In this way the model accounts for the self- limiting features of

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the population since the larger the population the less resources there are available to each member and the slower should be its rate of growth. This equation is often expressed alternatively as the Logistic equation

$$\frac{dP(t)}{dt} = r\left(1 - \frac{P(t)}{P_c}\right)P(t),\qquad(1.3)$$

where P_c, called the environmental carrying capacity, is the largest number of individuals that the environment is capable of supporting.
The solution of (1.3), given by

$$P(t) = \frac{P_c}{1 + \left[\frac{P_c}{P(o)} - 1\right]\exp(-rt)},$$

tends, for $r > 0$, asymptotically to P_c with increasing time.

Equation (1.3) was the standard approach for early deterministic population models and although it, and modifications of it, have been applied (as will be seen), with remarkable success to fit the growth curves of various populations, it has the major shortcoming of ignoring the possible influence of the age composition of a population upon its development. In fact the Logistic equation is based on a tacit assumption that the birth and death processes are age- independent.

There are numerous biological examples were age clearly plays a dominant role in the dynamics of a population and it was A.G. McKendrick [3], and H. von Foerster [4] who, in 1926 and 1959 respectively, independently proposed a partial differential equation which has played a unifying role in age-dependent population mathematics.

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The McKendrick-von Foerster equation (henceforth referred to as the M-F equation) is derived under the conditions that age and time are continuous variables; the population is closed to migration; the spatial variation of the population through time is ignored; and stochastic effects are not accounted for. In particular, in dealing with the M-F equation it is usually assumed that only females are counted. Males are present for reproductive purposes but are not specifically taken into consideration. This approach is adopted since, in general, the females of a population have a biologically well-defined beginning and end to their reproductive careers, while the reproductive behaviour of males is difficult to quantify.

The M-F equation describes the dynamics of such a one-sex population by means of an age-density or age-distribution function $\rho(a, t)$.

The quantity $\rho(a, t)da$ defines the number of individuals at time t with ages between a and $a + da$, and represents some kind of smoothing or statistical average of the true integer-valued population size. More precisely,

$$\rho(a, t) = \lim_{da \to p} \quad = \quad \frac{\text{Number of individuals aged } a \text{ to } a + da \text{ at time } t}{da} \quad \text{In}$$

particular, the number of individuals in the age bracket (a_1, a_2) at time t is given by

$$\int_{a_1}^{a_2} \rho(a, t)da, \tag{1.4}$$

so that the total population at time t is

$$P(t) = \int_0^{\infty} \rho(a, t)da. \tag{1.5}$$

To obtain his equation von Foerster [4], reasoned as follows:

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Assume that a small time increment $\triangle t$ has passed such that the age of each individual in the population is increased by $\triangle a$ (where the obvious requirement that clock time t and age time a be measured in the same units is imposed). Hence, the age distribution $\rho(a, t + \triangle t)$ at time $t + \triangle t$ would be the same as it was at time t if everyone was $\triangle a$ younger:

$$\rho(a, t + \triangle t) = \rho(a - \triangle a, t). \tag{1.6}$$

However, during the time interval $\triangle t$ there would be a loss of individuals in each age group due to death. This is given by

$$\mu(a, t)\rho(a, t) \triangle a,$$

where $\mu(a, t)$ is the prescribed age-specific death rate (also known as the mortality function), that is, the death rate at age a and time t per unit population of age a.

Thus, (1.6) becomes

$$\rho(a, t + \triangle t) = \rho(a - \triangle a, t) - \mu(a, t)\rho(a, t) \triangle a. \tag{1.7}$$

Assuming ρ is differentiable everywhere and expanding the two expressions of ρ about t and a yields

$$\rho(a, t) + \frac{\partial \rho}{\partial t} \triangle t + \dots = \rho(a, t) - \frac{\partial \rho}{\partial a} \triangle a + \dots - \mu(a, t)\rho(a, t) \triangle a, \tag{1.8}$$

while discarding higher powers in $\triangle a$ and $\triangle t$ and noting that $\triangle a = \triangle t$ leads to the M-F equation

$$\frac{\partial \rho(a, t)}{da} + \frac{\partial \rho(a, t)}{dt} = -\mu(a, t)\rho(a, t). \tag{1.9}$$

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Obviously the solution to this hyperbolic partial differential equation can only be completely determined by specifying two auxilliary conditions: An initial condition on the age distribution at some specified time, usually taken to be the age distribution at $t = 0$:

$$\rho(a, o) = \varphi(a), \tag{1.10}$$

and the boundary condition $\rho(o, t)$, denoting the number of births at any time t.

Hoppensteadt [5] rederived the M-F equation by basing his argument on the following two biologically plausible assumptions:

1. The change occurring in the population of age a at time t, over a time interval of length h, is proportional to the size of the population and the length of the interval. Thus,

$$\rho(a + h, t + h) - \rho(a, t) = -\mu(a, t)\rho(a, t)h, \tag{1.11}$$

where $\mu(a, t)$ is the age-specific death rate introduced earlier. Again, assuming ρ is differentiable, Taylor expanding the lead term and passing to the limit $h \to 0$ yields the M-F equation (1.9).

2. The number of individuals introduced into the population in the time

interval $(t, t+h)$ is[1]

$$h \int_0^\infty \beta(a,t)\rho(a,t)da, \qquad (1.12)$$

where $h\beta(a,t)$ is the average number of births produced by a female of age a in the interval $(t, t+h)$, with $\beta(a,t)$ being the prescribed age-specific fertility (also referred to as the fertility or fecundity function) of the population. By definition, $\beta(a,t)$ is the average number of offspring produced per unit time, by an individual of age a at time t.

If the birth rate $B(t)$ is defined as the rate of addition of newborns (individuals aged zero) to the population at time t, then clearly,

$$B(t) \equiv \rho(o,t) = \int_0^\infty \beta(a,t)\rho(a,t)da. \qquad (1.13)$$

As before, the initial condition

$$\rho(a,0) = \varphi(a),$$

is required for a unique solution of (1.9) to be specified.

$\varphi(a)$ is most often chosen to be a smooth function, becoming zero for large a, say $a \geq p$, where p is a fixed constant representing the maximum life span of the population. The assumption that there is a finite maximum

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[1] Actually Hoppensteadt defines the number of individuals in the age bracket (a_1, a_2) as

$$N \int_{a_1}^{a_2} \rho(a,t)da, \text{ and thus, } (1.12) \text{ as } Nh \int_0^\infty \beta(a,t)\rho(a,t)da,$$

where N is the population normalization constant. For convenience N has been set equal to 1 here, so that Hoppensteadt's definition of $\rho(a,t)$ and that already given are in agreement.

attainable age, (which is often assumed to be 100 years for human populations), ensures that the integrals (1.5) and (1.13) are evaluated over finite intervals, since necessarily $\rho(a,t) = 0$ for $a \geq p$. However, we shall adhere throughout to the convention of using the infinite integral.

Equations (1.9), (1.5), (1.10) and (1.13)[2] constitute the McKendrick-von Foerster (M-F) model of age dependent population growth and will be the focal point of this treatment of population dynamics.

The objective of this study was to survey the current state of information concerning age-dependent population models and to relate and synthesise as much of the theory and as many of the results as possible into a single presentation. In doing so a few results have been rederived along different lines and areas valuable to further research have been pointed out.

In the following chapter the M-F system is considered in depth and related to the Renewal equation, an alternative approach to modelling population growth.

This provides the foundation for the third chapter in which the M-F model is generalized to include modifications appropriate to specific situations, such as allowing for initial conditions $\rho(o,t)$ that are not of the form (1.13), and incorporating a harvest of members into the system.

The fourth chapter concerns the M-F system in which the mortality and fertility functions are so chosen that the basic equations of the theory reduce to a system of coupled nonlinear ordinary differential equations. The

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[2]The original McKendrick model involved μ and β being functions of age only. However, (1.9), (1.5), (1.10) and (1.13) are also referred to in literature as the M-F model.

emphasis here is upon the recent developments concerning the stability properties of such models.

The topic of the final chapters is that of the dynamics of interacting populations, in particular, predator-prey populations. While chapter 5 deals with such models in which age- dependence is ignored and in which the logistic equation plays a fundamental role, chapter 6, in contrast, covers predator-prey models in which the dynamics of one or both of the species is described by the McKendrick-von Foerster equation.

Chapter 2

The M-F system and its solution

The introductory chapter was deliberately vague about the functions $\mu(a, t)$ and $\beta(a, t)$ involved in the M-F model. The definitions of these are obviously essential to all that will follow and before presenting the solution of the M-F system these functions need to be elaborated upon.

It is unfair to attribute sole credit to McKendrick and von Foerster for the continuous time, age-dependent model since, in 1911, prior to their work, A.J. Lotka and F.R. Sharpe [15] developed an integral equation known as the Renewal equation to model the dynamics of age-dependent populations. However, we will see that these two approaches are simply different formulations of the same model since the M-F equation can be obtained from the Renewal equation and vice versa. The Renewal equation has been studied extensively, and we present its solution for the time- independent case $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$.

While $\rho(a, t)$ has been introduced as a differentiable function and μ and β

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as functions of age and time, this chapter concludes by overviewing Gurtin and MacCamy's classical paper [29], in which the M-F system is established and analysed for the case where ρ is not differentiable everywhere, and μ and β are functions of age and total population size $P(t)$. Theorems proving existence and uniqueness of solutions and conditions guaranteeing $\rho \in C^1$ are quoted. In particular, Gurtin and MacCamy's condition ensuring the stability of equilibrium solutions of the system is derived along different and somewhat simpler lines.

2.1 The functions $\mu(a,t)$, $\beta(a,t)$ and $\varphi(a)$.

Although the function $\mu(a,t)$ is used extensively in the literature on age-dependent population dynamics, a formal definition of it is seldom given. Fortunately, such has been provided by Impagliazzo [6] and Chiang [7], and in presenting their definitions we restrict attention for the moment to $\mu \equiv \mu(a)$.

Impagliazzo first defines the *average force of mortality* as

$$\bar{\mu} = \frac{d_i}{\ell(a_i)(a_{i+1} - a_i)},$$

where $\ell(a_i)$ is the number of individuals at the exact age a_i and d_i is the number of deaths over the age interval $[a_i, a_{i+1})$. Notice that it is not strictly correct to write $\ell(a_i) = \rho(a_i)$ since $\rho(a_i)$ represents the number of individuals at the exact age a_i *per unit age*, so that substitution of $\rho(a)$ for $\ell(a)$ in the above equation results in $\bar{\mu}$ being dimensionless and thus

not expressing a rate. Figure 2.1.1 reproduced from [6, p 13] indicates the average force of mortality data for a particular human population.

fig. 2.1.1

Average force of mortality based on data collected for a French population of 1746.
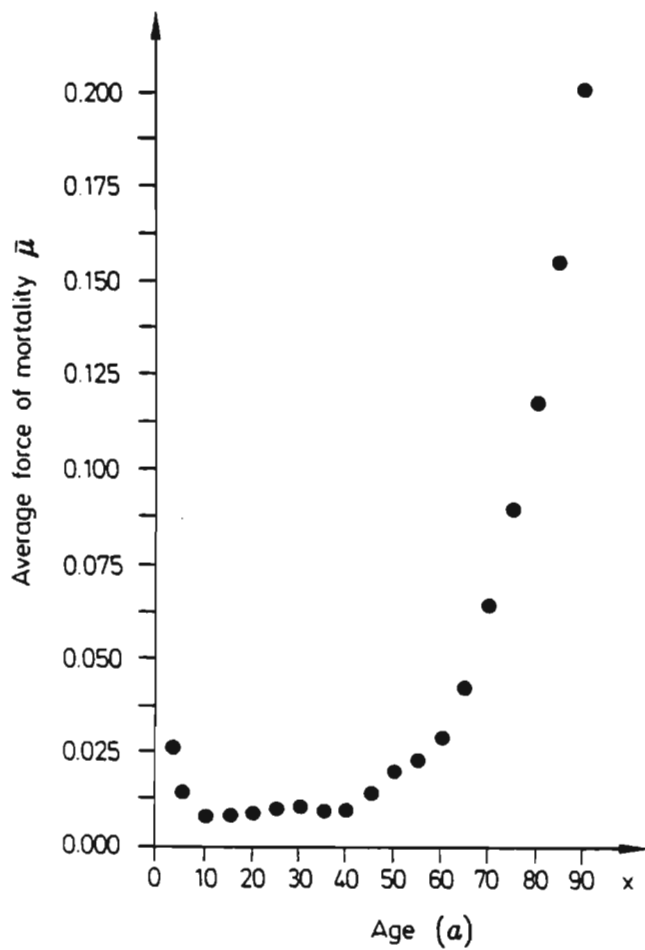
The *force of mortality* or equivalently the age-specific mortality rate $\mu(a)$, is the continuous function that results when the age interval $[a_i, a_{i+1})$ is allowed to approach zero in length. Thus, $\mu(a)$ expresses mortality as a time rate (which Impagliazzo stipulates as being an annual rate) at the precise moment of attaining age a.

The function $\pi(a)$ recurs frequently in quantitative population analyses. For a particular cohort of individuals, that is the group of individuals all born at the same time,

$$\pi(a) \quad = \quad \frac{\text{Number of individuals alive at exact age } a}{\text{Number of individuals born into the cohort}}$$

$$= \quad \frac{\ell(a)}{\ell(o)},$$

which in this case,

$$= \quad \frac{\rho(a)}{\rho(o)}.$$

Thus $\pi(a)$ defines the probability of surviving from birth to age a and as such is known as the *survivorship function*.

The formal definition of $\mu(a)$ is now given by

$$\mu(a) = -\frac{1}{\pi(a)} \frac{d}{da} \pi(a). \tag{2.1.1}$$

Impagliazzo establishes this in the following way:

Over an interval $[a_i, a_{i+1})$, the number of individuals of exact age a_{i+1} is given by the number of individuals of exact age a_i less the number of deaths that occur over the age interval, i.e.

$$\ell(a_{i+1}) = \ell(a_i) - d_i.$$

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Substituting this into the definition of $\bar{\mu}$ gives

$$\bar{\mu} = \left(1 - \frac{\ell(a + \Delta a)/\ell(a)}{\Delta a}\right),$$

where, for convenience we have set $a_{i+1} = a + \Delta a$ and $a_i = a$.

Rewriting the above expression as

$$\bar{\mu} = -\frac{1}{\ell(a)} \left(\frac{\ell(a + \Delta a) - \ell(a)}{\Delta a}\right),$$

and taking the limit as $\Delta a \to 0$ leads to

$$\mu(a) = -\frac{1}{\ell(a)} \frac{d}{da} \ell(a). \tag{2.1.2}$$

(Notice that replacing $\ell(a)$ by $\rho(a)$, which is acceptable in (2.1.2), yields the M-F equation for the case where the dependence of ρ and μ on time has been neglected.)

Now, making use of the definition of π, the formal definition (2.1.1) of $\mu(a)$ follows immediately from (2.1.2).

Definition (2.1.1) for $\mu(a)$ is most often encountered in the form

$$\pi(a) = \exp\left\{-\int_0^a \mu(\alpha)d\alpha\right\}, \tag{2.1.3}$$

which in turn implies that $\mu(a)$ cannot be a bounded function. For suppose that $\mu(a)$ is bounded over an age interval, then since $\pi(a)$ is bounded, specifically $\pi(a) \in [0, 1]$, we can allow the age variable to become as large as we please and are guaranteed of a probability of surviving to that age. In other words, survival to infinite age becomes possible.

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Hence $\mu(a)$ cannot be bounded, and for a biologically realistic population there must exist a maximum attainable age p such that

$$\int_0^a \mu(\alpha)d\alpha \to \infty \text{ as } a \to p, \text{ so that } \pi(a) \to 0 \text{ as } a \to p.$$

Figure 2.1.2 given in [6] indicates this property for the age- specific mortality function determined for the Danish population of 1967.

Fig 2.1.2

The age-specific mortality curve for the Danish population (females) of 1967
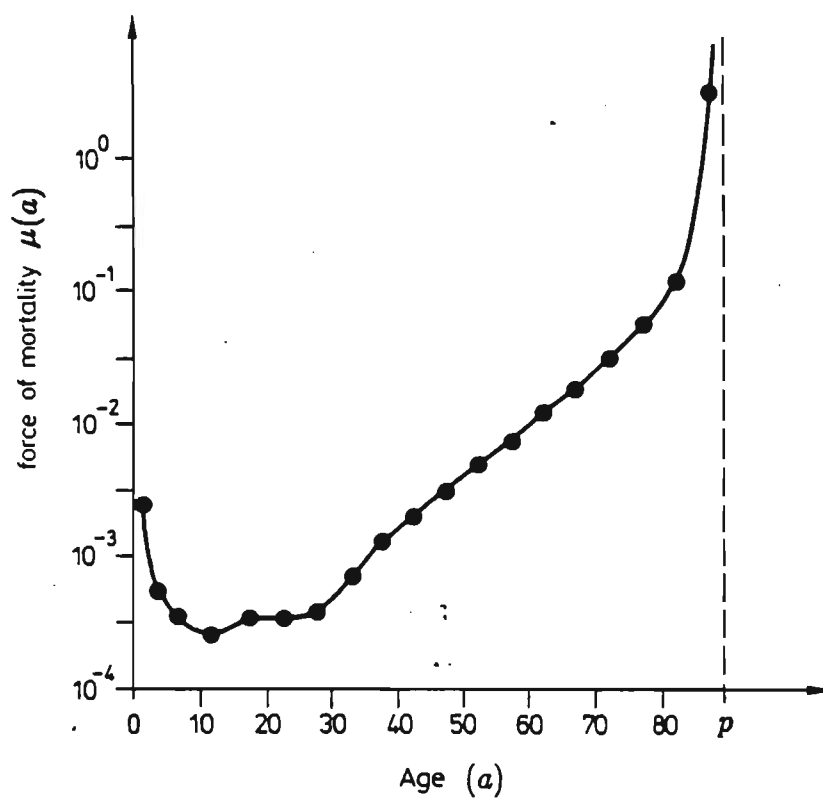
The definition of $\bar{\mu}$ given by Chiang [7], has identical meaning to that given by Impagliazzo but incorporates more information:

$$\bar{\mu} = \frac{d_i}{(a_{i+1} - a_i)(\ell(a_i) - d_i) + f_i(a_{i+1} - a_i)d_i}.$$

Here each of the d_i individuals that die between age a_i and a_{i+1} is assumed to live on the average, a fraction f_i of the interval. Hence, as for Impagliazzo's definition, $\bar{\mu}$ is a measure of

$$\frac{\text{the number of individuals dying in } [a_i, a_{i+1})}{\text{the number of years lived in } [a_i, a_{i+1}) \text{ by those alive at } a_i}.$$

Chiang applies this definition to data collected for a number of populations. For example, for the United States population of 1975, and for the age interval $a_i = 1$ year, $a_{i+1} = 5$ years, the value of $\ell(a_i)$ is 12,804,000, $d_i = 9060$ and $f_i = 0{,}4$ so that

$$\bar{\mu} = 0{,}0002 \text{ per person-year.}$$

Again $\mu(a)$ is obtained by allowing the age-interval to tend to zero in length. It appears that the simplest means of obtaining $\mu(a)$ is to apply definition (2.1.1) since information concerning $\pi(a)$ is documented for many populations in the form of *life tables*. A sample life table is given in Table 2.1 and applies to a population of vole mice (*microtus agrestis*) reared under laboratory conditions. In figure 2.1.3, $\pi(a)$ is given as a continuous function of age. (Table 2.1 and figure 2.1.3 also contain information concerning the fertility of the species which will be discussed shortly.)

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Age in weeks (a)	Life table π	Age-specific fertility rates β
8	0,83349	0,6504
16	0,73132	2,3939
24	0,58809	2,9727
32	0,43343	2,4662
40	0,29277	1,7043
48	0,18126	1,0815
56	0,120285	0,6683
64	0,05348	0,4286
72	0,02549	0,3000

Table 2.1: The Life Table and age-specific fertility rates of the *vole microtus agrestis* compiled by Andrewartha and Birch [8].

Fig. 2.1.3

The Life table and age-specific fertility curves for the *vole microtus agrestis* [8, p38]
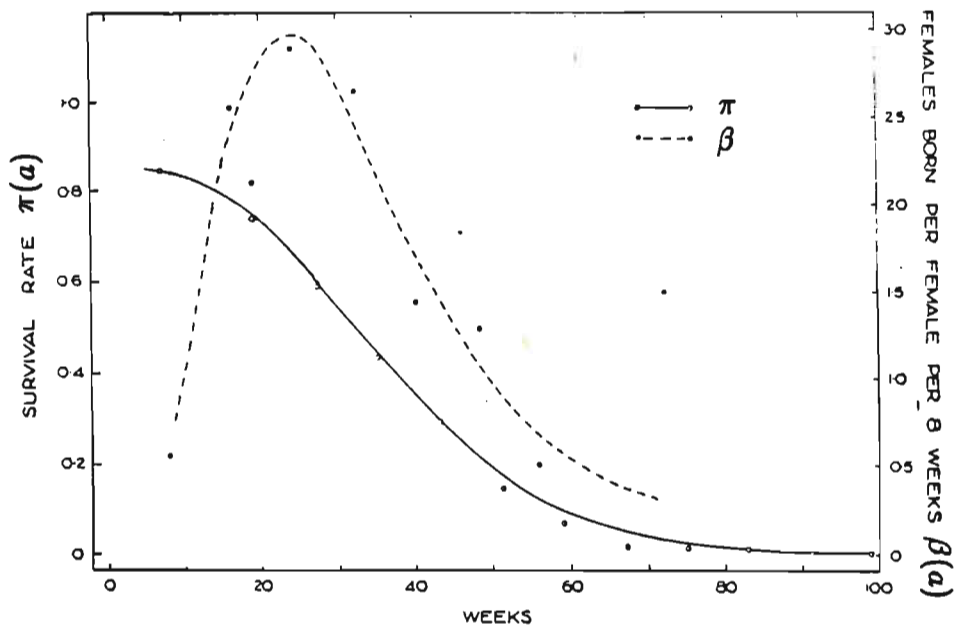
Andrewartha and Birch [8] obtained this information by following through the survival of a sample of the mice population from birth until the last member of the population died, recording the number of offspring produced as they aged. Only females were counted and the age-interval was chosen arbitrarily as eight weeks. Referring to table 2.1, the figures $a = 16$, $\pi = 0,73132$ for example, mean that from a sample of 100 mice of age zero approximately 73% survive to 16 weeks of age.

In [9] Keyfitz and Flieger document the life tables for numerous human populations. Whether the population be human or animal it is obvious, as Frauenthal [10] remarks, that a biologically realistic form of $\pi(a)$ must be

(i) continuous

(ii) differentiable

(iii) monotonically non-increasing; and as already mentioned

(iv) $0 < \pi(a) \leq 1$ for $0 \leq a < p$ and $\pi(p) = 0$,

where p represents the terminal age.

As an illustration we applied a polynomial regression to the survivorship data for the vole mouse population in order to determine an approximate form for $\mu(a)$.

The curve

$$\pi(a) \;=\; -8,916 \times 10^{-8} a^4 + 1,757 \times 10^{-5} a^3 - 1,029 \times 10^{-3} a^2$$

$$+4,744 \times 10^{-3} a + 0,8527,$$

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was found to fit the data with a regression coefficient of correlation 0,9998, a standard error of $\pm 6,912 \times 10^{-4}$ in the π estimate and standard errors of $\pm 2,200 \times 10^{-9}; \pm 3,538 \times 10^{-7}; \pm 1,930 \times 10^{-5}$ and $\pm 4,079 \times 10^{-4}$ in the respective coefficients.

Equation (2.1.1) then gave the following curve for $\mu(a)$:

Fig. 2.1.4

Approximate mortality curve for Andrewartha and Birch's vole mouse
population. (The behaviour of $\mu(a)$ over the interval $0 < a < 8$ is not
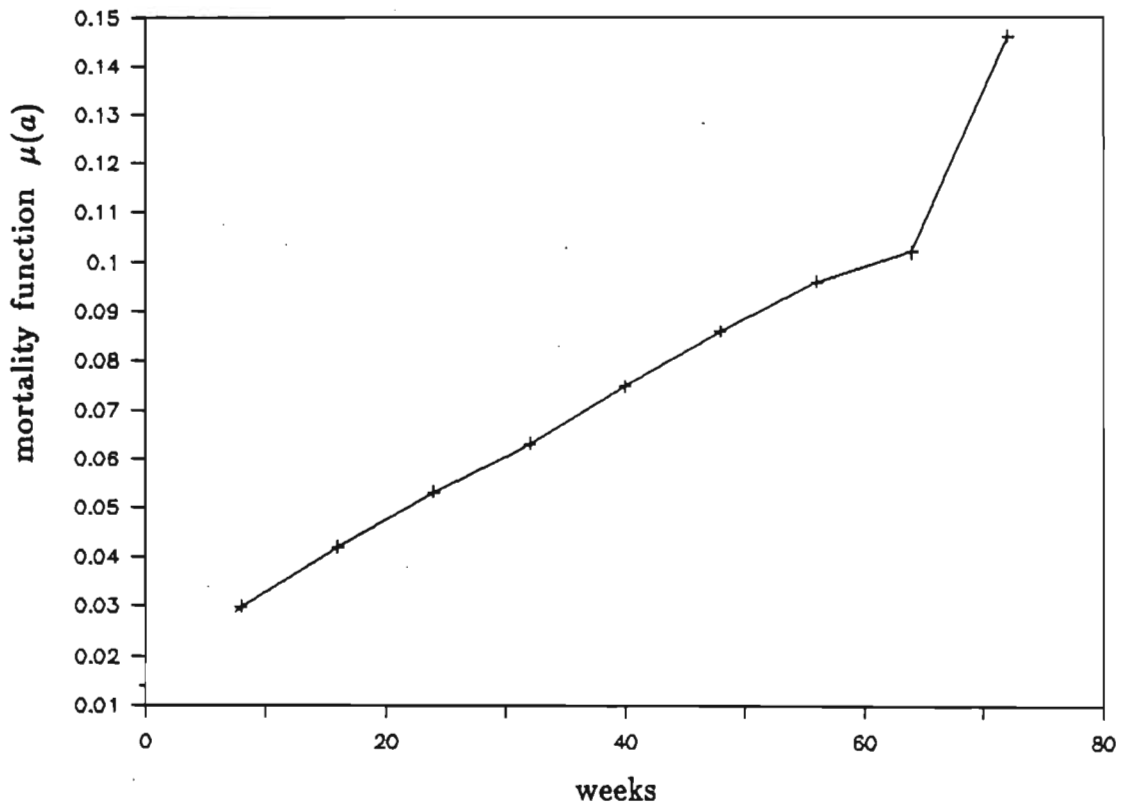
indicated since the behaviour of $\pi(a)$ here is not known. The current form
of $\pi(a)$ implies that $\mu(0) < 0$ - which is physically nonsensical.)

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Langhaar [11] proposes that a typical form of the mortality function is that of figure 2.1.5.

Fig. 2.1.5

The typical form of $\mu(a)$, [11, p201].
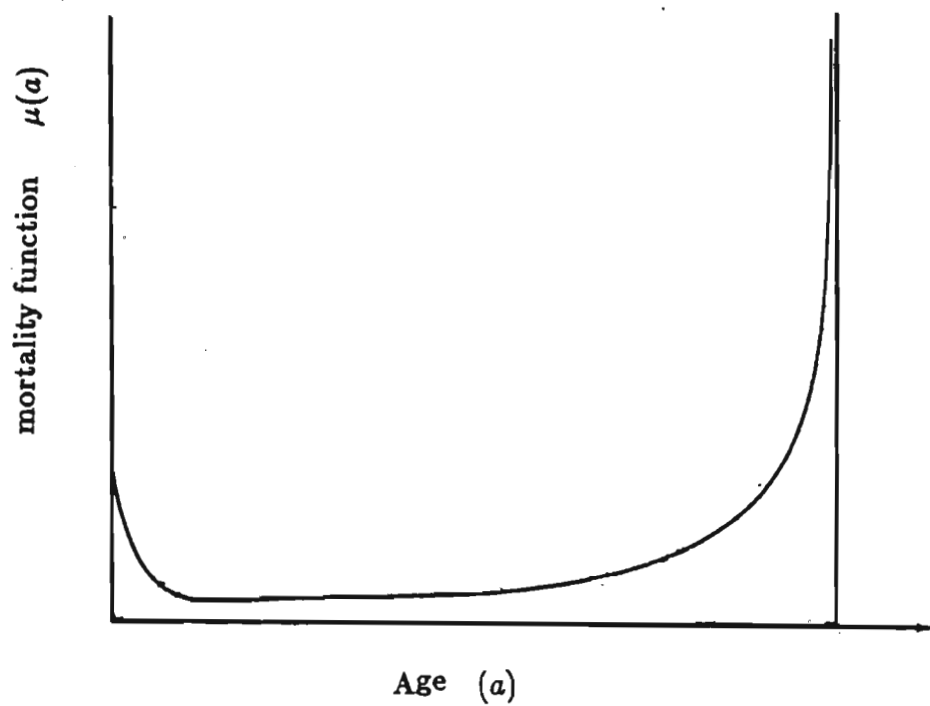
Thus $\mu(a)$ is large for either small (especially in the case of high infant mortality) or large a and reaches a relative minimum between these extreme values, and $\mu(a) \to \infty$ as $a \to p$. The mortality curve for the Danish population is in agreement with this typical behaviour. It is not known whether the vole mouse poulation exhibits the usual "high" infant mortality rate - information on the behaviour of $\pi(a)$ in the age-interval $0 < a < 8$ weeks and an accurate fit to this data might indicate this to be so. However, in this case $\mu(a)$ does show a rapid increase at the extreme end of the age-interval.

Turning now to the maternity function, quantitative population analyses most often assume β to be a function of age only. The maternity function is obtained from data of the number of female births to females of various ages. For example, if $\tilde{\beta}(a)$ gives the rate at which female offspring are produced by 100 000 females of age a, then $\beta(a) = 10^{-5}\tilde{\beta}(a)$. In [9], Keyfitz and Flieger record such fertility information for human populations of many countries.

As noted in [10], it is physically likely that $\beta(a)$ satisfies the properties of being

(v) continuous[1]

(vi) differentiable

(vii) $\beta(a) > 0$ for $m \le a \le n$ where m and n represent the lower and

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[1]While the possibility exists of $\beta(a)$ being sectionally continuous - this could be true of a population that is forbidden to produce during a certain age interval - we shall, for the most part, assume (v) to hold.

upper limits respectively of a female's fertile age span. (According to Frauenthal [10, p3], it is customary to assume that $m = 15$ and $n = 55$ for human populations.)

Further,

$$\beta(a) = 0 \text{ for} \qquad \begin{cases} 0 \le a < m \\ n < a \le p, \end{cases}$$

where $0 \le m < n \le p$, and p denotes the age of maximum survivorship.

(viii) $\beta(a)$ has a single maximum.

Evidently, the age-specific fertility curve for the vole mouse (figure 2.1.3) satisfies these conditions. In many of the situations covered in subsequent chapters the fertility function is assumed to be of the form

$$\beta(a) = \beta_0 a \exp(-\alpha a), \ \beta_0, \alpha = \text{ constants}, \ \beta_0 \ge 0, \alpha \ge 0, \qquad (2.1.4)$$

so that, for $\alpha > 0$, the typical behaviour of reproduction being greatest for individuals of a relatively young age and approaching zero at extreme ages is modelled.

Swart [12], in considering the controllability of the M-F system, works with the more general form

$$\beta(a) = f(a) \exp(-\alpha a), \qquad \alpha > 0 \qquad (2.1.5)$$

where $f(a)$ is an n-th degree polynomial. Of course, fertility behaviour of the type v-viii can be approximated by (2.1.5) to any required degree of accuracy.

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In particular, Nisbet and Gurney [13] choose the gamma- distribution

$$\beta(a) = \frac{\beta_0 \alpha^{n+1} a^n \exp(-\alpha a)}{n!}, \ \beta_0 \geq 0, \ \alpha > 0, \ n : \text{ integer,} \qquad (2.1.6)$$

Their illustration of the gamma-distribution for various values of n is given in figure 2.1.6.

Fig. 2.1.6

The shape of the gamma-distribution for a few values of n, [13, p 107].
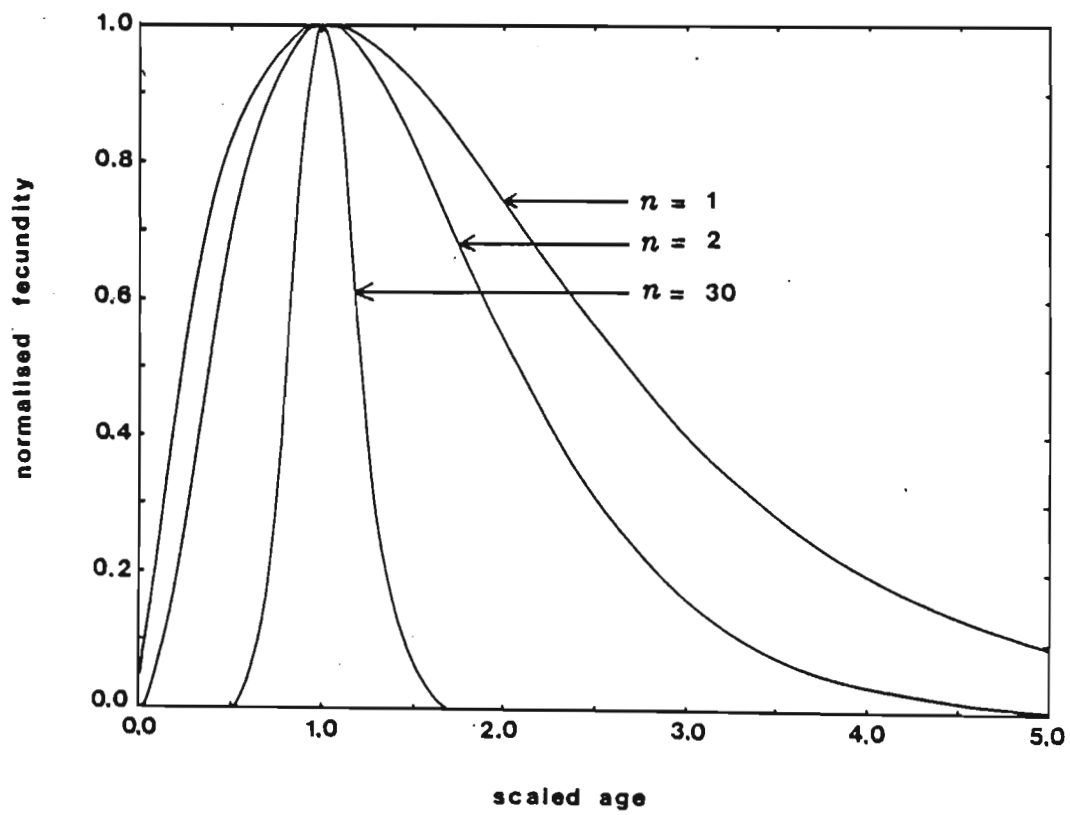
Nisbet and Gurney remark that while (2.1.6) may be a reasonable approximation to the fertility function of a population which reproduces at a fairly young age, it might not adequately allow for a "juvenile" phase during which reproduction does not occur. To model this new situation they construct a *displaced* gamma-distribution,

$$\beta(a) = \beta_0 h(a),$$

where

$$h(a) = \left\{ \begin{array}{l} 0 \text{ if } a < a_1 \\ g_n(a - a_1, a_2) \text{ if } a \geq a_1, \end{array} \right.$$

where the interval (o, a_1) represents the juvenile phase and where $g_n(a, \alpha)$ is given by

$$g_n(a, \alpha) = A_n^{-1} a^n e^{-\alpha a}, \text{ and } A_n = \max_{a \geq 0} \left\{ a^n e^{-\alpha a} \right\}.$$

To scale these functions Nisbet and Gurney introduce a parameter $a_2 = \frac{n}{\alpha}$. Figure 2.1.7 reproduced from [13] illustrates the typical form of the displaced gamma-distribution.

Fig. 2.1.7

The typical form of Nisbet and Gurney's displaced gamma- distribution
for a choice of parameters a_1, a_2 and n.
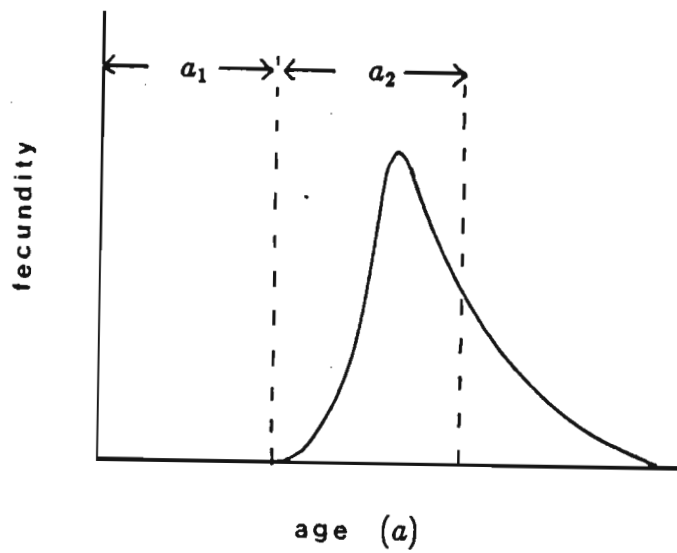
However, (2.1.4) will be the basic form of the fertility functions used in many of the applications that follow.

So far μ and β have been restricted as functions of age only. While this may be a valid assumption for populations which exhibit unchanging schedules of age-specific fertility and mortality rates from generation to generation, or which are examined over a short time interval, there are obviously situations for which the influence of time cannot be ignored. This would be true for example, of long-term human population studies and of studies of "underdeveloped" communities for which factors such as improved health care could lead in time, to a reduction in the mortality rate. It is a simple matter to include the dependence of time into the definitions of $\mu(a)$ and $\beta(a)$ given earlier. Thus $\beta(a,t)$ is now the average number of offspring to be produced per unit time by an individual of age a at time t, and from the definition of $\bar{\mu}$

$$\mu(a,t) = \lim_{da \to 0} \bar{\mu} = \lim_{da \to 0} \frac{d_i}{\ell(a,t)da},$$

where $\ell(a,t)$ is the number of individuals of exact age a at time t and d_i is the number of deaths over the age interval $[a, a+da)$.

This may be theoretically acceptable but presents difficulties as far as real applications are concerned. For example, while we may be able to record past and present behaviour of $\ell(a,t)$, its future behaviour cannot be determined and hence neither can $\mu(a,t)$. Similarly precise information about the future maternity development is simply not available from present day data. Thus, one must either estimate these rates or develop fertility and

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mortality functions which determine future rates by depending on the past behaviour of some demographic parameter. Models involving such choices of μ and β are included in chapter 3.

Finally, as far as $\varphi(a)$ is concerned we will, for the most part, consider

(ix) $\varphi(a)$ to be a C^1 function satisfying $\varphi(a) \to 0$ as $a \to \infty$,

as discussed in chapter 1, although attention will be given to the possibility of $\varphi(a)$ being sectionally continuous.

2.2 The Solution of the M-F model and the Renewal equation

A general solution of the M-F system is obtained by introducing the characteristic co-ordinates $(t - a = c,\ c = \text{constant})$ and integrating the ordinary differential equations which result. This procedure leads to

$$\rho(a,t) = \begin{cases} B(t-a)\exp\left\{-\int_0^a \mu(\alpha, t-a+\alpha)d\alpha\right\}, & t > a \\[2mm] \varphi(a-t)\exp\left\{-\int_0^t \mu(a-t+\tau, \tau)d\tau\right\}, & a \geq t. \end{cases} \qquad (2.2.1)$$

If the function $\rho(o,t) = B(t)$, given by

$$B(t) = \int_0^\infty \beta(a,t)\rho(a,t)da, \qquad (1.13)$$

were known, the dynamics of the population would be completely determined. Of course, $B(t)$ is not known, but it can be found from the integral equation obtained by substituting (2.2.1) into (1.13). It is not difficult to

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show that this results in

$$B(t) = G(t) + \int_0^t \beta(a,t)B(t-a)\pi(a,t-a)da, \qquad (2.2.2)$$

where

$$G(t) = \int_t^\infty \beta(a,t)\varphi(a-t)\sigma(a,t)da,$$

and where $\pi(a,t-a)$ and $\sigma(a,t)$ denote

$$\exp\left\{-\int_0^a \mu(\alpha,t-a+\alpha)d\alpha\right\}$$
$$\text{and} \quad \exp\left\{-\int_0^t \mu(a-t+\tau,\tau)d\tau\right\}, \quad \text{respectively.}$$

Hence, the full problem for $\rho(a,t)$ has been reduced to an integral equation for $B(t)$. (2.2.2) is known as a *Renewal* equation and will be seen to play a fundamental role in age-dependent population dynamics.

Clearly, the task of finding a solution to (2.2.2) is an important one in this analysis. Equation (2.2.2) having $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$, namely

$$B(t) = G(t) + \int_0^t \beta(a)B(t-a)\pi(a)da, \qquad (2.2.3)$$

where

$$G(t) = \int_t^\infty \beta(a)\varphi(a-t)\sigma(a,t)da = \int_t^\infty \beta(a)\varphi(a-t)\frac{\pi(a)}{\pi(a-t)}da, \quad (2.2.4)$$

is known as the linear Renewal equation or Lotka's Renewal equation after the biologist A.J. Lotka, who, in 1911, together with F.R. Sharpe [14], [15], proposed a method of solution that was to be the subject of much criticism. Before developing the mathematics which led to their classical

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solution and examining the criticisms raised against it, the assumptions concerning $\pi(a)$, $\beta(a)$ and $\varphi(a)$ need to be established. Lotka and Sharpe, in fact, placed no particular restrictions on these functions, but we shall give a more specific foundation to the problem and adopt the approach used by Lopez [16], who insists, for biological realism, that the conditions i, v, vi, viii apply to $\pi(a)$ and $\beta(a)$. In addition $\varphi(a)$ is assumed to satisfy ix.

It is also useful to point out some of the properties of (2.2.3). As was proved by Feller [17] there is always a unique solution, (which assures from the outset that the mathematical model does not contradict the real situation). Secondly, it can be shown (see Appendix 2.1) that under the above conditions $B(t)$ is a continuous function. Thirdly, since $\beta(a) = 0$ for $a > n$, it follows from (2.2.4) that $G(t)$ will vanish for $t > n$.

The essence of Lotka's method of solution consists in finding a family of functions $B(t)$ all of which satisfy (2.2.3) for $t > n$ and selecting among that family the particular function which satisfies (2.2.3) for $t \leq n$:

For $t > n$ we have

$$B(t) = \int_0^n \beta(a)B(t-a)\pi(a)da, \qquad (2.2.5)$$

or equivalently

$$B(t) = \int_m^n \beta(a)B(t-a)\pi(a)da.$$

Lotka chose the trial solution $B(t) = Ae^{rt}$, which will satisfy (2.2.5) if and

only if

$$\int_0^n e^{-ra}\beta(a)\pi(a)da = 1. \qquad (2.2.6)$$

It is not difficult to verify (see for example [18, p6], [10, p132]) that equation (2.2.6) known as the *characteristic equation* has a unique real root, r_1, (referred to as the *dominant* root); all other roots $\{r_j\} : j = 2, 3, ...$ appear in complex conjugate pairs with $Re\{r_j\} < r_1$; and $Re\{r_j\} \rightarrow -\infty$ as $j \rightarrow \infty$. Lotka assumed an infinite number of distinct simple roots of (2.2.6) and gave, without justification, the general solution to (2.2.5) as

$$B(t) = \sum_i A_i e^{r_i t}. \qquad (2.2.7)$$

This granted, the choice of coefficients

$$A_i = -\frac{F(r_i)}{H'(r_i)}$$

$$\text{where} \quad F(r_i) = \int_0^n G(a)e^{-r_i a}da \qquad (2.2.8)$$
$$\text{and} \quad H(r_i) = \int_0^n \beta(a)\pi(a)e^{-r_i a}da, \qquad (2.2.9)$$

guarantee (as Lotka proved, [19, p87]) that (2.2.7) will not only satisfy (2.2.5) but also the renewal equation (2.2.3).

It was not until William Feller published his paper [17] in 1941, that the above method received some justification and was placed on a sound mathematical basis. It is not the intention to present here, a detailed summary of the criticisms and corrections involved. These are given in [17]. Very briefly though, the relevant criticisms of Lotka's theory are mainly two: Lotka gave no reason to believe that there must be infinitely many roots

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of (2.2.6) and no assurance that the right-hand side of (2.2.7) converges; nor reason why there should be infinitely many *distinct* roots. Secondly, the expected number of births in the first n years which depends on the initial age structure and on the fertility and mortality schedules, represents a function that can assume a vast variety of forms and there is no guarantee that in all cases it can be decomposed into a sum of oscillations of the type given by (2.2.7).

Feller [17] discussed equation (2.2.3) under more general conditions (he assumed an infinite fertile age span) than have been imposed here and applying a Laplace Transform solution to (2.2.3) gave, by means of a number of theorems, conditions for the adequacy of Lotka's method. In particular, theorem 6 of [17] states that in order that the solution $B(t)$ of (2.2.3) be representable in the series expansion (2.2.7) where the series converges absolutely for $t > 0$, it is necessary that the Laplace Transform of $B(t)$

$$L(r) = \int_0^\infty e^{-rt} B(t) dt,$$

be a single-valued function, and it is necessary and sufficient that $L(r)$ admit an expansion

$$L(r) = \frac{F(r)}{1 - H(r)} = \sum \frac{A_i}{r - r_i},$$

where $A_i = -\dfrac{F(r_i)}{H'(r_i)}$; $F(r)$ and $H(r)$ are defined by (2.2.8) and (2.2.9); and where $\sum |A_i|$ converges absolutely.

(Theorem 6 is generalized in [17] to include the possibility of (2.2.6) having

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multiple roots. In this case (2.2.7) is replaced by

$$B(t) = \sum_i \sum_{j=1}^{\sigma_i} \left(A_{ij} / (j-1)! \right) t^{j-1} e^{r_i t}, \qquad (2.2.10)$$

where σ_i is the multiplicity of root r_i. The details of this are given in [17, p264].)

It was Lopez [16,pp 18-28] who then demonstrated by means of a detailed proof that the condition of Feller's Theorem 6 are satisfied when the finiteness of the fertile age span and the continuity of $B(t)$ are recognized. We have seen that these conditions are guaranteed by the requirements i, v, vii, and ix on π, β and φ. Moreover it is unlikely that the assumptions i, iii, iv, vi, vii, viii are ever violated for any real population, so that, working under the further assumption ix on φ, we can safely say that Lotka's classical solution provides a valid method for explicitly determining $B(t)$ and hence $\rho(a,t)$ for a real population for which $\beta \equiv \beta(a)$ and $\mu \equiv \mu(a)$. As Keyfitz and Smith state:

... "in demographic work the conditions of the theorem (theorem 6 of [17]) are always met."[2]

Given this assurance a useful consequence to demographic applications is the following:

It is evident from the properties of the roots of (2.2.6) that as $t \to \infty$

$$B(t) \to A_1 e^{r_1 t}, \qquad (2.2.11)$$

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[2][20, p.143]

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and that from (2.2.1) and from the expression (1.5) for $P(t)$ that

$$P(t) = \int_0^\infty B(t-a)\pi(a)da,$$

so that

$$P(t) \to A_1 e^{r_1 t} \int_0^\infty e^{-r_1 a}\pi(a)da \qquad \text{as } t \to \infty. \qquad (2.2.12)$$

Note then that since this last integral is a constant, (2.2.12) accords with the Malthusian growth pattern (1.1) where r_1 is analogous to the natural growth rate r.

More importantly (2.2.12) implies that

$$\rho(a,t) \to A_1 e^{r_1 t} e^{-r_1 a}\pi(a) \qquad \text{as } t \to \infty,$$

so that the proportion of individuals in any age group (a_1, a_2) given by

$$\frac{\int_{a_1}^{a_2} \rho(a,t)da}{\int_0^\infty \rho(a,t)da},$$

tends to the constant value

$$\frac{\int_{a_1}^{a_2} e^{-r_1 a}\pi(a)da}{\int_0^\infty e^{-r_1 a}\pi(a)da},$$

as $t \to \infty$.

Clearly any age-distribution of the form $\rho(a,t) = f(a)g(t)$ will exhibit such behaviour and is known as a *persistent* or *stable* age-distribution. Thus we have arrived at Lotka's well-known conclusion, namely, that a population which starts off with a known initial age-structure and is subjected from

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that moment to time independent fertility and mortality rates eventually grows exponentially at a rate r_1, and as it does so the population "stabilizes", in that the percentage of females in any age bracket remains the same for all values of time.

Before leaving Lotka's Method it is necessary to make mention of the quantity

$$R_0 = \int_0^\infty \beta(a)\pi(a)da. \tag{2.2.13}$$

This defines the *net reproduction rate*; that is, the average number of offspring expected to be born to a female during her life time. Comparing (2.2.6) and (2.2.13) it follows immediately that the dominant root r_1 is positive, zero or negative, depending on whether R_0 is greater than, equal to, or less than 1. According to (2.2.12) then, the size of R_0 determines (as is physically expected), whether the population grows, shrinks or becomes constant in size as time increases.

Since the mathematical theory for the linear Renewal equation (2.2.3) is well established much use has been made of it in projecting birth rates and future population sizes. Amongst others Keyfitz and Flieger [9], Keyfitz [21], Coale [22], Bellman and Cooke [23], and Pollard [24] make extensive use of this equation, particularly in human population contexts. Evidently the non-linear Renewal equations which result from μ and β being functions of variables other than age alone - for example we will encounter a situation where $\beta \equiv \beta(a, B(t - a))$ - present more difficulties. Various non-linear Renewal equations and the analysis concerning these will be dealt with in

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chapter 3.

Although we have seen that the Renewal equation can be derived from the M-F system, Lotka established his Renewal equation (2.2.3) from first principles. Thus, it is Lotka rather than McKendrick and von Foerster, who is often referred to as the instigator of age-dependent population dynamics. His contribution to population theory ("... the greatest single contribution ..."[3]) is contained in the series of papers ([14], [15], [19], [25], [26], [27], [28]) extending from 1907 to 1948; the core of his work being the linear Renewal equation (2.2.3).

It appears that the trend followed in modelling and analyzing age-dependent population systems is to use either the appropriate M-F system or the appropriate Renewal equation as the starting point. Having derived the Renewal equation from the M-F system it is worthwhile to demonstrate that the reverse is also possible. This is achieved without difficulty by first establishing the Renewal equation (2.2.2) from first principles.

Let $B(t)$ denote the rate of addition of newborns to the female population, that is the birth rate at time t. As for the M-F system, we suppose the initial age-distribution $\varphi(a)$, the age-specific death rate $\mu(a,t)$ and the age-specific fertility function $\beta(a,t)$ are known. Following the approach used by Hoppensteadt [18, pp 5,6] or Frauenthal [10, pp 130,131], it is convenient to divide the population into two groups: the females present at time $t = 0$ (initial population) and females born after time $t = 0$ (daughters, granddaughters, ... of the initial population). At any time t, all females

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[3][9, p 185]

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older than age t are in the first group, while all females younger than age t are in the second.

For the first group the density of females surviving from the initial population to attain age a at time t, $a \geq t$ is

$$\rho(a, t) = \varphi(a - t)\sigma(a, t), \qquad\qquad a \geq t, \qquad\qquad (2.2.14)$$

since

$$\sigma(a, t) = \exp\left\{ -\int_0^t \mu(a - t + \tau, \tau)d\tau \right\},$$

can be shown (see Appendix 2.2) to be the probability that an individual aged a at time t ($a \geq t$) survives from age $a - t$ to age a, and $\varphi(a - t)$ is the density of females in the initial population.

Each of these females will produce newborns at the rate $\beta(a, t)$ so that integrating $\beta(a, t)\sigma(a, t)\varphi(a - t)$ over all ages yields the total birth rate at time t due to the initial population, namely

$$\int_t^\infty \beta(a, t)\sigma(a, t)\varphi(a - t)da.$$

Likewise, in the second group consider the females of age a at time t. These were born at time $t - a$ at the rate $B(t - a)$. Appendix 2.2 indicates that the probability that an individual born at time $t - a$ survives to age a is given by

$$\pi(a, t - a) = \exp\left\{ -\int_0^a \mu(\alpha, \alpha + t - a)d\alpha \right\}. \qquad (2.2.15)$$

Therefore, the density of females in the second group at time t is

$$\rho(a, t) = B(t - a)\pi(a, t - a). \qquad\qquad (2.2.16)$$

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Again, each of these females will bear female offspring at the rate $\beta(a,t)$ so that their contribution to the birth rate at time t is

$$\int_0^t \beta(a,t)\pi(a,t-a)B(t-a)da.$$

Combining these results yields

$$B(t) = G(t) + \int_0^t \beta(a,t)B(t-a)\pi(a,t-a)da, \qquad (2.2.17)$$

where

$$G(t) = \int_t^\infty \beta(a,t)\varphi(a-t)\sigma(a,t)da.$$

Thus, we see that the construction of the Renewal equation (2.2.17), so called because it describes the way the population reproduces itself, involves establishing the solution to the M-F system,

$$\rho(a,t) = \begin{cases} B(t-a)\pi(a,t-a), & a < t \\ \varphi(a-t)\sigma(a,t), & a \geq t. \end{cases}$$

If one was not aware that this is the general solution of the M-F model, a routine differentiation exercise would confirm that $\rho(a,t)$ satisfies the M-F system for $t > 0$. However, to do so one would need the assurance that $\rho(a,t)$ is differentiable. Under the usual assumptions i-viii, on π and β, and $\varphi \in C^1$, $\rho(a,t)$ is differentiable everywhere. Shortly, we will encounter a generalized version of the M-F system that allows for the possibility that $\rho(a,t)$ is not differentiable everywhere and involves more general assumptions concerning μ, β and φ. However, (2.2.14) and (2.2.16) continue to satisfy this system. Thus, in either case and definitely in real situations

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where the functions involved are sufficiently smooth, the Renewal equation approach and the M-F system approach to modelling population dynamics are essentially equivalent. While a Renewal equation approach only yields information about $B(t)$, the solution of the M-F system also indicates the behaviour of the important functions $P(t)$ and $\rho(a,t)$. Of course, fundamental to both models is the solution of the Renewal equation.

A number of papers reviewed in chapter 3 involve a Renewal equation as the basis of the theory. Since the M-F equation is the focal point of this study the findings of these are extended to the appropriate M-F system, to obtain additional information about $P(t)$ and $\rho(a,t)$ for the populations concerned.

Having introduced the M-F system and the related Renewal equation, the fundamental theorems concerning this model need to be outlined.

2.3 Gurtin and MacCamy's non-linear M-F model

A classic paper in the field of age-dependent population dynamics is Gurtin and MacCamy's paper [29], (hereinafter referred to as GMC), which establishes the fundamental features and results concerning the M-F system by means of seven theorems. As these theorems provide the foundation for much of which is to follow, they are listed and discussed here in an overview of GMC.

GMC adopts a more general approach, defining a solution of the population

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problem up to time $T > 0$, as a non-negative function ρ on $\mathbf{R}^+ \times [0, T]$,
such that

$$D\rho(a, t) = \lim_{h \to 0} \frac{\rho(a + h, t + h) - \rho(a, t)}{h}$$

exists on $\mathbf{R}^+ \times [o, T]$;

$\rho(\bullet, t) \in L_1(\mathbf{R}^+)$;

$$P(t) = \int_0^\infty \rho(a, t) da, \qquad\qquad\qquad (2.3.1)$$

is continuous for $0 \le t \le T$, and

$$
\begin{array}{llll}
D\rho(a, t) & + \ \mu(a, P(t))\rho(a, t) = 0, & a > 0, 0 < t < T & (2.3.2) \\
B(t) & = \ \rho(o, t) = \int_0^\infty \beta(a, P(t))\rho(a, t) da, & 0 < t \le T & (2.3.3) \\
\rho(a, 0) & = \ \varphi(a), & a \ge 0. & (2.3.4)
\end{array}
$$

Clearly, if $\rho(a, t)$ is differentiable everywhere then $D\rho$ takes the usual form

$$D\rho = \rho_a + \rho_t.$$

Here then, the time dependence of both the mortality and fertility functions
is related to the total population size at time t and not to time itself. This
choice models those ecological (and human) situations in which the growth
of the population limits the availability of food, space and other resources,
and thus affects the survival and maternity behaviour of the population.
Typically, μ should increase with increasing P, and β should decrease with
increasing P. This dependence on $P(t)$ now introduces non-linearity into
the M-F equation and into the appropriate Renewal equation.

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GMC examines system (2.3.1 - 2.3.4) under a number of further assumptions:

1. The initial age-distribution $\varphi(a) \in L_1(\mathbf{R})$ is sectionally continuous. (Here we deviate from our usual assumption $\varphi(a) \in C^1$ to follow GMC's more rigorous approach.)

2. $\mu, \beta \in C(\mathbf{R}^+ \times \mathbf{R}^+)$; $\mu_P(a, P)$ and $\beta_P(a, P)$ exist for all $a \geq 0$, $P \geq 0$; $\mu(\bullet, P)$, $\mu_P(\bullet, P), \beta(\bullet, P)$ and $\beta_P(\bullet, P)$ as functions of P belong to $C(\mathbf{R}^+ : L_\infty(\mathbf{R}^+))^4$.

3. $\varphi \geq 0$, $\mu \geq 0$, $\beta \geq 0$.

It is pointed out in GMC that (2.3.3) is not required to hold at $t = 0$ and that by (2.3.4) this relation will be satisfied at $t = 0$ if and only if φ satisfies the compatibility condition

$$\varphi(0) = \int_0^\infty \beta(a, \Phi)\varphi(a)\,da; \ \Phi = \int_0^\infty \varphi(a)\,da. \qquad (2.3.5)$$

However, (2.3.5) is not imposed thus allowing for situations in which the initial age distribution is completely arbitrary.

As before, integrating (2.3.2) along the characteristics yields

$$\rho(a, t) = \begin{cases} B(t - a) \exp\left\{-\int_0^a \mu(\alpha, P(t - a + \alpha))\,d\alpha\right\}, & t > a \\ \varphi(a - t) \exp\left\{-\int_0^t \mu(a - t + \tau, P(\tau))\,d\tau\right\}, & a \geq t \end{cases} \qquad (2.3.6)$$

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[4] $L_\infty(\mathbf{R}^+)$ defines the space of functions bounded almost everywhere on $\mathbf{R}^+$.

$C(A : B)$ defines the set of all continuous functions from A to B.

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where

$$B(t) = \rho(o, t), \qquad\qquad (2.3.7)$$

so that a knowledge of P and B (along with μ, β and φ) completely determines $\rho(a, t)$ for all future time. Substitution of (2.3.6) into (2.3.1) and (2.3.3) leads to the integral equations, given in the form

$$P(t) = \int_0^t K(t-a, t, P) B(a) da + \int_0^\infty (L(a, t, P) \varphi(a) da, \qquad (2.3.8)$$

$$\begin{aligned} B(t) = {} & \int_0^t \beta(t-a, P(t)) K(t-a, t, P) B(a) da \\ & + \int_0^\infty \beta(a+t, P(t)) L(a, t, P) \varphi(a) da, \qquad (2.3.9) \end{aligned}$$

in GMC, where

$$\begin{aligned} K(\alpha, t, P) &= \exp\left\{ -\int_{t-\alpha}^t \mu(\alpha + \tau - t, P(\tau)) d\tau \right\} \\ & \qquad\qquad\qquad\qquad\qquad\qquad 0 \le \alpha \le t \\ L(\alpha, t, P) &= \exp\left\{ -\int_0^t \mu(\tau + \alpha, P(\tau)) d\tau \right\}. \end{aligned}$$

Notice that from (2.3.6) it follows that discontinuities in φ will propagate along the characteristics, and even if φ is continuous, (2.3.6) implies that ρ will be discontinuous across the characteristic $t = a$ unless

$$\lim_{t \downarrow 0} \rho(o, t) = B(0^+) = \varphi(o).$$

By (2.3.9)

$$B(0^+) = \int_0^\infty \beta(a, \Phi) \varphi(a) da.$$

Thus, when φ is continuous a necessary and sufficient condition for ρ continuous across $t = a$ is that (2.3.5) hold. In the physically unlikely case

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of (2.3.5) not being satisfied, $B(t)$ defined at $t = 0$ by (2.3.7) will not agree with B defined at $t = 0$ by (2.3.9). Gurtin and MacCamy overcome this technical difficulty by defining $B(t)$ by (2.3.7) for $t > 0$ and setting $B(0) = B(0^+)$.

It is easily confirmed that (2.3.9) reduces to Lotka's Renewal equation (2.2.3) for the case $\mu \equiv \mu(a), \beta \equiv \beta(a)$ and to (2.2.2) for $\mu \equiv \mu(a,t), \beta \equiv \beta(a,t)$. The integral equations (2.3.8), (2.3.9) provide the basis for most of the theorems established in GMC. Before listing these it is interesting to extend the previous note on discontinuities in φ to consider Langhaar's [11] discussion on discontinuities in $B(t)$. Langhaar deals with the M-F system for which $\mu = \mu(a,t)$, $\beta \equiv \beta(a,t)$ and hence with the Renewal equation (2.2.2) although his discussion would apply equally well to (2.3.9). He notes that if $G(t)$ or $\beta(a,t)$ develops a stepwise discontinuity at some time t_1 due to some cataclysmic event, then $B(t)$, given by (2.2.2) (or (2.3.9)), also has a stepwise discontinuity at t_1. Now equation (2.2.1), (or (2.3.6)) implies that if $B(t)$ has a stepwise discontinuity at $t = t_1$ the line $t - a = t_1$ is a stepwise discontinuity for $\rho(a,t)$. Such a discontinuity could be caused by a sudden increase (or decrease) in the fertility function $\beta(a,t)$. The population density $\rho(a,t)$ would then be higher (lower) on the side $t - a > t_1$ than on the side $t - a < t_1$. Langhaar illustrates this by supposing that the birth rate of a human population increases suddenly at $t = 0$ due to an event causing a sudden increase in fertility. Ten years later this jump has increased the population among children less than ten years but has not changed the age distribution among adults at all. "This observation

indicates why an increasing population ordinarily has a preponderance of young individuals and why there may be a shortage of young individuals in a decreasing population."[5]

The fundamental theorems of GMC are listed as follows:

Theorem 1

Let ρ be a solution of the population problem up to time $T > 0$. Then the total population P and the birth rate B satisfy the integral equations (2.3.8), (2.3.9) on $[0, T]$. Conversely, if P and B are non-negative continuous functions that satisfy (2.3.8), (2.3.9) on $[0, T]$ and if ρ is defined on $\mathbf{R}^+ \times [0, T]$ by (2.3.6), then ρ is a solution of the population problem up to time T.

This reaffirms that the M-F system approach and the Renewal equation approach are simply different formulations of the same model.

Theorem 2: Local Existence

There exists a $T > 0$ such that the population problem has a unique solution up to time T.

(The proof is a direct consequence of a fixed point argument [29, pp 286, 293].)

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[5][11, p 211]

Theorem 3

Let

$$\underline{\mu} = \inf_{a \geq 0,\, P \geq 0} \mu(a, P)$$

and suppose that

$$\bar{\beta} = \sup_{a \geq 0,\, P \geq 0} \beta(a, P) < \infty. \tag{2.3.10}$$

Further, let ρ be a solution of the population problem up to time T. Then for $0 \leq t \leq T$,

$$
\begin{aligned}
P(t) &\leq \Phi e^{\delta t} \\
B(t) &\leq \bar{\beta} \Phi e^{\delta t} \\
\rho(a, t) &\leq \bar{\beta} \Phi e^{-\underline{\mu} a} e^{\delta t} \qquad (a < t)
\end{aligned}
$$

and

$$\rho(a, t) \leq \|\varphi\|_t e^{-\underline{\mu} a} \qquad (a \geq t)$$

where

$$\delta = \bar{\beta} - \underline{\mu}, \quad \Phi = \int_0^\infty \varphi(a)\, da, \quad \|\varphi\|_t = \sup_{[0, t]} \varphi.$$

Thus, bounds for $B(t)$ and $P(t)$ are established under the assumption that a very reasonable result applies - it is physically most likely that $\beta(a, P)$ is uniformly bounded for all a and P. Further, these bounds could be useful to social planning - they are easy to compute and provide rough estimates of future populations sizes and birth rates. Notice too, that P and B can grow at most like $e^{\delta t}$ which agrees with the Malthusian Law (1.1). Another valuable consequence of (2.3.10) is Theorem 4.

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Theorem 4 : Uniqueness

Assume that (2.3.10) holds. Then the population problem has a unique solution for all time.

In formulating a population problem of the M-F type the most important questions are whether a solution to (2.3.9) and hence (2.2.1) exists and whether it is unique - such is necessary if the model is not to contradict the real situation. The value of Theorem 4 lies in the fact that existence and uniqueness are guaranteed by a condition that will apply to any real population.

The next theorem assures that the solution ρ will be a class C^1 function.

Theorem 5

Assume that $\varphi \in C^1(\mathbf{R}^+)$ with $\dot{\varphi} \in L_1(\mathbf{R}^+)$. Assume in addition that $\mu, \beta \in C^1(\mathbf{R}^+ \times \mathbf{R}^+)$ and that $\beta_a, \beta_P \in C(\mathbf{R}^+ \times \mathbf{R}^+ : L\infty(\mathbf{R}^+))$. Let ρ be a solution of the population problem up to time T. Then $\rho \in C^1(\mathbf{R}^+ \times [0, T])$ if and only if φ satisfies the compatibility condition (2.3.5) and

$$
\begin{aligned}
\dot{\varphi}(0) \; = \; & [\mu(0, \Phi) - \beta(0, \Phi)] \, \varphi(0) \\
& - \int_0^\infty \left[\beta_a(a, \Phi) + \beta_P(a, \Phi)\dot{\Phi} - \beta(a, \Phi)\mu(a, \Phi) \right] \varphi(a) da,
\end{aligned}
$$

(2.3.11)

where

$$
\dot{\Phi} = \varphi(a) - \int_0^\infty \mu(a, \Phi(a))\varphi(a) da.
$$

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It seems likely that in real situations these rather rigorous conditions can be relaxed, requiring instead that $\varphi, \dot{\varphi}, \mu, \beta, \beta_a, \beta_P$ be sufficiently smooth bounded functions.

A form of the age-distribution that will play a significant role throughout is the time-independent solution, $\rho(a,t) \equiv \rho(a)$ of (2.3.1 - 4). In this case (2.3.1 - 4) becomes

$$
\begin{aligned}
\rho_a &+ \mu(a, P^*)\rho = 0 & (2.3.12) \\
P^* &= \int_0^\infty \rho(a)da & (2.3.13) \\
B^* &= \rho(o) = \int_0^\infty \beta(a, P^*)\rho(a)da. & (2.3.14)
\end{aligned}
$$

A solution $\rho \in C^1(\mathbf{R}^+)$ of (2.3.12 - 14) is known as an *equilibrium age-distribution*. Clearly P^* and B^* are constants.

In studying equilibrium age-distributions the integral

$$
R(P) = \int_0^\infty \beta(a, P)\pi(a, P)da, \qquad (2.3.15)
$$

is important.

As for (2.2.15),

$$
\pi(a, P^*) = \exp\left\{-\int_0^a \mu(\alpha, P^*)d\alpha\right\}, \qquad (2.3.16)
$$

defines the probability of surviving from birth to age a in circumstances where the population size is held constant at P^* throughout the aging process. $R(P)$ indicates the number of children to be born to an individual when the population size is P.

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Theorem 6

Let $P > 0$ and assume that $\beta(\bullet, P)\pi(\bullet, P) \in L_1(\mathbf{R}^+)$. Then a necessary and sufficient condition that an equilibrium age-distribution exist with total population P^*, is that $R(P^*) = 1$. In this case the (unique) equilibrium age- distribution corresponding to P^* is given by

$$\rho(a) = B^*\pi(a, P^*), \qquad (2.3.17)$$

where

$$B^* = \frac{P^*}{\int_0^\infty \pi(a, P^*)da}.$$

We have seen that for the linear case $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$, the population grows, declines or tends to a constant value (the equilibrium value) depending on whether R_0 (as given by (2.2.13)) is greater than, less than or equal to 1. In this case R_0 is independent of P, and as pointed out in GMC it would be fortuitous for R_0 to equal 1. Here however R is a function of P, and it is likely that there exists at least one value of P for which $R(P) = 1$. Once this value of $P(P^*$ say) has been attained, the age-distribution maintains the same shape regardless of time progressing so that the number of individuals in any age group remains constant, and P remains at its fixed value of P^*.

Much recent work in population dynamics has concerned equilibrium age-distributions and their stability properties; some of this is discussed in subsequent chapters. In GMC the standard techniques are applied to investigate the stability of $\rho(a)$ having corresponding birth-rate B^* and total

population P^*. Considering "perturbations" $\xi(a,t)$ of $\rho(a)$ such that

$$
\begin{aligned}
\rho(a,t) &= \rho(a) + \xi(a,t) \\
P(t) &= P^* + \int_0^\infty \xi(a,t)da,
\end{aligned}
$$

substitution into (2.3.1 - 4) and linearization about the equilibrium position yields to the first order, the M-F variant

$$
D\xi + \mu(a, P^*)\xi + \omega p = 0
$$

$$
p(t) = \int_0^\infty \xi(a,t)da \tag{2.3.18}
$$

$$
\xi(o,t) = \int_0^\infty \beta(a, P^*)\xi(a,t)da + \kappa p(t),
$$

where

$$
\omega = B^* \mu_P(a, P^*)\pi(a, P^*), \qquad \text{and}
$$

$$
\kappa = B^* \int_0^\infty \beta_P(a, P^*)\pi(a, P^*)da.
$$

Gurtin and MacCamy then make the assumption that

$$
\xi(a,t) = \tilde{\xi}(a)e^{\gamma t}, \tag{2.3.19}
$$

with $\tilde{\xi}(a)$ and γ being complex, and derive a necessary and sufficient condition for the asymptotic stability of $\rho(a)$; namely, that all γ's satisfying the "gruesome"[6] transcendental equation (3.15) of [29, p 290] have negative real part.

---

[6] This is Nisbet and Gurney's (see [13,p 105]) description of equation (3.15) given in [29]. Nisbet and Gurney also analyse the system (2.3.18) but do not prescribe perturbations to be of the form (2.3.19). Necessary and sufficient conditions for local stability are given in terms of conditions on μ and β. The details of their work are given in [30].

The very lengthy final theorem of GMC, theorem 7, proves that this linear stability analysis is indeed valid.

However, as an alternative to GMC's method of obtaining (3.15) we have succeeded in deriving their result along somewhat simpler lines, by adopting instead a "Renewal equation approach" to the problem:

The appropriate Renewal equation for the system (2.3.1-4) is given by (2.3.9) but can be written instead in the more familiar form

$$B(t) = G(t) + \int_0^t \beta(a, P(t)) B(t - a) \pi(a, P(t)) da, \qquad (2.3.20)$$

where

$$G(t) = \int_t^\infty \beta(a, P(t)) \varphi(a + t) \sigma(a, t) da,$$

and $\pi(a, P(t))$ is given by

$$\pi(a, P(t)) = \exp\left\{ -\int_0^a \mu(\alpha, P(t - a + \alpha)) d\alpha \right\}.$$

As before, assuming $\beta(a, P(t)) = 0$ for $a > n$ implies that $G(t)$ will vanish for $t > n$, so that (2.3.20) becomes

$$B(t) = \int_0^n \beta(a, P(t)) B(t - a) \pi(a, P(t)) da, \ t > n,$$

or

$$B(t) = \int_0^\infty \beta(a, P(t)) B(t - a) \pi(a, P(t)) da, \ t > n, \qquad (2.3.21)$$

without any loss of generality.

To investigate the stability of (2.3.17) consider a perturbation of the form

$$P(t) = P^* + \delta e^{\gamma t}, \qquad (2.3.22)$$

where $P^* = \int_0^\infty \rho(a)da$; $|\delta|$ is small, and δ and γ are complex.

It is not difficult to verify that the birth-rate corresponding to (2.3.22) is of the form

$$B(t) = B^* + \in e^{\gamma t}, \qquad (2.3.23)$$

(where B^* is the birth-rate corresponding to P^*, $\in$ is a complex constant, and higher order terms in δ have been ignored).

Substitution in to (2.3.21) yields

$$
\begin{aligned}
\in e^{\gamma t} = {}& -B^* + \int_0^\infty \beta(a,P)B^*\pi(a,P)da + \\
& \int_0^\infty \beta(a,P) \in e^{\gamma(t-a)}\pi(a,P)da
\end{aligned}
$$

$$(2.3.24)$$

Now $\rho(a,t)$ is given by $B(t-a)\pi(a,P)$ for $t > a$ and $\rho(a)$ by (2.3.17), so that

$$
\begin{aligned}
\rho(a,t) - \rho(a) &= B(t-a)\pi(a,P) - B^*\pi(a,P^*) \\
&= \in e^{\gamma(t-a)}\pi(a,P) + B^*\left[\pi(a,P) - \pi(a,P^*)\right],
\end{aligned}
$$

from which we obtain

$$P - P^* = \int_0^\infty \in e^{\gamma(t-a)}\pi(a,P)da + B^* \int_0^\infty \left[\pi(a,P) - \pi(a,P^*)\right]da. \quad (2.3.25)$$

Expanding $\pi(a,P)$ in a power series in δ and ignoring higher order terms leads to

$$\pi(a,P) = \pi(a,P^*) - \pi(a,P^*)\left[\int_0^a \mu_P(\alpha,P^*)e^{\gamma(\alpha-a)}d\alpha\right]\delta e^{\gamma t} + \dots,$$

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so that (2.3.25) becomes

$$\delta e^{\gamma t} \simeq \int_0^\infty \in e^{\gamma(t-a)} \pi(a, P) da -$$

$$B^* \int_0^\infty \pi(a, P^*) \left[\int_0^a \mu_P(\alpha, P^*) e^{\gamma(\alpha-a)} d\alpha \right] \delta e^{\gamma t} da.$$

This in turn implies that

$$1 + B^* \int_0^\infty \pi(a, P^*) \left[\int_0^a \mu_P(\alpha, P^*) e^{\gamma(\alpha-a)} d\alpha \right] da$$

$$= \int_0^\infty \frac{\in}{\delta} e^{-a\gamma} \pi(a, P) da. \qquad (2.3.26)$$

On substituting (2.3.26) into (2.3.24) we obtain

$$\in e^{\gamma t} = B^* \left[R(P) - 1 \right] \int_0^\infty \frac{\in}{\delta} e^{-a\gamma} \pi(a, P) da \cdot \{$$

$$1 + B^* \int_0^\infty \pi(a, P^*) \left[\int_0^a \mu_P(\alpha, P^*) e^{\gamma(\alpha-a)} d\alpha \right] da \}^{-1}$$

$$+ \int_0^\infty \beta(a, P) \in e^{\gamma(t-a)} \pi(a, P) da. \qquad (2.3.27)$$

Expansion of $R(P)$ in a power series in δ, ignoring higher order terms yields

$$R(P) = R(P^*) + R'(P^*) \delta e^{\gamma t} + \dots$$

$$= 1 + \delta e^{\gamma t} \left[\int_0^\infty \beta_P(a, P^*) \pi(a, P^*) da - \right.$$

$$\left. \int_0^\infty \beta(a, P^*) \pi(a, P^*) \left[\int_0^a \mu_P(\alpha, P^*) e^{\gamma(\alpha-a)} d\alpha \right] da \right],$$

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from which (2.3.27) becomes

$$
\begin{aligned}
1 \;=\;& B^* \int_0^\infty e^{-a\gamma}\pi(a,P)da\, [\int_0^\infty \beta_P(a,P^*)\pi(a,P^*)\,da \\[4pt]
&- \int_0^\infty \beta(a,P^*)\pi(a,P^*)\left[\int_0^a \mu_P(\alpha,P^*)e^{\gamma(\alpha-a)}d\alpha\right]da]\bullet\{ \\[4pt]
&1\; + B^* \int_0^\infty \pi(a,P^*)\left[\int_0^a \mu_P(\alpha,P^*)e^{\gamma(\alpha-a)}d\alpha\right]da\}^{-1} \\[4pt]
&+ \int_0^\infty \beta(a,P)e^{-\gamma a}\pi(a,P)da,
\end{aligned}
\tag{2.3.28}
$$

which, setting $P = P^*$, is exactly equation (3.15) of GMC.

A solution of the form (2.3.22) will exist if and only if γ satisfies (2.3.28). Evidently if all γ's satisfying (2.3.28) have negative real parts, all perturbations will disappear in time and, as $t \to \infty$, $P(t) \to P^*$; in other words, the equilibrium position is stable. If there exists a root of (2.3.28) having non-negative real part the equilibrium is asymptotically unstable.

In the conclusion of GMC the special case

$$
\begin{aligned}
\mu(a,P) &\equiv \mu(P) \\
\beta(a,P) &\equiv \beta(P)e^{-\alpha a}, \qquad \alpha > 0,
\end{aligned}
\tag{2.3.29}
$$

is considered. This form of μ and β will not be discussed here but is dealt with in chapter 4. For the M-F system with μ and β described by (2.3.29) the stability criterion (2.3.28) is a polynomial in γ,

$$
\gamma^2 + \gamma\left[\mu(P^*) + \dot\mu(P^*)P^* - \frac{\dot\beta(P^*)\mu(P^*)P^*}{\beta(P^*)}\right] +
$$

$$
\left[\dot\mu(P^*) - \dot\beta(P^*)\right]\mu(P^*)P^* = 0,
\tag{2.3.30}
$$

where $\dot\mu$ and $\dot\beta$ denote differentiation with respect to P.

It is straight forward to verify that (2.3.30) will have negative real part roots if and only if

$$\dot{\mu}(P^*) - \dot{\beta}(P^*) > 0 \qquad (2.3.31)$$

and

$$\frac{\dot{\mu}(P^*)}{\mu(P^*)} > \frac{\dot{\beta}(P^*)}{\beta(P^*)} - \frac{1}{P^*} \qquad (2.3.32)$$

However, Gurtin and MacCamy incorrectly weaken (2.3.32) to allow for equality (see [29, p292]) and state that (2.3.31) will imply (2.3.32), so that (2.3.31) is a necessary and sufficient condition for the stability of the equilibrium age-distribution. Their statement clearly fails to hold when $\dot{\mu}(P^*) < 0$ and it is possible that $\dot{\mu}(P^*)$ is indeed negative. For example, we shall encounter a case later where,

$$\mu(P) = 1 + c - \alpha - (2c - q)P + (c - q)P^2, \ 0 < \alpha < 1, \ c > \alpha, \ c > q;$$

and $P^* = 1$.

Here $\dot{\mu}(P^*) = -q < 0$.

For the choice (2.3.29),

$$R'(P^*) = \frac{1}{\beta(P^*)} \left[\dot{\beta}(P^*) - \dot{\mu}(P^*) \right],$$

and from the above discussion, $R'(P^*) < 0$ is a necessary but not sufficient condition for the stability of the equilibrium age distribution, as is implied in GMC. In the next chapter variations of the expression (2.3.15) for R will be encountered. In each case the derivative of R with respect to an

appropriate variable will be seen to play an important role in stability criteria.

This summarizes the main results of GMC in which attention was given to the choice $\mu \equiv \mu(a, P)$, $\beta \equiv \beta(a, P)$. Chapter 3 deals with numerous other nonlinear variants of the M-F system, their solution and stability properties. The GMC results will be seen to form the basis of much of the theory involved.

Chapter 3

Non-linear Generalizations of the M-F model

With GMC's model and its results providing the initiative, much of the recent work in population theory has involved constructing and analysing various other generalizations of the M-F model. Such modifications have included incorporating dependence upon $\rho(a,t)$ into the fertility and/or mortality function; considering boundary conditions $\rho(o,t)$ that are not described by the usual integral (1.13); incorporating a harvest of members into the model; and, extending the M-F system to describe the dynamics of a two-sex population. The purpose of this chapter is to provide an overview of these and other generalization of the M-F model, to list and discuss the results of each, and to point out areas open to further research. Where details are omitted the references quoted provide a fuller account and indicate directions of other developments.

The salient feature of linearity ($\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$) of course, is that $B(t)$ and hence $\rho(a,t)$ can be explicitly calculated. The Renewal equations

which arise here are, in general, not as amenable to solution and we will see that the approach is not to seek an explicit solution but to investigate asymptotic behaviour of $B(t)$ and $P(t)$ by determining stability criteria on equilibrium solutions.

3.1   Dependence of β on past birth rate

It has been noted earlier that while at any given instant $\pi(a)$ (from which $\mu(a)$ can be deduced) and $\beta(a)$ can be determined from census data for the population, precise information about future survivorship and maternity behaviour is simply not available. One must either estimate these rates or develop fertility and mortality functions which determine future rates by depending on the past behaviour of some demographic parameter.

This is the approach used by Frauenthal [31] and Swick [32], [33] who consider a maternity function that depends upon the past female birth rate. In particular, their choice exploits the hypothesis of the economist and demographer R.A. Easterlin [34], that due to increased economic and social competition, females born in relatively large cohorts[1] tend to produce fewer children than those born in small cohorts. Very roughly the argument here is that those born in small cohorts have less peer- group job competition than those born in large cohorts, hence have more chance to succeed, and demonstrate this success by having more children. Implicit in this argument is the assumption that an individual can control her own fertility, so that the model developed would be most appropriate to human populations in

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[1]A cohort refers to a group of individuals all born at time t.

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developed countries.

Frauenthal [31] mentions that recent data for developed countries confirms that survivorship behaviour is relatively constant with time, so that, to a good approximation $\mu \equiv \mu(a)$, while the assumption is made that

$$\beta(a,t) \equiv \tilde{\beta}(a)\bar{\beta}(B(t-a)). \qquad (3.1.1)$$

$B(t-a)$ is the value of the birth rate at time $t-a$, but also serves as a measure of the initial size of the cohort born at time $t-a$. $\tilde{\beta}(a)$ is the underlying time- independent fertility function. Hence, the maternity behaviour of a female presently of age a at time t is a function of the size of the cohort into which she was born.

Frauenthal and Swick study the above situation using the Renewal Equation as the starting point. In reviewing [31], [32], [33] we shall instead apply the results of these papers to the appropriate nonlinear version of the M-F model, namely

$$\rho_a + \rho_t = -\mu(a)\rho \qquad (3.1.2)$$

$$P(t) = \int_0^\infty \rho(a,t)da \qquad (3.1.3)$$

$$B(t) = \rho(o,t) = \int_0^\infty \tilde{\beta}(a)\bar{\beta}(B(t-a))\rho(a,t)da \qquad (3.1.4)$$

$$\rho(a,0) = \varphi(a), \qquad (3.1.5)$$

where the biologically plausible assumption that $\mu(a)$, $\beta(a,t)$, $\varphi(a)$ are class C^1 functions has been made, so that ρ is at least differentiable as discussed in chapter 2.

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As found in chapter 2, the solution to (3.1.2 - 5) is given by

$$
\rho(a,t) = \begin{cases} B(t-a)\exp\left\{-\int_0^a \mu(\alpha)d\alpha\right\} = B(t-a)\pi(a), & t > a \\[2mm] \varphi(a-t)\exp\left\{-\int_0^t \mu(a-t+\xi)d\xi\right\}, & a \geq t \end{cases} \qquad (3.1.6)
$$

Recall too from the previous chapter that for $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$, R_0 equal to 1 (where R_0 is given by (2.2.13)) indicates that $B(t)$ tends to a constant value as time increases. Now, if in (3.1.1) the birth rate remains at a constant level B^* for a long time, $\beta(a,t)$ becomes a function of age only, so that to preserve consistency, $\tilde{\beta}(a)$ needs to be normalized such that

$$
R_0 = \int_0^\infty \tilde{\beta}(a)\pi(a)da = 1. \qquad (3.1.7)
$$

In this case the *net reproduction rate*, that is, the average number of daughters expected to be born to a female in the cohort $B(\tau)$ is given by

$$
R(B(\tau)) = \int_0^\infty \pi(a)\tilde{\beta}(a)\bar{\beta}(B(\tau))da, \qquad \tau = t - a.
$$

Since $\tau = t - a$ is constant with increasing time

$$
\begin{aligned}
R(B(\tau)) &= \bar{\beta}(B(\tau)) \int_0^\infty \tilde{\beta}(a)\pi(a)da \\
&= \bar{\beta}(B(\tau)),
\end{aligned}
$$

so that (3.1.1) becomes

$$
\beta(a,t) = \tilde{\beta}(a)R(B(t-a)),
$$

and Esterlin's hypothesis is satisfied if $R(B)$ is a decreasing function.

The focus of [31], [32], [33] is on describing the general properties of birth trajectories (that is, birth rates $B(t)$) as time increases. The following are essential to the criteria and results obtained:

- Denoting, as usual, the maximum age of childbearing by n, then substitution of (3.1.6), into (3.1.4), indicates that the birth rate for $t > n$ is described by[2]

$$B(t) = \int_0^\infty \tilde{\beta}(a) R(B(t-a)) \pi(a) B(t-a) da. \qquad (3.1.8)$$

- Letting $\rho(a)$ denote the equilibrium solution of (3.1.2 - 5) and

$$P^* = \int_0^\infty \rho(a) da = B^* \int_0^\infty \pi(a) da$$

$$B^* = \int_0^\infty \tilde{\beta}(a) R(B^*) \rho(a) da,$$

it is straightforward to verify that (3.1.8) has an equilibrium birth rate $B = B^*$, and the M-F system (3.1.2 - 5) has an equilibrium point (B^*, P^*) if and only if $R(B^*) = 1$.

- Expansion of $BR(B)$ about B^* leads to

$$BR(B) = B^* + (1 - w)(B - B^*) + g(B - B^*), \qquad (3.1.9)$$

where $w = -B^* R'(B^*)$ and $g(o) = 0 = g'(o)$, so that $w > o$ reflects Easterlin's hypothesis. Ignoring second order terms in (3.1.9) leads

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[2]where $\int_0^\infty$ can replace $\int_0^n$ without loss of generality.

to

$$R(B) = \left[1 + w\frac{(B^* - B(\tau))}{B(\tau)}\right] = \bar{\beta}(B(\tau)).$$

This perhaps justifies why Frauenthal [31] worked with the maternity function

$$\beta(a,t) = \tilde{\beta}(a)\left[1 + \alpha\left(\frac{B^* - B(t-a)}{B(t-a)}\right)\right] \qquad (3.1.10)$$

which he suggested as being the most realistic for a developed nation with effective fertility control. In (3.1.10) α is a constant and serves as a measure of the influence of cohort size upon the current maternity behaviour. B^* is a solution of $R(B^*) = 1$.

We restrict attention for the moment to (3.1.10) and to the analysis and results of [31]. The advantage of (3.1.10) is that the Renewal equation

$$B(t) = G(t) + \alpha B^* \int_0^t \pi(a)\tilde{\beta}(a)da + (1 - \alpha)\int_0^t B(t-a)\pi(a)\tilde{\beta}(a)da, \ t > 0,$$

$$(3.1.11)$$

(with $G(t)$ having the usual form), is linear and can thus be solved along the lines of Lotka's classical solution.

Instead of solving directly for $B(t)$, Frauenthal considers a birth rate $B(t)$ which is disturbed from its equilibrium position B^*, by making the substitution

$$B(t) = B^* + \tilde{B}(t), \qquad (3.1.12)$$

in (3.1.11). This leads to another Renewal equation

$$\tilde{B}(t) = \tilde{G}(t) + (1 - \alpha)\int_0^t \tilde{B}(t-a)\pi(a)\tilde{\beta}(a)da, \ t > 0, \qquad (3.1.13)$$

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where $\tilde{B}$ is the deviation of $B(t)$ from B^* and

$$\tilde{G}(t) = G(t) + B^* \left[\int_0^t \pi(a)\tilde{\beta}(a)da - 1. \right]$$

Assuming as usual that $\beta(a) = 0$ for $a > n$, so that $\tilde{G}(t) = 0$ for $t > n$ and further that

$$\tilde{B}(t) = \sum_{i=0}^{\infty} Q_i e^{r_i t}, \quad t > n, \tag{3.1.14}$$

leads to the analogue of (2.2.6)

$$\int_0^{\infty} e^{-ra}\tilde{\beta}(a)\pi(a)da = \frac{1}{1-\alpha} \quad . \tag{3.1.15}$$

This linear analysis sketches the proof of the theorem [31, Theorem I] which states that if all the roots of the characteristic equation (3.1.15) have negative real part then the equilibrium birth rate B^* is asymptotically stable. Notice that if $B(t)$ is of the form $B^* + \in e^{rt}$ for $t > n$ as in (2.3.23), then so is $P(t)$, since from (3.1.6), $\rho(a,t) = B(t-a)\pi(a)$ for $t > n$, so that

$$
\begin{aligned}
P(t) &= \int_0^{\infty} B(t-a)\pi(a)da \\
&= B^* \int_0^{\infty} \pi(a)da + \in e^{rt} \int_0^{\infty} \pi(a)e^{-ra}da \\
&= P^* + ke^{rt}, \ k = \text{ constant.}
\end{aligned}
\tag{3.1.16}
$$

Therefore, knowledge of the roots of (3.1.15) also indicates the asymptotic behaviour of the population size $P(t)$. With this in mind, we shall extend Frauenthal's results concerning $B(t)$ to make similar predictions about $P(t)$. Frauenthal points out that under the assumptions that $\pi(a)$ and $\beta(a)$ are continuous and that the fertile age- span is finite (recall the discussion

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of Lopez's proof in Chapter 2, section 2.2), (3.1.14) does represent the solution of the Renewal equation (3.1.13) for $t > 0$ where the coefficients Q_i can be determined along similar lines to the coefficients A_i of Lotka's solution ((2.2.7), (2.2.8), (2.2.9)). Instead of determining these coefficients and presenting a formal solution $B(t)$ of (3.1.11), Frauenthal investigates the qualitative behaviour of the birth trajectory with increasing time for all possible values of α:

1. $\alpha < 0$.   According to (3.1.10) this reflects the case where women born in large cohorts produce large numbers of children, contrary to Easterlin's hypothesis. The right-hand side of (3.1.15) is now less than unity. From (3.1.7) and the fact that $\pi(a) \geq 0$, $\tilde{\beta}(a) \geq 0$, it follows that only one real root $r = r_1$ of (3.1.15) exists and this root is greater than zero. The remaining roots $\{r_j\}$: $j = 2, 3, ...$, must occur in complex conjugate pairs with real parts less than r_1. Hence (3.1.14) indicates that $\tilde{B}$ grows exponentially so that $B(t)$ and $P(t)$ grow without bound.

2. $\alpha = 0$ corresponds to Lotka's time-independent model discussed in section 2.2 of chapter 2.

   More interesting cases occur for $\alpha > 0$, being consistent with Easterlin's postulate:

3. $0 < \alpha < 1$. Similar analysis to that of 1. confirms that the unique real root r_1 of (3.1.15) is less than zero. All the pairs of complex conjugate roots have real part less than r_1. Furthermore, it is shown

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that the dominant complex root (that is, the complex root having largest real part), has associated with it a period of oscillation about equal to f, where

$$f = \frac{1}{R_0} \int_0^\infty a\tilde{\beta}(a)\pi(a)da, \qquad (3.1.17)$$

defines the mean age of childbearing in a population for which $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$. Thus, if disturbed from the equilibrium position B^*, the birth trajectory $B(t)$ (or the population size $P(t)$), oscillates about B^* (P^*) with decreasing amplitude, eventually returning to B^* (P^*).

4. $\alpha > 1$. In this case all roots $\{r_j\} : j = 1, 2, 3, ...,$ are complex conjugate pairs. Let $\alpha = \alpha^*$ correspond to the case giving rise to a purely imaginary dominant root.

   (i) $\alpha = \alpha^*$. It is shown in [31] that the period of the undamped oscillation associated with this case is approximately equal to $2f$, so that $B(t)$ oscillates about B^* with constant amplitude. $P(t)$ will also exhibit undamped oscillations about P^*.

   (ii) $1 < \alpha < \alpha^*$. In this case the real part of the dominant root is less than zero and $B(t)$ oscillates about B^* with decreasing amplitude, eventually returning to B^*. (The same behaviour is predicted for $P(t)$.)

   (iii) $\alpha > \alpha^*$. Here the real part of the dominant root is greater than zero. As time increases, $B(t)$ oscillates about B^* with period

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approximately equal to $2f$ and increasing amplitude. Again $P(t)$ behaves similarly so that the population ultimately diverges to unbounded growth.

5. $\alpha = 1$. In this case the right-hand side of the characteristic equation (3.1.15) becomes unbounded. Setting $\alpha = 1$ in (3.1.11) it follows that for sufficiently large t $(t > n)$ $B(t)$ remains at its equilibrium value B^*. Necessarily, if $B(t) = B^*$, then

$$P(t) = \int_0^\infty B(t-a)\pi(a)da = \int_0^\infty B^*\pi(a)da = P^*.$$

Frauenthal's results provide a means then, of readily predicting the asymptotic character of $B(t)$ and $P(t)$ (and hence also $\rho(a,t)$), for populations which adjust their reproductive behaviour in accordance with the maternity function (3.1.10). The most salient feature of Frauenthal's model is its rather accurate explanation of a recent phenomenon observed in a number of developed countries. Apparently, in recent years bounded large amplitude oscillations in the birth rate have been observed, and in the United States the period of this oscillation has been found to be about 54 years. Keyfitz and Flieger [35] compute f, the mean age of childbearing for developed countries to be close to 27 years and Frauenthal's model predicts that for $1 < \alpha < \alpha^*$ a bounded solution occurs for $B(t)$ for which the natural period of oscillation is about $2f$, that is about 54 years. This agreement between observation and theoretical formulation is very encouraging. (3.1.10) with $1 < \alpha < \alpha^*$ is therefore indeed, as Frauenthal envisioned, a very realistic choice of the maternity function of a developed nation. A number

of other comments are added in [31]. Firstly, it is noted that $R(B(\tau))$ as given by

$$R(B(\tau)) = \int_0^\infty \pi(a)\beta(a,t)da, \qquad \tau = t - a,$$

can be written in this case as

$$R(B(\tau)) = (1 - \alpha) + \alpha\frac{B^*}{B(\tau)} \qquad (3.1.18)$$

so that for $0 < \alpha < \alpha^*$, $R(B(\tau))$ assumes a range of values. However, for this choice of parameters the model predicts that the population approaches a constant size. Hence, unlike the linear case $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$ and the nonlinear case $\mu \equiv \mu(a,P)$, $\beta \equiv \beta(a,P)$, R need not be precisely equal to one for a non-divergent solution to occur. In other words, a population can approach a constant size even though every cohort does not simply reproduce itself exactly.

Secondly, note by inspecting (3.1.18) that a drawback of the model is that for a range of values of α and $B(\tau)$, both negative and also large positive values of $R(B(\tau))$ can result. Both possibilities are inconsistent with the behaviour of a real population since, as Frauenthal points out, $R(B(\tau))$ would probably never be outside the range of about 1/2 to 2 for a developed country.

Finally, it is mentioned that the prediction that $B(t)$ will exhibit growing oscillations for $\alpha > \alpha^*$ is physically unlikely. Frauenthal argues that physical restrictions would prevent this sort of behaviour and proposes without mathematical proof that it is more reasonable to expect a limit cycle oscillation for $\alpha > \alpha^*$ If this were true the implications would be far reaching.

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"Such human institutions as the social security system and the educational system would have to evolve sufficient flexibility to cope with periodic fluctuations in numbers of people."[3] However, Frauenthal adds that no population has satisfied all the assumptions of his model for a sufficiently long time interval (in particular, the assumption that $\mu \equiv \mu(a)$ is not always accurate), to give the assurance that it is, in the long-term, an accurate model upon which such strategies can be based.

Swick [32], [33], on the other hand, considers Frauenthal's model with $R(B)$ and hence $\bar{\beta}(B(t-a))$ determined from (3.1.9) where in this case $\alpha = \omega = -B^* R'(B^*)$. Again $\omega > 0$, or equivalently, $R'(B^*) < 0$ reflects Easterlin's hypothesis.

Using standard perturbation theory Swick arrives at the following conclusions:

- If $0 < -B^* R'(B^*) < 1$ then each birth trajectory $B(t)$ starting in some neighbourhood of B^* approaches B^* with oscillations of decreasing amplitude.

- If $1 < -B^* R'(B^*) < \omega^*$ (ω^* being the purely imaginary root of (3.1.15)) then each birth trajectory starting near B^* approaches B^*, oscillating about B^* with period close to $2f$ (where f is defined by (3.1.17)).

- If $-B^* R'(B^*) > \omega^*$, then B^* is unstable.

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[3][31, p. 72]

Clearly the results of [31] are in agreement with these of [32] and [33]. We see then that the behaviour of the birth rate can be completely determined by the slope of the net reproduction rate $R(B)$ at the equilibrium B^*. Now the applicationof these results depends on the construction of a precise function to represent $R(B)$. This is understandably, as Swick explains, quite a difficult task.

The following result given in [32] formally proves what was observed in [31]: *Suppose that for $\omega = \omega^*$ (3.1.15) has the purely imaginary root $r^* i = \frac{2\pi i}{f^*}$, $f^* > 0$; that $nr^* i$ is not a root of (3.1.15) for $n \neq \pm 1$; and that $c(r^*) = \int_0^\infty s\bar{\beta}(s)\pi(s)\cos(r^* s)ds \neq 0$. Then B^* bifurcates at $\omega = \omega^*$ to a periodic solution of period near f^* (where $f^* = 2f$).*

For 1966 U.S. census data Swick shows that $\omega^* \simeq 2,3$ and $f^* = 2f \simeq 54$ years, so that combining the results of [31], [32] and [33] we have that for the choice of parameters $0 < \omega < 2,3$, B^* is asymptotically stable, but bifurcates at $\omega = 2,3$ to a periodic birth rate of period near 54 years.

Swick also mentions that it has not been established mathematically that these periodic solutions as asymptotically stable, but that numerical solutions strongly suggest that this is the case. He adds that the numerical solutions generated seem to imply that each birth trajectory does appraoch the periodic solution as a limit cycle, as Frauenthal proposed.

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3.2   Dependence of β on present birth rate

Rorres [36] investigates the case where the fertility function depends on $B(t)$, so that females "adjust" their fertility according to the present birth rate. The model studied is the M- F system having $\mu \equiv \mu(a,t)$, $\beta \equiv \beta(a,t,B(t))$ where explicit dependence on time is included and where, although not stated in [36], one would expect β to decrease with B.

In this case the net reproduction rate is given by

$$R(t,B(t)) = \int_0^\infty \beta(a,t,B(t))\pi(a,t)da.$$

By means of three theorems Rorres gives sufficient conditions for $B(t)$ to be contained in some interval (B',B'') for all t sufficiently large, or to approach an equilibrium value B^*. (Here an equilibrium birth rate is defined as any value $B^* > 0$ such that $R(t,B^*) \equiv 1$ for all $t > 0$.) As in [32] and [33] the quantity $R'(t,B^*)$ (where differentiation is with respect to B) plays a dominant role in the stability analysis of this paper. However, the conditions derived are complicated and do not have informative physical interpretation.

A more interesting model involving the dependence of β on $B(t)$ is Swick's [37] "welfare model." Swick argues that the most obvious deficiency in the cohort model (3.1.2 - 5) is the lack of any dependence in β and μ on the total size of the population, $P(t)$. He notes that although this seems to be more important in ecological than demographic applications, it can have impact even for human populations.

The "welfare model" (which Swick studies from a Renewal equation approach) involves $\beta \equiv \beta(a, B(t), P(t))$, $\mu \equiv \mu(a, P(t))$, and is so called since it is based on the assumption that the general welfare suffers when the population grows too large, and as a result, the fertility decreases and/or the mortality increases.

In particular, Swick works under the assumptions that μ is a constant and

$$\beta(a, B, P) = \bar{\beta}(B) N(P) \frac{\alpha^{n+1}}{n!} a^n \exp(-\gamma a), \ \gamma, \alpha > 0,$$

where $\bar{\beta}$ and N are unspecified functions of P and B respectively. Thus "population pressure" effects are assumed to affect β rather than μ.

Now, applying an ingenious technique introduced by Gurtin and MacCamy [38], Swick replaces the usual integral expressions for $B(t)$ and $P(t)$ by a system of ordinary differential equations. The details of this manipulation and the resulting system will not be elaborated upon here since Gurtin and MacCamy's technique and its applications is treated in detail in the next chapter. Suffice it to say that the technique is facilitated by β being of the form described above and by $\mu \equiv \mu(P)$ (or by μ being a constant as it is above), and that by applying eigenvalue analysis to the resulting set of O.D.E.'s, Swick readily obtains conditions on the parameters of the system guaranteeing that the equilibrium is stable.

3.3 Dependence of β on a weighted average of $\rho(a, t)$

In all of the models discussed so far the dependence of β on $B(t - a)$ or $B(t)$ (and $P(t)$) acts as a feedback mechanism, placing a degree of control on the growth of the population. This is also the case in another variation of the M-F model studied by Rorres [39], [40], in which β is a function of the "weight" $C(t)$ of the population, where the term weight is used in a generic sense denoting a scalar quantity which affects female fertility. More precisely, $C(t)$ is defined as a weighted average with respect to age of the age-density function, i.e.

$$C(t) = \int_0^\infty c(a)\rho(a, t)da, \tag{3.3.1}$$

where $c(a)$ is a given non-negative continuous function on $[\,o, \infty]$, not identically equal to zero. (This includes the case where $c(a) \equiv 1$ so that $C(t) \equiv P(t)$.) It also allows for different ages to be weighted differently to account for their possibly different ecological impacts on fertility. (Another possibility is to set $c(a)$ equal to the average weight of a female of age a, so that $C(t)$ is the biomass of the population - however, this has an unlikely application in human populations.)

This problem has also been analysed by Lamberti and Vernole [41] who consider the generalized form of the M-F Model,

$$D\rho(a, t) = -\mu(a)\rho(a, t) \tag{3.3.2}$$

$$C(t) = \int_0^\infty c(a)\rho(a, t)da \tag{3.3.3}$$

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$$B(t) = \rho(o,t) = \int_0^\infty \beta(a, C(t))\rho(a,t)da \qquad (3.3.4)$$

$$\rho(a,o) = \varphi(a) \qquad (3.3.5)$$

where $\varphi(a), \mu(a), \beta(a, C(t))$ are known bounded, nonnegative continuous functions of their variables. Notice that μ is assumed to be independent of the "weight" variable $C(t)$. As usual, $\mu(a)$ is defined so that

$$\lim_{a \to \infty} \int_0^a \mu(a)da = \infty$$

ensuring that $\pi(a) \to 0$ as $a \to \infty$.

In [41] existence and uniqueness of a nonnegative solution of (3.3.2 - 5), namely

$$\rho(a,t) = \begin{cases} B(t-a)\pi(a) & t > a \\ \varphi(a-t)\frac{\pi(a)}{\pi(a-t)} & t \le a, \end{cases}$$

are proved along similar lines to those of GMC.

The net reproduction rate, in this situation, is given by

$$R(C) = \int_0^\infty \beta(a, C(t))\pi(a)da,$$

and defines, as usual, the expected number of daughters to be born during the lifetime of a female when the "weight" of the population remains fixed at $C(t)$. Rorres and, Lamberti and Vernole give attention to investigating the local and global stability properties of an equilibrium age-distribution

$$\rho(a) = B^*\pi(a) \qquad (3.3.6)$$

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of the system (3.3.2 - 5). Once again, a necessary and sufficient condition for the existence of an equilibrium age-distribution is that there exists a $C^* > 0$ such that

$$\int_0^\infty \beta(a, C^*)\pi(a)da = 1. \tag{3.3.7}$$

As in GMC, Lamberti and Vernole remark that for the linear case ($\beta \equiv \beta(a)$) it would be fortuitous for equilibrium age distributions to exist but demonstrate that

$$If \ \lim_{c \to +\infty} \int_0^\infty \beta(a, C)da = 0 \ and \ \lim_{c \to 0} \int_0^\infty \beta(a, C)\pi(a)da > 1$$

then there exists an equilibrium age distribution.

As usual, in studying the local stability properties of (3.3.6) Rorres [39] disturbs $B(t)$ slightly from its equilibrium position B^* in order to determine conditions under which $B(t) \to B^*$ or equivalently $\rho(a, t) \to \rho(a)$ as $t \to \infty$. Setting

$$B(t) = B^* + \in e^{\gamma t} \tag{3.3.8}$$

implies that

$$C(t) = C^* + \delta e^{\gamma t}, \qquad \in, \delta, \gamma \text{ complex constants.}$$

Now substitution of (3.3.8) into (3.3.4), use of the relation $B^* = \frac{C^*}{D}$ where $D = \int_0^\infty c(a)\pi(a)da$, and linearization of the resulting equation about the equilibrium point C^* leads to an analogue of the stability equation (2.3.28) of GMC,

$$\int_0^\infty e^{-\gamma t} \left[\beta(a, C^*)\pi(a) + \frac{C^*}{D}R'(C^*)c(a)\pi(a)\right] da = 1. \tag{3.3.9}$$

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Theorem 1 of [39] states the expected: *If all the roots of (3.3.9) have negative real part then the equilibrium point (B^*, C^*) is locally stable.* Clearly, if any root of (3.3.9) has positive real part the equilibrium is unstable.

Rorres compares his criterion (3.3.9) to equation (2.3.28), remarking that GMC's detailed analogue indicates that the dependence of μ on $P(t)$(i.e. $C(t)$ with $c(a) \equiv 1$) as well as age adds to the complexity involved in deriving such a stability condition. However, in Chapter 2 we presented an alternative method to that used in GMC which enables (2.3.28) to be obtained without too much computational difficulty. Notice that since $R'(C^*) = \int_0^\infty \beta_C(a, C^*)\pi(a)da$, (3.3.9) is obtainable from (2.3.28) by replacing P^* with C^* and $\pi(a, P^*)$ with $c(a)\pi(a)$. Hence theorem 7 of GMC also guarantees that the linear analysis of [39] outlined above is indeed consistent.

Further stability criteria are given in [39] which involve the derivative of the net reproduction rate. It is noted that if $C^* R'(C^*) > 0$ then

$$\int_0^\infty \left[\beta(a, C^*)\pi(a) + \frac{C^*}{D}R'(C^*)c(a)\pi(a) \right] da = 1 + C^* R'(C^*) > 1$$

from which it is easy to verify that (3.3.9) has a unique, positive, real root. Thus, a necessary condition for local stability is that $C^* R'(C^*) < 0$. Rorres mentions that the ideal situation would be that a particular system is stable for all negative $C^* R'(C^*)$ and proceeds to give four criteria which will guarantee this. We shall limit attention to the case $c(a) \equiv 1$ since this has the widest physical applications. The relevant criteria are then twofold:

CRITERION 3

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Suppose $\mu'(a) \leq [\mu(a)]^2$ for all $a \geq 0$. Then P^* is stable if $R'(P^*) < 0$.

The case where μ is constant leads to

CRITERION 4

The equilibrium population size P^* is stable if $R'(P^*) < 0$.

Evidently these criteria have the advantage of being readily applicable. For example, suppose that

$$\beta(a, P) = \beta(P) a e^{-\alpha a} \quad , \alpha > 0$$
$$\text{and}$$
$$\mu \equiv c, \qquad c = \text{constant.}$$

Then $R(P) = \beta(P) \int_0^\infty a e^{-(\alpha+c)a} da$ and $R'(P^*) = \frac{\beta'(P^*)}{(\alpha+c)^2}$, so that $\beta'(P^*) > 0$ is a sufficient condition for the stability of the equilibrium value P^*.

We see again that the rate of change of the net reproduction rate with the "weight" function C (or population size P) is the essential demographic parameter in determining the local stability (or otherwise) of an equilibrium point.

In [40] Rorres proceeds to investigate the global stability character of equilibrium solutions of (3.3.2 - 5). Sufficient conditions for such stability are presented in detail. Lamberti and Vernole conclude their paper [41] by deriving a global stability result for the system (3.3.2 - 5) having $\beta(a, C) = \frac{\beta(a)}{1+C}$ where $\beta(a)$ is a continuous non-negative function. Thus $\beta(a, C)$ decreases with increasing $C(t)$, which for $C(t) \equiv P(t)$ reflects the situation where environmental pressures affect fecundity. We shall not discuss this result of [41] nor the results of [40] here, but will instead review another

variant of the M-F model proposed by Sinestari [42], [43] together with its local and global stability properties.

3.4   Dependence of β upon $\rho(a, t)$

Sinestrari constructs a modification of the M-F model reflecting the situation in which interactions that influence mortality and fertility are supposed to exist only between individuals of the same age. In particular Sinestrari works with the system

$$D\rho(a, t) = -\mu(a, t, \rho(a, t))\rho(a, t) \tag{3.4.1}$$

$$P(t) = \int_0^\infty \rho(a, t)da \tag{3.4.2}$$

$$B(t) = \rho(o, t) = \int_0^\infty \beta(a, t, \rho(a, t))\rho(a, t)da \tag{3.4.3}$$

$$\rho(a, o) = \varphi(a), \tag{3.4.4}$$

where the explicit dependence of β and μ on time allows one to account for the effects of seasonal variations, improved health care etc. The dependence of β and μ on $\rho(a, t)$ implies that at any instant t the rate at which an individual of age a produces children or dies depends on the individual's age *and* the number of individuals (females) of that age at the given time t. We can perhaps justify this choice by arguing that individuals of the same age have similar preferences and needs. Therefore, increasing the number of members in a particular age group limits the availability of necessary resources for that age group. Thus we expect, as Sinestari assumes, that

μ increases with ρ and β decreases with ρ. The latter assumption can also be regarded as a reflection of Easterlin's hypothesis.

Besides the usual assumptions that $\mu \geq 0$ be sectionally continuous; that $\int_0^\infty \varphi(a) \, da < \infty$; and that β and μ be known continuous, non-negative functions, the above requirements that $\mu(a, t, \rho)$ and $\beta(a, t, \rho)$ be respectively nondecreasing and non- increasing functions of ρ are imposed throughout [42] and [43].

Along the lines of the GMC paper Sinestrari establishes existence and uniqueness of solutions of (3.4.1 - 4); gives a priori bounds for the growth of $P(t)$ and $B(t)$ under the assumptions $\underline{\mu} = \inf \mu$, $\bar{\beta} = \sup \beta < \infty$; and proves theorems guaranteeing the existence, uniqueness, local and global stability of equilibrium age-distributions of (3.4.1 - 4). In what follows a few of these results are described.

Clearly, an equilibrium age-distribution of (3.4.1 - 4) must satisfy the system

$$\rho_a(a) = -\mu(a, \rho(a))\rho(a) \tag{3.4.5}$$

$$P^* = \int_0^\infty \rho(a) da \tag{3.4.6}$$

$$B^* = \rho(o) = \int_0^\infty \beta(a, \rho(a))\rho(a) da \tag{3.4.7}$$

Defining $F(B^*) = \int_0^\infty \beta(a, \rho(a)) \frac{\rho(a)}{B^*} da$, which is the usual net reproduction rate evaluated at B^*, a solution $\rho(a)$ of (3.4.5) satisfies the system if and only if

$$F(B^*) = 1. \tag{3.4.8}$$

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Sinestrari then demonstrates that $F(B^*)$ is non-increasing on $[0, \infty)$ so that there exists $F(0^+)$ and $F(+\infty)$, and further, that if $\mu(a, \rho)$ and $\beta(a, \rho)$ are strictly monotonic functions of ρ, then F is strictly decreasing. This leads in turn to necessary and sufficient conditions for the existence and uniqueness of equilibrium solutions, given as theorem 6 of [43]:

Theorem 6

If there are equilibrium age-distributions of (3.4.5 - 7) then $F(0^+) \geq 1$ and $F(+\infty) \leq 1$. Conversely, let $F(0^+) > 1$ and $F(+\infty) < 1$, then there exists equilibrium age-distributions. Moreover, if $\mu(a, \rho)$ and $\beta(a, \rho)$ are strictly monotonic functions of ρ then the equilibrium age-distribution is unique.

Theorem 7 of [43], along the lines of theorem 7 of GMC concerns the local stability of an equilibrium age-distribution:

Theorem 7

Let $\rho(a)$ be an equilibrium age-distribution such that the following condition holds

$$\int_0^\infty |\beta_\rho(a, \rho(a))\rho(a)+\beta(a, \rho(a))| \exp\left(-\int_0^a \mu_\rho(\alpha, \rho(\alpha))\rho(\alpha) + \mu(\alpha, \rho(\alpha))d\alpha\right) da < 1$$

$$(3.4.9)$$

then $\rho(a)$ is locally stable.

Notice from (3.4.8) that (3.4.9) is satisfied when

$$\beta_\rho(a, \rho) < 0 \text{ and } \beta_\rho(a, \rho)\rho + \beta(a, \rho) \geq 0 \qquad (3.4.10)$$

or when β does not depend on ρ and $\mu_\rho(a, \rho) > 0$.

Further, if $\beta_\rho \equiv 0 \equiv \mu_\rho$ then as expected, (3.4.9) reduces to the requirement that $R_0 < 1$, which as was seen in chapter 2, guarantees that the origin

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$(P^* = B^* = 0)$ is asymptotically stable; in other words that the population eventually becomes extinct.

Sinestrari concludes [43] with a theorem guaranteeing the global stability of a solution of (3.4.5 - 7):

Theorem 8

Let $\rho(a)$ be the unique nontrivial equilibrium age- distribution of (3.4.1 - 4). Suppose further that there exists an age interval (m, n) such that $\beta(a, \rho) > 0$ for $m < a < n$ and $\rho \geq 0$; $\varphi(a) \not\equiv 0$ in $[o, n]$; $\beta(a, \rho)\rho$ is a non-decreasing function of ρ; and that $\rho(a, t)$ is the corresponding solution of (3.4.1 - 4). Then

$$\lim_{t \to \infty} |\rho(a, t) - \rho(a)| = 0$$

uniformly for $a \in A$, $A = [o, p]$ where p represents the age of maximum survivorship.

The papers [42] and [43] present an interesting generalization of the M-F system and a wealth of results concerning it. Nevertheless, to obtain expressions for μ and β as functions of ρ for a particular population is evidently not an easy task. The interpretation of $\rho(a, t)$ is not as "straightforward" as those of $P(t)$ and $B(t)$, and it is difficult to conceptualize how μ and β would in fact change with ρ. However, Sinestrari has proposed the following expressions for μ and β in terms of ρ:

$$\mu(a, \rho) = d(a)e(\rho)$$

where $d(a)$ is a positive, continuous function having the form

$$d(a) = (p - a)^{-1}(1 + a)^{-1},$$

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(p denotes as usual, the maximum attainable age.)

Such a choice of $d(a)$ agrees with that proposed in chapter 2. Further $e(\rho)$ is assumed to be given by

$$e(\rho) = \begin{cases} \alpha\rho + \in, & 0 \leq \rho \leq \rho_1 \\ \bar{e}(\rho), & \rho_1 < \rho \leq \rho_2 \\ \rho^\sigma, & \rho > \rho_2 \end{cases}$$

where $\alpha, \in, \sigma > 0$ and $\bar{e}(\rho)$ is increasing and continuously differentiable on $\mathbf{R}^+$. Thus $e(\rho)$ increases linearly with ρ initially but after some critical value of ρ increases more rapidly perhaps due to the effects of increased food shortages and overcrowding.

$\beta(a, \rho)$ is assumed to be of the form $f(a)g(\rho)$, where $g(\rho)$ is a continuously differentiable decreasing function and $f(a)$ is continuous but positive only on the interval of fertility $[m, n]$. Hence $\beta(a, \rho)$ is bounded and thus biologically sensible.

Sinestrari applies the results of his paper [43] to this system. In particular, from the inequalities (3.4.10) it follows that an equilibrium age-distribution is stable if $g(\rho)$ is such that

$$\rho g'(\rho) + g(\rho) \geq 0, \tag{3.4.11}$$

a condition which can be readily tested.

We noted earlier that Sinestrari's choice $\beta \equiv \beta(a, t, \rho)$ was another means of modelling Easterlin's hypothesis. Frauenthal's [31] model incorporating this hypothesis yields more informative and applicable results than those of [42] and [43], since the Renewal equation involved is linear and can be solved

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explicitly. However, Frauenthal's model involves μ being a function of age only and an interesting project would be an analysis along the lines of GMC upon Frauenthal's model with $\beta \equiv \beta(a, B(t-a))$ and with $\mu \equiv \mu(a, P(t))$ so that the possibility of self-limiting effects are included in the mortality function.

3.5   The inclusion of a harvesting term

Incorporating a harvest of members into the M-F model leads to a further nonlinear variant. In [44] and [45] Brauer examines such a system:

$$\rho_a(a,t) + \rho_t(a,t) = -\mu(a, P(t))\rho(a,t) - v(a) \qquad (3.5.1)$$

$$P(t) = \int_0^\infty \rho(a,t)da \qquad (3.5.2)$$

$$B(t) = \rho(o,t) = \int_0^\infty \beta(a, P(t))\rho(a,t)da \qquad (3.5.3)$$

$$\rho(a,o) = \varphi(a), \qquad (3.5.4)$$

where $v(a)$ is the rate at which members of age a are harvested, so that

$$H = \int_0^\infty v(a)da < \infty,$$

the total number of members harvested per time is constant.

A model of this form would be appropriate to an animal population in which different age groups are harvested or preyed upon to different degrees or to a population (human or animal) in which an epidemic affects different age

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groups to different degrees - perhaps $v(a)$ is large for either small or large values of a.

Applying the method of characteristics to this harvesting problem gives

$$
\rho(a,t) = \begin{cases}
B(t-a)\exp\left\{-\int_0^a \mu^*(\alpha)d\alpha\right\} - \int_0^a v(y)\exp\left\{-\int_y^a \mu^*(\alpha)d\alpha\right\}dy, & t \geq a \\[3mm]
\varphi(a-t)\exp\left\{-\int_{a-t}^a \mu^*(\alpha)d\alpha\right\} - \int_{a-t}^a v(y)\exp\left\{-\int_y^a \mu^*(\alpha)d\alpha\right\}dy, & t < a
\end{cases}
\tag{3.5.5}
$$

where Brauer has set $\mu^* = \mu(\alpha, \; P(t-a+\alpha))$.

Substitution of the above into (3.5.2) and (3.5.3) results in the modified integral equations

$$
B(t) = b(t) + \int_0^t B(t-a)\beta(a, P(t))\exp\left\{-\int_0^a \mu^*(\alpha)d\alpha\right\}da - h_1(t) \tag{3.5.6}
$$

$$
P(t) = p(t) + \int_0^t B(t-a)\exp\left\{-\int_0^a \mu^*(\alpha)d\alpha\right\}da - h_2(t) \tag{3.5.7}
$$

with

$$
b(t) = \int_t^\infty \beta(a, P(t))\varphi(a-t)\exp\left\{-\int_{a-t}^a \mu^*(\alpha)d\alpha\right\}da \tag{3.5.8}
$$

$$
p(t) = \int_t^\infty \varphi(a-t)\exp\left\{-\int_{a-t}^a \mu^*(\alpha)d\alpha\right\}da \tag{3.5.9}
$$

$$
h_1(t) = \int_0^\infty v(y)\left[\int_y^{y+t} \beta(a, P(t))\exp\left\{-\int_y^a \mu^*(\alpha)d\alpha\right\}da\right]dy \tag{3.5.10}
$$

and

$$
h_2(t) = \int_0^\infty v(y)\left[\int_{y+t}^y \exp\left\{-\int_y^{y+t} \mu^*(\alpha)d\alpha\right\}da\right]dy, \tag{3.5.11}
$$

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(3.5.6) is now the appropriate Renewal equation for the system. (Notice that $\exp\left\{-\int_0^a \mu^*(\alpha)d\alpha\right\}$ is just the usual form of $\pi(a, P(t-a))$.)

It is not difficult to verify that when $\rho(a, t) \equiv \rho(a)$, that is, the age-distribution is an equilibrium age-distribution, these integral equations become

$$B^* \left[\int_0^\infty \beta(a, P^*) \exp\left\{ -\int_0^a \mu(\alpha, P^*)d\alpha \right\} da - 1 \right]$$

$$= \int_0^\infty \beta(a, P^*) \left[\int_0^a v(y) \exp\left\{ -\int_y^a \mu(\alpha, P^*)d\alpha \right\} dy \right] da \qquad (3.5.12)$$

$$P^* = B^* \int_0^\infty \exp\left\{ -\int_0^a \mu(\alpha, P^*)d\alpha \right\} da - \int_0^\infty \left[\int_0^a v(y) \exp\left\{ -\int_y^a \mu(\alpha, P^*)da \right\} dy \right] da.$$

$$(3.5.13)$$

(P^* and B^* represent as usual, the constant population size and birth-rate corresponding to $\rho \equiv \rho(a)$). From (3.5.12) it follows that in the absence of harvesting, i.e. $v(a) \equiv 0$

$$\int_0^\infty \beta(a, P^*) \exp\left\{ -\int_0^a \mu(\alpha, P^*)d\alpha \right\} = \int_0^\infty \beta(a, P^*)\pi(a, P^*)da = 1$$

$$(3.5.14)$$

which is the usual requirement that $R(P^*) = 1$. If there is harvesting then $v(a) > 0$ and (3.5.12) implies that

$$\int_0^\infty \beta(a, P^*)\pi(a, P^*)da > 1,$$

so that, in order to maintain equilibrium in the presence of harvesting, the average number of offspring per member must exceed 1.

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Notice too that from the "equilibrium equation"

$$\rho_a(a) = -\mu(a, P^*)\rho(a) - v(a),$$

and from the biologically reasonable assumption that

$$\rho(a, t) \to 0 \text{ as } a \to \infty$$

results the relation

$$\int_0^\infty \mu(a, P^*)\rho(a)da + \int_0^\infty v(a)da = \int_0^\infty \beta(a, P^*)\rho(a)da = B^*,$$

indicating, as expected, that for equilibrium to be maintained the birth rate must be equal to the net death rate plus the harvest rate.

In [44] and [45] Brauer investigates the qualitative behaviour of solutions of the integral equations (3.5.6) and (3.5.7) for various choices of μ and β. In particular the four cases $\beta \equiv \beta(a)$, $\mu \equiv \mu(P)$; $\beta \equiv \beta(P)$, $\mu \equiv \mu(P)$; $\beta \equiv \beta(a)$, $\mu \equiv \mu(a)$; and $\beta \equiv \beta(P)$, $\mu \equiv \mu(a)$ are studied. The first two cases lend themselves to a technique introduced by Gurtin and MacCamy [38], and mentioned earlier, which enables the system (3.5.1 - 4) to be reduced to a set of ordinary differential equations. As this technique and its applications are the subject of chapter 4 the analysis concerning these two cases will not be pursued here. Brauer's work on the latter cases will be briefly mentioned. Specifically (3.5.1 - 4) with $\beta \equiv \beta(a)$, $\mu \equiv \mu(a)$ provides an interesting contrast to the linear M-F model treated in detail in chapter 2.

(i) The choice $\beta \equiv \beta(a)$, $\mu \equiv \mu(a)$ transforms the integral equations (3.5.6) and (3.5.7) into

$$B(t) = b(t) + \int_0^t \beta(a)B(t-a)\pi(a)da - h_1(t) \quad (3.5.15)$$

$$P(t) = p(t) + \int_0^t B(t-a)\pi(a)da, -h_2(t) \quad (3.5.16)$$

with (3.5.15) being the analogue of Lotka's Renewal equation (2.2.3) for the harvested M-F model.

In chapter 2 it was shown that for the linear, unharvested model every age distribution tends to a persistent age distribution, $\rho(a,t) = f(a)g(t)$ as $t \to \infty$. In the harvested case the counterpart of a persistent age-distribution is a solution of the form $\rho(a,t) = f(a)g(t) - h(a)$. One can show by means of separation of variables (see [45, p.954]) the existence of solutions of the linear harvested model of the form

$$\rho(a,t) = \pi(a)\left[ce^{k(t-a)} - h(o) - \int_0^a \frac{v(y)}{\pi(y)}dy\right], \quad k,c = \text{ constants; } k \neq 0.$$

$$(3.5.17)$$

Substitution of (3.5.17) into (3.5.3) yields

$$\int_0^\infty \beta(a)\pi(a)e^{-ka}da = 1.$$

Clearly, if $k = 0$, $\rho(a,t)$ as given by (3.5.17) is an equilibrium age-distribution and $\int_0^\infty \beta(a)\pi(a)da = 1$. However, it was seen earlier that $\int_0^\infty \beta(a)\pi(a)da = 1$ only if there is no harvest, so that there is no solution with $k = 0$ if there is a harvest. In other words, if the maternity and mortality functions depend on age only and if there is harvesting there cannot be an equilibrium

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age-distribution. Moreover, persistent age-distributions either grow exponentially or tend to zero exponentially with time.

In order to examine the asymptotic behaviour of an age distribution Brauer studies the asymptotic behaviour of $B(t)$ by setting

$$B(t) = B_1(t) - B_2(t), \qquad (3.5.18)$$

where

$$B_1(t) = b(t) + \int_0^t \beta(a)B_1(t-a)\pi(a)\,da \qquad (3.5.19)$$

and

$$B_2(t) = h_1(t) + \int_0^t \beta(a)B_2(t-a)\pi(a)\,da. \qquad (3.5.20)$$

Now each of (3.5.19) and (3.5.20) is a linear Renewal equation with $b(t) \geq 0$ and $h_1(t) \geq 0$. As mentioned in chapter 2, Feller, in his paper [17], the purpose of which was to place Lotka's solution into correct mathematic context, presents a number of theorems concerning the linear Renewal equation. Applying Feller's results to (3.5.19), (3.5.20) Brauer shows that if

- $\int_0^\infty \beta(a)\pi(a)\,da < 1$ then $\lim_{t\to\infty} B_1(t) = 0$;

- $\int_0^\infty \beta(a)\pi(a)\,da \geq 1$ and r_1 is the largest real part root of $\int_0^\infty e^{r_i a}\beta(a)\pi(a)\,da = 1$, then $B_1(t) \sim c_1 e^{r_1 t}$ as $t \to \infty$;

- $\int_0^\infty \beta(a)\pi(a)\,da < 1$ then $\lim_{t\to\infty} B_2(t) > 0$;

- $\int_0^\infty \beta(a)\pi(a)\,da = 1$ then $B_2 \sim c_2 t$ as $t \to \infty$;

- $\int_0^\infty \beta(a)\pi(a)\,da > 1$ then $B_2(t) \sim c_2 e^{r_1 t}$ as $t \to \infty$.

Combining these results we see that if

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- $\int_0^\infty \beta(a)\pi(a)da \le 1$ then $B_1(t) - B_2(t)$ is negative for all sufficiently large t, indicating that $B(t)$ reaches zero in finite time;

- $\int_0^\infty \beta(a)\pi(a)da > 1$, then $B(t) \sim (c_1 - c_2)e^{r_1 t}$ \hfill (3.5.21)

as $t \to \infty$. Thus if $c_1 > c_2$ (the details for finding c_1 and c_2 can be found from [17] - as for the coefficients A_i of Lotka's solution the value of c_1 depends on $b(t)$ while that of c_2 depends on $h_1(t)$ and hence on $v(a)$), substitution of (3.5.21) into the appropriate form of (3.5.5), namely,

$$\rho(a,t) = \pi(a)\left[B(t-a) - \int_0^a \frac{v(y)}{\pi(y)}dy\right] \tag{3.5.22}$$

indicates that $\rho(a,t)$ approaches a persistent age- distribution as $t \to \infty$. On the other hand, if $v(a)$ is such that $c_1 < c_2$ then clearly $B(t)$ tends to zero in finite time. By (3.5.22) so does $\rho(a,t)$.

The conclusion for the harvested linear case then, is that every age-distribution either tends to a persistent age- distribution, which cannot be an equilibrium age-distribution, or vanishes identically for large t. This is in contrast to the unharvested counterpart in which equilibrium age-distributions are possible but extinction in finite time is not. Clearly the age-specific harvesting has to be carefully performed since the possibility of exponential growth would be disasterous if the harvested species is an undesirable one, such as an insect pest population, and the possibility of extinction is equally disasterous if the species harvested is a "desirable" type.

(ii) The choice $\beta \equiv \beta(P)$, $\mu \equiv \mu(a)$ obviously limits the applicability of the resulting model since the independence of age in β is an unlikely assumption

for most populations. However, we could argue that this choice could be used to model the behaviour of an animal population which is robust enough to exist off the minimum amount of food and other resources, with the effect that a reduction in food supplies etc. due to overcrowding, is more likely to result in reduced fecundity than in death. In other words "population pressure" effects primarily influence fertility rather than survivorship. The advantage of $\beta \equiv \beta(P)$ is that

$$B = \beta(P)P,$$

which follows from (3.5.3), and the model can be described by the single Volterra integral equation,

$$P(t) \quad = \quad p(t) \quad + \quad \int_0^t \pi(a)g(P(t-a))da - h_2(t) \quad (3.5.23)$$

$$\text{where} \qquad g(P) \quad = \quad \beta(P)P \qquad\qquad (3.5.24)$$

$$p(t) \quad = \quad \int_t^\infty \varphi(a-t)\frac{\pi(a)}{\pi(a-t)}da \qquad (3.5.25)$$

$$\text{and} \qquad h_2(t) \quad = \quad \int_0^\infty \frac{v(y)}{\pi(y)}\left[\int_y^{y+t} \pi(a)da\right] dy. \qquad (3.5.26)$$

The nonharvested form of (3.5.23),

$$P(t) = p(t) + \int_0^t \pi(a)g(P(t-a))da \qquad (3.5.27)$$

has been studied extensively by Londen [46], [47] and by Brauer [48]. Londen examines the question of boundedness of solutions of (3.5.27) and shows, under quite general hypotheses that every bounded solution tends to

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a limit as $t \to \infty$. In [48], (which preceeds [44] and [45]), Brauer gives a condition guaranteeing the boundedness of solutions under hypotheses which are appropriate to many population problems and derives conditions under which solutions cannot tend to zero. It is interesting, as Brauer points out in the introduction of [48], that (3.5.27) may also be used to describe the dynamics of a population afflicted with some disease - in this case $P(t)$ is the number of diseased members, $\pi(a)$ represents the probability that a diseased member survives to age a and $p(t)$ represents the number of diseased members who were already present at time $t = P$ and who are still alive at time t. Since g (which by definition (3.5.24) describes the number of members added to the population in unit time when the population size is P), depends only on the total number of diseased members, i.e. $g \equiv g(P)$, (3.5.27) would model a disease for which recovery from the disease confers negligible immunity, and which has a negligible incubation period since no delay terms are included in the integral equation.

In [44] and [45] Brauer modifies the results of [48] to apply to the harvested case (3.5.23). These are listed below

- If $\left[\int_0^\infty \pi(a)da\right]\left[\lim_{P \to \infty} \beta(P)\right] < 1$ then every nonnegative solution is bounded on $0 \le t < \infty$.

- If $g'(P) \int_0^\infty \pi(a)da$ is not identically equal to 1 on any P-interval then every bounded nonnegative solution tends to a limit P^* as $t \to \infty$ where P^* satisfies

$$P^* = -h_2(\infty) + g(P^*) \int_0^\infty \pi(a)da \qquad (3.5.28)$$

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and

$$h_2(\infty) = \int_0^\infty \pi(a) \left[\int_0^a \frac{v(y)}{\pi(y)} dy \right] da.$$

- If $h_2(\infty)$, which is related to the rate of harvesting, is so large that there are no solutions of (3.5.28) then every solution of (3.5.23) must reach zero in finite time; in other words the population has been harvested to extinction.

- The critical value of $h_2(\infty)$ for which this transition takes place is determined by $g'(P^*) \int_0^\infty \pi(a) da = 1$.

- An equilibrium age-distribution corresponding to a population size P^* is stable (in the usual sense of being relatively insensitive to perturbations) if

$$g'(P^*) \int_0^\infty \pi(a) da < 1,$$

and unstable if

$$g'(P^*) \int_0^\infty \pi(a) da > 1.$$

Since $g(P) = \beta(P)P$, (3.5.28) may be written as

$$P^* = -h_2(\infty) + P^* \beta(P^*) \int_0^\infty \pi(a) da,$$

and the above stability condition becomes

$$[P^* \beta'(P^*) + \beta(P^*)] \int_0^\infty \pi(a) da < 1$$

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$$\text{i.e.} \quad P^*\beta'(P^*)\int_0^\infty \pi(a)da < 1 - \left[1 + \frac{h_2(\infty)}{P^*}\right] = \frac{-h_2(\infty)}{P^*}$$

$$\text{or} \quad P^{*2}\beta'(P^*)\int_0^\infty \pi(a)da + h_2(\infty) < 0. \tag{3.5.29}$$

Thus, by means of a few criteria which appear to be computationally easy to verify, the behaviour of the harvested population is readily predicted. Notice too from (3.5.29), that $\beta'(P^*) < 0$ is a necessary condition for stability, but in the unharvested case $(h_2(\infty) = 0)$, $\beta'(P^*) < 0$, or equivalently $R'(P^*) < 0$[4] is necessary and sufficient for stability.

Brauer's papers [44], [45] provide a wealth of useful results for the harvested M-F model for which each of μ and β are functions of age only or functions of population size only. Not considered here is the behaviour of solutions for which μ and β depend on both of these variables and Brauer suggests that this would be worth further investigation. For example, one might attempt to obtain results for the system (3.5.1 - 4) having $\mu \equiv \mu(a)$, $\beta \equiv \beta(P)ae^{-\alpha a}$, $\alpha > 0$.

The literature on harvesting problems is extensive. Gurtin and Murphy [49], [50], for example consider the constant - effort harvesting model,

$$\frac{\partial \rho}{\partial a} + \frac{\partial \rho}{\partial t} + \mu(a, P(t))\rho + E(a,t)\rho(a,t) = 0 \tag{3.5.30}$$

coupled as usual with (3.5.2), (3.5.3), (3.5.4). Here $E(a,t)$ represents the "effort" with which individuals of age a are harvested at time t. (A discussion of the meaning of "effort" is given in section 5.6.) The total number

---

[4]Since $R'(P^*) = \beta'(P^*)\int_0^\infty \pi(a)da$

of individuals harvested at time t, per unit time is

$$\int_0^\infty E(a, t)\rho(a, t)da,$$

so that the total number harvested during a time interval $[0, T]$ is

$$\int_0^T \int_0^\infty E(a, t)\rho(a, t)da\ dt. \tag{3.5.31}$$

The problem posed is finding the function E which maximises the yield (3.5.31) subject to the dynamical equations (3.5.30), (3.5.2), (3.5.3) and the initial condition (3.5.4). The authors introduce assumptions which simplify the model sufficiently to permit explicit solutions of the optimization problem.

In a similar fashion, Rorres and Fair [51], study (3.5.1 - 4) at equilibrium, with $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$ and determine, by reformulating the problem as an optimal control problem, the harvest rate $v(a) \geq 0$ and terminal time A, which maximises the economic yield of the harvest, defined as

$$\int_0^A y(a)v(a)da,$$

$y(a)$ being the economic value of a single harvested female of age a, under the constraint that

$$\int_0^A c(a)\rho(d)da = 1.$$

Here $c(a)$ is the cost per unit time of maintaining a single unharvested female of age a.

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Sanchez, [52], on the other hand, incorporates a harvesting term into the original M-F model ($\mu \equiv \mu(a,t)$, $\beta \equiv \beta(a,t)$) which involves removing a fraction of the population which fall within a certain age group. For example, the author of [52] supposes that a fraction δ, $0 < \delta < 1$ of the population of age $a \geq c$ (c represents some chosen age) is harvested and replaces the usual partial differentiation equation by

$$\rho_a + \rho_t = -\mu(a,t)\rho - \delta\chi_{[c,\infty]}(a)\rho$$

where $\chi_A(a)$ is the characteristic function of the set A, i.e. $\chi_A(a)$ equals unity if $a \in A$ and zero otherwise. Solving the problem (integrating along the characteristics) and comparing the preharvested and postharvested birth rate and age- distribution indicates the influence of the harvesting strategy on the dynamics of the population. In another case Sanchez investigates the effect of harvesting a fraction of the population in an age interval $c < a < d$. In particular, it is assumed that μ and β are independent of time so that $B(t)$ and hence $\rho(a,t)$ can be explicitly calculated. The results of [52] and a discussion of these will not be given here. Notice though that these models do have useful physical application in that they would describe, for example, a game management strategy in which a proportion of the adult female population is culled, or the onset of a disease affecting only a fraction of a particular age group.

In a subsequent paper [53], Sanchez again assumes that only a fraction δ of the population of age $a \geq c$ is harvested, but supposes that there is a harvesting season of duration T during which harvesting occurs over a

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time interval of length h. It is assumed further that harvesting is periodic and that it occurs at the end of the season so that T is the time between harvesting periods. Under this seasonal harvesting strategy the M-F partial differential equation is replaced by

$$\rho_a + \rho_t = -\mu(a)\rho - \delta\chi_{[c,\infty]}(a)H(t)\rho$$

where

$$H(t) = \begin{cases} 0 \text{ if } nT < t < (n+1)T - h \\ 1 \text{ if } (n+1)T - h < t < (n+1)T, \quad n = 0, 1, 2, ... \end{cases}$$

Although μ and β are assumed to be independent of time in [53] the harvesting policy introduces time dependence into the modified M-F model. Consequently the population problem cannot be solved explicitly. However, Sanchez introduces a technique that enables two approximate time independent models whose birth rates bracket the true birth rate to be determined. In other words two functions $B_e(t)$ and $B_u(t)$, being solutions of respective time-independent renewal equations can be found such that the birth rate $B(t)$ of the seasonally harvested system satisfies

$$B_e(t) \leq B(t) \leq B_u(t).$$

A brief outline of the method is given in Appendix 3.1. The technique is very useful - one now has a means of determining at any time t, upper and lower estimates of the birth rate $B(t)$ and hence also of $\rho(a,t)$ and of the population size $P(t)$. This has practical consequences in regard to population control - the seasonal harvesting strategy that ensures that the population remains within some predetermined range can be determined.

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Sanchez's technique applies to M-F models satisfying $\mu \equiv \mu(a)$, $\beta \equiv \beta(a)$ and harvested according to his seasonal policy. As pointed out in [53] an area worthwhile to further study would be such harvested models with μ and β incorporating density-dependent terms.

3.6 Alternative expressions for the bounday condition $\rho(o, t)$

So far we have worked with the boundary condition

$$\rho(o, t) \equiv B(t) = \int_0^\infty \beta(a, t)\rho(a, t)da, \qquad (3.6.1)$$

but in some cases it becomes necessary to distinguish between $\rho(o, t)$ and $B(t)$ such that $\rho(o, t) \not\equiv B(t)$. For example, Di Blasio et al [54], [55] study the situation in which just after birth, there is a process Q controlling the passage of the newborn B into the youngest class of age $\rho(o, t)$, so that (3.6.1) is replaced by

$$\rho(o, t) = Q(B(t))B(t), \qquad (3.6.2)$$

where $B(t)$ has the usual form,

$$B(t) = \int_0^\infty \beta(a)\rho(a, t)da. \qquad (3.6.3)$$

This type of situation occurs in fish populations where $B(t)$ corresponds to the parental egg production rate (i.e. the number of newborn), Q to the proportion of newborn that survive to become fish, and hence $\rho(o, t)$ corresponds to the number of surviving newborn. More generally, (3.6.2) would

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describe circumstances in which shortage of food or other environmental limitations jeopardize the newborn's ability to survive. For any population in which cannibalism is prevalent the members of the population are themselves responsible for regulating $\rho(o,t)$ by eliminating some of the newborn when the number grows too large. One such choice for $\rho(o,t)$ given in [56] and dealt with again in chapter 6 is

$$\rho(o,t) = B(t) - \frac{cB(t)P(t)}{1+kB(t)} = B(t)\left[1 - \frac{cP(t)}{1+kB(t)}\right] = B(t)Q(B(t)),$$
$$c,k = \text{ positive constants}$$

Here $\frac{cB(t)P(t)}{1+kB(t)}$ determines the number of eggs eaten and depends on the product of the number of eggs available $B(t)$, and the number of "adults" $P(t)$. A satiation factor $(1+kB(t))$ is included to account for the fact that in times of large egg production there is a limit as to the number of eggs an adult can consume.

Di Blasio et al work under the assumptions that μ and β are (continuous) functions of age only, that the initial age-distribution φ is piecewise continuous and that

(1) $Q \geq 0$ is continuous and bounded on $\mathbf{R}^+$ and $q(x) = xQ(x)$ is piecewise continuously differentiable on $\mathbf{R}^+$.

Defining $E(t) = \rho(o,t)$ it is not difficult to show that the solution of the modified M-F system is in this case,

$$\rho(a,t) = \begin{cases} E(t-a)\pi(a) & \text{if } a < t \\ \\ \varphi(a-t)\frac{\pi(a)}{\pi(a-t)} & \text{if } a \geq t, \end{cases} \tag{3.6.4}$$

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with $\pi(a)$ having its usual meaning. The usual renewal equation for $B(t)$ is now replaced by

$$E(t) = \left(G(t) + \int_0^t \beta(a)E(t-a)\pi(a)da\right) Q\left(G(t) + \int_0^t \beta(a)E(t-a)\pi(a)da\right),$$
(3.6.5)

where, as in (2.2.3), $G(t)$ is described by

$$G(t) = \int_t^\infty \beta(a)\varphi(a-t)\frac{\pi(a)}{\pi(a-t)}da.$$

As is customary, the authors of [54] and [55] investigate the properties of the solutions of the M-F system by studying the integral equation (3.6.5). They prove the existence of a unique, non-negative solution for all $t \geq 0$ and give additional results ensuring that $\rho(a,t) > 0$ for $t \geq T$, $T > 0$. A means of estimating T is also provided. Particular emphasis is placed on the stability of equilibria and on the analysis of the stability region.

It is easy to see that an equilibrium solution of this population problem is given by

$$\rho(a) = E\pi(a),$$

where $E \geq 0$ satisfies

$$ERQ(ER) = E,$$
(3.6.6)

and, as usual, R is defined as

$$R = \int_0^\infty \beta(a)\pi(a)da.$$

Concerning the existence of equilibrium solutions two assumptions are imposed:

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(2) There exist solutions E_1 and E_2 of (3.6.6) such that $0 \le E_1 < E_2$ and further, $Q(x) > R^{-1}$ for $x \in (RE_1, RE_2)$ and $Q(x) < R^{-1}$ for $x \notin [RE_1, RE_2]$.

This assumption does not have meaningful physical interpretation but does ensure that two equilibrium age-distributions, $\rho_1(a) = E_1\pi(a)$ and $\rho_2(a) = E_2\pi(a)$, exist. Further, if $E_1 = 0$, then ρ_2 is the unique, non-trivial equilibrium.

(3) $q(x) = xQ(x)$ is non-decreasing on $\mathbf{R}^+$ and $q(x) > 0$ for $x > 0$; an assumption which implies that the greater the number of newborn the greater the number of survivors.

Amongst a number of stability theorems given in [54], [55], two are particularly concise:

Theorem 7, [56]

Let $0 < E_1 < E_2$. Then:

(i) $\rho_1(a) = E_1\pi(a)$ is unstable.

(ii) $\rho(a, t) \to \rho_2 = E_2\pi(a)$ uniformly as $t \to \infty$, or

(iii) $\rho(a, t) \to 0$ uniformly as $t \to \infty$.

Theorem 8, [56]

Let $0 = E_1 < E_2$. Then:

(i) $\rho(a, t) \to \rho_2(a) = E_2\pi(a)$ uniformly as $t \to \infty$

(ii) the trivial solution is unstable, (in other words, the population will not become extinct).

In conclusion Di Blasio et al apply these theorems to three known fishery models. The first of these, the Beverton-Holt model, involves

$$Q(x) = \begin{cases} c_0 = \dfrac{a}{b + x_0^\alpha} & \text{if } 0 \le x < x_0, \\[2ex] \dfrac{a}{b + x^\alpha}, & \text{if } x_0 \le x, \end{cases}$$

where a, b, α are constants, $a, b > 0$, $x_0 \ge 0$ and $0 < \alpha \le 1$. Thus $Q(x)$ is constant until some critical value of x (the number of newborn) is attained and decreases thereafter - perhaps due to the adults eating the eggs to reduce the increasing population pressure effects.

It is easily seen that Q and q satisfy assumptions (1) and (3). Furthermore, if

$$c_0 = \frac{a}{b + x_0^\alpha} > \frac{1}{R}, \tag{3.6.7}$$

then (2) holds with $E_1 = 0$.

From (3.6.6)

$$RE_2 = (aR - b)^{1/\alpha}$$

$$\text{i.e. } E_2 = \frac{(aR - b)^{1/\alpha}}{R}$$

Therefore, by theorem 8 we find that all solutions of this system tend to the unique non-trivial equilibrium age- distribution $\rho_2(a) = E_2 \pi(a)$ and $P(t) \to E_2 \int_0^\infty \pi(a) da$ as $t \to \infty$.

The second fishery model, the Chapman model, constructed to reflect the "recruitment process" of certain fish populations has

$$Q(x) = \begin{cases} ab & \text{if } x = 0, \\ \dfrac{b(1 - e^{ax})}{x} & \text{if } x > 0, \end{cases}$$

where $a, b > 0$ are known constants. Once again it is easily checked that Q and q satisfy (1) and (3). Furthermore $Q'(x) < 0$ so that if $ab > R^{-1}$ then (2) is satisfied with $E_1 = 0$ and E_2 given by

$$E_2 = b(1 - e^{aE_2R}).$$

Again, theorem 8 guarantees that all solutions of the M-F model tend to $E_2\pi(a)$ as $t \to \infty$.

In these cases, the results of Di Blasio et al have the advantages of being simple to confirm and of completely determining the asymptotic behaviour of solutions.

However, in the event of theorem 7 being satisfied, one needs a means of determining whether $\rho(a, t) \to 0$ or whether $\rho(a, t) \to \rho_2(a)$ as $t \to \infty$. Such is provided by theorem 6 of [56] which describes how the initial age-distribution influences the asymptotic behaviour of $E(t)$:

Theorem 6, [54]

Let p represent the maximum attainable age, let $p_1 = \sup \{a \in [0, p] : \beta(a) > 0\}$ and let $I_0 = [o, p_1]$. Then:

(i) if $\varphi(a) \geq c\pi(a)$ on I_0 with $c > E_1$, then $E(t) > E_1$ for $t \geq 0$ and $\lim_{t \to \infty} E(t) = E_2$.

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(ii) if $\varphi(a) < c\pi(a)$ on I_0 with $c < E_1$ then $E(t) < E_1$ for $t \geq 0$ and $\lim_{t \to \infty} E(t) = 0$.

(iii) if $\varphi(a) \geq E_2\pi(a)$ on I_0 then $E(t) \geq E_2$ for $t \geq 0$ and $\lim_{t \to \infty} E(t) = E_2$.

(iv) if $\varphi(a) \leq E_2\pi(a)$ on I_0 then $E(t) \leq E_2$ for $t \geq 0$.

This theorem applies to the third fishery model, mentioned in [54], the Depensatory model, for which

$$Q(x) = \frac{ax}{b + x^2}, \qquad x \geq 0; \; a, b > 0, \qquad (3.6.8)$$

so that the proportion of newborn that survive to become fish increases with x initially but decreases after the critical value, $x = b^{1/2}$ is reached - probably due again to the members of the population compensating for the increase in size by consuming the newborn.

Here too, Q and q satisfy (1) and (3). Moreover, since $Q'(x) > 0$ for $0 \leq x < b^{1/2}$ and $Q'(x) < 0$ for $x > b^{1/2}$, if we assume that $aR > 2b^{1/2}$ we have that there exist solutions $E_1, E_2, 0 < E_1 < E_2$, of (3.6.6) which in this case has the form

$$E^2 R^2 - EaR^2 + b = 0$$

and (2) is verified, as required.

In this case theorem 6 indicates then that if the initial age- distribution $\varphi(a)$ is "smaller" than $\rho_1(a) = E_1\pi(a)$ then all solutions of the M-F system tend to zero, while if $\varphi(a)$ is "greater" than $\rho_1(a)$ then all solutions tend to

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$E_1\pi(a)$ with increasing time. Thus, as the Di Blasio et al point out, $\rho_1(a)$ acts as a minimum viable level for the population.

A natural extension of the model proposed in [54] and a topic meriting further research is the combined system,

$$\rho_a + \rho_t = -\mu(a)\rho - v(a),$$

(a constant-effort strategy, $E(a)\rho(a,t)$ or a seasonal policy could also be considered),

$$P(t) = \int_0^\infty \rho(a,t)da$$

$$\rho(o,t) = B(t)Q(B(t))$$

$$B(t) = \int_0^\infty \beta(a)\rho(a,t)da.$$

This may be appropriate to a "bird of prey" population which consumes its newborn as a means of population control and which in turn is culled according to an age-dependent strategy as a further means of population control.

Often ordinary differential equation models are used to study the effects of harvesting. These could be of the form $\dot{P} = f(P) - h$ or $\dot{P} = f(P) - hP$, for example, where P represents the total population at time t, and h or hP the effects of harvesting. (Chapter 5 deals in detail with such harvested O.D.E. models in the predator-prey context.) Evidently the advantage of using age-dependent harvested models is that a more precise study of the effects of harvesting is possible: information relating not only to $P(t)$, but also to $B(t)$ and $\rho(a,t)$ can be obtained. Moreover, the harvesting policy

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can apply to a specific age-group or to a range of ages and not necessarily to the entire population as it does in the O.D.E. case.

3.7 Two-sex models

An obvious deficiency of the M-F model is that it involves only one function ρ, the age-distribution of the female population to model the dynamics of the entire population. A more complete description would require both males and females to be accounted for. This is the approach adopted by Sowummi [57] who modifies the M-F model to become:

$$
\begin{array}{rcll}
D\rho_i(a,t) & = & -\mu_i(a, P(t))\rho_i(a,t) & (3.7.1) \\
P_i(t) & = & \int_0^\infty \rho_i(a,t)da & (3.7.2) \\
\rho_i(o,t) & = & \int_0^\infty \beta_i(a, P(t))\rho_2(a,t)da & (3.7.3) \\
\rho_i(a,o) & = & \varphi_i(a) & (3.7.4)
\end{array}
$$

where $i = 1, 2$ represent the male and female function respectively and $P(t)$, $B(t)$ are the vector-valued functions $P \equiv (P_1, P_2)$, $B \equiv (B_1, B_2)$.

The model is said to be female dominant because of the dependence of (3.7.3) on $\rho_2(a,t)$ - which simply recognizes the fact that gestation is a female characteristic. Sowummi suggests that a male dominant formulation would be meaningful in a monogamous community with a relatively low male population - for example, in the aftermath of a war.

The work of GMC provides the guiding principle of this paper (the assumptions on all the parameters are much the same as in GMC) in which existence and uniqueness of the solution of (3.7.1 - 4) are proved, upper bounds of the female and male populations are established and necessary

and sufficient conditions for equilibrium are derived. Concerning the population bounds it is found, in comparison to theorem 3 of GMC that,

$$
P_1(t) \leq \begin{cases} \Phi_1 \exp\left\{-\underline{\mu}_1 t\right\} + \Phi_2 \exp \delta_2 t \frac{(1-\exp\{-(\underline{\mu}_1+\delta_2)t\})}{(\underline{\mu}_1+\delta_2)}, & \underline{\mu}_1 + \delta_2 \neq 0 \\ \\ \Phi_1 \exp\{-\underline{\mu}_1 t\} + \Phi_2 \exp \delta_2 t, & \underline{\mu}_1 + \delta_2 = 0 \end{cases}
$$

and

$$
P_2(t) \leq \Phi_2 \exp\{\delta_2 t\}
$$

where

$$
\Phi_i = \int_0^\infty \varphi_i(a)da, \qquad \underline{\mu}_i = \inf_{\substack{a > 0 \\ P \geq o}} \mu_i(a, P),
$$

$$
\bar{\beta}_i = \sup_{\substack{a > 0 \\ P \geq o}} \beta(a, P) < \infty, \quad \delta_i = \bar{\beta}_i - \underline{\mu}_i
$$

Notice then that the upper estimate of the female population at time t depends only on female parameters whereas that of the male population depends on both - a consequence of the female dominance of the model. As Sowummi points out, these bounds have the advantage of being easy to compute and of providing rough estimates which could be vital to social planning.

A specific two-sex system relevant to human populations has been constructed by Hoppensteadt [5]: It is assumed as before that

$$
\frac{\partial \rho_i}{\partial a} + \frac{\partial \rho_i}{\partial t} = -\mu_i(a, t)\rho_i, \qquad i = 1, 2
$$

where again μ_i denotes the death rates for male and female respectively

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but that the birth rates are given by

$$\rho_i(o,t) = \int_0^\infty \int_0^\infty \beta_i(a,t)c(a,a',t)da\ da',$$

where $c(a,a',t)$ represents the number of couples where the male has age a and the female has age a'. The initial numbers of couples are assumed to be known

$$c(a,a',o) = c_0(a,a'),$$

and further it is required that

$$c(a,o,t) = c(o,a',t) = 0 \text{ for all } a, a' \text{ and } t.$$

Hoppensteadt gives the dynamical equation for c as

$$\frac{\partial c}{\partial a} + \frac{\partial c}{\partial t} + \frac{\partial c}{\partial a'} = -\left[\triangle_1(a,t) + \triangle_2(a',t)\right]c - d(a,a',t)c + S(a,a',\rho_{1e},\rho_{2e}).$$

The function $d(a,a',t)$ describes the divorce rate and S describes the source of couples. S in turn depends on the numbers of males and females eligible for coupling which are given, respectively, by

$$\rho_{1e} = \rho_1(a,t) - \int_0^\infty c(a,a',t)da',$$

$$\rho_{2e} = \rho_2(a,t) - \int_0^\infty c(a,a',t)da.$$

Thus the full model is a complicated system of nonlinear equations. It is complicated further by the fact that S, known in demographic circles as the the marriage function, is very difficult to estimate. Hoppensteadt quotes forms of S that have been proposed but argues that these are inadequate.

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In its present form then, the model is of limited use for quantitative work. However as is usual practice, Hoppensteadt introduces simplifications that enable solution. In particular, he demonstrates that a solution is possible under the assumptions that the data depend on age only and that males have a selective advantage over females. In this case $\mu_1 < \mu_2$, $\beta_1 \geq \beta_2$ and the marriage function is likely to be proportional to the number of females,

$$S = k(a, a')\rho_{1e} = k_0(a')\delta(a - a')\rho_{1e},$$

where δ is the Dirac delta function, so that the further assumption is made that an individual can mate only with someone his own age. Although restrictive, it is not unlikely that these assumptions could be appropriate to certain human populations. Since Hoppensteadt's system has been constructed to model human population development, further work along these lines would always be of demographic value.

In sections (3.1)- (3.7) we have dealt with a number of nonlinear generalizations of the M-F model and touched upon the theory developed for these. Other work in this field includes

- Langhaar's [11] study of the M-F system with an "immigration function" $I(a, t)$, incorporated into the usual M-F equation, i.e.

$$\rho_a + \rho_t = I(a, t) - \mu(a, t)\rho;$$

- Griffel's [58] work on the inclusion of a death rate of the form $\mu \equiv d(a)\rho(a, t)$, $(\beta \equiv \beta(a))$ so that, as in [42], survival is dominated by competition with one's peers,

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- Coffman and Coleman's [59] study of the nonlinear system that results when $\mu \equiv \mu(a, \rho(a, t))$ and $B(t)$ is replaced by

$$\rho(o, t) = F(\rho(a_f, t)),$$

so that the number of births occurring at time t is given by a known function F, of the number of individuals of age a_f, a specified reproductive age;

- Cushing's [60] treatment of the M-F model for which $\mu \equiv \mu(a)$ and $\beta(t)$ is replaced by

$$\rho(o, t) = \int_0^t \left\{ g(t - s) \int_0^\infty \beta(a, s) \rho(a, s) da \right\} ds,$$

where $g(s) \geq 0$, $\int_0^\infty g(s) ds = 1$, is a *gestation period probability density function* describing the probability that a newborn produced at any time will bear a (female) member of the population s unit of time later. This gives recognition to the fact that in most populations the production of a new reproducing generation is "delayed" by gestation and maturation periods;

- the study, by Auslander et al [61], of the effects of "hereditary" influences by setting $\mu \equiv \mu(a, P(t))$, $\beta \equiv \beta(a, P(t - r))$, so that fecundity is affected by the size of the population at some time in the past.

Instead of elaborating upon these, in concluding this chapter brief mention is given to a specific generalization of the M-F model applied by Marsden and McCracken [62] to an insect population studied under laboratory conditions.

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3.8 Agreement between model and experiment

In one of the best known experiments in ecology the entomologist A.J. Nicholson (his work is recorded in [63] and [64]), maintained a population of sheep blowflies on a diet of chopped liver and sugar for several years, but deliberately limited the food supply to the adult flies. A limited food supply aggravated by competition among the adults prevented the flies from obtaining enough protein and this was reflected in reduced fecundity of the population.

In modelling this situation account must be taken of the nutritional state of the adult flies since this indirectly determines the rate of egg production. Accordingly, Marsden and McCracken [62][5] define a variable ξ which measures the nutritional state (eg. mass or "health") and propose that the situation is modelled by

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \frac{\partial (g\rho)}{\partial \xi} = -\mu\rho \qquad (3.8.1)$$

where $\frac{d\xi}{dt} = g(a, t, \xi, f)$ is the growth rate of ξ which depends on the food supply $f(t)$. The birth rate is then

$$B(t, \xi) = \rho(o, t, \xi) = \int_0^\infty \int_0^\infty \beta(a, t, \xi', \xi) d\xi' da, \qquad (3.8.2)$$

---

[5]This work of Marsden and McCracken is an extension of that of Oster and Auslander [65]

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and the equation of food abundance is chosen as

$$\frac{df}{dt} = u(t) - c(a, t, \rho), \qquad (3.8.3)$$

where $u(t)$ is the rate at which food is supplied to the population and $c(\cdot)$ is the consumption rate by the adult flies.

Marsden and McCracken select μ to be a constant and suggest reasonable empirical forms for $\beta(\cdot)$ and $c(\cdot)$ to be of the type,

Fig. 3.8.1

Constitutive Relations (Reproduced from [62]).

fecundity
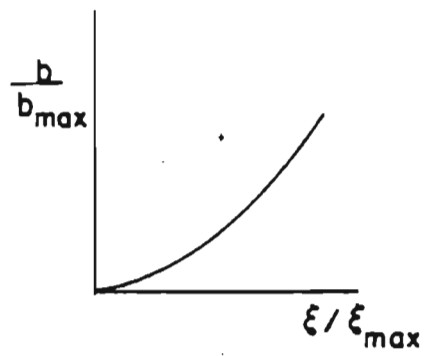
consumption

A numerical simulation of this model gave very good agreement with experiment, as figure 3.8.2, reproduced from [62], indicates :

Fig. 3.8.2

Comparison of simulated results with experimental data, [62, p344].

The details of this numerical simulation will not be given here, but are available in [62] and [65]. Of interest to Marsden and McCracken is the reason for the oscillation generated by the model. Their explanation in terms of a bifurcation mechanism is given in [62, pp 345-348].

The violent oscillations observed are biologically plausible since reduced food supply promoting reduced fecundity results in the next generation being smaller in size; but for this smaller generation the food supply is adequate and the fecundity, and hence the population size, can rebound to their maximum levels.

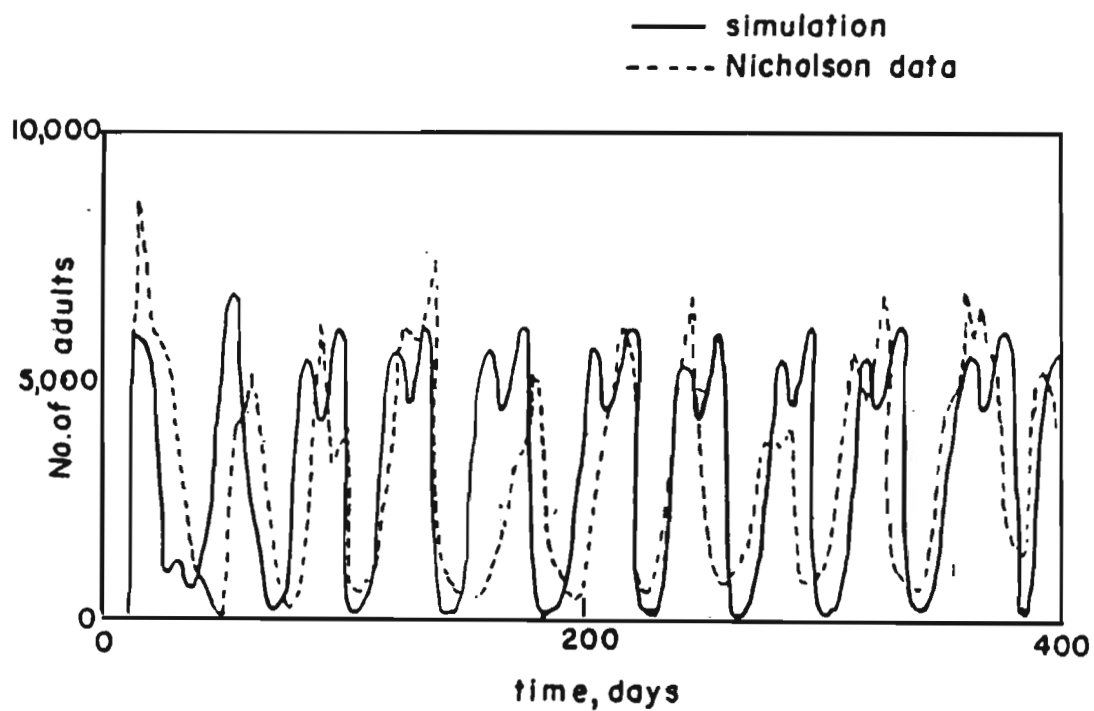Marsden and McCracken then go on to propose an M-F model for the dynamics of a particular wasp population studied by the ecologist C.B. Huffacker [61], in which regular oscillation in population numbers were observed. Again, numerical simulation of the model predicts oscillation similar to those observed experimentally. We see then that working within the M-F framework allows close agreement between the theoretical model and observed behaviour, and this strengthens our confidence in the use of the M-F system as a reliable means of modelling population development. Evidently though, the more detailed the model the more one has to rely on and develop numerical techniques for solution. The dilemma facing the ecological modeller is how much detail to incorporate in the mathematical models, for the ideal is to formulate rigorous but mathematically tractable systems.

An example of a fairly rigorous yet tractable model was provided by Frauenthal's [31] model of Easterlin's hypothesis, where the underlying assump-

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tions not only facilitated analytic solution of the system but also resulted in reasonable agreement between the model's predictions and recent U.S. population behaviour.

However, it appears that often biological realism is compromised in favour of mathematical tractability. For example, the assumption $\beta \equiv \beta(P)$ made in section 3.5 leads to an integral equation, the dynamics of which are fairly well understood, but it is unlikely that this assumption is true of many populations.

Similarly, it is difficult to imagine the assumption $\mu \equiv \mu(P)$ being appropriate to any population. However, under this assumption and the further assumption that $\beta \equiv \beta(P)a^n e^{-\alpha a}$, $\alpha > 0$, $n = 0, 1$, Gurtin and MacCamy [38] have unveiled an extremely useful "trick" which permits a full description of the population dynamics in terms of a few simple O.D.E.'s. In the next chapter this method is demonstrated and applied to a biochemical population for which these underlying assumptions are, in fact, quite realistic.

Chapter 4

The Gurtin and MacCamy Technique and its application

It was Gurtin and MacCamy [38] who discovered that the mathematical structure of the M-F system is such that the assumptions

$$\mu \equiv \mu(P)$$
$$\beta \equiv \beta(P)a^n e^{-\alpha a}, \ \beta(P) \geq 0, \ \alpha > 0, \ n = 0, 1,$$

allow the basic equations of the theory to be reduced to a system of coupled, nonlinear, ordinary differential equations. This assumption on μ obviously restricts the applicability of the resulting models. However, it would be realistic in situations where the bulk of the population does not die of old age; for example, a population of large game that is hunted or preyed upon to such an extent that death by old age is a rare event. Nevertheless, the technique has facilitated a wide variety of studies, providing much more extensive analysis than has been available for the integral formulation.

In what follows Gurtin and MacCamy's method is outlined and its appli-

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cation by Frauenthal and Swick [66], and Swart [67], [69] to age-structured biochemical population models is examined. In reviewing and relating the results of these papers particular emphasis is given to the existence of stable limit cycles.

4.1 The Gurtin and MacCamy "trick"

The basis of the technique which reduces the M-F system

$$\frac{\partial \rho}{\partial a} + \frac{\partial \rho}{\partial t} = -\mu(P(t))\rho \qquad (4.1.1)$$

$$P(t) = \int_0^\infty \rho(a,t)da \qquad (4.1.2)$$

$$\rho(o,t) \equiv B(t) = \int_0^\infty \beta(a,P(t))\rho(a,t)da \qquad (4.1.3)$$

$$\rho(a,0) = \varphi(a), \qquad (4.1.4)$$

to an equivalent problem involving ordinary different equations is the following:

Lemma [38, p. 200]

Assume that the mortality function μ is independent of age. Let ρ be a solution of (4.1.1) and let g be a (sufficiently smooth) function of age with

$$g(a)\rho(a,t) \to 0 \text{ as } a \to \infty. \qquad (4.1.5)$$

Define

$$G(t) = \int_0^\infty g(a)\rho(a,t)da, \qquad (4.1.6)$$

$$H(t) = \int_0^\infty g'(a)\rho(a,t)da. \qquad (4.1.7)$$

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Then

$$\dot{G} + \mu(P)G - g(0)B = H. \tag{4.1.8}$$

The proof follows simply from multiplying (4.1.1) by g and integrating from $a = 0$ to $a = \infty$ to obtain

$$\dot{G}(t) + \int_0^\infty g(a)\rho_a(a,t)da + \mu(P)G(t) = 0.$$

Integration of the second term by parts and use of (4.1.5) results in (4.1.8). Consider first the model involving $\beta \equiv \beta(P)e^{-\alpha a}$, i.e. $n = 0$. This assumption implies that fertility is a monotone decreasing function of age (and hence is maximum at age $a = 0$). Although this is biologically nonsensical, Gurtin and MacCamy [38] remark that it probably leads to a decent approximation in situations where the population reproduces at a fairly young age. However, its importance lies in the fact that (4.1.1 - 4) now becomes amenable to analysis being reducible to a pair of O.D.E.'s. This is achieved in [38] in the following way:

Equation (4.1.8) with $g \equiv 1$ has the form

$$\dot{P} + \mu(P)P - B = 0, \tag{4.1.9}$$

while (4.1.8) with $g(a) = e^{-\alpha a}$ yields

$$\dot{G} + \mu(P)G - B + \alpha G = 0, \tag{4.1.10}$$

where

$$G(t) = \int_0^\infty e^{-\alpha a}\rho(a,t)da = \frac{B}{\beta(P)}. \tag{4.1.11}$$

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Hence the M-F system reduces to

$$\dot{P} = -\mu(P)P + \beta(P)G \qquad (4.1.12)$$
$$\dot{G} = [-\mu(P) + \beta(P) - \alpha]\,G, \qquad (4.1.13)$$

from which $B(t), P(t)$ and hence $\rho(a,t)$ may be obtained.

The relevant initial conditions for this system are

$$P(0) = \int_0^\infty \varphi(a)da$$

$$G(0) = \int_0^\infty e^{-\alpha a}\varphi(a)da,$$

and follow from (4.1.2), (4.1.4) and (4.1.6). For convenience we will refer to system (4.1.12), (4.1.13) as system I.

The maternity function $\beta \equiv \beta(P)ae^{-\alpha a}$ (i.e. $n = 1$) provides a more realistic alternative to our previous choice. To derive the corresponding differential equation in this case, note firstly that (4.1.9) and (4.1.10) with $G(t)$ given by the first equality in (4.1.11), remain valid since they require only $\mu \equiv \mu(P)$ to be satisfied. Now Gurtin and MacCamy set

$$A(t) = \int_0^\infty ae^{-\alpha a}\rho(a,t)da, \qquad (4.1.14)$$
$$g(a) = ae^{-\alpha a},$$

and use the relation

$$\int_0^\infty g'(a)\rho(a,t)da = -\alpha A(t) + G(t),$$

so that (4.1.8) with G replaced by A gives

$$\dot{A} = -\mu(P)A - \alpha A + G.$$

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Finally, note that

$$B = \beta(P)A,$$

so that (4.1.9) and (4.1.10) lead to the system

$$
\begin{aligned}
\dot{P} &= -\mu(P)P + \beta(P)A && (4.1.15) \\
\dot{G} &= -\left[\mu(P) + \alpha\right]G + \beta(P)A && (4.1.16) \\
\dot{A} &= -\left[\mu(P) + \alpha\right]A + G. && (4.1.17)
\end{aligned}
$$

Equations (4.1.15), (4.1.16), (4.1.17) will be referred to as system II. The set of O.D.E.'s I and II now provide a means by which, theoretically at least, $B(t)$ and information concerning the behaviour of $P(t)$ may be obtained. Gurtin and MacCamy have analysed these systems quite extensively.

4.2 Analysis of systems I and II

As a further simplication Gurtin and MacCamy make the assumption

$$\beta(P) \equiv \beta_0, \qquad\qquad (4.2.1)$$

maintaining that one would generally expect a stronger dependence on P in the mortality function than in the maternity function; in other words, "population-pressure" effects are more likely to influence μ than β.

In this case, system I becomes

$$
\begin{aligned}
\dot{P} &= -\mu(P)P + B && (4.2.2) \\
\dot{B} &= \left[\gamma - \mu(P)\right]B, && (4.2.3)
\end{aligned}
$$

where

$$\gamma = \beta_0 - \alpha.$$

It is not difficult to verify, as is done in [38], that this system (4.2.2), (4.2.3) has the properties of

1. $\mathcal{L} = \{(B, P) \in \mathbf{R}_+^2 | B = \gamma P\}$ being an invariant set;

2. all equilibrium points lying on $\mathcal{L}$;

3. P obeying

$$\dot{P} = [\gamma - \mu(P)] P \text{ on } \mathcal{L}. \qquad (4.2.4)$$

An important consequence of these properties is given as a theorem in [38] and states that *the system* (4.2.2), (4.2.3) *has no closed orbits*.

For suppose that this system does have a closed orbit Ω. Then Ω must encircle at least one equilibrium point, and hence, by the above properties, must intersect $\mathcal{L}$. However, this is not possible and the above theorem follows.

In all the situations encountered so far we have not yet come across an explicit solution for $\rho(a, t)$. Gurtin and MacCamy provide such a solution in [38] by solving the system (4.2.2), (4.2.3). They first note that

$$\mu(P) = \frac{B}{P} - \frac{\dot{P}}{P} = \gamma - \frac{\dot{B}}{B},$$

follows from (4.2.2) and (4.2.3) and implies that

$$\frac{d}{dt}\left(\frac{P}{B}\right) + \gamma\left(\frac{P}{B}\right) = 1,$$

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and hence

$$\frac{P(t)}{B(t)} = \frac{P(0)}{B(0)}e^{-\gamma t} + \frac{1}{\gamma}\left(1 - e^{-\gamma t}\right). \tag{4.2.5}$$

Next, these authors confirm that

$$P(t)\exp\left\{\int_0^t \mu(P(z))dz\right\} = P(0) + B(0)\left[\frac{e^{\gamma t} - 1}{\gamma}\right], \tag{4.2.6}$$

and then demonstrate that for the linear choice

$$\mu(P) = b + cP, \ b > 0, c > 0, \tag{4.2.7}$$

(4.2.6) takes the form

$$\frac{P(t)}{P(0)} = \frac{(1-\xi)e^{-bt} + \xi e^{\tau t}}{1 + \eta - \Theta\ell - \eta(1-\xi)e^{-bt} + \ell e^{\tau t}} \tag{4.2.8}$$

where

$$\tau = \gamma - b = \beta_0 - \alpha - b$$

$$\xi = \frac{B(0)}{\gamma P(0)} \quad , \quad \eta = \frac{cP(0)}{b},$$

$$\ell = \frac{cB(0)}{\tau\gamma} \quad , \quad \Theta = \frac{\gamma}{b}.$$

Equations (4.2.5) and (4.2.8) lead to an expression for the birth rate B, and once P and B are known, substitution into the M-F solution (2.2.1), which in this case is

$$\rho(a,t) = \begin{cases} B(t-a)\exp\left\{-\int_0^a \mu(P(t-a+\alpha))\right\}d\alpha, & a < t \\ \varphi(a-t)\exp\left\{-\int_0^t \mu(P(\tau))d\tau\right\}, & a \geq t, \end{cases}$$

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yields $\rho(a, t)$.

Numerical calculations are carried out in [38] for the special case

$$\eta = \frac{1}{2}, \ \tau = b, \ \alpha = 4b, \ \xi = 1, \tag{4.2.9}$$

and

$$\varphi(a) = \begin{cases} \varphi_0, & 0 \le a \le a_0, \\ 0, & a > a_0. \end{cases}$$

(Gurtin and MacCamy point out that φ_0 and a_0 are not arbitrary; due to (4.2.9) $\frac{\varphi_0}{B(0)}$ is in fact equal to 0,70 and $\tau a_0 = 0,71$ (approximately).)

Figure 4.2.1 reproduced from [38, p 206] indicates the age- distribution $\rho(a, t)$ as a function of age for various times.

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fig. 4.2.1

Dimensionless age-distribution $\rho/B(0)$ as a function of dimensionless age τa for various values of dimensionless time τt. Here $\eta = \frac{1}{2}, \tau = b, \alpha = 4b$, and $\xi = 1$.

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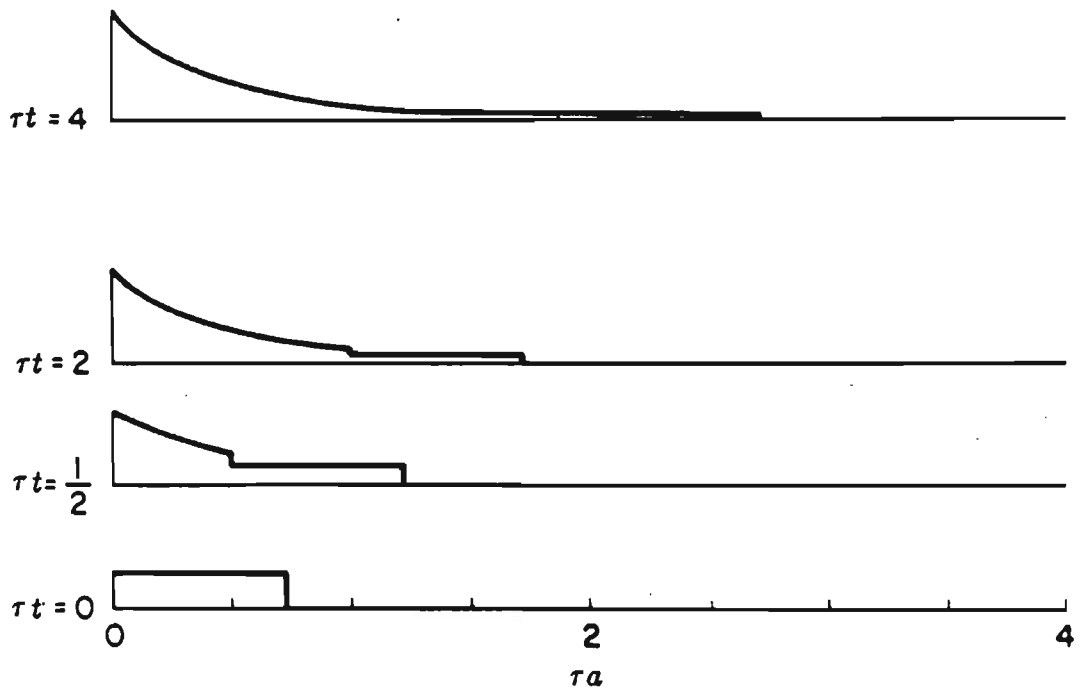
This figure provides an interesting picture of how $\varphi(a)$ progresses in time - we see that the "rectangular portion" of the curve corresponding to $\varphi(a)$ decreases in area as time increases indicating that the number of individuals in the intial population decreases as they age and ultimately tends to zero. The discontinuities observed arise due to the violation of the compatibility condition (2.3.5); instead $\varphi(0) \neq B(0)$. This inconsistency results in a discontinuity which propagates along the characteristic through $a = 0, t = 0$. Likewise, the discontinuity in φ at $a = a_0$ propagates along the characteristic through $a = a_0, t = 0$.

In addition, note from (4.2.8) that

$$P(t) \rightarrow \frac{\tau}{c} \quad \text{for} \quad \tau > 0,$$

$$P(t) \rightarrow 0 \quad \text{for} \quad \tau < 0.$$

Clearly figure 4.2.1 illustrates this approach of $\rho(a, t)$ with time to its equilibrium value

$$\rho(a) = \frac{\gamma\tau}{c} \exp\left\{-\mu(P^*)a\right\}.$$

Finally, Gurtin and MacCamy point out that this type of development of $P(t)$ with time is predictable from the observation that under the assumption (4.2.7) the differential equation (4.2.2) reduces to the classical Verhulst equation introduced in chapter 1,

$$\dot{P} + (\tau - cP)P = 0.$$

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Since (4.2.4) completely characterizes the population on the invariant set $\mathcal{L} = \{(B,P) \mid B = \gamma P\}$, the M-F system under the assumptions $\beta \equiv \beta_0 a e^{-\alpha a}$ and (4.2.7) will exhibit Verhulst behaviour whenever the initial data satisfies $B(0) = \gamma P(0)$, (i.e. $\xi = 1$), as was the case in the numerical example above.

In analyzing model II the authors of [38] express this system as

$$\dot{x} = -\mu(P)x + Mx,$$

where x is the column vector (P, G, A) and

$$M = \begin{bmatrix} 0 & 0 & \beta_0 \\ 0 & -\alpha & \beta_0 \\ 0 & 1 & -\alpha \end{bmatrix}.$$

Standard eigenvalue stability analysis of this system verifies the next theorem of [38], namely,

Under the assumptions $\beta(P) \equiv \beta_0 \geq 0$, $\mu(P) \geq \mu_0 > 0$, (where μ_0 is a constant), system II has no closed orbits. Moreover, if $\mu_0 + \alpha > \sqrt{\beta_0}$, then $P(t), G(t), A(t)$ and (hence) $B(t)$ tend to zero exponentially as $t \to \infty$.

Notice that the requirement $\mu_0 + \alpha > \sqrt{\beta_0}$ could be expressed alternatively as the requirement that the net reproduction rate $R(P)$ be less than unity since

$$R(P) \;=\; \int_0^\infty \beta(a, P) \exp\left\{ -\int_0^a \mu(\alpha, P)d\alpha \right\} da,$$

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$$= \frac{\beta_0}{[\alpha + \mu(P)]^2} \leq \frac{\beta_0}{[\alpha + \mu_0]^2} \, .$$

On the strength of this and the previous theorem, Gurtin and Mac-Camy conjecture that under reasonable assumptions concerning the functions $\mu(P)$ and $\beta(P)$ *system II has no closed orbits.* (i.e. no limit cycles).

This conjecture has been investigated by Frauenthal and Swick [66], and Swart [67], [68], who develop models, the dynamics of which counteract this claim.

4.3   A model for a biochemical population

Frauenthal and Swick [66] consider the dynamics of a continuously fed biochemical reactor in which a biological organism promotes a chemical reaction. An example of such a system would be a continuous fermentation reactor in which a yeast population converts sugar to alcohol. A reagent stream free of the biological organism flows into the tank and a product stream containing both living and dead organisms flows out. The mortality function must be defined so as to account for natural death and elimination by being carried out in the effluent stream.

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However, Frauenthal and Swick work with the M-F system for which

$$\mu \equiv \mu(P),$$

and

$$\beta \equiv \beta(P)e^{-\alpha a}, \quad \alpha > 0,$$

and maintain that the dependence of the mortality function on the population size P alone is a reasonable assumption since much of the mortality is actually due to the biological organism being washed out of the tank with the effluent stream.

They admit that the assumption on β is certainly unrealistic but, as we have seen, the M-F system can now be reduced to system I, a pair of coupled nonlinear O.D.E's.

In particular, Frauenthal and Swick assume that

$$\beta(P) = 1 + r - rP, \quad r > 0, \tag{4.3.1}$$

so that fertility decreases linearly with increasing population size, which is apparently consistent with experience for a number of species, and

$$\mu(P) = 1 + c - \alpha - (2c - q)P + (c - q)P^2, \tag{4.3.2}$$

where $0 < \alpha < 1$, $c > \alpha$, $c > q$. Hence $\mu(P)$ exhibits the typical form of being large for either small or large P - due to the respective effects of scarcity and crowding - and reaches a relative minimum between these extreme values.

From (4.1.13) of system I or from the requirement $R(P^*) = 1$, it follows that a necessary and sufficient condition for an equilibrium

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point (P^*, G^*) of system I to exist is that

$$-\mu(P) + \beta(P) - \alpha = 0,$$

which in this case gives $(P^*, G^*) = (1, 1 - \alpha)$.

We have seen that when $r = 0$ in (4.3.1), system I admits no limit cycle solutions. In investigating the possibility of limit cycles being generated for $r > 0$ and μ given by (4.3.2), Frauenthal and Swick first introduce the transformation

$$x = P - P^*,$$

$$y = G - G^*,$$

so that system I in this case becomes

$$\dot{x} = [q - (1 - \alpha)(1 + r)] x + y - rxy + (2q - c)x^2 - (c - q)x^3$$

$$(4.3.3)$$

$$\dot{y} = -(1 - \alpha)(r - q)x - (r - q)xy - (1 - \alpha)(c - q)x^2 - (c - q)x^2 y.$$

$$(4.3.4)$$

Routine calculation confirms that the characteristic equation corresponding to the linear portion of these equations is

$$\lambda^2 - [q - (1 - \alpha)(1 + r)]\lambda + (1 - \alpha)(r - q) = 0,$$

with roots

$$\lambda = \frac{1}{2}[q - (1 - \alpha)(1 + r)] \pm \frac{1}{2}\left\{\left([q - (1 - \alpha)(1 + r)]^2 - 4(1 - \alpha)(r - q)\right)\right\}^{1/2}.$$

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Denoting $(1 - \alpha)(1 + r)$ by q^*, it follows that if $r > (1 - \alpha)/\alpha$ then $\mathrm{Re}\,\lambda < 0$ for $q < q^*$, $\mathrm{Re}\lambda > 0$ for $q > q^*$, and at $q = q^*$, $\lambda = \pm i\left[(1 - \alpha)(r - q)\right]^{1/2} = \pm i\lambda_0$. Hence, reference to the necessary and sufficient conditions for Hopf bifurcation given in Appendix 4.1 indicates that the equilibrium (P^*, G^*) bifurcates at $q = q^*$ into a periodic solution with period near $\frac{2\pi}{|\lambda_0|}$.

Also outlined in Appendix 4.1 is an algorithm, which we refer to as Marsden and McCracken's algorithm, for determining whether the resulting periodic solution is asymptotically stable.

In applying this algorithm, the first step is to select co-ordinates such that with respect to these new co-ordinates the matrix of the linear part of system (4.3.3), (4.3.4) is

$$\begin{bmatrix} 0 & \lambda_0 \\ -\lambda_0 & 0 \end{bmatrix}.$$

Frauenthal and Swick achieve this by means of the transformation

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 1 & -1 \\ \lambda_0 & \lambda_0 \end{pmatrix} \begin{pmatrix} X \\ Y \end{pmatrix}.$$

The system (4.3.3), (4.3.4) then becomes (at $q = q^*$):

$$\begin{aligned}
\dot{X} = &\ \lambda_0 Y + 0,5\left[3q^* - c - (\lambda_0 + 1)r - (1 - \alpha)(c - q^*)/\lambda_0\right]X^2 \\
&+ 0,5\left[q^* - c + (1 + \lambda_0)r - (1 - \alpha)(c - q^*)/\lambda_0\right]Y^2 \\
&+ \left[c - 2q^* + (1 - \alpha)(c - q^*)/\lambda_0\right]XY \\
&- (c - q^*)X^3 + 2(c - q^*)X^2Y - (c - q^*)XY^2,
\end{aligned}$$

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$$\dot{Y} = -\lambda_0 X + 0,5\left[c - q^* + (\lambda_0 - 1)r - (1 - \alpha)(c - q^*)/\lambda_0\right]X^2$$
$$+ \quad 0,5\left[c - 3q^* + (1 - \lambda_0)r - (1 - \alpha)(c - q^*)/\lambda_0\right]Y^2$$
$$+ \quad \left[2q^* - c + (1 - \alpha)(c - q^*)/\lambda_0\right]XY$$
$$- \quad (c - q^*)X^2Y + 2(c - q^*)XY^2 - (c - q^*)Y^3.$$

The next step is to evaluate the Lyapunov function $\dddot{V}(o)$. It can be verified that in this case

$$\dddot{V}(o) = -3\pi\left[(c - q^*)(3r + q^* - 2c) + r(r - q^*)(c - 2q^*)\right] / \lambda_0(r - q^*),$$

so that $\dddot{V}(o) < 0$, in other words, the periodic solutions are stable, if and only if

$$D - (D^2 - E)^{1/2} < 4c < D + (D^2 - E)^{1/2},$$

where

$$D = 3(r + q^*) + r(r - q^*),$$
$$E = 8q^*\left[2r(r - q^*) + 3r + q^*\right].$$

To illustrate the qualitative nature of the limit cycles predicted by the theory, the authors of [66] simulate solutions for various parameter choices. The choice $r = 10, c = 10,5, \alpha = 0.9, \; q = 1,2(> q^* = 1,1)$ results in a stable limit cycle developing around the equilibrium point $(P^*, G^*) = (1; 0, 1)$.

Fig. 4.3.1

Solution winding out to the limit cycle in phase space for $r = 10; c = 10, 5; \alpha = 0, 9; q = 1, 2$. The cycle occurs about the equilibrium point $(P^*, G^*) = (1; 0, 1)$. (Reproduced from [66, p 504]).
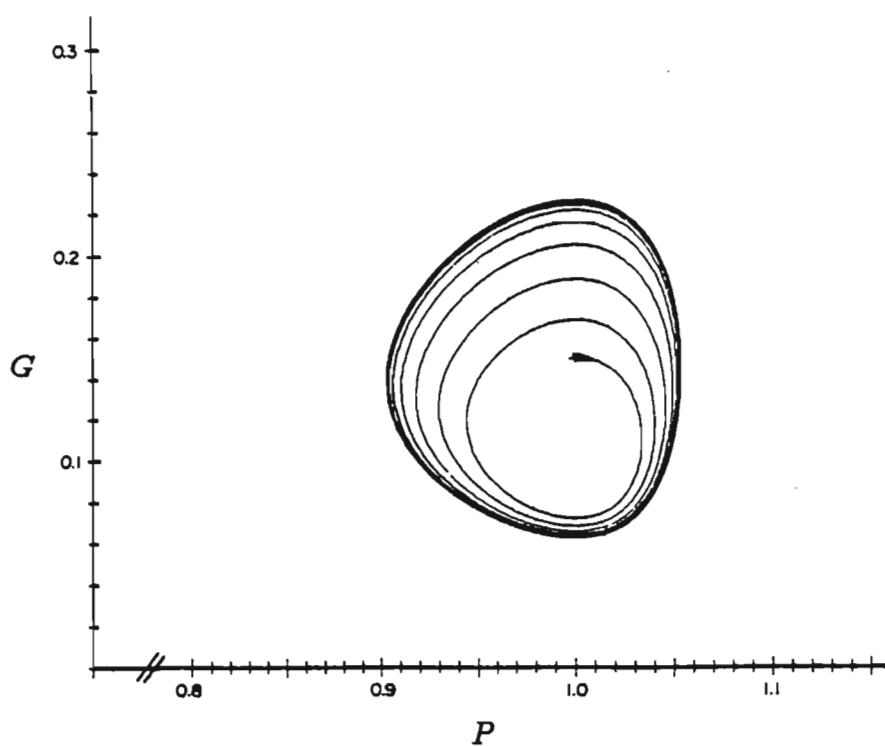
Fig. 4.3.2

The time trajectory of the limit cycles for $r = 10; c = 10, 5; \alpha = 0, 9; q = 1, 2$. The period of oscillation is about 7 time units. (Reproduced from [66 ,p 505].)
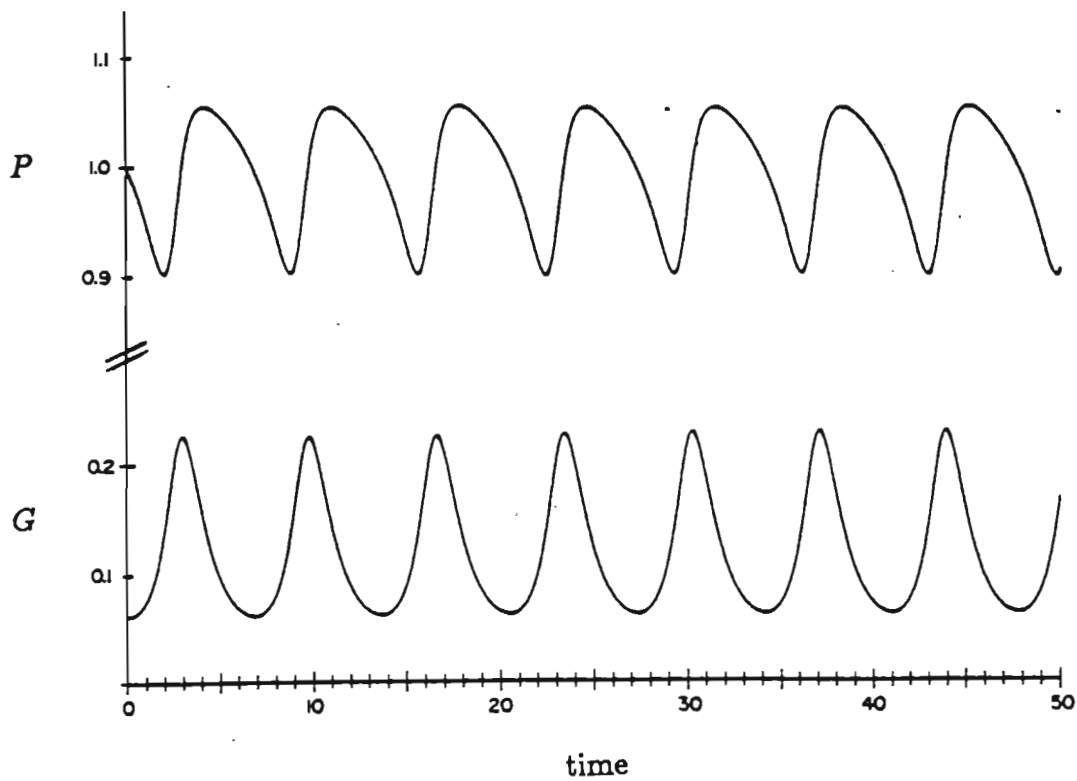
Frauenthal and Swick mention in conclusion, that although limit cycles of diverse sizes and natural periods were found as the parameters varied, the regions of parameter space which lead to stable limit cycle behaviour were rather small and that an arbitrary set of parameters (r, c, q, α) would more likely lead either to a stable point or to extinction. Nevertheless, their analysis has disproved Gurtin and MacCamy's conjecture.

4.4 A biochemical population model involving the general forms $\mu \equiv \mu(P)$, $\beta \equiv \beta(P)e^{-\alpha a}$.

Frauenthal and Swick's choice of mortality and fertility functions appears to be rather restrictive: $\mu(P)$ is very specialized and the linear decrease of β with P might not always be a realistic assumption. For this reason Swart [67] considers the general choice

$$\mu \equiv \mu(P),$$
$$\beta \equiv \beta(P)e^{-\alpha a}, \ \alpha > 0,$$

in the M-F model, and extends the results of [66] to a wider class of functions which are more likely to provide an accurate description of the "biochemical reaction tank" model.

In particular μ and β are prescribed as arbitrary positive class C^3 functions of P, containing the parameters $\sigma_1, ..., \sigma_n$, one of which is

the "preferred" bifurcation parameter and is denoted by σ.

As in [67] Swart introduces the transformation

$$
\begin{aligned}
x &= P - P^* \\
y &= G - G^*,
\end{aligned}
$$

into system I and obtains

$$
\dot{x} = -\mu(\sigma, x + P^*)(x + P^*) + \beta(\sigma, x + P^*)(y + G^*) \tag{4.4.1}
$$

$$
\dot{y} = \left[-\mu(\sigma, x + P^*) + \beta(\sigma, x + P^*) - \alpha \right](y + G^*). \tag{4.4.2}
$$

The linearized form of (4.4.1), (4.4.2) is then given by

$$
\begin{aligned}
\dot{x} &= A_1 x + A_2 y \tag{4.4.3} \\
\dot{y} &= A_3 x, \tag{4.4.4}
\end{aligned}
$$

where

$$
A_1 = -\mu(\sigma, P^*) - \dot{\mu}(\sigma, P^*)P^* + \dot{\beta}(\sigma, P^*)\frac{\mu(\sigma, P^*)}{\beta(\sigma, P^*)}P^*
$$

$$
A_2 = \beta(\sigma, P^*)
$$

$$
A_3 = -\left[\dot{\mu}(\sigma, P^*) - \dot{\beta}(\sigma, P^*)\right]\frac{\mu(\sigma, P^*)}{\beta(\sigma, P^*)}P^*.
$$

($\dot{\mu}$ and $\dot{\beta}$ denote differentiation with respect to P.) In addition, the roots of the characteristic equation of system (4.4.1), (4.4.2) are given by

$$
\lambda = \frac{1}{2}A_1 \pm \frac{1}{2}\left[A_1^2 + 4A_2 A_3\right]^{1/2},
$$

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so that if for certain values σ_0 of σ we have $A_1 = 0$, then

$$\lambda_0 = \pm i \left[-A_2 A_3\right]^{1/2}.$$

Since $A_2 > 0$, it follows that if $A_3 < 0$ then λ_0 is purely imaginary at $\sigma = \sigma_0$.

Evidently, a necessary condition for A_1 to be zero for some value σ_0 is that

$$\dot{\mu}(\sigma_0, P^*)\beta(\sigma_0, P^*) - \dot{\beta}(\sigma_0, P^*)\mu(\sigma_0, P^*) < 0, \qquad (4.4.5)$$

and a necessary and sufficient condition for A_3 to be negative is

$$\dot{\mu}(\sigma_0, P^*) - \dot{\beta}(\sigma_0, P^*) > 0. \qquad (4.4.6)$$

If, in addition to (4.4.5) and (4.4.6) being satisfied, we have that $A_1 < 0$ for $\sigma < \sigma_0$ and $\frac{\partial A_1}{\partial \sigma} > 0$ at $\sigma = \sigma_0$, then the Hopf criteria (Appendix 4.1) for bifurcation into periodic orbits are met.

Swart notes that under the usual biological assumption that

$$\dot{\beta}(\sigma, P) \leq 0,$$

the further condition

$$\dot{\mu}(\sigma_0, P^*) < 0,$$

follows immediately from (4.4.5). *Hence a strictly increasing mortality function cannot lead to bifurcation.* It follows from (4.4.6) then, that $\dot{\beta}(\sigma_0, P^*)$ may not be zero; in other words, in the case where $\beta(\sigma, P) \equiv$

β_0, $\beta_0 = $ constant, no closed orbits are possible, as was established earlier.

In applying the Marsden and McCracken algorithm, Swart first introduces the transformation

$$x = (A_2)^{1/2}X$$
$$y = (-A_3)^{1/2}Y,$$

into systems (4.4.1), (4.4.2). Having effected this transformation $\overset{..}{V}(o)$ is then determined. In particular, Swart demonstrates ([67, pp 5,6]) that a necessary and sufficient condition ensuring the existence of asymptotically stable periodic solutions is that

$$\left[-\mu^{-3}\beta(\dot{\mu} - \dot{\beta})\left\{(\beta/\mu)^{..}\right\}^{-1}\right]^{.} < 0,$$

when evaluated at P^*, σ_0.([]$^{.}$ denotes differentiation of the entire expression with respect to P and $\frac{\beta}{\mu}$$^{..}$ likewise, the second derivative of (β/μ) with respect to P.)

These results are then applied to the model

$$\beta(P) = ae^{-kP} + d$$

$$\mu(P) = be^{kP} - c + ge^{-kP}, \qquad k > 0, a, b, c, g, d \geq 0, \ g \geq c^2/4b,$$

which Swart describes as being restrictive but considerably more realistic than Frauenthal and Swicks choice (4.3.1), (4.3.2). Thereafter, conditions on the parameters of the model are derived under which bifurcation into stable limit cycles is indeed possible. Thus once again Gurtin and MacCamy's previous conjecture is proved wrong.

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4.5 A more realistic form for the maternity function and the Hopf bifurcation results for the model

As an improvement on the assumption $\beta \equiv \beta(P)e^{-\alpha a}$ of the previous models, Swart [68], examines the M-F system for which

$$\mu \equiv \mu(\sigma, P) \qquad (4.5.1)$$
$$\beta \equiv \beta(\sigma, P)f(a)e^{-\alpha a}, \alpha > 0, \qquad (4.5.2)$$

where μ is assumed to be a positive class C^1 function; β a positive class C^1 function with a non-positive derivative with respect to P (denoted by $\dot\beta$); σ a parameter (or set of parameters); and $f(a)$ represents a polynomial of degree n.

In order to reduce the M-F system involving (4.5.1), (4.5.2) to a set of O.D.E.'s, Swart constructs the weighting functions

$$K^i = \int_0^\infty \rho(a,t)f^i(a)e^{-\alpha a}da,$$

where $f^i(a)$ denotes the i-th derivative of $f(a)$ for $0 \le i \le n$. Applying the same technique of the lemma of section 4.1 where now $g(a) = f^i(a)$, $i = 0, ..., n$ we obtain the set of $n+2$ coupled O.D.E.'s:

$$\dot{P} = -\mu(\sigma, P)P + \beta(\sigma, P)K^0$$
$$\dot{K^i} = \beta(\sigma, P)f^i(o)K^0 - [\alpha + \mu(\sigma, P)]K^i + K^{i+1}, \ 0 \le i \le n-1$$
$$\dot{K^n} = \beta(\sigma, P)f^n(o)K^0 - [\alpha + \mu(\sigma, P)]K^n. \qquad (4.5.3)$$

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Notice that in this case $B(t) = \beta(\sigma, P)K^0$.

Swart specializes to the biologically realistic situation where $f(0) = 0$ and assumes, without loss of generality that $f^n(0) = 1$, so that K^n is simply the Laplace transform of ρ with respect to a. Furthermore, it is shown that a necessary and sufficient condition for the above system to have an equilibrium point (P^*, K^{*i}), $P^* > 0, i = 0, ..., n$, is that

$$\beta(\sigma, P^*)\left[\, f^n(o) + f^{n-1}(o)\,(\mu(\sigma, P^*) + \alpha) + ...\right.$$
$$\left. f^1(o)(\mu(\sigma, P^* + \alpha)^{n-1}\,\right] - (\mu(\sigma, P^*) + \alpha)^{n+1} = 0 \qquad (4.5.4).$$

Once again introducing the variables $x = P - P^*$, $y_i = K^i - K^{*i}$ in systems (4.5.3) leads to a set of O.D.E.'s which when linearized about the origin, has associated with it a lengthy characteristic equation of degree $n + 2$. Again the emphasis of [68] is on determining conditions under which Hopf bifurcation will take place for suitable values of σ. In particular, Swart produces an algorithm which ensures that the $n + 2$ roots of the characteristic equation consist of n real negative roots and one complex conjugate pair

$$\lambda_1 \pm i\lambda_2, \ \lambda_1 \leq 0, \ \lambda_2 > 0,$$

which becomes purely imaginary for some value σ_0 of σ. Roots of this nature obviously satisfy the root criteria of Appendix 4.1. In reviewing the content of [68] this algorithm will not be reproduced. Instead we will examine the cases $n = 1, n = 2$ which are simple enough to deal with without the aid of the algorithm.

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The case $n = 1$ corresponds to the maternity function

$$\beta \equiv \beta(\sigma, P)ae^{-\alpha a}, \ \alpha > 0,$$

a form often used to model fertility behaviour.

From the requirement $R(P^*) = 1$ or the "equilibrium point equation" (4.5.4), it follows that a necessary and sufficient condition for an equilibrium point to exist is

$$\beta(\sigma, P^*) - [\mu(\sigma, P^*) + \alpha]^2 = 0.$$

Further, the characteristic equation of the linearized system can be shown to be

$$\lambda^3 \ + \ \{2 \wedge + \mu AP^*\}\lambda^2 + \{2\mu \wedge + 2 \wedge AP^* + \mu\dot{\mu}P^*\}\lambda$$
$$+ \ \mu P^* \left\{2 \wedge \dot{\mu} - \dot{\beta}\right\} = 0, \tag{4.5.5}$$

where $\wedge = \mu + \alpha$, $A = \dot{\mu} - \mu\beta^{-1}\dot{\beta}$.

It is readily verified that the polynomial $\lambda^2 + a\lambda + b = 0$ will have roots of the type specified earlier if and only if $a = 0, b > 0$ for $\sigma = \sigma_0$; while $\lambda^3 + a\lambda^2 + b\lambda + c = 0$ will have such roots only if $a, b, c > 0$ and $ab - c = 0$ for $\sigma = \sigma_0$.

Hence, for the case $n = 1$ we require

$$2 \wedge \dot{\mu} - \dot{\beta} > 0 \qquad \text{at } \sigma_0, \tag{4.5.6}$$

and that

$$[2 \wedge + \mu + AP^*] \ [2\mu \wedge + 2 \wedge AP^* + \mu\dot{\mu}P^*] - \mu P^* \left[2 \wedge \dot{\mu} - \dot{\beta}\right] = 0,$$
$$\tag{4.5.7}$$

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for some value σ_0, in order that equation (4.5.5) has suitable roots.

(Of course, a cubic polynomial having complex roots can have only one complex conjugate pair so that the root criteria given here and the general requirement of Appendix 4.1 are equivalent in this case.) Equation (4.5.7) can be rewritten as

$$A \left[2 \wedge A + \mu \dot{\mu} \right] P^{*2} + \left[\dot{\mu}(3\mu + 2\alpha)^2 - \mu \dot{\beta}(7\mu + 3\alpha) \wedge \beta^{-1} \right] P^*$$

$$+2(2 \wedge +\mu) \wedge \mu = 0, \tag{4.5.8}$$

and since $\dot{\beta} \leq 0$ it becomes immediately obvious that if $\dot{\mu}(\sigma, P) \geq 0$ for all σ, then all coefficients of powers of P^* are positive, and therefore, for no value of σ can this equation be satisfied. Thus, if such a σ_0 exists it follows that

$$\dot{\mu}(\sigma_0, P^*) < 0.$$

In addition, it is not difficult to verify that if $\mu \geq 2\alpha$, then (4.5.8) cannot be satisfied for any σ. Hence, a necessary condition for the solution of (4.5.8) to exist and thus Hopf bifurcation to be possible is that

$$\mu(\sigma_0, P^*) < 2\alpha.$$

Returning to the "well-mixed reaction vessel" problem, Swart applies this analysis to the particular choice

$$\mu \equiv (c - \alpha)e^{-\sigma}e^P - c + (3\alpha - c)e^{\sigma}e^{-P},$$

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so that the mortality rate is large for either small or large P and reaches a minimum at an intermediate value of P, and

$$\beta \equiv (3\alpha - c)^2 e^{2\sigma} e^{-2P} a e^{-\alpha a},$$

where all parameters involved are positive constants. The restriction $\frac{6\alpha}{5} < c < 2\alpha$ guarantees that μ remains positive. Such a choice of μ and β is obviously very synthetic but Swart points out that it is biologically not completely impossible and provides a more realistic alternative to Frauenthal and Swick's model (4.3.1), (4.3.2).

Working through the previous analysis, one can verify that the characteristic roots are of the required form when σ has the value

$$\sigma_0 = (8\alpha - 3c)(3\alpha - c)(13\alpha^2 - 10\alpha c + 2c^2)^{-1},$$

and further that $\frac{\partial \lambda_1}{\partial \sigma}(\sigma_0)$ is indeed negative so that Hopf bifurcation does occur at σ_0. Whether this bifurcation can lead to stable limit cycles is a different matter, although, as mentioned in [68], computer simulation seems to indicate that stable limit cycles do arise provided c is close enough to 2α in value.

The case $n = 2$, and hence

$$f(a) = ra + sa^2, \quad r, s, > 0$$

provides a useful form of $\beta(a, P)$ since there are now more parameters with which to model the fertility behaviour and greater accuracy is possible. Adapting the previous analysis to this case Swart

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demonstrates that as for the choice $n = 1$, necessary conditions for Hopf bifurcation are that the function $\mu(\sigma, P)$ has a (locally) negative derivative, and that it "dips down" to below the value 2α.

Not only do the works of Frauenthal and Swick [66], and Swart [67], [68] conclusively disprove Gurtin and MacCamy's [38] original conjecture but they provide useful Hopf bifurcation criteria for the systems involved.

While our emphasis throughout this chapter has been on the existence of stable limit cycles, Gurtin and MacCamy's technique has facilitated a great deal of other analyses, some of which were mentioned in Chapter 3. In addition to these, Swart [12] makes use of this technique in considering controllability in age-dependent population dynamics. With the M-F system providing the underlying equations, it is assumed in [12] that μ is described by (4.5.1) which we have seen to be a reasonable assumption for the biochemical reaction tank model or for preyed- upon animal populations for which death by old-age is unlikely. Further, the fertility function is assumed to have the form (4.5.2). Applying Gurtin and MacCamy's technique Swart reduces the M-F system to the O.D.E. system (4.5.3) and then linearizes this system about the equilibrium point (P^*, K^{*i}) by setting $x = P - P^*$, $y_i = K^i - K^{*i}$, $u = \sigma - \sigma_0$. The linearized system is expressed in the state-space notation

$$\begin{pmatrix} \dot{x} \\ \dot{y}_i \end{pmatrix} = F \begin{pmatrix} x \\ y_i \end{pmatrix} + Gu,$$

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where details of F and G are given in [12, p. 239].

Swart shows that the matrix $B = [G, FG, F^2G, ..., F^{n+1}G]$ does not have maximal rank. In fact, B has rank 1. In other words, we have no guarantee that by suitably controlling the mortality function (by means of a particular culling strategy), an arbitrary initial state can be steered to a desired equilibrium state in finite time. However, Swart does demonstrate that it is possible to find a control which will bring the *total population* to a specified value in finite time. The details involved are too lengthy to repeat here but mention is made of this in conclusion to point out a further area of study that has been facilitated by Gurtin and MacCamy's clever technique.

Chapter 5

Age-independent predator-prey models

Although the emphasis in this treatment of population dynamics is on age-dependent models, specifically the M-F model, a mathematical study of populations would not be complete without attention being given to age-independent models. The work done in this field is vast and in this chapter the focus is primarily upon two species predator-prey models; particularly those described by the Lotka-Volterra or the more general Kolmogorov system of ordinary differential equations.

Furthermore, it is useful to study such predator-prey models here since these and their theory provide some groundwork for, as well as a contrast to, the predator-prey models examined in the next and final chapter, in which the dynamics of the one species is described by an age-independent Kolmogorov differential equation, and the dynamics of the other by an age- dependent M-F equation.

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In what follows the theory concerning harvested and unharvested Kolmogorov systems is first established, whereafter attention is given to specific predator-prey systems and to two other "multi-species" systems that have arisen out of attempts to model real-world situations.

5.1   The Lotka-Volterra model

In chapter 1 a brief review was given of the early deterministic O.D.E. models of single species population growth - in these, age distribution was not accounted for and the only variable was the population size $P(t)$. The logistic equation formed the canonical model.

The first step towards greater realism was to take into account the dependence of the species on its food supply, and this led to a study of predator-prey systems that has continued since the pioneering work of Lotka [69] and Volterra [70], [71][1]. The nonlinear model that they independently proposed extended the basic logistic equation to the system of quadratic differential equations:

$$
\begin{aligned}
\frac{dP_1}{dt} &= P_1(a - cP_2) \\
\frac{dP_2}{dt} &= P_2(-b + dP_1), \quad a, b, c, d > 0,
\end{aligned}
\tag{5.1.1}
$$

where $P_1(t)$, $P_2(t)$ are respectively the population sizes of the prey and predator; a and b are respectively the net birth rate of prey and

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[1] This paper by Scudo gives an interesting overview of the life of Vito Volterra and provides a concise, nontechnical description of his major contributions to mathematical ecology. Also supplied is a chronological list of Volterra's works, presented between 1901 and 1936.

net death rate of the predator *(per capita rates)*, in the absence of each other; and c and d relate to the interaction between the species: Clearly the prey growth rate is diminished proportionally to the number of interactions between prey and predator, while the predator population increases at a rate proportional to the interaction between it and its food supply.

It was Lotka who first proposed this model in 1925. In 1927, Volterra, being unaware of Lotka's work, presented the model again in [70]. Hence, system (5.1.1) is known as the Lotka-Volterra model. Neither Lotka nor Volterra restricted their work to predator-prey systems - depending on the signs of the constants, (5.1.1) can represent a species competing with another for the same resource or other types of two-species interactions.

May in his well-quoted text [72][2] presents a more generalized model of the dynamics of a community of m interacting species having population sizes $P_1, P_2, ..., P_m$ respectively. The model consists of the set of m O.D.E.'s

$$\frac{dP_i}{dt} = F_i(P_1(t), ..., P_m(t)), \qquad i = 1, ..., m, \qquad (5.1.2)$$

each F_i being a nonlinear function of the relevant interacting populations, describing the growth of the i-th species at time t. System (5.1.2) could apply to species in competition or co- operation, but here attention will mainly be upon predator-prey situations.

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[2] This text is referred to often and will henceforth be indicated as 'May'.

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Applying the usual standard stability analysis and denoting by $p_i(t)$ a small perturbation of $P_i(t)$ from the corresponding equilibrium value P_i^*, (obtained by solving the system $0 = F_i(P_1^*, ..., P_m^*)$) one arrives, by Taylor expansion, at the linearized approximation

$$\frac{dp_i(t)}{dt} = \sum_{j=1}^{m} a_{ij}\, p_i(t), \quad a_{ij} = \left(\frac{\partial F_i}{dP_j}\right)_{P_j = P_j^*}$$

i.e. $\quad \frac{d\bar{p}}{dt} = Ap(t),$

where $\bar{p}$ is the $m \times 1$ column matrix of the $p_i's$ and A is called the community matrix. Each of the elements a_{ij} of A describe the effect of species j upon species i near equilibrium and the sign of the eigenvalues of A determine the neighbourhood stability character of the system.

It is straightforward to verify that the eigenvalues of the community matrix of the Lotka-Volterra system (5.1.1) evaluated at the non-zero equilibrium point $\left(\frac{b}{d}, \frac{a}{c}\right)$ are purely imaginary,

$$\lambda = \pm i\sqrt{ab},$$

so that the system is said to be neutrally stable : the systems trajectories in the vicinity of the non-zero equilibrium point oscillate endlessly about the equilibrium point with a fixed amplitude that depends entirely on the initial conditions and with period approximately equal to $\frac{2\pi}{\sqrt{ab}}$. If perturbed from this equilibrium, the system will oscillate periodically with some new, fixed amplitude.

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This result provides the basis of an important ecological argument invoked by Elton [73] in 1958, and discussed in detail in May. Very briefly, Elton's hypothesis states that in nature, the stability of a system of interacting species is typically greater for structurally complex systems than for simple ones, (where roughly speaking, one system is said to be more complex than another if there are more species involved and/or greater interactions among species). According to May this hypothesis has, on occasion, been awarded the status of a mathematical theorem, part of the foundation of the claim being the fact that the Lotka-Volterra systems, unlike the single species logistic model, does not possess an asymptotically stable (non-zero) equilibrium.

However, May counteracted this claim mathematically by investigating n predator - n prey systems and found them to be in general less stable and never more stable than the simple two species model:

The analogue of the Lotka-Volterra model for an n- predator - n prey system is

$$\frac{dP_{1i}(t)}{dt} = F_i(t) \left[a_i - \sum_{j=1}^{n} c_{ij} P_{2j}(t) \right]$$

$$\frac{dP_{2i}(t)}{dt} = G_i(t) \left[-b_i + \sum_{j=1}^{n} d_{ij} P_{1j}(t) \right], i, j = 1, 2, ..., n, \ a_i, b_i, c_{ij}, d_{ij} > 0.$$

Restricting the above coefficients to be such that all populations at equilibrium have finite positive values, May demonstrates that the $2n$

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eigenvalues occur in n pairs, each pair having the form

$$\lambda = \varsigma + i\xi, \ -\varsigma - i\xi,$$

so that for every eigenvalue having a negative real part, there is a companion having a positive real part.

Consequently, either all eigenvalues have zero real parts, in which case the system is neutrally stable or, at least one eigenvalue has a positive real part indicating instability of the system. Hence, the more complex n predator - n prey system has at best the same stability properties as the predator- prey model, and in general is unstable rather than stable. Thus increasing stability of the system is not an automatic mathematical consequence of increasing multispecies complexity.

May points out that "while stability may usually go with complexity in the natural world (as evidence assembled by Elton seems to indicate) but not usually in general mathematical models is not really paradoxical. In nature we deal not with arbitrary complex systems but rather with ones selected by a long and intricate process ... Theoretical work should not try to prove any general theorem that 'complexity implies stability' but ... should focus on elucidating the very special sorts of complexity ... which may promote such mathematically atypical stability."[3] Such an exercise is beyond the scope of the material covered here.

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[3][72, pp 3,4]

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Returning to the Lotka-Volterra system, a simple but interesting exercise is to determine the effect of continuously removing constant proportions, h_1 and h_2 of the respective species from the system. This could occur due to a pesticide removing both predator and prey, or as a result of predation by a third species. The model now takes the form

$$\frac{dP_1}{dt} = P_1(a - h_1 - cP_2)$$

$$(5.1.3)$$

$$\frac{dP_2}{dt} = P_2(-b - h_2 + dP_1),$$

having the neutrally stable equilibrium point

$$\left(\frac{b + h_2}{d}, \frac{a - h_1}{c} \right),$$

provided that $a > h_1$. Hence, indiscriminate harvesting of this type increases the number of prey and decreases the number of predators. Scudo [71] explains that Volterra's research in the field of mathematical ecology was stimulated by a zoologist's observation that, during and after the first World War when fishing was severely limited, the proportion of predators among the total catch increased substantially. Volterra's harvested model model (5.1.3) explains this phenomenon.

Clearly, if the prey species is a "desired" species, harvesting is beneficial, while if the prey species is undesirable harvesting could be dangerous. As documented in [74], such a situation occurred in America,

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in 1868, when a population of scale insects was destroying the citrus industry. A beetle species was imported to prey upon the insect and kept the latter at bay until indiscriminate "harvesting" by the insecticide D.D.T. was initiated, removing both predator and prey. As predicted by (5.1.3) the prey (scale insect) population exploded and disaster ensued.

5.2 More realistic 1 predator - 1 prey systems

All parameters involved in the Lotka-Volterra model are constants, and while this model may be appropriate to a number of specific interacting populations, it is likely that in many cases the birth rates, death rates and interaction coefficients involved include density dependent effects. Here we review and comment on May's suggestions for enhancing the realism of the model.

(I) Accounting for the possibility of self-limiting effects, the per capita birth rate of the prey population becomes a function of its population density. A likely choice is to replace a by the logistic form

$$a \to r(1 - \frac{P_1}{k}), \qquad\qquad r = \text{constant},$$

where k is a carrying capacity set by the resource limitations. Thus, the population can increase up to a size k, after which

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crowding and food limitations etc., prevent further expansion. Other means of achieving a similar effect are,

$$a \rightarrow r \ell n \frac{k}{P_1},$$

$$a \rightarrow r \left(\frac{k}{P_1} - 1 \right),$$

$$a \rightarrow r \left(\left(\frac{k}{P_1} \right)^g - 1 \right), \qquad 1 \geq g > 0.$$

(II) In (5.1.1) the '$-cP_1P_2$' term describes the rate at which predators remove prey and is called the functional response. It indicates an unlimited attack capacity per predator which increases linearly with prey density. A more sensible and realistic functional response might be,

(i)

$$cP_1P_2 \rightarrow KP_2(1 - \exp\{-\ell P_1\}), \ \ell, K = \text{ constants}, \quad \ell > 0,$$

so that the net predator rate is proportional to P_1 for small prey populations but saturates to a constant, K, per predator for large values of P_1. A further alternative is

(ii)

$$cP_1P_2 \rightarrow \frac{KP_1P_2}{P_1 + D}, \ K, D = \text{ constants}, D > 0,$$

where D refers to some given value of prey population beyond which the predators capacity to capture gradually satiates.

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(III) As for the prey birth rate, the predator per capita death rate is also likely to be exacerbated by relatively high predator densities. We suggest that in many cases a possible replacement for b might be the quadratic function,

$$b \to w - uP_2 + vP_2^2; \qquad w, u, v = \text{non-negative constants,}$$

so that the per capita death rate exhibits the likely behaviour of being large for either small or large P_2 and reaches a minimum between these extremes.

(IV) In the Lotka-Volterra model, the per capita birth rate of the predator is proportional to prey abundance, (indicated by the term 'dP_1P_2'). As in (II) May suggests that dP_1P_2 could be more suitably replaced by expressions of the type (i) and (ii) indicating that excessive prey abundance does not imply unlimited proportional predator increase since there must be a limit to the extent that predators can benefit from an excessive amount of prey. Another possibility is $dP_1P_2 \to qP_2\sqrt{P_1}$, again implying a "less fast than linear" response of P_2 to P_1.

Finally, a substitute to (5.1.1) proposed in May is,

$$\frac{dP_2}{dt} = sP_2 \left[1 - \frac{P_2}{\gamma P_1}\right], \quad s, \gamma > 0,$$

so that the growth of the predator is of logistic form, with the conventional carrying capacity (P_c of (1.3)) being proportional to prey abundance.

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Assembling the above functions in various combinations suitable to the situation under consideration gives 1 predator - 1 prey models incorporating greater realism than the Lotka- Volterra system. Two specific examples are:

$$\frac{dP_1}{dt} = rP_1\left[1 - \frac{P_1}{k}\right] - \frac{KP_1P_2}{P_1 + D}$$

$$\frac{dP_2}{dt} = sP_2\left[1 - \frac{P_2}{\gamma P_1}\right] \tag{5.2.1}$$

and

$$\frac{dP_1}{dt} = rP_1\left[1 - \frac{P_1}{k}\right] - KP_2[1 - \exp(-\ell P_1)]$$

$$\frac{dP_2}{dt} = P_2[-b + \beta[1 - \exp(-mP_1)]]. \tag{5.2.2}$$

In the latter case the prey, in the absence of the predator, grows logistically while the predator, in the absence of prey, dies out exponentially.

5.3   The Kolmogorov Theorem

Most of the above and many other 1 predator - 1 prey systems modelled by O.D.E.'s can be written in the general form,

$$\frac{dP_1}{dt} = P_1F(P_1, P_2),$$

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$$\frac{dP_2}{dt} = P_2 G(P_1, P_2),$$

known as Kolmogorov's model. $F(P_1, P_2)$ and $G(P_1, P_2)$ describe the respective per capita growth rates of the two populations.

A.N. Kolmogorov [75], was responsible for deriving conditons which necessarily guaranteed that the above system possesses either a globally stable equilibrium point or a globally stable limit cycle.

Essentially Kolmogorov's theorem states that systems of the form (5.3.1) possess either a stable equilibrium point or a stable limit cycle provided that F and G are continuous functions of P_1 and P_2, with continuous first derivatives throughout the domain $P_1 > 0, P_2 > 0$[4] and that

(i) $\frac{\partial F}{\partial P_2} < 0$

(ii) $P_1 \left(\frac{\partial F}{\partial P_1} \right) + P_2 \left(\frac{\partial F}{\partial P_2} \right) < 0$

(iii) $\frac{\partial G}{\partial P_2} < 0$

(iv) $P_1 \left(\frac{\partial G}{\partial P_1} \right) + P_2 \left(\frac{\partial G}{\partial P_2} \right) > 0$

(v) $F(0, 0) > 0$.

In addition, there must exist quantities R, S, T, such that,

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[4]May [72] allowed for $P_1 \geq 0, P_2 \geq 0$, but clearly when $P_1 = 0, P_2 \geq 0$, (iii) and (iv) lead to a contradiction. We shall adopt Komogorov's [75] approach and require $P_1 > 0, P_2 > 0$.

(vi) $F(0, R) = 0,$ $R > 0$

(vii) $F(S,0) = 0,$ $S > 0$

(viii) $G(T,0) = 0,$ $T > 0$

(ix) $S > T.$

Conditions (i) - (ix) have interesting physical interpretation:

(i) the multiplication of the prey is slowed by the number of predators and, similarly,

(iii) the growth of the predators decreases with their population size, in other words the predator population is self- limited.

(ii) For any given ratio of the two species, the rate of increase of the prey is a decreasing function of population size while conversely,

(iv) that of the predators is an increasing function.

(v) If both populations are very small the prey multiply, but,

(vi) if there are too many predators (greater than R predators), the prey population cannot increase.

(vii) If there are too many prey they cannot multiply even in the absence of predators, in other words, S is the carrying capacity for the prey; and,

(viii) if there are T or less prey, the predators have insufficient sustenance to multiply.

(ix) Finally, if $S < T$ or $S = T$ the predators will disappear and the populations will reach a point of equilibrium at $P_1 = S$ and $P_2 = 0$. To prevent this "collapse" of the system it is required that $S > T$.

We refer to Minorsky [76] for a formal statement of the theorem and to Rescigno and Richardson [77], for a clear summary and extension of the results of Kolmogorov's paper. As the conditions (i) and (ix) imply, Kolmogorov interpreted (5.3.1) as describing the dynamics of predator-prey interactions. Rescigno and Richardson extend the interpretation of (5.3.1) to the cases of competitors and co-operators by altering the conditions on F and G. The proof of the theorem is given in [75] and is a direct consequence of the Poincaré-Bendixson theorem.

Often, the Kolmogorov theorem provides an easy alternative to the laborious Marsden and McCracken (M-M) algorithm introduced in chapter 4 and outlined in Appendix 4.1. This is illustrated by applying the two methods to a specific model investigated by Swart and Duffy [78], [79]:

Among the many predator-prey systems that have been studied is the elephant-tree ecology. Of interest here, as for other models of interacting species, is the stability properties of the system; in particular, the possible existence of stable limit cycles. Knowledge of such cycles provides bounds on future population sizes and thus could help

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in planning culling strategies. However, we see in section 5.4 that it is not always safe to plan harvesting policies from knowledge of the behaviour of nonharvested systems alone.

Swart and Duffy use the Caughley [80] model to describe the predator-prey dynamics for the elephant-tree system and show by means of the M-M algorithm that Hopf bifurcation into stable limit cycles may well occur. Necessary and sufficient conditions for such an occurrence are derived. In what follows, content of [78] is outlined.

Caughley's elephant-tree model has the form,

$$\frac{dP_1}{dt} = P_1\left[a - bP_1 - cP_2(P_1 + g)^{-1}\right]$$

$$\frac{dP_2}{dt} = P_2\left[-A + kP_1(P_2 + B)^{-1}\right], \quad a,b,c,g,A,k,B : \text{positive constants,}$$

where P_1 is the density of the trees (prey); P_2, the density of the elephants (predator); a, the initial rate of increase of the trees; b, the degree to which addition of a further unit of tree density depresses the rate of increase of the trees; c, the rate of elimination of trees per unit density of elephants; g, a threshold density of trees, (by threshold density is meant the minimum number of trees necessary for the survival of the trees - evidently if the trees are too sparse effective pollination and hence propagation of the population is not possible); A is the rate of decrease of the elephants in the absence of trees; k is the rate at which elephant decrease is ameliorated at a given ratio of trees to elephants; and B represents the threshold

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density of elephants.

The nontrivial equilibrium points of this system are

$$P_2^* = P_1^* k A^{-1} - B \qquad (5.3.3)$$

$$P_1^* = (2b)^{-1} \left\{ a - bg - ckA^{-1} + \left[(a - bg - ckA^{-1})^2 + 4b(ag + Bc) \right]^{1/2} \right\}$$

$$(5.3.4)$$

with the condition $P_1^* > ABk^{-1}$ ensuring that P_2^* is positive.

Linearizing the system about the equilibrium point (P_1^*, P_2^*) yields a community matrix having eigenvalues

$$\lambda = \frac{1}{2} \left[a - 2bP_1^* - cP_2^* g(P_1^* + g)^{-2} - AP_2^*(P_2^* + B)^{-1} \right] \pm \frac{1}{2} [D]^{1/2}$$

$$(5.3.5)$$

where

$$D = \left[a - 2bP_1^* - cP_2^* g(P_1^* + g)^{-2} - AP_2^*(P_2^* + B)^{-1} \right]^2$$

$$-4(P_2^* + B)^{-1} \left[ckP_1^* P_2^*(P_1^* + g)^{-1} - AP_2^*(a - 2bP_1^* - cP_2^* g(P_1^* + g)^{-2}) \right].$$

For Hopf bifurcation to occur (see Appendix 4.1) it is necessary that this expression may be written as $\lambda = \lambda_1 \pm i\lambda_2$, where $\lambda_1 \leq 0$ and $\lambda_2 > 0$, and that for some value of a preferred parameter, $\lambda_1 = 0$.

Thus, the authors consider the bifurcation condition

$$\lambda_1 = \frac{1}{2} \left[a - 2bP_1^* - cP_2^* g(P_1^* + g)^{-2} - AP_2^*(P_2^* + B)^{-1} \right] = 0, \quad (5.3.6)$$

and verify that under this assumption the corresponding value D_0 of D is indeed negative.

From (5.3.4) it follows that

$$A = ckP_1^* \left[(a - bP_1^*)(P_1^* + g) + Bc \right]^{-1}, \qquad (5.3.7)$$

which enables (5.3.6) to be rewritten as

$$(a - bg - 2bP_1^*) \left[(a - bP_1^*)(P_1^* + g) + Bc \right]^2 - ck(a - bP_1^*)(P_1^* + g)^2 = 0.$$
$$(5.3.8)$$

The choice of a bifurcation parameter is fairly arbitrary and Swart and Duffy select 'A' as such.

From (5.3.7) it follows that the condition $P_1^* > ABk^{-1}$ implies that $P_1^* < \frac{a}{b}$; so that throughout the analysis, the requirement $\frac{a}{b} > ABk^{-1}$ is essential.

Analysis of the roots of (5.3.8) indicates that this equation will have a single root $P_1^* < \frac{a}{b}$ if and only if

$$(a - bg)(ag + Bc)^2 - ckag^2 > 0. \qquad (5.3.9)$$

If (5.3.9) is satisfied (5.3.8) will have a root P_1^*, which, when substituted into (5.3.7) gives the "bifurcation value" A_0 of A.

Recall from chapter 4, that the M-M algorithm requires $\frac{\partial \lambda_1}{\partial A} > 0$ at A_0, for bifurcation to occur at A_0.

Making use of the fact that

$$\frac{\partial P_1^*}{\partial A} = ckA^{-2}P_1^* \left[(a - bg - ckA^{-1})^2 + 4b(ag + Bc) \right]^{-1/2},$$

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it is not difficult to show that $\frac{\partial \lambda_1}{\partial A} < 0$ at A_0, so that by choosing a new parameter $\mu = -A$ instead of A, it obviously follows that $\frac{\partial \lambda_1}{\partial \mu} > 0$ at $\mu = -A_0$ and that the necessary conditions for Hopf bifurcation are therefore satisfied for $A < A_0$.

Now, to determine whether these cycles are stable, Swart and Duffy apply the M-M algorithm, introducing the transformation

$$\begin{pmatrix} X \\ Y \end{pmatrix} = \begin{pmatrix} Ak^{-1} & \alpha \\ 1 & 0 \end{pmatrix} \begin{pmatrix} \bar{X} \\ \bar{Y} \end{pmatrix},$$

where $\alpha = (P_2^* + B)(2kP_2^*)^{-1}[-Do]^{1/2}$.

The linearized system of (5.3.2) then takes the form

$$\dot{\bar{X}} = F_1(\bar{X}, \bar{Y})$$

$$\dot{\bar{Y}} = F_2(\bar{X}, \bar{Y}),$$

of which in turn, the linearized form is

$$\dot{\bar{X}} = |\lambda_2|\bar{Y}$$

$$\dot{\bar{Y}} = -|\lambda_2|\bar{X},$$

where $\lambda_2 = \frac{1}{2}[-D_0]^{1/2}$, the form required for the application of the M-M algorithm.

Evaluating $\dddot{V}(o)$ as given in Appendix 4.1, Swart and Duffy obtain

$$\dot{V}(o) = 3\pi(4|\lambda_2|)^{-1}P_1^{*6}c^2k^3(P_1^* + g)\left[(a - bP_1^*)(P_1^* + g) + Bc\right]^{-1} \bullet$$

$$(a - bP_1^*)^{-2}(a - bg - 2bP_1^*)^{-1} \bullet V^*, \quad (5.3.10)$$

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where

$$V^* = BcP \{ L[2P_1^{*2}L^2 - 5P_1^{*2}LP + (2P_1^{*2} - gP_1^* - g^2)P^2]$$

$$- P_1^*(P_1^* + g)P^3 \} + L(P_1^* + g)^2 ck \{ -2gL^2 + (P_1^* + g)LP + P^2g \}$$

$$+ L^2P(P_1^* + g) \{ 2P_1^{*2}L^2 - 5P_1^{*2}LP + (2P_1^{*2} - gP_1^* - g^2)P^2 \},$$

and

$$P = a - bg - 2bP_1^*,$$

$$L = a - bP_1^*.$$

It is cleverly shown in [78], that for B large enough, V^* and hence $\ddot{V}(o)$ is negative, so that for all values of $A < A_0$ and B sufficiently large, the system (5.3.2) will exhibit stable limit cycles of period close to $2\pi|\lambda_2|^{-1}$.

We will instead apply the Kolmogorov theorem to the above elephant-trees system. In this case,

$$F = a - bP_1 - \frac{cP_2}{P_1 + g},$$

$$G = -A + \frac{kP_1}{P_2 + B},$$

and it is straightforward to verify that since all parameters involved are positive, conditions (i) - (v) are satisfied; while conditions (vi) - (ix) imply that $R = \frac{ag}{c}$, $S = \frac{a}{b}$, $T = \frac{AB}{k}$ and $\frac{a}{b} > \frac{AB}{k}$ respectively. The latter condition was encountered in Swart and Duffy's previous analysis.

Hence, according to Kolmogorov, providing $\frac{a}{b} > \frac{AB}{k}$, the system (5.3.2) possesses either a stable equilibrium point or a stable limit cycle.

As is well-known, the necessary and sufficient conditions for the system to possess local stability is that both eigenvalues (5.3.5) have negative real part. This requires that $u > 0$ and $v > 0$, where

$$u = AP_2^*(P_2^* + B)^{-1} - \left[a - 2bP_1^* - cP_2^*g(P_1^* + g)^{-2}\right],$$

$$v = cP_1^*(P_1^* + g)^{-1}kP_2^* - \left[a - 2bP_1^* - cP_2^*g(P_1^* + g)^{-2}\right]AP_2^*.$$

On the other hand, if either $u \leq 0$ or $v \leq 0$, Kolmogorov's theorem indicates that stable limit cycle behaviour ensues. Although the above is a neighbourhood stability analysis Kolmogorov's theorem ensures that, in this case, local and global stability are identical. Thus, the complete global stability character of the system is laid bare by simple and conventional neighbourhood analysis.

The above conditions on u and v are easy to test for any given set of parameters and it appears then, that the Kolmogorov theorem provides

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Fig. 5.4.1

Changes in the Hudson Bay Lynx and Hare populations during the period 1845 - 1935. (Reproduced from [72, p. 92].)

time in years

a far less laborious method for determining conditons under which stable limit cycles are possible, than does the M-M algorithm. Here we dealt with a specific system but May remarks that a great deal of the models that have been proposed for 1 predator - 1 prey systems satisfy the conditions of the theorem and hence possess either a stable point equilibrium or a stable limit cycle. He adds that these stable limit cycles provide satisfying explanations for those predator-prey communities in which populations are observed to oscillate in a rather reproducible manner. A well-documented case is that of the Hudson Bay Lynx-hare predator-prey systems referred to in [72]; see figure 5.3.1. For many years the explanation given associated this "cycling" phenomenom with the artificial, neutrally stable Lotka-Volterra oscillations. May maintains instead, the these observed oscillations are "surely the outcome of some stable limit cycle."[5]

A natural consequence of the Kolmogorov theorem being satisfied should be that $\ddot{V}(o)$ of the M-M algorithm is always negative - recall, that the calculation of $\dddot{V}(o)$ requires $\lambda = \pm i\lambda_2$, i.e. $u = 0$, so that, according to the previous discussion stable limit cycle behaviour must ensure.

This claim was investigated for the previous elephant- tree system: The conditions which the parameters are required to satisfy are,

$$\frac{a}{b} > ABk^{-1} \qquad (5.3.11)$$

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[5][72,p 92]

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and

$$a - bg - 2bP_1^* > 0, \qquad a - bP_1^* > 0, \qquad (5.3.12)$$

the latter two following from (5.3.7) and (5.3.8).

Realistically, the threshold density of trees g, must satisfy $g \geq 1$, which in turn, implies that $a > b$ since from (5.3.11)

$$0 < bP_1^* < \frac{a - bg}{2} < \frac{a - b}{2} < a - b. \qquad (5.3.13)$$

Yet, all attempts to show that $\dddot{V}(o)$ is negative under these restrictions were not successful. Moreover, if one attempts to prove that $\ddot{V}(o) < 0$ for the general system (5.3.1) satisfying the Kolmogorov conditions (i) - (ix) (see Appendix 5.1) one obtains an expression for $\ddot{V}(o)$ containing second and third derivatives of F and G about which the Kolmogorov theorem yields no information. Hence a result which appears to be evident is difficult to verify theoretically.

However, it was established (see Appendix 5.2) that under the additional conditions

$$P_1^* > g, \ a - bg - 6bP_1^* > 0, \qquad (5.3.14)$$

$\ddot{V}(o)$ is indeed negative.

Although this requirement appears to be rather contrived it was hoped that it would apply for biologically realistic parameter choices; so that the result $\ddot{V}(o) < 0$ would be confirmed in this case.

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In [79] Swart and Duffy give ranges of parameter values deduced from data gathered from several areas in Africa: c, the number of trees/km^2 destroyed per elephant/km^2 per year is considered to be of the order $\gamma 10$ with the maximum rate of destruction given by $c = 273$; while the growth rate a is of the order $\alpha 10^{-2}$ with the lowest rate given as $a = 0,02$. Apparently, k is the most difficult parameter to estimate and the value of $k = 2 \times 10^{-7}$ obtained as an average for two areas in Africa is known to vary considerably. The lowest threshold density for elephants that could be obtained was $B = 0,01$ elephant/km^2 and a realistic choice for the threshold density of trees is $g = 100$. In [79] attention was restricted to the situation where trees were given the 'best possible' chance of survival, namely the case where $b = 0$. However taking $b \neq 0$ it is most likely that b is 'close to zero' in value; according to typical data it was chosen to be of the order $\delta 10^{-5}$ or less.

Selecting parameter choices within these ranges and such that the restrictions imposed were satisfied, it was found that (5.3.14) held for many but not every combination of parameter values selected so that (5.3.14) is not a consequence of the parameters involved being biologically plausible.

The difficulty encountered in trying to show $\dddot{V}(o) < 0$ is puzzling. Nevertheless, we do conjecture that for the above elephant-tree system subject to the conditions of Kolmogorov's Theorem $\dddot{V}(o)$ is always negative. Proof of this would be a commendable exercise. Far more

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valuable though, would be proof that for a general system (5.3.1) satisfying (i)-(ix), the Lyapunov function $\overset{\cdots}{V}(o)$, defined in the M-M algorithm is negative.

As mentioned earlier, in [79] Swart and Duffy deal with the elephant-trees model under the restriction $b = 0$, so that the trees are assumed to be too sparse to significantly depress the growth rate of trees. In this case, the conditions of the Kolmogorov theorem fail to hold and to investigate the possibility of stable limit cycles, one has no choice but to apply the M-M algorithm. In doing so it is found in [79] that, in general, limit cycles will not occur; but that there does exist a narrow range of values which would lead to the existence of limit cycles in the populations. However, the period of such cycles would be so large that in practice one may discount entirely the possibility of stable limit cycles.

5.4   May's modification of the Kolmogorov Theorem

May, in [72] and [81], modified the Kolmogorov theorem stating without proof, that in many cases, the results remain valid when any of the inequalities (i), (ii), (iii), (iv) of the theorem are replaced by equalities. For example, he claims that the system (5.2.1) can be seen to have either a stable equilibrium point or a stable limit cycle even

though in this case,

$$P_1 \left(\frac{\partial G}{\partial P_1} \right) \; + \; P_2 \left(\frac{\partial G}{\partial P_2} \right) \; = 0,$$

and condition (viii) is violated. The reasons given by May are simply that "this can be seen if one uses the methods of Kolmogorov's theorem"[6] and further that the above equations can be "seen to be sensible limiting cases of more general predator-prey equations which do satisfy the criteria (of the theorem)."[7] May does not substantiate these reasons and his modification of the theorem has been challenged by Albrecht et al [82], who attempt to show it to be incorrect by means of a counter-example. They construct a model which satisfies May's relaxed 'Kolmogorov conditions' and which admits a continuum of neutrally periodic solutions - hence has neither a stable equilibrium point nor a stable limit cycle.

In reply to their findings May remarks (in a footnote concluding [82]), that firstly, the model chosen by Albrecht et al is contrived and does not have physical application and secondly, that while in addition to stable equilibrium points and stable limit cycles there may be classes of neutrally stable periodic solutions, these are unlikely to be of biological significance. He reiterates that whether inequalities are relaxed or not "the fact remains that essentially all the explicit 1 predator-1 prey models that have actually been propounded in the biological

[6] [81, p 902]
[7] [72, p. 88]

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literature exhibit either stable equilibrium points or stable limit cycle behaviour as the biological parameters are varied."[8] We know this to be true if the conditions of Kolmogorov's theorem are satisfied, but the work by Albrecht et al and the insufficient evidence that May gives for his claim suggest that, until it has been established by formal proof, the belief that the theorem remains valid even though inequalities are weakened, cannot be accepted.

Furthermore, Albrecht et al also suggest in [82], that under Kolmogorov's hypotheses there may be several possible configurations besides that of stable point or stable limit cycle. Thus, it appeared at first that the statement of the theorem given earlier, (which is that given in May before the inequalities are relaxed) is inaccurate. However, in consulting the discussion of Kolmogorov's theorem given in [77] it is apparent that all possible configurations do fall within the purview of 'stable point or stable limit cycle', so that our statement of the theorem is authentic.

Further work concerning the global stability properties of predator-prey systems has been produced by Liou and Cheng [83]. These authors adopt a less general approach than that of Kolmogorov and consider predator-prey systems described by the model

$$\frac{dP_1}{dt} = P_1 g(P_1) - P_2 h(P_1),$$

(5.3.15)

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[8] [82, p. 1074]

$$\frac{dP_2}{dt} = P_2(Kh(P_1) - b), \quad K, \text{ constant.}$$

This is just the Lotka-Volterra system (5.1.1) with the constant prey birth rate a; and the functional response term '$-cP_1P_2$,' as well as the predator birth rate term 'dP_1P_2' replaced by more realistic functions $g(P_1)$ and $h(P_1)$ respectively. Possible forms of $g(P_1)$ and $h(P_1)$ were discussed in section 5.2. Recall, that we discussed replacing a by

$$a \to r\left(1 - \frac{P_1}{k}\right) = g(P_1),$$

and $-cP_1P_2$ by

$$cP_1P_2 \to \frac{KP_1P_2}{P_1 + D} = KP_2h(P_1),$$

which was also an appropriate replacement for dP_1P_2. Liou and Cheng give four criteria (a), (b), (c) and (d) which together guarantee that the equilibrium point (P_1^*, P_2^*) is globally asymptotically stable in the domain $P_1 > 0, P_2 > 0$. ((a), (b) and (c) involve the properties of $g(P_1)$, $h(P_1)$ and $f(P_1) = \frac{P_1g(P_1)}{h(P_1)}$ and their derivatives, and are not difficult to verify; (d) is a rather complicated condition concerning the inverse function $\bar{f}$ of f over the interval $P_1^* < P_1 < k$, where (P_1^*, P_2^*) is a locally stable equilibrium such that $P_2^* = \frac{P_1^*g(P_1^*)}{h(P_1^*)}$, k is the prey carrying capacity, i.e. $g(k) = 0$, and $\bar{f} : [O, P_2^*] \to [P_1^*, k]$, since $f : [P_1^*, k] \to [O, P_2^*]$. Further details are given in [83, p. 65-67].)

Liou and Cheng list forms of $g(P_1)$ and $h(P_1)$ that arise in biological contexts, most of which were mentioned in section 5.2. They mention

that computer simulations indicate condition (d) of their paper to be satisfied for almost all combinations of these choices of g and h. Included in their list is those forms of g and h involved in system (5.2.2). Now, as for system (5.2.1) May claimed in [72, p 88] that (5.2.2) can be seen to possess either a stable point or a stable limit even though $\frac{\partial G}{\partial P_2} = 0$ and even though (5.2.2) is not strictly of the Kolmogorov form (5.3.1).

Assuming (d) to hold for system (5.2.2) it is not difficult to obtain, by means of the remaining criteria (a), (b), (c) of [83], ranges of parameter values for which Liou and Cheng's result holds and hence for which (5.2.2) has a globally stable equilibrium point. If one could show that, for parameter values outside of these ranges stable limit cycle behaviour ensues, May's claim would be established for this system. Even the assurance that (a), (b), (c) and (d) do apply to (5.2.2) would give credibility to May's statement.

The modification of the Kolmogorov theorem appears to be an unresolved area in mathematical ecology, and rigorous proof or disproof of the validity of the theorem under May's weakened conditions would settle this contention.

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5.5 The Incorporation of Enrichment and Harvesting into the Kolmogorov Model

In many practical situations one or both of the two species may be harvested and removed from the system. This could occur if, for example, one (or both) of the species is being used as a food supply for a third species.

Brauer, Soudack and Jarosch have studied this situation extensively and in this section the results of their papers [84], [85], [87], [88], are reviewed. Where details are omitted, these references provide proofs, refinements and explicit examples.

Brauer [84] first dealt with the non-harvested Kolmogorov model

$$
\begin{aligned}
\frac{dP_1}{dt} &= P_1 F(P_1, P_2, k) \\
\frac{dP_2}{dt} &= P_2 G(P_1, P_2),
\end{aligned}
\tag{5.5.1}
$$

where again P_1 and P_2 denote the prey and predator population sizes respectively and k, the limiting size to which the prey population can grow in the absence of predators (i.e. $F(k, o, k) = 0$), is explicitly indicated in the per capita growth rate function F, of the prey.

This paper does not yield much new information on 1 predator-1 prey systems but does introduce the concept of enrichment, investigating its effect on the stability of the system. Enrichment can take a number of forms, but is generally described by increasing the specie's

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food supply. For the prey species in this case, enrichment is described mathematically by an increase in the carrying capacity k. One would expect that enrichment of the prey's environment also leads to an increase in the predator population, so that in cases where the predator species is used as a food supply for a third species, enrichment of the prey environment may be a desirable goal for resource management. However, it may be that such enrichment tends to cause instability in the system and under study in [84] is the possibility of destroying the asymptotic stability of the system by increasing k.

Among a number of assumptions made in [84] are the following:

(A) F and its first-order partial derivatives are continuous for $P_1 > 0$, $P_2 > 0, k > 0$ and

$$\frac{\partial F}{\partial k}(P_1, P_2, k) > 0 \qquad \frac{\partial F}{\partial P_2}(P_1, P_2, k) < 0.$$

(B) G and its first-order partial derivatives are continuous for $P_1 > 0$, $P_2 > 0$ and

$$\frac{\partial G}{\partial P_1} > 0, \qquad \frac{\partial G}{\partial P_2} < 0.$$

(Actually, Brauer assumed $\frac{\partial G}{\partial P_2} \leq 0$, but in the light of the previous discussion on Kolmogorov's theorem and the weakening of inequalities, we shall restrict $\frac{\partial G}{\partial P_2}$ to be strictly negative. This means that there is intra-specific competition within the predator population i.e. its growth rate is restricted by the size of its

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population.) .

(C) F and G satisfy

$$\left(\frac{\partial F}{\partial P_1}\right)\left(\frac{\partial G}{\partial P_2}\right) - \left(\frac{\partial F}{\partial P_2}\right)\left(\frac{\partial G}{\partial P_1}\right) > 0 \quad \text{for } P_1 > 0, P_2 > 0, k > 0.$$

It will be seen that if the above expression is negative everywhere then no equilibrium point of (5.5.1) can be stable, so that (C) ensures the existence of stable equilibria.

Further, it is assumed that the equilibrium point $(P_1^*(k), P_2^*(k))$ is unique, that $F(k, 0, k) = 0$ for $k > 0$ and that the remaining conditions (ii), (iv), (v), (vi), (viii) and (ix) of Kolmogorov's theorem hold.

The main results of [86] can be stated as follows:

Theorem 1

Let (A), (B) and (C) hold. Then the prey and predator equilibrium populations, $P_1^*(k), P_2^*(k)$ are increasing functions of k.

Hence, as expected, enrichment of the prey's environment produces an increase in both the predator and prey equilibrium populations.

Theorem 2

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Let (A), (B) and (C) hold. Then an equilibrium point $(P_1^*(k), P_2^*(k))$ of (5.5.1) is asymptotically stable if

$$P_1^* \frac{\partial F}{\partial P_1}(P_1^*, P_2^*, k) + P_2^* \frac{\partial G}{\partial P_2}(P_1^*, P_2^*) < 0,$$

and unstable if

$$P_1^* \frac{\partial F}{\partial P_1}(P_1^*, P_2^*, k) + P_2^* \frac{\partial G}{\partial P_2}(P_1^*, P_2^*) > 0.$$

(Here and throughout $P_1^* \equiv P_1^*(k)$.)

This is easily seen from examining the eigenvalues of the community matrix of (5.5.1), namely

$$\lambda = \frac{1}{2}\left\{ \triangle_1 \pm \left[\triangle_1^2 - 4\triangle_2\right]^{1/2}\right\},$$

where

$$\triangle_1 = P_1^* \frac{\partial F}{\partial P_1}(P_1^*, P_2^*, k) + P_2^* \frac{\partial G}{\partial P_2}(P_1^*, P_2^*),$$

and

$$\triangle_2 = P_1^* P_2^* \left[\frac{\partial F}{\partial P_1}(P_1^*, P_2^*, k)\frac{\partial G}{\partial P_2}(P_1^*, P_2^*) - \frac{\partial F}{\partial P_2}(P_1^*, P_2^*, k)\frac{\partial G}{\partial P_1}(P_1^*, P_2^*)\right].$$

A direct consequence of Kolmogorov's theorem is then

Theorem 3

Let (A), (B) and (C) and the remaining conditions of the Kolmo-gorov theorem hold. Then (5.5.1) possesses either a stable

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equilibrium point or a stable limit cycle in the quadrant $P_1 > 0, P_2 > 0$.

Combining theorem 2 and theorem 3 we see that if k is increased to the value at which the equilibrium becomes unstable an oscillation must be set up. In particular, if

$$P_1 \frac{\partial F}{\partial P_1} \; + \; P_2 \frac{\partial G}{\partial P_2} > 0 \text{ at } (P_1^*(k), P_2^*(k), k), \qquad (5.5.2)$$

stable limit cycle behaviour ensures, while if

$$P_1 \frac{\partial F}{\partial P_1} \; + \; P_2 \frac{\partial G}{\partial P_2} < 0 \text{ at } (P_1^*(k), P_2^*(k), k),$$

the equilibrium is a stable point.

The above theorems express results that have been encountered previously. What is new and practically useful is a criterion for testing whether the system remains stable for all k or ultimately becomes unstable:

According to the above analysis an equilibrium point eventually becomes unstable as k is increased if

$$\lim_{k \to \infty} \left\{ P_1^*(k) \frac{\partial F}{\partial P_1} \left(P_1^*, P_2^*, k \right) + P_2^*(k) \frac{\partial G}{\partial P_2} \left(P_1^*, P_2^* \right) \right\} > 0. \qquad (5.5.3)$$

Calculating $\lim_{k \to \infty} P_1^*(k)$ and $\lim_{k \to \infty} P_2^*(k)$ and substituting into the expression

$$P_1 \frac{\partial F}{\partial P_1} (P_1, P_2, k) \; + \; P_2 \frac{\partial G}{\partial P_2} (P_1, P_2), \qquad (5.5.4)$$

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gives conditions under which (5.5.3) is satisfied. However, violation of (5.5.3) does not necessarily imply stability for all k unless we know that (5.5.4) is a monotone increasing function of k. If it is so, then (5.5.3) implies that the system becomes unstable under sufficient enrichment (which may be seen for example, in growth without bound of both species or in growing amplitude oscillations which might lead to extinction of one or both of the species as the systems trajectory approaches the axes of the quadrant), while negation of (5.5.3) implies the preservation of stability.

Brauer applies this last-mentioned result to system (5.2.1) encountered earlier. Here

$$F(P_1, P_2, k) = r\left[1 - \frac{P_1}{k}\right] - \frac{KP_2}{P_1 + D},$$

and

$$G(P_1, P_2) = s\left[1 - \frac{P_2}{\gamma P_1}\right].$$

Working through the above analysis, it is found that the derivative of (5.5.4) with respect to k is positive and that if $s > r$ the system remains stable under enrichment, while if $s < r$ there are values of γ for which enrichment causes destabilization. There is thus quite a delicate dependence of the qualitative behaviour of the system under enrichment on the parameters of the model, and this suggests the need in general, *for extreme caution in tampering with natural systems.* Indiscriminant enrichment of an environment with the hope of increasing a population could be dangerous in that the results may

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be very different from the intention.

In [85] Brauer et al extend the above theory to consider the effect of harvesting the predator population at a constant time rate on the stability of the system. They quote an example involving lake phytoplankton as predator and a particular nutrient as prey. Apparently, observations suggest large amplitude oscillation in both populations. Of interest is whether these oscillations could be "tamed" to stable limit cycle or stable point behaviour by suitable harvesting of the predator.

The system under study is

$$
\begin{aligned}
\frac{dP_1}{dt} &= P_1 F(P_1, P_2), \\
\frac{dP_2}{dt} &= P_2 G(P_1, P_2) - E,
\end{aligned}
\tag{5.5.5}
$$

where $E \geq 0$ is the constant rate at which predators are harvested, and where explicit dependence of F on k, the prey carrying capacity, is not indicated but is assumed. Evidently, for this system to be in the standard Kolmogorov form the second differential equation of (5.5.5) must be expressed as

$$
\frac{dP_2}{dt} = P_2 \bar{G}(P_1, P_2),
$$

where

$$
\bar{G}(P_1, P_2) = G(P_1, P_2) - \frac{E}{P_2}.
$$

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Brauer et al neglect to do this and require that conditions (A), (B) and (C), introduced earlier, continue to hold. However, we now have

$$\frac{\partial \bar{G}}{\partial P_2}(P_1, P_2) \;=\; \frac{\partial G}{\partial P_2}(P_1, P_2) + \frac{E}{P_2^2},$$

so that, in order for (B) to hold in this case, the values of P_2 need to be restricted to those satisfying

$$\frac{\partial G}{\partial P_2}(P_1, P_2) < -\frac{E}{P_2^2}. \qquad (B')$$

Furthermore, application of the Kolmogorov Theorem requires the existence of a constant T, such that $\bar{G}(T, 0) = 0$. This is clearly not possible for the above choice of $\bar{G}(P_1, P_2)$. Brauer et al do overcome this difficulty but before discussing this, the content of [85] is overviewed:

An equilibrium point is now a solution of the pair $P_1 F(P_1, P_2) = 0$, $P_2 G(P_1, P_2) = E$, and is denoted by $(P_1^*(E), P_2^*(E))$. As always, we require $P_1^*(E) > 0$, $P_2^*(E) > 0$. Furthermore, for $E = 0$ the equilibrium point $(P_1^*(0), P_2^*(0))$ is assumed to be unique with $P_1^*(0) > 0$, $P_2^*(0) > 0$. The implicit function theorem [86, p 185] guarantees the existence of an equilibrium point $(P_1^*(E), P_2^*(E))$ providing the community matrix of system (5.5.5), namely

$$C(E) = \begin{bmatrix} P_1^*(E)\frac{\partial F}{\partial P_1}(P_1^*, P_2^*) & P_1^*(E)\frac{\partial F}{\partial P_2}(P_1^*, P_2^*) \\[2mm] P_2^*(E)\frac{\partial G}{\partial P_1}(P_1^*, P_2^*) & P_2^*(E)\frac{\partial G}{\partial P_2}(P_1^*, P_2^*) + G(P_1^*, P_2^*) \end{bmatrix},$$

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where P_1^* denotes $P_1^*(E)$, is non-singular; in other words det $C(E) >$ 0 for $E \geq 0$. This condition holds for $E = 0$ since condition (C) is equivalently det$C(0) > 0$. (In addition Brauer et al demonstrate that for $E > 0$, the equilibrium points are always positive, so that the above requirement of $P_1^* > 0$, $P_2^* > 0$ is always valid for system (5.5.5).)

However, the criterion det$C(E) > 0$ for the existence of $(P_1^*(E),\ P_2^*(E))$ is not useful in practice since it requires $P_1^*(E)$ and $P_2^*(E)$ to be known. For this reason, a critical harvest rate determined by det $C(E_c) = 0$ is introduced in [85] so that the equilibrium point in the first quadrant exists for $0 \leq E < E_c$, disappears at E_c and fails to exist for $E > E_c$.

For example, the system having

$$F(P_1, P_2) = \frac{R}{P_1} - \frac{P_2}{P_1 + A},$$

$$G(P_1, P_2) = \frac{sA(P_1 - J)}{(J + A)(P_1 + A)},$$

with R, A, s, J being appropriate constants is mentioned in [85] as being used for the study of phytoplankton-nutrient population dynamics. The equilibrium points in this case are

$$P_1^*(E) = \frac{sAJR}{sAR - E(J + A)},$$

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$$P_2^*(E) = \frac{(sR - E)(J + A)}{sJ},$$

from which it is clear that

$$0 \leq E < \frac{sRA}{J + A},$$

ensures $P_1^*(E) > 0$. Hence, for this model, $E_c = \frac{sRA}{J + A}$.

Now, for $E = 0$, it is easily seen that a system trajectory in the $P_1 - P_2$ plane of a solution of (5.5.5) can approach the P_1 or P_2 axes tangentially but cannot cross an axis, since at $P_1 = 0$ and $P_2 = 0$ we have $\frac{dP_1}{dt} = 0 = \frac{dP_2}{dt}$. However, as Brauer et al note, for $E > 0$, $P_2 G(P_1, P_2) - E$ is negative for $P_2 = 0$, so that an orbit which comes near enough to the P_1 axis will cross it and at the crossing $\frac{dP_2}{dt} = -E < 0$. If $E > E_c$ a positive equilibrium point fails to exist; the predators are being harvested at a rate which exceeds their growth rate. Necessarily, $\frac{dP_2}{dt} < 0$ and the orbits will be drawn downwards to the P_1 axis, resulting in the biological catastrophe of the predator becoming extinct in finite time.

As usual, studying the stability properties of the system requires knowledge of the eigenvalues of the community matrix $C(E)$. Straight-forward calculation confirms that the eigenvalues are

$$\lambda = \frac{1}{2} \left\{ \triangle_1(E) \pm \left[(\triangle_1(E))^2 - 4 \triangle_2(E) \right]^{1/2} \right\},$$

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with

$$\Delta_1(E) = P_1^*(E)\frac{\partial F}{\partial P_1}(P_1^*, P_2^*) + P_2^*\frac{\partial G}{\partial P_2}(P_1^*, P_2^*) + G(P_1^*, P_2^*),$$

and

$$\Delta_2(E) = \det C(E) = P_1^*(E)P_2^*(E)\left[\frac{\partial F}{\partial P_1}(P_1^*, P_2^*)\frac{\partial G}{\partial P_2}(P_1^*, P_2^*)\right.$$

$$\left. -\frac{\partial F}{\partial P_2}(P_1^*, P_2^*)\frac{\partial G}{\partial P_1}(P_1^*, P_2^*)\right] + P_1^*(E)\frac{\partial F}{\partial P_1}(P_1^*, P_2^*)G(P_1^*, P_2^*).$$

Now, in order to apply Kolmogorov's theorem one needs to check that conditions (i) - (ix) apply to the *harvested* system. Clearly, if conditions (i), (ii), (iv), (v), (vi) hold for the unharvested system (5.3.1) they will also be true of the harvested case (5.5.5). However, as mentioned earlier, concerning condition (iii), the range of P_2 needs to be restricted in order that $\frac{\partial \tilde{G}}{\partial P_2} < 0$, for the harvested system. An equivalent interpretation of conditions (vii) - (ix) for the unharvested system is that the intersection of the prey isocline $F(P_1, P_2) = 0$ with the P_1 axis is to the right of the intersection of the predator isocline $G(P_1, P_2) = 0$ with the P_1 axis. Thus, for the harvested case (5.5.5), Brauer et al require that the intersection of $F(P_1, P_2) = 0$ with the P_1 axis be to the right of the intersection of $P_2G(P_1, P_2) = E$ with the P_1 axis, for conditions (vii) - (ix) to be satisfied. However, for $E > 0$, $P_2G(P_1, P_2) = E$ has the P_1 axis as an asymptote (since $\frac{dP_2}{dt} = 0$), and it appears that our requirements cannot be satisfied.

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The authors of [85] note though that if one considers a region bounded by the P_2 axis and a horizontal line $P_2 = \in$, with $\in$ chosen to be large enough so that the intersection of $F(P_1, P_2) = 0$ and $P_2 = \in$ is to the right of the intersection of $P_2 G(P_1, P_2) = E$ with $P_2 = \in$, then Kolmogorov's conditions (vii) - (ix) are satisfied in the first quadrant where $P_2 > \in$. If $E < E_c$ a positive equilibrium point exists and hence such an $\in$ can always be found.

Combining the above discussion with knowledge of the eigenvalues, we have that for values of P_1 and P_2 such that (A), (B'), (C) and Kolmogorov's conditions (ii), (iv), (v), (vi), as well as conditions (vii) - (ix) in the form apply to the harvested system, the system has a stable point for

$$P_1^*(E)\frac{\partial F}{\partial P_1}(P_1^*, P_2^*) + P_2^*(E)\frac{\partial G}{\partial P_2}(P_1^*, P_2^*) + G(P_1^*, P_2^*) < 0,$$

and bifurcates into a stable limit cycle for,

$$P_1^*(E)\frac{\partial F}{\partial P_1}(P_1^*, P_2^*) + P_2^*(E)\frac{\partial G}{\partial P_2}(P_1^*, P_2^*) + G(P_1^*, P_2^*) > 0.$$

Brauer et al define E_s to be the critical value of E for which such a transition occurs, i.e. $\triangle_1(E_s) = 0$. Thus harvesting at rates close to E_c and E_s can produce qualitative changes in the behaviour of the system, namely the real-life danger of predator extinction or, under Kolmogorov's conditions, the onset of stable oscillations.

The important concept of *practical stability* is introduced in [85]. By definition it implies that an orbit of a solution never comes closer to

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either axis than some preassigned distance. In this way the possibility of extinction of a species due to an oscillation approaching an axis very closely, is excluded. Brauer et al emphasise that the practical stability of a system may depend on its initial state and usually cannot be established by purely analytic means but often requires some numerical computation. So far, in our dealing with limit cycles we have not taken practical stability into account. It is evident though that we will need to do so. A good example is provided by system (6.4.2 - 4) of chapter 6 for which limit cycle behaviour is demonstrated but, which is definitely not practically stable: a more valid conclusion would be extinction of both species rather than regular, indefinite fluctuations in population numbers.

Brauer et al apply this analysis to three models which have arisen in separate biological contexts. They analyse the nature of solutions by first determining the equilibrium point as a function of E. Then, for specific parameter choices and $E < E_c$, $\triangle_1(E)$ and $\triangle_2(E)$ are computed and thus the nature of the equilibrium is determined.

The computer simulation and practical stability analyses for these systems are detailed in [85]. Instead of elaborating upon this work, brief mention will be made of some of the results obtained:

One of the models studied involves

$$F(P_1, P_2) = r\left(1 - \frac{P_1}{k}\right) - \frac{P_2}{P_1 + A}, \qquad G(P_1, P_2) = \frac{SA(P_1 - J)}{(J + A)(P_1 + A)},$$

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and calculations indicate that enrichment of the prey environment (i.e. increasing k) tends to create system oscillations, but that harvesting tends to stabilize these, even to the point of being able to change a limit cycle into an asymptotically stable equilibrium point. The safe harvesting terms, that is the value of E less than E_c which lead to a stable situation, increase with k. Hence, if one could assign a 'cost' to enrichment and a value to the harvested predator and derive a means of calculating an optimal enrichment and corresponding maximum safe harvest, one would obtain a valuable tool for resource management and control. Another point that arises is that the qualitative behaviour of the unharvested system gives no guide to the response to harvesting. For example, one system had an asymptotically stable point for $E = 0$ and developed limit cycles for certain values of $E > 0$, while another with a limit cycle for $E = 0$ exhibited stable point behaviour for values of $E > 0$. Thus, the behaviour before, in general, is not an indication of the behaviour after harvesting and a stable system may be destablized by harvesting. This warns against an intuitive approach to harvesting.

In [87] Brauer and Soudack investigate the Kolmogorov system in which both predator and prey are harvested according to the constant-yield strategy

$$\frac{dP_1}{dt} = P_1 F(P_1, P_2) - D$$

$$(5.5.6)$$

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$$\frac{dP_2}{dt} \quad = \quad P_2 G(P_1, P_2) - E,$$

where D and E are constants, not necessarily positively valued, since a negative harvest rate can be regarded as a rate of stocking. The basic assumptions of [87] are along the lines of [84] and [85], namely that

$$\frac{\partial F}{\partial P_1} < 0, \quad \frac{\partial G}{\partial P_1} > 0, \quad \frac{\partial G}{\partial P_2} < 0 \text{ for } P_1 > 0, P_2 > 0,$$

and there exist constants R, K, T, such that

$$
\begin{array}{ll}
F(K, O) = 0, & K > 0 \\
F(O, R) = 0, & R > 0 \\
G(T, O) = 0, & T > 0.
\end{array}
$$

Under study here is the asymptotic behaviour of solutions of the above system for different values of D and E and how this behaviour depends on D and E. Biologically this means the study of the effects of a variety of mechanisms such as increasing or decreasing the food supply of the predators and introducing or removing predators from the system. Brauer and Soudack analyse the trajectories of the system giving attention to the existence and nature of saddle points, equilibrium points and limit cycles. Their analysis is detailed and no application of Kolmogorov's Theorem is made. Emphasis is given to coexistence and extinction phenomena and regions of harvest rates for which the predator and prey coexist or for which either of the species becomes extinct in finite time are illustrated.

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As for the age-dependent harvested models of section 3.5, an extension of constant-yield harvesting is the study of constant- effort harvesting. This involves replacing D and E of (5.5.6) by DP_1 and EP_2 respectively, where D and E now represent harvesting efforts rather than rates, (a discussion of the meaning of "effort" is given in section 5.6). Notice that in this case the harvested model remains of the Kolmogorov type, since obviously, the constants D and E can be incorporated into the growth rate functions F and G respectively:

$$\frac{dP_1}{dt} = P_1 \bar{F}(P_1, P_2) = P_1(F(P_1, P_2) - D).$$

$$(5.5.7)$$

$$\frac{dP_2}{dt} = P_2 \bar{G}(P_1, P_2) = P_2(G(P_1, P_2) - E).$$

Thus, the Kolmogorov theorem can be tested and applied without any difficulty.

Brauer and Soudack's work on system (5.5.7) is detailed in [88]. As in [87] they examine how the asymptotic behaviour of the system varies for different values D and E of constant-effort harvesting or stocking.

Instead of elaborating upon their paper, attention is given to specific "multi-species" models that have arisen out of attempts to model real-world situations.

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5.6 A Two-species predator-prey model

A predator-prey system of ecological concern is the baleen whale and krill populations of the Southern Ocean. The number of baleen whales has been drastically reduced by excessive hunting and as a result there is a surplus of their principal food source, the Antarctic krill. There has been much discussion about exploiting this surplus krill, a rich source of Vitamin A, and already close on 100,000 tons per annum are harvested. (References to this information are available in [89].) However, the krill are also consumed by many other ocean creatures and the effect of krill- fishing on these as well as on the sparse baleen whales is a cause of concern. May et al [89] construct a simple, heuristic model of the situation in an attempt to predict the effect of various fishing strategies upon the whale and krill populations. In what follows, their model and its results are discussed.

Letting P_1 be the prey (krill) population and P_2 the predator (whale) population, May et al propose that the prey dynamics are described by

$$\frac{dP_1}{dt} = a_1 P_1 \left[1 - \frac{P_1}{k} \right] - b P_1 P_2, \qquad (5.6.1)$$

where a_1, as usual, represents the percapita growth rate of the krill, k is the carrying capacity of the environment, and the prey are consumed at a rate proportional to their density, bP_1 per predator, $b > 0$.

Similarly, a logistic equation describes the dynamics of the predator

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population

$$\frac{dP_2}{dt} = a_2 P_2 \left[1 - \frac{P_2}{\alpha P_1} \right], \tag{5.6.2}$$

with a_2 being the per capita growth rate of predators, α a positive constant expressing how many whales can be sustained on a population of one krill, and the carrying capacity of the whales being proportional to the amount of food available.

As mentioned in earlier sections, a particular type of harvesting practised in fishing (and other) industries is effort-harvesting where, fishing effort is measured in units appropriate to the fishery in question. According to Clark [90], in some cases the unit of measurement is simply the total number of vessel-days per unit time; in other cases more detailed information regarding the number of nets, lines etc. is available. Hence 'effort' can be a constant or a function of a number of variables. May et al assume that the krill population is harvested under a constant effort strategy at a rate $a_1 D$, where D denotes the constant fishing effort rescaled so that $D = 1$ corresponds to a fishing rate equal to the population's natural growth rate. The krill yield is then expressed as $y_1 = a_1 D P_1$. Similarly harvesting the whale population under constant effort at a rate $a_2 E$ gives a whale yield, $y_2 = a_2 E P_2$.

The harvested predator-prey system now becomes

$$\frac{dP_1}{dt} = a_1 P_1 \left[1 - \frac{P_1}{k} \right] - b P_1 P_2 - a_1 D P_1 \tag{5.6.3}$$

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$$\frac{dP_2}{dt} = a_2 P_2 \left[1 - \frac{P_2}{\alpha P_1}\right] - a_2 E P_2. \qquad (5.6.4)$$

May et al deal with the effects of different harvesting strategies on the system in terms of the concept of maximum sustainable yield (MSY): System (5.6.3), (5.6.4) is first reduced to

$$\frac{dX}{dt} = a_1 X [1 - D - X - \nu Y] \qquad (5.6.5)$$

$$\frac{dY}{dt} = a_2 Y [1 - E - \frac{Y}{X}], \qquad (5.6.6)$$

by setting $X = \frac{P_1}{k}$, $Y = \frac{P_2}{\alpha k}$, and where ν is the dimensionless parameter $\frac{b\alpha k}{a_1}$.

Routine calculation confirms that the equilibrium values for the krill and whale populations are respectively

$$X^* = \frac{1 - D}{1 + \nu(1 - E)}, \qquad Y^* = \frac{(1 - D)(1 - E)}{1 + \nu(1 - E)}, \qquad (5.6.7)$$

so that, as long as both D and E are less than unity, that is, the fish are being caught at a rate less than their natural replacement rate, there is a unique, and, as is easily verified, stable equilibrium. On the other hand, one can check that if harvesting of the whales is maintained at a level in excess of their natural growth rate, $E > 1$, then the system settles to the state $X^* = 1 - D$, $Y^* = 0$, while $D > 1$ guarantees extinction of both species, $X^* = 0$, $Y^* = 0$.
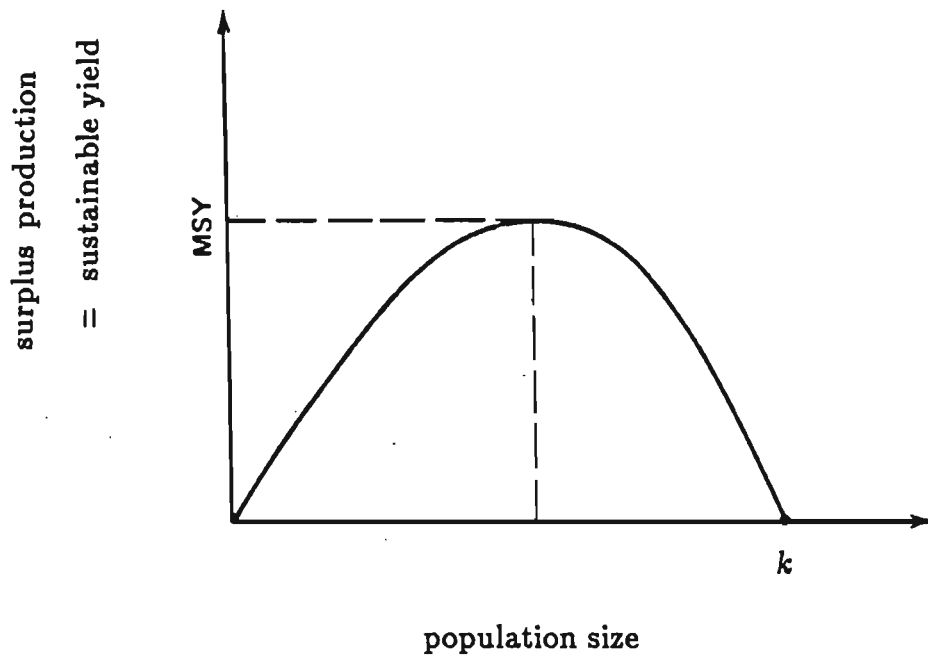
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Furthermore, the equilibrium krill and whale yields are

$$y_1 = \frac{(a_1 k)D(1-D)}{1+\nu(1-E)} \tag{5.6.8}$$

$$y_2 = \frac{(\alpha a_2 k)(1-D)E(1-E)}{1+\nu(1-E)}. \tag{5.6.9}$$

MSY is described in [90] as being the simplest possible management objective that accounts for the fact that a biological resource stock cannot be exploited too severely without eventual loss in productivity. The concept of MSY is based on a model of biological growth (see figure 5.5.1) that supposes that at any given population size less than a particular level k, a surplus production exists that can be harvested indefinitely without altering the stock level. If the excess is not removed by harvesting an increase in stock level results which ultimately approaches the environmental carrying capacity k, where excess production is reduced to zero.

Fig. 5.5.1

Clearly MSY is achieved at the population level where growth rate is maximised. (5.6.8), (5.6.9) give sustainable yields, since, corresponding to equilibrium populations of krill and whale, they can be continued indefinitely. For fixed E, the krill yield is maximized at $D = 0,5$ while for fixed D, the whale yield is maximized at

$$E = \frac{(1 + \nu) - \sqrt{1 + \nu}}{\nu}, \ \nu \neq 0.$$

The parameter ν can be regarded as a measure of the strength of interaction between whale and krill. When $\nu = 0$, so that "interference" by the whales is not considered, the krill population dynamics are described by a logistic equation. It is evident from (5.6.7) and (5.6.8) that y_1 and X^* decrease with increasing ν, so that the presence of whales has the expected effect of diminishing krill yield and depressing the equilibrium krill population by an amount that increases as ν increases.

Now in the absence of fishing $(D = E = 0)$ (5.6.7) gives

$$X^* = \frac{1}{1 + \nu}$$

which indicates that if $\nu = 1$ the whales are consuming krill at the point of MSY $(X^* = 0.5, \ P_1^* = \frac{k}{2})$ for the logistic equation; if $\nu > 1$ the whales are harvesting the krill in excess of MSY $(P_1^* < \frac{k}{2})$; while if $\nu < 1$ the krill are being consumed below the MSY level $(P_1^* > \frac{k}{2})$. According to May et al, much controversy surrounds the question of

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whether ν is expected to be close to one in natural predator-prey systems. For the baleen whale-krill system there is apparently inadequate data available to provide a reliable estimate for ν; but May et al mention that it is unlikely to be either very large or very small.

It is stressed in [89] that this type of MSY analysis is useful only if a harvested stock can be regarded as a single, isolated population. This was achieved earlier by setting $\nu = 0$ but if the harvested species have strong interactions $(\nu \neq 0)$, then MSY analysis applied to each species individually cannot serve as a guiding principle for management of the predator-prey system: Clearly, it is of no value to maximise (5.6.8/9) separately since these are interrelated and maximizing one reduces the other. In fact from (5.6.8) we see that y_1 is maximised by making E as large as possible, i.e. $E = 1$. But then (5.6.9) implies $y_2 = 0$, so that, to maximise krill yield we would need to harvest the whales to extinction. Conversely, the largest whale yield corresponds to no fishing for krill.

A better alternative is to study the situation from the point of maximizing a total weighted yield

$$y = y_1 + \gamma y_2,$$

where γ is a constant representing the relative value of the whales and the krill. γ could reflect relative economic value, processed weight, protein content etc. and clearly, large values of γ indicate the greater value of whales over krill and vice versa.

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Since y can be written as

$$y = \frac{ka_1(1-D)[D+\beta E(1-E)]}{1+\nu(1-E)}, \qquad \beta = \frac{\gamma\alpha a_2}{a_1}, \qquad (5.6.10)$$

y may now be maximised with respect to D and E to find the global optimum. Notice that as β increases in size, (5.6.10) indicates that

$$y \to \frac{ka_1(1-D)\beta E(1-E)}{1+\nu(1-E)}, \qquad (5.6.11)$$

while, if $\beta \to 0$

$$y \to \frac{ka_1(1-D)D}{1+\nu(1-E)}. \qquad (5.6.12)$$

Hence (5.6.11) is maximised at $D = 0$ while (5.6.12) is maximized when E is as large as possible. For large β then, it is best not to fish for krill at all but to leave the krill as food for the more valuable whales. However, if β is small, the optimum solution involves extinguishing the relatively valueless whales and harvesting only the krill.

Yet, these "all or nothing" strategies are rather inconsistent with attempts to preserve all species in the ecosystem. Only for a narrow band of intermediate β values will the optimum solution involve both predator and prey.

Although no concrete qualitative results are obtained, this model proposed by May et al does provide a basic framework that can be readily understood and expanded upon, and which gives insight into this predator-prey situation.

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We notice though, that system (5.6.3),(5.6.4) is a system of the Kolmogorov type (5.5.7). Yet Kolmogorov's condition (iv) fails to hold since in this case

$$P_1 \frac{\partial \bar{G}}{\partial P_1} + P_2 \frac{\partial \bar{G}}{\partial P_2} = 0.$$

If we had the assurance that Kolmogorov's theorem remains valid in this case, we would have a simple means of determining conditions on the parameters of the system under which either stable point behaviour or stable limit cycle behaviour is guaranteed. This would obviously have useful biological application. However, no mention or application of Kolmogorov's theorem is made in [89].

The next system to be examined is not of the predator-prey type - it involves a single species that is divided into three groups, such that its dynamics can be described by a "three-species" model. Mention is made of this here since this technique has implications for including age-structure into systems of differential equations.

5.7 A "three-species model" - the dynamics of a fox population infected with rabies.

The dynamics of a fox population infected with rabies - a directly transmitted viral infection of the nervous system to which fox populations are especially susceptible - has been modelled by Anderson

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[91], and Anderson et al [92] in attempts to investigate possible means of effectively checking the disease.

The fox population is divided into three separate groups: *susceptibles*, *infecteds* that are not yet infectious, and *infectious* individuals; each group having population densities X, I, Y respectively, (where density is measured as 'number per km^2'). The model does not account for recovered immune foxes because few survive the disease. Hence, the total fox density N is

$$N = X + I + Y.$$

The death rate of young foxes has been found to be density dependent, and it is assumed that the per capita death rate is linearly related to N. In particular, the net rate is assumed to be described by $(b + \gamma N)N$, where $\frac{1}{b}$ denotes fox life expectancy in the absence of resource limitations, and γ measures the influence of density dependence on the death rate. The per capita birth rate is assumed to be a constant a. By definition then, the per capita population growth rate is

$$r = a - b.$$

Apparently, in the absence of rabies, fox populations tend to increase up to some characteristic density and the logistic model

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{k} \right),$$

is chosen to describe this behaviour.

The following assumptions are imposed in [91] and [92]:

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- foxes contact rabies at a rate which is proportional to the number of encounters between susceptible and infectious foxes, βXY, where β is a transmission coefficient.

- foxes pass from the incubating to the infectious state at a per capita rate σ, such that the average incubation period is $\frac{1}{\sigma}$

- Rabid animals die at a constant per capita rate α so that their life expectancy is $\frac{1}{\alpha}$.

- Rabid foxes do not contribute to the reproductive effort of the population.

All these hypotheses allow for the set of equations:

$$\frac{dX}{dt} = rX - \gamma XN - \beta XY \tag{5.7.1}$$

$$\frac{dI}{dt} = \beta XY - (\sigma + b + \gamma N)I \tag{5.7.2}$$

$$\frac{dY}{dt} = \sigma I - (\alpha + b + \gamma N)Y, \tag{5.7.3}$$

with the sum of the above three giving

$$\frac{dN}{dt} = aX - (b + \gamma N)N - \alpha Y. \tag{5.7.4}$$

The 'basic reproduction rate', R, as discussed in [91], is defined as the expected number of secondary cases produced in the life time

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of an infectious individual when introduced into a population of k susceptible animals. Anderson justifies this as being

$$R = \frac{\alpha \beta k}{(\sigma + a)(\alpha + a)},$$

for systems (5.7.1 - 3).

By definition, rabies will be perpetuated within the population provided $R > 1$, which is equivalent to the condition that the fox population exceeds a threshold density, $k > k_T$ where

$$k_T = \frac{(\sigma + a)(\alpha + a)}{\beta \alpha}.$$

The case $R < 1$ or $k < k_T$ results in the fox population settling to its disease free equilibrium density k, so that rabies becomes extinct in the population; while if $R > 1$, rabies will alter fox abundance below the disease free level k to an equilibrium density N^* given by

$$N^* = \frac{(\sigma + a)(\alpha + a) - ar}{\alpha \beta - a\gamma}.$$

Depending on the choice of parameters, Anderson demonstrates that the equilibrium value N^* may be either a stable constant value (i.e. stable point) or that the system trajectory $N(t)$ may oscillate about N^* in a stable limit cycle, with cyclic solutions tending to arise if k is significantly larger than k_T.

It is interesting that for certain realistic parameter choices (we refer to [91, p 246] for a table of likely parameter values), the model predicts

stable cycles with periods in the general range 3 - 5 years. The authors note that such periods are precisely what is observed in Europe and North America, where a striking feature of the rabies disease in fox populations is the regular 3,4 or 5 year oscillations in fox density.

What is desired is a method of control that will maintain fox numbers below the critical threshold density k_T. In [91] and [92] four such methods are proposed.

(a) The first involves culling - a constant quota $\wedge$, of animals is removed annually. In the absence of rabies the population under such culling satisfies

$$\frac{dN}{dt} = rN \left[1 - \frac{N}{k} \right] - \wedge, \tag{5.7.5}$$

and has equilibrium points $0, N_1^*, N_2^*$ where

$$N_{1,2}^* = \frac{1}{2r} \left\{ kr \pm k\sqrt{r^2 - \frac{4r\wedge}{k}} \right\}, \qquad N_2^* > N_1^*. \tag{5.7.6}$$

It is straight forward to verify that the points 0, and N_2^* are locally stable while N_1^* is unstable.

From (5.7.6) it is evident that the largest admissible value that $\wedge$ can assume is $\wedge = \frac{rk}{4}$, and at this value the growth rate is at its maximum value (its "MSY" point), $N = \frac{k}{2}$.

If $\wedge > \frac{rk}{4}$, (5.7.6) admits only imaginary solutions and $N(t)$ tends to the stable state $N^* = 0$.

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For the purpose of disease control Anderson et al require $N_2^* < k_T$ and examine the two cases $k_T > \frac{k}{2}$ and $k_T < \frac{k}{2}$. It is not difficult to verify their results that:

A) If $k_T > \frac{k}{2}$ then culling at a rate

$$\frac{rk}{4} > \wedge > rk_T\left[1 - \frac{k_T}{k}\right],$$

will ensure a stable fox density below the threshold value k_T, while

B) if $k_T < \frac{k}{2}$ then necessarily $\wedge > \frac{rk}{4}$, and the only stable point is $N^* = 0$; in other words it is not possible to create a non-zero equilibrium fox density which is less than k_T.

(b) An alternative to such a culling programme is a constant effort harvesting strategy. For example, a constant number of man-hours per unit time could be devoted to culling. In this case the intrinsic per capita death rate changes from b to $b + \triangle b$ where $\triangle b$ is the additional mortality resulting from constant-effort culling. The model now becomes

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - \triangle bN,$$

which has non-zero equilibrium point $N^* = k\left(1 - \frac{\triangle b}{r}\right)$ which is stable.

Rabies will be eliminated providing $k\left(1 - \frac{\triangle b}{r}\right) < k_T$, or equivalently when $\frac{\triangle b}{r} > 1 - \frac{1}{R}$.

If R is large, as it apparently often is, $\triangle b$ must essentially equal r itself for rabies to be eliminated. Thus a substantial level of effort needs to be applied.

(c) The third alternative proposed involves vaccination. A category of immune foxes of population density $Z(t)$ is included into the model. Susceptibles are vaccinated at a per capita rate $\emptyset$ and immune animals lose their immunity at a per capita rate δ. The system (5.7.1 - 3), now becomes

$$\frac{dX}{dt} = a(X + Z) - (b + \gamma N)X - \beta XY - \emptyset X + \delta Z$$

$$\frac{dI}{dt} = \beta XY - (\sigma + b + \gamma N)I$$

$$\frac{dY}{dt} = \sigma I - (\alpha + b + \gamma N)Y$$

$$\frac{dZ}{dt} = \emptyset X - (\delta + b + \gamma N)Z$$

The equilibrium of interest is the disease free state having $Y^* = I^* = 0$, $N^* = k$ which can be shown to be stable providing $\emptyset > (a + \delta)(R - 1)$.

Defining the proportion of vaccinated foxes at equilibrium as

$$p = \frac{Z^*}{Z^* + X^*} = \frac{\emptyset}{\emptyset + a + \delta}$$

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it is shown in [91], [92] that $p > 1 - \frac{1}{R}$ results in rabies eradication. Once again, if R is large, considerable immunization effort needs to be applied and consequently, the disease would be difficult to bring under control.

(d) The final control strategy involves both culling and vaccination. Anderson et al demonstrate that under a constant effort culling programme that adds $\triangle b$ to the death rate and an immunization plan that vaccinates a proportion p of the fox population, the criterion

$$p + \frac{\triangle b}{r}(1 - p) > 1 - \frac{1}{R}$$

ensures that rabies is eradicated. Thus, if for example $R = 4$ it would be necessary to vaccinate 75% of foxes or cull at a rate 75% under a pure strategy; but under a combined plan, 50% of the population need to be culled and the remaining 50% immunized.

Of the number of problems involved in applying this combined strategy is that of operational timing - one wishes to avoid as far as possible, the culling of immunized foxes. Furthermore, we note that the above results seem to suggest that rabies will be difficult to control (either by culling, vaccination or both), once it has become established in the fox populaton, for then R is large and much greater than 1 in value. However, in low fox density habitats where k is close to k_T in value, i.e. R is not much greater than unity, such methods might provide effective means of control.

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This model illustrates how a rather complex situation can be quite effectively modelled by a system that involves just three variables and simple formulations. Clearly accuracy could be improved upon by incorporating, amongst others, spatial and stochastic effects and immigration terms. Nevertheless the close agreement between model predictions and the observed cyclic behaviour of rabies epidemics within fox populations suggests that the model provides quite a reliable basis for the design of control strategies.

5.8   A "three group model" of human population dynamics

The last model to be mentioned has been developed by Schweitzer and Dienes [93], and involves a similar approach to that of the previous model. In fact, it presents a means of incorporating age-structure into an age-independent differential equation system. Here a closed human population is modelled by a three-group system where the three groups Y, F, S are interpreted as,

Y = number of pre-reproductive people

F = number of reproductive people,

and S = number of post reproductive people.

The constant terms involved in the model are $b, k_Y, k_F, \mu_Y, \mu_S, \mu_F$ where b represents the average specific fertility measured in units $\frac{1}{\text{year}}$; k_Y, k_F denote the average rate constants for moving from one

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group into the next (i.e. aging) in units of $\frac{1}{\text{year}}$, and μ_Y, μ_F, μ_S are the average specific mortality rates for groups Y, F, S respectively in units $\frac{1}{\text{year}}$.

Unlike the population size, $P(t)$ of the M-F model, groups Y, F and S are assumed to account for both male and female members.

Combining these parameters the authors propose the following as a model of human population development (though it could also apply to animal populations).

$$\frac{dY}{dt} = bF - k_Y Y - \mu_Y Y \qquad (5.8.1)$$

$$\frac{dF}{dt} = k_Y Y - k_F F - \mu_F F \qquad (5.8.2)$$

$$\frac{dS}{dt} = k_F F - \mu_S S. \qquad (5.8.3)$$

The total population is clearly given by

$$N = Y + F + S, \qquad (5.8.4)$$

so that combining the above equations yields

$$\frac{dN}{dt} = bF - \mu_Y Y - \mu_F F - \mu_S S. \qquad (5.8.5)$$

Defining the growth rate r as

$$r = \frac{1}{N} \frac{dN}{dt},$$

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it follows from (5.8.5) that

$$r = CBR - CDR$$

where the crude birth rate (CBR) is defined as $\frac{bF}{N}$, and the crude death rate (CDR), as $\mu_y \frac{Y}{N} + \mu_F \frac{F}{N} + \mu_S \frac{S}{N}$.

In [93] the authors find an explicit solution to (5.8.1 - 3) which indicates that each of Y, F, S and N eventually grow exponentially with time, with r being the exponential growth constant in each case.

Recall from chapter 2 that within the M-F framework, a persistent age distribution $\rho(a,t) = f(a)g(t)$ is such that the proportion of the population in any age group remains constant as time increases. It is shown in [93] that the ratios $\frac{Y}{N}, \frac{F}{N}, \frac{S}{N}$ do not change with time, and again the population is said to be persistent.

In an application of this system to a concrete example - the 1967 United States population - Schweitzer and Dienes demonstrate that this three-group model is quite an effective tool for approximate calculations

From the 1967 U.S. data, the groups Y and F are chosen to be the number of individuals in the 0-14 and 15-45 year age groups respectively. S is then the remaining number of people. In addition, k_Y and k_F are chosen to be 0,07 and 0,03 respectively, since $0,07 \simeq \frac{1}{14}$ and $0,03 \simeq \frac{1}{30}$.

The actual U.S. data for 1967 are given in [93] as

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$$\text{Growth rate } r \qquad\qquad = \quad 0,0077$$

$$\text{Crude birth rate (CBR)} \quad = \quad 0,0174$$

$$\text{Crude death rate (CDR)} \quad = \quad 0,0097$$

$$\frac{Y}{N}(0-14) \qquad\qquad = \quad 0,300$$

$$\frac{F}{N}(15-45) \qquad\qquad = \quad 0,400$$

$$\frac{S}{N}(45-100) \qquad\qquad = \quad 0,300$$

$$b \qquad\qquad\qquad\qquad = \quad 0,044.$$

Now estimates for μ_Y, μ_F, μ_S are obtained by taking averages of the yearly specific death rates over each interval, (for example, μ_Y is obtained by finding the average of all the values of μ over the 0-14 age interval). This leads to the values,

$$\mu_Y = 0,002, \quad \mu_F = 0,0018, \quad \mu_S = 0,028.$$

These values can in turn be used in the relation defining CDR,

$$\text{CDR} = \mu_Y \frac{Y}{N} + \mu_F \frac{F}{N} + \mu_S \frac{S}{N}$$

and give

$$\text{CDR} = 0,00972,$$

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which is in close agreement with the actual CDR of 0,0097.

In solving the systems (5.8.1 - 3), the authors derive the relation

$$\frac{(r + k_Y + \mu_Y)(r + k_F + \mu_F)}{k_Y} = b. \qquad (5.8.6)$$

(Details of this manipulation are given in [93, p. 396].) Substituting the given value of r and those calculated for k_Y, k_f, μ_Y, μ_F, into the above equation gives

$$b = 0,045;$$

again, a very close agreement with the actual value of 0,044.

Thus, the three-group model provides a rather realistic quantitative description of the main characteristics of the population. However, in general, such close agreement is not always likely since the three-group model is a crude approximation to the actual age distribution and the underlying assumption that the growth rate r is a constant is not likely to be true of many populations.

The authors generalize the model to any number of groups and assign equal age intervals to each group by letting

X_1 denote the number of members 0 to 1 year old,
X_m, the number of members $m - 1$ to m years old,
X_i, the number of fertile members $i - 1$ to i years old,
X_j, the number of fertile members $j - 1$ to j years old,
X_{j+1}, the number of post-fertile members j to $j + 1$ years old,
b_m, the average specific fertility;
μ_m, the average specific mortality, and letting
k denote the rate constant for moving from one age group to the next (i.e. aging).

Again these constants are taken as the reciprocals of the age interval, expressed in years, to which they pertain.

It is most convenient to set $k = 1$ so that the O.D.E.'s describing the model become

$$\frac{dX_1}{dt} = \sum_i^j b_m X_m - X_1(1 + \mu_1)$$

$$\frac{dX_2}{dt} = X_1 - X_2(1 + \mu_2)$$

$$\vdots \qquad \vdots$$

$$\frac{dX_m}{dt} = X_{m-1} - X_m(1 + \mu_m)$$

$$\vdots \qquad \vdots$$

$$\frac{dX_n}{dt} = X_{n-1} - X_n(1 + \mu_n)$$

Since $N = \sum_1^n X_n$ we have

$$\frac{dN}{dt} = \sum_i^j b_m X_m - \sum_i^n \mu_m X_m - X_n.$$

Assuming again that the population is in constant growth then $\frac{dN}{dt} = rN$, and that each component grows exponentially, i.e.

$$\frac{dX_m}{dt} = r X_m = X_{m-1} - X_m(1 + \mu_m) \quad 2 \leq m \leq n,$$

one can determine the ratios of the population groups as

$$\frac{X_1}{X_2} = 1 + r + \mu_2$$

$$\vdots$$

$$\frac{X_m}{X_{m+1}} = 1 + r + \mu_{m+1} \tag{5.8.7}$$

$$\vdots$$

$$\frac{X_{n-1}}{X_n} = 1 + r + \mu_n$$

An interesting exercise is to refine the mesh by decreasing the size of the age groups in order to replace the current distribution by a continuous age distribution. We follow the approach used in [93] but extend the result to relate to the M-F equation:

The relations described by (5.8.7) for any arbitrary age interval scale become

$$\frac{X_{m-1}}{X_m} = 1 + \frac{r}{k} + \frac{\mu_m}{k}, \tag{5.8.8}$$

where $k = \frac{1}{\text{age interval}}$.

Now let $\rho(a)$ denote a continuous distribution such that for a particular value of a, $\rho(a) = X_m$.

We have then, that for small values of $\triangle a$,

$$X_{m-1} = \rho(a) - \frac{d\rho}{da} \triangle a,$$

so that

$$\frac{X_{m-1}}{X_m} = 1 - \frac{d\rho}{\rho da} \triangle a.$$

Using (5.8.8) and setting $\triangle a = \frac{1}{k}$, we obtain

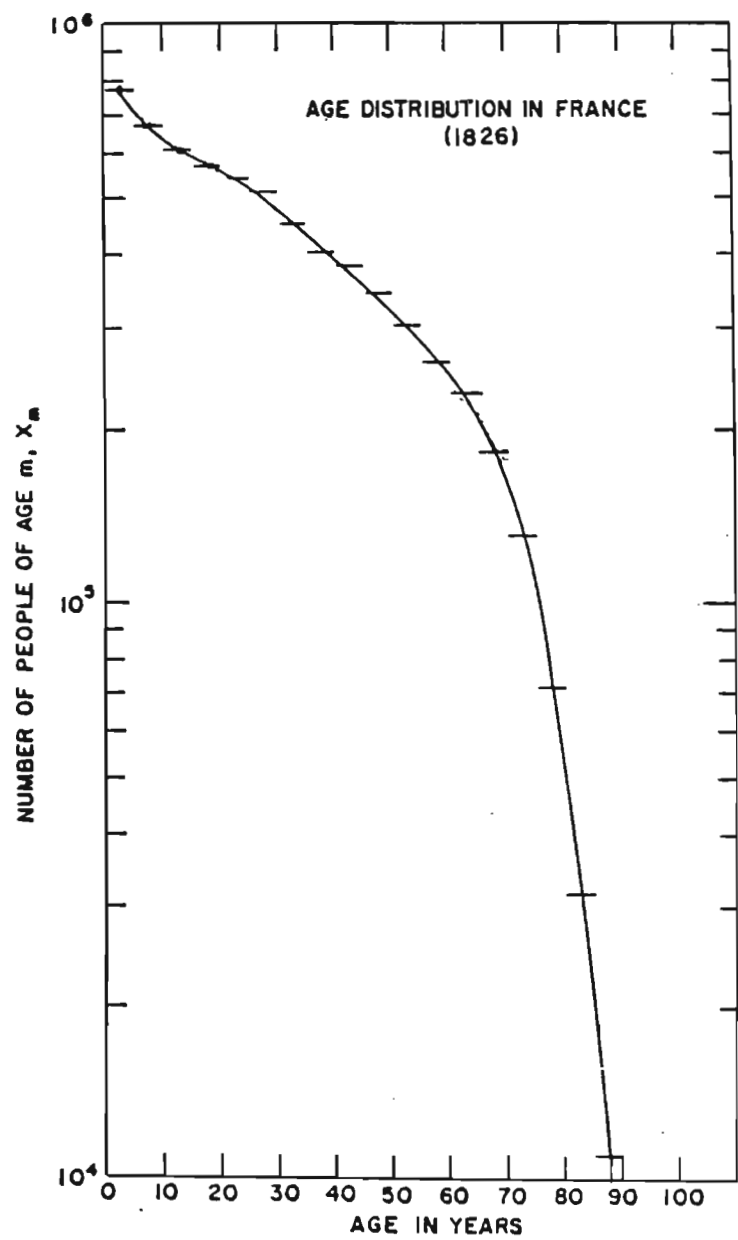$$1 - \frac{d\rho(a)}{k\rho(a)da} = 1 + \frac{r}{k} + \frac{\mu(a)}{k}.$$

This leads to

$$\frac{d\rho(a)}{da} = -(r + \mu(a))\rho(a), \qquad (5.8.9)$$

which is the time-independent form of the M-F equation with the usual expression for μ replaced by $r + \mu(a)$. This "new" form is what we expect since, in formulating the M-F equation, we do not assume a constant growth rate as was done here. If we apply the methods of chapter 1 used to derive the M- F equation and assume a constant growth rate r, and time independence in ρ, then necessarily we would arrive at (5.8.9). This agreement is encouraging and emphasises that such an age-independent model can provide a fairly accurate substitute for the M-F model.

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Finally, a specific population provides an interesting application of part of the above theory. Apparently, the population of France from 1770 to 1870 is characterised by a remarkably constant growth rate with $r = 0,004$. ([93] provides the relevant references.) To apply the results of the n-group model to this situation the authors fit a smooth curve to the population distribution data for 1826. Their diagram is reproduced below in figure 5.8.1.

Fig. 5.8.1

Age distribution for France in 1826, reproduced from [93, p 393]

Taking the segments between the data bars as straight lines, the slope of the curve between age groups X_m, X_{m-1} is given by
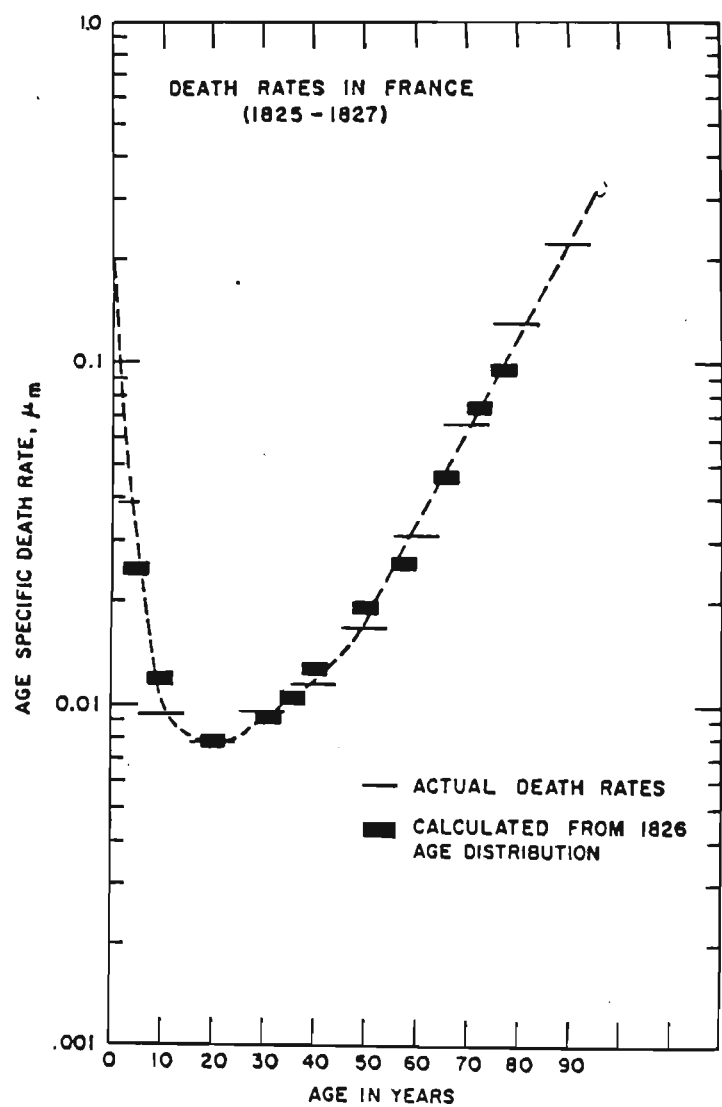
$$\frac{X_{m-1} - X_m}{\triangle a} \tag{5.8.10}$$

Now subtracting rX_m enables $\mu_m X_m$ and hence μ_m to be determined, since from (5.8.8) follows the equation

$$\frac{X_{m-1} - X_m}{\triangle a} - rX_m = \mu_m X_m.$$

The μ_m's obtained in this way are compared with the published death rates in figure 5.8.2 below, given as figure 2 of [93]. The agreement is clearly very good and demonstrates that the n-group system, a crude means of accounting for age- distribution, models this particular population very effectively.

Fig 5.8.2

Age specific death rates in France 1825 - 1827. The light bars represent actual death rates; the heavy bars have been calculated from the 1826 age distribution.

DEATH RATES IN FRANCE
(1825 – 1827)

ACTUAL DEATH RATES

CALCULATED FROM 1826
AGE DISTRIBUTION

AGE SPECIFIC DEATH RATE, μ_m

AGE IN YEARS

Hastings [94] has adopted a similar approach to modelling the dynamics of a predator-prey population. The prey species is divided into two classes - juvenile prey P_1^0 and adult prey P_1. Further it is assumed that the situation is such that the predator eats only young prey. The model has the form

$$\frac{dP_1^0}{dt} = bP_1 - aP_1^0 - P_2 f(P_1)$$

$$\frac{dP_1}{dt} = aP_1^0 - kP_1$$

$$\frac{dP_2}{dt} = P_2 f(P_1) - \ell P_2,$$

where P_2 denotes the number of predators, $f(P_1)$ determines the predation rate, b is the per capita birth rate of the prey, a is the rate at which the juvenile prey develop into adults, an k is the dea rate of adult prey, and ℓ is the death rate of the predators. This and related models are analyzed in [94] where conditions for local stability and numerical results are given. Smith and Mead [95] also consider predator-prey models of this form, examining how the stability character of the system changes for different parameter values.

However, in many cases, it is naive to view the state of a population as be specified by total population number alone and, although this technique of incorporating age structure into O.D.E. models can be effective, the other alternative, the use of the M-F equation, can

provide a means of modelling age-specific interactions with greater accuracy. It is to predator-prey systems into which age dependent effects are incorporated by means of an M-F equation that we now turn.

Chapter 6

Age-dependent
predator-prey models

The founding works of Lotka and Volterra, and McKendrick and von Foerster have initiated a long history of studies concerning the dynamics of interacting species without age-structure and those of single species with age-structure. Only much more recently has work in theoretical ecology included studies of the dynamics of interacting, age-structured models. In particular, Gurtin and Levine [96], [98], [104],Levine [97], [99], [102], and Frauenthal [56], have imposed an age-structure on a predator-prey system of the Lotka-Volterra (and the more general Kolmogorov) type by replacing the ordinary differential equation for the prey by an M-F partial differential equation.

Within this M-F/Kolmogorov framework, the effects of different patterns of age-selective predation can be examined by varying the assumptions on each model. Four types of predation are covered here,

namely - predation equally on all ages of prey; predation only on the very young; predation on all ages but with preference for the very young and very old; and finally, predation within the same population, that is, the predator and prey are the same species so that cannibalism occurs.

In what ensues the theory and results of the above papers are reviewed and related and our own comments and suggestions are added. Very little work has been produced on predator-prey systems that involve both predator and prey dynamics being described by M-F equations. Understandably, such systems can quickly become extraordinarily complex and seldom lend themselves to analytic study. In conclusion, mention is made of some of the work that has appeared in this field.

6.1   The M-F/Kolmogorov systems

Letting $\rho_1(a, t)$ denote the prey population density, it is assumed throughout that the prey population dynamics is described by an M-F equation

$$\frac{\partial \rho_1}{\partial a} + \frac{\partial \rho_1}{\partial t} = -\mu(a, t)\rho_1, \tag{6.1.1}$$

where the mortality function μ may be a function of age, time, prey population size and /or predator population size.

As usual, the total prey population is given by

$$P_1(t) = \int_0^\infty \rho_1(a,t)da, \qquad (6.1.2)$$

and the prey birth rate is given, at each time t, by a birth law of the form

$$B(t) = \int_0^\infty \beta(a)\rho_1(a,t)da. \qquad (6.1.3)$$

Here $\beta(a)$ is the fecundity function considered to be of the form

$$\beta(a) = \beta_0 a \exp(-\alpha a); \ \beta_0 \geq 0, \alpha \geq 0. \qquad (6.1.4)$$

The predator population is treated as an age-independent system, its evolution being described by the Lotka-Volterra (Kolmogorov) equation

$$\dot{P_2} = -bP_2 + cP_1P_2, \qquad (6.1.5)$$

where P_1 is given by (6.1.2) and $b > 0, c > 0$ are constants.

System (6.1.1 - 5) forms the underlying structure for the models that follow.

6.2 Two species: Indiscriminate predation model

In the case of age-indiscriminate predation, the assumption that the prey death function μ is linearly related to the total predator popu-

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lation P_2, i.e.

$$\mu(a, P) \equiv \mu(P_2) = \mu_0 + rP_2, \ \mu_0 > 0, \ r > 0,$$

is made. Thus the basic equations of the combined systems consist of (6.1.2 - 5), together with

$$\frac{\partial \rho_1}{\partial a} + \frac{\partial \rho_1}{\partial t} = (\mu_0 + rP_2)\,\rho_1. \qquad (6.2.1)$$

Although restrictive, the assumption that μ be independent of age may in some cases be valid, particularly if predation is so significant that survival of the prey depends primarily on the size of the predator population, with the result that death by old age is a rare event.

The value of μ being independent of age, of course, is that the system now lends itself to Gurtin and MacCamy's ([38]) moment technique.

Before applying the technique it is necessary to distinguish between the quantities $\rho_1(o, t)$ and $B(t)$. With the exception of the model of section 3.6, $B(t)$ has, until now, denoted the birth rate at time t and $B(t) = \rho_1(o, t)$. In this chapter $B(t)$ will be interpreted more specifically as the egg (or new born) production rate while $\rho_1(o, t)$ will denote the number of hatched eggs (live newborn) produced per unit time. Thus, we have the possibility that $\rho_1(o, t) \neq B(t)$ with their difference being the number of unhatched eggs (per unit time).

Where the predator is attracted equally to all ages of prey, it is assumed that $\rho_1(o, t) = B(t)$, since the newborn are no more vulnerable than the older prey.

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Applying Gurtin and MacCamy's moment technique and integrating (6.2.1) with respect to a, under the assumption that $\rho_1(a,t) \to 0$ as $a \to \infty$, one arrives at an equation for P_1. Similarly defining

$$A(t) = \int_0^\infty e^{-\alpha a} \rho_1(a,t) da \qquad (6.2.2)$$

and multiplying (6.2.1) by $\beta_0 a e^{-\alpha a}$ and $e^{-\alpha a}$ respectively, one obtains analogous equations for B and A.

The resulting system of equations is

$$
\begin{aligned}
\dot{P_1} &= -\mu_0 P_1 - r P_1 P_2 + B \\
\dot{B} &= -\gamma B - r B P_2 + \beta_0 A \\
\dot{A} &= -\gamma A - r A P_2 + B \\
\dot{P_2} &= -b P_2 + c P_1 P_2,
\end{aligned}
\qquad (6.2.3)
$$

where $\gamma = \mu_0 + \alpha$.

This closed set of coupled nonlinear ordinary differential equations is now amenable to analysis and solution.

In each of the four cases to be covered there will be a variation in (a) the survival rate of newborn which determines the relationship between $\rho_1(o,t)$ and $B(t)$, (b) the dynamics of the predator behaviour and (c) the functional dependence of the death function μ. In all, except one case, this functional dependence of μ will omit the inclusion of age.

Recall that in the absence of predators the quantity

$$R = \int_0^\infty \beta(a)\pi(a) da, \quad \pi(a) = \exp\left\{ -\int_0^a \mu(\alpha) d\alpha \right\},$$

which in this case becomes

$$R = \int_0^\infty \beta(a)e^{-\mu(P_2)a}da = \frac{\beta_0}{(\mu(P_2) + \alpha)^2} \qquad (6.2.4)$$

represents the net reproduction rate for the prey; that is, the expected number of offspring to be born to a member of the population in its natural life time. It is not difficult to show by means of eigenvalue analysis or using the stability equation (2.3.28) of chapter 2, that the equilibrium (0,0,0,0) of (6.2.3) is asymptotically stable if and only if $R < 1$. Hence to prevent extinction of the species it is assumed that $R > 1$, i.e. $\beta_0 > [\mu(P_2) + \alpha]^2$.

For convenience the ratios $x = \frac{A}{B}$, $y = \frac{B}{P_1}$ are introduced so that system (6.2.3) becomes

$$\begin{aligned}
\dot{P}_1 &= -\mu_0 P_1 - r P_1 P_2 + y P_1 \\
\dot{P}_2 &= -b P_2 + c P_1 P_2 \\
\dot{y} &= -\alpha y + \beta_0 xy - y^2 \\
\dot{x} &= 1 - \beta_0 x^2
\end{aligned} \qquad (6.2.5)$$

A theorem of [96] states an important result concerning system (6.2.5):

Let (P_1, P_2, y, x) be a solution of (6.2.5). Then $(P_1(t), P_2(t))$ converges, as $t \to \infty$, to a closed solution curve of the Lotka-Volterra equations

$$\begin{aligned}
\dot{P}_1 &= \omega P_1 - r P_1 P_2 \\
\dot{P}_2 &= -b P_2 + c P_1 P_2, \text{ where } \omega = -\gamma + \sqrt{\beta_0}.
\end{aligned}$$

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The result follows from proof that, as $t \to \infty$, $\frac{A}{B}$ and $\frac{B}{P_1}$ approach respectively, the constants

$$\frac{1}{\sqrt{\beta_0}} \text{ and } (-\alpha + \sqrt{\beta_0}),$$

at exponential rates.

Thus, this system involving age indiscriminate predation behaves like a predator-prey system in which age-structure is ignored; the P_1, P_2 co-ordinates of trajectories of (6.2.3) approach one of a continuum of neutrally stable closed curves as time increases.

Gurtin and Levine [96] find that this result can be generalised to the model for which the Lotka-Volterra predator equation is replaced by a more general Kolmogorov equation. Starting with the Kolmogorov model

$$\dot{P_1} = P_1 F(P_1, P_2) \qquad (6.2.6)$$

$$\dot{P_2} = P_2 G(P_1, P_2),$$

where $F(P_1, P_2)$, $G(P_1, P_2)$ satisfy conditions (i) - (ix) of the Kolmogorov theorem, they replace (6.2.6) by the M-F equation having $\mu = (\mu_0 - F(P_1, P_2))$, namely

$$\frac{\partial \rho_1}{\partial a} + \frac{\partial \rho_1}{\partial t} = -\left(\sqrt{\beta_0} - \alpha - F(P_1, P_2)\right)\rho_1, \qquad (6.2.7)$$

(where $\sqrt{\beta_0} - \alpha = \gamma - \alpha = \mu_0$).

We note that their choice of μ is biologically realistic since condition (i) of the Kolmogorov conditions requires that $\frac{\partial F}{\partial P_2} < 0$, which in turn

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implies that μ increases with increasing predator population, while for P_2 close to, or equal to zero, condition (ii) requires that $\frac{\partial F}{\partial P_1} < 0$ Hence μ increases with increasing prey population, and self-limitation effects within the prey population in the near absence of predators are accounted for.

On applying Gurtin and MacCamy's technique again, the model based on (6.2.6) and (6.2.7) reduces to

$$
\begin{aligned}
\dot{P}_1 &= -\mu_0 P_1 + P_1 F(P_1, P_2) + B \\
\dot{B} &= -\gamma B + B F(P_1, P_2) + \beta_0 A \\
\dot{A} &= -\gamma A + A F(P_1, P_2) + B \\
\dot{P}_2 &= P_2 G(P_1, P_2)
\end{aligned}
\qquad (6.2.8)
$$

Once again $x = \frac{A}{B}$ and $y = \frac{B}{P_1}$ satisfy the third and fourth equations of system (6.2.5) so that, by the previous theorem, x and y tend asymptotically to $\frac{1}{\sqrt{\beta_0}}$ and $(-\alpha + \sqrt{\beta_0})$ respectively, and (6.2.8) reduces to the Kolmogorov system

$$
\begin{aligned}
\dot{P}_1 &= P_1(\omega + F(P_1, P_2)) \\
\dot{P}_2 &= P_2 G(P_1, P_2).
\end{aligned}
\qquad (6.2.9)
$$

Since $F(P_1, P_2)$ satisfies Kolmogorov's conditions so does $\omega + F(P_1, P_2)$ and (6.2.9) possesses either a stable equilibrium or a stable limit cycle. Hence, depending on the parameters involved, the P_1, P_2 coordinates of trajectories of (6.2.8) converge as $t \to \infty$, to one of these

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solution possibilities. This result demonstrates again that the age-indiscriminate system behaves asymptotically like the corresponding predator-prey system in which age-structure is ignored.

Therefore ,incorporating age structure into the Kolmogorov model by means of a McKendrick-von Foerster equation for the prey population does not ultimately enhance the accuracy of the model. The reason why the age-indiscriminate model behaves in this way is clearly due to the omission of age-dependence in μ. This allows the M-F equation to be replaced by an O.D.E. which does not account for age structure. A more accurate model must necessarily include μ as a function of age.

6.3   Two species: "predation-on new-born" model

In the case where predation is on the young, it is assumed, for mathematical simplicty, that only newborn prey (or equivalently , only eggs) are eaten. The predator population is assumed to obey a Lotka-Volterra type equation, but now the birth rate $B(t)$, given by (6.1.3), is the underlying prey variable, i.e.

$$\dot{P_2} = -bP_2 + cBP_2. \qquad (6.3.1)$$

The age distribution $\rho_1(a, t)$ of the prey still obeys the evolution equation (6.1.1) but the death function μ is taken to be a constant with

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dependence on P_2 neglected, since predators have no effect on the survival of the prey past birth.

The number of newborn (eggs) $\rho_1(o,t)$ now equals $B(t)$ minus the number of newborn consumed. The model applied by Gurtin and Levine [96] in this case, assumes that this loss is proportional to the product of the number born and the number of predators, namely kP_2B, where k is a positive constant.

We have then,

$$\rho_1(o,t) = B(t) - kP_2(t)B(t). \qquad (6.3.2)$$

To avoid the problem of P_2 sufficiently large yielding $\rho_1(o,t) < 0$, $\rho_1(o,t)$ is defined more precisely as

$$\rho_1(o,t) = \max(B - kP_2B, 0).$$

Levine [97] replaces this function by the continuously differentiable approximation

$$\rho_1(o,t) = \frac{B}{1 + kP_2}, \quad k > 0 \qquad (6.3.3)$$

so that the number of surviving newborn decreases with P_2 in a saturating manner: and finds that the qualitative behaviour of the systems involving (6.3.2) or (6.3.3) remain the same.

As before, the systems (6.1.1 - 4), (6.3.1), (6.3.3), reduce to the autonomous system

$$\dot{P}_1 = -\mu_0 P_1 + \frac{B}{1 + kP_2}$$

$$\dot{B} = -\gamma B + \beta_0 A \tag{6.3.4}$$

$$\dot{A} = -\gamma A + \frac{B}{1 + kP_2}$$

$$\dot{P_2} = -bP_2 + cBP_2$$

Again the assumption $\beta_0 > \gamma^2$ ensures that the equilibrium $(0,0,0,0)$ corresponding to the extinction of both species is unstable. Stated differently this means that the prey population is self- sustaining in the absence of predators.
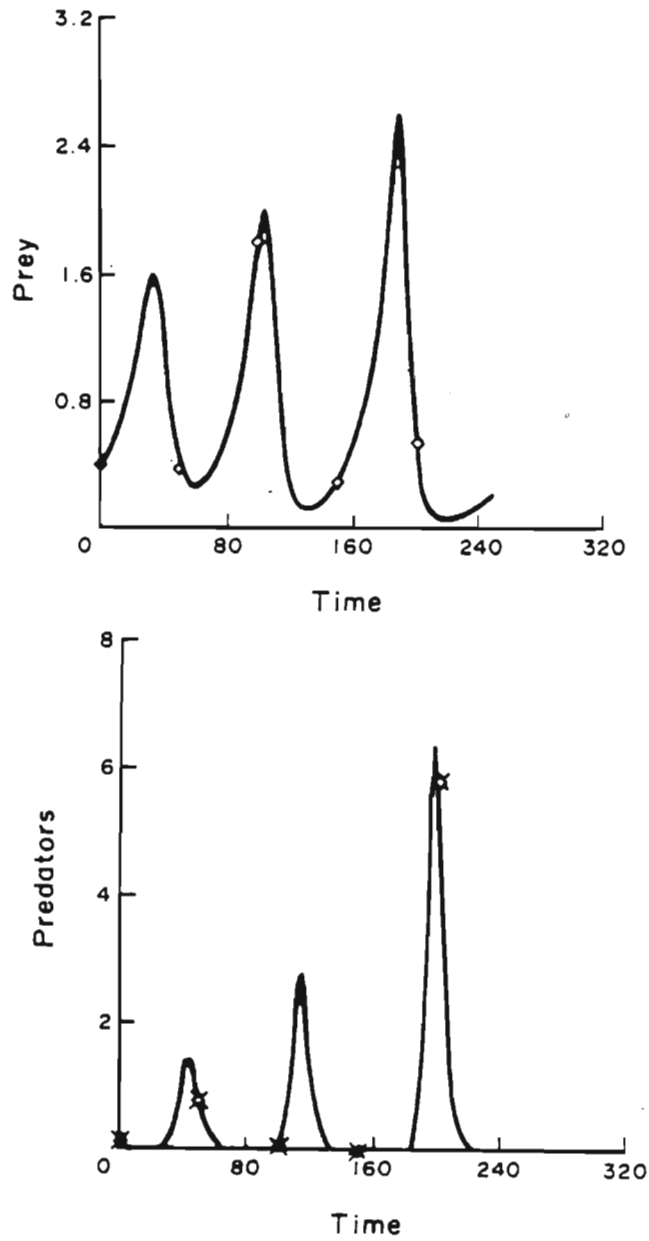
If $\beta_0 > \gamma^2$, the equations (6.3.4) have a single positive equilibrium at

$$\left(\frac{b\gamma^2}{\mu_0 c\beta_0}, \frac{b}{c}, \frac{b\gamma}{c\beta_0}, \frac{\beta_0 - \gamma^2}{k\beta_0} \right),$$

which can be shown to be unstable, since the Jacobian matrix has two negative eigenvalues and two complex conjugate eigenvalues with positive real part. Figure 6.3.1 reproduced from [97] shows the behaviour of the system (6.3.4) for typical parameter choices.

Fig. 6.3.1

Prey and predator populations as functions of time for equations (6.3.4) in the case where $\beta_0 = 5, \gamma = 2, b = c = \mu_0 = k = 1$.

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In fact Gurtin and Levine [96], and Levine [97], find that a consistent pattern emerges from computer data for every choice of parameters and initial conditions employed in (6.3.4) as long as $\beta_0 > (\mu_0 + \alpha)^2$ holds. The predator and prey populations oscillate with maxima increasing to infinity and minima decreasing to zero. Each local maximum for the prey population is followed by a maximum for the predator, then a minimum for the prey and a minimum for the predator, and so forth.

(It is noted in [97] that a mathematical proof of this qualitative behaviour has not been found, but attempts to explain it by variational methods are detailed in [97], [98] and [99].)

Nevertheless, although this model involving egg-eating predators is mathematically unstable, it could represent a biological phenomenon. Since the minima of both populations decrease to zero, the results correspond to extinction first of the prey and then of the predator. If the predators have alternative sources of food the model predicts extinction of the prey alone. This led Gurtin and Levine [96] to conjecture that the use of predators which selectively eat eggs or newborn could be a viable means of pest control. (An interesting application is Gurtin and Levine's reference to Carl Sagan's [100] theory that dinosaurs became extinct because mammals ate dinosaur eggs. The authors of [96] point out that although this theory cannot be accepted or rejected, they have provided a possible mathematical basis for it.)

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Once again we stress that the assumption that μ be constant is, in general, not an accurate one, but there are situations, as we mentioned earlier, for which we can justify its use. Should this assumption be appropriate, and should the remaining assumptions of system (6.3.4) be reasonable for the populations under consideration, then the above theory provides a clear description of the dynamics of the interacting populations.

Levine [97] considers enhancing the accuracy of the model described by (6.3.4) by accounting for the biological realities of self-limitation of the prey caused by limited food supply or overcrowding; and saturation of the predators appetite. He finds numerically that inclusion of these factors can have a stabilizing effect on the predator-prey system:

Levine models the effects of self-limitation by incorporating into the systems (6.1.1 - 4), (6.3.1), (6.3.3), a death function of the form

$$\mu = \mu_0 + sP_1, \; s > 0. \qquad (6.3.5)$$

(6.3.4) now becomes

$$
\begin{aligned}
\dot{P}_1 &= -\mu_0 P_1 - sP_1^2 + \frac{B}{1 + kP_2} \\
\dot{B} &= -\gamma B - sP_1 B + \beta_0 A \qquad (6.3.6) \\
\dot{A} &= -\gamma A - sP_1 A + \frac{B}{1 + kP_2} \\
\dot{P}_2 &= -bP_2 + cBP_2.
\end{aligned}
$$

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By applying eigenvalue analysis to this set of differential equations, Levine demonstrates how the stability properties of (6.3.6) change as s increases, that is, as the carrying capacity of the prey species decreases. In particular Levine establishes that the equilibrium can either be an asymptotically stable point or a stable limit cycle.

Secondly, satiation of the predator's appetite is accounted for in [97] in the following way: Until now the predator growth rate given by (6.3.1) depended on the total number of newborn prey consumed. However, there must exist a limit as to how much the predators can eat, and it would be more realistic for (6.3.1) to reflect this. Since $\frac{B}{1+kP_2}$ is the birth rate of prey minus the number of prey eaten, the number eaten can be shown to be $\frac{kBP_2}{1+kP_2}$.

Replacing BP_2 in (6.3.1) by this term leads to the new four-dimensional system

$$
\begin{aligned}
\dot{P_1} &= -\mu_0 P_1 + \frac{B}{1+kP_2} \\
\dot{B} &= -\gamma B + \beta_0 A \\
\dot{A} &= -\gamma A + \frac{B}{1+kP_2} \\
\dot{P_2} &= -bP_2 + \frac{ckBP_2}{1+kP_2}.
\end{aligned}
\qquad (6.3.7)
$$

The inclusion of $\frac{kBP_2}{1+kP_2}$ can also be interpreted as accounting for the effects of mutual interference of the predators since as P_2 increases,

the amount of prey available for consumption saturates to a constant value.

Again Levine demonstrates, by eigenvalue analysis of the Jacobian matrix at the unique positive equilibrium point of (6.3.7), that all eigenvalues have negative real part; hence the equilibrium point is stable.

Coleman and Frauenthal [101] extend this analysis to a model including both self-limitation effects for the prey, and appetite saturation for the predator. Their equilibrium point with both species present is shown to experience a Hopf bifurcation at a critical parameter and to manifest peculiarly shaped limit cycles.

In either of the above cases, these modifications evidently restore stable predator-prey coexistence in the two species model involving predation only on the very young.

This casts doubt now on the robustness of the previous extinction phenomena. In fact, the evidence suggests that only in the case where data collected for a predator-prey system indicates that the predator population can be treated as an age-independent system and that the assumption $\mu \equiv \mu_0$ is a valid one for the prey population (as it was for Nicholson's blowflies), can this strategy of pest control, by means of a predator eating the eggs or larvae of the prey, be potentially efficient.

6.4 Two-species: predation on all ages with extreme ages most vulnerable

According to Levine [102], there are numerous examples among insect populations, of predation only on the very young. However among vertebrates, predation is most likely to be on all ages but somewhat greater on the youngest and on the oldest members, since these are both very vulnerable.

In order to account for such a pattern of predation the death function of the prey must depend, in a complicated manner, on age.
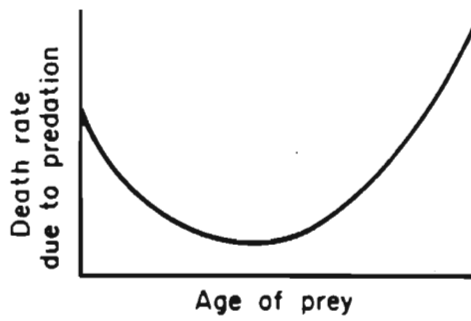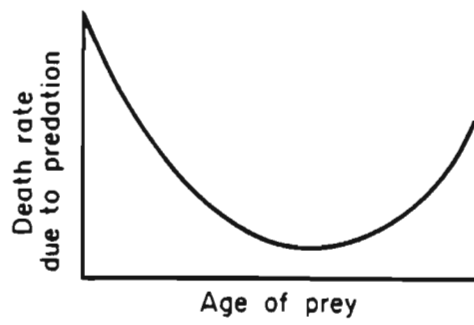
Levine [102], chooses the mortality function

$$\mu = \mu_0 + P_2(t)D(a),$$

having a component μ_0, which represents the age-independent natural death rate, and a component that is proportional both to the size of the predator population and to the predation rate $D(a)$. Possible forms of $D(a)$ illustrated in [102], are reproduced in figure 6.4.1.

Fig. 6.4.1

Schematic of two possible forms of the age-dependent predation function $D(a)$

$D(a)$ is expressed in the form

$$D(a) = r + \lambda_1 s_1(a) + \lambda_2 s_2(a) \qquad (6.4.1)$$

where r, λ_1 and λ_2 are positive constants with λ_1 and λ_2 measuring the amount of differential vulnerability among ages of prey. $s_1(a)$ is a function that is greatest for very young ages (eg. $c_1 \exp(-\nu_1 a); c_1, \nu_1 > 0$) and $s_2(a)$ is a function that is greatest for very old ages (eg. $c_2 \exp(\nu_2 a); c_2, \nu_2 > 0$).

Thus the equation for the prey population dynamics becomes

$$\frac{\partial \rho_1}{\partial a} + \frac{\partial \rho_1}{\partial t} + (\mu_0 + P_2(t)D(a))\, \rho_1 = 0, \qquad (6.4.2)$$

while the predator dynamics are assumed to be described by an age-weighted version of the Lotka-Volterra equation:

$$\dot{P}_2 = -bP_2 + cP_2 \int_0^\infty D(a)\rho_1(a,t)da. \qquad (6.4.3)$$

For the birth law the assumption is made that

$$\rho_1(o,t) = B(t) = \int_0^\infty \beta(a)\rho_1(a,t)da, \qquad (6.4.4)$$

where once again, $\beta(a)$ is assumed to be of the form (6.1.4), although Levine notes that the theory of [102] applies to more general forms of $\beta(a)$.

Regardless of its form, $\beta(a)$ must again obey the condition that ensures that the prey population is self-sustaining in the absence of

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predators, namely

$$R = \int_0^\infty \beta(a)e^{-\mu_0 a}da > 1.$$

Evidently, the inclusion of age dependence in this way, prevents the set of equations (6.1.4), (6.4.1), (6.4.2),(6.4.3), (6.4.4), from being transformed into a set of O.D.E.'s by means of Gurtin and MacCamy's moment technique.
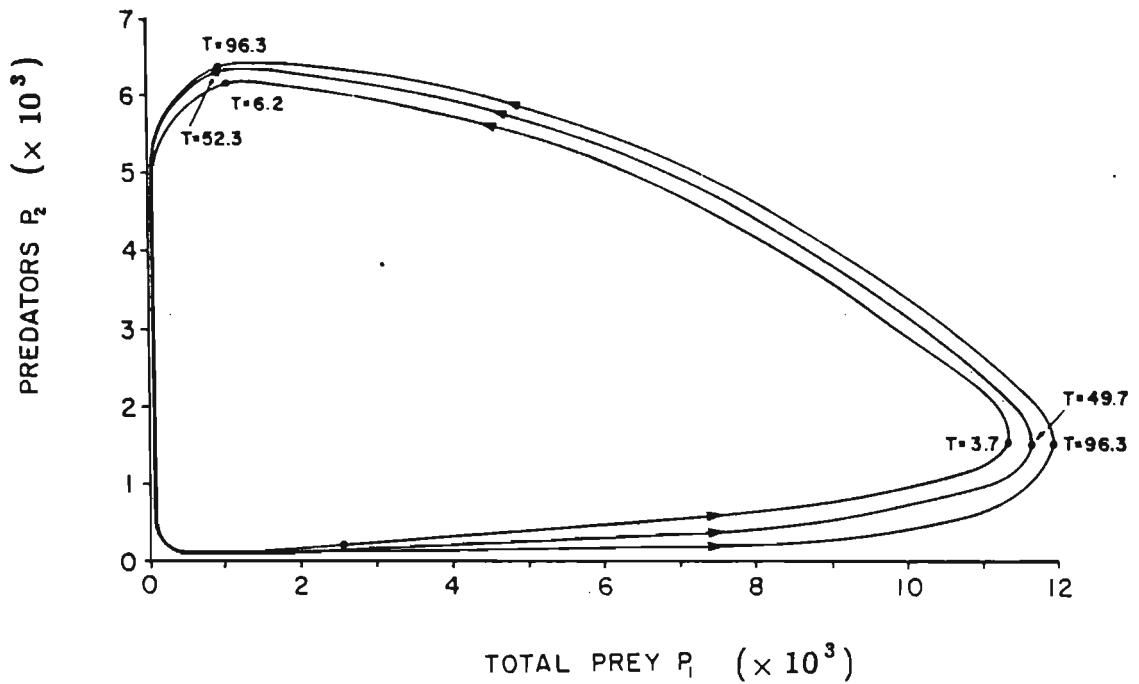
Notice though, that this system of mixed integrodifferential and partial differential equations does include both of the classes of systems described in sections 6.1 and 6.2 as special cases. The equations reduce to the "indiscriminate eating" system for $\lambda_1 = \lambda_2 = 0$, and to a simplified version of the "egg-eating" system when $D(a)$ is given by a constant multiple of the Dirac delta function.

Levine [102] examines system (6.1.4), (6.4.1 - 4) by means of a bifurcation theory for nonlinear integrodifferential equations developed by Cushing [103], treating λ_1 and λ_2 as bifurcation parameters. Levine's lengthy analysis will not be reproduced here - [98], [99], [102] and [103] provide the omitted details. The general result arising out of this work is that bifurcating periodic solutions exist for the system (6.1.4),(6.4.1 - 4), but that the stability properties of these solutions and the direction of bifurcation are not known. Levine [102] mentions that computer results hint that for many biologically reasonable parameter choices there are stable periodic solutions for $\lambda_1 > 0$, $\lambda_2 > 0$.

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Figure 6.4.2 given in [102] illustrates an example of such a result. The parameters were obtained from known data for a wolf / white- tailed deer predator-prey population. The simulations performed over a time interval of 100 years appear to show convergence to a periodic solution.

Fig. 6.4.2

Predator-prey oscillations generated by system (6.1.4), (6.4.1-4) using parameters appropriate to the wolf/white-tailed deer populations. ([102, p 913] provides the numerical parameter values and information concerning the time scale.

Levine remarks that this indicates stable co-existence between predator and prey. However, recalling the discussion of practical stability of the previous section we note that this limit cycle does not appear to be practically stable - the trajectories approach the predator axis rather closely and a more realistic conclusion would be extinction of the prey species. This in turn suggests that predation on the very young and very old might also provide a mechanism for biologically controlling certain prey populations.

6.5 One species: cannibalism

Cannibalism of the young has been documented in a variety of fish species such as perch, salmon and striped bass ([100]) and, it is commonly believed to function as a means of population control. The models that follow, were designed to test this belief. In each of these, (given in [100], [101], [104], [56]) it is assumed for mathematical simplicity, that only newborns are cannibalised.

The usual M-F/Kolmogorov system of the previous section is now replaced by the single M-F equation (6.1.1), with the subscript omitted.

Once again, (6.1.2) describes the total population size, (6.1.3) describes the birth rate, and the fecundity function is considered to be of the form (6.1.4).

In this case $\rho(o, t)$ represents the number of live newborn that survive

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cannibalism per unit time and it is assumed in [100], [101], [104], that

$$\rho(o,t) = g(B(t), P(t))B(t), \tag{6.5.1}$$

where $g(B, P)$ represents the fraction of newborns that survive cannibalism. Necessarily, $0 \leq g(B, P) \leq 1$.

Predation, or rather the conversion of newborn into food, is modelled by assuming that the death function μ of (6.1.1) depends on both $B(t)$ and $P(t)$, i.e.

$$\mu = f(B, P). \tag{6.5.2}$$

Once again the system (6.1.1-4), (6.5.1), (6.5.2), lends itself to the technique of Gurtin and MacCamy and reduces to the system of O.D.E.'s,

$$\begin{aligned}
\dot{P} &= -Pf(B,P) + Bg(B,P) \\
\dot{B} &= -Bf(B,P) - \alpha B + \beta_0 A \\
\dot{A} &= -Af(B,P) - \alpha A + Bg(B,P)
\end{aligned} \tag{6.5.3}$$

As usual, an additional assumption is needed to prevent extinction of the population. The net reproduction rate of the previous sections is replaced by the *net reproduction - survival rate* defined by

$$r(B,P) = g(B,P) \int_0^\infty \beta(a) e^{-f(B,P)a} da \tag{6.5.4}$$

$$= \frac{\beta_0 g(B,P)}{[f(B,P) + \alpha]^2}. \tag{6.5.5}$$

Since $e^{-f(B,P)a}$ is the probability of living to age a when the birth-rate is B and the total population size is P, $r(B, P)$ represents the

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expected number of surviving newborn born to a member of the population during its life-time.

Setting $\dot{P} = \dot{B} = \dot{A} = 0$ it follows that the relations

$$r(B, P) = 1, \qquad Pf(B, P) = Bg(B, P),$$

are necessary and sufficient for B and P to be co-ordinates of a nonzero equilibrium. The Jacobian matrix of (6.5.3) at (0,0,0) is

$$\begin{pmatrix} -\bar{\mu} & \gamma_0 & 0 \\ 0 & -(\bar{\mu} + \alpha) & \beta_0 \\ 0 & \gamma_0 & -(\bar{\mu} + \alpha) \end{pmatrix}$$

where $\bar{\mu} = f(0,0)$, $\gamma_0 = g(0,0)$ and it is assumed that $\bar{\mu}_0 > 0$.

A routine calculation confirms that the corresponding eigenvalues are

$$\lambda_1 = -\bar{\mu}, \; \lambda_2 = -\bar{\mu} - \alpha - \sqrt{\beta_0 \gamma_0}, \; \lambda_3 = -\bar{\mu} - \alpha + \sqrt{\beta_0 \gamma_0}.$$

From (6.5.5) it follows that, $r(0,0) < 1$ ensures all $\lambda_i < 0$, while $r(0,0) > 1$ results in $\lambda_1, \lambda_2 < 0$ and $\lambda_3 > 0$. In other words the equilibrium (0,0,0) is stable for $r(0,0) < 1$, but unstable for $r(0,0) > 1$.

As usual, the condition $r(0,0) > 1$ is imposed to prevent the possibility of extinction of the species. Gurtin and Levine [104], discuss three subcases of system (6.5.3):

A. In the first case cannibalism is important, not as a form of population control but as a primary source of food. The fraction

of surviving newborn is treated as a monotone increasing function of the ratio $\frac{B}{P}$, that is of the amount of available food per individual:

$$g(B, P) = Q(x), \ x = \frac{B}{P},\tag{6.5.6}$$

with $Q(x)$ increasing monotonically with x.

Setting $y = \frac{A}{P}$ in system (6.5.3) gives

$$
\begin{aligned}
\dot{x} &= -\alpha x + \beta y - Q(x)x^2 \\
\dot{y} &= -\alpha y + Q(x)x - Q(x)xy.
\end{aligned}
\tag{6.5.7}
$$

Gurtin and Levine analyse this system by considering possible transitions of the trajectories of the system. It is far more straight forward to apply standard linear stability analysis: (6.5.7) has a nonzero equilibrium point

$$(x^*, y^*) = \left(\frac{\sqrt{Q(x^*)\beta_0} - \alpha}{Q(x^*)}, \ \frac{\sqrt{Q(x^*)\beta_0} - \alpha}{\sqrt{Q(x^*)\beta_0}} \right),$$

which is positive providing

$$\sqrt{Q(x^*)\beta_0} > \alpha.\tag{6.5.8}$$

Introducing the variables $X = x - x^*$, $Y = y - y^*$, and substituting into (6.5.7) yields a system, the linearized form of which

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is

$$\dot{X} = X\left[-\alpha - 2Q(x^*)x^* - \dot{Q}(x^*)x^{*2}\right] + \beta_0 Y$$

$$\dot{Y} = X\left[Q(x^*) + \dot{Q}(x^*)x^* - \dot{Q}(x^*)x^* y^* - Q(x^*)y^*\right]$$

$$+ Y\left[-\alpha - x^* Q(x^*)\right].$$

The corresponding polynomial is given by

$$\lambda^2 + \lambda(2\alpha + 3Q(x^*)x^* + \dot{Q}(x^*)x^{*2}) +$$

$$(\alpha + 2Q(x^*)x^* + \dot{Q}(x^*)x^{*2})(\alpha + x^* Q(x^*)) +$$

$$(\dot{Q}(x^*)x^* + Q(x^*))(\beta_0 y^* - \beta_0) = 0., \qquad (6.5.9)$$

It is readily verified that the constant term of this polynomial is equivalently

$$2Q^2(x^*)x^* + \dot{Q}(x^*)(\sqrt{Q(x^*)\beta_0} - 2\alpha),$$

so that, since $\dot{Q}(x) > 0$, the further requirement that $\sqrt{Q(x^*)\beta_0} > 2\alpha$ guarantees that all coefficients of (6.5.9) are positive and hence that (6.5.9) has negative real part roots. The latter requirement is therefore necessary and sufficient for the stability of positive equilibria of (6.5.7). Moreover, if $\sqrt{Q(0)\beta_0} > 2\alpha$, the above result follows since $Q(x)$ is assumed to be monotonically increasing.

Now $P(t)$ can be obtained by solving

$$\dot{P} = P\left[-f(xP, P) + xQ(x)\right], \qquad (6.5.10)$$

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and since x approaches a limit $x^* > 0$, the asymptotic behaviour
of (6.5.10) is described by

$$\dot{P} = P\left[-f(x^*P, P) + x^*Q(x^*)\right].\qquad(6.5.11)$$

Due to self-limiting effects it is likely that $f(xP, P)$ is an increasing function of P. Under this assumption, it follows from the solution of (6.5.11) that

if $f(x^*P^*, P^*) = x^*Q(x^*)$ at some P^* then
$P(t) \to P^*$

if $f(x^*P^*, P^*) < x^*Q(x^*)$ for all P, then
$P(t) \to \infty$

while

if $f(0,0) > x^*Q(x^*)$, then
$P(t) \to 0$ as $t \to \infty$.

Such is the type of behaviour one would expect since $f(xP, P)$ is the death rate and $xG(x)$ can be thought of as the survival rate, (the number surviving birth, per unit population size), so that if for example, $f(x^*P^*, P^*) < x^*Q(x^*)$ a population "explosion" must result.

B. In the next case cannibalism is assumed to operate as a means of population control rather than as a means of obtaining food. For this reason g is chosen to depend explicitly on the total population P,

$$g(B, P) \equiv g(P).\qquad(6.5.12)$$

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It is assumed further that $g \in C^1$, that $g(P)$ decreases monotonicaly with P, and that $g(0) = 1$, implying that all newborn survive in the absence of predators.

(6.5.12) is augmented with the simplest possible assumption concerning f, namely

$$f(B, P) = \mu_0 = \text{ constant.}$$

In this case equations (6.5.3) take the form

$$
\begin{aligned}
\dot{P} &= -\mu_0 P + g(P) B \\
\dot{B} &= -(\mu_0 + \alpha) B + \beta_0 B z \\
\dot{z} &= g(P) - \beta_0 z^2,
\end{aligned}
\tag{6.5.13}
$$

where Gurtin and Levine [104] introduce $z = \frac{A}{B}$ for ease of analysis.

The Jacobian matrix at the unique positive equilibrium (P^*, B^*, z^*) can be shown to be

$$
\begin{pmatrix}
-\mu_0 + B^* g'(P^*) & \frac{(\mu_0 + \alpha)^2}{\beta_0} & 0 \\
0 & 0 & \beta_0 B^* \\
g'(P^*) & 0 & -2(\mu_0 + \alpha)
\end{pmatrix}.
$$

Further routine calculation confirms that all roots of the corresponding characteristic polynomial have negative real part, indicating that system (6.5.13) converges to a unique positive equilibrium.

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However, we note that it is often more realistic for $f \equiv f(P)$, so that density dependent effects are included in the mortality function. Replacing μ_0 in the previous model by $f(P)$ and working through the same analysis, we find that the Jacobian Matrix of the system at an equilibrium point (P^*, B^*, z^*), $z^* = \frac{f(P^*) + \alpha}{\beta_0}$, is

$$
\begin{pmatrix}
-f(P^*) - f'(P^*) + g'(P^*)B^* & g(P^*) & 0 \\
-f'(P^*)B^* & 0 & \beta_0 B^* \\
g'(P^*) & 0 & -2(f(P^*) + \alpha)
\end{pmatrix},
$$

having the characteristic polynomial

$$
\lambda^3 + \lambda^2 \{2(f(P^*) + \alpha) + f(P^*) + f'(P^*) - g'(P^*)B^*\}
$$

$$
+ \lambda \{g(P^*)f'(P^*)B + 2(f(P^*) + \alpha)[f(P^*) + f'(P^*) - g'(P^*)B^*]\}
$$

$$
2g(P^*)f'(P^*)B^*(f(P^*) + \alpha) - g(P^*)g'(P^*)B^*\beta_0 = 0.
$$

If $f(P)$ is strictly increasing and $g(P)$ is, as assumed earlier, strictly decreasing, the coefficients of the above equation are all positive so that the equilibrium point, (P^*, B^*, z^*) is stable. Thus, including the more realistic assumption that f is a monotone increasing function of P, does not alter the previous result. However, a biologically more plausible choice of $f(P)$, often used in analysis, is one that allows $f(P)$ to be large for either small or large P, and to reach a relative minimum between these extreme values. (Such a choice, was applied in the "biochemical

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reaction tank" models of chapter 4.) Work along these lines has been produced by Swick [105] who establishes conditions on $f(P)$ and $g(P)$ for the existence of periodic solutions of a model having much the same form as (6.5.3). Space does not permit this analysis to be repeated here and we refer to [105] for the details involved.

An extension on the models of A and B is model C of [104], in which cannibalism is considered to be both a means of population control and a source of food.

C. Here f and g are chosen to depend on both B and P. Defining

$$L(x, P) = f(xP, P), \quad Q(x, P) = g(xP, P); \quad x = \frac{B}{P},$$

it is assumed that $f(B, P)$ and $g(B, P)$ are class C^1 functions for $B \geq 0$, $P \geq 0$, so that $L(x, P)$ and $G(x, P)$ are class C^1 for $x \geq 0$, $P \geq 0$. For convenience the notation $Q(x, 0) = g(0, 0) = \gamma_0$, $L(x, 0) = f(0, 0) = \bar{\mu}$, $x \geq 0$ is introduced again.

In addition it is assumed that

$$(a)L > 0, \qquad (b)\frac{\partial L}{\partial x} \leq 0, \qquad (c)\frac{\partial L}{\partial P} \geq 0, \qquad (6.5.14)$$

$$(d)Q > 0, \qquad (e)\frac{\partial Q}{\partial x} > 0, \qquad (f)\frac{\partial Q}{\partial P} < 0, \text{ for } x > 0, \ P > 0,$$

and that

(a) $\gamma_0 = 1$

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(b) $\lim_{P \to \infty} \left[\sup_{z \ge 0} Q(x, P) \right] = 0$ \hfill (6.5.15)

(c) $\beta_0 > (\alpha + \bar{\mu})^2.$

Assumption (6.5.14b) asserts that the probability of dying decreases as the amount of food available per individual increases. (6.5.14c) states that the probability of dying increases with increasing population size. The restriction (6.5.14e) is analogous to the assumption that $Q(x)$ of model A be an increasing function of x. Assumption (6.5.14f) models cannibalism as a form of population control as it implies that the fraction of newborn surviving decreases with increasing population size. The assumptions (6.5.15 a,b) strengthen this last condition as they require that all newborn survive in the limit $P \to 0$ and that no newborn survive in the limit $P \to \infty$. Finally, (6.5.15c) indicates that as $P \to 0$ the net reproduction-survival rate $r(0,0)$, exceeds one.

Introducing the auxiliary variables

$$x = \frac{B}{P}, \ z = \frac{A}{B},$$

the associated system is now

$$
\begin{aligned}
\dot{P} &= P\left[-L(x, P) + xQ(x, P)\right] \\
\dot{x} &= x\left[-\alpha + \beta_0 z - xQ(x, P)\right] \\
\dot{z} &= Q(x, P) - \beta_0 z^2
\end{aligned}
\tag{6.5.16}
$$

Gurtin and Levine show by means of a detailed method involving Poincaré maps and the Brouwer fixed point theorem ([98], [99] or [104]

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provide the full details), that the above assumptions result in system (6.5.16) having either stable equilibria or periodic solutions. In [104] these authors remark that their method makes no statement about the stability of the periodic solution, but that computer simulations indicate stable limit cycle behaviour for a wide choice of parameters.

The results obtained for the models of A, B and C all seem to imply that a population which cannibalises itself can achieve a stable balance. In general $P(t)$ converges to a constant value or oscillates (in a stable fashion for most parameter choices) about a constant value. This lends support to the claim mentioned earlier, that cannibalism is a means of population control.

Gurtin and Levine ([98], [104]) point out that an analogy can be drawn between cannibalism and other population mechanisms which affect survival. In particular, they quote a reference [106] supporting the idea that there is a tendency for populations to compensate for increased mortality (due either to hunting or pollution) by a higher rate of egg survival. Thus, decreasing the population P, will increase the number of newborn which survive. This type of behaviour is also accounted for by (6.5.1) and (6.5.12) so that the models of B can also be applied to these situations.

According to Gurtin and Levine ([98], [104]) ecologists differ as to how effective this compensation is for mortality due to pollution. They discuss ([98, pp 158-160]) the recent proposal of building a power

plant near the Hudson River in the U.S.A. The utilities argued that the natural compensation mechanism of the fish (bass) population in the river would prevent the power plant from seriously reducing the bass numbers. Several counter- arguments have been given to this; the most notable being that mortality due to a power plant is harder to compensate for than mortality due to fishing or predation, because unlike fishermen and predators, power plants will not "go elsewhere" if fish become scarce.

Death in such a population due to pollution is age-dependent since apparently [99, p414], power plant pollution affects mostly the younger ages. Once again the assumption (6.5.1) as well as those of (6.5.14) and (6.5.15) can be a means of accounting for this, and as Levine [99] proposes, modifications to the previous model could shed light on the efficacy of compensation as a means of population control.

Frauenthal [56] has also studied a "cannibalism upon newborn" model of the form (6.5.3) but chooses $f(B,P)$ to be the linear function

$$f(B,P) = f(P) = \mu_0 + rP, \; \mu_0, r > 0,$$

and replaces (6.5.1) by

$$\rho(o,t) = \max\left\{B - \frac{BP}{1+kB}, \; 0\right\}; \; k > 0. \tag{6.5.17}$$

As usual, the egg reproduction rate $B(t)$ is given by

$$B(t) = \int_0^\infty \beta(a)\rho(a,t)da; \qquad \beta(a) = \beta_0 a e^{-\alpha a}, \; \alpha > 0.$$

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Frauenthal works under the assumption that all unhatched eggs are the victims of cannibalism, and that there are alternative food sources available for the adults, but these are not explicitly included in the model. Hence, the number of eggs eaten depends upon the product of the number of eggs and the number of adults, but with a satiation factor included, to account for the fact that in times when the amount of eggs produced is large, the amount consumed by the adults can only increase up until their customary appetite is satiated. Thus the number of cannibalized eggs is

$$B(t) - \rho(o, t) = \frac{B(t)P(t)}{1 + kB(t)}, \quad k > 0, \qquad (6.5.18)$$

which explains the choice of (6.5.17).

Strictly speaking, there should be one more multiplicative constant on the right hand side of (6.5.18); without loss of generality it can be absorbed into the parametrization, and $P and B$ can then be scaled by the same constant.

Under these changes (6.5.3) becomes

$$\dot{P} = -[\mu_0 + rP]P + \max\left\{B - \frac{BP}{1 + kB}, 0\right\}$$

$$(6.5.19)$$

$$\dot{B} = -[\mu_0 + \alpha + rP]B + \beta_0 A$$

$$\dot{A} = -[\mu_0 + \alpha + rP]A + \max\left\{B - \frac{BP}{1 + kB}, 0\right\}.$$

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(Frauenthal notes that this maximum function is inconvenient to treat analytically. When equations are solved analytically, the non-zero term in the maximum function is used and then checked a *posteriori* for suitability. In numerical simulations the maximum function is employed because it presents no computational difficulties.)

As this set of equations does not yield easily to analysis, Frauenthal proceeds to suppress certain features by setting some parameters to zero:

Firstly setting $r \equiv 0$, $k \equiv 0$ gives a model excluding carrying capacity and appetite satiation terms. By means of linearized stability analysis, it is not difficult to show that under the condition $\beta_0 > (\mu_0 + \alpha)^2$, all solutions approach the unique positive equilibrium

$$(P^*, B^*, A^*) = \left[1 - \frac{(\mu_0 + \alpha)^2}{\beta_0}\right] \left(1, \frac{\mu_0 \beta_0}{(\mu_0 + \alpha)^2}, \frac{\mu_0}{\mu_0 + \alpha}\right).$$

Setting $r \equiv 0, k > 0$, that is suppressing only the carrying capacity term, Frauenthal applies a numerical technique to illustrate the existence of a Hopf bifurcation. In particular, for the choice $\mu_0 = 0,015$, $\alpha = 1,0$, $k = 1,5$, and treating β_0 as a bifurcation parameter, numerical experimentation confirms that somewhere on the interval $2,83 < \beta_0 < 2,85$, the local properties of the equilibrium point switch from stable to unstable as β_0 is increased. Indeed, a Hopf bifurcation into a stable limit cycle is found to occur at $\beta_0 = 2,8368$.

Frauenthal applies this analysis to a specific situation: A crab popula-

tion (the Northern California Dungeness crab - references concerning it are listed in [56]), is known to practice cannibalism of its young. This species is harvested regularly by removing adult males and eversince this exploitation, large amplitude, periodic oscillations in the number of adult crabs have been observed.
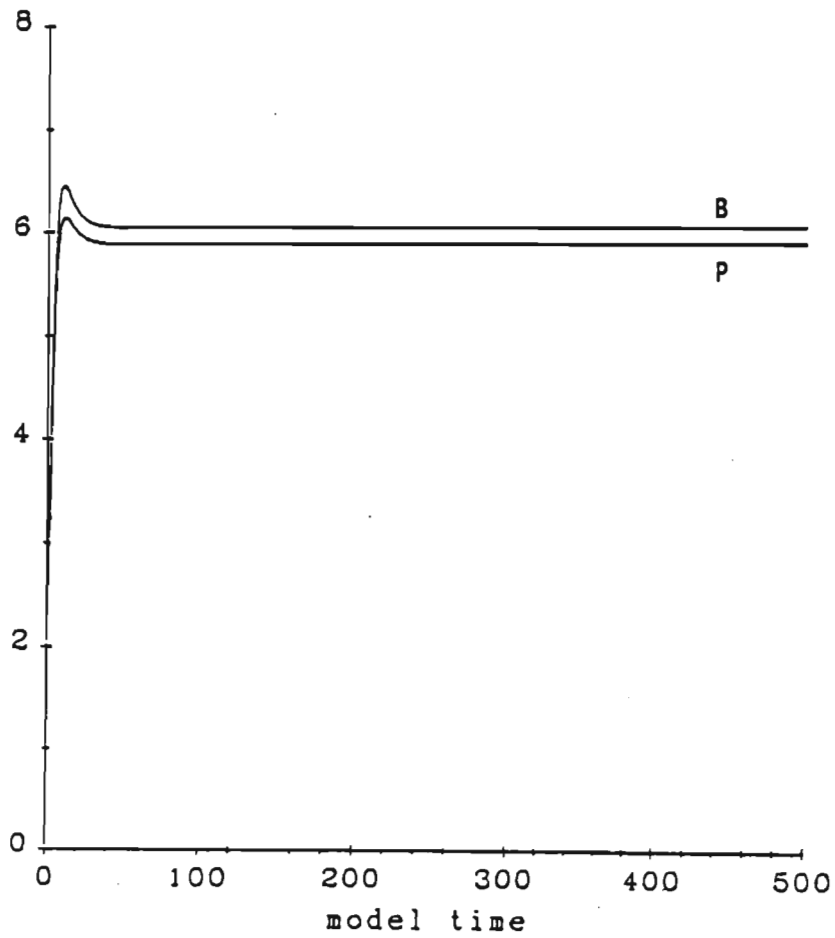
As pointed out in [56], one expects the effect of harvesting the male crabs to be a reduction in the value of the fertility as measured by β_0, since fewer males would make it difficult for females to find mating partners.

However, the model just mentioned predicts that an *increase* rather than a *decrease* in β_0 leads to the onset of stable cyclic behaviour and as such, does not appear to present an explanation for these observations.

However in concluding [56], Frauenthal studies the full model (6.5.19). By means of numerical methods it is shown that for fixed μ_0, r, α and k, the model manifests a shift from a stable point to a stable limit cycle as β_0 decreases from $5,0$ to about $4,8$. Taking $\beta_0 = 4,9$, it is shown in [56] that the only stable, positive equilibrium point is nonoscillatory so that the population approaches and then remains at this equilibrium point. A computer generated trace of this situation is shown in figure 6.5.1, reproduced from [56, p 96].
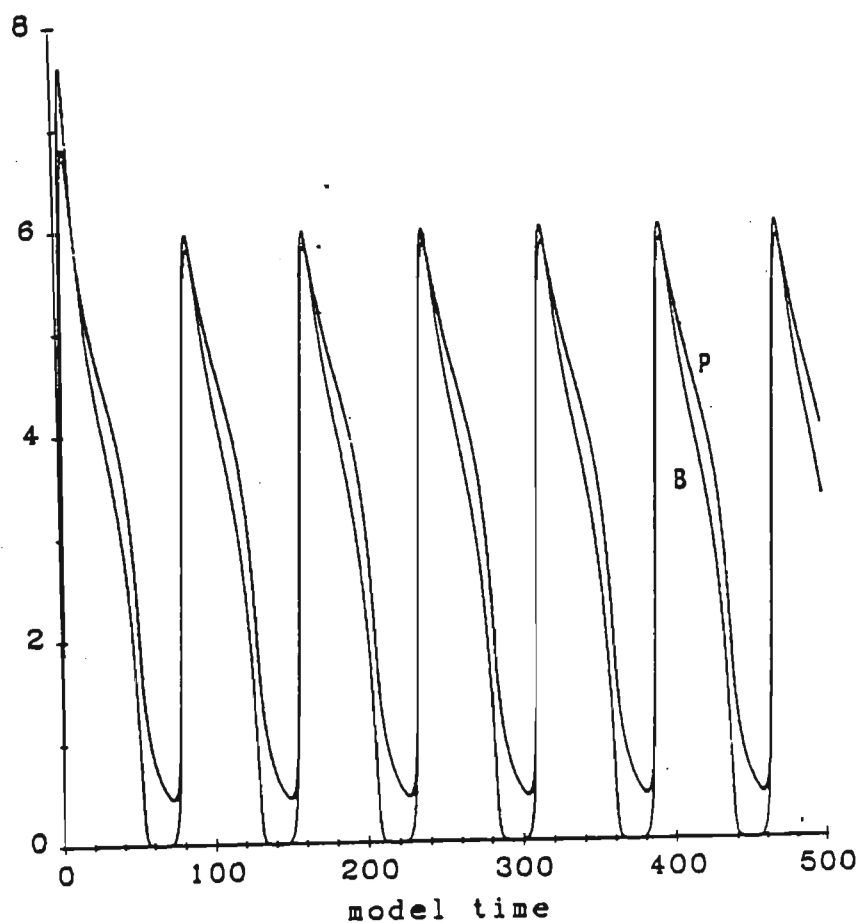
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Fig 6.5.1

Computer simulation of the model (6.5.19) with both carrying capacity and appetite satiation, for which $\mu_0 = 0,015, r = 0,07 \ \alpha = 1,0,$ $k = 1,5$ and $\beta_0 = 4,9.$

Supposing that an external effect reduces β_0 to 4,8, it is demonstrated that the stable nonoscillatory equilibrium point vanishes and the system shifts to exhibiting stable limit cycle behaviour about the only remaining positive equilibrium position. This solution is illustrated in figure 6.5.2, given in [56, p.97].

Fig. 6.5.2

Computer simulation of model (6.5.19) with both carrying capacity and appetite satiation, for which $\mu_0 = 0,015, r = 0,07, \alpha = 1,0, k = 1,5$ and $\beta_0 = 4,8$.

The reasons for this catastrophic behaviour are detailed in the Frauenthal reference and will not be reproduced here. With reference to the Dungeness crab population, Frauenthal has now proposed a mechanism explaining the onset of the regular cycles in the population size.

6.6   Harvested age-dependent predator-prey models

A natural extension of the theory of section (3.5) in which we examined harvested single species, age-dependent models, and that of section (5.5) where harvested age-independent predator-prey systems were dealt with, is to analyse harvested age-dependent predator-prey models.

As usual, the simplest type of harvesting to consider is constant-yield harvesting. For example, consider the age- indiscriminate predation model (6.1.2-5), (6.2.1) into which a constant-yield strategy $v(a)$, has been included for the prey so that,

$$H = \int_0^\infty v(a)da,$$

the total number of members harvested per time is constant. Suppose further that the predators are removed at a constant rate, K.

Thus (6.2.1) is replaced by

$$\frac{\partial \rho_1}{\partial a} + \frac{\partial \rho_1}{\partial t} = -(\mu_0 + rP_2)\,\rho_1 - v(a), \qquad (6.2.1)'$$

and (6.1.5) becomes

$$\dot{P_2} = -bP_2 + cP_1P_2 - K. \qquad (6.1.5)'$$

It is readily verified that Gurtin and MacCamy's moment technique still applies but that system (6.1.2), (6.1.3), (6.1.4), (6.1.5)', (6.2.1)' now reduces to

$$
\begin{aligned}
\dot{P_1} &= -\mu_0 P_1 - rP_1 P_2 + B - H \\
\dot{B} &= -\gamma B - rBP_2 + \beta_0 A - \beta_0 I \\
\dot{A} &= -\gamma A - rAP_2 + B - J \qquad (6.6.1) \\
\dot{P_2} &= -bP_2 + cP_1 P_2 - K,
\end{aligned}
$$

where

$$
\begin{aligned}
I &= \beta_0 \int_0^\infty a e^{-\alpha a} v(a)\,da, \text{ and} \\
J &= \int_0^\infty e^{-\alpha a}\,da.
\end{aligned}
$$

Eigenvalue analysis will yield conditions on the parameters of the model under which stable point behaviour is guaranteed. In particular, one can obtain information about the harvesting strategies that will ensure stable coexistence of predator and prey. Also, by choosing a parameter as a bifurcation parameter, analysis along the lines of

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that applied in chapter 4, could give ranges of values of H and K for which Hopf bifurcation into stable limit cycles results.

Similar analysis could be applied to the other age-selective predation models covered in this chapter.

Constant-effort harvested systems are not as amenable to analysis. We could replace K in $(6.1.5)'$ by KP_2, but replacing $v(a)$ in $(6.2.1)'$ by the usual substitute $E(a,t)\rho(a,t)$, prevents the application of the moment technique. If however we set $E(a,t) \equiv E(t)$, (which is the approach used by Gurtin and Murphy in [50], in studying a harvested single- species M-F model), so that the assumption is made that prey of all ages are harvested with equal intensity, then a system of O.D.E.'s can be obtained. For example,the age-indiscriminate predation model under constant-effort harvesting becomes (6.6.1), with each of H, I, J and K replaced by EH, EI, EJ and KP_2 respectively.

The inclusion of harvesting terms into predator-prey systems of the type discussed in this chapter is mentioned here because no literature seems to have appeared on this topic. With the material for these unharvested systems providing the basis, such further work would not be difficult, and might provide biologically valuable information for certain harvested predator- prey systems.

6.7 The use of M-F equations to describe the dynamics of both predator and prey

Among the few works that have appeared on this topic is Auslander, Oster, and Huffacker's [61] model of a general predator-prey system in which the life cycle of the predator is divided into two parts - adults and immature stages:

The M-F equation

$$\frac{\partial \rho_2}{\partial a} + \frac{\partial \rho_2}{\partial t} = -\mu_2(a,t)\rho_2, \tag{6.7.1}$$

is chosen to model the predator dynamics, where $\mu_2(a,t)$ is the predator mortality function.

The mortality function of the prey is taken to depend on the number of adult predators, the number of prey (thus including the likelihood of self-limitation), and on the number of prey at the age at which they are subject to predation. The prey dynamics are thus described by

$$\frac{\partial \rho_1}{\partial a} + \frac{\partial \rho_1}{\partial t} = -\mu_1(a,t,P_1,P_2,P_1^0,P_2^0)\rho_1, \tag{6.7.2}$$

where,

$$P_1 = \int_0^\infty \rho_1(a,t)da, \tag{6.7.3}$$

is the total number of prey,

$$P_1^0 = \int_{\epsilon}^{\epsilon+\delta} \rho_1(a,t)da, \qquad (6.7.4)$$

with $[\epsilon, \epsilon +\delta]$ denoting the age interval during which prey are subject to predation, is the number of prey attacked by predators and

$$P_2^0 = \int_{\alpha}^{\alpha+\gamma} \rho_2(a,t)da, \qquad (6.7.5)$$

is the number of adult predators. Here α and $\alpha + \gamma$ denote the onset of adulthood (i.e. breeding age) and maximum life expectancy respectively.

A realistic assumption for the birth rate of the predator is that it depends on the number of adult predators, that is, those in the age interval $(\alpha, \alpha + \gamma)$, and on the food supply, that is, the number of prey that can be consumed. Thus Auslander et al set

$$\rho_2(o,t) = \int_{\alpha}^{\alpha+\gamma} \beta_2(a,t,P_1^0)\rho_2(a,t)da. \qquad (6.7.6)$$

The birth rate of the prey is similarly defined as

$$\rho_1(o,t) = \int_{m}^{n} \beta_1(a,t,P_1^0(t-\tau))\rho_1(a,t)da, \qquad (6.6.7)$$

where (m,n) is the breeding age-interval for the prey.

The dependence of the maternity function at time t on $P_1^0(t-\tau)$, the number of prey τ time units earlier, is a sensible choice since if
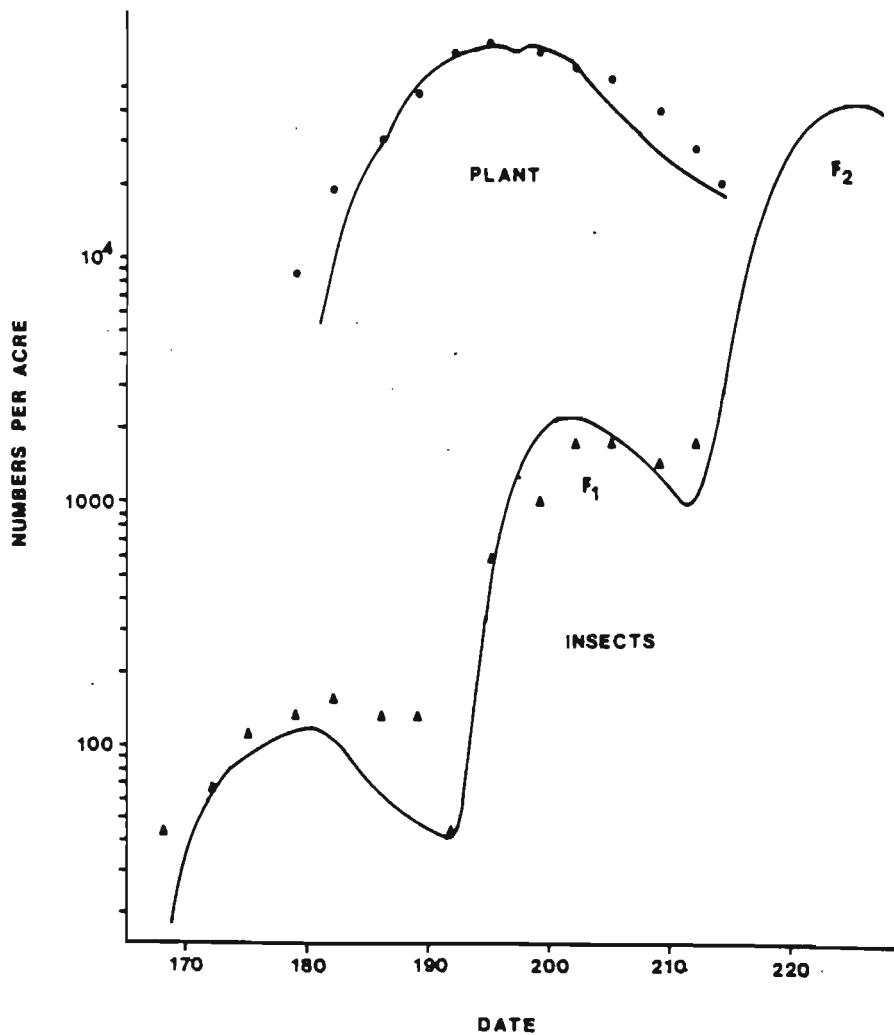
for example, predation in the past removes a large number of prey, there will be few adults in the present available for mating, and β_1 will subsequently be reduced.

The above system constitutes the Auslander et al predator-prey model. The next step is to choose functional forms for β_1, μ_1, β_2 and μ_2. Auslander et al do this by fitting curves to experimental data collected for a wasp-moth predator- prey system. Various simplications are made and forms for the mortality and fecundity functions are proposed. (Space does not permit this analysis to be repeated here but [61, pp 372-376] provides the omitted details.) However, the model remains far too complex to study analytically and must be examined through computer simulation. The simulations of [61] indicate that for many parameter choices the system exhibits a periodic solution and Auslander et al conjecture that this arises as a result of a Hopf bifurcation.

Feldman and Curry [107] have developed a system of M-F equations to represent the dynamics of a particular biological predator- prey system involving a species of weevil as the predator and a cotton plant (which they indicate as being an age-dependent system) as prey. Their model is very detailed and the assumptions concerning the birth rates, fecundity and death functions are far too lengthy to reproduce here. An iterative numerical technique is applied to approximate the solution and figure 6.7.1, given in [107, p399] illustrates the agreement between the theoretical and experimental data.

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Fig. 6.7.1

Model comparisons with experimental data for a boll weevil-cotton plant (*Gossypium hirsutum*) predator-prey system. Details of the time scale and other parameters are available in [107].

As for Nicholson's blowfly population mentioned in section (3.3.3), this excellent agreement emphasises the point that when age-structure is a relevant factor, and when the death, birth and fertility functions are modelled accurately, an M-F system can closely model reality.

It would be naive to concentrate on the M-F/Kolmogorov models alone as means of modelling real-world situations. The need for a high degree of realism so that the effect of untried harvesting (and other) strategies can be reasonably well predicted requires, in general, the use of M-F equations to model the dynamics of both predator and prey, and as such it becomes necessary to use and develop numerical techniques of solution.

Chapter 7

Conclusion

The emphasis throughout this study has been on investigating and relating the properties of a number of simple, conceptual M-F models. Complex M-F systems constructed to describe the dynamics of specific populations (although few in the current literature) have been purposely avoided, as the numerical methods involved in parameter estimation and solution of such systems could warrant a separate treatment.

The assumptions involved in the models examined were not always biologically plausible. Yet in concentrating on such analytic models, the necessary groundwork has been laid and useful quantitative and qualitative features of the M-F system have been established.

A number of uninvestigated topics worthwhile to further research have been highlighted. As a final example, consider the generalized M-F model that involves a logistic density dependent growth and density

dependent death rate such that the usual M-F equation becomes

$$\frac{\partial \rho}{\partial a} + \frac{\partial \rho}{\partial t} = -\mu(a,t,\rho)\rho \left[1 - \frac{\rho}{k(t)}\right],$$

where $k(t)$ represents a time-dependent carrying-capacity term. Brief mention is made of this model in [108], where Witten points out that numerical methods for equations of this type are sparse but that there is good reason for having to deal with such equations, both from a numerical as well as an analytic point of view.

This is by no means an exhaustive review of the current state of information concerning the M-F model - the references provided can be consulted for the directions of other developments. Nevertheless, in making accessible an overview of the literature concerning the M-F model, it is hoped that this study will provide incentive for further work in the field of age-dependent population dynamics.

Appendix 2.1

Lopez [16, p 11] proves that $B(t)$ is a continuous function by means of the following inductive argument: In section 2.2 it is established that

$$G(t) = \int_t^\infty \beta(a)\varphi(a-t)\sigma(a,t)da = \int_t^\infty \beta(a)\varphi(a-t)\frac{\pi(a)}{\pi(a-t)}da,$$

accounts for the expected number of births from mothers in the initial population while

$$B(t) = \int_0^t \beta(a)B(t-a)\pi(a)da,$$

accounts for the number of births to mothers who were born sometime between the initial moment and time t. If the assumptions (i), (v) and (ix) on π, β and φ hold, then necessarily $G(t)$ is continuous.

Denoting by $B_k(t)$ the expected number of births coming from the k-th generation of mothers, we have the recurrence relation

$$B_{k+1}(t) = \int_m^n \beta(a)B_k(t-a)\pi(a)da.$$

$(G(t) = 0$ for $t > n$ since $\beta(a) = 0$ for $a > n$.)

If $B_k(t)$ is continuous, then so is $B_{k+1}(t)$. This, together with the continuity of $B_1(t) = G(t)$, proves the continuity of $B_k(t)$ for all k. Now, the total number of births at time $t, B(t)$, can be attributed either to mothers from the first generation or to mothers from the

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second, and so on. In this way $B(t)$ can be expressed as a sum of a finite number of continuous functions and thus, will itself be continuous.

An alternative proof is given in [17, pp 249-250].

Appendix 2.2

The proof given here is along the lines of that presented by Langhaar [11, pp 201-202].

Let $\pi(a, T)$ denote the probability that an individual born at time T survives to age a. Of the N individuals born at time T the expected number that will survive to age a is $N\pi(a, T)$ and accordingly, the expected number that will survive to age $a + da$ is $N\pi(a, T) + N\pi_a(a, T)da$.

Hence, the expected number that will die in the age interval $(a, a + da)$ is $-N\pi_a(a, T)da$. From our discussion of $\mu(a, t)$ in section 2.1 it follows that $\mu(a, T + a)da$ is the proportion of individuals aged a at time $T + a$ that will die in the age interval $(a, a + da)$. Among the N individuals born at time T the expected number that will die in $(a, a + da)$ is the product of this proportion with $N\pi(a, T)$.

Thus,

$$-N\pi_a(a, T)da = N\pi(a, T)\mu(a, T + a)da.$$

Integrating and noting that $\pi(o, T) = 1$ yields

$$\pi(a, T) = \exp\left\{-\int_0^a \mu(\alpha, T + \alpha)d\alpha\right\}. \qquad (A.2.2.1)$$

Further, if an individual is of age a at time t and $t > a$ such that $T = t - a$, we have

$$\pi(a, t - a) = \exp\left\{-\int_0^a \mu(\alpha, t - a + \alpha)d\alpha\right\}.$$

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Now consider those individuals of age a at time t, but where $a \geq t$. At the initial time $t = 0$ (which we shall denote by time T' for the moment) these were of age $a - t$ and were born at time $T = T' - a + t$. We shall denote by $P(a - t, a, T)$ the probability that a randomly chosen individual of age $a - t$ who was born at time T will survive to age a.

Since survival from birth to age a may be regarded as survival to age $a - t$ followed by survival from age $a - t$ to age a, the theorem on the probability of the simultaneous occurrence of two events yields

$$P(a - t, a, T) = \frac{\pi(a, T)}{\pi(a - t, T)}.$$

Now substituting into (A.2.2.1) we have

$$P(a - t, a, T) = \frac{\exp\left\{-\int_0^a \mu(\alpha, T + \alpha)\right\} d\alpha}{\exp\left\{-\int_0^{a-t} \mu(\alpha, T + \alpha)\right\}} d\alpha$$

$$= \exp\left\{-\int_{a-t}^a \mu(\alpha, T + \alpha)\right\} d\alpha.$$

T can be replaced by $T' - a + t$, and since T' corresponds to the initial time $t = 0$ we obtain

$$P(a - t, a, t - a) = \exp\left\{-\int_{a-t}^a \mu(\alpha, \alpha + t - a) d\alpha\right\}.$$

In (2.2.14) the substitution $\tau = \alpha + t - a$ has been made in the above formula yielding

$$\sigma(a, t) = \exp\left\{-\int_0^t \mu(a - t + \tau, \tau) d\tau\right\}.$$

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Appendix 3.1

Sanchez's [53] technique is outlined here without justification. The reader is referred to [53,pp 363-367] for the omitted details.

To solve for $B_e(t)$ or $B_u(t)$ will require finding or approximating the roots of the characteristic equation

$$\int_0^\infty e^{-ra}\tilde{k}(a)da = 1,$$

where

$$\tilde{k}(a) = k(a) = \beta(a)\exp\left\{-\int_0^a \mu(\alpha)d\alpha\right\}, \ 0 \leq a \leq c$$

and

$$\tilde{k}(a) = k(a)\exp\left\{-\delta\left[\frac{a-c}{T}\right]h\right\}, \ a > c,$$

(in the case of $B_e(t)$ the last expression is multiplied by the factor $e^{-\delta h}$).

If the relation $0 < \int_0^\infty k(a)da < \infty$ is satisfied then the characteristic equation has a unique real root r_u and all other roots occur in complex conjugate pairs and satisfy $\text{Re}(r) < r_u$. Furthermore $B_u(t) = B_u\exp(r_u t) + 0[\exp(r_u t)]$ as $t \to \infty$ and similarly for $B_e(t)$ with corresponding real root r_e. Sanchez quotes references that provide numerical methods for determining these roots.

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Appendix 4.1

The concept of Hopf bifurcation is referred to often throughout this thesis. In [62, p 131] Marsden and McCracken give the following necessary and sufficient conditions for Hopf bifurcation of an equilibrium of a coupled system of $(n+2)$ O.D.E.'s for some value σ_0 of a parameter σ of the system: All roots of the $(n+2)$th degree characteristic equation of the linearized part of the system must have negative real parts in $\sigma < 0$; there must be a complex conjugate pair of roots,

$$\lambda(\sigma) = \lambda_1(\sigma) \pm i\lambda_2(\sigma),$$

such that for some value σ_0 of σ, $\lambda_1(\sigma_0) = 0$, $\lambda_2(\sigma_0) \neq 0$, and $\frac{\partial \lambda_1}{\partial \sigma}(\sigma_0) > 0$. The remaining roots must have negative real parts at $\sigma = \sigma_0$. Under these conditions the equilibrium bifurcates at $\sigma = \sigma_0$ to a periodic solution of the system with period near $\frac{2\pi}{|\lambda_2|}$.

Thus, the very nature of the solutions change at $\sigma = \sigma_0$ - they "bifurcate" from stable paths leading back to the origin into paths leading away from it and (possibly) into stable limit cycles around it, so that a new kind of dynamic "equilibrium" is obtained.

Marsden and McCracken proceed to derive an algorithm which indicates whether the resulting periodic orbits are stable. As the analysis involved is complicated, we outline the algorithm without justification. It is perhaps sufficient to note that the existence of stable limit cycles depends on the nature of a Lyapunov stability function V. (We

will restrict attention to the case $n = 0$ although the algorithm is not limited to two dimensional systems of differential equations.)

We shall represent the system of differential equations by

$$\dot{x} = f(x, y)$$
$$\dot{y} = g(x, y)$$

(1)

Let x^*, and y^* represent the equilibrium points,

i.e. $f(x^*, y^*) = g(x^*, y^*) = 0.$

Now introduce the new dependent variables

$$X = x - x^*$$
$$Y = y - y^*,$$

into system (1) so that it becomes

$$\dot{X} = F(X, Y)$$
$$\dot{Y} = G(X, Y),$$

(2)

having an equilibrium point at $(0,0)$.

Evaluate the characteristic equation of the matrix A corresponding to the linearised form of (2). Suppose that this equation has roots

$$\lambda = \lambda_1 \pm i\lambda_2,$$

which, for values of a parameter σ of the system satisfy the previous "root criteria", i.e.

$$\lambda(\sigma_0) = \pm i\lambda_2; \quad \sigma = \sigma_0.$$

Now introduce new co-ordinates $\bar{X}, \bar{Y}$ such that substitution into (2) yields the new system

$$\dot{\bar{X}} = \bar{F}(\bar{X}, \bar{Y})$$
$$\dot{\bar{Y}} = \bar{G}(\bar{X}, \bar{Y}),$$

(3)

for which at $\sigma = \sigma_0$, the linear part is

$$\dot{\bar{X}} = |\lambda_2|\bar{Y}$$
$$\dot{\bar{Y}} = -|\lambda_2|\bar{X}.$$

(Marsden and McCracken describe this step as finding vectors e_1 and e_2 so that $Ae_1 = -e_2$ and $Ae_2 = e_1$. A procedure for finding e_1 and e_2 is to find α and $\bar{\alpha}$, the complex eigenvectors, and then take $e_1 = \alpha + \bar{\alpha}$, $e_2 = i(\alpha - \bar{\alpha})$.)

The next step is to evaluate

$$\dddot{V}(o) \stackrel{def}{=} 3\pi \left(4|\lambda_2|^2\right)^{-1} [|\lambda_2|W_1 + W_2],$$

where

$$W_1 = \frac{\partial^3 \bar{F}}{\partial \bar{X}^3} + \frac{\partial^3 \bar{F}}{\partial \bar{X} \partial \bar{Y}^2} + \frac{\partial^3 \bar{G}}{\partial \bar{X}^2 \partial \bar{Y}} + \frac{\partial^3 \bar{G}}{\partial \bar{Y}^3}$$

$$W_2 = -\frac{\partial^2 \bar{F}}{\partial \bar{X}^2} \frac{\partial^2 \bar{F}}{\partial \bar{X} \partial \bar{Y}} + \frac{\partial^2 \bar{G}}{\partial \bar{Y}^2} \frac{\partial^2 \bar{G}}{\partial \bar{X} \partial \bar{Y}} - \frac{\partial^2 \bar{F}}{\partial \bar{Y}^2} \frac{\partial^2 \bar{F}}{\partial \bar{X} \partial \bar{Y}} +$$
$$+\frac{\partial^2 \bar{G}}{\partial \bar{X}^2} \frac{\partial^2 \bar{G}}{\partial \bar{X} \partial \bar{Y}} - \frac{\partial^2 \bar{F}}{\partial \bar{Y}^2} \frac{\partial^2 \bar{F}}{\partial \bar{Y}^2} + \frac{\partial^2 \bar{F}}{\partial \bar{X}^2} \frac{\partial^2 \bar{G}}{\partial \bar{X}^2},$$

where all these terms are evaluated at (0,0).

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If $\ddot{V}(o) < 0$ the periodic orbits are stable.

If $\ddot{V}(o) > 0$ the periodic orbits are unstable.

If $\ddot{V}(o) = 0$ the test yields no information.

Appendix 5.1

The fundamental equations are given by

$$\dot{P_1} = P_1 F(P_1, P_2, \sigma)$$

$$\tag{1}$$

$$\dot{P_2} = P_2 G(P_1, P_2, \sigma),$$

where σ is the chosen bifurcation parameter.

We assume the existence of an equilibrium point (P_1^*, P_2^*) where

$$F(P_1^*, P_2^*, \sigma) = G(P_1^*, P_2^*, \sigma) = 0.$$

In the usual way, the transformation $X = P_1 - P_1^*$, $Y = P_2 - P_2^*$ is made so that (1) becomes

$$\dot{X} = (X + P_1^*)F(X + P_1^*, Y + P_2^*, \sigma)$$

$$\tag{2}$$

$$\dot{Y} = (Y + P_2^*)G(X + P_1^*, Y + P_2^*, \sigma).$$

The linearised form of this system is then

$$\dot{X} = P_1^* F_1 X + P_1^* F_2 Y$$

$$\tag{3}$$

$$\dot{Y} = P_2^* G_1 X + P_2^* G_2 Y,$$

where

$$F_1 = \frac{\partial F}{\partial P_1}(P_1^*, P_2^*, \sigma), \quad F_2 = \frac{\partial F}{\partial P_2}(P_1^*, P_2^*, \sigma) \text{ etc.}$$

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The eigenvalues of this system are given by

$$\lambda = \frac{1}{2}(P_1^* F_1 + P_2^* G_2) \pm \frac{1}{2}\left[(P_1^* F_1 + P_2^* G_2)^2 - 4P_1^* P_2^*(G_2 F_1 - G_1 F_2)\right]^{\frac{1}{2}}.$$

(4)

One can verify from (ii) and (iv) of the Kolmogorov conditions that

$$\frac{P_2}{P_1} > \frac{F_1}{-F_2}$$

and

$$\frac{F_1}{-F_2} > \frac{P_2}{P_1} < \frac{G_1}{-G_2},$$

so that,

$$F_1 G_2 - G_1 F_2 > 0.$$

(5)

Also from Kolmogorov's condition (iv) we have that $G_1 > 0$.

It is immediately clear that if $F_1 \leq 0$ then Re $\lambda < 0$ and we have a stable solution that tends to (P_1^*, P_2^*) by the Poincaré-Bendixson Theorem.

If however $F_1 > 0$ and if $F_1 P_1^* + G_2 P_2^* < 0$ then the above result also follows.

If $F_1 P_1^* + G_2 P_2^* > 0$ then Re $\lambda > 0$, and the system is unstable. Thus, Hopf bifurcation can take place if

$$P_1^* F_1(P_1^*, P_2^*, \sigma) + P_2^* G_2(P_1^*, P_2^*, \sigma) = 0 \text{ for } \sigma = \sigma_0.$$

Then

$$\lambda = \pm i \left[P_1^* P_2^*(F_1 G_2 - G_1 F_2)\right]^{1/2} = i\delta,$$

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(where (5) indicates that the roots of (4) are imaginary).

In order to apply the Marsden and McKracken algorithm (see
Appendix 4.1) we need a transformation:

$$\begin{pmatrix} X \\ Y \end{pmatrix} = \begin{pmatrix} -P_2^* G_2 & \delta \\ P_2^* G_1 & 0 \end{pmatrix} \begin{pmatrix} X_1 \\ Y_1 \end{pmatrix},$$

so that (3) becomes

$$\begin{pmatrix} \dot{X}_1 \\ \dot{Y}_1 \end{pmatrix} = \begin{pmatrix} 0 & \delta \\ -\delta & 0 \end{pmatrix} \begin{pmatrix} X_1 \\ Y_1 \end{pmatrix},$$

the suitable form for the algorithm to apply.

Routine calculation confirms that

$$\dot{Y}_1 = \left(-\frac{P_2^*}{\delta} G_2 X_1 + Y_1 + \frac{P_1^*}{\delta} \right) F + \left(\frac{P_2^*}{\delta} G_2 X_1 + \frac{G_2 P_2^*}{\delta G_1} \right) G$$

$$\dot{X}_1 = \left(X_1 + \frac{P_2^*}{P_2^* G_1} \right) G.$$

The next step is to evaluate $\dddot{V}(0)$ as given in Appendix 4.1.
However, in doing so one obtains a lengthy expression involv-
ing second and third derivatives of F and G about which the
Kolmogorov theorem yields no information.

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Appendix 5.2

Notice that when $B = 0, V^*$ as defined on p. 163 is given by

$$V^* = L(P^* + g)^2 ckG + L^2 P(P_1^* + g) H.$$

where

$$H = 2P_1^{*2} L^2 - 5P_1^{*2} LP + \left(2P_1^{*2} - gP_1^* - g^2\right) P^2$$

$$G = -2gL^2 + (P_1^* + g)) LP + P^2 g.$$

Swart and Duffy [78] have shown that if B is large enough then $V^* < 0$ and hence $\dddot{V}(o) < 0$. Thus if we can show that $\frac{\partial V^*}{\partial B}$ is strictly increasing or decreasing, and that $V^* < 0$ for $B = 0$, the desired result that $\dddot{V}(o)$ is always negative, will follow.

Firstly, note that when $B = 0$, $G < 0$ and $H < 0$ will ensure $V^* < 0$.

It is straightforward to verify that G can be rewritten as

$$G = L \left(LP_1^* - b(P_1^* + g)^2\right) - bg(P_1^* + g) \left[2L - b(P_1^* + g)\right].$$

The expression

$$
\begin{aligned}
J &= bg(P_1^* + g) \left[2L - b(P_1^* + g)\right] \\
&= bg(P_1^* + g) \left[2a - 3bP_1^* - bg\right]
\end{aligned}
$$

is positive since $a - bg - 2bP_1^* > 0$ is assumed to hold and hence implies that

$$2a - 3bP_1^* - bg > 0.$$

We will now show that if

$$a - bg - 6bP_1^* > 0, \quad (\alpha)$$
$$\text{and} \quad P_1^* > g, \quad (\beta)$$

then

$$L\left(LP_1^* - b(P_1^* + g)^2\right) < 0, \ H < 0$$

and $\frac{\partial V^*}{\partial B} < 0$, all of which guarantee the desired result.

The expression $I = L(LP_1^* - b(P_1^* + g)^2)$ is equivalently

$$I = (a - bP_1^*)(aP_1^* - 2bP_1^{*2} - 2bP_1^*g - bg^2)$$

From (5.3.12) it follows that

$$0 \le P_1^* < \frac{a}{b}.$$

$$\text{When} \quad P_1^* = 0, \quad I < 0, \quad (1)$$
$$\text{When} \quad P_1^* = \tfrac{a}{b}, \quad I = 0. \quad (2)$$

Moreover,

$$\frac{\partial I}{\partial P_1^*} = -6bP_1^*(a - bP_1^*) + 4b^2 P_1^* g + (a - bg)^2.$$

Now, if (α) and (β) hold then

$$(a - bg)^2 > 6bP_1^*(a - bP_1^*).$$

Hence $\frac{\partial I}{\partial P_1^*} > 0$, so that (1) and (2) imply that

$$I < 0 \text{ for } 0 \le P_1^* < \frac{a}{b}.$$

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Hence (α) and (β) imply that $J > 0, I < 0$ and hence $G < 0$.

It is simple to verify that H can be rewritten as

$$H = 2P_1^{*2}Lb(P_1^* + g) - P_1^{*2}LP - gP^2(P_1^* + g) - 2P_1^*P(bg + bP_1^*).$$

Let k denote the sum of the first two terms of H. Then k can be expressed as

$$k = P_1^{*2}L(3bg + 4bP_1^* - a).$$

If (α) and (β) hold,

$$\begin{aligned}
\text{then} \quad & a - bg - 4bP_1^* - 2bP_1^* > 0 \\
\text{i.e.} \quad & a - bg - 4bP_1^* - 2bg > 0 \\
\text{i.e.} \quad & a - 3bg - 4bP_1^* > 0.
\end{aligned}$$

Hence $k < 0$ and thus $H < 0$.

Finally, $\frac{\partial V^*}{\partial B} = cP\{LH - P_1^*(P_1^* + g)P^3\}$, which under conditions (α) and (β) is negative since H is negative.

All these results confirm that $V^* < 0$ and hence $\dddot{V}(o) < 0$ for all parameter choices satisfying conditons (α) and (β).

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