To Bill, with Thanks and Best Wishes
Steve

UNIVERSITY OF STRATHCLYDE

"SIMPLE AGE-STRUCTURE MODELS OF LABORATORY INSECT POPULATIONS"

by

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ABSTRACT

The aim of the work reported is the formulation, analysis and application of analytically and computationally tractable age-structured models of laboratory insect populations. The simplified case of two developmental stages (immature and adult) is considered under different competition regimes. Both constant (Ch. 2 and 3) and differential (Ch. 4) aging are considered.

In Chapter 2 a general delay-differential equation describing the population dynamics of adults under two competition regimes is derived. The biological constraints upon the form of the functions in the equation are specified, and results on local stability, boundedness of solutions, and deterministic persistent fluctuations established. Useful relationships with difference equations are explored, and standard bifurcation results on the latter are shown to aid the analysis of the former. The results are illustrated by examining two models of the general type.

In Chapter 3 a particular delay-differential equation model is fitted to some classic data on the Australian sheep blowfly *Lucilia cuprina* (Wied). It is established that the quasi-periodic "cycles" in adult population numbers are deterministic persistent fluctuations, and that the qualitative differences in breeding patterns observed between different experiments (different competition regimes) are the result of a "humped" adult recruitment function.

In Chapter 4 general equations for a differentially aging two developmental-stage population are derived, and from these a single integro-differential equation for the adult population dynamics under "adult-only" competition is extracted. It is shown how the

choice of a gamma distribution with a shift in origin (matching well some observed maturation period distributions) makes local stability and numerical analyses straightforward. The behaviour of constant and distributed maturation period models is compared, and conclusions drawn about the occasions when the approximation (the former) is sufficient, and when the full distributed model (the latter) is required. The results and conclusions of the Case Study, Chapter 3, are justified in the light of this comparison.

ACKNOWLEDGMENTS

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NOTATION:

In the order: Roman lower case, Roman upper case, Greek. Subdivisions in order: single symbols, symbols with sub/superscripts, symbols including arguments, i.e. functions. Where relevant, the equation number where the notation is first used (or is defined), is given.

a	age
c	parameter in gamma distribution (Equation (4.4.9))
d	"scramble" parameter (Equation (2.7.14))
da	infinitesimal age-interval = dt
dr	infinitesimal immature stage-duration interval = dt
ds	infinitesimal adult stage-duration interval = dt
dt	infinitesimal time-interval
e	2.71828...
h	parameter related to larval food supply (Equation (3.4.3))
i	$i^2 = -1$
j,k	integers
m	constant *per capita* adult death rate (Equation (2.7.1))
p	integer order of gamma distribution (Equation (4.4.9))
r	time-to-date spent in immature developmental stage
s	time-to-date spent in adult developmental stage
t	time
v	parameter in difference equation analogue of Model (I) (Equation (2.7.10))
x	dummy age or time variable
c_o	parameter in recruitment function of Model (II) (Equation (2.7.14))
g_o	parameter controlling decline in *per capita* adult fecundity (Equation (3.3.3))
n_c	coherence number (Equation (3.5.3))

q_k	positive constants
t'	scaled time = t/τ
$f(a,t)$	age-density of individuals in the population at time t; constant aging
$f_A(s,t)$	stage-duration density of adults at time t; differential aging
$f_I(r,t)$	stage-duration density of immatures at time t; differential aging
$g(x;b)$	gamma distribution of integer order p, origin at $x = 0$
$n(t)$	small perturbation of adult population from equilibrium (Equation (2.4.2))
$u(a)$	normalised weighting function, with respect to age. (Equation (4.1.1))
$w(r)$	unnormalised distribution of maturation periods (Equation (4.4.1))
P	parameter related to per capita fecundity
Q	maximum per capita fecundity (Equation (3.3.3))
T	dominant period of either quasi-cycles, or persistent fluctuations (Equation (3.5.2))
A_0	adult population size at which total future recruitment rate is at a maximum
A_I	number of new adults introduced at start of experiment
A_{max}	maximum adult population size observed after the transient has passed
A_{min}	minimum adult population size observed after the transient has passed
A_L	lower bound on persistent fluctuations (Equation (1.5.5))
A_u	upper bound on persistent fluctuations (Equation (2.5.4))
A_t	adult population at time t in discrete time
A_T	adult population size at a turning point (Equation (2.5.3))
A^*	adult population steady state (Equation (2.4.1))
B_{max}	maximum value of $B(t)$
L_{LIM}	$Y_U - Y_L$: assymptotic maximum amplitude of scaled equation (Equation (2.7.11))

P_1	parameter related to maximum *per capita* fecundity in Model (I) (Equation (2.7.2))
P_2	parameter related to maximum *per capita* fecundity in Model (II) (Equation (2.7.14))
R_{max}	maximum future recruitment rate (Equation (2.5.2))
R'_{max}	R_{max}/A_0 (Equation (2.7.4))
S_1	average egg-to-adult survival under adult-only competition (Equation (3.3.2))
T_1	$(\tau_1/\tau_2)/(1+\tau_1/\tau_2)$ (Equation (4.7.6))
Y_I	A_I/A_0
Y_{max}	A_{max}/A_0
Y_{min}	A_{min}/A_0
Y_L	A_L/A_0
Y_u	A_U/A_0
Y_t	A_t/A_0
Y^*	A^*/A_0
$A(t)$	adult population at time t
$B(t)$	total birth rate at time t
$D_A(t)$	total adult death rate at time t
$D_I(t)$	total immature death rate at time t
$F(\cdot,\cdot)$	a non-linear function (Equation (4.1.1))
$G(A_t)$	generative function, discrete time (Equation (2.6.3))
$H(x)$	Heaviside step function at $x = 0$ (Equation (4.4.8))
$I(t)$	immature population at time t
$K(\tau_1/\tau_2 p)$	asymptotic value of $-\rho\tau/\alpha\tau$ (Equation (4.5.5))
$M(t)$	total maturation rate (out of immature stage) at time t, $M(t) = R(t)$
$R(t)$	total recruitment rate (into adult stage) at time t
$S_2(a)$	probability of survival to age a under conditions of immature-cohort competition; constant aging (Equation (3.4.2))
$U_j(t')$	$V_j(t)/B_{max}$ (Equation (4.7.4))

$V_j(t)$	one of p+1 auxilliary variables (Equation (4.6.2))
$Y(t)$	$A(t)/A_0$
α	partial derivative of $D_A(A)$ at $A = A^*$ (Equation (2.4.3))
γ	-1 times partial derivation of B(A) at $A = A^*$, discrete time (Equation (2.6.4))
Δt	small discrete time interval (Equation (2.6.1))
ε	small parameter (Equation (2.7.12))
ξ	$\theta+(\tau_1/\tau_2)\tan\theta$ (Equation (A2.17))
θ	$\tan\theta = \omega/c$ (Equation (A2.6)
λ	eigenvalue of solution to perturbation equation. $\lambda = -\mu+i\omega$
μ	real part of λ (Equation (2.4.6))
π	3.14159...
ρ	partial derivative of R(A) at $A = A^*$; constant aging (Equation (2.4.3)); = S_1 times partial derivative of B(A) at $A = A^*$, differential aging (Equation (4.5.4))
σ	standard deviation of g(x;p) (Equation (4.7.1)
τ	mean maturation period
ω	imaginary part of λ (Equation (3.5.2))
δ_F	Feigenbaum's delta (Equation (2.7.13))
θ_L	minimum feasible θ, given τ_1/τ_2 and p (Appendix 2)
θ_U	maximum feasible θ, given τ_1/τ_2 and p (Appendix 2)
τ_c	critical maturation period, at which instability first occurs; constant aging (Equation (2.4.5))
τ_1	minimum maturation period; differential aging (Equations (4.4.7))
τ_2	mean of g(x;p) (Equations (4.4.10)-(4.4.11))
$\beta(\cdot,t)$	*per capita* fecundity (age *or* stage duration specific)
$\beta_1(\cdot,t)$	$\beta(\cdot,t)$ under conditions of adult-only competition
$\beta_2(\cdot,t)$	$\beta(\cdot,t)$ under conditions of immature-cohort competition

$\delta(a,t)$	age-specific *per capita* death rate for the entire population; constant aging (Equation A1.1))
$\delta_A(\cdot,t)$	*per capita* adult death rate (age *or* stage-duration specific)
$\delta_I(\cdot,t)$	*per capita* immature death rate (age *or* stage-duration specific)
$\phi(r,t)$	*per capita* stage-duration specific maturation rate; differential aging
$\psi(r)$	observed frequency distribution of maturation times (Equation (4.4.4))

CHAPTER 1: INTRODUCTION

1.1 AGE STRUCTURE AND POPULATION DYNAMICS

In virtually any animal population there will be present, at any one time, individuals of a variety of different ages. Age dictates, to a great extent, the significance of an individual in a population: many of the important characteristics of an animal, such as fecundity, body size, growth rate and mortality, can be strongly age-dependent. In particular, it is generally true that an individual passes through some juvenile period, before becoming sexually mature and breeding according to a pattern that is characteristic of the species. There is a vast variety of animal 'life histories' ranging from those who breed once and then die, to those who breed more or less continually throughout most of their adult lives (a brief discussion of life history types is to be found in CHARLESWORTH (1980, Ch. 2); KREBS (1978, Ch. 10) contains many examples). Clearly, no single model, or class of models, could hope to describe the age-dependent effects upon population dynamics of all the possible life histories, so that if simple tractable population models incorporating some age-structure are sought, they must of necessity suffer from a restriction in range of application. Just as importantly, if the model construction is to be more than a mathematical exercise, appropriate data on a given population and its controlling mechanism must be available for model testing.

The difficulties of trying to understand the effects of age-structure on the dynamics of a field population are compounded by interactions (often age-specific themselves) between species and environmental variation, to the extent where the separation of dynamic features due to age-effects from those due to other causes is exceedingly difficult. In contrast, within the closed and controlled environment of the laboratory, age-structure effects can be investigated more or less in isolation, provided that an experimental animal is used which has a short generation time (in order that population data over a large number of generations can be collected in a relatively short time), and which can be readily aged. For these reasons, laboratory populations of insects, many of which have gratifyingly short generation times, and readily identifiable stages in the life-history (SOUTHWOOD 1966), have been among the chief sources of data on age-structure effects on population dynamics (most notably, the work of NICHOLSON (1950, 1954, 1957, 1960) on the Australian sheep blowfly, Lucilia cuprina Wied.)). It is natural therefore that models of laboratory age-structured populations should be particularly applicable to insect populations, and indeed the models developed and analysed in this thesis are explicitly insect population models.

1.2 MODELS INCORPORATING AGE-STRUCTURE

In Chapters 2 and 3 I shall be considering single-species models where the assumption is made that the length of the juvenile stage is the same for all individuals. This reflects a very general assumption that underlies almost all age-structure population models, namely that all individuals age uniformly. In Section (1.2.1) I shall briefly discuss these 'uniform aging' models, and then in Section (1.2.2) consider those few attempts at age-structure modelling when aging occurs at a different rate for each individual, a topic I return to in Chapter 4.

1.2.1 Uniform Aging

Historically there have been a number of approaches to the modelling of a uniformly aging population, based on a variety of continuous and discrete age/time formalisms. GOODMAN (1967) discusses the relationships between the various approaches in some detail while CHARLESWORTH (1980, Ch. 1) carefully sets out a number of alternative formulations, and NISBET & GURNEY (1982, Ch. 3) compare continuous and discrete time formalism, so that there is little need to go into detail here. However, the following is necessary background to Chapters 2 and 3.

The assumption of uniform aging allows all the age-structure models to be derived from a recurrence relation and a renewal condition. The recurrence relation describes the movement of individuals through the age-structure in small age and time steps, conditional upon survival, while the renewal condition is an integral equation (or the discrete time equivalent) defining the total birth rate as the sum of contributions from the fertile age-classes. Manipulating these two equations in different ways produces all the continuous and discrete time formalisms.

In continuous time, the age and time interval of the fundamental recurrence relation goes to zero, and a partial differential equation (equation A1.1) is obtained. The age-structure problem was first stated in this form by McKENDRICK (1926) (and later, independently, by von FOERSTER (1959)), but the earliest complete formulation was that of SHARPE & LOTKA (1911), and LOTKA (1925), who went directly from the recurrence relation to an integral equation, implicitly using the solution to the McKENDRICK equation en route. The two forms are completely equivalent, but historically, demographers have preferred the integral equation approach (c.f. POLLARD, 1973). For ecological population modelling the direct use of the McKENDRICK equation has become increasingly popular (e.g. SINKO & STEIFER 1967; AUSLANDER OSTER & HUFFAKER 1974; STREIFER 1974; OSTER 1976), with various simplifying assumptions permitting reduction of the partial differential equation to less complex balance equations (c.f. OSTER 1976). The differential equation models so widely used in the ecological literature are (if correct) in fact examples of age-structure equations simplified to the point where age-structure is ignored.

In discrete time age-structure models, the age and time step in the original recurrence relation remains finite, and so becomes the basic unit of age and time, i.e. there are a series of "age classes" through which individuals pass in "jumps". The common expression given to discrete time models is either a matrix equation, generally considered to date from LESLIE (1945, 1948), (but see POLLARD 1973, Ch. 4), or else high order difference equations (c.f. CHARLESWORTH 1980, Ch. 1). However, all discrete time age-structure models are approximations to a continuous time system (not only because their common ancestors are the recurrence relation and renewal condition mentioned above, but also because of the fundamental truth that time really is continuous on any ecological timescale), becoming exact only when breeding in the real population occurs at exactly and evenly spaced intervals. The main rationale for the use of the discrete time approximations is that they are computationally very much more tractable than the continuous time, exact equations, and simplifying assumptions can produce models whose analysis is trivial, the extreme case being the simple first order difference equations so common in ecological population modelling (e.g. MAY & OSTER 1976; VARLEY GRADWELL & HASSELL 1973, and references therein). However, there seems little reason to use such approximations if analytically and computationally tractable exact equations can be obtained. For this reason, delay-differential equations have been popular choices as population models (e.g. CASWELL 1972; ROSS 1972; MAY 1973; 1974a, 1981; CHOW 1974; MAY CONWAY HASSELL & SOUTHWOOD 1974; MAYNARD SMITH 1974, Ch. 3; BEDDINGTON & MAY 1975; STIRZAKEP 1975; TAYLOR & SOKAL 1976; KAPLAN & YORKE 1977; OSTER 1976; OSTER & IPAKTCHI 1978; GURNEY BLYTHE & NISBET 1980; NISBET & GURNEY 1982, Ch. 2 & 8), but those are usually used on an *ad hoc* basis, being rarely derived (MAYNARD SMITH 1974, OSTER 1976, PEREZ MALTA & COUTINHO, 1978, GURNEY BLYTHE

& NISBET 1980 and NISBET & GURNEY 1982, Ch. 8 being notable exceptions). A worrying feature is that the most common ad hoc delay-differential equation is the so-called "time-delayed logistic" (e.g. JONES 1962a, b; AUSLANDER et al 1974; MAY 1974a, Ch. 4). This equation was originally formulated by HUTCHINSON (1948) to describe, in a general way, the effects of delayed density-dependent regulation upon a growing population, and apparently can only be derived from the exact age-structure equations (i.e. The McKENDRICK (1926) equation and renewal condition) by removing all age-structure, and introducing an arbitrary time lag (see the derivation in AUSLANDER et al 1974)! Whatever its merits in other contexts, the time-delayed logistic is thoroughly inappropriate in age-structure modelling.

In Chapter 2 I derive from first principles (for the simplified case where there are just two developmental stages - immatures and adults - under certain resource competition regimes) a single delay-differential equation describing changes in the adult developmental class. I show that this delay-differential equation is readily analysed, and fit (in Ch. 3) a specific example to some of NICHOLSON's (1954) experimental results. GURNEY NISBET & LAWTON (1983), in a forthcoming publication, extend the derivation to include an arbitrary number of developmental classes, each with a characteristic length and competition regime.

1.2.2 Differential Aging

In all the models described so far, and in those examined in Chapters 2 and 3, all individuals in the population are assumed to age uniformly, so that the duration of a developmental stage is the same for all. Clearly in the real world this is not the case, as all biological features display a natural variation between individuals (BEGON (1983) discusses this variation at length, but even a cursory glance at published experimental results suffices to make the point abundantly clear).

Attempts to incorporate this natural variation into age-structure models have not met with great success. Explicit differential aging in the form of a forward diffusion term in McKENDRICK's (1926) equation has been suggested (OSTER & TAKAHASHI 1974; AUSLANDER *et al* 1974; OSTER 1976), but little appears to have been accomplished as regards model development and analysis. The most common approach has been to assume that there is some distribution of durations of a particular developmental stage (the immature stage) and simply insert this into a delay-differential equation to generalise the results of the latter (e.g. MAY 1973, 1974a; MACDONALD 1978). Unfortunately, the equations so produced are almost invariably inappropriate to age-structure modelling, as I show in Chapter 4 (although of course the same equations can express other biological processes, as they were originally formulated to do (e.g. VOLTERRA 1927)), and so most of the published work, performed on generalisations of the "time-delayed logistic", is of no relevance here (e.g. MAY 1973, 1974a, KAZARINOFF WAN & van den DRIESSCHE 1978; BARCLAY & van den DRIESSCHE 1975, CUSHING 1977, to choose a few). LEWIS (1972,

1977) has produced analytically tractable integral equation models, describing the flow of individuals through a "process" the duration of which is randomly distributed, and CUSHING (1980) investigates an integral equation model that incorporates (amongst other things) a distributed gestation period (although neither author chooses to include the effects of mortality during the distributed duration stage). Apparently no analytically and computationally tractable general mode of a differentially aging population has ever been formulated, and in Chapter 4 I attempt to do so, using an integro-differential equation formalism as the natural generalisation of the delay-differential equations of Chapter 2 and 3.

1.3 SOLUTIONS OF AGE-STRUCTURED MODELS

In Chapters 2-4 I shall be using delay-differential and integro-differential equations to describe the adult population dynamics of laboratory insect populations. As I shall show (Appendix 1 and Ch. 4), these equations are derived from partial differential equations like the McKENDRICK (1926) equations, and as such they have two solutions: one describing the dying off of individuals already present at the initial time, the second that of individuals born after that time (see SINKO & STREIFER 1967, and NISBET & GURNEY 1982, Ch. 3 for example). As a result, the complete future solution of the delay- or integro-differential balance equation requires an "initial history" of population numbers prior to the initial time that is itself a valid solution to the balance equation. For a laboratory population started by introducing a number of individuals into an empty apparatus (a cage, say), clearly there is no contribution from individuals older than the experiment, and the initial history is zero individuals for all past time. This leaves but one solution to be considered during the analytic and numerical treatment of the population models, which greatly increases their tractability.

Solving differential and delay-differential equations numerically is straightforward, provided a suitable algorithm and adequate computing facilities are available. The numerical analysis in Chapters 2 and 4 was performed using the UCSD PASCAL program SOLVER (MAAS, NISBET & GURNEY 1982) which utilizes a modified predictor-corrector algorithm, on a Western Digital Microengine. The older numerical analysis of Chapter 3 was performed on a Data General NOVA minicomputer using the program IVPS, a precursor to SOLVER.

CHAPTER 2 CONSTANT MATURATION PERIOD: GENERAL RESULTS

2.1 INTRODUCTION

In this Chapter I consider the dynamics of a laboratory insect population subdivided into two developmental classes, the immatures and the adults. With uniform aging and an "age-triggered" transition between classes, the length of time spent by any individual as an immature before transition to adulthood is constant - that is, there is a constant "maturation period", τ.

In Section (2.2) and Appendix 1 I deal with model formulation, and state the assumptions which permit the reduction of the modelling problem to the solution of a single delay-differential equation describing adult population dynamics. The biological constraints upon the forms of the functions in this general delay-differential equation are specified in Section(2.3) and rigorous results on stability, persistent fluctuations, and bounds of solutions are established (Sections (2.4) and (2.5)).

Some relationships between the delay-differential equation which I derive and simple first-order difference equations are explored in Section (2.6), and I show how some results on bifurcation in the latter can aid the analysis of the former. The results of some numerical analysis of two exemplary models are presented in Section (2.7).

An account of the work detailed in this Chapter has been published (BLYTHE NISBET & GURNEY 1982).

2.2 MODEL FORMULATION

The continuous time expression of the dynamics of a two developmental class, closed laboratory population must be of the form

$$\begin{cases} \dot{I}(t) = B(t) - M(t) - D_I(t) & (2.2.1) \\ \dot{A}(t) = R(t) - D_A(t) & (2.2.2) \end{cases}$$

where $(\dot{\ })$ denotes $\frac{d}{dt}$, $I(t)$ and $A(t)$ are the total numbers of immatures and adults, respectively, and $D_I(t)$ and $D_A(t)$ are their respective total death rates. $M(t)$ is the total maturation rate out of the immature class, and $R(t)$ the total recruitment rate into the adult class ($M(t)$ and $R(t)$ will be considered to be equal). In general, equation (2.2.1) and (2.2.2) will be rather intractable integro-differential equations (see Ch. 4), but by making certain assumptions about the biology of the organisms concerned, and about the manner in which they interact under conditions of competition for food, it is possible to extract a tractable general equation for adult population dynamics.

I will assume that the instantaneous adult death rate, $D_A(t)$, and birth rate, $B(t)$, are functions of the adult population size $A(t)$ only; and that competition occurs either in the adult developmental class only, (all adults competing equally) or in some immature age-class (all individuals of the same age competing). In Appendix 1 I show, given these assumptions and a constant sex ratio, that the instantaneous adult recruitment rate $R(t)$ is a function only of the size of the adult population at time $t-\tau$,

$$R(t) = R(A(t-\tau)) \qquad (2.2.3)$$

(where τ is the length of the maturation period). Hence the equation for the adult dynamics (2.2.2) is decoupled from that for the immature dynamics (2.2.1), and involves functions only of past and present adult population sizes:

$$\dot{A}(t) = R(A(t-\tau)) - D_A(A(t)) \qquad (2.2.4)$$

With appropriate choices of recruitment and death functions, equations like (2.2.4) are applicable in many contexts: specific population models have been examined by MAYNARD SMITH (1974 Ch. 3), BEDDINGTON & MAY (1975), TAYLOR & SOKAL (1976), OSTER & IPAKTCHI (1973), PEREZ et al (1978) (who also look at local stability of the non-linear equation), GURNEY BLYTHE & NISBET (1980), and MAY (1981), for example, whilst MACKEY & GLASS (1977), and GLASS & MACKEY (1979) use similar equations in the context of physiological control. Here, however, I shall be concerned only with adult population dynamics under the competition regimes stated.

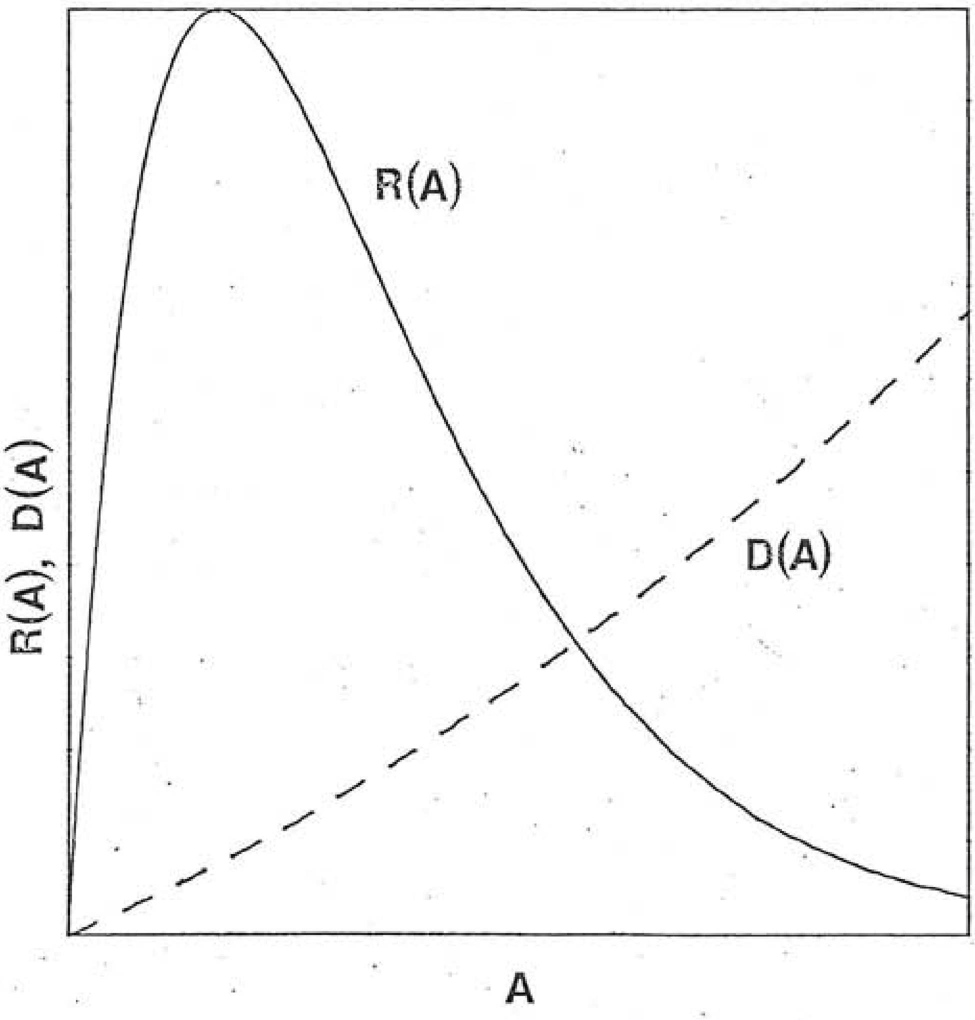


Fig. (2.1) - General forms for the recruitment (R(A)) and death ($D_A(A)$) rate functions under conditions of scramble competition.

2.3 REALISTIC RECRUITMENT AND DEATH FUNCTIONS

The functional forms of $R(A(t-\tau))$ and $D(A(t))$ specify the dynamics of the adult age-class in terms of responses to past and present population sizes. I will now identify the general features of these responses under different resource competition conditions, acting either in the adult age-class, or in some pre-adult cohort, with or without an Allee effect (the existence of a threshold population size, below which the population cannot sustain itself; MAY (1973)). It is useful to consider competition due to resource limitation in terms of classic "scramble" and "contest" behaviour, defined here as

Scramble: when available resources are partitioned equally amonst all individuals.

Contest: when a certain number of individuals are maintained at the expense of the rest.

When competition occurs in the adult age-class, if the *per capita* mortality between birth and sexual maturity is constant (Eq. (A1.10)), then the rate of recruitment at time t is proportional to the birth rate at time $t-\tau$. The birth rate will clearly be zero when the adult population size is zero, and under "scramble" competition will tend towards zero again for large population sizes (as the *per capita* share of the limited resources decreases), with some maximum birth rate occurring at an intermediate population size, so that a "humped" relationship exists between birth rate and population size as shown in Fig. (2.1). For "contest"

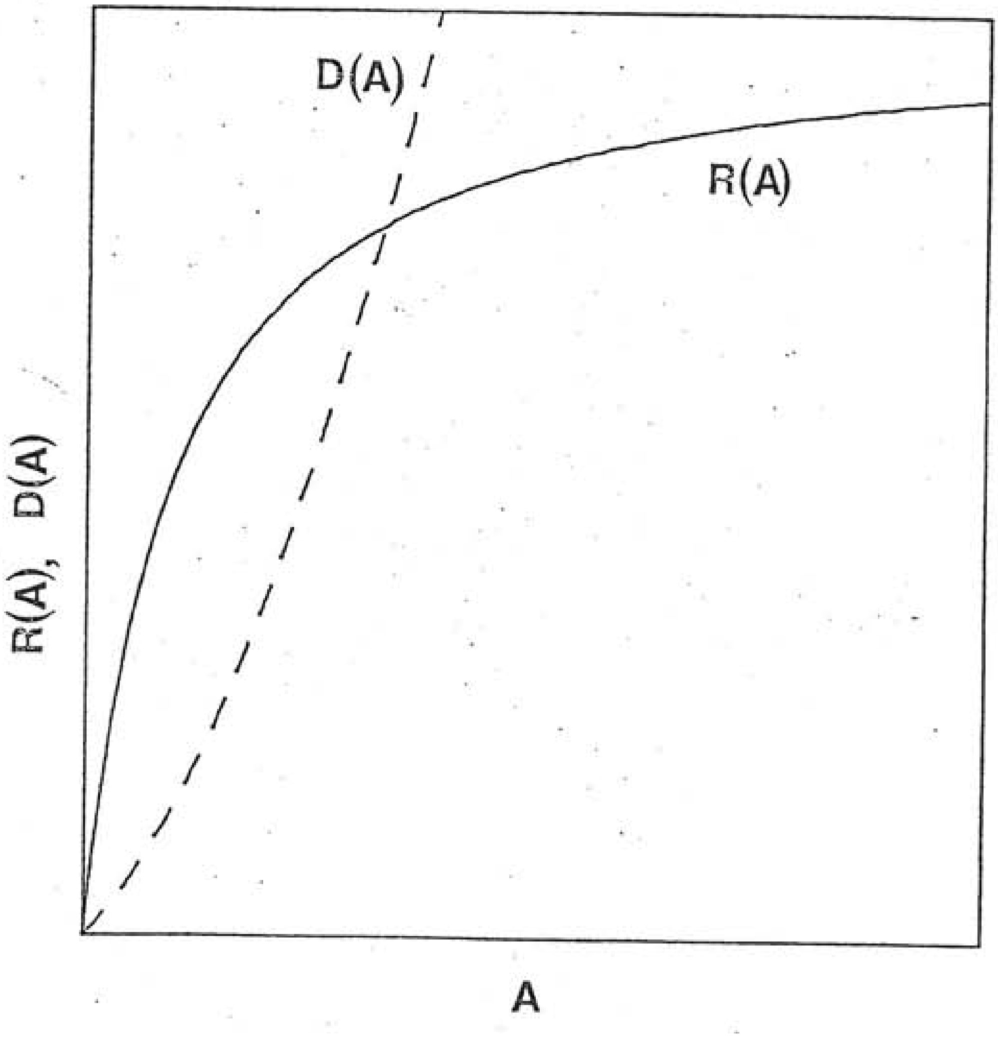


Fig. (2.2) - General forms for the recruitment (R(A)) and death ($D_A(A)$) rate functions under conditions of contest competition.

competition amongst adults, the unrestricted maintenance of a certain number of individuals, regardless of population size, ensures that there is no falling off of the birth rate for large population sizes greater than a certain value (see Fig. (2.2))..

If competition occurs amongst members of some cohort of pre-adult individuals, then the per capita offspring production of the adults can be expected to be constant, at the physiologically defined maximum value. Thus the response to competition is best considered in terms of survival to adulthood of members of the competing cohort. Under conditions of "scramble" competition, it is clear that the number of individuals surviving to adulthood will be zero when the cohort is empty, or when there are so many individuals of the competing age as to leave none with sufficient resources even to stay alive. It is reasonable to postulate that for cohort sizes between these extremes there will be a region where the total numbers surviving to adulthood has a maximum. Hence there is again a "humped" function, relating the rate of recruitment to the adult population and the size of the earlier, competing, cohort. For "contest" competition, the number of individuals from the competing age-cohort surviving to adulthood will not decrease at large cohort sizes (as some individuals will always get sufficient resources), but will remain at some maximum value. If density-dependence does not affect individuals at earlier ages, then the probability of survival from birth to the critical age can be taken to be a constant, so that the general form of the relationship between rate of recruitment to the adult population, and competing cohort size, is also the form of $R(A(t-\tau))$. Hence $R(A(t-\tau))$ for

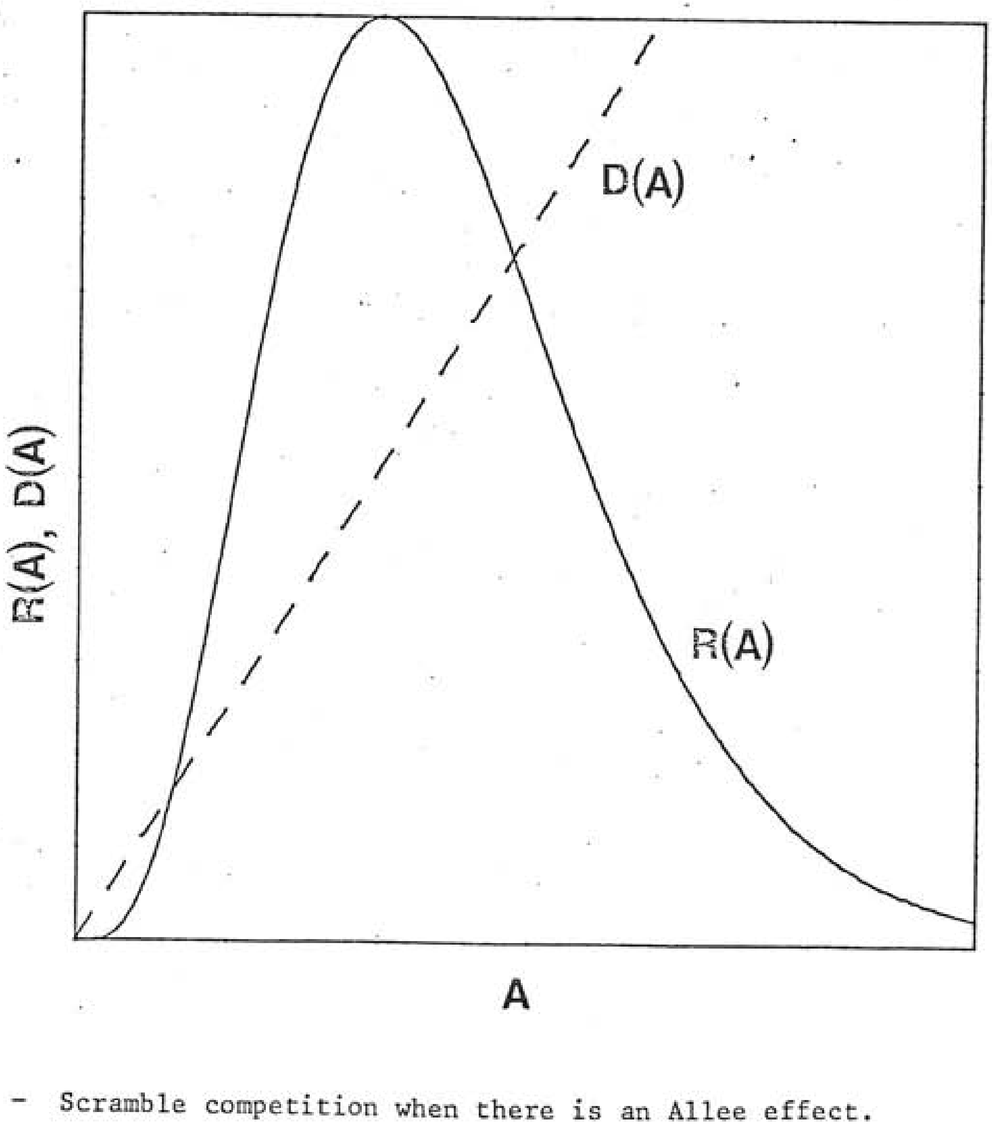


Fig. (2.3) - Scramble competition when there is an Allee effect. There are two steady state solutions, one of which (the lower) is always unstable.

"scramble" competition is again a "humped" function (Fig. (2.1)), whilst for "contest" competition $R(A(t-\tau))$ is characterised by a sustained maximum value (Fig. (2.2)). These functional forms are consistent with those traditionally used in difference equation formulations of "scramble" and "contest" competition (see HASSELL, 1978, Ch. 2, for example).

The adult death rate function, $D_A(A(t))$, is likely to be of relatively simple form, being zero at zero population, and rising continuously at greater population sizes. However, in general it is to be expected that there is greater density dependence in the per capita death rate (and hence more curvature of $D_A(A(t))$ under conditions of "contest" competition, (see Fig. (2.2)). I will show in section (2.4) that the characteristic shapes for $R(A(t-\tau))$ and $D_A(A(t))$ under "contest" conditions effectively preclude the appearance of persistent deterministic fluctuations.

An Allee effect can be readily incorporated into Eq. (2.2.4) by introducing a threshold into $R(A(t-\tau))$ for some small value of $A(t-\tau)$, such that when the adult population falls below this threshold value, the number of offspring surviving to attain future maturity will be too small to maintain the population (see Fig. (2.3)). For the sake of simplicity I will devote most attention to results for cases where an Allee effect is absent, except where these results would be radically altered or voided by the existence of such a population response.

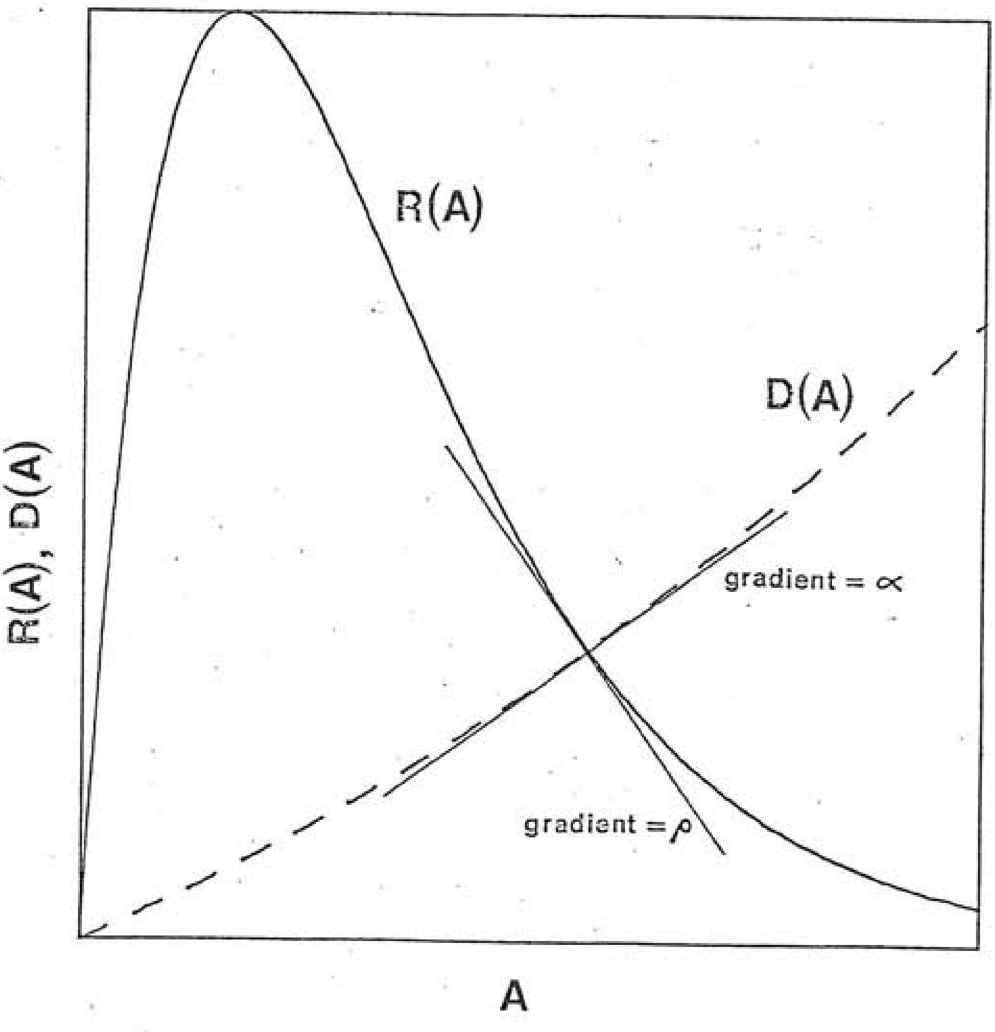


Fig. (2.4) - Interpretation of the two parameters α and ρ in the linearised equation (2.4.2). The two straight lines are tangential to the death and recruitment functions at the steady state A^*.

2.4 LOCAL STABILITY, AND PERSISTENT FLUCTUATIONS

If the population size A(t) attains a value at which it remains constant for a period at least as long as the delay in the system (τ), then it will not thereafter change (in the absence of external perturbations). This constant value is known as the steady state solution, A^*, and is clearly, from Eq. (2.2.4), a solution of the equation

$$R(A^*) = D_A(A^*) \qquad (2.4.1)$$

The fate of small perturbations n around A* (i.e. where $A = A^* + n$) is studied using the linearised equation

$$\dot{n}(t) = -\alpha n(t) + \rho n(t-\tau), \qquad (2.4.2)$$

where

$$\alpha \equiv \left(\frac{\partial D_A(A(t))}{\partial A(t)}\right)_{A=A^*}, \quad \text{and } \rho \equiv \left(\frac{\partial R(A(t-\tau))}{\partial A(t-\tau)}\right)_{A=A^*} \qquad (2.4.3)$$

For Eq. (2.2.4) α and ρ are geometrically interpretable as the gradients of $R(A(t-\tau))$ and $D_A(A(t))$, respectively, at the steady state (see Fig. (2.4)).

The behaviour of Eq. (2.4.2) is well known (e.g. EL'SGOL'TS 1966; DRIVER SASSER & SLATER 1973; MAYNARD SMITH 1974, Appendix to Ch. 3; NISBET & GURNEY 1982, Ch. 2) and is summarised in Fig. (2.5). When there is no Allee effect, the smallest possible steady state occurs when $D_A(A(t))$ is tangential to $R(A(t-\tau))$ (normally to the left of the peak in $R(A(t-\tau))$, i.e. $\rho = \alpha$, so that the region of interest lies below the line $\rho/\alpha = 1$. Beyond the local stability boundary the

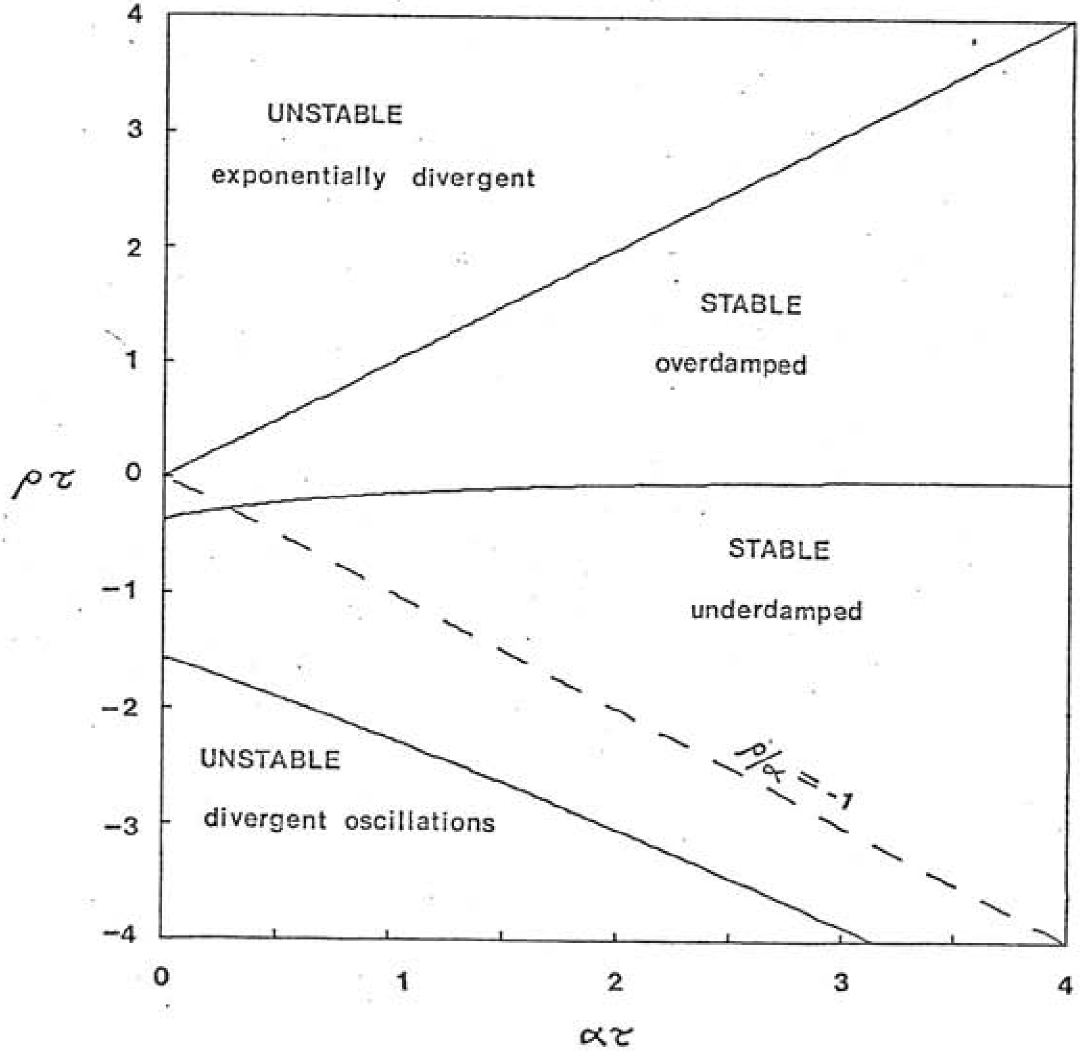


Fig. (2.5) - Behaviour of the linearised equation (2.4.1) in ($\alpha\tau,\rho\tau$)-space. From the constraints on the delay-differential equation $\alpha > 0$, and ρ can have any value.

population dynamics are controlled by non-linearities in the recruitment and death functions, and the locally linear analysis merely indicates divergent oscillations. KAPLAN & YORKE (1977) studied a general delay-differential equation similar to Eq. (2.2.4), but with a purely decreasing delayed function, and were able to prove, given suitable initial conditions, that if the linear analysis indicates this oscillatory local instability in the feasible region, then the corresponding behaviour in the non-linear equation will be limit cycles. I extend this result to the more biologically realistic model, Eq. (2.2.4), as follows.

It is clear from Fig. (2.5) that oscillatory local instability in Eq. (2.4.2) can only occur if $\rho < 0$. From the definition equation (2.4.3) it is clear that only those steady states lying on the right-hand, or falling, arm of $R(A(t-\tau))$ can become unstable in this manner. In the neighbourhood of such a steady state, equation (2.2.4) is equivalent to some member of KAPLAN & YORKE's (1977) general family, provided that fluctuations are of small enough amplitude. Thus, in the unstable region, but close to the local stability boundary, the solutions of Eq. (2.2.4) are small amplitude limit cycles. However, as soon as the amplitude of these limit cycles increases to the point where the minimum lies below the peak in the recruitment function, KAPLAN & YORKE's (1977) results become inapplicable, and more complex behaviour may occur.

Numerical studies using Eq. (2.2.4) with various "humped" $R(A(t-\tau))$ (see section (2.7)) support this argument, and it is now well known (MACKEY & GLASS 1977; OSTER & IPAKTCHI 1978; GLASS & MACKEY 1979;

GURNEY BLYTHE & NISBET 1980; MAY 1981) that when the fluctuation minimum crosses well below the peak in $R(A(t-\tau))$, the simple limit cycles may be replaced by a pattern of complicated (and possibly chaotic) behaviour (see Chapter 3). The existence of such behaviour means that although these fluctuations have bounds (see Section (2.3)), they cannot be called "limit cycles" any longer, and I shall refer to them as "presistent fluctuations" which may or may not be formally periodic.

The conditions for oscillatory local instability in the linear Eq. (2.4.2) are readily identified (for the full stability equations, see MAYNARD SMITH 1974, Appendix to Ch. 3, or NISBET & GURNEY 1982, Ch. 2). From Eqs. (2.4.1) and (2.4.3), the values of A^*, α and ρ do not depend on τ, but only upon the forms of $R(A(t-\tau))$ and $D_A(A(t))$, and each A^* defines a single α and ρ. These values, given general τ, in turn define a straight line in $(\alpha\tau,\rho\tau)$-space of the form

$$\frac{\rho}{\alpha} = \frac{\rho\tau}{\alpha\tau} = \text{constant} \qquad (2.4.4)$$

so that varying τ, with A^* held constant, merely moves the state-defining point in $(\alpha\tau,\rho\tau)$-space along such a line (eg. the line $\rho\tau/\alpha\tau = -1$ in Fig. (2.5)). Also, examination of the linearised stability equations (NISBET & GURNEY 1982, p. 42) reveals that the local stability boundary tends asymptotically with increasing τ to the line $-\rho/\alpha = 1$, so that if $-\rho/\alpha < 1$, then no value of τ will destabilize A^*, whereas if $-\rho\ \alpha > 1$, then there will be a finite delay sufficient to ensure instability.

The value of this critical delay, τ_c, at which a potentially unstable steady states will actually destabilise (stability for $0<\tau<\tau_c$, instability for $\tau > \tau_c$); can be calculated from the equations for the local stability boundary in $(\alpha\tau,\rho\tau)$-space (EL'SGOL'TS 1966), as

$$\tau_c = \frac{\cos^{-1}(\alpha/\rho)}{(\rho^2-\alpha^2)^{\frac{1}{2}}} . \qquad (2.4.5)$$

Hence, recalling the definitions of α and ρ, the conditions for the appearance of deterministically persistent fluctuations as solutions to Eq. (2.2.4) are that in the neighbourhood of some A*, the (delayed) recruitment rate function must be falling faster than the (undelayed) death rate function is rising, and that the delay must be "long enough". A comparison of Figs. (2.1) and (2.2) reveals that the first of these conditions can be fulfilled for some "scramble", but never for "contest" competition, so that persistent fluctuations would not be observed in the latter case. Furthermore, under "contest" conditions $\partial R(A)/\partial A$ remains positive, i.e. above the line $\rho = 0$ in Fig. (2.5) so that convergence is always of the non-oscillatory kind. This in turn implies that sustained quasi-cycles (bursts of coherent cycles, separated by periods of incoherent, noisy behaviour; see NISBET & GURNEY 1976, 1982 Ch. 7) will not be found under "contest".

It is also of interest to note what this stability analysis tells us about cases where there is an Allee effect. Here there is a lower steady state which, from Figs. (2.3) and (2.5), must be locally unstable, and where $R(A(t-\tau))$ rises faster than does $D_A(A(t))$. It follows from the stability equations for Eq. (2.4.2) (NISBET &

GURNEY 1982, p. 42) that the rate of the exponential divergence from this unstable steady state, μ, is given by the (real) solution to

$$\mu = -\alpha+\rho e^{-\mu\tau} \qquad \mu > 0 \tag{2.4.6}$$

from which it can be found, by differentiation with respect to τ, that

$$\frac{d\mu}{d\tau} = -\frac{\mu(\mu+\alpha)}{1+(\mu+\alpha)\tau} \qquad \mu, \alpha, \tau > 0. \tag{2.4.7}$$

From Eqs. (2.4.6) and (2.4.7) it is clear that as τ increases to infinity, μ decreases monotonically and asymptotically to zero. Hence a long time delay will increase the length of time a population will spend in the neighbourhood of an unstable steady state that is due to an Allee effect, a feature previously demonstrated by BEDDINGTON & MAY (1975) for a particular equation of type (2.2.4) in which the function has an Allee effect.

2.5 BOUNDEDNESS OF SOLUTIONS

If a population trajectory has a local maximum or minimum (denoted by A_T) at some time t, then setting $dA(t)/dt = 0$ in Eq. (2.2.4) gives the relation

$$R(A(t-\tau)) = D_A(A_T) \tag{2.5.1}$$

Further, $R(A(t-\tau))$ is by definition positive, and is bounded above, so that

$$0 \leqslant R(A(t-\tau)) \leqslant R_{max}, \tag{2.5.2}$$

where R_{max} is the maximum value of $R(A(t-\tau))$, and so is the asymptotic value of the recruitment function for "contest", and the value at the hump maximum for "scramble" (see Figs. (2.1) and (2.2)). Thus for any local maximum or minimum, A_T,

$$0 \leqslant D_A(A_T) \leqslant R_{max}, \tag{2.5.3}$$

so that there is both a (zero) lower bound and an upper bound on A_T. In the persistent fluctuation regime, which can exist only if competition is of "scramble" type, the maximum value attained once the transient behaviour has passed must be a turning point, so that there is an upper bound to solutions of Eq. (2.2.4), A_U, given by

$$D_A(A_U) = R_{max} \tag{2.5.4}$$

In addition to this rigorously established upper bound, there appears to be a non-zero lower bound. I have not managed to prove this, but numerical studies of several models strongly suggest that as the delay tends to infinity, so the dominant period of the fluctuations tends to a limit of 2τ (a result rigorously true on the local stability boundary, where $\omega\tau \to \pi$ as $\tau \to \infty$, so that the dominant period, $2\pi/\omega \to 2\tau$). At this limit, because of the "square" form of solutions to Eq. (2.2.4) (see Fig. (2.6) and section (2.6)), the absolute minimum population value attainable (A_L) must occur at a time τ after A_U, and so be a solution of

$$D_A(A_L) = R(A_U) \tag{2.5.5}$$

This lower bound is particularly significant when there is an Allee effect, since then extinction can be expected when the lower bound of fluctuations around the upper steady state reaches the lower unstable steady state. Using Eq. (2.5.5), the critical parameter values for a given model which will cause the population to become extinct for long enough τ (i.e. large enough fluctuations) can be found.

2.6 RELATIONSHIPS WITH DIFFERENCE EQUATIONS

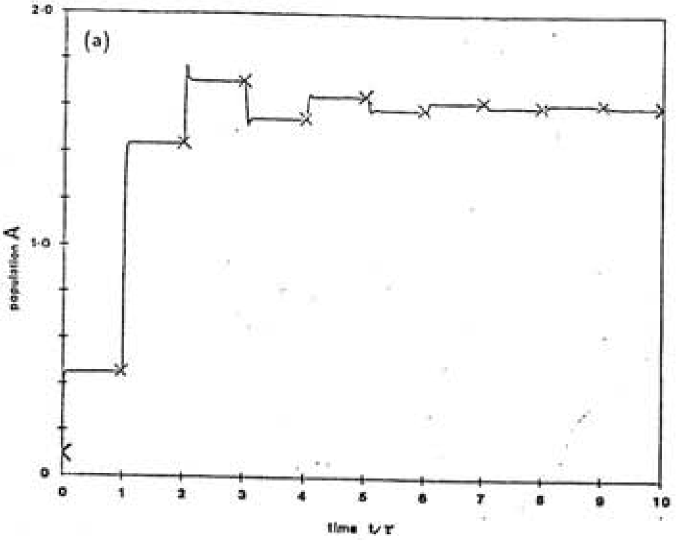
I now investigate the relationship between delay-differential population equations and the simple first-order difference equations commonly used in population biology. The obvious discrete time analogue of (2.2.4) is a difference equation with two distinct "delays", namely

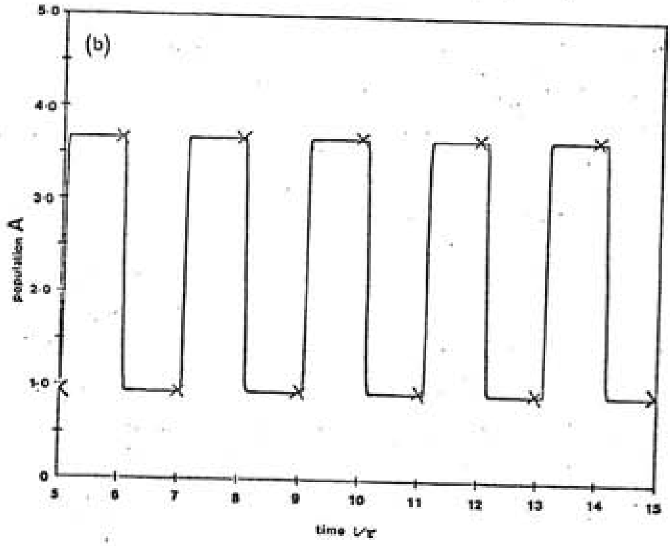
$$\frac{A_{t+\Delta t} - A_t}{\Delta t} = R(A_{t-\tau}) - D_A(A_t), \tag{2.6.1}$$

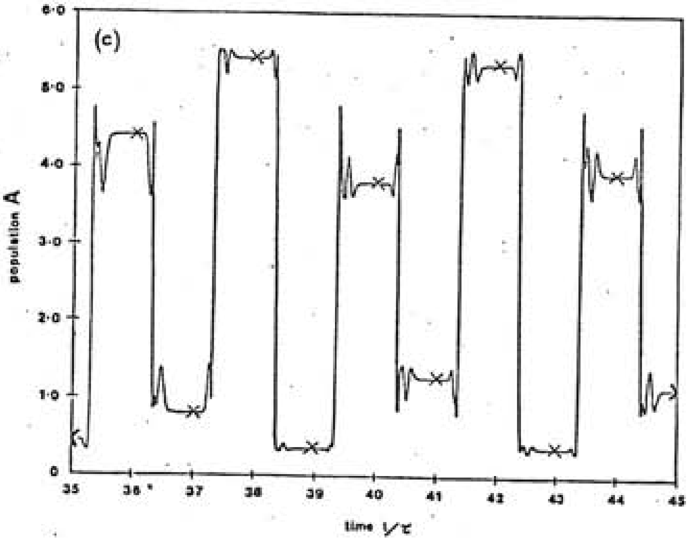
where the "long" delay τ is some integer multiple of Δt. Difference equations of the form have been widely studied in the fisheries literature (e.g. CLARK 1976, GOH 1980), and have occasionally been used for insect population models (e.g. READSHAW & CUFF (1980)). However it is not with equation (2.6.1) that I am here concerned, but rather with a much less obvious analogue, which derives from the fact that as the time delay τ in the delay-differential equation (2.2.4) becomes very long, this equation has solutions related to those of a simple <u>first-order</u> difference equation with only one delay. This is because, in the limit of large τ, the solution of (2.2.4) resembles a sequence of "steps" of duration τ (see Fig. (2.6)). At the end of each "step" the population trajectory is essentially flat, and thus the population sizes at the end of successive "steps" are related by

$$R(A_{t-\tau}) = D_A(A_t) \tag{2.6.2}$$

which is obtained by setting $dA(t)/dt = 0$ in Eq. (2.2.4). Equation (2.6.2) can readily be rearranged to give the first-order difference equation


(a)
population A
time t/τ
0
1·0
2·0
0 1 2 3 4 5 6 7 8 9 10


(b)
population A
time t/τ
0
1·0
2·0
3·0
4·0
5·0
5 6 7 8 9 10 11 12 13 14 15


(c)
population A
time t/τ
0
1·0
2·0
3·0
4·0
5·0
6·0
35 36 37 38 39 40 41 42 43 44 45

$$A_{t+\tau} = G(A_t), \quad A_I > 0 \tag{2.6.3}$$

where I will call $G(A_t)$ the "generative function", as it specifies the net reproduction from one generation to the next; A_I is the initial population size. Normally, if $D_A(A(t))$ is monotonic and not "excessively" non-linear, and $R(A(t-\tau))$ is "humped", then $G(A_t)$ will also be humped (see Fig. (2.7)). The fact that the difference equation (2.6.3) is closely related to a delay-differential equation like equation (2.2.4), when $dA(t)/dt$ is small was recognized by OSTER & IPAKTCHI (1978) and by MAY (1981); however, without knowledge of the asymptotic, "steplike" behaviour of the delay-differential equation, they were unable to fully exploit the relationship.

MAY & OSTER (1976) have examined the behaviour of Eq. (2.6.3) with "humped" $G(A_t)$ in some detail, and I shall restrict myself to mentioning those results which I intend to use. Not surprisingly perhaps, (2.6.3) has the same values for steady state, and for upper and lower bounds, as the analogous delay-differential equation (2.6.4). Further, it is clear from the above formulation of (2.6.3) that the conditions for local instability in the difference equation are equivalent to those already derived for (2.2.4) in the limit of large τ, namely

$$-\frac{\rho}{\alpha} = -\gamma \equiv \left(\frac{\partial G(A_t)}{\partial A_t}\right)_{A_t=A^+} > 1, \tag{2.6.4}$$

where $-\gamma$ is defined as the gradient of $G(A_t)$ at A^* (see Fig. (2.7)). It will usually be true of "humped" $G(A_t)$ that progressive steepening

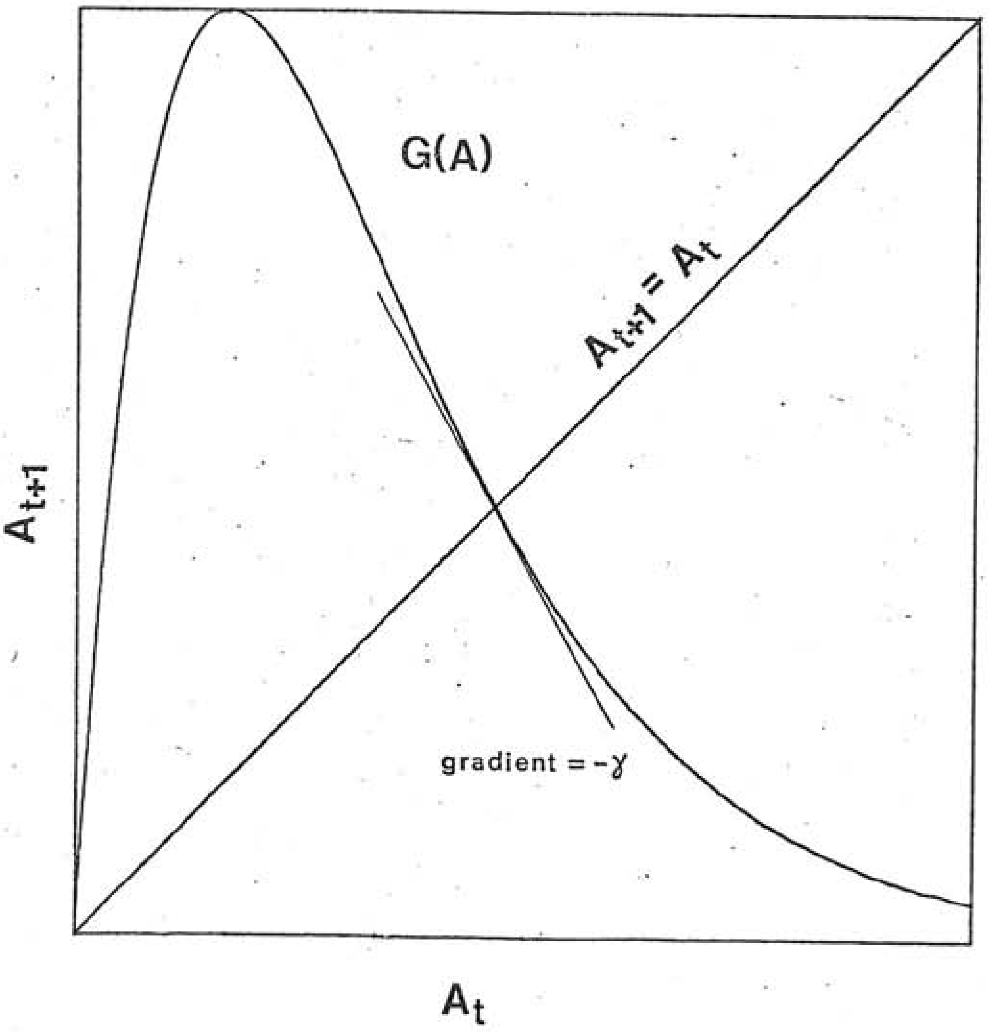


Fig. (2.7) - General "one-humped" shape for the generative function, $G(A_t)$, in Eq. (2.6.3) with normalised delay. $-\gamma$ is the gradient of the tangent to the generative function at the steady state A^*.

at A* using some variable parameter will cause an infinite series of bifurcations to appear, the first being when (2.6.4) is just satisfied, and a two-point cycle appears, subsequent ones occurring, over rapidly decreasing ranges of parameter values, as 2^k-point cycles (k = 2, 3, . . .) develop, until beyond some critical steepness in the generative function, "chaotic" solutions appear. This critical steepness can be found for any particular model using a rapidly converging algorithm described in Appendix A of MAY & OSTER (1976) MAY (1976) quotes a few mathematically entertaining examples which behave differently, while ALLWRIGHT (1978) gives an additional (sufficient) condition on the form of $G(A_t)$ that ensures period doubling and "chaos". However, the forms that produce different behaviour are sufficiently perverse that for modelling purposes, period doubling can be loosely regarded as being "normal" in equations of this type. In section (2.7) I show that normally the existence of bifurcations in the solutions of a delay-differential equation can be predicted, if the analogous first-order difference equation exhibits period doubling behaviour.

2.7 NUMERICAL EXAMPLES AND ILLUSTRATIONS

I will now illustrate the results on stability and boundedness of solutions, and on relationships with difference equations, using two equations of type (2.2.4). I will examine the behaviour of one in some detail, and then use the other to test the generality of this behaviour. Throughout, I will use one of the simplest possible functional forms for the death rate function,

$$D_A(A(t)) = mA(t), \quad m > 0, \qquad (2.7.1)$$

where m is the density-independent *per capita* death rate in the adult population. This permits concentration upon differences in the precise form and structure of the recruitment functions, which, as persistent fluctuations are to be considered, are both of "scramble" type.

2.7.1 Model (I)

For the first model, I choose the equation that I use in the Case Study (Chapter 3), namely

$$\dot{A}(t) = P_1 A(t-\tau)\exp(-A(t-\tau)/A_0) - mA(t) \qquad (2.7.2)$$

where P_1 is related to the maximum possible *per capita* fecundity. Equation (2.7.2) has rather cursorily been fitted to some of NICHOLSON's (1950, 1954, 1957, 1960) blowfly data by OSTER (1976) and OSTER & IPAKTCHI (1978), and more comprehensively by GURNEY BLYTHE & NISBET (1980), and NISBET & GURNEY (1982, Ch. 8). The direct discrete-time analogue of (2.7.2) (i.e. of the form (2.6.1)) has been fitted to the same data by READSHAW & CUFF (1980).

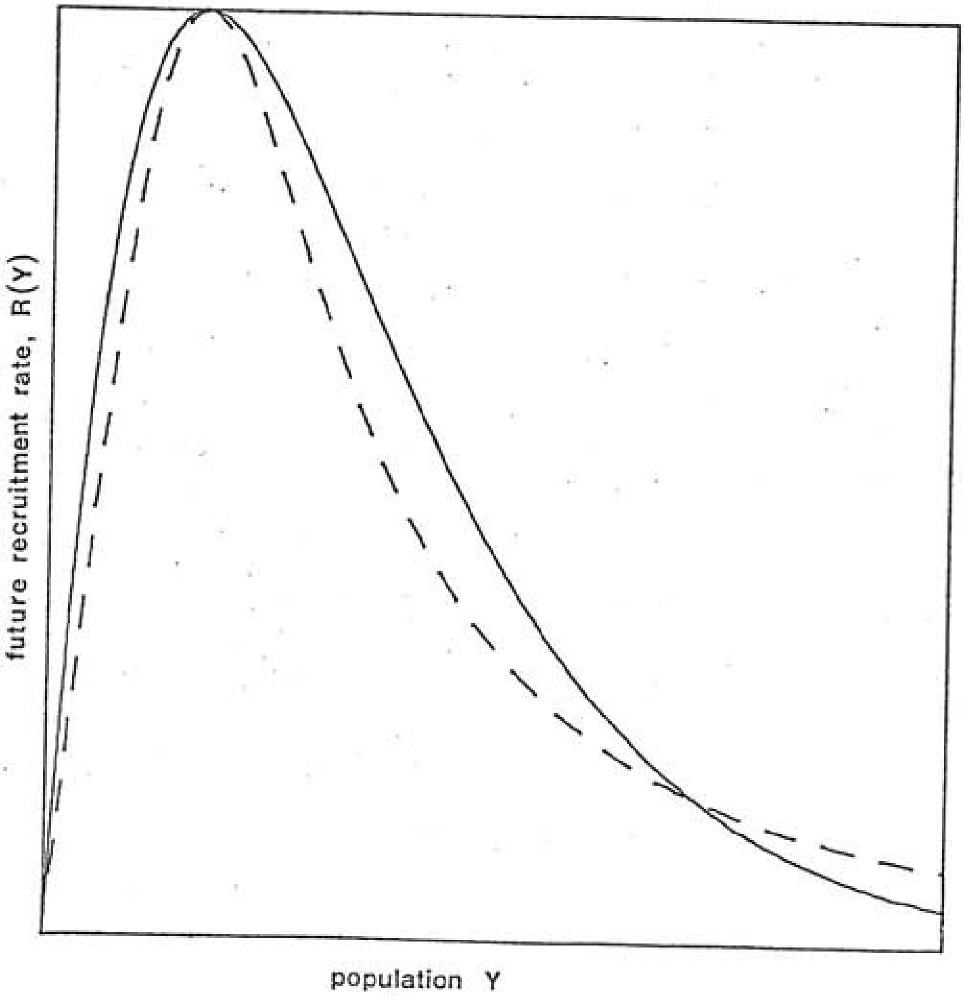


Fig. (2.8) - The normalised recruitment function for Model (I) (————), and Model (II), d = 3 (--------).

Equation (2.7.2) has the advantage of having A_0, the population size at which the total future recruitment rate is at a maximum, represented explicitly. It is advantageous to scale A(t) in terms of A_0 ($Y \equiv A/A_0$), so that (2.7.2) becomes

$$\dot{Y}(t) = P_1 Y(t-\tau)\exp(-Y(t-\tau)) - mY(t) \qquad (2.7.3)$$

As the peak height of $R(Y(t-\tau))$ is to be considered, and as I intend to compare models, it is more convenient to consider the controlling parameter space of (2.7.3) in terms of R'_{max} ($= R_{max}/A_0$, the scaled rate of future total recruitment), m and τ, rather than use P_1. For (2.7.3),

$$R'_{max} = P_1 \, e^{-1} \qquad (2.7.4)$$

so that, substituting this into Eq. (2.7.3), Model (I) becomes,

$$\dot{Y}(t) = R'_{max} Y(t-\tau)\exp(1 - Y(t-\tau)) - mY(t) \qquad (2.7.5)$$

(see Fig. (2.8)). Model (I) has a steady state solution, when $R'_{max} > me^{-1}$,

$$Y^* = 1 + \ell n \, (R'_{max}/m), \qquad (2.7.6)$$

and evaluation of the partial derivatives in Eq. (2.4.2) yields the general condition for potentially unstable steady states ($-\rho/\alpha > 1$)

$$R'_{max}/m > e, \qquad (2.7.7)$$

or equivalently, $Y^* > 2$. Fig. (2.9) shows the full local stability boundary, in the controlling ($R'_{max}\tau$, $m\tau$)-space, calculated parametrically from the linearised stability equations.

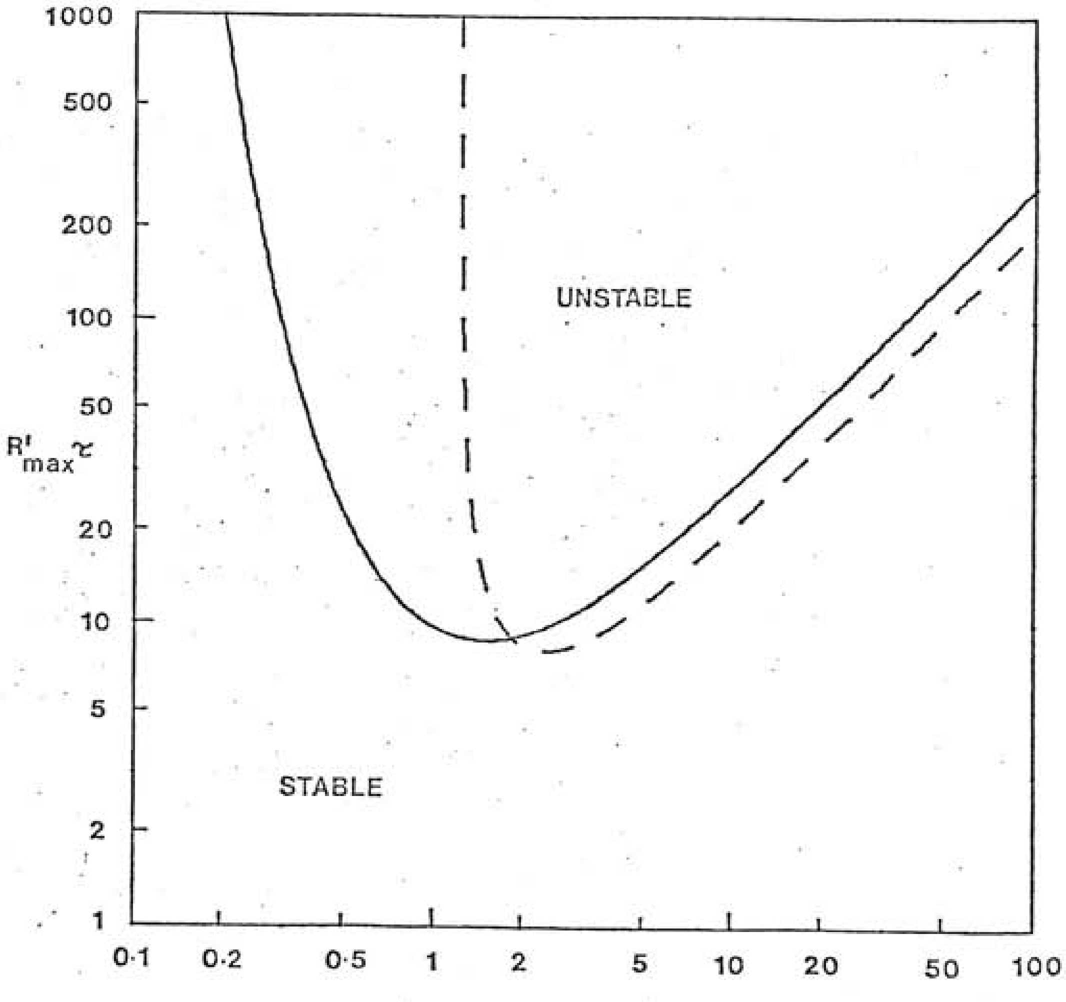


Fig. (2.9) - The local stability boundary for Model (I) (————) and Model (II), d = 3 (--------) in the common parameter space. Moving from bottom right to top left is equivalent to increasing Y^*; moving from bottom left to top right is equivalent to increasing τ.

Unfortunately, the behaviour in the persistent fluctuation region of parameter space cannot be simply characterised analytically, and it is usually necessary to resort to extensive numerical analysis. It is at this point that the methods outlined in sections (2.5) and (2.6) become useful. By considering the case where the delay is "infinite" and population trajectories "step-like", the discrete-time analogue of Model (I) can be constructed, and some insight into the dynamics of the continuous-time equation gained through study of the simple difference equation. Following the route of section (2.6), equation (2.7.5) becomes

$$0 = R'_{max} Y_{t-\tau} \exp(1 - Y_{t-\tau}) - mY_t, \qquad (2.7.8)$$

which can be rearranged to give

$$Y_{t+\tau} = (R'_{max}/m)\, Y_t \exp(1 - Y_t), \qquad (2.7.9)$$

the difference equation analogue of Model (I). Note that by setting $R'_{max}/m = \exp(v - 1)$, this equation becomes

$$Y_{t+\tau} = Y_t \exp(v - Y_t), \qquad (2.7.10)$$

which is a scaled version of a model with an impressive pedigree in population dynamics (MAY 1974b, 1975, 1976; MAY & OSTER 1976; these contain further references). A wealth of information on the dynamics of (2.7.4), a portion of which is summarised in Table (2.1), is available from these and other sources.

The series of values of R'_{max}/m which define the boundaries of behaviour in the discrete-time equation (2.7.9) (see Table (2.1))

Table (2.1) Dynamic Behaviour of the Difference Equation Analogues of Model (I) and Model (II) (d = 3)

Range of values of R'_{max}/m for which the two equations exhibit the stated type of behaviour.		
MODEL (I) (Eq. (2.7. 9))	MODEL (II) (Eq. (2.7.22)	Type of behaviour
0.368 - 1.000	0.667 - 1.000	Stable overdamped
1.000 - 2.718	1.000 - 2.000	Stable underdamped
2.718 - 4.600	2.000 - 4.829	Unstable: 2-point cycles
4.600 - 5.238	4.829 - 7.958	4-point cycles
5.238 - 5.392	7.958 - 9.217	8-point cycles
5.392 - 5.433	9.217 - 9.71[a]	16-point cycles or longer
5.433	9.71[a]	Chaotic solutions

[a] Not calculated exactly.

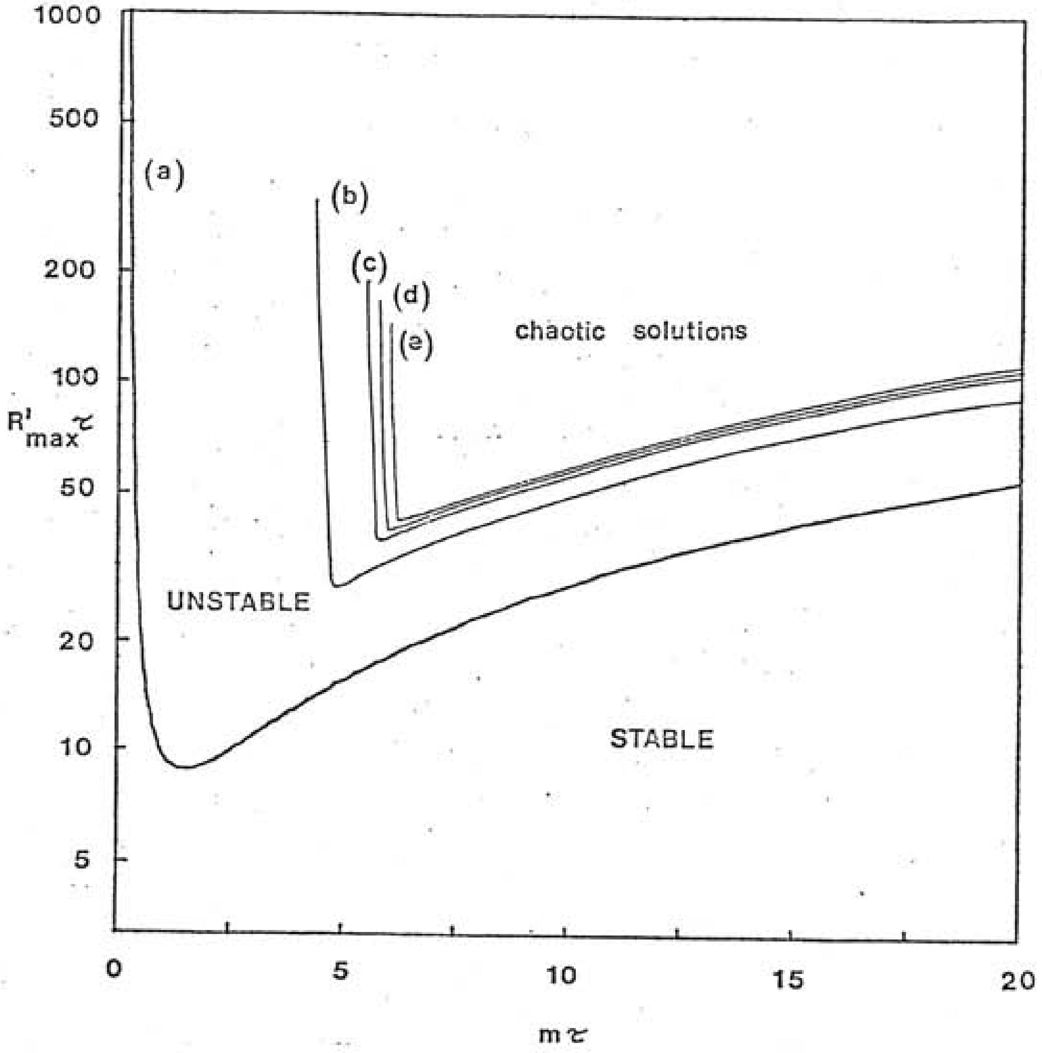


Fig. (2.10) - The approximate shape of the boundaries of behaviour for Model (I), in the persistent fluctuation regime beyond (a) the local stability boundary. At (b), (c), (d)... successive period-doublings occur, until at (e), solutions are apparently chaotic. For large τ, these boundaries tend towards the values of R'_{max}/m given in Table (2.1) for Eq. (2.7.9).

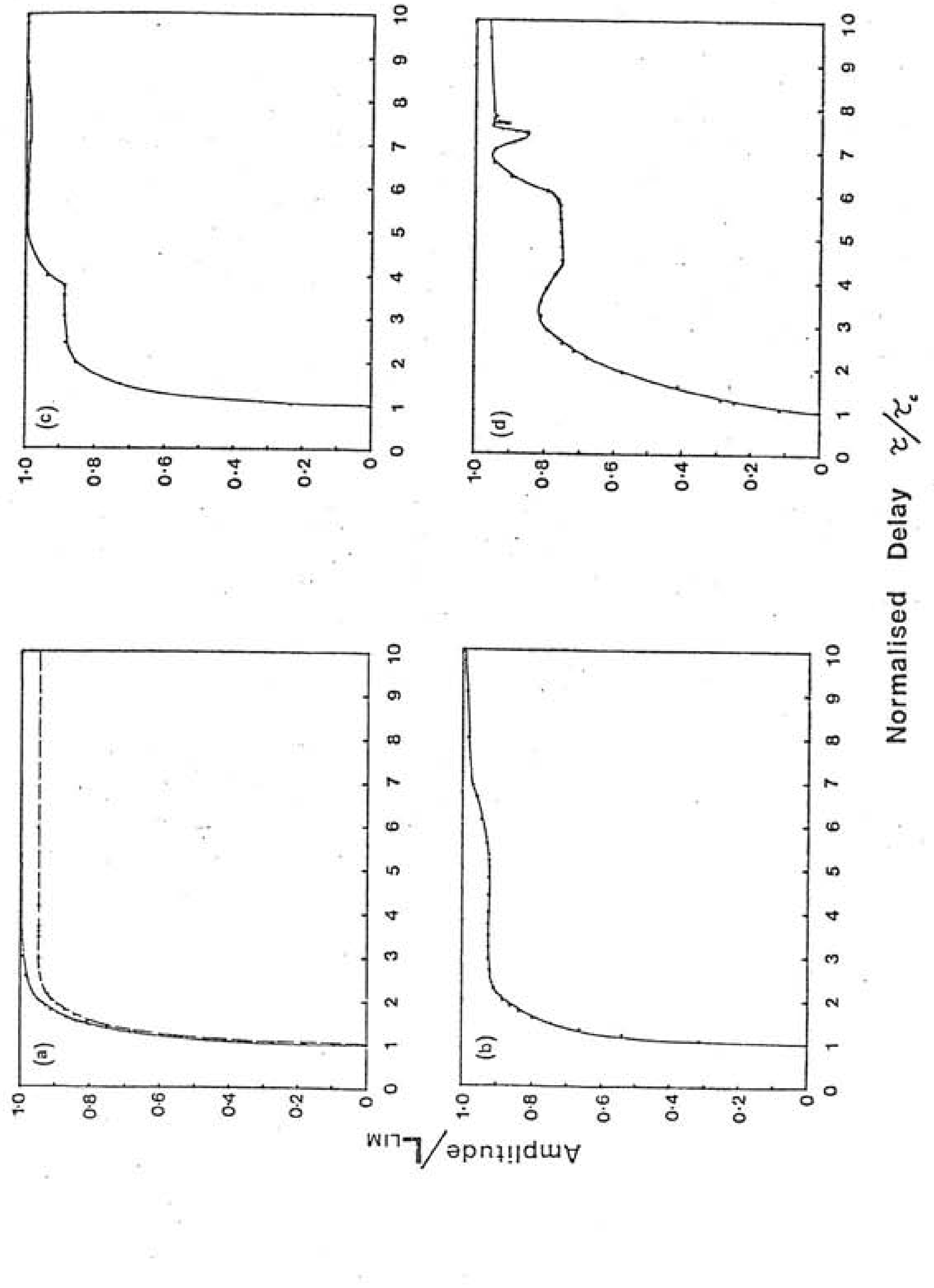
represent the asymptotic positions of the boundaries of corresponding behaviour in Model (I) as $\tau \to \infty$. In Fig. (2.10) I have plotted the approximate positions of some of the bifurcation boundaries for Model (I), obtained by taking a series of transects of increasing τ through $(R'_{max}\tau, m\tau)$-space. These boundaries (where period-doubling occurs in solutions of the delay-differential equation) are approximately the same shape as the local stability boundary, as might be expected, and they all approach their asymptotic value of R'_{max}/m rather quickly, as τ is increased. Thus, for any steady state which cannot produce chaotic solutions, the normalised formal repeat period (i.e. period/delay) can be determined when τ is very large, from the behaviour of the analogous difference equation.

I now examine the relationship between fluctuation amplitude and length of delay.

$$L_{lim} \equiv Y_U - Y_L, \qquad (2.7.11)$$

calculating Y_U and Y_L according to Eqs. (2.5.4) and (2.5.5), so that L_{lim} is the predicted asymptotic (as $\tau \to \infty$) amplitude for fluctuations in the non-linear region for the scaled equation (2.7.5). Fig. (2.11) is a plot of the fluctuation amplitude (maximum - minimum), as a proportion of L_{lim} against length of delay as a multiple of the critical delay (τ_c from Eq. (2.4.5)); a number of points worthy of note arise from consideration of this figure.

First, note that fluctuation amplitudes approach the asymptotic value, L_{lim}, as τ increases, and with one exception in Fig. (2.11), eventually become very close to this value. This exception is the


(a)
(b)
(c)
(d)
Amplitude/L_LIM
Normalised Delay τ/τc
0
0·2
0·4
0·6
0·8
1·0
0
1
2
3
4
5
6
7
8
9
10

result (see Fig. (2.11a)) for $R'_{max}\tau/m \simeq 4.14$, where the amplitude reaches about 95% of L_{lim} quite quickly, but is unable to exceed this value. This will be true for a very small range of values of $R'_{max}\tau/m\tau$ in each bifurcation "zone", where the fluctuation minimum has fallen well below the peak maximum, but where the next bifurcation has not occurred. In all other cases examined the asymptotic limit is eventually closely approached, taking a progressively larger τ/τ_c value to do so as $R'_{max}\tau/m\tau$ increases. A smooth rise in amplitude to the asymptotic value, as τ increases, is typical of solutions to equations of KAPLAN & YORKE's (1977) general family, and the similar behaviour for Model (I), with small amplitude limit cycles appearing just after the local stability boundary, and growing until the fluctuation minimum falls below the peak in $R(Y(t-\tau))$, confirms the argument of section (2.4).

A second point of interest in Fig. (2.11) is the curious variation in fluctuation amplitude in those transects passing through more than one behavioural region. What happens is best described by "following" such a transect (that for which there are just 2 bifurcations, say) as τ is increased (see Fig. (2.11b)). Immediately after the first bifurcation ($\tau = \tau_c$) the amplitude rises swiftly, until the depression of future population by (present) values well below the maximum in the recruitment function causes first a decrease, and then a levelling off in amplitude to occur. Amplitude stays approximately constant until $\tau/\tau_c \simeq 6$, when the second bifurcation occurs and there is an increase towards the asymptotic limit, L_{lim}. When there are three bifurcations (see Fig. (2.11c)), exactly the same pattern appears: initial growth followed by decline and levelling off at a reduced value, for the first two bifurcations, and approach to the asymptotic limit after the third. For the transect where $R'_{max}\tau/m\tau \simeq 14.7$ (see Fig. (2.11d)), which passes into the chaotic region, there is a long (and possibly infinite) series of bifurcations, with each of which, except for the last, there is an associated growth, decline and levelling off of fluctuation amplitude, occurring over a progressively decreasing range of τ/τ_c, and effecting a similarly decreasing change in the size of the observed amplitude.

At this point I will remark upon the fact that there are two parameters (R'_{max}/m, and τ), each of which has the characteristic that continuous increase will lead to the occurrence of a succession of bifurcations, with the range of parameter values between each successive bifurcation being progressively smaller. FEIGENBAUM (1978, 1979) has recently shown that for recursive relations of the form

$$Y_{j+1} = \varepsilon G(Y_j), \quad \varepsilon > 0, \ j = 0,1,2\ldots \tag{2.7.12}$$

exhibiting an infinite bifurcation sequence, the range of values of ε for each bifurcation will decrease according to a convergent progression to a universal value, δ_F, given by

$$\delta_F = \lim_{k\to\infty} \frac{(\varepsilon_{k+1} - \varepsilon_k)}{(\varepsilon_{k+2} - \varepsilon_{k+1})} = 4.66920\ldots \tag{2.7.13}$$

where k is the number of bifurcations in the sequence. It is clear that Eq. (2.7.9) is of the appropriate form, and that R'_{max}/m can be expected to converge to δ_F. This does indeed appear to happen -

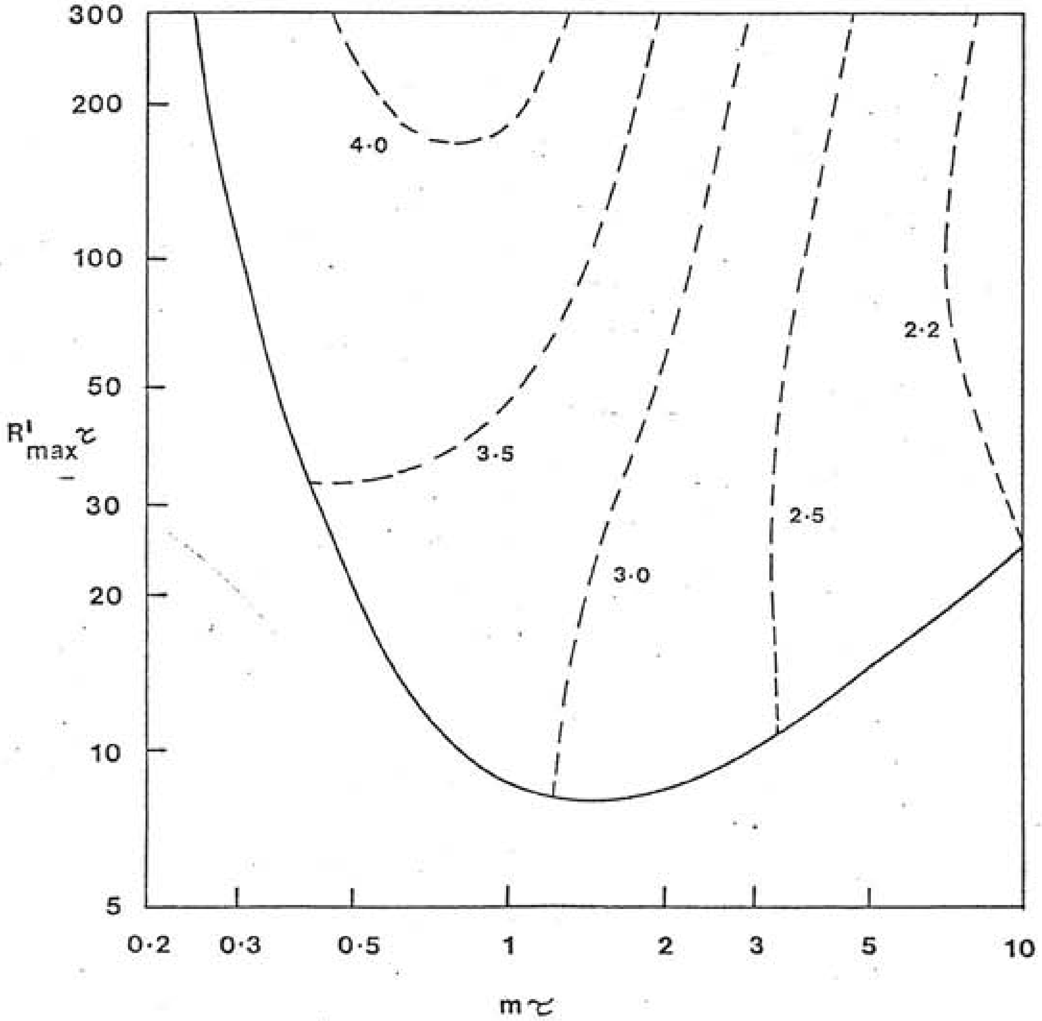


Fig. (2.12) - Contours of equal normalised dominant period (--------), T/τ, in the persistent fluctuation region of $(R'_{max}\tau, m\tau)$-space for Model (I).

the first part of the sequence can be followed in Table (2.1). However, it is also quite clear that τ is not a parameter of type ϵ, and it is not therefore surprising to find that the sequence of ranges of τ for the cases considered, do not appear to converge according to Feigenbaum's δ_F sequence. There is little, therefore, that can be said about behaviour when a large number of bifurcations have occurred, and I shall not dwell on this point.

In Fig. (2.12) I have plotted contours of the normalised dominant period (T/τ) in the persistent fluctuation region of $(R'_{max}\tau, m\tau)$-space for Model (I). It is clear that T/τ varies with both Y^* and τ. For small Y^*, increasing the delay τ causes a smooth and rapid decrease in T/τ towards an asymptotic value of 2τ. When Y^* is larger, this decline is not quite so rapid, but the asymptotic limit is the same, and for very large steady states, there is in fact an initial increase in the normalised dominant period, but again when τ becomes much longer, the limiting value of $T/\tau = 2$ is approached. This change of behaviour with the size of the steady state does not appear to be associated with the bifurcation sequence in the solution, except inasmuch as the simplest pattern occurs at the smallest (unstable) Y^*. It should be noted that when "following" a transect along a line of constant Y^* (and hence constant R'_{max}/m) that crosses a number of bifurcation boundaries, there is no abrupt change in the normalised dominant period at these boundaries - the formal repeat period of course doubles at each bifurcation, but curves of T/τ against τ are continuous.

This description of the behaviour of Model (I) in the non-linear regime seems to be quite self-consistent, and readily explicable in terms of what is understood of the dynamic processes involved. I will now examine the behaviour of the second equation.

2.7.2 Model (II)

I will first briefly examine the local stability properties of an equation with a rather more generalised recruitment function than that in Model (I), and then select a specific case chosen so as to make the recruitment functions of the two models as similar as possible, in order to compare behaviour. The delay-differential equation I have chosen is

$$\dot{A}(t) = \frac{P_2 A(t-\tau)}{1+c_0 A(t-\tau)^d} - mA(t), \qquad (2.7.14)$$

where P_2 is again a parameter related to the maximum possible *per capita* fecundity, and d essentially controls the rate of decline of $R(A(t-\tau))$ after the peak (i.e. a "scramble" parameter). The increased generality introduced by the extra parameter means that in this case the peak position, A_0, does not appear explicitly in the recruitment function, but is given by

$$A_0 = \left[c_0(d-1)\right]^{-1/d}. \qquad (2.7.15)$$

Again, A(t) is scaled in terms of $A_0 (Y = A/A_0)$, standardising the two models, so that (2.7.14) becomes

$$\dot{Y}(t) = \frac{P_1 Y(t-\tau)}{1+Y(t-\tau)^d/(d-1)} - mY(t), \qquad (2.7.16)$$

and if the scaled maximum future recruitment rate (R_{max}/A_0),

$$R'_{max} = P_2 \frac{d-1}{d} \qquad (2.7.17)$$

is again used as a model parameter, then Models (I) and (II) have a common parameter space, and (2.7.16) becomes

$$\dot{Y}(t) = \left(\frac{d}{d-1}\right) \frac{R'_{max}Y(t-\tau)}{1+Y(t-\tau)^d/(d-1)} - mY(t) \qquad \cdot (2.7.18)$$

which has the steady state solution

$$Y^* = \left[d(R'_{max}/m - 1) + 1\right]^{1/d}, \qquad (2.7.19)$$

and (potential) instability condition ($-\rho/\alpha > 1$)

$$R'_{max}/m > \left(\frac{d-1}{d-2}\right). \qquad (2.7.20)$$

There is an interesting result to be extracted from this elementary analysis of the local stability of the general equation (2.7.18). It is evident from Eq. (2.7.18) that the recruitment function is "humped" for all $d > 1$; however, according to Eq. (2.7.20) instability cannot occur, regardless of the length of the time delay, unless $d > 2$. This simply reflects the asymptotic behaviour of this choice of $R(Y(t-\tau))$: for large Y, R(Y) falls off as Y^{1-d}, and for $d < 2$ it is quite clear that the condition $-\rho/\alpha > 1$ cannot be satisfied with the given linear death rate, Eq. (2.7.1).

For the detailed comparison between Models (I) and (II), I choose a value of d which allows close matching of the shapes of the two recruitment functions; a value of $d = 3$ produces a curve sufficiently similar to that for Model (I) (see Fig. (2.8)). The example equation for Model (II) is therefore

$$\dot{Y}(t) = \frac{1.5R'_{max}Y(t-\tau)}{1+0.5Y(t-\tau)^3} - mY(t). \qquad (2.7.21)$$

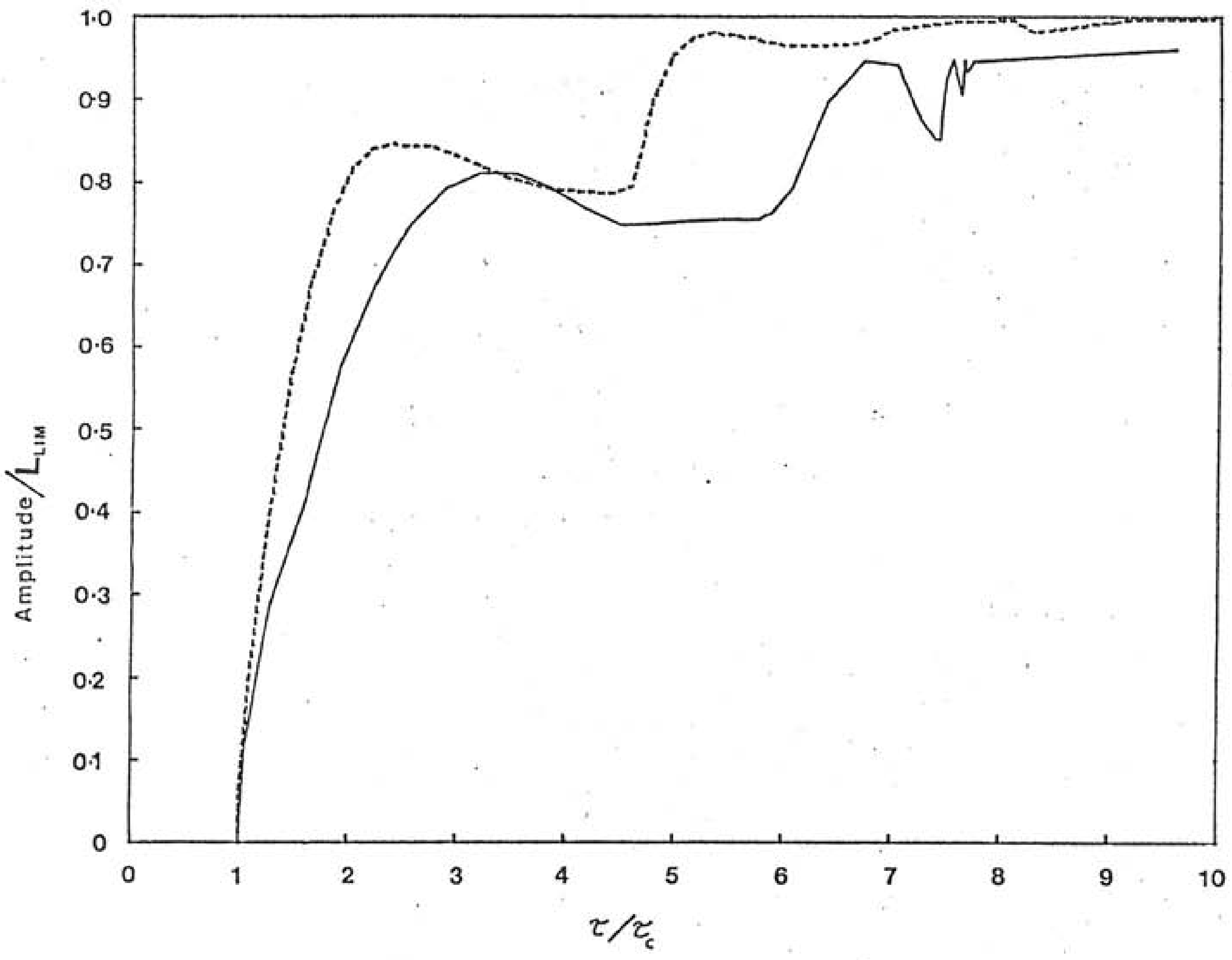
The local stability boundary for this equation eppears, with that for Model (I), in Fig. (2.9). It is immediately clear that the two models behave rather similarly for small Y*, but that for larger steady states the local stability boundaries diverge, with Model (II) being the more stable (larger τ_c required). This difference reflects the form of the recruitment functions in Fig. (2.8), for the two curves are very similar for steady states up to about two or three times the peak value, but their asymptotic behaviour is quite different, with (II) falling off rather less rapidly than (I), and so being more stable.

To locate the boundaries of behaviour in the persistent fluctuations regime, I again make use of the methods of section (2.6), and derive the discrete-time analogue of model (II), namely

$$Y_{t+\tau} = \frac{1.5(R'_{max}/m)Y_t}{1 + 0.5Y_t^3}. \qquad (2.7.22)$$

This equation has received rather less attention than (2.7.10), but a slightly more general form is mentioned by MAY & OSTER (1976, Table 1), and its local stability properties are briefly considered by MAYNARD SMITH (1974, Ch. 4).

Table (2.1) lists the boundaries of behaviour for Eq. (2.7.22), and it is clear that they are acceptably similar to those for the other difference equation analogue of Model (I), although the latter is a little more unstable. Numerical analysis indicates that the


1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
Amplitude/L_{LIM}
0
1
2
3
4
5
6
7
8
9
10
τ/τ_c

boundaries in Model (II) bear the same relationship to the asymptotic value, as given by the discrete-time equation (2.7.22) as is to be found with Model (I) and its difference equation analogue. It only remains then to demonstrate that the details of fluctuation amplitude and period variations in the two models are sufficiently similar in order to conclude that the properties observed in Model (I) are robust against changes in the detailed form of the recruitment function. In Fig. (2.13) I have plotted fluctuation amplitude against length of delay for a transect through the common parameter space. The transect is that for $R'_{max}\tau/m\tau \simeq 14.7$, and enters the chaotic regions of behaviour of both models, for long enough delay. While the results are certainly not identical (and it would be more than a little surprising if they were), they agree very closely upon the absolute amplitudes produced, and upon the appearance of the successive bifurcations, with Model (II) being again the more stable of the two. Clearly the general pattern of amplitude variation with delay length holds true for both models, even in the most intensely non-linear regimes, and it is safe to say that, within the bounds of experimental uncertainty, the qualitative predictions of the two models are virtually indistinguishable. As the death rate function, $D(A(t))$ is likely to be a much smoother function than $R(A(t-\tau))$ (see section (2.3)), it might be expected that variations in its specific form, and in the degree of non-linearity it possesses, would not alter the qualitative features of the general pattern of dynamic behaviour outlined above. This point is not pursued here, but some very cursory and superficial investigations indicate that this conclusion is a valid one.

The behaviour I have described is not, of course, generic for all "one-humped" functional forms of recruitment (see the example in

ALLWRIGHT 1978, for example), but on the basis of the detailed comparison between Models (I) and (II), and of some rather more cursory examinations of other "one-humped" forms for $R(A(t-\tau))$, I feel that I can say with some confidence that any sensible choice of analytic "humped" function can be used for the recruitment function in population equations of type (2.2.4), without introducing too many misleading model-specific effects.

2.8 DISCUSSION AND CONCLUSIONS

I have briefly stated the general conditions under which it is possible to express the dynamics of a population of mature adults using the delay-differential equation

$$\dot{A}(t) = R(A(t-\tau)) - D_A(A(t)) \qquad (2.8.1)$$

The use of Eq. (2.8.1) as a population model brings a number of advantages, being principally that there is no loss of the biologically important "fine detail" effects (discussed in detail in Ch. 3), as there is with discrete generation difference equation models, and at the same time that much of the burden of analysis, which goes with the use of models having more completely specified age-structure can be avoided, for the given competition regimes, when there is a constant maturation period.

I have examined the local stability properties of (2.8.1), and proposed a number of "tools" which can be used to simplify its analysis. The simple linear analysis of section (2.4) can be used to find the local stability boundary, and then the analogy with simple first-order difference equations can be exploited to locate the asymptotic position of the other bifurcation boundaries, so that for long enough "delay" τ the formal repeat time is known in multiples of the dominant period (which approaches 2τ as τ becomes very long). (It should be emphasized that the linear analysis does not provide any useful information about any bifurcation after the first despite certain claims to the contrary (e.g. PEREZ et al (1978)), a point made abundantly clear by OSTER & IPAKICHI's (1978) Fig. 11, and that without the methods of section (2.6), the only road to knowledge about the persistent fluctuation behaviour of (2.8.1) away from the local stability boundary is very extensive numerical analysis.) Furthermore, upper and lower bounds for the population size, after the transient has passed, can be calculated, and hence again for long enough τ, the approximate values of the absolute maximum and minimum excursions which are to be found in a given solution are known.

These "tools" should be particularly useful for helping to discover model-specific behaviour, so that a number of alternative models can be quickly and simply investigated, and any that departs from the general expected pattern, or is radically different from the others, can be eliminated without having to undertake lengthy numerical analysis on all of them. Of course, there are not sufficient tools available, exact or approximate, to do more than sketch some of the patterns of non-linear behaviour for (2.8.1), and if a full investigation of a particular equation is desired, as is the case in the following chapter, then there is little recourse but extensive numerical analysis.

CHAPTER 3 CASE STUDY: Modelling Laboratory Populations of *Lucilia cuprina*

3.1 INTRODUCTION

Some thirty years ago A.J. Nicholson performed a series of elegant laboratory experiments (BRILLINGER, GUCKENHEIMER, GUTTURP & OSTER 1980 report 145!) using as his experimental animal the Australian sheep blowfly *Lucilia cuprina* (Wied.) (NICHOLSON 1950, 1954, 1957, 1960). He maintained cultures of *L. cuprina* for extended periods of time (typically more than a year) under various resource supply regimes, and recorded the numbers present in, usually, one or two developmental classes, every second day. Portions of the resultant data have been widely reproduced in the literature, and considerable attention has been paid to the quasi-periodic fluctuations of population numbers evident in many of Nicholson's cultures (e.g. CLARK, GEIR, HUGHES & MORRIS 1967; VARLEY *et al* 1973, Ch. 2; AUSLANDER *et al* 1974; MAY 1974a, Ch. 4; MAYNARD SMITH 1974, Ch. 3; HASSELL LAWTON & BEDDINGTON 1976; OSTER 1976, 1981; OSTER & IPAKTCHI 1978; BRILLINGER *et al* 1980; CHARLESWORTH 1980, Ch. 1; GURNEY, BLYTHE & NISBET (1980, 1981); POOLE 1980; READSHAW 1981, READSHAW & CUFF 1980; NISBET & GURNEY 1982, Ch. 8).

The models which have been used to attempt to reproduce the observed quasi-periodic behaviour have been of many types, and vary from simple discrete-generation first-order difference equations (e.g. VARLEY *et al* 1973, Ch. 2), through delay-differential equations of assorted form (e.g. MAY 1974a, Ch. 4; MAYNARD SMITH 1974, Ch. 3;

OSTER 1976), to many-parameter full age-distribution models (e.g. OSTER & GUCKENHEIMER 1976) and purely statistical description (e.g. POOLE 1980; OSTER 1981). There has been little success however in producing simple, realistic and testable models capable of producing a reasonable quantitative fit to any of Nicholson's results, or of explaining the observed characteristics of the "cycles". In this Chapter, I present a delay-differential equation model of type (2.2.4) which goes some way towards achieving both. An account of this work has been published by GURNEY BLYTHE & NISBET (1980), and appears in more complete form in NISBET & GURNEY (1982, Ch. 8).

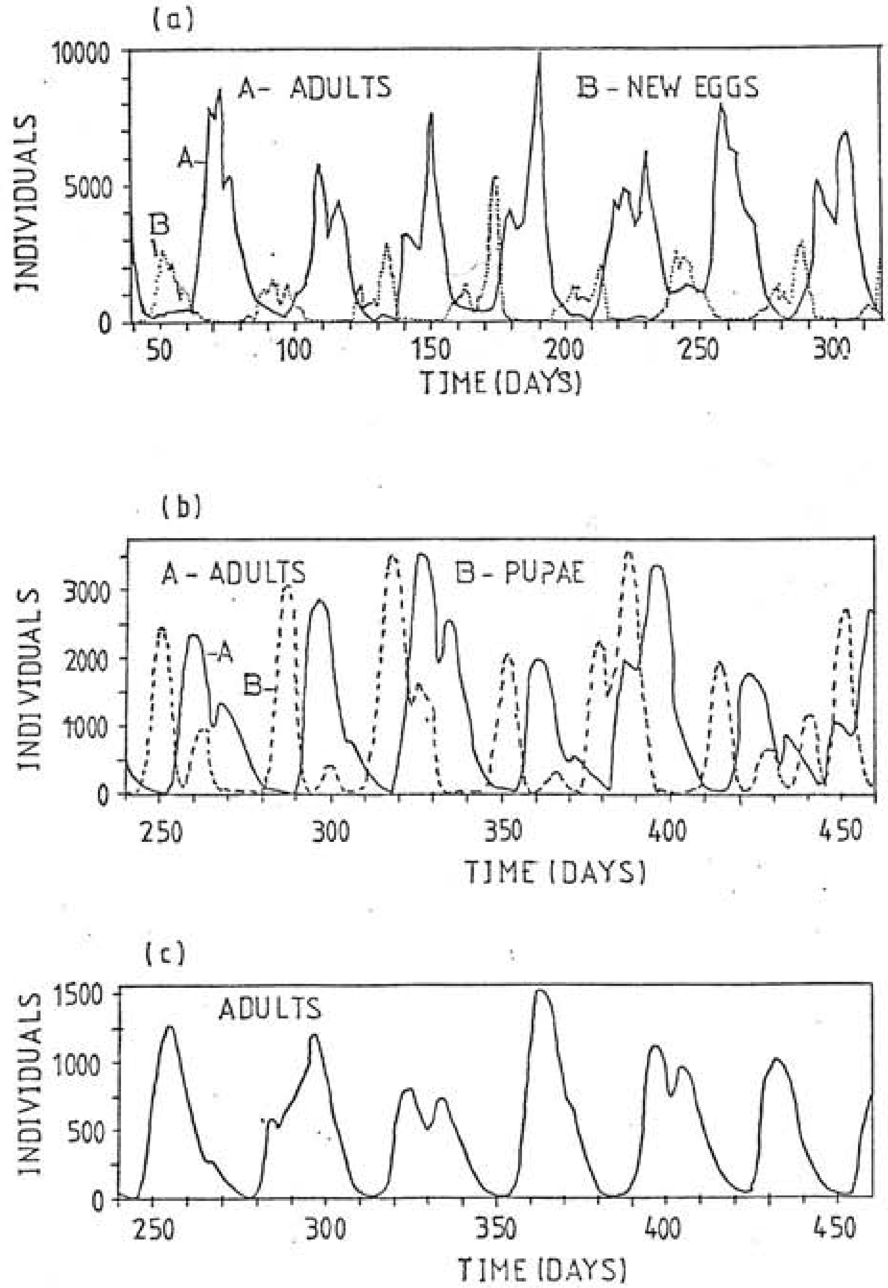


Fig. (3.1) - Quasi-periodic fluctuations in laboratory populations of *L. cuprina* (a) Adults food limited (b) Larval food limited (50g day^{-1}) (c) Larval food limited (25g day^{-1}). Data from Nicholson (1954)

3.2 MODELLING OBJECTIVES

Clearly, as the general equation developed in Chapter 2 is strictly applicable only where either adults alone compete, or whose competition occurs only amongst immature individuals of exactly the same age, a particular model can only be tested against data derived from experiments set up under these two competition regimes. In particular, I can make use of NICHOLSON (1954) results for adult-only competition (see Fig. (3.1(a)). Here, the Larvae had excess protein, in the form of liver, but the adults had a restricted supply (0.5 g ground liver day^{-1} added), although water and sugar were plentiful. Hence the adults competed equally amongst themselves for the protein to produce eggs, while the larvae did not compete for anything, i.e. "adult only" competition. Although Nicholson did not, apparently, perform any experiments where "within cohort" competition occurred, it was hypothesised (GURNEY BLYTHE & NISBET 1980) that this could be used to approximate the "larval food limited" experiments (Fig. (3.1(b,c)) - 50 g day^{-1} and 25 g day^{-1} liver added, respectively). This approximation has subsequently been justified, a point I shall return to in section (3.6).

While a simple strategic model such as Eq. (2.2.4) cannot be expected to provide a statistically "good" fit to the data, it must be capable of identifying and illuminating the important processes controlling the dynamics of the experimental population. In particular the mechanism producing the "cycles" in population fluctuation has to be identified, together with the controls on cycle characteristics (such as period and amplitude), and the qualitative features of the fluctuations made accessible to understanding (specifically, the difference in breeding behaviour between the two regimes: there are two well-separated generations per cycle for the larval food-limited case (Fig. (3.1(b and c))), but only one, rather smeared, generation per cycle in Fig. (3.1(a)). To do so, a particular choice of model, of the general type (2.2.4) must be chosen - that is, specific functions for $R(A(t-\tau))$ and $D_A(A(t))$ must be found.

3.3 ADULT COMPETITION

Despite the protein limitation in NICHOLSON's (1954) experiment (Fig. (3.1(a))), adults were provided with a surfeit of water and carbohydrates (in the form of sugar). *L. cuprina* adults can survive on a carbohydrate diet alone (ROBERTS & KITCHING 1974; GILMOUR 1961), so that little density-dependence in the *per capita* adult death rate is to be expected. Hence I assume a constant *per capita* death rate, m, as in the previous chapter, so that

$$D_A(t) = mA(t), \quad m > 0 \qquad (3.3.1)$$

From Appendix 1 (Eq. (A1.14)), the recruitment rate is given by

$$R(t+\tau) = S_1 A(t) \beta_1(A(t)) \qquad (3.3.2)$$

where S_1 is the average fraction of eggs laid which survive to become adults, and $\beta_1(A(t))$ is the *per capita* fecundity. The competition between adults is clearly of "scramble" type, so that $\beta_1(\cdot)$ must decrease with increasing A(t) (see section (2.3)). Because of its analytic simplicity, I choose the function

$$\beta_1(A(t)) = Q \exp(-A(t)/g_0) \quad Q, g_0 > 0 \qquad (3.3.3)$$

to specify the decline in $\beta_1(\cdot)$. Q is the maximum *per capita* fecundity, and g_0 controls the decrease of $\beta_1(\cdot)$. GURNEY *et al* (1983) have shown that Eq. (3.3.3) does indeed give an acceptable fit to NICHOLSON's (1954, 1957) data. Thus a good approximation to the future recruitment rate;

$$R(t+\tau) = S_1QA(t)\exp(-A(t)/g_0) \tag{3.3.4}$$

so that g_0 is revealed as being the value of $A(t)$ at which the future recruitment rate is at a maximum i.e. $g_0 = A_0$ (c.f. section (2.7)). Noting that

$$\begin{aligned} R'_{max} &= R_{max}/A_0 \\ &= S_1Qe^{-1} \end{aligned} \tag{3.3.5}$$

I can write down the full delay-differential equation model, for "adults only" competition, as

$$\dot{A}(t) = R'_{max}A(t-\tau)\exp(1-A(t-\tau)/A_o) - mA(t) \tag{3.3.6}$$

which is of course Model (I) of Chapter 2.

3.4 IMMATURE COHORT COMPETITION

As by definition the adults do not compete, adult *per capita* death rate should be truly density-independent, so that Eq. (3.3.1) holds, and *per capita* fecundity should not in this case decline with increasing adult population, but rather should remain at about the physiologically maximum value, Q. Hence, from Eq. (A1.19), the total future recruitment rate must be given by

$$R(t+\tau) = QA(t)S_2(QA(t)) \tag{3.4.1}$$

where $S_2(\cdot)$ is the probability of an individual in the competing cohort surviving to maturity, and is a decreasing function of QA(t). It is reasonable to assume that for small enough QA(t), $S_2(\cdot)$ tends towards its "excess food" value, S_1, so that I am free to choose a function decreasing from S_1 to zero as QA(t) increases. I choose

$$S_2(QA(t)) = S_1\exp(-QA(t)/h) \quad h > 0 \tag{3.4.2}$$

where h is a parameter related to the larval food supply. Clearly then future recruitment is given by

$$R(t+\tau) = S_1QA(t)\ \exp(-QA(t)/h) \tag{3.4.3}$$

so that, defining $A_0 \equiv h/Q$, and recalling Eq. (3.3.5), the adult population balance equation becomes

$$\dot{A}(t) = R'_{max}A(t-\tau)\exp(1-A(t-\tau)/A_0) - mA(t) \tag{3.4.4}$$

once again. Hence the same equation can be used to model "adult only" and "within cohort" competition, although clearly the parameters R'_{max} and A_0 must bear slightly different interpretations in the two competition regimes.

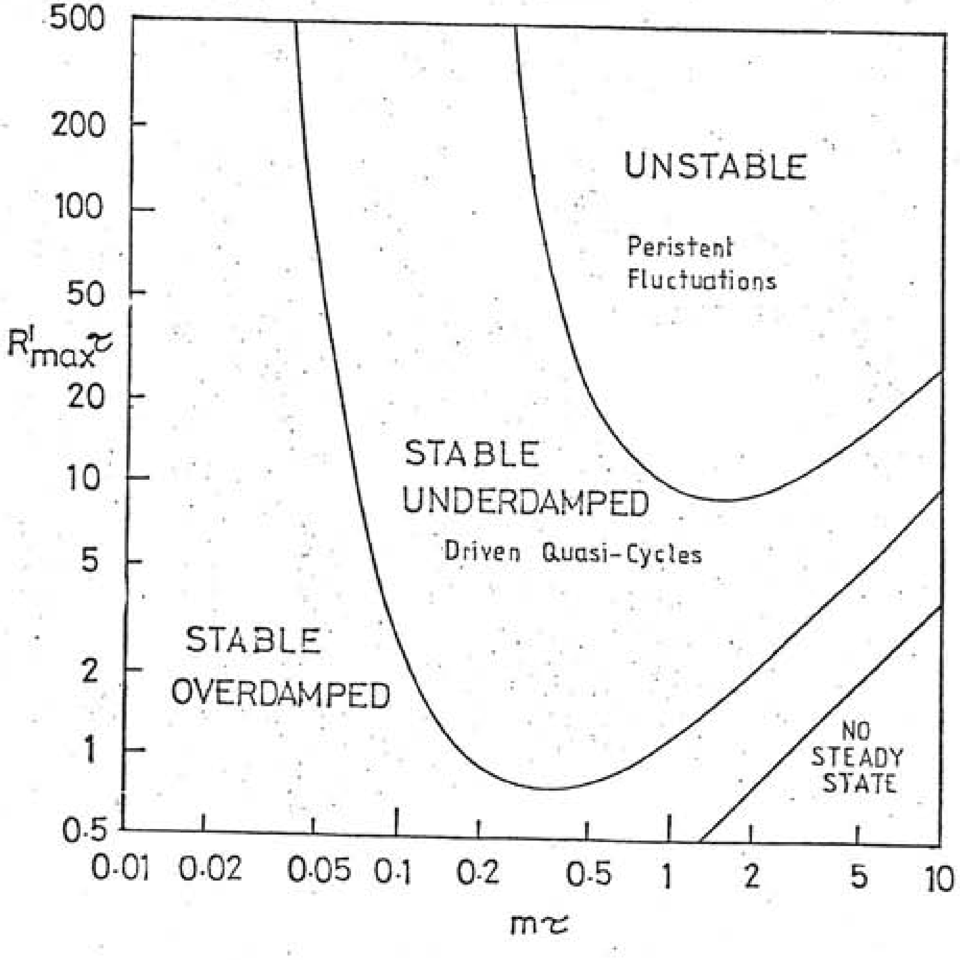


Fig. (3.2) - Boundaries of behaviour of the delay-differential equation (3.5.1) in the controlling ($R'_{max}\tau$, $n\tau$)-space.

3.5 MODEL BEHAVIOUR

Much of the analysis of Eq. (3.4.5) was performed in section (2.7) and need not be repeated here. However, it is necessary to reduce the number of free parameters in the model, to facilitate numerical analysis. By scaling $Y \equiv A/A_0$ and $R'_{max} = R_{max}/A_0$, as in Chapter 2, but also defining $t' \equiv t/\tau$, Eq. (3.4.5) reduces to

$$\dot{Y}(t') = (R'_{max}\tau)Y(t'-1)\exp(1-Y(t'-1)) - (m\tau)Y(t') \qquad (3.5.1)$$

which is completely controlled by the parameter groups $R'_{max}\tau$ and $m\tau$, providing the natural parameter space for plotting boundaries of behaviour used in Ch. 2. Fig. (3.2) illustrates the behaviour of (3.5.1) in $(R'_{max}\tau, m\tau)$-space, showing regions where solutions are overdamped, underdamped, or are persistent fluctuations. The curves in Fig. (3.2) were computed by transforming the relevant boundaries in $(\alpha\tau, \rho\tau)$-space.

Now, in a laboratory system with constant environment, there are only two mechanisms whereby the quasi-periodic fluctuations of Fig. (3.1(a-c)) could have arisen. Either they are the result of a deterministic, underdamped system being perturbed by demographic stochasticity (i.e. "endogenous resonant quasi-cycles" (NISBET & GURNEY 1982, Ch. 7)) or else they are similarly perturbed true deterministic persistent fluctuations. Thus both the "underdamped" region, and the "unstable" region of $(R'_{max}\tau, m\tau)$space (Fig. (3.2)) must be examined, and the quasi-periodic fluctuations arising therein suitably characterised.

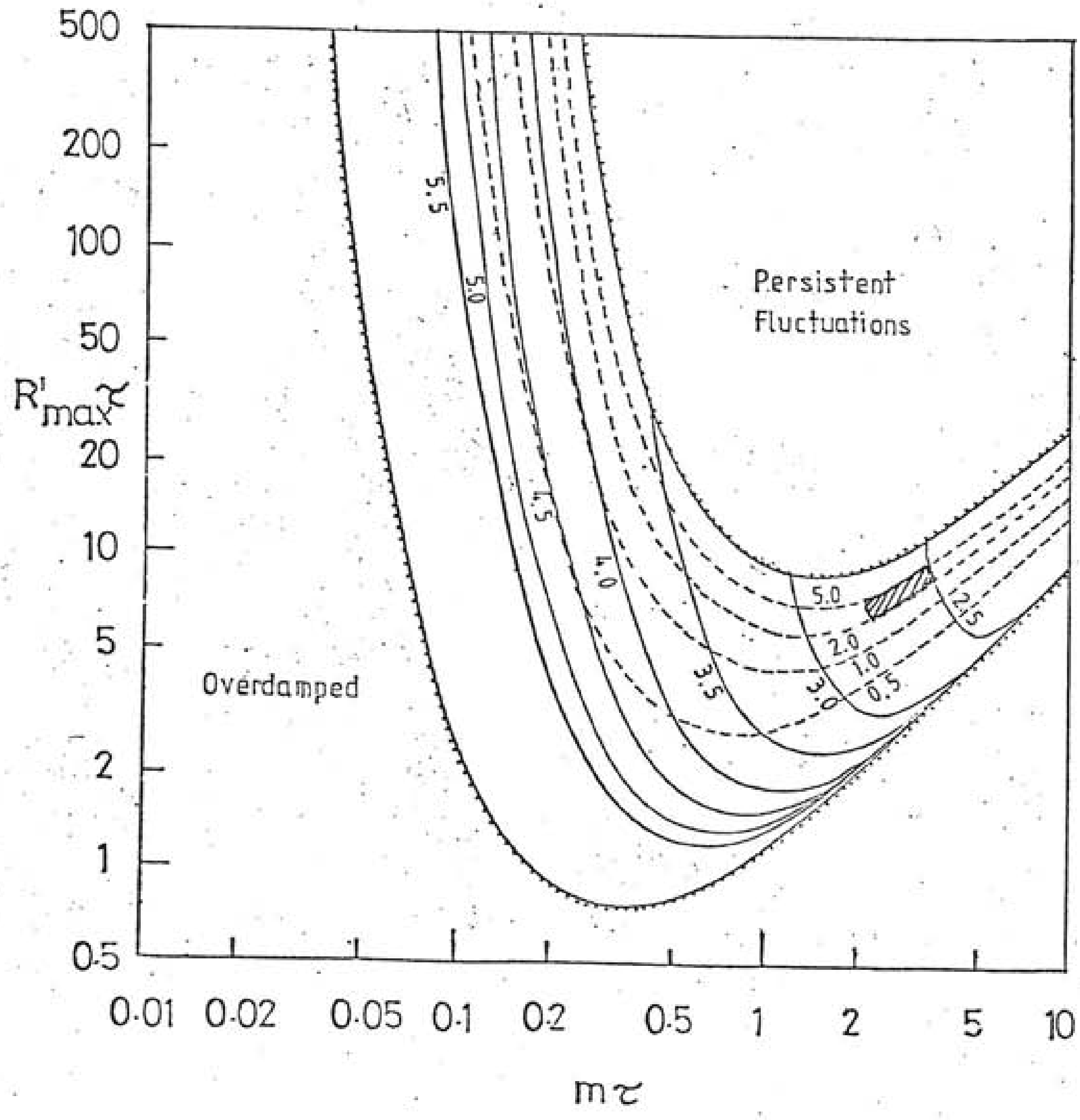


Fig. (3.3) - Characterisation of quasi-cyclic behaviour in the stable underdamped region of $(R_{max}\tau, m\tau)$-space equation (3.5.1). (————) contours of constant normalised period T/τ; (--------) contours of constant amplitude A_{max}/A_{min}. Shaded area is the fitted region of parameter space for the first experiment of Fig. (3.1) under the quasi-cycle hypothesis.

3.5.1 Quasi-cycles

The expected pattern of behaviour of quasi-cycles is the appearance of bursts of relatively coherent cyclic behaviour, interspersed with periods of incoherent noise (NISBET & GURNEY 1982, Ch. 7). The period of quasi-cycles themselves (T) will be very close to that of the damped oscillations, in the underlying underdamped system (op.cit.), and thus to a good approximation,

$$\frac{T}{\tau} \simeq \frac{2\pi}{\omega\tau} \qquad (3.5.2)$$

(here T is normalised with respect to the delay, τ; $\omega\tau$ is the normalised frequency of the damped oscillation). The amplitude of quasi-cycles is not computable, but another characteristic, the coherence number (n_c) can be estimated. Defining n_c as the number of cycles required for the amplitude of the damped oscillations of the underdamped region to fall by a factor of e, then to a good approximation (op.cit),

$$n_c \simeq \frac{\omega\tau}{2\pi\mu\tau} \qquad (3.5.3)$$

where $\mu\tau$ is the normalised real part of solutions to linearised equation (2.4.2) which controls the damping. Fig. (3.3) shows contours of normalised period (T/τ) and coherence number (n_c) for equation (3.5.1). By estimating T/τ and n_c for the real population fluctuations of Nicholson's experiments, fitted values of $R'_{max}\tau$ and $m\tau$ can be derived from Fig. (3.3) under the Quasi-cycle hypothesis, and compared with the real values to test that hypothesis.

TABLE 3.1 Fluctuation characterisation of Nicholson's (1954) data.

Experiment	T/τ	n_c	A_{max}/A_{min}
Adult Competition	2.6 ± 0.1	2 - 5	36 ± 17
Larval Competition ($50g\ day^{-1}$)	2.3 ± 0.1	2 - 5	77 ± 26
Larval Competition ($25g\ day^{-1}$)	2.37 ± 0.03	2 - 5	240 ± 160

From Fig. (3.1), and NICHOLSON (1954), the length of the immature stage, i.e. τ, is 14.8 ± 0.4 days, and so the normalised cycle periods (measured from Fig. (3.1), and divided by τ) are as given in Table (3.1), for the three experiments. Empirically it has been shown (NISBET & GURNEY 1982, Ch. 7) that the number of complete cycles appearing during one of the coherent "bursts" will be two to three times the coherence number as given by Eq. (3.5.3). Only six or seven "cycles" are visible in any of the sets of experimental results (Fig. (3.1)), so clearly n_c is not greater than two for any of them. An upper limit to n_c is not so forthcoming, but given the lack of sensitivity of $R'_{max}\tau$ values to changes in n_c in the region of parameter space dictated by the responses of T/τ given in Table (3.1), the estimated range

$$2 < n_c < 5 \qquad (3.5.4)$$

seems perfectly reasonable. The shaded area in Fig. (3.2) indicates the region of parameter space delineated by the intersection of the ranges of T/τ and n_c for the adult only competition experiment. For the sake of clarity I have not marked the corresponding regions for the other two experiments. In Table (3.2) I have tabulated the values of $R'_{max}\tau$ and $m\tau$ defining all three regions, that is, those <u>fitted</u> parameter values which the blowfly populations would have to have if the observed fluctuations are of quasi-cycle type.

TABLE 3.2 Fitted parameter values under the two hypotheses

	Persistent Fluctuation Hypothesis		Quasi-Cycle Hypothesis	
Experiment	$R'_{max}\tau$	$m\tau$	$R'_{max}\tau$	$m\tau$
Adult Competition	55±26	2.9±0.5	8.6±1.6	3.0±0.7
Larval Competition (50g day^{-1})	63±18	5.5±1.6	17±6	7.5±3.0
Larval Competition (25g day^{-1})	140±92	4.7±0.7	12±2	4.8±0.8

3.5.2 Deterministic Fluctuations

Deterministic, persistent fluctuations can be characterised by a dominant period, which, unlike the formal repeat period, varies smoothly throughout the unstable region of parameter space (see Ch. 2). Thus the values of T/τ used in section (3.5.2), and appearing in Table (3.1), are estimates also of the dominant period under the persistent fluctuations hypothesis. In this case I will also characterize the fluctuations by the relative amplitude. A_{max}/A_{min} (the ratio of maximum to minimum observed population size). In Fig. (3.4) I have plotted contours of T/τ and A_{max}/A_{min} for fluctuations in the unstable region of $(R'_{max}\tau,\ m\tau)$-space.

The measured values of A_{max}/A_{min} and T/τ for Nicholson's data appear in Table (3.1), and, using these values, I have identified the regions of $(R'_{max}\tau, m\tau)$-space required for the observed "cycles" to be of "persistent fluctuation" types (see the shaded areas in Fig. (3.4)).

The two sets of fitted parameter values, under the two hypotheses, appear in Table (3.2). In all three experiments, the fitted normalised death rates ($m\tau$) are virtually indistinguishable between the two hypotheses, whereas the fitted values of $R'_{max}\tau$ are very different. Thus by estimating $m\tau$ and (particularly) $R'_{max}\tau$ from the original data, it should be possible to differentiate between the two hypotheses.

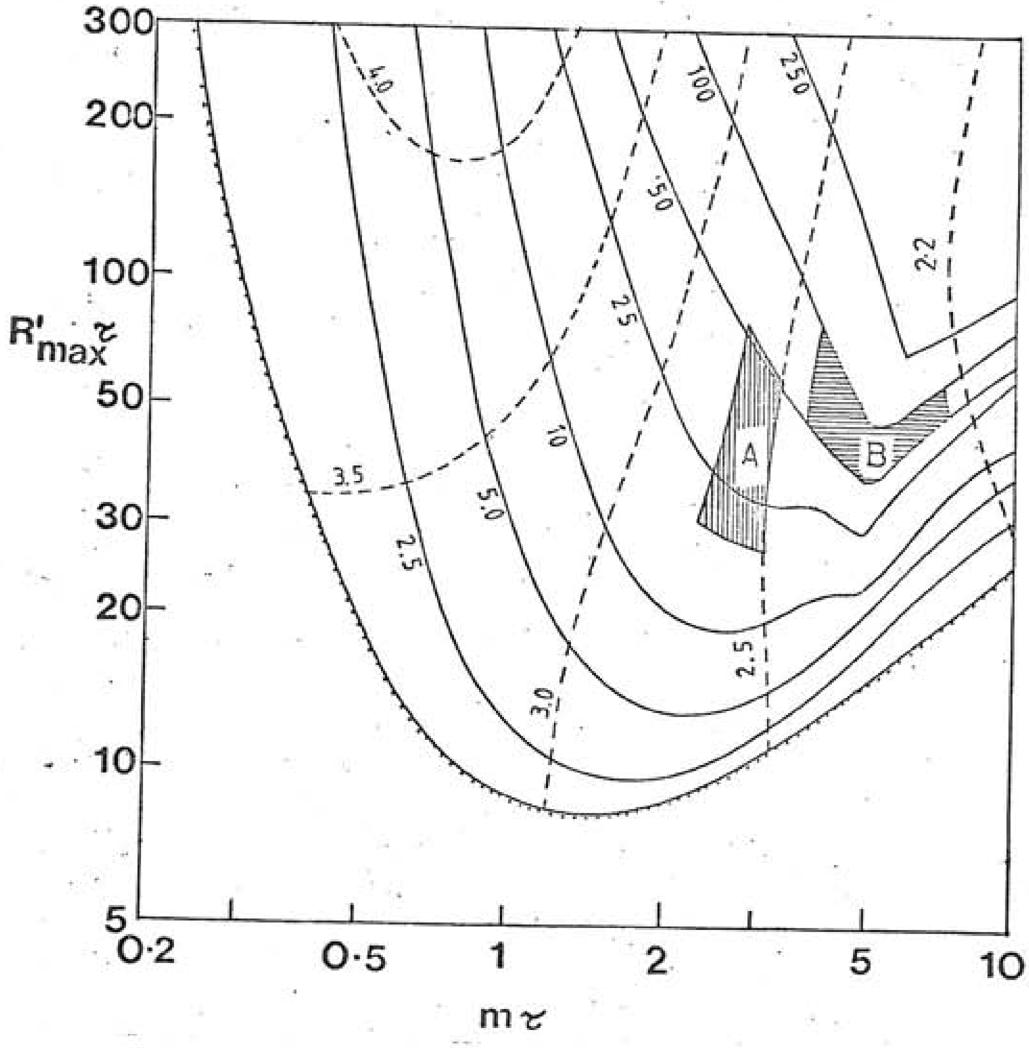


Fig. (3.4) - Characterisation of persistent fluctuation behaviour in the unstable region of $(R'_{max}\tau, m\tau)$-space for equation (3.5.1). (————) contours of constant normalised dominant period T/τ; (------) contours of constant amplitude A_{max}/A_{min}. Shaded areas (A) and (B) are the fitted regions of parameter space for the first two experiments of Fig. (3.1), under the persistent fluctuation hypothesis.

3.6 TESTING THE MODEL

I can obtain estimates of the true values of $m\tau$ in the adult food-limited case (Fig. (3.1(a)) and the 25g day^{-1} larvae food-limited case, as follows. It is clear from observation of these two data sets that egg-laying was at a minimum when the adult population was at the peak of each cycle, so that at a time τ(≃ 14.8 ± 0.4 days) later, recruitment to the adult population must have been at, or close to, zero. Thus in the last section of the falling arm of each cycle the delay-differential equation (3.4.5) reduces to

$$\dot{A}(t) \simeq -mA(t) \qquad (3.6.1)$$

which of course has the solution

$$A(t) \propto \exp(-mt). \qquad (3.6.2)$$

Hence, plotting $\ell n(A(t))$ against t (Fig. (3.5)), I can estimate m. The estimated $m\tau$ values for the two experiments are given in Table (3.3) (without information on reproductive behaviour, I cannot estimate $m\tau$ for the third experiment). Comparison with the fitted values in Table (3.2) confirms the conclusion that it is not possible to differentiate between them on the basis of death rates.

I can also estimate $R'_{max}\tau$ for the adult competition case. If B(t) is the total rate of egg-production, then clearly (from Appendix 1 and Eq. (3.3.3))

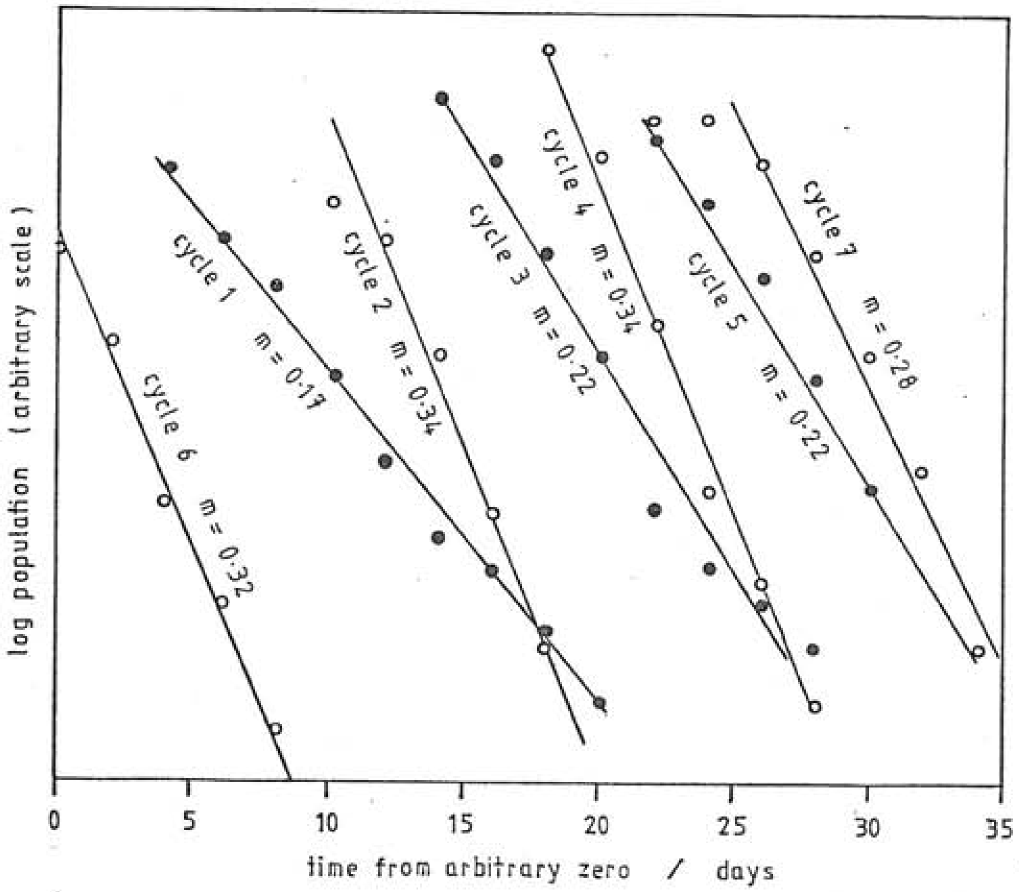


Fig. (3.5) - Estimating the per capita death rate, m, from the adult competition experiment of Fig. 3.1(a). Cycles 1, 3, and 5 are denoted by ● cycles 2, 4, 6 and 7 by O.

TABLE 3.3 Estimated Parameter Values

Experiment	$R'_{max}\tau$	$m\tau$
Adult Competition	48 ± 11	4.0 ± 0.5
Larval Competition (50 g day^{-1})	-	4.0 ± 0.6
Larval Competition (25g day^{-1})	-	-

$$B(t) = QA(t)\exp(-A(t)/A_0) \qquad (3.6.3)$$

Hence, if B_{max} (the maximum total birth rate),

$$B_{max} = QA_0e^{-1} \qquad (3.6.4)$$

and from Eq. (3.3.5),

$$R'_{max} = S_1Qe^{-1} \qquad (3.6.5)$$

so therefore

$$R'_{max} = S_1B_{max}/A_0 \qquad (3.6.6)$$

Thus by measuring (from Fig. (3.1(a))), the maximum total egg-laying rate (B_{max}) and the adult population size at which it occurs (A_0), and using the mean egg-to-adult survival probability S_1(= 0.91, NICHOLSON 1954), a range of $R'_{max}\tau$ values for the population in adult-only competition experiment can be found (Table (3.3)).

It is immediately clear that the estimated true $R'_{max}\tau$ (48 ± 11) is compatible with the persistent fluctuation hypothesis ($R'_{max}\tau$ = 55 ± 26), but not with the quasi-cycle hypothesis ($R'_{max}\tau$ = 8.5 ± 1.7), and I conclude that the "cycles" observed in Fig. (3.1(a)) are of persistent fluctuation type. Examination of Fig. (3.4) indicates that the dominant period of the persistent fluctuation observed under adult competition is controlled almost exclusively by the normalised death rate, $m\tau$, whereas the amplitude is controlled by both $R'_{max}\tau$ and $m\tau$ in some complicated manner, as expected from the conclusions of section (2.7).

Before turning to the results of the larval-food limited experiments (Fig. (3.1)(b,c)), I must consider briefly the justification for using a cohort-competition model. At the time of initial formulation (1979) the assumption that "within-cohort" competition was a reasonable approximation to the true immature competition regime was untestable. Recently however, GURNEY et al (1983) have shown that models incorporating uniform competition among all immatures - an obvious, strong alternative possibility - are incapable of producing cyclic fluctuations with periods greater than 2τ. As the cohort-competition model discussed in this chapter does predict cycles of long period, and, more importantly, the experimental data of Nicholson (Fig. (3.1) (b,c)) is characterised by cycles with periods greater than 2τ, there is strong evidence that not only is uniform competition ruled out for Nicholson's larval competition experiments, but that either cohort-competitors or some other form of asymmetric competition (the presence of some particularly advantaged or disadvantaged group) is occurring. LAWTON & HASSELL (1981) have recently shown that asymmetric competition is the norm in at least two-thirds of all well-documented cases of interspecific insect competition, so it should not be suprising if intraspecific competition is also often asymmetric.

Unfortunately, although the assumption that cohort competition is occurring in Nicholson's larval-food limited experiments (Fig. (3.1)(b,c)), is justified, the lack of egg-laying data for these experiments prevents me from estimating $R'_{max}\tau$, and thus differentiating between quasi-cycles and persistent fluctuations. However, given that the adult competition cyclic fluctuations (Fig. (3.1)(a)) are almost certainly of the latter type, there would have to be a very great change in the system dynamics indeed if the larval-competition "cycles" are to be of quasi-cyclic type. Very tentatively, therefore, I suggest that the quasi-periodic fluctuations observed in Fig. (3.1) are probably all of determinstic persistent fluctuation type.

3.7 FINE STRUCTURE - THE SEPARATION OF GENERATIONS

Apart from the mathematically interesting, but biologically not greatly relevant, details of period-doubling, there are other features of the dynamics of the delay-differential equation which are of biological importance. In Fig. (3.6) I have plotted four realisations of Eq. (3.5.1) for different points in ($R'_{max}\tau$, $m\tau$)-space, in order to illustrate the wide range of behaviour of which the model is capable, and to make qualitative comparisons with the experimental data. The solid line is (scaled) adult population, and the dashed line is the future recruitment rate (on a different scale, for clarity). The increasing complexity of the solutions (in the order (a)-(d)) is only partly a result of the period-doubling (the last solution shown, (d), is chaotic). The more important feature is the effect of the "humped" future recruitment curve, as discussed in Ch. 2. As adult population varies, so does $R(T+\tau)$, so that if (a) $A_{min} > A_0$ (the peak position for $R(t+\tau)$) both $A(t)$ as $R(t+\tau)$ will exhibit in the cycles, like KAPLAN & YORK's (1977) system. Once the amplitude of the $A(t)$ cycle is such that $A_{min} < A_0$ (Fig. (3.6(b))), then $R(t+\tau)$ will show a slight decrease, which will in turn effect the future adult population size. The result is that breeding behaviour can continue throughout the cycle, and there is only one generation per cycle, but with a certain amount of fine structure becoming evident. Increasing the adult population fluctuation amplitude further decreases A_{min} further below A_0, so that the resultant decrease in future recruitment at low population densities becomes pronounced, and each cycle now produces two bursts of eggs, which manifest as two separate

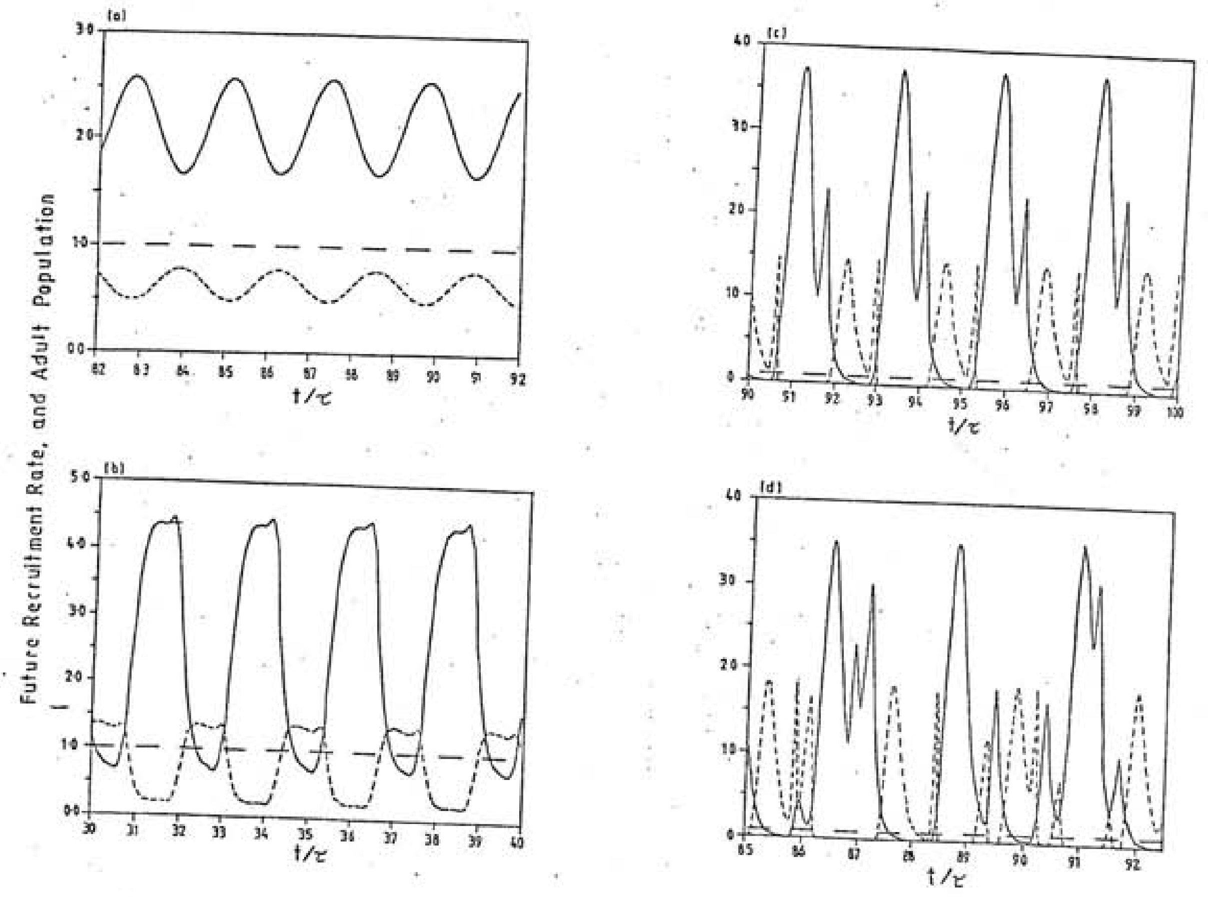


Fig. (3.6) - The qualitative features of the persistent fluctuations predicted by equation (3.5.1) (————) normalised adult population, $Y(t)$ (--------) normalised future recruitment $R(Y(t))/A_0$. The line (—— ——) is $Y(t) = 1.0$ i.e. $A(t) = A_0$, the position of the peak in $R(A)$. (a) - (d) represent solutions with different parameter values, and are referred to in the text.

generations entering the adult population in the future (Fig. (3.6(c))). When A_{min} becomes very small, the breeding behaviour is very complicated, with multiple bursts of eggs per cycle being possible (see Fig. (3.6(d))).

The solutions shown in Fig. (3.6(b) and (d)) have $R'_{max}\tau$ and $m\tau$ values corresponding approximately to the centres of gravity of the shaded areas in Fig. (3.4) for the adult competition and the 50 g day^{-1} larval food limited case, respectively. The predictions of the equation agree qualitatively well with the experimental results, in that separation of generations occurs for the latter case, but not for the former.

3.8 CONCLUSIONS

The model used to examine the population dynamics of *L. cuprina* in NICHOLSON's (1954) experiment thus provides a reasonable qualitative fit to the data, and reveals that the "cycles" observed by Nicholson are almost certainly deterministic persistent fluctuations, perturbed by demographic stochasticity. The normalised dominant period of these fluctuations is predominantly controlled by the parameter group $m\tau$, whereas the amplitude is strongly affected by all the model parameters.

Of considerable interest are the results on the appearance of discrete generations in "cycling" populations, due entirely to density effects, and the presence of a hump in the recruitment function. This mechanism allows delay-differential equation models to bridge some of the gap between continuous and discrete-time modelling.

The general results, and the comparison of models, of Ch. 2 give reassurance that the features of the model used here, and the conclusions reached, are not model specific (to be precise, not controlled by the details of the functions chosen for $R(Y)$ and $D_A(Y)$).

CHAPTER 4: DISTRIBUTED MATURATION PERIOD

4.1 INTRODUCTION

In this Chapter I return to the problem of incorporating differential aging into a population model. As in Chapters 2 and 3, I shall consider a laboratory population with just two developmental stages (immatures and adults), and shall therefore express differential aging by introducing variation among individuals in the "transit time" through the immature stage. The conventional expressions of adult population dynamics where there is such individual variation in the maturation period is an equation of the form

$$\dot{A}(t) = F(A(t), \int_{0}^{\infty} u(a)A(t-a)da) \qquad (4.1.1)$$

where $F(\cdot)$ is some generally non-linear function, and $u(a)$ is a normalised weighting function (e.g. MAY 1974a; OSTER 1976; MACDONALD 1978). I shall demonstrate in section (4.2) that a rigorous derivation does not lead to Eq. (4.1.1), but rather to an equation which is more obviously the generalisation of the delay-differential equations of Chapters 2 and 3.

After developing an appropriate formalism for modelling laboratory insect populations with "distributed" maturation period, under conditions of adult-only competition (4.3), I show how a general weighting function, that fits experimental data reasonably well, can permit a full local stability analysis to be performed, and make numerical analysis relatively simple (4.4 - 4.6). Finally, (4.7) I compare the stability and persistent fluctuation behaviour of models with constant and distributed maturation period, in an attempt to discover when the former type of model is an acceptable approximation, and when the more complete specification of the latter is required.

4.2 FORMULATION OF THE GENERAL EQUATIONS

In order to avoid the pitfalls that beset the user of *ad hoc* models such as Eq. (4.1.1), it is necessary to start from first principles. As I discussed in Chapter 1, the fundamental equations describing the constant aging process are a recurrence relation (for movement through the age-structure) and a renewal condition (for the birth rate), and it seems natural to look for a similar approach for differential aging. To simplify matters, I shall again divide the population into two developmental classes (immature and adults), so that an individual is born at the beginning of the immature stage, and (assuming that it survives) matures at some later time, entering the beginning of the adult stage. This suggests that there is a recurrence relation and a renewal condition for each developmental stage, and I shall now attempt to formulate these.

Clearly it is quite possible for two individuals that were born at time t to be in different developmental stages at some time t+x in the future. Because of this, the "age" of an individual is not a good indication of its functional "place" in the population, and instead I shall use the "time-to-date" spent in the immature, and in the adult developmental stages (the "stage-durations"), denoted by r and s, respectively. Hence I can denote by $f_I(r,t)dr$ and $f_A(s,t)ds$ the numbers of immatures and of adults in the small stage-duration intervals $(r,r+dr)$ and $(s,s+ds)$, respectively, at time t, and by $\delta_I(r,t)$ and $\delta_A(s,t)$ the respective immature and adult per capita death rates. I shall also define a per capita "maturation rate", $\phi(r,t)$, such that $\phi(r,t)dr$ is the average fraction of immature in the stage-duration interval $(r,r+dr)$ who mature into adults at time t.

Given the above definitions, it is easy to construct the two required recurrence relations. If I define infinitesimal stage-duration and time intervals dr, ds and dt, chosen for convenience to be equal, then the transitions between time - and stage-duration intervals are given by

$$\begin{cases} f_I(r,t+dt)dt = \{1-\phi(r-dt,t)dt\}\{1-\delta_I(r-dt,t)dt\}f_I(r-dt,t)dt & (4.2.1) \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad r,\ s > 0 & \\ f_A(s,t+dt)dt = \{1-\delta_A(s-dt,t)dt\} f_A(s-dt,t)dt & (4.2.2) \end{cases}$$

which, upon Taylor expansion of all functions to first order terms, neglecting higher order terms as $dt \to 0$, yield up a pair of partial differential equations similar to the McKENDRICK (1926) equation:

$$\begin{cases} \dfrac{\partial f_I(r,t)}{\partial t} + \dfrac{\partial f_I(s,t)}{\partial r} = -\ \phi(r,t)f_I(r,t) - \delta_I(r,t)f_I(r,t) & (4.2.3) \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad r,\ s > 0 & \\ \dfrac{\partial f_A(s_1t)}{\partial t} + \dfrac{\partial f_A(s,t)}{\partial s} = -\delta_A(s,t)f_A(s,t) & (4.2.4) \end{cases}$$

The renewal conditions are likewise simple to formulate. It is clear that the total maturation rate out of the immature population at time t (which is equal to the total recruitment rate into the adult population) in the total of the maturation rates of immatures at all r, i.e.

$$\begin{aligned} M(t) = R(t) &\equiv f_A(0,t) \\ &= \int_0^\infty \phi(r,t) f_I(r,t)\,dr \qquad (4.2.5) \end{aligned}$$

If I denote by $\beta(s,t)$ the per capita fecundity of adults of stage-duration s, then clearly the total birth rate at time t is given by

$$B(t) \equiv f_I(0,t) = \int_0^\infty \beta(s,t) f_A(s,t)\,ds \qquad (4.2.6)$$

By integrating over all r and s in Eqs. (4.2.3) and (4.2.4), respectively, and defining the total numbers of immatures and adults at time t as

$$I(t) \equiv \int_0^\infty f\,(r,t)\,dr \qquad (4.2.7)$$

and

$$A(t) \equiv \int_0^\infty f_A(s,t)\,ds \qquad (4.2.8)$$

respectively, then I regain the balance Eqs. (2.2.1) and (2.2.2), namely

$$\begin{cases} \dot{I}(t) = B(t) - M(t) - D_I(t) & (4.2.9) \\ \dot{A}(t) = R(t) - D_A(t) & (4.2.10) \end{cases}$$

(assuming no individuals achieve infinite r or s), where

$$D_I(t) \equiv \int_0^\infty \delta_I(r,t) f_I(r,t)\,dr \tag{4.2.11}$$

and

$$D_A(t) \equiv \int_0^\infty \delta_A(s,t) f_A(s,t)\,ds \tag{4.2.12}$$

are the total immature and adult death rates, as before.

Scant progress can be made in analysing the general integro-differential Eqs. (4.2.9) and (4.2.10), so I shall return to the consideration of a particular laboratory competition regime (that of adult-only competition) and try and extract analytically and computationally tractable equations.

4.3 ADULT COMPETITION

The assumptions which reduce the general Eqs. (4.2.11) and (4.2.12) to a description of adult-only competition are identical to those of Chapters 2 and 3, with one addition. As before, the *per capita* death rate is density-independent for the immatures, but density-dependent for the adults, and the *per capita* fecundity is likewise a function only of adult density. In addition, the *per capita* maturation rate is a function of the immature stage-duration, r, alone. Hence,

$$D_I(t) = \int_0^\infty \delta_I(r) f_I(r,t)\,dr, \tag{4.3.1}$$

$$D_A(t) = D_A(A(t)) = \delta_A(A(t))A(t), \tag{4.3.2}$$

$$B(t) = B(A(t)) = \beta_1(A(t))A(t), \tag{4.3.3}$$

and

$$M(t) = R(t) = \int_0^\infty \phi(r) f_I(r,t)\,dr \tag{4.3.4}$$

given Eqs. (4.3.1) - (4.3.4) the solution to the immature partial differential Eq. (4.2.3) is simply

$$f_I(r,t) = B(A(t-r))\exp\{-\int_0^r [\phi(x)+\delta_I(x)]dr\} \quad t > r \tag{4.3.5}$$

which, provided that the experiment to be modelled was started by the introduction of some new adults at t = 0 into an empty cage, is the only solution required.

Substituting (4.3.5) into (4.3.4) gives

$$M(t) = R(t) = \int_{0}^{\infty} w(r)B(A(t-r))dr \qquad (4.3.6)$$

where $$w(r) \equiv \phi(r)\exp\{-\int_{0}^{r} [\phi(r)+\delta_I(x)]dr\}, \qquad (4.3.7)$$

a result closely related to those of LEWIS (1972, 1977) who studied integral "flow" equations.

Thus the equation describing the adult population dynamics (Eq. (4.2.10)) is decoupled from that for the immature dynamics (Eq. (4.2.9)), so that

$$\dot{A}(t) = \int_{0}^{\infty} w(t)B(A(t-r))dr - D_A(A(t)) \qquad (4.3.8)$$

is the true generalisation of Eq. (2.2.4), for adult-only competition.

It is clear that Eq. (4.3.8) is not a special case of Eq. (4.1.1) the conventional "distributed-delay" equation. Indeed, as no single equation is capable, apparently, of fully characterising the population dynamics when there is immature competition and a distributed maturation period, and as Eq.(4.1.1) can only be a correct description of adult-only competition when the per capita fecundity is constant and the function F(·) involves no cross-multiplication of "delayed" and "undelayed" terms, all extensions of the time-delayed logistic are automatically ruled out as rigorous age-structure models (e.g. MAY 1974a; OSTER 1981), whatever their merits in describing other processes (e.g. VOLTERRA 1927; MACDONALD 1978).

The original modelling problem has now been reduced to making Eq. (4.3.8) analytically and computationally tractable, without loss of realism. The density-dependent total birth and death rates $B(\cdot)$ and $D_A(\cdot)$ produce no new difficulties, so I shall concentrate upon $w(\cdot)$, the weighting function.

4.4 THE WEIGHTING FUNCTION

The details of the definition of $w(r)$ are not, at first sight, encouraging. Even if explicit functions for $\phi(\cdot)$ and $\delta_I(\cdot)$ are known Eq. (4.3.7) will still produce what is likely to be a spectacularly intractable weighting function. Consider however a cohort of eggs, laid at some time $t-r$; then the biological meaning of the expression

$$w(r)dr = \phi(r)dr \exp\{-\int_0^r [\phi(x) + \delta_2(x)]dx\} \qquad (4.4.1)$$

is quite straightforward and unambiguous. From section (4.2), $\phi(r)dr$ is the proportion immatures in the stage-duration interval $(r, r+dr)$ who mature during that interval. The exponential term in (4.4.1) is simply the probability of surviving unmatured to a time r after birth. Combining these two definitions, Eq. (4.4.1) can be rewritten as

$$w(r)dr = \frac{\text{Number actually maturing in interval } (r,r+dr)}{\text{Initial cohort size}} \qquad (4.4.2)$$

Integrating over all r in Eq. (4.4.2) gives the relation

$$\int_0^\infty w(r)dr = \frac{\text{Total number ever maturing}}{\text{Initial cohort size}} \leqslant 1 \qquad (4.4.3)$$

which is precisely the quantity S_1 of Chapters 2 and 3, i.e. the average number of the original eggs which survive to achieve maturity. A comparison of Eqs. (4.4.2) and (4.4.3) suggests that a function $\psi(r)$ can be defined, such that

$$\psi(r)dr \equiv \frac{1}{S_1} w(r)dr \qquad (4.4.4)$$

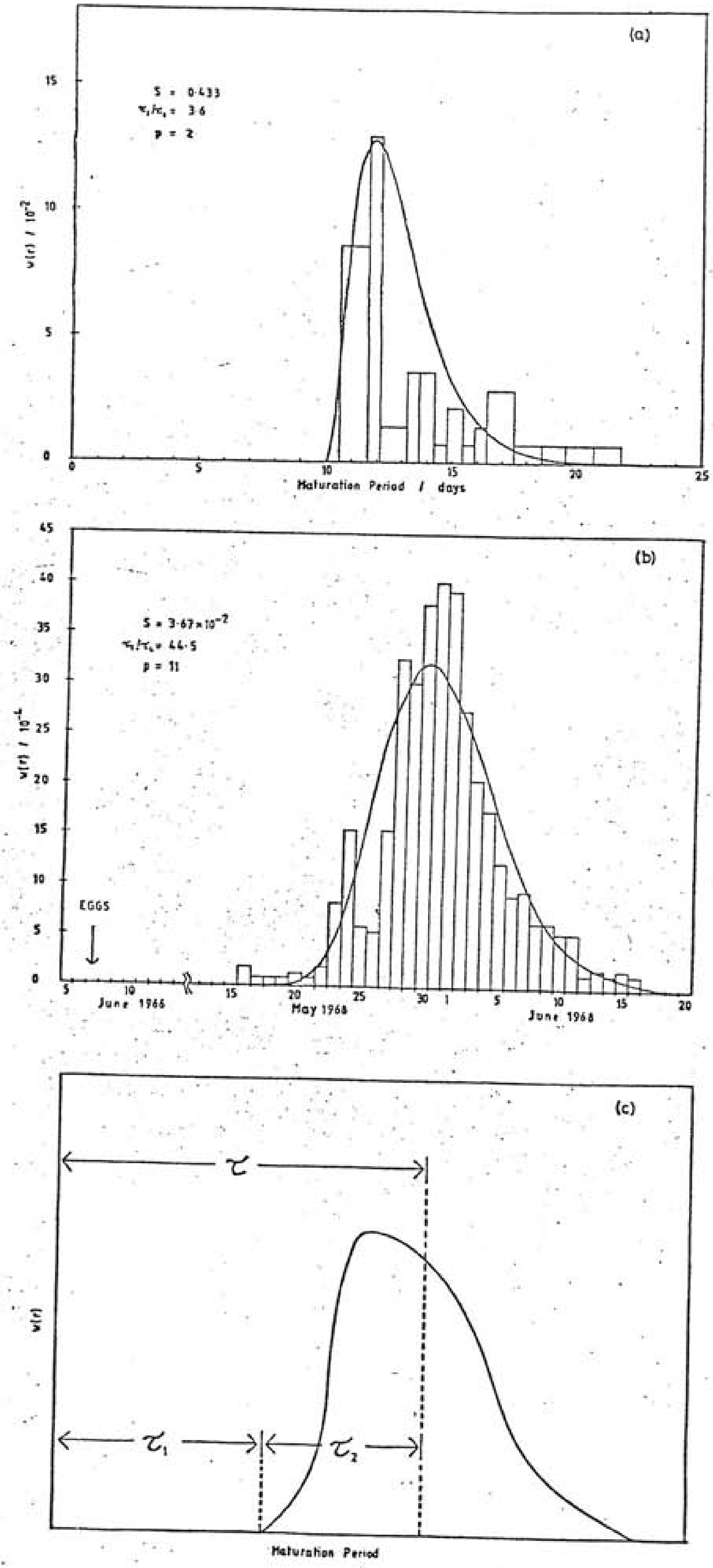
$$= \frac{\text{Number actually maturing during interval } (r, r+dr)}{\text{Total number ever maturing}} \qquad (4.4.5)$$

In other words $\psi(r)$ is the frequency distribution of maturation periods, and is thus, like S_1, easily experimentally measurable. Clearly the recruitment function in Eq. (4.3.8) can now be written as

$$R(t) = \int_0^\infty S_1\psi(r)B(A(t-r))dr \qquad (4.4.6)$$

with no loss of generality. By carefully choosing a function for $\psi(r)$, it is possible, as I show in sections (4.5) and (4.6) to extend the results of LEWIS (1977) and MACDONALD (1978), and to make the adult population balance Eq. (4.3.8) both analytically and computationally tractable. If the exercise is to have any value for practical modelling, however, the weighting function defined by such a choice must accurately reflect the variation in the maturation period observed in real populations.

In Fig. (4.1)(a,b), I have plotted the experimentally observed $w(r)$ for two insect species: (a) the blowfly Phaenicia sericata (ASH & GREENBERG 1975) and (b) the damselfly Pyrrhosoma nymphula (LAWTON 1970, and 1982 pers. comm.). The general pattern of such $w(r)$ is summarised in Fig. (4.1)(c):- there is some minimum


(a)
S = 0·433
τ_1/τ_2 = 3·6
p = 2
15
10
5
0
v(r) / 10^{-2}
0
5
10
15
20
25
Maturation Period / days
45
40
35
30
25
20
15
10
5
0
(b)
S = 3·67 × 10^{-2}
τ_1/τ_2 = 44·5
p = 11
v(r) / 10^{-4}
EGGS
5
10
June 1966
15
20
25
30
1
5
10
15
20
May 1968
June 1968
(c)
τ
τ_1
τ_2
v(r)
Maturation Period

maturation period τ_1, after which all individuals mature according to some distribution of maturation periods, with mean τ_2. This is of course by no means universal. However, a reasonably regular distribution, starting at some $r = \tau_1$, is sufficiently common that it can be considered usual. In fact, the $w(r)$ depicted in Fig. (4.1)(a,b) represent rather extreme examples of the pattern: P. sericata has an extremely short τ_1, followed by a broad, asymmetrical distribution, while for P. nymphula τ_1 is very long, and the distribution of emergence times relatively narrow and much more symmetrical. The choice of $\psi(r)$ must produce a $w(r)$ capable of these extreme curves, and any intermediate examples. I choose a function which has the minimum maturation period τ_1 specified by a shift in origin, and the distribution described by a standard general probability density function:

$$w(r) = S_1\ g(r-\tau_1;p)\ H(r-\tau_1) \qquad (4.4.7)$$

where

$$H(x) = \begin{cases} 0, & x < 0 \\ 1, & x \geq 0 \end{cases} \qquad (4.4.8)$$

is the Heaviside step function, and

$$g(x;p) = \frac{c^{p+1}}{p!}\, x^p\, e^{-cx} \qquad c > 0, \quad p \geq 1 \qquad (4.4.9)$$

the general gamma distribution of integer order p (strictly speaking, the Erlang distribution). The mean maturation period is obtained by adding the mean of $g(x;p)$ to τ_1, i.e.

$$\tau = \tau_1 + \tau_2 \qquad (4.4.10)$$

where

$$\tau_2 = \frac{p+1}{c} \qquad (4.4.11)$$

There are not usually any simple explicit analytic functions for $\phi(\cdot)$ and $\delta_I(\cdot)$ which, when substituted into Eq. (4.3.7) give exactly some member of the family of curves Eq. (4.4.7). However, it is possible to get arbitrarily close to any such curve by judiciously choosing $\phi(\cdot)$ and $\delta_I(\cdot)$, and the reverse process (choosing p and either $\phi(\cdot)$ or $\delta_I(\cdot)$) produces plausible forms for the unspecified function.

In Fig. (4.1)(a,b) I have plotted curves of $w(r)$, as given by Eq. (4.4.7), for the experimental data shown, fitted using a crude method of moments technique, with p taken to the nearest integer. Clearly, despite the great differences between the observed distributions, the "shifted gamma" form for $w(r)$ produces a reasonable fit to both. The gamma distribution itself is a common choice when a smooth continuous function, with a peak of adjustable width is required (e.g. LEWIS 1977; CUSHING 1977, 1980; MACDONALD 1978); however, to give a reasonable fit to real data either the distribution must be truncated (see SWICK 1981 for example), or else very large values of p must be used, to keep the probability of maturation at small r at a minimum. In neither case is the numerical analysis particularly easy. Using the gamma distribution, shifted to $r = \tau_1$ (first suggested by MACDONALD (1978, p25)), the local stability analysis is only marginally more complicated, and the numerical analysis is greatly facilitated, as I shall show in the following sections.

4.5 LOCAL STABILITY ANALYSIS

Before I can consider local stability, I require a formal definition of the steady-state solution to the integro-differential Eq. (4.3.8). I shall call $A^* \geqslant 0$ a steady-state solution if, given a history $A(t) = A^*$ for $-\infty < t \leqslant 0$, the subsequent solution is also $A(t) = A^*$ $(0 < t \leqslant 0)$. Clearly, if $A(t) = A^*$ over all time, then $dA(t)/dt = 0$ over all time, and Eq. (4.3.8) reduces to

$$\int_0^\infty w(r)B(A^*)dr = D_A(A^*) \tag{4.5.1}$$

so that A^* is revealed as any non-negative solution of

$$S_1 B(A^*) = D_A(A^*). \tag{4.5.2}$$

The steady state in the distributed maturation period system is thus identical with that of the constant maturation period system (see Eq. (2.4.1)).

The fate of small perturbations n around A^* can be examined in exactly the same manner as in Ch. 2, by substituting $A = A^*+n$ into Eq. (4.3.8), and expanding to terms of first order. The resulting linear equation is

$$\dot{n}(t) = -\alpha n(t) + \rho \int_0^\infty g(r-\tau_1;p)H(r-\tau_1)n(t-r)dr \tag{4.5.3}$$

using the weighting function of Eq. (4.4.7) (some of the local stability analysis can of course be performed for general $w(r)$, but not enough to be of much assistance), and where

$$\alpha \equiv \left[\frac{\partial D_A(A(t))}{\partial A(t)}\right]_{A=A^*} \quad \text{and} \quad \rho \equiv S_1 \left[\frac{B(A(t-r))}{A(t-r)}\right]_{A=A^*} \qquad (4.5.4)$$

α is exactly the same as for the constant maturation period equation of Ch. 2, namely the gradient of the death rate function at A^*. ρ is identical in value to the adult-only competition recruitment function gradient at A^* of Ch. 2 (Eq. (2.4.3)).

Appendix 2 contains a full local stability analysis of Eq. (4.5.3) for general p and τ_1, i.e. for any possible shape of weighting function permissible under Eq. (4.4.7). The results of the analysis are closely related to those of sections (2.4): there are now four controlling parameter groups, two of which ($\alpha\tau$ and $\rho\tau$) have direct counterparts in the constant maturation period system, and two of which (τ_1/τ_2 and p) are related to the shape of the weighting function. The local stability boundary in $(\alpha\tau,\rho\tau)$-space, for a given $\tau_1/\tau_2 > 0$ and $p \geqslant 1$, bears a strong resemblence to the discrete-delay boundary, and tends, as $t \to \infty$, some straight line (see Fig. (4.2)) of the form

$$-\frac{\rho\tau}{\alpha\tau} = K(\tau_1/\tau_2, p) \qquad (4.5.5)$$

where $K(\cdot) \to 1$ as the weighting function tends towards a delta-function (i.e. as τ_1/τ_2 and/or $p \to \infty$ (see Eq. (A2.21))). Thus, given τ_1/τ_2 and p, if a $-\rho\tau/\alpha\tau < K(\cdot)$, then there will be no τ large enough to destabilize (4.5.3), whereas if $-\rho\tau/\alpha\tau > K(\cdot)$, then there exists a finite τ sufficient to cause instability, exactly as in the constant maturation period case (Ch. 2). Here however there is no simple analytic expression for τ_c, and it must be calculated by solving Eqs. (A2.15) and A2.16).

There is a special case of w(r), as given by Eq. (4.4.7), for which the local stability boundary does not behave according to Eq. (4.5.5), namely when $\tau_1/\tau_2 = 0$ and $p = 1$, i.e. the broadest possible weighting function, with its origin at $r = 0$. Here the local stability boundary has the equation

$$-\rho\tau = (2 + \alpha\tau)^2 \qquad (4.5.6)$$

(I have used the Routh-Hurwitz criteria (MAY 1974a; NISBET & GURNEY 1982, Ch. 4) for the sake of clarity; the same results can be obtained using the methods of Appendix 2). Eq. (4.5.6) is clearly of quadratic form, and so does not tend to any straight line as $\tau \to \infty$. On the contrary, any straight line through the origin with gradient $-\rho\tau/\alpha\tau > 8$ will cross the local stability boundary twice in the feasible region of $(\alpha\tau, \rho\tau)$-space, i.e. not only is the system destabilised for "long enough" τ, but it is also restabilised for some "very long" τ (both values may be found as the roots of Eq. (4.5.6), solving for τ given, α and ρ). Numerical analysis confirms this result which is unusual, to say the least, with van den DRIESSCHE (1983) (for an epidemiological model with a distributed-duration immune phase) and SALEEM (1983) (for an age-structure model with age-dependent fecundity) having the only other examples of which I am aware where restabilisation at large delay occurs. In this case at least, the restabilising effect is almost certainly a purely mathematical artefact, and of no biological significance, as for any $\tau_1/\tau_2 > 0$ or any integer $p > 1$ the asymptotic behaviour of the local stability boundary is given by Eq. (4.5.5).

4.6 NUMERICAL ANALYSIS

The final advantage of the choice of the weighting function Eq. (4.4.7) is that numerical analysis is greatly facilitated. The unshifted gamma distribution is the basis of MACDONALD's(1978) "linear chain trick", which allows an integro-differential equation of the form (4.1.1) to be recast as a system of ordinary differential equations. Although his result does not apply to the age-structure equation (4.3.8), the extension of MACDONALD's(1978) technique is not difficult (in fact MACDONALD suggests 1978, p25 - (4.4.7) as a possible alternative weighting function, but does not make use of it). The important criterion for a weighting function is "degeneracy", i.e. an integral equation can be replaced by a set of differential equations if the weighting function satisfies the condition

$$\frac{d^j w(r)}{dr^j} = \sum_{k=0}^{j-1} q_k \frac{d^k w(r)}{dr^k}, \quad q_k \text{ constants} \qquad (4.6.1)$$

(FARGUE 1973; MACDONALD 1978, p15.)

In Appendix 3 I show that (4.4.7) possesses the correct properties, and demonstrate how, by defining p+1 arbitrary new variables,

$$V_j(t) = \int_{\tau_1}^{\infty} g(r-\tau_1;p+1-j)B(A(t-r))dr \quad , \quad j = 1,2..p+1 \qquad (4.6.2)$$

the integro-differential Eq. (4.3.8) (with w(r) given by (4.4.7)), can be rewritten as the system of p+2 equations,

$$\begin{cases} \dot{A}(t) = S_1 V_1(t) - D_A(A(t)) \\ \dot{V}_j(t) = c(V_{j+1}(t) - V_j(t)) \quad , \quad j=1,2\ldots p \\ \dot{V}_{p+1}(t) = c(B(A(t-\tau_1)) - V_{p+1}(t)) \end{cases} \qquad (4.6.3)$$

(recalling that c is a constant from Eq. (4.4.9)). Thus there are p linear, and one (possibly) non-linear, ordinary differential equations, and one usually non-linear delay-differential equation. The numerical analysis of the system of Eq. (4.6.3) thus requires initial values (i.e. at $t = 0$) for all p+2 variables, and an initial history ($-\tau \leqslant t < 0$) for A(t), all of which must be compatible with the history and initial values required for a direct solution of the integro-differential equation itself. Fortunately, for a laboratory experimental setup, all these values are forthcoming. It will be recalled that the experiment is initialised by the introduction of a number of new adults into an empty "cage" at time $t = 0$. Thus it is clear that $A(t) = 0$ for $-\infty \leqslant t < 0$, and that there is some positive initial value $A(0) = A_I$. It is clear from Eq. (4.6.2) that, given $A(t) = 0$ in the range of r covered by the integral, then all the variables would be zero also. Thus the specification of the system (4.6.5) is completed by the initial values and history

$$\begin{cases} A(t) = 0 \quad , \quad -\infty \leqslant t < 0 \\ A(0) = A_I > 0 \\ V_j(0) = 0 \quad , \quad j = 1,2\ldots p+1 \end{cases} \qquad (4.6.4)$$

4.7 CONSTANT V. DISTRIBUTED MATURATION PERIOD MODELS

Given that the local stability and numerical analysis of distributed maturation period models is now relatively straightforward, it is possible to systematically assess the differences between models where a full distribution is specified, and those where the constant maturation period approximation is used. First I shall make use of the results of section (4.5) to find out how narrow a distribution must be before the local stability properties are indistinguishable from those of the constant maturation period system, and then I shall, using a particular model, compare the persistent fluctuation behaviour of the two systems. Finally, I shall consider the consequences for modelling, and attempt to indicate when a full distribution is required in a model, and when the approximation is sufficient.

I shall occasionally make use of the quantity

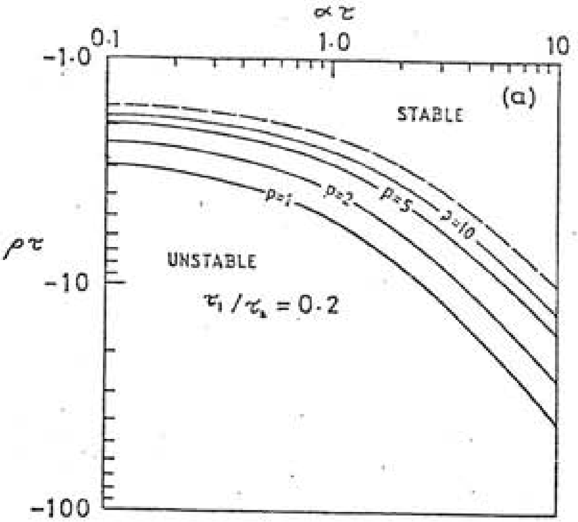
$$\sigma/\tau = \left[(1 + \tau_1/\tau_2)\sqrt{p+1}\right]^{-1} \qquad (4.7.1)$$

where $\sigma = \sqrt{p+1}/c$ is the standard deviation of the gamma distribution Eq. (4.4.9), and τ is the mean maturation period. σ/τ is a convenient approximate measure of the degree to which a given distribution differs from the broadest case on the one hand ($\tau_1/\tau_2 = 0$, $p = 1$: $\sigma/\tau = 1/\sqrt{2}$), and from the constant maturation period of exactly τ on the other (τ_1/τ_2 and p infinite, $\sigma/\tau = 0$).

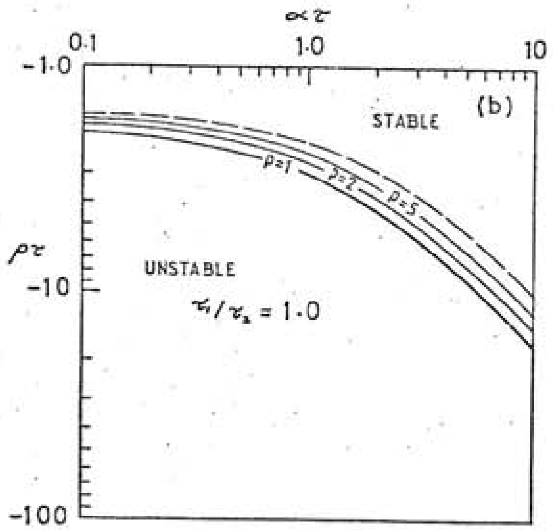
4.7.1 Local Stability Behaviour

In Fig. (4.2) I have plotted the local stability boundary of the distributed maturation period system for various τ_1/τ_2 and p, and of the constant maturation period Eq. (2.2.4), in $(\alpha\tau, \rho\tau)$-space (at Fig. (2.5)). Fig. (4.2)(a) shows the boundaries when $\tau_1/\tau_2 = 0.2$, with $1 \leq p \leq 10$ (i.e. $0.589 \geq \sigma/\tau > 0.251$). It is clear that even for quite large p (p = 10; the distribution is quite narrow), there is considerable disparity between the results of the constant and the distributed maturation period system. In Fig. (4.2)(b), $\tau_1/\tau_2 = 1.0$ (i.e. the average maturation period is twice the minimum), and here the agreement between the two systems is not unreasonable, even for fairly low p, but is certainly not exact. However when $\tau_1/\tau_2 = 5.0$ (Fig. (4.2)(c)) even the broadest of distribution (p = 1, i.e. $\sigma/\tau \simeq 0.118$) has an associated local stability boundary that is extremely close to that of the constant maturation period system, and for greater p the different curves becomes visually indistinguishable. For values of $\tau_1/\tau_2 > 5.0$, the same pattern holds - no value of p produces a local stability boundary significantly different from that of the constant maturation period system.

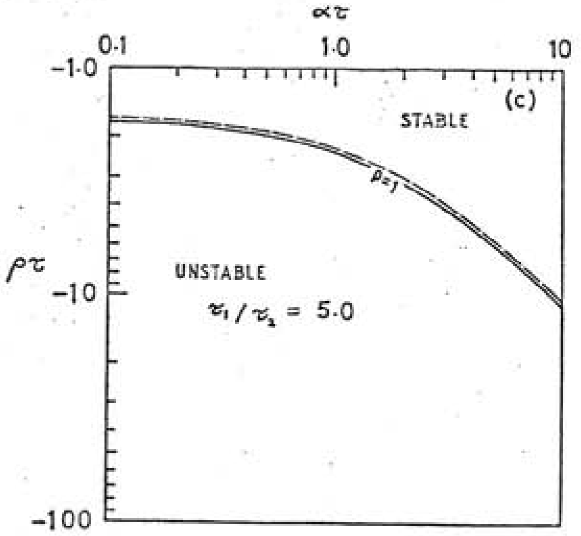
Thus, it would appear that for a maturation period distribution with τ_1/τ_2 greater than "about 5", the local stability properties are not significantly different from those predicted by the constant maturation approximation, regardless of the value of p. For τ_1/τ_2 much smaller than about 5, the details of the distribution shape begin to matter, and only a very narrow peak (p very large) can produce a local stability boundary close to the constant maturation period boundary. In terms of Eq. (4.7.1), it would appear that if



$\alpha\tau$
0.1
1.0
10
-1.0
-10
-100
$\rho\tau$
(a)
STABLE
UNSTABLE
$p=1$
$p=2$
$p=5$
$p=10$
$\tau_1/\tau_2 = 0.2$



$\alpha\tau$
0.1
1.0
10
-1.0
-10
-100
$\rho\tau$
(b)
STABLE
UNSTABLE
$p=1$
$p=2$
$p=5$
$\tau_1/\tau_2 = 1.0$



$\alpha\tau$
0.1
1.0
10
-1.0
-10
-100
$\rho\tau$
(c)
STABLE
UNSTABLE
$p=1$
$\tau_1/\tau_2 = 5.0$

$\sigma/\tau \leqslant 0.12$ then the local stability properties are adequately predicted by the approximation, but that by the time σ/τ is much more than twice this value, the complete distribution should not be ignored.

4.7.2 Persistent Fluctuations

Persistent fluctuations in solutions to the integro-differential Eq. (4.3.8) have the same upper bound (numerically) as that proved for the delay-differential equation of Ch. 2 (see section 2.5), and, likewise seem to have the same lower bound, but to further investigate differences in the predicted behaviour of the two systems, I must resort to numerical analysis of some particular model or models.

I chose the birth and death rates of the delay-differential equation of Ch. 2 ("Model I") and Ch. 3, i.e.

$$\begin{cases} B(t) = QA(t)\exp(-A(t)/A_0) & (4.7.2) \\ \\ D_A(t) = mA(t) & (4.7.3) \end{cases}$$

Substituting Eqs. (4.7.2) - (4.7.3) into Eq. (4.6.3), and scaling

$$Y \equiv A/A_0, \quad t' = t/\tau, \quad U = V/B_{max} \qquad (4.7.4)$$

with $c = (p+1)/\tau$ (Eq. (4.4.11)) produces the set of p+2 scaled equation for the distributed maturation system,

$$\begin{cases} \dot{Y}(t') = [R'_{max}\tau]U_1(t') - [m\tau]\ Y(t') \\ \dot{U}_j(t') = (p+1)(1+\tau_1/\tau_2)(U_{j+1}(t') - U_j(t')) \quad j=1,2\ldots p \\ \dot{U}_{p+1}(t') = (p+1)(1+\tau_1/\tau_2)(Y(t'-T_1)\exp(1-Y(t'-T_1))-U_{p+1}(t')) \end{cases} \tag{4.7.5}$$

where

$$T_2 \equiv \frac{\tau_1/\tau_2}{1+\tau_1/\tau_2} \tag{4.7.6}$$

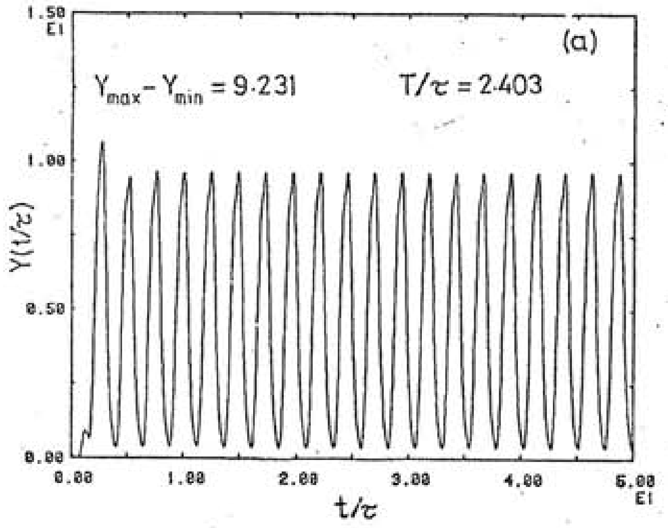
which is of course the generalisation of

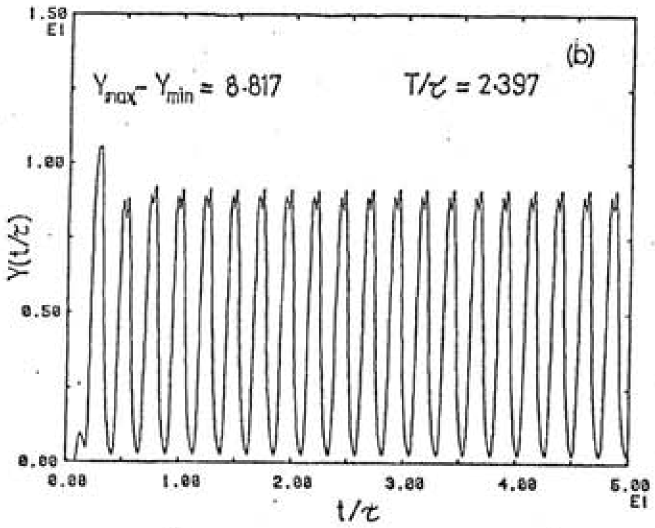
$$\dot{Y}(t') = [R'_{max}\tau]Y(t'-1)\exp(1-Y(t'-1))-(m\tau)Y(t') \tag{4.7.7}$$

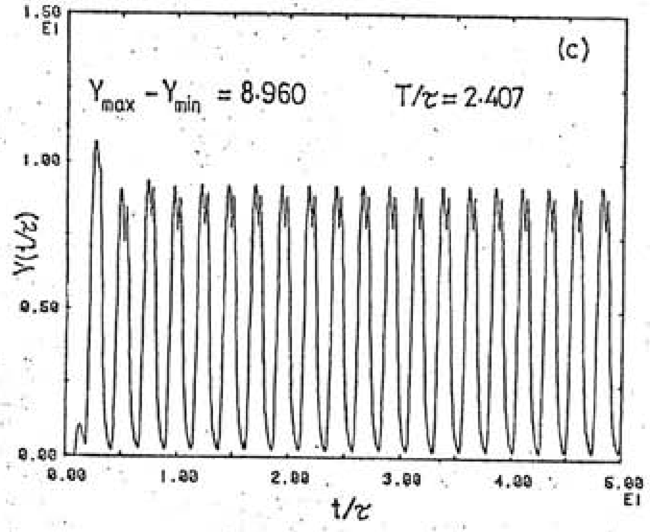
the constant maturation equation of Chs. 2 and 3. The initial history and initial values required to fully specify the problem are

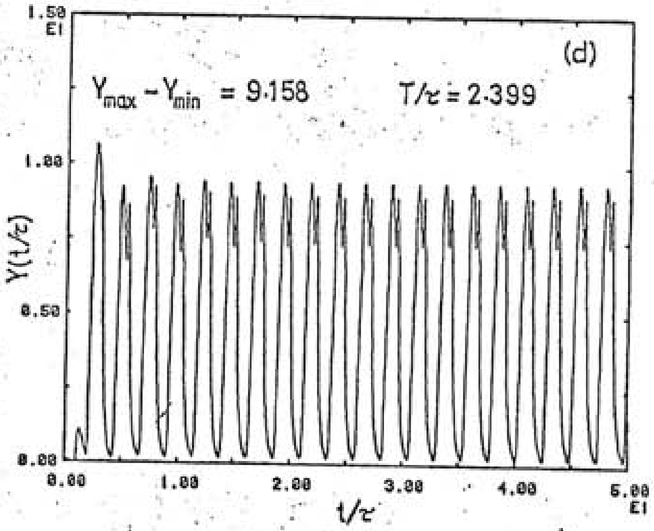
$$\begin{cases} Y(t') = 0 \quad -T_1 \leqslant t' < 0 \\ Y(0) = Y_I = A_0A_I > 0 \\ U_j(0) = 0 \quad j = 1,2\ldots p+1 \end{cases} \tag{4.7.8}$$

By choosing points in the common $(R'_{max}\tau, m\tau)$-space, and varying the parameters τ_1/τ_2 and p (as in section (4.7.1)), I can assess the importance of the details of the distribution of maturation periods upon the behaviour of (4.7.5) in the persistent fluctuation regime,


(a)
$Y_{max} - Y_{min} = 9.231$
$T/\tau = 2.403$
1.50 E1
1.00
0.50
0.00
$Y(t/\tau)$
0.00
1.00
2.00
3.00
4.00
5.00 E1
t/τ

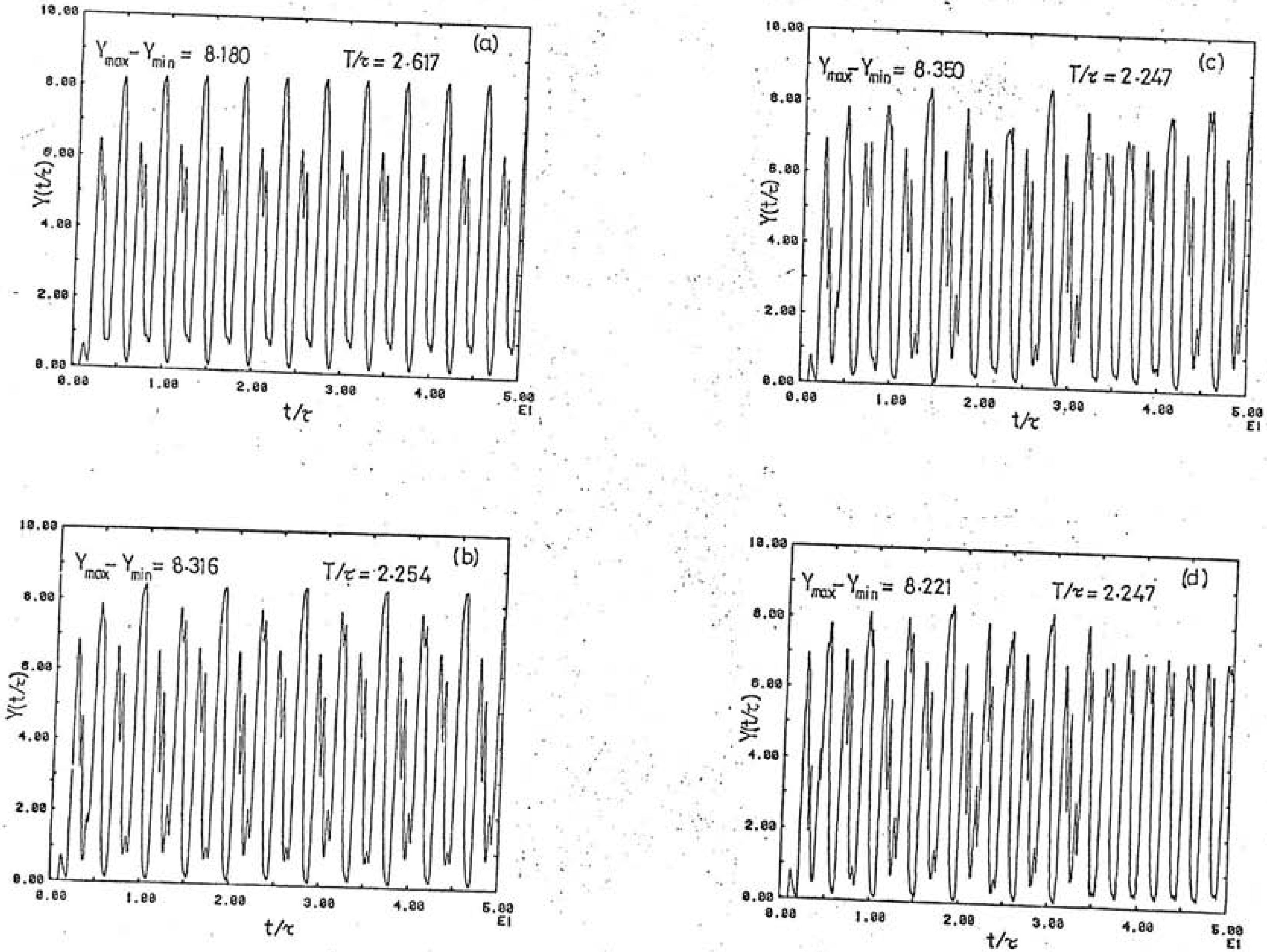

(b)
$Y_{max} - Y_{min} = 8.817$
$T/\tau = 2.397$
1.50 E1
1.00
0.50
0.00
$Y(t/\tau)$
0.00
1.00
2.00
3.00
4.00
5.00 E1
t/τ


(c)
$Y_{max} - Y_{min} = 8.960$
$T/\tau = 2.407$
1.50 E1
1.00
0.50
0.00
$Y(t/\tau)$
0.00
1.00
2.00
3.00
4.00
5.00 E1
t/τ


(d)
$Y_{max} - Y_{min} = 9.158$
$T/\tau = 2.399$
1.50 E1
1.00
0.50
0.00
$Y(t/\tau)$
0.00
1.00
2.00
3.00
4.00
5.00 E1
t/τ

and compare that behaviour with that of the approximation, Eq. (4.7.7). The first point I choose is $R'_{max}\tau = 47.8$, $m\tau = 4.0$, where the solution to Eq. (4.7.7) is periodic, but with some "fine structure", in the form of a double peak in each oscillation (Fig. (4.4)(d)). In Fig. (4.3)(a-c) I have plotted some solutions to Eq. (4.7.5), with the same $R'_{max}\tau$ and $m\tau$. I have chosen to keep $p=1$ and vary τ_1/τ_2 alone. It is clear that as τ_1/τ_2 is increased, the behaviour of (4.7.5) tends rapidly towards that of the limiting case, Eq.(4.7.7). At $\tau_1/\tau_2 = 3.0$ ($\sigma/\tau \simeq 0.177$; Fig. (4.3)(a)), although the fine structure predicted by the constant maturation period approximation is absent, there is close agreement between the dominant periods and amplitudes. At $\tau_1/\tau_2 = 5.0$ ($\sigma/\tau \simeq 0.118$, Fig. (4.3)(b)) the solution shows fine structure, and by the time $\tau_1/\tau_2 = 10.0$ ($\sigma/\tau = 0.064$, Fig. (4.3)(c)), the difference between the constant and the distributed maturation period models is unlikely to be experimentally detectable. By keeping τ_1/τ_2 constant, and varying p, the same kind of approach to the limiting case is observed.

Second, I choose the point $R'_{max}\tau = 51.5$, $m\tau = 6.0$ where Eq. (4.7.7) predicts chaotic fluctuations (Fig. (4.4)(d)). I shall alter τ_1/τ_2 once more, the time keeping p fixed at 2. For $\tau_1/\tau_2 = 5.0$ ($\sigma/\tau \simeq 9.62 \times 10^{-2}$; Fig. (4.4(a)) the solution to (4.7.5) is characteristic of a system that has undergone two bifurcations (i.e. the repeat period is twice the dominant fluctuation period), and while the fluctuation amplitude is reasonably well predicted by Eq. (4.7.7) (see Fig. (4.3)(a,d)), there is an appreciable difference between the periods of the two solutions, and clearly fine structure is ill-represented. At $\tau_1/\tau_2 = 5.0$


(a)
$Y_{max}-Y_{min}=$ 8·180
$T/\tau=$ 2·617
(b)
$Y_{max}-Y_{min}=$ 8·316
$T/\tau=$ 2·254
(c)
$Y_{max}-Y_{min}=$ 8·350
$T/\tau=$ 2·247
(d)
$Y_{max}-Y_{min}=$ 8·221
$T/\tau=$ 2·247
Y(t/τ)
t/τ
0.00
1.00
2.00
3.00
4.00
5.00
E1
2.00
4.00
6.00
8.00
10.00

($\sigma/\tau \simeq 5.25 \times 10^{-2}$; Fig. (4.4)(b)) a third bifurcation has occurred, with its associated period doubling; here both the maximum amplitude and the dominant period of the solution to Eq. (4.7.5) are well approximated by the constant maturation period system, and there is fair agreement between the transient behaviour predictions of the two equations (see Figs. (4.4)(b,d)). Fig. (4.4)(c) shows the solution of Eq. (4.7.5) when $\tau_1/\tau_2 = 15.0$ ($\sigma/\tau \simeq 3.05 \times 10^{-2}$); it is clear that the behaviour is very complicated, and does in fact appear to be chaotic, i.e. no repeat period was observed. Although the maximum amplitudes, dominant periods and transients of the distributed and constant maturation period equation solutions are in close agreement the approximation does not predict details of fine structure with any great accuracy.

It would seem, therefore, that the pattern of behaviour in the persistent fluctuation region of parameter space is too complicated for a single value of σ/τ to be able to indicate the accuracy of the approximation Eq. (4.7.7), as it was for the local stability boundary. However, the gross fluctuation characteristics (dominant period and maximum amplitude), which are probably principally controlled by $R'_{max}\tau$ and $m\tau$, are well predicted by the approximation, even for quite broad distributions, and the fine structure of solutions to the distributed maturation period system, although rather more sensitive to changes in τ_1/τ_2 and p is, when relatively uncomplicated, quite well predicted by the constant maturation period approximation.

4.8 DISCUSSION AND CONCLUSIONS

It is clear that the formulation of tractable models incorporating differential maturation, even for the simple two developmental stage population dealt with here, presents problems of analysis as yet unsurmounted, in the general case. Only for the restricted competition regime of adult-only competition has it so far been possible to extract an analytically and computationally tractable integro-differential equation model. The conventional ad hoc "distributed-delay" models can only under the most restricted and specific conditions be considered as accurate, and must in general be regarded as inappropriate to age-structure modelling.

Through the judicious choice of a general weighting function, I was able to extend the work of LEWIS (1977) and MACDONALD (1978), showing that a full local stability analysis can be performed for the general "adult-only competition" integro-differential equations, and that the numerical analysis of any particular model is relatively straightforward.

The results of sections (4.7.1) and (4.7.2) suggest that the amount of confidence that can be placed in a delay-differential equation model, as an approximation to a full distributed maturation period system, largely depends upon what is to be investigated. The local stability properties of the "distributed" system, and the gross fluctuation characteristics (i.e. the dominant period, and the observed maximum amplitude) of solutions can be estimated with considerable accuracy, even when the true distribution is not particularly close to being a delta-function at τ; the details of the fine structure of solutions, and the relationship between the dominant and the repeat period (the period-doubling behaviour), however, are much less accuratly approximated, except where they are both thoroughly uncomplicated.

This is rather less worrying than it might at first appear, for two reasons. Firstly, while the period-doubling behaviour of various population models has received a great deal of attention (e.g. MAY 1974b, 1975; MAY & OSTER 1976; PEREZ _et al_ 1978), there is no evidence to suggest that bifurcations after the first have much biological significance: their importance is largely mathematical, as an aid to charting the behaviour of a particular model, or class of models, as in Ch. 2. Thus, provided that the dominant periods, and the maximum amplitudes, of the approximation and of the "distributed" system solutions are very close, the details of the formal repeat time are unimportant. Secondly, and not unrelated, is the problem of initial value dependence. In the "chaotic" regime, the details of a given solution to a difference, delay-differential, or integro-differential equation will depend upon the initial value(s) (e.g. MAY 1975; OSTER 1981; MAY & OSTER 1976); also, for model parameter values taking the system close to some bifurcation, the transient part of the solution can be very long, and will of course be highly initial value dependent. It follows that, again, only the gross fluctuation characteristics of solutions to _either_ the constant or distributed maturation period systems can be relied upon to be accurate in detail. The existence and the magnitude of fine structure is determined by density effects (Ch. 3, and OSTER & IPAKTCHI 1978), and the details of the distribution of maturation periods are secondary influences.

It is natural to ask what these results indicate about the accuracy of delay-differential (constant maturation period) equations, as approximations to full distributed maturation period models of insect populations, and in particular how the results and conclusions of the Case Study (Chater 3) are affected. In an attempt to at least partially answer the first part of that question, I have compiled Table (4.1), the values of τ_1/τ_2 and τ of a few insect species under various experimental conditions. There is clear evidence of variation not only in the mean maturation period with temperature and humidity, as might be expected (MACKERRAS 1933; CHAPMAN 1969), but also of the shape of the distribution around this mean, as revealed by variations in τ_1/τ_2. Even if the (usually unknown) values of p which could be used to fit the original distributions were all uniformly high, there is a sufficient range of values of τ_1/τ_2 (from about one to about fifteen for the laboratory experiments) that for some at least of the cases in Table (4.1) - those with small τ_1/τ_2 - a delay-differential equation is likely to be quite inappropriate, while for others - large τ_1/τ_2 - the approximation would be perfectly satisfactory.

Unfortunately, NICHOLSON (1950, 1954, 1957, 1960) did not publish any details of the natural variation in maturation period that would permit a reconstruction of w(r), or even an estimate of τ_1/τ_2 and p. The only information of this sort for Lucilia cuprina of which I am aware is due to MACKERRAS (1933), who examined the life-histories of several species of blowfly. Some blowflies were kept in cubicles in an insectory, where the temperature, humidity and sunlight were "quite similar to those prevailing outside" (p 353); the mean temperature was thus about 20°C. The length of the maturation period of *L. cuprina* in the insectory varied between 14 and 21 days, with the mean delay at 17 days. Cage experiments at a temperature of 20 - 22°C produced *L. cuprina* with a range of maturation periods of only 14 - 16 days (MACKERRAS (1933) does not quote a mean value for these experiments). Increasing temperature reduced the maturation period, so that at 30°C, *L. cuprina* could mature in only 11 days. In the insectory, therefere, $\tau_1/\tau_2 \simeq 4.17$, and the fairly centrally placed mean suggests a reasonable degree of symmetry in the distribution, and hence a moderately large value of p, assuming that the shifted gamma distribution gives an acceptable fit. For the cage experiments, although the mean is not known, obviously $\tau_2 < 2$ days, so that $\tau_1/\tau_2 > 7$, and is quite likely to be at least twice this value, depending on the value of p, which is unfortunately quite unknown. While it would be dangerous to try and apply MACKERRAS's (1933) results too directly to the blowflies used by NICHOLSON (1954, 1957), under, no doubt, substantially different experimental conditions (certainly at a higher temperature: 25°C), it can be inferred with reasonable safety that neither τ_1/τ_2 or p is likely to be small and that they both could well be quite large. If so, then the results of sections (4.7.1) and (4.7.2) indicate that the delay-differential equation model of Chapter 3 should be substantially correct as regards the local stability behaviour, the gross fluctuation characteristics, and the *qualitative* features of the fine structure of solutions, and thus that the conclusions of Chapter 3 still stand.

TABLE (4.1)

REFERENCE	SPECIES	Laboratory Conditions Temp/^{o}C	R$_{1}$H/%	τ/days	τ_1/τ_2	S_1
ASH & GREENBERG (1975)	Phaenicia sericata	19	-	54.37	1.231	0.273
		27	-	15.98	1.672	0.433
		35	-	12.30	4.348	0.067
	Phaenicia pallescens	19	-	30.83	9.894	0.400
		27	-	13.31	4.762	0.727
		35	-	10.95	2.712	0.247
CLARKE & HOWITT (1975)	Anthonomus sigmatus	15.6	-	31.0	9.33	-
		21.1	-	23.5	14.7	-
		30.0	-	15.0	6.5	-
KIRK (1975)	Pterostichus chalcites	20 - 23	-	50.5	1.061	-
DELOACH & RABB (1971)	Winthemia manducae	24	100	32.0	3.923	-
MACKERRAS (1933)	Lucilia cuprina	20	-	17	4.67	-
		20 - 22	-	15 ± 1	>> 7	-
MADDOX & MAYFIELD (1979)	Amynothrips andersoni	24	-	24.0	3.0	-
PARTIDA & STRONG (1975)	Trogoderma variabile	37.8	50	35.53	9.075	0.0988
		32.2	70	34.16	4.545	0.328
		32.2	50	38.96	4.597	0.214
		32.2	30	40.40	5.314	0.351
		26.7	70	52.70	4.432	0.418
		26.7	50	57.33	9.759	0.408
		26.7	30	55.83	10.56	0.346
STRONG & MEAD (1975)	Trogoderma simplex	37.8	50	61.29	3.613	0.0252
		32.2	70	42.98	4.386	0.326
		32.2	50	48.06	4.302	0.330
		32.2	30	55.78	3.366	0.409
		26.7	70	71.21	4.011	0.287
		26.7	50	67.21	4.998	0.342
		26.7	30	70.72	2.992	0.277

CHAPTER 5 CONCLUSIONS AND SUGGESTIONS FOR FURTHER WORK

In this final Chapter I shall discuss the results and conclusions of the previous Chapters, and consider their implications, both in particular and in general, for the modelling of laboratory insect populations.

The objectives of the work reported in this thesis were the formulation, analysis and application of analytically and computationally tractable models of laboratory insect populations, when some account is taken of the population age-structure. The fulfilment of these objectives has met with considerable success. In Chapter 2 I developed a formalism for the study of populations undergoing constant aging, whereby under certain competition regimes, a single delay-differential equation encapsulates the adult population dynamics. A great deal of the behaviour of solutions to this equation can be studied analytically, and its numerical analysis is straightforward, given adequate computing facilities. In Chapter 3 I fitted such an equation to some of the classic data of NICHOLSON (1950, 1954, 1957, 1960), for laboratory populations of the sheep blowfly *Lucilia cuprina*, with considerable success, thereby gaining insight into the mechanisms producing the observed cyclic fluctuations in insect numbers. In Chapter 4 I managed to generalise the constant-aging approach of Chapter 2 and 3, and produce an equation which, under restricted competition conditions, describes the adult population dynamics of a differentially aging population, and which is both analytically and computationally tractable.

In general, the results presented in the foregoing Chapters are encouraging, and (it is hoped) useful. The occasions when these simple delay-differential and integro-differential equations can be used appropriately are now well defined, and all approximations clearly stated, which should prevent the kind of inadvertent misapplication that has led to the prevalence of the time-delayed logistic model. Any particular delay-differential equation model of the general type dealt with in Chapter 2 can be examined analytically, using the result on bounds, and on the asymptotic positions of bifurcation boundaries, to detect model-specific behaviour. Likewise, the results of Chapter 4 on distributed maturation period equations permit the testing, for a given model, of the effects of differential aging, and hence of the validity of the constant-aging approximation. While the local stability and numerical analyses of the distributed maturation period system are only marginally more difficult than those for the delay-differential equation approximation (so that if necessary accurate modelling is still possible), the full range of "tools" developed in Chapter 2 not as yet been extended to aid the analysis of the differential-aging system. The results and conclusions of Chapters 2 and 4 support those of Chaper 3, the case study - neither the precise functions used (for $R(\cdot)$ and $D_A(\cdot)$) in the delay-differential equation, nor the assumption of a constant maturation time should in this case make any significant difference to the dynamic behaviour of the fitted model.

At this point it is worth, I think, commenting upon one or two of the very general assumptions that I have made, throughout the thesis. First is the question of sex. I have not differentiated between the sexes in the population, so that all the vital rates (i.e. death, maturation, fecundity) have been given per individual, rather than per male or female. Clearly this is admissible only when there is no significant systematic difference between the death and maturation rates of the two sexes, and where the sex ratio is constant (so that the fecundity per adult is a constant fraction of the fecundity per adult female). I have no data on sex variation in *per capita* death rates, but can produce some for differences in maturation period, mostly from the sources listed in Table (4.1). CORBET (1952) (the damselfly *Pyrrhosoma nymphula*), BREWER & BACON (1975) (the Carrion Beetle *Silpha ramosa*), and MERTINS (1981) (the Odd Beetle *Thylodrias contractus*), for example, found no significant difference between male and female mean maturation periods in the species they studied. However, STRONG & MEAD (1975), and PARTIDA & STRONG (1975) found that for the two species of beetle that they studies (*Trogoderma simplex*, and *T. variabile*, respectively), males took significantly (statistically) less time to reach maturity than did females. In the blowfly *Lucilia cuprina*, according to MACKERRAS (1933), in a typical three-day span of emergences in cage experiments, the males tend to predominate on the first day, and the females on the third, with about equal numbers of both sexes on the second, indicating a slight difference in the mean maturation period between the sexes, but one that is almost certainly insufficient to alter the conclusions of Chapter 3. The adult sex ratio of many of these species is very close to being 1:1 (e.g. *Lucilia cuprina* (MACKERRAS 1933), and *Trogoderma simplex* (STRONG & MEAD 1975), or is at least approximately constant (e.g. *Pyrrhosoma nymphula* (CORBET 1952)), so that *per capita* and per female fecundities would not be incompatible.

Clearly, for some populations the sexually undifferentiated models of Chapters 2-4 are perfectly acceptable, but for others they could well be gross misrepresentations. The modelling of this latter type must involve an explicit two-sex formulation. While a considerable number of two-sex models have been produced, (see e.g. POLLARD (1973, Ch. 7) or CHARLESWORTH (1980)), these, usually formulated as matrix or integral equation systems, suffer from the same limitations of analytic and computational tractability as I discussed in the Introduction for age-structure models without sex. The development of two-sex versions of the constant-aging, and (especially) the differential-aging population equations of Chapters 2 and 4, respectively, remains a not inconsiderable task for the future.

Perhaps a more pressing problem arises from the assumption that the population under study has only two developmental stages, the first of which contains individuals who either do not compete (the "adult-only" competition regime), or who compete only with individuals of exactly the same age (the "within-cohort" competition of Chapters 2 and 3). For the constant aging case, GURNEY *et al* (1983) have recently extended the formalism to permit an arbitrary number of developmental stages, within each of which all individuals are functionally identical, and compete with one another accordingly. An intriguing variation on this theme permits the duration of each stage to be controlled by explicit or implicit time-dependence - essentially by involving some critical "physiological age" which must be reached before maturation out of a stage is possible (NISBET & GURNEY 1983). While this could admirably cater for the variation in the length of the mean maturation period of insects with environmental factors (see Table (4.1)), or indeed with population density, it offers no aid in describing the variation in the shape of the observed distribution (characterised by τ_1/τ_2 and p, in my approximation). There is thus as yet no way to produce analytically and computationally tractable population models incorporating density-dependence in the immature stage of a differentially aging population, much less develop the stage-duration regulation mechanisms of NISBET & GURNEY (1983). This too must be left for future work.

It is clear that many interesting problems of model formulation and analysis arise when the simplifying assumptions of a "sexless", two-developmental stage population are inappropriate. Nonetheless, I believe that the models and results presented in this thesis provide potentially useful tools for modelling many laboratory populations of insects, and that the results of the case study of Chapter 3, justified and reinforced by the details of the maturation period distribution and sex ratio discussed elsewhere in the thesis, provide strong supportive evidence for this belief.

APPENDIX 1 DERIVATION OF THE DELAY-DIFFERENTIAL EQUATION OF CHAPTERS 2 AND 3.

Let the age density for the population be f(a,t), such that f(a,t)da is the number of individuals aged between a and a + da, at time t. Then, if there is no immigration or emigration, the age-structured population dynamics are controlled by the McKENDRICK (1926) equation (see NISBET & GURNEY (1982, Ch. 3) for a derivation) and renewal condition,

$$\frac{\partial f(a,t)}{\partial t} + \frac{\partial f(a,t)}{\partial a} = -\delta(a,t)f(a,t) \qquad \text{(A1.1)}$$

and

$$B(t) \equiv f(0,t) = \int_0^\infty \beta(a,t)f(a,t)da \qquad \text{(A1.2)}$$

where $\delta(a,t)$ is the age-specific *per capita* death rate, $\beta(a,t)$ is the age specific *per capita* fecundity, and $B(t)$ the total birth rate. With a constant maturation period (i.e. length of immature developmental stage) τ, and a constant sex ratio, the total immature and total adult populations at time t are

$$I(t) \equiv \int_0^\tau f(a,t)da \qquad \text{(A1.3)}$$

and

$$A(t) \equiv \int_\tau^\infty f(a,t)da \qquad \text{(A1.4)}$$

respectively. The general solution to Eq. (A1.1) is

$$f(a,t) = f(0,t-a)\exp\{-\int_0^a \delta(x,t+x-a)dx\} \quad t > a \qquad (A1.5)$$

and, if the laboratory population is assumed to have been started at time t = 0 by "innoculating" an empty cage with adults, then the initial history and initial values required for the system to be fully specified are

$$\begin{cases} I(t) = 0 \quad , \quad t \leqslant 0 \\ A(t) = 0 \quad , \quad t < 0 \\ A(0) = A_I > 0 \end{cases} \qquad (A1.6)$$

Adult Competition

Assuming that fecundity depends only on the adult population size, A(t), then the renewal Eq. (A1.2) becomes

$$f(0,t) = B(t) = \beta_1(A(t))A(t) \qquad (A1.7)$$

Per capita death is assumed to be density-dependent but age-independent in the adult developmental class, and density-independent in all others, i.e.

$$\delta(a,t) = \begin{cases} \delta_I(a) & 0 \leqslant a < \tau \\ \delta_A(A(t)) & \tau \leqslant a \end{cases} \qquad (A1.8)$$

When $a = \tau$, and given (A1.8), the solution (A1.5) becomes

$$f(\tau,t) = B(t-\tau)\ \exp\{-\int_{0}^{\tau} \delta_I(x)dx\} \qquad t > \tau \tag{A1.9}$$

The exponential term is a constant (which I will call S_1) with respect to t, so that

$$f(\tau,t) = S_1 B(t-\tau) \tag{A1.10}$$

Integrating across the age ranges $0 \rightarrow \tau$, and $\tau \rightarrow \infty$ in (A1.1), the pair of balance equations (c.f. (2.2.1) and (2.2.2) are obtained;

$$\begin{cases} \dot{I}(t) = B(t) - f(\tau,t) - D_I(t) & \text{(A1.11)} \\ \dot{A}(t) = f(\tau,t) - D_A(A(t)) & \end{cases}$$

where

$$D_I(t) \equiv \int_{0}^{\tau} \delta_I(a) f(a,t) da \tag{A1.12}$$

and

$$D_A(A(t)) \equiv \delta_A(A(t))A(t) \tag{A1.13}$$

Combining Eqs. (A1.7) and A1.10) permits the definition

$$\begin{aligned} M(t) = R(t) \equiv f(\tau,t) &= S_1 B(A(t-\tau)) \\ &= R(A(t-\tau)) \end{aligned} \tag{A1.14}$$

so that the adult population equation decouples from the immature equation, to give Eq. (2.2.4):

$$\dot{A}(t) = R(A(t-\tau)) - D_A(A(t)) \qquad (A1.15)$$

Competition within pre-adult cohorts

Per capita fecundity is again age-independent, and may or may not be density-dependent, so in general

$$f(0,t) = B(t) = \beta_2(A(t))A(t) \qquad (A1.16)$$

When the pre-adult *per capita* death rate is density-dependent within a given cohort, then

$$\delta(a,t) = \begin{cases} \delta_I(f(a,t)) & , \quad 0 \leqslant a < \tau \\ \\ \delta_A(A(t)) & , \quad \tau \leqslant a \end{cases} \qquad (A1.17)$$

The solution, Eq. (A1.5) for $a = \tau$, is then

$$f(\tau,t) = f(0,t-\tau)\exp\{-\int_0^\tau f(x,t+x-\tau)dx \qquad (A1.18)$$

COLEMAN (1978) has proved, under assumptions identical with those used here, that this exponential is a function only of $f(0,t-\tau)$, so that

$$f(\tau,t) = f(0,t-\tau)S_2(f(0,t-\tau))$$

$$= B(t-\tau)S_2(B(t-\tau)) \qquad (A1.19)$$

$$= R(A(t-\tau)) \qquad (A1.20)$$

in my notation. Proceeding exactly as before for $D_I(t)$ and $D_A(t)$, the adult equation again decouples from the immature equation in (A1.11), and the result is, again, Eq. (2.2.4),

$$\dot{A}(t) = R(A(t-\tau)) - D_A(A(t)) \qquad \text{(A1.21)}$$

APPENDIX 2 LOCAL STABILITY OF THE DISTRIBUTED MATURATION PERIOD EQUATIONS

Assume a solution to Eq. (4.5.3) of the form

$$n(t) \propto e^{\lambda t} \quad , \quad \lambda = -\mu + i\omega \tag{A2.1}$$

Substituting this into its Eq. (4.5.3) gives

$$\alpha + \lambda = \rho \int_{0}^{\infty} g(r-\tau_1;p)H(r-\tau_1)e^{-\lambda r}dr \tag{A2.2}$$

The integral in Eq. (A2.2) is equivalent to the Laplace Transform of the shifted gamma distribution; hence (A2.2) becomes (WILLIAMS 1973; MACDONALD 1978)

$$\alpha + \lambda = \rho e^{-\lambda\tau_1} \frac{c^{p+1}}{(c+\lambda)^{p+1}} \tag{A2.3}$$

so that the stability equation from the Eq. (4.5.3) is

$$(\alpha + \lambda)\left(1 + \frac{\lambda}{c}\right)^{p+1} = \rho e^{-\lambda\tau_1} \tag{A2.4}$$

At the local stability boundary, $\mu=0$ i.e. (A2.4) has imaginary roots, hence,

$$(\alpha + i\omega)\left(1 + i\frac{\omega}{c}\right)^{p+1} = \rho e^{-i\omega\tau_1} \tag{A2.5}$$

To reduce Eq. (A2.5) to parametric equation for the local stability boundary, I follow an idea of MACDONALD's (1978). First, set

$$\tan\theta = \frac{\omega}{c} \tag{A2.6}$$

so that

$$(\alpha+i\omega)(\cos\theta+i\sin\theta)^{p+1} = \beta(\cos\theta)^{p+1}(\cos\omega\tau_1-i\sin\omega\tau_1) \tag{A2.7}$$

or

$$(\alpha+i\omega)(\cos[(p+1)\theta]+i\sin[(p+1)\theta]) = \rho\,(\cos\theta)^{p+1}\theta(\cos\omega\tau_1-i\sin\omega\tau_1) \tag{A2.8}$$

Equating real and imaginary parts in Eq. (A2.8), and dividing through by $\cos(p+1)\theta$ gives the pair of simultaneous equations

$$\left\{\begin{aligned} &\alpha - \omega\tan[(p+1)\theta] = \rho\cos\omega\tau_1(\cos\theta)^{p+1}/\cos[(p+1)\theta] && \text{(A2.9)}\\ &\omega + \alpha\tan[(p+1)\theta] = -\rho\sin\omega\tau_1(\cos\theta)^{p+1}/\cos[(p+1)\theta] && \text{(A2.10)}\end{aligned}\right.$$

which, after a little manipulation, give

$$\left\{\begin{aligned} &\alpha = \frac{-\omega}{\tan[(p+1)\theta+\omega\tau_1]} && \text{(A2.11)}\\ &\rho = \frac{-\omega}{(\cos\theta)^{p+1}\sin[(p+1)\theta+\omega\tau_1]} && \text{(A2.12)}\end{aligned}\right.$$

Recalling that $\omega = c\tan\theta = (p+1)/\tau_2$, (A2.11)-(A2.12) become

$$\left\{\begin{aligned} &\alpha = -\frac{1}{\tau_2}\,\frac{(p+1)\tan\theta}{\tan[(p+1)(\theta+\frac{\tau_1}{\tau_2}\tan\theta)]} && \text{(A2.13)}\\ &\rho = -\frac{1}{\tau_2}\,\frac{(p+1)\sin\theta}{(\cos\theta)^{p+2}\sin[(p+1)(\theta+\frac{\tau_1}{\tau_2}\tan\theta)]} && \text{(A2.14)}\end{aligned}\right.$$

Multiplying through both equations by τ (scales α and ρ), and recalling that $\tau = \tau_1 + \tau_2$, i.e. $\tau/\tau_2 = \tau_1/\tau_2 + 1$, Eq. (A2.13) - (A2.14) become, finally

$$\begin{cases} \alpha\tau = -\,(1+\tau_1/\tau_2)\,\dfrac{(p+1)\tan\theta}{\tan\left[(p+1)\zeta\right]} & \text{(A2.15)} \\[2ex] \rho\tau = -(1+\tau_1/\tau_2)\,\dfrac{(p+1)\sin\theta}{(\cos\theta)^{p+1}\sin\left[(p+1)\zeta\right]} & \text{(A2.16)} \end{cases}$$

where

$$\zeta = \theta+(\tau_1/\tau_2)\tan\theta \qquad \text{(A2.17)}$$

Equations (A2.15)-(A2.17) are thus the parametric equations for the local stability boundary of Eq. (4.5.5) in $(\alpha\tau,\rho\tau)$-space, given the parameters (τ_1/τ_2) and p. For population modelling, only $\alpha\tau > 0$ is of interest (c.f. Ch. 2), so, for solutions with θ in the first quadrant, Eq. (A2.15) indicates that

$$\pi/2 < (p+1)\zeta < \pi \qquad \text{(A2.18)}$$

i.e. (from (A2.17)),

$$\frac{\pi}{2(p+1)} < \theta + (\tau_1/\tau_2)\tan\theta < \frac{\pi}{(p+1)} \qquad \text{(A2.19)}$$

where solving for the upper and lower limits in (A2.19) gives the upper (θ_U) and lower (θ_L) limits of θ for which the parametric equations (A2.15) - (A2.16) give solutions with $\alpha\tau > 0$. Fig. (4.1) in the text illustrates local stability boundaries, with various τ_1/τ_2 and p.

I showed in Ch. 2 that the local stability boundary for the constant maturation period, delay-differential equation tends, as $\tau \to \infty$, to the straight line

$$-\frac{\rho\tau}{\alpha\tau} = 1 \tag{A2.20}$$

From Eq. (A2.15)-(A2.16) for the distributed maturation period system,

$$-\frac{\rho\tau}{\alpha\tau} = \frac{-1}{(\cos\theta)^{p+1}\cos\left[(p+1)\zeta\right]} \equiv K(\tau_1/\tau_2,p) \tag{A2.21}$$

As $\tau \to \infty$, so $\theta \to \theta_u$, so that in the limit the local stability boundary tends to the straight line;

$$-\frac{\rho\tau}{\alpha\tau} = \frac{1}{(\cos\theta_U)^{p+1}} \tag{A2.22}$$

which approaches the discrete delay result (Eq. (A2.20)) as τ_1/τ_2 and/or p becomes large.

APPENDIX 3 THE "LINEAR CHAIN TRICK" FOR DISTRIBUTED MATURATION PERIOD

The adult population balance equation can be written

$$\dot{A}(t) = S_1 V_1(t) - D_A(A(t)) \qquad (A3.1)$$

where $V_1(t)$ is the first in a series of p+1 auxiliary variables,

$$V_j(t) = \int_{\tau_1}^{\infty} g(r-\tau_1;p+1-j)B(A(t-r))dr, \quad j=1,2\ldots p+1 \qquad (A3.2)$$

Differentials with respect to time,

$$\frac{dV_j(t)}{dt} = \int_{\tau_1}^{\infty} g(r-\tau_1;p+1-j)\ \frac{\partial B(A(t-r))}{\partial t}\ dr, \quad j=1,2\ldots p+1 \quad (A3.3)$$

$$= -\int_{\tau_1}^{\infty} g(r-\tau_1;p+1-j)\ \frac{\partial B(A(t-r))}{\partial r}\ dr, \quad j=1,2\ldots p+1 \quad (A3.4)$$

$$= -\Big[g(r-\tau_1;p+1-j)B(A(t-r)\Big]_{r=\tau_1}^{r=\infty} + \int_{\tau_1}^{\infty} \frac{\partial g(r-\tau_1;p+1-j)}{\partial r}\ B(A(t-r))dr$$

$$(A3.5)$$

Now if $k \geqslant 1$, $g(0;k) = 0$ and

$$\frac{dg(x;k)}{dx} = c(g(x;k-1) - g(x;k)) \qquad (A3.6)$$

Also, $g(0;0) = c$ and

$$\frac{dg(x;0)}{dx} = -\ cg(x;0) \qquad (A3.7)$$

Finally $g(\infty;\text{all } k) = 0$. Hence Eq. (A3.5) becomes

$$\frac{dV_j(t)}{dt} = c\int_{\tau_1}^{\infty} g(r-\tau;p-j)B(A(t-r))dr - c\int_{\tau_1}^{\infty} g(r-\tau;p+1-j)B(A(t-r))dr$$

$$j = 1,2...p$$

$$(A3.8)$$

$$\frac{dV_{p+1}(t)}{dt} = cB(A(t-\tau_1)) - c\int_{\tau_1}^{\infty} g(r-\tau_1;0)B(A(t-r))dr \qquad (A3.9)$$

Recalling the definition of Eq. (A3.2), the integrals in Eq. (A3.8)-(A3.9) are replaced by various $V_j(t)$, so that the full description of the population dynamics is the system of p+2 equations

$$\begin{cases} \dfrac{dA(t)}{dt} = S_1 V_1(t) - D_A(A(t)) \\ \\ \dfrac{dV_j(t)}{dt} = c(V_{j+1}(t) - V_j(t)), \quad j=1,2...p \\ \\ \dfrac{dV_{p+1}(t)}{dt} = c(B(A(t-\tau_1))-V_{p+1}(t)) \end{cases} \qquad (A3.10)$$

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PUBLICATIONS

The following have appeared in print, and are bound into the Thesis after this page.

1. W.S.C. Gurney, S.P. Blythe, and R.M. Nisbet, "Nicholson's Blowflies Revisited," Nature(Lond.), 287, 17-21 (1980)

2. W.S.C. Gurney, S.P. Blythe, and R.M. Nisbet, "Reply to Readshaw and Cuff, 1981," Nature(Lond.), 292, 178 (1981)

3. S.P. Blythe, R.M. Nisbet, and W.S.C. Gurney, "Instability and Complex Dynamic Behaviour in Population Models with Long Time Delays," Theoretical Population Biology, 22, 147-176 (1982)

The following have been submitted for publication:

4. S.P. Blythe, R.M. Nisbet, and W.S.C. Gurney, "Formulating Population Models with Differential Aging," Proc. of an International Conference on Population Biology, (Edmonton, 1982), Springer-Verlag

5. S.P. Blythe, R.M. Nisbet, and W.S.C. Gurney, "The Systematic Formulation of Population Models with Distributed Maturation Period," Proc. of a Workshop on Mathematics in Medicine and Biomechanics, (Glasgow, 1982), Shiva

Also in preparation at time of submission;

6. S.P. Blythe, R.M. Nisbet, and W.S.C. Gurney, "Population Models with Distributed Maturation Period"

Reprinted from Nature, Vol. 287, No. 5777, pp. 17-21, September 4 1980

Nicholson's blowflies revisited

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A simple time-delay model of laboratory insect populations which postulates a 'humped' relationship between future adult recruitment and current adult population gives good quantitative agreement with Nicholson's classic blowfly data and explains the appearance of narrow 'discrete' generations in cycling populations.

NUMEROUS elementary ecology texts use as illustrative examples of oscillatory population fluctuations, data drawn from the comprehensive and elegant experiments performed by Nicholson[1,2] on laboratory cultures of the sheep blowfly *Lucilia cuprina*; in these, the population was regulated by the rate of food supply to either the adult population (Fig. 1*a*) or the larval population (Fig. 1*b*, *c*). Notwithstanding their popularity as alleged examples of oscillatory behaviour, the large, quasi-periodic population fluctuations observed by Nicholson are still very imperfectly understood. It is clear from the work of Maynard Smith[3] and May[4] that a combination of high fertility and long development delay must be primarily responsible, and the discrete-time model developed by Varley, Gradwell and Hassell[5] further suggests that a degree of 'overcompensation' in the controlling density dependence may be important. However, beyond these rather generalized insights progress has been slight. Despite a variety of more or less sophisticated attempts[4-6], no theoretical model has yet yielded a truly satisfactory quantitative fit to the time history of even a single culture, still less has it been possible to formulate a comprehensive framework within which the various subtly different experimental results can be systematically inter-related.

In this article, we seek to formulate a model capable of providing such a framework, but as an initially less grandiose target we shall try to answer a number of specific questions about Nicholson's blowfly data. First, we must identify the class of mechanism which produces the quasi-periodic fluctuations; are they self-sustaining limit cycles perturbed by experimental uncertainty and demographic stochasticity, or are they true quasi-cycles[7] driven by demographic or environmental stochasticity? Second, we wish to know what determines the period and amplitude of the cycles. Lastly and perhaps most interestingly, we wish to understand the observed patterns of breeding activity; specifically, why the two discrete generations per cycle observed in the larval food-limited case (Fig. 1*b*) occur at uneven time intervals, and why in the adult food-limited case (Fig. 1*a*) they merge into a single, almost continuous period of reproductive activity.

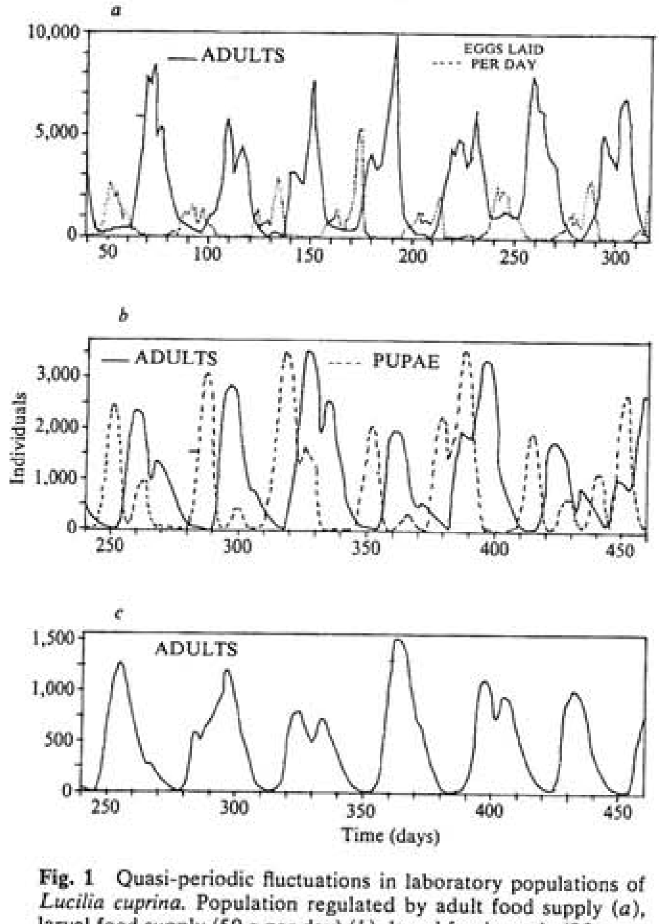

Fig. 1 Quasi-periodic fluctuations in laboratory populations of *Lucilia cuprina*. Population regulated by adult food supply (*a*), larval food supply (50 g per day) (*b*), larval food supply (25 g per day) (*c*). Data from ref. 1.

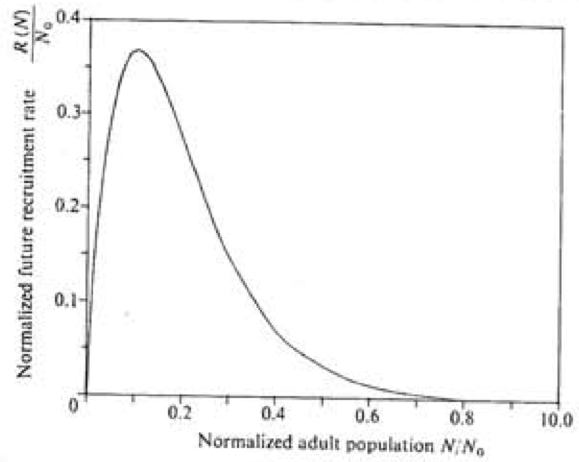

Fig. 2 Assumed dependence of future recruitment rate against present adult population.

The time-delayed logistic model

If it is to be capable of answering questions about the form and timing of generations, our model clearly cannot simply assume that generations are discrete; rather, it must make the initial assumption of overlapping generations and its dynamics must be such as to cause the spontaneous appearance of clearly marked discrete generations in the appropriate conditions. This implies that it must be formulated in terms of a differential, rather than a difference, equation. Probably the simplest single-species continuous time model capable of generating cyclic or quasi-cyclic fluctuations is the time-delayed logistic

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t}=rN\left[1-\frac{N(t-T_D)}{K}\right] \qquad (1)$$

May[4] showed that this model gave an acceptable gross fit to the adult population data shown in Fig. 1*a* with a delay time T_D of about 9 days, a value which he argued compared acceptably with the observed delay time. However, there are several serious objections to the time-delayed logistic model both in general and as a specific explanation of Nicholson's data. First, close examination of the life history data[2] shows that the appropriate experimental value of T_D is 14.8 ± 0.4 days, which implies that the discrepancy between 'best fit' and experimental values is worryingly large compared with the confidence interval in the best fit value (± 0.5 days). Second, the model "mixes up time-lagged and not time-lagged contributions" (R. M. May, personal communication) in a way which makes it a very poor paradigm for biological phenomena. However, even more serious than either of these objections is the fact that the time-delayed logistic model is entirely incapable of predicting two bursts of reproductive activity per adult population cycle. It is thus structurally incapable of explaining the results obtained by Nicholson in the larval food-limited regime.

A more realistic model

We now formulate an improved continuous time model of an insect population growing in an isolated laboratory culture. As the experimental data which will serve as the primary quantitative test of the model are mainly based on observations of adult population as a function of time, we begin by writing down a balance equation for the population of sexually mature adults, $N(t)$. The experimental conditions clearly preclude any immigration or emigration and thus the rate of change of N must simply be the difference between the total adult death rate (D) and the rate of recruitment to the adult population (R). If we assume that the *per capita* adult death rate has a time- and density-independent value δ, then

$$\frac{\mathrm{d}N}{\mathrm{d}t} = R - D = R - \delta N \tag{2}$$

The adult recruitment rate, R, should be evaluated by writing down analogous balance equations for all the life history stages of the species concerned. However, we can evade the resulting complexity (and increase the generality of our model) with the aid of three simplifying assumptions: (1) the rate at which eggs are produced depends only on the current size of the adult population; (2) all eggs which develop into sexually mature adults take exactly T_D time units to do so; (3) the probability of a given egg maturing into a viable adult depends only on the number of competitors of the same age. Together, these assumptions imply that the rate of recruitment at time t can only be a function of the size of the adult population at time $t - T_D$

$$R = R(N(t - T_D)) \tag{3}$$

so that the entire population dynamic can be expressed by a single delay-differential equation

$$\frac{\mathrm{d}N}{\mathrm{d}t} = R(N(t - T_D)) - \delta N(t) \tag{4}$$

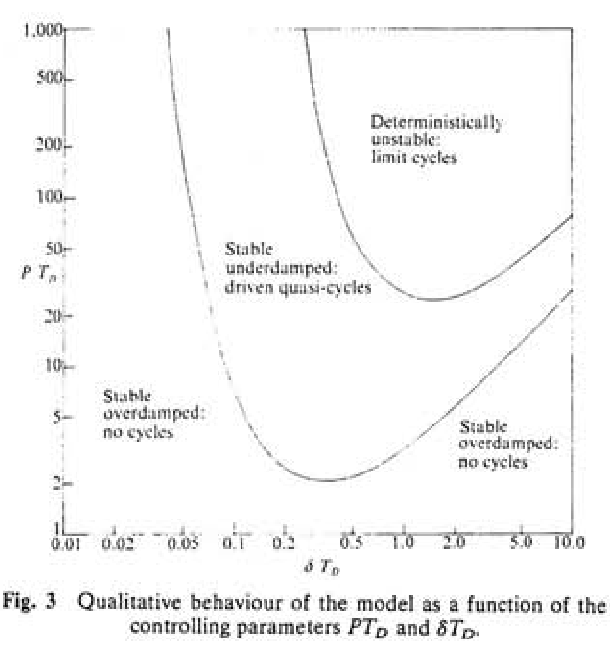

Fig. 3 Qualitative behaviour of the model as a function of the controlling parameters PT_D and δT_D.

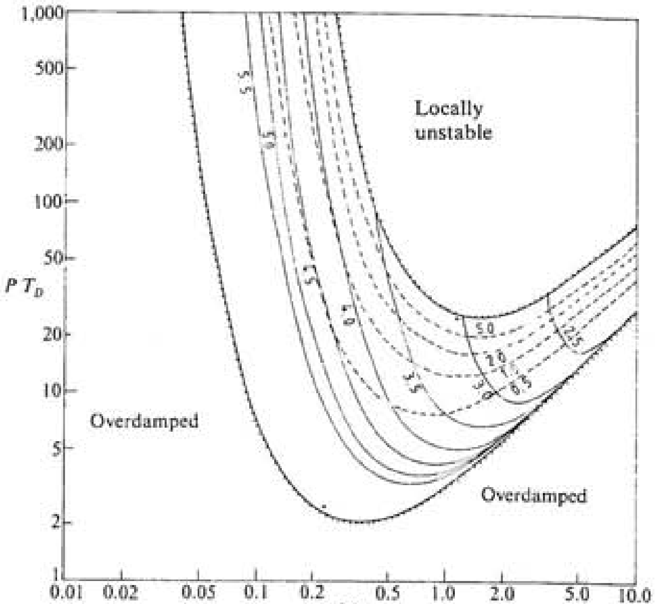

Fig. 4 Characterization of quasi-cyclic behaviour in the stable/underdamped region. Contours of constant normalized period T/T_D (———) and coherence number (– – – –) in the $PT_D/\delta T_D$ plane.

Although the recruitment rate function $R(N)$ can in principle be subject to experimental measurement, we wish our model to act as a paradigm for a rather larger class of similar models as well as provide a detailed fit to Nicholson's data, and we therefore seek rather to write down an appropriate algebraic form for $R(N)$. We consider first those experiments in which the only limiting factor is the rate at which food is supplied to the adult population. Here, egg to adult survival may reasonably be expected to be density independent, so that the rate of adult recruitment at time t will be directly proportional to the rate at which eggs were being laid at time $t - T_D$. Provided that the population sex ratio remains reasonably constant, it seems plausible to suppose that, in the presence of excess food, the total rate at which eggs are produced by a population of N adults will be directly proportional to N. However, when food is supplied at a limited rate, intraspecific competition will clearly act to reduce the average *per capita* fecundity of the members of large populations to well below its physiological saturation value. Indeed, where competition is of the 'scramble' type[1], it seems highly likely that very large populations will require the whole of their restricted food intake for physiological maintenance and will thus produce no offspring at all. Clear experimental evidence of such an effect can be found in Fig. 1*a*, which shows that in Nicholson's adult food-limited culture the total egg production rate drops to zero at high populations. Any plausible functional form for $R(N)$ must therefore go to zero as N becomes either very large or very small. In addition, it seems likely that most recruitment curves will display a single maximum (see Fig. 2) at an intermediate population whose size is determined by the available resources. We therefore choose to represent $R(N)$ by a simple function which displays all these properties

$$R(N) = PN \exp\{-N/N_0\} \tag{5}$$

where P is the maximum possible *per capita* egg production rate (corrected for egg to adult survival) and N_0 is the population size at which the population as a whole achieves maximum reproductive success.

In experiments in which the controlling factor is the rate of food supply to the larval population, the situation is at first sight entirely different. Here, the adults are always provided with excess food and thus always produce eggs at their physiological maximum rate. However, competition among the larvae now makes egg to adult survival highly density dependent, and indeed, Nicholson's batch culture experiments strongly suggest that when an age class is very large, none of its members will actually pupate successfully. Thus, within the limitations of our assumption that egg to adult survival is affected only by competition within a given age class, we can use equation (5) to describe recruitment in both the adult food-limited and the larval food-limited cases.

The dynamics of our model are thus always described by

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = PN(t - T_D) \exp\{-N(t - T_D)/N_D\} - \delta N(t) \tag{6}$$

which has a single non-trivial stationary state

$$N^* = N_D \ln(\widehat{P/\delta}) \tag{7}$$

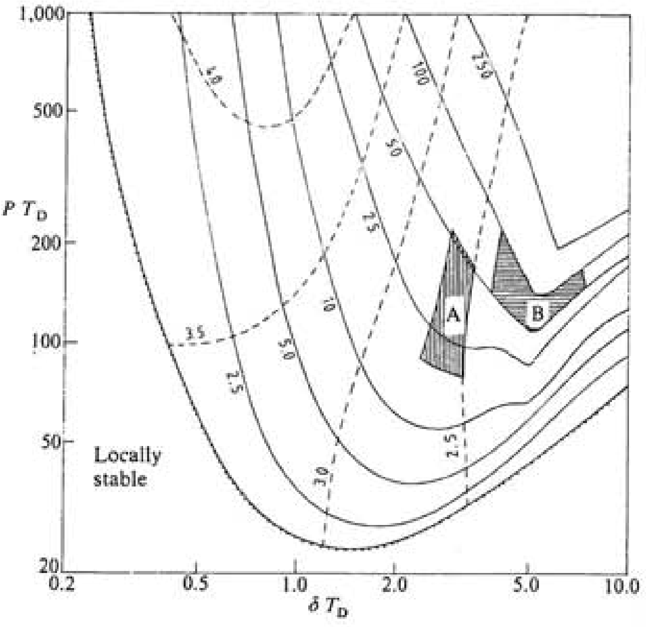

Fig. 5 Characterization of limit cycle behaviour in the locally unstable region. Contour of constant normalized period T/T_D (– – – –) and population ratio N_{max}/N_{min} (———) in the $PT_D/\delta T_D$ plane. The area marked A shows the best fit parameters for the data of Fig. 1*a* and the area marked B corresponds to the data of Fig. 1*b*.

It can easily be shown that the local stability of the steady state and the qualitative properties of the fluctuations about it are entirely controlled by the two quantities PT_D and δT_D, and in Fig. 3 we show the disposition in the $PT_D/\delta T_D$ plane of the various regions of qualitatively different behaviour. Because we seek to understand fluctuations which are at least quasi-periodic, we shall restrict our detailed analysis to the stable/underdamped (damped oscillatory) and locally unstable regions.

If the parameters of our deterministic model are in the stable/underdamped region, we would expect the demographic stochasticity present in a real system to induce quasi-cyclic population fluctuations consisting of bursts of relatively coherent cycles whose period is close to the deterministic natural period, interspersed with short periods of incoherent noise[7]. If we describe the return of an underdamped system to its deterministic equilibrium by a coherence number n_c, defined as the number of cycles over which the amplitude of the transient is reduced by a factor e, then it is found empirically[8] that when such a system is executing driven quasi-cycles, each burst of coherent cycles contains an average of roughly $3n_c$ cycles. Thus, in Fig. 4 we characterize the quasi-cyclic behaviour of our model in the stable/underdamped regime by plotting contours of constant normalized cycle period (T/T_D) and constant coherence number n_c on the appropriate part of the $PT_D/\delta T_D$ plane.

For model parameters in the locally unstable region, the exact solution of equation (6), which can be obtained by numerical integration, takes the form of a self-sustaining oscillation. For some parameter values this is a simple limit cycle, whereas for others it is a more complex cycle or is even formally aperiodic. In all cases, however, a spectral analysis of the solution reveals a

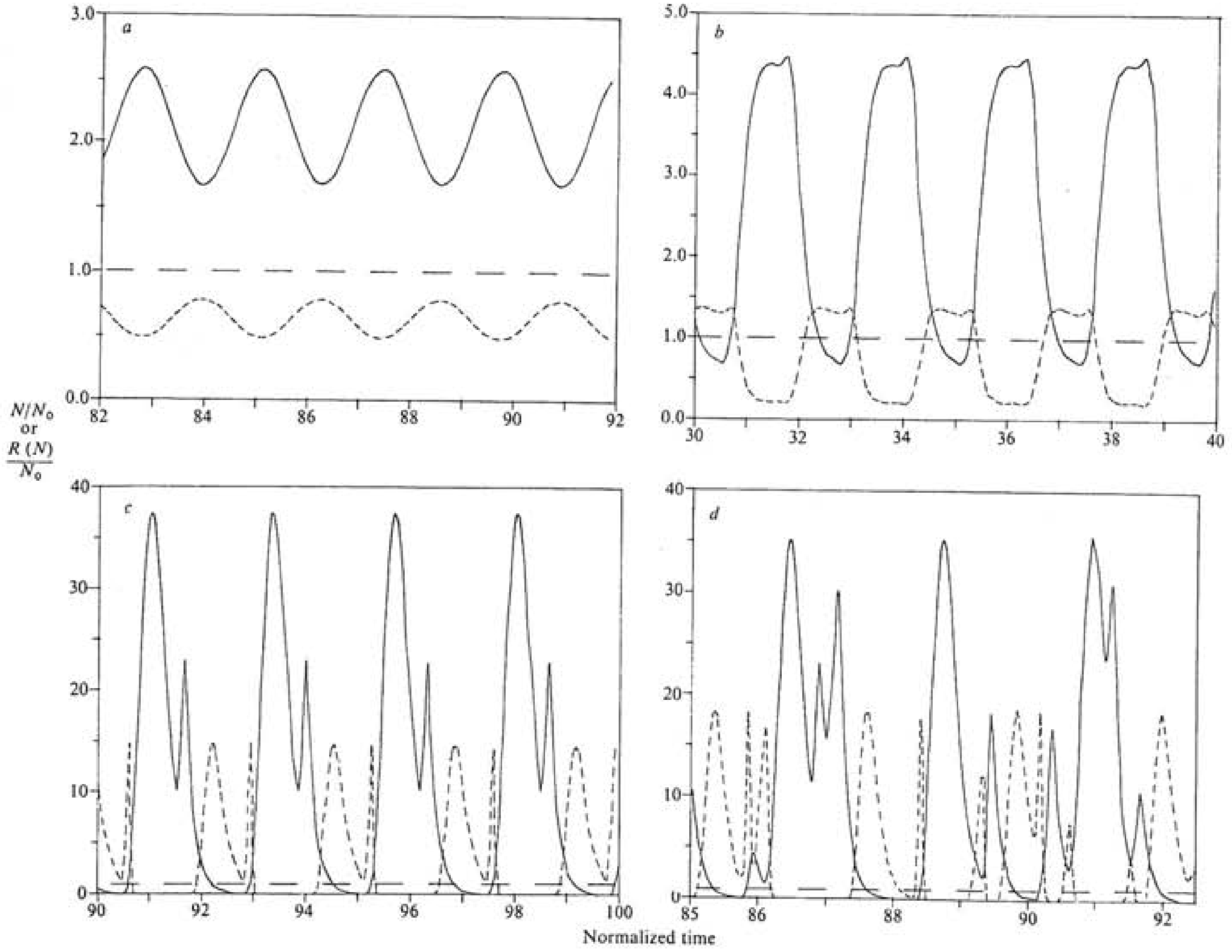

Fig. 6 Separation of generations in a cycling population. Normalized adult population (———) and normalized future recruitment rate (– – – –) as functions of time. *a*, $N_{min} \gg N_0$: continuous reproduction; *b*, $N_{min} \sim N_0$: one generation per cycle; *c*, $N_{min} \ll N_0$: two generations per cycle; *d*, $N_{min} \ll N_0$ and adult fluctuations aperiodic: complex generation pattern.

single clearly marked dominant period (T). We have therefore characterized the solutions in this region by the ratio of this dominant period to the development delay (T/T_D) and the ratio of maximum to minimum population observed during the cycle ($N_{\max}/N_{\min}$). In Fig. 5 we plot contours of these quantities in the appropriate part of the $PT_D/\delta T_D$ plane.

An experimental test

As a quantitative test of our model, we now determine the parameter values which give the best fit to the gross characteristics (T/T_D and $N_{\max}/N_{\min}$ or n_c) of the fluctuations in the adult population of Nicholson's blowfly cultures, and then compare these best fit values with independent experimental estimates of the same quantities. We restrict our attention to the adult food-limited case (Fig. 1*a*), because only here do the data allow us to make an accurate independent estimate of the maximum *per capita* fecundity (P).

There is no simple test which will tell us *a priori* whether the fluctuations shown in Fig. 1*a* are self-sustaining limit cycles or driven quasi-cycles, so we must determine the best fit parameters under both hypotheses. If we assume that the fluctuations are of limit cycle type, then our quantitative characterization requires us to measure the maximum to minimum population ratio $N_{\max}/N_{\min}$ and the normalized cycle period T/T_D; quasi-cyclic fluctuations we characterize by T/T_D and the coherence number n_c. Examination of Fig. 1*a* combined with our previous identification of the correct value of the delay T_D as 14.8 ± 0.4 days reveals that these quantities lie in the ranges

$$2.5 < (T/T_D) < 2.7; \quad 29 < (N_{\max}/N_{\min}) < 53; \quad 2 < n_c < 5 \qquad (8)$$

which enables us to infer from the contour maps given in Figs 4 and 5 that the best fit values of the controlling parameters PT_D and δT_D for the limit-cycle hypothesis are

$$PT_D = 150 \pm 70 \quad \delta T_D = 2.9 \pm 0.5 \qquad (9a)$$

and for the quasi-cycle hypothesis

$$PT_D = 23.5 \pm 4.5 \quad \delta T_D = 3.0 \pm 0.7 \qquad (9b)$$

Although the best fit values of δT_D required under the two hypotheses are essentially indistinguishable, it is clear that the appropriate values of PT_D differ by more than a factor of 6. Thus, an independent estimate of the maximum *per capita* fecundity P will provide a clear *a posteriori* test of the mechanism underlying the observed cycles. We can easily obtain such an estimate from the egg-laying rate data in Fig. 1*a* by recognizing that, because the adult population minima are clearly below the maximum of the total reproduction curve, the value of P is simply given by

$$Pe^{-1} = \frac{\text{Maximum rate of egg-laying}}{\text{population producing maximum reproduction}} \qquad (10)$$

The value of P thus inferred from Fig. 1*a* is in the range 7.4 per day $< P < 11.4$ per day, so that our final independent estimate of the controlling parameter PT_D is

$$PT_D = 130 \pm 30 \qquad (11)$$

which is clearly compatible with the value required under the limit cycle hypothesis and absolutely incompatible with the quasi-cycle hypothesis. This, together with the fact that an independent estimate of δT_D is in good general agreement with the values required under both hypotheses, gives us considerable confidence that the fluctuations observed by Nicholson in the adult food-limited case are of limit-cycle type.

Separate generations in cycling populations

Our rather simplistic initial characterization of the non-linear behaviour of equation (6) in the limit-cycle region in fact conceals a wealth of complexity, for the formal repeat period of the cycles can often be many times the empirically observed dominant period. The general pattern is very similar to that seen by Mackay and Glass[9] and May[10] in equations of similar structure; close to the local stability boundary the solution is a simple limit-cycle with period T, but moving deeper into instability produces a number of successive doublings of the repeat time until a region is reached where the solution is formally aperiodic (chaos). Beyond the chaotic region we again see cyclic fluctuations.

These variations in the fine structure of the adult population fluctuations, although mathematically fascinating, are likely to be hard to identify experimentally in the presence of realistic levels of experimental uncertainty. However, the accompanying variations in the predicted pattern of reproductive activity are not only sufficiently dramatic to be easily identified experimentally, but also provide a clear explanation of Nicholson's observation that, in certain experimental circumstances, breeding occurred in quasi-discrete 'generations' but that in others it was much more nearly continuous. The mechanism by which separation of generations can occur in our model is illustrated in Fig. 6. When the minimum adult population in the trough of the cycle ($N_{\min}$) is greater than the population size at which maximum total reproduction occurs, N_0, then breeding activity ($R(N)$) is essentially continuous with one broad peak per cycle (Fig. 6*a*). When $N_{\min}$ is slightly less than N_0 (Fig. 6*b*), the pattern is still much the same but the reproduction rate peak now has a distinctive 'double-humped' shape. However, when $N_{\min} \ll N_0$, the pattern changes dramatically. In simple cases such as Fig. 6*c*, each adult population peak generates two narrow discrete generations, whereas in more complex cases such as Fig. 6*d*, when the adult population variation is only quasi-periodic, the generations are also very variable in size.

We have tested the plausibility of this mechanism as an explanation of Nicholson's observations by comparing the patterns of breeding activity predicted by our model with best fit parameters determined from the adult population fluctuations shown in Fig. 1*a* and *b*. For the adult food-limited case (Fig. 1*a*), we predict a single double-humped peak per population cycle, whereas in the larval food-limited case (Fig. 1*b*), we predict that breeding should take place in clearly distinguishable generations occurring at uneven time intervals. It is clear from the egg-laying rate and pupal population data given in Fig. 1*a* and *b*, respectively, that this strongly marked qualitative change is indeed observed experimentally.

Conclusions

The model described above provides a satisfying qualitative fit to Nicholson's blowfly data, and its extreme simplicity thus allows us to deduce that the observed fluctuations arise from the combination of a long development delay with a single-humped total reproduction curve. Moreover, it seems clear that any model containing these two generic features must behave in a generally similar way, so that our picture of the way in which discrete generations may be spontaneously maintained in cycling populations should in fact be rather generally applicable.

This model may thus be the prototype of a family of models which will unify the hitherto diverse 'discrete generation' and 'overlapping generation' views of insect population dynamics and lead to a clearer understanding of the uneven timing of insect generations both in the constant environment of the laboratory and in the variable environments encountered in the field. However, considerable further development will be required before we can fully assess the potential of the framework provided by such models to elucidate the subtle systematic differences in behaviour between various populations. As the range of technically feasible modifications is immense, we strongly believe that further development can only be done efficiently in conjunction with a comprehensive experimental programme.

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The glass bead game

THE gap between theoretical and applied ecology seems to be widening. Indeed it is difficult to escape the worrying conclusion that some theoreticians are playing a version of Hermann Hesse's *Das Glasperlen Spiel*[1] or that they have little feeling for or understanding of biological problems. A particularly good example is the recent article by Gurney *et al.*[2] which attempts to provide a theoretical model to explain the oscillatory behaviour of laboratory populations of blowflies.

After reaching the esoteric conclusion that the blowfly cycles are "self-sustaining limit cycles" rather than "driven quasi-cycles", the authors proceed to use their model to explain the 'double-humped' nature of the cycles in terms of minimum population size ($N_{\min}$) in relation to the size at which the population achieves maximum reproductive success (N_0). The mathematics are correct, but in their zeal, the authors fail to notice Nicholson's own explanation of the 'double-hump' phenomenon (see Fig. 3 legend in ref. 3). He says "the lack of a clear inverse relation between the various low adult densities and the number of eggs produced is due to the fact that adults are mostly senile as the adult minima are approached, near the minima many are newly emerged and incapable of laying eggs, and subsequently highly fertile young individuals dominate". In other words, the fact that breeding occurred in 'quasi-discrete' generations is probably almost entirely a consequence of age-specific variation in the reproductive performance of the adult blowflies. As Gurney *et al.* ignore this variation their model must be seen as artefactual and spurious—a product of the 'game'.

Of less importance, but still worrying, is the promotion of "a satisfying qualitative fit" in the conclusions to "good quantitative agreement" in the abstract, and the failure to refer to similar published work[4,5]. In contrast, Readshaw and Cuff[6] have published a biologically realistic model of Nicholson's results which includes readily identifiable parameters. An age-specific version of the model would undoubtedly simulate the 'double-hump' but the data are not yet available.

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GURNEY *ET AL.* REPLY—Readshaw raises three scientific objections to the model described in our recent article[1]. We shall deal with these in turn.

The question of the nature of the mechanism responsible for the observed cycles is very far from 'esoteric'. Any moderately repetitive fine structure exhibited by a limit-cycle type of fluctuation carries readily extractable dynamic information, whereas the fine structure of a driven quasi-cycle is mainly 'noise' which only serves to obscure our view of the underlying population dynamic. Thus our judgement that detailed investigation of the fine structure of the cycles observed by Nicholson is a worthwhile exercise hinges on our unambiguous demonstration that they are limit cycles.

It is clear from our work that if average future recruitment bears any kind of humped relationship to current adult population then cycles which have minima well below the population size at which maximum overall reproductive success is achieved, must be accompanied by a 'discrete generation' pattern of breeding activity. A clear implication of Nicholson's[2,3] batch culture results displayed in Readshaw and Cuff's paper[4] is that just such a relationship exists for *Lucilia cuprina*, and there is thus no shred of evidence for their *ex cathedra* statement that the double-humped egg-laying rate curves observed by Nicholson are entirely the product of the age structure-dependent fecundity changes noted in Fig. 3 legend of ref. 3. However, such effects do provide a very plausible explanation of the observation that in four out of seven cycles shown the second peak of the double hump is considerably higher than the first.

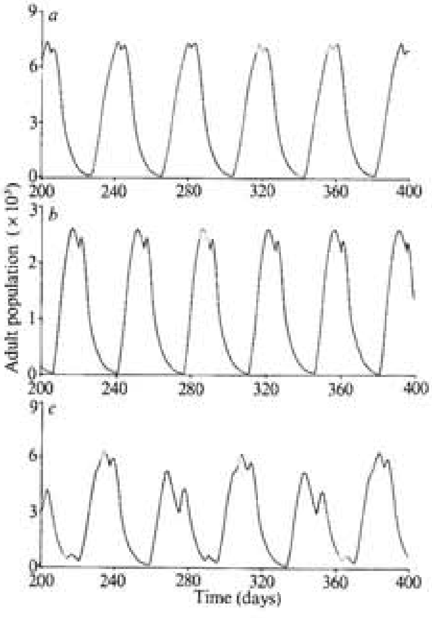

Fig. 1 Numerical solutions of Readshaw and Cuff's model equation[4]: $n(t+1) = 0.8n(t) + R(n(t-\tau))$. *a*, Adult food-limited case: $R = 10n$ when $n < 171$; $R = 1{,}795 - 0.503n$ when $171 < n < 3{,}569$; $R = 0$ when $n > 3{,}569$. $\tau = 15$ days. *b*, Larval food-limited case: $R = 10n(1 - \exp\{0.154 - 109.9/n\})$ when $n < 714$; $R = 0$ when $n > 714$. $\tau = 13$ days. *c*, Adult food-limited case with modified parameters: $R = 2.49n$ when $n < 600$; $R = 1{,}795 - 0.503n$ when $600 < n < 3569$; $R = 0$ when $n > 3{,}569$. $\tau = 15$ days.

The final objection of Readshaw is the claim that the fine structure predicted by our model must be 'spurious and artefactual' because their 'biologically reasonable' model predicts a limit cycle with no fine structure. This claim has no sound basis. Their model is effectively identical to ours except in the details of the functional form chosen for the recruitment rate function. In both experimental regimes considered the form chosen has a single hump with a maximum at a population size (N_0) comfortably in excess of the observed minimum population and thus there seems every reason to suppose that careful numerical analysis will reveal that their model predicts population cycles with a fine structure very similar to that shown in Fig. 6 of our paper[1]. Figure 1*a*, *b* shows that this is indeed the case. Furthermore, in the adult food-limited case (Fig. 1*a*) note that there is no direct experimental evidence for the value of N_0 implied by the parameters chosen by Readshaw and Cuff (171) and indeed that this value is considerably below the value of 600 that may be deduced from Nicholson's data (see Fig. 3 of ref. 3). If we abandon the attempt to force Readshaw and Cuff's piecewise linear approximation to the recruitment function to fit the behaviour of the population as $N \to 0$ and instead place the maximum of the curve somewhere near the correct value (Fig. 1*c*), then the structure predicted by their model becomes very strong indeed.

We conclude that the very simple mechanism proposed in our original article captures much of the spirit of the population dynamics underlying Nicholson's blowfly cycles and is thus a contribution to narrowing (rather than widening) the gap between theoretical and applied ecology.

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