INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION

INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
34100 TRIESTE (ITALY) - P.O.B. 586 - MIRAMARE - STRADA COSTIERA 11 - TELEPHONES: 224281/2/3/4/5/6
CABLE: CENTRATOM - TELEX 460392-I

SMR/99- 17

AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

THE SYSTEMATIC FORMULATION OF DELAY-DIFFERENTIAL MODELS OF AGE OR SIZE STRUCTURED POPULATIONS

R.M. NISBET

University of Strathclyde
Glasgow
Scotland

1. INTRODUCTION

The vital rates of individual organisms usually depend strongly on their chronological or physiological age. Thus the average vital rates which characterize the dynamics of a whole population of such organisms will remain constant over time only so long as the population retains a constant age-profile. Despite almost universal agreement on the evident corollary of this; namely that proper modelling of population fluctuations must require due attention to the dynamics of changes in the population age-distribution, the great majority of theoretical studies take little or no account of such changes.

It is our belief that the primary reason for this omission lies in the failure of any currently popular age-structure description to provide a modelling tool combining a useful degree of realism with an acceptable level of mathematical difficulty. The partial differential equation formalism orginally due to McKendrick (1926) and repopularised by von Foerster (1959) is the most rigorous and elegant available, but poses such horrendous technical difficulties that few analysts succeed in wringing from it any significant biological insight. The more popular matrix formalism (Leslie 1945) poses fewer technical problems but is seriously flawed as a modelling tool because its necessarily rigid assumption of equal length age classes precludes the realistic identification of such age classes with groups of functionally similar individuals (e.g. insect instars). The manifest failure of these two mathematically rigorous descriptions to come up with the biological goods has lead in turn to the use of a variety of ad hoc models based on sets of heuristically formulated delay-differential equations (see for example MacDonald 1978). Such models, although appealingly tractable, all carry the inherent flow that their lack of any mathematically rigorous foundation makes it hard to distinguish real (i.e. biologically real) dynamic subtlty from irrelevant artifacts of erroneous formulation.

In this paper we wish to argue that it is possible to set out a prescription which, under well defined simplifying assumptions, allows one to systematically formulate models which combine the rigour of the von Foerster approach with the mathematical docility of heuristic delay-differential models. The key element in this prescription is the realization that within most age-structured populations there are readily identifiable sub-populations whose members can, without serious error, be regarded as functionally identical (and thus, in particular, as having identical vital rates). If we write the number of individuals in the i^{th} such functional class at time t as $N_i(t)$ and think of a closed population (so as to exclude immigration and emigration) then it is self evident that the dynamics of the total population must be described by a set of differential equations of the general form

$$\dot{N}_i(t) = \text{recruitment} - \text{maturation} - \text{deaths}. \qquad (1)$$

The process of model formulation now focusses upon calculating the three terms on the right-hand side of this equation. The two difficult terms are the recruitment and maturation rates which describe moults, emergencies, pupation and so on, but it turns out that if any inter-class transition is triggered by a critical value of a single parameter (such as age, physiological age, size etc.) then the equivalent recruitment and maturation rates can be obtained rigorously from the von Foerster equation or one of its more complex cousins. In the remainder of this paper we shall concentrate on two particular cases: firstly inter-class transitions which take place at a critical age, and secondly transitions governed by body size (which is thought to be the critical factor in triggering many insect moults). However we would like to draw your attention also to some work which Stephen Blythe will be describing later in this session, in which he examines the possibility of similarly rigorous formulation of "distributed delay" models in which individual members of sub-populations differ in their aging rate.

2. AGE-DEPENDENT TRANSITIONS

We consider first the class of models in which transitions out of class i-1 into class i take place at age a_i, and transitions out of class i into class i+1 occur at age a_{i+1}, so that the duration of age class i is

$$\tau_i = a_{i+1} - a_i. \qquad (2)$$

We seek to calculate the magnitudes of the terms in the population balance equation (1) which we re-write more formally as

$$\dot{N}_i(t) = R_i(t) - M_i(t) - D_i(t). \qquad (3)$$

The death term is easy; we are assuming that all members of age class i have the same instantaneous per capita death rate $\delta_i(t)$ so

$$D_i(t) = \delta_i(t)N_i(t). \qquad (4)$$

The formal derivation of the recruitment and maturation terms (see Gurney, Nisbet and Lawton 1982) is considerably more complex, but it is rather easy to get a feel for the results with the aid of George Oster's analogy between the process of aging and the motion of a conveyor belt. By picturing age class i as a belt of length τ_i turning at constant unit speed (see fig. 1) we make it elementary to see that

1. The recruitment rate to the first age class (i=1 say) is just the total population reproduction rate, and thus, since all individuals in age class i at time t are deemed to have the same instantaneous per capita fecundity $\beta_i(t)$, must be given by

$$R_1(t) = \sum_i \beta_i(t) N_i(t). \tag{5}$$

2. For age classes other than the first, new recruits get onto the start of the belt by falling off the end of the previous one, so the rate of recruitment into class i must be exactly equal to the rate of maturation out of class i-1

$$R_i(t) = M_{i-1}(t) \qquad i>1. \tag{6}$$

3. Once on the belt individuals get off it only by dying (evaporating?) or falling off the end into class i+1. Thus if $P_i(t)$ is the probability that an individual falling onto the start of the belt at time $t-\tau_i$ is still alive to fall off the end at time t, then the rate of maturation out of age class i at time t is

$$M_i(t) = R_i(t-\tau_i) P_i(t) \tag{7}$$

The through age class survival $P_i(t)$ is quite complex to calculate rigorously (see Gurney et al loc. cit.) but fortunately there is a simple intuitive argument which yields the correct answer. We first define $\overline{\delta}_i(t)$ as the average death rate to which an individual maturing out of age class i at time t has been exposed during his sojorn in that age class, so that

$$\overline{\delta}_i(t) = \frac{1}{\tau_i} \int_{t-\tau_i}^{t} \delta_i(x)\,dx \tag{8}$$

and then see immediately that the through age-class survival probability $P_i(t)$ must be

$$P_i(t) = \exp\{-\tau_i \overline{\delta}_i(t)\} = \exp\{-\int_{t-\tau_i}^{t} \delta_i(x)\,dx\}. \tag{9}$$

3. PRACTICAL LUMPED AGE STRUCTURE MODELLING

In common with other delay-differential systems, the dynamic behaviour of lumped age-structure models is most readily investigated by judiciously selected numerical integrations. We have found that the evaluation of such integrals is noticeably facilitated by re-stating the integral equation (9) as a delay-differential equation plus an initial condition, and hence obtaining a model description consisting of pairs of delay-differential equations of the form

$$\dot{N}_i(t) = R_i(t) - R_i(t-\tau_i)P_i(t) - \delta_i(t)N_i(t) \tag{10a}$$

$$\dot{P}_i(t) = P_i(t)\,[\delta_i(t-\tau_i) - \delta_i(t)] \tag{10b}$$

where

$$R_i(t) = R_{i-1}(t-\tau_{i-1})P_{i-1}(t) \qquad i>1 \tag{11a}$$

$$R_1(t) = \sum_i \beta_i(t)N_i(t) \tag{11b}$$

and

$$P_i(0) = \int_{-\tau_i}^{0} \delta_i(x)\,dx \tag{12}$$

Once a suitable initial history has been constructed the system of equations can be integrated rapidly and effectively by a simple predictor-corrector algorithm such as that described by Maas, Nisbet and Gurney (1982). However, at this point we encounter an apparent impass, because the validity of equation (11a) hinges upon the entire historical record being itself a valid solution of equations (10) and (11). Thus we appear not to be able to solve the equations until we've constructed a prior history - by solving the equations!! The remedy for this difficulty lies in the fact that a totally empty system (all $N_i = 0$) is always a stationary solution of (10) and (11), so if we set

$$N_i(t) = 0 \qquad \text{for all } i \text{ and} \qquad t \geqslant 0 \tag{13}$$

then we have constructed a valid, if apparently uninteresting, initial history. Moreover, such an initial history is much less boring than it seems, because it corresponds to the actual prior state of a laboratory experiment which is initiated by the innoculation (at t = 0) of a previously empty culture vessel or enclosure. It thus only remains to model the innoculation process.

If we insist that the innoculated population shall have an arbitrary age distribution this is a very complex undertaking, but by restricting ourselves to "newly qualified" immigrants (e.g. newly laid eggs, newly emerged adults etc. etc.) we can reduce the problem to one which can be solved simply by modifying equation (11) to take account of an immigration rate $I_i(t)$ thus

$$R_i(t) = R_{i-1}(t-\tau_{i-1})P_{i-1}(t) + I_i(t) \qquad (14a)$$

$$R_1(t) = \sum_i \beta_i(t)N_i(t) + I_1(t) \qquad (14b)$$

and then setting all the I_i's to zero except during some short "innoculation period" just after $t = 0$.

4. GROWTH-DEPENDENT TRANSITIONS

In many species transitions between clearly defined functional classes (e.g. insect instars) occur not at a critical age but at a critical value of body size, body weight, or some other physiological parameter (Beddington Hassel and Lawton 1976). Provided that only a single critical factor is involved we can rather easily extend the formalism of section 2 to cover this case. As before the population balance equation for each functional class must of necessity take the general form

$$\dot{N}_i(t) = R_i(t)-M_i(t)-\delta_i(t)N_i(t) \qquad (15)$$

and our task is to discover the relationship between recruitment, maturation and reproduction. The formal mathematical derivation of the results we require (see Nisbet and Gurney 1983) from the general formalism due to Sinko and Streiffer (1967) is even more intimidating than before, but again Oster's conveyor belts come to our rescue. We now visualize distance along the belt as representing body size, so that (fig. 2) we regard size class i as a single belt spanning a size increment Δm_i and turning at a rate, $\dot{m}_i = g_i(t)$, determined by the instantaneous growth rate of the current population of the size class. By simply examining the picture we deduce at once that provided all newborns have the same weight (say $m = 0$):

1. Recruitment to the first size class is just the total population reproduction rate

$$R_1(t) = \sum_i \beta_i(t)N_i(t) \qquad (16a)$$

and

2. Recruitment to subsequent classes occurs only by maturation out of the previous class

$$R_i(t) = M_{i-1}(t) \qquad i>1. \qquad (16b)$$

Connecting the maturation rate out of class i to the recruitment rate into it is rather more complex in this case because the belt doesn't turn at a constant speed. To assist us in thinking about the problem we first define $\rho_B(t)$ and $\rho_E(t)$ to be the densities of individuals to be found at time t on the beginning and the end of the belt respectively. Now, since at time t, the belt is turning at speed $g_i(t)$ we know at once that

$$M_i(t) = g_i(t)\ \rho_E(t) \qquad (17)$$

and

$$\rho_B(t) = R_i(t)/g_i(t) \qquad (18)$$

Clearly if individuals maturing out of class i at time t entered it at a time which for reasons that will become clear in a moment we write as $t-\tau_i(t)$, then ρ_B and ρ_E must obey the relation

$$\rho_E(t) = \rho_B(t-\tau_i(t))P_i(t) \qquad (19)$$

where the through age-class survival $P_i(t)$ is now defined as

$$P_i(t) \equiv \exp\{-\int_{t-\tau_i(t)}^{t} \delta_i(x)dx\}. \qquad (20)$$

This (equation (19)) in turn enables us to combine equations (17) and (18) to yield a relationship between M_i and R_i

$$M_i(t) = g_i(t)\,\frac{R_i(t-\tau_i(t))}{g_i(t-\tau_i(t))}\,P_i(t). \qquad (21)$$

which becomes meaningful as soon as we can calculate the delay $\tau_i(t)$. But $\tau_i(t)$ simply represents the time taken by an individual maturing out of class i at time t to traverse that class (i.e. to achieve a size gain Δm_i). Thus, although it has now itself become a dynamically varying quantity, it is always defined by the recruitment that

$$\Delta m_i = \int_{t-\tau_i(t)}^{t} g_i(x)dx \qquad (22)$$

As we found in section 3, we can facilitate numerical analysis of this system by restating the two integral equations (20) and (22) as differential equations plus initial conditions. This yields a model description composed of sets of three delay-differential equations of the form

$$\dot{N}_i(t) = R_i(t) - \frac{g_i(t)}{g_i(t-\tau_i(t))} R_i(t-\tau_i(t))P_i(t) - \delta_i(t)N_i(t) \tag{23a}$$

$$\dot{P}_i(t) = P_i(t)\left[\frac{g_i(t)\delta_i(t-\tau_i(t))}{g_i(t-\tau_i(t))} - \delta_i(t)\right] \tag{23b}$$

$$\dot{\tau}_i(t) = 1 - \frac{g_i(t)}{g_i(t-\tau_i(t))} \tag{23c}$$

where, again as before, we modify the inter-class links to allow for "newly qualified" immigrants thus

$$R_1(t) = \sum_i \beta_i(t)N_i(t) + I_1(t) \tag{24a}$$

$$R_i(t) = R_{i-1}(t-\tau_{i-1}(t)) \frac{g_{i-1}(t)}{g_{i-1}(t-\tau_{i-1}(t))} P_{i-1}(t) + I_i(t) \tag{24b}$$

and where the initial states of the auxiliary variables P_i and τ_i are defined by

$$P_i(0) = \exp\{-\int_{-\tau_i(0)}^{0} \delta_i(x)dx\}, \tag{25a}$$

$$\int_{-\tau_i(0)}^{0} g_i(x)dx = \Delta m_i. \tag{25b}$$

As before we normally adopt the empty system ($N_i(t) = 0$ for i and $t \leq 0$) as our assumed prior history and start off the culture with a burst of immigration just after $t = 0$.

5. THE POPULATION DYNAMICS OF DAMSELFLY THEORETICA

To demonstrate the use of the formalism we have just developed, and also to illustrate the potential of "mixed mode" models in which some stages are size-controlled while others are age-controlled, we now formulate a strategic model of a generalized damselfly (*D. theoretica*). This model was suggested to us by some very elegant experiments of Lawton, Thomson & Thomson (1980) which showed that the damselfly *Ishnura elegans* can exhibit hugh variations in instar duration in response to changes in food supply. The model, illustrated in Fig. 3, is intended to explore the possibility of dynamic control mediated only by changes in instar duration, and postulates an organism with two life-history stages, larvae and adults, whose populations we shall write as L(t) and A(t) respectively. The population dynamics of the organism are as follows:

1. FOOD SUPPLY: larval food is supplied at a constant rate ϕ into a "pool" of size F(t), and is eaten by the larvae at a *per capita* rate E which depends on the availability of food, i.e. F(t). Thus we write

$$\dot{F}(t) = \phi - L(t)E(F(t)). \tag{26}$$

2. LARVAE:

   a) We assume that larvae grow at a rate directly proportional to their food intake rate, and mature into adults when they reach a critical size. Thus, from (23c) the dynamics of the development delay are

$$\dot{\tau}(t) = 1 - E(F(t))/E(F(t-\tau(t)). \tag{27}$$

   b) We assume that the larval death rate is a density independent constant Δ (per unit time), so that the through age-class survival P(t) is

$$P(t) = \exp\{-\tau(t)\Delta\} \tag{28}$$

   c) From equation (23a) we can see that if the adults produce eggs (i.e. newborn larvae!) at a rate R(t) then the larval population dynamic must be

$$\dot{L}(t) = R(t) - \frac{E(t)}{E(t-\tau(t))} \cdot R(t-\tau(t)).P(t) - \Delta.L(t) \tag{29}$$

3. ADULTS: We assume that adults have unlimited food supplies (or do not feed) so that they have a constant *per capita* fecundity and death rate β and δ respectively. Thus

$$R(t) = \beta A(t) \tag{30}$$

and

$$\dot{A}(t) = \frac{E(t)}{E(t-\tau(t))} \cdot R(t-\tau(t))P(t) - \delta A(t) \tag{31}$$

The dynamics of this model are fully discussed in Nisbet & Gurney (1983). Here it is sufficient to say that notwithstanding its postulation of entirely density *independent* birth and death *rates* the model (when equipped with a sensible functional form for E(F)) exhibits stable stationary states over large regions of its parameter space. The reason for this is very easy to understand: the density dependent length of the larval stage, combined with the loss of a constant fraction of the larval population per unit time, implies strong density dependence of egg to adult survival, and this "implicit density dependence" is just as capable of population stabilization as straightforwardly density dependent vital rates.

5. CONCLUSIONS

We have constructed a framework within which age and/or size structured populations can be modelled with a high degree of mathematical rigour using simple and comprehensible delay-differential equations. It cannot be overemphasized that the difference between such models and previously published *ad hoc* delay-differential models is that models formulated using our prescription are rigorously linked to an exact mathematical underpinning by a series of well-defined modelling assumptions, the principle one being that all members of each sub-population are functionally identical. Thus our prescription enables modellers to avoid the errors and pitfalls which so often accompany *ad hoc* model formulation - think on the time-delayed logistic model and be warned!

REFERENCES

Beddington, J.R., Hassel, M.P. and Lawton, J.H. (1976). "The Components of arthropod Predation II. The Predator rate of increase". Journal of Animal Ecology 45, 165-185.

von Foerster, H. (1959). "Some remarks on changing populations" in the Kinetics of Cellular Proliferation" (Ed. F. Stohlman Jr.) pp 382-407. Frame and Stratton, New York.

Gurney, W.S.C., Nisbet, R.M., and Lawton, J.H. (1983). "The Systematic Formulation of Tractable Single Species Population models incorporating Age Structure". Journal of Animal Ecology - in press.

Lawton, J.H., Thompson, B.A., and Thompson, D.J. (1980). "The effects of Prey Density on Survival & Growth of Damselfly Larvae" Ecological Entomology 5, 39-51.

Leslie, P.H. (1978). "On the use of matrices in certain population mathematics". Biometrika 33, 183-212.

Maas, P., Nisbet, R.M., and Gurney, W.S.C. (1982). "Solver-an adaptable program template for initial value problem solving". Applied Physics Industrial Consultants, University of Strathclyde, Glasgow.

McDonald, N. (1978). "Time lags in biological models". Springer-Verlag. Lecture notes in biomathematics Vol. 27.

McKendrick, A.G. (1926). Applications of Mathematics to Medical Problems. Proc. Edin. Math. Soc. 44, 98-130.

Nisbet, R.M. and Gurney, W.S.C. (1982). "The Systematic Formulation of population models for insects with dynamically varying instar duration". Submitted to Theoretical Population Biology.

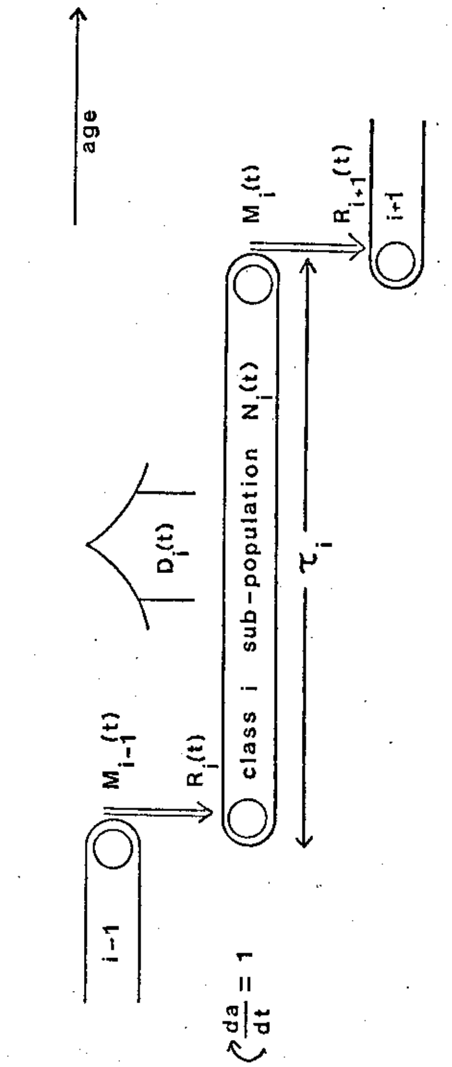
Sinko, J.W. & Streiffer, W. (1967). A new model for the Age-size structure of a population. Ecology 48, 910-918.

Figure Captions

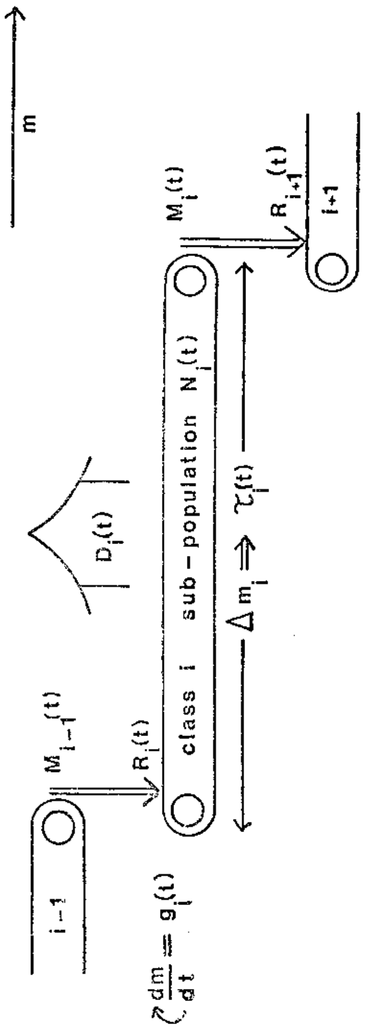
Figure 1 AGE DEPENDENT TRANSITIONS

Figure 2 SIZE DEPENDENT TRANSITIONS

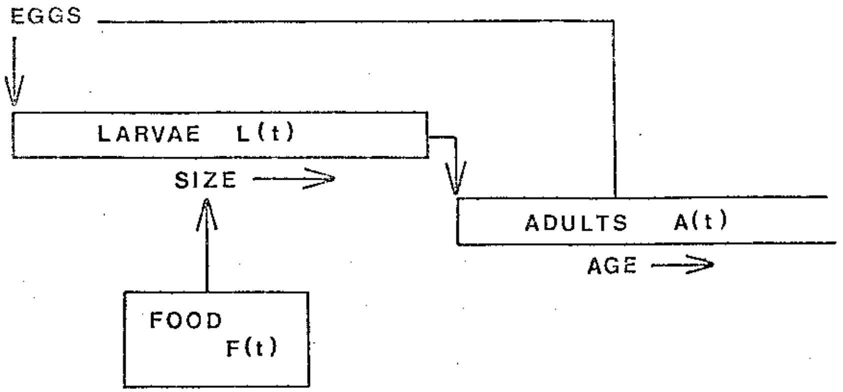
Figure 3 LIFE CYCLE OF DAMSELFLY THEORETICA



13


m
$M_i(t)$
$R_{i+1}(t)$
i+1
class i sub-population $N_i(t)$
$D_i(t)$
$\Delta m_i \Rightarrow \tau_i(t)$
$M_{i-1}(t)$
$R_i(t)$
i-1
$\tau \frac{dm}{dt} = g_i(t)$

14


EGGS
LARVAE L(t)
SIZE
ADULTS A(t)
AGE
FOOD F(t)