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The escalator boxcar train: Basic theory and an application to Daphnia population dynamics

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Basic Theory and an Application to Daphnia Population Dynamics

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(1) The various discrete and continuous time models for the dynamics of physiologically structured populations will be put into a contextual framework to elucidate the relations between them.
(2) We will first introduce the basic concepts (Section 1) and discuss in detail the assumptions underlying the discrete time Leslie matrix model for an age-structured population (Section 2). This somewhat lengthy introduction greatly facilitates the relaxation of these assumptions (section 3), which will at the same time show the relations between discrete and continuous time models (Section 4).
(3) As the main point a method is introduced to study continuous time models in a numerically consistent way that is readily interpreted in biological terms.
(4) Using the introduced method we studied the dynamics of a specific predator-prey system: a Daphnia population in interaction with its algal food source, in which the Daphnia population has an internal (age,size)-structure. The mechanisms that determine the dynamics of this system are discussed and compared with the results of a recent compilation of experimental data on Daphnia population dynamics.

Key Words & Phrases: physiologically structured population models, discrete time reproduction, continuous time reproduction, numerical methods, Leslie matrix models generalized, Daphnia population with age-size structure, oscillations.

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1. INTRODUCTION

One of the difficulties in modelling the dynamics of populations is to deal with those differences in behaviour of the individuals that exert a substantial influence upon these dynamics (Here and in the following 'behaviour' always refers to processes on the level of the individual that are important in a population dynamical sense. Examples of such processes are dying, giving birth and resource consumption). In many models these differences between individuals are simply ignored or it is assumed that the internal structure of the population does not change with time. Such an assumption allows the model builder to deal with an 'average' individual behaviour. The assumption is, however, often questionable.

The behaviour of any individual member of a population is usually determined by its physiological characteristics. As a result the dynamics of a population often depends upon the distribution of its individual members with respect to these physiological traits. A class of population dynamical models that take into account differences in individual behaviour due to differences in the physiological traits of the individual is commonly referred to as physiologically structured population models (The prefix physiologically is used to distinguish these models from those with a spatial structure).

In these structured population models the concepts of individual and population state play an

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important role. The 'physiological state' of an individual (or individual state, often abbreviated to i-state) is defined as a collection of variables (physiological traits) which (i) at any one time fully determines the contribution of the individual to the overall population dynamics and (ii) the future values of which are fully determined by their present values and the intervening environmental conditions as encountered by the individual. Examples of physiological state variables in this respect are age, size or energy reserve of an individual. In practice one wants to characterize the individual by a number of variables which is as small as possible, yet large enough to describe the individual behaviour in as much detail as is necessary for the dynamical phenomena under study.

The phrase 'fully determined', which is used in both parts of the definition above, requires some explanation. The first part of the definition refers to processes like dying and giving birth. Individuals clearly have a *chance* to die or to give birth that depends upon their physiological characteristics. In this paper we will assume that the population size is large enough to describe these *chance* processes within a group (cohort) of identical individuals by means of deterministic rates. Hence we will not deal with demographic stochasticity. The second part of the definition refers to processes like growing and ageing. We will neglect any stochastic variation in these processes among individuals with identical physiological states.

The population state can be conceived as a mathematical representation of the biological population, which takes into account not only the size of the population, but also its structure. Here 'structure' refers to the distribution of the individual members of the population with respect to the collection of physiological states that the individuals can attain (This collection is sometimes referred to as the 'physiological state-space'). Structured population models relate the dynamics of the population state to processes which take place on the level of the individual and which depend upon the physiological state of the individual. Hence structured population models provide a direct link between physiological and population ecology.

The age of an individual has often been used as the only 'physiological' state variable in structured population models. This was an obvious choice as the models usually originated from the field of human demography. Within this class of age-structured models a distinction can be made between continuous and discrete time models. We will briefly discuss these two types of age-structured models for the linear case, i.e. when there are no density dependent effects. In discrete time age-structured models (LEWIS, 1942; LESLIE, 1945) the biological population is represented by means of a column vector

$$\lambda(t) = \begin{bmatrix} \lambda_0(t) \\ \lambda_1(t) \\ \cdot \\ \cdot \\ \cdot \\ \lambda_{m-1}(t) \\ \lambda_m(t) \end{bmatrix}$$

where $\lambda_j(t)$ denotes the number of female individuals with an age between $j\Delta$ and $(j+1)\Delta$ at time t, where Δ is the width of an age class. The m-th age class contains the oldest female individuals of the population that are still reproductive. In these models the dynamics of the population is described on a discrete time basis and can be expressed in matrix notation as:

$$\lambda(t+\Delta) = A\lambda(t) \tag{1a}$$

where A is the so-called Leslie matrix:

$$A = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 & \cdots\cdots & F_m \\ P_0 & 0 & 0 & 0 & \cdots\cdots & 0 \\ 0 & P_1 & 0 & 0 & \cdots\cdots & 0 \\ 0 & 0 & P_2 & 0 & \cdots\cdots & 0 \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ 0 & 0 & 0 & 0 & \ldots P_{m-1} & 0 \end{bmatrix} \tag{1b}$$

and:

F_j represents the average number of daughters that will be alive at time $t+\Delta$, born in the interval t to $t+\Delta$ to females who were in the age group $j\Delta$ to $(j+1)\Delta$ at t.

P_j represents the probability that a female aged between $j\Delta$ and $(j+1)\Delta$ at time t will still be alive at time $t+\Delta$.

The matrix A describes the transition from the population state $\lambda(t)$ to the state $\lambda(t+\Delta)$ a time interval Δ later. This time step Δ, equal to the width of an age class, is usually used to scale both time and age, resulting in Δ as the unit of time. The population state $\lambda(t)$ is hence only considered at certain moments that are equally spaced in time.

The continuous time age structured models (Sharpe & Lotka, 1911; McKendrick, 1926; von-Foerster, 1959) are mathematically more demanding. The biological population is usually represented by means of a density function $n(t,a)$ over the age domain, such that

$$\int_{a_1}^{a_2} n(t,\xi)d\xi$$

denotes the number of individuals with an age between a_1 and a_2 at time t. In these models the dynamics of the population is specified on a continuous time basis by means of a hyperbolic partial differential equation (PDE), the so-called McKendrick equation, together with a special boundary condition:

$$\begin{cases} \dfrac{\partial n(t,a)}{\partial t} + \dfrac{\partial n(t,a)}{\partial a} = -d(a)n(t,a) \\ n(t,0) = \displaystyle\int_0^{\infty} b(\xi)n(t,\xi)d\xi \\ n(0,a) = \Psi(a) \end{cases} \tag{2}$$

where:

$n(t,a)$ is the density function (distribution) over the age axis.

$d(a)$ is the age specific individual death rate.

$b(a)$ is the age specific individual reproduction rate.

$\Psi(a)$ is the initial condition, i.e. the age distribution at $t=0$, which is assumed to be known.

The PDE in equation (2*a*) describes the ageing and dying processes of the individuals, while the boundary condition (2*b*) describes the reproduction process.

For many invertebrate and non-human vertebrate organisms other physiological attributes than age may be equally or more important. Body size is one of the most notable traits in this respect (Werner & Gilliam, 1984; Sauer & Slade, 1987). Moreover, in natural populations density dependent interactions often do occur. For these reasons the discrete and continuous time models have both been extended in various ways. Leslie matrix models have been reformulated to deal with size (Usher, 1966) or developmental stage (Lefkovitch, 1965; Werner & Caswell, 1977; Woodward, 1982) as the determining physiological state variable, while extensions to physiological states of higher dimensions also exist (SLOBODKIN, 1953). USHER (1972) gives an overview of the various developments of the Leslie matrix models, including models incorporating time lags, seasonal and random environmental changes and non-linear feedbacks. For a more recent and detailed overview of the theory and applications of matrix models we refer to CASWELL (1988).

Continuous time models have likewise been developed using size as the physiological state of an individual (BELL & ANDERSON, 1967; SINKO & STREIFER, 1967) or with non-linear feedbacks included into the model (GURTIN & MACCAMY, 1974) or both (MURPHY, 1983). Very recently the theoretical framework for physiologically structured population models has been described in some detail (METZ & DIEKMANN, 1986). This framework allows for physiological states which consist of an arbitrary number of variables (i.e. the physiological state-space can be of arbitrary finite dimension). The rates at which these physiological characteristics develop in time may depend on the physiological state itself as opposed to having just the constant value 1, which characterizes age. Moreover, these development rates as well as the birth and death rate may be time varying or may depend upon a set of dynamical variables, representing the state of the environment encountered by the population. Non-linear feedbacks from the population upon these rates can thus be incorporated by means of a feedback loop via an environmental variable. All these situations are covered by one general hyperbolic partial differential equation (METZ & DIEKMANN, 1986; See METZ ET AL. (1988) for a shorter and somewhat more biologically oriented exposition of this framework).

In general Leslie matrix models are conceptually and computationally simpler than continuous time models. The dynamics of the model population are, for example, easily computed by means of a matrix operation upon the population state vector (cf. equation (1)). In contrast, a correct interpretation of the hyperbolic PDE's occurring in continuous time models requires a heavy (functional) analytical framework that should not bother a biological model builder, while the dynamics of the population can usually only be computed by means of a complicated numerical technique. Such a numerical technique involves a discretization of the domain of the density function and replaces the PDE by an approximating system of ordinary differential equations (ODE's) which is then numerically integrated with respect to time. Recently a special numerical integration method has been developed for the type of PDE's occurring in structured population models (DE ROOS, 1988). For reasons that will be explained in a later section this method is called the *Escalator boxcar train.* The *Escalator boxcar train* can be applied to any situation that is covered by the general PDE given by METZ & DIEKMANN (1986, p. 92-96; see also METZ ET AL., 1988). For instance, the method is applicable even if more than one physiological characteristic of the individual determines its behaviour, i.e. if the physiological state space is higher dimensional.

If we apply one of the simplest numerical integration techniques, the forward-backward Euler discretization (or upwind differencing), with equal step sizes in both the time and age dimension to the McKendrick equation, the resulting numerical scheme is identical to expression (1), representing the standard Leslie matrix model (and the McKendrick equation can likewise be obtained as a limiting case of a Leslie matrix model by letting the width of an age class go to zero and hence the number of classes to infinity). Consequently the dynamics of an age-structured population that is described by the McKendrick equation can be studied numerically using a Leslie matrix model. This approximation is often applied and boils down to a subdivision of the individuals into age classes with an arbitrary width Δ, while within such an age class the individuals are assumed to have the same, usually intermediate age (see, however, Subsection 3.3 for a slightly different, mathematically more robust approximation with an identical underlying principle). It turns out that the *Escalator boxcar train* can be understood completely in biological terms without reference to the PDE, whose solution it (consistently) approximates, in much the same way as the Leslie matrix model can be understood without reference to the McKendrick equation. The aim of this paper, therefore, is to introduce and describe the *Escalator boxcar train* in such a way that it can be understood and used for numerical studies of structured population models by biologists, who do not want to be bothered by PDE's and their mathematical interpretation.

In the following sections the standard Leslie matrix model and its underlying assumptions will first be investigated in more detail. We will show that this model can also be expressed as a system of ordinary differential equations (ODE's) for two vectors that we will use to characterize the population. The elements of the first vector will denote the number of individuals in the cohorts that make up the population, the elements of the second vector will denote the *mean individual state* in these cohorts. In the context of the system of ODE's, that represents the standard Leslie matrix model, the assumptions will subsequently be relaxed. As a result we end up with a system of ODE's that is identical to the numerical scheme for the *Escalator boxcar train.* In a sense we will cover and link the range of situations from the standard Leslie matrix model to the general physiologically structured population models described by METZ & DIEKMANN (1986).

2. THE STANDARD LESLIE MATRIX MODEL

In the standard Leslie matrix model only the female population is considered. Given that the survival rates are sex independent and the sex-ratio is constant in time, the male individuals can simply be included without changing the entries in the matrix. In the following we will indeed assume that the model describes the dynamics of the total population.

Consider the following set of assumptions:

(1) The reproduction and survival rates of the individuals are only age dependent.
(2) These age dependent rates remain constant in time.
(3) Reproduction occurs in relatively short periods of time with fixed time intervals in between. This pulsed, periodic birth process results in cohorts of individuals with exactly the same age.

The standard Leslie matrix model for the dynamics of an age-structured population is based upon these assumptions and can consistently be expressed by the equation (1). (Note in this respect that a model does not refer to a set of equations. A model refers to an abstraction of the natural system we want to study, which we construct by making assumptions concerning the system. In turn this abstraction can be expressed by means of a set of equations. The latter translation from the model into a mathematical description must be done in a consistent way to avoid inadvertently making additional assumptions. Hence, the term 'consistent' implies that the resulting set of equations is unambiguously determined by the assumptions on which the model is based).

A pulsed, periodic reproduction process occurs, for example, in many fish populations, the dynamics of which are indeed often modelled using a standard Leslie matrix model (see, for example, JENSEN (1974), HORWOOD & SHEPHERD (1981), HORWOOD (1984), LEVIN & GOODYEAR (1980) and LEVIN (1981)). The fact that cohorts consist of individuals with exactly the same age ensures that the reproduction and survival rates for all individuals within a cohort are equal. This equality is used in the definitions of the entries in the matrix A of equation (1). Given a pulsed, periodic reproduction process the time and age step Δ is inherently determined by the fixed interval between consecutive reproduction times. In this situation also the age of each cohort of individuals is known exactly at every time. Together these ages of the different cohorts of individuals constitute the age distribution vector of the total population. If we consider age as a continuous variable and accordingly look for a representation of this age distribution over the range of attainable ages, it can be regarded as a distribution that is non-zero only at discrete age values, i.e. consists of a set of delta-functions (spikes), each spike representing a cohort of individuals. The distance between two such spikes is clearly equal to Δ.

Starting from the standard Leslie matrix model we will show that this model can also be expressed as a system of ordinary differential equations (ODE's). At the same time we will show the relation between the entries F_j and P_j in the matrix A and the age dependent individual reproduction and death rate $b(a)$ and $d(a)$, respectively, that occur in the McKendrick equation (2).

In the following we will focus upon the population dynamical processes during one reproduction cycle, consisting of a very short reproductive period and a relatively long inter-reproductive interval. Assume that the short reproductive phase has taken place just prior to $t = t^*$. At $t = t^*$ the population state is then given by $\lambda(t^*)$, specifying the number of individuals in each cohort. Implicitly, however, $\lambda(t^*)$ also contains all the information about the age of the individuals in each cohort. If Δ denotes the time interval between consecutive reproduction periods, the age of the individuals in the j-th cohort ($j=0,1,..,m$) at time $t=t^*$ equals $j\Delta$. We can make this more explicit by characterizing the population not only with the vector $\lambda(t)$, but also with a second vector:

$$\alpha(t) = \begin{bmatrix} \alpha_0(t) \\ \alpha_1(t) \\ \cdot \\ \cdot \\ \cdot \\ \alpha_{m-1}(t) \\ \alpha_m(t) \end{bmatrix}$$

where $\alpha_j(t)$ denotes the age of the individuals in the j-th cohort at time t. The introduction of $\alpha(t)$ is somewhat superfluous in a standard Leslie matrix model, but it facilitates a straightforward extension to situations that are not covered by the standard model. Note that the ages $\alpha_j(t)$ denote the age values, where the population age distribution is non-zero, i.e. denote the positions of the spikes.

Let τ denote the time elapsed since the last reproduction period at time t^*. During the inter-reproductive interval the individuals of the j-th cohort die at a rate that depends upon their age: $d(a)=d(\alpha_j(t^*+\tau))$. It is obvious that $\alpha_j(t^*+\tau)$ equals $j\Delta+\tau$. The process can be summarized by the following system of ODE's:

$$\begin{cases} \dfrac{d}{d\tau}\lambda_j = -d(\alpha_j)\lambda_j \\ \dfrac{d}{d\tau}\alpha_j = 1 \qquad j=0,\cdots,m \end{cases} \tag{3}$$

with initial conditions:

$$\begin{aligned} \lambda_j(\tau=0) &= \lambda_j(t^*) \\ \alpha_j(\tau=0) &= \alpha_j(t^*) = j\Delta \end{aligned} \tag{4}$$

We can solve this system of ODE's (3) for the number and age of the individuals in the j-th cohort still alive at the start of the next reproduction period at $t=t^*+\Delta^-$ (Here and in the following t^{*-} denotes the value of t just prior to t^*).

$$\begin{aligned} \lambda_j(t^*+\Delta^-) &= \exp\left\{-\int_0^\Delta d(\alpha_j)d\tau\right\}\lambda_j(t^*) = \exp\left\{-\int_0^\Delta d(j\Delta+\tau)d\tau\right\}\lambda_j(t^*) \\ \alpha_j(t^*+\Delta^-) &= \alpha_j(t^*)+\Delta = (j+1)\Delta \end{aligned} \tag{5}$$

At $t=t^*+\Delta^-$ these individuals produce a number of offspring dependent upon their age: $b(a)=b(\alpha_j(t^*+\Delta^-))$. Due to the pulsed, periodic birth process reproduction only takes place at certain specific ages of the individuals, i.e. $a=j\Delta$ ($j=0,....,m$). Therefore, the function $b(a)$ is only defined at these specific ages and represents the *number* of offspring produced (In mathematical language: the birth rate function consists of a collection of delta-functions). At the same time as reproduction takes place the individuals of all the age classes are shifted to the following age class, while the newborn individuals enter the 0-th age class:

$$\begin{cases} \lambda_0(t^*+\Delta) = \sum_{j=0}^{m} b(\alpha_j(t^*+\Delta^-))\lambda_j(t^*+\Delta^-) \\ \lambda_j(t^*+\Delta) = \lambda_{j-1}(t^*+\Delta^-) \\ \alpha_0(t^*+\Delta) = 0 \\ \alpha_j(t^*+\Delta) = \alpha_{j-1}(t^*+\Delta^-) = j\Delta \qquad j=1,....,m \end{cases} \tag{6}$$

The systems of equations (5) and (6) can be rewritten using equation (1) with:

$$P_j = \exp\left\{-\int_0^{\Delta} d(\alpha_j(t^*+\tau))d\tau\right\} = \exp\left\{-\int_0^{\Delta} d(j\Delta+\tau)d\tau\right\}$$

$$F_j = b(\alpha_j(t^*+\Delta^-))P_j = b((j+1)\Delta)P_j \tag{7}$$

It is now clear that the standard Leslie matrix model can also be expressed as the linear system of ODE's (3), describing the dynamics of the number and the age of the individuals in the various cohorts within an inter-reproductive interval, in combination with the reproduction process and renumbering operation specified by the system (6). The system of equations (7) shows the relation between the entries in the Leslie matrix A of equation (1) and the age dependent individual birth and death functions $b(a)$ and $d(a)$, respectively.

3. RELAXATION OF THE ASSUMPTIONS

3.1 Physiological state variables other than age.

As mentioned before, age is not always the most important trait in determining individual behaviour. For many invertebrate animals, for example, the size of an individual influences its rate of food intake, growth and reproduction to a much larger extent. To describe the dynamics of a population of such individuals, we have to generalize the standard Leslie matrix model to cover situations in which the vital rates, i.e. reproduction and death rate, depend upon an individual trait other than age. For convenience of formulation we will deal with the size of an individual as an example of a different physiological state variable, but for any other trait the following exposition will hold as well.

The generalization of the Leslie model formalism to size dependent vital rates is particularly straightforward, if we start from the system of ODE's (3) and the reproduction and renumbering expressions (6). Let s now denote size and $\sigma_j(t)$ the size of the individuals in the j-th cohort at time t. For a complete description we have to specify the size at birth of an individual, denoted by s_b, and the size dependent development rate, which will be denoted as $v(s)$. As in the previous section we focus upon one reproduction cycle (We also refer to that section for comparison and for the explanation of the various symbols). Within the inter-reproductive interval the individuals again die at a rate, that now depends upon their individual size: $d(s)=d(\sigma_j(t^*+\tau))$. The size of the individuals changes during this interval at a rate that depends upon size itself: $v(s)=v(\sigma_j(t^*+\tau))$. In formulae this is expressed as (compare the system of ODE's (3)):

$$\begin{cases} \dfrac{d}{d\tau}\lambda_j = -d(\sigma_j)\lambda_j \\ \dfrac{d}{d\tau}\sigma_j = v(\sigma_j) \qquad j=0,\ldots,m \end{cases} \tag{8}$$

with initial conditions:

$$\lambda_j(\tau=0) = \lambda_j(t^*)$$

$$\sigma_j(\tau=0) = \sigma_j(t^*)$$

Analytical integration of the system of equations (8) is only seldom possible. The solution of the ODE (8b) for σ_j, for instance, can only be found analytically with very special choices of $v(s)$. (An example of such a special choice is von Bertalanffy growth (VON BERTALANFFY, 1934)). Let us for a moment assume that such an analytical solution for σ_j does exist. Integration of (8a) from $t=t^*$ to $t=t^*+\Delta^-$ then leads to an expression equivalent with expression (5a) for the number of individuals in the j-th cohort still alive at the start of the next reproduction period:

$$\lambda_j(t^*+\Delta^-) = \exp\left\{-\int_0^{\Delta} d(\sigma_j)d\tau\right\}\lambda_j(t^*) \tag{9}$$

At $t=t^*+\Delta^-$ (now size dependent) reproduction and renumbering take place as before, leading to:

$$\begin{cases} \lambda_0(t^*+\Delta) &= \sum_{j=0}^{m} b(\sigma_j(t^*+\Delta^-))\lambda_j(t^*+\Delta^-) \\ \lambda_j(t^*+\Delta) &= \lambda_{j-1}(t^*+\Delta^-) \\ \sigma_0(t^*+\Delta) &= s_b \\ \sigma_j(t^*+\Delta) &= \sigma_{j-1}(t^*+\Delta^-) \qquad j=1,....,m \end{cases} \tag{10}$$

which are the analogues of the expressions (6). Formally these equations can then again be summarized by the Leslie matrix equation (1) with:

$$\begin{aligned} P_j &= \exp\left\{-\int_0^{\Delta} d(\sigma_j(t^*+\tau))d\tau\right\} \\ F_j &= b(\sigma_j(t^*+\Delta^-))P_j \end{aligned} \tag{11}$$

Apart from the solution of the ODE (8b) for σ_j, also the integral in expressions (9) and (11a) is often impossible to evaluate analytically. Therefore, to construct the Leslie matrix we usually have to turn to a numerical evaluation of these quantities. As an alternative solution method, however, it is computationally far more easy to integrate the system of ODE's (8) numerically from $t=t^*$ to $t=t^*+\Delta$ and subsequently apply the procedure described by (10). Many numerical integration methods to solve such systems of ordinary differential equations do exist, facilitating a straightforward application of this computational procedure. In the following subsections the same argument applies and we will therefore focus upon the extensions in the context of the system of ODE's (3) (or (8)) and the reproduction and renumbering expressions (6) (or (10)). We will leave out further expressions for the coefficients P_j and F_j that are formally possible, but computationally irrelevant.

Our way to extend the standard Leslie matrix model to size-structured populations differs in an important aspect from alternative methods. We continuously keep track of the position of a cohort of individuals within the size range that the individuals can attain. In the size based Leslie matrix models proposed by, for instance, USHER (1966) and GLASSER (1983) the attainable size range is subdivided a priori into fixed intervals of a certain width. Subsequently the transitions from one size class to another are described by means of transition probabilities. Essentially these size classes are equivalent to developmental stages. These size based models are hence identical to the developmental stage based model of LEFKOVITCH (1965). As one of the basic concepts we assumed that there was no stochastic variation among identical individuals in the development of the physiological state (= size). Our extension of the standard Leslie model to size-structured populations is consistent with this assumption (consistent in the sense as defined in section 2), in contrast with the models of USHER (1966) and GLASSER (1983). Of course, in certain biological situations the 'deterministic development' assumption is inappropriate and transition probability models may be preferable. These transition probability models (USHER, 1966; GLASSER, 1983), however, make no explicit assumptions concerning the development of a single individual (only implicitly by specifying the transition matrix). PLANT & WILSON (1986) have shown that in these models the variation in development between identical individuals depends upon the number of size classes that are distinguished. These models should hence be applied with care, since they can produce population dynamical phenomena that are not related to the behaviour of the individuals.

3.2 Time dependent vital rates.

Populations usually live in an environment that is far from constant in time. Two different types of environmental fluctuations can be distinguished. First, the environment may change in time due to some external factor. Obvious examples are seasonal climatic variation (temperature) and daily solar influx. This type of environmental fluctuation will be referred to as 'driven'. On the other hand, the population itself might induce environmental changes in time, leading to a feedback from the population to itself via the environment. An obvious example is the depletion of a natural resource. This situation will be referred to as 'interaction via the environment'.

Environmental fluctuations often bring about that the vital rates of an individual, i.e. the reproduction, death and development rate, fluctuate as well and hence are not constant in time. Let the state of the environment now be characterized by a set of variables:

$$E(t) = \begin{bmatrix} E_0(t) \\ E_1(t) \\ \cdot \\ \cdot \\ \cdot \\ E_{p-1}(t) \\ E_p(t) \end{bmatrix}$$

in which $E_i(t)$ denotes the state of the i-th environmental variable at time t. The number and nature of these variables is chosen in such a way that they constitute the minimal set of characteristics that describes the influence of the environment upon the individuals sufficiently well. The vital rates of an individual will now not only depend on its size s, but also on the environmental state $E(t)$. We will explicitly include these dependencies in our notation by using $b(E,s)$, $d(E,s)$ and $v(E,s)$ to refer to the individual reproduction, death and development rate, respectively.

In the case of a driven environment the state of the environment $E(t)$ is an explicit function of time and the vital rates $b(E,s)$, $d(E,s)$ and $v(E,s)$ are consequently explicit functions of time as well. It is easy to generalize the equations (8) and (10) from subsection 3.1 to cover this situation. Indeed we simply replace the time independent vital rates $b(s)$, $d(s)$ and $v(s)$ by their environment (and hence time) dependent counterparts $b(E,s)$, $d(E,s)$ and $v(E,s)$, respectively. This makes the direct evaluation of the entries in the Leslie matrix even more complicated if not impossible. Thus, the use of the alternative computational procedure, i.e. numerical integration of the system (8) and application of the reproduction and renumbering expressions (10) is strongly suggested (It should be noted that if the time dependence of the vital rates is periodic with a period equal to an integer fraction of Δ, this time dependence will not show up in the population state dynamics when evaluated at $t=t^*$, $t^*+\Delta$, $t^*+2\Delta$.... etc. only. In other words, in this situation we are still dealing with a time independent Leslie matrix model).

In the case of an interactive environment $E(t)$ itself will change with time due to some population influence. Clearly a feedback loop via the environment now exists, leading to non-linear population dynamics. The system of ODE's (8) must now be accompanied by an additional system, describing the dynamics of the environment:

$$\frac{d}{d\tau}E_j = f_j(E,\lambda,\sigma) \qquad j=0,....,p \tag{12}$$

The functions $f_j(E,\lambda,\sigma)$ must describe the internal dynamics of the j-th environmental variable as well as the population influence upon this environmental variable. For instance, in case the i-th environmental variable represents a food source, $f_i(E,\lambda,\sigma)$ should account for the growth rate of this food source itself and the feeding rate of the total population upon it. This system of ODE's (12) has to be integrated simultaneously with the system (8) from $t=t^*$ to $t^*+\Delta$. The dynamics of the population and its environment are now completely specified by the systems of equations (8), (10) and (12).

In the way described above we can straightforwardly and realistically incorporate environmental influences into the model. Obviously, a combination of a driven and interactive environment is also possible. In this case the state of the environment $E(t)$ is partly an explicit function of time and partly governed by a system of ODE's like (12). It should be noted that density dependent interactions within a population usually act via some environmental variable, e.g. food availability. These interactions hence constitute a feedback loop and can be incorporated immediately as described. If this is not the case and there is a *direct* density dependent effect of, for instance, the total population size upon the individual reproduction, death or development rate, we can add the total population size as one of the variables characterizing the environment. Any time we have to evaluate the right hand sides of the ODE's (8) the total population size is known and can hence be regarded as a 'driven' environmental variable. In this way VAN DEN BOSCH ET AL. (1988) investigate the effects of cannibalism in an age-structured population. More generally, a 'driven' environmental variable may be any function of the population state, characterized by $\lambda(t)$ and $\sigma(t)$, in addition to being a function of time itself.

3.3 Continuous reproduction.

The third assumption underlying the standard Leslie matrix model is definitely the most difficult to relax. As long as the reproduction process is pulsed in time the size distribution of the population consists of a set of spikes (delta-functions) at specific sizes, each spike representing a cohort of individuals. As we have seen, this type of spiked distribution is basic to the Leslie model formalism and even a prerequisite for the equations, presented in the previous subsections, to be a precise description of the population dynamics. Even a varying length of the inter-reproductive interval is covered by the formalism as long as the renumbering procedure is always applied at the same time as reproduction takes place. Continuous reproduction, however, leads to a continuous size distribution within the population. The population is then no longer naturally divided into distinct cohorts of individuals with identical size. At best we can use the Leslie model formalism as an approximation because the population dynamics is (more) properly described by a continuous time model.

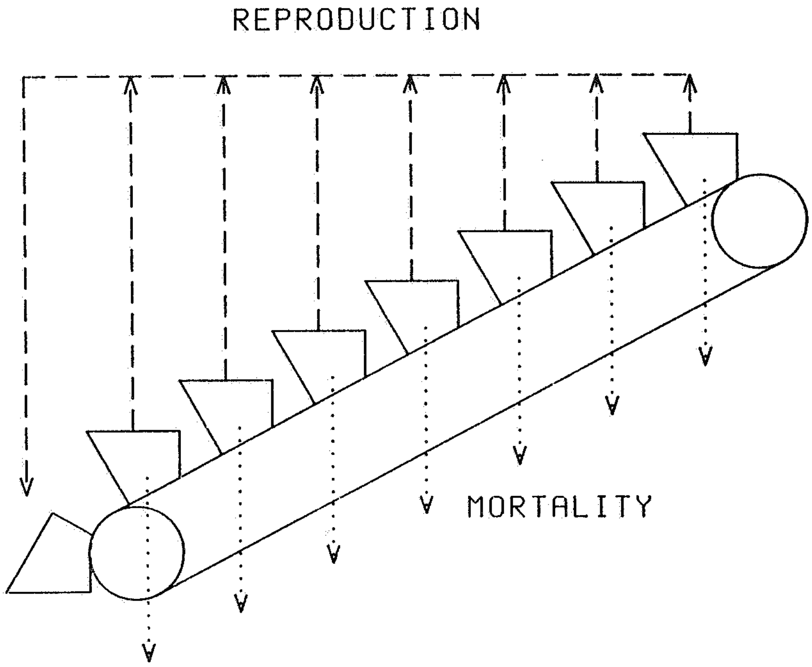

FIGURE 1. Visualization of the extended Leslie model formalism from subsection 3.3 as an elevating conveyor belt. The buckets on this belt represent the cohorts of individuals that are composed artificially. Individuals are lost from the cohorts due to mortality and all the newborn individuals are entering the cohort 'in creation' (the bucket coming up to the starting edge of the belt).

The main idea underlying the approximation is to replace the continuous population distribution by the spiked distribution type that is characteristic for the Leslie model formalism. (Obviously, we want to choose that member of the class of spiked distributions, which produces the best approximation to the continuous distribution). The evolution of this approximating distribution is subsequently described by means of a system of equations similar to (8) and (10). Since a natural subdivision of the population into cohorts no longer exists, we have to create them arbitrarily. Making more and hence smaller cohorts obviously improves the accuracy of the approximation, at the expense of more numerical labour.

At this point it should be stressed again that a central idea of the Leslie model formalism as described in the previous subsections is that cohorts of individuals are followed and stay together as an entity during their development through the size domain. This idea can best be visualized by an elevating conveyor belt as depicted in Figure 1. In the case of a pulsed reproduction process all the individuals in a bucket of this belt (=cohort) are piled up in one point, the (identical) size of the individuals within the cohort. In the case of a continuous reproduction process each bucket essentially transports a spread out heap of individuals. The approximation transforms the latter situation in the former one. As a consequence, a characteristic size value has to be selected within every cohort size range. This characteristic size value will indicate the support of the spike, which takes the place of the continuous distribution within the cohort. It is intuitively clear that this value should equal the *mean individual size* within a cohort. Therefore we introduce the column vector:

$$\mu(t) = \begin{bmatrix} \mu_0(t) \\ \mu_1(t) \\ \cdot \\ \cdot \\ \cdot \\ \mu_{m-1}(t) \\ \mu_m(t) \end{bmatrix}$$

where $\mu_j(t)$ denotes the *mean size* of the individuals in the j-th cohort (cf. $\alpha_j(t)$ and $\sigma_j(t)$). The approximation of the continuous size distribution now consists of the two vector quantities $\lambda(t)$ and $\mu(t)$, representing the total number of individuals and the mean individual size within each cohort, respectively.

Once the continuous distribution is approximated, the dynamics of the internal cohorts (i.e. all the cohorts except the one bordering the lower boundary of the size domain) are again described from $t=t^*$ to $t=t^*+\Delta$ by a system of ODE's comparable with system (8) from subsection 3.1:

$$\begin{cases} \dfrac{d}{d\tau}\lambda_j = -d(E,\mu_j)\lambda_j \\ \dfrac{d}{d\tau}\mu_j = v(E,\mu_j) \qquad j=1,....,m \end{cases} \tag{13}$$

The continuous reproduction process causes that at the instream point s_b of the size domain individuals continuously enter the first cohort (As the visualization in Figure 1 makes clear, the new bucket coming up to the start of the conveyor belt is filled continuously). In contrast, the discontinuous reproduction process from the previous subsections produced new cohorts of individuals instantaneously. In the case of a continuous reproduction process we have to describe the dynamics of this cohort 'in creation' in a continuous manner, i.e. by means of a system of ODE's. Moreover, after some period we have to stop adding to the particular cohort and start a new one, since this is not naturally imposed. For this purpose we will allow the entrance of newborn individuals into the cohort in creation for some time span Δ, whereafter the cohort is closed off and the formation of a new cohort is initiated. The time span Δ determines the size of the cohorts in the size domain and hence the accuracy of the approximation.

The ODE's describing the dynamics from $t=t^*$ to $t^*+\Delta$ of λ_0 and μ_0, the total number and mean size of the individuals in the cohort in creation therefore contain, apart from the usual death and development terms, also some terms due to the reproduction process. We will make the simplifying (but not necessary) assumption that the individuals of this cohort cannot reproduce themselves. As the other cohorts of individuals reproduce at a rate $b(E,\mu_j)\lambda_j$ the ODE describing the dynamics of λ_0 is easily derived as:

$$\frac{d}{d\tau}\lambda_0 = -d(E,\mu_0)\lambda_0+\sum_{j=1}^{m} b(E,\mu_j)\lambda_j$$

in which the first term is the usual mortality term and the last term describes the reproduction input to this cohort from all the cohorts present. (Note that the function $b(a)$ now represents the *rate* of reproduction, in contrast with the produced *number* of offspring from the previous subsections). The ODE for μ_0 can be derived by looking at the dynamics of the product quantity $\mu_0\lambda_0$, which can be interpreted as the total biomass of the youngest cohort. If *no* reproduction would take place, the cohort in creation would be equivalent to all the other cohorts. In that case the dynamics of λ_0 and μ_0 would be described by a system of ODE's equivalent with (13). Under this condition the ODE for the dynamics of $\mu_0\lambda_0$ would be:

$$\frac{d}{d\tau}\mu_0\lambda_0 = \lambda_0\frac{d}{d\tau}\mu_0+\mu_0\frac{d}{d\tau}\lambda_0 = v(E,\mu_0)\lambda_0-d(E,\mu_0)\mu_0\lambda_0$$

If reproduction occurs, the biomass of the youngest cohort additionally increases due to the inflow of newborn individuals. These individuals have identical size s_b at birth. The dynamics of $\mu_0\lambda_0$, including the reproduction terms, is then described by:

$$\frac{d}{d\tau}\mu_0\lambda_0 = \lambda_0\frac{d}{d\tau}\mu_0+\mu_0\frac{d}{d\tau}\lambda_0 = v(E,\mu_0)\lambda_0-d(E,\mu_0)\mu_0\lambda_0+\sum_{j=1}^{m} s_b b(E,\mu_j)\lambda_j$$

Note that the term due to reproduction equals the size at birth times the total reproduction input. We can now combine the equations for $d\lambda_0/d\tau$ and $d\mu_0\lambda_0/d\tau$ to arrive at the following system of ODE's:

$$\begin{cases} \dfrac{d}{d\tau}\lambda_0 = -d(E,\mu_0)\lambda_0+\displaystyle\sum_{j=1}^{m} b(E,\mu_j)\lambda_j \\ \dfrac{d}{d\tau}\mu_0 = v(E,\mu_0)+\dfrac{(s_b-\mu_0)}{\lambda_0}\displaystyle\sum_{j=1}^{m} b(E,\mu_j)\lambda_j \end{cases} \tag{14}$$

The occurrence of λ_0 in the denominator of the last ODE (14b) of this system causes some difficulties with the evaluation of $d\mu_0/d\tau$ at $\tau=0$. The values for μ_0 and $d\mu_0/d\tau$ can in principle be obtained by carefully taking the limit for $\tau\to 0$ in the system of ODE's (14). For computational purposes it is much more convenient, however, to replace the ODE for μ_0 with an approximately equivalent ODE for the quantity $\pi_0:=(\mu_0-s_b)\lambda_0$. This latter quantity characterizes the biomass of the first cohort relative to the size at birth s_b. Consequently the inflow of newborn individuals does not influence the dynamics of π_0. Since we replace the ODE for μ_0 by an ODE for π_0, the functions $d(E,s)$ and $v(E,s)$ cannot be evaluated at μ_0 anymore. We therefore approximate $d(E,\mu_0)$ and $v(E,\mu_0)$ by their first order Taylor expansion around s_b:

$$d(E,\mu_0) \simeq d(E,s_b)+(\mu_0-s_b)\frac{\partial}{\partial s}d(E,s_b)$$

$$v(E,\mu_0) \simeq v(E,s_b)+(\mu_0-s_b)\frac{\partial}{\partial s}v(E,s_b)$$

We also assume that higher order terms (i.e. all terms containing quadratic, cubic,.... expressions in π_0) in the resulting equations are negligible. The system of ODE's (14) is then replaced by the approximately equivalent system of ODE's for λ_0 and π_0:

$$\begin{cases} \dfrac{d}{d\tau}\lambda_0 = -d(E,s_b)\lambda_0 - \dfrac{\partial}{\partial s}d(E,s_b)\pi_0 + \sum_{j=1}^{m} b(E,\mu_j)\lambda_j \\ \dfrac{d}{d\tau}\pi_0 = v(E,s_b)\lambda_0 + \dfrac{\partial}{\partial s}v(E,s_b)\pi_0 - d(E,s_b)\pi_0 \end{cases} \tag{15}$$

The systems of ODE's (13) and (15) describe the dynamics of the internal cohorts and the cohort in creation, respectively, from $t=t^*$ to $t=t^*+\Delta$. At $t=t^*+\Delta$ the formation of the then youngest cohort is finished and the formation of a new cohort is initiated. At the same time renumbering of all the cohorts takes place to preserve their order. This leads to the following expressions that are the analogues of the system (10) (Note the differing expression for μ_1, due to the use of π_0):

$$\begin{cases} \lambda_0(t^*+\Delta) = 0 \\ \lambda_1(t^*+\Delta) = \lambda_0(t^*+\Delta^-) \\ \lambda_j(t^*+\Delta) = \lambda_{j-1}(t^*+\Delta^-) & j=2,....,m \\ \pi_0(t^*+\Delta) = 0 \\ \mu_1(t^*+\Delta) = s_b + \dfrac{\pi_0(t^*+\Delta^-)}{\lambda_0(t^*+\Delta^-)} \\ \mu_j(t^*+\Delta) = \mu_{j-1}(t^*+\Delta^-) & j=2,....,m \end{cases} \tag{16}$$

The systems of ODE's (13), (15) and the expressions (16), possibly accompanied by a system of ODE's like (12) to describe the environmental dynamics, constitute together an extension of the Leslie matrix formalism to cover situations in which all the assumptions of the standard model given in section 2 are relaxed.

4. THE LESLIE MODEL FORMALISM VERSUS CONTINUOUS TIME MODELS

Summarizing we can distinguish the following basic properties of the model formalism as discussed in the previous sections: the population dynamical behaviour of an individual is at any one time completely determined by its physiological state (size was used as an example in the discussion above), together with the state of the environment. The physiological state can assume values in some (one-dimensional) continuous domain, the physiological state-space (cf. size domain). Newborn individuals always enter this state-space at a fixed physiological state (cf. s_b). Finally, the population consists of a collection of cohorts of identical individuals.

Together these properties induce that the population distribution over the physiological state-space consists of a collection of delta-functions (spikes), each delta-function representing a cohort of individuals. The position of each delta-function represents the (mean) physiological state of the individuals within the cohort. A cohort of individuals is treated as an entity and hence stays together during the course of its existence. In (one of) the simplest situations the formalism reduces to a standard Leslie model, which can be expressed in matrix notation by equation (1). More generally, the model formalism can be expressed by the systems of equations (13), (15) and (16).

In case the reproduction process is continuous in time, however, the dynamics of the population is more consistently described by a continuous time model. METZ & DIEKMANN (1986, p.92-96) present a hyperbolic partial differential equation (PDE) for a general continuous time model. If the physiological state-space is one-dimensional this reduces to:

$$\begin{cases} \dfrac{\partial n(t,x)}{\partial t} + \dfrac{\partial v(E,x)n(t,x)}{\partial x} = -d(E,x)n(t,x) \\ v(E,x_b)n(t,x_b) = \int\limits_{x_b}^{\infty} b(E,x)n(t,x)dx \\ n(0,x) = \Psi(x) \end{cases} \tag{17}$$

where:

x	denotes the physiological state variable
$n(t,x)$	is the density function (distribution) over the physiological state-space, i.e. $n(t,x)dx$ equals the number of individuals with a physiological state in the range $x \rightarrow x+dx$
$v(E,x)$	is the individual development rate
$d(E,x)$	is the individual death rate
$b(E,x)$	is the individual reproduction rate
$\Psi(x)$	is the size distribution of the population at $t=0$

and all the individuals are born with state x_b. Moreover, the development rate $v(E,x)$ is such that it is not possible to reach physiological states less than x_b. If the environment is not constant in time or non-linear interactions exist within the population, this system of equations (17) is accompanied by a system of ODE's analogous to (12) describing the dynamics of the environment. The latter system may contain some weighted integrals of $n(t,x)$ accounting for the influence of the population upon its environment.

On the basis of purely numerical mathematical arguments de Roos (1988) developed a numerical integration method especially suited for the type of PDE exemplified by (17). This method is called the *Escalator boxcar train* following a publication of Goudriaan (1986) which contains some of the underlying ideas. The method is developed for the general case of a physiologically structured population model as presented by Metz & Diekmann (1986). This implies that the *Escalator boxcar train* is applicable to models with an arbitrary dimension of the physiological state and poses no restrictions at all upon the reproduction process, i.e. individuals may produce offspring with a state at birth that depends upon the physiological state of the parent, but individuals may also produce offspring with some specified distribution of the state at birth.

As a special characteristic, the *Escalator boxcar train* does not approximate the density function $n(t,x)$ itself at a set of points within its domain, as is usual with numerical integration methods for PDE's. Instead it approximates certain local moments of the distribution $n(t,x)$ over small non-overlapping subdomains, that together make up the relevant physiological state-space. Moreover, this subdivision of the state-space is dynamic itself. The subdomains move through the state-space in such a way that all the individuals with a physiological state within a certain subdomain remain in that subdomain during the numerical integration. The moments of the distribution within the subdomains are readily interpreted in biological terms as numbers of individuals, mean individual state, variance around the mean individual state, etc. The approximation by means of moments also implies, that the method does not make any assumption about the continuity of the density function $n(t,x)$ itself, but makes essential assumptions about the continuity of the functions $v(E,x)$, $d(E,x)$ and $b(E,x)$. Thus the integration method is readily applicable even if the density function $n(t,x)$ consists of a set of delta-functions (which is the case when the reproduction is synchronized completely at certain time points). Another advantage of the method is the relative ease with which any order of accuracy is attained by simply including more moments of the distribution $n(t,x)$. The second order Escalator boxcar train only includes two local moments of $n(t,x)$, the total number and mean physiological state of the individuals in a subdomain, while the third order method also includes the variance around this mean state. A comparable method to reformulate the PDE that represents a continuous time model into a system of ODE's was proposed by Streifer & Istock (1973). Apart from a not completely consistent third order approximation the main difference between their method and the *Escalator boxcar train* is the subdivision of the physiological state-space into non-overlapping subdomains. The method of STREIFER & ISTOCK (1973) only approximates the dynamics of the number of individuals, the mean physiological state and the variances around this mean state of the total population.

More important from the biological point of view, however, is that the second order *Escalator boxcar train* in its simplest form, i.e. for models with a one-dimensional physiological state that are represented by the system of equations (17), is identical with the extension of the Leslie model formalism of subsection 3.3. Thus the systems of ODE's (13), (15) and possibly (12) together with the renumbering procedure specified by the expressions (16) not only denote a model formalism derived from the standard Leslie matrix model, but also a numerical integration technique for the type of hyperbolic PDE occurring in a continuous time model. Obviously, the basic properties of the Leslie model formalism and the *Escalator boxcar train* are identical (compare the moving subdomains within the state-space with cohorts of individuals). The *Escalator boxcar train* can likewise be visualized as the elevating conveyor belt from Figure 1 (hence its name).

Together the Leslie matrix formalism and the *Escalator boxcar train* cover and link a score of (superficially unrelated) models for the dynamics of physiologically structured populations, which differ in the nature of the physiological state and the characteristics of the birth, death and development processes. The relationship between the Leslie model formalism and the *Escalator boxcar train* implies that the numerical method has a direct biological interpretation. Conversely the *Escalator boxcar train* indicates a way to extend the Leslie model formalism to more complex situations, in which for instance the individual behaviour is determined by more than one physiological trait (i.e. the physiological state assumes values in a higher dimensional state-space). Such a situation will be exemplified in the following sections, in which we will study a structured population model for the dynamics of a *Daphnia* population feeding on a self renewing algal food source. In this model the individual behaviour will be determined by the age and the size of the individuals. More complicated reproduction processes than 'all individuals are born with an equal physiological state' can also be incorporated into the formalism. If we interpret μ_j and $\nu(E,\mu_j)$ as vector quantities, the equations (13) and (16), that deal with the internal cohort dynamics, immediately generalize to these more complex situations. The equations describing the dynamics of the cohort(s) in creation are always comparable with the equations (15). Slight technical differences may, however, arise from a complicated reproduction process. For a complete discussion we refer to DE ROOS (1988).

5. POPULATION DYNAMICAL EFFECTS OF SIZE DIFFERENCES IN DAPHNIA

A large number of experimental and theoretical studies has focussed upon the dynamics of *Daphnia* species in both field and laboratory populations. MCCAULEY & MURDOCH (1987, see also MURDOCH & MCCAULEY, 1985) have compiled and analyzed the data of more than 20 of these studies of *Daphnia* field populations in addition to the data of 8 laboratory populations. They distinguish three patterns of dynamics exhibited by interacting field populations of *Daphnia* and algae, following the typical algal bloom in spring:

I. Both the *Daphnia* and the algal population appear stable (A population is assumed to be stable if the standard deviation of the logarithm of the density is less than 0.08)
II. *Daphnia* and algal populations display joint cycles.
III. The *Daphnia* population exhibits cyclic behaviour,the algal population appears stable.

The data suggested that all types of dynamics can arise in the same structural system, probably by means of quantitative changes in parameters. Moreover, on the basis of the similarity between the dynamics of laboratory and field populations of *Daphnia* MCCAULEY & MURDOCH (1987) conjecture that all three types of dynamics arise from the interaction between *Daphnia* and algae and in particular that the cycles are internally driven.

The cyclic fluctuations displayed by the *Daphnia* populations have a dominant period close to the generation time of *Daphnia* (25-45 days). According to McCauley & Murdoch (1987) a cycle is initiated by a burst of reproduction at low population densities, giving rise to a population peak that mainly consists of juveniles. Food availability subsequently decreases, leading to a suppression of reproduction and a slowing down of juvenile growth. After a long period of declining densities a small number of mostly adult individuals survive to initiate the next cycle (McCauley & Murdoch, 1987). The severe changes in demography of the *Daphnia* population during one cycle demonstrate the major influence of the individual age/size differences on the overall population dynamics.

The outlined picture of the population dynamics of *Daphnia* raises several questions: is it possible that all three types of dynamics can occur in the same structural system by mere quantitative changes in the parameters? If so, what causes the system to change from one type of dynamics to the other? These questions we studied in more detail using an (age,size)-structured population model of a *Daphnia* population in interaction with its algal food source. The complete, more mathematically oriented analysis of the model (equilibria, stability analysis, etc.) will be published elsewhere (de Roos et al., in prep.). In this paper we illustrate the application of the *Escalator boxcar train* method to this model and present some interesting conclusions that were specifically obtained using the numerical method.

5.1. Models of the individual behaviour of Daphnia.

The construction of any physiologically structured population model starts with the modelling of the individual behaviour. Several alternative models exist for the allocation of ingested energy to growth and reproduction in individual *Daphnia* (Sinko & Streifer, 1969; Paloheimo et al., 1982; Kooijman, 1986a; Lynch, 1988; Gurney et al., 1988). These models clearly differ in the significance they attach to empirical observations versus a priori considerations. The models introduced by Sinko & Streifer (1969), Paloheimo et al.(1982) and Lynch (1988) are essentially collections of empirical functions, that mimic the experimental observations on growth and reproduction for individuals of different sizes and ages at different food levels. The models described by Kooijman (1986a) and Gurney et al. (1988) are to a larger extent derived from a priori assumptions concerning the energy flows and transformations within an individual *Daphnia* and are hence of a more mechanistic nature. The Kooijman model is the most strongly based upon these a priori assumptions. This model is especially suited to gain insights of a more general nature, possibly in expense of the exact mimicing of empirical observations on *Daphnia.* It has, for instance, been used to study the relation between body size and various physiological variables (Kooijman, 1986b,c) in a wide range of animal species.

For our investigations we used a simplified version of the Kooijman model which was introduced by Kooijman & Metz (1984). Our choice is mainly motivated by the simplicity and the mechanistic nature of the model, which allows an easy interpretation of population dynamical phenomena in terms of individual characteristics. Although various details of the model deserve a fair amount of (biological) criticism, we believe that the model captures the main features of the energy channelling in an individual *Daphnia.* Future investigations should reveal how modifications of these model aspects influence the results of the original model that are already valuable in itself.

In the Kooijman-Metz model individual *Daphnia* are characterized by their length l and their age a. The model describes the growth and reproduction of an individual *Daphnia* as a function of food availability. In accordance with our goal to study the interaction between a *Daphnia* population and its algal food source, the environment is hence completely characterized by only one variable: the prevailing food density or concentration of edible algae, denoted by x. Derivations of the model equations from a priori assumptions on the energy channelling to maintenance, growth and reproduction can be found in Kooijman & Metz (1984) and Metz et al. (1988) and we refer to these places for an in depth explication of the model. Here we will only present a general description.

Individual animals of different sizes are assumed to have the same allometric relations, so that surface area and (wet) weight are proportional to l^2 and l^3, respectively. The length of an individual is therefore a convenient measure of its size. Food intake is assumed to be proportional to surface area, which is plausible for a filter-feeder like *Daphnia.* In addition, the food intake at any given size of an individual depends on the prevailing food availability following a Holling type II functional response.

Under conditions of abundant food the ingested energy is allocated in fixed proportions to maturation and reproduction on the one hand and to maintenance and growth on the other. Reproduction is therefore proportional to food intake (and hence to surface area). The energy requirements for maintenance take precedence over energy allocation to growth and are assumed proportional to the weight of an individual. The energy cost per unit weight increase is assumed constant as is the energy cost of producing a neonate. Individuals are born with a fixed length, while maturation stops and reproduction starts after reaching a fixed juvenile length.

At low food densities this energy channelling picture is changed a bit. If the default energy allotment to maintenance and growth is not enough to cover maintenance requirements alone, ingested energy is allocated in such a way that growths stops, maintenance requirements are just met and the remaining energy is put into reproduction. An individual that cannot meet its maintenance requirements from the energy it ingests dies instantaneously. Additional death causes are random deaths due to, for example, predation and death from old age, i.e. by reaching a maximum lifespan.

This description can be represented by the following equations for the individual behaviour (KOOIJMAN & METZ, 1984; METZ ET AL., 1988). The feeding rate of an individual *Daphnia* upon the algal food population is:

$$I(x,l) = v_x f(x) l^2 \tag{18}$$

where v_x is the maximum ingestion rate per unit surface area and $f(x)=\xi x/(1+\xi x)$ describes the dependency of the food intake rate upon the food availability. This function is equivalent with a Holling type II functional response, scaled between 0 and 1. The parameter ξ is the shape parameter of this functional response (i.e. $1/\xi$ is the food density at which the intake rate at a certain length is half the maximum rate). Table I contains a complete reference list of the symbols used to designate the various variables and parameters, together with their default values.

Growth in weight is following a slightly adapted von Bertalanffy growth equation (see e.g. BEVERTON & HOLT, 1957). Using the assumption that surface area and weight are proportional to l^2 and l^3, respectively, the equation can be reformulated into an equivalent equation describing the growth in length (see METZ & DIEKMANN (1986), pg. 21-22, for the derivation):

$$\begin{aligned} \frac{dl}{dt} &= g(x,l) = \gamma(l_m f(x) - l) && \text{for } l<l_m f(x) \\ &= 0 && \text{otherwise} \end{aligned} \tag{19}$$

In this equation l_m and $l_m f(x)$ are the maximum lengths that an individual can attain under conditions of infinite food availability and under the prevailing food conditions, respectively. The parameter γ designates the rate constant of growth.

The birth rate $b(x,l)$ is given by:

$$\begin{aligned} b(x,l) &= 0 && \text{for } l_b<l<l_j \\ &= r_m f(x) l^2 && \text{for } l_j<l<l_m f(x) \\ &= \frac{r_m}{(1-\kappa)}(f(x)l^2 - \frac{\kappa l^3}{l_m}) && \text{otherwise} \end{aligned} \tag{20}$$

The parameters l_b and l_j represent the length at birth and the juvenile length, respectively, r_m is the maximum reproduction rate per unit surface area (recall the proportionality of the reproduction rate with the food intake and hence the surface area) and κ is the default fraction of ingested energy allocated to growth and maintenance. When $l=l_m f(x)$ the default energy allocation to growth and maintenance just suffices to cover maintenance requirements alone. Hence, when $l>l_m f(x)$ growth stops (eq. 19b) and energy is redirected from the default reproduction allotment to cover maintenance completely (eq. 20c).

Symbol	Default value	Description	Units
Variables:			
a		age	$d(ays)$
l		length	mm
x		concentration of edible algae	cell.ml^{-1}
Parameters:			
l_b	0.8	length at birth	mm
l_j	2.5	length at maturation	mm
l_m	6.0	maximum attainable length under infinite food availability	mm
γ	0.15	time constant of growth	d^{-1}
ξ	7.0E-6	shape parameter of the functional response.	$ml.$cell^{-1}
ν_x	1.8E6	maximum feeding rate per unit surface area	cell.$mm^{-2}.d^{-1}$
κ	0.3	default fraction of ingested energy channelled to growth and maintenance	-
r_m	0.1	maximum reproduction rate per unit surface area	$mm^{-2}.d^{-1}$
δ		random death rate of *Daphnia*	d^{-1}
$a_{\max}$	70	maximum lifespan of *Daphnia*	d
α	0.5	maximum algal growth rate	d^{-1}
C		carrying capacity of the algae	cell.ml^{-1}

TABLE I. Symbol reference list for the variables and parameters used in the Kooijman-Metz model. The default parameter values are extracted from Kooijman & Metz (1984) and Kooijman (1986a). The parameters δ and C are variable.

The death rate of the individuals equals:

$$d(x,a,l) = \delta \qquad \text{for } a<a_{\max},\ l<\frac{l_m f(x)}{\kappa}$$
$$= \infty \qquad \text{otherwise} \tag{21}$$

in which δ is the random death rate and $a_{\max}$ is the maximum attainable lifespan. When $l>l_m f(x)/\kappa$ an individual cannot cover its maintenance requirements anymore from the energy ingested and instant death occurs.

The last equation concerns the dynamics of the algal food population. We have described the autonomous dynamics of the algal population by means of the (unstructured) logistic growth equation:

$$R(x) = \alpha x(1-x/C) \tag{22}$$

in which α is the maximum growth rate and C is the carrying capacity.

5.2. Applying the Escalator boxcar train.

The previous section contained all the ingredients for a continuous time model of the dynamics of an (age,size)-structured *Daphnia* population feeding on a dynamical algal food source. The complete set of equations that describe the individual behaviour as well as the overall population dynamics (PDE, boundary condition, etc.) are given in the appendix. Here we will only show how to construct from the modelled individual behaviour the systems of ODEs that are used to study numerically the dynamics of the population. We thus circumvent as many mathematical intricacies as possible.

The *Escalator boxcar train* method was introduced in subsection 3.3 for the situation in which only one physiological characteristic of the individual, its size, determined the population dynamical behaviour and all individuals were born with equal size at birth. The extension to take into account more physiological variables is, however, straightforward if we interpret the variables μ_i and π_0 and the function v in the equation (13), (15) and (16) as vector quantities. In the context of the present model let $\lambda_j(t)$ again denote the number of individuals in the j-th cohort. The quantity μ_j is now assumed to be a vector with two elements $\mu_j^a(t)$ and $\mu_j^l(t)$ that represent the mean age and mean length, respectively, of the individuals in the j-th cohort. In the same way the development rate v is a vector with two elements $v^a(x,a,l)$ and $v^l(x,a,l)$ that describe the development rate in age and length, respectively. Obviously $v^a(x,a,l)$ equals the constant value 1, while in the present model $v^l(x,a,l)$ equals the individual growth rate $g(x,l)$ from equation (19). The ODE for μ_j (eq. 13b) is thus replaced by two ODEs for μ_j^a and μ_j^l. We arrive at the following system of ODEs for the dynamics of an internal cohort (refer to Figure 1: all the cohorts except the one entered by newborns):

$$\begin{cases} \dfrac{d}{d\tau}\lambda_j & = & -d(x,\mu_j^a,\mu_j^l)\lambda_j \\ \dfrac{d}{d\tau}\mu_j^a & = & v^a(x,\mu_j^a,\mu_j^l) = 1 \\ \dfrac{d}{d\tau}\mu_j^l & = & v^l(x,\mu_j^a,\mu_j^l) = g(x,\mu_j^l) \qquad\qquad j=1,\dots,m \end{cases} \tag{23}$$

in which $d(x,a,l)$ is the individual death rate from equation (21). The system of equations (23) is clearly analogous with (13).

The equations describing the dynamics of the cohort in creation (see Figure 1: the cohort entered by newborns) are somewhat more complicated because of the partial derivatives appearing in (15). As in subsection 3.3 we characterize the cohort in creation with the quantity λ_0 that denotes the number of individuals in the cohort and with π_0 which now is a vector quantity with elements indicated by $\pi_0^a(t)$ and $\pi_0^l(t)$. Corresponding to the interpretation of π_0 in subsection 3.3 the element π_0^a can be interpreted as the product $\mu_0^a\lambda_0$, the 'age mass' of the first cohort (relative to the age at birth: 0), and the quantity π_0^l as $(\mu_0^l-l_b)\lambda_0$, the 'length mass' of the first cohort with respect to the length at birth. The dynamics of λ_0, π_0^a, π_0^l are now described by the following system of ODEs:

$$\begin{cases} \dfrac{d}{d\tau}\lambda_0 & = & -d(x,0,l_b)\lambda_0 - \dfrac{\partial d}{\partial a}(x,0,l_b)\pi_0^a - \dfrac{\partial d}{\partial l}(x,0,l_b)\pi_0^l + \sum\limits_{j=1}^{m} b(x,\mu_j^l)\lambda_j \\ & = & -\delta\lambda_0 + \sum\limits_{j=1}^{m} b(x,\mu_j^l)\lambda_j \\ \dfrac{d}{d\tau}\pi_0^a & = & v^a(x,0,l_b)\lambda_0 + \dfrac{\partial v^a}{\partial a}(x,0,l_b)\pi_0^a + \dfrac{\partial v^a}{\partial l}(x,0,l_b)\pi_0^l - d(x,0,l_b)\pi_0^a \\ & = & \lambda_0 - \delta\pi_0^a \\ \dfrac{d}{d\tau}\pi_0^l & = & v^l(x,0,l_b)\lambda_0 + \dfrac{\partial v^l}{\partial a}(x,0,l_b)\pi_0^a + \dfrac{\partial v^l}{\partial l}(x,0,l_b)\pi_0^l - d(x,0,l_b)\pi_0^l \\ & = & g(x,l_b)\lambda_0 + \dfrac{\partial}{\partial l}g(x,l_b)\pi_0^l - \delta\pi_0^l \end{cases} \tag{24}$$

in which $g(x,l)$ and $d(x,a,l)$ are again given by equation (19) and (21) and $b(x,l)$ is the birth rate function from equation (20). We furthermore assumed that for the individuals in this cohort $d(x,a,l)=\delta$, i.e. that the newborn individuals can always meet their maintenance requirements and instant death does not occur (see eq. 21). This system of ODEs (24) can be derived from equation (15) by carefully interpreting the quantities v and π_0 as vector quantities, not only in (15) but also in the Taylor expansion of the functions d and v preceding it (see subsection 3.3). The systems of ODEs (23) and (24) describe the dynamics of the cohorts during the time interval Δ that intervenes the moments of closing the present cohort in creation and starting a new one. Hence, at the end of this time interval the following renumbering operation is carried out, which is completely equivalent with (16):

$$\begin{cases} \lambda_0(t^*+\Delta) & = 0 \\ \lambda_1(t^*+\Delta) & = \lambda_0(t^*+\Delta^-) \\ \lambda_j(t^*+\Delta) & = \lambda_{j-1}(t^*+\Delta^-) \qquad j=2,\ldots.,m \\ \pi_0^a(t^*+\Delta) & = 0 \\ \mu_1^a(t^*+\Delta) & = \dfrac{\pi_0^a(t^*+\Delta^-)}{\lambda_0(t^*+\Delta^-)} \\ \mu_j^a(t^*+\Delta) & = \mu_{j-1}^a(t^*+\Delta^-) \qquad j=2,\ldots.,m \\ \pi_0^l(t^*+\Delta) & = 0 \\ \mu_1^l(t^*+\Delta) & = l_b+\dfrac{\pi_0^l(t^*+\Delta^-)}{\lambda_0(t^*+\Delta^-)} \\ \mu_j^l(t^*+\Delta) & = \mu_{j-1}^l(t^*+\Delta^-) \qquad j=2,\ldots.,m \end{cases} \tag{25}$$

Finally we have to specify the ODE that describes the dynamics of the only environment variable in the present model, i.e. the concentration of edible algae. These dynamics are determined by algal growth and *Daphnia* grazing:

$$\frac{dx}{dt} = R(x)-I_{tot}(x) \tag{26a}$$

in which $R(x)$ describes the internal dynamics of the algal population as given by (22) and $I_{tot}(x)$ represents the grazing rate of the total *Daphnia* population upon the algal food source. This grazing rate can be calculated from the various cohort variables in the following way:

$$I_{tot}(x) = \sum_{j=1}^{m} I(x,\mu_j^l)\lambda_j = \sum_{j=1}^{m} \nu_x f(x)(\mu_j^l)^2\lambda_j \quad \text{if} \quad \lambda_0 = 0$$

and (26b)

$$I_{tot}(x) = \sum_{j=1}^{m} I(x,\mu_j^l)\lambda_j + I(x,l_b+\frac{\pi_0}{\lambda_0})\lambda_0 = \sum_{j=1}^{m} \nu_x f(x)(\mu_j^l)^2\lambda_j + \nu_x f(x)(l_b+\frac{\pi_0}{\lambda_0})^2\lambda_0 \quad \text{if} \quad \lambda_0>0$$

Note that the grazing rate of the individuals in the cohort in creation is determined by first applying a transformation (equivalent to (25)) to obtain the mean length of the individuals already present in this cohort and then using this mean length to calculate the feeding rate of the cohort. This method to determine the grazing rate ensures that the system of equations (23)-(26) is a numerically consistent approximation to the continuous time structured population model specified in the appendix (DE ROOS, 1988).

5.3. Some population consequences of the Kooijman-Metz model

We used the systems of ODEs and renumbering equations (23)-(26) to study numerically the dynamics of the (age,size)-structured model of a *Daphnia* population in interaction with the algal food population. The parameter values used for the numerical study are derived from KOOIJMAN & METZ (1984) and KOOIJMAN (1986a). They refer to a population of *Daphnia magna* Strauss feeding on *Chlorella* sp. (cell weight 1.4 10^{-5} μg; KOOIJMAN, pers. comm.). Kooijman & Metz estimated the values of the feeding parameters v_x and ξ using data of MCMAHON & RIGLER (1963). WATTS & YOUNG (1980) have noted that the feeding rates found by McMahon & Rigler are relatively high, probably due to the fact that starved *Daphnia magna* were used for the experiments. Using the equations (25) and (26) it can be shown, however, that only the product of these parameters influences the dynamics of the model. This product $v_x\xi$ can be interpreted as the maximum filtering rate per unit surface area per day. With our choice of v_x and ξ the product amounts to 12.6 $ml.mm^{-2}.\text{day}^{-1}$, which agrees fairly well with other estimates found in the literature (PORTER ET AL., 1982: 13.5 $ml.mm^{-2}.\text{day}^{-1}$). The value of ξ only determines the absolute level of the algal population density. Essentially all the algal densities should be viewed relative to $1/\xi$, the food density at which the individual intake rate is half the maximum rate. The ODEs were integrated in time using a 2-nd order Runge-Kutta integration method with automatic step size correction (see, for instance, PRESS ET AL., 1986). The renumbering equations (26) were applied at time intervals of length $\Delta=0.25$ day.

The numerical results show that the model exhibits three different types of dynamics. The *Daphnia* and algal population either both approach a stable equilibrium state or display joint cycles. We can, however, distinguish two basic types of oscillatory behaviour with a range of intermediate patterns. The type of dynamics that occurs at high values of the carrying capacity of the algal population and high values of the *Daphnia* death rate is exemplified in Figure 2. Characteristic properties of this type of dynamics are the larger cycle amplitude exhibited by the algae in respect to the amplitude of the *Daphnia* cycles and the phase lag between *Daphnia* and algae of approximately 1/4 period (*Daphnia* is lagging behind). This type of oscillations resembles the predator-prey cycles exhibited by the classic Lotka-Volterra models. The complete analysis of the model (DE ROOS ET AL., in prep.) shows that these oscillations are induced by a mechanism that is also the basis of the well-known 'paradox of enrichment': even if both populations should start out in an equilibrium situation, a slight deviation in the algal population would force the system into the oscillatory behaviour. Initially the reaction of the *Daphnia* population on such a disturbance is too slow and hence the algal population can escape the control imposed by the *Daphnia*. Subsequently the *Daphnia* overcompensate this lagging behind and oscillations result.

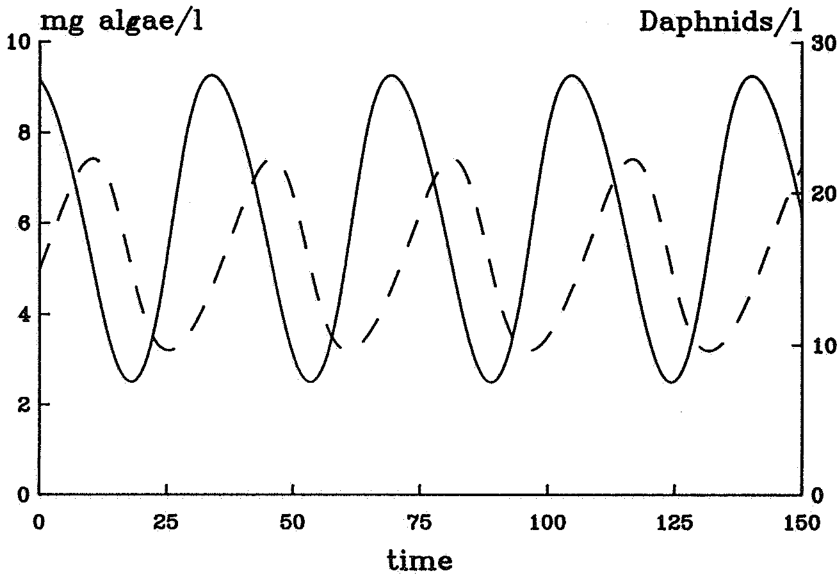

FIGURE 2. Dynamical behaviour of the algal (———) and *Daphnia* (– – – – –) population at a high carrying capacity of the algae ($C=1.0E6$) and a high death rate of the *Daphnia* ($\delta=0.25$). The other parameters have their default values ($\Delta=0.25$).

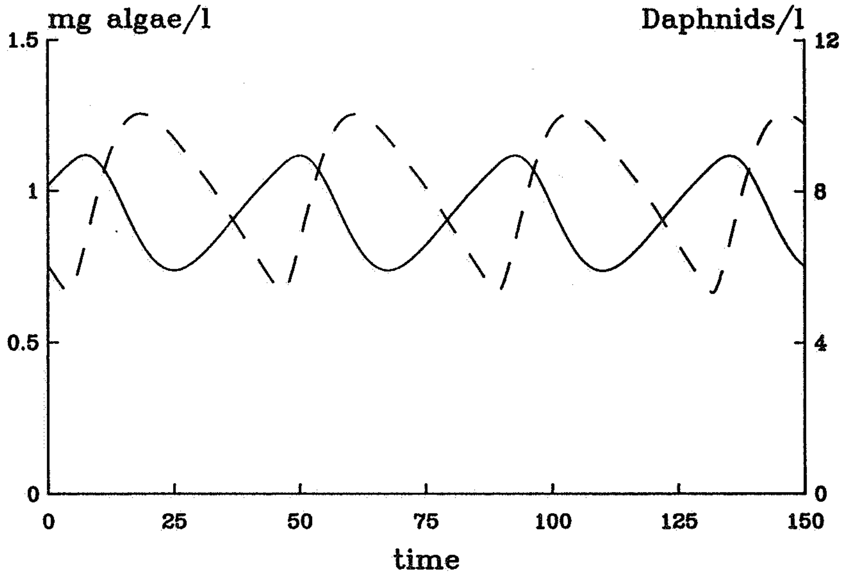

FIGURE 3. Dynamical behaviour of the algal (———) and *Daphnia* (– – – – –) population at a low carrying capacity of the algae ($C=2.0E5$) and a low death rate of the *Daphnia* ($\delta=0.05$). The other parameters have their default values ($\Delta=0.25$).

The second type of oscillatory behaviour occurs at low carrying capacities of the algal population and low death rates of the *Daphnia.* Figure 3 gives an example. Characteristic for this type of oscillations is the larger amplitude of the *Daphnia* in comparison with the algal population and a phase lag between *Daphnia* and algae of 1/2 period. It turns out that these oscillations are completely due to the delay introduced by the juvenile period. This time delay forces the *Daphnia* population to oscillate and subsequently induce antiphase oscillations in the algal density. Obviously the internal size-structure of the *Daphnia* population is playing an important part in these oscillations. Especially the fact that an individual *Daphnia* must grow to a certain size before it can start reproducing seems to be a key factor. The algal population merely follows the changes in the *Daphnia.*

On the basis of our numerical studies we conjecture that the predator-prey type of oscillations that we observed in the model is comparable with the type II dynamics distinguished by McCauley & Murdoch (1987, see also before). Therefore, these type II dynamics are probably driven by the 'prey escape' mechanism that we described. On the other hand we believe that the second type of oscillations that we observed is comparable with the type III dynamics of McCauley & Murdoch. Although the algal population is oscillating, these oscillations stay well within the bounds that McCauley & Murdoch use for their stability criterion. These type III dynamics are therefore likely to be caused by the juvenile delay of the *Daphnia.*

We conclude that although our model is rather crude in several aspects, we are able to reproduce three types of dynamics that are comparable with the patterns found in field studies. One of these types is completely due to the internal size-structure of the *Daphnia* population, which shows the significance of incorporating physiological structure in population dynamical models in certain situations. Our results make it plausible that the three types of dynamics observed in field populations of *Daphnia* and algae indeed can arise in the same structural system by mere changes in parameters. Moreover, the model analysis sheds some light on the possible mechanisms underlying these types of dynamics.

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Appendix

In this appendix we will give the complete set of equations describing the model that was investigated in this study. We refer to table I for a summary of the used variables and parameters. From subsection 5.1 we extract the equations describing the growth, death and reproduction behaviour of an individual:

growth:

$$\frac{dl}{dt} = g(x,l) = \gamma(l_m f(x) - l) \qquad \text{for } \; l < l_m f(x)$$

$$= 0 \qquad \text{otherwise}$$

death:

$$d(x,a,l) = \delta \qquad \text{for } \; l < \frac{l_m f(x)}{\kappa}, \quad a < a_{\max}$$

$$= \infty \qquad \text{otherwise}$$

reproduction:

$$b(x,l) = 0 \qquad \text{for } \; l_b < l < l_j$$

$$= r_m f(x) l^2 \qquad \text{for } \; l_j < l < l_m f(x)$$

$$= \frac{r_m}{(1-\kappa)}\left(f(x) l^2 - \frac{\kappa l^3}{l_m}\right) \qquad \text{otherwise}$$

in which $f(x) = \frac{\xi x}{1+\xi x}$ represents the functional response.

The grazing rate of an individual *Daphnia* upon the algal food population is described by:

$$I(x,l) = v_x f(x) l^2$$

Following the lines set out by METZ & DIEKMANN (1986) we arrive at the following set of equations describing the population behaviour:

$$\begin{cases} \dfrac{\partial n(t,a,l)}{\partial t} + \dfrac{\partial n(t,a,l)}{\partial a} + \dfrac{\partial g(x,l)n(t,a,l)}{\partial l} = -d(x,a,l)n(t,a,l) \\ n(t,0,l_b) = \int\limits_0^{a_{\max}} \int\limits_{l_b}^{l_m} b(x,l)n(t,a,l)dlda \\ n(0,a,l) = \Psi(a,l) \end{cases}$$

in which $n(t,a,l)$ is the density function representing the population and $\Psi(a,l)$ is the initial condition at $t=0$ that is assumed to be known. The first equation represents the growth, ageing and death processes of the individuals in the population, while the second equation represents the reproduction process. These equations have to be coupled to an ODE describing the dynamics of the algal food population to complete the specification of the model:

$$\frac{dx}{dt} = R(x) - \int\limits_0^{a_{\max}} \int\limits_{l_b}^{l_m} I(x,l)n(t,a,l)dlda$$

$$x(0) = x_0$$

with $R(x)$ the (autonomous) logistic growth dynamics of the algal population:

$$R(x) = \alpha x(1-x/C)$$