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## STUDYING THE DYNAMICS OF STRUCTURED POPULATION MODELS: A VERSATILE TECHNIQUE AND ITS APPLICATION TO *DAPHNIA*

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**Abstract.**—We introduce a versatile model formulation, called the *escalator boxcar train*, that can be used to study the dynamics of populations structured by age, size, or any other physiological trait. Spanning the entire spectrum between the classical, age-structured, Leslie matrix models and continuous-time, physiologically structured population models, it combines the computational ease of the matrix models with the flexibility of the continuous-time models; it allows the population dynamics to depend on an arbitrary number of individual characteristics and can account for nonlinear interactions of the population with its (fluctuating) environment, for density dependence in individual behavior, and for a continuous reproduction process. Application of the technique to a model for the dynamics of a *Daphnia* population reveals that a food-dependent maturation delay induces a very specific type of population cycle, in which the demography of the population plays a major role. The influence of "growth-curve plasticity," that is, the change in size at each age with a change in food density, on individual feeding behavior (at higher food densities individuals are larger and hence eat more) is a potential mechanism to stabilize the dynamics. The influence of growth-curve plasticity on reproduction (primarily the increase in maturation delay with a decrease in food density) greatly destabilizes the system.

Matrix models constitute a class of models for the dynamics of a population that incorporate individual variability. Originally formulated for populations in which the individual age was the main source of variability (Lewis 1942; Leslie 1945), these models have been modified subsequently to deal with size (Usher 1966; Glasser 1983) or developmental stage (Lefkovich 1965; Werner and Caswell 1977; Woodward 1982) as the key individual characteristic. Matrix models have been widely used in biological research because of their simplicity and tractability. A recent overview (Caswell 1989) shows that they are a powerful tool for analyzing, for example, the impact of life-history characteristics on population dynamics, the influence of the present population state on its growth potential, and the sensitivity of the dynamics to quantitative changes in vital rates. How-

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ever, as Caswell (1989) also noted, matrix models are not suitable for studying the dynamics of a population whenever the environment is not constant.

McKendrick (1926) introduced an entirely different type of model for an age-structured population. It describes the dynamics of the age distribution on a continuous-time basis using a partial differential equation, usually referred to as the McKendrick-von Foerster equation. This type of model has been developed to such an extent that it can be used to describe the dynamics of a population that is living in a fluctuating environment owing to external forcing or to the interaction between the environment and the population itself. In addition, it also applies to situations in which more than one physiological trait of the individuals (e.g., age, size, and energy reserves) has a strong influence on individual reproduction and mortality (see Metz and Diekmann 1986 for a detailed overview of the theory, and see Metz et al. 1988 for a more biologically oriented introduction). In contrast to matrix models, these models, which we refer to as continuous-time, physiologically structured models, are mathematically and computationally difficult to analyze, because they always give rise to a partial differential equation. The analysis is especially hard when the environment is not constant.

These two classes of models seem very remote from each other, and both seem to have their own specific restrictions in biological research. In this article, we show that they are actually the end points of a spectrum and how they can be related to each other. The entire spectrum is spanned by a technique that is called the *escalator boxcar train* (EBT; Goudriaan 1986; De Roos 1988). Although the technique was originally developed as a computational method for partial differential equations, it also constitutes an extension of matrix models. Being intermediate between matrix models and continuous-time models, the escalator boxcar train combines the computational ease of the former with the flexibility of the latter: it can be applied to model the dynamics of a population, including interactions with its environment, while an arbitrary number of physiological traits of the individuals can influence their behavior.

The mathematical derivation of the escalator boxcar train as an approximation of a partial differential equation model has been published elsewhere (De Roos 1988). In this article we show its relation to the matrix models and how the technique spans the entire spectrum from the simple, age-structured Leslie matrix model to the continuous-time, physiologically structured models. We illustrate the technique and its flexibility with an application to a structured model for the dynamics of a *Daphnia* population in which the individuals feed on a dynamically varying population of algae. In this case two individual characteristics (age and size) have an influence on the individual's behavior. Moreover, the growth and reproduction of individual *Daphnia* depend on the density of algae in their environment, which itself is strongly influenced by the feeding of the *Daphnia* population. Computations of the population dynamics that are obtained with the escalator boxcar train show that the dependence of feeding, growth, and reproduction on food density and individual size has a stabilizing as well as a destabilizing influence on the dynamics. The underlying mechanisms are identified and discussed.

#### THE ESCALATOR BOXCAR TRAIN

The escalator boxcar train extends the age-structured Leslie matrix model on the following major points:

1. Other physiological traits as the key individual characteristics: we generalize the model for a size-structured population
2. A fluctuating environment and density dependence: we show how to account for a fluctuating food density in the model, for which the individuals in the population compete
3. A continuous reproduction process: in principle, the Leslie matrix model describes the dynamics of an age-structured population with pulsed reproduction, although it is often used as a (crude) approximation in case of continuous reproduction; we introduce a more consistent way to handle continuous reproduction

The key step in achieving these goals is to switch to an alternative, though fully identical, mathematical formulation of the original age-structured population model introduced by Leslie (1945). In essence, we write down a set of equations that specifies on a continuous-time basis exactly the same model as the Leslie matrix equation describes on a discrete-time basis. In view of the similarity of our alternative formulation to the escalator boxcar train, the numerical method for continuous-time models (De Roos 1988), we refer to it as the escalator boxcar train formulation. The EBT formulation is not appropriate for studying, for example, the eigenvalues of the Leslie matrix model or the sensitivity of these eigenvalues to parameter changes or for estimating the parameters in the matrix model (see Caswell 1989). However, we claim that for computation of population dynamics the EBT formulation is only slightly more complicated than the matrix formulation. More important, the EBT formulation allows a relatively straightforward generalization of the model on the three major points mentioned above.

The original Leslie matrix model (Lewis 1942; Leslie 1945) can be represented as

$$\begin{pmatrix} \lambda_0(t+1) \\ \lambda_1(t+1) \\ \lambda_2(t+1) \\ \vdots \\ \lambda_n(t+1) \end{pmatrix} = \begin{pmatrix} F_0 & F_1 & F_2 & \dots & F_n \\ P_0 & 0 & 0 & \dots & 0 \\ P_1 & 0 & \dots & \dots & 0 \\ \vdots & \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & P_{n-1} & 0 \end{pmatrix} \begin{pmatrix} \lambda_0(t) \\ \lambda_1(t) \\ \lambda_2(t) \\ \vdots \\ \lambda_n(t) \end{pmatrix}, \quad (1a)$$

where, assuming that the population census directly follows a pulse of reproduction,  $\lambda_i(t)$  denotes the number of (female) individuals present at time  $t$  in the  $i$ th age class or cohort, that is, with an age of  $i$  time units (a time unit equals the width of an age class and hence the time interval between two reproduction pulses),  $F_i$  represents the number of individuals in age class 0 at time  $t+1$  produced per individual in age class  $i$  at time  $t$ , and  $P_i$  is the survival probability

of an individual in age class  $i$ . In matrix notation this can be written as

$$\lambda(t+1) = A\lambda(t). \quad (1b)$$

The matrix  $A$  is often referred to as the Leslie matrix.

How can this process be described on a continuous-time basis? The quantities  $\lambda_i(t)$  actually decrease continuously owing to mortality during the time interval between successive birth pulses, while the age of the individuals increases continuously. If  $q(a)$  denotes the instantaneous mortality rate (i.e.,  $q(a)da$  is the chance that an individual of age  $a$  dies within a small interval  $da$ ) and  $\alpha_i(t)$  denotes the age of the individuals in the  $i$ th cohort, these changes can be described by the equations

$$d\lambda_i/dt = -q(\alpha_i)\lambda_i \quad (2)$$

and

$$d\alpha_i/dt = 1.$$

The latter equation of this system of ordinary differential equations (ODEs) is obvious in the context of the Leslie matrix model (age progresses just as fast as time) but plays an important role in its extensions.

Reproduction at time  $t+1$  is determined by the maternity function  $m(a)$ , which is defined as the expected number of (female) offspring per (female) individual of age  $a$ , and by the number of individuals that have survived since the previous census. If  $\lambda_i(t+1^-)$  and  $\alpha_i(t+1^-)$  denote the number and age, respectively, of individuals in the  $i$ th cohort just prior to the birth pulse at time  $t+1$ , and  $\lambda_i(t+1^+)$  and  $\alpha_i(t+1^+)$  denote the same quantities immediately afterward, the number and age of the newborn individuals equal

$$\lambda_0(t+1^+) = \sum_{i=1}^n m[\alpha_i(t+1^-)]\lambda_i(t+1^-) \quad (3)$$

and

$$\alpha_0(t+1^+) = 0,$$

respectively. As reproduction occurs, the individuals in all the other cohorts instantaneously "age" one time unit and hence end up in the next cohort; that is, the current cohorts are renumbered

$$\lambda_{i+1}(t+1^+) = \lambda_i(t+1^-) \quad (4)$$

and

$$\alpha_{i+1}(t+1^+) = \alpha_i(t+1^-),$$

for  $i = 0, \dots, n-1$ . In the present case the latter quantities simply equal  $i+1$ .

The ODEs (2), in combination with the reproduction scheme (3) and the renumbering process (4), represent our alternative formulation of the matrix equation (1a). The two formulations are entirely equivalent descriptions of the same pro-

cess, as we show in Appendix A. The quantities  $P_i$  and  $F_i$  in equation (1a) can be expressed in terms of the instantaneous mortality rate  $q(a)$  and the maternity function  $m(a)$  (see App. A):

$$P_i = \exp \left\{ - \int_0^1 q[\alpha_i(t+\xi)]d\xi \right\} = \exp \left\{ - \int_0^1 q(i+\xi)d\xi \right\} \quad (5a)$$

and

$$F_i = m[\alpha_i(t+1)]P_i = m(i+1)P_i. \quad (5b)$$

#### EXTENSIONS OF THE STANDARD MODEL

The escalator boxcar train formulation of the standard matrix model is especially suitable for incorporating size and/or food dependence or continuous reproduction into the model. In these cases, it is not even possible to describe the model in general with a matrix equation like equation (1a). The equations of the escalator boxcar train formulation, however, are always comparable with equations (2), (3), and (4) and are consequently easy to solve by existing numerical integration methods. These computations are only slightly more complicated than the computations required by the Leslie matrix model. The EBT formulations of the standard age-structured and the extended models are summarized in table 1, which clearly shows their similarity. A computer implementation of the complete escalator boxcar train technique is available from the first author.

Many other extensions of the standard age-structured model exist, incorporating, for example, size (Usher 1966; Ghasser 1983), developmental stage (Lefkovich 1965; Werner and Caswell 1977; Woodward 1982; Hughes 1984), or even both size and age (Slobodkin 1953) as the key individual characteristics (see Usher 1972 and Caswell 1989 for an overview of all the developments). Our approach differs, because all extended models derived below are continuous-time, physiologically structured population models (Metz and Diekmann 1986; Metz et al. 1988) or consistent numerical approximations thereof. Thus, all these models can be expressed in terms of a partial differential equation.

#### Size-dependent Dynamics

For many animals (e.g., cladocerans and many fish species) the size of the individual organism determines its rate of feeding, growth, and reproduction to a much larger extent than its age. The dynamics of the population might be seriously affected by this size dependence, since growth in size, in contrast to aging, can fluctuate in time. In this section we replace the age of an individual with its size, leaving the remaining structure of the standard model unchanged.

The size of an individual is denoted by  $s$ . If reproduction and mortality depend on size, the instantaneous mortality rate  $q$  and the maternity function  $m$  are functions of size rather than age. Accordingly we write  $q(s)$  and  $m(s)$  instead of  $q(a)$  and  $m(a)$ . Growth in size often also depends on the size itself. Hence the growth rate is described by some function  $g(s)$ , dependent on  $s$ . It is assumed that individuals are born with a certain fixed size  $s_b$ .

Symbols	Definitions	Model Equations
<b>A. Standard age-structured model:</b>		
$a$	Individual age	
$\lambda_i(t)$	Number of individuals in the $i$ th cohort	Continuous-time dynamics for all cohorts, in between two reproduction pulses:
$\alpha_i(t)$	Age of all individuals in the $i$ th cohort	
$q(a)$	Age-dependent mortality rate	$\begin{cases} \frac{d\lambda_i}{dt} = -q(\alpha_i)\lambda_i \\ \frac{d\alpha_i}{dt} = 1 \end{cases} \quad i = 0, \dots, n$
$m(a)$	Age-dependent maternity function	
		Reproduction equations yielding cohort with newborns (at integral values of $t$ ):
		$\begin{cases} \lambda_0(t+1^+) = \sum_{i=0}^{i=n} m[\alpha_i(t+1^-)]\lambda_i(t+1^-) \\ \alpha_0(t+1^+) = 0 \end{cases}$
		Renumbering equations for all other cohorts (at integral values of $t$ ):
		$\begin{cases} \lambda_{i+1}(t+1^+) = \lambda_i(t+1^-) \\ \alpha_{i+1}(t+1^+) = \alpha_i(t+1^-) \end{cases} \quad i = 0, \dots, n-1$
<b>B. Size-structured model:</b>		
$s$	Individual size	
$s_b$	Individual size at birth	Continuous-time dynamics for all cohorts, in between two reproduction pulses:
$\lambda_i(t)$	Number of individuals in the $i$ th cohort	
$\sigma_i(t)$	Size of all individuals in the $i$ th cohort	$\begin{cases} \frac{d\lambda_i}{dt} = -q(\sigma_i)\lambda_i \\ \frac{d\sigma_i}{dt} = g(\sigma_i) \end{cases} \quad i = 0, \dots, n$
$q(s)$	Size-dependent mortality rate	
$m(s)$	Size-dependent maternity function	
$g(s)$	Size-dependent growth rate	
		Reproduction equations yielding cohort with newborns (at integral values of $t$ ):
		$\begin{cases} \lambda_0(t+1^+) = \sum_{i=0}^{i=n} m[\sigma_i(t+1^-)]\lambda_i(t+1^-) \\ \sigma_0(t+1^+) = s_b \end{cases}$
		Renumbering equations for all other cohorts (at integral values of $t$ ):
		$\begin{cases} \lambda_{i+1}(t+1^+) = \lambda_i(t+1^-) \\ \sigma_{i+1}(t+1^+) = \sigma_i(t+1^-) \end{cases} \quad i = 0, \dots, n-1$
<b>C. Food-dependent size-structured model:</b>		
$s$	Individual size	
$s_b$	Individual size at birth	Continuous-time dynamics for all cohorts, in between two reproduction pulses:
$x$	Food density in the environment	
$\lambda_i(t)$	Number of individuals in the $i$ th cohort	$\begin{cases} \frac{d\lambda_i}{dt} = -q(x, \sigma_i)\lambda_i \\ \frac{d\sigma_i}{dt} = g(x, \sigma_i) \end{cases} \quad i = 0, \dots, n$
$\sigma_i(t)$	Size of all individuals in the $i$ th cohort	

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$q(x, s)$	Mortality rate (depends on both food density and individual size)	Reproduction equations yielding cohort with newborns (at integral values of $t$ ):	$\begin{cases} \lambda_0(t+1^+) = \sum_{i=0}^{i=n} m[x, \sigma_i(t+1^-)]\lambda_i(t+1^-) \\ \sigma_0(t+1^+) = s_b \end{cases}$
$m(x, s)$	Maternity function (depends on both food density and individual size)		
$g(x, s)$	Individual growth rate (depends on both food density and individual size)	Renumbering equations for all other cohorts (at integral values of $t$ ):	$\begin{cases} \lambda_{i+1}(t+1^+) = \lambda_i(t+1^-) \\ \sigma_{i+1}(t+1^+) = \sigma_i(t+1^-) \end{cases} \quad i = 0, \dots, n-1$
$I(x, s)$	Individual feeding rate (depends on both food density and individual size)		
$R(x)$	Rate at which food is regenerating in or being added to the environment	Dynamics of food density in the environment:	$\frac{dx}{dt} = R(x) - \sum_{i=0}^{i=n} I(x, \sigma_i)\lambda_i$
<b>D. Food-dependent size-structured model with continuous reproduction:</b>			
$\Delta$	Time between renumbering operations	Continuous-time dynamics for the zeroth cohort (until first renumbering operation):	$\begin{cases} \frac{d\lambda_0}{dt} = -q(x, s_b)\lambda_0 - q_s(x, s_b)\pi_0 + \sum_{i=0}^{i=n} b(x, \mu_i)\lambda_i^* \\ \frac{d\pi_0}{dt} = g(x, s_b)\lambda_0 + g_s(x, s_b)\pi_0 - q(x, s_b)\pi_0 \end{cases}$
$s$	Individual size		
$s_b$	Individual size at birth	Continuous-time dynamics for all other cohorts, in between two renumbering operations:	$\begin{cases} \frac{d\lambda_i}{dt} = -q(x, \mu_i)\lambda_i \\ \frac{d\mu_i}{dt} = g(x, \mu_i) \end{cases} \quad i = 1, \dots, n$
$x$	Food density in the environment		
$\lambda_i(t)$	Number of individuals in the $i$ th cohort	Renumbering equations and new initial values for cohort with newborns (at $\Delta$ time intervals):	$\begin{cases} \lambda_i(t+\Delta^+) = \lambda_0(t+\Delta^-) \\ \mu_i(t+\Delta^+) = s_b + \frac{\pi_0(t+\Delta^-)}{\lambda_0(t+\Delta^-)} \\ \lambda_0(t+\Delta^+) = 0 \quad \pi_0(t+\Delta^+) = 0 \\ \lambda_{i+1}(t+\Delta^+) = \lambda_i(t+\Delta^-) \\ \mu_{i+1}(t+\Delta^+) = \mu_i(t+\Delta^-) \end{cases} \quad i = 1, \dots, n-1$
$\pi_0(t)$	Total size mass, relative to $s_b$ , of the individuals in the zeroth cohort		
$\mu_i(t)$	Mean size of the individuals in the $i$ th cohort	Renumbering equations for all other cohorts (at $\Delta$ time intervals):	$\begin{cases} \mu_{i+1}(t+\Delta^+) = \mu_i(t+\Delta^-) \end{cases} \quad i = 1, \dots, n-1$
$q(x, s)$	Mortality rate (depends on both food density and individual size)		
$b(x, s)$	Instantaneous birth rate (depends on both food density and individual size)	Dynamics of food density in the environment:	$\frac{dx}{dt} = R(x) - \sum_{i=0}^{i=n} I(x, \mu_i)\lambda_i^*$
$g(x, s)$	Individual growth rate (depends on both food density and individual size)		
$I(x, s)$	Individual feeding rate (depends on both food density and individual size)		
$R(x)$	Rate at which food is regenerating in or being added to the environment		
$q_s, g_s$	Derivatives of $q$ and $g$ with respect to $s$		

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NOTE.—In A, B, and C, reproduction takes place at integral values of  $t$ . Time values of  $t^-$  and  $t^+$  indicate the moments immediately before and after  $t$ , respectively. The  $n$ th cohort is the last cohort that plays a role in the dynamics of the population.

\* Include the zeroth cohort if  $\lambda_0 \neq 0$ . Take  $\mu_0 := s_b + \pi_0/\lambda_0$ .

The size-dependent vital rates, introduced above, form the ingredients of our size-structured population model. Owing to the pulsed reproduction process, the population again consists of distinct cohorts of individuals, which are now size classes. Consequently, a cohort can be characterized by the number of individuals in the cohort, denoted as before by  $\lambda_i(t)$ , and by the size of the individuals in the cohort, which we denote by  $\sigma_i(t)$ . One of the basic assumptions of our models (and of continuous-time, physiologically structured population models in general) is that growth in size is deterministic, that is, individuals of the same size grow at the same rate, which is valid as long as the variability among identical individuals is not too large. The assumption implies that all the individuals in a specific cohort have the same size,  $\sigma_i(t)$ .

The size-structured model is now simply derived from the standard age-structured model by replacing all the age-dependent functions with their size-dependent equivalents and replacing the ODE for  $\alpha_i$  with an analogous ODE for  $\sigma_i$  (see table 1). The right-hand side of this latter equation equals the growth rate  $g$  evaluated at  $\sigma_i$ , just as the right-hand side of the ODE for  $\alpha_i$  equaled one, the rate of aging. Comparison of parts A and B of table 1 shows clearly the similarity between the models.

The size-structured model introduced here can be formulated in terms of a matrix equation (1a) only for specific choices of the growth function,  $g(s)$ , for instance, when  $g(s)$  describes a von Bertalanffy growth curve (von Bertalanffy 1934; see App. A). The expressions for the quantities  $P_i$  and  $F_i$  with such a specific  $g(s)$  are very similar to expressions (5) for the age-structured model (see App. A).

#### *Food-dependent Dynamics*

One of the main restrictions of the standard model is the assumption that the environment is constant and that the death rate, growth rate, and maturity function (at a certain age or size) therefore do not change over time. In general, however, these rates are not constant at all, either because they are influenced by fluctuating environmental factors or because they are density-dependent. As opposed to the standard model, the EBT formulation can be used to model almost any system in which the environment changes over time or in which density-dependent mechanisms influence individual behavior. As an example, we will show in this section how it can be applied to a situation in which the vital rates are influenced by the availability of food in the environment, for which the individuals in the population compete. In the section Further Extensions and Discussion we will discuss in more detail how it can account for a fluctuating environment and density-dependent mechanisms in general.

Therefore, if  $x$  denotes the food density in the environment of the population, we will assume in the following that  $q$ ,  $g$ , and  $m$  are functions of both  $s$  and  $x$  and we will hence denote them by  $q(x, s)$ ,  $g(x, s)$ , and  $m(x, s)$ , respectively.

For the formulation of our population equations, the dependence of the functions  $q$ ,  $g$ , and  $m$  on  $x$  does not make a difference: The equations for the food-dependent model are completely identical to the equations for the (food-independent) size-structured model, except that all the vital rates now depend on

both size and food density (see table 1, pt. C). However, if the food density in the environment is not an explicit function of time, as, for example, in a laboratory experiment with a completely controlled food availability, we have to describe the dynamics of the food concentration itself.

The dynamics of the food density are determined by two processes: the regeneration of the food within the environment (or the rate at which food is added to the environment) and the feeding by the individuals of our size-structured population. Assume that  $R(x)$  is the rate of regeneration (addition) of food ( $R[x]$  could, for instance, be the logistic equation). Further assume that  $I(x, s)$  is the feeding rate of an individual of size  $s$  at a food density  $x$ . Since the structure of the population is entirely known in terms of the number,  $\lambda_i(t)$ , and size,  $\sigma_i(t)$ , of individuals in the various cohorts, the population's feeding rate can be determined by summing all the individual feeding rates; that is, it equals  $\sum_{i=0}^n I(x, \sigma_i) \lambda_i$ . The dynamics of the food density is now described by an ODE, of which the right-hand side is simply the balance between regeneration/addition and the population feeding rate (see table 1, pt. C). This ODE has to be solved simultaneously with the equations for  $\lambda_i$  and  $\sigma_i$ , the number and size of the individuals in the  $i$ th cohort. Owing to this dynamic food density, it is no longer possible to formulate the model by using an explicit matrix equation.

#### *Continuous Reproduction*

The change from pulsed to continuous reproduction is certainly the most complicated of the extensions. A pulsed reproduction process implies that a newborn cohort arises more or less instantaneously. Even if the reproduction pulses are not equally spaced in time, the model from the previous section can be used, as long as the renumbering and reproduction operations are carried out at the time of a reproduction pulse. Continuous reproduction implies that the population does not consist of distinct cohorts of individuals with an identical size but is characterized by a continuous distribution of the individuals over a whole range of sizes. The mathematically correct formulation of the model would now employ a quite complicated partial differential equation, comparable with the age-structured model introduced by McKendrick (1926; Metz and Diekmann 1986). However, the technique developed in the previous sections can be used as a consistent approximation to this equation.

The basis of the EBT formulation consists of the subdivision of the population into distinct cohorts of individuals, the description of the dynamics of the number and size of the individuals in these cohorts by ODEs, and the renumbering/shifting of these cohorts at equidistant time intervals, when a new cohort is formed. Therefore, using the EBT formulation as an approximation for the continuous-reproduction model involves imposing a subdivision of the population into cohorts of individuals and describing how new cohorts arise from the continuous inflow of newborn individuals.

Assume that initially the population at time  $t$  can be subdivided into cohorts of more or less identical individuals. One such cohort can again be characterized by the number of individuals in it and by a representative size for these individuals. Since even within the cohort the individuals are no longer completely identi-

cal owing to the continuous size distribution, the mean size of the individuals in the cohort is chosen as the representative size value. This mean size of the individuals in the  $i$ th cohort is denoted by  $\mu_i(t)$ . The dynamics of the quantities  $\lambda_i(t)$  and  $\mu_i(t)$  characterizing the cohorts are described by a set of ODEs similar to those in the previous section (see table 1, pt. D), with  $\sigma_i$  (the identical size of the individuals) replaced by  $\mu_i$  (the mean size of the individuals).

In contrast to the situations considered so far, the cohort of individuals that are born between time  $t$  and  $t + 1$  does not arise instantaneously at  $t + 1$ , but the inflow of newborn individuals into this cohort is spread out over the whole time interval. Therefore, the dynamics of this cohort, which we shall call the "cohort in creation" as opposed to the "internal" cohorts that are already present in the population, should also be described on a continuous-time basis, that is, by ODEs. Upon reaching time  $t + 1$  this cohort now becomes an internal cohort itself, while a new cohort in creation is started up for the individuals that will be born during the next time unit. We have to impose this transformation of the cohort in creation into an internal cohort and its replacement by a new cohort in creation, because distinct cohorts no longer arise naturally. The choice of lumping all the individuals born between  $t$  and  $t + 1$  into one cohort is also arbitrary: The length of the time interval during which individuals are lumped into the same cohort can be chosen freely. In the following we therefore assume that all individuals that are born between time  $t$  and  $t + \Delta$  ( $\Delta$  is referred to as the cohort width) are lumped into the same cohort. The transformation and replacement of the cohort in creation are hence carried out at time  $t + \Delta$ ,  $t + 2\Delta$ ,  $t + 3\Delta$ , and so on (the significance of the value of  $\Delta$  will be discussed in the next subsection).

The cohort in creation is again characterized by the number of individuals it contains and by a representative size measure. In accordance with the internal cohorts, the number and mean size of the individuals in the cohort in creation are denoted by  $\lambda_0(t)$  and  $\mu_0(t)$ , respectively. Unfortunately, the mean size,  $\mu_0(t)$ , of the individuals is not an appropriate choice to describe the dynamics of this cohort, since its value and its dynamics are undefined at the time that the cohort is started, that is, when it is empty (see App. B). The dynamics of the cohort is hence described in terms of  $\lambda_0(t)$  and the quantity  $\pi_0(t)$ , defined as

$$\pi_0(t) := [\mu_0(t) - s_b] \lambda_0(t). \quad (6)$$

The quantity  $\pi_0(t)$  can be interpreted as the total biomass of the individuals in the cohort in creation at time  $t$  relative to the size at birth,  $s_b$ . The ODEs describing the dynamics of the quantities  $\lambda_0(t)$  and  $\pi_0(t)$  are derived in Appendix B and presented in table 1, part D. At the empty start of a cohort in creation both the number of individuals,  $\lambda_0(t)$ , and the (relative) biomass of these individuals,  $\pi_0(t)$ , obviously equal zero. The ODE for  $\lambda_0(t)$  contains terms due to the reproduction. Instead of the maternity function  $m(x, s)$  that characterized the pulsed reproduction, these terms now involve the instantaneous reproduction rate, that is, the number of newborns per unit of time produced by one individual. This rate is assumed to depend on both size and food density and is denoted by  $b(x, s)$ .

At time  $t + \Delta$  the cohort in creation is transformed into an internal cohort and

the internal cohorts themselves are renumbered. At this time the characterizing size measure  $\pi_0(t)$  has to be transformed into the mean size of the individuals, the quantity characterizing an internal cohort. For this reason the transformation of the zeroth cohort into the first cohort is slightly more complicated, the renumbering equations for all other cohorts are identical to the ones from the previous sections. The ODE describing the dynamics of the food density does not change either. The whole set of equations for the continuous-reproduction model is given in table 1, part D.

#### *Further Extensions and Discussion*

The equations in part D of table 1 approximate the dynamics of a size-structured, continuously reproducing population in which the individuals are competing for a common food source. The mathematically correct description involves a complicated partial differential equation, which is given in Appendix B. The equations in part D of table 1 were derived from the original age-structured Leslie matrix model on the basis of biological arguments. The same equations have been derived from the partial differential equation by application of the escalator boxcar train. Just like the popular Runge-Kutta methods for numerical integration of ordinary differential equations, the escalator boxcar train is a numerical integration method for the partial differential equations in physiologically structured population models (De Roos 1988). This method constitutes a consistent approximation of the original partial differential equation, which means that the approximation is better with smaller values of the cohort width,  $\Delta$  (actually, the approximation error scales with the square of  $\Delta$ ). Therefore, if the equations in part D of table 1 are used to study the dynamics of a population interacting with its environment, the actual model under study is a continuous-time, physiologically structured model. Smaller values of  $\Delta$  imply a better approximation of the dynamics but also increase the number of cohorts,  $n$ , that are still playing a role in the population dynamics. The number of cohorts,  $n$ , can be kept within bounds by eliminating cohorts that contain numbers of individuals near zero owing to mortality or cohorts that are for other reasons dynamically negligible. The fact that the escalator boxcar train essentially constitutes an approximation of a continuous-time model also implies that further extensions of the model described in the previous sections are relatively easy. Two will be discussed here; for further extensions see De Roos (1988). If more than one physiological trait of the individuals influences their dynamics, say size and age, the functions describing the vital rates of an individual (feeding, death, growth, and reproduction) depend on both size and age. Consequently, we have to characterize every cohort not only by the mean size but also by the mean age of the individuals, and we have to add the necessary ODEs and renumbering equations. In essence, these new equations are, however, completely comparable with the equations in part D of table 1 (see the next section for an example).

In general, we can distinguish two different types of environmental influences on the individual death, growth, and reproductive rates, which can be characterized as "feedback" and "external forcing." The dynamic food density in our models is representative of a situation in which a feedback loop exists from the

population to the environment (owing to feeding) and back (owing to the influence of the food density on the vital rates). This type of environmental influence on individual behavior we will call an "interactive" environment. As we have shown, the EBT formulation accounts for such an interaction with the environment, using a separate ODE to describe the dynamics of the environmental variable. This ODE specifies the precise functional form of the feedback between the population and its environment.

In contrast, the death, growth, and reproductive rates of an individual may fluctuate owing to time-varying, external factors such as seasonal climatic variation, temperature, and daily solar influx. This type of influence on individual behavior we will call a "driving" environment. To account for such a driving environmental factor in the model, the functions for the individual death, growth, and reproduction rates should again explicitly incorporate this dependence on the environmental variable, as in the food-dependent model described in the section Food-dependent Dynamics. However, it is not necessary to specify a separate ODE for the variable itself. Since the population does not influence the environmental factor directly, it is an explicit function of time (of the year, the day, etc.).

These two classes of environmental influences also automatically cover almost any consistently formulated type of density dependence in the vital rates (note that for every individual the total population is just a characteristic of its environment). Density dependences that influence individual behavior in an indirect manner, such as competition for a common resource, always act through a feedback loop via the environment and are hence incorporated into the model as an interactive environment. Density dependences that affect individual behavior directly, such as cannibalism, can be accounted for by a driving environmental variable. The total population size or any other measure of the population may be seen as a driving environmental variable, since its value can be assessed at every moment from the state of the total population, that is, the quantities  $\lambda_i(t)$  and  $\mu_i(t)$ , and a separate ODE for its dynamics is therefore not needed.

The representation of the environment in terms of a single key factor, such as food density in the food-dependent model can easily be extended to more than one environmental variable. In this case the environmental variables could be of both the interactive and the driving types. The EBT formulation could thus account for a situation in which the environment is characterized, for example, by food density, temperature, and total population size. The dynamics of each interactive environmental variable should in this case be described by a separate ODE.

#### AN APPLICATION TO DAPHNIA POPULATION DYNAMICS

The interaction between *Daphnia* populations and their algal food source constitutes an example in which physiological differences between individual *Daphnia*, primarily differences in size, have been conjectured to play an important role in the dynamics of the total population (Murdoch and McCauley 1985; McCauley and Murdoch 1987). In a large survey of the dynamics of *Daphnia* populations in

both field and laboratory situations McCauley and Murdoch (1987) distinguished three main patterns of dynamics:

1. Both the *Daphnia* and the algal population appear stable
2. *Daphnia* and algal populations display joint cycles
3. The *Daphnia* population exhibits cyclic behavior; the algal population appears stable

The cyclic fluctuations displayed by the *Daphnia* populations have a dominant period close to the generation time of *Daphnia* (25–45 d). According to McCauley and Murdoch (1987), a cycle is initiated by a burst of reproduction at low population densities, giving rise to a population peak that consists mainly of juveniles. Food availability subsequently decreases, which leads 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 and Murdoch 1987). The severe changes in demography of the *Daphnia* population during one cycle demonstrate the major influence of the individual age and/or size differences on the overall population dynamics.

On the basis of the similarity between the dynamics of laboratory and field populations of *Daphnia*, McCauley and Murdoch (1987) conjecture that all three types of dynamics arise from the interaction between *Daphnia* and algae within the same structural system, probably by means of quantitative changes in parameters, and in particular that the cycles are internally driven. We have recently investigated these conjectures (De Roos et al. 1990), using a model of energy channeling to growth and reproduction introduced by Kooijman and Metz (1984). Feeding, growth, and reproduction of individuals in the model depend on their size (length),  $x$ , and on the density of algae,  $x$ , in the environment, while mortality depends primarily on the individual age,  $a$ . Here, we present some results that were obtained by the escalator boxcar train technique to illustrate its potential.

#### The Kooijman-Metz Model

The Kooijman-Metz model uses a rather simple description of the energy budget of an individual *Daphnia* (see Kooijman and Metz 1984 and Metz et al. 1988 for a complete derivation and experimental underpinning). However, it incorporates the main features common to most models of individual *Daphnia* behavior (Sinko and Streifer 1969; Paloheimo et al. 1982; Kooijman 1986; Gurney et al. 1990): (1) the feeding rate of individual *Daphnia* strongly increases with individual size and is an increasing but decelerating function of food density, (2) individual *Daphnia* mature on reaching a fixed size, and (3) ultimate size and growth rate increase with food availability.

Individuals of different sizes are assumed to have the same allometric relations, so that surface area and (wet) weight are proportional to  $s^2$  and  $s^3$ , respectively. Food intake is assumed to be proportional to surface area and depends at a given size on the prevailing food density, following a Holling Type II functional response. Ingested energy is allocated in fixed proportions to maturation and reproduction on the one hand and to maintenance and growth on the other, as

TABLE 2

SYMBOL, REFERENCE LIST FOR THE VARIABLES AND PARAMETERS USED IN THE KOOIJMAN-METZ MODEL.

Symbol	Default Value	Description	Units
<b>Variables:</b>			
<i>a</i>		Age	d
<i>s</i>		Size	mm
<i>x</i>		Concentration of edible algae	cells · mL <sup>-1</sup>
<b>Parameters:</b>			
<i>s<sub>b</sub></i>	.8	Size at birth	mm
<i>s<sub>j</sub></i>	2.5	Size at maturation	mm
<i>s<sub>m</sub></i>	6.0	Maximum attainable size	mm
<i>γ</i>	.15	Time constant of growth	d <sup>-1</sup>
<i>ξ</i>	7.0 × 10 <sup>-6</sup>	Shape parameter of the functional response	mL · cell <sup>-1</sup>
<i>v<sub>1</sub></i>	1.8 × 10 <sup>6</sup>	Maximum feeding rate per unit of surface area	cells · mm <sup>-2</sup> · d <sup>-1</sup>
<i>k</i>	.3	Default fraction of ingested energy channeled to growth and maintenance	
<i>r<sub>m</sub></i>	.1	Maximum reproduction rate per unit of surface area	mm <sup>-2</sup> · d <sup>-1</sup>
<i>δ</i>	Variable	Random death rate of <i>Daphnia</i>	d <sup>-1</sup>
<i>A<sub>max</sub></i>	70	Maximum lifetime of <i>Daphnia</i>	d
<i>α</i>	.5	Maximum algal growth rate	d <sup>-1</sup>
<i>C</i>	Variable	Algal carrying capacity	cells · mL <sup>-1</sup>

NOTE.—The default parameter values are based on experimental data for *Daphnia magna* feeding on *Chlorella* sp. and are extracted from Kooijman and Metz (1984) and Kooijman (1986). The parameters *δ* and *C* are variable.

long as the fraction allocated to maintenance and growth together is sufficient to meet maintenance requirements alone. If not, ingested energy is allocated in such a way that growth stops, maintenance requirements are just met, and the remaining energy is put into reproduction. Under abundant food conditions reproduction is therefore proportional to food intake (and hence to surface area). The energy requirements for maintenance always take precedence over growth and reproduction and are assumed to be proportional to individual weight. The energy cost per unit of weight increases and the energy cost of producing a neonate is assumed to be constant. Individuals die owing to background mortality, old age (i.e., by reaching a maximum life span), and starvation (i.e., if the individual cannot meet its maintenance requirements anymore).

The variables and parameters used in the *Daphnia* population model are given in table 2, while the equations that describe the feeding, growth, reproduction, and mortality of individual *Daphnia* and the growth rate of the algal food population are given in table 3. The algal population is assumed to exhibit logistic growth in the absence of *Daphnia*. The default parameter values are derived from Kooijman and Metz (1984) and Kooijman (1986) and are characteristic of a population of *Daphnia magna* feeding on *Chlorella* species (cell weight, 1.4 × 10<sup>-5</sup> μg; S. A. L. M. Kooijman, personal communication).

TABLE 3

EQUATIONS THAT DESCRIBE THE FEEDING, GROWTH, REPRODUCTION, AND MORTALITY OF INDIVIDUAL *DAPHNIA* (FOLLOWING KOOIJMAN AND METZ 1984) AND THE GROWTH RATE OF THE ALGAE IN THE ENVIRONMENT

Individual feeding rate:	$f(x, s) = v_1 f(x) s^2$	where $f(x) = \frac{\xi x}{1 + \xi x}$
Growth rate in size:	$g(x, s) = \gamma(s_m f(x) - s)$	for $s < s_m f(x)$ otherwise
Instantaneous birth rate:	$b(x, s) = 0$	for $s_b < s < s_j$ for $s_j \leq s < s_m f(x)$ otherwise
Instantaneous mortality rate:	$= \frac{r_m}{(1-k)} \left( f(x) s^2 - \frac{k s^3}{s_m} \right)$	
Autonomous algal dynamics:	$R(x) = \alpha x \left( 1 - \frac{x}{C} \right)$	for $a < A_{max}$ and $s < s_m f(x)$ otherwise

*The Escalator Boxcar Train Formulation of the Kooijman-Metz Model*

The EBT formulation of the Kooijman-Metz model is given in table 4. As explained in the section Further Extensions and Discussion, every internal cohort is now characterized by the number of individuals in the cohort,  $\lambda_i(t)$ , their mean size,  $\mu_i^s(t)$ , and their mean age,  $\mu_i^a(t)$ . The equations for the continuous-time dynamics and the renumbering of these cohorts are comparable with the equations for the model from the section Continuous Reproduction (cf. table 1, pt. D, and table 4).

The cohort in creation is characterized by its number of individuals,  $\lambda_0(t)$ , the total biomass,  $\pi_0^b(t)$  (relative to the size at birth,  $s_b$ ), and the total "age mass" (cumulative age of all individuals),  $\pi_0^a(t)$  (relative to the age 0 at birth). The latter quantity is defined as

$$\pi_0^a(t) := \mu_0^a(t) \lambda_0(t), \tag{7}$$

in which  $\mu_0^a(t)$  represents the mean age of the individuals in the (nonempty) cohort (cf. the definition of  $\pi_0^a(t)$ ).

The most important differences between the formulations in table 1, part D, and table 4 occur in the ODEs describing the dynamics of  $\lambda_0(t)$ ,  $\pi_0^b(t)$ , and  $\pi_0^a(t)$ . More specifically, in the ODE for  $\lambda_0(t)$  both the derivative of the mortality rate with respect to size,  $q_s$ , and the derivative of the mortality rate with respect to age,  $q_a$ , appear (table 4). Also in the ODE for  $\pi_0^b(t)$  the derivative of the growth rate with respect to size,  $g_s$ , and the derivative of the growth rate with respect to age,  $g_a$ , occur. Although for the present model some of these derivatives

TABLE 4  
ESCALATOR BOXCAR TRAIN FORMULATION FOR THE KOOIJMAN-METZ *DAPHNIA* MODEL

<p>Continuous-time dynamics for the zeroth cohort (until first renumbering operation):</p>	$\left\{ \begin{aligned} \frac{d\lambda_0}{dt} &= -q(x, 0, s_b)\lambda_0 - q(x, 0, s_b)\pi_0^{\delta} \\ &\quad - q_0(x, 0, s_b)\pi_0^{\delta} + \sum_{i=1}^{i=n} h(x, \mu_i^i)\lambda_i^* \\ \frac{d\pi_0^{\delta}}{dt} &= g(x, s_b)\lambda_0 + g(x, s_b)\pi_0^{\delta} \\ &\quad + g_0(x, s_b)\pi_0^{\delta} - q(x, 0, s_b)\pi_0^{\delta} \\ \frac{d\pi_0^{\delta}}{dt} &= \lambda_0 - q(x, 0, s_b)\pi_0^{\delta} \end{aligned} \right.$
<p>Continuous-time dynamics for all other cohorts, in between two renumbering operations:</p>	$\left\{ \begin{aligned} \frac{d\lambda_i}{dt} &= -q(x, \mu_i^i, \mu_i^i)\lambda_i \\ \frac{d\mu_i^i}{dt} &= g(x, \mu_i^i) \\ \frac{d\mu_i^i}{dt} &= 1 \end{aligned} \right. \quad i = 1, \dots, n$
<p>Renumbering equations and new initial values for cohort with newborers (at <math>\Delta</math> time intervals):</p>	$\left\{ \begin{aligned} \lambda_i(t + \Delta^+) &= \lambda_0(t + \Delta^-) \\ \mu_i^i(t + \Delta^+) &= s_b + \lambda_0(t + \Delta^-) \\ \mu_i^i(t + \Delta^+) &= \frac{\pi_0^{\delta}(t + \Delta^-)}{\lambda_0(t + \Delta^-)} \\ \lambda_0(t + \Delta^+) &= 0, \quad \pi_0^{\delta}(t + \Delta^+) = 0, \quad \pi_0^{\delta}(t + \Delta^+) = 0 \end{aligned} \right.$
<p>Renumbering equations for all other cohorts (at <math>\Delta</math> time intervals):</p>	$\left\{ \begin{aligned} \lambda_{i+1}(t + \Delta^+) &= \lambda_i(t + \Delta^-) \\ \mu_{i+1}^i(t + \Delta^+) &= \mu_i^i(t + \Delta^-) \quad i = 1, \dots, n-1 \\ \mu_{i+1}^{i+1}(t + \Delta^+) &= \mu_i^i(t + \Delta^-) \end{aligned} \right.$
<p>Dynamics of food density in the environment:</p>	$\frac{dx}{dt} = R(x) - \sum_{i=0}^{i=n} f(x, \mu_i^i)\lambda_i^*$

\*Include the zeroth cohort if  $\lambda_0 \neq 0$ : Take  $\mu_0^0 := s_b + \pi_0^{\delta}/\lambda_0$ .

always equal zero, we have included them to show how an extension to more individual traits in the model generally affects the equations. We did not include these additional terms in the ODE for  $\pi_0^{\delta}(t)$ , because all derivatives of the rate of aging obviously equal zero.

The renumbering equations for the cohort in creation are again similar to the equation for the continuous-reproduction model (cf. table 1, pt. D, and table 4). Note that the equations for  $\mu_i^i(t + \Delta)$  and  $\mu_i^i(t + \Delta)$  are equivalent except that individuals are born with age zero and size  $s_b$ . Also note that if the ingestion or reproduction rates of the newborn individuals should depend on age, the contribution of the zeroth cohort has to be included if  $\lambda_0 \neq 0$ , with  $\mu_0^0 := \pi_0^{\delta}/\lambda_0$  (cf.  $\mu_0^0$ ). In other words, the quantities  $\pi_0^{\delta}$  characterizing the cohort in creation always

have to be converted to their  $\mu_0$  analogues, before calculating, for example, the feeding or reproduction of the cohort.

*Size-Structure Influences on Daphnia Population Dynamics*

The numerical computations carried out with the escalator boxcar train for the Kooijman-Metz population model show that the *Daphnia* and algal populations display either one of two distinct types of oscillatory dynamics or approach a stable equilibrium. The first type of fluctuation is found with low values for both the *Daphnia* background mortality,  $\delta$ , and the algal carrying capacity,  $C$ . The second type of fluctuation is found with high values for both parameters. Increasing  $\delta$  and  $C$  from low values to high values causes a gradual shift from the first type of oscillation to the second. A stable equilibrium occurs primarily at intermediate to high levels of the *Daphnia* background mortality and low values of the carrying capacity.

At low values of  $\delta$  and  $C$ , the oscillations in *Daphnia* density have a relatively large amplitude compared to the oscillations in the algal density (fig. 1a). Moreover, the two populations cycle almost in antiphase, that is, maxima in the *Daphnia* density coincide with minima in the algal density and vice versa. The demographic structure of the *Daphnia* population exhibits drastic changes during a cycle (fig. 1b): A cycle is initiated by the maturation of a large number of individuals, which gives rise to a peak of reproduction. The large number of *Daphnia* subsequently brings down the algal density to low levels, which induces a decrease in reproduction and a slowing down of juvenile development. The algal density can recover as soon as the background mortality has sufficiently decreased the *Daphnia* population, which gives rise to a new burst of maturing *Daphnia*.

The slowing down and subsequent speeding up of juvenile development in this first type of oscillatory behavior result in large fluctuations in the time delay between the birth of a *Daphnia* and the onset of its reproduction. This variable maturation delay is the main cause of the oscillations. In contrast, the mean adult fecundity shows little variation during a cycle. Since at its maximum density the *Daphnia* population consists largely of juvenile individuals, the mean individual size within the *Daphnia* population fluctuates in antiphase with its density. This mitigates fluctuations in the total feeding rate of the *Daphnia* population and is the main reason for the smaller amplitude in algal density. The cycles with these parameter values are completely induced by the *Daphnia* life history; the predator-prey interaction between *Daphnia* and algae does not play a direct role (De Roos et al. 1990).

With high values of  $\delta$  and  $C$ , the oscillatory dynamics looks very much like the predator-prey cycles that are known from classical models of the Lotka-Volterra type. The amplitude in algal density is larger than the amplitude in *Daphnia* density, and the *Daphnia* lags behind by roughly 1/4 period (see fig. 2a). The demographic structure of the *Daphnia* population is also relatively stable during a cycle (fig. 2b): The proportion of juveniles versus adults is roughly constant. The relatively high algal density results in a short maturation delay that appears to fluctuate very little. The adult fecundity, however, shows large fluctuations,

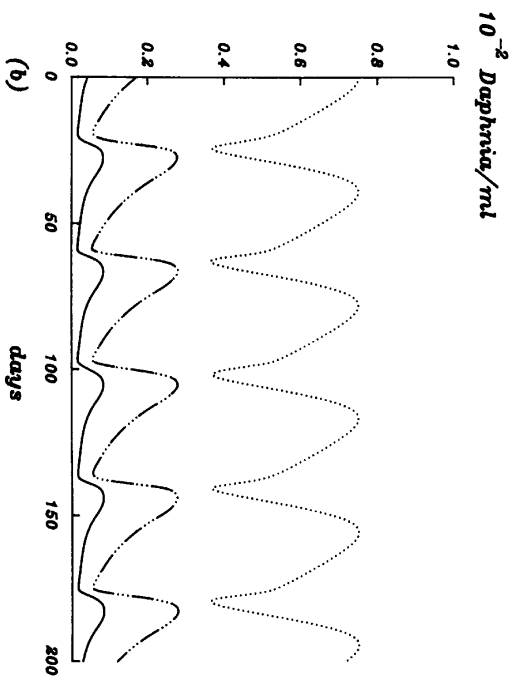
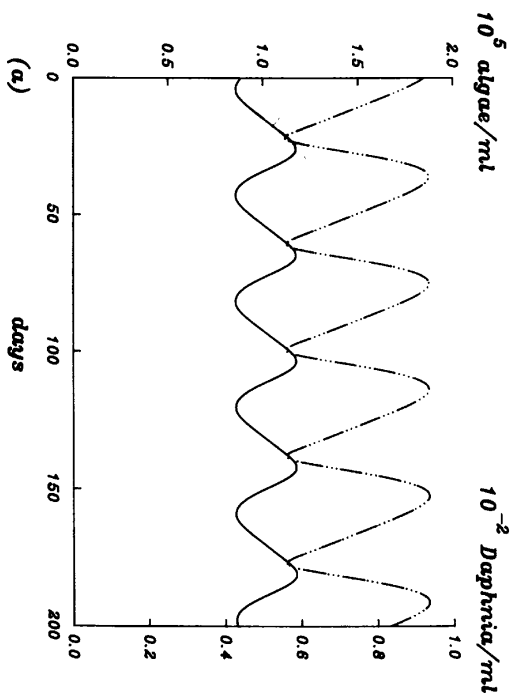


FIG. 1.—Dynamic behavior of the *Daphnia* model with a low *Daphnia* death rate ( $\delta = 0.055$ ) and a low algal carrying capacity ( $C = 2.0 \times 10^5$ ). *a*. Simulated *Daphnia* (dots and dashes) and algal (solid line) densities. *b*. Population birth rate (solid line) and density of juvenile (dotted line) and adult (dots and dashes) *Daphnia*.

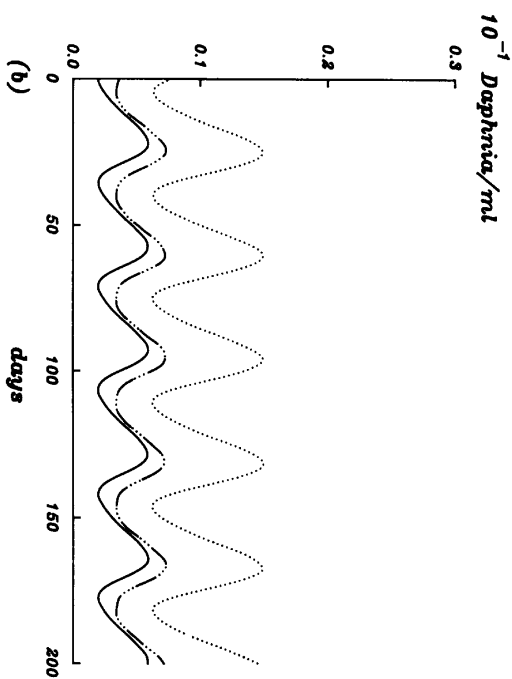
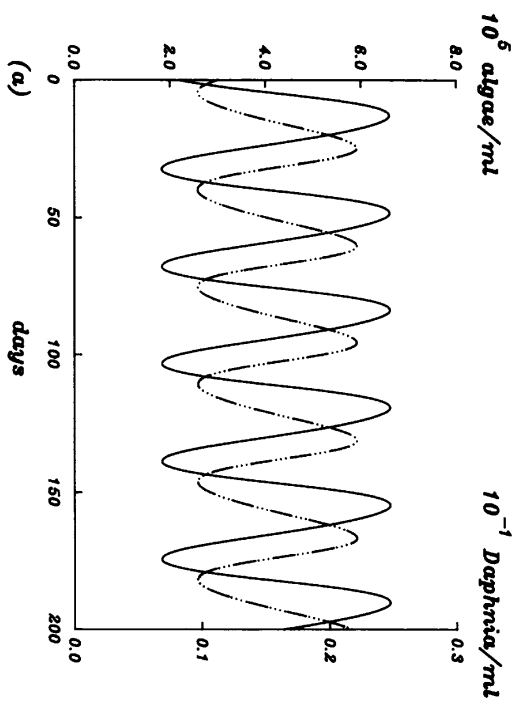


FIG. 2.—Dynamic behavior of the *Daphnia* model with a high *Daphnia* death rate ( $\delta = 0.25$ ) and a high algal carrying capacity ( $C = 1.0 \times 10^6$ ). *a*. Simulated *Daphnia* (dots and dashes) and algal (solid line) densities. *b*. Population birth rate (solid line) and density of juvenile (dotted line) and adult (dots and dashes) *Daphnia*.

partly owing to the fact that at the algal maximum the mean size of the adult *Daphnia* attains a maximum as well. This type of oscillation results from the interaction between the algae and the *Daphnia*; the life history of the *Daphnia* hardly plays a role. More specifically, the cycles arise because the algae escape the control imposed by the *Daphnia* during the increasing phase of the cycle and can hence grow unrestrictedly for a while. For this reason, we have referred to these (classical predator-prey or paradox-of-enrichment) cycles as "prey-escape" cycles (De Roos et al. 1990).

The two types of cycles displayed by our model resemble the two classes of fluctuating dynamics found by Murdoch and McCauley (1985; McCauley and Murdoch 1987). On the basis of the amplitudes of the *Daphnia* and the algae and the phase shift between their fluctuations, the type 2 dynamics distinguished by McCauley and Murdoch (1987) may be identical to our prey-escape cycles, while McCauley and Murdoch's type 3 dynamics may be identical to our maturation-delay cycles. These last two also appear similar with respect to the demography during the cycle, although they differ in some details (for instance, the initiation of a cycle by the maturation of a large number of *Daphnia*). The similarity between the two types of cycles displayed by the model and the two distinguished by McCauley and Murdoch supports their main idea that the different types of dynamics can arise by quantitative changes in the vital rates. Moreover, the model results provide insight into potential mechanisms underlying the two types of dynamics.

With a higher food level, both the ultimate size and the growth rate of the *Daphnia* increase. This results in a change in the growth curve (the size of an individual as a function of its age), a phenomenon we refer to as "growth-curve plasticity" (De Roos et al. 1990). The growth-curve plasticity affects both individual feeding and reproduction: Higher food levels on the one hand result in a shorter maturation delay and on the other in a larger size at every single age, which in turn increases the individual feeding and reproduction capacity. The influence on reproduction is destabilizing, mainly because of the change in the maturation delay. On the other hand, the influence on feeding is stabilizing, because it allows adjustment to low food densities by inducing smaller sizes and hence reducing the individual feeding rate.

These two opposing effects of growth-curve plasticity have as an effect that, with the same values for the *Daphnia* background mortality and the algal carrying capacity, the two populations can either be in stable equilibrium or display cyclic behavior. Even coexistence of two different types of cyclic behavior is possible with the same parameter values (De Roos et al. 1990). It is unclear to what extent this coexistence of different dynamic patterns with the same parameter values is of importance in natural systems, but the influence of growth-curve plasticity on feeding, in particular, seems to be a potentially important mechanism that can stabilize predator-prey interactions.

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APPENDIX A

COMPARISON OF ESCALATOR BOXCAR TRAIN AND MATRIX FORMULATIONS  
THE AGE-STRUCTURED MODEL

In this section we show the equivalence of the escalator boxcar train and the matrix formulation for the basic age-structured model. Assume that the last reproduction pulse took place at time  $t^*$  and that the population state at that time was given by the vector quantities  $\lambda_i(t^*)$  and  $\alpha_i(t^*)$ , the number and age of the individuals in the various cohorts, respectively. Let  $\tau$  denote the time elapsed since this last reproduction pulse. Integration of the second ODE in equations (2) yields

$$\alpha_i(t^* + \tau) = \alpha_i(t^*) + \tau = i + \tau. \tag{A1}$$

The first ODE in equations (2) is subsequently integrated to yield an expression for  $\lambda_i(t^* + \tau)$ , while the above expression is used to replace  $\alpha_i$ :

$$\lambda_i(t^* + \tau) = \exp \left\{ - \int_0^\tau q[\alpha_i(t^* + \xi)] d\xi \right\} \lambda_i(t^*) = \exp \left\{ - \int_0^\tau q(i + \xi) d\xi \right\} \lambda_i(t^*). \tag{A2}$$

At the start of the next reproduction pulse at time  $t^* + 1^-$  (as before,  $t^* + 1^-$  denotes the value of  $t$  just prior to  $t^* + 1$ ), the number and age of the individuals in the  $i$ th cohort still alive are hence

$$\lambda_i(t^* + 1^-) = \exp \left\{ - \int_0^1 q[\alpha_i(t^* + \xi)] d\xi \right\} \lambda_i(t^*) = \exp \left\{ - \int_0^1 q(i + \xi) d\xi \right\} \lambda_i(t^*)$$

$$\text{and} \tag{A3}$$

$$\alpha_i(t^* + 1^-) = \alpha_i(t^*) + 1 = i + 1.$$

Applying the reproduction equations (3) and the renumbering scheme (4) to the quantities  $\lambda_i(t^* + 1^-)$  and  $\alpha_i(t^* + 1^-)$ , we obtain the following expressions for  $\lambda_i(t^* + 1^+)$  and  $\alpha_i(t^* + 1^+)$ , the number and age, respectively, of the individuals in the  $i$ th cohort after the reproduction pulse, in terms of  $\lambda_i(t^*)$  and  $\alpha_i(t^*)$ :

$$\lambda_{0,t^*+1^+} = \sum_{i=0}^n m[\alpha_i(t^* + 1^-)] \lambda_i(t^* + 1^-) = \sum_{i=0}^n m(i + 1) \exp \left\{ - \int_0^1 q(i + \xi) d\xi \right\} \lambda_i(t^*),$$

$$\alpha_{0,t^*+1^+} = 0,$$

$$\lambda_{i,t^*+1^+} = \lambda_i(t^* + 1^-) = \exp \left\{ - \int_0^1 q(i + \xi) d\xi \right\} \lambda_i(t^*), \tag{A4}$$

and

$$\alpha_{i,t^*+1^+} = \alpha_i(t^* + 1^-) = i + 1,$$

for  $i = 0, \dots, n - 1$ . These equations can also be written as equation (1a) with the following expressions for  $P_i$  and  $F_i$  in terms of the instantaneous mortality rate  $q(a)$

the maternity function  $m(a)$ :

$$P_i = \exp \left\{ - \int_0^1 q[\alpha_i(t) + \xi] d\xi \right\} = \exp \left\{ - \int_0^1 q(t + \xi) d\xi \right\} \quad (A5)$$

and

$$F_i = m[\alpha_i(t + 1)]P_i = m(t + 1)P_i.$$

The expressions show the relation between the entries in the Leslie matrix  $A$  of equations (1) and the age-dependent maternity and individual mortality functions,  $m(a)$  and  $q(a)$ , respectively, and hence the equivalence of the EBT and the Leslie matrix formulation.

#### THE SIZE-STRUCTURED MODEL

If we want to express the size-structured model in terms of a matrix formulation, we can formally follow the same derivation as presented for the age-structured model (see above). Formal integration of the ODE for  $\lambda_i(t)$  and application of the reproduction and renumbering equations for the size-structured model (see table 1, pt. B) would yield

$$P_i = \exp \left\{ - \int_0^1 q[\sigma_i(t + \xi)] d\xi \right\} \quad (A6)$$

and

$$F_i = m[\sigma_i(t + 1)]P_i.$$

These are only formal expressions, because, in order to have explicit expressions for  $P_i$  and  $F_i$ , we need an expression for  $\sigma_i(t)$  as an explicit function of time. In general, such an expression, which must be the solution of the ODE for  $\sigma_i(t)$  (see table 1, pt. B), cannot be found. Only with very special choices of the growth function  $g(s)$  does an analytical solution for  $\sigma_i(t)$  exist. An example of such a special choice is von Bertalanffy growth (von Bertalanffy 1934). Moreover, even with an analytical function for  $\sigma_i(t)$  it is likely that the integral in the expression for  $P_i$  can only be evaluated numerically. For this reason the EBT formulation is probably easier for studying the dynamics of the population.

#### APPENDIX B

In this appendix we derive the ordinary differential equations that describe the dynamics of the cohort in creation between  $t$  and  $t + \Delta$ . Apart from the usual death and development terms, these equations also contain some terms due to the reproduction process. For the time being we make the simplifying (but not necessary) assumption that the individuals of the cohort in creation itself do not reproduce.

If no reproduction at all took place, the cohort in creation would be identical to all other cohorts. The dynamics of  $\lambda_0(t)$  and  $\mu_0(t)$ , the number and mean size of the individuals, would be described by

$$d\lambda_0/dt = -q(x, \mu_0)\lambda_0 \quad (B1)$$

and

$$d\mu_0/dt = g(x, \mu_0)$$

(compare table 1). The product quantity  $\mu_0\lambda_0$  represents the total biomass of the individuals in the cohort in creation. Its dynamics can be derived from equations (B1) by applying the product rule for differentiation:

$$d\mu_0\lambda_0/dt = \lambda_0 d\mu_0/dt + \mu_0 d\lambda_0/dt = g(x, \mu_0)\lambda_0 - q(x, \mu_0)\mu_0\lambda_0. \quad (B2)$$

The function  $b(x, s)$  is assumed to describe the reproduction rate of an individual of size  $s$  at a food density  $x$ . Hence, if reproduction does occur, the total reproduction from

individuals in the  $i$ th internal cohort equals  $b(x, \mu_i)\lambda_i$ . Summing these contributions from all the internal cohorts yields for the dynamics of  $\lambda_0$  the following ODE:

$$d\lambda_0/dt = -q(x, \mu_0)\lambda_0 + \sum_{i=1}^n b(x, \mu_i)\lambda_i. \quad (B3)$$

The last summation term in this ODE describes the inflow of newborn individuals from all the internal cohorts. Since individuals are born with a size  $s_b$ , the total increase in biomass due to reproduction equals the product of  $s_b$  and the summation term in equation (B3). The dynamics of the quantity  $\mu_0\lambda_0$  representing the biomass of the cohort in creation is therefore described by

$$d\mu_0\lambda_0/dt = \lambda_0 d\mu_0/dt + \mu_0 d\lambda_0/dt = g(x, \mu_0)\lambda_0 - q(x, \mu_0)\mu_0\lambda_0 + \sum_{i=0}^n s_i b(x, \mu_i)\lambda_i. \quad (B4)$$

By substituting equation (B3) into equation (B4) we can derive the ODE for  $\mu_0$  which leads to the following set of equations:

$$d\lambda_0/dt = -q(x, \mu_0)\lambda_0 + \sum_{i=1}^n b(x, \mu_i)\lambda_i \quad (B5)$$

and

$$d\mu_0/dt = g(x, \mu_0) + [s_b - \mu_0]\lambda_0 \sum_{i=1}^n b(x, \mu_i)\lambda_i.$$

The occurrence of  $\lambda_0$  in the denominator of the last ODE of this system causes some difficulties if  $\lambda_0 = 0$ . For computational purposes it is therefore much more convenient to replace this equation by an ODE for the quantity  $\pi_0 := (\mu_0 - s_b)\lambda_0$ . This latter quantity is a measure of the biomass of the individuals in the cohort, though relative to the size at birth,  $s_b$ . Since the biomass of a newborn individual equals  $s_b$ , the inflow of newborn individuals into the cohort in creation does not influence the dynamics of this quantity,  $\pi_0$ . The ODE for  $\pi_0$  can be derived from the equality

$$\frac{d\pi_0}{dt} = \frac{d(\mu_0 - s_b)\lambda_0}{dt} = \frac{d\mu_0\lambda_0}{dt} - s_b \frac{d\lambda_0}{dt}$$

and expressions (B3) and (B4). However, since we replace the ODE for  $\mu_0$  with an ODE for  $\pi_0$ , the functions  $g$  and  $g$  cannot be evaluated at  $\mu_0$  anymore. Therefore,  $g(x, \mu_0)$  and  $g(x, \mu_0)$  are approximated by their first-order Taylor expansions around  $s = s_b$ :

$$q(x, \mu_0) \approx q(x, s_b) + (\mu_0 - s_b)q_s(x, s_b) \quad (B6)$$

and

$$g(x, \mu_0) \approx g(x, s_b) + (\mu_0 - s_b)g_s(x, s_b),$$

in which  $q_s$  and  $g_s$  represent the derivatives of  $q(x, s)$  and  $g(x, s)$  with respect to  $s$ .

The system of ODEs in equations (B5) is hence replaced by the following, equivalent system of ODEs for  $\lambda_0$  and  $\pi_0$ :

$$d\lambda_0/dt = -q(x, s_b)\lambda_0 - q_s(x, s_b)\pi_0 + \sum_{i=1}^n b(x, \mu_i)\lambda_i \quad (B7)$$

and

$$d\pi_0/dt = g(x, s_b)\lambda_0 + g_s(x, s_b)\pi_0 - q(x, s_b)\pi_0.$$

These equations describe the dynamics of the cohort in creation from its start at time  $t$  until its transformation into an internal cohort at  $t + \Delta$ . If the individuals in the cohort in

creation reproduce themselves, this reproduction can be included in the summation term in the first ODE in equations (B7) as long as  $\lambda_0 \neq 0$ . The reproductive contribution equals  $b(x, \mu_0) \lambda_0$ , just like the contributions of the other cohorts, while the quantity  $\mu_0$  is defined as  $s_b + \pi_0/\lambda_0$ , as long as  $\lambda_0 \neq 0$ .

The equations that describe the continuous-reproduction model more correctly make use of a partial differential equation. The escalator boxcar train formulation is only a numerical approximation of this equation. The more consistent model formulation can be derived by following the lines set out by Metz and Diekmann (1986; Metz et al. 1988):

$$\partial n(t, s)/\partial t + qg(x, s)n(t, s)/\partial s = -q(x, s)n(t, s),$$

$$g(x, s_b)n(t, s_b) = \int_{s_b}^{\infty} b(x, s)n(t, s)ds,$$

$$n(0, s) = \Psi(s), \quad (B8)$$

$$dx/dt = R(x) - \int_{s_b}^{\infty} l(x, s)n(t, s)ds,$$

and

$$x(0) = x_0,$$

in which  $n(t, s)$  is a density function over the size range  $[s_b, \infty)$ , which represents the population, and  $\Psi(s)$  and  $x_0$  are the initial conditions at time  $t = 0$ , which are assumed to be known. The functions  $g$ ,  $q$ , and  $b$  are the same as in the EBT formulation.

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