

# Population Models Incorporating Physiological Structure: A Quick Survey of the Basic Concepts and an Application to Size-Structured Population Dynamics in Waterfleas

J. A. J. METZ, A. M. DE ROOS and F. VAN DEN BOSCH

## 1 Introduction

In this chapter we give a survey of the modeling methodology for physiologically structured populations developed in Metz and Diekmann (1986) with a stress on simple techniques and applications. The main application considered is a size- (and age-) structured model for *Daphnia* population dynamics based on the ideas in Kooijman and Metz (1984). Although admittedly considerably simplified, this model appears to be able to generate all three types of observed *Daphnia* population behavior distinguished by Murdoch and McCauley (1985), a feat not (yet) reproduced by any of its competitors.

### 1.1 Why Structure?

Any mathematical model, just as any experiment, necessarily entails a good deal of simplification. The idea is to study mechanisms in their bare essentials, unobscured by all the wonderful detail present in nature. The ultimate aim is to help unravel the natural network of cause and effect by elucidating the general principles pertaining to its links. Therefore any simplifications made by the modeler, or rather any complexity retained, should directly bear on the principles he or she is searching for; and model and observation should be confronted judiciously, taking each for what it is worth.

In the classical lumped models of population dynamics, all individuals are treated as if they were the same. This is a useful ploy when the essentials of the population process under study can be captured in a few empirically meaningful parameters that do describe the gross interactions among individuals.

Usually the individuals making up a population are far from the same, and quantities like per capita birth and death rates are but "population properties", i.e., averages over the whole population, instead of direct reflections of chances common to all individuals. This often precludes the in-depth quantitative confrontation of lumped models with real data.

A second limitation of lumped models is that the essence of many mechanisms determining population behavior is directly related to precisely those individual differences referred to above, as, for example, when food scarcity af-

fects reproduction mainly indirectly, by keeping individuals longer in the non-reproductive size range.

Apparently there is a need for modeling strategies, and corresponding mathematical toolboxes, that not only take into account the total size of a population but also its structure, where "structure" refers to any subdivision on the basis of one or more traits of the individuals. In this paper we shall concentrate on physiological structure, where the adjective "physiological" serves to single out traits such as age or size, which reflect dynamical processes in the individual.

### 1.2 State Representations

Below we shall often need corresponding concepts on the individual and the population levels. The prefixes *i*- and *p*- will be used as distinguishing qualifiers.

#### 1.2.1 The *i*-State

The fact that we are looking for models with a mechanistic pretension means that we cannot just use any collection of *i*-traits: the traits considered should together qualify as *i*-state.

Loosely speaking, a collection of variables qualifies as the state of a system if (1) the behavior (output) of the system at time  $t$  is fully determined by the values of these variables plus the condition of the environment (input) at  $t$ , and (2) the values of these variables at  $t + \tau$  are fully determined by their values at  $t$  plus the intervening environmental history. Here "fully determined" should be interpreted in a stochastic sense: taking account of the past does not improve the prediction, all its influence is channeled through the present state.

Below we shall allow *i*-outputs to be stochastic, but we shall consider only deterministic *i*-state movements. We shall moreover assume that we may characterize the *i*-state by a finite list of continuous variables; in other words, the *i*-state will be a finite dimensional vector. The components of the *i*-state vector we call *i*-state variables.

*Example:* If the probability of producing offspring as well as offspring number, the probability of dying, and the feeding rate of an individual (i.e., the population-dynamically relevant *i*-behavior) all depend only on its size and the current food conditions, and if growth only depends on the current size and the current food conditions, size qualifies as *i*-state.

*i*-State representations can be constructed using either mechanistic, i.e., physiological, or purely empirical, input-output-based, considerations. Examples of state variables of a physiological provenance are size and energy reserves; examples of state variables constructed from input-output data are (physiological) age and development index.

#### 1.2.2 The *p*-State

The tenet of the physiologically structured population methodology as set out in Metz and Diekmann (1986) is that we should take the *p*-state to be a frequency

Institute of Theoretical Biology, University of Leiden, Groenhovensstraat 5, 2311 BT Leiden, The Netherlands

Size-Structured Populations  
B. Ebenman and L. Persson (Eds.)

distribution over the space of possible  $i$ -states  $\Omega$ . This frequency distribution serves as the mathematical counterpart of the real population present in nature. The dynamics of the  $p$ -state takes the form of a continual shifting of this frequency distribution due to the continuous movement of individuals through  $\Omega$  in the course of their lives, combined with local decreases due to deaths, and local increases as a result of births. Any  $p$ -outputs, such as for example total population size or food consumption, can be calculated as integrals of this frequency distribution with some weighting function.

Implicit in this picture of a population is the assumption that all individuals experience the same environmental inputs, such as food availability or predator density. Biologically this is equivalent to the individuals (or the environment) mixing homogeneously on the time scale of the processes under study.

A final assumption will be that we are dealing with large total numbers of individuals, so that we can phrase our models in a deterministic fashion. This also entails that we can represent the  $p$ -state by a density function  $n$ , where  $n(t, x) dx$  is the number (or rather number per unit of area of volume) of individuals in a little  $\Omega$ -volume of size  $dx$  around the  $i$ -state  $x$ . (If you are not familiar with vector notation, please imagine that we are dealing with scalar  $i$ -states only. There really is not a great difference.)

### 1.3 Concluding Remarks

The argument so far may be summarized in the following recipe for the construction of a physiologically structured population model:

1. Track down an appropriate set of  $i$ -state variables (e.g., size and age) and determine the corresponding  $i$ -state space  $\Omega$ .
2. Find expressions for the deterministic motion of the  $i$ -state (growing, "proceeding of time"), in dependence on the  $i$ -state itself and the environmental conditions.
3. Find expressions for the rate of occurrence of the stochastic jump contributions (deaths, births), again in dependence on  $i$ -state and environment.

To this we have to add:

4. Write down equations for the  $p$ -state incorporating those features, and, last but not least,
5. analyze the resulting  $p$ -equations to distil relevant biological information.

Step (4) will be covered in general terms in Section 2. There we shall also consider two equivalent alternative equations which can be of considerable help when it comes to step (5). If that section seems unduly abstract we ask you to bear with us, as the examples in the next sections probably will clarify the issue (and if it is really too much: Subsections 2.2 and 2.3 can, if necessary, be skipped on first reading).

As yet there are few general procedures for dealing with step (5), but neither are there for lumped population models of any complexity. In Section 3 we shall give some indication of what can be done. The example in that section has size

as its main  $i$ -state variable in accordance with the theme of this volume. However, the reason why we worked so hard on studying this example to begin with, is that size usually exerts a quite drastic influence on the population dynamical behavior of ectotherms, making it an  $i$ -state variable worthy of a great deal of attention.

## 2 Population Equations

### 2.1 The $p$ -Equation

In this subsection we shall discuss in general terms the basic differential equation for the  $p$ -state, expressing the balance of all the infinitesimal contributions to the change in  $n(t, x)$ . For more details you are referred to Metz and Diekmann (1986) and the references therein.

To simplify the discussion, we shall start by assuming that the  $i$ -state is one-dimensional, so that we can make the imagery of a shifting frequency distribution somewhat more concrete by visualizing the population as a heap of sand lying on a conveyor belt, with  $x$  the distance from the start of the belt, as depicted in Fig. 1. Only this conveyor does not move everywhere with the same velocity: at time  $t$  and position  $x$  the local velocity equals the speed of movement of the  $i$ -state,  $v[E(t), x]$  where  $E(t)$  is the condition of the environment at time  $t$ . If you wish you may think of  $x$  as size, and of  $v[E(t), x]$  as the growth rate of individuals of size  $x$  at food availability  $E(t)$ .

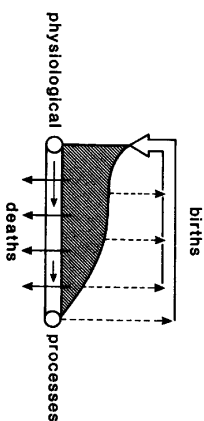
If we neglect births and deaths, we can calculate the change in the number of individuals between  $x$  and  $x + dx$ ,  $\partial n(t, x) dx / \partial t$ , by subtracting the outstream at  $x + dx$ ,  $v[E(t), x + dx] n(t, x + dx)$ , from the instream  $v[E(t), x] n(t, x)$  at  $x$ . Next we divide through by  $dx$ . Adding births and subtracting deaths finally gives

$$\frac{\partial n(t, x)}{\partial t} = \frac{\partial v[E(t), x] n(t, x)}{\partial x} + b_t[E(t), x] n(t, x), \quad (1a)$$

where the index  $I$  is added to indicate that we are dealing with a birth rate and a per-capita death rate pertaining to the interior of  $\Omega$ .

The fact that  $v$  depends on  $x$  has an interesting consequence. A conveyor belt can only move at different speeds at different places if it contracts wherever it slows down and expands wherever it speeds up. Where it contracts the sand cumulates, as the same amount of sand has to be accommodated on a smaller amount of length, and where it expands the sand spreads out. To see how this effect is accounted for in Eq. (1a) we write

Fig. 1. Conveyor belt representation of a physiologically structured population with a one-dimensional  $i$ -state space



$$\frac{\partial v n}{\partial x} = v \frac{\partial n}{\partial x} + \frac{\partial v}{\partial x} n.$$

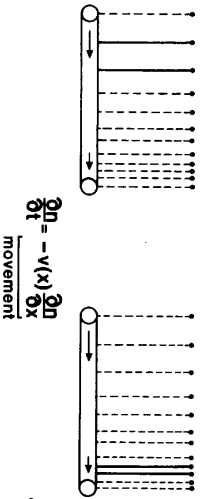
If  $n$  had represented the heights of a collection of rigid sticks riding along with the conveyor belt, as depicted in Fig. 2A, only the term  $v \partial n / \partial x$  would have appeared in our equation (we would then of course also miss out the birth and death terms). The term  $\partial v / \partial x n$  takes care of mass conservation;  $-\partial v / \partial x$  is positive where the conveyor belt contracts and negative where it expands.

Apart from the deaths represented by  $\mu_1 n$ , some more deaths may be implicit in the combination of our assumptions about  $\Omega$  and Eq. (1a). If the conveyor belt is of finite length, say that it ends at  $x_{max}$ , and  $v[E(t), x_{max}]n(t, x_{max}) > 0$ , then there is a net loss of sand at the end. This occurs for example when  $x$  represents age, and we decide to idealize a near constant duration of life by letting everybody die at exactly  $x_{max}$  [a mathematical alternative is formally to extend  $\Omega$  beyond  $x_{max}$ , and to set  $n(t, x)$  equal to zero for  $x > x_{max}$ ].

Our balance law expressed in (1a) has to be completed by indicating what happens at the start of the conveyor belt. We shall denote the corresponding  $i$ -state as  $x_b, x_b < x_{max}$ , where the  $b$  symbolizes that this usually is the place where newborns start their lives [the main exception are purely size-dependent models

**ELASTIC CONVEYOR BELT**

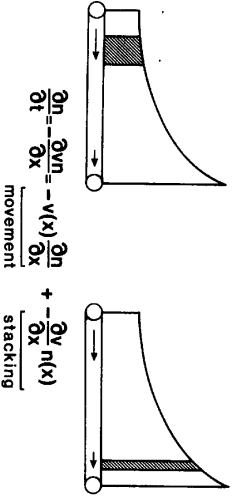
pure transport



$$\frac{\partial n}{\partial t} = -v(x) \frac{\partial n}{\partial x}$$

movement

transport plus mass conservation



$$\frac{\partial n}{\partial t} = -v(x) \frac{\partial n}{\partial x} + \frac{\partial v}{\partial x} n(x)$$

movement      stacking

Fig. 2. The effect of local speed changes of the conveyor belt

in which individuals multiply by dividing; it is to accommodate such models as well, that we introduced the term  $b_1$  in Eq. (1a)]. Equating the rate at which individuals enter  $\Omega$  past  $x_b$  to the birth rate at the boundary,  $b_B$ , gives

$$v[E(t), x_b]n(t, x_b) = b_B(t, x_b). \tag{1b}$$

[Note that the second argument in  $b_B(t, x_b)$  takes a fixed value; it is introduced only as a preparation for the case of higher dimensional  $\Omega$ .]

The  $p$ -equation is completed by giving recipes for calculating the birth rates by summing the births coming from all different sorts of parents

$$b_B(t, x_b) = \int_{\Omega} \beta_B[E(t), x_b, y]n(t, y)dy,$$

$$b_1(t, x) = \int_{\Omega} \beta_1[E(t), x, y]n(t, y)dy, \tag{1c}$$

where  $\beta_B$  and  $\beta_1$  are the per capita birth rates (usually either  $\beta_1$  or  $\beta_B$  is zero), and by giving recipes for calculating the relevant  $p$ -outputs  $F_i, i = 1, \dots, k$ . The latter are necessarily of the form

$$F_i(t) = \int_{\Omega} f_i[E(t), x]n(t, x)dx. \tag{1d}$$

An example is  $k = 2, F_1$  the population feeding rate, and  $F_2$  the population size, in which case we should choose  $f_1$  to be the food-availability and  $i$ -state-dependent  $i$ -feeding rate, and  $f_2[E(t), x] = 1$ .

All the quantities  $v, \mu_1, \beta_B, \beta_1$ , and  $f_i$  in theory at least may depend on the condition of the environment. Whether this also is the case in practice depends on the particular biological problem under consideration. For a given course of the environment Eq. (1) is linear, which is an important mathematical asset. However, we may also make the environment dependent on the  $p$ -output, either indirectly, for example by letting  $v$  depend on food availability and writing down an equation for the food dynamics which contains the  $p$ -feeding rate as one of its terms, or directly, for example by letting the death rate  $\mu_1$  include a component due to cannibalism, thus making the coupled equations nonlinear. It is especially this possibility of incorporating feedbacks through the environment which allows us to study all sorts of interesting biological questions.

The generalization of Eq. (1a) to higher dimensional  $\Omega$  (see Fig. 3) is

$$\frac{\partial n(t, x)}{\partial t} = - \sum_i \frac{\partial v_i[E(t), x]n(t, x)}{\partial x_i} + b_1(t, x) - \mu_1[E(t), x]n(t, x), \tag{2a}$$

where the  $v_i$  denote the components of the  $i$ -state velocity in the direction of the coordinate axes. The generalization of Eq. (1b) is

$$h(x_b, v[E(t), x_b])n(t, x_b) = b_B(t, x_b) \text{ for } x_b \in \partial_+ \Omega, \tag{2b}$$

where  $h$  denotes the so-called "inward normal" at the instream boundary  $\partial_+ \Omega$  (i.e., a vector of unit length orthogonal to  $\partial_+ \Omega$  pointing into  $\Omega$ ) and  $\langle \dots \rangle$  denotes the inner product. The corresponding Eqs. (2c) and (2d) look exactly the same as their one-dimensional counterparts.

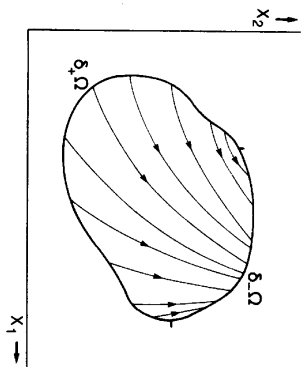


Fig. 3. A hypothetical two dimensional i-state space  $\Omega$

2.2 The Cohort Representation

We can also look at a population as a collection of cohorts. The cohort representation and the representation as a frequency distribution over an i-state space coincide only in the purely age-dependent case.

In the general case it is not sufficient to distinguish cohorts by how long ago they were born,  $a$  (from age). We also have to distinguish between individuals born with different i-states  $x_b$ . Moreover we have to keep track of the i-state of the individuals making up a cohort,  $x(t, a, x_b)$ . As the cohorts themselves are necessarily infinitesimally small, we introduce a density function  $m$  such that  $m(t, a, x_b) dx_b da$  equals the number of individuals having ages in an age bracket of size  $da$  around  $a$  and birth states in a small  $\Omega_b$ -volume of size  $dx_b$  around  $x_b$ , where  $\Omega_b$  is the set of possible birth states. By the same argument as in the previous section (we just have many age conveyor belts moving in parallel, one for each value of  $x_b$ ) we find that  $m$  satisfies

$$\frac{\partial m(t, a, x_b)}{\partial t} = -\frac{\partial m(t, a, x_b)}{\partial a} - \mu_1[E(t), x(t, \bar{x}, x_b)]m(t, a, x_b), \tag{3a}$$

together with

$$m(t, 0, x_b) = \int_0^1 \int_{\Omega_b} \beta[E(t), x_b, x(t, a, y_b)]m(t, a, y_b) dy_b da + b_0(t, x_b), \tag{3b}$$

where  $b$  is the birth rate, split up according to birth state  $x_b$ ,  $\beta$  is equal to either  $\beta_a$  or  $\beta_l$  depending on which of them is nonzero, and  $b_0$  represents the births from parents present at the start of the experiment; as these parents may be of mixed origins, and hence may have experienced different environmental histories, we cannot assume a simple relation between their i-state and their age plus state at birth even when the latter quantities are known.

To arrive at an equation for  $x(t, a, x_b)$  we first consider the case where  $x$  is size so that we may visualize  $x$  as the heights of a collection of growing sticks hitching a ride on the same conveyor belts as the cohorts. This picture has already made its appearance in the previous subsection, except that there the sticks did stay the same length. To account for the growth of the sticks we just add a growth term  $v[E(t), x(t, a, x_b)]$  at the right hand side:

$$\frac{\partial x(t, a, x_b)}{\partial t} = \frac{\partial x(t, a, x_b)}{\partial a} + v[E(t), x(t, a, x_b)], \tag{3c}$$

$$x(t, 0, x_b) = x_b. \tag{3d}$$

For the general case we only have to interpret  $v, x$  and  $x_b$  as vectors.

To calculate  $b_0$  we split up the parent population into "cohorts" characterized by their i-state  $y$  at  $t = 0$ . The cohort i-states as a function of time and initial cohort i-state we shall denote as  $x_0$ , and the corresponding density function representing the cohort sizes as  $m_0$ . Then

$$b_0(t, x_b) = \int_{\Omega} \beta[E(t), x_b, x_0(t, y)]m_0(t, y) dy. \tag{3e}$$

Moreover  $m_0$  and  $x_0$  satisfy the equations

$$\frac{\partial m_0(t, y)}{\partial t} = -\mu_1[E(t), x_0(t, y)]m_0(t, y), \quad m_0(0, y) = n(0, y), \tag{3f}$$

and

$$\frac{\partial x_0(t, y)}{\partial t} = v[E(t), x_0(t, y)], \quad x_0(0, y) = y. \tag{3g}$$

We complete the cohort representation by indicating how we should calculate the p-outputs:

$$F_l(t) = \int_0^1 \int_{\Omega_b} f_l[E(t), x(t, a, x_b)]m(t, a, x_b) dx_b da + F_{0l}(t), \tag{3h}$$

where  $F_{0l}(t)$  denotes the contribution by the survivors from the parent population,

$$F_{0l}(t) = \int_{\Omega} f_l[E(t), x_0(t, y)]m_0(t, y) dy. \tag{3i}$$

2.3 An Integral Equation for the Birth Rate

Equations (2) and (3) may both rightfully be considered generalizations of the McKendrick (Von Foerster) partial differential equation of age dependent population theory. The counterpart of Lotka's integral equation is

$$b(t, x_b) = \int_0^1 \int_{\Omega_b} B[E(t), a, x_b, y_b]b(t-a, y_b) dy_b da + b_0(t, x_b), \tag{4a}$$

where  $B[E(t), a, x_b, y_b] dx_b$  is the rate at which individuals born a time units ago in i-state  $y_b$  produce offspring in an  $\Omega_b$ -volume of size  $dx_b$  around  $x_b$ .  $b_0$  has already been defined above. This equation has to be completed with a number of equations from which  $B$  can be calculated. We first express  $B$  in the per-capita birth rate  $\beta$  and the probability  $\mathcal{P}$  that a prospective parent survived from its birth a time units ago to the present:

$$B[E(t), a, x_b, y_b] = \beta[E(t), x_b, x(t, a, y_b)] \mathcal{F}(t, a, y_b) \quad (4b)$$

$x$  satisfies Eq. (3c), for future reference here renamed into (4c), just as before, together with

$$x(t, 0, y_b) = y_b, \quad (4d)$$

and  $\mathcal{F}$  satisfies

$$\frac{\partial \mathcal{F}(t, a, y_b)}{\partial t} = -\frac{\partial \mathcal{F}(t, a, y_b)}{\partial a} - \mu_1[E(t), x(t, a, y_b)] \mathcal{F}(t, a, y_b), \quad (4e)$$

together with

$$\mathcal{F}(t, 0, y_b) = 1. \quad (4f)$$

The p-outputs can be calculated from

$$F_i(t) = \int_0^1 \int_{a_0}^1 f_i[E(t), x(t, a, y_b)] \mathcal{F}(t, a, y_b) b(t-a, y_b) dy_b da + F_{0i}(t). \quad (4g)$$

For any realistic population model both  $b_0(t, x)$  and  $F_{0i}(t)$  go to zero for large time. Therefore Eq. (4) suffices for the study of the long-term behavior of the population. If we wish to study an initial value problem we may just add (3e) to (3g) plus (3i).

## 2.4 Concluding Remarks

Equations (2), (3) and (4) are fully equivalent, Chapter III Section 4 of part A of Metz and Diekmann (1986) gives the formal mathematical machinery for transforming them into each other. However, they are not equivalent in the case with which they can be used in various applications: some problems are more easily investigated using (2) and others using (3) or (4). For example, in De Roos (1988) an efficient numerical technique is developed for the treatment of physiologically structured population models by what is essentially an unusual discretization of (3) in combination with an expansion procedure applied to (2). The various *Daphnia* simulations below were all performed using this technique. Therefore it is a good idea to keep them all three in mind, and to switch equations, and associated imagery, whenever there seems to be an advantage in doing so.

## 3 Example: *Daphnia* Population Dynamics

### 3.1 Introduction

In this section we shall treat in some detail a size- (and age-) structured model for the population dynamics of ectotherms. This model was originally developed with an eye on the waterflea *Daphnia magna*. Its experimental underpinning for different constant food availabilities is discussed in Kooijman and Metz (1984).

Various mathematical and biological fine points in the derivation of the p-equation, as well as further refinements of the model structure are considered in Diekmann et al. (1984), Metz and Diekmann (1986), Heijmans and Metz (1986), and Thieme (1988).

A number of detailed and complicated *Daphnia* models have been proposed (Sinko and Streifer 1969) or are currently under investigation, notably by Lynch (in press), by Nisbet, Gurney, McCauley and Murdoch (in prep), and by Kooijman (1986a, Kooijman, Van der Hoewen and Van der Werf in press). This presence of alternative, competing, frameworks adds a good deal to the scientific interest of the *Daphnia* work. At the two extremes, Lynch's model is mainly a collation of empirical curves pertaining to various aspects of the overall individual physiology, whereas Kooijman's model is to a large extent based on a priori considerations. The models by Nisbet and coworkers, and by Kooijman include energy reserves as a third i-state variable, in addition to size and age. This is especially important at times of rapid changes in food availability. Kooijman's model is a direct extension of the model described below. In contrast to the models by Lynch and by Nisbet and coworkers it was never meant to specifically mimic the known details of *Daphnia* physiology, but to provide insights of a general nature. Various papers by Kooijman (1986b, c, 1988) i.a. attest to its usefulness for collating data on individual growth physiology from all over the animal kingdom.

For the sake of tractability, we shall temporarily neglect the undoubted presence of energy reserves, as well as any other refinements. We just had to learn our trade in easy steps. Moreover, results from the simple model already are of considerable interest in their own right. After all, the search for principles that is science should be guided by a plethora of particulars. A logical next step should be investigating how our present results stand up against the various modifications that have been proposed.

## 3.2 Model Formulation

### 3.2.1 The i-Model

Below I will denote length and age. These are the i-state variables. The environment is characterized by only one variable, food availability (i.e., density or concentration)  $x$ . A survey of the identifiable parameter combinations together with their interpretation can be found in Table 1.

The model formulation starts from the simplified picture of an animal shown in Fig. 4, plus the assumption that animals of different sizes have similar geometries, so that surface area and (wet) weight are proportional to  $l^2$  and  $l^3$  respectively. Below we shall just identify these quantities; this only affects the values of the various proportionality constants. Food intake is assumed to be proportional to surface area and to depend on food availability through a hyperbolic functional response. The energy gained is channeled either to reproduction or basal metabolism plus growth in fixed proportions  $1 - \kappa$  and  $\kappa$ . Growth results only after basal metabolism has had its share, which is assumed to be proportional to the animal's weight, with proportionality constant  $\zeta$ . (All energetic



tween  $l_b$  and  $l_m = \kappa v / \zeta$ . This defines  $\Omega$ . Following the lines laid out in Section 2.1 we arrive at the p-equation

$$\frac{\partial n}{\partial t} = -\frac{\partial g n}{\partial l} - \mu n \quad \text{for } l < l(x)$$

$$n = 0 \quad \text{for } l > l(x)$$

$$g(x, l_b) n(t, l_b) = b(t) \quad (8a)$$

$$b(t) = \int_{l_b}^{l^*} \beta(x, l) n(t, l) dl. \quad (8b)$$

In the general case  $\Omega$  is a subset from the square spanned by the ages from 0 to  $a_{\max}$  and the lengths from  $l_b$  to  $l_m$ . The p-equation becomes

$$\frac{\partial n}{\partial t} = -\frac{\partial n}{\partial a} - \frac{\partial g n}{\partial l} - \mu n \quad \text{for } l < l(x)$$

$$n = 0 \quad \text{for } l > l(x) \quad (9a1)$$

$$n(t, 0, l) = b(t) \delta(l - l_b) \quad (9a2)$$

$$b(t) = \int_{\Omega} \beta(x, l) n(t, a, l) dl da, \quad (9b)$$

where  $\delta(y)$  denotes the Dirac delta function, i.e., a "function" which is zero everywhere except for an "infinitely high peak" at  $y = 0$  such that the surface area under this peak is exactly one.

The delta function in Eq. (9a2) is due to the fact that all young are born in one point of the one-dimensional instream boundary  $a = 0$  only, instead of being spread out over that boundary. Worse still, because all individuals in a cohort experience exactly the same environmental history they stay together. Therefore the density function  $n$  develops the same degeneracy, spawned by the delta function on the boundary (see Fig. 5). All the mass is concentrated on just a one dimensional curve in  $\Omega$ , the current, or period, age-length relation. As a result calculations using Eq. (9), even though still possible, are slightly unpleasant.

The idea of a cohort representation developed in Section 2.2 provides the way out. We just sweep all the mass onto the age axis, and write down the usual equation for the age distribution  $n(t, a)$  plus a separate equation which updates the

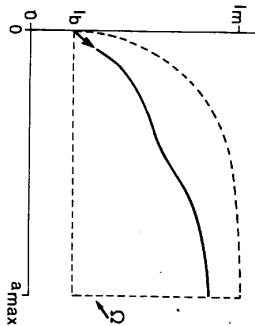


Fig. 5. The *Daphnia* i-state space, and the support of the population distribution (the current, or period, age length relation)

current age length relation  $l(t, a)$  (think again of that conveyor belt planted with growing sticks):

$$\frac{\partial n}{\partial t} = -\frac{\partial n}{\partial a} - \mu n \quad \text{for } l(t, a) < l(x)$$

$$n = 0 \quad \text{for } l(t, a) > l(x) \quad (10a)$$

$$n(t, 0) = b(t)$$

$$\frac{\partial l}{\partial t} = -\frac{\partial l}{\partial a} + g(x, l)$$

$$l(t, 0) = l_b \quad (10b)$$

$$b(t) = \int_0^{a_{\max}} \beta[l(t, a)] n(t, a) da. \quad (10c)$$

For the food dynamics we shall make three different choices. We start in Section 3.3 with

$$x(t) = x, \quad a \text{ parameter}. \quad (11)$$

In Section 3.4 we shall consider a chemostat-type food dynamics in which food is fed to the experimental tank at a rate  $\alpha$  per unit of volume, and removed again at a relative rate  $\beta$ , for example through decay or washout. The resulting environment equation is

$$\frac{dx}{dt} = \alpha - \beta x - v f(x) \int_0^{a_{\max}} l^2(t, a) n(t, a) da. \quad (12)$$

In this equation the feeding rate to the tank,  $\alpha$ , will be treated as a free parameter. In preparing the figures the relative decay rate  $\beta$  was kept fixed at  $0.5 \text{ d}^{-1}$ . Finally we shall consider self-renewing food, which we shall represent by the environment equation

$$\frac{dx}{dt} = \alpha x (1 - x/\beta) - v f(x) \int_0^{a_{\max}} l^2(t, a) n(t, a) da. \quad (13)$$

In this equation we shall treat the carrying capacity  $\beta$  as a free parameter. In preparing the figures the maximum capacity for self-renewal  $\alpha$  was set to either  $2 \text{ d}^{-1}$  (Fig. 10) or  $0.5 \text{ d}^{-1}$  (Fig. 11).

### 3.3 Constant Food Availability

When food availability is kept constant, the coupling between the equation for the current age-length relation and the age distribution goes only one way. The biological interpretation as well as Eq. (10b) (think of the conveyor belt interpretation again) both tell us that in that case the current age-length relation quickly stabilizes to the usual Von Bertalanffy growth curve, dependent only on the fixed, *Daphnia* parameters and the value of  $x$ . This in turn lets Eq. (10a) plus

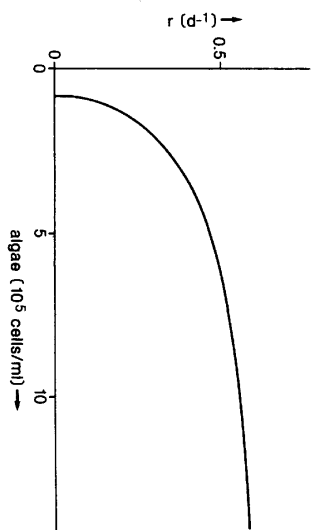


Fig. 6. Intrinsic rate of natural increase as a function of food density for the *Daphnia* model

Eq. (10c) degenerate into the usual equations of age dependent population theory in constant environments.

Figure 6 shows how the intrinsic rate of natural increase  $r$  would depend on food availability if there were no random deaths. From this figure one can immediately determine  $r$  for more realistic values of  $\phi$  using

$$r(\phi, x) = r(0, x) - \phi. \quad (14)$$

Random deaths just act as a constant dilution without affecting the composition of the population.

$r$  is seen to increase with  $x$ , in accordance with biological intuition. The critical value of the food concentration above which the population eventually grows and below which it eventually declines, we shall call  $x_c$ . To calculate  $x_c$  we just set  $r = 0$  in the characteristic equation. Alternatively we may go back to the  $i$ -equations and use the property that at  $x_c$  individuals produce on average exactly one young during their lifetime. (NB: The property of eventual exponential growth or decline under constant environmental conditions holds almost universally for structured population models, but the ability to write down a characteristic equation in just the intrinsic rate of natural increase is tightly linked to the existence of a finite collection of selected states such that any individual has to pass through at least one of these states during its life-time. In our *Daphnia* model this collection consists of the unique state at birth:  $a = 0, 1 = l_0$ .)

### 3.4 Dynamical Food

#### 3.4.1 Introduction

The results of the previous subsection could have been obtained just as easily direct from the  $i$ -model. The main reason for going through the complicated business of writing down  $p$ -equations is that this allows us to study the effect of food limitation.

Since the early work by Pratt (1943) a good number of papers on *Daphnia* population dynamics have been published. A detailed survey of published data on laboratory and (semi-)natural waterflea populations led Murdoch and

McCauley (1985; see also McCauley and Murdoch, 1987) to distinguish three qualitatively different types of dynamical behavior: (i) stable equilibrium, (ii) predator-prey oscillations, in which both the *Daphnia* and the food algae fluctuate with the same period, and (iii) pure *Daphnia* oscillations in combination with a barely fluctuating algal population. One of the challenges to the modeler is to reproduce all three types of behavior, including the elusive type (iii) oscillations, by means of just one model for the *Daphnia* population. In the next subsections we shall try to convince you that our *Daphnia* model is at least potentially capable of doing precisely this, plus producing a fourth type of oscillation, in which the *Daphnia* and the food are in antiphase instead of the usual one-quarter phase lag characteristic of predator-prey oscillations.

#### 3.4.2 The Stability of the Internal Equilibrium

At equilibrium the *Daphnia* population should neither grow nor decline. Apparently the value of the food density at equilibrium,  $\hat{x}$ , is set wholly by the *Daphnia* dynamics, making  $\hat{x} = x_c$ ; provided, of course, that  $x_c < x_0$ , the equilibrium of the food population in the absence of any *Daphnia*. If  $x_c > x_0$ , *Daphnia* goes extinct.

The equilibrium age-length relation is again a Von Bertalanffy growth curve. Formally this can be derived from Eq. (10b) with  $l(a)$  substituted for  $l(t, a)$ , making  $\partial l / \partial t = 0$ . In the same manner we can calculate  $\hat{n}(a)$  from Eq. (10a) after we have also set  $b(t) = b$ . The result is  $\hat{n}(a) = b \mathcal{F}(a)$ , where  $\mathcal{F}(a) = \exp(-\phi a)$  is the fraction of *Daphnids* that survives to age  $a$ . Substituting both results in either Eq. (12) or (13) finally leads to an explicit, though slightly cumbersome, expression for  $b$ .

Apparently the combination of the food and *Daphnia* dynamics leads to a unique interior equilibrium.

When we try to study the stability of the equilibrium we by necessity enter into a rather shady realm. At the present state of the art we cannot fall back on existing theory to answer even the first questions about existence and uniqueness of solutions to our full population equations. (That such questions are not trivial can be seen from the fact that Thieme (1988) has shown that Eq. (10) can indeed be rigged such that it does not allow a solution; fortunately the combination of conditions leading to this somewhat bizarre phenomenon is such that we feel safe in ignoring it for our present considerations.) However, we shall boldly plunge into the deep, and just assume that all the usual dynamical systems theorems hold good. This also means that the calculations which we describe below in general terms were formal only; the fact that the results of, for example, formal stability calculations and numerical solutions of the full population equations gave consistent results inspires some trust.

We start our study of the internal equilibrium by observing that it exists if and only if the trivial equilibrium, in which the *Daphnia* population is extinct, is unstable. By changing either  $a$  or  $\beta$  depending on the food dynamics or  $\phi$  we can let the interior equilibrium disappear or appear at will. When it appears it does so from the trivial equilibrium. The general results from bifurcation theory about the exchange of stability then imply that close to the trivial equilibrium it should

be stable. Moreover the absence of any other interior equilibria implies that it can only become unstable by merging with a, stable or unstable, limit cycle, in a so-called Hopf bifurcation.

To study the stability of the internal equilibrium more closely we can linearize Eq. (10) together with either Eq. (12) or (13). After going through the usual motions of substituting trial solutions which depend on time as  $\exp(-\lambda t)$  we end up, after a lot of messy algebra, with a characteristic equation in just the one complex variable  $\lambda$ . As in the case of constant  $x$ , this is made possible by the fact that all individuals have to pass through a unique  $i$ -state at birth. The Hopf bifurcation result cited above implies that we do not have to look for any real  $\lambda$ 's crossing zero. Therefore we can set  $\lambda = i\omega$ ,  $\omega$  real, and look for any parameter combinations which make this happen. Any stability changes are bound to occur at such parameter values. The stability diagrams in the next two subsections were all calculated in this way. The details of the calculations, which are not completely trivial, we hope to publish elsewhere.

### 3.4.3 Chemostat Food Dynamics

Figure 7 shows the stability diagram for the chemostat food dynamics [Eq. (13)]. It can be seen that the predatory death rate  $\phi$  exerts a fairly dominating influence, especially at high feeding rates to the tank  $a$ . Any changes in the food decay rate  $\beta$  change only the size of the peninsula that juts out from the unstable continent into the mare stabilitatis, but not the behavior of the stability boundary at high feeding rates.

Interestingly enough, Fig. 7 does not give the whole dynamical picture, as stability of the equilibrium may go together with the existence of a stable limit cycle. This happens in the area surrounding the peninsula, in particular in the bay separating the peninsula from the continent. As yet we have no idea of the extent of this feature.

Figure 8 shows the pattern of oscillations at high  $a$ . Observe that food and *Daphnia* are in clear antiphase. The phase relations between food and *Daphnia*

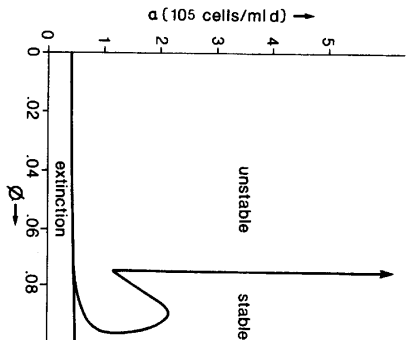


Fig. 7. The stability boundary for the interior equilibrium for the *Daphnia* model with chemostat food dynamics:  $a$  feeding rate to the tank,  $\phi$  random death (harvesting) rate

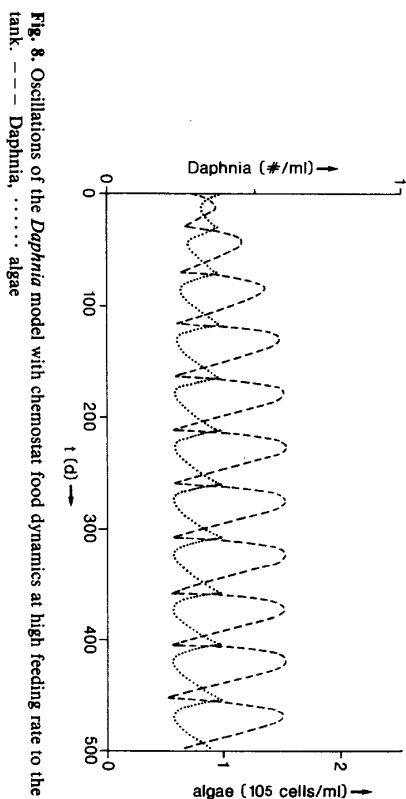


Fig. 8. Oscillations of the *Daphnia* model with chemostat food dynamics at high feeding rate to the tank. --- *Daphnia*, ..... algae

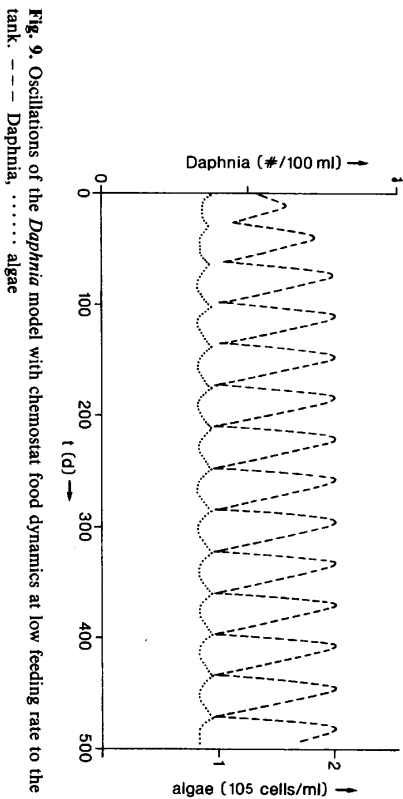


Fig. 9. Oscillations of the *Daphnia* model with chemostat food dynamics at low feeding rate to the tank. --- *Daphnia*, ..... algae

also provide a clue to the mechanism driving the oscillations. One feature which is not visible in Fig. 8, is that births occur in sharp peaks, starting with a very steep increase followed by a fairly gentle decline. The drop in food concentration coincides with the birth peak. When the new crop of young ages, their number, and that of their parents, decreases. This allows the food to recover. When the firstborns of a crop have grown large enough they start the new birth peak. So far this is just the variable maturation time scenario of Nisbet and Gurney (1984). However, this is not the whole story. To complete it we have to return to our picture of the conveyor belt. While rolling on it also contracts, pushing all the young from one birth cycle closer and closer together, so that when they reach reproductive size they do so almost simultaneously. This effect strongly contributes to the oscillatory tendency of the model.

At low  $\alpha$  the birth peaks become much more gentle and the decrease in the food starts to lag somewhat behind. Moreover, the effect of the deaths on the population feeding rate is largely compensated for by growth. Figure 9 shows an example. It can be observed that the food fluctuates only very mildly, well within the 20% criterion used by Murdoch and McCauley to define their type (iii) oscillations. These oscillations are made possible by the size structure: Even though both *Daphnia* numbers and *Daphnia* biomass do fluctuate considerably, the total *Daphnia* surface area, and therefore the *Daphnia* feeding rate, stays much more constant. Moreover, due to the fact that at low  $\alpha$  there are only few *Daphnia* around these fluctuations in feeding rate have only a relatively minor impact on the food population.

### 3.4.4 Self-Renewing Food

Figure 10A shows the stability diagram for the self-renewing food dynamics [Eq. (13)], and Fig. 10B a corresponding stability diagram for the unstructured predator-prey model

$$\begin{aligned} \frac{dx}{dt} &= \alpha x(1-x/\beta) - u f(x) N \\ \frac{dN}{dt} &= [v f(x) - \phi] N. \end{aligned} \quad (15)$$

The maximum capacity for self-renewal of the food  $\alpha$  is same in both diagrams, and the same applies to the shape parameter  $\xi$  in the functional response. However, the two remaining parameters  $u$  and  $v$  do not bear any simple relation to the *Daphnia* parameters. They were chosen only for the likeness of the corresponding stability diagrams.

Here too there exist shoals in the mare stabilitatis where the stable limit cycle extends beyond the peninsula.

Finally Fig. 11 shows some typical predator-prey cycles in which *Daphnia* lags a quarter period behind its food.

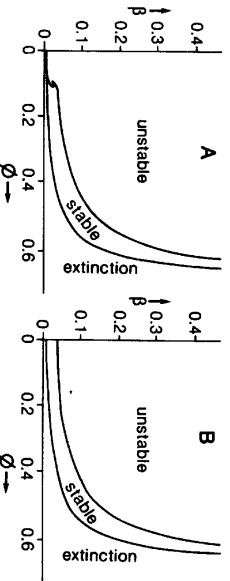


Fig. 10. A The stability boundary for the interior equilibrium for the *Daphnia* model with self-renewing food. B The stability boundary for an unstructured model, with the parameters without counterparts in the *Daphnia* model chosen to maximize the likeness to A.  $\beta$  carrying capacity of the food in the absence of *Daphnia*;  $\phi$  random death (harvesting) rate

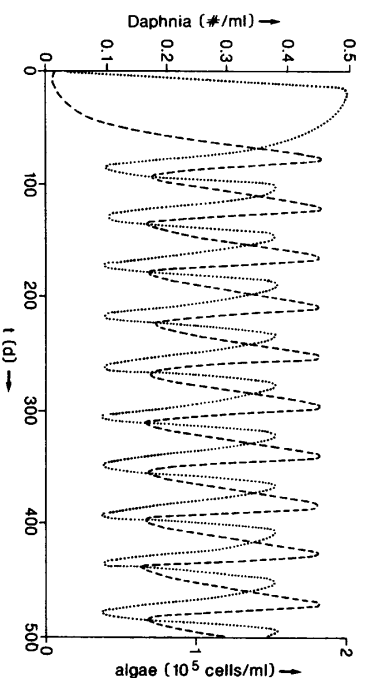


Fig. 11. Predator-prey oscillations in the *Daphnia* model with self-renewing food

Apparently the unstructured model [Eq. (15)] captures the dynamical essentials of an interaction where one species feeds upon an other quite well, at least in a qualitative sense. However, our failure to find any clear relation between the parameters  $u$  and  $v$  and the parameters characterizing individual behavior is symptomatic of its weaknesses. It is not clear a priori how one should arrive at a quantitative match over a range of different circumstances. It is here that structured models, in which all the parameters have well-defined empirical counterparts, have at least the potential to score higher.

## 4 Concluding Remarks

We hope that the previous sections have convinced you that one does not need to be a mathematician to deal with physiologically structured population models. What matters is the interplay between reasoning in terms of individual behavior, a good use of the conveyor belt analogy, and some formal mathematical manipulations. Of course there is some quite deep mathematics hidden underneath, but we can safely leave that to the mathematicians.

A second message was that an almost necessary condition for making life simple is that all individuals are bound to pass through one, or a few, selected states. In particular, when everybody is born equal, many calculations reduce to those for the age-dependent problem.

One good reason to replace the more conventional lumped models by their structured counterparts, is that usually only the latter allow a clear mechanistic interpretation of the model parameters. What we are interested in ultimately is mechanistic insight. Models are just a tool.

But structured models may also have interesting dynamical properties special to their kind!

*Acknowledgments.* We thank Odo Diekmann for giving the Dutch structured population movement its impetus, Bas Kooijman, Roger Nisbet, Bill Gurney and Ed McCauley for many exasperating but

fruitful discussions about *Daphnia*, Anneke Leopoldt for calculating stability boundaries for the *Daphnia* model with chemostat food dynamics and for writing the first simulation programs, Erik Evers for calculating stability boundaries for the case of self-renewing food, Peter Hock for drawing the figures, and the organizers of the Falsterbo workshop for a good job and a pleasant week.

## 5 References

- Beverton RH, Holt SJ (1957) The dynamics of exploited fish populations. H M Sin Off, London
- De Roos AM (1988) Numerical methods for structured population models, the escalator boxcar train. *Nucl Meth Part Diff Equ* 4(3):173–195
- Diekman O, Metz JAJ, Kooijman SALM, Heijmans HJAM (1974) Continuum population dynamics with an application to *Daphnia magna*. *Nieuw Arch Wisk* (4) 2:82–109
- Heijmans HJAM, Metz JAJ (1986) Small parameters in structured population models and the Trotter-Kato theorem. *REP AM-R* 8603, Cent Math Comput Sci, Amsterdam
- Kooijman SALM (1986a) Population dynamics on basis of budgets. In: Metz JAJ, Diekmann O (eds) The dynamics of physiologically structured populations. Springer, Berlin Heidelberg New York, pp 266–297 (Springer lecture notes in biomathematics, vol 68)
- Kooijman SALM (1986b) Energy budgets can explain body size relations. *J Theor Biol* 121:269–282
- Kooijman SALM (1986c) What the hen can tell about her eggs: egg development on the basis of energy budgets. *J Math Biol* 23:163–185
- Kooijman SALM (1988) The Von Bertalanffy growth rate as a function of physiological parameters: a comparative analysis. In: Hallam TG, Levin SA (eds) Mathematical ecology. World Sci, pp 3–45
- Kooijman SALM, Metz JAJ (1984) On the dynamics of chemically stressed populations: the deduction of population consequences from effects on individuals. *Ecotox Environ Saf* 8:254–274
- Kooijman SALM, van der Hoeren N, van der Werf DC (in press) Population consequences of a physiological model for individuals. *Funct Ecol*
- Lynch M (in press) The life history consequences of resource depression. *Ecology*
- McCauley E, Murdoch WW (1987) Cyclic and stable populations: plankton as a paradigm. *Am Nat* 129:97–121
- Metz JAJ, Diekmann O (eds) (1986) The dynamics of physiologically structured populations. Springer, Berlin Heidelberg New York (Springer lecture notes in biomathematics, vol 68)
- Murdoch WW, McCauley E (1985) Three distinct types of dynamic behaviour shown by a single planktonic system. *Nature* (London) 316:628–630
- Nisbet RM, Gurney WSC (1984) "Stage-structure" models of uniform larval competition. In: Levin SA, Hallam TG (eds) Mathematical ecology. Proceedings Trieste 1982. Springer, Berlin Heidelberg New York, pp 97–113 (Springer lecture notes in biomathematics, vol 54)
- Pratt DM (1943) Analysis of population development of *Daphnia* at different temperatures. *Biol Bull* 85:116–140
- Sinکو JW, Streifer W (1969) Applying models incorporating age-size structure of a population to *Daphnia*. *Ecology* 50:608–615
- Thieme HR (1988) Well-posedness of physiologically structured population models for *Daphnia magna*. *J Math Biol* 26:299–317

# Dynamics of Age- and Size-Structured Populations: Intraspecific Competition

B. EBENMAN

## 1 Introduction

In most organisms different aged individuals differ in size and morphology. In some taxa the body weight of individuals within species spans 4 or more orders of magnitude (Werner and Gilliam 1984). The radical changes in morphology accompanying metamorphosis in organisms with complex life cycles is well known to all biologists. Such variation within a species will have important evolutionary and population dynamic consequences. In this chapter I will discuss the implications of such differences in size/morphology on the intensity of competition between age classes, and show that competition between age classes can have interesting population dynamic consequences.

In many animals the individuals change their resource use as they develop from newborns to adults. Such niche changes during the life cycle will affect intraspecific competition and hence population dynamics. The strength of competition between different-aged individuals will often depend on their patterns of growth or on the form of their life cycles (Polis this Vol.; Wilbur this Vol.). In most organisms with complex life cycles, like amphibians, holometabolous insects and many marine invertebrates, there is no competition between the juveniles and adults (Wilbur 1980). In organisms with "simple" life cycles (i.e., organisms not undergoing metamorphosis), like reptiles, fishes and hemimetabolous insects, the niche differences between the age classes are in most cases not so pronounced. Instead, individuals in different age classes partly overlap in their use of resources (Polis 1984; Werner and Gilliam 1984). Finally, among birds and mammals – which are almost fullgrown at the age of independence – there is probably seldom any significant ecological segregation between the age classes. This is also often the case for plants (e.g., Goldberg 1987).

With the help of general discrete-time models with two age classes I have investigated how competition between adults and juveniles affects population dynamic behavior. I will first review results from a model of a purely age-structured population (Ebenman 1987 and 1988) and later compare these results with new results from a model that also incorporates size-structure.

## 2 Age-Structured Populations

There is a rather large literature on the effects of density dependence on the dynamic behavior in age-structured populations (reviewed by Nisbet and Gurney

Department of Biology, Linköping University, 581 83 Linköping, Sweden