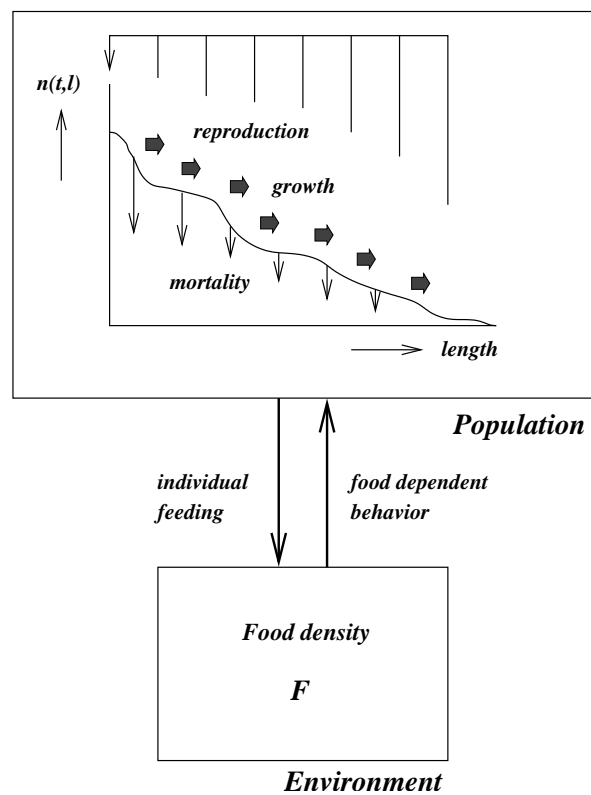


From Individual Life History to Population Dynamics using Physiologically Structured Models



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Chapter 1

Age-structured models

1.1 Traditional versus individual-based models

Developing theory necessarily implies deriving an abstraction of the real-world system of interest and formulating a logical representation of that system. The abstraction process itself involves making choices about the relevant details one wants to incorporate and the appropriate scale of complexity that minimally has to be represented by the model. Most of the current theory in population and community ecology bases itself on an abstraction that adopts the population as the basic unit. Hence, models in population and community ecology often have as a general form :

$$\frac{dN_i}{dt} = f_i(N_1, \dots, N_q) N_i \quad i = 1, \dots, q \quad (1.1)$$

Here the variables N_i represent the number of individuals making up population i or the total amount of biomass of this population. The functions $f_i(N_1, \dots, N_q)$ represent the per-capita growth rate of population i .

It is very important to stress that in these traditional approaches the *population* is modeled. In other words, the modeling involves deriving mathematical functions that describe how the population changes over time. The variable N_i is used to denote the *state* of the population, it characterizes and distinguishes one population from another. N_i is also referred to as the *population state*.

The recipe for population change is determined by the per-capita growth rate $f_i(N_1, \dots, N_q)$. In a closed population this per-capita growth rate is a balance between reproduction and mortality of *individuals*. This indicates an important philosophical problem of population-level models: the processes that change a population take place at the level of the individual organisms, which are, however, not represented in the model itself, since the basic abstraction unit adopted is the population. Generally, the per-capita growth rates $f_i(N_1, \dots, N_q)$ are nonetheless derived on the basis of knowledge about individual reproduction and death.

Consider the basic Lotka-Volterra predator-prey model:

$$\frac{dF}{dt} = rF - aFC \quad (1.2a)$$

$$\frac{dC}{dt} = \epsilon aFC - \mu C \quad (1.2b)$$

In these equations F and C represent the abundance of prey (food) and predators (consumers), respectively. The parameter r represents the exponential growth rate of prey in the absence of the predator, while μ represents the death or mortality rate of the predators in the absence of prey. Encounters between prey and predators are assumed to follow the *mass action law* and are hence proportional to the product of the abundances F and C . The parameter a represents the attack rate of predators, which equals the area or volume that a predator searches through during a single unit of time. The parameter ϵ represents the conversion efficiency, *i.e.* the efficiency with which predators convert consumed prey into offspring.

Clearly, the model functions describing how the population abundances will change over time are derived by making assumptions about individual-level processes like mortality and encounters between prey and predators. Since in reality the dynamics of the population are the cumulative result of all reproduction and death events happening to its individuals, we can only be certain that the model (1.2) correctly reflects these dynamics if one of the two following conditions holds:

- All individuals are functionally identical, meaning that they have identical birth and death rates, or
- The individuals can be represented by an average type and this average does not change over time.

These conditions already hint at the importance of *population structure*, *i.e.* its composition in terms of different types of individuals that are present, in addition to the *population abundance*, which only refers to the total number of individuals present. The last of the conditions above expresses that traditional population-level models may correctly capture the dynamics of groups of different individuals, if the composition is relatively constant over time. Hence, especially when the composition of a population changes over time traditional population models may be expected to generate predictions with little relation to the natural system of interest.

Individuals are generally far from identical and individual variability is actually one of the most fascinating aspect of biology in general. In addition, populations are seldomly characterized by a constant structure or composition. Figure 1.1 shows one of the classic time series in population ecology, the dynamics of the blowfly *Lucilia cuprina* in experiments carried out by Nicholson (1954). The dynamics clearly show that the population at certain times is made up almost exclusively by the adult individuals, while at other times only pupae are present in the population. These two facts imply that the predictions of population-level models in most cases do not represent exactly the accumulated changes of its constituting individuals. At best the population-level models provide an approximation, but how well it approximates the accumulated changes in the entire collection of individuals is unclear.

To improve our modeling of the population dynamics we have to change perspective: Instead of adopting the population as our basic unit of interest and modeling its fate, we adopt the individual as our basic entity and model its fate over time. Structured or individual-based models implement this change in perspective and can hence be considered to be based on an entirely different paradigm for studying the dynamics of populations. In the following I will use the term *physiologically structured population model*, abbreviated as *PSPM*, as a general name for models that

- explicitly model individuals and their life history, and

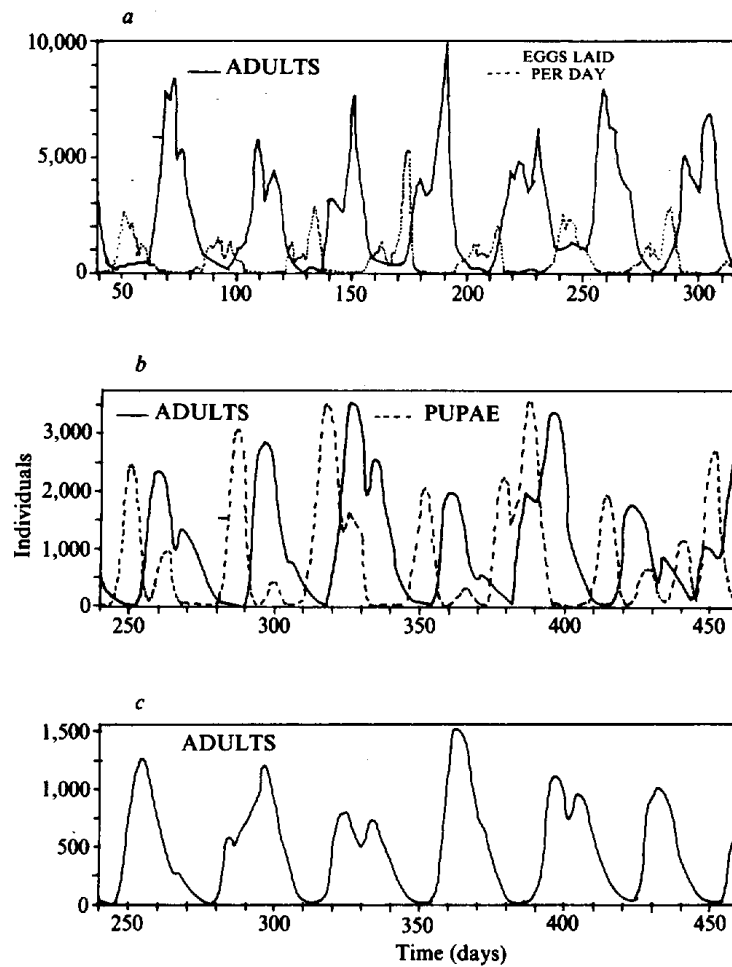


Figure 1.1: Quasi-periodic fluctuations in laboratory populations of *Lucilia cuprina*. Population regulated by adult food supply (a), larval food supply (50 g per day) (b), larval food supply (25 g per day) (c). Data from Nicholson (1954).

- derive population-level model descriptions by keeping book of the individual-level life history events (e.g. reproduction, mortality) without making any further assumptions at the population-level itself.

Hence, PSPMs focus mainly on the state of the individual and the changes therein over time. The *individual state* (or *i-state*) is therefore the most important state concept in PSPMs, while the population state is only of secondary importance. Because individual-level events like reproduction, mortality but also development are often also influenced by the environment that an individual lives in, for example, by food availability, it is also necessary to introduce the *environmental state* (or *E-state*) to characterize the environment in which an individual lives (From a strict system theoretical sense this concept actually does not qualify as a real “state”, but we will disregard this theoretical inconsistency in our discussions). More extensive discussions about the *i-state*, *E-state* and *p-state* will follow in the next chapter, here we just introduce these three concepts with short descriptions:

- Individual or *i-state*: a set of (physiological) variables that characterizes an individual

and is used to distinguish individuals from each other.

- Environmental or E -state: a set of variables, e.g. food density, density of predators, that characterizes the environment in which the focal individual lives.
- Population or p -state: the mathematical construct to represent all individuals making up the biological population. The choice of this mathematical construct depends on the details of the modeled individual life history. It may be a vector of age- or size-class densities or a continuous distribution over an age- or size-interval.

Different modeling frameworks exist to account for the individual life history in population dynamic models. The most well known class of models are the age- or size-structured matrix models (Caswell 2001). The numerous studies involving matrix models by Caswell (2001, see also Caswell 1989) exemplify how mathematical modeling can provide major contributions to answer ecological questions. Another well known class of models are the continuous-time, discrete-stage structured models popularized by Gurney and Nisbet (1998), which are formulated in terms of delay-differential equations. The most flexible and hence most daunting class of models are the physiologically structured population models sensu Metz and Diekmann (1986, see also de Roos 1997), which are often formulated in terms of partial differential equations. Our main focus will be on this latter class of models, as they account most consistently for individual life histories in population dynamic models, but we will discuss the matrix and stage-structured models wherever the life history allows for an exact reduction to one of these two types of models.

For the PSPMs sensu Metz and Diekmann (1986) a method has been developed to numerically integrate the set of partial differential equations, representing the population model. This numerical method is referred to as the *Escalator Boxcar Train* or *EBT*-method (de Roos 1988; de Roos et al. 1992a; de Roos 1997). Apart from a numerical method the EBT can also be seen as an alternative framework for modeling structured populations, which explicitly and rigorously accounts for the individual life history. In this and the following chapters we will consider the EBT as such an alternative modeling framework and hence derive EBT-formulations for the case studies of interest. We consider this a more intuitive introduction to the concepts behind physiologically structured population models, which circumvents the often intimidating presentation of the partial differential equations.

1.2 A simple model for Pacific salmon

The Pacific ocean is the home of seven different species of so-called Pacific salmon. Several of these species have recently been listed as threatened under the U.S. Endangered Species Act. Our interest here is on two of these species, coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*). Populations of coho salmon in California have declined significantly in abundance over the past century, while in contrast chinook salmon maintained higher abundances (Hill et al. 2003). Salmon have a semelparous life history strategy. Late in the year, adults migrate from the ocean back to their natal stream, where spawning occurs. After spawning, the adults die. The eggs hatch next spring. The newborn individuals are referred to as “parr” as long as they are younger than 1 year. Parr remain in freshwater for 1 year before migrating to the sea, at which stage they are referred to as “smolts”. Smolts are individuals with an age between 1 and 2 years. One of the major differences between the life histories of coho and chinook salmon in the California Current is that female coho salmon

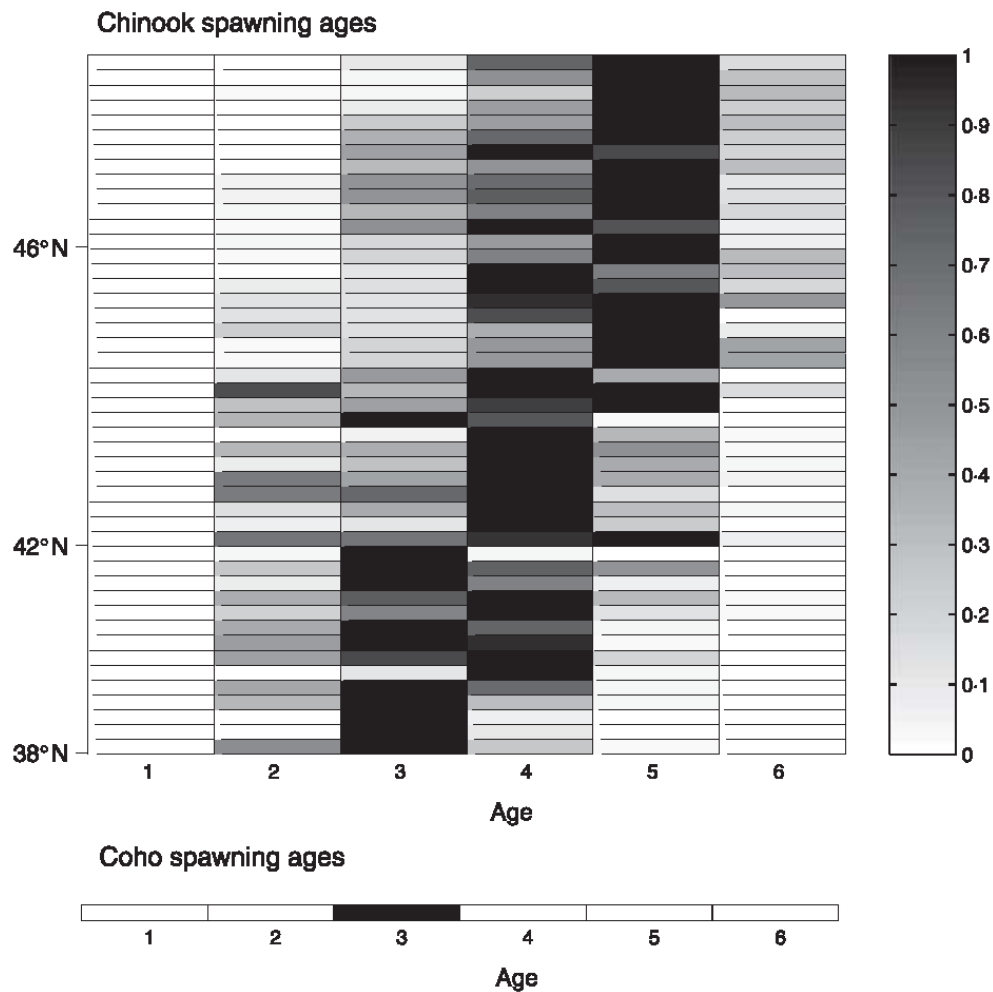


Figure 1.2: Spawning age distribution for female chinook and coho salmon from the California Current. Data from Hill et al. (2003).

typically stay in the ocean for 18 months and return for spawning in their natal stream when they are 3 years old. In contrast, female chinook salmon stay for a more variable length of time in the ocean and spawn over a range of years, primarily at the dominant ages of 3-6 years (Hill et al. 2003). These reproductive patterns are referred to as obligate semelparity and indeterminate semelparity, respectively (Begon et al. 1996). Figure 1.2 illustrates this difference in spawning behavior of female coho and chinook salmon for populations in the California Current.

Hill et al. (2003) present a simple, age-structured model for the dynamics of a population of coho or chinook salmon. Their model is formulated as a density-independent, matrix model (Caswell 2001). It is based on the following set of assumptions about the life history of the salmon individuals:

- *Mortality*: individuals experience mortality primarily during migration, both when migrating as smolt (1-2 years old) from their natal stream to the ocean, as well as when they migrate as adult back to their natal stream to spawn. Mortality of individuals in the ocean is negligible. The mortality that migrating juvenile individuals experience

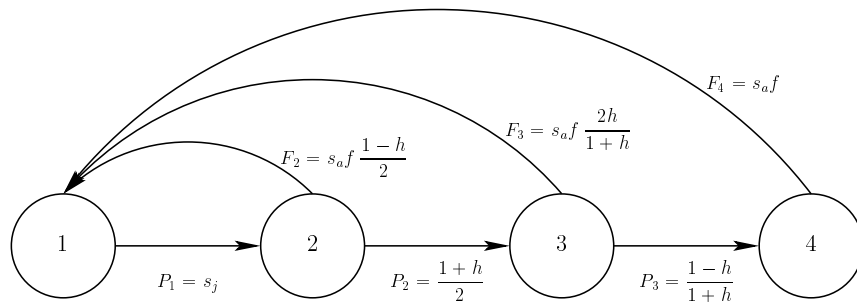


Figure 1.3: Life-cycle graph for an age-classified salmon population. Each node in the graph represents an age class and the arrows connecting the nodes represent the contribution of individuals in age class i make to the number of individuals in age class j ($j = 1, \dots, 4$) during one time interval. s_j is the probability a juvenile survives from age 1 to age 2. s_a is the probability that a returning adult survives to reproduce. f is the number of offspring produced per adult that survive to age 1. h is the proportion of adults that reproduce at age 3. See text for details.

results in individuals having a probability s_j to survive their migration to the ocean (i.e. the survival probability from parr to smolt equals s_j). The mortality of returning adults results in these individuals having a probability s_a to survive their migration back to their natal stream.

- *Reproduction:* individuals return to their natal stream to spawn at an age of 2, 3 or 4 years old. With probability h they return to spawn at an age of 3 years, with probability $(1-h)/2$ they return to spawn at either age 2 or 4 years old. On successful return to their natal stream, having survived the migration, they spawn a number of eggs that eventually yield f 1-year old individuals. Fecundity is assumed to be independent of the age at which adults spawn. The parameter f hence is a product of the number of eggs produced and the survival probability from 0 to 1 year old.
- *Development:* since both mortality and reproduction are determined by the age of an individual, development from the neonate to the juvenile and eventually the adult stage is age-dependent, as well. Although Hill et al. (2003) do not explicitly state the assumptions about individual development we point them out here to be consistent with later case studies, in which development is explicitly modeled.

Figure 1.3 shows the life cycle graph of the salmon, which incorporates all of these assumptions. A life cycle graph is a graphical representation of the main life stages that can be distinguished in the individual life history plus the possible transitions from one stage to the other (Caswell 2001). The matrix model of Hill et al. (2003) tracks the number of individuals that are exactly 1 year old just before they start migrating to the ocean and the number of 2, 3 and 4 year old individuals in the ocean before these older individuals migrate back to their natal stream to spawn.

Hill et al. (2003) study the dynamics of the model as a function of the parameter h , which determines the variance in the age of reproduction. More precisely, h is the fraction of female individuals that spawn at an age of 3 years. Figure 1.4 illustrates the spawning age distribution of females for 3 different values of the parameter h . Note that of all individuals that do not spawn at an age of 3 years (i.e. a fraction $1-h$ of all females), exactly 50% are

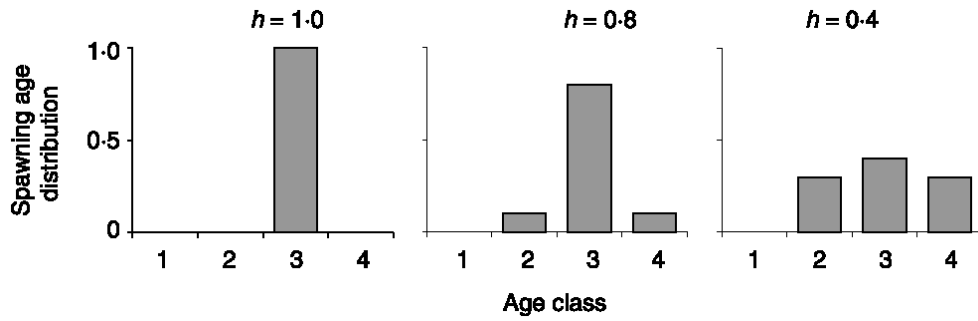


Figure 1.4: Spawning age distribution as a function of h . Decreasing h increases the variance in the age of reproduction. The variance in reproductive age ranges between 2- and 4-years olds is distributed symmetrically around year 3. Figure redrawn from Hill et al. (2003).

assumed to spawn at an age of 2 years, while the other 50% spawns at an age of 4 years. Female coho salmon reproduce almost exclusively reproduce at an age of 3 years and hence $h = 1$. For this choice of parameters the life cycle graph simplifies considerably as shown in Figure 1.5.

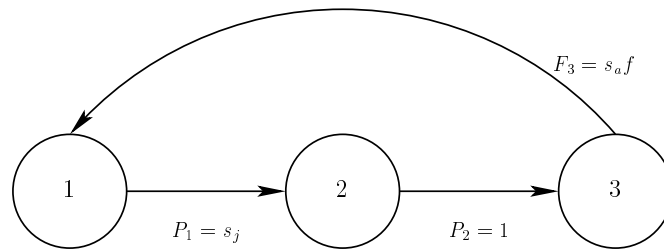


Figure 1.5: Life cycle graph for coho salmon. The graph is identical to the life cycle graph shown in Figure 1.3, but for a choice $h = 1$.

On the other hand, chinook salmon have a more variable distribution of spawning ages. As a default parameter value we will assume that only 60% of all female chinook salmon spawns at the age of 3 years, while 20% spawns either at an age of 2 or 4 years. For this parameter choice $h = 0.6$, the life cycle graph for chinook salmon simplifies to the graph shown in Figure 1.6.

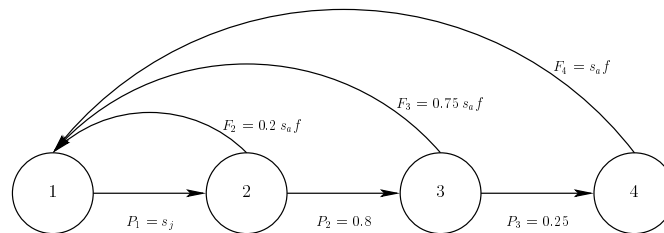


Figure 1.6: Life cycle graph for chinook salmon. The graph is identical to the life cycle graph shown in Figure 1.3, but for a choice $h = 0.6$.

Mathematically the salmon population model can now be expressed as an age-dependent matrix model. For coho salmon the model tracks the dynamics of the number of 1 year old individuals, just before their migration to the ocean, the number of 2 year old smolts and the number of 3 year old adults, shortly before their migration back to the spawning sites. Let

these three densities be denoted by $n_1(t)$, $n_2(t)$ and $n_3(t)$, respectively, and let $\mathbf{n}(t)$ denote the vector with these three densities as its elements:

$$\mathbf{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \end{pmatrix}$$

The time argument of $\mathbf{n}(t)$, $n_1(t)$, $n_2(t)$ and $n_3(t)$ indicates that these variables refer to the population densities in a particular year t . The time point within this particular year, at which the population is censused, is fixed and the matrix model describes the changes in the densities from that particular moment to the same moment exactly one year later, in the year indicated by $t + 1$. Unfortunately, Hill et al. (2003) do not explicitly state at which moment within the year they consider the population census to take place and a closer look at the life cycle graph as presented by these authors (see Figure 1.3) reveals that determination of the population census time is not straightforward either. We will not discuss this issue here further and only consider the changes in densities from one year to the next.

The recipe determining the changes in coho salmon densities from year t to $t + 1$ can be written in matrix notation as follows:

$$\begin{aligned} \begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \end{pmatrix} &= \begin{pmatrix} 0 & 0 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \end{pmatrix} \\ &= \begin{pmatrix} 0 & 0 & s_a f \\ s_j & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \end{pmatrix} \end{aligned} \tag{1.3}$$

If we define the matrix \mathbf{A} as

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & s_a f \\ s_j & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} \tag{1.4}$$

equation (1.3) can be written in a more condensed form as:

$$\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t) \tag{1.5}$$

using the matrix \mathbf{A} and the vector of coho salmon densities \mathbf{n} at time t and $t + 1$, respectively. The model for chinook salmon is slightly more complicated, because in addition to the densities of 1, 2 and 3 year old individuals, which were accounted for in the coho salmon model, also the density of 4 year old adults, just before their migration back to the spawning site, has to be accounted for. Let the variables $m_1(t)$, $m_2(t)$, $m_3(t)$ and $m_4(t)$ denote the densities of the these 4 year classes of chinook salmon in a particular year t . From the life cycle graph shown in Figure 1.6 we can now infer that the changes in these densities from one year to the

next can be described by the following equation:

$$\begin{aligned} \begin{pmatrix} m_1(t+1) \\ m_2(t+1) \\ m_3(t+1) \\ m_4(t+1) \end{pmatrix} &= \begin{pmatrix} 0 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix} \begin{pmatrix} m_1(t) \\ m_2(t) \\ m_3(t) \\ m_4(t) \end{pmatrix} \\ &= \begin{pmatrix} 0 & 0.2 s_{af} & 0.75 s_{af} & s_{af} \\ s_j & 0 & 0 & 0 \\ 0 & 0.8 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{pmatrix} \begin{pmatrix} m_1(t) \\ m_2(t) \\ m_3(t) \\ m_4(t) \end{pmatrix} \end{aligned} \quad (1.6)$$

This equation can again be written in more condensed form by defining a matrix \mathbf{B} as:

$$\mathbf{B} = \begin{pmatrix} 0 & 0.2 s_{af} & 0.75 s_{af} & s_{af} \\ s_j & 0 & 0 & 0 \\ 0 & 0.8 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{pmatrix} \quad (1.7)$$

and a vector $\mathbf{m}(t)$ with as elements the 4 age class densities of chinook salmon:

$$\mathbf{m}(t) = \begin{pmatrix} m_1(t) \\ m_2(t) \\ m_3(t) \\ m_4(t) \end{pmatrix} \quad (1.8)$$

Using these variables the age-dependent matrix model for chinook salmon can be expressed as:

$$\mathbf{m}(t+1) = \mathbf{B} \mathbf{m}(t) \quad (1.9)$$

The equations (1.5) and (1.9) represent the population-dynamic model for coho and chinook salmon, respectively. Hill et al. (2003) use these models to answer questions about the influence of variance in the spawning age distribution on the persistence of the population. The aim of their study is explain the difference in response that has been observed for coho and chinook salmon populations to changing environmental conditions. Our interest here primarily is on formulating population-dynamic models and less on the questions that can be addressed with the models derived. We hence conclude our discussion of the models here and refer to the paper by Hill et al. (2003) for a presentation of their biological implications.

1.3 EBT-formulation of the Pacific salmon model

The basic idea of the EBT-technique is to follow *cohorts of identical individuals* throughout their entire life history. A cohort refers here to all individuals that are born at the same time with identical physiological properties and traits, *i.e.* with the same *i*-state at birth. These cohorts are followed throughout their entire life cycle, from the time that the cohort is formed, *i.e.* when the individuals are born, through their development into juvenile and adult stages till all individuals making up the cohort have died and the cohort has gone extinct. One of the basic assumptions of the EBT-technique is that cohorts of identical individuals will remain identical throughout their life. Hence, there is no divergence in *i*-state among individuals within the same cohort.

1.3.1 Coho salmon

Given the life cycle of coho salmon presented in Figure 1.5 it is clear that the population will always consist of cohorts of identical individuals. Age is the defining trait that completely determines the stage in the life cycle of the individual organism and hence determines its vital rates (*i.e.* reproductive activity and mortality risk). In other words, individual age is the only variable making up the i -state, which makes divergence between individuals born at the same time with the same i -state impossible. As described, salmon eggs hatch at basically the same time during the year and (naturally) all individuals are born with age 0. Hence, every year a single new cohort of individuals with the same i -state at birth is produced. Apart from individuals that die, these cohorts progress through the different life stages (parr, smolt, adult), governed by age, and finally die after spawning. The semelparous life style of salmon moreover ensures that cohorts of individuals go extinct at a relatively well-defined point in time: namely right after they have spawned their eggs at the age of 3 years.

To start our derivation of the EBT-formulation of the coho salmon population dynamic model, we will focus on the cohort of newborn individuals that is born at time $t = T$. The EBT-formulation follows the fate of this cohort continuously throughout their life history and hence the time t is a continuous variable. We will assume that eggs hatch every year at the same time, that is at time $t = T, T + 1, T + 2, \dots$. The number of hatching individuals at time T , which we will indicate with $N_0(T)$, equals the product of the number of adult individuals that spawned and the number of hatchlings that these adults each produced, *i.e.* their fecundity. The adults are approaching 3 years of age and actually die in autumn, some time before the eggs they produce hatch. We will indicate the time at which the adults spawn with $t = T^-$ to indicate that it is some time before the hatching of the eggs at $t = T$. A more detailed specification of the moment of spawning is possible, but not necessary for the purpose of the model formulation. If the number of spawning adults at this particular time is indicated with the variable $N_2(T^-)$ (the subscript 2 indicates that the adults are only 2 years old and turning 3) and each adult individual produce exactly E eggs, the number of hatchlings $N_0(T)$ is related to the number of spawners following:

$$N_0(T) = E N_2(T^-) \quad (1.10)$$

Note that one way of looking at this equation is that it implies that all spawning, adult individuals are identical, since they produce exactly the same number of eggs E . Another way of looking at this equation is that E represents the expected number of eggs, which a single adult produces. In this case one has to assume that the total number of adults is always so large that the total number of hatchlings produced exactly equals the expected value of this (intrinsically stochastic) variable. In other words, due to the large number of spawning individuals, the variance in the number of hatchlings produced is negligible.

After birth the individuals of the newborn cohort age and some of the individuals possible die. The age of the individuals in the newborn cohort we will indicate with the variable $A_0(t)$, which represents the i -state of the individuals. The mathematical recipe for development in this i -state is obvious:

$$\frac{dA_0}{dt} = 1, \quad A_0(T) = 0 \quad (1.11)$$

which in mathematical terms expresses that all individuals in the cohort start out with age 0 at the time of their birth $t = T$ and develop in age at unit rate.

The mortality process of the individuals in the cohort will be modeled by specifying an *instantaneous mortality rate* $d(a)$, which may depend on the age of the individual, a . The

meaning of an instantaneous mortality rate is not immediately straightforward. A more intuitive quantity that characterizes the death or survival of an individual organism is its survival probability, *i.e.* its probability to still be alive at a particular age a . Let $S(a)$ denote this survival probability up to age a . The instantaneous mortality rate $d(a)$ at age a is now defined as the rate of decline in the survival probability $S(a)$, provided that an individual is still alive at age a . In other words, the instantaneous mortality rate equals the *relative* rate of decrease in $S(a)$:

$$d(a) = -\frac{1}{S(a)} \frac{dS(a)}{da} \quad (1.12)$$

Note that the minus sign appears as the mortality rate is a positive quantity and the survival probability only decreases over time. The definition directly leads to the following differential equation determining the dynamics of the survival probability of the survival probability $S(a)$:

$$\frac{dS}{da} = -d(a)S \quad S(0) = 1 \quad (1.13)$$

The initial condition $S(0) = 1$ is self evident. The ODE can be formally solved through integration by parts, yielding:

$$S(a) = e^{-\int_0^a d(\xi) d\xi} \quad (1.14)$$

Since the $N_0(t)$ individuals in the cohort experience an instantaneous mortality rate $d(a)$ at age a , their decrease in number through mortality follows the differential equation:

$$\frac{dN_0}{dt} = -d(A_0)N_0 \quad N_0(T) = EN_2(T^-) \quad (1.15)$$

in which we have accounted for the initial condition (1.10), which relates the number of hatchlings at time $t = T$ to the number of spawning adults. The dynamics of the cohort born at time $t = T$ is therefore completely described by the following system of 2 ODEs:

$$\begin{cases} \frac{dN_0}{dt} = -d(A_0)N_0, & N_0(T) = EN_2(T^-) \\ \frac{dA_0}{dt} = 1, & A_0(T) = 0 \end{cases} \quad (1.16a)$$

$$\quad (1.16b)$$

These two ODEs describe the decrease in the number of individuals in the cohort born at time $t = T$ due to mortality and describe their development, *i.e.* aging. Since individuals spawn and die at an age of 3 year, the population of coho salmon is made of individuals that are between 0 and 1 year old, which we have indicated with the variable $N_0(t)$, individuals that are between 1 and 2 year old, which we will indicate with the variable $N_1(t)$ and adult individuals with and age between 2 and 3 year old, which we indicate with $N_2(t)$. Provided that the age-dependent mortality rate $d(a)$ is specified for all ages between 0 and 3 years, the mortality and aging of the individuals in the older cohorts will be described by analogous systems of ODEs. Hence, the dynamics of the entire population can be described by the sets of ODEs

$$\begin{cases} \frac{dN_i}{dt} = -d(A_i)N_i & (1.17a) \end{cases}$$

$$\begin{cases} \frac{dA_i}{dt} = 1 & i = 0, 1, 2 & (1.17b) \end{cases}$$

as long as no new cohort arises.

But, at time $t = T + 1$, when the individuals in the cohort we focused on up to now are 1 year old, a new reproduction event takes place and hence a new cohort of hatchlings has to be accounted for in our population model. This causes a bit of a bookkeeping problem. Which index are we going to use to designate the new cohort? The choice is in some sense arbitrary, but we have consistently made the choice to always give a new cohort of hatchlings the index 0 and to renumber all existing cohorts in the population by adding 1 to their index. Therefore, at the next time of an reproduction event, when $t = T + 1$, a new cohort of hatchling individuals, with abundance indicated by $N_0(t)$ and individual age by $A_0(t)$, will arise, given by

$$\begin{cases} N_0(T + 1) = E N_2(T + 1^-) & (1.18a) \\ A_0(T + 1) = 0 & (1.18b) \end{cases}$$

At the same time all older cohorts are renumbered to keep the appropriate order in the indexes. This renumbering operation is mathematically described by the following set of equations.

$$\begin{cases} N_i(T + 1) = N_{i-1}(T + 1^-) & (1.19a) \\ A_i(T + 1) = A_{i-1}(T + 1^-) & i = 1, 2 \quad (1.19b) \end{cases}$$

Note that in both sets of equations the notation $N_i(T + 1^-)$ (or $A_i(T + 1^-)$) refers to the abundance (or age) of the individuals in cohort i just before $t = T + 1$. Also note that all adult individuals that become 3 years of age reproduce, but do not survive. Hence, their density $N_2(T + 1^-)$ only occurs in equation (1.18a) and nowhere else.

This completes the EBT-formulation for the population dynamic model for coho salmon. The model formulation consists of 3 parts:

1. The integration of all sets of (two) ODEs that track the mortality and aging of individuals (*i.e.* the individual life history) in the different cohorts between two points in time at which reproduction occurs. The integration of these ODEs is carried out numerically using standard methods for the numerical integration of differential equations, such as the Runge-Kutta methods (Press et al. 1988).
2. The creation of a new cohort of hatchlings at the moment that a reproduction event occurs, and
3. The renumbering of all non-hatchling cohorts to conserve an appropriate order in the indexes of the cohorts. Notice that this part is purely a bookkeeping issue and has little to do with the model of the individual life history.

For the coho salmon model a summary of these three model stages and the equations pertaining to them is provided in Table 1.1.

Equivalence with the matrix model

Having completed the EBT-formulation of the population dynamic model for coho salmon, it is now instructive to consider the equivalence of the EBT-formulation derived in the previous section with the matrix model that was derived in section 1.2 (see eq. (1.3)). We will show in

Table 1.1: EBT-formulation of the population dynamic model of coho salmon

A. Definitions	
a	individual age
$N_i(t)$	number of individuals in cohort i at time t
$A_i(t)$	age of individuals in cohort i at time t
$d(a)$	instantaneous mortality rate for individuals with age a
E	number of eggs spawned by an adult individual at age 3

B. Model equations	
Continuous-time dynamics for all cohorts, in between two reproduction events	$\begin{cases} \frac{dN_i}{dt} = -d(A_i) N_i \\ \frac{dA_i}{dt} = 1 \end{cases} \quad i = 0, 1, 2$
Creation of new cohort during reproduction event at $t = T, T + 1, T + 2, \dots$	$\begin{cases} N_0(t) = E N_2(t^-) \\ A_0(t) = 0 \end{cases}$
Renumbering equations for all non-newborn cohorts at $t = T, T + 1, T + 2, \dots$	$\begin{cases} N_i(t) = N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \end{cases} \quad i = 1, 2$

this section that the EBT-formulation is completely identical to the matrix model, provided we choose the parameter E and the age-dependent, instantaneous mortality rate $d(a)$ appropriately. The basic idea is that we derive expressions for the parameters s_j , s_a and f in the matrix model in terms of the parameter E and the function $d(a)$ of the EBT-formulation. The expressions will show how E and $d(a)$ have to be chosen to have complete congruence between the two model formulations.

To start with consider the parameter s_j in the matrix model, which represents the probability that an individual survives from age $a = 1$ to age $a = 2$ (see section 1.2 for a description of this parameter). In the EBT-formulation survival was determined by the instantaneous mortality rate $d(a)$ or equivalently by the survival function

$$S(a) = e^{-\int_0^a d(\xi) d\xi}$$

(see equation (1.14)). The probability to survive from age $a = 1$ to age $a = 2$, provided that the individual is alive at age $a = 1$, is given by:

$$\frac{S(2)}{S(1)} = \frac{e^{-\int_0^2 d(\xi) d\xi}}{e^{-\int_0^1 d(\xi) d\xi}} = e^{-\int_1^2 d(\xi) d\xi}$$

Therefore, if the instantaneous mortality rate $d(a)$ is chosen in such a way that

$$e^{-\int_1^2 d(\xi) d\xi} = s_j \quad (1.20)$$

the EBT-formulation models the survival from individuals of exactly 1 year old to the age of 2 year in a completely identical way as the matrix model. Note, however, that the identity (1.20) can be fulfilled in a large number of different ways. For example, the identity would hold, if

$$d(a) = -\ln s_j, \quad \text{for } 1 \leq a < 2$$

but would equally hold for a choice

$$d(a) = \begin{cases} -2 \ln s_j & \text{for } \leq a < 1.5 \\ 0 & \text{for } 1.5 \leq a < 2 \end{cases}$$

In short, there is no unique choice for the instantaneous mortality rate $d(a)$ that fulfills the identity (1.20). This fact can be looked upon in two different ways:

- for the EBT-formulation of a structured population model more detailed assumptions are required than for the corresponding matrix model, as the age-dependence of the instantaneous mortality rate has to be specified completely and not just the survival probability from one year to the next, but
- because of these more detailed assumptions the EBT-formulation represents in more detail the entire life history of the individuals in the population, as it keep tracks of the decrease in survival probability throughout the entire year and not just of the survival from one year to the next.

This more detailed, but at the same time more rigorous representation of the individual life history in EBT-formulations is one of its most important properties. In the simple case study considered here, in which density dependence does not play a role and in which individual age constitutes the i -state, these properties are not so important. Hence, the use of the EBT-formulation is in this case a bit of an overkill and the use of the matrix model should be preferred for simplicity reasons. Of course, the reason that we derive an EBT-formulation for this case at all is to actually show its congruence with more well-known model formulations. Next, consider the parameter s_a . In the matrix model the number of 3 year old adults was censused just before their migration back into their natal stream to spawn. The parameter s_a represented the probability that an adult would survive the migration and indeed reach its spawning grounds. In the EBT-formulation the quantity $N_2(T^-)$ was used to denote the number of adults of 3 years old just before they spawned, *i.e. after* migration. In essence, this implies that it is assumed that adults migrate some time in their third year of life, when they are between 2 and 3 years old. The probability s_a should hence be related to the survival probability of adult individuals from the age $a = 2$ to the age $a = 3$ years. In mathematical terms:

$$e^{-\int_2^3 d(\xi) d\xi} = s_a \quad (1.21)$$

which expression is completely analogous to the one derived earlier for the parameter s_j (see equation (1.20)). As discussed above for the identity (1.20), the instantaneous mortality

rate $d(a)$ for $2 \leq a < 3$ is not unambiguously defined by the condition (1.21). Again the EBT-formulation represents the individual life history in more detail and more explicitly.

Finally, the parameter f in the matrix model (1.3) represented the number of 1 year old individuals that survived from the eggs produced by a spawning adult individual in the year before. This parameter thus incorporates two different elements, which are explicitly represented in the EBT-formulation: the number of eggs E produced by a spawning individual and the survival probability, $S(1)$, up to an age of 1 year old. Given the expression (1.14) for the survival probability $S(a)$, we can derive the following identity:

$$f = E S(1) = E e^{-\int_0^1 d(\xi) d\xi} \quad (1.22)$$

which ensures the congruence between the matrix model and the corresponding EBT-formulation. Given that 2 quantities, E and $d(a)$ for $0 \leq a < 1$, of the EBT-formulation are involved in this identity, the latter condition is even less restrictive than the conditions (1.20) and (1.21), in the sense that there are a large number of choices to be made for E and $d(a)$ that keep the identity of the matrix model and the EBT-formulation intact.

The conclusion of the analysis in this section is that the matrix model and the EBT-formulation are completely identical, provided that the 3 conditions (1.20), (1.21) and (1.22) are satisfied. Both models hence yield the same results, but to do so the EBT-formulation requires a more detailed and more explicit representation of the individual life history (*i.e.* the instantaneous mortality rate $d(a)$ in this case) than the matrix model.

1.3.2 Chinook salmon

The EBT-model for the population dynamics of coho salmon, derived in the previous section, can be readily extended to account for the dynamics of chinook salmon as well, as the only difference between the two species is the variance in the spawning age distribution. Chinook salmon obviously exhibit more variance in the age at which they spawn, as clearly shown in Figure 1.2. However, the data presented in Figure 1.2 do not show clearly how this observed variability is related to the individual life history. For that, we would have to follow over time a single cohort of individuals, born in the same year, and score how many of these individuals spawn at which age, provided that they survive. Figure 1.2 represents a more aggregated data set involving multiple cohorts from different years that are most probably also not all equally abundant. The figure exemplifies a common problem in formulating an individual-based population model that the data available not always provide unambiguous information about the life history, as the data frequently relate to population-level measurements. To circumvent the difficulty we will simply follow Hill et al. (2003) in their assumption that a fixed fraction h of a cohort spawns at an age of 3 years, while a fraction $(1 - h)/2$ of these individuals spawns at an age of 2 years and a equal fraction at an age of 4 years old.

We will adopt $h = 0.6$ as the default parameter value, such that equal fractions of 20% of the individuals in a cohort spawn at the age of 2 or 4 years old, respectively, while the bulk 60% of the individuals spawn at the age of 3 years. To derive the EBT-formulation these fractions will be translated into the probability that an individual of age a , having survived up to the moment of reproduction, will spawn and die, instead of wait another year. This probability will be denoted by the age-dependent function $p(a)$, which is naturally only defined for the discrete values $a = 1, 2, 3$ and 4, since spawning can only occur at these fixed moments in the life cycle of an individual. A fraction $1 - p(a)$ of the individuals reaching age a will thus skip

Table 1.2: EBT-formulation of the population dynamic model of chinook salmon

A. Definitions	
a	individual age
$N_i(t)$	number of individuals in cohort i at time t
$A_i(t)$	age of individuals in cohort i at time t
$d(a)$	instantaneous mortality rate for individuals with age a
E	number of eggs spawned by an adult individual at age $a = 1, 2, 3$ or 4
$p(a)$	spawning probability of an individual with age $a = 1, 2, 3$ or 4

B. Model equations	
Continuous-time dynamics for all cohorts, in between two reproduction events	$\begin{cases} \frac{dN_i}{dt} = -d(A_i) N_i \\ \frac{dA_i}{dt} = 1 \end{cases} \quad i = 0, \dots, 3$
Creation of new cohort during reproduction event at $t = T, T + 1, T + 2, \dots$	$\begin{cases} N_0(t) = E \sum_{i=1}^3 p(A_i(t^-)) N_i(t^-) \\ A_0(t) = 0 \end{cases}$
Renumbering equations for all non-newborn cohorts at $t = T, T + 1, T + 2, \dots$	$\begin{cases} N_i(t) = (1 - p(A_{i-1}(t^-))) N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \end{cases} \quad i = 1, \dots, 3$

reproduction and wait for a later spawning event. Obviously, no individual spawns at age 1, hence $p(1) = 0$. Of all adult individuals reaching the age of 2 year, 20% spawns and thus $p(2) = 0.2$. From the remaining 80% of the cohort, which waits till a later age, 75% spawns at the age of 3 years (this represents exactly 60% of the number of individuals in the cohort that survived to a reproductive age at all). Therefore, $p(3) = 0.75$. Finally, individuals that reach the age of 4 years always spawn, i.e. $p(4) = 1$. Therefore, the age-dependent probability to spawn at age a is given by:

$$p(a) = \begin{cases} 0 & \text{for } a = 1 \\ 0.2 & \text{for } a = 2 \\ 0.75 & \text{for } a = 3 \\ 1.0 & \text{for } a = 4 \end{cases} \quad (1.23)$$

In the model presented by Hill et al. (2003), it was assumed that all individuals with an age of 2 years or older experience a negligible background mortality and hence have a survival probability equal to 1. Only when adults migrate back to their spawning site they have a lower probability to survive equal to s_a . An individual hence does not pay any price for postponing spawning to a later age. This assumption is crucial for the derivation of the values for $p(a)$ presented above. If mortality, other than during migration, would have occurred for

adult individuals it should have been accounted for in the derivation of the values for $p(a)$. We leave it as an exercise to the reader to think about how the age-dependent probabilities $p(a)$ would be related to the observed spawning age distribution of a particular cohort in case adult mortality is not negligible.

Because multiple cohorts of chinook salmon are assumed to spawn at the same time, the total number of hatchlings produced in a particular year is a sum over the contributions from the adult individuals of 2, 3 and 4 years old. If the hatching of eggs is taking place at time $t = T$, the number of individuals in the newborn cohort is hence given by:

$$N_0(T) = E \sum_{i=0}^3 p(A_i(T^-)) N_i(T^-)$$

Note that at time $t = T$ the individual in the cohort with index $i = 0$ and index $i = 3$ are exactly 1 and 4 years old. Also note that we silently introduced the variables $N_3(t)$ and $A_3(t)$ to represent the number and age of the individuals in the cohort that is between 3 and 4 years old.

The state of the newborn cohort at the time of hatching therefore equals:

$$\left\{ \begin{array}{l} N_0(T) = E \sum_{i=0}^3 p(A_i(T^-)) N_i(T^-) \\ A_0(T) = 0 \end{array} \right. \quad \begin{array}{l} (1.24a) \\ (1.24b) \end{array}$$

The facultative spawning also has to be accounted for in the renumbering equations (*cf.* equations (1.19)), since only a fraction $1 - p(a)$ of the present individuals survives this reproduction event at time $t = T$. Hence, the number of adult individuals has be adjusted, such that the renumber equations become:

$$\left\{ \begin{array}{l} N_i(T) = (1 - p(A_{i-1}(T^-))) N_{i-1}(T^-) \\ A_i(T) = A_{i-1}(T^-) \end{array} \right. \quad \begin{array}{l} (1.25a) \\ i = 1, \dots, 3 \quad (1.25b) \end{array}$$

Note that our definition of the probabilities $p(a)$, allows us to write these renumbering equation in the above, compact form. Even though individuals at age $a = 1$ are not adult yet, the definition of $p(a) = 0$ for $a = 1$ makes it possible to write a single set of renumbering equations for all existing cohorts in the population. A summary of all model equations is provided in Table 1.2.

Equivalence with the matrix model

It is once again instructive to consider the congruence between the EBT-formulation for the chinook salmon model and the corresponding matrix model derived in section 1.2. It will turn out that the conditions to be satisfied for complete congruence between the matrix and the EBT-model are slightly different than in the model for coho salmon. In the coho salmon model we accounted for the mortality experienced by adults during migration by an appropriate choice for the instantaneous mortality rate $d(a)$ for $2 \leq a < 3$. In case of the chinook salmon model this is no longer possible, because individuals that do not spawn at an age of 3 years old, do all survive and spawn at a later age. This issue was already discussed

in the previous section, where it was pointed out that individuals do not pay a price for skipped spawning. As a consequence, to reach complete congruence between the matrix and the EBT-model, we have to assume that

$$d(a) = 0 \quad \text{for } a \geq 2 \quad (1.26)$$

The parameter s_a in the matrix model, representing the probability for an adult to survive its migration back to the spawning sites, can now only be accounted for in the EBT-formulation by incorporating it in the expected number of eggs produced per adult individual. If we consider an adult individual in the matrix model just before it starts its migration back to the spawning site, it is expected to give rise to a number of 1 year old individuals equal to $s_a f$ in the following year. In the EBT-formulation, such an adult individual on average gives rise to

$$E S(1) = E e^{-\int_0^1 d(\xi) d\xi}$$

1 year old individuals in the following year. Hence, for congruence between the matrix model and the EBT-formulation, we have to impose the condition:

$$s_a f = E e^{-\int_0^1 d(\xi) d\xi} \quad (1.27)$$

As an aside, please note that the conditions (1.26) and (1.27) would also have ensured congruence between the matrix model and the EBT-formulation for the coho salmon model, which once again reinforces the idea that different EBT-formulations with different parameter values and/or choices for life history function like $d(a)$ can all correspond to the same matrix model! Regarding the mortality between an age of $a = 1$ and $a = 2$ the coho and chinook salmon model do not differ. Hence, the final condition, relating the parameter s_j in the matrix model to the instantaneous mortality rate $d(a)$ in the EBT-model remains unchanged (*cf.* equation (1.20)):

$$e^{-\int_1^2 d(\xi) d\xi} = s_j \quad (1.28)$$

The definition of the probabilities $p(a)$ (equation (1.23)) together with the conditions (1.26), (1.27) and (1.28) on the parameter E and the age-dependent function $d(a)$ ensure that the EBT-model for chinook salmon is fully identical to the matrix model presented in section 1.2. As discussed in section 1.3.1, the EBT-formulation is based on more detailed and more explicit assumptions concerning the individual life history, especially on the instantaneous mortality rate $d(a)$. Hence, EBT-models with different choices for E and $d(a)$ may all be identical to the matrix model, as long as the conditions on E and $d(a)$ are satisfied. Of course, the condition that $d(a) = 0$ for $a \geq 2$ uniquely determines this part of the mortality rate function, leaving only flexibility in the choice of E and $d(a)$ for $0 \leq a < 2$.

1.4 Nursery competition in coho salmon

In the previous section it was argued that the EBT-formulation incorporated more explicit assumptions about the individual life history, in our example specifically the individual survival, and represented this life history in more detail. In addition to this property, the full

power of the EBT-approach will arguably only show up in cases in which density dependence plays a role in one way or the other. To illustrate this point we will in this section formulate a variant of the population dynamic model for coho salmon, in which newborn individuals compete with each other and therefore experience density dependent mortality. This type of competition is often referred to as nursery competition. We will both formulate an EBT-model and a corresponding matrix-type model.

Let us assume that newborn individuals experience a mortality rate that increases linearly with their density, due to competition for available resources. In the EBT-formulation we could account for such density dependence in mortality by assuming as functional form for the age-dependent mortality function, $d(a)$, as follows:

$$d(a) = \begin{cases} \mu_0 + \mu_1 N_0(t) & \text{for } 0 \leq a < 1 \\ \mu_0 & \text{otherwise} \end{cases} \quad (1.29)$$

in which the variable $N_0(t)$ refers to the number of individuals with an age between 0 and 1 year that are present at time t . The parameter μ_0 can be interpreted to represent a background mortality level that is density independent. The parameter μ_1 governs the strength of the density dependence in the mortality. The instantaneous mortality rate now not only depends on the age of an individual, but also on the number of conspecifics around, so we should actually write $d(a, N_0(t))$ for completeness. However, we will suppress this dependence on $N_0(t)$ for brevity.

To complete the model it remains to specify numerical values of the three parameters E , μ_0 and μ_1 and to specify the state of the initial population at $t = 0$. When done, the dynamics can be computed following the 3 basic stages of the EBT-procedure presented on page 12 with the sets of equations shown in Table 1.1. The basic model has remained completely the same, the assumption about nursery competition only involves changing the specification of one of the functions that describe life history processes.

In the matrix model (1.3) for the population dynamics of coho salmon, we have to account in a different way for the density dependence of newborn individuals, since individuals with an age between 0 and 1 year old are not explicitly represented in the model. The number of 1 year old individuals produced by all the adults present at a particular time is given by:

$$s_a f n_3(t)$$

which linearly depends on the number of spawning individuals $n_3(t)$. One way, which is frequently used to account for density dependence among the newborn individuals is to replace this linear dependence on the number of spawning individuals by a Ricker function (Ricker 1953) to describe the total number of offspring produced:

$$s_a f n_3(t) \exp(-c n_3(t)) \quad (1.30)$$

in which c is a parameter that determines the strength of the density dependence. Because of this modification the matrix \mathbf{A} shown in equation (1.4) will now depend on the density $n_3(t)$:

$$\mathbf{A}(\mathbf{n}) = \begin{pmatrix} 0 & 0 & s_a f \exp(-c n_3(t)) \\ s_j & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} \quad (1.31)$$

The EBT-formulation of this nursery competition process explicitly specifies how the density dependence operates at every point in time, as it relates the instantaneous mortality rate

$d(a)$ to the number of individuals present at that time. In contrast, the matrix model only specifies the overall outcome of the reproduction process and the density dependent mortality during the first year of life by modeling the number of 1 year old individuals that remain at time $T + 1$ from the spawning by adult individuals at time T .

The relevant question now is whether the density dependent parameter c in equation (1.30) and more generally the functional form of this Ricker-type of equation can be related to the density dependent mortality rate $d(a)$ given by equation (1.29). We can address this question by considering the ODE of the EBT-formulation that describes the decrease in the number of newborn individuals, $N_0(t)$, which are born at time $t = T$:

$$\frac{dN_0}{dt} = -(\mu_0 + \mu_1 N_0) N_0, \quad N_0(T) = E N_2(T^-) \quad (1.32)$$

This ODE is identical to the ODE (1.16a), but with $d(a)$ replaced by its functional form (1.29). Remember that $N_2(T^-)$ represents the number of spawning adults, which hence corresponds to the quantity $s_a n_3(t)$ in the matrix model (remember that in the EBT-model the adult migration mortality was accounted for in the mortality rate $d(a)$ for ages between $a = 2$ and $a = 3$). The ODE (1.32) can be solved explicitly, yielding:

$$N_0(t) = \frac{\mu_0 e^{-\mu_0 t} N_0(T)}{\mu_0 + \mu_1 (1 - e^{-\mu_0 t}) N_0(T)} \quad (1.33)$$

This solution determines a relationship between the number of 1 year old individuals at time $t = T + 1$, $N_1(T + 1) = N_0(T + 1^-)$ (*cf.* equation (1.19a)), and the number of spawning adults at time $t = T$, $N_2(T^-)$:

$$N_1(T + 1) = \frac{\mu_0 e^{-\mu_0} E N_2(T^-)}{\mu_0 + \mu_1 (1 - e^{-\mu_0}) E N_2(T^-)} \quad (1.34)$$

From this equation it is clear that relationship between the number of 1 year old individuals at time $T + 1$ is a saturating function of the number of spawning adults at time T , as opposed to the hump-shaped form that is represented by the Ricker function (1.30). To represent the nursery competition, in which the newborn mortality rate linearly increases with newborn density, in the matrix model, we hence have to assume that the number of 1 year old individuals at time $t + 1$ is related to the number of adults, $n_3(t)$, at time t following:

$$\frac{s_a f n_3(t)}{1 + c n_3(t)} \quad (1.35)$$

This functional form is also known as the Beverton-Holt stock-recruitment relationship (Beverton and Holt 1957), which was originally postulated to represent the relationship between spawning stock biomass and recruitment in fish populations. Using the Beverton-Holt functional form, the density dependent matrix \mathbf{A} becomes:

$$\mathbf{A}(\mathbf{n}) = \begin{pmatrix} 0 & 0 & \frac{s_a f}{1 + c n_3(t)} \\ s_j & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} \quad (1.36)$$

Given specific choices for the parameters E , μ_0 and μ_1 in the EBT-formulation, complete correspondence between this formulation and the matrix model can now be achieved by

choosing the parameters s_j , s_a , f , and c according to the following identities:

$$s_j = e^{-\mu_0} \quad (1.37a)$$

$$s_a = e^{-\mu_0} \quad (1.37b)$$

$$f = E e^{-\mu_0} \quad (1.37c)$$

$$c = \frac{\mu_1 (1 - e^{-\mu_0}) e^{-\mu_0}}{\mu_0} E \quad (1.37d)$$

With these choices for s_j , s_a , f , and c the conditions (1.20) and (1.21) are satisfied and ensure that the stock-recruitment relations (1.34) and (1.35) are identical to each other¹.

Whether the more often used Ricker stock-recruitment relationship or the Beverton-Holt relationship is used in the matrix model makes a very significant difference: With the Ricker function the matrix model predicts the occurrence of population cycles, complex dynamics and chaos, like exhibited by the well-known logistic map (May 1974). In contrast, with the Beverton-Holt relationship the matrix model only exhibits fixed-point dynamics for all values of the parameters.

1.5 Summary and conclusions

In terms of model formalism, the basic idea of the EBT-technique is to follow cohorts of identical individuals throughout their entire life history and account for all life history events of importance: growth, development, reproduction and death. New cohorts are added to the population when individuals are born, while cohorts of which all individuals have died are removed from the population.

From a practical point of view, the population dynamics is computed in a 3 stage procedure, involving

1. The numerical integration of all sets of ODEs that determine the life history of the individuals in a cohort, more specifically their development (aging) and mortality,
2. The creation of a new cohort of individuals at the moment that a reproduction event occurs, and
3. The renumbering of all existing cohorts in the population at the moment of a reproduction event to conserve an appropriate order in the indexes of the cohorts.

From the preceding sections, in which the EBT-formulations for the matrix models of section 1.2 have been derived we can draw two important conclusions:

- In comparison with the matrix models for salmon population dynamics, discussed in section 1.2, the EBT-formulation of these models incorporates more explicit assumptions about the individual life history and hence represents the life history in more detail. Most clearly this is illustrated by the fact that in the density-independent matrix model only the survival probability from one year to the next has to be specified. In contrast,

¹In fact, the derivation of the expression for the parameters f and c is a bit subtle, as it requires that the variable $N_2(T^-)$ in equation (1.34) is substituted by the product $s_a n_3(t)$, which occurs in the matrix model. Equating the right-hand side of the result to the expression shown in equation (1.35) then leads to identities (1.37c) and (1.37d)

in the EBT-formulation the entire age-dependent function for the individual death rate $d(a)$ has to be specified. Different choices for this age-dependent function may lead to the same survival probability from year to year, which makes the EBT-approach both more detailed as well as more specific.

- Also when density dependence plays a role, the EBT-formulation of the models accounts more explicitly and in more detail for the way in which the density dependence operates. Accounting for nursery competition in the EBT-model for coho salmon turned out to be straightforward and only involve the specification of the appropriate dependence of the mortality function $d(a)$ on newborn density. In contrast, to derive a corresponding matrix model involved the derivation of an explicit solution for the dynamics of the number of newborn individuals during their first year of life and a proper matching between the parameters in the matrix model and the EBT-model. The resulting matrix model incorporates a Beverton-Holt stock-recruitment relationship, as opposed to the Ricker-type relation that is often assumed as a phenomenological representation of the nursery competition process.

Because of these properties we consider the EBT-formulations of the population dynamics more *mechanistic*, i.e. even when they are fully identical to the matrix model formulation these model formulations incorporate a more specific representation of the individual life history processes, such as mortality, reproduction and interactions with other individuals.

Chapter 2

Size structure and environmental feedback

Before embarking on the study of models in which individual body size plays a dominant role, we will first discuss in more detail and more formally the different state concepts, *i*-state, *E*-state and *p*-state, that were already introduced in the previous chapter. The introduction of these 3 different states is necessitated by the fact that we are formulating a mathematical model: as a consequence, we need a mathematical representation of the object, the dynamics of which we aim to describe. The relevant objects in a PSPM are the individual, the environment it lives in and finally the population it is a member of.

2.1 The individual state or *i*-state

The individual state or *i*-state is a collection of, usually physiological, statistics that characterizes the individual organism and that is used to distinguish individuals from each other. Variables that are often used as elements of the individual state are the age of the individual, its size, its developmental stage or, in case of plants, the amount of foliage. Formally, the individual state should be a collection of individual properties

1. that at any one time completely determines, possibly together with the present state of its environment, the individual's probability to die or give birth and its influence on the environment (its contribution to the overall population dynamics), and
2. whose future values are completely determined by its present values plus the time course of the intervening environmental history, as encountered by the individual.

In practice only a limited number of such variables are used to characterize individuals. In the previous chapter the age of an individual was the only *i*-state-variable, *i.e.* age was the single element making up the *i*-state. In this chapter individual body size will constitute the *i*-state, such that again the *i*-state is represented by only a single variable. There is a very important difference between age and body size as *i*-state variable: aging always proceeds at unit rate, while growth in size is far more variable. Often the rate of growth in body size not only depends on the current body size of an individual, but also on the state of the environment in which it lives, for example, on the food density. This makes that predictions of size-structured models are often fundamentally different than those of age-structured models

and hence that the influence of growth and development on populations and communities is not sufficiently appreciated (de Roos and Persson 2004).

The two conditions on the i -state that are posed above already make clear that the i -state should be chosen such that it fully determines the most important life history processes of an individual: growth, development, reproduction, death and the interactions of the individual with its environment, for example, with its resources or predators. To model the life history of an individual organism mathematical functions have to be derived that specify how the rates at which these life history processes proceed, depend on the current i -state and on the properties of the environment that the individual lives in. This individual-level, life history model constitutes the ultimate core of the PSPM.

2.2 The environmental state or E -state

In most of the models considered in chapter 1, the events that occurred during the individual life history, being reproduction and death, were only influenced by the age of the individual. Hence, the fate of a single individual was assumed to be fully determined by its own i -state, *i.e.* its age, and by nothing else. In reality, such a situation almost never occurs: the main events in the individual life history, development, death and reproduction, are almost always a function of both the i -state as well as the environment that the individual lives in. This influence of the environment on life history is often referred to in general terms as *phenotypic plasticity*. However, since there is, as far as we know, no unambiguous definition of the term phenotypic plasticity, we will avoid using it.

The influence of the environment that an individual lives in on its life history can take many different forms. Three distinct classes can be recognized, illustrated by the following examples:

1. *Abiotic modulation*: life history processes are often strongly dependent on abiotic factors, like temperature. At lower temperatures, development slows down, which in some cases has led to the recognition of the *physiological age* of an individual and to the definition of the concept of *degree days*. In addition, to a slower development, also other processes like reproduction, feeding, and mortality tend to proceed at a slower rate at lower temperatures. This type of environmental influence we will refer to as *abiotic modulation*, since it is a completely external factor that neither the individual itself, nor the population it belongs to, nor any other population in the community that the population is part of can influence. As opposed to the following two classes, this type of environmental influence therefore does not lead to density dependence!
2. *Direct density dependence*: In many classical models in population biology, like the most basic logistic growth equation, the population abundance itself is assumed to directly influence the vital rates. More mechanistic examples of direct density dependence are represented by cannibalism of adult individuals on younger or smaller conspecifics or the interference between predator individuals of the same species. This type of environmental influence on the individual life history clearly depends on how many individuals constitute the population: at very low densities the influence will become negligible, while the influence will become stronger the more abundant the population is. Therefore, this density dependence operates in a very direct way, because it is the population abundance that directly modifies the vital rates.
3. *Environmental feedback*: The last class of environmental influence we will refer to as

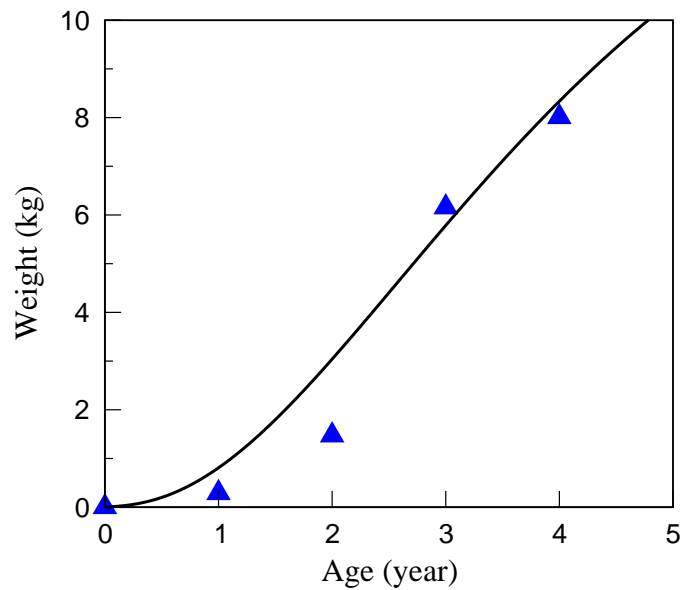


Figure 2.1: Weight-age relationship for chinook salmon in Lake Ontario. Average weight-at-age data reported by Rand and Stewart (1998) for the period 1990-1991 are shown together with a vonBertalanffy growth curve (Von Bertalanffy 1957) fitted by eye (see text for details).

environmental feedback, even though this is a bit of a misnomer. The most obvious example of environmental feedback is the influence of resource levels on individual growth and development, reproduction and possibly mortality. In turn, resource levels in the environment will be influenced by the feeding of the individuals and hence will be more depressed at higher population densities. Environmental feedback hence also represents a form of density dependence, but one that operates indirectly: high population densities will lead to lower resource levels, which in turn will slow down individual growth and development, as well as negatively affect individual reproduction and survival.

The terms introduced for the last two categories of environmental influence, direct density dependence and environmental feedback, are slightly ambiguous. Both types of environmental influence represent density dependent effects and both types can be considered to be a feedback mechanism of the population abundance on the life history of its individuals. The main distinction is in the direct or indirect manner in which the density dependence or feedback operates. We could hence have referred to the two types as direct and indirect density dependence. Alternatively, in de Roos (1997) the two types are referred to as *feedback functions* and *feedback loops*. The importance is that the two types of influence represent density dependence and population feedback, but have either a direct or an indirect type of operation. The terminology used to distinguish the two from one another is only semantics.

Next to the *i*-state, the environmental state plays a very important role in PSPMs. Every factor that can modify the life history of an individual organisms and that is not one of its own physiological traits, is considered part of its environment. Hence, also all other members of the population it is itself part of are considered part of its environment. The environment is hence defined in such a way that any population- or community-level influence on the fate of an individual organism operates via its environment.

The way in which the dynamics of the environment are incorporated into the PSPM depends

on the type of environmental influence that is modeled. In case of abiotic modulation, the state of the environment changes over time in a pre-determined manner. For example, to account for seasonal temperature variation in a PSPM, one has to specify a priori the pattern of the daily temperature as a function of the time of year. An example of direct density dependence was already encountered in section 1.4 on nursery competition in coho salmon. Here, the density of newborn individuals at a particular time, $N_0(t)$, influenced the individual-level, *per capita* mortality rate of the individuals. The variable $N_0(t)$ was already part of the population-level model and its dynamics are hence following directly from the PSPM. In contrast, if reproduction and death would depend on the resource levels in the environment and these resources have an autonomous dynamics even in the absence of populations that consume them, the PSPM has to be extended by a dynamic model for the resources themselves. Examples of this type of environmental feedback will be discussed later in this chapter.

2.3 The population state or p -state

The population state is the mathematical object or construct that represents a biological population in a dynamic model. In traditional, population-dynamic models, which are exclusively formulated at the population level, it is the only state concept. In structured population models, however, it plays a less important role and is subsidiary to the i -state and E -state. The latter two states play fundamental roles in the model of the individual life history, which constitutes the core of any PSPM. The p -state only plays a role in the bookkeeping process that translates the individual-level, life-history dynamics into its population consequences.

The form of the p -state strongly depends on the model of the individual life history. In the previous chapter the population was represented by a vector of cohort densities, for example, the vector

$$\mathbf{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix} \quad (2.1)$$

represented the population of chinook salmon in the age-structured matrix model of section 1.2. Also in the corresponding EBT-formulation of the model the population was represented by a vector of cohort densities, but each cohort was also characterized by the age of the individuals in the cohort. Hence, a full characterization of the salmon population incorporates both the number of individuals in the different cohorts as well as their age. The population state could hence be written as a matrix:

$$\begin{pmatrix} N_0(t) & A_0(t) \\ N_1(t) & A_1(t) \\ N_2(t) & A_2(t) \\ N_3(t) & A_3(t) \end{pmatrix} \quad (2.2)$$

or as two vectors,

$$\begin{pmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{pmatrix}, \quad \begin{pmatrix} A_0(t) \\ A_1(t) \\ A_2(t) \\ A_3(t) \end{pmatrix} \quad (2.3)$$

one specifying the cohort abundances, the other the age of their individuals.

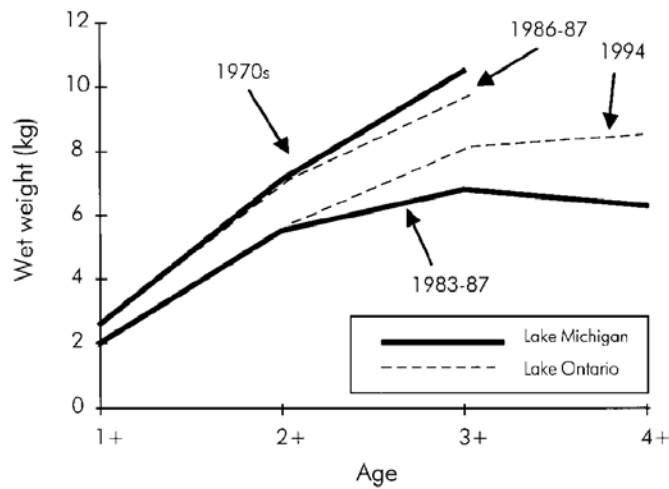


Figure 2.2: Weight-at-age for sexually mature hatchery chinook salmon from Lake Michigan and Lake Ontario. Figure redrawn from Rand and Stewart (1998), showing sampling data from Strawberry Creek, Wisconsin (Lake Michigan) and Salmon River, New York (Lake Ontario). Both reductions in size-at-age and delays in age-at-maturity have occurred in these populations over time.

In general, in an EBT-model the population is made up of distinct cohorts of individuals. Each of these cohorts is characterized by a number of variables, specifying the number of individuals in the cohort and their average i -state (age, size or any other physiological variable). The p -state in an EBT-model is hence the conjunction of these sets of variables that characterize each cohort separately. When the number of cohorts in a population is always the same, as is the case for the semelparous salmon populations, the p -state has a constant dimension. In later chapters we will, however also encounter situations in which the number of cohorts making up a population varies over time. In that case, the dimension of the p -state is not pre-determined, but shrinks or expands with the number of cohorts present.

Finally, in case reproduction does not occur in discrete events over time, as we have considered up to now, the population essentially consists of individuals that span a continuum of ages and/or sizes. A more appropriate representation of the population in such a cases would be a continuous distribution over an age- or size-interval. We will not discuss this possibility in more detail here, as it mostly plays a role in more mathematical studies of PSPMs.

2.4 Size dependence in life history of chinook salmon

In chapter 1 age-structured models were formulated to describe the population dynamics of chinook salmon. All life history processes in these models were hence related to the age of an individual salmon, the variable representing the i -state. In many fish species, however, individual body size plays a much more prominent role in the life history than age. Chinook salmon is no exception to this rule. Newborn chinook salmon weigh approximately 4 g, while adult individuals of 4 years or older may weigh up to 10 kg! Individuals may hence exhibit a weight increase with a factor of $10^3 - 10^4$ during their lifetime. Figure 2.1 shows data presented by Rand and Stewart (1998) of the average weight of chinook individuals at different ages. These authors present further evidence for a decline in weight-at-age as well as

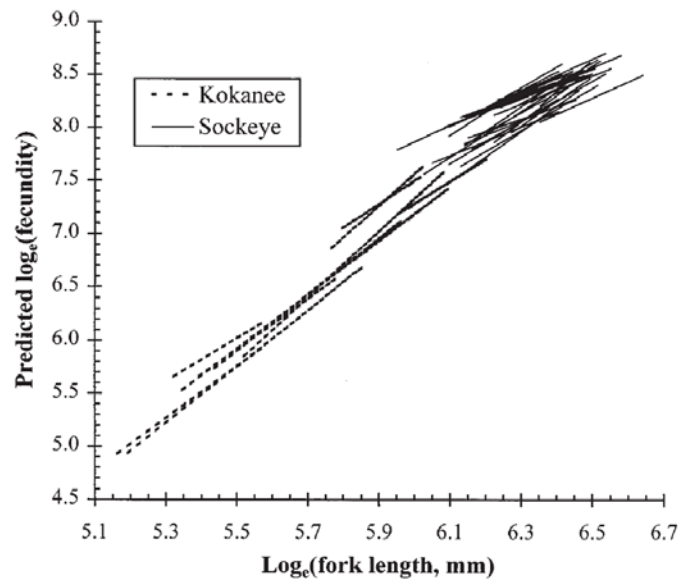


Figure 2.3: Relationship between fecundity and fork length for 11 populations of kokanee and 46 populations of sockeye salmon. Only the regression lines to the actual data on $\log_e(\text{fecundity})$ versus $\log_e(\text{fork length})$ are shown for different populations from Japan, Canada and the US. Figure redrawn from McGurk (2000).

age-at-maturity over time as a result of food limitation (see Figure 2.2). This food limitation is argued to mainly result from low densities of adult alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), which constitute the main prey fish species of the chinook salmon.

The differences in body size has substantial consequences for the individual life history processes, especially for individual reproduction and mortality. Figure 2.3 shows regression lines for a large number of populations of a different species of Pacific salmon, *Oncorhynchus nerka*. One variant of this species, referred to as sockeye salmon, is anadromous and hence migrates out into the ocean. The other variant, called kokanee salmon, is nonanadromous and remains in freshwater throughout its life. The data indicate a significant positive relationship between the body size of the female salmon and the number of eggs produced when spawning. For chinook salmon Healey (2001) showed that a relative constant fraction of 20-25% of the body weight of a female salmon consists of gonad mass. This gonadal investment translates in the production of roughly 550 – 750 eggs per kilogram body weight. Heath et al. (1999) showed even larger variation in the number of eggs produced per kilogram body weight of female chinook salmon, ranging from 600-1200 eggs per kilogram.

Mortality is equally dependent on individual body size, especially in the early stages of life. In general, larger individuals have a higher probability to survive. The pattern may strongly depend, however, on the environment that the individuals live in. Figure 2.4 shows survival data for 0^+ fry of nasu salmon (*Oncorhynchus nasou*) over a 3-week experimental period. In the absence of predators, small individuals indeed have a higher mortality risk, but in the presence of predators survival of all size classes of individuals tends to be equal. Here, the selectivity of the predator, which size of prey fish is prefers to forage on, equalizes the survival probability of the salmon fry. In general, however, survival of small individuals tend to correlate positively with body size, as is also shown in Figure 2.5.

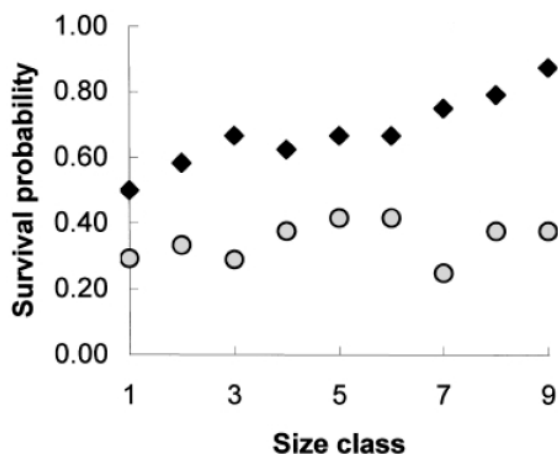


Figure 2.4: Survival probability for different size classes of 0^+ fry of nasu salmon *Oncorhynchus nasou*. Survival was measured over a 3-week experimental period in the absence (diamonds) or the presence (circles) of a fish predator. Figure redrawn from Reinhardt et al. (2001).

The data on the influence of body size on life history processes, such as reproduction and mortality, indicate that for many fish species, age does not really qualify as an appropriate statistic to characterize the state of individual. At least, Figure 2.4 clearly shows that similarly aged, 0^+ chinook salmon have different survival probabilities, dependent on how big they are. More generally, body size is one of the most important traits of an individual organism in many species and a much stronger determinant of the fate of an individual organism than individual age. It determines to a large extent the type and strength of ecological interactions that the individual is subjected to and influences most, if not all, key life-history processes, including food choice, foraging capacity, growth, development, reproduction and mortality (Peters 1983; Werner 1988). The importance of body size is related to the fact that over 80% of all species grow and develop throughout their entire life (Werner 1988). Only mammals and birds exhibit little, and if so rather rapid, growth during their life, such that body size may be less important than age for these taxonomic groups.

2.5 An age- and size-structured life history model for chinook salmon

For chinook salmon it seems far more appropriate to choose body size as the variable that describes the individual state and hence to formulate a size-structured model for its population dynamics. When body size is adopted as z -state we have to model how life history processes, such as reproduction and mortality, depend on it. In contrast to the age-structured models discussed in the previous chapter, however, we now also have to describe how body size changes over the life time of an individual. In other words, next to the modeling of reproduction and mortality, which were also part of an age-structured model, we have to add a functional description how an individual grows over time as a function of its own size. This adds an important process to the model of individual life history.

We first discuss the modeling of individual growth, using the data presented in Figure 2.1.

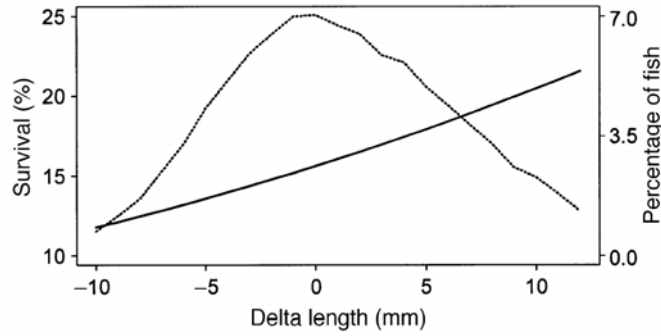


Figure 2.5: Survival as a function of body length in chinook salmon. The solid, increasing line depicts percent survival as a function of the deviation of individual body length from the population average length. The dotted line indicates the fraction of fish in the salmon cohort with that particular body length. Figure redrawn from Zabel and Achord (2004).

The data presented were used to fit a vonBertalanffy growth curve (Von Bertalanffy 1957), describing the weight, $W(a)$, of an individual at age a . The growth curve $W(a)$ is the solution of the following ODE:

$$\frac{dW}{da} = 3\gamma \left(W_\infty^{1/3} W^{2/3} - W \right), \quad W(0) = W_0 \quad (2.4)$$

The right-hand side of this ODE describes the instantaneous growth rate in weight for an individual with a particular weight W . The parameters of the ODE are the initial weight at birth, W_0 , the cubic root of the ultimate weight at very old age, $W_\infty^{1/3}$ and the growth rate constant γ . The ODE can be solved explicitly by recasting the equation in terms of the cubic root of the individual weight. Define

$$s = W^{1/3} \quad (2.5)$$

The variable s , which we will refer to as individual size, hence represents a length-type of measure of individual body size. Substitution of the relationship (2.5) into the ODE (2.4) yields the following ODE for s :

$$\frac{ds}{da} = \gamma (s_\infty - s), \quad s(0) = s_0 \quad (2.6)$$

in which

$$s_\infty = W_\infty^{1/3} \quad (2.7)$$

and

$$s_0 = W_0^{1/3} \quad (2.8)$$

The ODE (2.6) can be solved in a straightforward manner yielding:

$$s(a) = s_\infty - (s_\infty - s_0) e^{-\gamma a} \quad (2.9)$$

An explicit function for the weight-at-age function $W(a)$ can be derived using the relationship (2.5), yielding

$$W(a) = \left(W_\infty^{1/3} - \left(W_\infty^{1/3} - W_0^{1/3} \right) e^{-\gamma a} \right)^3 \quad (2.10)$$

This last age-dependent function $W(a)$ has been fitted to the data points presented in Figure 2.1 to estimate the parameters $W_\infty^{1/3}$ and γ , while Rand and Stewart (1998) provide an estimate for the remaining parameter W_0 equal to 0.004 kg.

Given the choice of s ($= W^{1/3}$) as our length-based measure of individual body size, the individual life history is now modeled using 3 size-dependent functions:

- $g(s)$, the individual growth rate. This function represents the right-hand side of the ODE that describes the growth of the individual in body size:

$$\frac{ds}{dt} = g(s) \quad s(0) = s_0 \quad (2.11)$$

in which the parameter $s_0 = 0.16$ equals the cubic root of the weight of a newborn individual at birth ($W_0 = 0.004$) and the growth function $g(s)$ is defined as

$$g(s) = \gamma(s_\infty - s) \quad (2.12)$$

with parameters $\gamma = 0.4$ and $s_\infty = 2.5$. Inspection of Figure 2.1 shows that the fit of the vonBertalanffy growth curve to the data is not that good. In particular, it seems that the individuals grow far more rapidly between an age of 2 and 3 years old, corresponding to the period in which they have migrated out into the ocean. This change in habitat possibly involves a change in food availability as well, which might explain the rapid growth of the individuals in this period. For the sake of simplicity we will, however, ignore these aspects of the salmon life history and model individual growth in size with the growth function (2.12).

It should be pointed out that the growth process is described in a deterministic manner, *i.e.* given the size of an individual its growth rate is uniquely determined. This also implies that individuals that start out have the same size at birth will always remain identical to each other. In section 1.3 it was already pointed out that this was one of the basic assumptions on which the EBT-formalism is based.

- $E(s)$, the number of eggs produced when spawning. Figure 2.3 made clear that the fecundity of female salmon depends on the female body size. Data presented by Healey (2001) and Heath et al. (1999) indicated that per kilogram body weight chinook salmon produce somewhere between 500 and 1200 eggs. For the function $E(s)$ we will hence assume the simple relationship

$$E(s) = \beta s^3 \quad (2.13)$$

with scaling constant $\beta = 700$. This function implies that the number of eggs produced at spawning scales linearly with individual body weight ($= s^3$) and that per kilogram weight 700 eggs are produced.

- $d(s)$, the instantaneous mortality rate. Given the variability in size-dependent survival patterns observed in natural systems, due to, for example, the type and density of predators present, we will consider only a very simple form of size-dependence in mortality rate, following the relationship

$$d(s) = \mu_\infty - (\mu_\infty - \mu_0) e^{-s/s_\mu} \quad (2.14)$$

The function $d(s)$ hence is a decreasing function of our body size measure s , takes on the values μ_0 and μ_∞ for very small and very large individual, respectively, while it falls

Table 2.1: Age/size-structured life history model of chinook salmon

A. i-state variables and life history parameters			
<i>Symbol</i>	<i>Unit</i>	<i>Value</i>	<i>Interpretation</i>
a	y		individual age
s	$\text{kg}^{1/3}$		individual body size
s_0	$\text{kg}^{1/3}$	0.16	body size of newborn individual
s_∞	$\text{kg}^{1/3}$	2.5	maximum body size
γ	y^{-1}	0.4	growth rate constant
β	kg^{-1}	700	weight-specific fecundity
μ_0	y^{-1}	2	mortality rate of very small individual
μ_∞	y^{-1}	1	mortality rate of very large individual
s_μ	$\text{kg}^{1/3}$	0.5	body size scaling constant of mortality

B. Life history model equations	
<i>Function</i>	<i>Interpretation</i>
$g(s) = \gamma (s_\infty - s)$	growth rate in body size
$E(s) = \beta s^3$	number of eggs spawned by an adult individual
$d(s) = \mu_\infty - (\mu_\infty - \mu_0) e^{-s/s_\mu}$	instantaneous mortality rate
$p(a) = \begin{cases} 0 & \text{for } a = 1 \\ 0.2 & \text{for } a = 2 \\ 0.75 & \text{for } a = 3 \\ 1.0 & \text{for } a = 4 \end{cases}$	age-specific spawning probability

off with s at a rate determined by the parameter s_μ . The choice of the functional form of $d(s)$ is rather arbitrary and not based on any particular data. Data on mortality rate are usually extremely difficult to obtain, let alone on the scaling of mortality with size and/or age. Mortality is therefore often the most arbitrary part of a life history model. Using the functional form above allows us to explore how increasing levels of newborn mortality (increasing value of μ_0) affects the population dynamics. A workable set of default parameters for the chinook salmon model developed here is $\mu_\infty = 1/\text{year}$, $\mu_0 = 2/\text{year}$ and $s_\mu = 0.5 \text{ kg}^{1/3}$.

What remains to be specified is the probability that an adult will spawn in a particular year. As discussed in section 1.2 chinook salmon spawn either at an age of 2, 3 and 4 year old. Hence, the timing of spawning is not governed by individual size, but by individual age. This implies that to correctly describe the life history of chinook salmon the choice of individual body size as the only variable of the i -state will not suffice. Both age and size have to be taken into account to fully describe the fate of an individual and these variables hence constitute together the i -state. In contrast to the models developed in the previous chapter, the model

developed here is based on a two-dimensional i -state, *i.e.* one that contains two elements. For the probability to spawn at a particular age a , denoted by the function $p(a)$, we will adopt the same formulation as in section 1.3.2 (see equation (1.23)):

$$p(a) = \begin{cases} 0 & \text{for } a = 1 \\ 0.2 & \text{for } a = 2 \\ 0.75 & \text{for } a = 3 \\ 1.0 & \text{for } a = 4 \end{cases} \quad (2.15)$$

Table 2.1 summarizes the variables, parameters and functions that together constitute the age- and size-dependent life history model for chinook salmon derived above.

2.6 Age- and size-structured EBT-model for chinook salmon

On the basis of the life history model for chinook salmon derived in the previous section it is relatively straightforward to formulate the model for the population dynamics of the salmon. In principle, the model is close to the model presented in Table 1.2, except for the fact that in addition to keeping track of the age of the individuals in all the cohorts, we also have to keep track of the body size of the individuals. Let the variable $S_i(t)$ denote the body size of all the individuals in cohort i (remember that we have assumed that all individuals are born with the same body size and hence they remain identical in body size throughout their life). At the time of birth $S_i(t)$ equals s_0 , the body size of a newborn individual. Subsequently, the dynamics of the body size in the cohort follows the differential equation

$$\frac{dS_i}{dt} = g(S_i) \quad (2.16)$$

which is simply the growth equation for an individual with a particular body size s .

Each cohort of individual is now characterized by three variables: the number of individuals in the cohort, $N_i(t)$, the age of the individuals in the cohort, $A_i(t)$, and the body size of the individuals in the cohort, $S_i(t)$. The dynamics of these variables after birth is fully determined by the following set of ODEs:

$$\begin{cases} \frac{dN_i}{dt} = -d(S_i) N_i & (2.17a) \end{cases}$$

$$\begin{cases} \frac{dA_i}{dt} = 1 & (2.17b) \end{cases}$$

$$\begin{cases} \frac{dS_i}{dt} = g(S_i) & i = 0, 1, 2, 3 & (2.17c) \end{cases}$$

This set of equations incorporates both the size-dependent growth rate $g(s)$, as well as the size-dependent mortality rate $d(s)$.

At the beginning of a new year, when a reproduction event is taking place, a new cohort is created. Let's assume that these reproduction events take place at $t = T, T + 1, T + 2, \dots$. The individuals are born with age 0 and body size s_0 , while the total number of offspring

Table 2.2: Age/size-structured EBT-model of a chinook salmon population

A. Population variables	
$N_i(t)$	number of individuals in cohort i at time t
$A_i(t)$	age of individuals in cohort i at time t
$S_i(t)$	body size of individuals in cohort i at time t

B. Population model equations	
Continuous-time dynamics for all cohorts, in between two reproduction events	$\left\{ \begin{array}{l} \frac{dN_i}{dt} = -d(S_i) N_i \\ \frac{dA_i}{dt} = 1 \\ \frac{dS_i}{dt} = g(S_i) \end{array} \right. \quad i = 0, \dots, 3$
Creation of new cohort during reproduction event at $t = T, T + 1, T + 2, \dots$	$\left\{ \begin{array}{l} N_0(t) = \sum_{i=1}^3 E(S_i(t^-)) p(A_i(t^-)) N_i(t^-) \\ A_0(t) = 0 \\ S_0(t) = s_0 \end{array} \right.$
Renumbering equations for all non-newborn cohorts at $t = T, T + 1, T + 2, \dots$	$\left\{ \begin{array}{l} N_i(t) = (1 - p(A_{i-1}(t^-))) N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \\ S_i(t) = S_{i-1}(t^-) \end{array} \right. \quad i = 1, \dots, 3$

produced is given, as before, by the product of the fecundity, the probability of spawning at age a and the number of individuals in the different adult cohorts:

$$\left\{ \begin{array}{l} N_0(T) = \sum_{i=0}^3 E(S_i(T^-)) p(A_i(T^-)) N_i(T^-) \\ A_0(T) = 0 \\ S_0(T) = s_0 \end{array} \right. \quad \begin{array}{l} (2.18a) \\ (2.18b) \\ (2.18c) \end{array}$$

(*cf.* equation (1.24)). The only difference with the age-structured model developed in section 1.3.2 is the fecundity of the adult now depends on their body size, $E(S_i)$.

Finally, for bookkeeping reasons we have to renumber all the older cohorts in the populations to keep order in the indices. The renumbering equations also have to account for the facultative spawning, as was the case for the age-structured model (*cf.* equations (1.25)), since only a fraction $1 - p(a)$ of the present individuals survives this reproduction event at time $t = T$.

Hence, the renumber equations become:

$$\begin{cases} N_i(T) = (1 - p(A_{i-1}(T^-))) N_{i-1}(T^-) & (2.19a) \\ A_i(T) = A_{i-1}(T^-) & (2.19b) \\ S_i(T) = S_{i-1}(T^-) & i = 1, \dots, 3 \quad (2.19c) \end{cases}$$

Note once again that our definition of the probabilities $p(a)$, allows us to write these renumbering equation in the above, compact form. Even though individuals at age $a = 1$ are not adult yet, the definition of $p(a) = 0$ for $a = 1$ makes it possible to write a single set of renumbering equations for all existing cohorts in the population. All population-level equations describing the dynamics of the age- and size-structured chinook salmon population are summarized in Table 2.2.

2.7 Environmental feedback: a dynamic resource model

Despite its rather intimidating formulation, the model derived in the previous section is a linear model, *i.e.* it is completely density independent. As a consequence, the population dynamics it predicts is rather boring and straightforward: ultimately the population will grow exponentially with a constant exponential growth rate. We could of course again incorporate nursery competition into the model, as was done in section 1.4 in the model for coho salmon. Whether or not nursery competition is accounted for, the incorporation of the size-dependence into the model is in reality rather superfluous. Essentially the model is a fully age-structured and can be reformulated into an age-structured matrix model if nursery competition is not playing a role. For, the growth in body size, as modeled by the ODE (2.11), can be solved to yield an explicit relationship between the age and the size of an individual, as shown by equation (2.9):

$$s(a) = s_\infty - (s_\infty - s_0) e^{-\gamma a} \quad (2.20)$$

Using this relationship between age and size of an individual, we could replace all the size-dependent functions by age-dependent functions. For example, the size-dependent fecundity $E(s)$ an individual adult with size s could be replaced by the age-dependent function:

$$E(a) = \beta (s_\infty - (s_\infty - s_0) e^{-\gamma a})^3 \quad (2.21)$$

Also for the size-dependent mortality rate $d(s)$ an equivalent age-dependent function can be derived using the size-age relationship (2.20). Therefore, as long as an explicit relationship between body size and age can be derived, the population dynamic model is essentially an age-structured model and can be reformulated into a fully identical age-structured analogue. The invariant size-age relation is, however, not very likely to occur under any set of natural conditions. Growth in size is usually very flexible and often depends on external factors, most importantly on resource availability and temperature. Size-structured population models only become interesting if this dependence of growth on resource availability, especially, is accounted for and if the resource density itself is dynamic.

For chinook salmon the data presented in Figure 2.2 showed that indeed resource limitation played a role in the changes that occurred in the size-at-age relationship over several years. Rand and Stewart (1998) argued that chinook individuals in Lake Michigan remained smaller

Table 2.3: Age/size-structured life history model of chinook salmon with food dependence

A. <i>i</i>-state variables and life history parameters			
<i>Symbol</i>	<i>Unit</i>	<i>Value</i>	<i>Interpretation</i>
a	y		individual age
s	kg ^{1/3}		individual body size
s_0	kg ^{1/3}	0.16	body size of newborn individual
s_m	kg ^{1/3}	2.5	maximum body size at very high food levels
γ	y ⁻¹	0.4	growth rate constant
β	kg ⁻¹	700	weight-specific fecundity
μ_0	y ⁻¹	2	mortality rate of very small individual
μ_∞	y ⁻¹	1	mortality rate of very large individual
s_μ	kg ^{1/3}	0.5	body size scaling constant of mortality
α	g/kg ^{2/3}	1	maximum ingestion rate scaling constant
F_h	g/L	0.5	body size scaling constant of mortality

B. Life history model equations	
<i>Function</i>	<i>Interpretation</i>
$g(s, F) = \gamma \left(s_m \frac{F}{F_h + F} - s \right)$	growth rate in body size
$E(s) = \beta s^3$	number of eggs spawned by an adult individual
$d(s) = \mu_\infty - (\mu_\infty - \mu_0) e^{-s/s_\mu}$	instantaneous mortality rate
$p(a) = \begin{cases} 0 & \text{for } a = 1 \\ 0.2 & \text{for } a = 2 \\ 0.75 & \text{for } a = 3 \\ 1.0 & \text{for } a = 4 \end{cases}$	age-specific spawning probability
$I(s, F) = \alpha s^2 \frac{F}{F_h + F}$	resource ingestion rate

in the 1980's than in the 1970's due to lower prey fish availability. A simple way of incorporating this resource dependence into the life history model of chinook salmon is to assume that the maximum size that individuals can reach increases with resource availability, following a hyperbolic relationship:

$$s_\infty = s_m \frac{F}{F_h + F} \quad (2.22)$$

A mechanistic underpinning for this relationship between ultimate body size s_∞ and resource density F can be found in Kooijman and Metz (1984), Kooijman (1993) and Kooijman (2000) (Note that here and below I use the term resource and food indiscriminately). The two

parameters in the equation above represent the maximum body size s_m under very high (actually infinite) resource levels and the resource density F_h at which the largest size reached by an individual is half this maximum.

Using the food-dependent expression (2.22) for the ultimate body size at a particular food density, the growth rate now becomes both size- and food-dependent, as follows:

$$g(s, F) = \gamma \left(s_m \frac{F}{F_h + F} - s \right) \quad (2.23)$$

A food-dependent growth rate alone, however, does not lead to any density dependence in the population model. For that, there has to be a feedback effect from the salmon population on its resource. As long as the food density F is constant, the entire life history of an individual is still independent of its environment and the model is linear and age-structured. Feedback of the salmon population on its own resource availability comes about because the individuals forage on it and hence deplete it. We model the resource ingestion rate, denoted with the function $I(s, F)$, with the following equation:

$$I(s, F) = \alpha s^2 \frac{F}{F_h + F} \quad (2.24)$$

The choice for this functional form of the resource ingestion rate is related to the choice for the expression (2.23) for the growth rate $g(s)$. This set of two equations can be derived from considerations about the energy budget of the individual organism as developed in Kooijman and Metz (1984), Kooijman (1993) and Kooijman (2000). We will discuss this issue in a later chapter.

Incorporating the expressions for the size- and food-dependent growth and ingestion rate, $g(s, F)$ and $I(s, F)$, respectively, into the size-structured model derived in the previous sections (see Tables 2.1 and 2.2) completes the formulation of the model describing the life history of chinook salmon as a function of its own age and size and the resource availability in the environment.

At the population level the most substantial difference due to the introduction of food-dependence in individual life history is that now also the dynamics of the food density itself has to be modeled. Obviously, food density varies continuously over time through feeding by the salmon and through its own regrowth or replenishment. The total foraging of salmon equals the sum of the feeding of all the cohorts presents, *i.e.*

$$\sum_{i=0}^3 I(S_i, F) N_i(t)$$

where S_i is the current body size of the individuals in cohort i and N_i is the number of these individuals. The regrowth of food can be modeled in a variety of ways, most commonly used is the logistic growth equation. However, for simplicity we will model regrowth of food by means of the semi-chemostat growth equation:

$$\rho (K - F)$$

in which the parameter K refers to the maximum density of food that can be attained and ρ is the time constant of regrowth. The semi-chemostat growth equation models a growth process, in which the regrowth is largely independent of the current food density itself, for

Table 2.4: Age/size-structured EBT-model of a chinook salmon population with dynamic resource

A. Population variables and parameters			
<i>Symbol</i>	<i>Unit</i>	<i>Value</i>	<i>Interpretation</i>
$N_i(t)$	#/L		number of individuals in cohort i at time t
$A_i(t)$	y		age of individuals in cohort i at time t
$S_i(t)$	$\text{g}^{1/3}$		body size of individuals in cohort i at time t
$F(t)$	g/L		resource density in the environment
ρ	y^{-1}	0.01	semi-chemostat resource regrowth rate
K	g/L	1.0	maximum resource density in absence of consumers

B. Population model equations	
Continuous-time dynamics for all cohorts, in between two reproduction events	$\begin{cases} \frac{dN_i}{dt} = -d(S_i) N_i \\ \frac{dA_i}{dt} = 1 \\ \frac{dS_i}{dt} = g(S_i, F) \end{cases} \quad i = 0, \dots, 3$
Creation of new cohort during reproduction event at $t = T, T + 1, T + 2, \dots$	$\begin{cases} N_0(t) = \sum_{i=1}^3 E(S_i(t^-)) p(A_i(t^-)) N_i(t^-) \\ A_0(t) = 0 \\ S_0(t) = s_0 \end{cases}$
Renumbering equations for all non-newborn cohorts at $t = T, T + 1, T + 2, \dots$	$\begin{cases} N_i(t) = (1 - p(A_{i-1}(t^-))) N_{i-1}(t^-) \\ A_i(t) = A_{i-1}(t^-) \\ S_i(t) = S_{i-1}(t^-) \end{cases} \quad i = 1, \dots, 3$
Dynamics of resource density in the environment	$\frac{dF}{dt} = \rho(K - F) - \sum_{i=0}^3 I(S_i, F) N_i(t)$

example, through inflow of food from outside the system or from refuges or because food or prey are recruited from smaller size classes of individuals that the consumers can forage on.

The dynamics of F is now a balance between an increase through regrowth and a decrease through foraging, described by the ODE:

$$\frac{dF}{dt} = \rho(K - F) - \sum_{i=0}^3 I(S_i, F) N_i(t) \quad (2.25)$$

An initial condition for the food density at time $t = 0$, $F(0)$, has to be specified to complete

this ODE. To compute the population dynamics, the ODE has to be integrated numerically at the same time as the ODEs (2.17) for the dynamics of the statistics representing a cohort of individuals. At the time that a reproduction event occurs, there is no change to the food density whatsoever. Therefore, the numerical integration of ODE (2.25) alongside the integration of the cohort ODEs is the only thing needed to account for a dynamic food component in the age and size-structured population model for chinook salmon.

Table 2.4 summarizes this population dynamic model for chinook salmon in case of a dynamic resource. It is the first example of a model, in which population size structure plays a pivotal role and which can not be reduced to a corresponding age-structured model. The dynamics resource in the model is a clear example of an environmental feedback, one of the three mechanisms of environmental influence on population dynamics, discussed on page 2.2: on the one hand the individual-level processes, mainly growth in body size in this case, depend on the current resource availability, on the other hand the salmon population as a whole depletes the resource and hence negatively affects its individuals, but in an indirect way. This way of modeling density dependence, by means of an environmental factor that influences the life history of the *individual*, but that itself is only affected by the *population* as a whole, has become extremely important in the theory of PSPMs: as discussed by Diekmann et al. (2003) it is the basis for methods to numerically calculate the equilibrium of a PSPM, as well as for evolutionary analyses using these models. We refer to Claessen and de Roos (2003) for a more intuitive introduction to these advanced methods.

2.8 Summary and conclusions

From a conceptual point of view, accounting for population size structure and size dependence of individual life history is not very different from the age-dependent modeling that was discussed in the previous chapter. Still, the basic idea of the EBT-technique is to follow cohorts of identical individuals throughout their entire life history and account for all life history events of importance: growth, development, reproduction and death. New cohorts are added to the population when individuals are born, while cohorts of which all individuals have died are removed from the population. The major difference is that the use of body size as an *i*-state variable requires that an additional life history process is modeled: individual growth and development. Also, choosing more physiological variables (both age and size) to represent the *i*-state has been shown to be a relatively straightforward extension of the population-level model: it requires that additional equations have to be specified for the body size of the individuals in each cohort, which are analogous to the equations for the age of the individuals in the cohort. The incorporation of environmental feedback loops requires that additional equations (ODEs) are specified for the dynamics of these factors over time. This contrasts with direct density-dependent mechanisms, such as the nursery competition discussed in section 1.4, which do not require the population-level model to be extended with additional equations.

From a practical point of view, the population dynamics is still computed in 3 stages, but which now encompass 4 different procedures:

1. The numerical integration of all sets of ODEs that determine the life history of the individuals in a cohort, more specifically their development, aging and mortality.
2. The simultaneous integration of the ODEs that determine the dynamics of all environmental factors, such as food density. These ODEs are coupled with the cohort ODEs

through the influence these factors (*i.e.* food density) have on individual life history and, in turn, the population-level feedback of the cohorts on them, for example through feeding.

3. The creation of a new cohort of individuals at the moment that a reproduction event occurs, and
4. The renumbering of all existing cohorts in the population at the moment of a reproduction event to conserve an appropriate order in the indexes of the cohorts.

An important conclusion from section 2.7 is that size-structured population models can always be reformulated into a corresponding age-structured model, as long as individual growth and development is invariant, *i.e.* does not depend on environmental conditions. Hence, the dependence of individual growth and development on, for example, food density makes for a crucial difference. Once again, this reinforces the earlier conclusion that the power of the EBT-formalism primarily resides in its more detailed and explicit representation of individual life history and of the density dependence involved in this life history.

Chapter 3

Continuous reproduction

In the preceding chapters we have only discussed situations in which reproduction occurred at discrete moments in time. This pulsed reproduction process implies that a newborn cohort arises more or less instantaneously and that hence the population is naturally subdivided into discrete cohorts of identical individuals. Even for species, for which reproduction does take place as distinct events, but at irregularly spaced moments in time, the EBT-formalism, such as shown in Table 2.4, can be applied, as long as the renumbering and reproduction operations are carried out at the time of a reproduction event. However, in case reproduction is a process that takes place continuously through time, the EBT-formalism in Table 2.4 does not suffice any longer. It should be noted that at the level of an individual organism, reproduction is always a discrete event, but considered at the population level offspring may be produced more or less continuously. This is comparable with the mortality process, which at the level of individuals is of course a discrete process, but at the cohort or population level may be considered as a continuous decline in the total number of individuals present.

The change from pulsed to continuous reproduction significantly complicates the formulation of an EBT-model. Continuous reproduction implies that the population does not consist of distinct cohorts of individuals with an identical size (*i*-state), but is characterized by a continuous distribution of the individuals over a whole range of sizes. The mathematically correct formulation of the model would employ a quite complicated partial differential equation, comparable with the age-structured model introduced by McKendrick (1926). This partial differential equation formalism will be presented in chapter 4. Originally, the EBT has been developed as a numerical technique to study the class of partial differential equations that occur in PSPMs with continuous reproduction. The derivation of the method as a numerical integration scheme for these equations can be found in de Roos (1988). The technique is hence suited to account for continuous reproduction, but the resulting formulation is less intuitive from a biological perspective than the formulation for populations with a discrete reproduction process, such as exemplified by the model in Table 2.4. In the current chapter we discuss how the EBT can be adapted to account for continuous reproduction. The biological system, used here to illustrate the formulation of such an EBT-model, is the waterflea *Daphnia pulex*, which feeds on the alga *Chlamydomonas reinhardtii*. This system has frequently been the focus of structured-population modeling (see, e.g., Nisbet et al. 1989) because of the large amount of biological information available at both the individual and population levels. In the next section we will first introduce a simple size-structured model for the life history of individual *Daphnia*.

3.1 Modeling the life history of *Daphnia*

A large amount of biological data shows that the size of an individual *Daphnia* greatly influences its behavior, more specifically, larger individuals have higher food consumption, basal metabolism and reproduction rate. Many different models have been developed to describe the life history of *Daphnia*, i.e. its feeding, reproduction, and growth, as a function of its body size and the current food density. The model presented here was first proposed by Kooijman and Metz (1984) and models these relations using simple assumptions about the gathering, assimilation, and allocation of energy. Although simple, the model incorporates features common to most models of individual *Daphnia* behavior (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.

In contrast to the original Kooijman-Metz model, the model used here assumes, for ease of presentation, that *Daphnia* individuals can shrink. Biologically this assumption is hard to defend, but it has only minor effects on the dynamics (see de Roos et al. 1990). This is only a summary of the model; for a complete derivation and experimental underpinning, see Kooijman and Metz (1984) and Metz et al. (1988).

The length of an individual *Daphnia* is denoted by ℓ , and it is assumed that individuals of different length are isomorphic, such that their surface area and their volume scale as ℓ^2 and ℓ^3 , respectively. At birth the individual length of *Daphnia* tends to vary relatively little, and hence, individuals are assumed to be born with a fixed length indicated by ℓ_b . Individual length also determines, to a large extent, the distinction between juveniles and adults; maturation occurs at a more or less fixed length, denoted by ℓ_j .

Assume that the feeding of *Daphnia* is a surface-related process; then, the isomorphy assumption guarantees that the maximum ingestion rate, I_{max} , scales with the squared length:

$$I_{max} = \nu \ell^2,$$

where ν is a proportionality constant that can be interpreted as the maximum ingestion rate per unit of surface area. There is good evidence (Kooijman and Metz 1984; Kooijman 1986; McCauley et al. 1990) that the amount of food consumed depends nonlinearly on the ambient food density, following a Holling Type-II functional response. Together with the allometric relation for I_{max} , this implies that the food ingestion rate $I(\ell, F)$ of an individual *Daphnia* with length ℓ at food density F is

$$I(\ell, F) = \nu \ell^2 \frac{F}{F_h + F}. \quad (3.1)$$

In the Kooijman-Metz model, the conversion efficiency of ingested food into assimilated food is assumed constant, as are the energy required to produce a single offspring and the energy needed per unit of biomass increase via somatic growth. The pivotal assumption in the model is that a *fixed proportion* of the assimilate is used for development and reproduction, while the remaining part is used to cover maintenance and, if possible, somatic growth. From this

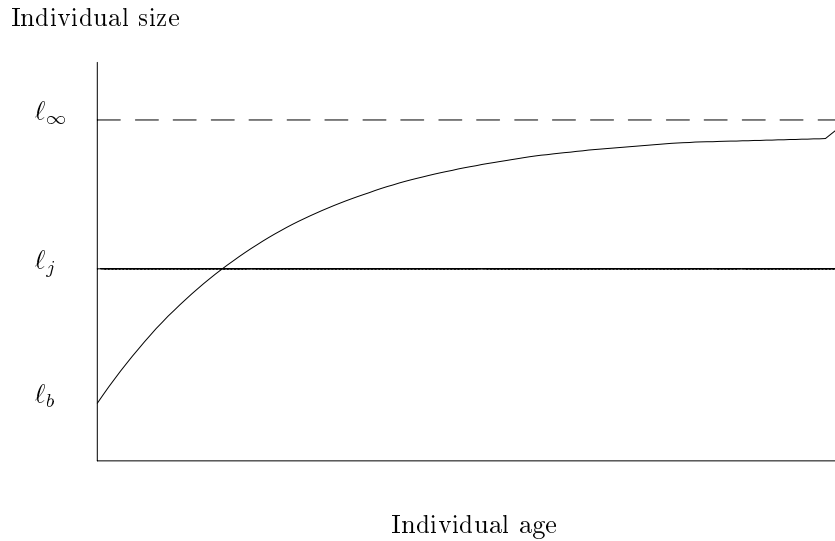


Figure 3.1: Length-age relation for an individual *Daphnia* at constant food density. The resulting length-age relation is the von Bertalanffy growth curve illustrated here. ℓ_∞ indicates the ultimate size reached at the current constant food density and equals $\ell_m F_c / (F_h + F_c)$, where $F = F_c$ is the constant food density.

assumption, it follows that the fecundity of adult *Daphnia* is directly proportional to food ingestion and can hence be described by the function

$$b(\ell, F) = \begin{cases} r_m \ell^2 \frac{F}{F_h + F} & \text{if } \ell > \ell_j \\ 0 & \text{if } \ell \leq \ell_j \end{cases} \quad (3.2)$$

where $b(\ell, F)$ denotes the rate at which adult *Daphnia* produce offspring per unit of time. The parameter r_m is a proportionality factor indicating the maximum reproduction rate per unit of surface area. Juvenile individuals ($\ell < \ell_j$) are assumed to channel the same proportion of their energy into reproduction and development as adults do, but to use it first to develop their reproductive organs. Note that in case of continuous reproduction an *instantaneous reproduction rate* $b(\ell, F)$ is specified, as opposed to, for example, the fecundity function $E(s)$, which was used to model reproduction in the chinook salmon model (see equation (2.13)).

The remaining amount of assimilated energy is spent on basal metabolism and growth. Metabolic requirements are assumed to be proportional to individual volume (ℓ^3) and take precedence over growth. Using these assumptions, together with a bit of formula manipulation (Kooijman and Metz 1984; de Roos et al. 1990), leads to the expression for the rate of growth in length, $g(\ell, F)$:

$$\frac{d\ell}{dt} = g(\ell, F) = \gamma \left(\ell_m \frac{F}{F_h + F} - \ell \right). \quad (3.3)$$

Here, γ is again a proportionality constant, while ℓ_m can be interpreted as the maximum length a *Daphnia* reaches under conditions of abundant food. Note that equation (3.3) allows $g(\ell, F)$ to become negative if F is small, which implies that somatic tissue is used to cover maintenance requirements with a concurrent decrease in length. This reflects the assumption that individuals can shrink under low food conditions, mentioned above.

Table 3.1: Length-structured life history model for *Daphnia pulex* feeding on *Chlamydomonas reinhardtii*

A. <i>i</i>-state variables and life history parameters			
<i>Symbol</i>	<i>Unit</i>	<i>Value</i>	<i>Interpretation</i>
ℓ	mm		individual length
ν	mgC/mm ²	0.007	maximum ingestion rate scaling constant
F_h	mgC/L	0.164	half-saturation food density in functional response
ℓ_b	mm	0.6	length at birth
ℓ_j	mm	1.4	length at maturation
ℓ_m	mm	3.5	maximum length at very high food levels
γ	d ⁻¹	0.11	growth rate constant
r_m	mm ⁻²	1.0	maximum reproduction rate scaling constant
μ	d ⁻¹	0.05	size-independent, background mortality rate

B. Life history model equations	
<i>Function</i>	<i>Interpretation</i>
$g(\ell, F) = \gamma \left(\ell_m \frac{F}{F_h + F} - \ell \right)$	growth rate in length
$b(\ell, F) = \begin{cases} r_m \ell^2 \frac{F}{F_h + F} & \text{if } \ell_j < \ell \\ 0 & \text{if } \ell \leq \ell_j \end{cases}$	reproduction rate
$d(\ell, F) = \mu$	instantaneous mortality rate
$I(\ell, F) = \nu \ell^2 \frac{F}{F_h + F}$	Feeding rate

The growth equation (3.3) we have encountered before in the food-dependent life-history model for chinook salmon, derived in section 2.7. If the food density is constant, such that $F = F_c$, equation (3.3) can be solved explicitly (see equation (2.20)) and predicts that an individual grows according to the von Bertalanffy growth curve (Von Bertalanffy 1957), approaching asymptotically the ultimate size at that food level, $\ell_m F_c / (F_h + F_c)$ (see Figure 3.1):

$$\frac{d\ell}{da} = \gamma \left(\ell_m \frac{F_c}{F_h + F_c} - \ell \right)$$

$$\Rightarrow \ell(a) = \ell_m \frac{F_c}{F_h + F_c} - \left(\ell_m \frac{F_c}{F_h + F_c} - \ell_b \right) e^{-\gamma a}. \quad (3.4)$$

The symbol ℓ_∞ will be used to indicate the maximum attainable size at a particular food density:

$$\ell_\infty = \ell_m \frac{F}{F_h + F}.$$

Mortality is modeled in a very simple manner by assuming that all individuals are exposed to the same background mortality risk, independent of their size. Hence, the mortality rate $d(\ell, F)$ equals:

$$d(\ell, F) = \mu. \quad (3.5)$$

The preceding expressions modeling the life history of *Daphnia* are summarized in Table 3.1.

3.2 Size-structured EBT-model for *Daphnia*

The conceptual basis of the EBT formulation consists of (1) the subdivision of the population into distinct cohorts of individuals, (2) the description of the dynamics of the number and size of the individuals in these cohorts using ODEs and (3) the renumbering of the indices of these cohorts at equidistant time intervals, when a new cohort is formed. In the absence of pulsed reproduction and a natural subdivision into discrete cohorts, the EBT formulation can at best serve as a numerical approximation of a model with continuous reproduction. Its application as such necessitates imposing a subdivision of the population into cohorts of individuals and describing how new cohorts arise from the continuous inflow of newborn individuals. These cohorts are in this case no longer consisting of completely identical individuals, but even within a cohort there is some amount of variability in the i -state of the different individuals. The idea is now to lump individuals in such a way into cohorts that this within-cohort variability is negligibly small.

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. Given the length-dependence in the life history model of *Daphnia*, derived in the previous section, we will adopt the individual length as the characteristic measure of body size and hence as i -state. Since even within the cohort the individuals are not completely identical anymore due to the continuous size distribution, the *mean* length of the individuals in the cohort is chosen as the representative length value. This mean length of the individuals in the i^{th} cohort is denoted by $L_i(t)$. The dynamics of the quantities $N_i(t)$ and $L_i(t)$ characterizing the cohorts are described by a similar set of ODEs as in the previous section:

$$\begin{cases} \frac{dN_i}{dt} = -d(L_i, F) N_i & (3.6a) \\ \frac{dL_i}{dt} = g(L_i, F) & i = 0, 1, 2, \dots \end{cases} \quad (3.6b)$$

Note that these equations would be exact if there was no variation in individual length within a cohort and all individuals would have an identical body length equal to $L_i(t)$. It can be shown mathematically that in case individual body lengths within a cohort span an interval from ℓ to $\ell + \Delta_\ell$, the approximation of the ODEs (3.6) to the exact dynamics of the total number of individuals and their mean length scales with Δ_ℓ^2 , i.e. in a quadratic way with the variation in individual length (de Roos 1988). Hence lumping individuals into cohorts with smaller size ranges rapidly leads to a better approximation of the “real” dynamics.

In contrast to the situations considered so far, the cohort of individuals that are being 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 *boundary cohort* as opposed to the *internal cohorts* that are already present in the population, should also be described on a continuous-time basis, i.e. using ODEs. Upon reaching time $t + 1$ this cohort now becomes an internal cohort itself, while a new boundary cohort is started up for the individuals that will be born during the next time unit. We have to impose this transformation of the boundary cohort into an internal cohort and its replacement by a new boundary cohort, because distinct cohorts do not arise naturally anymore. The choice to lump 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, which are born between time t and $t + \Delta$, are lumped into the same cohort. The transformation and replacement of the boundary cohort is hence carried out at time $t + \Delta, t + 2\Delta, t + 3\Delta, \dots$ (The significance of the value of Δ will be discussed later on this chapter).

The boundary cohort 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 length of the *Daphnia* in the boundary cohort are denoted by $N_0(t)$ and $L_0(t)$, respectively. If *no* reproduction at all would take place, the boundary cohort would be identical to all other cohorts and the dynamics of $N_0(t)$ and $L_0(t)$ would be described by:

$$\begin{cases} \frac{dN_0}{dt} = -d(L_0, F) N_0 & (3.7a) \\ \frac{dL_0}{dt} = g(L_0, F) & (3.7b) \end{cases}$$

Let's consider the product of $N_0(t)$ and $L_0(t)$. This product can be interpreted as the total length of all individuals together in the boundary cohort. The dynamics of the product can be derived from the equations above by applying the product rule for differentiation:

$$\begin{aligned} \frac{d(L_0 N_0)}{dt} &= N_0 \frac{dL_0}{dt} + L_0 \frac{dN_0}{dt} \\ \Rightarrow \frac{d(L_0 N_0)}{dt} &= g(L_0, F) N_0 - d(L_0, F) L_0 N_0 \end{aligned}$$

In the model of the individual life history of *Daphnia* the function $b(\ell, F)$ represents the reproduction rate of an individual with length ℓ at the current food density $F(t)$. Hence, if reproduction does occur, the total rate at which individuals in cohort i produce offspring equals $b(L_i, F) N_i$. Summing the contributions of all cohorts in the population yields the following expression for the total population fecundity:

$$\sum_i b(L_i, F) N_i. \quad (3.8)$$

The newborn individuals represented by this total population birth rate are all accumulated into the current boundary cohort. The dynamics of the number of individuals in the boundary cohort hence become:

$$\frac{dN_0}{dt} = -d(L_0, F) N_0 + \sum_i b(L_i, F) N_i \quad (3.9)$$

which accounts on the one hand for the mortality process of the individuals that have recently been born and on the other hand for the addition of newborns.

Since all individuals are born with an identical size at birth ℓ_b , the increase in the product of L_0 and N_0 due to reproduction equals the product of ℓ_b and the sum (3.8). The dynamics of the quantity $(L_0 N_0)$ is therefore described by the ODE:

$$\begin{aligned} \frac{d(L_0 N_0)}{dt} &= N_0 \frac{dL_0}{dt} + L_0 \frac{dN_0}{dt} \\ &= g(L_0, F) N_0 - d(L_0, F) L_0 N_0 + \ell_b \sum_i b(L_i, F) N_i \end{aligned} \quad (3.10)$$

An ODE for the mean length L_0 can now be derived by substitution of the ODE (3.9) into equation (3.10) and solving for dL_0/dt . This leads to the following set of ODEs, describing the dynamics of $N_0(t)$ and $L_0(t)$, the number and mean length, respectively, of the newborn individuals in the boundary cohort:

$$\left\{ \begin{aligned} \frac{dN_0}{dt} &= -d(L_0, F) N_0 + \sum_i b(L_i, F) N_i & (3.11a) \\ \frac{dL_0}{dt} &= g(L_0, F) + \frac{(\ell_b - L_0)}{N_0} \sum_i b(L_i, F) N_i & (3.11b) \end{aligned} \right.$$

The occurrence of N_0 in the denominator of the ODE (3.11b) causes a problem if $N_0 = 0$, which occurs when a new boundary cohort is created. The mean length $L_0(t)$ of the individuals is hence not an appropriate choice to describe the dynamics of the boundary cohort, since its value and its dynamics are undefined at the time that the cohort is started, *i.e.* when it is empty. For computational purposes it is therefore much more convenient to describe the dynamics of the boundary cohort in terms of $N_0(t)$ and the quantity:

$$B_0(t) := (L_0(t) - \ell_b) N_0(t) \quad (3.12)$$

$B_0(t)$ is a measure of the total length of all individuals in the boundary cohort together, though relative to the length that individuals have when born, ℓ_b . This choice to calculate the total length of all individuals in the boundary cohort relative to ℓ_b is convenient, because it makes the dynamics of $B_0(t)$ independent of the reproduction process. The ODE for $B_0(t)$ can be derived from the equality

$$\frac{dB_0}{dt} = \frac{d(L_0(t) - \ell_b) N_0}{dt} = \frac{d(L_0 N_0)}{dt} - \ell_b \frac{dN_0}{dt}$$

Substitution of the ODEs (3.9) and (3.10) into this expression yields:

$$\left\{ \begin{aligned} \frac{dN_0}{dt} &= -d(L_0, F) N_0 + \sum_i b(L_i, F) N_i & (3.13a) \\ \frac{dB_0}{dt} &= g(L_0, F) N_0 - d(L_0, F) B_0 & (3.13b) \end{aligned} \right.$$

However, in these equations the evaluation of the functions $g(\ell, F)$ and $d(\ell, F)$ at $\ell = L_0$ poses a problem, as the individuals in the boundary cohort are not characterized by their

average length L_0 . Therefore, $g(L_0, F)$ and $d(L_0, F)$ are replaced by their first-order Taylor expansions around $\ell = \ell_b$:

$$g(L_0, F) \approx g(\ell_b, F) + (L_0 - \ell_b) \frac{\partial}{\partial \ell} g(\ell_b, F) \quad (3.14)$$

and

$$d(L_0, F) \approx d(\ell_b, F) + (L_0 - \ell_b) \frac{\partial}{\partial \ell} d(\ell_b, F) \quad (3.15)$$

in which $\frac{\partial}{\partial \ell} g(\ell, F)$ and $\frac{\partial}{\partial \ell} d(\ell, F)$ represent the partial derivatives of the functions $g(\ell, F)$ and $d(\ell, F)$, respectively, with respect to length ℓ .

Using these approximations the system of ODEs (3.13) can be replaced by the following, equivalent system of ODEs for the dynamics of N_0 and B_0 , respectively:

$$\left\{ \begin{array}{l} \frac{dN_0}{dt} = -d(\ell_b, F)N_0 - \frac{\partial}{\partial \ell} d(\ell_b, F)B_0 + \sum_i b(L_i, F)N_i \end{array} \right. \quad (3.16a)$$

$$\left\{ \begin{array}{l} \frac{dB_0}{dt} = g(\ell_b, F)N_0 + \frac{\partial}{\partial \ell} g(\ell_b, F)B_0 - d(\ell_b, F)B_0 \end{array} \right. \quad (3.16b)$$

If the individuals in the boundary cohort reproduce themselves, this reproduction can be included into the summation term in the ODE (3.16a) as long as $N_0 \neq 0$. The reproductive contribution equals $b(L_0, F)N_0$, just like the contributions of the other cohorts, while the quantity L_0 is defined as

$$L_0 = \ell_b + \frac{B_0}{N_0} \quad (3.17)$$

as long as $N_0 \neq 0$.

At time $t + \Delta$ the boundary cohort is transformed into an internal cohort and the internal cohorts themselves are renumbered. At this time the characterizing size measure $B_0(t)$ has to be transformed into the average size of the individuals, the quantity characterizing an internal cohort. Equation (3.17) specifies the appropriate transformation. The transformation of the 0th cohort into the 1st cohort is hence more complicated than in the EBT-models that we have encountered up to now (*cf.* Table 3.2).

$$\left\{ \begin{array}{l} N_1(t^* + \Delta) = N_0(t^* + \Delta^-) \end{array} \right. \quad (3.18a)$$

$$\left\{ \begin{array}{l} L_1(t^* + \Delta) = \ell_b + \frac{B_0(t^* + \Delta^-)}{N_0(t^* + \Delta^-)} \end{array} \right. \quad (3.18b)$$

$$\left\{ \begin{array}{l} N_0(t^* + \Delta) = 0 \end{array} \right. \quad (3.18c)$$

$$\left\{ \begin{array}{l} B_0(t^* + \Delta) = 0 \end{array} \right. \quad (3.18d)$$

The last two equations of this transformation specify the initial values of N_0 and B_0 for the new boundary cohort that is going to be created.

The renumbering equations for all internal cohorts are identical to the ones from the previous sections:

$$\left\{ \begin{array}{l} N_i(t^* + \Delta) = N_{i-1}(t^* + \Delta^-) \end{array} \right. \quad (3.19a)$$

$$\left\{ \begin{array}{l} L_i(t^* + \Delta) = L_{i-1}(t^* + \Delta^-) \end{array} \right. \quad i = 2, 3, \dots \quad (3.19b)$$

Finally, as in the food-dependent EBT-model for the dynamics of the chinook salmon, the ODE describing the dynamics of the food density incorporates a semi-chemostat regrowth

Table 3.2: Length-structured EBT-model for *Daphnia pulex* feeding on *Chlamydomonas reinhardtii*

A. Population variables and parameters			
<i>Symbol</i>	<i>Unit</i>	<i>Value</i>	<i>Interpretation</i>
$N_i(t)$	#/L		number of individuals in cohort i at time t
$L_i(t)$	mm		average length of individuals in cohort i at time t
$B_0(t)$	mm/L		Length-based measure of individuals in cohort 0 at time t
$F(t)$	mgC/L		resource density in the environment
ρ	d ⁻¹	0.5	semi-chemostat resource regrowth rate
K	mgC/L	0.25	maximum resource density in absence of consumers

B. Population model equations			
Continuous-time dynamics for boundary cohort during cohort cycle	$\begin{cases} \frac{dN_0}{dt} = -d(\ell_b, F)N_0 - \frac{\partial}{\partial \ell} d(\ell_b, F)B_0 + \sum_{i>0} b(L_i, F) N_i \ddagger \\ \frac{dB_0}{dt} = g(\ell_b, F)N_0 + \frac{\partial}{\partial \ell} g(\ell_b, F)B_0 - d(\ell_b, F)B_0 \end{cases}$		
Continuous-time dynamics for other cohorts during cohort cycle	$\begin{cases} \frac{dN_i}{dt} = -d(L_i, F)N_i \\ \frac{dL_i}{dt} = g(L_i, F) \end{cases} \quad i = 1, 2, \dots$		
Transformation and new initial values for boundary cohort at end of cohort cycle ($t = t^*, t^* + \Delta, t^* + 2\Delta, \dots$)	$\begin{cases} N_1(t^* + \Delta) = N_0(t^* + \Delta^-) \\ L_1(t^* + \Delta) = \ell_b + \frac{B_0(t^* + \Delta^-)}{N_0(t^* + \Delta^-)} \\ N_0(t^* + \Delta) = 0 \\ B_0(t^* + \Delta) = 0 \end{cases}$		
Renumbering equations for other cohorts at end of cohort cycle ($t = t^*, t^* + \Delta, t^* + 2\Delta, \dots$)	$\begin{cases} N_i(t^* + \Delta) = N_{i-1}(t^* + \Delta^-) \\ L_i(t^* + \Delta) = L_{i-1}(t^* + \Delta^-) \end{cases} \quad i = 2, 3, \dots$		
Dynamics of resource density in the environment	$\frac{dF}{dt} = \rho(K - F) - \sum_i I(L_i, F) N_i(t) \ddagger$		

\ddagger Include the boundary cohort in the summation if $N_0 \neq 0$; use $L_0 = \ell_b + B_0/N_0$.

process of the food density plus the total population feeding of the *Daphnia* on the algae. This total foraging pressure is the sum of all the foraging pressures over the various cohorts

in the population:

$$\frac{dF}{dt} = \rho(K - F) - \sum_i I(L_i, F) N_i(t) \quad (3.20)$$

(cf. equation (2.25)). The foraging pressure by individuals in the boundary cohort has to be included into the summation term in the above ODE as soon as $N_0 \neq 0$. The rate of foraging equals $I(L_0, F)N_0$, just like the contributions of the other cohorts, where the quantity L_0 is defined by equation (3.17).

3.3 Summary and conclusions

The population-level equations derived in the previous section are summarized in Table 3.2. They give an approximate description of 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 partial differential equation, which is further discussed in chapter 4. The EBT can hence be viewed as a numerical method to integrate the partial differential equations in physiologically structured population models (de Roos 1988), analogous to the popular Runge-Kutta methods for numerical integration of ordinary differential equations. It provides a consistent approximation of the original PDE, which means that the approximation is better with smaller values of the cohort width Δ (Actually the approximation error scales with the square of Δ). Therefore, if the equations, as shown in Table 3.2, are used to study the dynamics of a *Daphnia* population interacting with its resource, the actual model under study is a continuous-time, physiologically structured model. Smaller values of Δ imply that a better approximation to the model dynamics is achieved, but also increase the number of cohorts that are still playing a role in the population dynamics. This number of cohorts can be kept within bounds by eliminating cohorts that contain numbers of individuals near 0 due to mortality or cohorts that are for other reasons dynamically negligible. In general the number of cohorts in the population may hence vary over time, depending on the distribution of the individuals over all possible size values. This contrasts with the models for salmon population dynamics, discussed in earlier chapters, because in these models the number of cohorts was always the same. From a modeling point of view the changing number of cohorts implies that the dimension of the system of ODEs that has to be solved varies over time, which makes the numerical integration a slightly non-standard process. Conceptually, however, the changing dimension is close to the biological reality: the number of cohorts in a population may vary over time and since the dynamics of each cohort is described by a set of ODEs, so will the dimension of the full set of equations.

The EBT-formulation of a model with continuous reproduction was derived above, starting from the EBT-models discussed in previous chapters. In section 4.6 an alternative derivation of the EBT-formulation is provided, as a numerical approximation to the partial differential equation that analytically describes the physiologically structured population model. The ODEs describing the dynamics of the boundary cohort constitute the major difference with the EBT-models presented in earlier chapters. Because of the continuous reproduction process calculating the population dynamics now is a 2 stage process, involving

1. The numerical integration of all ODEs that describe the continuous time dynamics in between two renumbering operations. These ODEs describe the life history, more specifically their development, aging and mortality, of the individuals in the boundary cohort with newborn individuals as well as in all internal cohorts. In addition, a number

of the ODEs describe the dynamics of all environmental factors, such as food density. These ODEs are coupled with the cohort ODEs through the influence these factors (*i.e.* food density) have on individual life history and, in turn, the population-level feedback of the cohorts on them, for example through feeding.

2. At regularly (or irregularly) spaced moments in time, the integration of the ODEs is halted and a transformation plus renumbering operation is carried out. The old boundary cohort is transformed into an internal cohort, while all internal cohorts in the population are renumbered to conserve an appropriate order in the indexes of the cohorts. A new, empty boundary cohort is created to accumulate the newborn individuals over the next integration cycle.

The relevant equations describing the EBT-formulation of a physiologically structured population model with continuous reproduction are exemplified by the EBT-model for *Daphnia* population dynamics, shown in Table 3.2.

Chapter 4

Mathematical analysis

In the previous chapters we have discussed EBT-models for physiologically structured populations from an intuitive point of view with a strong emphasis on how to study these models numerically. The current chapter is intended as a more formal introduction to the mathematical aspects of PSPMs. The main aim is to illustrate the mathematical representation of the models using partial differential equations (PDEs) and to show how equilibria of PSPMs and their stability can be sometimes computed analytically. The mathematical background of the modeling framework and the justification of the equations are discussed only when necessary for a better understanding of the biological aspects of the models. This chapter is an adapted version of the introduction provided in de Roos (1997).

PSPMs belong to the general class of “individual-based” models, which describe the dynamics of a population in terms of the behavior of its constituent individuals. The class of PSPMs that we focus on is restricted by the following restrictions:

1. Spatial distribution is completely neglected. All individuals experience the same, spatially homogeneous environment. More technically, individuals are assumed to mix quickly and randomly, such that the “mass-action law” applies, and the interactions can be completely described in terms of the densities (de Roos et al. 1991; Metz and de Roos 1992).
2. Only large populations are considered. In principle, the population can consist of infinitely many types of individuals, but *of each type* a sufficiently large number is assumed to be present that demographic stochasticity plays no role. Assuming this “law of large numbers” ensures that an inherently stochastic process, such as the death of individuals, can be approximated by a deterministic description.
3. The growth and development of individuals is assumed to be deterministic. This implies that two identical individuals develop in exactly the same way. As a consequence, identical individuals always remain identical.

From these restrictions it is clear that the PSP models considered here are deterministic approximations of essentially stochastic processes. They constitute only part of the entire class of PSP models (for other situations, see the more in-depth discussions in Metz and Diekmann 1986; Metz and de Roos 1992; Diekmann et al. 1994 and Diekmann and Metz 1995). It should also be noted that the mathematical theory of PSP models is still actively evolving. According to recent theory, PSP models should be formulated as integral equations

(or abstract renewal equations), as opposed to the partial differential equations (PDEs) used up to now. This “cumulative” formulation in terms of integral equations is claimed to be more natural, more elegant, and technically superior (Diekmann et al. 1994; Diekmann and Metz 1995). I do not discuss these developments but stick to the PDE formalism to stay in line with the tradition of writing population-dynamic models as differential equations. (As an aside, note that although the EBT-technique for numerical study of PSP models was developed on the basis of the PDE formalism, it is actually formulated in terms of integral quantities and, hence, is close in spirit to the new “cumulative” formulation of the models.)

The traditional sequence for discussing the theory of structured populations begins with age-structured models, followed by size-structured models, and eventually leads to models with more than one structuring variable. This is a roughly chronological introduction, since age-structured PDE models were introduced by McKendrick (1926) and VonFoerster (1959), size-structured population models date back to the work of Bell and Anderson (1967), and Sinko and Streifer (1967) discussed a structured-population model that distinguishes both age and size. This chapter takes a different approach and discusses the formulation and analysis of a size-structured model for a specific biological situation: the population dynamics of the waterflea *Daphnia pulex*, which feeds on the alga *Chlamydomonas reinhardtii*. The size-structured model of its life history was already formulated in section 3.1. The formulation and analysis of the resulting population model is discussed in the sections 4.2, 4.5, 4.7, and 4.8. These sections, together with section 3.1 describing the life history model, constitute a closed, independent story. The remaining sections of this chapter discuss the theory in a more general context.

4.1 Modeling the Individual and Its Environment

4.1.1 The Individual Behavior

The i -state and E -state have already been discussed formally in chapter 2. The entire collection of values that the i -state can possibly attain is referred to as the *individual state space*, or *i -state space*. For *Daphnia* the i -state space is the entire range of lengths that can possibly be observed in the species, which according to section 3.1 equals the size range between ℓ_b and ℓ_m . The i -state space is often indicated by Ω .

Once the i -state and E -state are selected as the characteristics of an individual and its environment that completely determine its behavior, the form of this dependence has to be specified. The behavior of individuals consists essentially of four processes: development, which refers to the changes in i -state over time; mortality; reproduction; and the influence of the individual on its environment, such as the influence of feeding on the current food density. All these behavioral processes are specified in terms of instantaneous rates because the dynamics of the population are described on a continuous-time basis in terms of differential equations. The discussions to follow focus on the formal definition of these rates and their relation to observable, biological data.

Development

The i -state changes over time in a fully deterministic fashion, since two individuals with identical i -states are assumed to be identical forever and the i -state and E -state together determine the development of the individual. Formally, the individual development rate,

$g(x, E)$, is the rate of change of the individual state variable x at the current time, as a function of the variable itself and the current environmental state E .

Consider an individual, born with an individual state equal to x_b at $t = 0$. The change in i -state is described by the ODE

$$\frac{dx}{dt} = g(x, E). \quad (4.1)$$

This equation only fixes the current developmental rate of the individual. Because the environmental variable E can change over time, as a result of external factors or influences of the population itself, this ODE determines the entire development of the individual, only if the time course of the E -state is given. In the *Daphnia* example, food density and length determine the current individual growth rate, but without information on the entire future of the food density the future sizes of the individuals are also unknown.

To relate individual behavior to experimental data, it is useful to consider individuals that are all born with a fixed size x_b and live after birth in a constant environment; that is, $E(t)$ is equal to some constant E_c for all t . Such a scenario corresponds to a study in which a cohort of identical individuals is followed over their entire life under constant conditions. Under such conditions we can usually derive expressions for observable quantities such as the relation between the age and the i -state of the individuals in the cohort. These expressions involve the instantaneous rates in the model and can therefore be used to determine these rates experimentally. Hence, the scenario of individuals living in a constant environment E_c recurs frequently in this and the following sections.

If individuals are born with i -state x_b and live in a constant environment E_c , their i -state at every age is given by the formal solution of the ODE (4.1). At age a such individuals have an i -state $X(a, E_c)$:

$$X(a, E_c) = x_b + \int_0^a g(X(\zeta, E_c), E_c) d\zeta. \quad (4.2)$$

Little or no analytical investigation is possible if the integral in (4.2) has no closed form. I therefore assume that this integral can be solved analytically. Consequently, the i -state of individuals at age a in the “constant-environment scenario” is explicitly given by a function $X(a, E_c)$, which can be referred to as the (i -state)-age relation.

In the *Daphnia* example, the specific choice of $g(\ell, F)$ allows for an explicit solution of the length-age relation when the food density is constant. The resulting curve is known as the von Bertalanffy growth curve, the general form of which is illustrated in Figure 3.1.

Mortality

Individual mortality is governed by the instantaneous mortality rate, $d(x, E)$, defined as the rate at which the probability of survival from birth to i -state x decreases with time. This definition implies that the product $d(x, E) \Delta t$ equals the probability that an individual with i -state x , living in an environment E , will die within a small time interval Δt . To relate this rate to observable data, it is again useful to consider an individual that has been born with i -state x_b and lives in a constant environment E_c . The survival probability for such an individual can be characterized by the survival function, $S(x, E_c)$, defined as the probability that an individual survives and reaches an i -state x , while living in a constant environment E_c .

The individual is born with i -state x_b and therefore $S(x_b, E_c) = 1$. According to the definition of the instantaneous mortality rate, the dynamics of $S(x, E_c)$ are governed by the ODE

$$\frac{dS(x, E_c)}{dt} = -d(x, E_c) S(x, E_c),$$

where $S(x_b, E_c) = 1$. The right-hand side of this ODE depends implicitly on time because the i -state x changes over time, following the relation (4.2). For the changes of $S(x, E_c)$ with the i -state x ,

$$\begin{aligned} \frac{dS(x, E_c)}{dx} &= \frac{dS(x, E_c)}{dt} \frac{dt}{dx} = -\frac{d(x, E_c)}{g(x, E_c)} S(x, E_c) \\ \Rightarrow S(x, E_c) &= \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right), \end{aligned} \quad (4.3)$$

which explicitly relates the survival function to the instantaneous growth and mortality rates. The probability that an individual dies with i -state x is given by the probability density function $H(x, E_c)$:

$$\begin{aligned} H(x, E_c) &= -\frac{dS(x, E_c)}{dx} \\ &= \frac{d(x, E_c)}{g(x, E_c)} S(x, E_c) \\ &= \frac{d(x, E_c)}{g(x, E_c)} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right). \end{aligned} \quad (4.4)$$

If $g(x, E_c)$ has been determined from observations on the (i -state)-age relation in the constant environment E_c , each of these equations could be used to determine the instantaneous death rate $d(x, E_c)$. Most readily, it is determined from the decrease in the log-transformed survival function with increasing i -state x , which equals the quotient of the individual death and growth rates at x :

$$-\frac{d}{dx} \ln(S(x, E_c)) = -\frac{1}{S(x, E_c)} \frac{dS(x, E_c)}{dx} = \frac{d(x, E_c)}{g(x, E_c)}.$$

When chronological age is used as the i -state, the function g always has the value 1, but the relations derived in this section still apply. For example, the survival function becomes

$$S(a, E_c) = \exp\left(-\int_0^a d(\zeta, E_c) d\zeta\right),$$

where the variable a is now used instead of x to identify age as the i -state. This relation seems to contain an integral over a rate $d(a, E_c)$ with a dimension (time^{-1}). However, the integral must be a dimensionless quantity to appear in the exponential function, which it is not if the integrand (i.e., the quantity to be integrated) carries the dimension (time^{-1}). In reality, the function $d(a, E_c)$ is divided by a rate function that is always equal to 1, which makes the dimension of the integrand equal to (age^{-1}) and the integral indeed dimensionless. This obscure occurrence of the unit developmental rate in age should be stressed, since it will be encountered in later sections as well.

Formal expressions of the expected value of the i -state and age at death are given in Appendix A.

Reproduction

Reproduction is modeled by specifying the instantaneous birth or reproduction rate, $b(x, E)$, defined as the rate of production of offspring by an individual of i -state x experiencing an environment state E . The quantity $b(x, E) \Delta t$ gives the number of offspring that an individual with an i -state equal to x , living in an environment with E -state E , produces within a small time interval Δt .

In a constant environment, E_c , the integral

$$\int_0^a b(E_c, X(\zeta, E_c)) d\zeta$$

gives the cumulative number of offspring an individual living in these conditions has produced by the time it reaches age a , given that it did not die. In cohort studies, the cumulative number of offspring can hence be used to determine $b(x, E)$. By a change of variables in the equation above, this cumulative number of offspring can be expressed in terms of x :

$$\int_0^a b(X(\zeta, E_c), E_c) d\zeta = \int_{x_b}^{X(a, E_c)} b(x, E_c) \frac{da}{dx} dx = \int_{x_b}^{X(a, E_c)} \frac{b(x, E_c)}{g(x, E_c)} dx.$$

It follows that the cumulative number of offspring produced by a surviving individual living under constant environmental conditions E_c between its birth with i -state x_b and the time it reaches the i -state x is equal to:

$$\int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \quad (4.5)$$

If $g(x, E_c)$ has been determined from experimental observations on the (i -state)-age relation in the constant environment, E_c , the instantaneous reproduction rate, $b(x, E_c)$, is most readily determined from the increase in the cumulative number of offspring with x . This increase equals the ratio of the individual reproduction and growth rates at x :

$$\frac{d}{dx} \int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi = \frac{b(x, E_c)}{g(x, E_c)}.$$

Experimental observations often involve the first reproduction event of an individual. The i -state at which reproduction first occurs can be calculated using the same approach used for survival. The probability that an individual has not yet reproduced by the time it has reached an i -state x , given that it survives, equals

$$\exp \left(- \int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \right).$$

The probability that it first reproduces when it has an i -state x , again conditional on survival, is

$$\frac{b(x, E_c)}{g(x, E_c)} \exp \left(- \int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \right).$$

These expressions are completely analogous to the survival function and the probability distribution of the state at death, respectively, in the discussion on the mortality rate. Their derivation proceeds along the same lines and is therefore left as an exercise.

Appendix A of this chapter gives formal expressions for the expected i -state and age of the individual when it first reproduces.

Influence on the Environment

The last component of individual behavior to be modeled is its influence on the environment. As described in section 2.2, the types of feedback or density dependence can be categorized as direct density dependence and environmental feedback loops.

Direct density dependence involves statistics, such as population size, the number of juveniles or adults, and total biomass, that exert a direct density-dependent influence on the individual life history. Deriving expressions for such population statistics (see section 4.3) requires introducing the population state. In general, these expressions involve a weighting function, $\phi(x)$, which indicates the contribution of an individual of i -state x to the density-dependent influence. For the total population size, all individuals are weighted equally and $\phi(x) \equiv 1$. To determine the number of juvenile or adult individuals, set $\phi(x) \equiv 1$ for all i -states that represent juveniles or adults, respectively, and $\phi(x) \equiv 0$ otherwise. If individual mass is taken as the i -state x and the total population biomass is the statistic of interest, $\phi(x) = x$, because individuals contribute to the population biomass in accordance with their current i -state. In general, the weighting function ϕ depends only on the i -state x . In special cases, it can also depend on the current E -state or the i -state of other individuals. For example, to model cannibalism of older or larger individuals on younger or smaller individuals, a weighting function $\phi(x', x)$ is needed that depends on both the i -state x' of the cannibal and the i -state x of its victim (van den Bosch et al. 1988).

Environmental feedback loops involve environmental variables, the dynamics of which are specified by an ODE. For each environmental variable E , a function $I(x, E)$ must be formulated that specifies the rate at which an individual with i -state x decreases or increases E . A classic example is the resource density experienced by an individual. The function $I(x, E)$ in this case models the resource consumption rate (see the *Daphnia* example).

4.1.2 The Dynamics of the Environment without Individuals

In case of abiotic modulation (see section 2.2) the environmental variables that modulate the individual life history are explicit functions of time. Their functional form must be specified. Annual temperature fluctuations could, for example, be modeled as a sinusoidal function of time.

To model an environmental feedback loop, the dynamics of the environmental variable must be described in the absence of the structured population. The logistic growth rate of the algal population in the *Daphnia* example is typical.

4.1.3 Some Remarks on Notation

Discussing the *Daphnia* example in parallel with the general theory of PSP models raises some problems of notation. In general, I use x and E to denote the i -state and E -state, respectively, as long as no specific physiological or environmental traits have been attached to

these two states. In the *Daphnia* example, individual length and the food density appear as *i*-state and *E*-state, respectively, and therefore, I use ℓ and F in discussions of this particular model. I use g , b , d , and I to denote the functions that model development, reproduction, mortality, and environmental interactions of the individuals. These functions can therefore appear with different arguments, for example $g(x, E)$ as opposed to $g(\ell, F)$, depending on the context of the discussion.

4.1.4 Recipe for Model Construction

1. Choose the set of physiological traits that determine individual behavior as *i*-state variables, denoted by x .
2. Choose the set of variables that characterize an individual's environment and influence its behavior as *E*-state variables, denoted by E .
3. Describe the individual behavior as a function of the *i*-state and the *E*-state, including developmental rate, $g(x, E)$; mortality rate, $d(x, E)$; reproduction rate, $b(x, E)$; and individual influences on its environment, the weighting functions $\phi(x)$ for the direct density-dependent factors and the rate functions $I(x, E)$ for indirect density-dependent factors.
4. Specify the "explicitly given" environmental forcing functions as a function of time, $E_{exp}(t)$.
5. Describe the autonomous dynamics of the "dynamically varying" environmental variables, $R(E_{dyn})$.

4.2 The Size-Structured *Daphnia* Population Model

The simplest, *unstructured*-population model for the interaction between *Daphnia* and algae is the Rosenzweig-MacArthur model:

$$\frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K} \right) - I_{max} \frac{F}{F_h + F} C, \quad (4.6a)$$

$$\frac{dC}{dt} = \epsilon I_{max} \frac{F}{F_h + F} C - \mu C, \quad (4.6b)$$

in which F and C represent the density of algae and *Daphnia*, respectively; α and K denote the maximum growth rate and the carrying capacity of the algae, respectively; I_{max} and F_h are the maximum feeding rate and the half-saturation food level of the *Daphnia* functional response; and ϵ and μ are the conversion efficiency and per capita mortality rate of *Daphnia*, respectively. Here, we have assumed that the regrowth of algae in the absence of *Daphnia* follows a logistic growth process.

In this unstructured model the total number of *Daphnia*, denoted by C , represents the biological population in the model. An analogous representation of the biological population is needed for the size-structured model. In addition to the total number of individuals, it must also contain information about their sizes. Given that individual size lies in the continuous interval $[\ell_b, \ell_m)$ and the assumption that the number of individuals is large, an appropriate

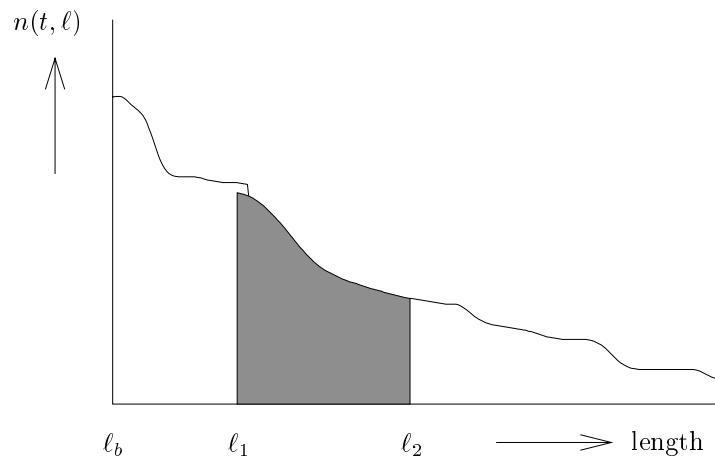


Figure 4.1: Mathematical representation of the *Daphnia* population in the structured model. The density function $n(t, \ell)$ constitutes the mathematical representation of the *Daphnia* population in the structured model. The hatched surface under the curve between $\ell = \ell_1$ and $\ell = \ell_2$ equals the integral of $n(t, \ell)$ over this length interval and represents the number of *Daphnia* with a length between these two bounds.

mathematical representation of the population is a density function. This density function, denoted by $n(t, \ell)$, gives the distribution of individuals as a function of ℓ at time t . It is important to understand that only the integral of $n(t, \ell)$ can be interpreted as a number of individuals; that is,

$$\int_{\ell_b}^{\ell_m} n(t, \ell) d\ell$$

equals the total population size at time t . In general, the integral

$$\int_{\ell_1}^{\ell_2} n(t, \ell) d\ell$$

gives the total number of *Daphnia* with length ℓ between ℓ_1 and ℓ_2 (see Fig. 4.1).

The interpretation of $n(t, \ell)$ itself (as opposed to its integral) is problematic. One can loosely think of the quantity $n(t, \ell) \Delta\ell$ as the number of individuals with a length in a (small) interval $[\ell, \ell + \Delta\ell)$. Since these $n(t, \ell) \Delta\ell$ individuals all have a feeding rate equal to $I(\ell, F)$ (Table 3.1), their total feeding rate equals the product $I(\ell, F) n(t, \ell) \Delta\ell$. Taking the limit $\Delta\ell \rightarrow 0$ and integrating the product function gives the total feeding rate of all individuals with a length between ℓ_1 and ℓ_2 :

$$\int_{\ell_1}^{\ell_2} I(\ell, F) n(t, \ell) d\ell.$$

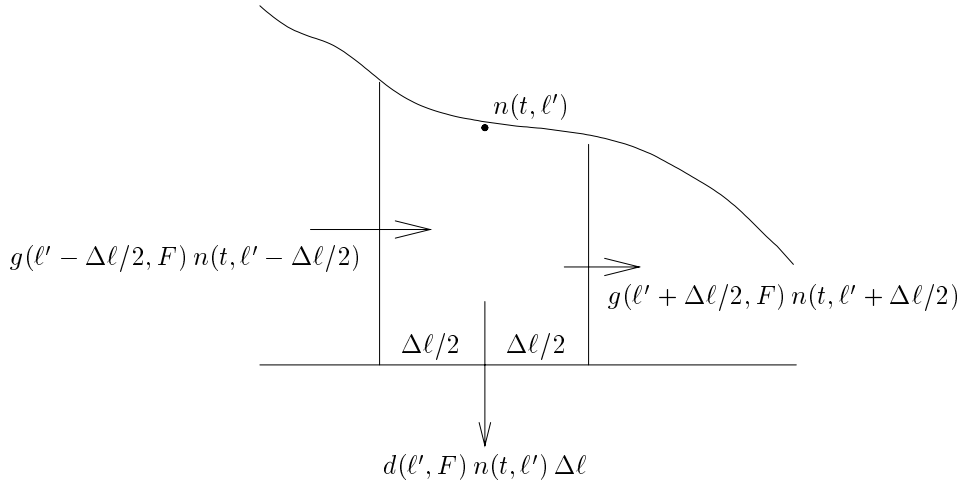


Figure 4.2: The derivation of the partial differential equation for $n(t, \ell)$.

The ODE (4.6a) for algal density in the unstructured model (4.6) makes it clear that in the size-structured model the dynamics of algal density must also equal the balance between the growth of the algae and the feeding rate of the total *Daphnia* population. This total feeding rate is given by the integral of $I(\ell, F) n(t, \ell)$, given above with $\ell_1 = \ell_b$ and $\ell_2 = \ell_m$. Therefore, in the size-structured *Daphnia* model, the dynamics of algal density are described by

$$\frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K} \right) - \int_{\ell_b}^{\ell_m} I(\ell, F) n(t, \ell) d\ell, \quad (4.7)$$

which resembles the ODE (4.6a) in the unstructured model.

Once the state of the *Daphnia* population has been represented by the density function $n(t, \ell)$, a partial differential equation (PDE) governing its dynamics can be derived by considering a small size interval of width $\Delta \ell$ around a specific length $\ell = \ell'$ (see Fig. 4.2). Within a small time interval Δt (small enough that $g(\ell', F) \Delta t \ll \Delta \ell$), the number of individuals in this length interval changes because (1) smaller individuals enter the interval by growing, (2) individuals at the upper end of the interval grow out of it, and (3) individuals disappear through death.

The flux across the lower bound ($\ell = \ell' - \Delta \ell/2$) is the rate at which individuals enter the interval as a result of growth. This flux is proportional to the rate at which a single individual grows across the boundary and to the number of individuals doing so, that is, to the product of the growth rate and the density at this value of ℓ : $g(\ell' - \Delta \ell/2, F) n(t, \ell' - \Delta \ell/2)$. Analogously, the rate at which individuals leave the interval at the high end equals the product of the growth rate and the local density at $\ell = \ell' + \Delta \ell/2$: $g(\ell' + \Delta \ell/2, F) n(t, \ell' + \Delta \ell/2)$. Finally, the rate at which individuals disappear because of death equals the product of the death rate and the number of individuals with a length in the small interval of size $\Delta \ell$: $d(\ell', F) n(t, \ell') \Delta \ell$. Note that this last expression uses the “law of large numbers”: in a small time interval, Δt , every individual in the interval around $\ell = \ell'$ has a probability of dying equal to $d(\ell', F) \Delta t$. The law of large numbers allows us to replace the *number* of individuals dying during the small time interval, which clearly is a stochastic variable, by its *expected* value!

Multiplying all rates by the considered time interval Δt , and adding the various contributions (see Fig. 4.2), yields a balance equation for the difference between the number of individuals, $n(t + \Delta t, \ell') \Delta \ell$, at time $t + \Delta t$ and the number of individuals, $n(t, \ell') \Delta \ell$, at time t :

$$\begin{aligned} n(t + \Delta t, \ell') \Delta \ell - n(t, \ell') \Delta \ell = \\ - g(\ell' + \Delta \ell/2, F) n(t, \ell' + \Delta \ell/2) \Delta t + g(\ell' - \Delta \ell/2, F) n(t, \ell' - \Delta \ell/2) \Delta t \\ - d(\ell', F) n(t, \ell') \Delta \ell \Delta t. \end{aligned}$$

It is instructive to check the dimensions in this equation. Note that the dimensions of $g(\ell, F)$, $n(t, \ell)$, and $d(\ell, F)$ are (length·time⁻¹), (number·length⁻¹), and (time⁻¹), respectively. Next, dividing both sides by the product $\Delta t \Delta \ell$ leads to

$$\begin{aligned} \frac{n(t + \Delta t, \ell') - n(t, \ell')}{\Delta t} = \\ - \frac{g(\ell' + \Delta \ell/2, F) n(t, \ell' + \Delta \ell/2) - g(\ell' - \Delta \ell/2, F) n(t, \ell' - \Delta \ell/2)}{\Delta \ell} \\ - d(\ell', F) n(t, \ell'). \end{aligned}$$

Taking the limits $\Delta t \rightarrow 0$ and $\Delta \ell \rightarrow 0$ in such a way that $g(\ell', F) \Delta t \ll \Delta \ell$, the left-hand side of this equation can be recognized as the partial derivative of $n(t, \ell)$ at $\ell = \ell'$ with respect to time t , while the first term on the right-hand side equals the partial derivative of the product $g(\ell, F) n(t, \ell)$ at $\ell = \ell'$ with respect to length ℓ . After dropping the primes, this limiting procedure results in the following partial differential equation for the density function $n(t, \ell)$:

$$\frac{\partial n(t, \ell)}{\partial t} = - \frac{\partial g(\ell, F) n(t, \ell)}{\partial \ell} - d(\ell, F) n(t, \ell). \quad (4.8)$$

This PDE describes only the dynamics of the density function $n(t, \ell)$ in the interior of the interval $[\ell_b, \ell_m]$ and incorporates the influence of individual growth and death in the two terms on the right-hand side. It must be supplemented with a boundary condition that specifies the density at the lower end ($\ell = \ell_b$) of the interval, at every time t , to complete the model. Since individuals are born at length ℓ_b , it is clear that this boundary condition should involve reproduction. The form of the boundary condition can be derived by integrating the left and right sides of the PDE (eq. 4.8) from $\ell = \ell_b$ to $\ell = \ell_m$, as follows:

$$\begin{aligned} \int_{\ell_b}^{\ell_m} \frac{\partial n(t, \ell)}{\partial t} d\ell = - \int_{\ell_b}^{\ell_m} \frac{\partial g(\ell, F) n(t, \ell)}{\partial \ell} d\ell - \int_{\ell_b}^{\ell_m} d(\ell, F) n(t, \ell) d\ell \\ \Rightarrow \frac{d}{dt} \int_{\ell_b}^{\ell_m} n(t, \ell) d\ell = g(\ell_b, F) n(t, \ell_b) - g(\ell_m, F) n(t, \ell_m) - \int_{\ell_b}^{\ell_m} d(\ell, F) n(t, \ell) d\ell. \end{aligned}$$

The last equation has a clear biological interpretation. The left-hand side is the rate of change in the total number of individuals in the population. These changes should equal the balance between births and deaths. The last term on the right-hand side is the total mortality rate

Table 4.1: Population-Level Equations of the Size-Structured Model for the Interaction between *Daphnia* and Algae

<i>Daphnia</i> dynamics	$\frac{\partial n(t, \ell)}{\partial t} + \frac{\partial g(\ell, F) n(t, \ell)}{\partial \ell} = -d(\ell, F) n(t, \ell)$ $g(\ell_b, F) n(t, \ell_b) = \int_{\ell_b}^{\ell_m} b(\ell, F) n(t, \ell) d\ell$
Algal dynamics	$\frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K}\right) - \int_{\ell_b}^{\ell_m} I(\ell, F) n(t, \ell) d\ell$
Initial conditions	$n(0, \ell) = \Psi(\ell)$ $F(0) = F_0$

Note. — The functions $g(\ell, F)$, $b(\ell, F)$, $d(\ell, F)$, and $I(\ell, F)$, modeling the individual behavior, are specified in Table 3.1.

in the population (cf. the total population feeding rate in the ODE, eq. 4.7). Since ℓ_m is an asymptotic length that no individual can reach, $g(\ell_m, F) n(t, \ell_m) \equiv 0$. This leads to the conclusion that $g(\ell_b, F) n(t, \ell_b)$ should equal the total population birthrate. Analogous to the total population feeding rate in the ODE (eq. 4.7) and the total population death rate in the derivation above, this total population birthrate equals the integral of the product of the individual birthrate, $b(\ell, F)$, and the population density, $n(t, \ell)$, over the reachable size interval $[\ell_b, \ell_m]$. The boundary condition with which to supplement the PDE (eq. 4.8), therefore, has the form

$$g(\ell_b, F) n(t, \ell_b) = \int_{\ell_b}^{\ell_m} b(\ell, F) n(t, \ell) d\ell. \quad (4.9)$$

It should be noted that the product $g(\ell_b, F) n(t, \ell_b)$ is natural, since it makes both sides of the condition a rate, with dimension (number·time⁻¹).

This completes the size-structured model for *Daphnia*: starting from an initial state of both the *Daphnia* and the algal populations, the equations derived here determine the future dynamics of both. For the algal population, the initial state consists of an initial algal density. The initial state of the *Daphnia* population is more complicated; it must specify the initial size distribution as well as initial numbers. Thus, the density function $n(t, \ell)$ at $t = 0$ is specified as a function of ℓ :

$$n(0, \ell) = \Psi(\ell),$$

$$F(0) = F_0.$$

Here, $\Psi(\ell)$ denotes the density function characterizing the initial *Daphnia* population and F_0 denotes the initial algal density. The full set of equations for the size-structured *Daphnia* population model is summarized in Table 4.1, and Figure 4.3 shows a schematic illustration of the actions that these equations specify.

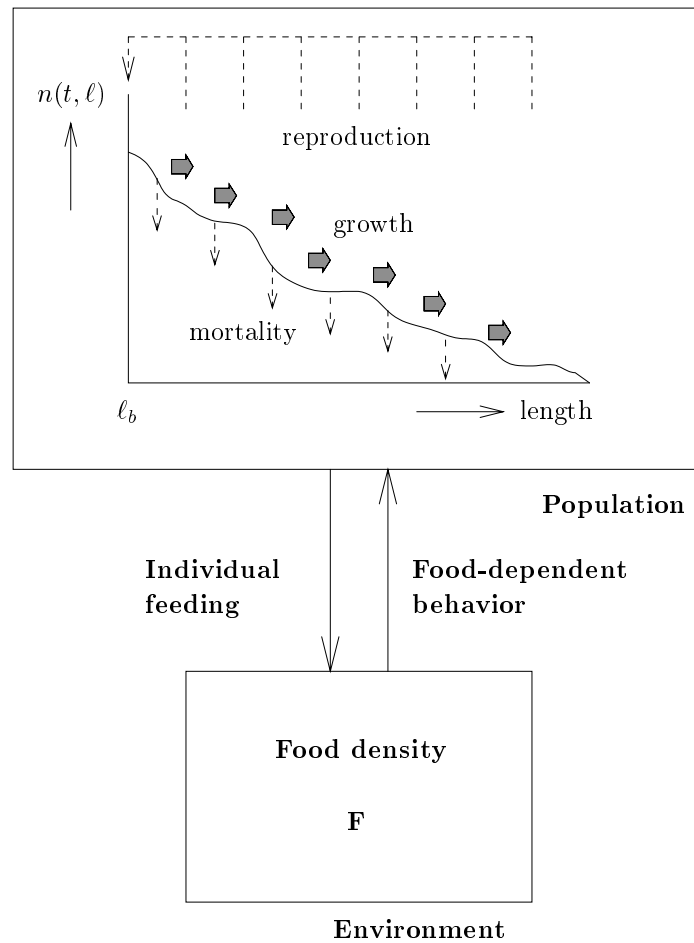


Figure 4.3: Schematic representation of the *Daphnia* population model, specified in Table 4.1. Growth and mortality influences on $n(t, l)$ are described by the partial differential equation, the reproduction influence by the boundary condition in Table 4.1. Individual behavior, mainly reproduction and growth, depends on food density. Food dynamics are described by an ordinary differential equation incorporating the feeding influence of individual *Daphnia*.

4.3 The Model at the Population Level

4.3.1 The Population State and Its Statistics

In section 2.3 the population or p -state was already introduced as the mathematical representation of the biological population. In physiologically structured models, the state of the individuals can generally take its value from a continuous individual state space. As a consequence, the p -state in these models can be represented by a distribution or density function over the individual state space Ω . (The choice of a density function as the p -state is connected to the PDE formalism. The recently developed “cumulative formulation” leads to different p -states.)

Note that the integral of the density function is interpreted as a number of individuals. Integration over the entire individual state space, Ω , gives the total number of individuals in

the population. Integration over part of Ω gives the number of individuals with an i -state in the part considered. More generally, any population statistic $\Phi(t)$ of biological interest can be written as a weighted integral of the population density function over the individual state space, Ω :

$$\Phi(t) = \int_{\Omega} \phi(x) n(t, x) dx. \quad (4.10)$$

In this equation $\phi(x)$ is an arbitrary weighting function defined on Ω . The total population size is obtained by assuming that $\phi(x) = 1$ for all x . The number of juvenile and adult individuals is obtained by assuming $\phi(x) = 1$ for values of the i -state that pertain to juvenile and adult individuals, respectively, and assuming that $\phi(x) = 0$ otherwise. If x refers to the weight of an individual, setting $\phi(x) = x$ gives the total population biomass at time t . These are just a few examples to show that population statistics of interest are weighted integrals of the density function $n(t, x)$ over the individual state space, Ω .

Section 4.1 discussed how an individual can influence components of its environment, like the ambient food density, that in turn exert an influence on the individual behavior via a feedback loop. In the *Daphnia* model, the total population feeding rate appears in the ODE for food density as an integral of the density function $n(t, \ell)$ weighted by the individual feeding rate (see eq. 4.7). The behavior of an individual can also be influenced directly by the population itself (cf. feedback functions in section 4.1). The acting variable in direct density dependence is generally also a weighted integral of $n(t, x)$ over the state space Ω . Instead of appearing in an ODE that describes the dynamics of an environmental variable, it occurs as an independent variable in the individual growth, birth, or mortality rate.

4.3.2 Other Individual State Variables

Although the size-structured model of section 4.2 is formulated with specific choices for the functions $g(\ell, F)$, $b(\ell, F)$, $d(\ell, F)$, and $I(\ell, F)$ (see Table 3.1), its form is representative of any structured-population model in which (1) both the i -state and the E -state are one-dimensional (i.e., consist of a single variable), (2) all individuals are born with a fixed identical state at birth, and (3) the E -state acts as a feedback loop for the structured population. To obtain a general formulation of such a structured-population model, the variables ℓ and F in the population equations of Table 4.1 can be replaced everywhere with the unspecified variables x and E . The general formulation is couched in terms of the functions $g(x, E)$, $b(x, E)$, $d(x, E)$, and $I(x, E)$, which model the individual behavior (see section 4.1), and the density function $n(t, x)$ characterizing the state of the structured population. The bounds of the integrals that occur in these formulas (cf. Table 4.1) must be chosen so that the integration is over the appropriate range of reachable i -state values, usually the entire i -state space Ω .

Models in which the chronological age a of the individuals constitutes the i -state form a special class of these one-dimensional structured-population models. Age-structured models involve only the functions $b(a, E)$, $d(a, E)$, and $I(a, E)$, since the growth rate g in age equals one. An age-structured model is therefore comparable to any other structured model, except that the function g is replaced everywhere by the constant 1. This special form of g (see also section 4.1) disguises the exact interpretation of various terms in the equations, since rates and densities are no longer easily distinguished. For example, the boundary condition in an

age-structured model is

$$n(t, 0) = \int_0^{\infty} b(a, E) n(t, a) da$$

(cf. eq. 4.9). Notwithstanding its form, the left-hand side of this equation still has to be interpreted as a rate, since it is essentially the product of the rate of aging (one) and the density at age zero.

4.3.3 More Environmental State Variables

Changing the interpretation of the environmental state variable, or characterizing the environment by more than a single variable, involves a relatively straightforward generalization of the model discussed in section 4.2. This is in sharp contrast with adding more individual state variables, which is discussed in section 4.9.

The E -state can be a vector of environmental variables, consisting of a mixture of abiotic modulation or forcing factors, direct density-dependent mechanisms, and feedback loops (see section 2.2). Each environmental forcing factor must be specified as an explicit function of time. Every direct density-dependent mechanism involves specifying a weighted integral of $n(t, x)$ (cf. eq. 4.10), using a weighting function $\phi(x)$. For every feedback loop, an ODE has to be added to the model to describe both the autonomous dynamics of the environmental variable and the influence of the structured population on its current value. Last but not least, the dependence of individual behavior on each environmental variable must be modeled. A higher-dimensional E -state makes the model more complicated but not qualitatively different.

4.4 Constant Environments: Linear, Density-Independent Models

In this section it is assumed that the environmental state is characterized by a vector of variables, E_c , that remain constant over time. This assumption eliminates density-dependent interactions between individuals because such interactions, by definition, act via the changing state of the environment. (The assumption of a constant environment and the absence of density-dependent interactions also exclude feedback functions among the environmental state variables; see section 4.1). In the absence of density dependence, the population either grows or declines exponentially, depending on the number of offspring produced, on the average, by a single individual during its life. The models discussed in this section are, therefore, linear and density-independent. Note that this discussion is important for the analysis of equilibria in density-dependent models as well, since the environment at equilibrium is also constant in time.

A *Daphnia* population in the laboratory, with constant ambient food density, is an example of a system considered here. Evidently, exponential population growth or decline means that such an experimental system cannot exist for a long time, but structured-population models allow us to compute, for example, the population growth rate as a function of the life-history characteristics of the individuals. For ease of presentation, the i -state is assumed to comprise a single variable, although the discussion also applies to higher-dimensional cases.

Since the environment is constant, the only equations of interest are those relating to the structured population:

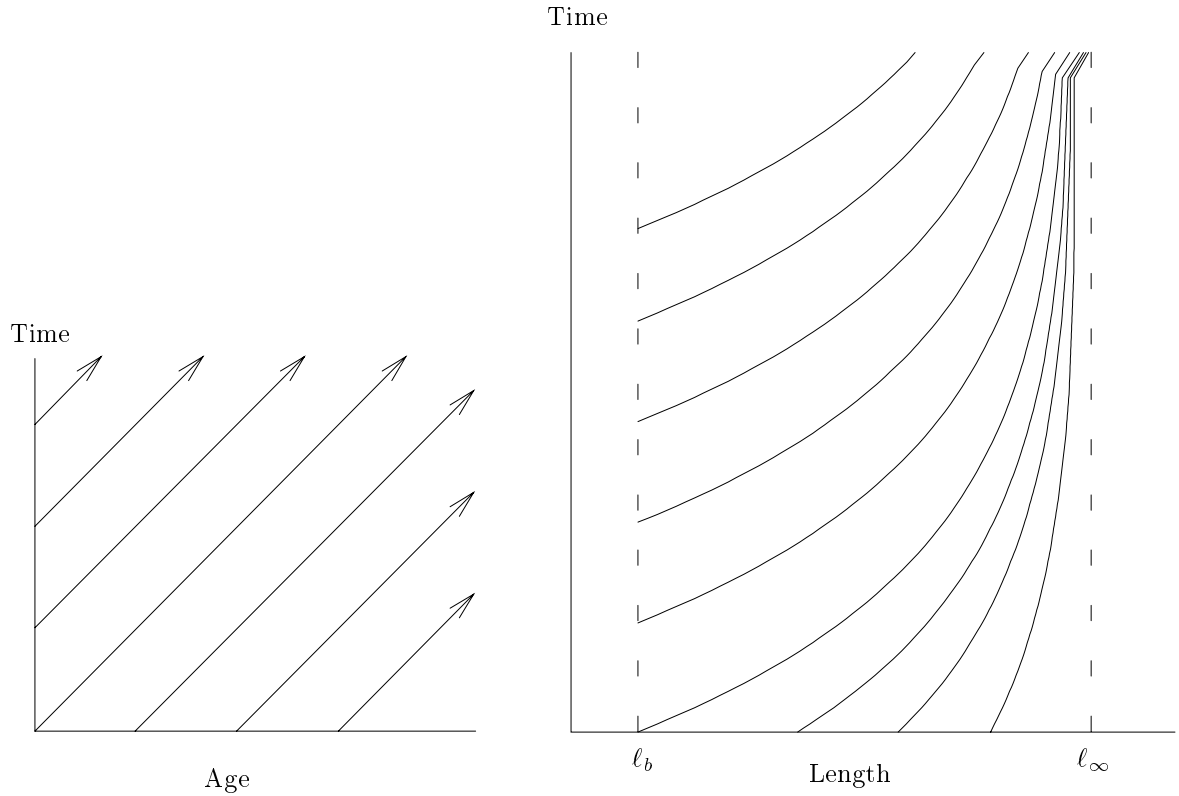


Figure 4.4: Characteristics of the partial differential equation for an age-structured population (*left*) and for the size-structured, *Daphnia* model (*right*). For *Daphnia*, food density F_c is assumed constant over time, such that the ultimate length ℓ_∞ equals $\ell_m F_c / (F_h + F_c)$. The characteristics can most easily be interpreted as the trajectories or paths through the (*i*-state)-time plane, followed by the individuals during their lifetime. The characteristics originating on the *x*-axis pertain to members of the initial population; those originating on the *y*-axis (*left*) or on the vertical line $\ell = \ell_b$ (*right*) to individuals born later.

$$\frac{\partial n(t, x)}{\partial t} = -\frac{\partial g(x, E_c) n(t, x)}{\partial x} - d(x, E_c) n(t, x), \quad (4.11a)$$

$$g(E_c, x_b) n(t, x_b) = \int_{x_b}^{x_m} b(x, E_c) n(t, x) dx, \quad (4.11b)$$

$$n(0, x) = \Psi(x). \quad (4.11c)$$

Here, the *i*-state space Ω is the interval $[x_b, x_m)$, and individuals are born with *i*-state x_b . As usual, $n(t, x)$ is the density function characterizing the population state, and $g(x, E_c)$, $d(x, E_c)$, and $b(x, E_c)$ model individual development, mortality, and reproduction as a function of its state x in the (constant) environment, E_c .

First, the concept of characteristics has to be introduced. *Characteristics* are curves in the

space, spanned by the i -state coordinate and time — here, the plane $\Omega \times \mathbb{R}^+$ — along which the changes in the density function n are described by an ordinary differential equation, if the derivative used in this ODE is the total (material) derivative of n :

$$\frac{Dn}{Dt} = \frac{\partial n(t, x)}{\partial t} + g(x, E_c) \frac{\partial n(t, x)}{\partial x}.$$

In the general theory of partial differential equations, the characteristics are sometimes curves in the three-dimensional space spanned by the i -state x , time t , and density n . The characteristics, as defined here, are the projections of these latter curves on the two-dimensional plane spanned by the i -state and time. These two meanings of the term characteristics are used interchangeably. Most important, the characteristics, as defined here, can be interpreted biologically as the trajectories that individuals follow through the (x, t) -plane, if they do not die. Figure 4.4 shows the characteristics for an age-structured model and the size-structured model used in the *Daphnia* example. The ODE for the changes in the density n along the characteristics turns out to be linear and is explicitly solvable. The phrase integration along characteristics refers to obtaining the solution of the PDE (4.11a) by deriving and integrating this linear ODE for the density n along the characteristics. To explain the method of integration along characteristics, a bit of rather complicated notation is required.

Let the variable θ be proportional to time with the moment in time when $\theta = 0$ not yet fixed. Mathematically, the characteristics (in the sense used here) can be defined as all those curves in the (x, t) -plane, for which

$$\frac{dt}{d\theta} = 1, \tag{4.12a}$$

$$\frac{dx}{d\theta} = g(x, E_c). \tag{4.12b}$$

This definition implies that

$$\frac{dx}{dt} = g(x, E_c), \tag{4.13}$$

which is just the ODE describing individual development. The characteristics constitute an infinite collection of curves in the (x, t) -plane with an identical form but different origins: if an individual is born at time t_b with i -state x_b , its development through the (x, t) -plane follows the characteristic that originates in (x_b, t_b) . Alternatively, if an individual is already present when $t = 0$, with an i -state x_0 , it will follow the characteristic through the (x, t) -plane, which originates in $(x_0, 0)$ (see Fig. 4.4). Therefore, the set of characteristics comprises all the $(i$ -state)-time relations of individuals that are born at different times t_b with i -state x_b or that are already present at time 0 with i -state x_0 . Let $\theta = 0$ correspond to a particular time and i -state, denoted by $t_{\theta=0}$ and $x_{\theta=0}$, respectively, and referred to as the *origin* of the characteristic. The origin is (x_b, t_b) if the characteristic pertains to individuals born at time $t_b > 0$ with i -state x_b , or is $(x_0, 0)$ if the characteristic pertains to a member of the initial population. The variable θ indicates the position along the characteristic. For the characteristics followed by the members of the initial population θ is identical to time because here $\theta = 0$ corresponds to $t = 0$. Analogously, for the characteristics followed by the individuals born after $t = 0$, θ is identical to the age of the individuals (see Fig. 4.4).

To derive the ODE for $n(t, x)$ along a particular characteristic, its derivative with respect to

θ is calculated by considering t and x explicitly as functions of θ :

$$\begin{aligned} \frac{dn(t(\theta), x(\theta))}{d\theta} &= \frac{\partial n(t(\theta), x(\theta))}{\partial t} \frac{dt}{d\theta} + \frac{\partial n(t(\theta), x(\theta))}{\partial x} \frac{dx}{d\theta} \\ &= \frac{\partial n(t(\theta), x(\theta))}{\partial t} + g(x(\theta), E_c) \frac{\partial n(t(\theta), x(\theta))}{\partial x} \\ &= -\frac{\partial g(x(\theta), E_c)}{\partial x} n(t(\theta), x(\theta)) - d(x(\theta), E_c) n(t(\theta), x(\theta)). \end{aligned}$$

In the first two steps of the derivation, the chain rule of differentiation and the equations (4.12) for the characteristics are used to resolve the derivative $dn/d\theta$. The notations $t(\theta)$ and $x(\theta)$ indicate that both time and i -state, respectively, are considered explicit functions of θ . In the last step, the PDE (4.11a) is used to eliminate the partial derivatives of n . The following, linear ODE results for the value of $n(t(\theta), x(\theta))$ along a particular characteristic parameterized by θ :

$$\frac{dn(t(\theta), x(\theta))}{d\theta} = -\left(d(x(\theta), E_c) + \frac{\partial g(x(\theta), E_c)}{\partial x}\right) n(t(\theta), x(\theta)).$$

This ODE can be solved for the density $n(t(\theta), x(\theta))$ when $\theta = \theta_1$:

$$n(t(\theta_1), x(\theta_1)) = n(t_{\theta=0}, x_{\theta=0}) \exp\left(-\int_0^{\theta_1} \left[d(x(\theta), E_c) + \frac{\partial g(x(\theta), E_c)}{\partial x}\right] d\theta\right). \quad (4.14)$$

Equation (4.14) shows that the density, n , at a specific point $(x(\theta_1), t(\theta_1))$ is a function of its value at the origin $(x_{\theta=0}, t_{\theta=0})$ and the intervening values of $x(\theta)$ along the characteristic. The density changes through mortality and the change in developmental rate. The appearance of $d(x(\theta), E_c)$ in (4.14) indicates that the density decreases along the characteristic because of individual deaths. In addition, the density can increase or decrease because characteristics converge or diverge, respectively, in the (x, t) -plane. This explains the occurrence of $\partial g(x(\theta), E_c)/\partial x$ in (4.14). Where characteristics converge, individuals with smaller x values have higher developmental rates, and hence, $\partial g(x(\theta), E_c)/\partial x$ is negative. This results in an increase in the density along the characteristic (see eq. 4.14). Intuitively, the increase can be understood if we consider all individuals with i -state between x_1 and x_2 at time t . If no mortality takes place, the number of these individuals remains constant, which fixes the integral over the density function at a constant value. However, if the two characteristics passing through x_1 and x_2 at time t converge, the range of i -state values, over which these individuals are distributed, gets smaller with time. Together with the constant integral, this decrease in range implies that the value of the density function has to increase, on the average (see also Fig. 4.4). For diverging characteristics, an analogous reasoning holds.

The use of $t(\theta_1)$ and $x(\theta_1)$ in equation (4.14) implies that the coordinates of the characteristics in the (x, t) -plane can be given explicitly as functions of the parameter θ . This depends on the existence of a closed-form solution for the ODEs (4.12). Since θ is proportional to time, ODE (4.12a) implies that

$$T(\theta_1, t_{\theta=0}) = \theta_1 + t_{\theta=0},$$

where $T(\theta_1, t_{\theta=0})$ is the time coordinate of the point parameterized by $\theta = \theta_1$ along the characteristic with its origin at coordinates $(x_{\theta=0}, t_{\theta=0})$. For what follows, assume that an

explicit solution for the ODE (4.12b) is known. The function $X(\theta_1, x_{\theta=0}, E_c)$ indicates the i -state coordinate of the point along the characteristic with its origin at $(x_{\theta=0}, t_{\theta=0})$. The function $X(\theta_1, x_{\theta=0}, E_c)$ depends on the form of the developmental rate $g(x, E_c)$ and cannot be given in general. Moreover, since development usually depends on the (constant) state of the environment, E_c also appears as an argument in the function $X(\theta_1, x_{\theta=0}, E_c)$.

In addition to the functions $T(\theta_1, t_{\theta=0})$ and $X(\theta_1, x_{\theta=0}, E_c)$ for the coordinates along a specific characteristic, the derivation that follows also requires an explicit expression for the inverse of $X(\theta_1, x_{\theta=0}, E_c)$ with respect to its first argument. This inverse is indicated by $\tau(x, x_{\theta=0}, E_c)$ and can be interpreted as the time it takes to develop from an initial i -state $x_{\theta=0}$ to a final i -state x . Therefore,

$$\tau(X(\theta_1, x_{\theta=0}, E_c), x_{\theta=0}, E_c) = \theta_1$$

and

$$X(\tau(x_1, x_{\theta=0}, E_c), x_{\theta=0}, E_c) = x_1.$$

To illustrate the rather complicated notation, the expressions for these functions will be derived for the *Daphnia* example model. The food density is assumed equal to the constant F_c . As discussed in section 3.1, the growth in length ℓ under constant food conditions is

$$\frac{d\ell}{dt} = g(F_c, \ell) = \gamma(\ell_m h(F_c) - \ell),$$

in which the functional response is defined as

$$h(F) = \frac{F}{F_h + F}.$$

The ODE for ℓ can be solved explicitly. If a characteristic is considered with its origin located at length and time coordinates $(\ell_{\theta=0}, t_{\theta=0})$, the analogue of the function $X(\theta, x_{\theta=0}, E_c)$ is a function $L(\theta, \ell_{\theta=0}, F_c)$, given by

$$L(\theta, \ell_{\theta=0}, F_c) = \ell_m h(F_c) - (\ell_m h(F_c) - \ell_{\theta=0}) e^{-\gamma\theta}$$

(cf. also the length-age relation in eq. 3.4). Figure 4.4 illustrates that all individuals born after $t = 0$ follow characteristics to the left and above the characteristic originating at $(\ell_b, 0)$. Hence, $\ell_{\theta=0}$ is taken to be equal to ℓ_b for these individuals and $t_{\theta=0}$ is identified with their time of birth. The members of the initial population all follow characteristics to the right and below the characteristic that originates at $(\ell_b, 0)$. As natural choices for the origins of these characteristic, let $t_{\theta=0}$ equal zero and $\ell_{\theta=0}$ be the length of these individuals at $t = 0$. The function $L(\theta, \ell_{\theta=0}, F_c)$ specifies the length of individuals after growing for a period of θ time units at a constant food density F_c , given that they started out with initial length $\ell_{\theta=0}$. The analogue of the function $\tau(x, x_{\theta=0}, E_c)$ is a function $A(\ell, \ell_{\theta=0}, F_c)$, defined as

$$A(\ell, \ell_{\theta=0}, F_c) = \frac{1}{\gamma} \ln \left(\frac{\ell_m h(F_c) - \ell_{\theta=0}}{\ell_m h(F_c) - \ell} \right).$$

This equality is obtained by solving the relation

$$L(\theta, \ell_{\theta=0}, F_c) = \ell$$

for θ . $A(\ell, \ell_{\theta=0}, F_c)$ can be interpreted as the time it takes an individual at a constant food density, F_c , to grow from length $\ell_{\theta=0}$ to length ℓ .

The functions $X(\theta, x_{\theta=0}, E_c)$ and $\tau(x, x_{\theta=0}, E_c)$ can be used to obtain a formal solution for the linear model (4.11). Equation (4.14) can be rewritten as

$$\begin{aligned}
 n(t(\theta_1), x(\theta_1)) &= n(t_{\theta=0}, x_{\theta=0}) \exp \left(- \int_0^{\theta_1} \left[d(x(\theta), E_c) + \frac{\partial g(x(\theta), E_c)}{\partial x} \right] d\theta \right) \\
 &= n(t_{\theta=0}, x_{\theta=0}) \exp \left(- \int_{x_{\theta=0}}^{x(\theta_1)} \left[d(x, E_c) + \frac{\partial g(x, E_c)}{\partial x} \right] \frac{d\theta}{dx} dx \right) \\
 &= n(t_{\theta=0}, x_{\theta=0}) \exp \left(- \int_{x_{\theta=0}}^{x(\theta_1)} \frac{d(x, E_c) + \partial g(x, E_c)/\partial x}{g(x, E_c)} dx \right) \\
 &= n(t_{\theta=0}, x_{\theta=0}) \frac{g(x_{\theta=0}, E_c)}{g(x(\theta_1), E_c)} \exp \left(- \int_{x_{\theta=0}}^{x(\theta_1)} \frac{d(x, E_c)}{g(x, E_c)} dx \right).
 \end{aligned} \tag{4.15}$$

For the members of the initial population, the density $n(t_{\theta=0}, x_{\theta=0})$ can be replaced by the initial density function $\Psi(x)$ from (4.11c) because $(x_{\theta=0}, t_{\theta=0})$ is $(x, 0)$. Substitution into equation (4.15) yields the following equation for the dynamics of this part of the population:

$$n(t, X(t, x, E_c)) = \frac{g(x, E_c)\Psi(x)}{g(X(t, x, E_c), E_c)} \exp \left(- \int_x^{X(t, x, E_c)} \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi \right). \tag{4.16}$$

By definition, members of the initial population with i -state x at $t = 0$ have an i -state equal to $X(t, x, E_c)$ at time t .

For individuals born after $t = 0$, the origin of the characteristic $(x_{\theta=0}, t_{\theta=0})$ is (x_b, t_b) , where t_b refers to the time of the birth of these individuals. The dynamics of the part of the population born after $t = 0$ can therefore be described by

$$n(t, x) = \frac{g(x_b, E_c)n(t - \tau(E_c, x, x_b), x_b)}{g(x, E_c)} \exp \left(- \int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi \right). \tag{4.17}$$

Here, the time of birth t_b of individuals that have reached i -state x at time t has been replaced by

$$t_b = t - \tau(x, x_b, E_c),$$

following the definition of the function $\tau(x, x_b, E_c)$. Since $t_b > 0$, it is clear that equation (4.17) holds only as long as $t > \tau(x, x_b, E_c)$.

Together, equations (4.16) and (4.17) specify the entire solution of the linear PDE (4.11a) along its characteristics: equation (4.16) relates to the initial population, and equation (4.17) relates to individuals born after $t = 0$. In any realistic situation with a nonzero death rate, the initial population dies out, in the meantime making a diminishing contribution to the long-term dynamics. The initial population does play a role in short-term dynamics and

models exist in which its influence does not become negligible (see, e.g., Metz and Diekmann 1986, chapter 2). In general, however, for the long-term behavior of the linear model (4.11), the dynamics of interest are described by equation (4.17).

If $B(t, E_c)$ is defined as the total population birthrate for a population living in the constant environment E_c , equation (4.17) can also be written as

$$n(t, x) = \frac{B(t - \tau(E_c, x, x_b), E_c)}{g(x, E_c)} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right).$$

Substitution into the boundary condition (4.11b) leads to the following integral equation:

$$B(t, E_c) = \int_{x_b}^{x_m} B(t - \tau(x, x_b, E_c), E_c) \frac{b(x, E_c)}{g(x, E_c)} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) dx. \quad (4.18)$$

Provided that $\tau(x, x_b, E_c)$ (the time it takes an individual to develop from x_b to x when living in a constant environment, E_c) is a known function of its three arguments, this renewal equation relates the total population birthrate at time t to its history.

Equation (4.18) shows that the linear model does not allow a stable-equilibrium solution. An equilibrium would imply that the birthrate B is constant over time. Substitution of a constant birthrate $\bar{B}(E_c)$ into (4.18) leads to an expression involving only parameters; no dynamic variables appear. Hence, the constant birthrate occurs for only very specific parameter combinations, such that every individual, on the average, produces exactly a single offspring during its lifetime. For almost all parameter combinations, individuals produce more or fewer offspring. Because an equilibrium is not feasible and the model does not incorporate any density dependence, the population ultimately grows or declines exponentially. Substituting the exponential trial solution,

$$B(t, E_c) = B_0 e^{\lambda t},$$

into the renewal equation (4.18) leads to the following characteristic equation:

$$\Pi(\lambda, E_c) = 1, \quad (4.19)$$

in which

$$\Pi(\lambda, E_c) = \int_{x_b}^{x_m} e^{-\lambda\tau(x, x_b, E_c)} \frac{b(x, E_c)}{g(x, E_c)} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) dx.$$

The last exponential function appearing in the integrand is the survival function $S(x, E_c)$, given in equation (4.3). The characteristic equation can therefore also be written as

$$\Pi(\lambda, E_c) = \int_{x_b}^{x_m} e^{-\lambda\tau(x, x_b, E_c)} \frac{b(x, E_c)}{g(x, E_c)} S(x, E_c) dx = 1. \quad (4.20)$$

The integral expression for $\Pi(\lambda, E_c)$ when $\lambda = 0$ resembles equation (4.5), which gives the number of offspring produced by a surviving individual in a constant environment, E_c , between its birth with i -state x_b and the time it reaches i -state x . In $\Pi(0, E_c)$, however, the integration is carried out over $[x_b, x_m)$, that is, over the entire life history of the individual, and the reproductive contribution at every i -state x is weighted with the probability $S(x, E_c)$ of

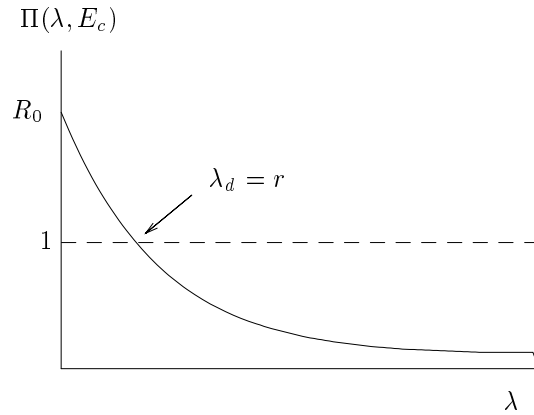


Figure 4.5: The general form of the characteristic equation (4.20) for a structured population model

surviving to that i -state. This quantity, $\Pi(0, E_c)$, is often referred to as the net reproduction R_0 :

$$R_0 = \Pi(0, E_c) = \int_{x_b}^{x_m} \frac{b(x, E_c)}{g(x, E_c)} S(x, E_c) dx. \quad (4.21)$$

By definition, R_0 is the expected number of (female) offspring produced by one female individual throughout her life when density-dependent factors can be neglected, for example, when population densities are infinitesimally low.

Net reproduction, R_0 , is sometimes also referred to as the expected lifetime reproduction of an individual. The integral in (4.19) can also be evaluated when $\lambda \neq 0$. The resulting quantity, $\Pi(\lambda, E_c)$, is a strictly decreasing function of λ with a positive second derivative. Therefore, there exists exactly one simple real root to the characteristic equation (4.19) (see Fig. 4.5). This single real root is referred to as the dominant eigenvalue λ_d of the linear model (4.11). It is the ultimate, exponential growth or decline rate of the population and is often called the intrinsic population growth rate. In the biological literature, this quantity is often indicated by r . The characteristic equation (4.19) is important because it relates the intrinsic population growth rate to the entire life history of the individuals and to the constant environmental conditions E_c . Figure 4.5 also makes clear that a positive (or negative) population growth rate corresponds to R_0 's being larger (or smaller) than unity:

$$R_0 > 1 \iff r > 0, \quad R_0 < 1 \iff r < 0,$$

which is intuitively clear given the interpretation of R_0 .

Although the population eventually grows or declines exponentially, and the density function $n(t, x)$ for every value x does so as well, the form of the density function ultimately becomes

constant over time:

$$\begin{aligned} n(t, x) &\sim e^{-\lambda\tau(x, x_b, E_c)} \frac{b(x, E_c)}{g(x, E_c)} S(x, E_c) \\ &= e^{-\lambda\tau(x, x_b, E_c)} \frac{b(x, E_c)}{g(x, E_c)} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) dx. \end{aligned} \quad (4.22)$$

This means that the composition of the population, in terms of the proportions of individuals with an i -state in various classes, becomes constant. The constant form of the density function is referred to as the *stable state distribution*.

For realistic choices of the functions g , b , and d , the characteristic equation (4.19) cannot be solved explicitly. For simple choices of the functions, the integral might have a closed-form solution, but even then the resulting equation is transcendental. Hence, the value of λ_d has to be obtained numerically. In general, there are infinitely many roots (eigenvalues) of the characteristic equation (4.19), although only the dominant one is real. The others are complex and form a collection of complex conjugate pairs. The real parts of these complex pairs are, in all practical situations, smaller than the value of the single real eigenvalue, accounting for the adjective dominant. The remaining eigenvalues determine the rate at which the population attains the stable state distribution (4.22).

These equations can be simplified for age-structured populations, for which $x_b = 0$, $x_m = \infty$, $g(x, E_c) \equiv 1$, and most important, $\tau(x, x_b, E_c) = a$. With these substitutions and the replacement of the variable x by a to indicate age, the renewal equation (4.18) becomes

$$\begin{aligned} B(t, E_c) &= \int_0^\infty B(t-a, E_c) b(a, E_c) \exp\left(-\int_0^a d(\zeta, E_c) d\zeta\right) da \\ &= \int_0^\infty B(t-a, E_c) b(a, E_c) S(a, E_c) da. \end{aligned}$$

This equation is known as Lotka's integral equation for the dynamics of an age-structured population (Sharpe and Lotka 1911; Roughgarden 1979). The characteristic equation (4.19) for the age-structured model becomes

$$\begin{aligned} \int_0^\infty e^{-\lambda a} b(a, E_c) \exp\left(-\int_0^a d(\zeta, E_c) d\zeta\right) da &= 1 \\ \Rightarrow \int_0^\infty e^{-\lambda a} b(a, E_c) S(a, E_c) da &= 1. \end{aligned}$$

This is Euler's equation (Roughgarden 1979) for the computation of the intrinsic population growth rate of an age-structured population, in which the product of the natality function, $b(a, E_c)$, the survival function, $S(a, E_c)$, and an exponential weighting function $\exp(-\lambda a)$ is integrated over the entire individual life history. Therefore, the renewal equation (4.18) and the characteristic equation (4.19) can be interpreted as the analogues of Lotka's integral equation and Euler's equation, respectively, for an arbitrary i -state variable x .

4.5 The Equilibrium of the *Daphnia* Model

The equilibria of the *Daphnia* model can in principle be studied using the model formulation in Table 4.1. It turns out to be more convenient, however, to reformulate the model as an age-dependent problem. Because of the positive mortality rate, the initial population plays an exponentially diminishing role. The long-term dynamics, including the approach to equilibrium, are determined by the individuals born after time zero. The deterministic growth in length, described by the ODE (3.3), ensures that individuals follow a unique growth trajectory, depending only on their initial length and the food density. Since all individuals start at the same initial length ℓ_b and all experience the same environmental food density, individuals born at the same time remain identical, while they always differ from individuals born at different times. In other words, after the initial population becomes negligible, the length of an individual is uniquely related to its chronological age. Of course, this length-age relation can change over time owing to changing food density; but at any moment in time, individual length and age form a one-to-one relation. Thus, the *Daphnia* population can be completely characterized in terms of a density function $m(t, a)$, representing the age distribution of the population, together with a length-age relation $L(t, a)$, which specifies at every time t the unique relation between individual length and age. The possible age range is $[0, \infty)$.

Like the integral of the population size distribution $n(t, \ell)$, the integral

$$\int_{a_1}^{a_2} m(t, a) da$$

represents a total number of *Daphnia*, but now of individuals at time t with an age between a_1 and a_2 . Since the function $L(t, a)$ relates age to length at time t , the following equality holds:

$$\int_{a_1}^{a_2} m(t, a) da = \int_{L(t, a_1)}^{L(t, a_2)} n(t, \ell) d\ell.$$

(The total number of *Daphnia* with an age between a_1 and a_2 must equal the total number of *Daphnia* with a length between the corresponding bounds $L(t, a_1)$ and $L(t, a_2)$.) The right-hand side of this equation can be rewritten by a change in variables as

$$\int_{L(t, a_1)}^{L(t, a_2)} n(t, \ell) d\ell = \int_{a_1}^{a_2} n(t, L(t, a)) \frac{d\ell}{dt} \frac{dt}{da} da = \int_{a_1}^{a_2} n(t, L(t, a)) g(L(t, a), F) da,$$

which shows that $m(t, a)$ and $n(t, \ell)$ are formally related to each other by

$$m(t, a) \equiv n(t, L(t, a)) g(L(t, a), F).$$

This equivalence can be used to express any (weighted) integral of $n(t, \ell)$ as an integral of

$m(t, a)$. For example, the population birthrate can be rewritten as

$$\begin{aligned} \int_{\ell_b}^{\ell_m} b(\ell, F) n(t, \ell) d\ell &= \int_0^{\infty} b(L(t, a), F) n(t, L(t, a)) \frac{d\ell}{dt} \frac{dt}{da} da \\ &= \int_0^{\infty} b(L(t, a), F) n(t, L(t, a)) g(L(t, a), F) da \\ &= \int_0^{\infty} b(L(t, a), F) m(t, a) da. \end{aligned}$$

The PDE describing the dynamics of $m(t, a)$ can be derived using the same bookkeeping arguments as were used to derive the PDE for $n(t, \ell)$ (see Fig. 4.2). This leads to

$$\frac{\partial m(t, a)}{\partial t} = -\frac{\partial m(t, a)}{\partial a} - d(L(t, a), F) m(t, a). \quad (4.23)$$

In this equation the death rate, $d(L(t, a), F)$, indirectly depends on the individual age via its dependence on the individual length. In the *Daphnia* model this does not make a difference, because $d(L(t, a), F) \equiv \mu$, which is independent of length and hence age. In the example model, the relevant PDE therefore equals

$$\frac{\partial m(t, a)}{\partial t} + \frac{\partial m(t, a)}{\partial a} = -\mu m(t, a). \quad (4.24)$$

The boundary condition for the PDE (4.23) can be derived by integrating both sides of the equation over the reachable age range $[0, \infty)$ (cf. the derivation of eq. 4.9):

$$\begin{aligned} \int_0^{\infty} \frac{\partial m(t, a)}{\partial t} da &= -\int_0^{\infty} \frac{\partial m(t, a)}{\partial a} da - \int_0^{\infty} d(L(t, a), F) m(t, a) da \\ \Rightarrow \frac{d}{dt} \int_0^{\infty} m(t, a) da &= m(t, 0) - m(t, \infty) - \int_0^{\infty} d(L(t, a), F) m(t, a) da. \end{aligned}$$

As in the derivation of the boundary condition (4.9), this leads to the conclusion that $m(t, 0)$ should equal the population birthrate:

$$m(t, 0) = \int_0^{\infty} b(L(t, a), F) m(t, a) da. \quad (4.25)$$

Note that the developmental rate g does not disappear from the left-hand side but is simply equal to one.

In the *Daphnia* model, the birthrate, $b(\ell, F)$, equals zero when $\ell < \ell_j$. The age at which individuals reach this juvenile-to-adult threshold is indicated by the function $A_j(t)$, which equals the current duration of the juvenile stage. Because of the time dependence of the length-age relation, the value of $A_j(t)$ varies in time. The definition of $A_j(t)$ implies that it fulfills the condition

$$L(t, A_j(t)) = \ell_j. \quad (4.26)$$

The juvenile period, $A_j(t)$, is only implicitly defined by (4.26), but an explicit expression is possible if the entire length-age relation is known. By substitution of the functional form for $b(\ell, F)$, given in Table 3.1, the population birthrate can be rewritten using the function $A_j(t)$, such that the boundary condition (4.25) becomes

$$m(t, 0) = \int_{A_j(t)}^{\infty} r_m h(F) (L(t, a))^2 m(t, a) da; \quad (4.27)$$

$h(F)$ is used as before to denote the *Daphnia* functional response $F/(F_h + F)$.

The population feeding rate can also be rewritten using the density function $m(t, a)$ and the length-age relation, $L(t, a)$, so that the ODE (4.7) describing the dynamics of the food density becomes

$$\frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K}\right) - \int_0^{\infty} I(L(t, a), F) m(t, a) da. \quad (4.28)$$

After substituting the expression for $I(L(t, a), F)$ (see Table 3.1), this ODE simplifies to

$$\frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K}\right) - \int_0^{\infty} \nu h(F) (L(t, a))^2 m(t, a) da. \quad (4.29)$$

The equation for the dynamics of the length-age relation, $L(t, a)$, has to be derived separately. Clearly,

$$L(t, 0) = \ell_b, \quad (4.30)$$

since at birth all individuals have length ℓ_b , whatever their time of birth. Consider the change in length in a small time interval Δt . An individual with age a has length $L(t, a)$ at time t , and length $L(t + \Delta t, a + \Delta t)$ at the end of the interval Δt . The difference between these lengths is the growth increment during the interval, which equals $g(L(t, a), F) \Delta t$. Equating the two yields an expression for the growth in length during the time interval Δt

$$\frac{L(t + \Delta t, a + \Delta t) - L(t, a)}{\Delta t} = g(L(t, a), F).$$

Expanding the term $L(t + \Delta t, a + \Delta t)$ to the first order and taking the limit $\Delta t \rightarrow 0$ leads to the following PDE for the dynamics of the length-age relation, $L(t, a)$:

$$\frac{\partial L(t, a)}{\partial t} + \frac{\partial L(t, a)}{\partial a} = g(L(t, a), F). \quad (4.31)$$

Substituting the expression for $g(\ell, F)$ from Table 3.1 leads to the following result

$$\frac{\partial L(t, a)}{\partial t} + \frac{\partial L(t, a)}{\partial a} = \gamma (\ell_m h(F) - L(t, a)). \quad (4.32)$$

The initial states of the *Daphnia* population and the algal food density now have to be specified by means of an initial condition for $m(0, a)$, an initial condition for $L(0, a)$, and the initial value for the food density $F(0)$:

$$m(0, a) = \Psi(a), \quad L(0, a) = \Lambda(a), \quad F(0) = F_0.$$

Table 4.2: Equations of the *Daphnia* Population Model after Reformulation as an Age-Structured Problem

<i>Daphnia</i> dynamics	$\frac{\partial m(t, a)}{\partial t} + \frac{\partial m(t, a)}{\partial a} = -\mu m(t, a)$ $m(t, 0) = \int_{A_j(t)}^{\infty} r_m h(F) (L(t, a))^2 m(t, a) da$ $\frac{\partial L(t, a)}{\partial t} + \frac{\partial L(t, a)}{\partial a} = \gamma (\ell_m h(F) - L(t, a))$ $L(t, 0) = \ell_b$ $L(t, A_j(t)) = \ell_j$
Algal dynamics	$\frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K}\right) - \int_0^{\infty} \nu h(F) (L(t, a))^2 m(t, a) da$
Initial conditions	$m(0, a) = \Psi(a)$ $L(0, a) = \Lambda(a)$ $F(0) = F_0$

Note. — The function $h(F) = F/(F_h + F)$ refers to the *Daphnia* functional response. The expressions for the individual growth, death, reproduction, and feeding rates are already incorporated.

Here, $\Psi(a)$ and $\Lambda(a)$ are age-dependent distributions and F_0 is a scalar quantity. Since the reformulated, age-dependent model is used only for the computation and analysis of equilibria, these initial conditions are of lesser importance but are given for completeness.

This reformulation of a size-structured model into an age-structured model, involving a density function for the number of individuals and a function describing the unique relation between individual age and size, was first introduced by Murphy (1983). In her honor it has also been called the “Murphy trick” (Metz and Diekmann 1986); it makes the model more amenable to further analysis, such as the computation of equilibria and analysis of their stability. The entire set of equations derived in this section by applying the Murphy trick is summarized in Table 4.2. Once again, the long-term dynamics of the models summarized in Tables 4.1 and 4.2 are identical after the influence of the initial population has become negligibly small.

If an equilibrium of the *Daphnia* model exists, all dynamic variables should approach a constant value over time, including the environmental food density. The equilibrium food density is indicated by \tilde{F} . A constant food density leads to an equilibrium length-age relation, denoted by $\tilde{L}(a, \tilde{F})$, which satisfies the PDE (4.32) and the accompanying boundary condition (4.30):

$$\frac{\partial \tilde{L}}{\partial a} = \gamma (\ell_m h(\tilde{F}) - \tilde{L}), \quad \tilde{L}(0, \tilde{F}) = \ell_b. \quad (4.33)$$

This equation can be solved explicitly for the equilibrium length-age relation:

$$\tilde{L}(a, \tilde{F}) = \ell_m h(\tilde{F}) - (\ell_m h(\tilde{F}) - \ell_b) e^{-\gamma a}. \quad (4.34)$$

The equilibrium age at which individuals reach the juvenile length ℓ_j , and hence mature, is indicated by the function $\tilde{A}_j(\tilde{F})$, which must fulfill its definition (4.26):

$$\tilde{L}(\tilde{A}_j(\tilde{F}), \tilde{F}) = \ell_m h(\tilde{F}) - (\ell_m h(\tilde{F}) - \ell_b) e^{-\gamma \tilde{A}_j(\tilde{F})} = \ell_j,$$

which allows an explicit solution:

$$\tilde{A}_j(\tilde{F}) = \frac{1}{\gamma} \ln \left(\frac{\ell_m h(\tilde{F}) - \ell_b}{\ell_m h(\tilde{F}) - \ell_j} \right). \quad (4.35)$$

Because of the occurrence of $h(\tilde{F})$ in this relation, \tilde{F} is used as an explicit-function argument of \tilde{A}_j .

The density function $m(t, a)$, representing the age distribution of the *Daphnia* population, is the only dynamic quantity remaining. When the system approaches an equilibrium, this function also becomes time- (but not age-) independent. The constant age distribution of the *Daphnia* population in equilibrium is denoted by $\tilde{m}(a)$. Because $\tilde{m}(a)$ has to fulfill the PDE (4.24), it can be obtained from

$$\frac{\partial \tilde{m}}{\partial a} = -\mu \tilde{m}, \quad (4.36)$$

which implies that

$$\tilde{m}(a) = \tilde{m}(0) e^{-\mu a}. \quad (4.37)$$

The equilibrium age distribution of the *Daphnia* is an exponentially decreasing function of age with a decay parameter equal to μ . (The assumption that the death rate, μ , is independent of length and food is drastic, but it makes the equilibrium calculations and the analysis of its stability much simpler; see section 4.7.)

The equilibrium length-age relation (4.34), age distribution (4.37), and duration of juvenile period in equilibrium (4.35) can be substituted for $L(t, a)$, $m(t, a)$, and $A_j(t)$, respectively, in the boundary condition (4.24):

$$\begin{aligned} \tilde{m}(0) &= \int_{\tilde{A}_j(\tilde{F})}^{\infty} r_m h(\tilde{F}) (\tilde{L}(a, \tilde{F}))^2 \tilde{m}(a) da \\ &= \int_{\tilde{A}_j(\tilde{F})}^{\infty} r_m h(\tilde{F}) (\tilde{L}(a, \tilde{F}))^2 \tilde{m}(0) e^{-\mu a} da. \end{aligned}$$

Both sides of this equation can be divided by $\tilde{m}(0)$ to yield the first condition for the equilibrium of the *Daphnia* model:

$$\int_{\tilde{A}_j(\tilde{F})}^{\infty} r_m h(\tilde{F}) (\tilde{L}(a, \tilde{F}))^2 e^{-\mu a} da = 1. \quad (4.38)$$

This equilibrium condition is derived using only the equations for the dynamics of the *Daphnia* population; the ODE (4.29) describing the food dynamics has not been used at all.

Apart from the growth, reproduction, and mortality parameters, the food density \tilde{F} is the only unknown quantity in equation (4.38), which thus determines its equilibrium value. On the left-hand side of (4.38), the term $\exp(-\mu a)$ can be recognized as the survival function of an individual *Daphnia* (the probability that it survives to age a). The quantity $r_m h(\tilde{F}) (\tilde{L}(a, \tilde{F}))^2$ is the reproduction rate at age a (see also Table 3.1). The product of the survival function and the reproduction rate at age a is integrated over the interval $[\tilde{A}_j(\tilde{F}), \infty)$, which represents the part of the lifespan during which an individual *Daphnia* is adult and reproduces. Thus, the left-hand side of the equilibrium condition (4.38) equals the expected number of offspring an individual *Daphnia* produces during its entire life when living at a constant food density \tilde{F} . At equilibrium, an individual should just replace itself; hence, the expected number of offspring equals one.

The interpretation of the equilibrium condition (4.38) indicates an important aspect of the *Daphnia*-algal system: in purely exploitative systems, in which individuals compete only for a common resource, the equilibrium resource density is fully set by the life-history characteristics of the consumer, in such a way that, on the average, every individual consumer just replaces itself. Population statistics of the consumer play no role in determining the equilibrium resource level. Only the equations for the *Daphnia* dynamics are necessary to obtain a condition for the equilibrium food density, \tilde{F} . This food density in turn completely determines the composition of the consumer population: the length-age relation (4.34) is fixed by the food density, and the age distribution (4.37) is fixed up to a multiplicative factor $\tilde{m}(0)$. The latter is also true when the death rate differs among individuals, since it can depend only on individual length and the food density, not on statistics of the *Daphnia* population. Equation (4.29) describing the food dynamics determines only the absolute size of the *Daphnia* population in equilibrium; the length-structure is fixed by the food density imposed by the *Daphnia* themselves.

The expected number of offspring of a *Daphnia* individual, in an environment where the food density is equal to its carrying capacity K , can be calculated by substituting $\tilde{F} = K$ in the left-hand side of equation (4.38):

$$\int_{\tilde{A}_j(K)}^{\infty} r_m h(K) (\tilde{L}(a, K))^2 e^{-\mu a} da. \quad (4.39)$$

If this expected number of offspring is larger than one, a *Daphnia* population can at least grow and establish itself in a “virgin” food environment. In addition, this guarantees the existence of at least one solution for $\tilde{F} \in [0, K]$ in equation (4.38), since its left-hand side equals zero when $\tilde{F} = 0$ ($h(0) = 0$). Because the functional response $h(F)$ is a monotonically increasing function, the equilibrium length-age relation (4.34) is an increasing function of \tilde{F} as well. From equation (4.35) one can deduce that the age at maturation decreases monotonically with the equilibrium food density, \tilde{F} . These monotonicity arguments imply that the left-hand side of the equilibrium condition (4.38) increases with \tilde{F} and that the equilibrium food density is unique.

The ODE (4.29), describing the food dynamics, governs the absolute size of the equilibrium *Daphnia* population. Both sides of this ODE equal zero at equilibrium. Substitution of the equilibrium length-age relation (4.34) and equilibrium age distribution (4.37) for $L(t, a)$ and

$m(t, a)$, respectively, in the right-hand side of the equation yields

$$\alpha \tilde{F} \left(1 - \frac{\tilde{F}}{K} \right) - \int_0^{\infty} \nu h(\tilde{F}) (\tilde{L}(a, \tilde{F}))^2 \tilde{m}(0) e^{-\mu a} da = 0. \quad (4.40)$$

Because \tilde{F} is determined by equation (4.38), the only unknown remaining is $\tilde{m}(0)$, the value of the equilibrium age distribution of the *Daphnia* population at age zero. The boundary condition (4.27) equates this value to the population birthrate of *Daphnia*. Let \tilde{B} refer to the population birthrate of *Daphnia* at equilibrium. Substituting $\tilde{m}(0) = \tilde{B}$ in the equation above results in the second equilibrium condition for the *Daphnia* model:

$$\tilde{B} = \frac{\alpha \tilde{F} \left(1 - \frac{\tilde{F}}{K} \right)}{\int_0^{\infty} \nu h(\tilde{F}) (\tilde{L}(a, \tilde{F}))^2 e^{-\mu a} da}. \quad (4.41)$$

The equilibrium population birthrate is an explicit function of the equilibrium food density, which is determined by equation (4.38). Given \tilde{B} , the rest of the age distribution is calculated from equation (4.37).

The pair of scalar values (\tilde{F}, \tilde{B}) determined by the conditions (4.38) and (4.41) constitutes the equilibrium state of the *Daphnia* model. The entire composition of the population can be calculated from these two values using the relations derived above. The integrals in (4.38) and (4.41) can be solved explicitly, given the particular form of the equilibrium length-age relation (4.34) and the simple, exponential survival function $\exp(-\mu a)$ of the *Daphnia* model. However, the relation resulting from solving the integral in (4.38) is a nonlinear, implicit equality from which the value of \tilde{F} can only be determined numerically. It is generally the case that the equilibrium equations can be solved only with numerical techniques, even for relatively simple models like the one considered here. Many numerical root-finding routines are available in popular computer software packages. Solving for the equilibrium also requires biologically realistic values for the parameters, which is sometimes the hardest problem of all.

When both the *i*-state and the *E*-state are one-dimensional, that is, consist of a single variable, the equations for the structured population completely determine the value of the *E*-state at equilibrium. This is true whether the *E*-state variable constitutes a feedback loop, as in the *Daphnia* model considered here, or a direct density-dependent feedback function. Because the individual behavior depends only on the *i*-state and *E*-state (see section 4.1), this constant *E*-state fixes the relative composition of the structured population in equilibrium, that is, the age or size distribution of the population. If the *E*-state variable constitutes a feedback loop, the ODE describing its dynamics determines the absolute size of the structured population in equilibrium. In case of a feedback function, this absolute size is set by the equilibrium value of the *E*-state itself. For example, if the total population size directly influences individual behavior, its value at equilibrium is determined by the equations (PDE and boundary condition) describing the dynamics of the structured population. But since the total population size equals the integral of the density function, its equilibrium value immediately fixes the multiplication constant in the equilibrium density function of the population.

Even if the *E*-state is a vector of variables, the equilibrium of the structured-population model is fully specified in terms of a set of scalar values for all environmental state variables and

a scalar value for the total population birthrate. Given these values, the definitions of the different state concepts (section 4.1) ensure that the entire composition of the structured population can be calculated. That the E -state together with the total population birthrate completely determines the equilibrium of the structured population is intimately linked to the single i -state with which individuals can be born. Generalizations of this last point are difficult and are discussed briefly in section 4.9.

4.6 Numerical Exploration of Dynamics

The dynamics of a structured population model can be studied by integration of the governing set of equations (PDE, boundary condition, and accompanying ODEs) over time, starting from a specified initial state. Many methods have been developed for the numerical solution of such ordinary and partial differential equations. Ready-made recipes have been presented by, for example, Press et al. (1988). The combination of a PDE with a boundary condition that involves an integral of the solution $n(t, \ell)$ itself (eq. 4.9) is, however, rather unusual. The *Escalator Boxcar Train*, which has been extensively discussed in the previous chapters, has therefore been developed specifically for physiologically structured population models. As explained before, its central idea is inspired by the biological origin of the equations, making it powerful and flexible enough to be applied to any kind of structured-population model (de Roos 1988). In previous chapters the EBT-method was derived starting from an age-structured Leslie-matrix model on the basis of heuristic arguments. As a complementary approach, I derive the EBT method here from a mathematical perspective, that is, by considering the density function $n(t, \ell)$ as the object of study.

I begin by subdividing the range $[\ell_b, \ell_m)$ into small intervals, each spanning a certain range of individual lengths, such that individuals within a single interval can be classified as roughly similar. Assume, therefore, that a set of points ℓ_i have been chosen so that the entire range $[\ell_b, \ell_m)$ is covered by the intervals

$$\Omega_i = [\ell_i, \ell_{i+1}), \quad i = 1, \dots, Z.$$

The assumption implies that $\ell_1 = \ell_b$ and $\ell_{Z+1} = \ell_m$. The selection of the intervals Ω_i is not described here; it will become clear that the method itself generates the subdivision of $[\ell_b, \ell_m)$ automatically. The total number of individuals with a length in the interval Ω_i is given by

$$N_i(t) = \int_{\ell_i}^{\ell_{i+1}} n(t, \ell) d\ell \quad (4.42)$$

(cf. section 4.2); and the average length of these individuals is

$$L_i(t) = \frac{\int_{\ell_i}^{\ell_{i+1}} \ell n(t, \ell) d\ell}{N_i(t)}. \quad (4.43)$$

The cohort with index i is assumed to be fully characterized by its total number of individuals, $N_i(t)$, and their average length, $L_i(t)$. Biologically, the population then is a collection of cohorts. Mathematically, the density function $n(t, \ell)$ is approximated by a set of delta functions (measures) of size $N_i(t)$ at length $\ell = L_i(t)$.

Integrals of the type that occur in the boundary condition (4.9) and the ODE (4.7) can be written as a sum of integrals over the intervals Ω_i :

$$\int_{\ell_b}^{\ell_m} \phi(\ell) n(t, \ell) d\ell = \sum_{i=1}^Z \int_{\ell_i}^{\ell_{i+1}} \phi(\ell) n(t, \ell) d\ell.$$

In this expression the function $\phi(\ell)$ is used to denote a general weighting function for $n(t, \ell)$. Using a Taylor expansion of the function $\phi(\ell)$ around the value $\ell = L_i(t)$, the integral over the interval Ω_i can be approximated by

$$\begin{aligned} \int_{\ell_i}^{\ell_{i+1}} \phi(\ell) n(t, \ell) d\ell &= \int_{\ell_i}^{\ell_{i+1}} \phi(L_i) n(t, \ell) d\ell + \int_{\ell_i}^{\ell_{i+1}} \phi'(L_i) (\ell - L_i) n(t, \ell) d\ell \\ &+ \frac{1}{2} \int_{\ell_i}^{\ell_{i+1}} \phi''(L_i) (\ell - L_i)^2 n(t, \ell) d\ell + \dots \end{aligned}$$

The definition (4.43) of $L_i(t)$ implies that the term involving $\phi'(L_i)$ vanishes in this expression. The integral over the entire range $[\ell_b, \ell_m)$ can therefore be approximated up to second-order precision by the following sum:

$$\int_{\ell_b}^{\ell_m} \phi(\ell) n(t, \ell) d\ell = \sum_{i=1}^Z \phi(L_i(t)) N_i(t). \quad (4.44)$$

Hence, all population statistics of interest (those occurring in the boundary condition of eq. 4.9, the food-dynamics ODE of eq. 4.7, and the total population size or biomass) can be computed as a weighted sum over the cohort statistics.

For the dynamics of the quantities $N_i(t)$ and $L_i(t)$, the EBT method assumes that, barring death, cohorts of individuals stay together indefinitely. Individuals never switch to other cohorts. This implies that the boundary values ℓ_i change over time following the ODE (3.3) describing the individual growth in length:

$$\frac{d\ell_i}{dt} = g(\ell_i, F). \quad (4.45)$$

As long as all boundary values ℓ_i develop according to this ODE, individuals never cross the boundary and enter another cohort. The intervals Ω_i are moving through the length range $[\ell_b, \ell_m)$ and expanding (or shrinking), if the growth rate increases (or decreases) with ℓ .

The dynamics of $N_i(t)$ are described by the following ODE

$$\begin{aligned} \frac{dN_i}{dt} &= \frac{d}{dt} \int_{\ell_i}^{\ell_{i+1}} n(t, \ell) d\ell \\ &= \int_{\ell_i}^{\ell_{i+1}} \frac{\partial n(t, \ell)}{\partial t} d\ell + n(t, \ell_{i+1}) \frac{d\ell_{i+1}}{dt} - n(t, \ell_i) \frac{d\ell_i}{dt} \end{aligned}$$

$$\begin{aligned}
&= \int_{\ell_i}^{\ell_{i+1}} \frac{\partial n(t, \ell)}{\partial t} d\ell + n(t, \ell_{i+1})g(\ell_{i+1}, F) - n(t, \ell_i)g(\ell_i, F) \\
&= \int_{\ell_i}^{\ell_{i+1}} \frac{\partial n(t, \ell)}{\partial t} d\ell + \int_{\ell_i}^{\ell_{i+1}} \frac{\partial g(\ell, F) n(t, \ell)}{\partial \ell} d\ell \\
&= - \int_{\ell_i}^{\ell_{i+1}} d(\ell, F) n(t, \ell) d\ell.
\end{aligned}$$

The first step in this derivation uses Leibnitz' rule for the derivative of an integral when the integration bounds are not constant, and the last step exploits the PDE (4.8) to replace the time and length derivatives of $n(t, \ell)$. A more complicated derivation, proceeding along the same lines, yields the ODE for the dynamics of $L_i(t)$:

$$\begin{aligned}
\frac{dL_i}{dt} &= \frac{d}{dt} \frac{\int_{\ell_i}^{\ell_{i+1}} \ell n(t, \ell) d\ell}{N_i(t)} \\
&= \frac{\int_{\ell_i}^{\ell_{i+1}} \ell \frac{\partial n(t, \ell)}{\partial t} d\ell + \ell_{i+1} n(t, \ell_{i+1}) \frac{d\ell_{i+1}}{dt} - \ell_i n(t, \ell_i) \frac{d\ell_i}{dt}}{N_i(t)} - \frac{\int_{\ell_i}^{\ell_{i+1}} \ell n(t, \ell) d\ell \frac{dN_i}{dt}}{(N_i(t))^2} \\
&= \frac{\int_{\ell_i}^{\ell_{i+1}} \ell \frac{\partial n(t, \ell)}{\partial t} d\ell + \ell_{i+1} n(t, \ell_{i+1})g(\ell_{i+1}, F) - \ell_i n(t, \ell_i)g(\ell_i, F)}{N_i(t)} - \frac{L_i(t) \frac{dN_i}{dt}}{N_i(t)} \\
&= \frac{\int_{\ell_i}^{\ell_{i+1}} \ell \frac{\partial n(t, \ell)}{\partial t} d\ell + \int_{\ell_i}^{\ell_{i+1}} \frac{\partial \ell n(t, \ell) g(\ell, F)}{\partial \ell} d\ell}{N_i(t)} - \frac{L_i(t) \frac{dN_i}{dt}}{N_i(t)} \\
&= \frac{\int_{\ell_i}^{\ell_{i+1}} g(\ell, F) n(t, \ell) d\ell}{N_i(t)} - \frac{\int_{\ell_i}^{\ell_{i+1}} (\ell - L_i(t)) d(\ell, F) n(t, \ell) d\ell}{N_i(t)}.
\end{aligned}$$

The ODEs for $N_i(t)$ and $L_i(t)$ do not form a solvable system, because they involve weighted integrals over the density function $n(t, \ell)$. To obtain a closed, solvable system, the functions

$d(\ell, F)$ and $g(\ell, F)$ are approximated, as in the derivation of equation (4.44), by their Taylor expansion around $\ell = L_i(t)$. Higher-order terms involving squares and higher powers of the difference $\ell - L_i(t)$ are neglected. This leads to the following set of ODEs describing the approximate dynamics of $N_i(t)$ and $L_i(t)$:

$$\begin{cases} \frac{dN_i}{dt} = -d(L_i, F) N_i & (4.46a) \\ \frac{dL_i}{dt} = g(L_i, F) & i = 0, \dots, Z \end{cases} \quad (4.46b)$$

(*cf.* equation (3.6)). These equations show that the dynamics of the total number and average length of a cohort of individuals with lengths distributed over a small interval Ω_i can be approximated by the dynamics of a similar group of individuals, but now all having a length exactly equal to this average value. Of course, the approximation is better, the smaller the difference $\ell - L_i(t)$ and hence the interval Ω_i .

The ODEs (4.46) describe the dynamics of cohorts that are already present in the population, but they do not account for reproduction. The cohorts that are already present are called internal cohorts. Since the value of the lowest interval bound, $\ell_1(t)$, changes over time following the ODE (4.45), all newborn individuals have a length within a widening interval $[\ell_b, \ell_1(t)]$. This cohort is the boundary cohort. The boundary cohort is characterized by the total number of individuals it contains:

$$N_0(t) = \int_{\ell_b}^{\ell_1} n(t, \ell) d\ell. \quad (4.47)$$

Since the number of individuals within the interval is initially zero, their average length is initially not defined. In other words, equation (4.43) cannot be used to calculate the average length of the boundary cohort because the denominator might equal zero. A slightly different quantity is therefore employed to capture information on how the distribution of individuals within the interval $[\ell_b, \ell_1(t)]$ changes over time:

$$B_0(t) = \int_{\ell_b}^{\ell_1} (\ell - \ell_b) n(t, \ell) d\ell. \quad (4.48)$$

The choice of the weighting factor $(\ell - \ell_b)$ in this integral makes the resulting equations slightly simpler, since newborn individuals have $\ell = \ell_b$ and hence do not contribute to this statistic.

Formal differentiation of $N_0(t)$ with respect to time yields (after some manipulation) the following ODE:

$$\frac{dN_0}{dt} = - \int_{\ell_b}^{\ell_1} d(\ell, F) n(t, \ell) d\ell + g(\ell_b, F) n(t, \ell_b).$$

The derivation of this ODE runs completely analogous to the derivation presented above for the ODE describing the dynamics of $N_i(t)$. The special feature of the ODE for $N_0(t)$ is the appearance of the term $g(\ell_b, F) n(t, \ell_b)$ in the right-hand side. This term occurs because the lower bound of the interval $[\ell_b, \ell_1(t)]$ does not change with time as do all other bounds $\ell_i(t)$

(see eq. 4.45). This term is, however, the left-hand side of the boundary condition (4.9). It can therefore be replaced by the total population birthrate:

$$\frac{dN_0}{dt} = - \int_{\ell_b}^{\ell_1} d(\ell, F) n(t, \ell) d\ell + \int_{\ell_b}^{\ell_m} b(\ell, F) n(t, \ell) d\ell.$$

Because the average length of the newborn individuals in the boundary cohort is not defined as a characterizing statistic, the function $d(\ell, F)$ is instead expanded around the value $\ell = \ell_b$. Terms involving squared or higher powers of the difference $\ell - \ell_b$ are again neglected. Moreover, the integral representing the population reproduction rate is replaced by the appropriate summation (see eq. 4.44), involving the cohort measures $N_i(t)$ and $L_i(t)$. These substitutions lead to the following ODE approximating the dynamics of $N_0(t)$:

$$\frac{dN_0}{dt} = -d(\ell_b, F) N_0 - \frac{\partial}{\partial \ell} d(\ell_b, F) B_0 + \sum_{i=1}^Z b(L_i, F) N_i.$$

Although the summation in the last term is essentially over all cohorts, the contribution of those cohorts for which $L_i(t) \leq \ell_j$ is of course zero (see Table 3.1).

Formal differentiation of $B_0(t)$ with respect to time yields the ODE

$$\frac{dB_0}{dt} = \int_{\ell_b}^{\ell_1} g(\ell, F) n(t, \ell) d\ell - \int_{\ell_b}^{\ell_1} (\ell - \ell_b) d(\ell, F) n(t, \ell) d\ell.$$

Again, the functions $d(\ell, F)$ and $g(\ell, F)$ are replaced by their Taylor expansion around the boundary value $\ell = \ell_b$, neglecting squared or higher powers of $\ell - \ell_b$. This yields an ODE for the approximate dynamics of $B_0(t)$:

$$\frac{dB_0}{dt} = g(\ell_b, F) N_0 + \frac{\partial}{\partial \ell} g(\ell_b, F) B_0 - d(\ell_b, F) B_0.$$

The dynamics of the boundary cohort can therefore be approximated by the following set of ODEs:

$$\left\{ \begin{array}{l} \frac{dN_0}{dt} = -d(\ell_b, F) N_0 - \frac{\partial}{\partial \ell} d(\ell_b, F) B_0 + \sum_{i=1}^Z b(L_i, F) N_i \end{array} \right. \quad (4.49a)$$

$$\left\{ \begin{array}{l} \frac{dB_0}{dt} = g(\ell_b, F) N_0 + \frac{\partial}{\partial \ell} g(\ell_b, F) B_0 - d(\ell_b, F) B_0 \end{array} \right. \quad (4.49b)$$

(*cf.* equation (3.16))

The dynamics described by the ODEs (4.46) and (4.49) for the Z internal cohorts and the single boundary cohort approximate the dynamics described by the PDE (4.8) and its boundary condition (4.9). They can be studied using any integration method to numerically solve systems of ordinary differential equations (e.g., the Runge-Kutta method). The boundary cohort cannot, however, be continued indefinitely, because the interval $[\ell_b, \ell_1(t))$ would become large and the approximation would break down. Therefore, a renumbering operation at regular time intervals Δt is a crucial part of the EBT method, as explained in detail in previous chapters. This renumbering operation transforms the current boundary cohort into an

internal cohort and initializes a new, empty boundary cohort. At the same time, all internal cohorts are renumbered to make room for the new internal cohort and to keep them in order. Internal cohorts that have become negligible can be discarded.

If a renumbering procedure has just taken place when $t = t^*$, the population consists of internal cohorts characterized by the quantities $N_i(t^*)$ and $L_i(t^*)$ ($i = 1, \dots, Z$) and an empty boundary cohort for which $N_0(t^*) = 0$ and $B_0(t^*) = 0$. Between t^* and $t^* + \Delta t$, the ODEs (4.46) and (4.49) are solved numerically. At $t^* + \Delta t$, the following transformations are applied ($t^* + \Delta t^-$ is used in these equations to denote the value of the variables prior to the transformation):

$$\begin{cases} N_i(t^* + \Delta t) = N_{i-1}(t^* + \Delta t^-) \\ L_i(t^* + \Delta t) = L_{i-1}(t^* + \Delta t^-) & i = 2, 3, \dots, N_1(t^* + \Delta t) = N_0(t^* + \Delta t^-) \\ L_1(t^* + \Delta t) = \ell_b + \frac{B_0(t^* + \Delta t^-)}{N_0(t^* + \Delta t^-)} \\ N_0(t^* + \Delta t) = 0 \\ B_0(t^* + \Delta t) = 0 \end{cases} \quad (4.50a)$$

$$(4.50b)$$

$$(4.50c)$$

$$(4.50d)$$

$$(4.50e)$$

(*cf.* equations (3.18) and (3.19)). The first two equations simply renumber the internal cohorts. The equation for $L_1(t^* + \Delta t)$ converts the quantity B_0 into the average length of the individuals in the new cohort with index one. The last two equations reset the values for the boundary cohort so that it is empty. Transforming the boundary cohort and starting a new, empty one increase the number of ODEs to solve by two; but the number of ODEs can decrease because some of the internal cohorts are discarded. The number of quantities with which the structured population is characterized, and hence the number of ODEs to solve, can therefore change in the renumbering procedure.

In the long run, the time interval Δt between renumbering operations determines the intervals $\Omega_i(t)$. The choice of Δt determines the initial width of the interval $[\ell_b, \ell_1(t))$ at the moment that the boundary cohort is transformed into the internal cohort with index one. Because the bounds subsequently change according to the ODE (4.45), this initial width also determines the length interval spanned by the cohort at a later time. The initial population has only to be subdivided, one way or another, into a collection of cohorts; after that, the choice of Δt completely determines this subdivision. Smaller values of Δt imply that the dynamics of the PDE (4.8) are better approximated at the expense of a larger number of cohorts to keep track of and more ODEs to solve simultaneously.

The ODE (4.7) describing the dynamics of the food density must be solved simultaneously with the ODEs (4.46) and (4.49). Following equation (4.44), the integral occurring in (4.7)

is replaced by the appropriate sum of the cohort statistics:

$$\left\{ \begin{array}{l} \frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K}\right) - \sum_{i=1}^Z I(L_i, F) N_i \quad \text{if } N_0(t) = 0 \\ \frac{dF}{dt} = \alpha F \left(1 - \frac{F}{K}\right) - \sum_{i=1}^Z I(L_i, F) N_i - I\left(\ell_b + \frac{B_0}{N_0}, F\right) N_0 \quad \text{if } N_0(t) > 0 \end{array} \right. \quad (4.51)$$

The second equation shows that the boundary cohort must be taken into account if $N_0(t) > 0$ (note that this complication does not occur in the approximation of the total population birthrate in eq.4.49, since the newborn individuals cannot yet reproduce). As for the internal cohorts, the function $I(\ell, F)$ must be evaluated at the average length of the individuals in the boundary cohort, which equals $\ell = \ell_b + B_0(t)/N_0(t)$.

This completes the formulation of the EBT method. For the *Daphnia* model, the resulting set of equations has already been presented Table 3.2, but for a semi-chemostat regrowth process of the algae. These equations are a consistent approximation of the original PDE and boundary condition (de Roos and Metz 1991). When the numerical solutions obtained with the EBT method can be compared with analytical results, the method has proved accurate (see, e.g., de Roos et al. 1990).

4.7 Stability Analysis of the *Daphnia* Equilibrium

In addition to numerical explorations of dynamics, studies of unstructured-population models usually involve some kind of bifurcation analysis of attractors (e.g., equilibria, limit cycles). Often this analysis is restricted to finding the boundary that separates parameter values for which the equilibrium is attractive from those for which it is repelling. Ideally, when studying a structured-population model, one would also like a complete inventory of the changes in dynamics that occur with changes in model parameters. Equilibria can disappear or become biologically irrelevant in certain parameter regions, a stable equilibrium can become unstable, or a limit cycle can arise that ultimately leads to persistent fluctuations in densities. Structured-population models can be expected to exhibit the same richness of dynamics found in unstructured models. In contrast to the theory for models formulated in terms of ODEs, the techniques and general theory for a complete bifurcation analysis of structured-population models is not readily available.

The *Daphnia* model, however, is simple enough to make a linear stability analysis feasible. The outcome indicates whether, and for which parameter values, the *Daphnia* population and the food density return to their equilibrium states (computed in section 4.5) following a small perturbation away from those states. The issue to resolve is whether small perturbations of the equilibrium grow or decrease with time and, hence, whether the equilibrium is locally stable. In addition to numerical simulations, this analysis is most frequently applied in studies of structured-population models (see, e.g., de Roos et al. 1990; van den Bosch and de Roos 1996).

To explain the procedure for a structured-population model, it is useful to recapitulate the local stability analysis of the basic model (4.6). The first step is to linearize the equations, assuming that the system is close to the equilibrium. The resulting, linear equations can be solved explicitly by searching for exponential solutions. In all derivations below, I use exponential trial solutions right from the start to keep the presentation as short as possible.

Any internal equilibrium of the basic model (4.6) is a pair of nonzero values (\tilde{F}, \tilde{C}) , for which the right-hand sides of the ODEs vanish. The stability of such an equilibrium is determined by assuming that the prey and predator populations are close, but not equal, to their equilibrium densities. The small deviations between actual and equilibrium densities are assumed to grow or decrease exponentially over time:

$$\begin{aligned} F(t) &= \tilde{F} + \Delta_F e^{\lambda t}, \\ C(t) &= \tilde{C} + \Delta_C e^{\lambda t}, \end{aligned} \tag{4.52}$$

where Δ_F and Δ_C are the initial perturbations of the prey and predators. These expressions for $F(t)$ and $C(t)$ are substituted into the ODEs (4.6) to obtain a set of equations describing the fate of the deviations $\Delta_F e^{\lambda t}$ and $\Delta_C e^{\lambda t}$:

$$\begin{aligned} \frac{d(\Delta_F e^{\lambda t})}{dt} &= \alpha \left(\tilde{F} + \Delta_F e^{\lambda t} \right) \left(1 - \left(\tilde{F} + \Delta_F e^{\lambda t} / K \right) \right) - I_{max} \frac{\tilde{F} + \Delta_F e^{\lambda t}}{F_h + \tilde{F} + \Delta_F e^{\lambda t}} \left(\tilde{C} + \Delta_C e^{\lambda t} \right), \\ \frac{d(\Delta_C e^{\lambda t})}{dt} &= \epsilon I_{max} \frac{\tilde{F} + \Delta_F e^{\lambda t}}{F_h + \tilde{F} + \Delta_F e^{\lambda t}} \left(\tilde{C} + \Delta_C e^{\lambda t} \right) - \mu \left(\tilde{C} + \Delta_C e^{\lambda t} \right). \end{aligned}$$

The left-hand sides of these equations involve only the time derivatives of $\Delta_F e^{\lambda t}$ and $\Delta_C e^{\lambda t}$ because $d\tilde{F}/dt = d\tilde{C}/dt = 0$. Since the deviations $\Delta_F e^{\lambda t}$ and $\Delta_C e^{\lambda t}$ are assumed to be small, the terms on the right-hand sides can be replaced by their first-order Taylor expansion around the equilibrium state (\tilde{F}, \tilde{C}) . All second- and higher-order terms involving $\Delta_F e^{\lambda t}$ and $\Delta_C e^{\lambda t}$ are hence neglected. Together with an evaluation of the time derivatives, this yields the following set of algebraic equations:

$$\begin{aligned} \lambda \Delta_F e^{\lambda t} &\approx \alpha \left(1 - 2\tilde{F}/K \right) \Delta_F e^{\lambda t} - I_{max} \frac{F_h}{(F_h + \tilde{F})^2} \tilde{C} \Delta_F e^{\lambda t} - I_{max} \frac{\tilde{F}}{F_h + \tilde{F}} \Delta_C e^{\lambda t} \\ \lambda \Delta_C e^{\lambda t} &\approx \epsilon I_{max} \frac{F_h}{(F_h + \tilde{F})^2} \tilde{C} \Delta_F e^{\lambda t} + \epsilon I_{max} \frac{\tilde{F}}{F_h + \tilde{F}} \Delta_C e^{\lambda t} - \mu \Delta_C e^{\lambda t} \end{aligned}$$

The last two terms in the second equation cancel, because $d\tilde{C}/dt = 0$ at equilibrium. Dividing both sides by $e^{\lambda t}$, the equations can also be expressed in matrix form as

$$\mathbf{J}(\lambda) \begin{pmatrix} \Delta_F \\ \Delta_C \end{pmatrix} = \mathbf{0}, \tag{4.53}$$

in which

$$\mathbf{J}(\lambda) = \begin{pmatrix} \alpha \left(1 - 2\tilde{F}/K \right) - I_{max} \frac{F_h}{(F_h + \tilde{F})^2} \tilde{C} - \lambda & -I_{max} \frac{\tilde{F}}{F_h + \tilde{F}} \\ \epsilon I_{max} \frac{F_h}{(F_h + \tilde{F})^2} \tilde{C} & -\lambda \end{pmatrix}.$$

If both Δ_F and Δ_C are not zero, equation (4.53) holds only if

$$\det \mathbf{J}(\lambda) = 0. \tag{4.54}$$

Given initial perturbations Δ_F and Δ_C and the linear equations determining their time evolution, the change over time of these perturbations is, in general, described by a sum of

contributions that are all of the form $\exp(\lambda t)$. The value of λ in each contribution corresponds to a root of the equation (4.54), and the number of these roots determines the number of different contributions. It follows that as long as the real part of all the roots λ is negative, the initial perturbations decline and the internal equilibrium is locally stable. The roots λ of equation (4.54) are the eigenvalues of the basic model in the neighborhood of its equilibrium state (\tilde{F}, \tilde{C}) . Equation (4.54) is called the characteristic equation of the model.

The characteristic equation (4.54) is a second-order polynomial in λ with two, possibly complex roots λ_1 and λ_2 . It can be shown that if a complex number $\sigma + i\omega$ is a root of equation (4.54), its complex conjugate, $\sigma - i\omega$, is also a root. The most interesting case occurs when the equilibrium loses its stability because such a pair of complex conjugates crosses the imaginary axis from the left to the right half of the complex plane (implying that σ turns from negative to positive). Such a loss of stability may lead to a limit cycle, in which the prey and predator exhibit persistent periodic oscillations, although this is not universally true. At the particular parameter values at which this loss of stability occurs, the characteristic equation (4.54) has a pair of purely imaginary roots, $\lambda = \pm i\omega$ ($\sigma = 0$). If the *Daphnia* mortality rate μ is the parameter of interest, the value of μ where equilibrium stability changes can be found by solving for μ and ω the equation

$$\det \mathbf{J}(i\omega) = 0. \quad (4.55)$$

Equation (4.55) depends indirectly on μ because the equilibrium state (\tilde{F}, \tilde{C}) is a function of μ . This condition is actually two equations, one for the real part and one for the imaginary part of $\det \mathbf{J}(i\omega)$. For the basic model (4.6), it can be shown that equation (4.55) permits simultaneous solutions of μ and ω only if the trace of the matrix $\mathbf{J}(\lambda)$, when $\lambda = 0$, is positive for the particular value of μ . The matrix $\mathbf{J}(0)$ is the Jacobian matrix of the basic model (4.6), evaluated at the equilibrium state (\tilde{F}, \tilde{C}) . A negative trace of the Jacobian matrix is one of the two Routh-Hurwitz criteria for an equilibrium of a set of two ODEs to be stable. The other Routh-Hurwitz criterion — for stability of such an equilibrium, the determinant of the Jacobian matrix should be positive — is always fulfilled for this model.

The linear stability analysis of the structured *Daphnia* model follows the same procedure. The states of the population and the food density are assumed to be close, but not identical, to the equilibrium state computed in section 4.5. The deviations from the equilibrium are assumed to grow or decrease exponentially. A set of linear equations is derived for the time evolution of these deviations, in which only first-order terms are included. This allows the derivation of a characteristic equation analogous to (4.54) for the eigenvalues of the model in the neighborhood of the equilibrium state. The equation is solved for the value of a single parameter at which there exists a pair of purely imaginary eigenvalues, $\lambda = \pm i\omega$. This parameter value corresponds to a point on the stability boundary of the model. At this boundary the internal equilibrium loses its stability, and limit cycles can arise.

Although the conditions (4.38) and (4.41) show that the equilibrium state of the *Daphnia* model is entirely determined by the food density \tilde{F} and the population birthrate \tilde{B} , it is convenient to start the stability analysis of the equilibrium from a characterization in terms of the equilibrium food density, \tilde{F} , the equilibrium age distribution, $\tilde{m}(a)$, the equilibrium length-age relation, $\tilde{L}(a, \tilde{F})$, and the duration of the juvenile period in equilibrium, $\tilde{A}_j(\tilde{F})$. To simplify the notation, neglect the explicit food dependence in these last two quantities and simply write $\tilde{L}(a)$ and \tilde{A}_j instead of $\tilde{L}(a, \tilde{F})$ and $\tilde{A}_j(\tilde{F})$, respectively.

When the population and the food density are close to their equilibrium states and the deviations from the equilibrium are assumed to grow or decrease exponentially, the actual

state of the system is

$$\begin{aligned}
 F(t) &= \tilde{F} + \Delta_F e^{\lambda t}, \\
 m(t, a) &= \tilde{m}(a) + \Delta_m(a) e^{\lambda t}, & \Delta_m(0) &= \Delta_B, \\
 L(t, a) &= \tilde{L}(a) + \Delta_L(a) e^{\lambda t}, & \Delta_L(0) &= 0, \\
 A_j(t) &= \tilde{A}_j + \Delta_A e^{\lambda t}.
 \end{aligned} \tag{4.56}$$

For the basic model, it was sufficient to assume that prey and predator densities were close to their equilibrium values. Equation (4.56) incorporates deviations between the current and equilibrium values of both the population age distribution and the length-age relation at every age a . Then, Δ_B , which can be interpreted as the initial perturbation in the total population birthrate, is used as shorthand for the deviation in the population age distribution at age 0, $\Delta_m(0)$. The relation $\Delta_L(0) = 0$ follows from the assumptions that all individuals are born with the identical length at birth, ℓ_b , and that hence $L(t, 0) = \ell_b$ under all circumstances.

Appendix B shows in detail how substitution of the relations (4.56) into the model equations of Table 4.2 yields a set of equations for the time evolution of the deviations Δ_F , $\Delta_m(a)$, $\Delta_L(a)$, and Δ_A . Using Taylor expansion of the functions describing the individual behavior (Table 3.1) and neglecting all higher-order terms, this eventually leads to a system of equations for the eigenvalues λ in the neighborhood of the equilibrium state:

$$\mathbf{U}(\lambda) \begin{pmatrix} \Delta_B \\ \Delta_F \end{pmatrix} = \begin{pmatrix} U_{11}(\lambda) & U_{12}(\lambda) \\ U_{21}(\lambda) & U_{22}(\lambda) \end{pmatrix} \begin{pmatrix} \Delta_B \\ \Delta_F \end{pmatrix} = \mathbf{0}. \tag{4.57}$$

Like equation (4.53), this equation is linear in the perturbation of the total population birthrate Δ_B and the food density Δ_F . As in the unstructured model, the equation implies that the eigenvalues of the model are the roots of the following characteristic equation:

$$\det \mathbf{U}(\lambda) = 0. \tag{4.58}$$

In contrast to the matrix \mathbf{J} , however, the elements of \mathbf{U} are nonlinear functions of λ . In

Appendix B the following expressions are derived for the elements of \mathbf{U} :

$$\begin{aligned}
U_{11}(\lambda) &= \int_{\tilde{A}_j}^{\infty} r_m h(\tilde{F}) (\tilde{L}(a))^2 e^{-(\mu+\lambda)a} da - 1, \\
U_{12}(\lambda) &= \int_{\tilde{A}_j}^{\infty} r_m h(\tilde{F}) (\tilde{L}(a))^2 \tilde{B} e^{-\mu a} da \frac{h'(\tilde{F})}{h(\tilde{F})} \\
&\quad + \left\{ \frac{r_m \ell_m (h(\tilde{F}))^2 \ell_j^2}{\ell_m h(\tilde{F}) - \ell_j} \tilde{B} e^{-\mu \tilde{A}_j} \frac{1 - e^{-(\lambda+\gamma)\tilde{A}_j}}{\lambda + \gamma} \right. \\
&\quad \left. + 2\gamma r_m \ell_m (h(\tilde{F}))^2 \int_{\tilde{A}_j}^{\infty} \tilde{L}(a) \tilde{B} e^{-\mu a} \frac{1 - e^{-(\lambda+\gamma)a}}{\lambda + \gamma} da \right\} \frac{h'(\tilde{F})}{h(\tilde{F})}, \\
U_{21}(\lambda) &= - \int_0^{\infty} \nu h(\tilde{F}) (\tilde{L}(a))^2 e^{-(\mu+\lambda)a} da, \\
U_{22}(\lambda) &= R'(\tilde{F}) - \lambda - \int_0^{\infty} \nu h(\tilde{F}) (\tilde{L}(a))^2 \tilde{B} e^{-\mu a} da \frac{h'(\tilde{F})}{h(\tilde{F})} \\
&\quad + \left\{ 2\gamma \nu \ell_m (h(\tilde{F}))^2 \int_0^{\infty} \tilde{L}(a) \tilde{B} e^{-\mu a} \frac{1 - e^{-(\lambda+\gamma)a}}{\lambda + \gamma} da \right\} \frac{h'(\tilde{F})}{h(\tilde{F})}.
\end{aligned}$$

In these expressions, $R'(\tilde{F})$ and $h'(\tilde{F})$ denote the derivative with respect to food density of the algal growth rate $R(F)$ and the *Daphnia* functional response $h(F)$ evaluated at the equilibrium \tilde{F} . In general, the characteristic equation (4.58) has infinitely many roots that all correspond to eigenvalues of the model in the neighborhood of the equilibrium state. Because the equilibrium is unstable as soon as a single eigenvalue has a positive real part, the (pair of) eigenvalue(s) with the largest real part is crucial for stability. This is often referred to as the dominant (pair of) eigenvalue(s). In practice, this dominant (pair of) eigenvalue(s) is the only one that can be readily localized in numerical explorations. Hence, other roots can for practical purposes be ignored.

If the natural mortality rate of *Daphnia* μ , is our parameter of interest, the particular value of μ at which the equilibrium loses its stability and limit cycles may arise can be found by solving for μ and ω the equation

$$\det \mathbf{U}(i\omega) = 0. \quad (4.59)$$

Again, this is actually a set of two equations, one for the real part and one for the complex part of $\det \mathbf{U}$. Such equations can generally be solved with appropriate, numerical root-finding procedures (e.g., the Newton-Raphson method; Press et al. 1988). Moreover, because the elements of the matrix \mathbf{U} are functions of the food density \tilde{F} and population birthrate \tilde{B} , the equilibrium conditions (4.38) and (4.41) must be solved simultaneously with (4.59). The entire set of equations may be so complicated that finding a solution is problematic.

The value for μ satisfying equation (4.59) is a point on the stability boundary of the model, as in the unstructured model. Such a stability boundary can be constructed in a plane of two parameters by varying one of the two in a stepwise manner over a range of values, while at every step solving for the value of the other parameter at which the equilibrium loses its stability. This procedure is illustrated in the next section. The nature of the dynamics once the equilibrium is unstable can be verified only by using numerical explorations close to the stability boundary.

4.8 Some Results and Implications for *Daphnia*

This section includes a discussion of some conclusions from numerical investigations of the equilibrium, stability, and dynamics of the *Daphnia* model with logistically growing algae. Many of these results are part of an extensive investigation of a slightly more complicated model (de Roos et al. 1990), which assumes that individual *Daphnia* have a maximum life span and cannot shrink during times of food shortage. The life span assumption results in negligible, quantitative differences in the model predictions. The assumption that individuals cannot shrink implies that energy destined to be spent on reproduction must be rechanneled to cover basic metabolic needs during bouts of starvation, when the allocation rule of the model discussed here would predict individual weight loss. The equilibrium and its stability are completely unaffected by the non-shrinking assumption, because in equilibrium individuals never shrink. The only differences in the model predictions concern the oscillatory dynamics when the equilibrium is unstable. If individuals can shrink, the oscillations are far more pronounced, although the remaining characteristics of the cycles in population structure and density are the same (de Roos et al. 1990).

4.8.1 Existence and Stability of the Internal Equilibrium

Figure 4.6 shows the stability diagram as a function of the background *Daphnia* mortality rate μ and the carrying capacity K of the algae. Three different regions can be distinguished in this diagram: (1) a region with parameter combinations (μ, K) in which the *Daphnia* population becomes extinct; (2) a region with a stable equilibrium, and (3) a region in which the *Daphnia* and algal populations cycle indefinitely. The existence boundary, separating the first and second regions, has been determined by numerically solving for the carrying capacity, K , at which the expected number of offspring produced by a single *Daphnia* individual equals unity (see eq. 4.39). This specific value of K was determined for $\mu = 0.01, 0.02, 0.03, \dots, 0.30$. Comparing expression (4.39) with the equilibrium condition (4.38), from which the equilibrium food density is determined, it can be concluded that this minimum value of K for the existence of an equilibrium exactly equals the food density imposed by the *Daphnia* population in a stable equilibrium state. This equivalence of the minimum resource density for existence and the imposed equilibrium level is a general characteristic of purely exploitative systems.

The boundary between the stable equilibrium and the region of population oscillations has been determined by numerically solving for the value of the carrying capacity that satisfies both the bifurcation condition (4.59) and the equilibrium conditions (4.38) and (4.41). The particular K value was computed for $\mu = 0.01, 0.02, 0.03, \dots, 0.30$. Numerical studies of the dynamics were subsequently conducted to determine the type of dynamics arising when the equilibrium is unstable (de Roos et al. 1990), that is, for parameter combinations above the

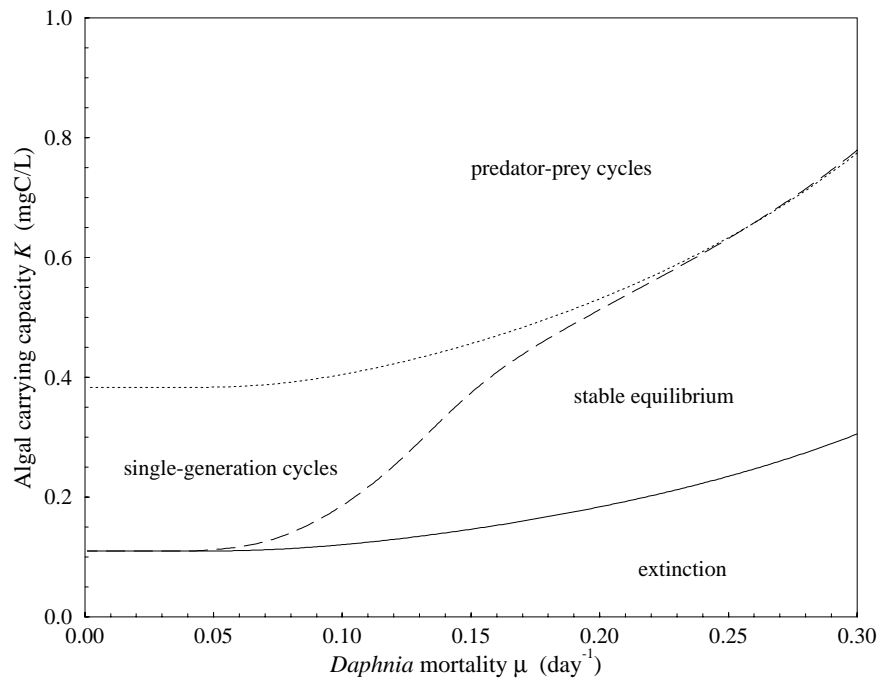


Figure 4.6: Stability diagram of the size-structured model for the dynamics of a *Daphnia pulex* population feeding on *Chlamydomonas reinhardtii* with logistic growth of the latter. The logistic growth rate parameter α equals 0.5, other parameters as in Table 3.1. *Solid line*, existence boundary; *dashed line*, stability boundary; *dotted line*, prey-escape boundary, approximately separating the parameter region with classical predator-prey oscillations from the region with single-generation oscillations (following de Roos et al. 1990).

stability boundary. On the basis of these simulations, the region of population oscillations can be subdivided into two parts. In one, the fluctuations are similar to the oscillations found in the unstructured model (4.6). This type of oscillation is usually referred to as predator-prey, paradox-of-enrichment, or prey-escape cycles (Rosenzweig 1971; de Roos et al. 1990). In the second part, roughly located at low values for both μ and K , the fluctuations are due to size-dependent growth and reproduction, and are referred to as single-generation or time-lag cycles (Gurney and Nisbet 1985).

An approximate boundary between the paradox-of-enrichment cycles and single-generation cycles can be determined by comparing the stability criteria for the structured *Daphnia* model and its unstructured analogue (4.6). This prey-escape boundary, marking the transition to the classical predator-prey cycles, is likely to occur in all models in which the individuals of an exploiter population with a saturating functional response compete with each other only indirectly for a (logistically) growing resource (de Roos et al. 1990). The transition is related to the ability of the resource to escape the control of the consumer population (for an approximate criterion for this “prey-escape boundary”, see de Roos et al. 1990). The loss of control is due to the saturating functional response. In the *Daphnia* model, as K increases, the oscillations gradually change from single-generation to predator-prey cycles without a catastrophic transition. The prey-escape boundary is, therefore, not as sharp as the boundary that separates the stable and unstable regions. Nonetheless, it indicates the

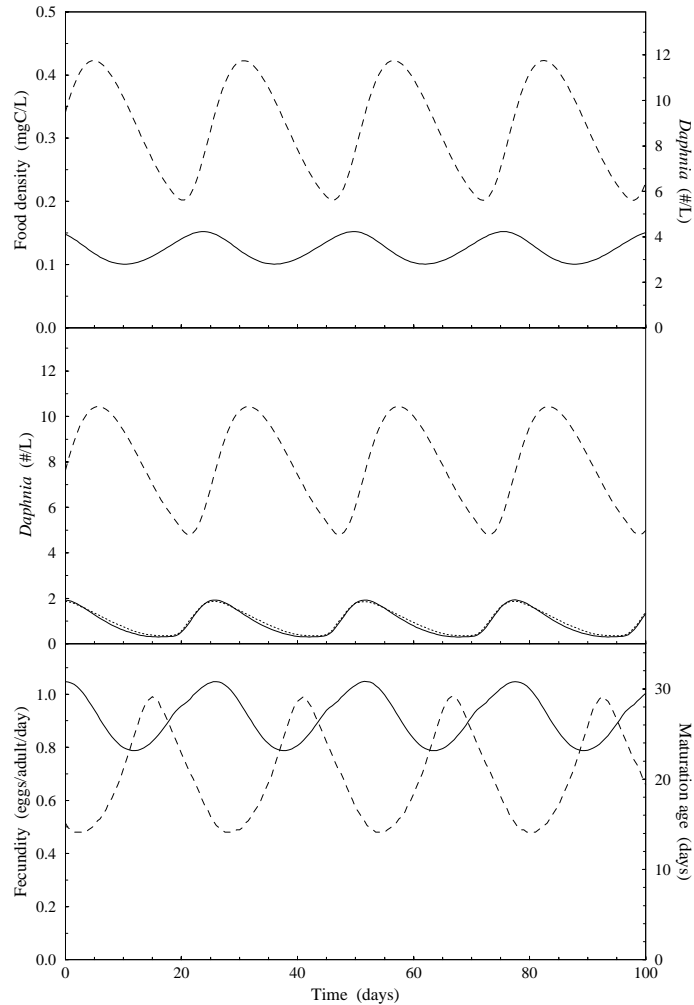


Figure 4.7: Single-generation dynamics in the *Daphnia* model. Parameters: *Daphnia* mortality rate, $\mu = 0.11$; algal carrying capacity, $K = 0.25$; all others as in Figure 4.6. *Top*, algal biomass (*solid*) and total number of *Daphnia* (*dashed*) per liter. *Middle*, number of neonate (*dotted*), juvenile (*dashed*), and adult (*solid*) *Daphnia* per liter. *Bottom*, length of the juvenile period (*dashed*) and adult fecundity (*solid*).

extent of the parameter region for which single-generation and predator-prey cycles can be expected to occur, a prediction that is confirmed by numerical simulations.

Figure 4.6 shows the location of the prey-escape boundary as defined by de Roos et al. (1990) for the *Daphnia* model studied here. With parameter combinations above this line the observed dynamics are roughly similar to classical predator-prey oscillations, below it the observed dynamics correspond to single-generation cycles.

The main feature of Figure 4.6 is the large area of the parameter space in which classical predator-prey cycles are predicted by both the structured and unstructured *Daphnia* models. Eventually, these cycles always occur because the carrying capacity of the algae increases. As shown by McCauley and Murdoch (1990), this prediction by the model is at odds with experimental observations on natural and semi-natural populations of *Daphnia*, where prey-escape cycles are hard to find. The mechanism behind the prey-escape cycles suggests that any model of a purely exploitative consumer feeding on a logistically growing resource with

a saturating functional response would disagree with the results of McCauley and Murdoch (1990, de Roos et al. 1990). The discrepancy between the model prediction of predator-prey cycles and the apparent lack of such cycles in experimental and natural populations was addressed by Murdoch et al. (1998), who discusses various hypotheses that could explain the discrepancy.

4.8.2 Population Oscillations Induced by Size Structure

Figure 4.7 shows a typical example of the single-generation oscillations that are induced by the size structure and size-dependent behavior of the *Daphnia* population. These results are obtained by numerically integrating the ODEs of Table 3.2. Both the *Daphnia* and algal populations fluctuate with a period of roughly 26 days. The maximum *Daphnia* density is approximately twice the minimum, whereas for the algae, the ratio of maximum to minimum density is less (Fig. 4.7, *top panel*). At any time, the *Daphnia* population contains one dominant cohort (*middle panel*). Both these features agree reasonably well with cycles observed in natural and laboratory *Daphnia* populations (Murdoch and McCauley 1985; McCauley and Murdoch 1987). This suggests that the aspects of individual behavior included in the *Daphnia* model play an important role in the dynamics of real-world *Daphnia* populations.

Figure 4.7 also shows results that shed doubt on this suggestion, however. The bottom panel of the figure shows that the single-generation oscillations are primarily due to fluctuations in the length of the juvenile period, which varies by a factor of about two. It appears that the number of adults at any time determines whether a new population birth pulse is generated. In contrast, adult fecundity fluctuates less and never reaches low values. This seems at odds with the experimental observations presented by McCauley and Murdoch (1987). Although these authors concluded that real-world *Daphnia* populations display mainly delay-driven cycles, with retarded juvenile growth and suppressed adult fecundity as important causal mechanisms, it is actually the latter that seems to be the driving force behind the oscillations. Whenever fecundity is determined, it turns out to fluctuate dramatically (McCauley and Murdoch 1987, Figs. 7, 9). Although juvenile development is indeed slower than under high-food conditions, McCauley and Murdoch (1987) showed no evidence that this delay drives the cycles. Moreover, large fluctuations in adult fecundity agree with the observation in natural *Daphnia* populations that the surviving adults of a dominant cohort, at the end of their life, initiate a new dominant cohort (McCauley and Murdoch 1987).

Figure 4.8 shows more clearly why single-generation cycles are generated by the model. This figure displays the size structure of the *Daphnia* population during one entire oscillation of the simulation presented in Figure 4.7. A considerable cohort of individuals is stopped in their development just before reaching maturity. Within a short time (about four days), all mature, leading to a new birth pulse. As adults, they continue to reproduce while mortality decreases their number. The first of their offspring do not develop quickly enough to reach maturity before food conditions deteriorate and development slows. Hence, the front of the new cohort is again stopped shortly before reaching maturity. The individuals that are born later from the same adult cohort can catch up with the front, because smaller individuals are assumed to be more efficient. This leads to a “piling up” of individuals just before the size at maturation, ℓ_j , which starts a new cycle after some time. It is mainly this piling-up mechanism (i.e., the variable delay of the juvenile period) that drives the single-generation cycles, as opposed to the length of the juvenile delay itself (de Roos et al. 1990). As an obvious consequence, it is not the last, surviving adults of a dominant cohort that start a new

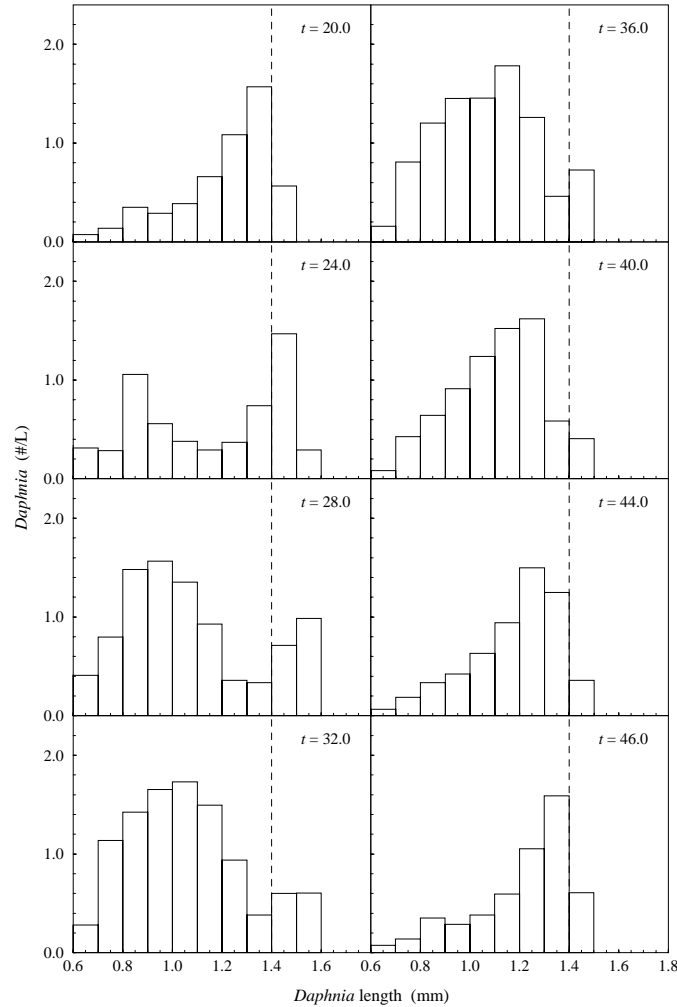


Figure 4.8: Changes in the size distribution of *Daphnia* during one complete cycle of the simulation presented in Figure 4.7. *Dashed line*, length ℓ_j at which individuals mature.

cycle (requiring a substantial fluctuation in adult fecundity) but the bulk of the dominant cohort shortly after they mature.

The predictions of the *Daphnia* model hence seem to agree superficially with observations of natural and laboratory populations of *Daphnia*, but they differ dramatically on closer inspection. As far as experimental data are available, the cycles in real-world *Daphnia* populations seem to be driven primarily by the changing fecundity of the adult *Daphnia*, whereas the model predicts dynamics that are driven primarily by the changing number of adults in the population. These changes in number come about by the large fluctuations in the length of the juvenile period. How the large fluctuations in adult fecundity arise in experimental populations, without inducing large-amplitude predator-prey cycles, is an unresolved question.

4.9 General Perspective

This chapter has dealt with the mathematical formulation of models for physiologically structured populations and the techniques that are most commonly applied to analyze them. These

techniques include equilibrium computations, stability analysis, and numerical simulations. Only relatively simple models could be dealt with in this chapter; the general class of PSP models is much broader and allows for the investigation of more-complicated scenarios. This last section puts the theory presented here in a more general perspective. Possible extensions will be discussed using the model formulation that is obtained after the application of the Murphy trick (section 4.5).

Although the general discussions about the model at the individual and population levels (sections 4.1, 4.3, and 4.4) are phrased in terms of an i -state and E -state of arbitrary dimension, they are illustrated with a model in which only a single variable for the i -state and E -state appeared. Sections 4.1 and 4.3 show in some detail how to extend the E -state to any arbitrary, finite number of variables, but they do not touch on more i -state variables.

As it turns out, increasing the number of i -state variables is only moderately complicated, as long as all newborn individuals have the same state at birth. This can be illustrated by incorporating direct age dependence into the *Daphnia* model (Table 4.2). The functions describing individual growth, reproduction, mortality, and feeding now depend on three quantities: the individual length, the individual age, and the current food density. This dependence can be expressed by writing $g(L(t, a), a, F)$, $b(L(t, a), a, F)$, $d(L(t, a), a, F)$, and $I(L(t, a), a, F)$ to represent the model of the individual behavior. Then, all functions are seen to depend on age both directly and indirectly through the relation between age and length, $L(t, a)$. The direct age dependence of the mortality rate d does not invalidate the PDE (4.23) for the *Daphnia* age distribution $m(t, a)$. A similar argument holds for the individual reproduction, feeding, and growth rates that occur in the equations (4.25), (4.28), and (4.31), respectively. All age-independent rates can hence be straightforwardly replaced by age-dependent functions. The basic set of PDEs, ODEs, and boundary conditions does not change.

Because of the additional age dependence, equilibrium computations and stability analysis are probably more difficult, but not qualitatively different. Only the sets of ODEs that are used to approximate the model for numerical simulations must be extended. Equation (4.46) must be supplemented with an equation for the mean age of the individuals in a cohort. The appropriate equation is identical to the ODE for dL_i/dt , except that the growth rate g is replaced by the unit developmental rate in age. Similarly, the system of ODEs (4.49) has to be extended with an equation that is identical to the ODE for dB_0/dt except for the substitution of g by unity (and consequently all derivatives of g by zero). The equation describes the development of the quantity that characterizes the age distribution of the individuals within the boundary cohort. (For a version of the *Daphnia* model that incorporates such additional age dependence, see de Roos et al. 1992b.)

Extending the i -state with a physiological characteristic other than age is possible, at the expense of adding another PDE. For example, assume that the strict relation between individual length and weight assumed in the *Daphnia* model does not hold, but that the weight of an individual with a specific length can vary. Furthermore, assume that individuals are born with a fixed weight w_b . A weight-age relation $W(t, a)$ can now be introduced to keep track of the weight of the individuals as a function of their age. The dynamics of $W(t, a)$ can be described by a PDE of the form

$$\frac{\partial W(t, a)}{\partial t} + \frac{\partial W(t, a)}{\partial a} = z(L(t, a), W(t, a), F),$$

where $W(t, 0) = w_b$ (cf. eq. 4.31; boundary condition 4.30). In this equation the function $z(L(t, a), W(t, a), F)$ denotes the growth rate in weight, as a function of food density,

individual length, and individual weight. These three variables now influence all individual-level functions. In addition to the function $z(L(t, a), W(t, a), F)$, the model is specified in terms of the functions $g(L(t, a), W(t, a), F)$, $b(L(t, a), W(t, a), F)$, $d(L(t, a), W(t, a), F)$, and $I(L(t, a), W(t, a), F)$, modeling growth in individual length, reproduction, mortality, and feeding, respectively. As with the introduction of age dependence, adding weight as an i -state variable also requires extending the systems of ODEs (4.46) and (4.49) with equations that are analogous to the ODEs for dL_i/dt and dB_0/dt . These equations must describe the change in mean weight of the individuals in an internal cohort and a boundary cohort, respectively, and hence involve the function $z(L(t, a), W(t, a), F)$ instead of $g(L(t, a), W(t, a), F)$. (For an example of the analysis of a PSP model of this sort, see van den Bosch and de Roos 1996.)

The crucial aspect of all these models is that the identical state at birth, together with deterministic growth and developmental rates, ensures an eventual one-to-one relation between the i -state and individual age. The members of the initial population can obviously have i -states that form a cloud of points in the three-dimensional i -state space defined by age, length, and weight. After their death, however, the i -states of all individuals at any time make up a one-dimensional curve through this three-dimensional i -state space, originating in the point that represents the state at birth of an individual. This holds even when the state at birth of the individuals changes over time! Essentially, more complicated PSP models therefore involve either a larger number of possible states at birth or non-deterministic growth and development in the i -state.

If individuals can be born with one of a finite collection of i -states at birth, a PSP model can still be formulated (and possibly analyzed) using the framework discussed here. All individuals are identified with the state with which they are born, and the entire population can be subdivided on that basis into a finite number of subpopulations. The model would be formally analogous to a model with more than a single structured population, although the subpopulations may be coupled by the reproduction process when the state at birth of the offspring is not the same as the parent's state at birth.

Turning from the PDE framework to the "cumulative" formulation (Diekmann et al. 1994; Diekmann and Metz 1995), it may even be possible to allow for an infinite range of i -states at birth, or for non-deterministic growth and development in the i -state, which is one of the hardest restrictions to relax in the current framework. Although the model formulation might be theoretically possible, whether and what kind of analysis is possible for such a model, remains absolutely unclear. I also know of no study that analyzed any specific, more complicated example. This reemphasizes the fact that the field of modeling physiologically structured populations is still developing, with respect both to the general theory and to the detailed studies of examples. Readers interested in more-complicated models and their analysis may find some solace in the book by Metz and Diekmann (1986) on which most of the theory presented here is based, but more likely they will have to wait until the theoretical state of the art has been developed further.

Appendix A

Some Formal Calculations Relating to Individual Death and Reproduction

Consider a cohort of individuals living in a constant environment E_c , and assume that the individual state space Ω consists of the interval $[x_b, x_m)$, in which x_b is the i -state at birth and x_m is the asymptotic i -state that long-living individuals approach (formally, when their age, a , approaches infinity).

Integration of the distribution of the state at death (4.4) from x_b to x_m yields

$$\begin{aligned} \int_{x_b}^{x_m} H(x, E_c) dx &= \int_{x_b}^{x_m} \frac{d(x, E_c)}{g(x, E_c)} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) dx \\ &= -\exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) \Big|_{x=x_b}^{x=x_m} \\ &= S(x_b, E_c) - S(x_m, E_c). \end{aligned}$$

$S(x_b, E_c)$ equals 1 by assumption. The value of $S(x_m, E_c)$ necessarily equals 0 because no individual lives long enough (infinitely long!) to attain the asymptotic i -state x_m . Essentially this poses a condition on the instantaneous mortality rate, $d(x, E_c)$, which should ensure that $S(x_m, E_c) = 0$, that is, that indeed no individual lives forever. From the definition of $H(x, E_c)$ it can be concluded that its expected value equals the average i -state at which an individual dies. Integration by parts of this expectation yields an equation that relates this average i -state at death to the survival function $S(x, E_c)$:

$$\begin{aligned} \int_{x_b}^{x_m} x H(x, E_c) dx &= \int_{x_b}^{x_m} x \frac{d(x, E_c)}{g(x, E_c)} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) dx \\ &= -x \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) \Big|_{x=x_b}^{x=x_m} + \int_{x_b}^{x_m} \exp\left(-\int_{x_b}^x \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) dx \\ &= x_b + \int_{x_b}^{x_m} S(x, E_c) dx. \end{aligned}$$

If the expected lifetime of an individual is of interest, the probability density function of the age at which an individual dies can be derived as follows (cf. the definition and derivation of H):

$$\begin{aligned} -\frac{dS(X(a, E_c), E_c)}{da} &= -\frac{dS(X(a, E_c), E_c)}{dt} \frac{dt}{da} \\ &= d(X(a, E_c), E_c) S(X(a, E_c), E_c) \\ &= d(X(a, E_c), E_c) \exp\left(-\int_{x_b}^{X(a, E_c)} \frac{d(\xi, E_c)}{g(\xi, E_c)} d\xi\right) \\ &= d(X(a, E_c), E_c) \exp\left(-\int_0^a d(X(\zeta, E_c), E_c) d\zeta\right). \end{aligned}$$

The resulting expression is analogous to the distribution of the state at death given in function (4.4). It is a probability density function with an integral equal to 1. Its expected value can again be derived

by integration by parts:

$$\begin{aligned}
& \int_0^{\infty} a d(X(a, E_c), E_c) \exp \left(- \int_0^a d(X(\zeta, E_c), E_c) d\zeta \right) da \\
&= -a \exp \left(- \int_0^a d(X(\zeta, E_c), E_c) d\zeta \right) \Big|_{a=0}^{a=\infty} + \int_0^{\infty} \exp \left(- \int_0^a d(X(\zeta, E_c), E_c) d\zeta \right) da \\
&= \int_0^{\infty} \exp \left(- \int_0^a d(X(\zeta, E_c), E_c) d\zeta \right) da.
\end{aligned}$$

The last integral equals the average age individuals reach, given that the death rate, $d(x, E_c)$, and the (i -state)-age relation, $X(a, E_c)$, are known.

As mentioned in the text, the first reproduction event is, from a probabilistic point of view, comparable with the death of an individual. Therefore, it is relatively straightforward to see that the expected i -state at which an individual gives birth for the first time is given by

$$\begin{aligned}
& \int_{x_b}^{x_m} x \frac{b(x, E_c)}{g(x, E_c)} \exp \left(- \int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \right) dx \\
&= -x \exp \left(- \int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \right) \Big|_{x=x_b}^{x=x_m} + \int_{x_b}^{x_m} \exp \left(- \int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \right) dx \\
&= x_b + \int_{x_b}^{x_m} \exp \left(- \int_{x_b}^x \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \right) dx.
\end{aligned}$$

Like the arguments that led to the condition $S(x_m, E_c) = 0$, this derivation must also assume that individuals reproduce with probability 1 if they live long enough, which is biologically realistic. The exact assumption states that

$$\exp \left(- \int_{x_b}^{x_m} \frac{b(\xi, E_c)}{g(\xi, E_c)} d\xi \right) = 0.$$

The expected age at which an individual reproduces for the first time is given by

$$\begin{aligned}
& \int_0^{\infty} a b(X(a, E_c), E_c) \exp \left(- \int_0^a b(X(\zeta, E_c), E_c) d\zeta \right) da \\
&= -a \exp \left(- \int_0^a b(X(\zeta, E_c), E_c) d\zeta \right) \Big|_{a=0}^{a=\infty} + \int_0^{\infty} \exp \left(- \int_0^a b(X(\zeta, E_c), E_c) d\zeta \right) da \\
&= \int_0^{\infty} \exp \left(- \int_0^a b(X(\zeta, E_c), E_c) d\zeta \right) da.
\end{aligned}$$

The integrand in the first expression is the probability density function for an individual to reproduce for the first time at age a (cf. the derivation for the expected lifetime of an individual above). The expected age is, of course, equivalent to the “time till first reproduction.”

Appendix B

Derivation of the Characteristic Equation of the *Daphnia* Model

To derive the matrix $\mathbf{U}(\lambda)$ in the characteristic equation (4.58), the approximations (4.56) for the population state and food density in the neighborhood of the equilibrium are to be substituted into the model equations of Table 4.2. The equations are then linearized and solved as far as possible to obtain the elements of $\mathbf{U}(\lambda)$. In the following, function symbols subscripted with F or ℓ — for example, $d_F(\ell, F)$ and $d_\ell(\ell, F)$ — refer to the partial derivatives of the function with respect to F and ℓ , respectively.

Substituting $m(t, a) = \tilde{m}(a) + \Delta_m(a) e^{\lambda t}$ into the PDE (4.23) leads to the following derivation:

$$\begin{aligned}
\frac{\partial \Delta_m(a) e^{\lambda t}}{\partial t} + \frac{\partial \tilde{m}(a)}{\partial a} + \frac{\partial \Delta_m(a) e^{\lambda t}}{\partial a} &= -d\left(\tilde{L}(a) + \Delta_L(a) e^{\lambda t}, \tilde{F} + \Delta_F e^{\lambda t}\right) (\tilde{m}(a) + \Delta_m(a) e^{\lambda t}) \\
&\approx -d(\tilde{L}(a), \tilde{F}) \tilde{m}(a) - d_\ell(\tilde{L}(a), \tilde{F}) \Delta_L(a) e^{\lambda t} \tilde{m}(a) \\
&\quad - d_F(\tilde{L}(a), \tilde{F}) \Delta_F e^{\lambda t} \tilde{m}(a) - d(\tilde{L}(a), \tilde{F}) \Delta_m(a) e^{\lambda t} \\
\Rightarrow \frac{\partial \Delta_m(a)}{\partial a} &= -(\lambda + \mu) \Delta_m(a) \\
\Rightarrow \Delta_m(a) &= \Delta_B e^{-(\lambda + \mu)a}.
\end{aligned} \tag{B1}$$

In the first step, the function $d(\ell, F)$ is replaced with its first-order Taylor expansion around the equilibrium values \tilde{F} and $\tilde{L}(a)$. All higher-order terms involving the deviates Δ_F , $\Delta_L(a)$, and $\Delta_m(a)$ are neglected. These manipulations constitute the linearization step, since a linear equation for $\Delta_m(a)$ results. In the second step, the partial derivatives of the function d are replaced with the appropriate expressions from Table 3.1. In addition, the equilibrium condition (4.36) for $\tilde{m}(a)$ is used to simplify the equation. Both sides of the equation can be divided by $e^{\lambda t}$, which removes the time dependence. These manipulations lead to a simple differential equation for $\Delta_m(a)$ that can be solved explicitly, as shown in the last equation. The symbol Δ_B is used as shorthand for $\Delta_m(0)$. Obviously, $\Delta_m(a)$ is an explicit function of Δ_B only, involving no other small deviates.

Analogous to the derivation above, the approximation $L(t, a) = \tilde{L}(a) + \Delta_L(a) e^{\lambda t}$ is substituted into the PDE (4.31):

$$\begin{aligned}
\frac{\partial \Delta_L(a) e^{\lambda t}}{\partial t} + \frac{\partial \tilde{L}(a)}{\partial a} + \frac{\partial \Delta_L(a) e^{\lambda t}}{\partial a} &= g\left(\tilde{L}(a) + \Delta_L(a) e^{\lambda t}, \tilde{F} + \Delta_F e^{\lambda t}\right) \\
&\approx g(\tilde{L}(a), \tilde{F}) + g_\ell(\tilde{L}(a), \tilde{F}) \Delta_L(a) e^{\lambda t} + g_F(\tilde{L}(a), \tilde{F}) \Delta_F e^{\lambda t} \\
\Rightarrow \frac{\partial \Delta_L(a)}{\partial a} &= -(\lambda + \gamma) \Delta_L(a) + \gamma \ell_m h'(\tilde{F}) \Delta_F \\
\Rightarrow \Delta_L(a) &= \frac{\gamma \ell_m h'(\tilde{F})}{\lambda + \gamma} \left(1 - e^{-(\lambda + \gamma)a}\right) \Delta_F.
\end{aligned} \tag{B2}$$

In the first step of this derivation, the equation is linearized by using the Taylor expansion of the function $g(\ell, F)$, neglecting higher-order terms. In the second step, the partial derivatives of g are replaced with their appropriate expression (see Table 3.1), and the equilibrium condition (4.33) is

used for simplification. A linear, time-independent differential equation for $\Delta_L(a)$ results, which can be solved to obtain an explicit expression for $\Delta_L(a)$ as a function of Δ_F only. The function $h'(\tilde{F})$ in this (and all following equations) is the derivative of the *Daphnia* functional response $h(F)$, evaluated at the equilibrium food density, \tilde{F} .

Substituting the relations $F(t) = \tilde{F} + \Delta_F e^{\lambda t}$, $L(t, a) = \tilde{L}(a) + \Delta_L(a) e^{\lambda t}$, and $m(t, a) = \tilde{m}(a) + \Delta_m(a) e^{\lambda t}$ into the ODE (4.29) for the food density gives

$$\begin{aligned}
\frac{d\Delta_F e^{\lambda t}}{dt} &= R(\tilde{F} + \Delta_F e^{\lambda t}) \\
&\quad - \int_0^\infty I(\tilde{L}(a) + \Delta_L(a) e^{\lambda t}, \tilde{F} + \Delta_F e^{\lambda t}) (\tilde{m}(a) + \Delta_m(a) e^{\lambda t}) da \\
&\approx R(\tilde{F}) + R'(\tilde{F}) \Delta_F e^{\lambda t} \\
&\quad - \int_0^\infty I(\tilde{L}(a), \tilde{F}) \tilde{m}(a) da - \int_0^\infty I_\ell(\tilde{L}(a), \tilde{F}) \Delta_L(a) e^{\lambda t} \tilde{m}(a) da \\
&\quad - \int_0^\infty I_F(\tilde{L}(a), \tilde{F}) \Delta_F e^{\lambda t} \tilde{m}(a) da - \int_0^\infty I(\tilde{L}(a), \tilde{F}) \Delta_m(a) e^{\lambda t} da \\
\Rightarrow (R'(\tilde{F}) - \lambda) \Delta_F &- \int_0^\infty 2\nu h(\tilde{F}) \tilde{L}(a) \Delta_L(a) \tilde{m}(a) da \\
&- \int_0^\infty \nu h'(\tilde{F}) (\tilde{L}(a))^2 \Delta_F \tilde{m}(a) da - \int_0^\infty \nu h(\tilde{F}) (\tilde{L}(a))^2 \Delta_m(a) da = 0.
\end{aligned} \tag{B3}$$

The function $R'(\tilde{F})$ is the derivative of the algal growth function $R(F)$, evaluated at the equilibrium food density, \tilde{F} . This derivation is analogous to the previous two. The linearization, which involves the partial derivatives of the *Daphnia* ingestion rate $I(\ell, F)$, and the simplification step, which uses the equilibrium condition (4.40), now leads to an algebraic equality. The first three terms of this equality are all linear expressions of Δ_F , since $\Delta_L(a)$ has been derived above as an explicit function of Δ_F . The coefficients of Δ_F in these three terms together constitute the element $U_{22}(\lambda)$ in the matrix $\mathbf{U}(\lambda)$. The last term in the equality is a linear function of Δ_B by virtue of the relation between $\Delta_m(a)$ and Δ_B derived above. This term constitutes the element $U_{21}(\lambda)$ in the matrix $\mathbf{U}(\lambda)$.

The remaining two elements of the matrix $\mathbf{U}(\lambda)$ are obtained from the linearization of the boundary condition (4.27). This boundary condition contains the current duration of the juvenile period $A_j(t)$ as a lower bound in the integral. If the state of the system is perturbed away from the equilibrium state, the juvenile delay changes as well. At every time, however, $A_j(t)$ fulfills the condition $L(t, A_j(t)) = \ell_j$. By substituting the approximations $L(t, a) = \tilde{L}(a) + \Delta_L(a) e^{\lambda t}$ and $A_j(t) = \tilde{A}_j + \Delta_A e^{\lambda t}$ into this

equality, a relation between Δ_A and $\Delta_L(\tilde{A}_j)$ can be derived:

$$\begin{aligned}
\ell_j &= L(t, \tilde{A}_j + \Delta_A e^{\lambda t}) \\
&= \tilde{L}(\tilde{A}_j + \Delta_A e^{\lambda t}) + \Delta_L(\tilde{A}_j + \Delta_A e^{\lambda t}) e^{\lambda t} \\
&\approx \tilde{L}(\tilde{A}_j) + \frac{\partial \tilde{L}(\tilde{A}_j)}{\partial a} \Delta_A e^{\lambda t} + \Delta_L(\tilde{A}_j) e^{\lambda t} \\
\Rightarrow \Delta_A &= \frac{-\Delta_L(\tilde{A}_j)}{g(\ell_j, \tilde{F})}.
\end{aligned} \tag{B4}$$

The linearization step involves the Taylor expansion of the function $\tilde{L}(a)$ around the equilibrium value $a = \tilde{A}_j$. Recognizing that $\ell_j = \tilde{L}(\tilde{A}_j)$ and $\partial \tilde{L}(\tilde{A}_j)/\partial a = g(\ell_j, \tilde{F})$ following equation (4.33), Δ_A can be expressed in terms of $\Delta_L(\tilde{A}_j)$ and is hence also linearly related to Δ_F .

Linearization of the boundary condition (4.27) involves substitution of all approximate values given by (4.56):

$$\begin{aligned}
&\tilde{m}(0) + \Delta_B e^{\lambda t} \\
&= \int_{\tilde{A}_j + \Delta_A e^{\lambda t}}^{\infty} b(\tilde{L}(a) + \Delta_L(a) e^{\lambda t}, \tilde{F} + \Delta_F e^{\lambda t}) (\tilde{m}(a) + \Delta_m(a) e^{\lambda t}) da \\
&\approx \int_{\tilde{A}_j}^{\infty} b(\tilde{L}(a), \tilde{F}) \tilde{m}(a) da + \int_{\tilde{A}_j}^{\infty} b_\ell(\tilde{L}(a), \tilde{F}) \tilde{m}(a) \Delta_L(a) e^{\lambda t} da + \int_{\tilde{A}_j}^{\infty} b_F(\tilde{L}(a), \tilde{F}) \tilde{m}(a) \Delta_F e^{\lambda t} da \\
&\quad + \int_{\tilde{A}_j}^{\infty} b(\tilde{L}(a), \tilde{F}) \Delta_m(a) e^{\lambda t} da - b(\ell_j, \tilde{F}) \tilde{m}(\tilde{A}_j) \Delta_A e^{\lambda t} \\
\Rightarrow \Delta_B &= b(\ell_j, \tilde{F}) \tilde{m}(\tilde{A}_j) \frac{\Delta_L(\tilde{A}_j)}{g(\ell_j, \tilde{F})} - \int_{\tilde{A}_j}^{\infty} 2r_m h(\tilde{F}) \tilde{L}(a) \tilde{m}(a) \Delta_L(a) da \\
&\quad - \int_{\tilde{A}_j}^{\infty} r_m h'(\tilde{F}) (\tilde{L}(a))^2 \tilde{m}(a) \Delta_F da - \int_{\tilde{A}_j}^{\infty} r_m h(\tilde{F}) (\tilde{L}(a))^2 \Delta_m(a) da = 0.
\end{aligned} \tag{B5}$$

The linearization step in the derivation above is complicated by the fact that $\tilde{A}_j + \Delta_A e^{\lambda t}$ occurs in the lower bound of the integral. The perturbation of this integral bound can be approximated to first order by the term $-b(\ell_j, \tilde{F}) \tilde{m}(\tilde{A}_j) \Delta_A e^{\lambda t}$. The remaining steps to linearize and simplify (using the equilibrium condition for $\tilde{m}(0)$) are identical to the derivation (B3). The resulting equality contains the expressions for the elements $U_{11}(\lambda)$ and $U_{12}(\lambda)$ in $\mathbf{U}(\lambda)$: the first and last term of the equality are both linear functions of Δ_B on the basis that $\Delta_m(a)$ is related to Δ_B . The coefficients of these terms constitute the element $U_{11}(\lambda)$. Because $\Delta_L(a)$ is a function of Δ_F , all remaining terms in the equality are proportional to Δ_F . The three coefficients together form the basis of the element $U_{12}(\lambda)$. This completes the derivation of the characteristic equation (4.58).

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