

CHAPTER 5

The impact of population structure on population and community dynamics

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5.1 Introduction

In a book on theoretical ecology a chapter on structured population models will inevitably, but perhaps unjustly, stand out, as so much of current theory in population ecology is based on unstructured rather than on structured models. Every student in ecology will, at some point, have studied the seminal models for competition and predation introduced by Lotka (1925) and Volterra (1926). Far fewer students, however, will have encountered structured population models, such as the age-structured model introduced by Sharpe and Lotka (1911) or the age-structured matrix model proposed by Leslie (1945). Text books in general ecology (Begon et al. 2005) discuss unstructured population models in quite some detail, while even text books in theoretical ecology (Yodzis 1989) may devote only a few subsections to structured models.

The term structured population models itself is used rather loosely for a wide variety of different models. For the purpose of this chapter, the term hence needs a more precise definition, as it is simply impossible to discuss all types of structured population models. Unstructured population models effectively treat all individuals in the population as identical, such that it is only necessary to keep track of the total population abundance, in terms of the number of individuals, their density, or their total biomass. But the birth and death rates that

ultimately determine the changes in the number of individuals in a population are never the same for all individuals. An individual always starts out life as a juvenile, incapable of reproduction or replication, whatever species the individual belongs to. Birth and death rates thus vary with the age of the individual, its developmental stage, spatial location or its genotype, among many other factors. In a very general sense, any population dynamic model that takes differences between individuals into account can be referred to as structured. However, in this chapter, I will restrict myself to discussing models that account for differences between individuals resulting from the developmental process that individuals go through during their life history. “Ontogenetically structured population models” would be an appropriate name for this class of models, referring to the ontogeny or individual life history that the models are aimed to capture. Instead, in the literature ontogenetically structured population models are indicated as age-structured, stage-structured, size-structured or physiologically structured population models. In what follows, I will use the general term structured population model and in particular the abbreviation SPM to indicate models that account for differences between individuals arising from their ontogeny and thereby explicitly exclude models that account for the spatial, genetic, behavioral or any other type of structure of a population.

5.2 State concepts in SPMs

All SPMs have at their core a model representation of the individual life history. This life history representation may be more or less detailed and more data-driven or more model-based, but structured population models in effect are based on data or assumptions about the individual life history. They translate this individual-level representation to the population level by bookkeeping operations. Population dynamics, therefore, truly emerges from the individual life history processes. In contrast, unstructured population models are based on mathematical functions that describe the population dynamic processes themselves as a function of population-level quantities such as densities or biomasses. Unstructured models are thus based on population-level assumptions. Structured and unstructured population models can therefore also be classified as individual-based versus population-based approaches of modelling ecological dynamics.

The first step when modelling any system, be it a community, a population, or an individual, is to identify the quantities that characterize the state of the system. These state variables have to be chosen such that they capture all relevant information about the history of the system to determine its dynamics and hence its future. In unstructured population models the choice of the state of the system only requires a choice between representing populations by their numerical densities or their biomass. The state of the system is then determined by the (numerical or biomass) abundance of all the populations that the unstructured model accounts for. The dynamics of the system, that is the growth of the populations and their interactions, subsequently has to be specified (modelled) dependent on the state variables (abundances of all populations). In SPMs the choice of the state of the system is more complex, because the basis of such models is formed by a representation or model of the individual life history, whereas the aim of the SPM is to describe the changes in populations. To capture these different levels of biological organization Metz and Diekmann (1986) introduced the distinction between the state of an individual, also referred to as *individual* or *i-state*, the state of the population, referred to as

population or *p-state*, and the state of the environment that the individuals live in (*environmental* or *E-state*).¹

The concepts of *i-*, *p-*, and *E-state* are fundamental and powerful (Metz and Diekmann 1986; Metz and de Roos 1992; Caswell and John 1992; Caswell 2001). To formulate a SPM, we have to start asking the question which characteristics, quantities or traits of the individual organism play the most important role in its life history and have the largest impact on its birth and death rate. Is it the age of the individual? Then the *i-state* would be made up by individual age and we would end up with an age-structured model. More often, however, the body size of an individual is the most important life history trait of an individual, such that body size is the appropriate choice for the *i-state* and a size-structured population model would result. Given a choice of the individual state, the choice of the population or *p-state* is rather straightforward as the distribution, be it a discrete distribution or a continuous density function, over all possible *i-states*.

More important than the choice of the *p-state*, is arguably the choice of the environmental or *E-state*. This choice forces us to consider which factors have an influence on the individual's reproduction, mortality, and development, apart from its own traits. Are there no factors other than the individual state variables (age or size) influencing the life history processes (reproduction, mortality and development)? In that case, the individual is apparently living in a constant environment, its life history is independent of any external factors and in particular independent of population density. Abiotic factors like temperature that vary over time can influence the individual life history and hence be part of the environmental state. But temperature is generally not changed by the individuals in a population themselves and their life history will hence unfold in a time-varying environment, but again, independent of any population impact. However, if individuals would compete with other individuals for example for nesting sites, the

¹ For clarity I use environmental or *E-state*, even though from a system theory point of view the use of "state" is not appropriate (Metz and de Roos 1992).

reproductive success of an individual will depend on how many competitors there are around. In this case, the environmental or E -state would have to include as an E -state variable the number of individuals in the population that are competing for the nest sites. As yet another example, if the life history processes depend on food availability in the environment and the individuals of the population together are capable of depleting this food availability through their foraging, food density would be an appropriate choice as E -state variable.

These last two examples of possible E -states both give rise to a feedback of the population on the individual life history, in other words, they involve density dependence. However, the first example, competition for nest sites, is a direct form of density dependence, whereas, in the second example, competition for food, the density dependence operates indirectly through a quantity (food density) other than population abundance itself, but whose dynamics is influenced by the population. The premise of distinguishing the i -, p -, and E -state is that density dependence or population feedback always operates through the E -state. Vice versa, if the environment (E -state) is unaffected by the population the life history of an individual unfolds in a way that is independent of other individuals in the environment.

The extensive discussion of the individual and environmental state emphasizes the need to carefully think about the biology of the system we want to study when formulating a SPM. What individual traits influence the individual life history? What are the most important elements of the environment that individuals are facing during their life? Given their basis in individual life history and combined with the concept of environmental or E -state, SPMs allow for a faithful representation of the ecology of the system in a population dynamic model. Many examples of structured population models in the literature, however, account for density dependence by simply making the individual birth, death or development rate a function of the (numerical) abundance of the population. This is obviously a simplifying assumption, which may not correctly reflect how density dependence operates mechanistically in the modelled ecological system (except when density

dependence operates through some form of direct competition for example for nest sites or through interference competition) and which may thus lead to misleading results. In short, one form of density dependence is not necessarily the same as the other, often the devil is in the details.

5.3 Types of structured population models

A SPM can either describe the changes in the state of a population continuously through time or can describe the state of the structured population at discrete points in time only. Similarly, the individual state variable that is adopted in the model can be continuous or discrete. For example, with age as a continuous i -state variable every individual in the population will be characterized by its age, which may adopt any positive value. Alternatively, all individuals can be grouped into a limited number of distinct age classes. Often, four different types of SPMs are recognized based on the choice between discrete and continuous representation of the time and the i -state variable in the model (Caswell et al. 1997 see Table 5.1).

For each of these four types of SPMs, a different mathematical framework is used to formulate the model: matrices, integral projection equations, ordinary or delay differential equations, and partial differential equations.

Matrix models (Caswell 2001) classify individuals in discrete stages on the basis of their i -state variable (age or size). If k such stages are distinguished, the population state is a vector $(n_1(t), \dots, n_k(t))^T$ representing the number of individuals in each of the stages. The model then describes the dynamics of the structured population using a population projection matrix \mathbf{A} by:

$$\begin{aligned} \begin{pmatrix} n_1(t+1) \\ \vdots \\ n_k(t+1) \end{pmatrix} &= \mathbf{A} \begin{pmatrix} n_1(t) \\ \vdots \\ n_k(t) \end{pmatrix} \\ &= \begin{pmatrix} a_{11} & \dots & a_{1k} \\ \vdots & \ddots & \vdots \\ a_{k1} & \dots & a_{kk} \end{pmatrix} \begin{pmatrix} n_1(t) \\ \vdots \\ n_k(t) \end{pmatrix} \end{aligned} \quad (5.1)$$

Table 5.1 Types of structured population models (adapted from Caswell et al. (1997) with references to monographs about them).

		Time dynamics	
		Discrete	Continuous
Individual state representation	Discrete	Matrix models (Caswell 2001)	Stage-structured models (Murdoch et al. 2003)
	Continuous	Integral projection models (Ellner et al. 2016)	Physiologically structured population models (de Roos and Persson 2013)

Each of the elements a_{ij} of the population projection matrix \mathbf{A} describes the number of individuals that will be in stage i at time $t + 1$ per individual in stage j at time t .

In integral projection models (IPMs; Rees et al. 2014; Ellner et al. 2016) individuals are characterized by a continuous i -state variable z , often referring to the individual body size. The population state in IPMs is a density function $n(t, z)$ representing the density of individuals with i -state z at time t . The integral of $n(t, z)$ over the interval from a to b :

$$\int_a^b n(t, z) dz$$

equals the number of individuals with an i -state in the interval $[a, b]$. IPMs describe the dynamics of the population with an integral equation, which in its simplest form can be written as:

$$n(t + 1, z) = \int_{\Omega} (F(z, z') + S(z') G(z, z')) n(t, z') dz' \tag{5.2}$$

In this equation the function $G(z, z')$ represents the probability that an individual with i -state z' at time t will have i -state z at time $t + 1$, $S(z')$ is the probability that an individual with i -state z' at time t survives till time $t + 1$ and the function $F(z, z')$ models the density of offspring with an i -state z produced between time t and $t + 1$ by an individual with i -state z' . The interpretation of the function $F(z, z')$, and similarly the function $G(z, z')$, is analogous to the interpretation of $n(t, z)$ in that the integral

$$\int_a^b F(z, z') dz$$

equals the number of offspring with an i -state in the interval $[a, b]$ produced between time t and $t + 1$ by an individual with i -state z' at time t .

Continuous-time stage-structured models can be described by a system of ordinary or delay-differential equations (Nisbet and Gurney 1983; Murdoch et al. 2003). For example, consider a model with only 2 stages, juveniles and adults with densities $J(t)$ and $A(t)$ at time t , respectively. The population dynamics can then be described by a system of two ordinary differential equations (ODEs; see for examples de Roos et al. 2007; Schreiber and Rudolf 2008):

$$\begin{aligned} \frac{dJ}{dt} &= \beta A - \gamma J - \mu J \\ \frac{dA}{dt} &= \gamma J - \mu A \end{aligned} \tag{5.3}$$

In these ODEs the parameter β represents the per capita reproduction rate (fecundity) of an adult individual, γ the per capita maturation rate of a juvenile individual and μ the per capita mortality rate of juveniles and adults. This formulation in terms of ODEs, however, assumes that every juvenile individual, irrespective how long time they have spent in the juvenile stage, has a probability per unit time to mature equal to γ . The probability distribution for the juvenile stage duration τ then follows an exponential distribution with a mean equal to $1/\gamma$.

Alternatively, the dynamics of the population can be described by a system of delay-differential

equations (DDEs; see for examples Nisbet and Gurney 1983; de Roos and Persson 2003):

$$\begin{aligned}\frac{dJ}{dt} &= \beta A(t) - \beta A(t - \tau) e^{-\mu\tau} - \mu J(t) \\ \frac{dA}{dt} &= \beta A(t - \tau) e^{-\mu\tau} - \mu A(t)\end{aligned}\quad (5.4)$$

This formulation assumes that all individuals that are born at time t all mature at the same time after exactly τ time units. The juvenile stage duration is therefore for all individuals the same. The recruitment rate to the adult stage at time t therefore equals the birth rate τ time units prior, $\beta A(t - \tau)$, multiplied by the probability that an individual survives its juvenile period, $e^{-\mu\tau}$.

Like IPMs physiologically structured population models (PSPMs) also characterize an individual by a continuous i -state variable, for example, the individual body size s . The population state is, in that case, a density function $n(t, s)$ representing the density of individuals with body size s at time t . The integral

$$\int_{s_1}^{s_2} n(t, s) ds$$

equals the number of individuals with a body size in the range s_1 to s_2 . Classically, in a PSPM the population dynamics is described by a partial differential equation (PDE) of the form:

$$\frac{\partial n(t, s)}{\partial t} + \frac{\partial g(s)n(t, s)}{\partial s} = -\mu(s)n(t, s) \quad (5.5)$$

in which the function $g(s)$ represents the growth rate in body size of an individual with size s and $\mu(s)$ represents the mortality rate of such an individual. To complete the model specification the PDE has to be supplemented with a boundary condition of the form:

$$g(s_b) n(t, s_b) = \int_{s_b}^{\infty} \beta(s) n(t, s) ds \quad (5.6)$$

Here it is assumed that newborn individuals have a size at birth equal to s_b and the function $\beta(s)$ represents the rate at which offspring is produced by an individual with body size s . The boundary condition matches the total rate at which offspring is produced by the population (right-hand side of the equation) to the rate at which individuals enter

the possible body size range at the lower end (left-hand side of the equation). The partial differential equation (5.5) with its boundary condition (5.6) is often referred to as the McKendrick–von Foerster equation. However, with body size as i -state variable it was first studied by Bell and Anderson (1967) and introduced into ecology by Sinko and Streifer (1967, 1969).

The equations presented previously for matrix, integral projection, stage-structured, and physiologically structured population models are the simplest representatives of these four types of SPMs. More complex examples of matrix models can be found in Caswell (2001), of IPMs in Ellner et al. (2016 for IPMs), of stage-structured models in Murdoch et al. (2003), and of PSPMs in Metz and Diekmann (1986) and de Roos and Persson (2013). These four types of SPMs, however, differ not just in their mathematical formulation, but also in some subtle, more biological aspects.

Data-driven or function-based life history model:

Discrete-time SPMs (matrix and IPMs) are formulated in terms of quantities that can be directly measured in experiments or collected empirically. The matrix elements a_{ij} in Equation (5.1), for example, are identical to or constructed from (i) the i -state of an individual at time $t + 1$ given its i -state at time t , (ii) its survival probability and (iii) the number of offspring it produces between time t and $t + 1$. These quantities are all directly measurable. The model of the individual life history in discrete-time SPMs is therefore often data-driven, consisting of generalized linear or additive models fitted to the life history observations.

In contrast, continuous-time SPMs are formulated in terms of *rates of change*, more specifically the vital rates, i.e., the reproduction, development and mortality rate. These vital rates are not directly measurable and can only be inferred indirectly from the quantities that discrete-time SPMs use directly as input: the i -state of individuals at time $t + 1$ given their state at time t , their probability to survive and the number of offspring they produce during this time interval. A continuous-time SPM is therefore usually formulated by choosing a priori specific functional forms for the vital rates as functions of the i -state of the individual and possibly

the environmental state. For example, a common assumption in PSPMs with body size as i -state variable is that growth in body size follows von Bertalanffy growth with growth rate,

$$g(s) = K(s_{\infty} - s)$$

in which $g(s)$ represents the rate of change in body size s , s_{∞} is the ultimate size an individual can reach, and the parameter K characterizes how rapidly this ultimate size is approached. Appropriate values for the parameters in these vital rate functions are subsequently inferred from experimental or empirical observations. Furthermore, these functions for the vital rates often have a mechanistic basis. Many continuous-time size-structured models are, for example, based on an underlying model for the energy acquisition and use of an individual. The assumptions about energy acquisition and use implemented in such a dynamic energy budget model (Kooijman 1993; Kooijman 2010; Lika and Nisbet 2000) then translate into functional forms of the individual growth rate in body size and reproduction rate as a function of body size and food availability in the environment. With a mechanistic basis for the vital rate functions the model for the individual life history is also easily extended to conditions for which measurements are not directly available. So it is rather straightforward to make the rates in a dynamic energy budget model temperature dependent using established rules for the scaling of physiological rates with temperature (Kooijman 2010; Lindmark et al. 2019). In discrete-time, data-driven SPMs accounting for temperature dependence in the life history model requires demographic observations of individuals at different temperatures.

Linear and non-linear models: The dynamics of linear population models is independent of the population state itself, whereas in non-linear models the population state has an influence on the dynamics. Linear, density-independent SPMs always lead in the long run to exponential growth of the population, irrespective of the type of SPMs that is used. In principle, all four different types of SPMs also allow for density dependence in population dynamics, but they differ in how they account for such density dependence. A good example of how density dependence tends to be incorporated in

data-driven, discrete-time SPMs is provided by Childs et al. (2011), who present a density dependent integral projection model (IPM) for Soay sheep. The life history model in this IPM is constructed by fitting generalized linear and additive models to observations of survival, fecundity and changes in body size at three different densities of the population. This results in a phenomenological representation of density dependence, which does not specify the mechanism by which such density dependence occurs. It also does not consider whether the population density (to which all individuals contribute equally) is an appropriate measure for the strength of the density dependence or that individuals in different stages contribute to a different extent to this density dependence.

In contrast, continuous-time SPMs tend to be far more explicit and mechanistic about the form of density dependence. For example, the model for cannibalistic interactions in a single fish population analysed by Claessen et al. (2000) models explicitly the basic resource that all cannibalistic individuals compete for, the impact of each of the cannibalistic individuals on this basic resource dependent on its body size, the mortality imposed by cannibalistic individuals of particular body sizes on smaller-sized conspecifics and the energy gains that cannibalistic individuals derive from eating their conspecifics. Density dependence thus occurs in this model through different mechanisms, exploitative competition for a shared resource and cannibalism, and both mechanisms are explicitly accounted for in the model in a functional, non-phenomenological manner.

Deterministic or stochastic individual development: The four types of SPMs differ in the extent to which they can and do represent variation between individuals that at one particular time have the same i -state value (for example, individuals that are born at the same time with the same i -state). Individual development in PSPMs is always deterministic and hence variation will never arise between two individuals born with the same i -state at the same time. At the other extreme, the premise of IPMs is that individuals with the same current i -state will exhibit variation in their i -state at the next time step. Matrix and continuous-time stage-structured models can account for variation in individual

development, more specifically individual stage duration, but can also be formulated to exclude any such variation (see de Valpine et al. 2014 for an excellent discussion of this topic). The two systems of differential equations (5.3) and (5.4) exemplify how different formulations can capture either an exponential distribution of the juvenile stage duration or a fixed juvenile stage duration in an otherwise identical stage-structured population model. Different implementations may thus differ in the individual life history that SPMs represent, and the model results should hence also be carefully interpreted in the light of such possible differences.

Ecological complexity and mathematical tractability: Matrix models, IPMs, stage-structured models and PSPMs differ in the level of complexity in the life history and the ecological interactions of individuals that they can and tend to handle. In matrix models, IPMs and stage-structured models individuals are usually distinguished from each other by a single trait, commonly age, size, or stage (but see Caswell et al. 2018 for a recent synthesis of age \times stage classified matrix models). The majority of matrix models and IPMs model a single population in a density-independent setting (but see Table 1 in Rees et al. 2014 for exceptions). These models are hence more geared toward demographic analysis, that is to studying the growth rate and structure of a population in relation to the rates of individual reproduction, development and mortality, as well as the sensitivity of population growth rate and structure in response to changes in these vital rates. In contrast, virtually all continuous-time stage-structured models and PSPMs are non-linear or density dependent. In PSPMs individuals are furthermore frequently characterized by more than a single i -state variable (e.g., de Roos et al. 1990; Persson et al. 1998; Claessen et al. 2000; de Roos et al. 2002). Continuous-time SPMs are hence more geared toward analyzing the interactions between individuals of the same or different species. The flip side of the complexity that the different model types can handle is the ease of their analysis. To analyze linear, density-independent matrix models the substantial power of linear algebra can be brought to bear. This allows for numerous, demographic aspects to be studied using matrix models. For

IPMs something similar holds, as following their formulation and parameterization these models are usually discretized into a large matrix model for analysis. Non-linear, continuous-time SPMs are by comparison more difficult to analyze and in practice often studied only with numerical simulations of the dynamics at particular parameter values. A more powerful and more complete analysis of model dynamics is possible using the theory on bifurcations in non-linear dynamical systems (Kuznetsov 1998). Bifurcation analysis is however up to now only used to a limited extent to assess the generality and robustness of observed dynamics in ecological models. Methods for bifurcation analysis of continuous-time stage-structured models in terms of delay-differential equations (Engelborghs et al. 2002) and PSPMs (Kirkilionis et al. 2001; Diekmann et al. 2003; de Roos 2008) have been developed in recent years as well. These methods form the basis for a recently developed software package to analyze bifurcations in the ecological and evolutionary dynamics of PSPMs (de Roos 2018a), which only requires as input the functions describing development, reproduction and mortality of individuals throughout their life history and functions describing the interactions of these individuals with their environment.

Summarizing, both discrete- and continuous-time SPMs have at their core a model representation of the individual life history, but as discussed previously, they differ in a number of aspects, including in how they represent the life history. The different types of SPMs therefore also serve different purposes and have different strengths and weaknesses. It would be quite ridiculous to claim that one particular framework is better than the other, each of the four types of SPMs is better at something than the others. Roughly speaking, matrix and integral projection models are better suited to analyse life history observations, infer their implications and explore the consequences of variability of individual development between otherwise identical individuals on population growth. On the other hand, continuous-time SPMs, in particular PSPMs, allow for mechanistic representations of individual-level processes, like energetics and in particular the interactions of an individual organism with its environment, including individuals of the same or other

populations. They are therefore better suited to analyse how particular mechanisms or aspects of the life history or ecology of an individual would affect the population and community dynamics.

5.4 Ecological consequences of changing population structure

Recent years have seen two prominent developments in the field of structured population modelling: first, integral projection models (IPMs) have become more and more popular with an increasing number of new applications (see Rees et al. 2014; Ellner et al. 2016 for examples). Second, physiologically structured population models (PSPMs) have been used to analyze the consequences of ontogenetic development as a fundamental life history process for population dynamics and community structure (de Roos and Persson 2013). These latter studies have revealed the importance of the population composition or size-structure and the changes therein with changing ecological conditions for the dynamics and persistence of species. In this section I will provide a summary of the highlights of this newly emerging body of ecological theory and a discussion of how this body of theory adds to or contrasts with predictions of unstructured models.

As pointed out in an earlier section physiologically structured population models (PSPMs) can account for substantial complexity in individual life history and the ecological interactions of the individual with its environment. A range of life history and ecological scenarios has been analyzed using PSPMs: consumer-resource interactions, in which consumers forage on a single shared resource throughout life with consumer reproduction occurring continuously (de Roos et al. 1990; de Roos et al. 2008; de Roos et al. 2013) or as discrete pulses in time (Persson et al. 1998; de Roos and Persson 2001); consumers exploiting multiple resources throughout life (Schellekens et al. 2010; Nakazawa 2011; van Leeuwen et al. 2013; Wollrab et al. 2013; Nakazawa 2015) or adaptively switching between different resources (de Roos et al. 2002); dynamics and community structure of cannibalistic (Claessen et al. 2000) and tritrophic systems with one (de Roos and Persson 2002) or multiple size-selective predators (de Roos

et al. 2008); among others. This variety might lead one to expect a lot of rather specific insights into dynamics and community structure, but surprisingly some very general understanding has emerged.

5.4.1 Juvenile and adult-driven population cycles

Most PSPMs studied to date characterize individuals by their body size and use a model of individual energetics to describe the somatic growth and reproduction of individuals at different body sizes. In these dynamic energy budget (DEB) models energy assimilation from food equals energy allocation to growth, reproduction and metabolic maintenance. DEB models generally predict growth rate and ultimate body size to be determined by food availability (Kooijman and Metz 1984; Kooijman 2010; Persson et al. 1998; Lika and Nisbet 2000), as is representative for the growth patterns of invertebrate and ectotherm vertebrate species. Only one energy budget model has been published that considers growth in structural mass (excluding energy reserves) and ultimate size to be genetically determined (de Roos et al. 2009; de Roos and Persson 2013), which would better reflect the growth patterns of mammals and birds. Growth in total body mass (including reserves) and reproduction, however, are in all DEB models dependent on food availability and on individual body size. Individuals at different body sizes may hence respond differently to changes in food availability, which has implications for population dynamics.

Consider, for example, a scenario in which small, juvenile individuals are more efficient foragers than adults in the sense that there are low food densities at which adults have a negative energy balance while juveniles can still ingest sufficient food to meet their metabolic maintenance requirements. Reproduction will then halt at low food densities that allow juvenile growth in body size to continue. In consumer-resource systems this type of juvenile-adult asymmetry leads to cycles in population density with reproduction only occurring when juvenile biomass is low and stopping as soon as the increasing density of juveniles suppresses food

availability to too low levels (see Figure 5.1, left panel). The intraspecific interactions among differently sized consumers thus cause the reproduction to become pulsed in time. Furthermore, as a result of these reproduction pulses the (juvenile) population becomes dominated by a single cohort of individuals that is born within a short period of time. Alternatively, when small, juvenile individuals have higher maintenance requirements per unit biomass than adults, population cycles also emerge as a

consequence of juvenile-adult asymmetry. In this case, adults reproduce continuously, but juvenile growth slows down when adult density becomes too high (see Figure 5.1, right panel). High adult densities hence slow down the juvenile maturation rate, leading to a decrease in adult density and in reproduction. In turn, the decrease in reproduction causes the juvenile density to decline and the cyclic dynamics to restart. Besides the difference between pulsed and continuous reproduction juvenile- and

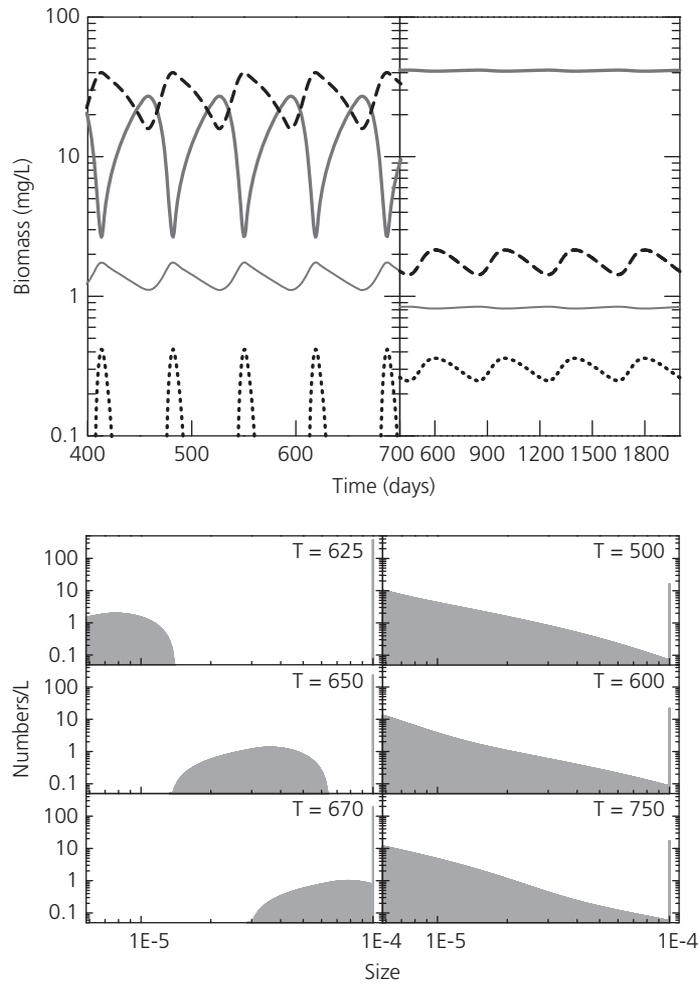


Figure 5.1 Population cycles emerge as a consequence of consumer life history. *Top*: Two types of population cycles emerge as a consequence of the consumer life history, when either juvenile (*left*) or adult (*right*) consumers can withstand lower resource densities. Panels show densities of juvenile (*thick solid line*), adult (*thick dashed line*) and resource biomass (*thin solid line*) as well as daily biomass production through reproduction (*dotted line*). *Bottom*: Changes over time in population size distribution in the two types of population cycles shown in the top panels. Panels redrawn with permission from de Roos and Persson (2013, Figures 9.2 and 9.3, respectively).

adult-driven cycles (Figure 5.1) differ from each other in a range of aspects, including the amplitude of the cycles, the duration of the juvenile period and the adult lifespan (de Roos and Persson 2003; de Roos and Persson 2013).

These population cycles are caused by the asymmetry in the energetics between juveniles and adults. The ingestion rate and maintenance requirements of an individual determine, together with the efficiency with which ingested food is assimilated and converted into new tissue, how much new biomass an individual of a particular body size produces at a given food density through growth and reproduction. Because of the juvenile-adult asymmetry there are food densities at which either juveniles or adults are just staying alive without contributing to consumer population growth. The asymmetry may be only stage-dependent or may occur between any two individuals with a different body size, the two types of cycles show up irrespectively and occur with both continuous and pulsed reproduction of consumers (Persson et al. 1998; de Roos and Persson 2003; de Roos and Persson 2013; Persson and de Roos 2013). Population cycles due to within-stage or between-stage interactions have been extensively studied in continuous-time stage-structured models as well (Gurney et al. 1980; Nisbet and Gurney 1982; Nisbet and Gurney 1983; Gurney and Nisbet 1985). They are also referred to as “single-generation” cycles, because throughout a cycle the population is dominated by a single generation of individuals (Gurney and Nisbet 1985). The juvenile- and adult-driven cycles shown in Figure 5.1 are in essence equivalent to single-generation cycles, although in continuous-time stage-structured models the single-generation cycles have not been linked to the energetic asymmetry between individuals in different stages.

5.4.2 Biomass overcompensation

The occurrence of juvenile- or adult-driven population cycles, originating from the asymmetry in energetics between juveniles and adults or more generally between individuals of different body sizes, is one of the two general findings that have emerged from the analysis of PSPMs, in which individuals are characterized by their body size. The

second general finding is the occurrence of biomass overcompensation (de Roos et al. 2007; de Roos and Persson 2013), which term refers to the phenomenon that the biomass of a particular size-class of individuals or of the entire population increases as opposed to decreases with an increase in mortality experienced by the individuals (see Figure 5.2). Biomass overcompensation is also a consequence of the asymmetry in energetics between individuals in different stages or with different body sizes. Consider for example that juvenile consumers are more efficient foragers than adults and hence have a more positive energy balance (see Figure 5.2, top-left and bottom row). This would imply that at low food availability adult reproduction is very limited or even stops, whereas juvenile growth and maturation can still progress. In a consumer-resource equilibrium at low consumer mortality adult reproduction would hence constitute a more severe bottleneck in consumer life history which contributes more to controlling the population at equilibrium than juvenile growth and maturation. If consumer mortality would be slightly higher, the total consumer biomass in equilibrium will be lower and resource density will consequently be higher. Because of the reproduction bottleneck, the higher resource density leads to a larger, relative increase in the rate at which newborn consumers are produced, than in the rate at which juveniles mature and recruit to the adult stage. This difference in response between the recruitment rate to and the maturation rate out of the juvenile stage exceeds the increased loss rate due to the higher mortality and thus leads to a higher equilibrium biomass density of juvenile individuals despite the higher mortality they experience.

Analysis of simple size-structured population models have revealed that even a little bit of asymmetry between juveniles and adults is sufficient to result in biomass overcompensation or juvenile- or adult-driven population cycles (de Roos et al. 2013; Persson and de Roos 2013). These analyses have also shown that the two most important conditions for *symmetry* in energetics between juveniles and adults to occur are: (i) mortality is size- and stage-independent and (ii) the mass-specific, per-unit biomass production rate of new biomass through somatic growth and reproduction is the same for

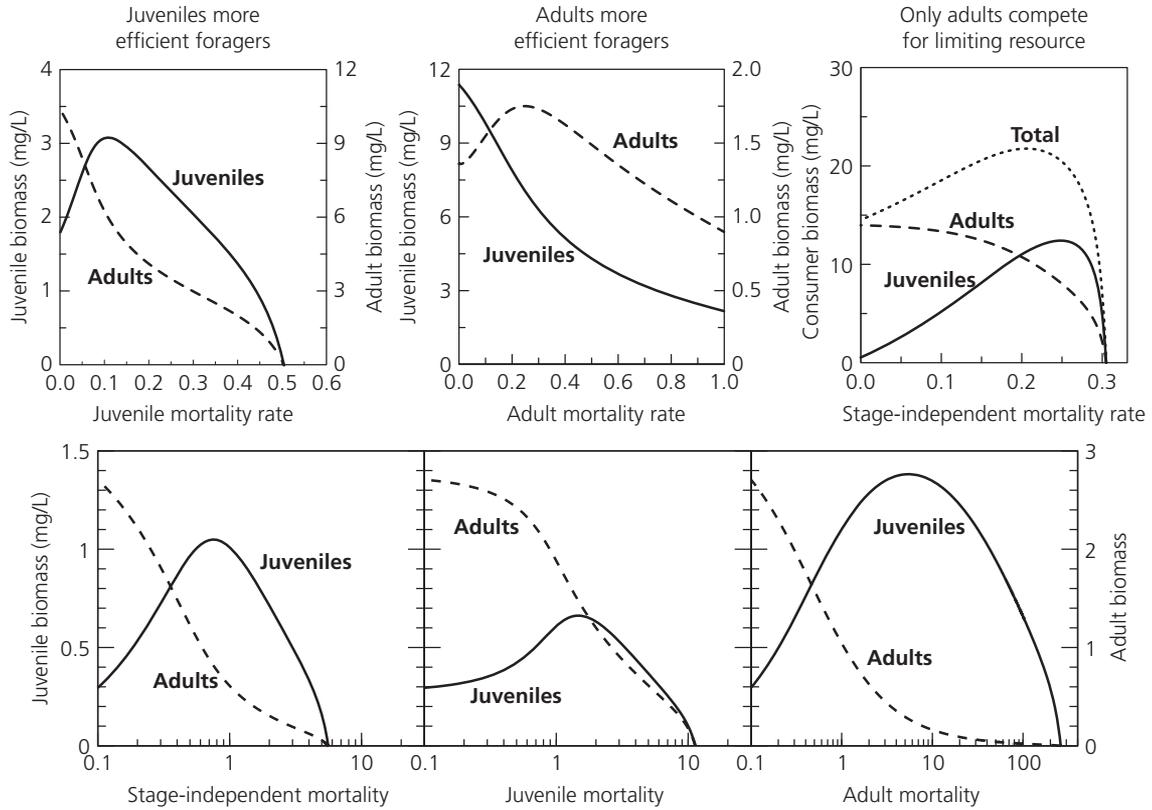


Figure 5.2 Biomass overcompensation emerges as a consequence of consumer life history. *Top*: Types of biomass overcompensation that emerge as a consequence of the consumer life history, when either juvenile (*left*) or adult (*middle*) consumers are more efficient foragers or when only adults compete for a limiting resource (*right*). *Bottom*: Biomass overcompensation in response to increases in stage-independent (*left*), juvenile (*middle*) and adult mortality (*right*) in case juveniles are more efficient foragers than adults. Solid and dashed lines refer to juvenile and adult biomass densities, respectively.

Panels redrawn with permission from de Roos and Persson (2013, Figure 3.5 and 3.6), and de Roos et al. (2007, Figure 1).

individuals of all body sizes (de Roos et al. 2013). The latter condition holds when the quantity

$$\frac{g(s, R) + \beta(s, R)s_b}{s} \quad (5.7)$$

is independent of body size s , where $g(s, R)$ and $\beta(s, R)$ equal the growth rate in body size and the fecundity, respectively, at size s and resource density R . Only when these symmetry conditions hold, will an increase in individual mortality leave the population size distribution unchanged, and will the life history processes not result in population cycles. In other words, only in case of ontogenetic symmetry in energetics will population structure not play a role whatsoever and will the results of PSPMs be

equivalent to the results of unstructured population models for species interactions. The insights from those unstructured population models therefore apply under these limiting conditions of ontogenetic symmetry in energetics.

Biomass overcompensation does not refer to a temporary or transient increase in the biomass of a particular stage but is an equilibrium phenomenon. It, moreover, can occur irrespective of the type of increase in mortality, whether this increase is the same for all individuals, or whether only specific stages or size classes experience the increased mortality (Figure 5.2, bottom row). Effectively, it is the increase in equilibrium food density that causes the biomass overcompensation, while the increased mortality is only the means to increase this

equilibrium food density and this occurs irrespective of whether the mortality increase is stage- or size-dependent or not. Abrams (Abrams and Matsuda 2005; Abrams 2009) was the first to propose that population density could increase with increasing mortality and dubbed this the “Hydra” effect. Biomass overcompensation resembles the Hydra effect but differs from it in some important aspects (Schröder et al. 2014). Most importantly, the Hydra effect deals with the number of individuals in a population and does not distinguish between small juveniles and large adults. In contrast, biomass overcompensation deals with stage-specific or total population biomass and comes about because of an increase in energetic efficiency of consumers at higher mortality levels. Maintenance requirements play a crucial role in this higher efficiency at higher mortality rates (de Roos 2018b). In consumer-resource systems at low consumer mortality most of the resource ingested by consumers is spent on maintenance costs for all consumers together and only little is used effectively for either juvenile growth and maturation or for adult reproduction. With an increase in consumer mortality the loss to maintenance requirements is smaller and the ratio between effective production and ingestion, either the reproduction rate per unit of ingested resource by adults or the maturation rate per unit of ingested resource by juveniles, increases. This increased efficiency subsequently leads to overcompensation in either juvenile or adult biomass. The two life history elements that are sufficient for such overcompensation to occur are differences between juveniles and adults and significant energy requirements to cover metabolic maintenance costs (de Roos 2018b).

5.4.3 Community consequences of biomass overcompensation

In unstructured models of ecological communities, a competitor or a predator of a particular focal population only changes its density, usually in a negative manner. In PSPMs, however, competitors and predators of a focal population not only change its overall density but also its population structure. Furthermore, competitors or predators may not affect all individuals in the focal population

equally but only have an impact on a subset of them. For example, predation mortality tends to be much higher for smaller than for larger sized individuals of a prey population. Because of biomass overcompensation predation on a specific size range of prey individuals may result in an increase in the biomass of this particular size class of prey (cf. Figure 5.2, bottom-middle panel). In contrast to the negative impact of predators on their prey population that is intuitively expected on the basis of unstructured models, size-selective predators can change the size-structure of their prey population and thus have a positive effect on the availability of their own prey. Through this positive feedback, biomass overcompensation in a prey population has ramifications for the persistence of species at higher trophic levels that feed on the prey as it gives rise to the presence of alternative stable community states or facilitation among predators. These effects are absent in case of ontogenetic symmetry and hence quite distinct from existing unstructured theory about basic trophic modules.

Consider for example a tritrophic food chain consisting of a basic resource, a consumer or prey and a predator population. Unstructured population models predict the occurrence of a unique community equilibrium under all conditions, whereby the length of the food chain increases with the productivity of the basic resource and decreases with the mortality rate of the top predator (Oksanen et al. 1981). Alternative stable states therefore do not occur (McCann and Yodzis 1995). In contrast, if the prey population is size-structured and predators would only forage on juvenile prey, biomass overcompensation in juvenile prey would lead to the occurrence of alternative stable community states, one with and one without predators, for certain ranges of basic resource productivity or predator mortality rates (Figure 5.3). Biomass overcompensation in juvenile prey occurs when juveniles have a greater energy efficiency, because they have higher ingestion rates relative to their energetic needs. When predators are absent and juvenile prey do not experience increased mortality relative to adults, the prey population is then dominated by adults, while juvenile biomass is relatively low due to low adult population fecundity (Figure 5.2; bottom-middle panel). If a

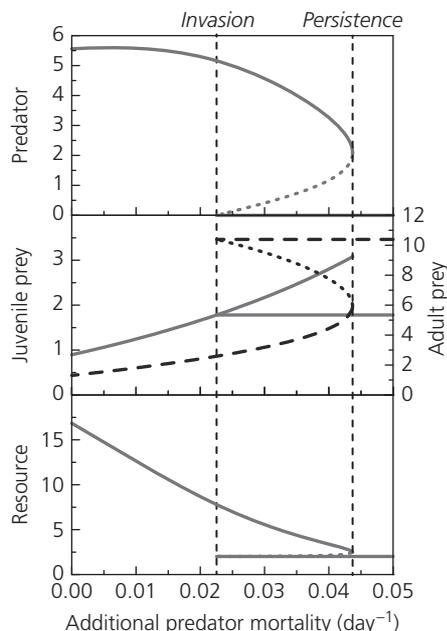


Figure 5.3 Emergent Allee effect for predators in a stage-structured food chain. Changes in equilibrium biomass of basic resource (*bottom*), juvenile (*middle, solid lines*) and adult prey (*middle, dashed lines*), and top predator (*top panels*) with increasing predator mortality in excess of background levels. Predators forage exclusively on juvenile prey. Stable equilibria are indicated with solid or dashed lines, unstable equilibria with dotted lines. For mortality rates between 0.023 and 0.044, one unstable and two stable equilibria co-occur. Panels redrawn with permission from de Roos and Persson (2013, Figure 4.4).

predator that selectively feeds on juvenile prey is present, though, the predation mortality it imposes on juvenile prey causes an overcompensatory increase in juvenile prey biomass (Figure 5.2; bottom-middle panel). In an equilibrium with predators the juvenile prey biomass is therefore higher as opposed to lower than in an equilibrium without predators (Figure 5.3). This change in the size-structure of the prey population induced by predation mortality allows for the occurrence of alternative community states with and without predators. As a consequence, once present the predator may persist at higher mortality rates than those for which it would be able to invade an equilibrium community state from which it is absent. The phenomenon that predators through predation change the size-structure of their prey

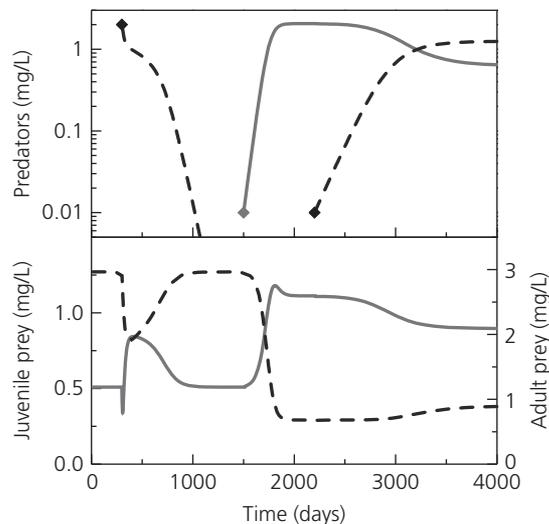


Figure 5.4 Emergent facilitation between generalist and stage-specific predators in a stage-structured food chain. Invasion dynamics of a generalist (*top, solid lines*) and a stage-specific predator of juvenile prey (*top, dashed lines*) into an equilibrium of resource, juvenile (*bottom, solid lines*), and adult prey (*bottom, dashed lines*). Generalist and specialist predators forage equally on both juvenile and adult prey and exclusively on juvenile prey, respectively. Invasion of juvenile-specialized predators at $t = 300$ into the prey-only equilibrium is unsuccessful, despite the high initial density, whereas generalist predators can invade successfully even from low density ($t = 1500$). Generalist predator invasion allows for subsequent, successful invasion of specialist predators from low density ($t = 2200$). Panels redrawn with permission from de Roos and Persson (2013, Figure 5.1).

population and thus promote their own food availability has been termed an emergent Allee effect because it is based on purely exploitative predation of prey (de Roos and Persson 2002), in contrast to most mechanisms causing Allee effects.

Biomass overcompensation in prey populations may also lead to positive effects among predators of the same prey that differ in the range of body sizes of prey they select, a phenomenon referred to as *emergent predator facilitation*. This facilitation can occur between stage-specific predators that forage on two entirely different stages of prey or between a generalist predator that forages on all prey stages and a stage-specific predator foraging on either juvenile or adult prey only (Figure 5.4). For example, in case juveniles have a greater energy efficiency due to higher ingestion rates relative to their energetic

needs, the increase in juvenile biomass with mortality is independent of the size-selectivity of the mortality (Figure 5.2; bottom panels). Analogous to how the increase in juvenile biomass with juvenile mortality forms the basis of the emergent Allee effect discussed previously, the increase with either stage-independent or adult-specific mortality forms the basis of emergent facilitation. Through this juvenile biomass overcompensation a generalist predator can increase the food availability for a predator foraging on juvenile prey only and allow this juvenile-specialized predator to invade under conditions that do not allow for its invasion in the absence of the generalist predator (Figure 5.4). Persistence of the predator feeding only on juveniles may then crucially depend on the presence of the generalist predator. If juvenile and adult prey individuals feed on different resources, predator facilitation may also be bidirectional, in that both predators need each other to persist (mutual predator facilitation) (de Roos and Persson 2013).

Ontogenetic asymmetry between juveniles and adults of the same species may not only come about through intrinsic differences in energetic efficiency between the stages but may also arise because the stages feed on different resources that have different productivities. Schreiber and Rudolf (2008) showed that alternative stable states could occur in case the juveniles and adults of a consumer species feed on different resources. The alternative community states differ in that they are either dominated by juveniles, in case juvenile resource is in short supply and maturation is more resource limited than fecundity, or by adults if adult resource is in short supply and consequently fecundity is more resource limited than maturation. Gradual changes in either juvenile or adult resource supply can in this case lead to abrupt regime shifts. For example, a gradual increase in juvenile resource supply will induce an abrupt shift from a juvenile-dominated consumer-resource equilibrium at low juvenile resource supply to an adult-dominated consumer-resource equilibrium at high juvenile resource supply. A predator feeding only on juvenile consumers will be able to establish itself in the consumer-resource equilibrium occurring at low juvenile resource supply (Figure 5.5). Once established, the predator will keep the juvenile biomass

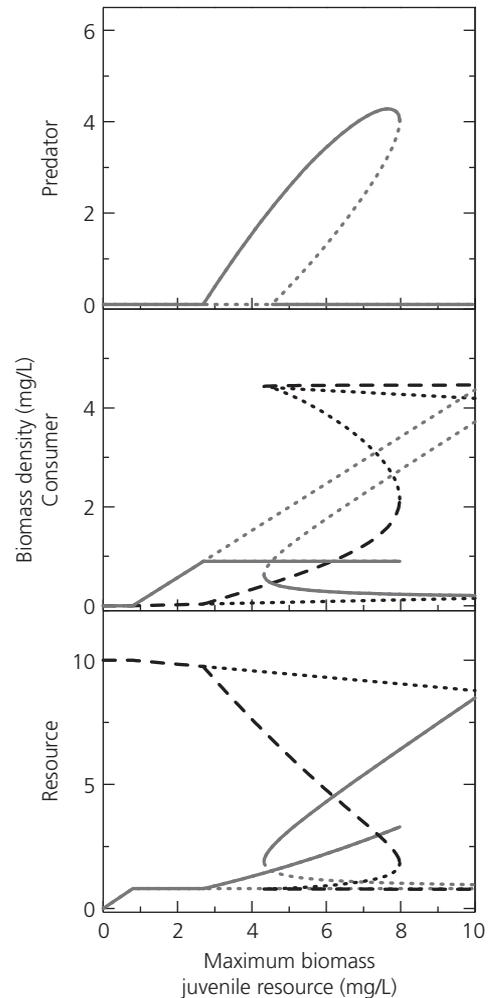


Figure 5.5 Emergent predator exclusion in a stage-structured food chain with different resources for juvenile and adult prey. Changes in equilibrium biomass of basic resources (*bottom*), consumer (prey, *middle*), and juvenile-specialized predator (*top panels*) with increasing maximum density of resource 1, foraged on by juvenile consumers. Solid lines refer to juvenile consumer biomass or their exclusive resource 1; dashed lines to adult consumer biomass or their exclusive resource 2. Consumers experience a complete niche shift from resource 1 to resource 2 at maturation. Stable equilibria are indicated with solid or dashed lines; unstable equilibria with dotted lines. Panels redrawn with permission from de Roos and Persson (2013, Figure 6.6).

constant when productivity of the juvenile resource increases, while juvenile resource density and adult consumer biomass increase, and adult resource

density decreases with this change in productivity (Figure 5.5). The ratio between juvenile and adult consumer biomass therefore decreases, which will lead to an abrupt shift to the adult-dominated consumer-resource equilibrium at high productivity of the juvenile resource. In this adult-dominated equilibrium state the juvenile biomass density is too low for the juvenile-specialized predator to survive. In contrast to unstructured food chain models, which predict that increasing productivity of the basic resource increases the density of the top predator, the ontogenetic niche shift in the prey makes the predator go extinct with increasing productivity of the resource that its main prey, juvenile consumers, is foraging on. This phenomenon is also referred to as *emergent predator exclusion* (Persson and de Roos 2013).

These examples of consequences of ontogenetic asymmetry in energetics between juveniles and adults for community structure represent only three of the many possible feeding modules. The phenomena are considered emergent (emergent Allee effect, emergent facilitation and emergent predator exclusion) because they arise as a consequence of the life history processes of the prey, in particular the biomass overcompensation that results from the ontogenetic asymmetry in energetics between juvenile and adult prey, whereas the community effect occurs at the higher trophic level of the predators exploiting this prey. In all feeding modules analyzed so far, the changes in size distribution that predators induce in their prey population readily give rise to the occurrence of alternative stable states (de Roos and Persson 2013).

5.5 Interfacing theory and data

A current trend in theoretical ecology is that models are to an increasing extent required to have a tight link to empirical and experimental data. This is especially true for structured population models as they necessarily include more detail and hence require more assumptions about the individual life history than unstructured population models. However, unlike the other types of structured populations models PSPMs also offer a larger scope for confronting model predictions with empirical or

experimental data. PSPMs are built on a function-based life-history model, in which the life history is shaped by environmental variables that in turn are influenced by the dynamics of the population abundance and composition. Model predictions about the individual life history are therefore to a considerable extent shaped by this population feedback on life history and only loosely related to the underlying model assumptions. As a consequence, PSPMs generate virtually independent predictions at both the individual as well as the population level that can be confronted with data to determine the relevance of the generated model results (de Roos and Persson 2001). For example, if an equilibrium state occurs under certain conditions in a size-structured population model, the model not only generates predictions about the total population abundance or biomass, but also about its size-distribution, whether it is stunted or not, and about the ratio of juveniles and adults in the population. In addition to these population level predictions, the model also generates predictions about the shape of the growth curve as a function of age that the individuals follow in the equilibrium state, about the duration of their juvenile period and the maximum size they reach in their life.

Persson et al. (2007) used this predictive capacity of PSPMs at both the individual and population level to test whether the abrupt changes in the fish community of Lake Takvatn (Norway) following a short period of culling of the dominant fish species in the lake, Arctic char (*Salvelinus alpinus*), represented a shift between two alternative stable states of the fish community. Before the experimental manipulation the fish community was dominated by Arctic char, ever since brown trout (*Salmo trutta*), a predator of juvenile Arctic char, had gone extinct decades earlier. Because the high density of Arctic char in the lake meant that individual char only reached medium body sizes around 20 cm, it was decided in view of the importance of char for sport fisheries to cull the population during a period of four years. This short-term manipulation of the char population resulted in a reduction in the density of Arctic char and an unexpected recovery of the brown trout population (Figure 5.6, top-left panel), which has by now persisted for over 20 years (Persson et al. 2013). In

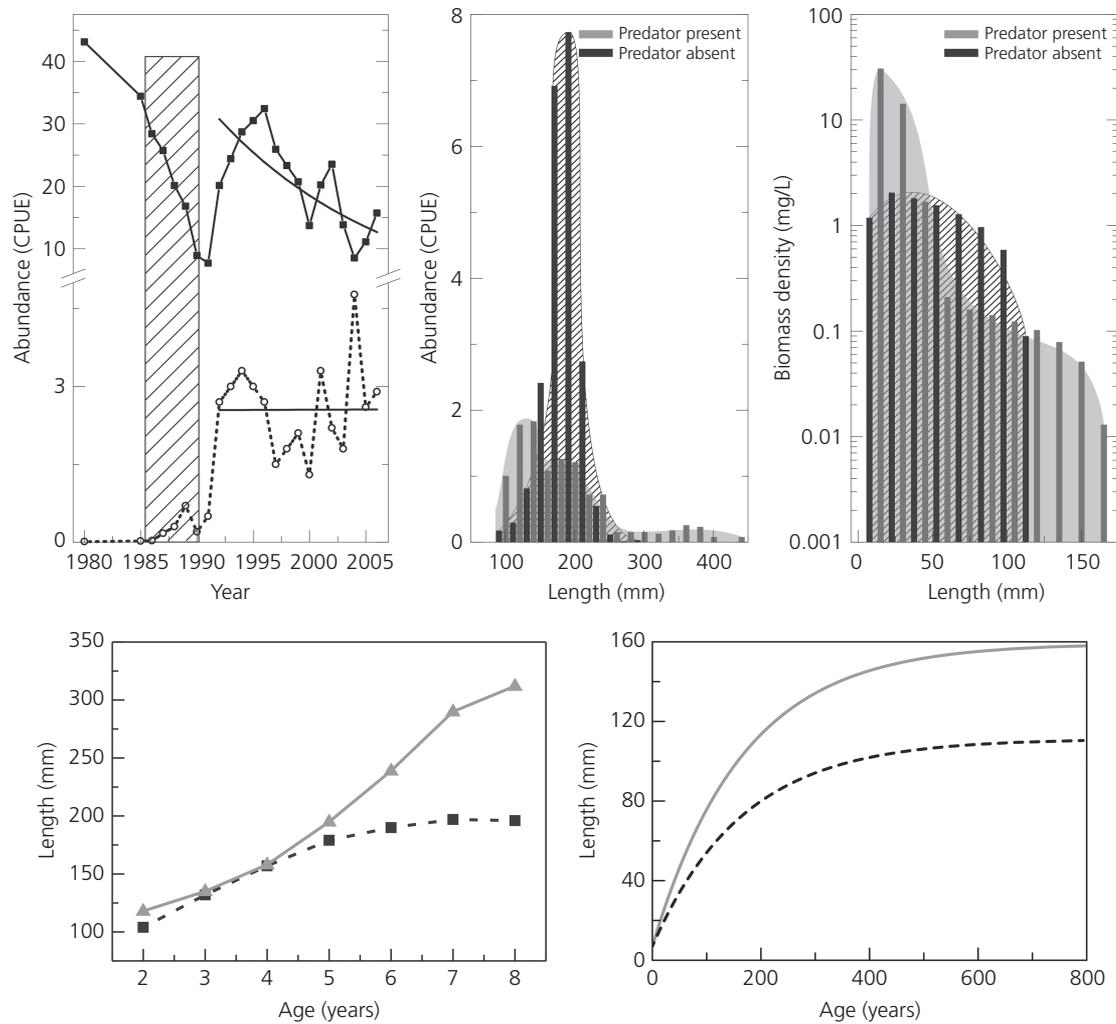


Figure 5.6 Confronting model predictions of the fish community dynamics in Lake Takvatn with empirical data. *Top, left:* Changes in the abundance (catch per unit effort defined as capture per gill net per 24 hours) of brown trout (*open circles, dashed line*) and Arctic char (*closed squares, solid line*) in Lake Takvatn, 1980–2006. Heavy fishing of Arctic char took place from 1984 to 1989 (*hatched area*). Thin, solid curves starting in 1991 represent trend lines. *Top, middle:* Size distribution of Arctic char in Lake Takvatn in 1980 (predator absent; *black bars and hatched convex hull*) and 1994 (predator present; *grey bars and filled convex hull*). *Top, right:* Prey size-distribution in the two alternative stable community states with (*grey bars and filled convex hull*) and without predators (*black bars and hatched convex hull*) as predicted by a generic tritrophic food-chain model of a basic resource, a size-structured consumer and a top-predator foraging on small-sized consumers only (see de Roos and Persson 2013, pp. 136–45). *Bottom, left:* Average individual growth curves of Arctic char in Lake Takvatn before (*black closed squares and dashed line*) and after the culling period (*grey closed triangles and solid line*). *Bottom, right:* Individual growth curves of consumers in the two alternative stable community states with (*grey solid line*) and without predators (*black dashed line*) shown in the top-right panel.

Top-left, top-middle, top-right and bottom-left panels redrawn and adapted with permission from de Roos and Persson (2013 Figure 4.17, 4.19, 4.10 and 4.18, respectively) using data from Persson et al. (2007).

this new community state predation of brown trout prevents severe intraspecific competition among char, such that individual growth in body size is no longer limited by strong density dependence and individuals reach larger sizes (sometimes up to 50 cm; Figure 5.6, bottom-left panel). Due to their larger sizes and the reduced intraspecific competition the total reproduction rate of the Arctic char population has increased leading to an increase in density of Arctic char smaller than 15 cm. In the presence of a dominant brown trout population, the density of both small and large Arctic char individuals was therefore substantially higher than in the absence of predators (Figure 5.6, top-middle panel), even though Arctic char smaller than 15 cm constitute the main prey of brown trout. The experimental observations regarding the change in individual growth curves and population size-distribution are in line with the qualitative predictions of a generic tritrophic food-chain model of a basic resource, a size-structured consumer and a top-predator foraging on small-sized consumers only (see de Roos and Persson 2013, pp. 136–45), even though the latter model is not specifically parameterized for the Arctic char-brown trout interaction and comparison between modelled and observed size distributions is difficult because of the difference in catchability of individuals of different body sizes. On the basis of a confrontation of seven different model predictions with the empirical data Persson et al. (2007) argued that the fish communities before and after the culling of Arctic char represented two alternative stable states, brought about by an emergent Allee effect in brown trout.

5.6 On generality and model specificity

A chapter on SPMs can not ignore the question whether or not the model results derived from a SPM are general or not and in particular whether they are more or less general than results from unstructured population models. Theoretical results are only relevant if they apply to a range of systems and situations. Unstructured population models are often considered more general than structured models, as the latter make more explicit and more system-specific assumptions about the individual life history (Holling 1966;

May 2001; Evans et al. 2013). The background for this view is two-fold: First, unstructured population models tend to be based on fewer assumptions and often involve fewer functions and parameters and are therefore considered to apply to a wider variety of systems. This view is inspired by May's (2001) plea for a strategic modelling approach that "sacrifices precision in an effort to grasp at general principles ... to provide a conceptual framework for the discussion of broad classes of phenomena". As a second reason, for unstructured population models it is often possible to derive analytical results, whereas structured population models can often only be analyzed using numerical techniques. Numerical results are considered less general, as they depend on the particular values of the model parameters for which the results have been derived.

It can, however, also be argued that unstructured population models poorly represent ecological systems, as they consider all individuals identical and thus model populations essentially as collections of elementary particles. Unstructured models have even inspired classic textbooks in ecology to define population dynamics as "the variations in time and space in the sizes and densities of populations," where population density is defined as "the numbers of individuals per unit area" (Begon et al. 2005; Turchin 2013). This perspective again emphasizes changes in numbers of individuals and neglects differences between them. Therefore, in the current ecological paradigm population dynamics arises only as a consequence of two processes: individual reproduction and mortality. And yet, life history is the most fundamental feature that sets individual organisms apart from elementary particles in physics or molecules in chemistry. Individual development throughout life history constitutes an essential and uniquely ecological process. Furthermore, individual development is unlike other factors, such as for example spatial heterogeneity or genetic variability, that may be argued to influence population dynamics. The impact of both spatial heterogeneity and genetic variability can be controlled and even eliminated by choosing an appropriate, experimental setup. In fact, some of the most classic ecological experiments (Tilman 1982) have been carried out in well-stirred chemostats or

using parthenogenetic species (McCauley and Murdoch 1990). In contrast, individual development can never be eliminated by any experimental design, as it is in fact the first process that invariably takes place after the birth of an individual, before reproduction and mortality will ever occur. In my opinion, individual development is therefore also a constituent part of population dynamics just like reproduction and mortality. Structured population models are based on this premise that not only reproduction and mortality, but also individual development shapes the dynamics of a population and that the population is not equivalent to just the number of its individuals, but that the composition or structure of the population (the distribution of the individuals over the possible individual states) is equally important, a fact that is supported by numerous ecological studies (e.g., Olson et al. 2001; Klemetsen et al. 2002). I therefore in general do support May's plea for a strategic modelling approach, but at the same time argue that ignoring individual development in population and community models may be an unjustified oversimplification.

5.7 Outlook

Undoubtedly, the individual life history of a species plays a very important role in its ecology and its evolution. Nonetheless, current ecological theory, in particular theory about population interactions and community dynamics, accounts only to a limited extent for the influence of life history as it is mostly based on unstructured models. Similarly, evolutionary theory about individual life history is often based on a density-independent, fitness-maximization principle and mostly ignores the ecological interactions that shape an individual's life history. Analysis of evolutionary dynamics within an ecological context involving intra- and interspecific interactions is possible using the framework of Adaptive Dynamics (Metz et al. 1996; Dieckmann 1997), but only few adaptive dynamics studies up to now have considered more detailed life histories. Physiologically structured population models (PSPMs) offer ample possibilities to address general questions about the consequences of individual life history on ecological and evolutionary dynamics, in particular facilitated by the recent

development of software for their analysis (de Roos 2018a). These developments allow for addressing exciting and novel ecological and evolutionary questions in the years to come. However, as a cautionary closing note it is important to consider the desired complexity of a PSPM. When formulating a PSPM one often has a particular ecological scenario or system in mind that one wants to capture in the model. It is then quite easy to give in to the natural tendency to tailor the model more and more to this ecological situation, by incorporating an increasing amount of detail (something I also do too often). However, making more detailed assumptions greatly limits the generality of the model predictions. I therefore advocate a certain middle ground of model complexity, in which certain qualitative features of the individual life history are captured by the model with reference to a range of ecological systems, while all the time carefully weighing the benefits of incorporating further aspects of a life history against the costs of a decrease in generality of its results. Furthermore, once a particular pattern emerges from a PSPM with detailed assumptions the generality of the pattern and its mechanistic causes can be investigated by simplifying the PSPM, while preserving the elements that are involved in generating the pattern. For example, juvenile and adult-driven population cycles were first described as results from a model that mimicked in quite some detail the foraging of roach (*Rutilus rutilus*) on zooplankton. Later studies, however, with much more simplified models (de Roos and Persson 2003; Persson and de Roos 2013) revealed that these cycles occurred commonly whenever there is a competitive asymmetry between juveniles and adults. Similarly, biomass overcompensation was first found in a consumer-resource model, in which the consumer population was characterized by a complete size distribution (de Roos and Persson 2002), but was later on shown to also occur in stage-structured models (de Roos et al. 2007; de Roos 2018b), provided that juvenile and adult individuals differ in their energetic requirements, i.e., there is asymmetric competition for resources between them, and metabolic maintenance costs require a significant amount of energy. I would argue that this approach of model simplification is necessary and greatly benefits the generality of the developed theory.

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