

CHAPTER ONE

Summary

A Bird's-Eye View of Community and Population Effects of Ontogenetic Development

Why start with summarizing the contents of a book? In the present case we see at least two good reasons. First, the amount of information provided in our book is without doubt quite massive. A summary provides an overview of the many topics that we cover and, we hope, reduces the risk that the reader will get lost in details and can no longer see the forest through the trees. Second, and partly related to the first reason, a number of, in our mind, novel and fundamental insights (some of them were not even known to us when we started to write the book!) are advanced. Here a summary serves the purpose of clearly showing how different chapters fit together in a general framework with respect to model approaches as well as results obtained. Reading this summary chapter will show you the different types of community modules that we analyze (summarized in figure 1.3) and give you a clear impression of the results and insights that we present in this book. Most of all, we hope it will serve as an encouragement to delve in more detail into the chapters that follow.

HISTORICAL BACKGROUND

Ecology has a long tradition of building theory about the dynamics of populations and the structure of communities that emerge from it. The early foundations for this theory were established by the pioneering work of Alfred Lotka and Vito Volterra, who formulated the most simple models for the dynamics of populations engaged in competitive and predator-prey interactions. Lotka-Volterra models have been used widely and form the basis of most, if not all, of our current theory on population and community processes. Because of their simplicity Lotka-Volterra models have often been viewed as leading

to predictions that are general and representative for many different systems. And yet, these models completely ignore one of the most important processes in an individual's life history—one that is, moreover, unique to biology: development.

Lotka-Volterra models use population abundance as the state variable to characterize a population and describe changes therein using rather abstract demographic and community parameters such as population growth rates and coefficients of interaction between species. The dynamics of a population is described as the balance between reproduction and mortality, which increase and decrease abundance, respectively. In essence, these two processes are not unique to biological systems, as synthesis of particles from substituent elements and degradation of particles also occurs in, for example, chemical systems. Analogously, increases and decreases in population abundance result from the reproduction and mortality, respectively, of individual organisms. However, no individual organism of any species can reproduce right after it has been born, nor is its chance to die the same throughout all stages of its life history. Individual organisms go through an ontogenetic development, which is a major component of their life history. In fact, given that many individuals die before they manage to reproduce, ontogenetic development can be considered the most prominent life history process after mortality.

The intricacies of an individual's life history, including its ontogenetic development, have forever fascinated ecologists and have been studied extensively. Nonetheless, the absence of ontogenetic development as an important life history process from the core models of ecological theory has not been cause for major concern, nor has it been considered an important omission. The progression through different life stages has been accounted for in matrix models that focus on the potential of population growth of single populations, but when considering interactions between species and models of larger communities, the simplification of the population to a number of individuals without distinguishing between these individuals has been the rule. Basic ecological models thus ignore without much qualm the most prominent process in an individual's life history, one that is unique to biological systems and has no counterpart in physical and chemical systems.

The most important aspect of ontogenetic development in virtually all species is an increase in body size. Body size, in turn, determines to a large extent an individual's ecology in terms of its feeding, growth and reproduction rate, the food sources it can exploit, and the predators to which it is exposed. Moreover, in most species growth in body size is plastic, dependent on the environmental conditions the individual experiences, in particular, the availability of

food resources that are required for its maintenance, growth, and reproduction. The consequences of such plastic and food-dependent ontogenetic development for the dynamics of populations and the structure of communities are the subject of this book. We investigate these population and community consequences using a collection of models that differ in the amount of detail with which the individual life history is represented (figure 1.1). All models account for growth in body size as the most important aspect of ontogenetic development and rigorously adhere to a mass-conservation principle. Thus, they explicitly account for the processes by which energy is acquired (feeding) and through which energy is spent (maintenance, growth, and reproduction). We also confront the predictions derived from these models as much as possible with experimental and empirical data that we either collected ourselves or that are available in the literature. More specifically, we present experimental and/or empirical evidence for the majority of phenomena that we deduce from our model analysis.

We use two basic model formulations: a fully size-structured model formulation with an explicit handling of continuous size distributions and a stage-based formulation with two stages (juveniles, adults). Most important, the latter can be shown to be a faithful approximation to the fully size-structured model formulation, as model results of the two formulations are completely identical under equilibrium conditions. In the stage-based formulation, the juvenile stage increases in biomass as a result of adult reproduction and somatic growth of juvenile individuals, whereas adult biomass increases as a result of maturation of juvenile biomass into adult biomass (figure 1.1, top panel). Significantly, all these rates are dependent on the resource biomass level. Biomass is lost from the system through mortality and energetic costs for maintenance. In the fully size-structured model formulation, individuals grow in body size over ontogeny to reach maturity at a specific size (figure 1.1, bottom panel). The rate of increase in size is a function of net intake (intake minus maintenance costs). Net intake and reproduction rates are also in this case dependent on resource biomass density.

A crucial question to ask when considering community effects of ontogenetic development is whether it matters that basic ecological models ignore this process when modeling population dynamics. In our opinion, the answer is obviously yes, as we otherwise would not have written this book. The book underpins this assertion by presenting the major consequences of ontogenetic development for community structure and population dynamics. Furthermore, we will show that the conditions under which development does *not* have a significant community influence represent only a limiting case. We hence

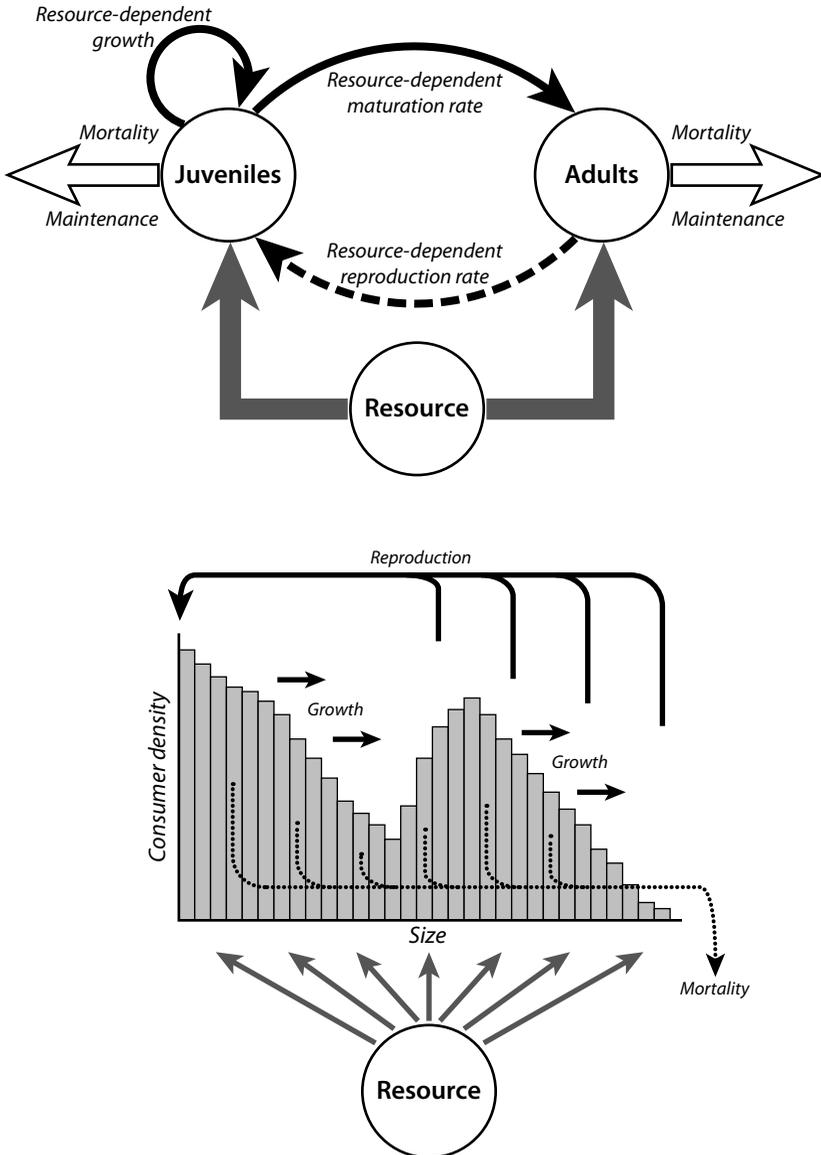


FIGURE 1.1. Schematic representation of the two basic types of models used in the different chapters. *Top panel:* The consumer life cycle as a dynamic system represented by a two-stage biomass model where biomass is generated from ingested resources (solid gray arrows), lost through mortality and maintenance (open arrows), and channeled between the juvenile and the adult stages through maturation and reproduction, respectively (solid black arrow, dashed black arrow). In

postulate that the ecological theory based on Lotka-Volterra models is all but a limiting case of a more general population and community theory.

BIOMASS OVERCOMPENSATION

Arguably the most important finding presented in the book is that an increase in mortality of a population can lead to an increase in its biomass, which runs counter to all our intuitive ideas about the consequences of mortality. Figure 1.2 illustrates this phenomenon using the stage-based formulation schematically presented above for a consumer population, but in contrast to what is assumed in figure 1.1, juvenile and adult individuals forage on two different resources with otherwise exactly identical mass-specific feeding rates (this model is analyzed further in chapter 6). When individual consumers forage to an equal extent on both resources (50 percent foraging effort on both resource 1 and 2, respectively), irrespective of whether they are juvenile or adult, an increase in mortality of all consumers leads to the intuitively obvious result that total consumer biomass decreases (figure 1.2, left). Furthermore, the increase in mortality does not change the ratio between juvenile and adult consumer biomass in equilibrium. The relative composition of the population hence remains the same. Note that we have assumed in this model that individual consumers do vary in their body size as they grow from their size at birth to mature at an adult body size, but that per unit of biomass, the rates of feeding, maintenance, and mortality are the same for all consumers. The fact that both juveniles and adults exploit both resources to an equal extent makes them identical on a mass-specific basis.

When juvenile consumers exclusively feed on resource 1 and at maturation switch to exclusively feeding on resource 2, the response of the population to an increase in mortality of all individuals is quite different: a higher mortality translates into a higher total biomass of the population, mainly because the

addition, juvenile biomass increases through somatic growth (*circular solid black arrow*). *Bottom panel*: The consumer life cycle as a dynamic system represented by a physiologically or fully size-structured population model. Biomass is generated from a size-dependent intake of the resource (*gray arrows*) and lost through mortality (*dotted arrow*) and maintenance costs. Individuals grow as a function of energy intake minus maintenance costs (*black horizontal arrows*). At a fixed size they start to reproduce (*vertical and horizontal black arrow*). In both formulations, all biomass growth and recruitment processes depend on resource availability.

biomass density of juvenile consumers increases significantly, whereas adult consumer biomass only decreases with mortality, as before (figure 1.2, right). This positive relationship between mortality and biomass density in equilibrium we refer to as *biomass overcompensation*. Biomass overcompensation comes about because the relative composition of the population changes with changing conditions, that is, mortality. Note that we refer to an increase in standing stock equilibrium biomass and *not* to an increase in a population dynamic rate process, such as the population reproduction rate, with increasing mortality. The latter is in fact more understandable and has been discussed before in the literature.

ONTOGENETIC (A)SYMMETRY IN ENERGETICS

When does biomass overcompensation occur? This question brings us to another important concept presented in the book, that of *ontogenetic symmetry in energetics*. In classical Lotka-Volterra models all individuals are by definition the same and thus characterized by equal rates of feeding, maintenance, reproduction, and mortality. As we will show, the population dynamics models that account for individual growth in body size throughout life history and hence for the population size structure, presented in figure 1.1 above, can under specific conditions be simplified to a single ordinary differential equation for the changes in total population biomass over time. More specifically, the classical, bioenergetics model presented by Yodzis and Innes (1992) represents an example of such a model, which looks like an unstructured population model that characterizes the population with a single state variable: population biomass. At the same time, the Yodzis and Innes model can also be shown to exactly describe the dynamics of a fully size-structured population, in which all individuals experience the same mortality and per unit of body mass produce the same amount of new biomass through either somatic growth in body size or production of offspring. The condition that allows for simplifying a size-structured model to a simple model for total population biomass we refer to as *ontogenetic symmetry in energetics*, because of the symmetry between individuals of different body sizes (i.e., in different stages in their development) in the efficiency with which they convert ingested food into new biomass. Under conditions of ontogenetic symmetry, size-structured population dynamics do not differ from the dynamics of unstructured populations: increases in mortality lead to the expected decrease in total population biomass, and changing external conditions such as mortality or food supply do not change the relative population composition.

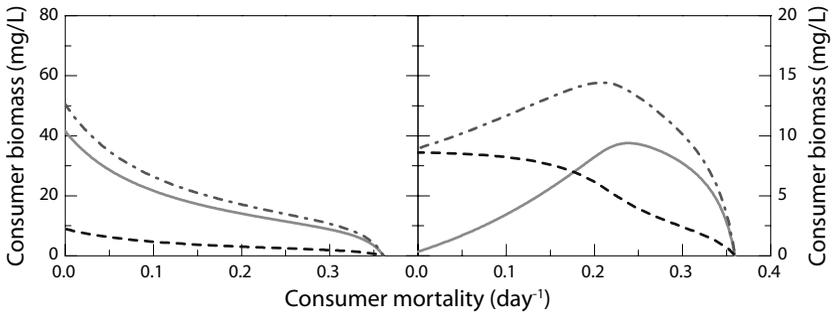


FIGURE 1.2. Changes in juvenile (*light-gray solid lines*), adult (*black dashed lines*), and total consumer biomass (*dark-gray dotted-dashed lines*), with increasing mortality targeting all consumers equally in a consumer-resource model in which juvenile and adult consumers either forage to the same extent on two different resources (*left*; $q_{J,1} = q_{J,2} = q_{A,1} = q_{A,2} = 0.5$, see box 6.2) or switch from exclusively foraging on resource 1 as juvenile to foraging exclusively on resource 2 as adult (*right*; $q_{J,1} = q_{A,2} = 1$, $q_{J,2} = q_{A,1} = 0$, see box 6.2). See boxes 6.1 and 6.2 for model equations and parameters, respectively. Results pertain to a consumer population with characteristic adult body weight equal to $W_A = 0.0001$ gram and maximum density of resources 1 and 2 equal to $R_{\max,1} = 100$ mg/L and $R_{\max,2} = 18$ mg/L, respectively.

The results shown in the right panel of figure 1.2 hence occur because of *ontogenetic asymmetry* between juvenile and adult consumers. In particular, juveniles and adults differ because we have assumed that they forage on different resources that are produced at different rates. Figure 1.2 represents a situation with a high productivity of resource 1, on which the juveniles forage, whereas resource 2, exclusive to adult consumers, is in short supply. Juvenile and adult consumers thus experience very different feeding regimes. At low mortality this leads to a domination of the population by adults, because adult resource is limited in equilibrium. Adult consumers then use most of their intake to cover their maintenance costs, and reproduction is low. At the same time, juvenile resource density is high, leading to rapid growth of juveniles from their size at birth to their maturation size and early maturation.

Hence, at low mortality a bottleneck occurs in the adult stage of the consumer life history. An increase in mortality relaxes this bottleneck, as it decreases adult biomass and increases the availability of resource for the surviving adults. The latter, positive effect is so substantial that total reproduction by all adults together increases with increasing mortality. In turn, this increase in total

reproduction translates into an increase in biomass of juveniles, which continue to experience high food availability and can cash in on the high supply of their resource. The biomass overcompensation hence occurs because individual consumers differ in their energetics, which results in a differential change in maturation and reproduction rate when an increase in mortality relaxes the intraspecific competition and resource densities increase. The differential change in maturation and reproduction rate leads to a change in population composition and ultimately to a more efficient use of the supplied resources.

Biomass overcompensation occurs when the ontogenetic symmetry in energetics is broken. In physics, symmetry breaking is known to bring a system from a disorderly state, which occurs in the symmetric case, into one of two definite states that are robust against small changes as opposed to the symmetric state. Analogously, we can identify two distinct regimes of ontogenetic asymmetry in energetics. First, if juveniles are energetically less efficient than adults, a bottleneck in development during the juvenile stage will mostly limit the population at equilibrium when mortality is low. Then, the population tends to be dominated at equilibrium by juveniles. Increases in mortality will generically decrease juvenile biomass but increase adult biomass. Second, if adults are energetically less efficient, a bottleneck in reproduction will limit the population at equilibrium when mortality is low, leading to adults making up the largest part of population biomass under these circumstances. Increases in mortality will then decrease adult biomass but increase juvenile biomass. These two regimes of ontogenetic asymmetry, either juvenile development or adult reproduction limiting a population at equilibrium, are like two sides of a coin. A state of ontogenetic symmetry represents the dividing line between them. Just as in physics, the system states that are observed in the symmetric case, which in our case refers to the type and nature of community equilibria or the type of population dynamics predicted by a model, are sensitive to small changes in the energetic status of juveniles and adults. This is the reason why we postulate that classic ecological theory based on Lotka-Volterra models only covers a limiting case of the more general theory, which also encompasses cases with asymmetric conditions of individual energetics.

Biomass overcompensation occurs for almost all parameter combinations in different size-structured, consumer population models irrespective of the precise details of the individual life history that are accounted for in these models. Figure 1.2 does represent an extreme example, in that even total population biomass increases with increasing mortality. In general, however, it is more likely to find that total population biomass decreases and only the biomass density of juveniles or that of adults increases in response to mortality. Stage-specific biomass overcompensation, for example, occurs when adults and juveniles share

the same resource but differ in their mass specific intake rate (figure 1.3, top row, left module). It is hence a generic phenomenon, although the precise form of biomass overcompensation may depend on model details (see chapter 3 for details). Crucial for its occurrence is the fact that individuals require energy to cover the costs for maintaining themselves, an aspect of individual life history that is often ignored in Lotka-Volterra models.

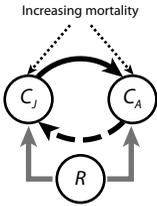
EMERGENT COMMUNITY EFFECTS OF BIOMASS OVERCOMPENSATION

Under conditions of population regulation at equilibrium by limited juvenile development, the equilibrium density of adult biomass will not only increase in response to increases in mortality that targets all consumers equally but also in response to increases in mortality that target only juveniles or only adults. The same holds for the increase in juvenile equilibrium biomass with increasing mortality: it occurs irrespective of whether mortality targets only juveniles, only adults, or both juveniles and adults equally (chapter 3; figure 1.3, top row, left module). Biomass overcompensation hence occurs irrespective of the precise size-dependency of the mortality imposed. This result immediately reveals the possible community consequences of biomass overcompensation. For example, consider that juvenile equilibrium biomass increases in response to increased juvenile mortality. If this mortality is imposed by a predator species foraging on these juveniles, predators will experience a higher availability of food (i.e., more juvenile consumer biomass) the higher the mortality they impose on these juveniles. Thus, a positive feedback emerges between the stage-specific mortality that stage-specific predators impose and their food availability.

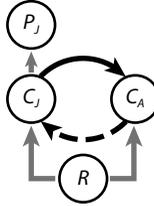
At the population level, this positive feedback gives rise to an *emergent Allee effect* (chapter 4; figure 1.3, top row, middle module): low densities of predators fail to build up a population, as the predation mortality they impose on juvenile consumers is not sufficient to raise juvenile biomass density to levels that are high enough for predator persistence. In contrast, a high predator density will lead to an increase in juvenile consumer biomass that is sufficient for predator persistence. Over significant ranges of resource productivity and predator mortality, this threshold behavior will imply that both an equilibrium without predators as well as a coexistence equilibrium of consumers and predators is stable. The Allee effect, as embodied by the threshold predator density for persistence and the bistability between equilibria with and without predators present, does not result from any specific model ingredient but

Community structure

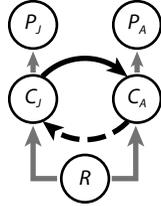
Chapter 3
Biomass overcompensation



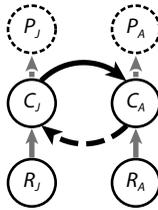
Chapter 4
Emergent Allee effects



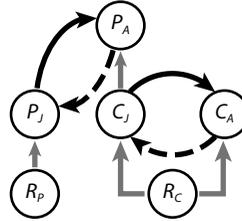
Chapter 5
Emergent facilitation



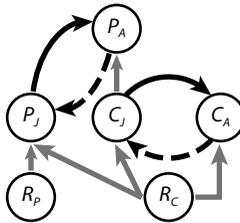
Chapter 6
Ontogenetic niche shifts



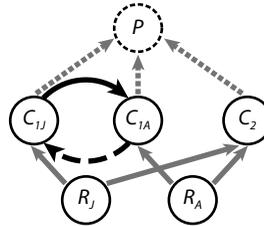
Chapter 6
Ontogenetic niche shifts



Chapter 7
Mixed interactions

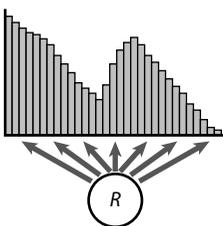


Chapter 8
Interspecific competition and predation

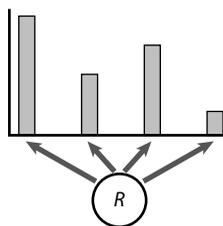


Population dynamics

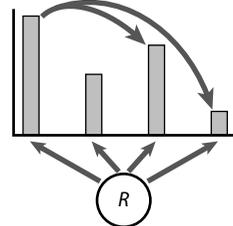
Chapter 9
Consumer-resource dynamics



Chapter 10
Consumers with pulsed reproduction



Chapter 11
Cannibalism



emerges as a consequence of the ontogenetic development of the consumers that the predators prey on. Emergent Allee effects can occur for predators that specialize either on juvenile consumers or on adult consumers, depending on whether the consumer population in absence of predators is regulated by limited reproduction or development, respectively. They also occur in a far more detailed size-structured model that accounts for size-structure in both prey and predator population and in which prey vulnerability is a continuous function of both prey and predator body size (figure 1.1, bottom panel; see chapter 4 for details). Furthermore, there is convincing evidence from an experimental manipulation of the fish community in an entire lake that corroborates the occurrence of emergent Allee effects in natural systems.

A second type of emergent community effect, *emergent facilitation* between different stage-specific predators (chapter 5; figure 1.3, top row, right module), occurs because juvenile biomass in equilibrium also increases in response to an increase in adult mortality. Consider the effect of an adult-specialized predator species imposing predation mortality on adult consumers. This will translate into a higher density of juvenile biomass in equilibrium and thus to a higher food availability for a predator species that specializes on juvenile consumers. Through the changes in the consumer population stage-structure, the adult-specialized predator thus benefits the juvenile-specialized predator. We will show that as a consequence the juvenile-specialized predator may only be able to persist in the presence of the adult-specialized predator that competes with it for the same prey species (chapter 5). Extinction of the adult-specialized predator then necessarily leads to extinction of the juvenile-specialized predator as well. Such facilitation of the juvenile-specialized predator by the

FIGURE 1.3. Principal trophic modules (R for resource, C for consumer, P for predator) considered in the different chapters. Gray arrows represent ingestion, black solid arrows maturation, and black dashed arrows reproduction. Dashed gray arrows and dashed circles represent variations on the basic feeding relations and trophic modules (indicated by solid gray arrows and solid circles) investigated in the different chapters. Dotted black arrows represent different types of additional mortality to which consumers are exposed. In chapters 3, 4, 6, and 7, both types of model, illustrated in figure 1.1, are used to investigate community structure, whereas chapters 5 and 8 use the stage-structured model only. Chapters 9, 10, and 11 use the physiologically structured model (figure 1.1, bottom panel) with either continuous (chapter 9) or pulsed (chapters 10 and 11) reproduction.

adult-specialized predator occurs over significant ranges of predator mortality. The reverse phenomenon, facilitation of the adult-specialized predator by a juvenile-specialized predator, also occurs readily, but for conditions in which the consumer population in absence of predators is mostly regulated in equilibrium by limited juvenile development. Biomass overcompensation in consumer populations in response to mortality thus indirectly gives rise to positive effects at higher trophic levels, either within the same predator population (emergent Allee effect) or among predators that forage on different size ranges of consumers (emergent facilitation).

ONTOGENETIC NICHE SHIFTS IN CONSUMER LIFE HISTORY

In many species the ecology of individuals changes drastically with increases in body sizes. Some of these changes are quantitative in nature, such as increases in the rate of foraging and maintenance. Individuals may, however, also switch diet and forage on completely different resources as juveniles and adults. Such qualitative changes in ecology throughout individual life history are referred to as ontogenetic niche or diet shifts. Figure 1.2 already illustrates that more complex outcomes of population dynamics can be expected in cases where individuals change their diet at maturation, as it even allows for overcompensation in total population biomass.

In cases where juveniles and adults share a single resource, their energetic efficiency determines whether at low mortality the population at equilibrium is regulated by slow juvenile development or by low adult reproduction. In contrast, these two modes of population regulation support two alternative stable states when juveniles and adults have different diets. Under the same conditions of resource productivity and mortality, the population may equilibrate either in a stable state in which juvenile development is limited or in one in which adult reproduction is limited. This bistability between a development-controlled and a reproduction-controlled equilibrium of the consumer-resource system generically occurs over a wide range of resource productivities (chapter 6).

Ontogenetic niche shifts in consumer life history and the ensuing bistability between a development-controlled and a reproduction-controlled equilibrium have implications for the occurrence of emergent effects at higher trophic levels (chapter 6; figure 1.3, second row, left module). In particular, because total consumer biomass can increase with an increase in mortality that targets

all consumers equally (figure 1.2) an emergent Allee effect can in this case occur for a generalist predator that feeds on both juvenile and adult consumers, which is impossible when juvenile and adult consumers share a single resource. For stage-specific predators the bistability between a development-controlled and a reproduction-controlled equilibrium of consumers implies that predators may be able to invade and persist only in one of these two stable states, in which the consumer stage they forage on dominates the consumer population, whereas the food density they encounter in the alternative consumer equilibrium is too low for population growth. As a consequence, increasing the productivity of, for example, the resource that juvenile consumers forage on, eventually leads to extinction of a stage-specific predator species that specializes on the juvenile consumers. Similarly, increasing productivity of the resource for adult consumers leads to extinction of an adult-specialized predator species. Together, however, the juvenile-specialized and adult-specialized predator species can persist for all combinations of resource productivity that lead to extinction of one of the predators when alone. Thus, through the ontogenetic niche shift in consumer life history, the emergent facilitation between two stage-specific predators becomes reciprocal, whereas this facilitation is always only one-sided (either juvenile-specialized predators facilitate adult-specialized ones or vice versa) in cases where juvenile and adult consumers share a resource (chapter 6).

ONTOGENETIC NICHE SHIFTS IN PREDATOR LIFE HISTORY

Many predator species do not prey on consumers throughout their entire life; as a juvenile they forage on smaller-size alternative resources. Predators hence often also exhibit an ontogenetic niche shift in their life history from basic resource-feeding to predation (figure 1.3, second row, right module). The occurrence of ontogenetic niche shifts in the life history of predators of size-structured consumers allows for the possibility of multiple (up to three) stable community equilibria under the same conditions of resource productivity. An ontogenetic niche shift of predators from feeding on their exclusive, alternative resource as a juvenile to preying on juvenile consumers as an adult allows for the occurrence of a stable coexistence equilibrium of consumers and predators that is regulated by limited predator reproduction, next to a stable coexistence equilibrium that is regulated by limited predator development (chapter 6). If the predator preys on a consumer population that in absence of

predators is regulated by limited reproduction, it may in addition experience an emergent Allee effect. In combination with the two types of coexistence equilibria, the emergent Allee effect allows for the occurrence of three different stable community states over certain ranges of resource productivity: (1) a stable consumer-only equilibrium without predators; (2) a stable coexistence equilibrium regulated by limited predator development during its juvenile stage; and (3) a stable coexistence equilibrium regulated by limited predator reproduction.

The type of regulation of the predator population at equilibrium has consequences for both the composition of the consumer species it preys on as well as for the life history of the predators themselves (chapter 6). When limited development regulates the predator population at equilibrium, most intraspecific competition for food among predators occurs in the niche during which they feed on their alternative resource, while intraspecific competition in the predatory niche is negligible. As a consequence, the predation mortality imposed on consumers is generally low, such that the consumer population tends to be regulated by limited reproduction and dominated by adults (note that we concentrate here on the more likely scenario of predators foraging on juvenile consumers, which in turn are more efficient in their energetics than adult consumers).

If individual predators can grow in body size even after maturation, this high adult consumer density allows individual predators to reach very large body sizes, albeit only a few individuals manage to do so. In contrast, in the coexistence equilibrium with limited reproduction regulating the predator population, intraspecific competition is negligible in the resource-feeding niche of juvenile predators and mostly occurs in the predatory niche. Even if predators can grow in body size after maturation, they will not manage to do so, because food for adult predators is limited. Juvenile consumers experience high predation mortality in this coexistence equilibrium. This in turn leads to high resource densities for consumers, fast development of surviving juveniles, and high reproduction of adult consumers. If they are capable of somatic growth after maturation, the few surviving adult consumer individuals can in this coexistence state reach body sizes that are close to their maximum. In cases where consumers and predators can both grow in body size after maturation these two stable coexistence equilibria can be aptly distinguished as the “stunted-consumer” and the “stunted-predator” equilibrium, on the grounds that in either equilibrium individuals of one of the two species reach body sizes that are only slightly larger than their maturation size, whereas the other species grows to body sizes close to its maximum.

When juvenile predators forage on a basic resource before switching to predation on consumers, the possibility arises that they compete in this resource-feeding niche with their future prey. This type of mixed interaction between consumers and predators, which can also be classified as intraguild predation or life-history omnivory, is considered to be a major force structuring natural communities (figure 1.3, third row, left module). Diet overlap between consumers and juvenile predators restricts the coexistence possibilities of consumers and predators (chapter 7). However, this outcome crucially depends on the extent to which adult predators need to feed on consumers to successfully reproduce. If adult predators can feed on the basic resource as well and gain sufficient energy from it for reproduction, they may drive consumers to extinction over large ranges of resource productivity (chapters 6 and 7). On the other hand, if preying on consumers is necessary for predator reproduction, consumers are never driven to extinction by predators (chapter 7).

Consumers and predators then coexist in stable equilibrium, in which predators dominate and overrule the competitive advantages of consumers through the predation mortality they impose. Consumers may become dominant owing to their advantage in resource competition, in which case the density of the resource that consumers and juvenile predators share becomes so low that juvenile predators experience a severe bottleneck in their development. Ultimately, this drives the predator to extinction. Rather than leading to a balance between the competitive advantage of the consumer and the top-down suppression by the predator, mixed interactions, in which predators rely on the presence of consumers for persistence, thus lead to the occurrence of bistability between a competition-driven community state without predators present and a predation-driven coexistence state (chapter 7).

COMPETITION BETWEEN CONSUMERS WITH AND WITHOUT ONTOGENETIC NICHE SHIFTS

Figure 1.2 suggests that consumers that experience a niche shift in their life history from feeding on resource 1 as a juvenile to feeding on resource 2 as an adult may be able to exploit the available resources more efficiently at higher levels of mortality than at lower mortality. This change in efficiency with increasing mortality turns out to have major consequences for coexistence of different consumer species that compete for the same resources. Consumers that specialize on different resources in different stages of their life history are referred to as ontogenetic specialists. In contrast, ontogenetic

generalists do not change their pattern of resource usage throughout their life history.

In competition for two basic resources an ontogenetic specialist and an ontogenetic generalist can coexist in a stable equilibrium for certain combinations of resource productivity (chapter 8; figure 1.3, third row, right module), while for other combinations of resource productivity either the ontogenetic specialist outcompetes the generalist or vice versa. The diet shift in itself thus leads to niche partitioning between the specialist and the generalist, even in cases where both consumers are energetically equally efficient (chapter 8). In general, the range of resource productivities for which the ontogenetic specialist outcompetes the generalist is larger when specialists do not switch completely from foraging on resource 1 as a juvenile to foraging on resource 2 as an adult, but rather when both juveniles and adults exploit both resources to a varying extent.

Ontogenetic specialists also outcompete ontogenetic generalists over larger ranges of resource productivity when mortality is high, which is not surprising given the increase in energetic efficiency of specialists with increasing mortality illustrated in figure 1.2. This increase in competitive ability with increasing mortality has very counterintuitive consequences for the coexistence of ontogenetic specialists and generalists in the presence of shared predators. The classic idea is that shared predators can promote the coexistence of an inferior and a superior competitor species, only if in the presence of predators the dominance of superior competitors is countered by higher predation mortality. Such predator-mediated coexistence of competitors thus relies on a trade-off for the two competitors between their competitive ability and vulnerability to predation.

When consumers go through an ontogenetic niche shift, however, this trade-off is not necessary for coexistence of the two competitors in the presence of a shared predator, as a consequence of the increase in energetic efficiency with higher mortality of ontogenetic specialists. More specifically, we show that an ontogenetic specialist with a significant competitive disadvantage, such that it is always outcompeted by the ontogenetic generalist in the absence of predators, can outcompete the generalist when predators are present. This reversal of competitive dominance occurs even if the ontogenetic specialist is the preferred prey of the predators and predators attack specialists at a higher rate than generalists (chapter 8). Hence, even with a double handicap, both a competitive and a predatory disadvantage, the ontogenetic specialist outcompetes the generalist over a significant range of resource productivities when predators are present as a consequence of the fact that the adaptability of its population stage structure allows it to exploit resources more efficiently when mortality increases.

ONTOGENETIC (A)SYMMETRY IN ENERGETICS AND POPULATION DYNAMICS

In simple but generic models that account for the size structure of a consumer population, ontogenetic symmetry in energetics leads to the same type of dynamics as observed in Lotka-Volterra predator-prey models: If resource growth is logistic, classical predator-prey cycles occur at high resource carrying capacity. If resource growth follows semichemostat dynamics and resource productivity is hence independent of resource density, the size-structured consumer-resource system approaches a stable equilibrium, as unstructured Lotka-Volterra models would. In contrast, size-structured consumer-resource models predict qualitatively different types of dynamics to occur in the two different regimes of ontogenetic asymmetry in energetics, which are characterized by either juveniles or adults being more efficient in acquiring food and/or their use of assimilated energy.

With semichemostat resource dynamics (i.e., constant resource productivity independent of resource density) size-structured consumer-resource models (figure 1.3, bottom row, left module) predict regular population cycles to occur in both regimes of ontogenetic asymmetry (chapter 9). The characteristics of these population cycles are, however, quite different in the two regimes. In cases where juvenile consumers are more efficient in their acquisition and use of energy, juveniles tend to outcompete all older and larger conspecifics, because their higher efficiency allows them to survive at lower resource densities. As a consequence, cycles in population density with large amplitude occur, in which the population is dominated by one and the same cohort of individuals throughout the entire cycle. In these so-called *juvenile-driven* cycles adult consumers are not continuously present in the population but only occur when the dominant cohort matures. Following maturation a dominant cohort produces a pulse of offspring that makes up the next dominant cohort. Their more efficient use of energy allows the offspring cohort to drive their parents to extinction, thereby monopolizing the population entirely. The life history of individual consumers in these population cycles resembles the consumer life history in a population equilibrium that is regulated by limited adult reproduction: juvenile growth in body size is fast, leading to short juvenile periods and high juvenile survival, while adult fecundity is low and adult lifespan is short. Moreover, the ratio between juvenile and adult consumer density is low during these cycles, as it is in a reproduction-controlled equilibrium state.

In cases where adult consumers are more efficient in their acquisition and use of energy, population cycles also occur over large ranges of parameters, but the amplitude of these so-called *adult-driven* cycles is much smaller

(chapter 9). The composition of the consumer population during these cycles is relatively constant, with juveniles and adults coexisting continuously throughout the cycle. Juvenile growth in body size is in this case slow and is further retarded when a pulse of consumers matures. The retardation of juvenile development and the consequent long juvenile period and low juvenile survival are major factors giving rise to the cycles. Adult fecundity and the ratio between juvenile and adult density are both high. These characteristics closely resemble the characteristics of an equilibrium state regulated by limited juvenile development.

In many aspects juvenile-driven and adult-driven population cycles thus resemble the consumer equilibrium states, regulated by limited reproduction and limited development, respectively. Both types of cycles have a period that is close to the duration of the juvenile stage, which distinguishes them from the classic predator-prey cycles occurring in unstructured Lotka-Volterra type models. When resource growth is logistic as opposed to following semichemostat dynamics, the size-structured consumer population exhibits complex dynamics as a result of an interaction between the cyclic tendency originating from the ontogenetic asymmetry in energetics and the cyclic tendency embodied in classic predator-prey cycles (chapter 9). In cases where adult consumers are more efficient in their energy use, this interplay results in the occurrence of two types of cycles over large ranges of parameters: one large-amplitude cycle that resembles the classic predator-prey cycle and another, with smaller amplitude, resembling the adult-driven ontogenetic cycle. In cases where juvenile consumers are more efficient in their use of energy, however, such bistability does not occur, and the resulting dynamics are more of a mixed type, in-between the juvenile-driven ontogenetic cycles and classic predator-prey cycles.

Juvenile-driven and adult-driven population cycles also occur in size-structured consumer-resource models that in more detail represent specific ecological systems. These cycles therefore seem to be robust population dynamic patterns, which occur independently of rather drastic changes in model assumptions—for example, whether reproduction occurs continuously throughout the year or only as a pulsed event in the beginning of summer (chapter 10; figure 1.3, bottom row, middle module). The type of ontogenetic asymmetry, whether juveniles or adults are energetically more efficient, determines which type of cycle ensues.

Other types of intraspecific interaction may annul the size-dependent, intraspecific competitive relations between juveniles and adults and thus suppress the occurrence of population cycles. As a particularly well-studied example, cannibalism of juveniles by adult conspecifics may stabilize

juvenile-driven population cycles that result from ontogenetic asymmetry in energetics (chapter 11; figure 1.3, bottom row, right module). However, the interplay between size-dependent competition for resources and size-dependent cannibalism also gives rise to new population dynamics phenomena. At low intensity, cannibalism of juveniles by adults completely cancels out the competitive advantage of juveniles, leading to rapid juvenile growth and low juvenile survival, while adult cannibals reach body sizes that are only slightly larger than their size at maturation. In a number of aspects this type of cannibal-driven dynamics resembles the “stunted-predator” equilibrium state that we observed in mixed interaction systems, in which juvenile predators compete for resources with consumers they prey on as adults (chapter 7). The cannibal-driven dynamics can be viewed as a single-species version of this “stunted-predator” dynamics.

At higher intensities of cannibalism, we also find a single-species analogue of the “stunted-consumer” equilibrium that occurred in mixed interaction systems (chapters 7 and 11). In this case a few adult cannibals can reach large (giant) body sizes, while the population as a whole is mainly regulated by resource competition among small juveniles. This competition leads to slow juvenile development, long juvenile periods, and relatively high juvenile survival. Because the mixed interaction now occurs within one and the same cannibalistic population, the two states are not simultaneously stable. Rather, the population alternates over time between these two regimes, giving rise to a new type of dynamics that we refer to as “dwarf-and-giant” cycles (chapter 11). In such cycles, periods of cannibal-driven and competition-driven dynamics alternate, in which the population is mainly regulated by top-down suppression of juveniles through cannibalism and competition for resources among juveniles, respectively. An extensive dataset on experimental lake systems supports model predictions for the occurrence of these dynamics in a number of cannibalistic systems (chapter 11).

Formulation and parameterization of detailed size-structured population models, as exemplified by the consumer-resource model (chapter 10) and the cannibal-resource model (chapter 11) that we study, requires the availability of large amounts of experimental data to carefully parameterize the various functions (for example, size-dependent feeding and maintenance rates, and energy allocation rates to growth and reproduction) describing individual life history. This data “hunger” of detailed models can be seen as a disadvantage, but detailed models also provide the advantage that they allow for extensive confrontation of model predictions against empirical data. In particular, they allow for more than just testing empirical observations on population-level statistics, such as the amplitude and periodicity of cycles. A major, but rather

unknown advantage of detailed size-structured models is that they make predictions about individual life history under conditions of density dependence and population feedback. Because they do not directly result from and hence are rather independent of the model assumptions, these predictions can be used for tests of model performance against observations on life history in natural situations. For both the size-structured, consumer-resource and the cannibalism model, such tests reveal the close match between model predictions and empirical data (chapters 10 and 11).

GENERALIZATION

The population and community effects of ontogenetic development that are discussed above have all been derived for systems in which the growth rate in body size during the ontogeny of individual organisms strongly depends on the availability of food. Although this is valid for the large majority of species, the growth patterns of mammals and many bird species is much less influenced by food availability and is more under genetic control. Several lines of evidence suggest, however, that the insights we obtained also hold more generally, for example, for systems in which growth rate in body size is largely independent of food availability and genetically more predetermined.

When growth in body size is genetically predetermined, it is not the supply (i.e., availability) of food that determines the energetics of individual organisms but the demands on energy for growth, maintenance, and reproduction. Such demand-driven energetics necessitate that energy storage of individual organisms in the form of reserve (i.e., fat) tissue is explicitly accounted for in population dynamic models, as the predetermined costs for somatic growth and maintenance have to be covered from these reserves in times of food shortage. We show that as a rule biomass overcompensation also occurs in a size-structured consumer-resource model based on demand-driven energetics of individual organisms (chapter 12). This biomass overcompensation again results from differential responses in maturation and reproduction rate, when intraspecific competition is relaxed and resource density increases at higher mortality levels. The changes in maturation rate, however, do not result from a shorting of the juvenile period, which is constant given the predetermined growth rate in body size. Rather, the changes in maturation and reproduction rate now result from differential changes in the amount of energy storage by juvenile and adult consumers when resource density increases.

This size-structured consumer-resource model based on demand-driven energetics also displays the same two types of population cycles that we identified

for size-structured models for consumers with supply-driven energetics (compare chapters 9 and 12). Juvenile-driven and adult-driven cycles occur when juveniles and adults are more efficient in their acquisition and use of energy, respectively. Moreover, the cycle characteristics in the demand-driven size-structured model in most major aspects resemble the characteristics of the two types of cycles in supply-driven, size-structured consumer-resource models. Lastly, theoretical considerations and experimental evidence also suggest that adult-driven cycles may be an important dynamic feature of populations of unicellular organisms as well.

Altogether, these lines of evidence hint at the generality of the distinct phenomena that we have revealed for the two different regimes of ontogenetic asymmetry, governed by a higher energetic efficiency of either juveniles or adults. Above all, we hope it will convince readers also to consider ontogenetic development in their own research as a major and important life history process shaping population and community dynamics.

Enjoy reading the details in the subsequent chapters!