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Chapter 1

General Introduction

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Outline

The main paradigms in population and community ecology are based on mathematical models that assume equal ecological interactions for all individuals in the population. These models are also referred to as unstructured models, and have provided important insights about the functioning of natural systems. However, accounting for variation in ecological interactions between individuals (*i.e.* intraspecific variation in ecological interactions), can help to even better understand the dynamics of populations and communities. Ontogenetic development is an important source of intraspecific variation in ecological interactions. Ontogenetic development refers to the changes in size, shape, physiology or maturity status of an individual that occur during its lifetime. Recently, ecological theory has been developed that accounts for the intraspecific variation in ecological interactions that arises from ontogenetic development (De Roos et al. 2013). This body of theory uses structured population models, which in contrast to unstructured models, can account for differences between individuals. Not only are the dynamics from structured models richer, they also overthrow many of the paradigms from unstructured ecological theory.

The crucial feature that leads to the dissemblance in dynamics between structured and unstructured theory is the *ontogenetic asymmetry* in energetics and mortality of an individual. Ontogenetic asymmetry implies that the mass-specific rates of resource ingestion, biomass production and mortality, change with individual body size (De Roos and Persson 2013). Thus, in case of ontogenetic asymmetry, ontogenetic development leads to intraspecific variation in ecological interactions. Structured ecological theory readily connects ontogenetic asymmetry in individual organisms to the dynamics of populations and communities (reviewed in De Roos and Persson 2013).

The next step is to understand the eco-evolutionary implications of ontogenetic asymmetry. This thesis takes this step by studying the evolutionary causes and consequences of ontogenetic asymmetry. After this introductory chapter, chapters 2 and 3 study whether and how selection can explain ontogenetic asymmetry in a basic ecological setting. In chapters 4 and 5, the ecological and evolutionary consequences of ontogenetic asymmetry for the long-term persistence of species in more complex ecological communities are studied. Finally, chapter 6 describes an example of how evolution can lead to more complexity in ecological communities.

The remainder of this chapter shortly describes the approach and some insights from the ecological theory that is based on unstructured models. Thereafter, reasons to develop theory that includes ontogenetic development will be discussed, and examples of the consequences of ontogenetic asymmetry for the dynamics of populations and communities will be given. Finally, a more specific description of the research questions of the following chapters will be presented.

Unstructured ecological theory

A main objective in ecology is to understand mechanisms and processes that govern the dynamics of natural populations and communities for a broad range of species and systems. A theoretical approach towards this goal is to use dynamic models that describe interacting populations, such as consumer-resource models (Murdoch et al. 2003), competition models (MacArthur 1970; Tilman 1980, 1982), models of three species trophic modules (Holt and Polis 1997; McCann et al. 1998; Polis and Holt 1992; Polis et al. 1989) and models describing multi-species food webs (De Ruiter et al. 1995; May 1972; McCann 2011). Many of the paradigms about how populations and communities function and persist have been developed through the strategic use of these models.

As an example of such paradigms, modeling studies have helped to realize that the fate of species co-depends on their dynamic, biotic environment. Furthermore, species impact their own environment and in such a way affect their own success. Therefore, fitness is not a static predefined trait, but rather it depends on the functioning of species in their dynamic environment. Another example is the work devoted to studying the conditions and mechanisms that lead to stable coexistence of species communities. Theory predicts that in constant environments, the number of competing species cannot be higher than the number of resources (Gause 1934; Hardin 1960). In natural communities there are often many species coexisting on a limited number of resources, and theoretical research has been valuable in discovering the potential mechanisms that enable many species to coexist on a limited number of resources (Chesson 2000; Huisman and Weissing 1999).

One way to link consumer-resource interactions to larger food webs is to study the dynamics of trophic modules (Bascompte and Melián 2005; Kondoh 2008). These are components within the greater food web, containing three or four species in different configurations. Examples of trophic modules are the diamond food web (Wollrab et al. 2013), where species compete for a resource and share a common predator, apparent competition (Holt 1977), in which case two species only interact through a shared predator, and intraguild predation (IGP), which describes a predator and a prey that also compete for a resource (Polis and Holt 1992; Polis et al. 1989). IGP appeared to be common in food webs (Bascompte and Melián 2005; Polis 1991; Polis and Myers 1985). Numerous fish, amphibian, reptile and insect species are engaged in IGP (Persson 1988), and this interaction can also be found in zooplankton communities (Toscano et al. 2016). However, early theoretical work showed limited potential for coexistence of intraguild predators with intraguild prey. This finding stimulated more research on the mechanisms that enhance coexistence in intraguild predation systems (*e.g.* Diehl and Feißel 2000; Diehl and Feissel 2001; Mylius et al. 2001).

Many of the above models are population-level models (De Roos and Persson 2005), as their formulation begins by considering population-level processes. A population-level viewpoint considers ecosystems as trophic pyramids, in which the nodes are populations composed of identical individuals (De Roos and Persson 2005). Implicitly, this approach assumes that existing intraspecific variation between individuals within a population is negligible, in terms of its impact on population-level processes, and hence can be ignored. Therefore, all individuals are considered to have identical ecological interactions. This concerns both the *type* of interaction (*e.g.* feeding, predation or competition) as well as the *strength* of the interaction (*e.g.* rates of resource feeding, or competitive ability). For intraguild predation systems, this implies that all intraguild predators simultaneously hunt for intraguild prey and feed on the shared resource. In addition, it also implies that all intraguild predators have identical rates of resource feeding and identical predation rates. Because of the lack of internal structure in such a population, population-level models are also called unstructured models. An important consequence of the assumption that all individuals are identical, is that these models delimit population dynamics to mere changes in population numbers or total population biomass. The life histories of individual organisms are therefore only represented by the processes of reproduction and mortality, which respectively lead to an increase and a decrease in population density.

Ontogenetic development: an important life history process

However, beyond the two key processes of reproduction and mortality, an important life-history process is ontogenetic development. Ontogenetic development can be regarded as the collection of changes in the state of an individual that occur during its life, in terms of changes in size, shape, physiology, maturity status, or behavior. It is well recognized that ontogenetic development plays a major role in the life of all species, as there are no species that reproduce immediately after birth (De Roos and Persson 2013). In any species, individuals must first grow in size and develop maturity before they can commence reproduction. One of the most striking and critical features of ontogenetic development is ontogenetic body size growth. In many species, the differences in size between newborns and adults can span several orders of magnitude (De Roos and Persson 2013). Also, the preponderance of species with complex life cycles or metamorphosis is illustrative for the importance of ontogenetic development in nature.

Ontogenetic development unavoidably creates intraspecific variation in ecological interactions (DeAngelis and Mooij 2005), as the nature of many ecological processes changes as a result of ontogenetic development. For example, juveniles and adults

can compete for resources that are important for their growth and reproduction, and juveniles might be better or weaker competitors. Alternatively, in many species juveniles and adults consume different resources and occupy different habitats, either as a result of ontogenetic niche shifts or metamorphosis (Werner 1988; Werner and Gilliam 1984). Juveniles and adults may also experience differences in predation, because of different predators or different predation rates. To return to the example of intraguild predation, in many cases the competition and predation between intraguild predators and prey are separated between different life stages of the intraguild predator. In these so-called life history intraguild predation systems (LHIGP: Hin et al. 2011; Pimm and Rice 1987; Van de Wolfshaar et al. 2006), juvenile intraguild predators compete with intraguild prey, while adult intraguild predators feed on intraguild prey.

Intraspecific variation in ecological interactions that originates from ontogenetic development can have significant consequences for ecological and evolutionary processes. Population-level models cannot account for this variation, as these models do not consider differences between individuals. Studying the population and community consequences of ontogenetic development therefore requires a different modeling approach. A framework is needed that describes the important life history processes of individuals (ontogenetic development, reproduction and mortality), and subsequently translates these individual-level dynamics to the population and community level (De Roos and Persson 2001; Diekmann and Metz 2010). Such an approach is used by structured population models. In the next section I will introduce this modeling approach and subsequently describe how ontogenetic development can change the dynamics of populations and communities.

Structured ecological theory

Structured population models start by describing the ecology and key life history processes of individuals. The population and community-level dynamics then emerge from the individual-level processes (De Roos and Persson 2001; Diekmann and Metz 2010; Metz and Diekmann 1986). Structured population models keep track of the individuals separately or track the distribution that describes the (relative) abundance of different types of individuals, *i.e.* the population structure or population composition. Changes in the population composition make the dynamics of structured population models more complex compared to unstructured models. A structured modeling approach that incorporates ecological interactions with descriptions of life histories is provided by the framework of physiologically structured population models (PSPMs; De Roos 1997; De Roos et al. 1992; Metz and Diekmann 1986). The core ideas of this framework are outlined in box 1.1.

Ontogenetic (a)symmetry

In order to understand the consequences of ontogenetic development for the dynamics of populations and communities, one needs to specify the conditions under which ontogenetic development does not lead to changes in ecological interactions. For this we use the condition of *ontogenetic symmetry*, which applies if and only if the mass-specific ingestion rate, the mass-specific biomass production rate and the mortality rate of an individual do not change with individual body size (De Roos et al. 2013). Any deviation from the conditions of ontogenetic symmetry leads to *ontogenetic asymmetry*. In case of ontogenetic asymmetry, either the mass-specific resource ingestion rate, the mass-specific biomass production rate or the mortality rate changes with individual body size (De Roos et al. 2013). Ontogenetic symmetry describes the conditions under which ontogenetic development does not lead to deviations in the strength of ecological interactions. Conversely, ontogenetic asymmetry introduces changes in strength of ecological interactions during ontogeny through changes in the resource intake, biomass productivity or mortality.

There are many sources of ontogenetic asymmetry in natural populations. For example, the biomass production rate of an individual depends on both the energy assimilated from food and the amount of energy required for maintenance metabolism. When these two processes scale differently with body size, this leads to ontogenetic asymmetry through changes in the mass-specific biomass production. Also, ontogenetic asymmetry will readily result from ontogenetic diet shifts or metamorphosis, through a shift in mass-specific ingestion or mass-specific biomass production rates. Size-dependent mortality is also an important source of ontogenetic asymmetry. These different examples suggest that ontogenetic asymmetry applies to individuals in most, if not all species.

In population-dynamical equilibrium, ontogenetic asymmetry leads to a difference in productivity between different life stages. For the whole population, the rate of biomass production through growth or reproduction must necessarily equal the rate of biomass loss through mortality, in order to remain at population equilibrium. When in one life stage biomass production exceeds biomass loss, this net gain of biomass must be compensated for in the other life stage (De Roos et al. 2007). Therefore, in the latter life stage a net biomass loss must occur.

Ontogenetic asymmetry in a consumer species with a distinct juvenile and adult life stage, for example, translates into *juvenile-adult asymmetry*, when the population is at equilibrium (De Roos et al. 2013). Juvenile-adult asymmetry implies a difference in net biomass productivity between juvenile and adult life stages. When the juvenile life stage is a net source of biomass, the adult life stage is a net sink of biomass. Consequently, population-level maturation rate in biomass exceeds population-level

Box 1.1: Physiologically structured population models (PSPMs)
Ecological models that describe interacting populations and also incorporate an explicit description of individual life history (that can depend on these ecological interactions) are referred to as physiologically structured population models (PSPMs; De Roos 1997; De Roos et al. 1992; De Roos and Persson 2001; Metz and Diekmann 1986). A PSPM uses structuring variables (individual-states or *i*-states), such as age, size or energy reserves, to distinguish different individuals. Individuals can only differ with respect to their *i*-state value and individuals that have same *i*-state values are considered fully identical by the PSPM. The population of all individuals is tracked by the *p*-state (from population-state), which is a measure that describes the distribution of all individuals within the *i*-state space (the collection of all possible *i*-states). The specification of a PSPM lies in describing the *i*-state dynamics, which reflect life history processes. The rate of change of an *i*-state can depend on the current *i*-state value (*e.g.* body size, amount of energy reserve), on the state of the environment (the *E*-state, *e.g.* resource density) or on the *p*-state or some scaled version of the *p*-state (*e.g.* predator pressure from cannibalism). All assumptions of a PSPM pertain to the specification of the *i*-state dynamics or the dynamics of the environment. No further population-level assumptions are required. Ecological interactions within a PSPM framework occur between two structured populations or between a structured population and the environment (*e.g.*, a size-structured consumer population feeding of an unstructured resource). In many PSPMs, a Dynamic Energy Budget (DEB) model is used to describe the *i*-state dynamics. A DEB model describes the rates of uptake, allocation and use of energy and nutrients for energy-demanding processes within an organism, such as growth, reproduction and maintenance metabolism (Kooijman 2010). Using a DEB model confines the individual life history to what is physically possible, as organisms have to adhere to the principle of mass and energy conservation. For example, organisms need to take up energy from the environment to grow and reproduce and cannot use the same amount of energy twice. The resource input of the DEB model can be an environmental variable in the PSPM. The joint feeding of all individuals depletes resource densities, which limits growth and reproduction through the dynamics of the DEB model. In such a way density-dependence is introduced through a dynamic feedback between consumer feeding and resource renewal.

reproduction rate in biomass. The biomass turn-over through the life cycle is in this case regulated mostly by reproduction (De Roos et al. 2007). Alternatively, when the adult life stage is a net source of biomass and the juvenile stage is a net sink of biomass, the population-level reproduction rate in biomass exceeds the population-level maturation rate in biomass. In this case, the biomass turn-over is regulated mostly by maturation.

Ontogenetic development can thus lead to changes in the strength of ecological interactions through ontogenetic asymmetry. Ontogenetic asymmetry in turn leads to an asymmetry in the productivity of different life stages when the population is in equilibrium. Next, I will describe how ontogenetic asymmetry affects dynamics of populations and communities.

Population and community consequences of ontogenetic asymmetry

Structured population models have revealed considerable effects of ontogenetic asymmetry on the dynamics of populations and communities (reviewed in De Roos et al. 2013). Ontogenetic asymmetry leads to phenomena through changes in population composition. The most important consequence for community dynamics is *biomass overcompensation*, which is the phenomenon that (stage-specific) biomass density increases with increasing mortality (De Roos et al. 2007).

Biomass overcompensation occurs because mortality relaxes competition for resources and in this manner indirectly increases resource density. In case of ontogenetic asymmetry this will lead to a disproportionate increase in the production rate of the life stage that limits the population-level biomass turn-over most. As a consequence, the equilibrium biomass density in the other life stage increases. In a maturation-regulated population, mortality leads to an increase in maturation rate and this increases adult biomass density. In a reproduction-regulated population, mortality increases the reproduction rate and this increases juvenile biomass density.

Biomass overcompensation is a robust phenomenon and has been demonstrated to occur in several empirical systems (Cameron and Benton 2004; Ohlberger et al. 2011; Reichstein et al. 2015; Schröder et al. 2014). It occurs when different life stages share a resource, or feed on separate resources that differ in productivity. It occurs independent of whether mortality is increased in the sink or the source life stage, or in both simultaneously (De Roos and Persson 2013). Also, biomass overcompensation happens irrespective of life-history details and whether reproduction occurs continuously throughout the year or with a seasonal pattern (Soudijn 2016).

Biomass overcompensation differs from the Hydra effect, which describes a (time-averaged) positive mortality response in the cyclic dynamics of unstructured consumer-resource models (Abrams 2009). The essential ingredients for the occurrence of the Hydra effect are a positive correlation between resource productivity and resource density (as in logistic resource growth) and a saturating consumer functional response (Schröder et al. 2014). An increase in consumer mortality will change the amplitude and period of the consumer-resource cycle, which can lead to an increase in time-averaged consumer density. Biomass overcompensation occurs because of energetic bottlenecks in life history of the consumer and is independent of the type of resource growth, or the consumer functional response.

Biomass overcompensation creates a positive feedback between the mortality rate and the biomass density of a life stage. This allows stage-specific predators to increase their own prey availability, which results in an emergent Allee effect for the predator (De Roos and Persson 2013; De Roos et al. 2003*b*). Through a similar mechanism, two

stage-specific predators are able to mutually facilitate each other's persistence (De Roos et al. 2008*a*).

Besides biomass overcompensation, ontogenetic asymmetry can induce cohort cycles in the population dynamics (De Roos and Persson 2013). These arise through changes in competitive ability during ontogeny. Competitively superior individuals require lower resource densities to cover their maintenance needs than competitively inferior individuals. Size-dependent changes in competitive ability arise when mass-specific ingestion rates change in a different way with size than mass-specific biomass production rates. When juveniles are superior competitors, they outcompete their parents by suppressing resource density. This will lead to juvenile-driven cohort cycles (De Roos and Persson 2003). Alternatively, adult-driven cycles occur when adults are superior competitors. In this case, destabilization occurs because of an increase in the juvenile period, caused by limited food availability, combined with a sudden increase in fecundity and adult biomass when the dominant cohort matures (De Roos and Persson 2003, 2013).

The omnipresence of ontogenetic asymmetry and its strong effects on the structure and dynamics of populations and communities, raises the question of how ontogenetic asymmetry evolves. Under which conditions does selection favor ontogenetic asymmetry, and how do ecological factors affect selection on the strength and direction of ontogenetic asymmetry? Furthermore, how does selection on ontogenetic asymmetry affect the long-term potential for persistence of species and food webs? These are the main questions that will be addressed in this thesis and answering these questions requires a framework that integrates ecological interactions with the evolution of life histories. The next section will motivate such a framework and introduce the more specific research questions of the following chapters.

Studying the eco-evolutionary dynamics of ontogenetic asymmetry

There are at least two reasons why ecological interactions must be accounted for when studying the evolutionary origins of life histories. The first is that life histories are plastic and vary with ecological conditions, such as resource availability (Claessen et al. 2000; Van Kooten et al. 2007) and predation (Pfennig et al. 2010). The second reason is that optimal life histories and ecological dynamics influence each other through an eco-evolutionary feedback. As life history decisions affect ecological interactions, in turn, the ecological interactions determine which life history strategy returns the highest fitness and is selected for. This leads to a constant feedback between evolutionary change and ecological response (Ferrière and Legendre 2013; Palkovacs and Post 2008; Post and Palkovacs 2009).

Studying the eco-evolutionary dynamics of ontogenetic asymmetry thus requires an approach that incorporates both ecological interactions and eco-evolutionary feedbacks. The theory of adaptive dynamics provides such an approach. The concepts and rationale of adaptive dynamics are discussed in box 1.2. This thesis will combine the structured models as described in box 1.1, with the adaptive dynamics approach to study the evolutionary origin of ontogenetic asymmetry and its consequences for the persistence of populations. The specific research questions will be motivated next.

Chapter 2 and 3 study the evolution of ontogenetic asymmetry in a basic ecological setting. This involves a size-structured consumer population feeding on an unstructured resource. The life history of the consumer is described by a simple dynamic energy budget (DEB) model (Kooijman 2010; Lika and Nisbet 2000). In this DEB model, the rate of maximum resource ingestion and the rate of maintenance metabolism follow power functions of body mass. The exponents in these power functions determine the body-mass scaling of energy intake (through resource ingestion) and energy expenditure (through maintenance metabolism). Biomass production of the consumer equals the difference of energy intake and energy expenditure. The scaling of biomass production with body mass therefore depends on the scaling exponents of both maximum ingestion and maintenance metabolism.

Chapter 2 shows that there is strong selection towards an equal body-mass scaling of energy supply and energy expenditure, but only under limited conditions do these scaling exponents evolve exactly to ontogenetic symmetry (linear scaling of both energy supply and energy expenditure with body size). The type of ontogenetic asymmetry that evolves leads to higher mass-specific resource ingestion and mass-specific biomass production for either juveniles or adults. As a consequence, one life stage becomes a net source of biomass, while the other life stage becomes a net sink of biomass. Which life stage becomes a net source depends on the size-dependency of mortality and the extent of pre- and post-maturation growth. Furthermore, the evolved type of ontogenetic asymmetry (equal scaling exponents of maximum ingestion and maintenance metabolism) ensures that all individuals require the same resource density to cover their maintenance costs. This neutralizes intraspecific competition and stabilizes population dynamics.

Chapter 3 extends the approach of chapter 2 and studies whether ontogenetic asymmetry can arise from multiple processes that determine the body-mass scaling of energy supply. In addition to the scaling of maximum ingestion rate with body mass, in chapter 3 the scaling of energy supply is also determined by the attack rate scaling. Chapter 3 shows that ontogenetic asymmetry does not evolve from considering separate scaling processes for energy supply. This result is also consistent between two different trade-offs that are considered.

Box 1.2: Adaptive dynamics

Adaptive dynamics (Geritz et al. 1998; Metz 2012; Metz et al. 1995) is an approach for studying adaptive phenotypic evolution in ecological models that describe interacting populations. Adaptive dynamics distinguishes between resident and mutant phenotypes. Initially, the population consists only of the resident phenotype (*i.e.* is monomorphic) and resides at its population dynamical attractor (*e.g.* stable equilibrium point, limit cycle). Evolutionary change occurs when mutants with a slightly different phenotype invade and take over the population-dynamical attractor of the resident. Whether the mutant invades and replaces the resident not only depends on the phenotype of the mutant, but also on the environment in which the mutant invades. In turn, this environment depends on the resident trait, because it is the resident that determines the population dynamical equilibrium in which mutants invade. The fitness of the mutant is hence a function of the trait values of both the mutant and the resident. The tools of adaptive dynamics provide methods to quickly assess the long-term outcome of many subsequent rounds of mutant-resident interactions. The dynamics between mutants and residents make adaptive dynamics a framework in which evolutionary change explicitly depends on ecological dynamics.

Chapter 4 and 5 consider an intraguild predation (IGP) system to study the consequences of ontogenetic asymmetry in a more complex community than the basic ecological setting of chapters 2 and 3. Size-dependent interactions can readily induce ontogenetic asymmetry in IGP systems. For example, an ontogenetic diet shift in the intraguild predator (in case of life-history IGP (LHIGP); Hin et al. 2011; Rudolf 2007; Van de Wolfshaar et al. 2006) leads to a difference in the mass-specific ingestion and the mass-specific biomass production rate between juvenile and adult intraguild predators. Also, cannibalism is common in LHIGP systems and increases both adult mass-specific production and juvenile mortality.

Chapter 4 shows that the ontogenetic asymmetry that arises from cannibalism disrupts the stable persistence of intraguild predators, irrespective of the type of change in diet that the intraguild predator exhibits during its life. Cannibalism leads to a shift from a reproduction- to a maturation-regulated population. In a maturation-regulated population, juvenile intraguild predators suffer from competition with intraguild prey. With increasing levels of cannibalism, the competition in the juvenile stage becomes too severe for stable predator persistence.

Chapter 5 builds on chapter 4, by studying how ontogenetic asymmetry in resource ingestion and biomass production evolves in response to cannibalism in an IGP system. It is assumed that intraguild predators can evolve to increase juvenile biomass production and resource ingestion by increasing juvenile specialization on the shared resource. Such an increase could potentially offset the negative effects of competition in the juvenile life stage under high levels of cannibalism. Alternatively, evolution of adult specialization will increase intra- and interspecific predation rates. This leads

to an increase in ingestion and biomass production for adults. However, a genetic constraint between the life stages is assumed to prevent concurrent specialization of both life stages on their respective food source. Hence, the direction and strength of ontogenetic asymmetry in the intraguild predator can evolve through selection on an ontogenetic trade-off in resource specialization.

Chapter 5 shows that in absence of cannibalism, selection on this ontogenetic trade-off leads to an increase in specialization of one life stage, at the expense of feeding performance in the other life stage. Ultimately, this increasing specialization of one life stage shifts the community dynamics to a state in which predators can no longer persist. Consequently, selection on the ontogenetic trade-off in absence of cannibalism leads to evolutionary suicide of the intraguild predator. Cannibalism prevents evolutionary suicide by stabilizing selection on the ontogenetic trade-off in resource specialization.

Chapter 4 and 5 thus show that cannibalism has a central role in LHIGP systems. Cannibalism can inhibit persistence of intraguild predators on ecological timescales (chapter 4), but also stabilizes evolutionary dynamics and prevents evolutionary suicide (chapter 5). It is therefore important to understand the conditions that inhibit or promote the evolution of cannibalism. Chapter 6 addresses this topic in the more applied and practical context of fisheries-induced evolution. In chapter 6 a model for the population dynamics of cannibalistic Arctic char (*Salvelinus alpinus)* is formulated. With this model the eco-evolutionary interaction between cannibalism and fisheries-induced mortality on large char individuals is investigated. It is shown that fisheries-induced mortality promotes the evolution of cannibalism, by changing the stabilizing selection on cannibalism resulting from costs associated with cannibalistic feeding, into positive directional selection. This leads to a double effect of mortality on the population. The fisheries-induced mortality decreases population biomass directly, but also selects for even higher rates of cannibalism, which further reduces population density. The interaction between ecological and evolutionary effects of harvesting severely increases vulnerability of cannibalistic Arctic char populations to high levels of mortality.

Finally, chapter 7 summarizes the main findings of the preceding chapters and discusses how these results contribute to understanding the conditions under which ontogenetic asymmetry evolves in basic and more complex ecological communities.

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