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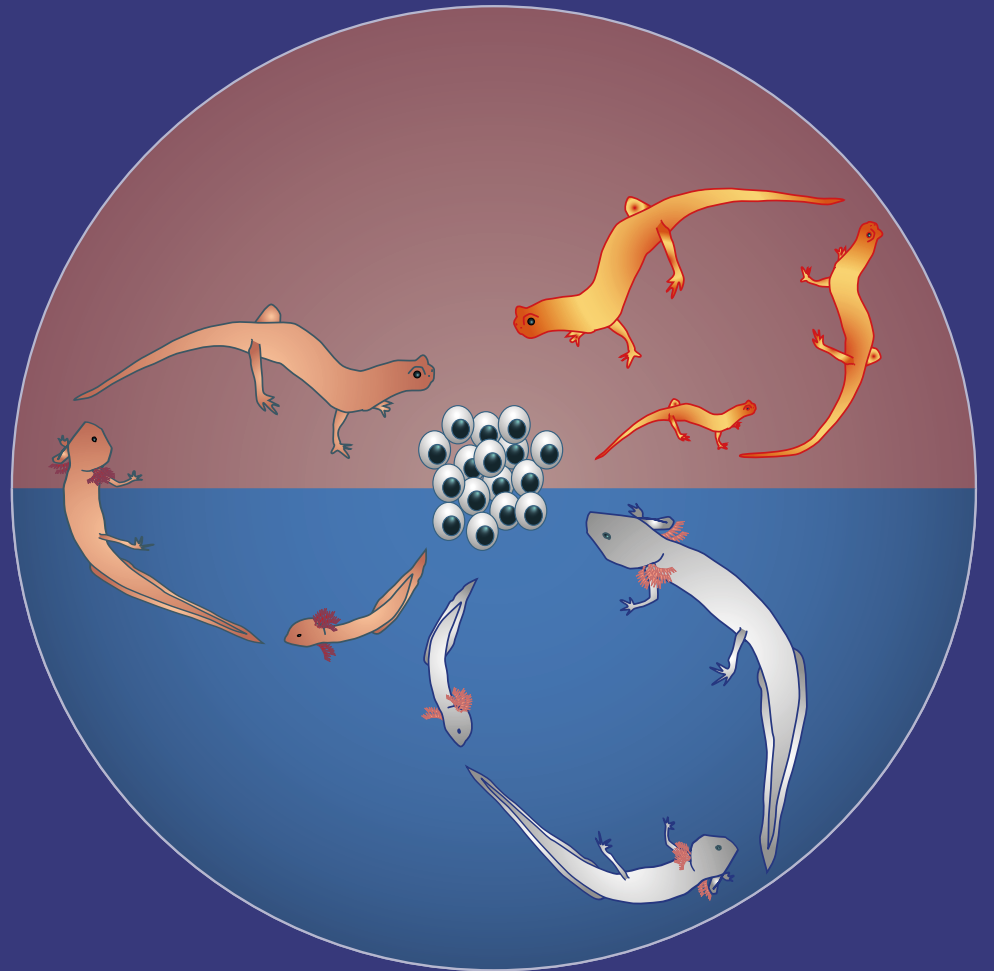
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# Evolution of complex life cycles

Hanna ten Brink



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2018



Evolution  
of  
Complex  
Life Cycles

by  
Hanna ten Brink

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of  
Complex  
Life Cycles

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ter verkrijging van de graad van doctor

aan de Universiteit van Amsterdam

op gezag van de Rector Magnificus

prof. dr. ir. K.I.J. Maex

ten overstaan van een door het College voor Promoties ingestelde commissie,

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CHAPTER

1

## GENERAL INTRODUCTION

Hanna ten Brink

### 1.1 Background

Voracious caterpillars change into elegant butterflies and swimming tadpoles become hopping frogs. The offspring of asymmetrical flatfish just look like typical, upright swimming, baby fish, and the offspring of most crustaceans (e.g., lobster) bear little resemblance to the adult form. All these species possess a metamorphosis and undergo a radical shift in their morphology, behavior and habitat during their lives. Metamorphosis has not only fascinated biologists but is also a recurrent theme in the classical literature. The famous Roman poet Ovid wrote the narrative poem "The Metamorphoses", consisting of more than 250 myths where humans change to animals, trees or stars, animals into humans, ivory becomes flesh and blood is turned into flowers. In Franz Kafka's *Metamorphosis* (1915), one morning poor Gregor Samsa "found himself transformed in his bed into a monstrous vermin". Each child is familiar with the brothers Grimm fairy tale of the frog that changes into a handsome prince after he is kissed by a princess. Even though these mysterious transformations in the literature are a fascinating topic, this thesis is not about such types of metamorphoses but about the biological process of an animal that undergoes a relatively abrupt life-history transition at a certain point in its life.

There is a continuous gradient from direct developing species that only experience a diet shift during their ontogeny to species that have a complex life cycle with an abrupt ontogenetic change in morphology, behavior, or physiology (Werner 1988; Werner and Gilliam 1984) (see box 1.1 for the definitions of these terms). Among fish for example, size-specific shifts in food type are common without large changes in morphology (Werner and Gilliam 1984). Hemimetabolous insects, such as dragonflies and grasshoppers, undergo some morphological changes during development, but the changes are gradual and not spectacular (Brown 1977). Holometabolous insects, such as bees and butterflies, on the other hand, undergo sharp and abrupt metamorphoses that separate the different life stages. Werner (1988) estimated that approximately 80% of all animal species undergo a metamorphosis during their life cycle. Additionally, a large proportion of species without a metamorphosis have a clear shift in diet during their ontogeny.

Fossil evidence and phylogenetic distributions of complex life cycles indicate that this strategy evolved more than two hundred million years ago in insects (Labandeira and Sepkoski 1993) and amphibians (Wassersug 1975). In marine invertebrates this was already in the Cambrian period (500 Mya) (Strathmann 1993). It has even been suggested that the common ancestor of all animals already had a biphasic life cycle, with a pelagic larva and a benthic adult stage (Jägersten 1972). The ubiquity of complex life cycles is therefore probably not the result of many evolutionary origins but rather of their ecological success. Even though a complex life cycle is apparently a suc-

cessful strategy, it also got lost several times in evolutionary history. Via, for example, the evolution of direct development (e.g., in some frog species; Callery et al. 2001) or the evolution of paedomorphosis (e.g., in salamanders; Bonett et al. 2014a). This then raises the question why are complex life cycles so pervasive and under which ecological conditions did they evolve? Why did some species lose a complex life cycle while others did not?

During metamorphosis individuals can rebuild their body plan (e.g., Aguirre et al. 2014). It has therefore been hypothesized that metamorphosis evolved such that individuals can occupy different niches during their life or specialize on different tasks (Moran 1994). Taxa that nowadays exhibit a sharp and abrupt metamorphosis between different life stages have evolved from a situation where the changes from newborn to adult were more continuous. In insects and marine invertebrates it has been shown that the morphological divergence between different life stages has increased during the course of evolution (Brown 1977; Nielsen 1998). Furthermore, the ancestors of frogs looked more like the metamorphosing stage than the larvae or adults of present-day species (Wassersug and Hoff 1982). Gradually the different life stages became morphologically more distinct from each other and ultimately a metamorphosis evolved. Fossils of early amphibians showed that an ontogenetic shift from feeding under water as a larva to feeding on land as an adult was a crucial factor for the evolution of this metamorphosis (Schoch 2009). Based on these observations it is thought that ontogenetic changes in niche were the first steps in evolutionary history towards complex life cycles (Nielsen 1998; Persson 1988; Schoch 2009; Werner 1988). To understand why complex life cycles have evolved and why they are so successful, it is therefore necessary to understand how ontogenetic niche shifts have evolved.

Given the ubiquity of ontogenetic niche shifts and complex life cycles, there is surprisingly little theory on the evolution of these life-history strategies (but see Ebenman 1992; Istock 1967; Werner 1988; Werner and Gilliam 1984). Istock (1967) argued that a metamorphosing population, where larvae and adults can adapt completely independent from each other, is evolutionary unstable. When one of the two life stages is slightly better adapted than the other, selection will favor the reduction and ultimately loss of the other stage (Istock 1967). A metamorphosing population will therefore always evolve to a population without metamorphosis. In contrast to the idea of metamorphosis as being inherently unstable, Ebenman (1992) showed that a metamorphosing population, in which different life stages exploit different food sources, can hardly be invaded by a mutant without a complex life cycle and is therefore evolutionarily very successful. Other studies by Werner and Gilliam (1984) and Werner (1988) mainly focused on the optimal timing of niche shifts and metamorphosis and do not really investigate how complex life cycles arose in the first place. They argue that complex life cycles are selected for in order to maximize growth rates and mini-

### **Box 1.1: Definitions**

**Adult:** The mature stage of an animal species.

**Adaptive dynamics:** A mathematical framework to model evolution in an ecological setting.

**Complex life cycles (CLC):** A life history where individuals abruptly change their morphology, habitat, behavior, physiology, and/or diet at a certain point in their lives.

**Direct development:** A life history where individuals are born with the adult morphology. The larval stage is completely absent or develops within the parent.

**Juvenile:** The life stage of a species that mostly resembles the adult but is not yet mature.

**Larva:** The free-living developmental stage of a species that differs in morphology from the adult stage.

**Maturation:** The transition from the non-reproducing juvenile to the mature adult stage.

**Metamorphosis:** A life-history transition from the free-living larval stage to the (non-mature) juvenile stage.

**Ontogeny:** The development of an individual over its lifetime.

**Ontogenetic niche shift:** A change in food source and/or habitat use over the course of ontogeny.

**Pedomorphosis:** A derived life history where individuals never metamorphose and reach maturation with the larval morphology.

**Physiologically structured population model (PSPM):** A model that characterizes individuals by some state (e.g., size, age, sex or genotype).

mize mortality rates at each size. When the growth rate in one stage is greatly reduced compared to another stage, there would be selection to reduce the time spent in this stage and therefore to change the timing of the niche shift and/or metamorphosis.

What these studies have in common is that they assume fixed growth, mortality, and reproduction rates for a certain strategy. The impact of individuals on their environment is not taken into account. The fitness of an individual depends crucially on growth and reproduction, which are in most species largely determined by food intake (de Roos and Persson 2013). Both metamorphosis and niche shifts during ontogeny will change the food intake of an individual, and result in a change in its fitness. If changing niches during ontogeny increases the fitness of an individual, this trait can in principle spread in the population. However, if individuals start exploiting a different food source, this will affect the densities of the food sources that are used by the population. This will in turn alter the profitability of the niche shift and thereby the fitness of the shifting individual. Hence, this feedback loop between the individuals and the environment should be taken into account when studying the ecological conditions promoting the evolution of complex life cycles.

The aim of this thesis is to provide new insights into the evolutionary gain and loss of ontogenetic niche shifts and complex life cycles, taking into account the feedback loop between individuals and their environment. Ontogenetic niche shifts, metamorphosis, direct development and paedomorphosis (box 1.1) evolved long ago (e.g., Strathmann 1993; Wolfe 2017). The ecological conditions that promoted the evolution of these life-history strategies have probably changed considerably since then. To better understand the ecological conditions that have led to the gain and loss of complex life cycles, it is therefore useful to study an evolutionary model. While there are many ecological factors (e.g., dispersal, predation, or mate finding) that can promote the evolutionary gain or loss of complex life cycles, this thesis focuses on one aspect specifically; the effect of food availability.

## 1.2 Modeling biological evolution

Concepts such as 'survival of the fittest', 'the struggle for existence' and simple Mendelian inheritance are familiar to first-year biology students and even to laymen, yet evolution is a tremendously complex process. Traits almost never follow simple Mendelian inheritance, where one gene, consisting of two alleles, corresponds to one trait. Instead, traits are often controlled by multiple genes, which furthermore consist of more than two alleles. Additionally, the fitness of an individual depends on many factors, such as the presence of competitors and predators, food availability and environmental conditions. Even though evolution can occur on ecological timescales, it is usually a relatively slow process which makes evolutionary experiments often difficult.

Theoretical models help to better understand evolution and can avoid the difficulty of evolutionary experiments. Models are, however, always simplifications of the real system. The more complex and detailed the model, the harder it becomes to understand the mechanisms leading to a certain result. Therefore, when modeling evolution, simplifications are essential to gain new insights. What to include and exclude in a particular model depends a lot on the question that the modeler tries to answer. Someone interested in the molecular mechanisms underlying metamorphosis needs a different approach than someone that wants to study how a gene that affects the timing of metamorphosis can spread in the population. Every approach that models biological evolution is in a way always a caricature of the system under study since simplifying assumptions have to be made.

One approach, the framework of adaptive dynamics, provides the fundamental tools to study evolution in an ecological context (Geritz et al. 1998). It is, therefore, the appropriate modeling framework for understanding the evolution of complex life cycles. Adaptive dynamics allows for the study of evolution in a detailed ecological setting, often at the cost of ignoring genetic detail. Adaptive dynamics assumes that the

focal population consists only of individuals with one specific, the so-called resident phenotype and evaluates whether or not a mutant with a slightly different phenotype has a positive growth rate and will hence increase in the population. It furthermore assumes that the ecological time scale is much faster than the evolutionary time scale. Therefore, mutant individuals appear infrequently, such that a beneficial mutant becomes fixed in the population and that the ecological dynamics reach a stable attractor before the next mutant arises. The success of a mutant depends not only on its own phenotype but also on the environment it encounters. Since the environment is determined by the strategy of the resident population, the fitness of a mutant depends indirectly also on the phenotype of the resident population (Geritz et al. 1998).

### 1.3 Size-structured population models

The approach of adaptive dynamics has been applied to many evolutionary problems, such as the evolution of specialization in resource utilization (e.g., Egas et al. 2004 and Nurmi and Parvinen 2013), evolution of habitat choice (e.g., Ravnigné et al. 2009) and evolution of life-history parameters such as survival and reproduction (e.g., White et al. 2006). Most studies of adaptive dynamics use unstructured ecological models, where all individuals within the population are identical (but see Claessen and Dieckmann 2002).

Individuals do, however, grow during their life. After an individual is born it needs to at least double in size before it can reproduce. In many species newborn individuals increase several orders in magnitude in mass before they are mature (Werner and Gilliam 1984). Differently sized individuals differ in rates of food intake, mortality, maintenance, and reproduction (de Roos and Persson 2013). As a result, individuals in different life stages have different effects on the environment and on the population dynamics. Juvenile individuals, for example, do not reproduce and therefore do not contribute to the growth of a population. Adults, on the other hand, do reproduce but do not always eat (e.g., in many Chironomidae). Differently sized individuals can furthermore experience different selection pressures, which can lead to implicit trade-offs between the different life stages.

Ontogenetic niche shifts and metamorphosis are by definition processes that take place during an individual's development, and an individual's ontogeny should therefore be taken into account when modeling complex life cycles. The framework of physiologically structured population models (PSPMs, de Roos and Persson 2001) allows for intraspecific variation among individuals, such as differences in size or age, and can therefore be used to study complex life cycles. In PSPMs, all assumptions pertain to the individual level and the population dynamics than emerge from these individual-level processes. The state of an individual, characterized by variables such as size, age,

or energy reserves, determines an individual's development, mortality, reproduction and its effect on the environment (e.g., food levels or conspecifics). PSPMs are completely deterministic, which implies that all individuals with the same state develop in an identical way.

## 1.4 Outline of the thesis

This thesis will combine physiologically structured population models and the adaptive dynamics framework to study under which ecological conditions complex life cycles can evolve.

Since it is thought that ontogenetic changes in niche have been the first step in evolutionary history towards life cycles with a metamorphosis, chapters 2 and 3 study how ontogenetic niche shifts can evolve. In both chapters it is assumed that there are two different types of food present. One of these food sources, the primary food source, is available for all consumers. The secondary food source, on the other hand, is only available for large consumers. Small individuals are too small to handle this food source, which is for example the case for many piscivorous fish species that need to reach a certain size before they are large enough to feed upon other fish (Mittelbach and Persson 1998). The two types of food are considerably different from each other, for example plant material and insects, such that an individual specialized in feeding on one food source is not very efficient in feeding on the other.

Chapter 2 studies when consumers switch to the secondary food source and if individuals can specialize in feeding on this new food source. Specialization on the secondary food source comes at a cost since it reduces specialization on the primary food source. This leads to a trade-off between early and late foraging success. A stage-structured consumer-resource model is used to study the evolution of ontogenetic niche shifts.

While in chapter 2 it is assumed that the population is in a stable equilibrium, size-structured populations often exhibit different types of population cycles (de Roos and Persson 2003, 2013; Persson et al. 1998). The evolutionary analysis of non-equilibrium population dynamics is, however, much harder compared to equilibrium conditions, especially for structured populations. Since it has been shown that non-equilibrium dynamics can have a profound effect on the evolutionary behavior of systems (Hoyle et al. 2011; Nurmi and Parvinen 2013; White et al. 2006), chapter 3 investigates how the type of population cycles affect the evolution of ontogenetic niche shifts.

In chapter 4 it is studied under which ecological conditions metamorphosis can evolve in species that change niches over their life cycle. During metamorphosis individuals can rebuild their body plan. This allows individuals to specialize on multiple niches during their lives. However, metamorphosis is an energetically costly process

(e.g., Geffen et al. 2007) and is, furthermore, quite risky (e.g., Wassersug and Sperry 1977). In this chapter it is studied when the benefits of metamorphosis outweigh the costs such that it can evolve.

While metamorphosis is the dominant life-history strategy in the animal kingdom, it disappeared several times during the evolutionary history. Chapter 5 shows under which conditions metamorphosis disappears, either via the evolution of direct development or via the evolution of paedomorphosis. Given that metamorphosing species crucially depend on multiple niches for their survival and growth, I especially focus on the evolutionary loss of metamorphoses under deteriorating food conditions.

In chapter 6 I summarize the results of the thesis and discuss the implications of the results on the understanding of the evolution of complex life cycles.



**A PARENT-OFFSPRING TRADE-OFF LIMITS THE  
EVOLUTION OF AN ONTOGENETIC NICHE SHIFT**

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## Abstract

Many free-living animal species, including the majority of fish, insects, and amphibians, change their food and habitat during their life. Even though these ontogenetic changes in niche are common, it is not well understood which ecological conditions have favored the evolution of these shifts. Using an adaptive dynamics approach, we show that it is evolutionarily advantageous to switch to an alternative food source in the course of ontogeny when this results in a higher intake rate for the switching consumers. Individuals are, however, not able to specialize on this new food source when this negatively affects the performance early in life on the original food source. Selection on these early life stages is so strong that in species with a complete diet shift, evolution results in large juveniles and adults that are maladapted to the alternative food source while their offspring are specialized on the original food source when young. These outcomes suggest strong selection to decouple the different life stages, such that they can maximize their performance on different food sources independently from each other. Metamorphosis could be a way to decouple the different life stages and therefore evolve in species that feed on multiple food sources during their life.

## 2.1 Introduction

Almost all free-living animal species change their niche during their life. The best-known examples are species with a metamorphosis, such as frogs and butterflies, that change not only their diet and habitat but also their complete morphology over their lifetime. Less well-known examples of species changing their niche include fish (e.g., many piscivorous fish feed on zooplankton when small; Mittelbach and Persson 1998), reptiles (e.g., lizards are often carnivorous early in life but switch to herbivory later; Werner and Gilliam 1984), and invertebrates (e.g., spiders include larger food items in their diet when they grow larger; Turner 1979). These so-called ontogenetic niche shifts are the rule rather than the exception in the animal world (Werner and Gilliam 1984).

A common explanation for the evolution of ontogenetic niche shifts is that shifting niches is a way to maximize somatic growth rate at each size (Werner 1988; Werner and Gilliam 1984). Larger individuals often gain access to food sources and habitats that they cannot use when small. Furthermore, growth of an individual will change its energy requirements and also its feeding efficiency on different food sources (Werner and Gilliam 1984). Therefore, the profitability of a given prey type generally changes with increasing body size. By changing niches, species can optimize growth rates across the life cycle. Werner and Gilliam (1984) have shown that the population growth rate is maximized when individuals shift between niches in such a way that the ratio of mortality to growth is minimized at each size. However, this explanation for the evolution of ontogenetic niche shifts is based on individual-level optimization and does not take into account the feedback between an individual and its environment (other individuals of the population, food densities, etc.). Changing niches over ontogeny will affect food densities and thereby the profitability of the different diets. This change in food densities will in turn change the optimal strategy of an individual. Therefore, when studying the evolution of ontogenetic niche shifts one should take into account the feedback between the environment, in particular food densities, and the different strategies of individuals. Although the optimal timing for ontogenetic niche shifts has been investigated in such a context (Claessen and Dieckmann 2002), it is not well understood which ecological conditions have favored the evolution of ontogenetic niche shifts in the first place. The aim of this article is to gain insight into how ontogenetic niche shifts can evolve, taking into account the feedback between the environment and the individuals.

In this study we investigate which food conditions promote the evolution of an ontogenetic niche shift in species where large individuals have access to an alternative food source, assuming that there is a trade-off between early and late foraging success. Different food sources often require different morphologies to be effectively uti-

lized (Hjelm et al. 2000; Werner 1977). Hence, species that change their food source use over their lifetime experience different selection pressures on their morphologies in different phases of their life. Whereas some species (e.g., many frog species) undergo sharp and abrupt metamorphoses to accommodate such ontogenetic changes in selection pressure, other species (e.g., the banded watersnake *Nerodia fasciata*; Vincent et al. 2007) cope with ontogenetic niche shifts only through allometric changes in body form to modify feeding morphology and thereby their efficiency on different food sources. There are, however, limits to the extent that allometric growth can change the morphology of an organism. Changing diet during ontogeny can therefore lead to a trade-off between early and late foraging success, since specialization on one food source comes at the expense of specialization on the other (Werner and Gilliam 1984). Of course, it would be advantageous for a species with an ontogenetic niche shift to be able to specialize independently on the different food sources to get rid of the trade-off between early and late foraging success. However, life stages often cannot evolve independently from each other because of genetic correlations between the stages (Schluter et al. 1991). Perch (*Perca fluviatilis*), for example, switch from pelagic zooplankton to benthic macroinvertebrates and ultimately other fish over their ontogeny (Persson 1988). It has been hypothesized that perch are susceptible to morphological trade-offs, which will reduce efficiency in each of these niches, compared to a species that specializes in only one niche (Bergman and Greenberg 1994; Persson 1988). Hjelm et al. (2000) indeed showed that such a trade-off in body morphology between the benthic and piscivorous niches exists.

In this study we assume that there is an original food source available for all individuals and an alternative food source that, because of size constraints, is available only for large juveniles and adults but not for small juveniles, as, for example, occurs in many fish species that start life as planktivores but become piscivores when they have reached a size advantage over their potential prey (Mittelbach and Persson 1998). We further assume that the two food sources occur either in the same habitat or in two nonoverlapping habitats. When they occur in the same habitat (e.g., plankton and prey fish in a pelagic environment), there is only selection on the foraging skills (attack rates) of the consumers on the two food sources. On the other hand, when the food sources occur in two nonoverlapping habitats (e.g., the pelagic and benthic parts of a lake), there is, in addition to selection on these foraging skills, selection for the food/habitat preference. For the purpose of this study we define the ontogenetic niche as the combination of this food/habitat preference and the foraging skills of the consumer. First, we investigate for which food source productivities individuals specialize to an alternative food source when it occurs in the same habitat as the original food source. Second, we study how both the food source use and the specialization on the different food sources evolve when they occur in two nonoverlapping habitats. To take

into account how ecological interactions can affect evolution, we use the framework of adaptive dynamics. Adaptive dynamics provides the fundamental tools to study evolution in an ecological context (Dieckmann and Law 1996; Geritz et al. 1998) and is therefore an appropriate framework to study the evolution of ontogenetic niche shifts in the context of possible population feedback on food sources. [1mm]

## 2.2 Model and methods

### Population dynamics

We model the population dynamics of a consumer population feeding on two food sources, using the stage-structured biomass approach as developed in de Roos et al. (2008). Such a stage-structured biomass model captures the dynamics of a continuous size distribution, ranging between the size at birth of neonate individuals and the (fixed) size of the non-growing adult individuals, while keeping track of the changes in biomass only in one or more juvenile body-size classes and the class of nongrowing adult individuals. In contrast to the original formulation of this stage-structured biomass framework, however, we analyze a simplified version in which possible starvation conditions of consumers are ignored, as on an ecological time scale the consumer-resource model always approaches a stable equilibrium that precludes individual starvation. Since ontogenetic niche shifts generally occur between the larval and juvenile stages, before sexual maturation (e.g., in fish, amphibians, marine invertebrates, and the ancestor of holometabolous insects; Sehnaal et al. 1996), we divide the juvenile stage into two classes, small juveniles (S) and large juveniles (L). It is assumed that the population feeds on two food sources that possibly occur in two distinct habitats. One of the food sources, the original food source ( $X_1$ ), is available for all individuals, while the other food source, the alternative food source ( $X_2$ ), is available only for large juvenile and adult (A) consumers. When the two food sources occur in the same habitat, the consumer experiences the food sources as intermixed in space and can feed on both food sources simultaneously. When the two food sources occur in two nonoverlapping habitats, individuals have to choose which food source to feed on. In this case there is, for large individuals, a trade-off between foraging on  $X_1$  and foraging on  $X_2$  that is absent when the food sources occur in the same habitat. To capture these differences in feeding behavior, we use the following spatially implicit multispecies mass-specific functional response (McCann et al. 2005) for large juveniles and adults foraging in two habitats of the same size:

$$\frac{f_1 a_1 X_1 + f_2 a_2 X_2}{1 + h(f_1 a_1 X_1 + f_2 a_2 X_2)}, \quad (2.1)$$

where  $f_1 = \beta + (1 - \beta)\phi$  and  $f_2 = \beta + (1 - \beta)(1 - \phi)$ . In this equation,  $\beta$  is the amount of spatial overlap of the two food source habitats,  $\phi$  is the relative preference for the original food source, and  $a_1$  and  $a_2$  are the mass-specific attack rates on the original

and alternative food source, respectively. When  $\beta = 1$ , the two food source habitats overlap completely and the two food sources are intermixed in space. In this case, the preference parameter  $\phi$  is obsolete and selection acts only on the attack rates  $a_1$  and  $a_2$ . Alternatively, when  $\beta = 0$ , the two food sources occur in two nonoverlapping habitats, and individuals need to choose which food source to forage on. The parameters  $f_1$  and  $f_2$  determine the fraction of time large individuals search for the original and the alternative food source, respectively. The following set of differential equations describes the ecological dynamics of the biomass densities of the consumer and the food sources:

$$\begin{aligned}
 \frac{dX_1}{dt} &= \delta(X_{1,\max} - X_1) - \frac{qa_1X_1S}{1+hqa_1X_1} - \frac{f_1a_1X_1(L+A)}{1+h(f_1a_1X_1+f_2a_2X_2)}, \\
 \frac{dX_2}{dt} &= \delta(X_{2,\max} - X_2) - \frac{f_2a_2X_2(L+A)}{1+h(f_1a_1X_1+f_2a_2X_2)}, \\
 \frac{dS}{dt} &= v_S(X_1)S + v_A(X_1, X_2)A - \gamma_S(v_S, \mu_S)S - \mu_S S, \\
 \frac{dL}{dt} &= \gamma_S(v_S, \mu_S)S + v_L(X_1, X_2)L - \gamma_L(v_L, \mu_L)L - \mu_L L, \\
 \frac{dA}{dt} &= \gamma_L(v_L, \mu_L)L - \mu_A A.
 \end{aligned} \tag{2.2}$$

Default parameter values of the model are listed in table 2.1. The food sources follow semi-chemostat dynamics with a turnover rate of  $\delta$  and will reach equilibrium densities of  $X_{1,\max}$  and  $X_{2,\max}$ , respectively, in the absence of the consumer population. The consumers feed according to a type 2 functional response on the food sources. The stage-structured biomass approach is based on the assumption that the rates of food intake and maintenance are linearly related to the body size of individual consumers. Since feeding efficiencies often change over ontogeny (Werner 1988) we include the factor  $q$  to modulate the attack rate of the smallest individuals. When  $q = 1$ , all stages have the same mass-specific attack rate on the original food source. For values of  $q$  larger (smaller) than 1, the smallest individuals are more (less) efficient in feeding on the original food source than larger sized individuals. Ingested food is assimilated with efficiency  $\sigma$  and first used to cover maintenance costs. All individuals have a mass-specific maintenance rate of  $T$  per unit biomass. The difference between mass-specific food intake and maintenance costs determines the mass specific net biomass production of individuals:

$$\begin{aligned}
 v_S(X_1) &= \sigma \frac{qa_1X_1}{1+hqa_1X_1} - T, \\
 v_L(X_1, X_2) &= v_A(X_1, X_2) = \sigma \frac{f_1a_1X_1 + f_2a_2X_2}{1+h(f_1a_1X_1 + f_2a_2X_2)} - T.
 \end{aligned} \tag{2.3}$$

Juveniles invest all their net biomass production in growth in body size, while adults convert all their net biomass production into new offspring. It is assumed that adults

do not grow anymore and have an identical size  $M_A$ . We assume that small and large juveniles and adults experience constant background mortality rates of  $\mu_S$ ,  $\mu_L$ , and  $\mu_A$ , respectively. Juveniles mature into the next stage (large juveniles or adults) after reaching a certain size. Offspring are born at a size  $M_A z_1 z_2$ . The parameters  $z_1$  and  $z_2$  represent the ratio between the smallest and largest sizes of individuals within the small-juvenile and large-juvenile stages, respectively. The mass-specific maturation functions depend on the net biomass production, the mortality rate, and the size range ( $z_1$  or  $z_2$ ) over which an individual grows in a certain stage. The form of the maturation functions has been derived from an underlying, fully size-structured population model to ensure the exact identity between all equilibrium states in the stage-structured biomass model and its fully size-structured analog (see de Roos et al. (2008) for details). The mass-specific maturation functions for small and large juveniles, respectively, are given by:

$$\begin{aligned}\gamma_S(v_S, \mu_S) &= \frac{(v_S - \mu_S)}{1 - z_1^{(1 - \mu_S/v_S)}}, \\ \gamma_L(v_L, \mu_L) &= \frac{(v_L - \mu_L)}{1 - z_2^{(1 - \mu_L/v_L)}}.\end{aligned}\quad (2.4)$$

Notice that starvation conditions are ignored which implies that  $v_S(X_1)$ ,  $v_L(X_1, X_2)$ , and  $v_A(X_1, X_2)$  are always positive and therefore  $\gamma_S(v_S, \mu_S)$ , and  $\gamma_L(v_L, \mu_L)$  as well.

### Evolutionary traits

The niche of an individual is determined by the preference for a certain food source (determined by the parameter  $\phi$ ) and how well the consumer is specialized on this food source (determined by the attack rates). We assume that specialization on one food source comes at the expense of specialization on the other, leading to a trade-off between early and late foraging success. This means that small juveniles that are specialized on the original food source have a low efficiency on the alternative food source as adults and, vice versa, that adults that are highly specialized on the alternative food source produce offspring that perform badly on the original food source. To incorporate this in the model, we adopt a simple linear trade-off between the two mass-specific attack rates  $a_1$  and  $a_2$ , which is given by

$$\begin{aligned}a_1 &= \psi A_{\max}, \\ a_2 &= A_{\max} - a_1 = (1 - \psi) A_{\max}.\end{aligned}\quad (2.5)$$

In these equations  $\psi$  is the relative specialization on the original food source and  $A_{\max}$  is the maximum value the attack rates can have. A value of  $\psi = 1$  means that individuals are completely specialized in feeding on the original food source. In this case

individuals cannot feed on the alternative food source at all. For low values of  $\psi$ , individuals are very efficient in feeding on the alternative food source and not very efficient in feeding on the original food source. Note that  $\psi$  can never have a value of 0 because in that case individuals cannot feed on the original food source at all, since  $a_1 = 0$ . The smallest individuals depend on this food source for their growth and therefore need to be able to feed on this.

The relative preference for a certain food source is determined by the parameter  $\phi$ . A value of  $\phi = 1$  means that large individuals have a strong preference for (the habitat with) the original food source. Vice versa, a value of  $\phi = 0$  means that large individuals have a strong preference for (the habitat with) the alternative food source. When the food sources occur in the same habitat ( $\beta = 0$ ), large individuals experience both food sources as completely intermixed in space and therefore forage on both food sources. In this case, the parameter  $\phi$  drops out of the model formulation, and evolutionary considerations of the food preference of large individuals are irrelevant.

When the two food sources occur in two nonoverlapping habitats ( $\beta = 1$ ), both  $\phi$  and  $\psi$  evolve. Parameter  $\psi$  is a morphological trait that affects the foraging skills of an individual for its whole lifetime. Parameter  $\phi$ , however, is more a behavioral trait that determines the food source preference of an individual. This trait affects large juveniles and adults but not small juveniles, since they can feed only on the original food source. Therefore, the parameter  $\phi$  determines a trade-off only for large individuals between feeding on the original and feeding on the alternative food source, while parameter  $\psi$  represents a trade-off between early and late foraging success.

### Evolutionary analysis

For the evolutionary analysis the framework of adaptive dynamics is used (Dieckmann and Law 1996; Geritz et al. 1998). Adaptive dynamics is based on the assumptions that individuals reproduce asexually, that the population is completely monomorphic, and that small mutations occur randomly. These mutations occur infrequently, such that the mutant trait either spreads or dies out and the population has reached its ecological attractor before the next mutant arises. The ecological timescale is therefore considered much faster than the evolutionary timescale. The success of a mutant depends on its strategy and on the environment it encounters. In our model, the environment that a mutant experiences consists of the two food source densities, which are in equilibrium with the resident population and thus depend on the strategy of the resident ( $\bar{X}_1(\phi, \psi)$  and  $\bar{X}_2(\phi, \psi)$ ). The fitness of a mutant depends, therefore, not only on its own strategy but also indirectly on the strategy of the resident. From here onward we use, for simplicity, the notation  $X_1$  and  $X_2$  to refer to the equilibrium densities of the food sources set by the strategy of the resident. The lifetime reproductive output,  $R_0$ , can be used as a measure of invasion fitness (Mylius and Dieckmann 1995). For the lifetime



reproductive output of a mutant the notation  $R_0((\phi', \psi') | (\phi, \psi))$  is used to indicate that it depends on both its own strategy  $(\phi', \psi')$  and the strategy of the resident population  $(\phi, \psi)$  through its dependence on the food source densities that are set by the resident. A mutant can invade only if  $R_0((\phi', \psi') | (\phi, \psi)) > 1$ . This new population can then subsequently be invaded by another mutant that has an invasion fitness that exceeds unity. In this way, the population experiences a succession of mutations and evolves in the direction of the selection gradient

$$\frac{\partial R_0(\mathbf{y}' | \mathbf{y})}{\partial \mathbf{y}'}, \quad (2.6)$$

where  $\mathbf{y}$  is the trait vector  $(\phi, \psi)$ . The point where the selection gradient becomes 0 is the evolutionarily singular strategy (ESS), which can be evolutionarily unstable or stable. In the latter case, no other mutant can invade in the population. If the singular strategy is evolutionarily unstable, evolutionary branching can occur (Geritz et al. 1998).

The lifetime reproductive output of an individual equals the probability of surviving until adulthood times the expected number of offspring produced over the lifetime of an adult. The survival probability until adulthood depends on the duration of the juvenile period and the mortality rate. Since juveniles mature into the next size class when reaching a certain size, the juvenile period depends on the growth rate and the size range over which a juvenile grows. The probability of surviving to the next size class can be shown to equal

$$\frac{\mu_S}{z_1 v_S(X_1)} \quad (2.7)$$

for small juveniles and

$$\frac{\mu_L}{z_2 v_L(X_1, X_2)} \quad (2.8)$$

for large juveniles (box 3.1 in de Roos and Persson 2013). All the net biomass production of adult individuals, which, given their size  $M_A$  equals  $M_A v_A(X_1, X_2)$ , is used for reproduction. Since offspring are born at a size  $M_A z_1 z_2$  the reproduction rate (number of individuals per day) of a single adult equals  $\frac{v_A(X_1, X_2)}{z_1 z_2}$ . The average lifetime of an adult equals  $\frac{1}{\mu_A}$ . The lifetime reproduction of a mutant is then given by:

$$R_0((\phi', \psi') | (\phi, \psi)) = \frac{v_A(X_1, X_2, \phi', \psi')}{\mu_A z_1 z_2} \frac{\mu_S}{v_S(X_1, \phi', \psi')} \frac{\mu_L}{v_L(X_1, X_2, \phi', \psi')}. \quad (2.9)$$

In this equation, the notations  $v_S(X_1, \phi', \psi')$ ,  $v_L(X_1, X_2, \phi', \psi')$  and  $v_A(X_1, X_2, \phi', \psi')$  are used for the net biomass production of small juvenile, large juvenile, and adult mutants, respectively, in the environment set by the resident population.

### Model analysis

When the two food sources occur in the same habitat, only parameter  $\psi$  evolves. In this case, we calculate and classify all possible ESSs for different parameter combinations,

using the PSPManalysis software package (de Roos 2016). This software numerically computes the (ecological) equilibrium of the model as a function of any parameter, using the computational approach as described in Kirkilionis et al. (2001), Diekmann et al. (2003) and de Roos (2008). The basic idea behind this method is to solve for the equilibria of a physiologically structured population model by iteratively computing the resource densities for which the lifetime reproductive output of an individual equals 1. To compute the latter, the individual life history is computed by integrating a set of coupled ordinary differential equations that describe how the survival, fecundity, growth, and feeding of an individual changes over its lifetime. The PSPManalysis automatically detects and classifies ESSs according to the classification of Geritz et al. (1998). The package can continue these singular points as a function of a second model parameter (see de Roos 2016 for details).

To analyze the evolutionary dynamics when two traits evolve simultaneously, we use the canonical equation of adaptive dynamics to study to which attractor the system evolves. The canonical equation is a deterministic approximation of the evolutionary trajectory of traits, assuming infinitesimally small mutations (Dieckmann and Law 1996; Durinx et al. 2008), see Appendix 2.A for more details. We assume that, initially, all individuals forage on the original food source ( $\phi = 1$ ) and are specialists on this food source as well ( $\psi = 0.9$ ). A value of  $\psi = 0.9$  means that large individuals are able to feed on the alternative food source but are not very efficient in doing so. We deliberately choose a value of  $\psi < 1$  to ensure that large individuals are able to feed on the alternative food source. A value of  $\psi = 1$  means that large individuals cannot feed on the alternative food source at all, and in this case there is no selection pressure on  $\psi$  or  $\phi$ . We use PSPManalysis to simulate the evolutionary dynamics when both parameters evolve. In addition, we use a C-based simulation program to simulate the evolutionary dynamics in parameter areas where there are two ecologically stable equilibria.

### Parameterization

All biomass densities are expressed in milligrams per liter, and time is expressed in days. Per capita mortality rates ( $\mu_S$ ,  $\mu_L$  and  $\mu_A$ ) are stage specific, while the other consumer parameters are either mass specific (maintenance rate, attack rate, and maximum ingestion rate) or dimensionless and therefore the same for all three stages. For the adult body weight ( $M_A$ ) a value of 0.1 mg is chosen; the weight of a newborn individual is 0.001 mg. Both  $z_1$  and  $z_2$  have a value of 0.1, which means that small and large juveniles mature to the next stage after they have achieved a tenfold increase in their weight. Following de Roos and Persson (2013; box 3.4), we assume that the mass-specific maintenance rate, the mass-specific attack rate, the mass-specific maximum ingestion rate (which is the inverse of the handling time), and the per capita mortality rate are proportional to the quarter power of the adult body size (Brown et al. 2004;

Peters 1986). Hence, all these rates scale as  $cM_A^{-0.25}$ , with different scaling constants  $c$ , where  $M_A$  is expressed in grams. The scaling of all rates with adult body mass also implies that, qualitatively, model predictions are independent of the choice of  $M_A$ . Varying  $M_A$  changes the timescale over which evolutionary change occurs but not the end points. Scaling constants are chosen for invertebrate species. For the mass-specific maintenance rate a scaling constant of 0.01 is chosen (Brown et al. 2004; de Roos and Persson 2013; Yodzis and Innes 1992). For the mass-specific maximum ingestion rate a scaling constant of 0.1 is chosen (de Roos and Persson 2013; Hansen et al. 1997), such that the handling time scales with  $10 M_A^{0.25}$ . For the background mortality rate a scaling constant of 0.002 is used (Gillooly et al. 2001) for large juveniles and adults. Mortality rates are often size specific and often decrease with size (e.g., Hampton 2000; Sogard 1997). To take this into account, we use for small juveniles a scaling constant of 0.002 or 0.004, to study how increased juvenile mortality affects the results. Ingested biomass of both food sources is assimilated with an efficiency of 0.5 (Peters 1986). For the food sources turnover rate we assume a value of 0.1 per day, which is equal to the metabolic rate of an adult with a body size of 0.1 mg. In this way the food source turnover rate takes place at approximately the same rate as consumer turnover through metabolism. The maximum food source densities and the mass-specific attack rates are the only volume-related parameters in the model. Changing the values of these parameters has a qualitative effect on model dynamics only when these changes affect the products  $a_1 \cdot X_{1,\max}$  or  $a_2 \cdot X_{2,\max}$ . Changes in attack rate and maximum food source densities that leave these products unaffected merely represent a scaling of the volume in which the system exists and therefore change model dynamics only quantitatively. The attack rates are determined by parameters  $\psi$ ,  $A_{\max}$ , and  $q$ . We adopt a maximum value of 0.06 for the scaling constant of the mass-specific attack rate with  $M_A^{-0.25}$ , such that  $a_1 = 0.6$  when  $\psi = 1$ . Therefore,  $A_{\max} = 0.6$ . For parameter  $q$  we assume a value of 1 or 1.2. In the first case, all individuals have the same mass-specific attack rate. In the latter case, small juveniles are 1.2 times as effective in feeding on the original food source as large individuals.

**Table 2.1:** Parameters of the model

Parameter	Default Value	Unit	Description
$\delta$	.1	day <sup>-1</sup>	Food source turnover rate
$\sigma$	.5	-	Conversion efficiency
$A_{\max}$	.6	L mg <sup>-1</sup> day <sup>-1</sup>	Maximum mass-specific attack rate
$h$	1	day	Mass-specific handling time
$T$	.1	day <sup>-1</sup>	Mass-specific maintenance rate
$M_A$	.1	mg	Adult weight
$z_1$	.1	-	Body size ratio of smallest and largest individuals in small-juvenile size range
$z_2$	.1	-	Body size ratio of smallest and largest individuals in large-juvenile size range
$\mu_L, \mu_A$	.02	day <sup>-1</sup>	Mortality rate of large juveniles and adults
$\mu_S$	.02 or .04	day <sup>-1</sup>	Mortality rate of small juveniles
$q$	1 or 1.2	-	Relative efficiency of small juveniles in feeding on $X_1$
$X_{1,\max}, X_{2,\max}$	variable	mg L <sup>-1</sup>	Maximum biomass density of food sources 1 and 2
$\phi^*$	0 - 1	-	Relative preference for food source 1 by large juveniles and adults
$\psi^*$	0 - 1	-	Relative specialization on food source 1

\*Parameter can change because of evolution

### 2.3 Results

A mutant that increases its feeding rate at any life stage increases its lifetime reproductive output (equation 2.9). An increase in the feeding rate in the juvenile stages will increase the somatic growth rate of the mutant, while an increase in the feeding rate in the adult stage will increase its reproduction rate. A mutant that has a higher food intake (which increases with the product of food density, the attack rate, and the preference) than the resident can therefore invade. The most advantageous strategy for large individuals is therefore to search for the food source that is the most abundant and specialize on this food source as well. However, the smallest individuals can feed only on the original food source, and their growth and survival critically depend on this food source. Since we assume that specialization on one food source comes

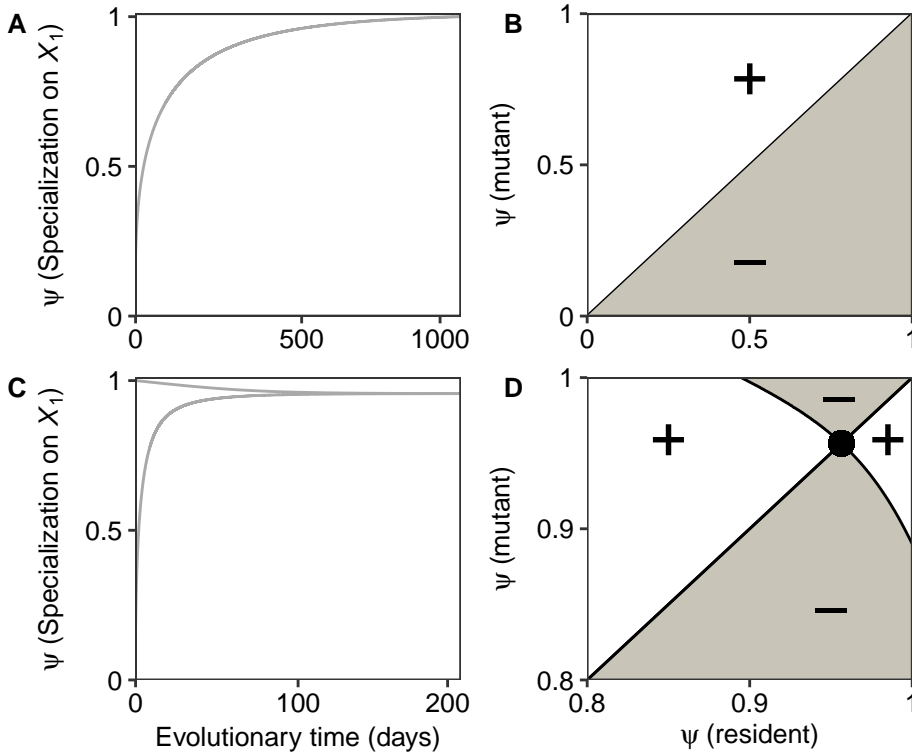
at the expense of specialization on the other, this leads to a trade-off between early and late foraging success. Because of this trade-off, large individuals that specialize on the alternative food source produce offspring that are maladapted to the original food source. In the first part of this section, we study the evolution of ontogenetic niche shifts when the two food sources occur in the same habitat ( $\beta = 1$ ). In this case, only the specialization  $\psi$  evolves. In the second part, we consider the case where the two food sources occur in two nonoverlapping habitats ( $\beta = 0$ ).

### **Two food sources occurring in the same habitat**

When the two habitats overlap completely, the consumer does not need to choose between habitats and can therefore feed on both food sources simultaneously. In this case, there is selection only on the foraging skills of the consumer ( $\psi$ ), that is, on the attack rates ( $a_1$  and  $a_2$ ) on the two food sources. Depending on the value of  $X_{2,\max}$ , we find two qualitatively different evolutionary outcomes. Individuals either completely lose their ability to forage on the alternative food source or they do feed on the alternative food source but are not very efficient in doing so ( $a_2$  remains low).

Figure 2.1A shows how specialization  $\psi$  evolves when the maximum density of the alternative food source is very low. Independent of the initial value of  $\psi$ , it will always evolve to 1 (figures 2.1A, 2.1B). Individuals will therefore lose their ability to feed on the alternative food source ( $a_2 \rightarrow 0$ ) and will feed only on the original food source. In this case, large individuals cannot eat the alternative food source, even though it occurs in the same habitat, because they do not have the right morphology to do so. When  $X_{2,\max}$  is very low, the density of the alternative food source is much lower than that of the original food source. It is therefore beneficial for large individuals to specialize completely on the original food source and thereby ignore the alternative food source.

Figure 2.1C shows a typical evolutionary time course for intermediate and high values of  $X_{2,\max}$ . Independent of the initial value,  $\psi$  always evolves to values just below 1. The pairwise invasibility plot of figure 2.1D shows that this ESS is convergent stable. Therefore, once this point is reached, no other mutant can invade in the population. Because specialization  $\psi$  evolves to high values, individuals broaden their diet when they grow larger, but they are not very efficient in feeding on the alternative food source (the attack rate  $a_2$  remains close to 0). Apparently, the trade-off between early and late foraging success hinders specialization on the food source used later in life.



**Figure 2.1:** Evolutionary outcome when the two food sources occur in the same habitat ( $\beta = 1$ ) for both a low (A, B) and a high (C, D) value of  $X_{2,\max}$ . A, Change in the specialization parameter  $\psi$  over evolutionary time, starting from  $\psi = 0.2$ , when  $X_{1,\max} = 3$  and  $X_{2,\max} = 0.8$ . Parameter  $\psi$  evolves to a value of 1, meaning that individuals will completely lose the ability to feed on the alternative food source. B, Pairwise invasibility plot (PIP) for  $X_{1,\max} = 3$  and  $X_{2,\max} = 0.8$ , showing that  $\psi$  always evolves to a value of 1 independent of the starting values. White areas indicate positive invasion fitness and gray areas negative invasion fitness. C, Change in the specialization parameter  $\psi$  over evolutionary time, starting from two different initial conditions ( $\psi = 1$  or  $\psi = 0.16$ ), when  $X_{1,\max} = 3$  and  $X_{2,\max} = 2.5$ . Independent of the starting value,  $\psi$  evolves to a value of 0.96, meaning that large individuals are specialized on the original food source and are not very efficient in feeding on the alternative food source. D, PIP showing the location of the evolutionarily singular strategy for  $X_{1,\max} = 3$  and  $X_{2,\max} = 2.5$ . Independent of the initial value,  $\psi$  will always evolve to a value of 0.96. White areas indicate positive invasion fitness and gray areas negative invasion fitness. Evolutionary time units are arbitrary in A and C (see app. 2.A).

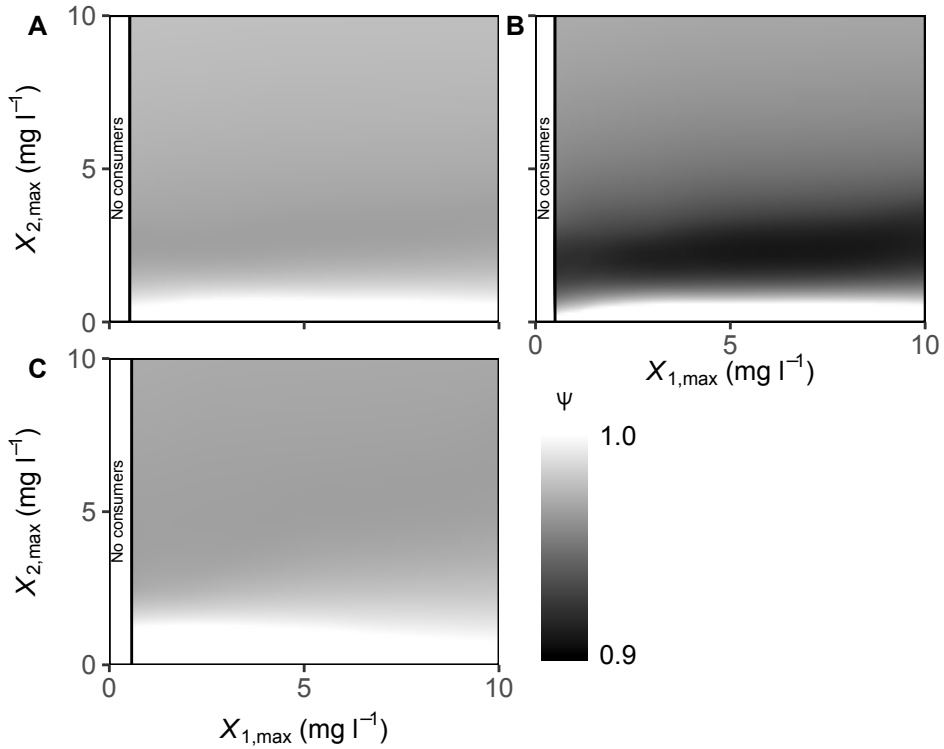
Figure 2.2A shows to which value  $\psi$  evolves as a function of  $X_{1,\max}$  and  $X_{2,\max}$ . Specialization  $\psi$  always evolves to a convergent stable strategy (CSS). When the maximum density of the alternative food source is very low,  $\psi$  evolves to a value of 1, meaning that individuals have lost their feeding ability on the alternative diet ( $a_2 = 0$ ). The alternative food source is therefore not exploited at all, and an ontogenetic niche shift does not evolve. For increasing values of  $X_{2,\max}$ ,  $\psi$  evolves to slightly lower values (minimum value of specialization  $\psi$  equals 0.95,  $a_2 = 0.03$ ), meaning that large individuals can feed on the alternative food source but are not very efficient in feeding on this food source. Surprisingly, for very high values of  $X_{2,\max}$  the CSS value of  $\psi$  increases again, and large individuals become even more inefficient in feeding on the alternative food source. Increasing  $X_{2,\max}$  will increase adult food availability and therefore fecundity. This will increase competition among small juveniles. Apparently, it is in that case even more important for small juveniles to be highly specialized on the original food source. In summary, large individuals cannot specialize on the alternative food source, even when this food source is very abundant, when this negatively affects their offspring. Because of the habitat overlap, individuals do broaden their diet over their lifetime, but they are not very good at feeding on the alternative food source.

Since the minimum prey size a consumer can eat often increases with consumer size (Werner 1988), we also study the evolution of specialization  $\psi$  when small juveniles have an attack rate 1.2 times that of large juveniles and adults per gram body weight on the original food source. The form of the trade-off between the attack rates remains the same for all stages (equation 2.5). Figure 2.2B shows that even in this case, individuals specialize on the original food source and are not very efficient in feeding on the alternative food source. When small individuals are better competitors for the original food source than larger ones,  $\psi$  can evolve to slightly lower values, compared to the situation where all stages have the same competitive abilities. This is possible because the trade-off in feeding efficiencies affects small juveniles to a lesser extent than large juveniles and adults.

Mortality rates often decrease with body size (e.g., Hampton 2000; Sogard 1997). We study the effect of size-dependent mortality by increasing the per capita mortality rate for small juveniles to 0.04 while keeping the other parameters the same. Figure 2.2C shows that the results are comparable to those of the model analysis with equal mortality rates for all stages. As before, we find that consumers do not specialize on the alternative food source when this negatively affects the performance of small juveniles.

### Two food sources occurring in two nonoverlapping habitats

When the two habitats do not overlap at all,  $\phi$  determines on which food source the large individuals feed. When  $\phi = 0$ , for example, there is a complete ontogenetic diet shift and large individuals feed only on the alternative food source. We refer to the



**Figure 2.2:** Evolutionary outcome for different combinations of  $X_{1,\max}$  and  $X_{2,\max}$  when the two habitats completely overlap ( $\beta = 1$ ). A, All individuals experience the same per capita mortality rate and have the same foraging abilities on the original food source, independent of their size. For very low values of  $X_{2,\max}$ , the value of the specialization parameter  $\psi$  evolves to 1. For increasing values of  $X_{2,\max}$   $\psi$  first decreases to a minimum of 0.95. For higher values of  $X_{2,\max}$  the value of  $\psi$  increases again. B, All individuals experience the same per capita mortality rate, but small juveniles are 1.2 times as efficient in feeding on the original food source as larger individuals. As in A,  $\psi$  first decreases with increasing  $X_{2,\max}$  and increases afterwards. Specialization  $\psi$  now evolves to lower values, compared to the case where all individuals have the same competitive abilities. However,  $\psi$  still evolves to relatively high values (minimum value equals 0.9). C, All individuals have the same foraging ability on the original food source, but small juveniles experience a higher mortality rate than the large juveniles and adults. The minimum value to which  $\psi$  can evolve is 0.95.

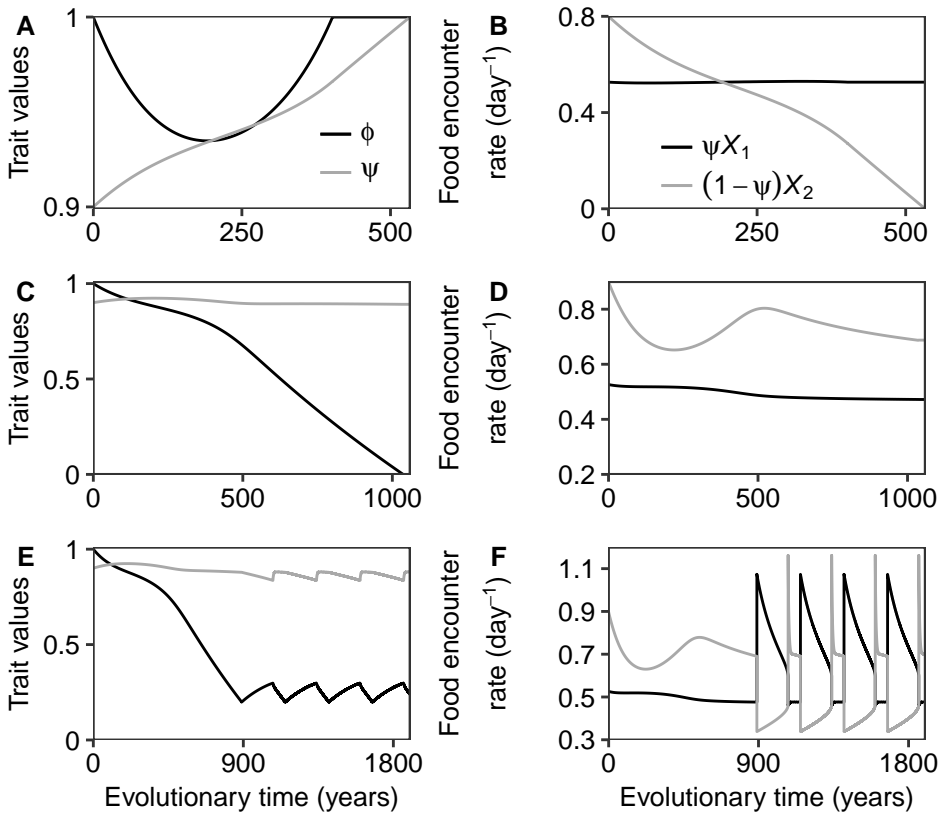


parameter  $\phi$  as the food choice (equivalent to habitat choice in this case) and to  $\psi$  as the (degree of) specialization on the original food source. Since we are interested in the question how a niche shift can evolve in species that do not have one, we assume that initially all individuals feed on the original food source ( $\phi = 1$ ) and are specialized in feeding on the original food source ( $\psi = 0.9$ ,  $a_1 = 0.54$ ,  $a_2 = 0.06$ ). We used the canonical equation of adaptive dynamics to study the evolutionary dynamics of the model for many different combinations of maximum food source densities. We found three qualitatively different evolutionary outcomes, which are described below.

Figure 2.3A shows a typical evolutionary time series that occurs for most combinations of  $X_{1,\max}$  and  $X_{2,\max}$ . Food specialization  $\psi$  always increases over evolutionary time and will evolve to its maximum value, which equals 1. Food choice  $\phi$  first decreases over evolutionary time but increases later and ultimately evolves to a value of 1 as well. This evolutionary pattern can be explained by the change in the specialization-adjusted food source densities over evolutionary time, which are shown in figure 2.3B. Initially, food choice  $\phi$  will evolve to lower values, since large individuals can increase their food intake by feeding on the alternative food source (first part of figure 2.3B). However, at the same time specialization  $\psi$  increases, since there is apparently selection for increased feeding efficiency on the original food source (figure 2.3A). Because of this increase in specialization  $\psi$ , large individuals become less efficient on the alternative food source, and it is no longer beneficial to feed on this food source (last part of figure 2.3B). Therefore, the direction of evolutionary change in food choice  $\phi$  reverses, and it will now evolve to higher values. Ultimately, both food choice  $\phi$  and specialization  $\psi$  evolve to their maximum values, which equals 1 for both parameters. In this case, no niche shift evolves, and the consumers even lose their capability to consume the alternative food source.

Figure 2.3C shows a typical evolutionary time series when the maximum density of the alternative food source is very high while the maximum density of the original food source has low or intermediate values. In this case, food choice  $\phi$  evolves to a value of 0 while the specialization  $\psi$  evolves to a value slightly lower than 1 (in figure 2.3C  $\psi = 0.89$ ,  $a_2 = 0.07$ ,  $a_1 = 0.53$ ). When  $X_{2,\max}$  is very high, it is beneficial for large individuals to feed on the alternative food source, independent of the value of specialization  $\psi$  (figure 2.3D). Therefore, food choice  $\phi$  will evolve to a value of 0, and the consumers have a complete ontogenetic diet shift. However, even though large individuals feed completely on the alternative food source, specialization on the new food source is not possible, and specialization  $\psi$  evolves to relatively high values. Even when the productivity of the alternative food source is very high, the trade-off between early and late foraging success hinders specialization on the food source used later in life.

When both  $X_{1,\max}$  and  $X_{2,\max}$  are very high, the results are comparable to the situation described above. Even though large individuals spend most of their time search-



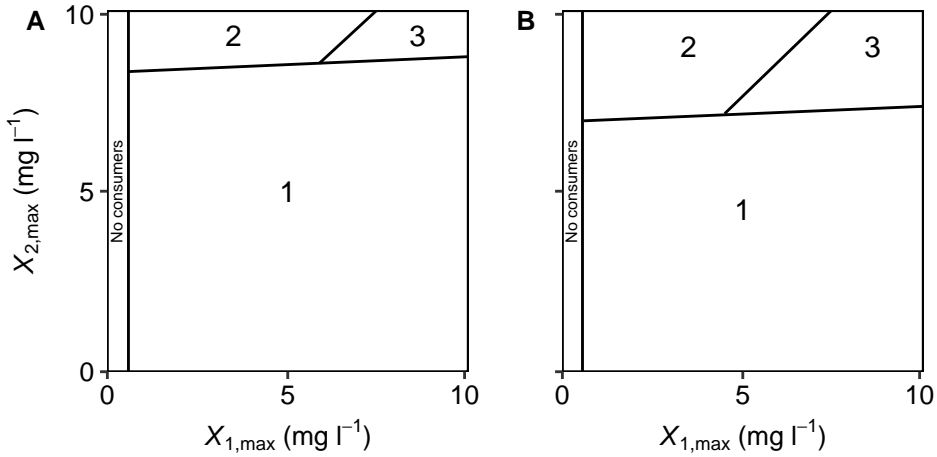
**Figure 2.3:** Evolutionary time series for different values of  $X_{1,\max}$  and  $X_{2,\max}$  showing how the evolutionary traits (A, C and E) and the equilibrium food densities (B, D and F) change over evolutionary time when the two food sources occur in two nonoverlapping habitats. Evolutionary time units are arbitrary in A, C and E (see appendix A). The profitability of a certain food source is determined by its density and the degree of specialization of consumers on the food source. The food source encounter rates ( $X_1 * a_1$  and  $X_2 * a_2$ ) are therefore plotted to show which food source is the most profitable to forage on. A,  $X_{1,\max} = 1$  and  $X_{2,\max} = 8$ . In this case both  $\phi$  and  $\psi$  will evolve to a value of 1, and individuals will feed only on the original food source and even lose their ability to feed on the alternative food source. B,  $X_{1,\max} = 1$  and  $X_{2,\max} = 8$ . Initially, the alternative food source is the more profitable food source for large individuals to forage on. However, because of the evolutionary change in specialization  $\psi$  (see A), the original food source becomes more profitable over evolutionary time. C,  $X_{1,\max} = 6$  and  $X_{2,\max} = 9$ . For high values of  $X_{2,\max}$  a complete diet shift will evolve ( $\phi = 0$ ) but large individuals are not very efficient in feeding on the alternative food source ( $\psi = 0.89$ ). D,  $X_{1,\max} = 6$  and  $X_{2,\max} = 9$ . Even though the efficiency with which large individuals feed on the alternative food source remains low, the alternative food source is for large individuals the most profitable food source to forage on. E,  $X_{1,\max} = 8$  and  $X_{2,\max} = 9$ . When both  $X_{1,\max}$  and  $X_{2,\max}$  are very high, the population will never reach an evolutionary end point. The two parameters will therefore always change over time. In this case, the large individuals spend most of their time in the habitat with the alternative food source ( $\phi = 0.2 - 0.3$ ) but are not very efficient in feeding on this food source ( $\psi = 0.84 - 0.88$ ). F,  $X_{1,\max} = 8$  and  $X_{2,\max} = 9$ . Because both the specialization  $\psi$  and the food choice  $\phi$  change over evolutionary time, the food source profitabilities fluctuate as well.

ing for food in the habitat with the alternative food source, they never specialize on this food source. However, in this case the population never reaches an ESS. Figure 2.3E shows a typical evolutionary time series when the two traits always change over evolutionary time. The evolutionary cycling occurs because the ESS corresponds to an equilibrium that is ecologically unstable. For low values of food choice  $\phi$ , when the overlap in diet between small and large consumers is small, there are two stable ecological equilibria, separated by an unstable equilibrium (for a more detailed discussion about this bistability when small and large consumers feed on different food sources, see Schreiber and Rudolf (2008) and Guill (2009)). In one of the stable ecological equilibria, specialization  $\psi$  evolves to lower values while food choice  $\phi$  evolves to higher values. The evolutionary directions are reversed in the other stable equilibrium. Because the equilibrium that is evolutionarily stable is ecologically unstable, it is never reached, and the system always cycles between different values of food choice  $\phi$  and specialization  $\psi$ . In this case, the consumers exhibit a partial diet shift but are never specialized on the alternative food source. The profitabilities of the two food sources also change over time because of the evolutionary cycling (figure 2.3F).

Figure 2.4A shows the boundaries of the parameter regions in the  $X_{1,\max}$  -  $X_{2,\max}$  space where the different evolutionary outcomes described above occur. For most combinations of  $X_{1,\max}$  and  $X_{2,\max}$  an ontogenetic niche shift cannot evolve, and the alternative food source remains unexploited. For very high values of  $X_{2,\max}$ , large individuals spend most or even all of their time searching for the alternative food source. However, large individuals will never specialize on the alternative food source. When a complete ontogenetic diet shift evolves, the lowest value to which the specialization  $\psi$  can evolve equals 0.88. When there is evolutionary cycling, the minimum value that specialization  $\psi$  can reach equals 0.83.

When smaller individuals are more efficient in feeding on the original food source than large individuals ( $q = 1.2$ ), we find qualitatively the same results (figure 2.4B). As before, for most combinations of  $X_{1,\max}$  and  $X_{2,\max}$  an ontogenetic diet shift does not evolve. For high values of  $X_{2,\max}$ , the alternative food source is exploited by large individuals, but they cannot specialize on this new food source. The minimum value to which specialization  $\psi$  can evolve is slightly lower than that in the situation where all individuals have the same competitive abilities. Furthermore, the parameter area for which consumers exploit the alternative food source is slightly larger. A diet shift never evolves when the small individuals experience an increased per capita mortality rate of 0.04 (figure not shown). The alternative food source always remains unexploited in this case.

To summarize, an ontogenetic diet shift can evolve only for very high values of  $X_{2,\max}$ , but specialization on the alternative diet is never possible. Increasing the competitive abilities of the smallest individuals increases the parameter area where a com-



**Figure 2.4:** Evolutionary outcome for different combinations of  $X_{1,max}$  and  $X_{2,max}$  when the two habitats are completely separated in space ( $\beta = 0$ ). For low values of  $X_{2,max}$  no diet shift can evolve, because the density of the alternative food source is very low (area indicated with 1). For very high values of  $X_{2,max}$  a complete diet shift can evolve, but the consumers are not specialized on this diet ( $\psi$  between 0.88-0.92). For very high values of both  $X_{1,max}$  and  $X_{2,max}$  (area 3), the population will never reach an evolutionary endpoint. While large individuals feed most of their time on the alternative food source ( $\phi = 0 - 0.45$ ), they are not very efficient in feeding on this food source. A: All individuals experience the same per capita mortality rate and have the same foraging abilities on the original food source, independent of their size. The minimum value to which  $\psi$  evolves when there is a complete diet shift is 0.88. In the parameter area where there is evolutionary cycling, the minimum value that  $\psi$  can reach equals 0.83. B: All individuals experience the same per capita mortality rate, but small juveniles are 1.2 times as efficient in feeding on the original food source compared to larger individuals. The minimum value that  $\psi$  can reach equals 0.77 in the area where there is evolutionary cycling and 0.87 in the area where a complete diet shift evolves.

plete ontogenetic diet shift can evolve. On the other hand, increasing the mortality rate of the smallest individuals will decrease the parameter area where a complete ontogenetic diet shift can evolve.

## 2.4 Discussion

In this study, we found that it is advantageous for individuals to broaden their diet or even completely switch to an alternative diet during ontogeny when this increases their food intake. Surprisingly, however, consumers do not specialize on the alternative food source when this negatively affects the performance of small juveniles. Small juveniles are not able to feed on the alternative food source and are therefore completely dependent on the original food source for their survival and growth. Apparently, it is important that performance of small juveniles is high, so that they mature quickly into the next stage. Even though adults might increase their reproduction rate if they specialize on the alternative food source, this would, because of the trade-off between early and late foraging success, result in offspring that do not perform very well in the first part of their life cycle. Those individuals are outcompeted early in their life by individuals that are better foragers on the original food source. It therefore turns out to be evolutionarily more important to produce a few offspring that are excellent competitors than to produce many offspring that are not very efficient in feeding during the first part of their lives. The trade-off between early and late foraging success impedes the evolution of an ontogenetic niche shift. Large individuals are able to broaden or change their diet over their lifetime, but they always have a low efficiency on the food source used later in their life.

When the two food sources occur in the same habitat, it is even harder for large individuals to specialize on the alternative food source, compared to a situation where the two food sources are separated in space. Because of the overlap, large juveniles and adults always have access to both food sources, while small juveniles can feed only on the original food source. This larger food availability for large juveniles and adults leads to a high reproduction rate of new offspring. Because of the many offspring produced, competition in the small-juvenile stage is very strong (de Roos et al. 2007). This impedes specialization of larger individuals on the alternative food source if that leads to maladapted offspring and thus even stronger competition in this stage. Therefore, when the two food sources overlap in space, consumers expand their niche over ontogeny but can never specialize on the alternative food source.

Previous studies assumed that switching niches during ontogeny is a way to maximize growth rates across the life history (Werner, 1988; Werner and Gilliam, 1984). These studies did not consider the ecological conditions that might favor the evolution of ontogenetic niche shifts in the first place and mainly focused on the timing of the shift. We showed that there is a strong feedback between environment and strategy and that this feedback should be taken into account, as it determines whether an ontogenetic niche shift evolves or not.

A critical assumption in our study is that the different life stages are correlated, such that specialization of large individuals on the alternative food source results in offspring that are not very efficient in feeding on the original food source. We showed that this trade-off prevents specialization on the alternative food source, even when this food source is very abundant. It is, however, difficult to observe this prediction in empirical systems, because to do so would require comparison of morphologies and feeding efficiencies of populations, ecotypes, or closely related species with and without an ontogenetic niche shift. As far as we know, there is only one empirical study that gives some support to our prediction (Shedd et al. 2015). While most kokanee salmon feed only on macroinvertebrates, there is one population in Alaska that switches to piscivory during ontogeny (Shedd et al. 2015). Even though the diet of large individuals consists almost solely of fish, the morphology of these fish is not adapted to piscivory. While there is only limited evidence for a trade-off between early and late foraging success, there are, however, many studies (e.g., Jones et al. 2013; Svanback and Eklov 2003; Werner 1977) that show that morphological traits that facilitate feeding on a certain type of food (e.g., algae) are different from morphological traits that facilitate feeding on another type of food (e.g., fish). On the basis of these observations, we think that it is reasonable to assume the trade-off between early and late foraging success.

When small individuals are relatively more efficient in feeding on the original food source than large individuals, the results are qualitatively the same. However, compared to the situation where all individuals have the same foraging abilities, large individuals can now specialize slightly more on the alternative food source. In this case, the trade-off between early and late foraging success is less strong, since small juveniles are less affected than large juveniles and adults. In the absence of this trade-off, it is therefore to be expected that specialization on the alternative food source is possible. Hence, in species with an ontogenetic niche shift there is probably strong selection to break up the correlation between different stages when the alternative food source is very abundant. It is often thought that metamorphosis has evolved to decouple the different life stages and allows for the independent evolution of stage-specific traits (Moran 1994). It is, however, still unclear to what extent metamorphosis can decouple different life stages. Some studies have reported independent evolution of larval and adult traits (Parichy 1998; Saenko et al. 2012), while others have found strong correlations of traits between different stages (Fellous and Lazzaro 2011; Gower and Webster 2004). Apparently, some traits expressed in different life stages can evolve independently, while other traits are correlated.

Even if metamorphosis can break up the correlations between different life stages, such that they can evolve independently, metamorphosis also entails costs. During metamorphosis, some species cannot feed at all (e.g., holometabolous insects) or feeding becomes less efficient (e.g., flatfishes Geffen et al. 2007). Since metamorphosis

costs energy, species often lose body mass during the transformation from larva to juvenile (Downie et al. 2004; Thiyagarajan et al. 2003). Furthermore, metamorphosing individuals are often more vulnerable to predation and therefore often experience high mortality rates (e.g., Wassersug and Sperry 1977). Metamorphic chorus frogs (*Pseudacris triseriata*), for example, are not well adapted to either land or water, compared to pre- and post-metamorphic individuals, and experience high predation risk by the garter snake (*Thamnophis sirtalis*). It remains a question for further research under which ecological conditions the potential benefits from metamorphosis can outweigh its disadvantages.

We have shown that a change in diet over an individual's lifetime could promote the evolution of metamorphosis. However, factors other than diet could explain the origin of metamorphosis as well, such as dispersal, mate finding, or habitat selection (Moran 1994). A shift in diet could therefore also be a result of the selection for, for example, dispersal. Even though other factors might have driven the evolution of metamorphosis as well, it is thought that a shift in diet often has been the first step in evolutionary history toward complex life cycles with metamorphosis. Fossils of early amphibians, for example, showed that not the habitat shift but the shift in diet from feeding under water as a larva to feeding on land as an adult was a crucial factor for the evolution of metamorphosis (Schoch 2009). It would be interesting to study whether metamorphosis is more likely to evolve because of a diet shift or because of other factors, such as dispersal.

In cases when two food sources occurred in different habitats, we studied only the evolutionary dynamics, assuming that initially a niche shift did not exist. It is, however, possible that there are other evolutionary attractors present that can be reached when starting from different ancestral states. We did not study the global evolutionary behavior of the system and looked only at the evolutionary dynamics, starting from one particular situation, because the main question that we are interested in is how a niche shift can evolve in species that do not have one. Therefore, the simplifying assumption was made to look only at the evolutionary dynamics on a local scale. Further work will address whether there are multiple evolutionary attractors present in the system when starting from different initial conditions.

A limitation of this study is that we analyzed only a linear trade-off function, where every increase in the attack rate on the alternative food source leads to an equal decrease in the attack rate on the original food source. There are, however, different trade-off shapes possible, and the shape of the trade-off function can have dramatic effects on the evolutionary outcome (e.g., Egas et al. 2004; Kisdi 2001). A different trade-off shape could, for example, lead to evolutionary branching (Geritz et al. 1998). It is, however, beyond the scope of this article to evaluate the effects of different trade-off shapes on the evolution of ontogenetic niche shifts.

Another simplifying assumption in this study is that of determinate growth of individuals. We assumed that individuals stop growing after reaching maturity, which is not always true. A shift in diet might increase growth rates and therefore allow for larger adult body sizes. Larger-sized individuals often have higher fecundity, which makes it even more profitable to change diet. It has been shown in a model for parasites that ontogenetic host switching can evolve because of the advantage of an increased body size at maturity and higher fecundity (Parker et al. 2003). However, Parker et al. (2003) used a density-independent model and did not take into account the feedback between individuals and the environment. While this might be valid for parasitic organisms, we believe that the feedback between environment and the different strategies of individuals cannot be ignored when studying diet shifts in free-living animals.

To analyze the robustness of our result with regard to major changes in both the model structure and the model parameters, we analyzed a fully size-structured population model (appendix 2.B). This model is an extension of the model described by Persson et al. (1998) but includes an additional food source. Growth is indeterminate, and the maximum size of individuals depends on the food source densities. The attack rates were modeled as hump-shaped functions of the body mass of an individual. Because of these specific functions, large individuals become less efficient on the original food source. The model was parameterized for the interaction between roach (*Rutilus rutilus*) and two zooplankton food sources. We found again that individuals do not specialize on the food source used later in life. This analysis shows that our results do not depend on the parameterization or the specific assumptions of the stage-structured biomass model, such as determinate growth and the linear increase of the attack rate with increasing size.

Given the high number of species with ontogenetic niche shifts, one must conclude that this is a very successful life-history strategy. We showed that individuals switch to an alternative diet later in life as a way to maximize food intake. However, it is not possible to specialize on the alternative food source if this leads to maladapted offspring. There is therefore probably selection to decouple the different life stages such that they can specialize independently on their different food sources. The evolution of metamorphosis could be a way to break up the trade-off between performances on different diets between different life stages. Our results hence suggest that the evolution of an ontogenetic niche shift could induce the evolution of a metamorphosis.

## Acknowledgments

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## Appendix 2.A Canonical equation

The canonical equation of adaptive dynamics is a deterministic approximation describing the rate of evolution in a population that is mutation limited and where mutation steps are small (Dieckmann and Law 1996; Durinx et al. 2008). The evolutionary rate of change of a trait is proportional to the selection gradient and depends furthermore on the production rate of mutants, their establishment chance and the mutational covariance matrix. Because the degree of food specialization  $\psi$  is a morphological trait while food choice  $\phi$  is a behavioural trait, we assumed the traits to be completely independent from each other, therefore the mutational covariance matrix, which equals in this case the identity matrix, does not play a role in the evolutionary trajectories. The rate of change of traits  $\mathbf{y}$  in a monomorphic, size structured population can then be described as

$$\frac{d\mathbf{y}}{d\tau} = \frac{T_f}{T_s} \frac{\hat{n}\mu}{\sigma^2} \frac{\partial s(\mathbf{y}'|\mathbf{y})^\top}{\partial \mathbf{y}'} \Big|_{\mathbf{y}'=\mathbf{y}} \quad (2.10)$$

where  $\tau$  spans the evolutionary timescale (Durinx et al. 2008). In this equation  $T_s$  is the expected lifespan of an individual,  $T_f$  the average age at giving birth,  $\hat{n}$  the size of the population in equilibrium,  $\mu$  the mutation probability per birth event,  $\sigma^2$  the variance of the offspring trait distribution and  $\frac{\partial s(\mathbf{y}'|\mathbf{y})}{\partial \mathbf{y}'} \Big|_{\mathbf{y}'=\mathbf{y}}$  the selection gradient. Because we have an explicit expression for  $R_0$ , we use this as a measure of invasion fitness. The relation between  $R_0$  and the invasion fitness  $s(\mathbf{y}'|\mathbf{y})$  is given by  $s(\mathbf{y}'|\mathbf{y}) = \frac{\log(R_0(\mathbf{y}'|\mathbf{y}))}{T_f}$  (Durinx et al. 2008). Because we studied the evolutionary change of two traits in a single population,  $T_s$  and  $\hat{n}$  are equal for both equations and only scale the evolutionary rates but do not change the evolutionary endpoints.

Furthermore, by assuming that the size and variance of the mutations are equal for both traits, the mutation rates and the selection gradients are the only factors that determine the evolutionary trajectories. The food source preference  $\phi$  of an individual can evolve fast and this could even happen on an ecological timescale because of learning (e.g. Slagsvold and Wiebe 2007). On the other hand,  $\psi$  evolves probably more slowly since it is a morphological trait. We assume therefore that the mutation rate of trait  $\phi$  is higher than the mutation rate of trait  $\psi$ . The canonical equation for the two traits now simplifies to:

$$\begin{cases} \frac{d\phi}{d\tau} = C_1 \frac{\partial R_0(\phi'|\phi)}{\partial \phi'} \Big|_{\phi'=\phi} \\ \frac{d\psi}{d\tau} = C_2 \frac{\partial R_0(\psi'|\psi)}{\partial \psi'} \Big|_{\psi'=\psi} \end{cases} \quad (2.11)$$

where we choose  $C_1$  to be ten times higher than  $C_2$ . Decreasing (increasing)  $C_1$  decreases (slightly increases) areas 1 and 2 in figure 2.4 but does not qualitatively change the evolutionary outcomes. The evolutionary time units can be considered arbitrary since they are freely adjustable through the choice of the constants  $C_1$  and  $C_2$ .

## Appendix 2.B Robustness of the results

We found that individuals can broaden or shift their diet when they grow larger. However, specialization on the new diet is not possible when this negatively affects the smallest individuals. To check the robustness of this outcome with regard to major changes in the model structure and model parameters, we studied the evolution of ontogenetic niche shifts using a fully size-structured population model assuming that the resources occur in the same habitat ( $\beta = 1$ ). The model is an extension of the consumer-resource model described by Persson et al. (1998). In contrast to the model of Persson et al. (1998) we assume continuous reproduction and equilibrium conditions. We extend the model by introducing a second, unstructured, resource population.

The feeding, growth, reproduction and mortality of an individual are assumed to be functions of two variables, irreversible and reversible mass, referred to as  $x$  and  $y$ , respectively. Irreversible mass is structural mass such as bones and organs and cannot be starved away. On the other hand, reversible mass (such as fat, muscle tissue and, in the case of adults, gonads) can be used to cover basic metabolism during starvation. There is a maximum ratio of reversible mass to irreversible mass which equals  $q_j$  for juveniles and  $q_a$  for adults. Newborn individuals are born with irreversible mass  $x_b$  and the maximum amount of reversible mass ( $q_j x_b$ ). When reaching size  $x_f$  individuals become adults. Total body length, attack rates and handling times are assumed to only depend on irreversible mass (Persson et al. 1998) through the quantity  $w = x(1 + q_j)$ . Similar to the main text we assume that there are two resources, both following semi-chemostat dynamics. One food source, the original food source, is available for all individuals, while the alternative food source is only available after an individual has reached a certain size ( $w > w_{\min} = x_{\min}(1 + q_j)$ ). We assume that the attack rates on both food sources are humpshaped functions of the body mass of an individual:

$$a_1(w) = A_1 \left( \frac{w}{w_0} \exp\left(1 - \frac{w}{w_0}\right) \right)^\alpha \quad (2.B1)$$

$$a_2(w) = \begin{cases} 0 & w \leq w_{\min} \\ A_2 \left( \frac{w - w_{\min}}{w_0} \exp\left(1 - \frac{w - w_{\min}}{w_0}\right) \right)^\alpha & \text{otherwise.} \end{cases} \quad (2.B2)$$

In these equations  $A_1$  and  $A_2$  are the maximum attack rates that can be reached when the body size of an individual equals  $w_0$  and  $w_0 + w_{\min}$  on the original and alternative resource respectively. The exponent  $\alpha$  determines how fast the attack rates increase with body size for small individuals. To incorporate a trade-off between foraging skills on the two different food sources, we again assume a linear trade-off between the two maximum attack rates ( $A_1$  and  $A_2$ ). The same function as in the main text is used

(equation 2.5) for the trade-off between  $A_1$  and  $A_2$ :

$$\begin{aligned} A_1 &= \psi A_{\max} \\ A_2 &= (1 - \psi) A_{\max}. \end{aligned} \quad (2.B3)$$

We assume a holling type 2 functional response, therefore the resource ingestion of an individual can be written as

$$I(X_1, X_2, w) = \frac{a_1(w)X_1 + a_2(w)X_2}{1 + h(w)(a_1(w)X_1 + a_2(w)X_2)} \quad (2.B4)$$

whereby

$$h(w) = \zeta_1 + \zeta_2 w^{-\zeta_3} e^{\zeta_4 w}. \quad (2.B5)$$

The total energy intake of an individual equals the resource intake rate multiplied by a conversion factor  $k_e$ . Assimilated energy is first used to cover maintenance costs. The metabolic demands per unit of time is a function of both irreversible and reversible mass and can be described by a power function

$$E_m(x, y) = p_1 (x + y)^{p_2}. \quad (2.B6)$$

Juveniles allocate a fraction  $\kappa_j(x, y)$  of the net-biomass production (the difference between the food assimilation and maintenance cost of an individual)  $E_g(X_1, X_2, x, y) = k_e I(X_1, X_2, w) - E_m(x, y)$  to growth in irreversible mass, following

$$\kappa_j(x, y) = \frac{y}{(1 + q_j)q_j x}. \quad (2.B7)$$

The remaining part is allocated to growth in reversible mass. Adults allocate a fraction  $\kappa_a(x, y)$  to growth in irreversible mass, a fraction  $q_j \kappa_a(x, y)$  to growth in reversible mass and the remainder  $(1 - (1 + q_j)\kappa_a)$  to reproduction. The fraction  $\kappa_a(x, y)$  allocated to reversible mass equals

$$\kappa_a(x, y) = \frac{y}{(1 + q_a)q_a x}. \quad (2.B8)$$

The number of eggs an individual adult produces per unit of time

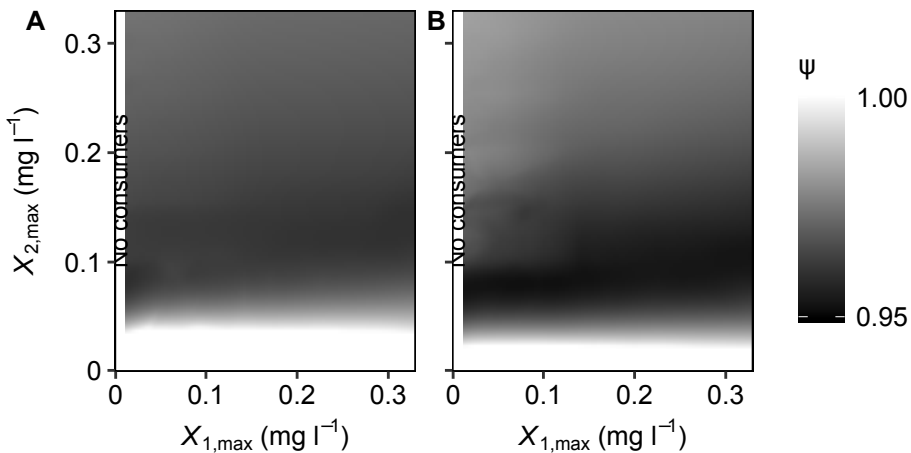
$$b(x, y, X_1, X_2) = \begin{cases} (1 - (1 + q_j)\kappa_a(x, y))E_g(x, y, X_1, X_2)\eta & x > x_f \\ 0 & \text{otherwise} \end{cases} \quad (2.B9)$$

where  $\eta$  is a conversion factor. A more detailed description of the model can be found in Persson et al. (1998). Metabolic demands and handling time are parameterized for the interaction between a planktivorous fish population of roach *Rutilus rutilus* and two zooplankton populations as food source following Persson et al. (1998). Parameters are listed in table 2.B1.

Since we take only into account the situation where the two habitats completely overlap ( $\beta = 1$ ), only specialization  $\psi$  evolves. Using the PSPManalysis software package (de Roos 2016) we calculated to which value  $\psi$  evolves for different combinations of  $X_{1,\max}$  and  $X_{2,\max}$ . To test how the size at which the alternative resource becomes available influences the evolution of ontogenetic niche shifts, we did the calculations for two different values of  $x_{\min}$ .

All evolutionarily singular strategies found were evolutionarily stable attractors (CSSs). We found again that specialization on the alternative resource is not possible (figure 2.B1A). Even when individuals can feed on the alternative resource when they are relatively small ( $x_{\min} = 0.01$  while size at birth  $x_b = 0.000804$ ), individuals specialize on the original resource (figure 2.B1B).

This analysis shows that our results are robust to substantial differences in model structure and parameters. In contrast to the stage-structured biomass model, adults can still grow and their maximum size depends on the food source densities. For the stage-structured biomass model we assumed equal mass-specific handling times. We have now assumed mass-specific functions for both the attack rate and the handling time (Persson et al. 1998). While in the main text the model was parameterised for an invertebrate species, we have now parameterised the model for a vertebrate species (*Rutilus rutilus*).



**Figure 2.B1:** Evolutionary outcome for different combinations of  $X_{1,\max}$  and  $X_{1,\max}$  when the two habitats completely overlap for the fully size-structured model. We used two different values for  $x_{\min}$ , the irreversible mass at which the alternative resource becomes available. A:  $x_{\min} = 1$ . B:  $x_{\min} = 0.01$ . Parameter  $\psi$  will always evolve to high values.

**Table 2.B1:** Parameters of the model

Parameter	Default Value	Unit	Description
$\delta$	0.5	$\text{day}^{-1}$	Resource growth
$X_{1,\max/2,\max}$	variable	$\text{mg L}^{-1}$	Maximum biomass density of food source 1 and 2
$x_b$	0.000804	g	Irreversible mass of newborns
$x_{\min}$	0.01 or 1	g	Irreversible mass at which alternative resource becomes available
$x_f$	5	g	Irreversible mass at maturation
$A_{\max}$	$1 \cdot 10^5$	$\text{L day}^{-1}$	Maximum attack rate
$w_0$	17.42	g	Effective body mass at which maximum attack rate is attained
$\alpha$	0.93	-	Size scaling exponent of the attack functions
$\zeta_1$	0.00036	$\text{day mg}^{-1}$	Constant used in the handling time function
$\zeta_2$	0.00745	$\text{day mg}^{-1} \text{g}^{\zeta_3}$	Constant used in the handling time function
$\zeta_3$	0.68	-	Slope of decline in handling time at small consumer sizes
$\zeta_4$	$1.15 \cdot 10^{-3}$	$\text{g}^{-1}$	Slope of increase in handling time at large consumer sizes
$p_1$	0.033	$\text{g}^{1-p_2} \text{day}^{-1}$	Metabolic constant
$p_2$	0.77	-	Metabolic constant
$k_e$	0.00061	-	Conversion factor
$q_j$	0.742	-	Constant determining maximum juvenile reversible mass
$q_a$	1	-	Constant determining maximum adult reversible mass
$\eta$	0.5	-	Gonad-offspring conversion
$\mu$	0.01	$\text{day}^{-1}$	Background mortality rate

\* These values are the original values from Persson et al. (1998) divided by  $1.1 \cdot 10^{-2}$  (the weight of a prey individual) to express prey densities in milligram  $\text{l}^{-1}$  instead of individuals  $\text{l}^{-1}$ .



**LARGE AMPLITUDE CONSUMER-RESOURCE  
CYCLES ALLOW FOR THE EVOLUTION OF  
ONTOGENETIC NICHE SHIFTS IN CONSUMER LIFE  
HISTORY**

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## Abstract

In many size-structured populations individuals change resources during the course of their ontogenetic development. Different resources often require different adaptations to be effectively exploited. This leads to a trade-off between small and large individuals in direct developing species. Specialization on the resource used later in life turns out to be hardly possible in case of equilibrium dynamics. However, size-structured populations often exhibit population cycles. Non-equilibrium dynamics can change evolutionary behavior when compared with equilibrium dynamics. Here, we study the evolution of specialization on a secondary resource that is only available for large individuals, using the framework of adaptive dynamics. We show that in case of small amplitude cycles, specialization on a secondary resource is hardly possible, either because this will decrease the resource intake of large individuals or because this will severely increase competition among small individuals such that they cannot mature. Specialization on a secondary resource is often possible in case the population exhibits large amplitude cycles. Specialization now increases the resource intake of large individuals and therefore prevents starvation. While specialization increases competition among small individuals, maturation is still possible in case of large amplitude cycles. We furthermore show that in our model small and large amplitude cycles coexist and that there is therefore evolutionary bistability.



### 3.1 Introduction

Many animal species change their niche during their life (Werner and Gilliam 1984). Most research has focussed on the optimal timing of these ontogenetic niche shifts (Claessen and Dieckmann 2002; Werner and Hall 1988; Werner 1988), whereas it is not well understood why they evolved in the first place. Although it may be beneficial for individuals to change resource use over ontogeny (Werner and Gilliam 1984), there is also a cost connected to shifting diets. A morphology that allows individuals to feed on a certain food type is not necessarily efficient when feeding on a different food type (e.g., Andersson 2003; Hjelm et al. 2003; Meyer 1989). In direct developing species this leads to a trade-off between early and late foraging success; individuals can either specialize in feeding on the resource they use early in life or in feeding on the resource they use later in life (e.g., Hjelm et al. 2000). It has been shown in a theoretical study that such a trade-off limits the evolution of ontogenetic niche shifts. While individuals are able to broaden their diet during ontogeny, individuals adopt a morphology specialized in feeding on the primary resource and are therefore not very efficient in utilizing the resource used later in life (chapter 2 of this thesis). However, some species (e.g., many piscivorous fish) have a morphology specialized in feeding on the resource used later in life. How did such life-history strategies evolve?

Most theoretical studies on the evolution of life-history traits, including studies on the evolution of ontogenetic niche shifts (e.g., Claessen and Dieckmann 2002 and chapter 2 of this thesis) assume equilibrium population dynamics, despite the fact that ecological systems can show different types of dynamics, such as limit cycles or chaos. Ecological dynamics affect evolutionary dynamics and vice versa, it is therefore no surprise that the evolutionary behavior of a system can be affected by the type of population-dynamical attractor (Hoyle et al. 2011; Nurmi and Parvinen 2013; White et al. 2006).

Taking into account the effect of the type of population dynamics on the evolutionary behavior is potentially important in studying ontogenetic niche shifts. Ontogenetic niche shifts occur by definition at some point during an individual's development. The timing of such switches is largely determined by the size of an individual (Werner and Gilliam 1984). It is therefore appropriate to study the evolution of ontogenetic niche shift with the use of size-structured population models. Size-structured populations often exhibit population cycles and the type of population fluctuation is determined by the competitive ability of individuals (de Roos and Persson 2003, 2013; Persson et al. 1998). Population cycles cause fluctuations in resources as well, which in turn will determine whether feeding and specialization on a certain diet is beneficial or not. It is therefore expected that the type of population cycles can affect the evolution of ontogenetic niche shifts.

In this paper we study the effect of the type of population dynamics on the evolution of ontogenetic niche shifts. We use a size-structured consumer-resource model and the adaptive dynamics approach (Durinx et al. 2008; Geritz et al. 1998). We assume a single consumer population utilizing two alternative resources. One resource is available for all individuals while the other resource is only available for large individuals. A trade-off between foraging abilities is assumed, the more efficient an individual uses one resource, the less efficient it can use the other. Previous works showed that under equilibrium conditions specialization on the resource only available for large individuals is not possible when this negatively affects offspring performance (chapter 2 of this thesis). In this work we investigate if this result holds under non-equilibrium conditions as well.

### 3.2 Model and methods

#### Model description

We use a simple dynamic energy budget model for individual consumers of different sizes. Our model extends the Kooijman-Metz model (de Roos et al. 1990; Kooijman and Metz 1984) by introducing a second resource population and starvation mortality. The derivations of the functions of this model with one resource have been described before (de Roos et al. 1990; Kooijman and Metz 1984). We therefore only shortly outline the model below, the set of equations and functions describing the model in more detail are listed in table 3.1 and 3.2 respectively.

**Table 3.1:** Model equations

Equation	Description
$\frac{dX_1}{dt} = \delta(X_{1,\max} - X_1) - \int_{\ell_b}^{\ell_m} I_1(X_1, X_2, \ell) c(t, \ell) d\ell$	Dynamics resource 1
$\frac{dX_2}{dt} = \delta(X_{2,\max} - X_2) - \int_{\ell_v}^{\ell_m} I_2(X_1, X_2, \ell) c(t, \ell) d\ell$	Dynamics resource 2
$\frac{\partial c(t, \ell)}{\partial t} + \frac{\partial g(X_1, X_2, \ell) c(t, \ell)}{\partial \ell} = -(\mu + S(X_1, X_2, \ell)) c(t, \ell)$	Consumer size distribution dynamics
$g(X_1, X_2, \ell_b) c(t, \ell_b) = \int_{\ell_b}^{\ell_m} b(X_1, X_2, \ell) c(t, \ell) d\ell$	Population birth rate

Consumers are born with size  $\ell_b$ , get access to the secondary resource at size  $\ell_v$  and subsequently mature into adults at a length  $\ell_j$ . We define small juveniles as all

individuals with a body length smaller than  $\ell_v$ . Immature individuals with a body size equal to or larger than  $\ell_v$  are regarded as large juveniles.

The growth of both resources follows semi-chemostat dynamics with a turnover rate of  $\delta$ . The maximum densities that the primary and the secondary resource can reach in the absence of the consumers equals  $X_{1,\max}$  and  $X_{2,\max}$ , respectively. We assume that the two resources occur in the same habitat and that only large juveniles and adults can feed on both resources. Resource ingestion follows a Holling-type-2 functional response and is proportional to the squared length of an individual with proportionality constant  $I_m$ . In the original model description, the size-dependent resource ingestion for consumers only foraging on the primary resource is formulated as

$$I_1(X_1, \ell) = I_m \xi X_1 / (1 + \xi X_1) \ell^2. \quad (3.1)$$

In this equation  $\xi$  is the shape parameter of the functional response. Ingested food is assimilated with a conversion efficiency  $\sigma$ , of which a fixed fraction  $\kappa$  is used for maintenance and growth in body mass, where mass is proportional to cubed individual length with proportionality constant  $\beta$ . The remainder of the assimilated food is invested in maturation (juveniles) and reproduction (adults). Maintenance takes precedence over growth and is also proportional to the cubed length of an individual with proportionality constant  $\chi$ . Growth in mass ( $= \beta \ell^3$ ) hence equals  $\kappa \sigma I_m \xi X_1 / (1 + \xi X_1) \ell^2 - \chi \ell^3$ , which leads after some rewriting (see de Roos et al. 1990) to the following expression for the growth rate in length of small individuals ( $\ell < \ell_v$ ) feeding solely on the primary resource:

$$g(X_1, \ell) = \gamma (\ell_m \xi X_1 / (1 + \xi X_1) - \ell), \quad (3.2)$$

where  $\gamma (= \chi / (3\beta))$  represents the growth rate constant. Parameter  $\ell_m (= \kappa \sigma I_m / \chi)$  is the maximum size individuals can reach under very high food conditions. This parameter is a composite parameter that among others depends on the proportionality constant  $I_m$  relating food intake at ad-libitum food supply to the squared length of an individual (de Roos et al. 1990; Kooijman and Metz 1984). Not only this maximum size  $\ell_m$ , but also the birthrate parameter  $r_m$  (see below) depends implicitly on  $I_m$ .

In the current model formulation Holling's disc equation is used to model the consumer's functional response such that

$$I_1(X_1, \ell) = a_1 X_1 / (1 + h a_1 X_1) \ell^2, \quad (3.3)$$

where  $a_1 = I_m \xi$  and  $h = 1 / I_m$ . The growth of an individual feeding only on the primary resource (equation 3.2) is now reformulated as

$$g(X_1, \ell) = \gamma (\ell_m h a_1 X_1 / (1 + h a_1 X_1) - \ell). \quad (3.4)$$

We choose this formulation for the functional response to ease the extension to a secondary resource and to be able to use a trade-off between the two attack rates, which is in line with chapter 2 of this thesis. In the new model formulation, food intake of large individuals ( $\ell \geq \ell_v$ ) feeding on two resources equals

$$I_2(X_1, X_2, \ell) = (a_1 X_1 + a_2 X_2) / (1 + h(a_1 X_1 + a_2 X_2)) \ell^2. \quad (3.5)$$

Using the same assumptions as before, growth of large individuals then follows

$$g(X_1, X_2, \ell) = \gamma(\ell_m h(a_1 X_1 + a_2 X_2) / (1 + h(a_1 X_1 + a_2 X_2)) - \ell). \quad (3.6)$$

Under sufficient food conditions adults ( $\ell \geq \ell_j$ ) produce offspring at a rate

$$b(X_1, X_2, \ell) = r_m h \frac{a_1 X_1 + a_2 X_2}{1 + h(a_1 X_1 + a_2 X_2)} \ell^2 \quad (3.7)$$

where the parameter  $r_m (= (1 - \kappa) \sigma I_m / (\beta \ell_b^3))$  represents the proportionality constant relating fecundity at ad-libitum food availability to squared individual length (de Roos et al. 1990; Kooijman and Metz 1984).

When the fraction  $\kappa$  of assimilated energy is not sufficient to cover maintenance costs, growth ceases and energy allocated to reproduction is reduced (table 3.2). When the total amount of ingested food is not enough to pay maintenance costs, individuals die instantaneously. When the size of individuals is close to the size at which this instantaneous death occurs, consumers suffer already from increased starvation mortality  $S(X_1, X_2, \ell)$  (table 3.2). Note that because large individuals have access to two resources while small individuals have only access to a single resource, the size at which starvation occurs is different depending on the size class of a consumer (table 3.2).

The density function  $c(t, \ell)$  represents the size distribution of the consumer population at time  $t$ . Since individual consumer biomass is assumed proportional to cubed length with proportionality constant  $\beta$ , integral

$$\int_{\ell_1}^{\ell_2} \beta \ell^3 c(t, \ell) d\ell \quad (3.8)$$

gives the total biomass of the consumers with a length between  $\ell_1$  and  $\ell_2$  at time  $t$ . Equation 3.8 is used to calculate the biomass densities of the three different consumer size-classes.

We assume that the two resources require different morphological adaptations to be effectively utilized. We therefore use a simple linear trade-off between the attack rate on the primary and the secondary resource

$$\begin{aligned} a_1 &= (1 - \psi) A_{\max}, \\ a_2 &= \psi A_{\max}. \end{aligned} \quad (3.9)$$

**Table 3.2:** Functions of the model

Function	Expression	Description
$I_1(X_1, X_2, \ell)$	$\begin{cases} \frac{a_1 X_1}{1+h a_1 X_1} \ell^2 & \text{if } \ell < \ell_v \\ \frac{a_1 X_1}{1+h(a_1 X_1 + a_2 X_2)} \ell^2 & \text{otherwise} \end{cases}$	Ingestion of resource 1
$I_2(X_1, X_2, \ell)$	$\begin{cases} 0 & \text{if } \ell < \ell_v \\ \frac{a_2 X_2}{1+h(a_1 X_1 + a_2 X_2)} \ell^2 & \text{otherwise} \end{cases}$	Ingestion of resource 2
$\ell_\infty(X_1, X_2, \ell)$	$\begin{cases} \ell_m h \frac{a_1 X_1}{1+h a_1 X_1} & \text{if } \ell < \ell_v \\ \ell_m h \frac{a_1 X_1 + a_2 X_2}{1+h(a_1 X_1 + a_2 X_2)} & \text{otherwise} \end{cases}$	The length at which somatic growth stops given the current food conditions
$\ell_s(X_1, X_2, \ell)$	$\ell_\infty / \kappa$	Length of instantaneous death
$\ell_{\text{crit}}(X_1, X_2, \ell)$	$\ell_s - q_s(\ell_s - \ell_\infty)$	Length at which starvation occurs
$g(X_1, X_2, \ell)$	$\begin{cases} \gamma(\ell_m h \frac{a_1 X_1}{1+h a_1 X_1} - \ell) & \text{if } \ell < \ell_v \leq \ell_\infty \\ \gamma(\ell_m h \frac{a_1 X_1 + a_2 X_2}{1+h(a_1 X_1 + a_2 X_2)} - \ell) & \text{if } \ell_v \leq \ell \leq \ell_\infty \\ 0 & \text{otherwise} \end{cases}$	Growth rate
$b(X_1, X_2, \ell)$	$\begin{cases} 0 & \text{if } \ell < \ell_j \\ r_m h \frac{a_1 X_1 + a_2 X_2}{1+h(a_1 X_1 + a_2 X_2)} \ell^2 & \text{if } \ell_j \leq \ell \leq \ell_\infty \\ \frac{r_m}{1-\kappa} (h \frac{a_1 X_1 + a_2 X_2}{1+h(a_1 X_1 + a_2 X_2)} - \kappa \frac{\ell}{\ell_m}) \ell^2 & \text{if } \ell_j \leq \ell > \ell_\infty \end{cases}$	Reproduction rate
$S(X_1, X_2, \ell)$	$\begin{cases} 0 & \text{if } \ell \leq \ell_{\text{crit}}(X_1, X_2, \ell) \\ \mu_s(\ell - \ell_{\text{crit}}) & \text{if } \ell_{\text{crit}} < \ell < \ell_s \\ \infty & \text{if } \ell > \ell_s \end{cases}$	Starvation mortality

For brevity of notation function arguments have been omitted where possible

In this equation parameter  $\psi$  is the relative degree of specialization on the secondary resource. Such a trade-off between  $a_1$  and  $a_2$  directly affects resource intake, growth, birth, and death but does not change the composite parameters  $\ell_m$  and  $r_m$ . Note that the diet of large individuals is determined by the two resource densities and the degree of specialization. When the resource densities fluctuate over time, the diet of large individuals changes on an ecological timescale.

The parameterization of the model is based on a planktivorous fish foraging on two unstructured resources (de Roos and Persson 2002). Default parameters can be found in table 3.3. We will study the evolution of  $\psi$  for different supply rates ( $\delta X_{2,\text{max}}$ ) of the secondary resource, to do so we varied  $X_{2,\text{max}}$  while keeping  $\delta$  constant.

#### **Model analysis**

We use the framework of adaptive dynamics (Durinx et al. 2008; Geritz et al. 1998) to study the evolution of specialization on a secondary resource. Since the model lacks an analytical solution we use the EBT-method (de Roos 1997; de Roos et al. 1992) to study both the ecological dynamics and the evolutionary behavior of the model numerically. The ecological dynamics were studied by integrating the model over long time periods while varying parameter  $\psi$  with small steps (See box 3.5 in de Roos and Persson 2013 for an explanation of this procedure).

To calculate if a mutant can invade we start with a single, resident consumer population with a certain trait value  $\psi_{\text{res}}$ , that is settled at its ecological attractor. We then introduce two mutant populations. One mutant with a trait value of  $\psi_{\text{mut}}$  and as a control one population with exactly the same trait value  $\psi_{\text{res}}$  as the resident population. Since we are only interested if these mutants can invade in the environment set by the residents, the mutants themselves do not affect the resources. We introduce these mutant populations by assuming that for 1000 days a few newborn mutants are produced at the same time as the resident population reproduces. Because the resident population is at its ecological attractor, the control mutant population that has exactly the same degree of specialization as the resident population will in the long run not change in size after these 1000 days. To check if the other mutant population grows or shrinks we compare after 2,000,000 days the size of the mutant population with the size of the control population. If the mutant population is larger than this control population this mutant can invade, if it is smaller it cannot. This step is repeated for many trait combinations of  $\psi_{\text{res}}$  and  $\psi_{\text{mut}}$  to construct the pairwise invasibility plots (PIPs).

In addition to studying the evolution of specialization  $\psi$  for the different types of population cycles, we also studied this in case of equilibrium dynamics using the PSPManalysis software package (de Roos 2016). The PSPManalysis packages automatically detects and classifies evolutionary singular strategies according to the classification of Geritz et al. (1998). The package can compute where the mutant has a positive and negative growth rate and can in this way construct a PIP (see de Roos 2016 for details). Even though the steady state of the size-structured model is unstable and hence not an ecological attractor, we nonetheless analyze the evolutionary dynamics in this steady state because the resource fluctuations in case of small-amplitude population cycles (see below) are close to the constant resource densities in the (unstable) equilibrium state. The analysis thereby provides insights into the mechanisms that prevent the evolution of specialization in case of small-amplitude cycles.

**Table 3.3:** Standard parameters of the model

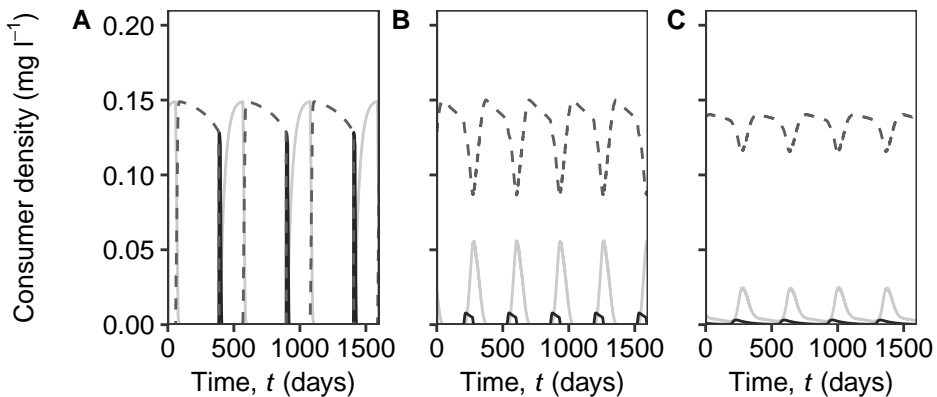
Parameter	Description	Default Value	Unit
$\delta$	Resource turnover rate	0.1	day <sup>-1</sup>
$X_{1,\max}$	Maximum biomass density of resource 1	0.09	mg l <sup>-1</sup>
$X_{2,\max}$	Maximum biomass density of resource 2	variable	mg l <sup>-1</sup>
$\ell_b$	Length at birth	7	mm
$\ell_v$	Length at which secondary resource becomes available	40	mm
$\ell_j$	Length at maturation	110	mm
$\ell_m$	Maximum length	300	mm
$h$	Handling time	10	day mm <sup>2</sup> mg <sup>-1</sup>
$A_{\max}$	Maximum value of the attack rate	6.667	day <sup>-1</sup> mm <sup>-2</sup> l
$\kappa$	Proportion invested in maintenance and growth	0.7	-
$\gamma$	Von Bertalanffy growth rate	0.006	day <sup>-1</sup>
$r_m$	Proportionality constant of reproduction	0.003	day <sup>-1</sup> mm <sup>-2</sup>
$\mu$	Background mortality	0.01	day <sup>-1</sup>
$\mu_s$	Scaling constant of starvation mortality	0.2	day <sup>-1</sup>
$q_s$	Threshold fraction for onset starvation mortality	0.3	-
$\beta$	Length to weight proportionality constant	$9 \cdot 10^{-3}$	mg mm <sup>-3</sup>

### 3.3 Results

We will first show the different types of ecological dynamics that can be found in the model. Secondly, we discuss the costs and benefits of specialization on a resource that is only available for large individuals. Thirdly, we will discuss how specialization on the secondary resource evolves or not, depending on the type of population dynamics.

#### Ecological dynamics

The consumer population displays, in the absence of an ontogenetic niche shift ( $\psi = 0$ ), three different types of cycles. One large amplitude single-cohort cycle, in which the population is dominated by a single cohort throughout its lifetime, and two types with intermediate and low amplitude where there are multiple cohorts present at the same time (figure 3.1). The different types of cycles do sometimes co-occur. Figure 3.2 shows, for two different values of  $X_{1,\max}$ , where the different type of cycles occur as a function of the supply rate of the secondary resource and the degree of specialization  $\psi$ . The two small amplitude cycles disappear in case individuals are more specialized on the secondary resource. Stable equilibrium dynamics do not occur for the chosen parameter values.

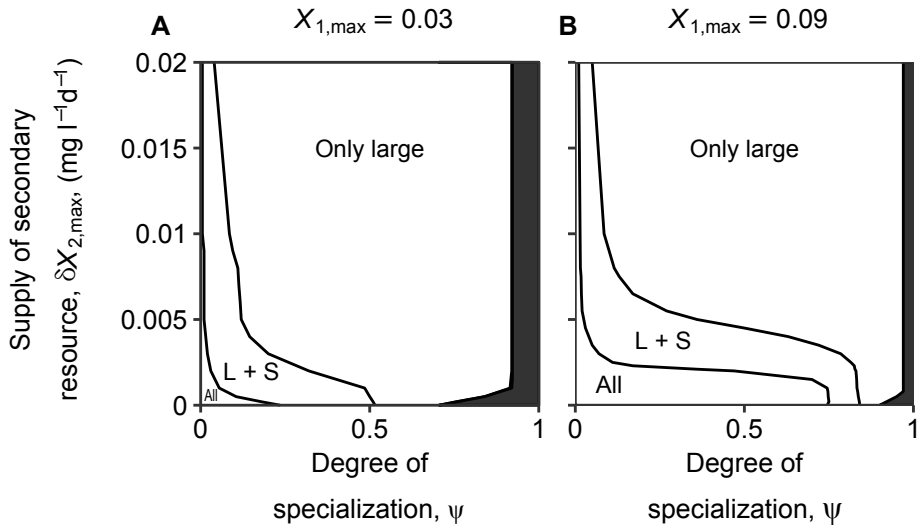


**Figure 3.1:** Three different types of oscillatory dynamics can be found in the Kooijman-Metz model. Depending on the initial conditions, the population fluctuations have a high (A), intermediate (B) or low (C) amplitude. Biomass density ( $\text{mg l}^{-1}$ ) of small juveniles (grey, solid line), large juveniles (darkgrey, dashed line), and adults (black, solid line) over time (days). The secondary resource is not exploited ( $\psi = 0$ ), other parameter values as in table 3.3.

Since we are mainly interested in how the type of dynamics influences the evolution of specialization on a secondary resource, we choose parameter  $X_{1,\max} = 0.09 \text{ mg l}^{-1}$ . For this parameter value, the three different types of population cycles



co-occur for most values of the degree of specialization on the secondary resource,  $\psi$ , the trait under evolution. In this way we ensure that if we observe different evolutionary behaviors, this is caused by the type of dynamics, and not by a change in parameter values.



**Figure 3.2:** Occurrence of the three types of population cycles (large (L), small (S) and intermediate) as a function of the degree of specialization on the secondary resource ( $\psi$ ) and the supply rate of this resource ( $\text{mg l}^{-1} \text{day}^{-1}$ ) for two values of  $X_{1,\max}$ , the maximum value of the primary resource ( $\text{mg l}^{-1}$ ). The dark areas indicate the parameter range where there is no viable population. Parameter values as in table 3.3.

### Costs and benefits of specialization on a secondary resource

A mutant can invade a resident population when its long-term average per capita growth rate is positive in the environment set by the resident population (Metz et al. 1992). A mutant's per capita growth rate is determined by the number of offspring it produces, which in our model depends on the time until maturation and the survival and reproduction rate. The trade-off between specialization on the primary and secondary resource (equation 3.9) implies that small juveniles that are more specialized on the secondary resource, always grow slower compared to individuals that are less specialized on the secondary resource. Small juveniles do not have access to the secondary resource and do therefore not benefit from a morphology specialized in feeding on this resource. In the first part of the life cycle specialization on the secondary

resource is therefore always disadvantageous since it slows down growth. Specialization on the secondary resource can therefore only evolve if this initial disadvantage is compensated for later in life. Specialization on the secondary resource is for large individuals only advantageous when this will increase their growth and reproduction rate. Since growth and reproduction depend in our model on the resource intake,  $X_2 > X_1$  is a necessary, but not sufficient, condition for specialization to be advantageous.

#### **The type of population dynamics affects the evolutionary outcome**

Figure 3.3 shows PIPs for three different supply rates of the secondary resource (results for other supply rates are shown in appendix 3.A). The evolution of the specialization parameter  $\psi$  is highly affected by the type of population dynamics.

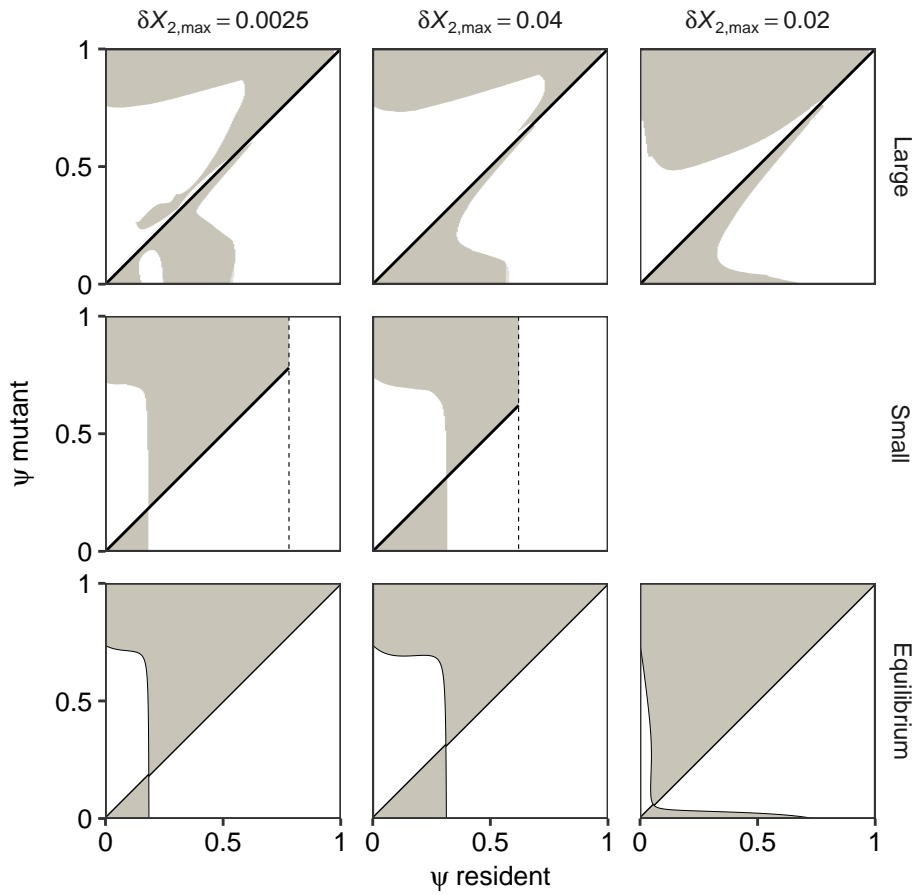
In case of large amplitude cycles, parameter  $\psi$  can evolve to very high values, meaning that individuals specialize in feeding on the secondary resource (upper row in figure 3.3). While the evolutionarily stable strategies (ESSs) are for all supply rates convergent and evolutionary stable (CSS), the PIPs show that a mutant that is substantially different from the resident strategy can invade, which might in principle lead to a dimorphic population. It is, however, beyond the scope of this paper to study how these two subpopulations subsequently evolve.

When the population displays small amplitude cycles, the specialization parameter  $\psi$  evolves to low values for most supply rates of the secondary resource (figure 3.A1 and middle row in figure 3.3). This implies that individuals have a morphology that is efficient in feeding on the primary resource, but not very efficient in feeding on the secondary resource. Interestingly, the evolutionary result is the same for intermediate amplitude cycles (figure 3.A1 in appendix 3.A) and when equilibrium dynamics are assumed (bottom row in figure 3.3). The ESSs in this case are all convergent stable strategies.

Note that for high supply rates of the secondary resource, both the small and intermediate amplitude cycles occur only for low values of the specialization parameter  $\psi$  (figure 3.2B). Since for low values of parameter  $\psi$  the selection gradient is in this case positive (figure 3.3), evolution takes specialization parameter  $\psi$  to the boundary of existence of the small or intermediate amplitude dynamics, at which point attractor switching to the large amplitude cycles occurs. Evolution will subsequently drive parameter  $\psi$  to the CSS value of these large amplitude cycles.

We will first discuss the mechanisms that prevent the specialization parameter  $\psi$  to evolve to high values in case of small amplitude cycles. Secondly, we will show why consumers evolve a morphology highly specialized in feeding on the secondary resource in case of large amplitude cycles.

Because the evolutionary dynamics are qualitatively the same for small and intermediate amplitude cycles and when equilibrium dynamics are assumed (figure 3.3 and



**Figure 3.3:** Pairwise invasibility plots for different types of population dynamics and different values of the supply rate of the secondary resource ( $\text{mg l}^{-1}\text{day}^{-1}$ ). The grey areas indicate negative invasion fitness, the white areas positive. The dotted lines in the PIPs for small amplitude cycles indicate where this type of cycles disappears. Parameter values as in table 3.3.

3.A1), we will, for convenience, analyze evolution in the context of such equilibrium dynamics, even for high values of the supply rate of the secondary resource, for which the small and intermediate amplitude cycles disappear (figure 3.A1). This approach will allow us to better unravel the mechanisms that prevent the specialization parameter  $\psi$  to evolve to high values.

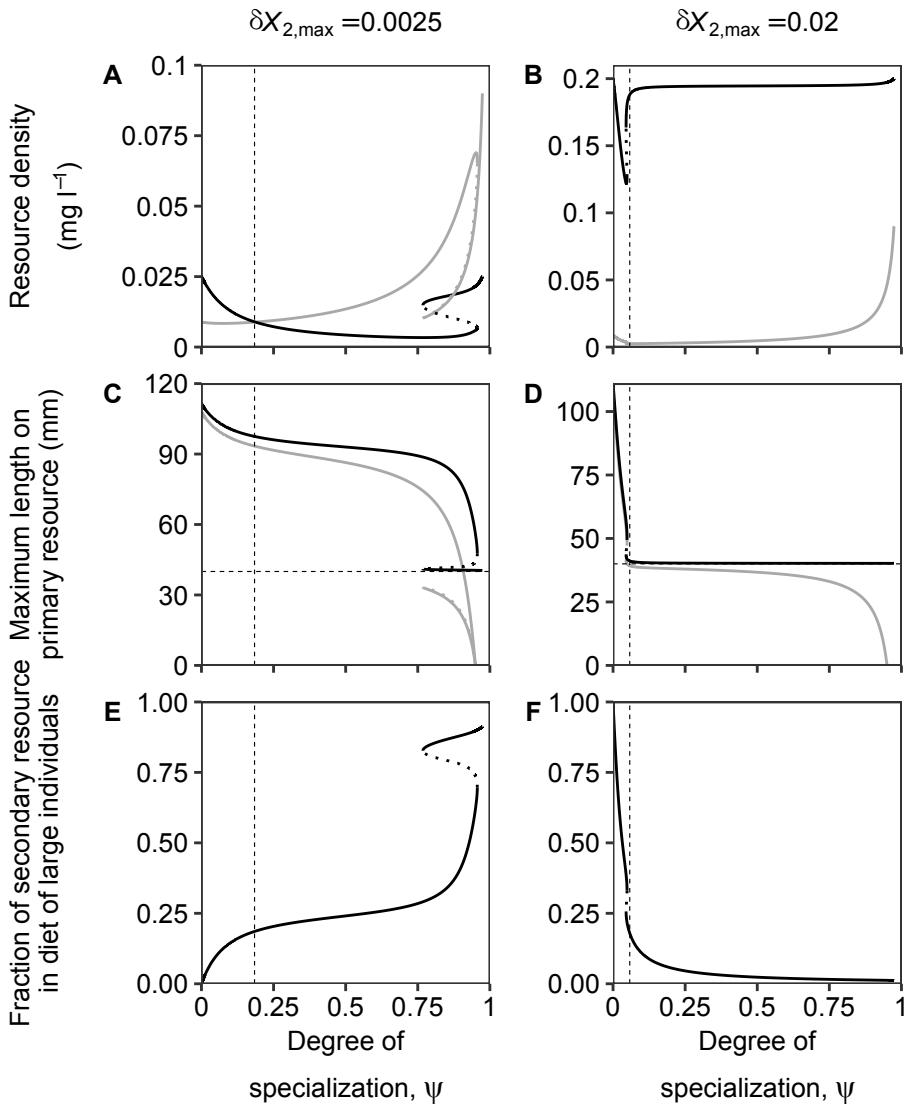
### **Evolution of specialization under equilibrium conditions and in case of small amplitude cycles**

Figures 3.3 and 3.A1 show that under equilibrium population dynamics, the CSS of the specialization parameter  $\psi$  initially increases with increasing supply rates, but ultimately decreases again to low values. Only for a small range of supply rates of the secondary resource, the specialization parameter  $\psi$  can evolve to relatively high values (figure 3.A1).

Figure 3.4A shows the equilibrium densities of the two resources as a function of the degree of specialization  $\psi$  of the resident population in case of a low supply rate of the secondary resource. This figure shows that the density of the secondary resource is higher than the density of the primary resource in case the resident population is not or only slightly specialized in feeding on the secondary resource. Therefore, a mutant that specializes more on the secondary resource than the resident will increase its resource intake and can invade. Vice versa, the primary resource is more abundant than the secondary resource in case the resident population has a morphology highly specialized on the secondary resource (figure 3.4A). In this case a mutant that is less specialized has a higher resource intake than the resident and can therefore invade. The specialization parameter  $\psi$  therefore evolves to a value such that  $X_1 = X_2$  (figure 3.4A). Since individuals have a morphology specialized in feeding on the primary resource, the diet of large individuals consists mainly of this resource in the CSS (figure 3.4E).

Increasing the supply rate of the secondary resource increases the value of  $\psi$  where the densities of both resources are equal. Therefore, the specialization parameter  $\psi$  initially evolves to higher values with increasing supply rates (figure 3.3 and 3.A1). For high supply rates specialization on a secondary resource is, however, impeded by the trade-off between small and large individuals.

Figure 3.4B shows that for high supply rates, the density of the secondary resource is always higher than the density of the primary resource, independent of the level of specialization. Large individuals almost exclusively forage on the secondary resource as soon as the specialization parameter  $\psi > 0$  (figure 3.4F). It is for large individuals therefore beneficial to specialize on the secondary resource. Nonetheless, the parameter  $\psi$  does not evolve to high values (figure 3.3).



**Figure 3.4:** Upper panels: Densities of the primary (grey line) and secondary (black line) resource ( $\text{mg l}^{-1}$ ) in equilibrium as a function of the degree of specialization of the resident population. Middle panels: The maximum size (mm) individuals can reach when only feeding on the primary resource as a function of the degree of specialization (black line). The grey line indicates the maximum size that mutant individuals that are slightly more specialized in feeding on the secondary resource ( $\psi_{\text{mut}} = \psi_{\text{res}} + 0.01$ ) can reach in the environment set by the resident strategy. The horizontal dashed line indicates a length of 40 mm, the size at which the second resource becomes available. Bottom panels: The fraction of the secondary resource in the diets of large individuals ( $\ell > \ell_v$ ). The dotted sections of the equilibrium curves correspond to equilibria that are saddle points. The vertical dashed lines indicate the location of the CSS. Parameter values as in table 3.3.

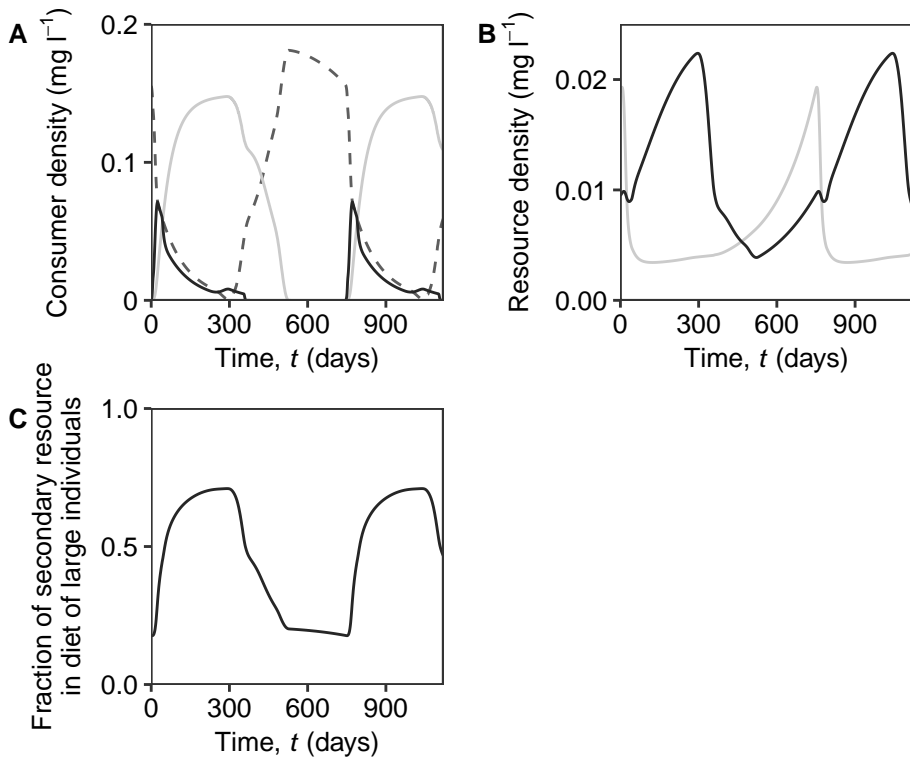
Because large individuals have a lot of food available as soon as  $\psi > 0$ , the adults of the resident population produce many offspring that depress the density of the primary resource. The competition for this primary resource is so intense, that the maximum size that small juveniles can reach while feeding on this resource, is barely above the threshold value for switching to the secondary resource (horizontal dashed line in figure 3.4D). Since mutant individuals with a slightly larger value of  $\psi$  than the resident are less effective in feeding on the primary resource (equation 3.9), they are not able to reach the size threshold needed to switch to the secondary resource. These mutant individuals will never mature and cannot invade the resident population.

To summarize, for low supply rates the specialization parameter  $\psi$  evolves to low values since further specialization on a secondary resource decreases the resource intake of large individuals (figure 3.4A). While large individuals do include the secondary resource in their diet, they mainly feed upon the primary resource (figure 3.4E). For high supply rates, large individuals feed mainly upon the secondary resource (figure 3.4F). It is therefore for large individuals beneficial to evolve a morphology specialized in feeding on this abundant resource. However, competition among the abundant small individuals prevents the specialization parameter  $\psi$  to evolve to high values. Only for intermediate values of the supply rate, some specialization can evolve (figure 3.3 and 3.A1) since in that case increasing the specialization parameter  $\psi$  is beneficial for large individuals while at the same time competition among the smallest individuals is not severe enough to prevent specialization on the secondary resource.

#### **Evolution of specialization in case of large amplitude cycles**

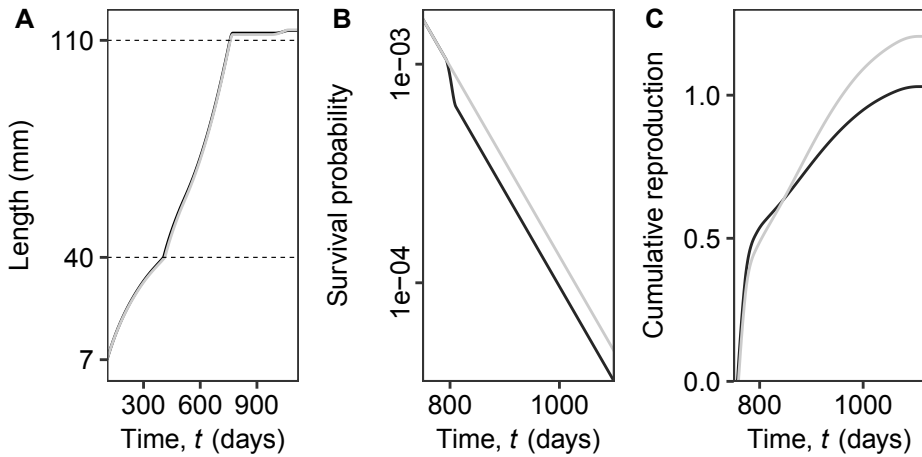
When the population exhibits large amplitude cycles, the specialization parameter  $\psi$  can evolve to high values for most supply rates (figure 3.3 and 3.A1). To explain why the degree of specialization  $\psi$  evolves to high values we will first discuss in detail the ecological dynamics (figure 3.5 and 3.7). We show in these figures a resident population with a strategy of  $\psi = 0.3$ , the ecological dynamics are however qualitatively the same for different values of  $\psi$ . In figure 3.6 and 3.8 we show the growth, survival probability and reproductive output of a resident individual ( $\psi = 0.3$ ) and a mutant that is slightly more specialized on the secondary resource ( $\psi = 0.31$ ). We will first explain how the degree of specialization evolves in case of low supply rates (figure 3.5 and 3.6), secondly we explain how the degree of specialization evolves for high supply rates (figure 3.7 and 3.8).

Figure 3.5A shows that at day 0 a cohort of large juveniles matures and starts to reproduce at a high rate. Shortly afterward, the population mainly consists of small juveniles. Since these juveniles only feed on the primary resource, the density of this resource is low, while that of the secondary resource is high (figure 3.5B). Around day 300, small juveniles start to mature to the large juvenile size class (figure 3.5A) and in-



**Figure 3.5:** Large amplitude cycles in case of low supply rates of the secondary resource. A: Density ( $\text{mg l}^{-1}$ ) of small juveniles (grey, solid line), large juveniles (darkgrey, dashed line) and adults (black, solid line) over time (days). B: Densities ( $\text{mg l}^{-1}$ ) of the primary (grey) and secondary (black) resource over time. C: Fraction of the secondary resource in the diet of large individuals.  $\delta X_{2,\max} = 0.0025 \text{ (mg l}^{-1} \text{ day}^{-1})$ ,  $\psi = 0.3$ , other parameters as in table 3.3.

clude the secondary resource in their diet (figure 3.5C). Therefore, the density of the secondary resource decreases while the density of the primary resource increases (figure 3.5B). Around day 750, large juveniles mature into adults (figure 3.5A and 3.6A) that reproduce a new, abundant cohort of offspring (figure 3.5A). These offspring subsequently decrease the primary resource to very low levels (figure 3.5B), causing a high starvation mortality among their parents, which in turn leads to an increase in the secondary resource. A mutant that is slightly more specialized on the secondary resource has therefore more food available than the residents ( $X_2 > X_1$ ), starves less (grey line figure 3.6B), and therefore produces more offspring (figure 3.6C). Because mutants are less effective on the primary resource they grow slightly slower (figure 3.6A), start reproducing later, and initially have a lower reproductive output than residents (first part of figure 3.6C). However, since the survival probability of the resident is lower than that of the mutant (figure 3.6B), the mutant reproductive output catches up with the resi-

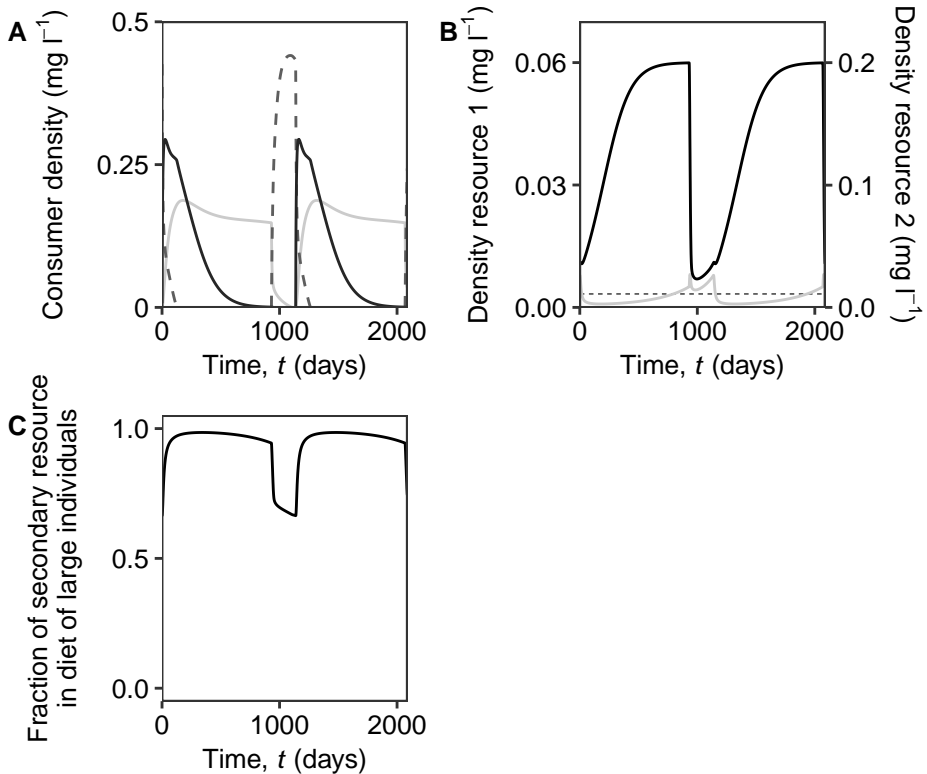


**Figure 3.6:** Differences in growth (A), survival (B) and reproduction (C) of an individual of the resident population (black lines) and a mutant individual (grey lines) in the environment set by the resident population when the supply rate of the secondary resource is low (see figure 3.5 for the corresponding population dynamics). Panel A: Growth of a resident individual and a mutant born at day 107. The dashed lines indicate when the secondary resource becomes available (at a size of 40 mm) and when the individual matures (at a size of 110 mm). Panel B: Resident adults starve because of a lack of food while mutant adults stay alive in the environment set by the resident population and continue to reproduce. Panel C: Cumulative reproduction of a resident adult and a mutant adult over time in the environment set by the resident.  $\delta X_{2,\max} = 0.0025$  ( $\text{mg l}^{-1}\text{day}^{-1}$ ),  $\psi_{\text{res}} = 0.3$ ,  $\psi_{\text{mut}} = 0.31$ , other parameters as in table 3.3.

dent around day 850 (figure 3.6C). Since the reproductive output of a mutant individual is ultimately higher than that of an individual of the resident population, it can invade in the population and the specialization parameter  $\psi$  will evolve to high values.

When the supply rate of the secondary resource is high, the specialization parameter  $\psi$  evolves to high values as well (figure 3.3 and 3.A1). However, the mechanism behind the evolution of specialization is in this case different. As with low supply rates, the cycle starts off at day 0 with a cohort of large juveniles maturing and starting to reproduce (figure 3.7A). However, because the supply rate of the secondary resource is high, many more offspring are produced compared to the case where the supply rate was low. Competition among the smallest individuals is therefore very high and growth is slow (figure 3.8A). Initially, the density of the primary resource is for both resident and mutant individuals too low to reach the size where the secondary resource becomes available (figure 3.7B). Over time the density of small individuals decreases because of background mortality (figure 3.7A). This leads to an increase in the density of the primary resource such that maturation to the next size class is possible (figure 3.7B). Around day 930 the first juvenile matures to the next stage. The secondary re-

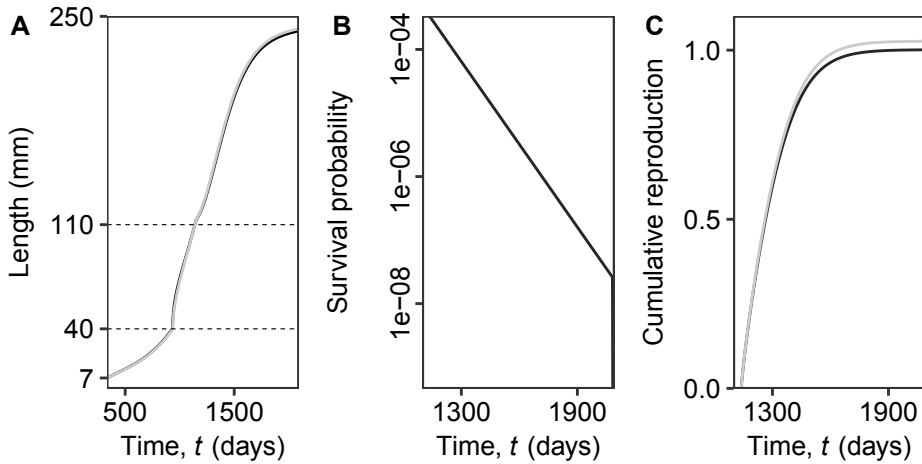




**Figure 3.7:** Large amplitude cycles in case of high supply rates of the secondary resource. A: Density ( $\text{mg l}^{-1}$ ) of small juveniles (grey solid line), large juveniles (darkgrey, dashed line) and adults (black, solid line) over time (days). B: Densities ( $\text{mg l}^{-1}$ ) of the primary (black) and secondary (grey) resource over time. The dotted line indicates the density of the primary resource that is necessary for resident individuals to reach a size of 40 mm. C: Fraction of the secondary resource in the diet of large individuals.  $\delta X_{2,\text{max}} = 0.02 \text{ (mg l}^{-1} \text{ day}^{-1})$ ,  $\psi = 0.3$ , other parameters as in table 3.3.

source is now available and since it is very abundant (figure 3.7B), growth is accelerated (figure 3.8A). Around day 1100 the first large juveniles mature into adults (figure 3.7A and 3.8A). These adults can continue to grow since there is lots of the secondary resource available (figure 3.8A). The reproduction rate is therefore very high, leading to a large number of offspring (figure 3.7A). Even though these offspring decrease the density of the primary resource to very low levels (figure 3.7B), starvation among adults does not occur (figure 3.8B) since large individuals feed almost exclusively on the very abundant secondary resource (figure 3.7C).

Mutant individuals that are more specialized on the secondary resource initially grow slower. However, as soon as these mutants have access to the secondary resource, they grow faster and can reproduce more (figure 3.8C), since the density of the



**Figure 3.8:** Differences in growth (A), survival (B) and reproduction (C) of an individual of the resident population (black lines) and a mutant individual (grey lines) in the environment set by the resident population when the supply rate of the secondary resource is high (see figure 3.7 for the corresponding population dynamics). Panel A: Growth of a resident individual and a mutant born at day 335. The dashed lines indicate when the secondary resource becomes available (at a size of 40 mm) and when the individual matures (at a size of 110 mm). Panel B: The survival probability of resident adults and mutant adults is equal. Adults do not starve when a new cohort arrives because they can feed on the secondary resource. Panel C: Cumulative reproduction of a resident adult and a mutant adult over time in the environment set by the resident.  $\delta X_{2,\max} = 0.02$  ( $\text{mg l}^{-1}\text{day}^{-1}$ ),  $\psi_{\text{res}} = 0.3$ ,  $\psi_{\text{mut}} = 0.31$ , other parameters as in table 3.3.

secondary resource is always higher than the density of the primary resource. Under equilibrium conditions, the specialization parameter  $\psi$  could not evolve to high values when the supply rate was high since this increased competition among the smallest individuals such that they could not grow to the next size class (figure 3.4D). When the population exhibits large amplitude cycles, the primary resource increases as soon as the small juveniles of the resident population start to forage on the secondary resource. This allows some mutant individuals to reach the threshold size for feeding on the secondary resource somewhat later. Since the secondary resource is very abundant, mutants can make up for the delay in the first part of their life and ultimately produce more offspring (figure 3.8C).

### 3.4 Discussion

In this paper we studied the evolution of ontogenetic niche shifts under non-equilibrium dynamics. We showed that specialization on a resource that is only available for large individuals is hardly possible in case of small-amplitude cycles, intermediate-amplitude cycles, or equilibrium conditions. Surprisingly, while there are two different types of small amplitude cycles, the evolutionary behavior is exactly the same in both (figure 3.A1). While it was shown before that specialization on a secondary resource is hardly possible under equilibrium conditions (chapter 2 and 4 of this thesis), we here reveal the mechanisms that prevent this.

Our results show that different ecological dynamics lead to different selection pressures and therefore to very different evolutionary outcomes. These differences occur because of the different ecological conditions that individuals experience depending on the type of population cycles. Notably, these different types of population cycles are all internally generated and co-occur for the same parameter set. In case of large amplitude cycles and low supply rates of the secondary resource, adults experience high juvenile-driven starvation mortality, which makes it advantageous to specialize on a secondary resource. These starvation conditions do not occur in case of small amplitude cycles or equilibrium conditions. In case of equilibrium conditions and high supply rates of the secondary resource, the constant presence of small individuals suppresses the primary resource to such low levels that less efficient individuals cannot grow sufficiently to reach the second feeding niche. While competition for the primary resource is still severe in case of large amplitude cycles, the maturation of the dominant cohort to the next size class releases competition for the primary resource during a short time-interval, allowing less efficient individuals to mature.

It has been shown before that non-equilibrium dynamics can lead to different evolutionary outcomes compared to equilibrium conditions (Hoyle et al. 2011; Nurmi and Parvinen 2013; White et al. 2006). White et al. (2006) and Hoyle et al. (2011) showed with the use of a discrete-time model that under non-equilibrium conditions and with certain trade-offs, evolutionary branching is possible in ecological scenarios that do not allow for branching under equilibrium conditions. Nurmi and Parvinen (2013) looked into the evolution of resource specialization and identified evolutionary scenarios, such as evolutionary suicide, that were only found under non-equilibrium conditions. Our work differs in two main aspects from these results. First, we show that different evolutionary outcomes are possible for the same set of parameters. Dependent on the initial conditions, the consumer population can exhibit three types of population cycles and two different evolutionary outcomes. There is thus not only ecological but also evolutionary bistability.

A second difference is that independent of the type of population dynamics, we always find convergent stable strategies (CSSs, Geritz et al. 1998). The type of population dynamics only affects the location of these CSSs. This is in contrast with the work of White et al. (2006), Hoyle et al. (2011) and Nurmi and Parvinen (2013) who all find that non-equilibrium dynamics change the type of evolutionary attractor, e.g., from an evolutionary repeller to an evolutionary branching point. Furthermore, all these studies find changes in the type of evolutionary attractor in case of non-linear trade-offs but not for linear trade-offs (Hoyle et al. 2011; Nurmi and Parvinen 2013; White et al. 2006). We found different evolutionary outcomes depending on the type of dynamics, even though we assumed a linear trade-off between the attack rates on the primary and secondary resource. Using different trade-offs could maybe lead to even more distinct evolutionary outcomes, depending on the type of population dynamics. However, the effect of different trade-off functions on the evolution of niche shifts is beyond the scope of this study.

Even though specialization on a secondary resource is possible in case of large amplitude cycles, it would still be beneficial for individuals to be effective on the primary resource as well. Small individuals depend on this resource for their growth and they can therefore reproduce earlier on in their life when they are more effective in feeding. Metamorphosis allows for the independent evolution of stage-specific traits, such that juveniles can specialize on the primary resource while adults specialize on the secondary resource (Moran 1994). It has been shown that, under equilibrium conditions, metamorphosis can evolve to increase the level of specialization of small individuals on the primary resource, even though metamorphosis is very costly for larger individuals (chapter 4 of this thesis). While there is probably selection to increase juvenile performance, it is still an open question if the benefits of better specialized juveniles outweigh the costs of metamorphosis in case of large amplitude cycles.

The large amplitude single cohort cycles that allow for the evolution of specialization on a secondary resource occur because small individuals can, in the absence of an ontogenetic niche shift, outcompete their parents (de Roos et al. 1990). Due to the differences in scaling between intake (with a power of  $2/3$ ) and metabolic demands (with a power of 1) with body weight, smaller individuals can withstand lower resource levels than larger individuals. Large amplitude cycles where adults quickly die after reproducing because of juvenile-induced starvation mortality, are common predictions of size-structured consumer resource models (de Roos and Persson 2003, 2013; Persson et al. 1998). We therefore expect that our result is not specific for the chosen model formulation, but can be found in many size-structured models.

In summary, we showed that the type of population cycles have a striking effect on the evolution of ontogenetic niche shifts. The evolutionary outcome can be completely reversed when the type of population dynamics change. These results have

important consequences, since population cycles resulting from size-dependent interactions are a common observation in natural systems (Murdoch et al. 2002). It is therefore of importance to consider the effect of the type of population cycles when studying the evolution of life-history traits.

### Acknowledgments

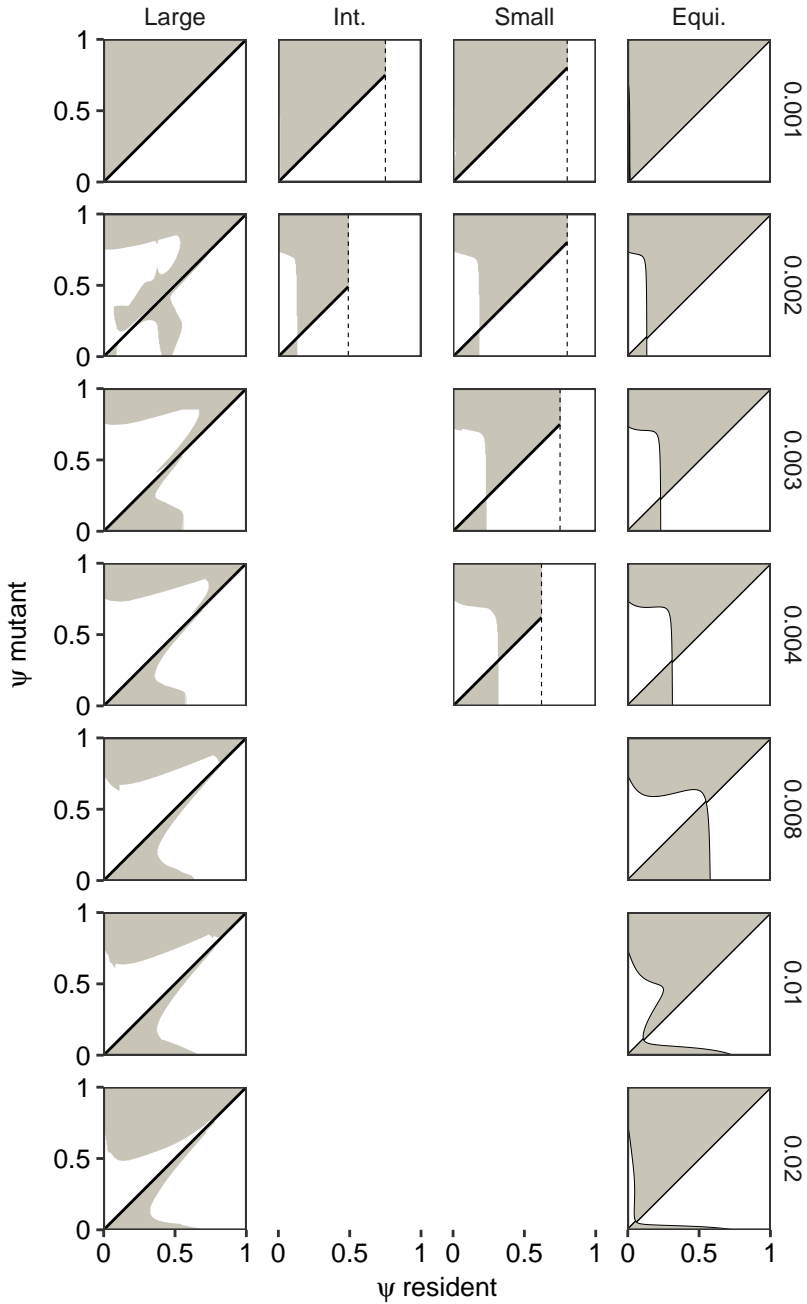
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### Appendix 3.A Pairwise invasibility plots

In this appendix we show pairwise invasibility plots (PIPs) for many different supply rates of the secondary resource.

Figure 3.A1 shows that the PIPs for small and intermediate amplitude cycles are similar to the PIPs where equilibrium dynamics are assumed. The specialization parameter  $\psi$  initially evolves to higher values with increasing supply rates. Because the secondary resource is available at high density, it is beneficial for individuals to specialize in feeding on that resource. However, for high values of the supply rate, parameter  $\psi$  will evolve to very low values. This implies that consumers are very efficient in feeding on the primary resource and not on the secondary resource. Competition among the smallest individuals hinders specialization on the resource used later in life.

The specialization parameter  $\psi$  evolves to high values in case of large amplitude cycles (figure 3.A1). Only when the supply rate is very low ( $0.001 \text{ mg l}^{-1} \text{ day}^{-1}$ ), individuals will specialize in feeding on the primary resource.



**Figure 3.A1:** Pairwise invasibility plots for different types of population dynamics and different values of the supply rate of the secondary resource ( $\text{mg l}^{-1} \text{day}^{-1}$ ). The grey areas indicate negative invasion fitness, the white areas positive. The dashed line in the PIPs for intermediate and small amplitude cycles indicates where these types of cycles disappear. Parameter values as in table 3.3.





**THE EVOLUTIONARY ECOLOGY OF  
METAMORPHOSIS**

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Under review in *The American Naturalist*

### Abstract

Almost all animal species undergo metamorphosis, even though empirical data show that this life-history strategy evolved only a few times. Why is metamorphosis so widespread and how has it evolved? Here we study the evolution of metamorphosis using a fully size-structured population model in conjunction with the adaptive-dynamics approach. We assume that individuals compete for two food sources, one of these, the primary food source, is available to individuals of all sizes. The secondary food source is available only to large individuals. Without metamorphosis, unresolvable tensions arise for species faced with the opportunity of specializing on such a secondary food source. We show that metamorphosis can evolve as a way to resolve these tensions, such that small individuals specialize on the primary food source, while large individuals specialize on the secondary food source. We find, however, that metamorphosis only evolves when the supply rate of the secondary food source exceeds a high threshold. Individuals postpone metamorphosis when the ecological conditions under which metamorphosis originally evolved deteriorate, but will not abandon this life-history strategy, even if it causes population extinction through evolutionary trapping. In summary, our results show that metamorphosis is not easy to evolve but, once evolved, it is hard to lose. These findings can explain the widespread occurrence of metamorphosis in the animal kingdom despite its few evolutionary origins.

## 4.1 Introduction

Metamorphosis is widespread in the animal kingdom (Werner 1988). Salamanders, frogs, butterflies, and ants all abruptly change their morphology at a certain point during their lives. Also many fish species – e.g., salmon and flatfish (McMenamin and Parichy 2013), crustaceans such as lobsters and barnacles (Haug and Haug 2013), and jellyfish (Holstein and Laudet 2014) – undergo a period of postembryonic remodelling of their body plan. In this paper, we aim to understand which ecological conditions promote the evolution of metamorphosis in free-living species that change their diet over their life cycle. Metamorphosis is here defined as the morphological change that takes place at the transition from the larval to the juvenile life stage.

It is commonly thought that metamorphosis has evolved to decouple different life stages, such that larvae and adults can evolve independently from each other in response to different selection pressures (Moran 1994). This allows individuals to adopt different phenotypes during their life cycle, each specialized on different tasks such as dispersal, mate finding, or food acquisition (Moran 1994). A body plan that is needed for efficient mate finding, for example, may often be very different from a body plan needed for efficient feeding (Moran 1994). However, genetic correlations among the phenotypes expressed during different life stages prevent their independent evolution (Schluter et al. 1991). This is because adaptations beneficial for one life stage can be disadvantageous for another life stage. The adaptive decoupling hypothesis predicts that metamorphosis breaks up these genetic correlations and therefore permits the independent evolutionary response of phenotypes expressed during different life stages (Moran 1994). Although many studies have shown that genetic correlations persist, to some extent, across the metamorphic boundary, so that larval traits keep influencing post-metamorphic performance (Aguirre et al. 2014; Crean et al. 2011; Fellous and Lazaro 2011), there is considerable evidence that metamorphosis allows for the decoupling of phenotypic evolution (Aguirre et al. 2014; Moran 1994; Parichy 1998; Saenko et al. 2012). While metamorphosis can therefore be highly beneficial for organisms, it typically is a costly process. For instance, species not only often lose body mass during metamorphosis, but also tend to be more vulnerable to predation (Geffen et al. 2007; Wassersug and Sperry 1977). This raises the question under which ecological conditions the benefits of metamorphosis can outweigh its disadvantages.

Metamorphosis is likely to be especially advantageous in species that change diet during ontogeny. It has even been suggested that ontogenetic changes in diet constituted the first steps in evolutionary history toward life cycles with metamorphosis (Ebenman 1992; Nielsen 1998; Schoch 2009; Wassersug 1975; Werner and Hall 1988; Wilbur 1980). Species with an ontogenetic diet shift face a fundamental trade-off between their performance early and late in life, since different food types often require

different morphologies (Ebenman 1992; Svanback and Eklov 2003; Werner 1977). Recent research has shown that individuals will change their diet during ontogeny when this increases their energy intake (chapter 2 of this thesis). However, it is not possible for individuals to specialize on a new food source when this overly much reduces their performance on the food source they depend on early in life (chapter 2 of this thesis). These results suggest that strong selection pressures exist toward decoupling the phenotypes expressed during different life stages, so that an individual's performance on different food sources can be maximized as independently as possible. Although most animal species undergo metamorphosis, only a few theoretical studies have investigated the origin of metamorphosis in species exhibiting ontogenetic diet shifts during their life cycle (Ebenman 1992; Istock 1967; Werner and Hall 1988). One of the first analyses of this problem is presented in the paper by Istock (1967). Using an age-structured model, Istock (1967) examined whether a population in which individuals undergo metamorphosis could invade and persist in a community of species without metamorphosis. In his model, the two different life stages interfaced by metamorphosis occupy separate niches and evolve independently from each other. Istock (1967) argued that a population in which individuals undergo metamorphosis can invade, but never persist, in a community of species without metamorphosis. On this basis, he concluded that metamorphosis is an evolutionarily unstable strategy. In contrast to Istock, Ebenman (1992) considered fitness maximization at the individual level in an age-structured model and concluded that metamorphosis easily evolves in species that change resources during ontogeny. Other theoretical studies of the evolution of metamorphosis have mainly focused on the optimal timing of metamorphosis (Werner 1988; Werner and Gilliam 1984), and not on the question under which conditions metamorphosis evolves in the first place.

An important shortcoming of all aforementioned studies is that they do not take into account the feedback between individuals and their environment. In most species, growth and reproduction, which crucially influence fitness, are largely determined by food intake (de Roos and Persson 2013). Diet shifts and metamorphosis change this food intake, and thus, also the densities of the different food sources. This change in food densities, in turn, alters the food intake of individuals and therefore their fitness. Hence, the feedback loop between individuals and their environment cannot be ignored when studying the evolution of metamorphosis.

Here we study the origin of metamorphosis in species that undergo an ontogenetic diet shift, taking into account the just highlighted feedback loop between individuals and their environment. To do so, we use a size-structured consumer-resource model in conjunction with the adaptive-dynamics approach. Adaptive-dynamics theory enables the exploration of evolution in realistic ecological contexts (Dieckmann and Law 1996; Geritz et al. 1998; Metz et al. 1992). We assume that individuals are limited to for-

aging on a primary food source when they are small. Larger individuals additionally have access to a secondary food source, occurring in a different habitat. Individuals choose their habitat so that their food intake is optimized. Furthermore, we assume that individuals can specialize on the consumption of either the primary food source or the secondary food source, leading to a trade-off between their foraging successes early and late in life. It has been shown before that such a trade-off hinders specialization on the secondary food source (chapter 2 of this thesis) and might therefore promote the evolution of metamorphosis. However, since metamorphosis is costly, we assume that metamorphosing individuals lose body mass and have a high probability of dying.

To understand the ecological conditions that allow for the evolution of metamorphosis, we first study how specialization on the secondary food source is hindered by the aforementioned trade-off. On this basis, we examine if and to what extent metamorphosis evolves, depending on the supply rate of the secondary food source. Lastly, we investigate if and when metamorphosis disappears when the ecological conditions under which it has evolved change.

## 4.2 Model and methods

### Population dynamics

We use a size-structured consumer-resource model based on the model described by Persson et al. (1998) to study the evolution of metamorphosis in species changing their diet during ontogeny. In contrast to Persson et al. (1998), we assume, for the sake of simplicity, continuous reproduction and equilibrium conditions. Extending the model by Persson et al. (1998), we introduce a second food source. Both food sources are assumed to be unstructured. The primary food source, with population density  $X_1$ , is available to all individuals, whereas the secondary food source, with population density  $X_2$ , is available only to individuals exceeding a threshold size. Both food sources follow semi-chemostat dynamics and reach densities of  $X_{1,\max}$  and  $X_{2,\max}$  in the absence of the consumer population. It is assumed that the two food sources occur in two distinct habitats of equal size (it has been shown previously that relaxing this assumption has little impacts on results; chapter 2 of this thesis).

The feeding, growth, reproduction, and mortality of an individual are functions of two individual-state variables, measuring an individual's irreversible mass (such as bones and organs) and its reversible mass (such as fat, gonads, or liver tissue), denoted by  $x$  and  $y$ , respectively. The maximum attainable reversible body mass is given by  $y_{\max} = q_1 x$ , where  $q_1$  is a dimensionless scaling constant describing an individual's maximum fraction of reversible to irreversible mass (Persson et al. 1998). An individual's total body length, attack rate, and handling time are assumed to depend only on

its standardized body mass  $w = x + y_{\max} = x(1 + q_j)$  (Persson et al. 1998). In general, an individual's reversible mass can be used, and thus diminished from  $y_{\max}$ , for two purposes: to cover its basic metabolism under starvation conditions and to be invested in metamorphosis (see section 'Evolving traits and life-history trade-offs'). When population dynamics are equilibrated, starvation conditions do not occur, so an individual's reversible mass is fully available for covering its costs of metamorphosis.

Newborn individuals are born at an irreversible body mass  $x_b$  and are assumed to possess the maximum amount  $q_j x_b$  of reversible body mass. Since starvation conditions do not occur, the ratio between irreversible and reversible mass is constant until individuals reach the threshold body mass at which metamorphosis can occur: larvae (L) potentially undergo metamorphosis and become juveniles (J) when reaching the standardized body mass  $w_j$ . Juveniles mature into adults (A) and start reproducing when reaching the standardized body mass  $w_A$ . The secondary food source becomes available to individuals after reaching the standardized body mass  $w_{\min}$ .

The foraging rates of individuals initially increase with their body mass, because of enhanced visual capacity and locomotion ability, but then again decrease with body mass when individuals are larger, because of a reduced ability to perceive small prey and to make fine-tuned maneuvers. To describe this fundamental dependence of an individual's attack rates on its standardized body mass in foraging on the primary and secondary food sources, we use the following hump-shaped functions (figure 4.1), respectively,

$$a_1(w) = A_1 \left[ \frac{w}{w_0} \exp\left(1 - \frac{w}{w_0}\right) \right]^\alpha \quad (4.1a)$$

$$a_2(w) = \begin{cases} 0 & w \leq w_{\min} \\ A_2 \left[ \frac{w - w_{\min}}{w_0} \exp\left(1 - \frac{w - w_{\min}}{w_0}\right) \right]^\alpha & \text{otherwise.} \end{cases} \quad (4.1b)$$

In these equations,  $A_1$  and  $A_2$  are the maximum attack rates individuals can reach when their body mass equals  $w_0$  and  $w_0 + w_{\min}$  on the primary and secondary food sources, respectively. The parameter  $\alpha$  determines how strongly the attack rates on the primary and secondary food sources increase and decrease around the peaks at  $w_0$  and  $w_0 + w_{\min}$ , respectively. In the absence of an ontogenetic diet shift and all else being equal,  $\alpha$  determines the competitive ability of an individual of a given size, which can be characterized by the food density at which the individual can just meet its maintenance requirements (Persson et al. 1998). By choosing the value  $\alpha = 0.6$ , we assume that small individuals have, in the absence of an ontogenetic diet shift, a higher competitive ability than large individuals (Persson et al. 1998).

We assume a Holling-type-2 functional response; therefore, the food intake of an individual with standardized body mass  $w$  can be written as

$$I(X_1, X_2, w) = \frac{\phi(w)a_1(w)X_1 + [1 - \phi(w)]a_2(w)X_2}{1 + h(w)\{\phi(w)a_1(w)X_1 + [1 - \phi(w)]a_2(w)X_2\}} \quad (4.2a)$$

whereby the handling time  $h(w)$  equals

$$h(w) = \zeta_1 + \zeta_2 w^{-\zeta_3} e^{\zeta_4 w}. \quad (4.2b)$$

In equation 4.2a,  $\phi(w)$  is the fraction of time individuals spend searching for the primary food source. We assume that individuals show optimal foraging behaviour and therefore allocate their time searching for each food source in such a way that they maximize their food intake, which implies

$$\phi(w) = \frac{1}{1 + \exp(\sigma[a_2(w)X_2 - a_1(w)X_1])}. \quad (4.3)$$

In this equation, the parameter  $\sigma$  determines the steepness of the sigmoid curve at equal food source profitabilities,  $a_2(w)X_2 = a_1(w)X_1$  (de Roos et al. 2002). The energy-intake rate of an individual equals its food-intake rate multiplied by a conversion factor  $k_e$ . Assimilated energy is first used to cover maintenance costs. An individual's metabolic-cost rate allometrically increases with its total body mass  $x + y$ ,

$$E_m(x, y) = p_1(x + y)^{p_2}. \quad (4.4)$$

The biomass-production rate of larvae and juveniles is given by the difference between their energy-intake rate and their maintenance-cost rate,

$$E_g(X_1, X_2, x, y) = k_e I(w, X_1, X_2) - E_m(x, y) \quad (4.5)$$

Of this biomass production, larvae and juveniles allocate a fraction  $\kappa_J(x, y)$  to growth in irreversible mass,

$$\kappa_J(x, y) = \frac{y}{(1 + q_J)q_J x}, \quad (4.6a)$$

with the remaining fraction being allocated to growth in reversible mass. Since adults also invest in reproduction, they allocate a lower fraction  $\kappa_A(x, y)$  to growth in irreversible mass,

$$\kappa_A(x, y) = \frac{y}{(1 + q_A)q_A x}, \quad (4.6b)$$

with the remainder being allocated to growth in reversible mass and reproduction. To ensure that individuals always invest in reversible mass in such a way that the ratio of  $y$  to  $x$  either remains at or is restored to  $q_J$  and that reproduction does not take place

when  $y < q_j x$  (Persson et al. 1998), we assume that adults allocate a fraction  $\kappa_R(x, y)$  to reversible mass according to

$$\kappa_R(x, y) = \begin{cases} 1 - \kappa_A(x, y) & y < q_j x \\ [1 - \kappa_j(x, y)] \frac{\kappa_A(x, y)}{\kappa_j(x, y)} & \text{otherwise.} \end{cases} \quad (4.7)$$

The remaining fraction  $1 - \kappa_A(x, y) - \kappa_R(x, y)$  of the biomass production is invested in reproduction. The number of eggs an individual adult produces per unit of time therefore equals

$$b(x, y, X_1, X_2) \begin{cases} 0 & y < q_j x \\ [1 - \frac{\kappa_A(x, y)}{\kappa_j(x, y)}] E_g(x, y, X_1, X_2) \eta / ((1 + q_j) x_b) & \text{otherwise.} \end{cases} \quad (4.8)$$

where the factor  $\eta$  converts from energy to body mass. A more detailed description of the model specified here can be found in Persson et al. (1998).

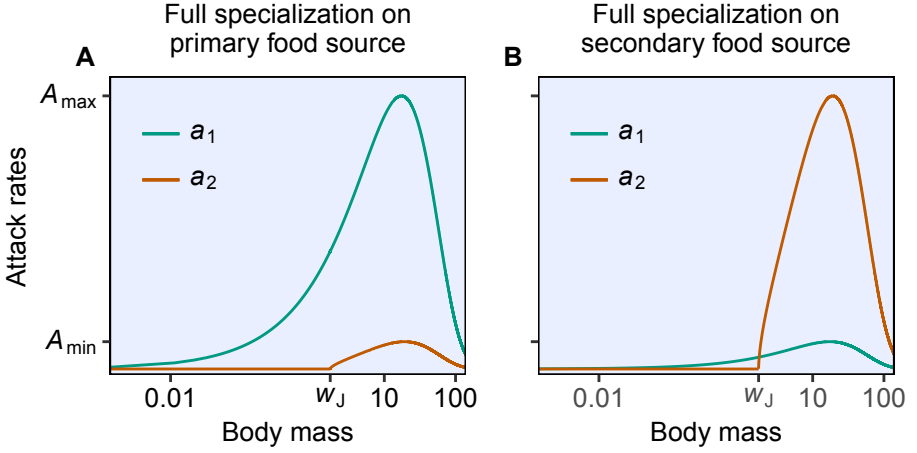
Because an individual's total body mass  $x + y$  equals its standardized body mass  $w$  before metamorphosis, and since its reversible body mass  $y$  is restored to  $y_{\max} = q_j x$  soon after metamorphosis, so that its total body mass again equals its standardized body mass, we will from now on simply use the term body mass to refer to the standardized body mass  $w$ .

Following Persson et al. (1998), metabolic costs and handling times are parameterized for the interaction between a planktivorous fish population of roach *Rutilus rutilus* and two zooplankton populations as food sources. Our model should, however, be interpreted as a more general consumer-resource model describing the interaction between two food sources and a size-structured consumer. All parameter values related to energetics are based on a reference temperature of 19 °C. Processes taking place during the winter season are ignored. Model variables are listed in table 4.1, and model parameters are listed in table 4.2 together with their default values.

### **Evolving traits and life-history trade-offs**

We assume that the two food sources require two different morphologies to be effectively utilized. This means that a morphology that is optimal for feeding on the primary food source is not very efficient in feeding on the secondary food source, and vice versa. We furthermore assume that metamorphosis can decouple the morphologies at different life stages such that an individual can adopt different morphologies before and after metamorphosis. To incorporate this, we consider a linear trade-off between the two attack-rate constants  $A_{1i}$  and  $A_{2i}$  within a certain life stage (larvae, juveniles, or adults;  $i = L, J, \text{ or } A$ ), assuming that these constants can vary between





**Figure 4.1:** In the absence of metamorphosis individuals can either specialize on the primary (A) or on the secondary (B) food source. The figure shows the attack rates ( $1 \text{ day}^{-1}$ ) on the primary food source (green) and secondary food source (orange) as functions of a consumer's body mass ( $g$ ). A: Individuals do not undergo metamorphosis and are fully specialized on the primary food source ( $\psi_i = 0$  for all life stages  $i = L, J, \text{ or } A$ ). B: Individuals do not undergo metamorphosis and are fully specialized on the secondary food source ( $\psi_i = 1$  for all life stages  $i$ ). Parameter values are as shown in tables 4.2 and 4.3.

$A_{\min}$  and  $A_{\max}$ ,

$$\begin{aligned} A_{1i} &= (1 - \psi_i)(A_{\max} - A_{\min}) + A_{\min}, \\ A_{2i} &= \psi_i(A_{\max} - A_{\min}) + A_{\min}. \end{aligned} \quad (4.9)$$

In these equations,  $0 \leq \psi_i \leq 1$  is the relative degree of specialization of a life stage ( $i = L, J, \text{ or } A$ ) on the secondary food source. The value  $\psi_i = 0$  means that individuals in life stage  $i$  are completely specialized on the primary food source and not very efficient in feeding on the secondary food source (figure 4.1A). Conversely, the value  $\psi_i = 1$  means that individuals in life stage  $i$  are completely specialized on the secondary food source and not very efficient in feeding on the primary food source (figure 4.1B). In the absence of metamorphosis, the degree of specialization is equal for all three life stages ( $\psi_L = \psi_J = \psi_A$ ).

Because larger individuals can feed on the secondary food source, whereas smaller individuals cannot, there is a possible conflict between maximizing feeding performance across all life stages. For small individuals, it is important to specialize on the primary food source, while later in life it becomes important to specialize on the secondary food source as well. Metamorphosis can decouple the different life stages such that they can adapt independently from each other – it unlinks the specialization between the different life stages. In other words, individuals with metamorphosis that

specialize on the secondary food source later in life are not specialized on the primary food source, but this does not affect their offspring. Metamorphosis decouples the different stages as follows

$$\psi_A = \psi_J = \min(1, \psi_L + \theta), \quad (4.10)$$

where  $\theta$  is the extent of the metamorphosis. Individuals without metamorphosis have the same morphology over their lifetime ( $\psi_L = \psi_J = \psi_A$ ), whereas individuals with full metamorphosis can specialize on the primary food source when small and on the secondary food source when large. Figure 4.3A shows how the attack rates of an individual that undergoes full metamorphosis change with its body mass. Since the benefits of metamorphosis depend on an individual's body mass, we examine the body mass at metamorphosis as one of the evolving traits.

Metamorphosis is an energetically costly process (Geffen et al. 2007; Sheridan and Kao 1998; Thiyagarajan et al. 2003). We therefore assume that individuals have to invest reversible mass to cover those costs. When individuals reach the body size at which they may undergo metamorphosis ( $x = x_j$  and  $y = q_j x_j$ ), they lose  $\theta x_j (q_j - q_s)$  of their reversible body mass. In this equation, the parameter  $q_s$  is the ratio of  $y$  to  $x$  of an individual immediately after full metamorphosis ( $\theta = 1$ ). The lower  $q_s$ , the more expensive is the metamorphosis.

Metamorphosis is not only energetically costly, but can also be risky. For example, in some species, metamorphosing individuals are more vulnerable to predation compared to pre- and post-metamorphic individuals (Hadfield 2000; Wassersug and Sperry 1977). Furthermore, during metamorphosis there is a high risk of developmental mistakes in phenotypic expression. Therefore, we assume that individuals may die during metamorphosis with probability  $p\theta$ . The parameter  $p$  is the probability of dying during metamorphosis when undergoing full metamorphosis ( $\theta = 1$ ). Parameters related to specialization and metamorphosis are listed in table 4.3, and the corresponding evolving traits are listed in table 4.1.

### Evolutionary dynamics

We use adaptive-dynamics theory (Dieckmann and Law 1996; Geritz et al. 1998; Metz et al. 1992) to study how the specialization  $\psi_L$  of larvae, the extent  $\theta$  of metamorphosis, and the body mass  $w_j$  at metamorphosis evolve. Specifically, we consider populations that evolve through the fixation of small and rare mutations in these traits, while otherwise being monomorphic. This gives rise to evolutionary rates that are proportional to the selection gradient (Dieckmann and Law 1996). We thus use the canonical equation of adaptive-dynamics theory (Dieckmann and Law 1996; Durinx et al. 2008) to determine the resultant evolutionary trajectories. For simplicity, we assume that the studied traits evolve independently from each other, which means that the mutational

variance-covariance matrix is proportional to the identity matrix. For the three dimensionless evolving traits  $\psi_L$ ,  $\theta$ , and  $w_J/g$ , we arbitrarily chose a value of 0.01 for the product of mutation probability per birth event, mutation variance, and variance in the number of offspring (Durinx et al. 2008). Since all evolutionary endpoints we have found in this study possess strong convergence stability changing these values only alters the evolutionary rates, but has no effect on the evolutionary outcomes (Leimar 2009)

Evolutionarily singular strategies (Geritz et al. 1998) are defined by the vanishing of the evolutionary rates of all considered traits, corresponding to the absence of any directional selection. We continue trait combinations at these potential evolutionary outcomes as functions of the supply rate of the secondary food source and determine whether the evolutionarily singular strategies are convergence stable and/or evolutionarily stable following Geritz et al. (1998) and Leimar (2009). To study how the evolution of metamorphosis depends on the supply rate  $\delta X_{2,\max}$  of the secondary food source, we vary  $X_{2,\max}$  while keeping  $\delta$  constant.

### Model analysis

All analyses are performed using the PSPManalysis software package (de Roos 2016). Based on the computational approach described by Kirkilionis et al. (2001), Diekmann et al. (2003), and de Roos (2008), the PSPManalysis package numerically computes the ecological equilibrium of physiologically structured population models as a function of any model parameter, by iteratively computing the food-source densities for which the lifetime reproductive success  $R_0$  of an individual equals 1. In nonlinear size-structured models,  $R_0$  depends on an individual's size-specific rates of feeding, growth, mortality, and fecundity, so the PSPManalysis package numerically integrates a set of coupled ordinary differential equations that describe how these rates change over an individual's lifetime.

The PSPManalysis package can automatically detect and classify evolutionarily singular strategies according to the classification of Geritz et al. (1998). The package can numerically continue these evolutionarily singular strategies as functions of any (second) model parameter (de Roos 2016). The package can furthermore calculate derived quantities such as the expected food intake of an individual during its lifetime. We use these quantities to calculate the expected fraction of the secondary food source in the diet of juveniles and adults ( $w > w_J$  or  $w > w_{\min}$  in the absence of metamorphosis) to characterize the degree of the ontogenetic diet shift.

**Table 4.1:** Model variables and evolving traits

Variable	Description	Range	Unit
$X_1$	Density of primary food source	from 0 to $X_{1,\max}$	$\text{mg l}^{-1}$
$X_2$	Density of secondary food source	from 0 to $X_{2,\max}$	$\text{mg l}^{-1}$
$x$	Irreversible body mass	Larger than $x_b$	g
$y$	Reversible body mass	From $q_j x_b$ to $y_{\max} = q_j x$	g
$\psi_i$	Degree of specialization of larvae, juveniles or adults ( $i=L, J, \text{ or } A$ ) on the secondary food source	From 0 - 1	-
$\theta$	Extent of metamorphosis	From 0 - 1	-
$w_j$	Standardized body mass at metamorphosis	Larger than $w_b$	g

**Table 4.2:** Model parameters and their default values from Persson et al. (1998)

Parameter	Description	Default Value	Unit
$\delta$	Food-source turnover rate	0.1	day <sup>-1</sup>
$X_{1,\max}$	Maximum biomass density of primary food source	0.055	mg l <sup>-1</sup>
$X_{2,\max}$	Maximum biomass density of secondary food source	Variable	mg l <sup>-1</sup>
$x_b$	Irreversible body mass of newborns	0.000804	g
$w_A$	Standardized body mass at maturation	8.71	g
$w_0$	Standardized body mass at which maximum attack rate is attained on primary resource	17.42	g
$\alpha$	Size scaling exponent of the attack functions	0.6	-
$\zeta_1$	Constant in handling-time function	0.00036*	day mg <sup>-1</sup>
$\zeta_2$	Constant in handling-time function	0.00745*	day mg <sup>-1</sup> g <sup><math>\zeta_3</math></sup>
$\zeta_3$	Slope of decrease in handling time at small consumer sizes	0.68	-
$\zeta_4$	Slope of increase in handling time at large consumer sizes	1.15 10 <sup>-3</sup>	g <sup>-1</sup>
$p_1$	Metabolic constant	0.033	g <sup>1-p<sub>2</sub></sup> day <sup>-1</sup>
$p_2$	Metabolic exponent	0.77	-
$k_e$	Metabolic conversion factor	0.00061*	-
$q_J$	Constant determining maximum reversible body mass	0.742	-
$q_A$	Constant in adult energy-allocation function	1	-
$\eta$	Gonad-offspring conversion	0.5	-
$\mu$	Background mortality rate	0.01	day <sup>-1</sup>

Note: \*These values are the original values from Persson et al. (1998) divided by  $1.1 \cdot 10^{-2}$  (the mass of a prey individual) to express prey densities in mg l<sup>-1</sup> instead of individuals l<sup>-1</sup>.

**Table 4.3:** Model parameters and their default values related to specialization and metamorphosis

Parameter	Description	Default Value	Unit
$A_{\max}$	Maximum value of the attack-rate constants $A_1$ and $A_2$	$10^5$	$\text{l day}^{-1}$
$A_{\min}$	Minimum value of the attack-rate constants $A_1$ and $A_2$	$10^4$	$\text{l day}^{-1}$
$w_{\min}$	Standardized body mass at which the secondary food source becomes available	1.742	g
$\sigma$	Constant in habitat-switching rate	10	$\text{day g}^{-1}$
$q_s$	Ratio of reversible to irreversible body mass immediately after full metamorphosis	0.2	-
$\rho$	Probability of dying during full metamorphosis	0.5	-

### 4.3 Results

In the first part of this section, we show that – in the absence of metamorphosis – the trade-off between foraging success early and late in life impedes specialization on the secondary food source. In the second part, we show that metamorphosis can evolve to allow individuals to specialize on the primary food source when small and on the secondary food source when large. In the last part, we show that metamorphosis can evolve only under limited ecological conditions; however, once evolved, it is a very robust life-history strategy.

#### **Without metamorphosis individuals specialize on the primary food source**

It has been shown before that, even when it is beneficial for individuals to change diet during their ontogeny, specialization on a new food source is not possible in the absence of metamorphosis (chapter 2 of this thesis). These results are mostly corroborated by the analysis of our current model, and therefore we describe our corresponding analysis only briefly.

In contrast to the model in chapter 2, we assume that food choice is a behavioral trait and does not evolve. Because of the choice of the trade-off function (equation 4.9) and the energy-maximizing feeding function (equation 4.3), large individuals ( $w > w_{\min}$ ) always include both food sources in their diet. However, when the fraction of the secondary food source in the diet is graphically indistinguishable from 0 or 1, we will state, for convenience, that large individuals completely feed on the primary or the secondary food source, respectively. In this section, we assume that metamorphosis is absent ( $\theta = 0$ ) and only specialization evolves. Without metamorphosis, all individuals have the same morphology ( $\psi_L = \psi_J = \psi_A$ , which we denote by  $\psi$ ), so body mass  $w_J$  at metamorphosis disappears from the model formulation. For low values of both the specialization trait  $\psi$  and the supply rate of the secondary food source, there are two stable ecological equilibria, separated by an unstable one. Nevertheless, for any given initial value of  $\psi$ , evolution always reaches the same evolutionary outcome, independent of the initially realized ecological equilibrium. We therefore ignore this ecological bistability, since it is inconsequential on the evolutionary timescale. All evolutionary outcomes described in this subsection are continuously stable strategies (CSSs), and therefore locally evolutionarily stable (Geritz et al. 1998).

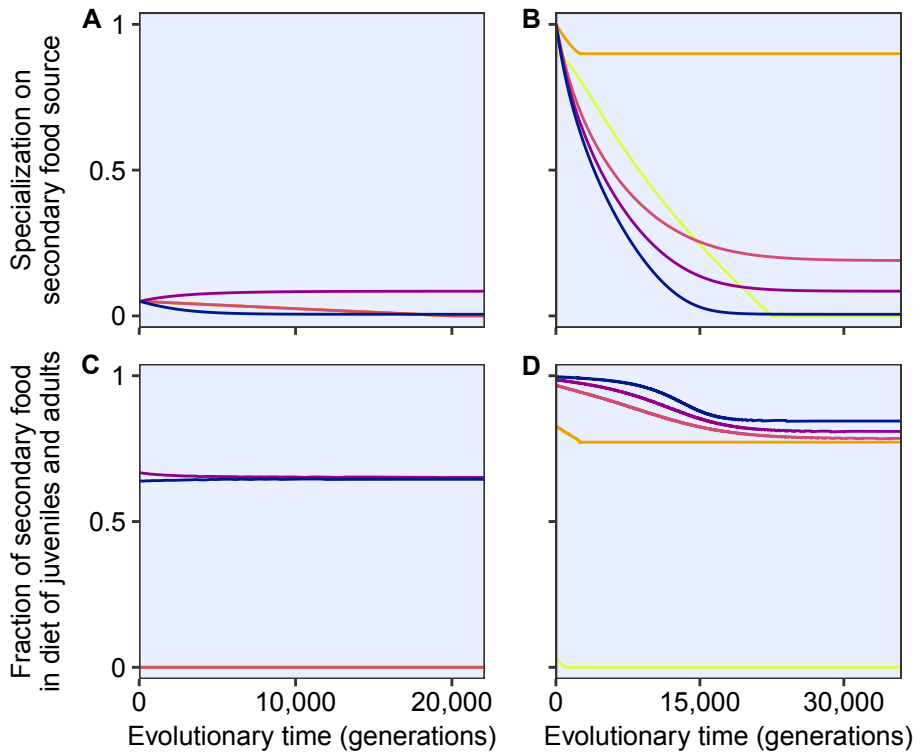
Specialization on a secondary food source is not possible when individuals are initially specialized on the primary food source (figure 4.2A), independent of the supply rate of the secondary food source. For low and intermediate supply rates, large individuals do not feed on the secondary food source (figure 4.2C). There is therefore no reason to evolve a specialization on this food source. When the supply rate is high, large individuals do feed on the secondary food source (figure 4.2C); however, no specializa-

tion evolves in this case either. The reason for this is subtle, but can be understood as follows. Because large individuals have access to the secondary food source, they have high rates of growth and reproduction. This leads to a high number of offspring and therefore to strong competition among those offspring for the primary food source. Individuals that are more specialized on the secondary food source produce offspring that are not very efficient in this feeding early in life. Such individuals are therefore outcompeted by individuals that are more specialized in feeding on the primary food source early in life (chapters 2 and 3 of this thesis).

When individuals are initially specialized on the secondary food source, they evolutionarily lose this specialization in case of low and high supply rates of the secondary food source, but not in case of intermediate supply rates (orange line in figure 4.2B). When the supply rate is high, individuals lose their specialization for the reason already mentioned, namely that competition is very severe among the smallest individuals so that it is more important to grow fast than to reproduce fast (chapter 2 of this thesis). In contrast, when the supply rate of the secondary food source is low, large individuals do not feed on it (yellow line in figure 4.2D) – even not when they are specialized in doing so. Therefore, it is in this case not beneficial even for large individuals to be specialized on this unused food source. Only for intermediate supply rates of the secondary food source, specialization is possible (orange line in figure 4.2B). In this case, large individuals mainly feed on the secondary food source (figure 4.2D), but since this food is not too abundant, competition among the smallest individuals is not severe enough to promote specialization on the primary food source. Notice that, as a consequence, the smallest individuals end up in this case being poor foragers on the food source that is available to them.

These results underscore that, without metamorphosis, unresolvable tensions arise for species faced with the opportunity of specializing on a secondary food source. Even though large individuals mainly feed on this food source, specialization is only possible for a narrow range of conditions, in which case small individuals pay high costs as they end up having poor foraging capacity (see appendix 4.A for more details). Accordingly, a decoupling of the morphologies expressed during different life stages is favored by strong selection pressures, such that large individuals can specialize on the secondary food source without negatively affecting their offspring's specialization on the primary food source. Even in the rare cases in which specialization on the secondary food source evolves without metamorphosis, there still is selection for metamorphosis, so as to allow small individuals to specialize again on the primary food source.





**Figure 4.2:** Evolutionary dynamics of specialization in the absence of metamorphosis for five different supply rates of the secondary food source. Specialization on the secondary food source is possible only under limited conditions (A, B), even when large individuals feed mainly on the secondary food source (C, D). A, B: Evolutionary dynamics of specialization when individuals are initially specialized on the primary food source (A) or secondary food source (B). C, D: Resultant changes in the fraction of the secondary food source in the diet of large individuals when individuals are initially specialized on the primary food source (C) or secondary food source (D). Light-colored lines indicate lower supply rates of the secondary food source, whereas dark-colored lines indicate higher supply rates:  $\delta X_{2,\max}$ =0.0011 (light green), 0.0022 (orange), 0.0066 (dark pink), 0.011 (purple), or 0.022 (dark blue)  $\text{mg l}^{-1} \text{day}^{-1}$ . In A, the light-green, orange, dark-pink, and dark-blue lines lie on top of each other; in C, this is the case for the light-green, orange, and dark-pink lines, as well as for the purple and dark-blue lines. The initial value of  $\psi = \psi_L = \psi_J = \psi_A$  equals 0.1 (A, C) or 1 (B, D). Other parameter values are as shown in tables 4.2 and 4.3.

**Metamorphosis evolves to enable independent specialization**

In this and the following subsection, we study the joint evolution of the extent  $\theta$  of metamorphosis, the body mass  $w_J$  at metamorphosis, and the specialization  $\psi_L$  of larvae. Metamorphosis breaks up the trade-off between the attack rates on the two food sources, so that small individuals can be specialized on the primary food source even when large individuals are specialized on the secondary food source (figure 4.3A). We find that metamorphosis can evolve either to enable large individuals to specialize on the secondary food source (figure 4.3B) or to enable small individuals to specialize on the primary food source (figure 4.3C).

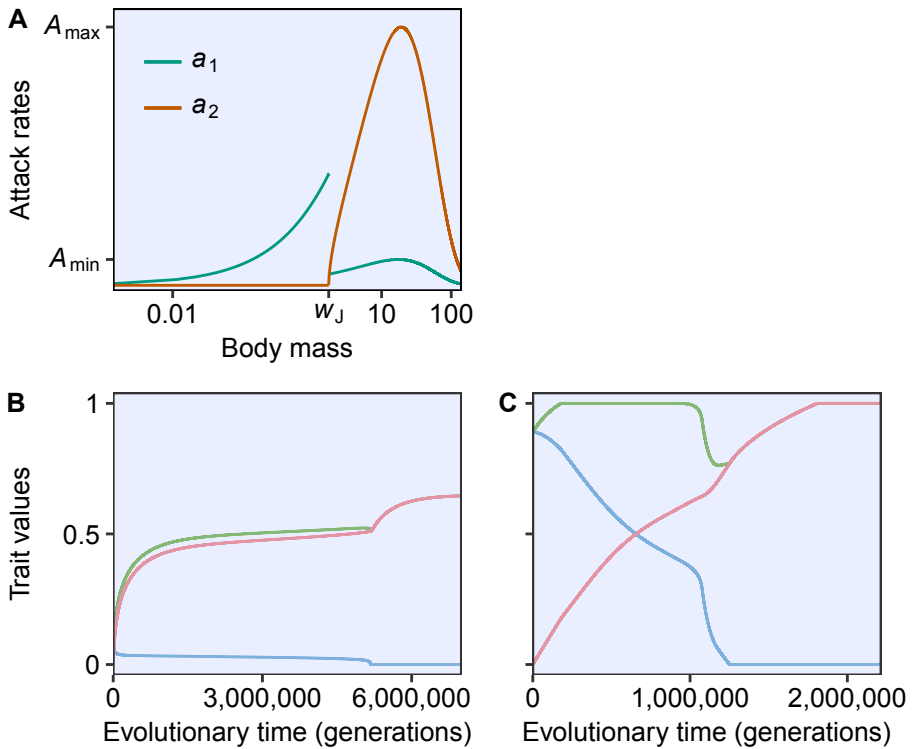
Figure 4.3B shows an evolutionary time series that is typical when individuals initially are mainly specialized on the primary food source and the supply rate of the secondary food source is high enough for large individuals to include the secondary food source in their diet. The extent of metamorphosis (red line in figure 4.3B) increases over evolutionary time, while the specialization trait  $\psi_L$  of larvae (blue line in figure 4.3B) slightly decreases over evolutionary time. Large individuals therefore partly specialize on the secondary food source (green line in figure 4.3B), whereas small individuals fully specialize on the primary food source ( $\psi_L = 0$ ).

Figure 4.3C shows an evolutionary time series that is typical when individuals are initially specialized on the secondary food source. We find that even in this case, metamorphosis evolves such that small and large individuals can specialize on the primary and secondary food sources, respectively. The extent  $\theta$  of metamorphosis (red line in figure 4.3C) increases over evolutionary time, while larvae become more and more specialized on the primary food source as their specialization trait  $\psi_L$  decreases (blue line in figure 4.3C). Since  $\psi_L$  evolves faster than  $\theta$ , as the former is subject to stronger selection than the latter, adults become temporarily less specialized on the secondary food source. Ultimately, however, a full metamorphosis evolves, so that small individuals are fully specialized on the primary food source ( $\psi_L = 0$ ), whereas large individuals are fully specialized on the secondary food source ( $\psi_J = \psi_A = 1$ ). In this case, large individuals thus invest in metamorphosis not to improve their own performance, but to improve the performance of their offspring. Accordingly, the morphology of small individuals, which was initially specialized on feeding on the secondary food source, diverges over evolutionary time from that of large individuals.

In summary, metamorphosis can evolve either to enable large individuals to specialize on the secondary food source (figure 4.3B) or to enable small individuals to specialize on the primary food source (figure 4.3C).

**Metamorphosis only evolves when the supply rate exceeds a high threshold**

In the first subsection above, we have shown that specialization on the secondary food source is hardly possible without metamorphosis. For simplicity, we now therefore fo-



**Figure 4.3:** Metamorphosis can evolve such that individuals are specialized on the primary food source when small and on the secondary food source when large. A: Attack rates ( $1 \text{ day}^{-1}$ ) on the primary food source (green) and the secondary food source (orange), as functions of a consumer's body mass (g) when individuals undergo full metamorphosis. B, C: Evolutionary dynamics of the extent of metamorphosis (red) and of the specialization on the secondary food source for larvae (blue) and for juveniles and adults (green) when individuals are initially specialized on the primary food source (B) or secondary food source (C). Parameters:  $\delta X_{2,\max} = 0.011$  (B), or  $0.0022$  (C)  $\text{mg l}^{-1} \text{ day}^{-1}$ . The body mass at metamorphosis is  $w_{\min} = 1.742$  g in A, which approximately equals the body mass at which metamorphosis eventually evolves to occur in B and C. Other parameter values are as shown in tables 4.2 and 4.3.

cus on the conditions under which metamorphosis evolves when individuals are initially specialized on the primary food source (figure 4.3B). In appendix 4.B, we analogously show under which conditions metamorphosis evolves when individuals are initially specialized on the secondary food source.

The extent  $\theta$  of metamorphosis and the larval specialization  $\psi_L$  on the secondary food source jointly determine the specialization on the secondary food source of juveniles and adults according to equation 4.10. We find that, for an initial value of  $\psi_L = 0$ ,  $\psi_L$  never evolves away from zero, so  $\psi_J = \psi_A = \theta$  (equation 4.10). It is hence sufficient to study and discuss the joint evolution of  $\theta$  and the body mass  $w_J$  at metamorphosis.

Figure 4.4A shows that metamorphosis originates abruptly when the supply rate of the secondary food source becomes sufficiently high. Surprisingly, however, metamorphosis is not lost when the supply of the secondary food source decreases, which results in population extinction through evolutionary trapping when this supply becomes too low. These results can be explained by the trade-off between the attack rates and the feedback between the food sources and the consumers as follows. We have seen above that, in a population in which individuals do not undergo metamorphosis, specialization on the secondary food source is not possible; therefore, individuals have a low foraging efficiency on this food source. For low values of the supply rate  $\delta X_{2,\max}$  of the secondary food source, individuals barely feed on it (figure 4.4B), and therefore it does not pay to evolve a metamorphosis, since the costs are very high while the benefits are low. The fraction of secondary food in the diet of large individuals increases with increasing supply rates, even though individuals are not specialized in feeding on this food source ( $\psi_L = \psi_J = \psi_A = 0$ , figure 4.4B). After  $\delta X_{2,\max}$  has reached a certain threshold such that the secondary food source is a substantial part of the diet of large individuals (after the dotted line in figure 4.4B), it becomes beneficial to invest in metamorphosis. A small investment in metamorphosis increases the feeding efficiency on the secondary food source, which in turn increases the fraction of this food source in the diet of large individuals. Because of this higher fraction of the secondary food source in the diet of large individuals, it is beneficial to invest even more into metamorphosis. Therefore, the degree of metamorphosis can suddenly evolve from 0 to high values, so that small individuals have a morphology specialized on feeding on the primary food source while large individuals have a morphology specialized on feeding on the secondary food source.

While increasing the extent of metamorphosis will increase the food intake of large individuals and therefore their birth rate, metamorphosis is always costly: metamorphosis decreases the probability that an individual survives until adulthood and slows down maturation, because of the energy investment metamorphosis requires. When the supply rate of the secondary food sources increases, the extent of metamorphosis evolves to lower values because of these costs (figure 4.4A). When the supply rate of

the secondary food source is high, there is plenty of food available for the metamorphosed individuals. In this case, the gains of increased efficiency do not outweigh the costs of investing more in metamorphosis; in other words, the necessity for changing morphology decreases with increasing supply rate of the secondary food source.

### **Once evolved metamorphosis does not disappear when conditions change**

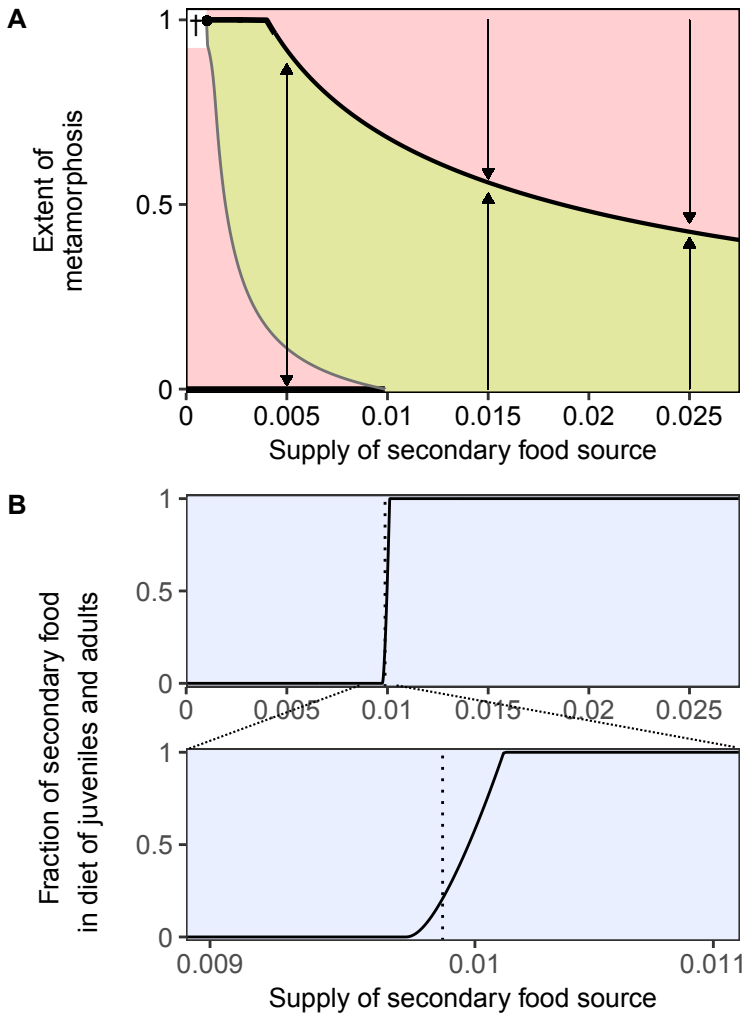
Once metamorphosis has evolved, it does not disappear when the secondary food source becomes less productive. Remarkably, the extent of metamorphosis even increases when the supply rate of the secondary food source decreases (figure 4.4A). This seemingly paradoxical result can be explained by the fact that metamorphosed individuals are specialized on the secondary food source and do not feed on the primary food source at all. Individuals investing less in metamorphosis thereby increase their foraging efficiency on the primary food source when large, but do not benefit from this, since this food source is not used after metamorphosis. Conversely, individuals investing more in metamorphosis increase their foraging efficiency on the secondary food source, which is beneficial when the supply rate of this food source diminishes.

Surprisingly, when the supply rate of the secondary food source is very low, metamorphosis does not disappear. Instead, the population ultimately goes extinct (figure 4.5B). We show in figure 4.5A that the less productive the secondary food source, the later in life metamorphosis occurs. With decreasing values of the supply rate of the secondary food source, there is less of it available, which makes it beneficial for individuals to postpone their metamorphosis and feed on the primary food source for longer. Because metamorphosed individuals are very efficient in feeding on the secondary food source, they will continue to feed on it even though its supply rate decreases. Our findings indicate that there is no selection to reduce the extent of metamorphosis when the supply rate of the secondary food source is decreasing. The size at metamorphosis is, however, always smaller than the size at maturation. Adults rely therefore mainly on the secondary food source for their reproduction. When the supply of this food source becomes too low, adults do not have enough food to reproduce and the population goes extinct. Since the population's evolutionary attractor collides with its extinction boundary, metamorphosis can be an evolutionary trap (Dieckmann and Ferriere 2004; Ferriere and Legendre 2013).

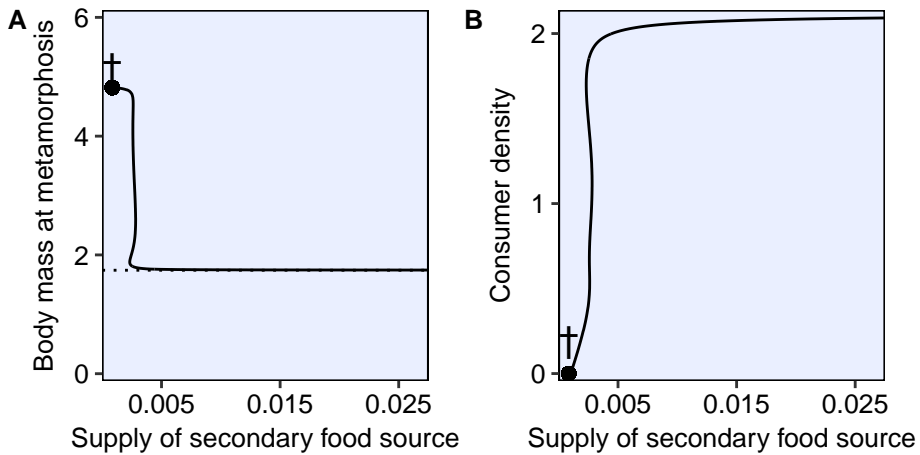
### **Robustness of results**

Our results turn out to be robust under many different parameter combinations. Different values of the model parameters  $X_{1,\max}$ ,  $w_{\min}$ ,  $\rho$ ,  $q_s$ ,  $\alpha$ , all give the same qualitative pattern (appendix 4.D).

Interestingly, for very high values of  $X_{1,\max}$ , metamorphosis ceases to be an evolutionary trap. Because of our assumption that individuals always have a positive feeding



**Figure 4.4:** Metamorphosis originates abruptly (A) when the supply rate of the secondary food source becomes sufficiently high, so that a significant fraction of the diet of large individuals consists of the secondary food source (B). When metamorphosis has evolved, it is not lost when the supply rate of the secondary food source decreases, which results in population extinction through evolutionary trapping when this supply becomes too low. A: Evolution of the extent of metamorphosis as a function of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{ day}^{-1}$ ). Thick black lines indicate continuously stable strategies (CSSs), whereas the thin grey line indicates evolutionary repellers. Arrows show the direction of evolution. In the red area, evolution decreases the extent of metamorphosis, whereas in the green area, evolution increases the extent of metamorphosis. The population cannot persist in the white area marked with a dagger (†). B: Fraction of the secondary food source in the diet of juveniles and adults in the absence of metamorphosis ( $\psi_L = \psi_J = \psi_A = 0$ ), as a function of the supply rate of the secondary food source. The vertical dotted line indicates the critical supply rate at which the extent of metamorphosis evolves away from zero, which happens once – in the absence of metamorphosis – a significant fraction of the diet of juveniles and adults consists of the secondary food source. Parameter values are as shown in tables 4.2 and 4.3.



**Figure 4.5:** The lower the supply rate of the secondary food source, the later in life individuals undergo metamorphosis (A). Because metamorphosis does not disappear with a diminishing supply of the secondary food source, the population experiences evolutionary trapping and goes extinct when the secondary food source becomes too scarce (B). In that case, population extinction occurs at the filled circles marked with a dagger (†). A: Body mass (g) at which individuals undergo metamorphosis at the CSSs shown in figure 4.4A, as a function of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{ day}^{-1}$ ). The dotted line indicates the body mass at which the secondary food source becomes available to individuals. B: Consumer density (per 1000 l) at the CSSs shown in figure 4.4A, as a function of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{ day}^{-1}$ ). Parameter values are as shown in tables 4.2 and 4.3.

rate on the primary food source (equations 4.1b and 4.9), large individuals can survive on the primary food source alone when its supply rate is sufficiently high, even though they are not specialized in doing so. When the secondary food source becomes scarce while the primary food source is sufficiently abundant, individuals solely feed on the primary food source, metamorphosis disappears, and the population persists (figure 4.D1D in appendix 4.D).

#### 4.4 Discussion

Here we have shown that metamorphosis can evolve to break up the phenotypic correlation between different life stages, such that small individuals are specialized on a primary food source while large individuals are specialized on a secondary food source. Our findings suggest that metamorphosis can evolve only under limited ecological conditions. When the supply rate of the secondary food source is very high, such that the density of this food source is much higher than that of the primary food source, large individuals switch to feeding on the secondary food source even though they do not have the morphology ideally suited to utilizing it. Metamorphosis then

evolves to allow large individuals to specialize on the secondary food source without negatively affecting the performance of their offspring in feeding on the primary food source. When the supply rate of the secondary food source is lower, metamorphosis can evolve only when individuals are initially specialized in feeding on it. Specialization on the secondary food source can only evolve under limited conditions, but if these are met, metamorphosis evolves to allow small individuals to specialize on the food source available early in life.

Although it has been shown before that metamorphosis evolves in species with an ontogenetic diet shift as soon as its benefits outweigh its costs (Ebenman 1992), we have additionally shown here that a population with metamorphosis does not easily lose this life-history strategy when the ecological conditions under which it evolved change. Moreover, when the ecological conditions for metamorphosed individuals become very unfavorable, the population will often go extinct. Metamorphosis can therefore be an evolutionary trap. Since this evolutionary trap co-occurs with a viable evolutionary attractor, it is possible, in principle, that the population escapes extinction by evolving back to a non-metamorphosing life-history strategy. However, we show in appendix 4.C why this is rather unlikely. A population in which individuals undergo metamorphosis can rarely be invaded by a mutant, recombinant, or immigrant that does not undergo metamorphosis. Conversely, a population that does not undergo metamorphosis can almost always be invaded by individuals undergoing metamorphosis. Metamorphosis changes the efficiencies of the consumers on the different food sources, which in turn change the food densities and therefore the benefits and costs of metamorphosis. Hence, this feedback loop between individuals and their environment is crucial for understanding the evolution of metamorphosis, and should not be ignored.

The common ancestor of all animal species probably had a complex life cycle with a pelagic larva stage and a benthic adult stage, separated by metamorphosis (Jägersten 1972). There is a long-standing debate in evolutionary biology about the origin of these pelago-benthic life cycles. While the dominant view is that the ancestral metazoan was a pelagic larva-like animal and that later in evolutionary history a benthic juvenile/adult stage was added to its life cycle (e.g., Jägersten 1972; Nielsen 2013), there is an alternative view suggesting that the ancestral metazoan was a benthic adult-like animal (e.g., Page 2009; Raff 2008; Sly et al. 2003). Here we have assumed that the ancestral state of the consumer had a larval morphology and that the adult morphology evolved later through the evolution of metamorphosis. However, we have also showed that in case individuals start with the adult morphology (after specialization on the secondary food source), metamorphosis can evolve as a way to include a specialized larval morphology in their life cycle. Therefore, even though we have assumed the larval morphology as the ancestral state, our results suggest that it is also possible that



the adult morphology is ancestral and that only later in evolutionary history the larval state evolved.

While metamorphosis is widespread in the animal kingdom, the loss of the pre-metamorphic life stage has occurred in several species, e.g., in many marine invertebrates (Pechenik 1999) and in some frog species (Callery et al. 2001) via the evolution of direct development. In our model, a loss of the larval stage is impossible, since the smallest individuals need to feed upon the primary food source in order to metamorphose. To test under which conditions metamorphosing individuals evolve toward a life history with direct development, a different approach is therefore needed. In species with direct development, the elimination of the larval stage occurred in association with the production of larger offspring (Callery et al. 2001; Moran 1994). In marine invertebrates, for example, species that undergo metamorphosis produce smaller offspring than related species that skip the larval stage (Marshall et al. 2012). For future studies, it would be interesting to see under which ecological conditions adults evolve to produce larger offspring, such that the larval stage can be skipped and species evolve direct development.

Another pathway by which metamorphosis can disappear is the evolution of paedomorphosis, through which individuals mature while keeping the larval morphology (as happens, e.g., in many newts and salamanders). We have found that individuals evolve to paedomorphosis only when the supply rate of the primary food source is very high (appendix 4.D). In this case, metamorphosis disappears when the secondary food source becomes scarce, so individuals evolve to retain the same larval morphology throughout their ontogeny. This is in line with empirical work that shows that paedomorphosis evolves when conditions for the post-metamorphic stage are unfavorable (Bonett et al. 2014a). For most supply rates of the primary food source, however, individuals only postpone metamorphosis when the post-metamorphic niche deteriorates. Since in our model metamorphosis always takes place before maturation, paedomorphosis does not evolve in these cases. We have assumed that the body mass at maturation is fixed. In future research, it would be interesting to study whether paedomorphosis could evolve more easily in a model in which the body mass at maturation evolves as well.

In this study we have examined the evolution of metamorphosis in species changing their diet during their life cycle. However, factors other than diet could also explain the origin of metamorphosis, such as dispersal, mate finding, predator avoidance, or habitat selection (Moran 1994). Many insects have, for example, a non-feeding adult stage that is specialized on dispersal and mate finding. The traits needed for these tasks may be maladaptive during the feeding stage (Moran 1994). Metamorphosis could therefore evolve to separate tasks over the life cycle. Additionally, predators might force species to change their habitat during their life cycle. For example, results

of a recent experiment suggest that the transition from water to land in marine blenny fish has been promoted by the presence of aquatic predators (Ord et al. 2017). In future research, it would be interesting to study whether metamorphosis is more likely to evolve because of a diet shift or because of other factors such as dispersal or predation pressure. Further work could also address the question under which ecological conditions either the larval or the adult stage evolves into a non-feeding stage.

Here we have modeled metamorphosis as a discrete life-history transition. While metamorphosis can occur within a few minutes or hours (e.g., in marine invertebrates; Hadfield 2000), it is often a relatively slow process that may take weeks or months (e.g., in amphibians; Downie et al. 2004). Taxa that nowadays exhibit a sharp and abrupt metamorphosis between different life stages have evolved from situations in which the changes from newborn to adult were more continuous. For example, in insects and marine invertebrates, it has been shown that the morphological divergence between different life stages has increased during the course of evolution (Brown 1977; Nielsen 1998). Furthermore, the ancestors of frogs looked more like the metamorphosing stage than the larvae or adults of present-day species (Wassersug and Hoff 1982). Gradually, the different life stages became morphologically distinct, and ultimately, a metamorphosis evolved. Since the transitory stage cannot be well adapted to the needs addressed by either the larval or the adult morphology, there is probably a high selection pressure to concentrate the developmental events during this transition, so as to decrease the duration of the transformation. In our current study, the duration of metamorphosis is not taken into account, while in reality it is an important aspect of metamorphosis – suggesting another avenue of promising future research.

Fossil evidence and phylogenetic distributions of metamorphosis indicate that metamorphosis has evolved more than two hundred million years ago in insects (Labandeira and Sepkoski 1993) and amphibians (Wassersug 1975). In marine invertebrates, this evolution occurred already earlier, in the Cambrian period, 500 million years ago (Strathmann 1993). It has even been suggested that the common ancestor of all animals already underwent a metamorphosis, with a pelagic larva stage and a benthic adult stage (Jägersten 1972). This early metamorphosis got lost in some phyla, e.g., in the Ctenophora and the Chaetognata, while it re-evolved again in only a few cases (Jägersten 1972). The abundant occurrence of metamorphosis is thus not due to a high frequency of origination, but due to its persistent ecological success (Moran 1994). Our findings here are in line with these observations. We have shown that metamorphosis can evolve only under limited ecological conditions. However, once evolved, it is a very successful life-history strategy that will not easily disappear through further evolution.

## Acknowledgments

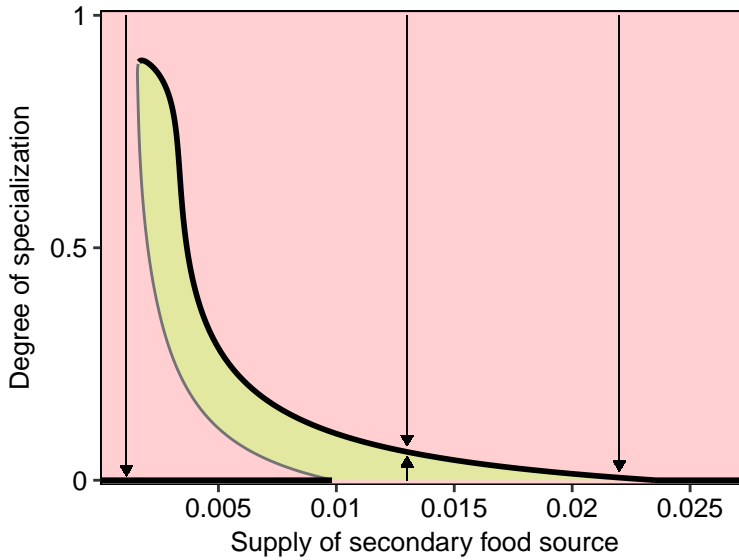
This research was supported by funding from the European Research Council under the European Union's Seventh Framework Programme (FP/2007-2013) / ERC Grant Agreement No. 322814. Part of the research reported here was done during the Young Scientist Summer Program (YSSP) in the Evolution and Ecology program (EEP) at the International Institute for Applied Systems Analysis (IIASA), Laxenburg, for which HtB received a grant from the Dutch Science Foundation (NWO) and a grant from IIASA.

## Appendix 4.A Evolution of specialization

In the absence of metamorphosis, the degree of specialization on the secondary food source is equal for all three life stages ( $\psi_L = \psi_J = \psi_A$ ). In this appendix, we show and briefly discuss the evolutionary bifurcations of this uniform degree of specialization, which we denote by  $\psi$ , as a function of the secondary food source's supply rate (figure 4.A1).

When the supply rate of the secondary food source is low, individuals evolve to be fully specialized on the primary food source ( $\psi = 0$ ). Since the secondary food source is very scarce in this case, individuals do not change diet during their ontogeny and only feed upon the primary food source. There is therefore no reason for them to specialize on the secondary food source (figure 4.A1). Specialization on the secondary food source neither evolves when the supply rate of the secondary food source is high (figure 4.A1). In this case, the trade-off between foraging success early and late in life impedes the evolution of specialization, as the benefits of specialization on the secondary food source late in life are outweighed by the high associated costs of such specialization early in life.

For intermediate supply rates of the secondary food source, two alternative evolutionary outcomes are separated by an evolutionary repeller. Depending on the initial value of the specialization trait  $\psi$  individuals either fully specialize on the primary food source ( $\psi = 0$ ) or specialize on the secondary food source to some extent ( $0 < \psi < 1$ ). When individuals are initially fully specialized on the primary food source, they hardly include the secondary food source in their diet, and therefore does not evolve away from 0. In contrast, above the threshold value of  $\psi$  associated with the evolutionary repeller, a substantial fraction of the diet of large individuals consists of the secondary food source, and in this case further specialization on the secondary food source evolves. When individuals are initially fully specialized on the primary food source, this second evolutionary outcome is realized only when mutational steps are large enough for a mutant to arise with a value of that exceeds that of the evolutionary repeller. Alternatively, when mutational steps are small, a high degree of specialization on the secondary food source can evolve from a full specialization on the primary food source only when the supply rate of the secondary food source is initially so high that  $\psi$  evolves away from zero, and this is followed by a decrease in the supply rate of the secondary food source, so that increases further, causing individuals to become even more specialized on the secondary food source (figure 4.A1).

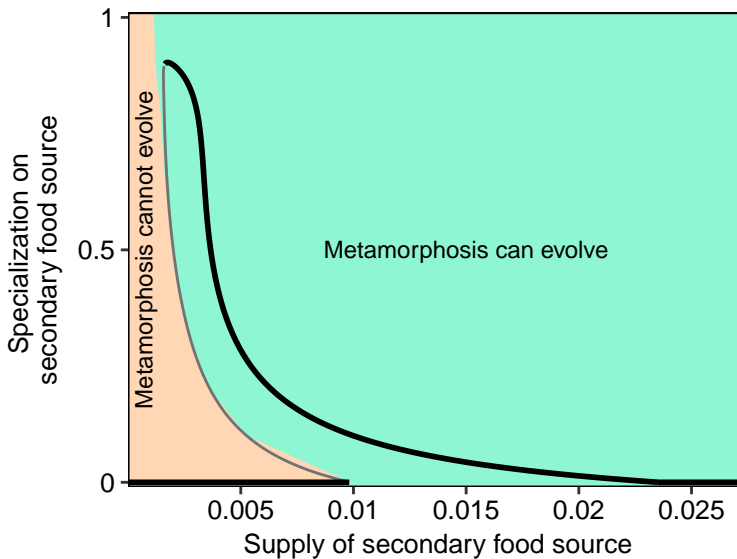


**Figure 4.A1:** Evolution of specialization on the secondary food source as a function of the supply rate of the secondary food source in the absence of metamorphosis. Black lines indicate continuously stable strategies (CSSs), whereas the thin grey line indicates evolutionary repellers. Arrows show the direction of evolution. In the red area, evolution decreases the degree of specialization on the secondary food source, whereas in the green area, evolution increases this degree of specialization. For intermediate values of the supply rate of the secondary food source, there are two continuously stable strategies with no specialization or partial specialization on the secondary food source, respectively. Parameter values are as shown in 4.2 and 4.3.

## Appendix 4.B Evolution of metamorphosis after specialization

In this appendix, we examine the conditions under which metamorphosis can evolve when individuals are initially specialized on the secondary food source.

Figure 4.B1 illustrates when metamorphosis starts to evolve as a function of the supply rate of the secondary food source and the initial value of the specialization trait. Metamorphosis evolves when individuals are not specialized on the secondary food source ( $\psi = 0$ ) and the supply rate of the secondary food source is high, or when this supply rate is low (but not too low) and some initial specialization on the secondary food source exists. Whether or not metamorphosis starts to evolve is hardly influenced by the body mass at metamorphosis (not shown). In case metamorphosis can evolve (mint-green area in figure 4.B1), the extent of metamorphosis evolves to a high value (upper branch of CSSs in figure 4.4).

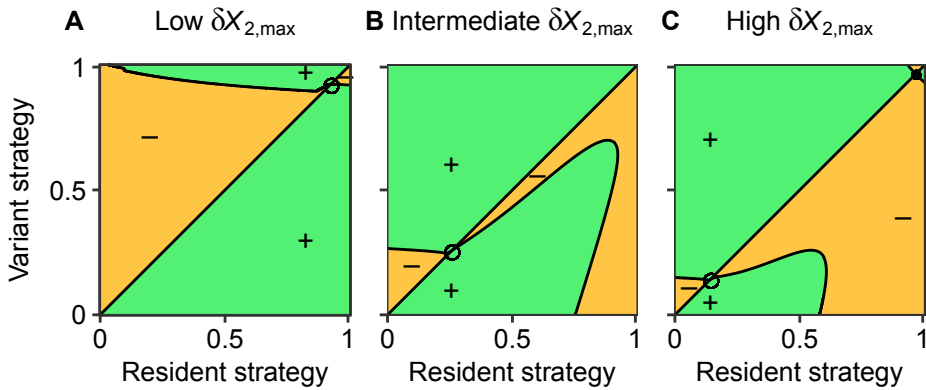


**Figure 4.B1:** Overview of conditions under which metamorphosis starts to evolve as a function of the supply rate of the secondary food source and the initial degree of specialization on the secondary food source,  $\psi_L = \psi_J = \psi_A$  when  $\theta = 0$ . The figure also shows the outcomes of evolution when the specialization trait  $\psi = \psi_L = \psi_J = \psi_A$  evolves in the absence of metamorphosis (as in figure 4.A1), demonstrating that metamorphosis evolves approximately when the initial value of  $\psi$  exceeds the value of the evolutionary repeller in figure 4.A1, and in particular, when it equals the value of the positive CSS in figure 4.A1. The initial value of  $w_j$  is 1.742 g; other parameter values are as shown in tables 4.2 and 4.3.

## Appendix 4.C Evolutionary rescue is hardly possible

In this appendix, we demonstrate that the evolutionary rescue of a metamorphosing population is hardly possible when environmental conditions change.

Figure 4.4A shows that metamorphosis does not disappear when the supply rate of the secondary food source decreases. Ultimately, the population will go extinct for very low supply rates (figure 4.5B). This evolutionary trap occurs for parameter values for which also a viable evolutionary attractor exists (figure 4.4A). It would therefore be possible, in principle, that the population escapes extinction by evolving back to a non-metamorphosing life history. Examination of the pairwise invasibility plots shows that this is rather unlikely (figure 4.C1). For most values of the supply rate  $\delta X_{2,\max}$  of the secondary food source, a population with metamorphosis cannot be invaded by a variant (mutant, recombinant, or immigrant) without metamorphosis (figures 4.C1B and 4.C1C). When  $\delta X_{2,\max}$  is low, the population is of very small size (figure 4.5B) and therefore can easily move away from the optimal strategy because of genetic drift. However, the pairwise invasibility plots in figures 4.C1B and 4.C1C show that variants that undergo metamorphosis can always invade, which makes it very unlikely that metamorphosis disappears because of genetic drift. For a small range of values of  $\delta X_{2,\max}$  close to the extinction boundary, a population with full metamorphosis can be invaded by a variant that has a smaller degree of metamorphosis, provided the variant strategy is sufficiently different from the resident strategy (figure 4.C1A). In this case, evolutionary rescue is possible; however, the population's size for these values of the supply rate is very small (figure 4.5B), which makes it highly susceptible to extinction through demographic or environmental stochasticity before a suitable variant strategy appears.



**Figure 4.C1:** Evolutionary rescue is hardly possible for a metamorphosing population on the brink of extinction. A: Pairwise invasibility plot for the extent of metamorphosis at a low supply rate of the secondary food source. Green areas indicate where the variant strategy can invade the resident strategy (positive invasion fitness), while orange areas indicate where this is not possible (negative invasion fitness). The open circle indicates the location of the evolutionary repeller. B: Pairwise invasibility plot at an intermediate supply rate. C: Pairwise invasibility plot at a high supply rate. The filled circle indicates the location of the continuously stable strategy (CSS). For simplicity, we assume that the other two evolving traits,  $\psi_L$  and  $w_j$ , have values at the CSS of the population with metamorphosis and do not evolve. Parameters:  $\delta X_{2,\max} = 0.0011$  (A), 0.0031 (B), or 0.0044 (C)  $\text{mg l}^{-1} \text{ day}^{-1}$ ;  $\psi_L = 0$  and  $w_j = 4.82$  (A), 1.78 (B), or 1.76 (C) g. Other parameter values are as shown in tables 4.2 and 4.3.



## Appendix 4.D Robustness of results

In this appendix, we study the robustness of our results by investigating the evolution of specialization and metamorphosis for different parameter combinations.

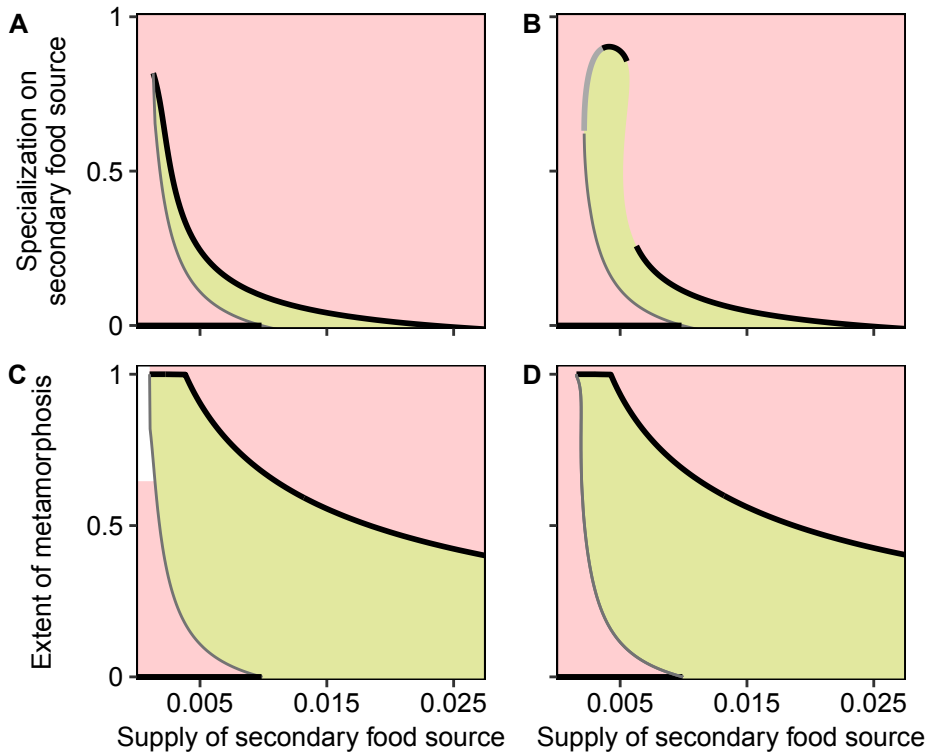
Figure 4.D1 shows how two different choices of the supply rate of the primary food source affect the evolution of specialization and metamorphosis (decreased in left column, increased in right column). Decreasing this supply rate does not qualitatively change the evolutionary outcomes (figures 4.D1A,C). In contrast, when this supply rate is increased, a small interval of the supply rate of the secondary food source appears in which evolutionary branching can occur when only the specialization trait evolves (thick grey line in figure 4.D1B). Since evolutionary branching can occur only when the population is initially specialized on the secondary food source and only for a limited range of conditions (when  $\delta X_{1,\max}$  is high and  $\delta X_{2,\max}$  is intermediate), we do not study this potential for evolutionary branching in further detail. Figure 4.D1B also shows a discontinuous change in the continuously stable strategy (CSS) of the specialization trait  $\psi$  (vertical edge of green area). This happens because two alternative stable ecological equilibria exist for intermediate supply rates of the secondary food source. One of these ecological equilibria disappears when the supply rate of the secondary food source is increased, which leads to an abrupt transition in the evolutionary outcome.

When the supply rate of the primary food source is very high, metamorphosis disappears when the supply rate of the secondary food source is decreased, which implies that metamorphosis in this case is not an evolutionary trap (figure 4.D1D). For high supply rates of the primary food source, metamorphosed individuals can survive and reproduce while feeding only on the primary food source, even though they have a morphology that is not specialized on doing so. When the supply rate of the secondary food source diminishes, the food available to metamorphosed individuals decreases, but there is always enough of the primary food source left in order for them to survive. Since we assume optimal foraging, individuals will exclusively forage on the primary food source when the secondary food source is rare. At this point, the selection pressure on metamorphosis is negative because of the associated costs, and metamorphosis disappears (figure 4.D1D). Notice that this evolutionary outcome occurs only because we assume that large individuals (with body masses  $w > w_{\min}$ ) can always forage on both food sources, independent of their morphology.

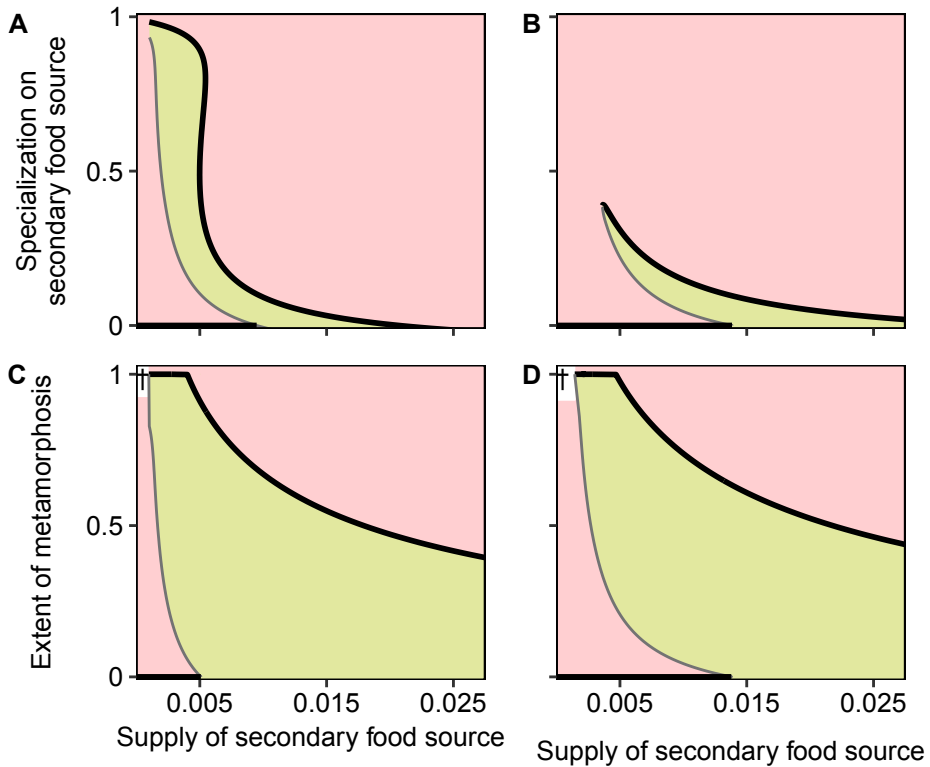
Figure 4.D2 shows that changing the body mass at which the secondary food source becomes available to individuals (decreased in left column, increased in right column) does not qualitatively change the evolution of specialization, nor the evolution of metamorphosis. When the secondary food source is available only to large individuals, specialization on it is not possible, even not when individuals are initially already specialized on this food source (figure 4.D2B). Because individuals need to grow a lot before the secondary food source becomes available to them, it is even more important for them to be specialized on the primary food source than when the secondary food source is available already to small individuals (figure 4.D2A). Decreasing the body mass at which the secondary food source becomes available to individuals decreases the supply rate of the secondary food source at which metamorphosis can start to evolve (figure 4.D2C,D). Because the secondary food source is available early in life, it is beneficial to invest in metamorphosis already when the supply rate of the secondary food source is relatively low.

Since changing the costs of metamorphosis does not affect the evolution of specialization, we show in figure 4.D3 only how changing these costs (increased in left column, decreased in right column) affect the evolution of metamorphosis. We consider in turn the mortality costs of metamorphosis and the energetic costs of metamorphosis. The risk of dying during metamorphosis largely determines to which extent metamorphosis can evolve (figure 4.D3A,B), but does not affect the supply rate of the secondary food source at which metamorphosis can start to evolve. The energetic costs of metamorphosis influence only slightly the extent to which metamorphosis evolves (figure 4.D3C,D).

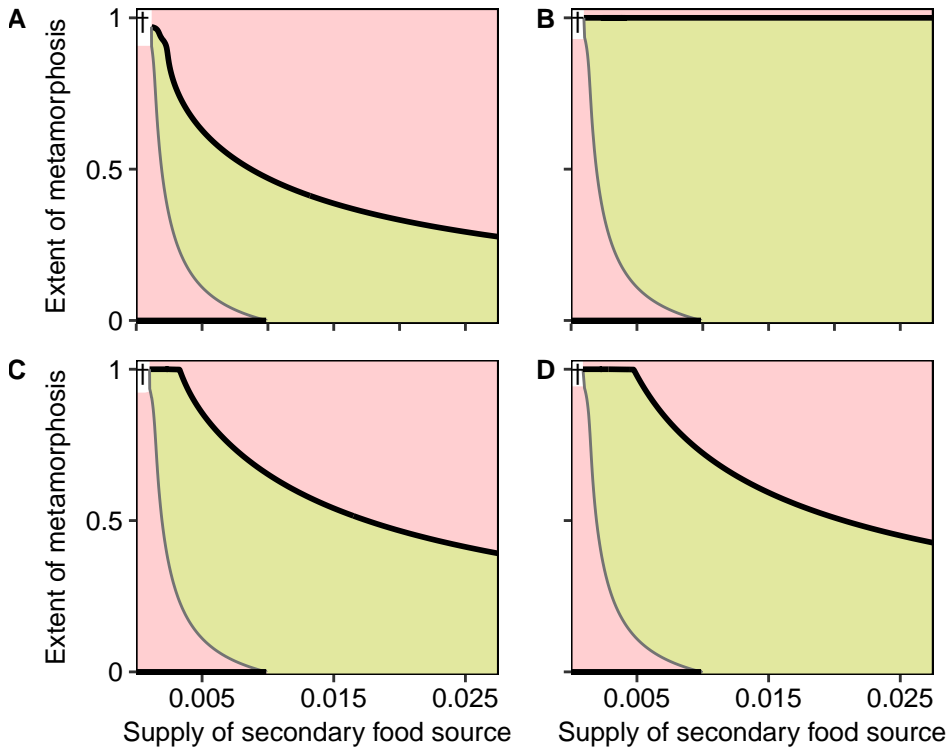
In figure 4.D4, we show the evolution of specialization and metamorphosis for  $\alpha = 0.93$ , which is increased relative to the value  $\alpha = 0.6$  used in the main text. The parameter  $\alpha$  determines how strongly the attack rates on the primary and secondary food sources increase and decrease around their peaks at  $w_0$  and  $w_0 + w_{\min}$ , respectively. In the absence of an ontogenetic diet shift and all else being equal,  $\alpha$  determines the competitive ability of an individual of a given body mass, which can be characterized by the food density at which the individual can just meet its maintenance requirements (Persson et al. 1998). A value of  $\alpha = 0.93$  means that in the absence of an ontogenetic diet shift differently sized consumers have more or less similar competitive abilities. In this case, specialization on the secondary food source is never possible (figure 4.D4A). For this higher value of  $\alpha$ , small individuals are much more affected by the trade-off between specialization on the primary and secondary food sources. Nevertheless, the evolution of metamorphosis is not influenced by  $\alpha$  (figure 4.D4B).



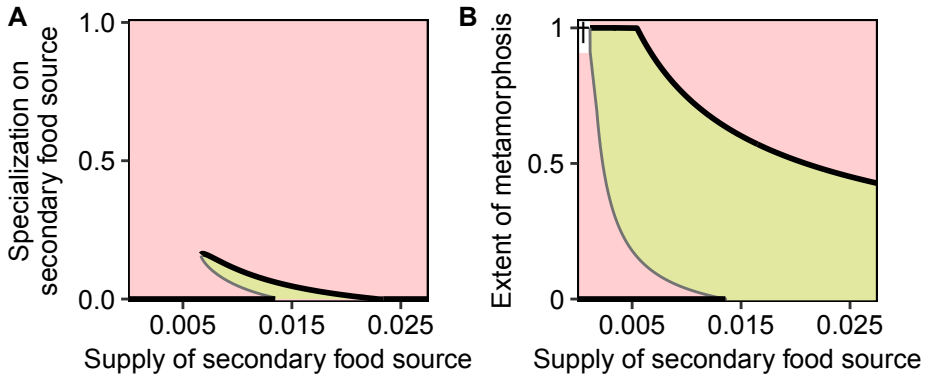
**Figure 4.D1:** Effects of changing the supply rate of the primary food source. Evolution of specialization on the secondary food source (A and B) in the absence of metamorphosis, and evolution of metamorphosis (C and D) when there initially is no specialization on the secondary food source, as functions of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{ day}^{-1}$ ) for two different values of the supply rate of the primary food source (A and C, decreased relative to main text; B and D, increased relative to main text). Thick black lines indicate continuously stable strategies (CSSs), thin grey lines indicate evolutionary repellers, and the thick grey line in B indicates evolutionary branching points. Arrows show the direction of evolution. In the red areas, evolution decreases the degree of specialization (A and B) or the extent of metamorphosis (C and D), whereas in the green areas, evolution increases the degree of specialization or the extent of metamorphosis. The population cannot persist in the white area marked with a dagger ( $\dagger$ ). Parameters:  $X_{1,\max} = 0.022$  (A, C) or  $0.11$  (B, D)  $\text{mg l}^{-1}$ . Other parameter values are as shown in tables 4.2 and 4.3.



**Figure 4.D2:** Effects of changing the body mass at which the secondary food source becomes available to individuals. Evolution of specialization on the secondary food source (A and B) in the absence of metamorphosis and evolution of metamorphosis (C and D) when there initially is no specialization on the secondary food source, as a function of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{ day}^{-1}$ ) for two different values of the body mass at which the secondary food source becomes available to individuals (A and C, decreased relative to main text; B and D, increased relative to main text). Note that specialization on a secondary food source is not possible in case individuals gain access to it too late in life (B). Thick black lines indicate continuously stable strategies (CSSs), whereas thin grey lines indicate evolutionary repellers. Arrows show the direction of evolution. In the red areas, evolution decreases the degree of specialization (A and B) or the extent of metamorphosis (C and D), whereas in the green areas, evolution increases the degree of specialization or the extent of metamorphosis. The population cannot persist in the white areas marked with a dagger (†). Parameters:  $w_{\min} = 0.88$  (A, C) or 6 (B, D). Other parameter values are as shown in tables 4.2 and 4.3.



**Figure 4.D3:** Effects of changing the costs of metamorphosis. Evolution of metamorphosis when there initially is no specialization on the secondary food source, as a function of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{ day}^{-1}$ ) for (A and B) two different mortality costs of metamorphosis and (C and D) two different energetic costs of metamorphosis (A and C, increased relative to main text; B and D, decreased relative to main text). A:  $\rho = 0.9$ , which means that individuals undergoing full metamorphosis ( $\theta = 1$ ) have a probability of 0.1 to survive metamorphosis. B:  $\rho = 0$ , which means that metamorphosis does not decrease survival. C:  $q_s = 0$ , which means that full metamorphosis requires individuals to invest all their reversible body mass into metamorphosis. D:  $q_s = 0.742 = q_f$ , which means that metamorphosis does not require an investment of reversible body mass. Other parameter values are as shown in tables 4.2 and 4.3. Thick black lines indicate continuously stable strategies (CSSS), whereas thin grey lines indicate evolutionary repellers. Arrows show the direction of evolution. In the red areas, evolution decreases the extent of metamorphosis, whereas in the green areas, evolution increases the extent of metamorphosis. The population cannot persist in the white areas marked with a dagger (†).



**Figure 4.D4:** Effects of changing how strongly the attack rates on the primary and secondary food sources increase and decrease around their peaks. Evolution of specialization on the secondary food source (A) in the absence of metamorphosis and evolution of metamorphosis (B) when there initially is no specialization on the secondary food source, as functions of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ) for  $\alpha = 0.93$  (increased relative to main text). Specialization on the secondary food source is never possible in this case (A). Other parameter values are as shown in tables 4.2 and 4.3. Thick black lines indicate continuously stable strategies (CSSs), whereas thin grey lines indicate evolutionary repellers. Arrows show the direction of evolution. In the red areas, evolution decreases the degree of specialization (A) or the extent of metamorphosis (B), whereas in the green areas, evolution increases the degree of specialization or the extent of metamorphosis. The population cannot persist in the white area marked with a dagger (†).

**METAMORPHOSIS, AN EVOLUTIONARY DEAD END?**

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## Abstract

While most animal species undergo metamorphosis, several species have evolved life cycle modifications to avoid complete metamorphosis. Some species, e.g. many salamanders and newts, have deleted the adult stage via a process called paedomorphosis. Others, e.g. some frog species and marine invertebrates, do no longer have a distinct larval stage and reach maturation via direct development. It is not well understood which ecological conditions can lead to the loss of metamorphosis, either via the evolution of paedomorphosis or via the evolution of direct development. Here we show with the use of a size-structured consumer-resource model in conjunction with the adaptive-dynamics approach, that metamorphosis often is an evolutionary dead end which leads to the extinction of a population when the environment deteriorates. Only under limited ecological conditions metamorphosis can disappear via the evolution of paedomorphosis or direct development. When the adult habitat deteriorates, individuals postpone metamorphosis, this will lead to a (partial) paedomorphic population in case the larval habitat is very favorable. Vice versa, in case the larval habitat deteriorates, individuals will produce larger offspring and in concert accelerate metamorphosis, leading to direct development in case the adult habitat is highly favorable. With a phylogenetic approach we furthermore show that among amphibians the evolution of direct development is indeed, as we hypothesize, preceded by the evolution of larger egg sizes.



## 5.1 Introduction

What do the Puerto Rican tree frog *Eleutherodactylus coqui*, the axolotl (*Ambystoma mexicanum*) and the flat periwinkle (*Littorina obtusata*, a marine sea snail), have in common? They all have lost the ability to metamorphose, something their ancestors still did. Both the tree frog and the sea snail lost metamorphosis via the evolution of direct development, their offspring are born with the adult morphology. The axolotl, on the other hand, retains the larval morphology and lost the adult stage via the evolution of paedomorphosis. In contrast to metamorphosing salamanders, adult axolotls possess gills and remain their whole life aquatic. How did these life-history strategies evolve?

Even though some species have lost the ability to metamorphose, metamorphosis is the dominant life-history strategy in the animal kingdom (Werner 1988). We define metamorphosis here as the morphological change that takes place at the transition from the free-living larval to the juvenile stage. This morphological change allows for the effective exploitation of different niches during an individual's life (Moran 1994). It has been shown before in a theoretical study that metamorphosis is difficult to evolve, but, once evolved it is a very successful strategy that is not lost easily (chapter 4 of this thesis). Since metamorphosing species often depend on multiple niches for their growth and reproduction, they are vulnerable to habitat degradation since a metamorphosing population can already go extinct if only one of the two habitats becomes unsuitable (Rudolf and Lafferty 2011). Metamorphosis is furthermore both a risky and energetically costly process (e.g. Geffen et al. 2007; Wassersug and Sperry 1977). It is therefore likely that under some ecological conditions individuals evolve a life-history strategy without metamorphosis.

The evolution of direct development is one pathway by which metamorphosis can disappear. In direct developing species the adult features form during the embryonic stage and are present at hatching (Callery et al. 2001). Species with direct development lack a free-living larval stage. Direct development evolved at least 10 times in anurans (Hanken 1999) and at least twice in salamanders (in the lungless salamanders, Wake and Hanken 1996). Direct development is also a common life-history strategy among marine invertebrates (e.g. Marshall et al. 2012) and the default strategy among mammals. While there are many studies that describe the morphological and hormonal development of direct developing species (e.g. Callery et al. 2001; Schweiger et al. 2017), from an ecological point of view it is not well understood how and why direct development evolved. It is likely that unfavorable conditions for larvae select for the evolution of direct development. Life-history data of marine invertebrates for example show that planktonic species, where individuals are born with the adult morphology, are more common in unproductive environments (Marshall et al. 2012). Empirical

data furthermore show that direct development is associated with the production of larger offspring (e.g. Callery et al. 2001; Marshall et al. 2012; McEdward 2000), but it is unknown if direct development leads to the evolution of larger offspring or the other way around.

Metamorphosis can also be lost via the evolution of paedomorphosis, where individuals retain the larval features during their whole life cycle. Paedomorphosis is common in salamanders (Denöel et al. 2005) but for example absent in frogs (Elinson and del Pino 2012). Paedomorphosis can evolve when individuals change the relative timing of developmental events (heterochrony). When the size at maturation is decreased, while the size at metamorphosis stays the same, individuals mature while keeping the larval morphology (progenesis). Paedomorphosis can also evolve when individuals increase the size at which they metamorphose, such that metamorphosis takes place very late in life after individuals have matured (neoteny) (Bonett et al. 2014*b*). Both progenesis and neoteny can ultimately lead to paedomorphic individuals.

There are several hypotheses regarding the loss of metamorphosis via the evolution of paedomorphosis (Whiteman 1994; Wilbur and Collins 1973). The 'paedomorph advantage hypothesis' states that paedomorphosis evolves under good larval conditions and harsh adult conditions (Whiteman 1994; Wilbur and Collins 1973). Because they occupy different ecological niches in different stages of their development, individuals that optimally use the larval niche, have a higher fitness than individuals that switch to the unfavorable adult niche. It is therefore evolutionary advantageous to skip metamorphosis and always keep the larval morphology. Alternatively, under the 'best of a bad lot' hypothesis paedomorphs originate in case of unfavorable larval conditions. Because larval growth is in this case very slow, individuals never reach the minimum size needed in order to metamorphose (Whiteman 1994). The theoretical models underlying these hypotheses only assume that there is some variation in growth rates among individuals which leads to differences in fitness. They do not include any feedback between the individuals in the population and their environment and are mainly used to explain variation in developmental mode within populations (e.g. Bonett et al. 2014*a*; Whiteman et al. 2012; Wilbur and Collins 1973). Individuals that metamorphose have a different impact on the environment (e.g. food densities) than paedomorphic individuals (e.g. Denöel and Joly 2001), and the success of an individual therefore depends on the strategy of the other individuals in the population. Hence, it is necessary to take this feedback loop between the strategy of individuals and their environment into account when studying the evolution of paedomorphosis.

The aim of this paper is to better understand when paedomorphosis and direct development can evolve in an initially metamorphic population. To do so, we use a fully size-structured consumer resource model where the consumer forages on two types of food. These food sources require different morphologies to be effectively utilized.

While large individuals can feed upon both food sources, small individuals can only feed upon the primary food source, since they are too small to handle the secondary food source. Individuals are born with a morphology specialized in feeding on the primary food source. At a certain size individuals undergo metamorphosis and develop a morphology specialized in feeding on the secondary food source. While metamorphosis allows for the efficient exploitation of the two food sources, we assume that it is an energetically costly process. We will study the evolutionary response of the metamorphosing population in relation to deteriorating food conditions. Since the benefits and costs of metamorphosis depend on the food densities and these densities are in turn affected by the strategy of the consumers, it is important to take into account the feedback loop between the environment and the consumer individuals. We therefore use the framework of adaptive-dynamics (Geritz et al. 1998) to study the evolutionary loss of metamorphosis.

We first study how metamorphosing individuals will respond to changes in the supply rate of the primary food source. We find that there is selection to produce larger offspring when the primary food source becomes less productive. Secondly, we study how changes in the supply rate of the secondary food source affects life-history traits of metamorphosing individuals. We show that diminishing supply rates lead to individuals that postpone metamorphosis. Thirdly, we study under which ecological conditions metamorphosis can disappear through the evolution of direct development or paedomorphosis. In line with the results in chapter 4 of this thesis we find that metamorphosis is hard to lose, even when this leads to the extinction of the population. Paedomorphosis and direct development can only evolve under limited conditions. Finally, we test our predictions regarding the evolution of direct development in amphibians with the use of a phylogenetic comparative framework (Pagel 1994).

## 5.2 Model and methods

### **Model**

To understand under which ecological conditions metamorphosis can disappear we use an extension of the size-structured consumer-resource model described by Persson et al. (1998). Below we describe the most important aspects of the model, a more detailed model description can be found in appendix 5.A and in chapter 4 of this thesis.

The growth and fecundity of an individual depends on its food intake. We assume that consumers have access to two food sources that each require a different morphology to be effectively utilized by the consumers. The primary food source is available for all consumers while the secondary food source is only available for individuals with a body mass larger than  $w_{\min}$ . Both the primary and secondary food source follow semi-chemostat dynamics with a turn-over rate of  $\delta$  and will, in the absence of con-

sumers, reach a maximum density of  $X_{1,\max}$  and  $X_{2,\max}$ , respectively. Metamorphosis decouples the morphologies expressed at different life stages such that an individual can adopt different morphologies before and after metamorphosis. Initially, the consumer has three life stages; larvae (L), juveniles (J) and adults (A). Larvae are born with body mass  $w_b$  and metamorphose into juveniles at a body mass of  $w_j$ , juveniles subsequently mature into adults and start reproducing when reaching a body mass of  $w_A$ . The morphology of an individual is described by the relative degree of specialization  $\psi_i$  ( $i = L, J$ , or  $A$ ) on the secondary food source; a value of  $\psi_i = 0$  means that individuals are completely specialized in feeding on the primary food source, conversely, a value of  $\psi_i = 1$  means that individuals are completely specialized in feeding on the secondary food source.

The morphology of larvae is determined by parameter  $\psi_L$ . The morphology of postmetamorphs (juveniles and adults) is determined by two traits, the extent of metamorphosis  $\theta$  and the larval specialization parameter  $\psi_L$  following

$$\psi_A = \psi_J = \min(1, \psi_L + \theta). \quad (5.1)$$

Note that  $\psi_L$ ,  $\psi_J$ , and  $\psi_A$  have values between 0 and 1. Individuals that undergo metamorphosis lose part of their body mass and furthermore have a probability of  $\rho\theta$  to die during metamorphosis. We refer to the larval morphology in case a life stage is specialized in feeding on the primary food source ( $\psi_i = 0$ ) and to the adult morphology in case a life stage is (partly) specialized in feeding on the secondary food source ( $\psi_i > 0$ ).

Metamorphosis can disappear in several ways. Paedomorphosis, where all individuals have the larval morphology, can evolve when the degree of metamorphosis  $\theta$  evolves to a value of 0 or when the body mass at metamorphosis  $w_j$  evolves to values larger than the body mass at maturation  $w_A$ . As a consequence, individuals will first mature before they metamorphose or even never reach the size at metamorphosis at all. Direct development, where all individuals adopt the adult morphology, can evolve in case the body mass at birth  $w_b$  is larger than the body mass at metamorphosis  $w_j$ , such that metamorphosis takes place before individuals are born. In this case the mothers pay for the costs of the metamorphosis of their offspring (see appendix 5.A).

To study how paedomorphosis and direct development can evolve we study the evolution of four traits; the two traits that determine the morphology of an individual ( $\psi_L$  and  $\theta$ ), the body mass at metamorphosis  $w_j$  and the body mass at birth  $w_b$ . We use the framework of adaptive-dynamics to study the evolution of these four traits (Geritz et al. 1998).

We assume that initially larvae are completely specialized on the primary food source ( $\psi_L = 0$ ) while postmetamorphs are (partly) specialized on the secondary food source ( $\theta > 0$ ), which is the case when the supply rates of both food sources are high

(see chapter 4 of this thesis). To understand which ecological conditions lead to the disappearance of metamorphosis, we track this evolutionary singular strategy (ESS) predicted by the model for decreasing values of the supply rate of either the primary ( $\delta X_{1,\max}$ ) or the secondary ( $\delta X_{2,\max}$ ) food source. We decrease the supply rates by varying  $X_{1,\max}$  and  $X_{2,\max}$  while keeping  $\delta$  constant. We assume that the body mass at which the secondary food source becomes available  $w_{\min}$  does not evolve. Since this parameter is possibly very important in the evolutionary outcome, we also investigate the effect of this parameter.

For most values of  $w_{\min}$ , the evolutionary singular strategies found possess strong convergence stability and therefore correspond to a CSS (Leimar 2009). In case  $w_{\min}$  is very low and the supply rates of both food sources are high, the selection gradient vanishes for an ecological steady state that is dynamically unstable (saddle point) and hence not an ecological attractor. We used the canonical equation of adaptive dynamics (Dieckmann and Law 1996; Durinx et al. 2008) to study how the four traits evolve in this case. For simplicity we assume that all evolutionary traits evolve independently from each other, we therefore used the identity matrix for the mutational covariance matrix. In appendix 5.B we show that even though the four evolving traits always vary over evolutionary time, they stay close to the strategy with a vanishing selection gradient that gives rise to an ecologically unstable steady state. We therefore ignore this subtlety in the result section and will refer to the strategy with a vanishing selection gradient as an ESS irrespective of its ecological instability.

Even though there are four traits evolving in our model, for clarity we do not always show how all of these traits change for changing supply rates. We show the evolutionary endpoints of body mass at birth  $w_b$  and at metamorphosis  $w_j$  in case of diminishing supply rates of the primary food source and the degree of metamorphosis  $\theta$  and the body mass at metamorphosis  $w_j$  in case of diminishing supply rates of the secondary food source. All analyses are performed using the PSPManalysis software package (de Roos 2016). This software package allows for the equilibrium and evolutionary analysis of physiologically structured population models (see chapter 4 of this thesis for more details). A more detailed description of the model and the evolutionary analysis can be found in appendix 5.A.

### Phylogenetic comparative analyses

We use a phylogenetic comparative analysis to test the correlation between the evolution of direct development and larger offspring. A dated phylogenetic tree including 2871 amphibian species was obtained from Pyron and Wiens (2013). Data for direct development and egg size were obtained from the AmphiBIO database (Oliveira et al. 2017) and matched against the phylogenetic data. From the entries in this database we used breeding strategy 'Dir' to indicate whether species reproduce via direct devel-

opment or not (binary) and 'Offspring\_size\_min\_mm' as a measure of egg size. As the latter trait is continuous, and our analyses (see below) can only handle binary data, we defined large eggs as  $\geq$  the average across amphibians, and small eggs as  $<$  the average. The average was 2.857 mm. In total, we obtained direct development data for 79% of the species ( $n = 2265$ ) and egg size data for 28% of the species ( $n = 795$ ) for which we also had phylogenetic data ( $n = 2871$ ).

We tested for correlated evolution between direct development and large egg sizes in a phylogenetic comparative framework (Pagel 1994). To do so, we calculated the log marginal likelihood of an independent and a dependent model. In the independent model it is assumed that transitions in the two traits (between no direct development and direct development and between no large eggs and large eggs) occur completely independently from each other. The evolution of direct development does in this independent model not depend on the presence of large eggs and, vice versa, the evolution of large eggs is independent of the type of developmental mode. We compare the fit of this model with a dependent model where the two traits are correlated. In this model, the transition rates of both traits depend on the state of the other trait. It is assumed that the probability that two traits change at exactly the same time equals zero (Pagel 1994). There are therefore in total 8 transition rates calculated. These analyses were carried out in BAYESTRAITS v3 (Meade and Pagel 2017).

We ran five replicate Markov chain Monte Carlo (MCMC) chains for models of independent evolution and dependent (correlated) evolution, using a reversible jump hyper prior with an exponential prior between 0 and 100 and using a stepping stone sampler (Xie et al. 2011) to obtain estimates of the log marginal likelihoods. These MCMC chains were run for 5000000 generations and we discarded a 10% burnin. Support for correlated evolution was calculated using log Bayes Factors as follows:

$$2 \cdot (\log \text{marginal likelihood (dependent model)} - \log \text{marginal likelihood (independent model)}) \tag{5.2}$$

in which a log Bayes Factor  $> 10$  indicates strong support for the more complex model (in this case the dependent model, and thus for correlated evolution).

In case we found support for correlated evolution, we evaluated transition rates to assess whether the transition towards direct development is conditional on the evolution of large egg sizes. The significance of this was tested by comparing Bayes Factors of the full, dependent model (no constraints) to a constraint model. In this constraint model we assume that large eggs and small eggs may equally likely be present when direct development evolves. The constraint model therefore only calculates 7 transition rates (in contrast to 8 transition rates in the full, dependent model). We compare again the log marginal likelihoods of both models to test which model fits the data the best (Pagel 1994).

### 5.3 Results

In chapter 4 of this thesis we found that metamorphosis can evolve as a way to relax the trade-off between early and late foraging success. Metamorphosis is, however, costly and it can therefore only evolve when the secondary food source is very abundant. As soon as the supply rate of this food source reaches a high threshold, metamorphosis evolves abruptly. Once evolved, metamorphosis does often not disappear when the supply rate of the secondary food source diminishes. There is therefore evolutionary bistability; for many supply rates of the secondary food source there are two evolutionary attractors, one where individuals undergo metamorphosis and a second attractor where individuals do not metamorphose. Here, we study the evolutionary response of a metamorphosing population to deteriorating food conditions. We therefore only study how the traits in the CSS of a metamorphosing population respond to decreasing supply rates and we ignore how a non-metamorphosing population responds to changing supply rates.

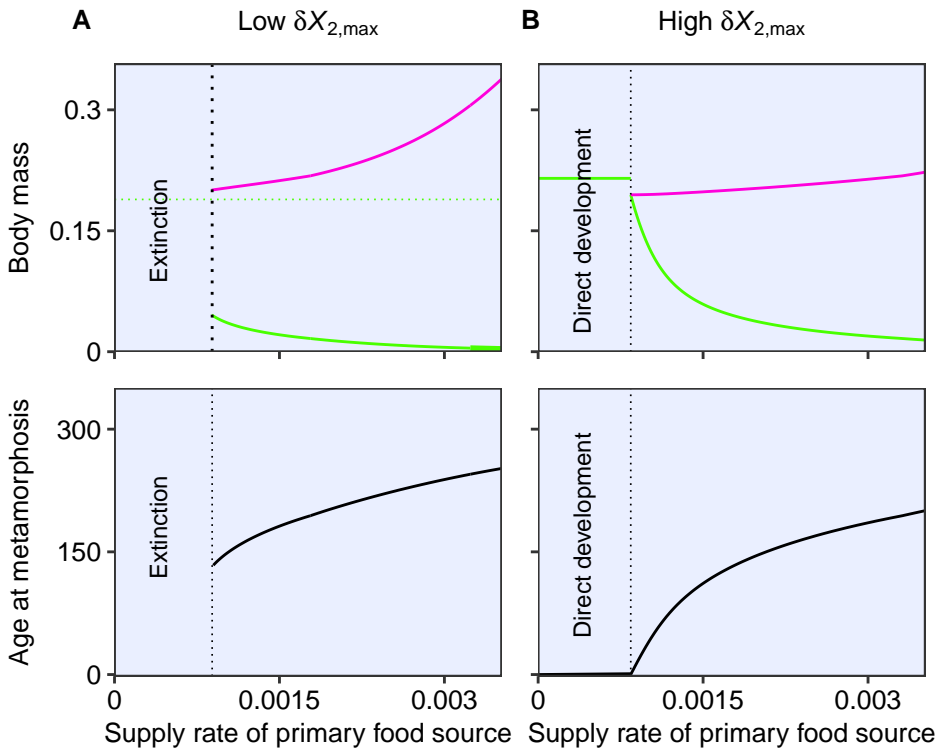
In the first part of this section we show that individuals produce larger offspring when the primary food source deteriorates. While this sometimes leads to the evolution of direct development, the population often goes extinct when the primary food source becomes too scarce. In the second part we show how a metamorphosing population adapts to deteriorating conditions of the secondary food source. We show that paedomorphosis can evolve but that, again, the population can also go extinct in case the supply rate of the secondary food source becomes too low. In the third section we show that for most parameter settings metamorphosis is an evolutionary trap in the sense that it leads to the extinction of a metamorphosing population when one of the food sources becomes too scarce. In the last section we show with a phylogenetic comparative analysis that the evolution of large egg sizes preceded the evolution of direct development in amphibians.

#### **Evolution of larger offspring when the primary food source deteriorates**

When the primary food source deteriorates there is selection to reduce the period where individuals depend on this food source. There is therefore an evolutionary response to a diminishing supply rate of the primary food source such that individuals produce larger offspring and furthermore metamorphose at a smaller body mass (top panels of figure 5.1). By increasing the body mass at birth  $w_b$  and decreasing the body mass at which individuals undergo metamorphosis  $w_j$ , individuals will metamorphose at an earlier age (bottom panels in figure 5.1).

Since individuals depend crucially on the primary food source when their body mass is less than  $w_{\min}$ , it is of importance to produce offspring that are large enough to immediately start feeding on the secondary food source when the primary food

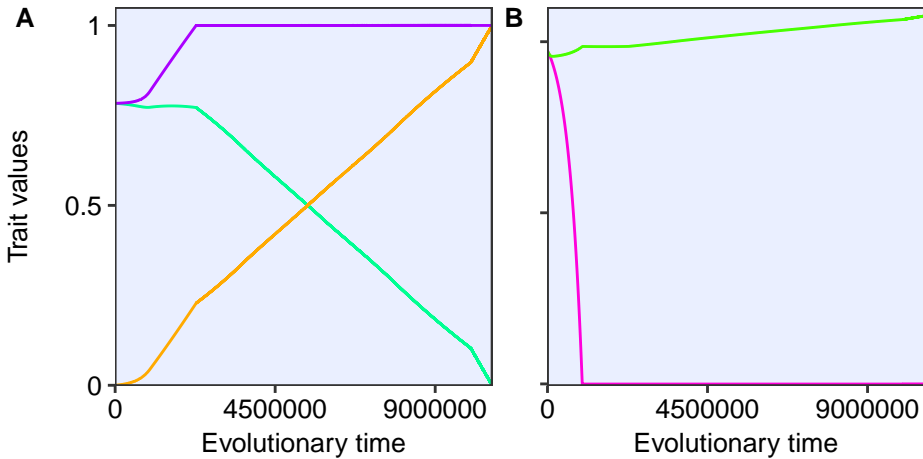
source is very scarce or even absent. Producing large offspring is energetically more expensive than producing small offspring. Adults that produce larger offspring therefore need more food in order to produce a single offspring compared to adults that produce smaller offspring. There is thus a trade-off between producing many small individuals that depend on the primary food source for a long time or producing a few big individuals that do not rely on this food at all. For most supply rates of the secondary food source, the density of this food is not high enough for individuals to produce offspring large enough to completely skip the primary food source. The population therefore often goes extinct in case of diminishing supply rates of the primary food source, even though the body mass at birth increases (figure 5.1A).



**Figure 5.1:** Body mass (g) at birth (green), body mass at metamorphosis (light purple) (top panels) and age at metamorphosis (bottom panels) at the CSS for decreasing values of the supply rate of the primary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ) for low (A) and high (B) supply rates of the secondary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ). For low supply rates of the primary food source the population either goes extinct (A) or evolves direct development (B). The dotted green line in the top panel of A shows the minimum body mass at birth that is necessary to skip the primary food source. Parameters:  $\delta X_{2,max} = 0.0066$  (A) or  $\delta X_{2,max} = 0.011 \text{ mg l}^{-1}$  (B);  $w_{min} = 0.1742$  gram. Other parameter values are as shown in tables 5.A3 and 5.A4.



When the supply rate of the secondary food source is very high, direct development can evolve (figure 5.1B and figure 5.2). The body masses at birth and at metamorphosis evolve such that at a certain point individuals metamorphose before they are born (vertical dotted line in figure 5.1B). At this point, individuals do no longer feed on the primary food source. We show in figure 5.2 how the traits change over evolutionary time as soon as metamorphosis takes place before birth. Because metamorphosis is still costly (the costs are now paid by the mother, appendix A), there is selection to reduce the extent of metamorphosis  $\theta$  (mint-green line) while at the same time it is beneficial to increase specialization parameter  $\psi_L$  (orange line) such that all individuals have a morphology fully specialized on the secondary food source (dark purple line). Because individuals no longer pay the costs of metamorphosis, the size at birth will evolve to higher values (figure 5.2) since adults have more energy available to produce large offspring. This results in a sudden jump in the body mass at birth as soon as direct development evolves (top panel in 5.1B). Since we are only interested in how a metamorphosing population responds to decreasing supply rates, we do not show in figure 5.1B when a direct developing species would again re-evolve metamorphosis when the supply rate of the primary food source increases.



**Figure 5.2:** Evolutionary dynamics, starting from a metamorphic initial population, of the extent of metamorphosis ( $\theta$ , mint-green) the larval specialization parameter  $\psi_L$  (orange) and the resulting specialization on the secondary food source for all individuals (dark purple) (A) and the body mass at birth ( $w_b$ , green) and at metamorphosis ( $w_j$ , light purple) (B) in gram. Parameters:  $\delta X_{1,\max} = 0.00084$ ,  $\delta X_{2,\max} = 0.011 \text{ mg l}^{-1}$  and  $w_{\min} = 0.1742$  gram. Other parameter values are as shown in tables 5.A3 and 5.A4.

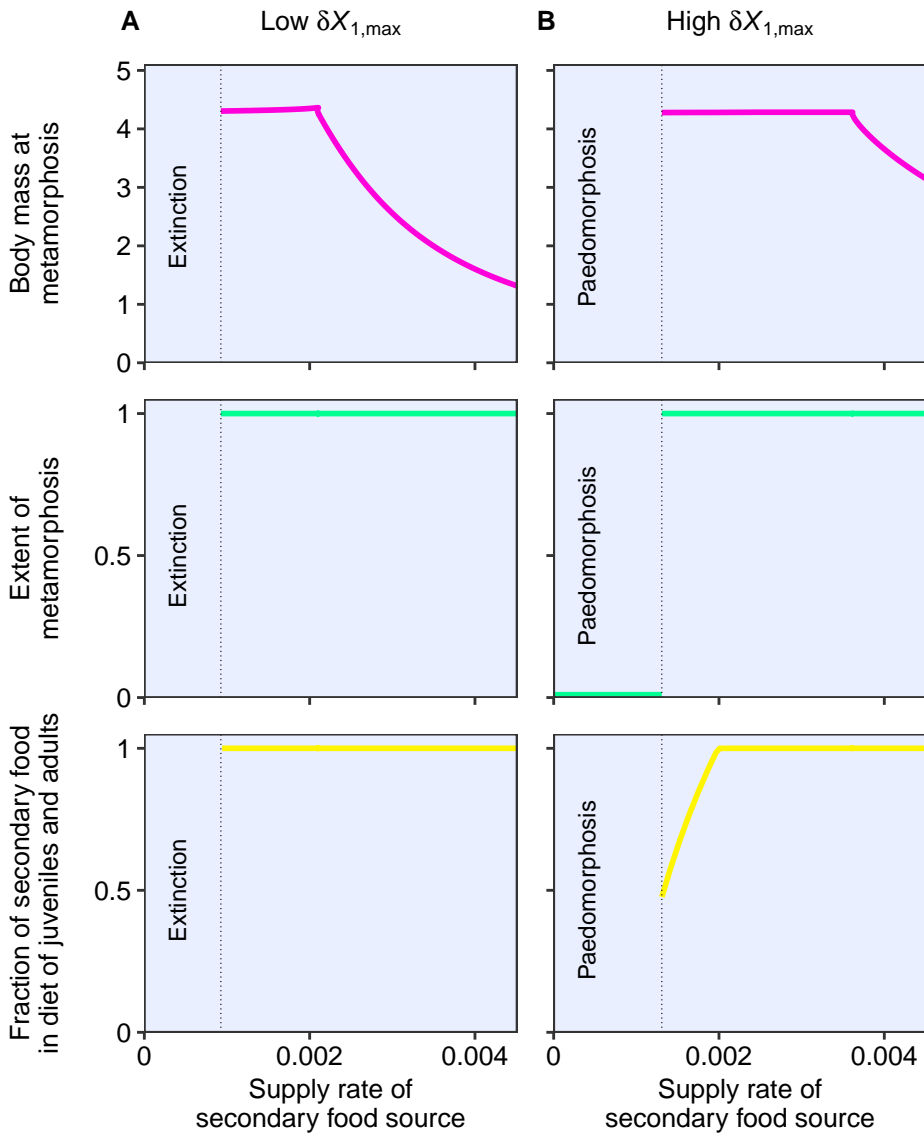
### **Evolution of a postponed metamorphosis when the secondary food source deteriorates**

When the supply rate of the secondary food source diminishes, there is an evolutionary response to postpone metamorphosis (top panels in figure 5.3). When the supply rate of the secondary food source decreases, there is less of it available. It is therefore beneficial for individuals to postpone metamorphosis such that they are specialized on the primary food source for longer.

Individuals are, after metamorphosis, very efficient in feeding on the secondary food source. For most supply rates of the primary food source they therefore only feed on the secondary food source after metamorphosis (bottom panel in figure 5.3A). Because of this, there is no selection to reduce the extent of metamorphosis (middle panel in figure 5.3A). Hence, adults rely completely on the secondary food source for their reproduction, such that when this food source becomes too scarce, reproduction diminishes and the population goes extinct (figure 5.3A).

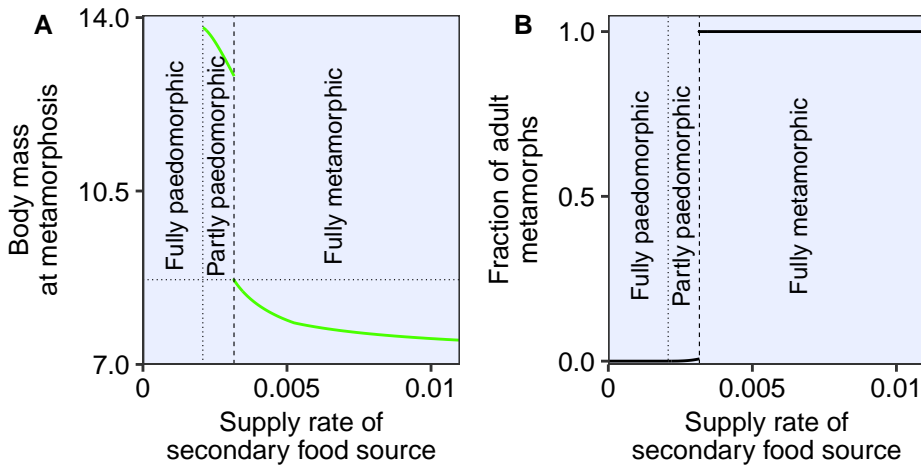
Paedomorphosis, where all individuals adopt the larval morphology, evolves abruptly in case the supply rate of the primary food source is very high while that of the secondary food source is low (figure 5.3B). Even though postmetamorphs are not specialized in feeding on the primary food source, the high availability of the primary resource makes that they now do include this food in their diet when the secondary food source becomes scarce (bottom panel figure 5.3B). For very low supply rates of the secondary food source, a large fraction of the diet of large individuals consists of the primary food source. It is therefore beneficial to specialize on the primary food source. As soon as individuals reduce the extent of their metamorphosis, however, they become less efficient in feeding on the secondary food source and more efficient in feeding on the primary food source (equation 4.10). Therefore, individuals will include more of the primary food source in their diet which in turn selects for a less pronounced metamorphosis. Because of this autocatalytic effect of a decrease in metamorphosis, paedomorphosis evolves abruptly as soon as the supply rate of the secondary resource drops below a certain threshold (dotted line in figure 5.3B).

The results in chapter 4 of this thesis show that metamorphosis can only re-evolve as soon as the supply rate of the secondary food source reaches a high threshold (not shown in figure 5.3). There is therefore a second evolutionary attractor present for many supply rates of the secondary food source where individuals do not metamorphose. Since we are only interested in how a metamorphosing population responds to decreasing supply rates, this attractor is not represented.



**Figure 5.3:** Body mass (g) at metamorphosis (top panel), the extent of metamorphosis (middle panel) and the fraction of the secondary food source source in the diet of juveniles and adults (bottom panel) at the CSS as a function of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ) for low (A) and high (B) supply rates of the primary food source. Parameters:  $\delta X_{1,\max} = 0.0055$  (A) or  $\delta X_{1,\max} = 0.011 \text{ mg l}^{-1} \text{day}^{-1}$  (B);  $w_{\min} = 0.01742$  gram. Other parameter values are as shown in tables 5.A3 and 5.A4.

In case the secondary food source is only available for very large individuals (high value of  $w_{\min}$ ), there is a second mechanism by which paedomorphosis can evolve. Because only the largest individuals can make use of the secondary food source, metamorphosis takes place relatively late in life (figure 5.4A). When the supply rate of the secondary food source diminishes, individuals postpone metamorphosis (as in figure 5.3), such that metamorphosis takes place just before maturation (vertical dashed line in figure 5.4). In contrast to figure 5.3, figure 5.4 shows that in this case the mass at metamorphosis continues to increase with decreasing supply rates of the secondary resource. When the mass at metamorphosis exceeds the mass at maturation there is a discrete change in the body mass at metamorphosis such that individuals postpone metamorphosis until they have reached a very large body mass. Because of this, most adults die before metamorphosis takes place and only a few actually undergo metamorphosis (figure 5.4B). For even lower values of the supply rate metamorphosis takes place at a body mass that not a single individual actually reaches (vertical dotted line in figure 5.4). Even though metamorphosis has not really disappeared ( $\theta > 0$ ), the population appears to be paedomorphic since not a single individual undergoes metamorphosis. How such a paedomorphic population re-evolves a metamorphosis when the supply rate of the secondary food sources increases, is not investigated.



**Figure 5.4:** Body mass at metamorphosis (A) and the fraction of adults in the population that have metamorphosed (B) at the CSS as a function of the supply rate of the secondary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ). The horizontal dotted line in A indicates at which body mass individuals mature. The vertical lines indicate where the population becomes partly (dashed) or fully (dotted) paedomorphic.  $\delta X_{1,\max} = 0.055 \text{ mg l}^{-1} \text{day}^{-1}$ ;  $w_{\min} = 6.97 \text{ gram}$ . Other parameter values are as shown in tables 5.A3 and 5.A4.

### When does metamorphosis disappear?

In the previous two sections we showed that direct development and paedomorphosis can evolve in case of diminishing supply of the primary and the secondary food source, respectively. In this section we show how these results depend on the supply rates of the two food sources and the body mass at which the secondary food source becomes available.

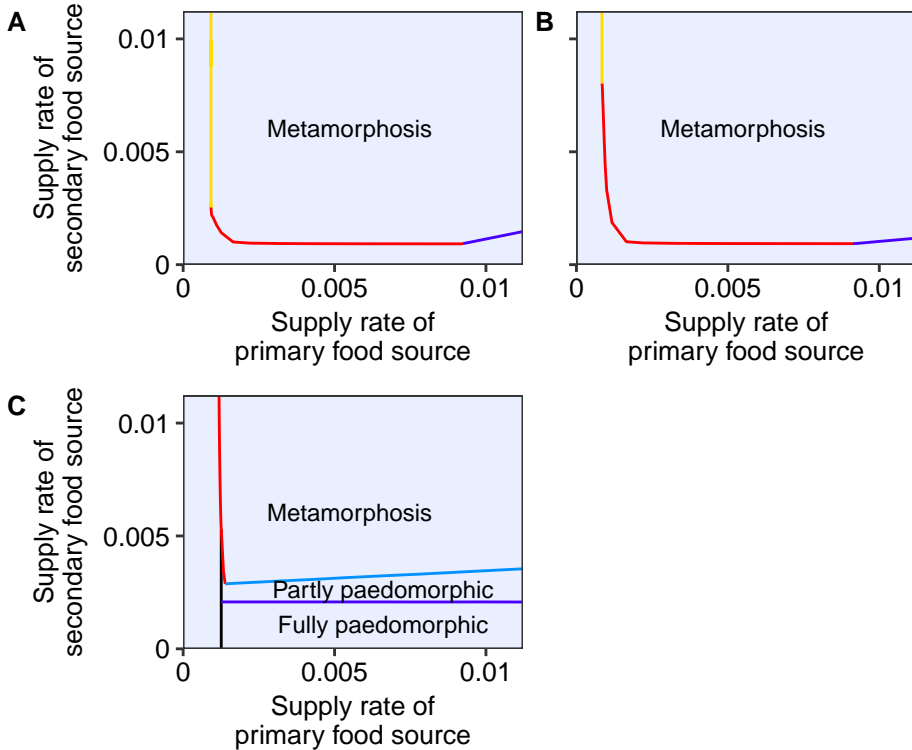
In case individuals have access to the secondary food source very early in life, direct development almost always evolves in case the supply rate of the primary food source diminishes (yellow line figure 5.5A). Because the secondary food source is already available for small individuals, direct development can evolve relatively easy because individuals can skip the primary food source even when they are born with a relatively small body mass. For very low supply rates of the secondary food source, however, adults do not have enough food available to produce offspring large enough to skip the primary food and the population goes extinct in case the supply rate of this food becomes too low (red line in figure 5.5A).

When the secondary food source is available somewhat later in life, direct development can only evolve when the supply rate of the primary food source is high (yellow line in figure 5.5B), otherwise the population goes extinct in case the supply rate of the primary food source becomes too low (red line 5.5B). Adults can only produce offspring large enough to skip the primary food source when there is a lot of the secondary food source available. For even higher values of  $w_{\min}$  direct development can not evolve at all (e.g. figure 5.5C), even not when the supply rate of the secondary food source is very high. In this case the population always goes extinct when the supply rate of the primary food source diminishes.

For most values of  $w_{\min}$  paedomorphosis only evolves in case the supply rate of the primary food source is very high (figure 5.5A and 5.5B). In this case postmetamorphs also feed on the primary food source, which leads to selection to reduce the extent of metamorphosis when the supply rate of the secondary food source decreases (figure 5.3B). However, for most supply rates of the primary food source, the population goes extinct in case the secondary food source deteriorates (red lines in figures 5.5A and 5.5B). Only when the secondary food source is available very late in life paedomorphosis evolves easily (blue lines in figure 5.5C).

To summarize, a metamorphosing population often goes extinct in case one of the two food sources diminishes. Direct development can evolve in case the secondary food source is available early in life and when the supply rate of this food source is high. The earlier the secondary food source is available, the lesser the supply rate of this food source that is necessary for the evolution of direct development. Paedomorphosis, on the other hand, evolves when the supply rate of the primary food source is

very high. When the secondary food source is only available for very large individuals paedomorphosis evolves relatively easily.



**Figure 5.5:** Two-parameter plots showing where an initially metamorphic population goes extinct (red lines), becomes (partly) paedomorphic (blue lines) or evolves direct development (yellow lines) as a consequence of decreasing supply rates of the primary and secondary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ) for different values of the body mass at which the secondary food source becomes available ( $w_{\min}$ ). A (partly) paedomorphic population goes extinct at the black line in C.  $w_{\min} = 0.01742$  (A),  $w_{\min} = 0.1742$  (B), or  $w_{\min} = 6.97$  (C). Other parameter values are as shown in tables 5.A3 and 5.A4.

### Direct development only evolves in amphibians after the evolution of large eggs

Our model results show that before direct development evolves, there is selection for increased offspring size (top panels in figure 5.1). While a correlation between developmental mode and offspring size has been observed before (e.g. Callery et al. 2001; Marshall et al. 2012; McEdward 2000), this correlation has not been tested in a phylogenetic framework.

We found very strong support for correlated evolution between direct development and large egg sizes within the amphibians, i.e. the average log Bayes Factor over all five parallel runs was 23.4 in favor of the dependent model (Table 5.C1 in appendix C). To test if the transition to direct development indeed depends on the presence of large eggs, we furthermore compared the Bayes Factor of the fully dependent model to a constrained model where we assumed that the transition rate to direct development does not depend on egg size. The dependent model performed significantly better than the model in which we constrained the transition to direct development to be independent of egg size (Bayes Factor of 11.6).

Table 5.1 shows the conditional transition rates of the two traits, estimated by the dependent model. The presence of direct development is indicated with  $D=1$ , the presence of metamorphosis with  $D=0$ . Large eggs are referred to as  $E=1$ , small eggs as  $E=0$ . The parameter  $P(E = 1 \rightarrow 0 \mid D = 1)$  for example, is the estimated transition probability per million years from large to small eggs in case individuals mature via direct development. These transition rates strongly support the prediction that direct development cannot evolve unless large egg size has evolved first, i.e. the transition from metamorphosis to direct development is zero if small eggs are present (table 5.1). The transition rates furthermore show that the loss of direct development is extremely rare when the lineage has large egg sizes (table 5.1). All other transition scenarios are equally likely (see Table 5.1). It is therefore for example possible that after direct development has evolved, small eggs evolve again.

**Table 5.1:** Transition probabilities per million years between developmental modes (trait D) and large egg size (trait E) for the correlated (dependent) model of evolution resulting from Bayesian Markov chain Monte Carlo analyses in BayesTraits. '0' refers to absence of the trait, '1' refers to presence.

Transition rate	Median estimate (Transitions/Million years)
$P(D = 0 \rightarrow 1 \mid E = 0)$	0
$P(D = 0 \rightarrow 1 \mid E = 1)$	0.004462
$P(D = 1 \rightarrow 0 \mid E = 0)$	0.004528
$P(D = 1 \rightarrow 0 \mid E = 1)$	0
$P(E = 0 \rightarrow 1 \mid D = 0)$	0.004783
$P(E = 0 \rightarrow 1 \mid D = 1)$	0.004646
$P(E = 1 \rightarrow 0 \mid D = 0)$	0.004785
$P(E = 1 \rightarrow 0 \mid D = 1)$	0.004485

## 5.4 Discussion

In this chapter we have shown that a metamorphosing population evolves in response to changing conditions in such a way that individuals reduce their dependence on the deteriorating food source. While this can lead to the evolution of either direct development or paedomorphosis, we also showed that metamorphosis tends to be an evolutionary dead end. Since metamorphosing species often crucially depend on two (or more) habitats for their growth, survival and reproduction, they are hypersensitive to habitat loss (Rudolf and Lafferty 2011) and a metamorphosing population often goes extinct when one of the two food sources becomes too scarce.

We have found that there is selection to produce larger offspring and to decrease the body mass at metamorphosis in case the food source that larvae crucially depend on deteriorates. Larger offspring require less food to reach the metamorphosis size threshold and have therefore an advantage when the larval food source is scarce. In case adults are able to produce large enough offspring to skip this primary food source, direct development can evolve in order to avoid the dependence on the declining food source. It has often been observed in marine invertebrates (e.g. Marshall et al. 2012) and amphibians (e.g. Callery et al. 2001) that direct developing species produce larger eggs compared to related indirect developing species. Our phylogenetic analysis indeed strongly supports our hypothesis that among amphibians the evolution of large eggs preceded the origin of direct development. Our finding that before direct development evolves metamorphosis occurs earlier in life remains to be tested.

Instead of producing larger offspring, individuals can also adapt to bad larval conditions by enhancing parental care, for example by nursing their offspring. Parental care can greatly increase survival and growth rates of offspring and is therefore a good strategy when the larval food source is of poor quality. However, taking care of your offspring is energetically costly (e.g. Smith and Wootton 1995) and will reduce the number of offspring an individual can produce. Individuals will therefore face a similar trade-off as is the case for producing larger offspring, they can either produce many offspring without taking care of them or produce a few and spend lots of energy in their upbringing. It is therefore likely that, as in the case for producing large offspring, the evolution of parental care depends on the conditions of the adult habitat. It has been shown in frogs that the evolution of large egg size typically precedes the evolution of parental care (Summers et al. 2006) and it would be interesting for further research to study how these two strategies interact with the evolution of direct development in case ecological conditions change.

We have shown that a deteriorating adult habitat is associated with a delayed metamorphosis, a high risk of extinction and, under some circumstances, the evolution of paedomorphosis. Our results show that a prerequisite for the evolution of paedo-



morphosis is that the ontogenetic niche shift at metamorphosis is incomplete, such that postmetamorphs keep utilizing the larval niche (the primary food source) even after metamorphosis. Part of these results are in line with empirical work that showed with a phylogenetic approach that the occurrence of paedomorphosis in plethodontid salamanders is correlated with inhospitable environments for terrestrial adults (Bonett et al. 2014a). Bonett et al. (2014a) furthermore showed that the rate of extinction in paedomorphic lineages is much higher than in metamorphic lineages. The authors suspect that the limited dispersal abilities of paedomorphs have caused these high extinction rates. However, our results indicate that these high extinction rates can also be explained by a different mechanism; populations that evolve in the direction of paedomorphosis are very vulnerable to extinction since they depend on the bad adult habitat for their reproduction. While we looked at changes in the supply rate of the postmetamorphic food source, the work of Bonett et al. (2014a) looked at the effect of climatic conditions such as temperature and precipitation. However, the effect of an inhospitable environment for postmetamorphs is comparable to low food conditions since both will reduce reproduction and survival. In another paper they furthermore showed, in line with our results, that a delay in the age at metamorphoses preceded the evolution of paedomorphosis (Bonett et al. 2014b). A similar phylogenetic approach as used by Bonett et al. 2014a,b could be used to test if metamorphosis indeed occurs at relatively larger body masses in case of unfavorable adult habitats, if the evolution of paedomorphosis is related to relative good larval conditions and whether or not paedomorphosis is associated with incomplete niche segregation between larvae and postmetamorphs.

While we found that it is difficult to evolve paedomorphosis, this life-history strategy has evolved several times in salamanders (Hanken 1999). One explanation for this contrasting result is that we only considered the evolution in body mass at metamorphosis. However, paedomorphosis can also evolve when individuals accelerate maturation (i.e. reduce the body mass at maturation), a process known as progenesis (Denöel et al. 2005; McMahan and Hayward 2016). It might be easier to evolve paedomorphosis in case individuals can also mature at a smaller body size. Interestingly, there are no known cases of paedomorphosis in anurans. A possible explanation for this is that it is physically not possible for the tadpole stage to possess characters needed for reproduction (Wassersug 1975). However, tadpoles of *Xenopus laevis* that fail to metamorphose are able to develop gonads. Furthermore, tadpoles of the paradoxical frog *Pseudis paradoxa* also have fully developed gonads (Downie et al. 2009). Metamorphosis takes place at very large body sizes in the paradoxical frog, indicating that this species is evolving in the direction of paedomorphosis (Downie et al. 2009).

Studies of facultative paedomorphosis in salamanders indicate that the onset of metamorphosis is probably not only dependent on body mass but also on age and

growth conditions (Denöel et al. 2005), leading to some plasticity in the timing of metamorphosis. Paedomorphic individuals do not only arise when the larval growth conditions are very favorable (e.g. Denöel and July 2001), but also when larvae do not grow fast enough to reach the critical size that is needed to undergo metamorphosis (Whiteman 1994; Whiteman et al. 2012, i.e. best of a bad lot hypothesis). To better understand the conditions under which paedomorphosis can evolve, it would be interesting to also take into account both age and body mass at metamorphosis and maturation.

We found that the body mass at which the secondary food source becomes available ( $w_{\min}$ ) largely influences if direct development and paedomorphosis can evolve or not. When the secondary food source is already available for small individuals, direct development evolves easily while paedomorphosis is often not possible. Vice versa, when the secondary food source is only available for large individuals, direct development can often not evolve but paedomorphosis evolves easily. These results indicate that there is strong selection to change the body mass at which individuals have access to the secondary food source in case one of the two food sources become too scarce. While including this trait in the evolutionary analysis will probably facilitate the evolution of direct development and paedomorphosis, there are certain size limits to what you can do with a certain morphology (Werner 1988) and therefore limits to which extent  $w_{\min}$  can evolve. Piscivorous fish are for example limited by their gape size and need to be of a certain size before they are large enough to consume other fish (e.g. Mittelbach and Persson 1998). Because of these constraints we have chosen to not let  $w_{\min}$  evolve and only study how changing this parameter changes the result.

In appendix 5.D we show that changing the ontogenetic scaling of the attack rates changes for which supply rates of the secondary food source direct development can evolve. In case small individuals are very efficient feeders on their food source, direct development can hardly evolve and the population will ultimately go extinct in case the primary food source becomes too scarce. However, because small individuals are very efficient in feeding on the primary food source, the population can deal with very low supply rates of the primary food source. These results show that the ability to evolve direct development do not only depend on the supply rates of the different food sources but are also influenced by the size-dependent ingestion capacity of individuals.

We have assumed a constant mortality rate for all individuals, independent of an individuals body mass. This is of course a very simplistic assumption since mortality is often size dependent, with high mortality rates among the smallest individuals (e.g. Sogard 1997). However, we expect that changing this assumption will not qualitatively change our results. When small individuals experience elevated mortality levels, there is probably a stronger selection to produce large offspring. However, adults will nonetheless need a substantial amount of food to produce those large offspring.

Therefore, the evolution of direct development, which is constraint by the food availability for adults, will probably not evolve more easily in case of size dependent mortality.

Together, our results demonstrate that metamorphosis is a very successful strategy that is not easily lost. However, metamorphosis comes with a risk since it also makes individuals dependent on multiple food sources. An evolutionary response to changing conditions can prevent extinction, but this is often not possible.

### Acknowledgments

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## Appendix 5.A Detailed model description

### Model description

We assume that there are two, unstructured, food sources present. Both the primary and secondary food source follow semi-chemostat dynamics with turnover rate  $\delta$ , and will reach, in the absence of consumers, a density of  $X_{1,\max}$  and  $X_{2,\max}$  respectively. The primary food source, with density  $X_1$ , is available for all individuals while the secondary food source, with density  $X_2$ , is only available for large individuals. The two food sources require two different morphologies to be efficiently utilized by the consumers.

We assume that a consumer consists of two different forms of mass, irreversible mass  $x$  such as bones and organs and reversible mass  $y$  such as fat. The reversible mass of an individual can be invested in metamorphosis or used to cover its basic metabolism under starvation conditions. For simplicity we assume equilibrium conditions and ignore starvation conditions; an individual's reversible mass is therefore fully available for covering the costs of metamorphosis. The body length, attack rate and handling time of an individual depend only on its standardized body mass  $w = x + y_{\max} = x(1 + q_j)$  (Persson et al. 1998), where  $y_{\max}$  is the maximum attainable amount of reversible body mass. Parameter  $q_j$  is a dimensionless scaling constant describing an individual's maximum ratio of reversible to irreversible mass.

**Table 5.A1:** Model variables

Variable	Description	Range	Unit
$X_1$	Density of primary food source	From 0 to $X_{1,\max}$	$\text{mg l}^{-1}$
$X_2$	Density of secondary food source	From 0 to $X_{2,\max}$	$\text{mg l}^{-1}$
$x$	Irreversible body mass	Larger than $x_b$	g
$y$	Reversible body mass	From $q_j x_b$ to $y_{\max}$	g

Newborn larvae (L) are born at an irreversible body mass  $x_b$  and the maximum attainable amount of reversible mass  $y = q_j x_b$ . The total body mass at birth equals  $w_b = (1 + q_j) x_b$ . The ratio between irreversible and reversible mass is constant until individuals reach standardized body mass  $w_j$  and metamorphose into juveniles. Individuals lose an amount  $\theta x_j (q_j - q_s)$  of their reversible body mass during metamorphosis. In this equation  $\theta$  is the extent of the metamorphosis and parameter  $q_s$  is the ratio of  $y$  over  $x$  of an individual immediately after full metamorphosis ( $\theta = 1$ ). After metamorphosis the reversible body mass  $y$  is over time restored to  $y_{\max} = q_j x$  (see below) such that the total body mass  $x + y$  again equals its standardized body mass. We therefore use the term body mass to refer to the standardized body mass  $w$ . Juveniles mature into adults (A) and start reproducing when reaching standardized body mass

$w_A$ . The secondary food source  $X_2$  becomes available after individuals have reached standardized body mass  $w_{\min}$ .

The size-dependent attack rate on the primary and secondary food source are described by two hump-shaped functions following

$$a_1(w) = A_{1i} \left[ \frac{w}{w_0} \exp\left(1 - \frac{w}{w_0}\right) \right]^\alpha \quad (5.A1a)$$

$$a_2(w) = \begin{cases} 0 & w \leq w_{\min} \\ A_{2i} \left[ \frac{w-w_{\min}}{w_0} \exp\left(1 - \frac{w-w_{\min}}{w_0}\right) \right]^\alpha & \text{otherwise.} \end{cases} \quad (5.A1b)$$

In these equations  $\alpha$  determines how strongly the attack rates on the primary and secondary food sources increase and decrease around the peaks at  $w_0$  and  $w_0 + w_{\min}$ , respectively. Parameters  $A_{1i}$  and  $A_{2i}$  are the maximum attack rates an individual can reach on the primary and secondary food source when its standardized body mass equals  $w_0$  and  $w_0 + w_{\min}$ , respectively. We assume that there is a linear trade-off between these two maximum attack-rate constants within a certain life stage ( $i = L, J$  or  $A$ ),

$$\begin{aligned} A_{1i} &= (1 - \psi_i)(A_{\max} - A_{\min}) + A_{\min}, \\ A_{2i} &= \psi_i(A_{\max} - A_{\min}) + A_{\min}. \end{aligned} \quad (5.A2)$$

In these equations,  $0 \leq \psi_i \leq 1$  is the relative degree of specialization on the secondary food source of a certain life stage. A value of  $\psi_i = 0$  means that individuals in life stage  $i$  are completely specialized in feeding on the primary food source and not very efficient in feeding on the secondary food source. Vice versa, a value of  $\psi_i = 1$  means that individuals are very efficient in feeding on the secondary food source while they are not very efficient in feeding on the primary food source.

Metamorphosis can decouple the different life stages such that individuals can be specialized on the primary food source as larvae and on the secondary food source as juveniles and adults. Metamorphosis decouples the different life stages as follows

$$\psi_A = \psi_J = \min(1, \psi_L + \theta), \quad (5.A3)$$

in this equation parameter  $\theta$  is the extent of the metamorphosis. Individuals that undergo metamorphosis lose part of their body mass as described above and furthermore have a probability of  $\rho\theta$  to die during metamorphosis.

The food intake of an individual with standardized body mass  $w$  can be written as

$$I(X_1, X_2, w) = \frac{\phi(w)a_1(w)X_1 + [1 - \phi(w)]a_2(w)X_2}{1 + h(w)\{\phi(w)a_1(w)X_1 + [1 - \phi(w)]a_2(w)X_2\}} \quad (5.A4a)$$

whereby the handling time  $h(w)$  equals (following Persson et al. 1998)

$$h(w) = \zeta_1 + \zeta_2 w^{-\zeta_3} e^{\zeta_4 w}. \quad (5.A4b)$$

We assume that individuals show optimal foraging behavior and allocate their time searching for each food source in such a way that food intake is maximized. This implies that  $\phi(w)$ , the fraction of time individuals spend searching for the primary food source equals

$$\phi(w) = \frac{1}{1 + e^{\sigma(a_2(w)X_2 - a_1(w)X_1)}}. \quad (5.A5)$$

In this equation parameter  $\sigma$  determines the steepness of the sigmoid, food-selection curve at equal food source profitabilities,  $a_1(w)X_1 = a_2(w)X_2$  (de Roos et al. 2002). The form of equation 5.A1 and 5.A5 imply that large individuals ( $w > w_{\min}$ ) always include both food sources in their diet. We will, however, for convenience state that individuals only feed upon the primary or secondary food source in case the fraction of the secondary food source in the diet of large individuals is graphically indistinguishable from 0 or 1, respectively.

The total energy-intake of an individual equals its food-intake rate multiplied by a conversion factor  $\kappa_e$ . Total net-energy intake is first used to cover maintenance costs. The metabolic demands per unit of time is a function of both irreversible and reversible mass of a consumer and can be described by a power function following

$$E_m(x, y) = p_1(x + y)^{p_2}. \quad (5.A6)$$

Larvae and juveniles allocate a fraction  $\kappa_j(x, y)$  of the net-biomass production (the difference between the food assimilation and maintenance cost of an individual)  $E_g(X_1, X_2, x, y) = k_e I(X_1, X_2, w) - E_m(x, y)$  to growth in irreversible mass, following

$$\kappa_j(x, y) = \frac{y}{(1 + q_j)q_j x}. \quad (5.A7a)$$

The remaining part is allocated to growth in reversible mass. Since adults also invest in reproduction they allocate a lower fraction  $\kappa_A(x, y)$  to growth in irreversible mass following

$$\kappa_A(x, y) = \frac{y}{(1 + q_A)q_A x}, \quad (5.A7b)$$

with  $q_A > q_j$ , the remainder is invested in reversible mass and reproduction. To ensure that individuals will always invest in reversible mass in such a way that the ratio of  $y$  to  $x$  either remains or is restored to  $q_j$  and that reproduction does not take place when  $y < q_j x$  (Persson et al. 1998) we assume that adults invest a fraction  $\kappa_R(x, y)$  of their net-energy production in reversible mass according to the function (see chapter 4 of this thesis):

$$\kappa_R(x, y) = \begin{cases} 1 - \kappa_A(x, y) & y < q_j x \\ (1 - \kappa_j(x, y)) \frac{\kappa_A(x, y)}{\kappa_j(x, y)} & \text{otherwise.} \end{cases} \quad (5.A8)$$

The remainder fraction of the adult net-biomass production  $(1 - \kappa_A(x, y) - \kappa_R(x, y))$  is invested in reproduction. The number of eggs an individual adult produces per unit of time then equals

$$b(x, y, X_1, X_2) \begin{cases} 0 & y < q_J x \\ (1 - \frac{\kappa_A(x, y)}{\kappa_J(x, y)}) E_g(x, y, X_1, X_2) \eta / w_b & \text{otherwise.} \end{cases} \quad (5.A9)$$

where  $\eta$  is a conversion factor.

### Direct development

We assume that in case metamorphosis takes place before individuals are born ( $w_J < w_b$ ), the costs of metamorphosis are paid by the mother. This means that a fraction of the eggs ( $\rho\theta$ ) does not survive. It is furthermore more costly to produce an egg because the energetic costs of metamorphosis have to be paid as well. The number of eggs an individual adults produces per unit of time therefore equals

$$b(x, y, X_1, X_2) \begin{cases} 0 & y < q_J x \\ (1 - \rho\theta)(1 - \frac{\kappa_A(x, y)}{\kappa_J(x, y)}) E_g(x, y, X_1, X_2) \eta / (w_b + \theta x_J (q_J - q_s)) & \text{otherwise.} \end{cases} \quad (5.A10)$$

in case metamorphosis takes place before individuals are born. It is likely that metamorphosis is less costly in case the mothers pay for it. However, changing the costs of metamorphosis after birth does not change the results (unpublished results).

Metabolic demands and handling time are parameterized for the interaction between a planktivorous fish population of roach *Rutilus rutilus* and two zooplankton populations as food sources following Persson et al. (1998). The model should, however, be interpreted as a more general consumer-resource model describing the interaction between two food sources and a size-structured consumer. All rates were scaled to a daily basis, all parameter values related to energetics are based on a reference temperature of 19°C. Processes taking place during the winter season are ignored. We assume that eggs have a minimal mass of  $1 \cdot 10^{-4}$  gram, which is the smallest egg size observed for cold-blooded aquatic invertebrates (Hendriks and Mulder 2008). Model variables are listed in table 5.A1, the evolving parameters in table 5.A2 and standard parameter values in tables 5.A3 and 5.A4.

### Evolutionary dynamics

To study under which conditions metamorphosis disappears we use the framework of adaptive dynamics (Dieckmann and Law 1996; Geritz et al. 1998). Adaptive dynamics assumes that a population is monomorphic and that evolution in this population occurs because of the fixation of very small and rare mutations. The extent of metamorphosis  $\theta$ , specialization parameter  $\psi_L$ , the the body mass at birth  $w_b$  and

the body mass at which metamorphosis takes place  $w_J$  can all evolve. For the latter two we assume that the amount of irreversible mass at metamorphosis ( $x_J$ ) and birth ( $x_b$ ) evolve while parameter  $q_J$ , that determines together with the irreversible mass  $x$  the total body mass, does not evolve. We assume that initially both supply rates are high ( $\delta X_{1,\max} = \delta X_{2,\max} = 0.011 \text{mg l}^{-1} \text{day}^{-1}$ ) and individuals undergo metamorphosis ( $\theta > 0$ ). In this case there is only a single evolutionary singular strategy (ESS), which is defined by the vanishing of the selection gradient of all considered traits. We track this ESS for different values of  $w_{\min}$  as a function of the supply rate of either the primary or secondary food source and determine whether these strategies are convergence stable and/or evolutionary stable following Geritz et al. (1998) and Leimar (2009).

**Table 5.A2:** Evolving traits

Variable	Description	Range	Unit
$\psi_L$	Degree of specialization of larvae on the secondary food source	From 0 to 1	-
$\theta$	Extent of metamorphosis	From 0 to 1	-
$w_J$	Body mass at which individuals undergo metamorphosis	Larger than $w_b$	g
$w_b$	Body mass of newborns	Larger than 0.0001	g



**Table 5.A3:** Standard parameters of the model from Persson et al. (1998)

Parameter	Description	Default Value	Unit
$\delta$	Food source turnover rate	0.1	day <sup>-1</sup>
$X_{1,\max}$	Maximum biomass density of primary food source	variable	mg l <sup>-1</sup>
$X_{2,\max}$	Maximum biomass density of secondary food source	variable	mg l <sup>-1</sup>
$w_A$	Standardized body mass at maturation	8.71	g
$w_0$	Standardized body mass at which maximum attack rate is attained on primary food source	17.42	g
$\alpha$	Exponent in attack-rate functions	0.93	-
$\zeta_1$	Constant in handling-time function	0.00036*	day mg <sup>-1</sup>
$\zeta_2$	Constant in handling-time function	0.00745*	day mg <sup>-1</sup> g <sup><math>\zeta_3</math></sup>
$\zeta_3$	Slope of decrease in handling time at small consumer sizes	0.68	-
$\zeta_4$	Slope of increase in handling time at large consumer sizes	$1.15 \cdot 10^{-3}$	g <sup>-1</sup>
$p_1$	Metabolic constant	0.033	g <sup>1-<math>p_2</math></sup> day <sup>-1</sup>
$p_2$	Metabolic exponent	0.77	-
$k_e$	Metabolic conversion factor	0.00061*	-
$q_j$	Constant determining maximum reversible body mass	0.742	-
$q_A$	Constant in adult allocation function	1	-
$\eta$	Gonad-offspring conversion factor	0.5	-
$\mu$	Background mortality rate	0.01	day <sup>-1</sup>

Note: \*These values are the original values from Persson et al. (1998) divided by  $1.1 \cdot 10^{-2}$  (the weight of a prey individual) to express prey densities in milligram l<sup>-1</sup> instead of individuals l<sup>-1</sup>.

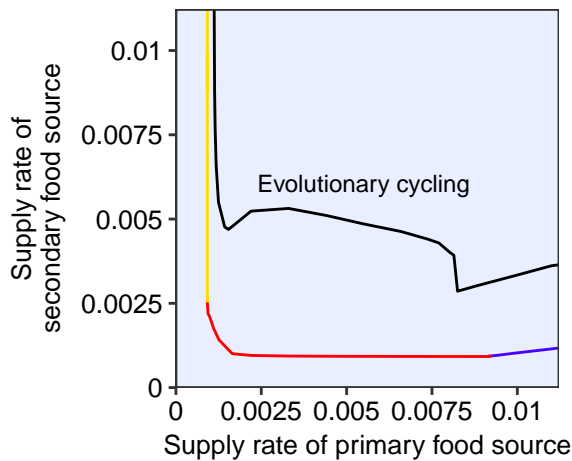
**Table 5.A4:** Parameters related to specialization and metamorphosis

Parameter	Description	Default Value	Unit
$A_{\max}$	Maximum value of the attack rate constants $A_1$ and $A_2$	$1 \cdot 10^5$	$\text{l day}^{-1}$
$A_{\min}$	Minimum value of the attack rate constants $A_1$ and $A_2$	$1 \cdot 10^4$	$\text{l day}^{-1}$
$w_{\min}$	Standardized body mass at which the secondary food source becomes available	0.01742, 0.1742 or 6.97	g
$\sigma$	Constant in habitat-switching rate	10	$\text{day mg}^{-1}$
$q_s$	Ratio of reversible to irreversible body mass immediately after full metamorphosis	0.2	-
$\rho$	Probability to die during full metamorphosis	0.5	-

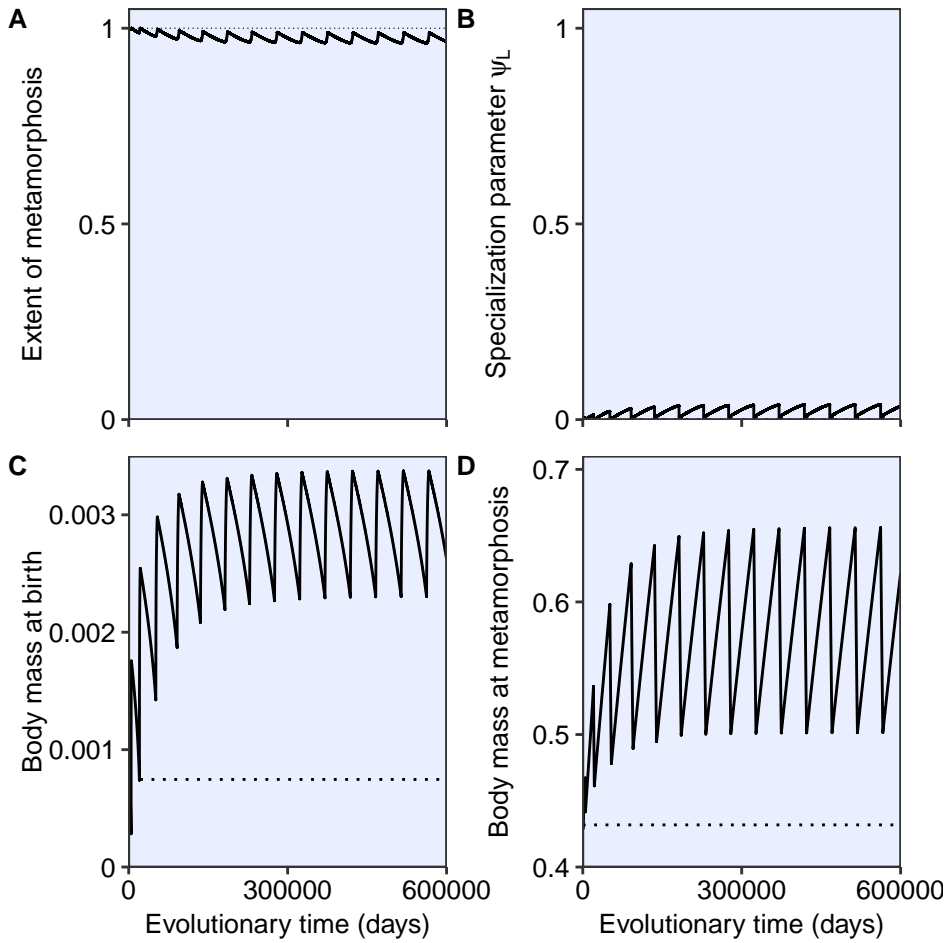
## Appendix 5.B Evolutionary cycling

In this appendix we show how the four traits evolve in case there is no stable evolutionary endpoint.

In case the secondary food source is already available for very small individuals ( $w_{\min} = 0.01742$ ), the evolutionary singular strategy is for many combinations of the two food supply rates absent. The black line in figure B1 indicates the parameter area where this is the case. The reason for this is that there are two stable ecological equilibria, separated by an unstable equilibrium. The life history strategy for which the selection gradient equals 0 is in this case located on the ecologically unstable equilibrium branch and can therefore never be reached (we will refer to this particular life history strategy as an unstable ESS, even though this is in the context of adaptive dynamics somewhat of a misnomer). In each of the two stable equilibrium states evolution takes the evolving strategies to the boundary of the existence of this equilibrium, at which point the system switches to the other ecological stable equilibrium. As a consequence, the four traits keep on changing over evolutionary time. Since there is no stable ESS occurring for these parameter values, the traits stay relatively close to the trait values that characterize the unstable ESS (figure B2). For low supply rates of the secondary food source, the ESS is located on a stable ecological attractor (figure B1).



**Figure B1:** Two-parameter plot showing where the population goes extinct (red lines), becomes pedomorphic (blue lines), evolves direct development (yellow lines) and where the evolutionary singular strategy is absent (above the black line) as a function of the supply rates of the primary and secondary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ).  $w_{\min} = 0.01742$ , other parameter values are as shown in tables 5.A3 and 5.A4.



**Figure B2:** Evolutionary dynamics of the extent of metamorphosis (A), both in gram, the specialization parameter  $\psi_L$  (B), the body mass at birth (C) and metamorphosis (D) in case life history strategy for which the selection gradient vanishes corresponds to an unstable ecological equilibrium. The dotted lines indicate the value of the trait in the ESS in the ecologically (and hence evolutionary) unstable equilibrium.  $\delta X_{1,\max} = 0.0055$ ,  $\delta X_{2,\max} = 0.0088 \text{ mg l}^{-1} \text{ day}^{-1}$ , and  $w_{\min} = 0.01742 \text{ gram}$ . Other parameters are as shown in tables 5.A3 and 5.A4.

## Appendix 5.C Log marginal likelihoods

In this appendix we show the log marginal likelihoods for the three different models. These indicate strong support for the dependent model over the independent model, as well as strong support for the dependent model over the dependent constrained model.

**Table 5.C1:** Log marginal likelihood for the dependent, independent, and constrained dependent models obtained from Markov chain Monte Carlo (MCMC) in BayesTraits, for the evolution of direct development and large egg size on the amphibian phylogeny. For each of the models, five independent MCMC chains were run for 5000000 generations, discarding 10% as burnin. The average log marginal likelihoods for the dependent, independent and constrained dependent models were used to calculate a log Bayes Factor.

	Dependent model	Independent model	Constrained dependent model
MCMC 1	-597.05	-610.12	-602.74
MCMC 2	-598.05	-608.1	-603.72
MCMC 3	-599.87	-610.31	-603.24
MCMC 4	-596.35	-608.8	-606.66
MCMC 5	-598.65	-611.24	-603.17
Average log marginal likelihood	-597.99	-609.71	-603.91
Log Bayes Factor (dependent vs independent)	23.44		
Log Bayes Factor (dependent vs constrained dependent)	11.6		
$P(D = 0 \rightarrow 1 \mid E = 0) =$			
$P(D = 0 \rightarrow 1 \mid E = 1)$			

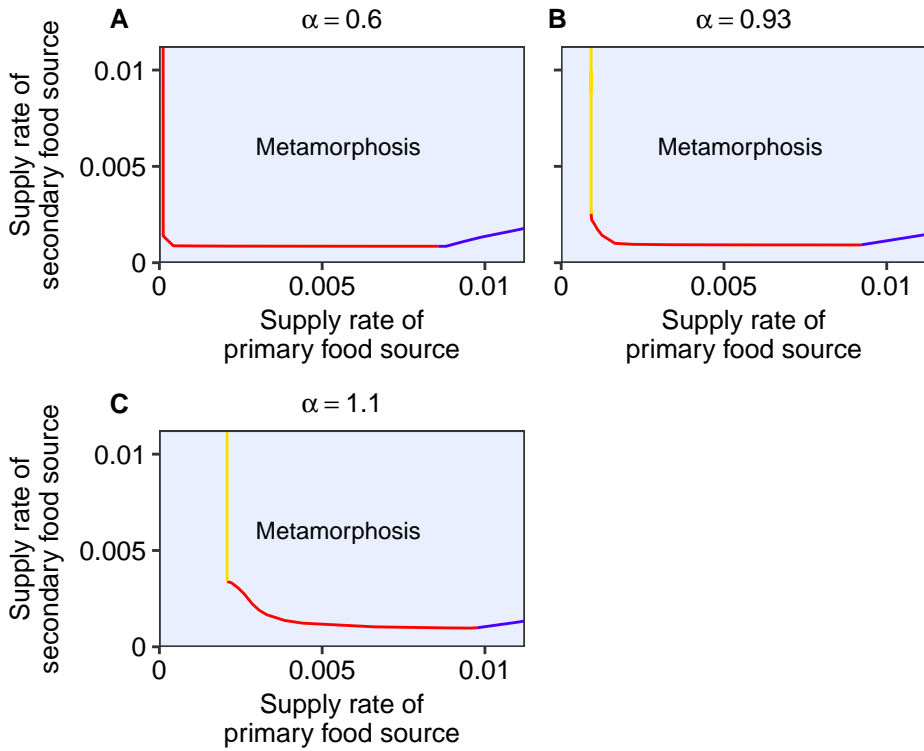
## Appendix 5.D The effect of $\alpha$

In this appendix, we study how changing parameter  $\alpha$  affects our result. Parameter  $\alpha$  determines how fast the attack rates on the primary and secondary food source increase and decrease around the peaks at  $w_0$  and  $w_0 + w_{\min}$ , respectively. This parameter affects, among other things, how effectively the smallest individuals can forage on the primary food source. The lower  $\alpha$ , the higher the attack rates of the smallest individuals. When  $\alpha = 0.6$ , small individuals need less food to survive compared to larger individuals. In case  $\alpha = 1.1$ , it is the other way around and small individuals need more food in order to survive compared to large individuals. When  $\alpha = 0.93$  individuals require more or less the same amount of food for their survival (Persson et al. 1998).

Figure 5.D1 shows that changing parameter  $\alpha$  does affect the evolutionary response to decreasing supply rates of the primary food source but hardly affects how the population responds to decreases in the supply rate of the secondary food source. Changing  $\alpha$  affects the attack rate of small individuals more strongly than that of large individuals (equation 5.A1), which explains why  $\alpha$  hardly influences how the population responds to changes in the supply rate of the secondary food source, since this food source is only eaten by larger individuals.

For low values of  $\alpha$ , the population will ultimately go extinct in case the primary food source becomes too scarce. Direct development does not evolve. When the primary food source is very low there is hardly an evolutionary response to produce larger offspring. Because small offspring are very efficient on the primary food source, they can grow even when this food source is scarce. Producing larger offspring is therefore not profitable because it will decrease the number of offspring an individual produces while it hardly decreases the time until metamorphosis. Only when the supply rate of the secondary food source is very high (e.g.  $0.02 \text{ mg l}^{-1} \text{ day}^{-1}$ ) direct development will evolve (not shown in the figure). Note that because small individuals are very efficient in feeding, the population can survive for much lower supply rates of the primary food source compared to higher  $\alpha$  values.

In case  $\alpha = 1.1$  direct development evolves for lower supply rates of the primary food source compared to the situation where  $\alpha = 0.93$ . Because for high values of  $\alpha$  small individuals are much less efficient on the primary food source, the selection pressure to produce large individuals is higher.



**Figure 5.D1:** Two-parameter plots showing where the population goes extinct (red lines), becomes paedomorphic (blue lines) and evolves direct development (yellow lines) as a consequence of decreasing the supply rates of the primary and secondary food source ( $\text{mg l}^{-1} \text{day}^{-1}$ ) for different values of  $\alpha$ , which determines the competitive ability of an individual of a given size.  $\alpha = 0.6$  (A),  $\alpha = 0.93$  (B), or  $\alpha = 1.1$  (C);  $w_{\min} = 0.01742$ , other parameter values are as shown in tables 5.A3 and 5.A4.





CHAPTER

6

## GENERAL DISCUSSION

Hanna ten Brink

## 6.1 Introduction

*"...She raised her hands to Heaven, and exclaimed, 'Forever may you live in that mud-pool!' The curse as soon as uttered took effect, and every one of them began to swim beneath the water, and to leap and plunge deep in the pool. [...] Their ugly voices cause their bloated necks to puff out; and their widened jaws are made still wider in the venting of their spleen. Their backs, so closely fastened to their heads, make them appear as if their shrunken necks have been cut off. Their backbones are dark green; white are their bellies, now their largest part. Forever since that time, the foolish frogs muddy their own pools, where they leap and dive." - Ovid, The metamorphoses, book IV, translated by Brookes More.*

The Roman poet Ovid described in his poem "The metamorphoses" how the goddess Latona transformed barbarian peasants into croaking frogs. Although Ovid perceived metamorphosis as so miraculous that it must be evidence of divine intervention, scientific inquiry has emphasized that complex life cycles, where individuals undergo metamorphosis to drastically change their morphology at a certain point in their life, have originated through natural selection. Even though complex life cycles are ubiquitous in the animal kingdom, it is still not well understood which ecological conditions favored the evolution of this life-history strategy.

It has been hypothesized that metamorphosis evolved as an adaptation to allow individuals to occupy different niches during their life (the adaptive decoupling hypothesis, Moran 1994). In this thesis I first explore under which ecological conditions an ontogenetic niche shift can evolve when there is a trade-off between performance early and late in life (chapter 2 and 3). Second, I studied if metamorphosis evolves as a mechanism to relax this trade-off (chapter 4). Even though metamorphosis is a common life-history strategy, some species lost their ability to metamorphose over evolutionary time. In chapter 5 I studied under which conditions metamorphosis will disappear. In this chapter, I summarize and discuss the results and implications of the preceding chapters.

## 6.2 Evolution of ontogenetic niche shifts

Species that have an abrupt and extreme metamorphosis, such as frogs and insects, appeal to the imagination. In contrast to metamorphosis, ontogenetic niche shifts can occur much more subtly. Many species change their diet or habitat during their life without undergoing large morphological changes in body form (Werner and Gilliam 1984). Some lizard species, for example, often switch from a carnivorous diet to a herbivorous diet during ontogeny (Durtsche 2004). A specialized feeding morphology that

allows individuals to feed on a certain food type is not necessarily efficient when feeding on a different food type. Individuals might not simultaneously be specialized in consuming the food they eat early on in life as well as the food they eat later on in life. Without metamorphosis, species that feed on different food types over the course of their lives would face a trade-off.

The results in chapter 2 show that this trade-off between early and late foraging efficiency limits the evolution of ontogenetic niche shifts. Large individuals do broaden or even completely shift their diet if this increases their food intake. However, they can not evolve a morphology specialized in feeding on this new food source when this negatively affects their offspring's feeding performance on the original food source. While this result is robust against changes in parameter values and specific model assumptions (chapter 4 and appendix 2.B of chapter 2), this result does not always hold under non-equilibrium conditions (chapter 3). The results in chapter 3 show that competition among the smallest individuals is the mechanism that prevents specialization on the food source used later in life in case of equilibrium conditions and small amplitude cycles. Surprisingly, specialization is possible in case of large amplitude cycles, which cause the food sources to fluctuate as well. Therefore, there are periods with not enough food available for large individuals to balance their energy requirements. This leads to starvation among the largest individuals. Specialization on a secondary food source prevents this starvation and is therefore selected for. While there is still strong competition among the smallest individuals, this competition is released for a short period when individuals mature to the next size class. This allows less efficient larvae to grow and ultimately reproduce. A crucial feature allowing for the evolution of specialization on the secondary food source in this case, is therefore that only a single cohort of individuals, born within a narrow time window, dominates the population during its juvenile phase.

A critical model assumption in these chapters is that specialization on one food source comes at a cost of specialization on the other food source. While there is ample empirical evidence that some body morphologies are better adapted in feeding on a certain food type than others (e.g., Jones et al. 2013; Werner 1977), there is not much work that shows a trade-off between early and late foraging success. It is rather difficult to empirically show the existence of such a trade-off, since it would require the comparison of feeding efficiencies and morphologies of closely related species with and without an ontogenetic niche shift. The recently isolated kokanee salmon (*Oncorhynchus nerka*) from Jo-Jo Lake, Alaska, is such an example. This population was allopatrically isolated from other lakes 200 to 1600 years ago (Shedd et al. 2015). While kokanee are typically planktivorous throughout their lives, individuals in Jo-Jo lake switch to a piscivorous diet during their ontogeny (Shedd et al. 2015). Piscivorous individuals, however, do not have many of the morphological adaptations needed in order

to be efficient piscivores (Shedd et al. 2015). While the authors suggest that the limited genetic variation has inhibited specialization to a more piscivorous diet, the results in chapter 2 suggest an alternative hypothesis; adaptation to the food source used later in life could be prevented by a trade-off between early and late foraging success.

The results of chapter 2 and 3 suggest that specialization on a food source used later in life is often not possible in species without a metamorphosis. However, some species that shift niches during ontogeny have high feeding performance as adults. For example, some piscivorous fish such as pikeperch have a morphology specialized in feeding on fish while their young need to feed upon zooplankton in order to grow large enough to make the switch to piscivory (Mittelbach and Persson 1998). How did these life-history strategies evolve? Below I will discuss several explanations for the discrepancy between such observations from natural systems and the model results.

Changes in feeding morphology do not always lead to a reduced foraging efficiency. Several studies have indicated that as a result of morphological differences only the foraging success on one of the resources changes (Andersson 2003 (Arctic charr); Osenberg et al. 1992 (sunfish); Thompson 1992 (grasshoppers)). For example, young-of-the-year Arctic charr individuals (*Salvelinus alpinus*) that were reared on two different diets developed different morphologies (Andersson 2003). Individuals that were raised on zooplankton had a higher attack rate on zooplankton than individuals raised on benthic macroinvertebrates. In contrast, there was no difference between the two types in performance on the benthic diet. This study shows that there is not always a trade-off in foraging efficiencies for one type of morphology.

Not all ontogenetic changes in diet lead to a trade-off between foraging success early and late in life. Young lizards, for example, lack the gut bacteria needed to efficiently digest plant material (Cooper and Vitt 2002). They obtain the necessary intestinal flora by eating faeces of older individuals. In the meantime they feed upon insects. The adaptations for these lizards to switch to a plant-based diet accumulate over time and do probably not require an actual morphological change in body form.

It might be possible that specialization on a secondary food source evolves in case this food source is available very early in life. The model in chapter 2, for example, assumes that small individuals need a tenfold increase in body mass before they can switch to the secondary food source. The earlier the secondary food source is available, the shorter the period where individuals crucially depend on the primary food source for their growth. This might relax the selection to have very efficient offspring and therefore allow specialization on the food source used later in life. Piscivorous fish whose diet almost completely consists of fish seem to switch much earlier from planktivory to piscivory compared to species whose diet does only partly consists of fish (Mittelbach and Persson 1998). It would be useful to study if the latter have a less specialized feeding morphology for piscivory compared to the first.

Competition among the smallest individuals, which prevents specialization on a secondary food source, might be released by several ecological or environmental factors. The results of chapter 3 show, for example, that large cohort cycles allow for the specialization on the secondary food source. While competition among larvae is still severe, the maturation of the dominant cohort to the next size class releases this competition for a short time-interval such that less efficient individuals can mature. Predation might be argued to also reduce the competition among the smallest individuals and thereby allow for specialization on the secondary food source. This is, however, not very likely since higher mortality rates among the smallest individuals will probably first select for fast maturation to avoid predation risk. It was, for example, shown in chapter 2 that increased mortality rates among the smallest individuals make specialization on a secondary food source less likely.

Fluctuations in the productivities of the food sources might also allow for specialization on a secondary food source. The productivities of many primary producers fluctuate over time, e.g., because of seasonality. It has been shown that large fluctuations in resource productivity can lead to periods of starvation among consumers (Soudijn and de Roos 2017). The results of chapter 3 indicate that such periods of starvation may allow for the evolution of specialized adults. The population cycles observed in chapter 3 are all internally driven and result from size-dependent interactions. It remains to be tested if and when externally driven fluctuations lead in an analogous fashion to the evolution of individuals with a feeding morphology specialized in feeding on the secondary food source.

A last explanation for the absence of a trade-off between early and late foraging efficiency, is that some species with an ontogenetic niche shift do have a (cryptic) metamorphosis. Metamorphosis allows for the restructuring of an individual's body plan and can therefore promote an ontogenetic niche shift (Moran 1994 and chapter 4 of this thesis). While metamorphosis is commonly defined as a drastic change in morphology in a short amount of time (e.g. Schoch 2009), morphological changes can also occur much more subtly and gradually (e.g., Rötzer and Haug 2015). Such morphological adaptations can help individuals to specialize on a different food source later in life. Mice, and maybe other mammals as well, are an example of species with a cryptic metamorphosis. While mammals are commonly regarded as direct developers, it has been shown that mice undergo some restructuring of their intestines during weaning. This restructuring is under influence of thyroid hormones, which is an ancestral feature of metamorphosis in chordates (Laudet 2011).

### 6.3 The evolutionary gain and loss of metamorphosis

The results of chapter 2 and 3 show that it can be advantageous to switch diet during ontogeny. However, in the presence of a trade-off between foraging efficiencies on different food sources, specialization on the food source used later in life can only evolve under limited conditions. Species that face the opportunity to specialize on such a food source therefore experience selection pressures to relax this trade-off. One possible way to do so is through a metamorphosis.

The results in chapter 4 show that metamorphosis can indeed evolve to allow individuals to specialize on different food sources during their life. Even though metamorphosis is costly, it will evolve when the food source used later in life is very abundant. Interestingly, as soon as life stages are slightly decoupled due to a metamorphosis, there is selection for a more pronounced metamorphosis such that pre- and post-metamorphs become morphologically more distinct from each other. Once evolved, metamorphosis is a very robust strategy that is not easily lost (chapter 4 and 5). Metamorphosing populations respond to changing food conditions by either increasing or decreasing the length of the pre-metamorphic period. This change in the timing of metamorphosis can under some conditions lead to the evolution of paedomorphosis or direct development (chapter 5).

The evolution of metamorphosis has only been studied under equilibrium conditions and it is still unknown if there is also selection for metamorphosis in case of non-equilibrium dynamics. Under non-equilibrium conditions, species can evolve a specialized adult stage in the absence of a metamorphosis (chapter 3). The results of chapter 4 show, however, that metamorphosis can evolve even if individuals have a morphology specialized in feeding on the food source used later in life. Metamorphosis will now evolve as a way to improve larval performance. This result suggests that a metamorphosis is always beneficial in case of a conflict between different life stages. The ecological conditions under which metamorphosis can evolve, however, might be different in the case of non-equilibrium conditions.

The chapters of this thesis describe the evolution of ontogenetic niche shifts and metamorphosis as a way to more effectively acquire food sources, which in turn leads to faster growth and increased reproduction. However, there might be other factors than food driving the evolution of complex life cycles, such as predation, interspecific competition or hostile environments. Predation is for example the main reason for blenny fish to move ashore for short periods of time (Ord et al. 2017). Further research could provide answers about the conditions of evolving a complex life cycle as a way to escape predation or competition.

The results of this thesis do shed some light on how factors other than diet can promote the evolution of complex life cycles. If changing niches increases the survival,

growth or reproduction of an individual, it can evolve since this will ultimately increase  $R_0$ , the lifetime reproductive output. It is therefore possible that factors other than food acquisition can select for an ontogenetic niche shift. However, when the transition to this new niche requires specific morphological and/or physiological adaptations, these can probably only evolve when it does not negatively affect the competitive ability of small individuals that have not yet shifted (chapter 2). There will probably be selection to relax this trade-off, but how likely is it that such a trade-off between early and late success selects for the ability to metamorphose? The results in chapter 4 show that metamorphosis, which is inherently costly, can only evolve if the secondary niche is very profitable. This would mean that in case of predation or a hostile environment as the driving factor of the niche shift, the mortality risk in the secondary niche has to be much lower compared to the primary niche in order for metamorphosis to evolve. However, individuals need food in order to survive, grow, and reproduce and because of the niche shift it is expected that post-metamorphs become dependent on a new food source. The availability of this new food source is an important factor in determining if metamorphosis can evolve or not, even if the niche shift was initially driven by factors other than diet. An alternative would be to evolve to a life-history strategy where individuals do not feed after shifting niches, which is for example the case in some insects species (e.g., some mayflies). It is for such species necessary to build up enough reserves during the larval period in order to reproduce as adults. Therefore, the availability of food in the larval habitat will play a crucial role in the evolution of such life-history strategies. To conclude, mortality risks may facilitate the evolution of metamorphosis but it is likely that, ultimately, food availability is the main driver that determines if metamorphosis evolves or not.

## 6.4 Some speculations on the role of metamorphosis for the vertebrate transition to land

About 375 millions of years ago, during the Devonian period, the first vertebrates, the tetrapods, moved out of the water onto land. This transition was preceded by the colonization of land by plants and invertebrates (Clack 2012). The fish-tetrapod transition has been one of the greatest evolutionary events in the history of vertebrates, leading to a sudden radiation of many new species including the origin of mammals. The transition to a terrestrial habitat requires fundamental changes of an animals morphology and physiology (Ashley-Ross et al. 2013). How and why this transition evolved is of great interest and still heavily debated (Long and Gordon 2004). The tetrapod transition to land is very hard to study since there is very little fossil data available, let alone ontogenetic data. Consequently, there is not much known about the life history of the earliest tetrapods (Olori 2015). Furthermore, there is still much debate going on

about the exact phylogeny of the tetrapods (e.g., Clack 2012; Olori 2015). The evolution of a metamorphosis might have played an important role in the vertebrate transition to land and the results of this thesis allow to speculate about the factors that drove tetrapods to leave the water.

Fossil data show that there was a spectrum of developmental modes in the early amphibians (Schoch 2001, 2009), one of the two extant tetrapod groups. The vast majority of early amphibians underwent some gradual morphological change during ontogeny that allowed adults to make short trips ashore. Even though individuals could move to the land, they were not very good in doing so (Schoch 2009). A rapid transformation from the larval to juvenile stage, as is observed in modern amphibians, only evolved tens of millions years after the first tetrapod had gained ground (Schoch 2001, 2009). It has been shown that not the transition to land, but a change in feeding mode, selected for life histories with a rapid, condensed, metamorphosis (Schoch 2009). Feeding on land requires a very different morphology than feeding in the water (e.g., Ashley-Ross et al. 2013). The results of this thesis show that the ability to metamorphose can indeed evolve to allow individuals to gain a different feeding mode later in life (chapter 4). The establishment of metamorphosis in the early amphibians subsequently allowed for selection to act in different ways on the different life stages, resulting in more specialized larvae and adults (Schoch 2010).

Much less is known about the transition to land in the ancestor of amniotes, the second group of modern tetrapods comprising birds, reptiles and mammals. Amniotes are regarded as the first truly terrestrial vertebrates. Amniotes possess direct development and either lay their eggs on land or fully develop within their mother. But how did the mainly aquatic ancestor of the amniotes evolve to a fully terrestrial direct developing species?

The results of this thesis suggest that metamorphosis might have played a crucial role in the transition to land in the ancestors of the amniotes. While the earliest tetrapods already made some excursions on land as adults, the results of chapter 2 and 3 show that adaptation to such a new habitat is unlikely to evolve when this negatively affects the aquatic larvae. There is growing evidence that most adaptations seen in early tetrapods already had a function in the aquatic environment (Clack 2012; Schoch 2001) and therefore were beneficial for all life stages. However, in order to feed on land, a different morphology is needed that conflicts with feeding in water (Ashley-Ross et al. 2013). One scenario is that the largely unexploited terrestrial food sources during the late Devonian selected for large individuals specialized in feeding on this. The results in chapter 4 show that this will subsequently select for metamorphosis. After the establishment of metamorphosis there might have been selection to reduce the time in the less favorable aquatic habitat and therefore to evolve direct development (chap-



ter 5). The evolution of the amniote egg subsequently allowed individuals to become completely independent from the aquatic environment.

An alternative scenario is that metamorphosis was not involved in the transition to land. Selection may have acted on all life stages equally to move to a terrestrial habitat. This terrestrial lifestyle subsequently selected for the amniote egg in order to improve hatching success. In this thesis it was assumed that the larval stages always crucially depended on the primary food source and that only after the establishment of metamorphosis individuals could skip this larval niche by producing large eggs (chapter 5). Further research is needed to find out the likelihood of evolving from an aquatic to a terrestrial life style without a metamorphosis.

Fossil information suggests that in lineages related to or even leading to the amniotes different developmental modes existed, including life histories with metamorphosis. The seymouriamorph *Discosauriscus* had a very long aquatic larval period and gradually changed into an adult form that was likely terrestrial (Sanchez et al. 2008). On the other hand, Klembara (2007) showed that *Seymouria sanjuanensis*, a tetrapod from the Lower Permian, had a very early metamorphosis. This may indicate that this species was evolving towards direct development in order to skip the larval habitat (as shown in chapter 5). Unfortunately there is very little fossil information available for the period where full terrestriality in the amniotes evolved (Carroll 2001). Furthermore, eggs are in general not very well fossilized (Clack 2012), which makes it hard to infer how terrestriality evolved in the amniotes and if metamorphosis indeed played a role. The question how amniotes became fully terrestrial will probably only be resolved when there is a more complete knowledge of fossils of stem-taxa leading to the amniotes.

## 6.5 Conclusions

To conclude, the results presented in this thesis help to better understand how complex life cycles evolved and, especially, why metamorphosis is so ubiquitous in nature. While incorporating the feedback loop between individuals and their environment lead to some fundamental new insights regarding the evolution of ontogenetic niche shifts and metamorphosis, the models analyzed in this thesis are still very simple and raise many more new questions. For example, the evolution of complex life cycles has, in this thesis, only been studied in a basic ecological setting, with one species consuming two food sources. How can complex life cycles evolve in a more complex ecological scenario, e.g., in the presence of a competitor? The success of a mutant does in that case not only depend on the strategy of the resident population but also on the strategy of the competitor. It remains to be tested how more complex community structures affect the evolution of complex life cycles.

An important insight of this thesis is that the life-history strategy of a species depends a lot on its evolutionary history and not only on the current ecological conditions. The results of chapter 4 and 5 show that metamorphosis does not originate easily, but once evolved it does not often disappear when conditions change. This implies that a species with a metamorphosis can be very successful in a similar environment as where another, non-metamorphic, species can thrive as well. This result is fundamentally different from previous work on the evolution of complex life cycles where there is only a single successful strategy possible for a certain set of ecological conditions. This difference results from the inclusion of the feedback loop between the environment and the strategy of the individuals. A metamorphic species has a different effect on the environment than a non-metamorphic species and will therefore experience different selection pressures. The results in this thesis demonstrate that taking into account the interactions between ecology and evolution is needed in order to understand why certain life-history strategies are commonly observed in nature.





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## SUMMARY

### Evolution of complex life cycles

Frogs are born as tadpoles and butterflies as caterpillars. These animals have a complex life cycle. Somewhere during their lives, the larval form transforms abruptly into the adult form in a process known as metamorphosis. Not only frogs and butterflies have such complex life cycles, also ladybugs, flatfish, lobsters, salmon, eel, and many other species drastically change their body form during their life. In fact, the majority of animal species have a metamorphosis. Yet, fossil evidence suggests that metamorphosis only evolved a few times in evolutionary history. Why then is metamorphosis so commonly seen in nature? A few species have lost the ability to metamorphose over evolutionary time. One such example is the axolotl (*Ambystoma mexicanum*). In contrast to its evolutionary ancestor, this salamander species retains the larval morphology over its lifetime and does not metamorphose. Why did the axolotl and other species lose metamorphosis while others did not?

During metamorphosis the animal body is transformed and rebuilt. This can be advantageous, because it allows species to efficiently exploit different niches during their life. Butterflies, for example, feed on nectar. However, they start their lives as caterpillars, built for nibbling on juicy leaves. To be able to feed on nectar, butterflies need a feeding straw, which caterpillars do not have. Metamorphosis allows the leaf-eating caterpillar to transform into a nectar-consuming butterfly. While metamorphosis can be beneficial for species that change their niche during their development, the process itself is very costly. The energetic costs of rebuilding the body are high and individuals are vulnerable to predation during metamorphosis. Furthermore, individuals that metamorphose are often dependent on two or more habitats for their growth, survival, and reproduction. If the conditions in just one of these habitats deteriorate too much, a metamorphosing species can go extinct.

Not all species that change niches during development have a metamorphosis. Some species, e.g. many fish species, only change their diet during their life, without drastic changes in morphology. It is thought that such ontogenetic niche shifts, have been the first steps in evolutionary history towards complex life cycles where individuals undergo metamorphosis. Consequently, to understand why complex life cycles have evolved and why they are so successful, it is necessary to understand how and why ontogenetic niche shifts have evolved. The aim of this thesis is to understand under which ecological conditions niche shifts and metamorphosis may have

evolved. Niche shifts and metamorphosis are life-history strategies that evolved millions of years ago. Little is however known about the ecological conditions that promoted their evolution. To better understand why metamorphosis and niche shifts are so ubiquitous in the animal kingdom, it is therefore useful to study the evolution of these life-history strategies with an evolutionary model.

Chapter 2 and 3 describe the conditions under which species switch their diet during development, and whether they evolve a morphology specialized in feeding on the food source used early or later in life. Large individuals are assumed to have access to two different types of food, the primary and secondary. Newborn individuals are considered too small to eat the secondary food source and can only feed upon the primary. The two food types are substantially different from each other, such that a morphology that is efficient for feeding on one type of food, is not very useful in exploiting the other food type.

The results in chapter 2 show that, under equilibrium conditions, it is beneficial for individuals to switch diets during their development when this increases their food intake. Even though large individuals then forage mainly on the secondary food source, they cannot evolve a morphology specialized for exploiting this type of food. The mechanisms that prevent specialization on a food source used later in life is studied in detail in chapter 3. Shifting diets increases the food intake of adults, which results in a higher reproduction rate. Because adults produce many offspring, competition for food is very strong among the smallest individuals. It is therefore of crucial importance for small individuals to be very effective at feeding on the scarce, primary food source. Individuals with a morphology that is slightly maladapted in feeding on this food type, are outcompeted by better adapted individuals. As a result, specialization on a secondary food source stands no chance.

Chapter 3 shows that the competition among the smallest individuals is somewhat alleviated when the population exhibits large population fluctuations. When the dominant cohort matures, there is a small timeframe during which less efficient larvae can escape competition and subsequently mature to the larger size class. Since these individuals are more efficient at feeding on the secondary food source as adults, they can produce many offspring. Therefore, specialization on a food source used later in life can evolve in case the population exhibits large population cycles.

Chapter 4 describes under what conditions metamorphosis can evolve as a mechanism to relax the tradeoff between foraging on the primary or secondary food source. Because metamorphosis is costly, it can only evolve when the secondary food source is abundant. Interestingly, as soon as life stages are slightly decoupled by metamorphosis, there is selection to evolve a more pronounced metamorphosis, such that pre- and postmetamorphs become morphologically more distinct from each other. When the conditions change under which metamorphosis initially evolved, metamorphosis

often does not disappear. Metamorphosis is therefore not easy to evolve, but, once evolved, it is hard to lose.

Even though metamorphosis is common in the animal kingdom, some species have lost metamorphosis through the evolution of direct development or paedomorphosis. Direct developers are born with the adult morphology. Paedomorphic individuals, in contrast, retain the larval morphology during their whole life. In chapter 5 it is studied under which conditions metamorphosis can disappear. The results in this chapter show that metamorphosis is most of the time an evolutionary dead end. If the availability of one of the two food sources that metamorphosing species uses deteriorates, the species often goes extinct. When the food source eaten by large individuals becomes scarce, there is an evolutionary response to postpone metamorphosis. This can, under some conditions, lead to the evolution of paedomorphosis, where individuals become mature while having the larval morphology. Vice versa, when the food source eaten by small individuals becomes scarce, it is beneficial to quickly metamorphose such that the secondary food source can be exploited earlier. Larger offspring reach the size at which they can metamorphose earlier, and are therefore selected for when the food source eaten by small individuals becomes scarce. This can sometimes lead to the evolution of direct development, where individuals are born with the adult morphology. The hypothesis that the evolution of direct development was preceded by the evolution of larger eggs was tested among amphibians with the use of a phylogenetic framework. The results of this analysis indeed strongly support the predictions of the evolutionary model.

To summarize, the work in this thesis shows that metamorphosis can be beneficial for species that change niches during their life. Since metamorphosis is costly, it only evolves under very favorable habitat conditions. Once evolved, however, metamorphosis is a robust strategy that does not easily disappear. Metamorphosis allows species to efficiently exploit multiple niches during their lives. While this is beneficial under favorable food conditions, metamorphosing species are vulnerable to habitat degradation since they depend on several food sources for their growth, survival and reproduction. Direct development and paedomorphosis can evolve as a way to deal with deteriorating conditions. The findings in this thesis explain the empirical observation that metamorphosis is ubiquitous in the animal kingdom, despite only a few evolutionary origins.





## SAMENVATTING

### **De evolutie van complexe levenscycli**

Kikkers worden geboren als dikkopjes en vlinders worden geboren als rupsen. Deze diersoorten hebben een zogenaamde complexe levenscyclus: ze veranderen op een bepaald moment in hun leven relatief abrupt van gedaante door middel van een metamorfose. Niet alleen kikkers en vlinders hebben een complexe levenscyclus, ook lieveheersbeestjes, platvissen, kreeften, zalm, paling en vele andere diersoorten veranderen radicaal van uiterlijk gedurende hun leven. Op basis van fossielen denken we dat levenscycli met een metamorfose maar een paar keer afzonderlijk van elkaar zijn geëvolueerd. Desondanks ondergaat de meerderheid van alle diersoorten op aarde een metamorfose. Waarom komt metamorfose zo vaak voor in het dierenrijk?

Een aantal soorten is het vermogen tot metamorfose ergens in de evolutionaire geschiedenis kwijtgeraakt. Een voorbeeld is de axolotl (*Ambystoma mexicanum*). Deze salamandersoort blijft gedurende zijn hele leven in het larvale stadium en heeft, in tegenstelling tot zijn evolutionaire voorouder, geen metamorfose. Waarom is de axolotl zijn metamorfose kwijtgeraakt terwijl andere salamandersoorten nog wel van gedaante wisselen?

Tijdens de metamorfose wordt het lijf van een dier omgebouwd. Dit kan voordelig zijn omdat het een individu in staat stelt om gedurende verschillende stadia van zijn leven, op succesvolle wijze, verschillende leefgebieden en voedselbronnen te benutten. Vlinders hebben bijvoorbeeld vaak een lange tong waarmee ze goed nectar uit bloemen kunnen drinken. Maar vlinders worden geboren als rupsen, experts in het vreten van sappige blaadjes. Rupsen hebben zo'n lange tong helemaal niet nodig. Metamorfose zorgt ervoor dat de blaadjes-vretende rups kan veranderen in een nectardrinkende vlinder. Alhoewel metamorfose voordelig kan zijn, is het ondergaan van een metamorfose een energieverblindende en risicovolle aangelegenheid. Het kost een boel energie om een lijf om te bouwen en individuen zijn tijdens de metamorfose gemakkelijke prooien voor hongerige roofdieren. Bovendien zijn soorten met een metamorfose vaak afhankelijk van twee of meerdere leefgebieden en/of voedselbronnen voor hun groei, overleving en voortplanting. Als de omstandigheden in slechts één van die leefgebieden achteruitgaat, kan dit er al toe leiden dat een soort met een metamorfose uitsterft.

Niet alle diersoorten die gedurende hun leven structureel naar een ander leefgebied of voedselbron overstappen, hebben een metamorfose. Sommige soorten voeden

zich in een latere levensfase met een voedselbron die drastisch verschilt van de voedselbron uit eerdere levensstadia, zonder dat hun lichaam veel verandert. Zo eten veel vissen als ze jong zijn zoöplankton en als ze ouder zijn andere vissoorten. We noemen zo'n verandering een 'ontogenetische niche shift'. Een niche shift is een verandering van plek in het ecosysteem, ontogenetisch betekent dat die verandering ergens in de ontwikkeling van het individu plaatsvindt. We denken dat ontogenetische niche shifts, dus het structureel overstappen naar een andere voedselbron, de eerste stap geweest is in de evolutie van complexe levenscycli waarbij individuen een metamorfose hebben. Het is daarom belangrijk om te snappen hoe en waarom deze ontogenetische niche shifts zijn geëvolueerd om te kunnen begrijpen waarom metamorfose is ontstaan.

Het doel van dit proefschrift is om te begrijpen onder welke ecologische omstandigheden ontogenetische niche shifts en metamorfoses kunnen evolueren. Deze strategieën zijn miljoenen jaren geleden ontstaan en we weten maar heel weinig over de ecologische omstandigheden van die tijd. Bovendien is het heel lastig om de evolutie van bijvoorbeeld metamorfose met een experiment te onderzoeken, onder andere omdat evolutie vaak een langzaam proces is. Daarom gebruik ik wiskundige modellen om te onderzoeken welke omstandigheden in theorie leiden tot de evolutie van ontogenetische niche shifts en metamorfoses. Met een model is het mogelijk om meer inzicht te krijgen over de evolutie van deze strategieën. Bovendien kan een model leiden tot nieuwe hypotheses over mogelijke ecologische relaties die belangrijk zijn voor de evolutie van niche shifts en metamorfoses.

In hoofdstuk 2 en 3 kijk ik naar de omstandigheden waarin ontogenetische niche shifts kunnen evolueren. In mijn wiskundige modellen neem ik aan dat grote individuen twee soorten voedsel tot hun beschikking hebben; de eerste en de tweede voedselbron. Individuen die net geboren zijn, zijn te klein om van de tweede voedselbron gebruik te kunnen maken, zij eten dus alleen de eerste voedselbron. De twee voedselbronnen zijn behoorlijk verschillend van elkaar, denk bijvoorbeeld aan planten en insecten. Omdat de voedselbronnen zo van elkaar verschillen, is een lichaam dat goed is voor het eten van de eerste voedselbron minder geschikt voor het eten van de tweede voedselbron en vice versa.

In hoofdstuk 2 laat ik zien dat het evolutionair voordelig is om tijdens het leven van voedselbron te wisselen als dit de voedselinname verhoogt. Dit resultaat is niet echt verrassend, hoe meer voedsel een individu heeft, hoe meer nakomelingen het kan krijgen. Opvallend is dat het niet mogelijk is voor individuen zonder metamorfose om een lichaam te evolueren wat gespecialiseerd is in het eten van de tweede voedselbron, zelfs niet als grote individuen alleen maar dit voedsel eten en de eerste voedselbron links laten liggen. In hoofdstuk 3 kijk ik met een ander type model in detail naar het mechanisme wat er nou voor zorgt dat specialisatie op de tweede voedselbron niet mogelijk is in dieren zonder metamorfose. Dieren veranderen alleen van voedselbron

als dit hun voedselinname verhoogt. Omdat volwassenen hierdoor meer voedsel tot hun beschikking hebben, kunnen ze meer nakomelingen maken. Doordat er vervolgens zoveel nakomelingen zijn, ontstaat onder hen heel veel onderlinge concurrentie voor de eerste voedselbron. Het is daarom van essentieel belang dat pasgeboren individuen heel goed zijn in het eten van deze schaarse eerste voedselbron. Individuen die een uiterlijk hebben wat een klein beetje minder goed is in het eten van dit voedsel, worden door beter aangepaste individuen weggeconcurrerd. Omdat specialisatie op de tweede voedselbron ervoor zorgt dat individuen minder goed worden in het eten van de eerste voedselbron, kan die specialisatie niet evolueren.

In hoofdstuk 2 is de populatie in ecologisch evenwicht. Dit houdt in dat de samenstelling (het aantal individuen in een bepaalde levensfase) en grootte van de populatie niet veel verandert op een ecologische tijdschaal. In hoofdstuk 3 onderzoek ik de evolutie van ontogenetische niche shifts in een populatie die niet in evenwicht is, maar voortdurend fluctueert. Bij een bepaald soort fluctuatie is het wél mogelijk om specialisatie op de tweede voedselbron te evolueren. Bij dit type fluctuatie bestaat de populatie op een zeker tijdstip voornamelijk uit één generatie, bijvoorbeeld pasgeboren individuen of juist alleen maar grote, volwassen dieren. Als individuen van zo'n fluctuerende populatie van voedselbron wisselen als ze groter worden, is specialisatie op die tweede voedselbron wel mogelijk. De reden hiervoor is dat de competitie voor de eerste voedselbron in een fluctuerende populatie niet altijd even sterk is. Als de meeste individuen uit een jonge generatie zijn overgegaan op het eten van de tweede voedselbron, is er heel weinig concurrentie voor de eerste voedselbron. Een mutant die niet zo goed is in het eten van deze voedselbron kan nu ongestoord eten en op die manier toch volwassen worden. Omdat deze individuen juist wél heel goed zijn in het eten van de tweede voedselbron, krijgen ze veel meer nakomelingen dan individuen die juist goed zijn in het eten van de eerste voedselbron. Specialisatie op de tweede voedselbron kan daarom evolueren op het moment dat de populatie grote fluctuaties heeft.

In hoofdstuk 4 onderzoek ik de evolutie van metamorfose. Ik neem in dit hoofdstuk aan dat metamorfose ervoor kan zorgen dat soorten zich zowel op de eerste als op de tweede voedselbron kunnen specialiseren. Omdat metamorfose erg duur is, kan het alleen evolueren als de tweede voedselbron in overvloed aanwezig is. Een opvallend resultaat is dat metamorfose zichzelf versterkt. In eerste instantie verschillen individuen voor en na de metamorfose maar een klein beetje in uiterlijk. Bij de volgende generaties gaan die verschillen steeds meer toenemen. Als de ecologische omstandigheden waaronder metamorfose is geëvolueerd veranderen, verdwijnt metamorfose niet. Het belangrijkste resultaat van hoofdstuk 4 is dat metamorfose niet makkelijk evolueert, maar als het eenmaal geëvolueerd is, verdwijnt het niet als de omstandigheden veranderen.

In hoofdstuk 5 kijk ik onder welke omstandigheden metamorfose kan verdwijnen. In dit hoofdstuk toon ik aan dat metamorfose bijna altijd een evolutionair doodlopende weg is. Als de beschikbaarheid van slechts één van de twee voedselbronnen schaars wordt, sterft een soort met metamorfose daarom vaak uit. Alleen als de andere voedselbron ruimschoots aanwezig is, kan er een strategie evolueren waardoor de populatie in stand blijft. Een evolutionaire reactie om toch te overleven als de tweede voedselbron, die door grote individuen gegeten wordt, verslechterd, is om pas later in het leven metamorfose te ondergaan. Onder specifieke omstandigheden leidt dit tot de evolutie van “paedomorfose”: individuen worden dan volwassen terwijl ze de larvale morfologie behouden. Omgekeerd, als de eerste voedselbron, die voornamelijk door jonge individuen wordt gegeten, verslechterd, is het evolutionair voordelig om juist eerder in het leven metamorfose te ondergaan. Hierdoor kunnen individuen sneller van de tweede voedselbron eten. Er is bovendien selectie voor het produceren van grotere nakomelingen. Hoe groter je bij je geboorte bent, hoe sneller je de tweede voedselbron kan gaan eten. Deze evolutionaire ontwikkeling leidt soms tot de evolutie van “directe ontwikkeling”: individuen worden geboren met het uiterlijk van volwassenen. De hypothese dat de evolutie van een directe ontwikkeling wordt voorafgegaan door de evolutie van grotere nakomelingen, hebben we getest in de amfibieën met behulp van een fylogenetisch methode. Hierbij hebben we gekeken naar de aanwezigheid van grote eieren en een directe ontwikkeling in de evolutionaire stamboom van de amfibieën. De resultaten van deze analyse ondersteunen de hypothese van het evolutionaire model.

De resultaten in dit proefschrift laten zien dat metamorfose voordelig is voor soorten die van ecologische rol veranderen in hun leven. Omdat metamorfose heel duur is, kan het alleen evolueren onder hele goede ecologische omstandigheden. Zodra het geëvolueerd is, is metamorfose een robuuste strategie die niet snel verdwijnt als omstandigheden veranderen. Metamorfose zorgt ervoor dat soorten in hun leven gebruik kunnen maken van meerdere voedselbronnen. Alhoewel dit voordelig is onder goede omstandigheden, zijn soorten met een metamorfose erg kwetsbaar voor achteruitgang van het leefgebied, juist omdat ze afhankelijk zijn van meerdere voedselbronnen. Directe ontwikkeling en paedomorfose zijn twee strategieën die kunnen evolueren als een manier om met deze verslechterende omstandigheden om te gaan. De resultaten in dit proefschrift kunnen verklaren waarom metamorfose zo vaak voorkomt in het dierenrijk. Metamorfose evolueert zelden, maar als het eenmaal aanwezig is, verdwijnt deze strategie niet snel.

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# AUTHOR CONTRIBUTIONS

## **2 A Parent-Offspring Trade-Off Limits the Evolution of an Ontogenetic Niche Shift**

*Hanna ten Brink and André M. de Roos*

HtB and AMdR designed the research. HtB analyzed the model and wrote the first version of chapter. HtB and AMdR contributed to later versions of the chapter.

## **3 Large amplitude consumer-resource cycles allow for the evolution of ontogenetic niche shifts in consumer life history**

*Hanna ten Brink and André M. de Roos*

HtB and AMdR designed the research. HtB analyzed the model and wrote the first version of chapter. HtB and AMdR contributed to later versions of the chapter.

## **4 The evolutionary ecology of metamorphosis**

*Hanna ten Brink, André M. de Roos and Ulf Dieckmann*

HtB and UD designed the research. HtB analyzed the model and wrote the first version of chapter. HtB, AMdR, and UD, contributed to later versions of chapter.

## **5 Metamorphosis, an evolutionary dead end?**

*Hanna ten Brink, Renske Onstein and André M. de Roos*

HtB and AMdR designed the model analysis. RO and HtB designed the phylogenetic analysis. RO analyzed the phylogenetic analysis. HtB analyzed the model and wrote the first version of chapter. HtB and AMdR contributed to later versions of the chapter.



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