Evolution of complex life cycles

ten Brink, J.A.

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CHAPTER 4

THE EVOLUTIONARY ECOLOGY OF METAMORPHOSIS

Hanna ten Brink
André M. de Roos
Ulf Dieckmann

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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 $X_{1,\text{max}}$ and $X_{2,\text{max}}$ 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 $y_{\text{max}} = q_j x$, where $q_j$ 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 $w = x + y_{\text{max}} = x(1 + q_J)$ (Persson et al. 1998). In general, an individual’s reversible mass can be used, and thus diminished from $y_{\text{max}}$, 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 $w_{\text{min}}$.

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,

\begin{align}
a_1(w) &= A_1 \left(\frac{w}{w_0} \exp(1 - \frac{w}{w_0})\right)^{\alpha} \\
a_2(w) &= \begin{cases} 0 & w \leq w_{\text{min}} \\ A_2 \left[\frac{w - w_{\text{min}}}{w_0} \exp(1 - \frac{w - w_{\text{min}}}{w_0})\right]^{\alpha} & \text{otherwise.} \end{cases}
\end{align}

In these equations, $A_1$ and $A_2$ are the maximum attack rates individuals can reach when their body mass equals $w_0$ and $w_0 + w_{\text{min}}$ 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 $w_0 + w_{\text{min}}$, 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 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 \( y < q_j x \) \cite{Persson1998}, we assume that adults allocate a fraction \( \kappa_R(x, y) \) to reversible mass according to

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

\[
b(x, y, X_1, X_2) \begin{cases} 
0 & y < q_j x \\
\frac{1 - \kappa_A(x, y)}{\kappa_J(x, y)} E_g(x, y, X_1, X_2) \eta / ((1 + q_j x_b)) & \text{otherwise}.
\end{cases}
\] (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 \cite{Persson1998}.

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 \( y_{\text{max}} = q_j x \) 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 \cite{Persson1998}, metabolic costs and handling times are parameterized for the interaction between a planktivorous fish population of roach \textit{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.

\section*{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; \( i = L, J, \) or \( A)\), assuming that these constants can vary between
4.2 Model and methods

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

$$A_{1i} = (1 - \psi_i)(A_{\text{max}} - A_{\text{min}}) + A_{\text{min}},$$

$$A_{2i} = \psi_i(A_{\text{max}} - A_{\text{min}}) + A_{\text{min}}. \quad (4.9)$$

In these equations, $0 \leq \psi_i \leq 1$ is the relative degree of specialization of a life stage ($i = \text{L, J, or A}$) 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 ($\psi_\text{L} = \psi_\text{J} = \psi_\text{A}$).

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

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 ($l \text{ day}^{-1}$) 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 $i = \text{L, J, or A}$). 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.
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

$$\psi_A = \psi_I = \min(1, \psi_L + \theta),$$

(4.10)

where $\theta$ is the extent of the metamorphosis. Individuals without metamorphosis have the same morphology over their lifetime ($\psi_L = \psi_I = \psi_A$), whereas individuals with full metamorphosis can specialize on the primary food source when small and on the secondary food source when large. Figure 4.3 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 ($x = x_I$ and $y = q_I x_I$), they lose $\theta x_I (q_I - q_s)$ 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 $w_I$ 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
4.2 Model and methods

The 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 $\delta X_{2,\text{max}}$ of the secondary food source, we vary $X_{2,\text{max}}$ 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 $w > w_{\text{min}}$ in the absence of metamorphosis) to characterize the degree of the ontogenetic diet shift.
### Table 4.1: Model variables and evolving traits

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Range</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$X_1$</td>
<td>Density of primary food source</td>
<td>from 0 to $X_{1,\text{max}}$</td>
<td>mg l$^{-1}$</td>
</tr>
<tr>
<td>$X_2$</td>
<td>Density of secondary food source</td>
<td>from 0 to $X_{2,\text{max}}$</td>
<td>mg l$^{-1}$</td>
</tr>
<tr>
<td>$x$</td>
<td>Irreversible body mass</td>
<td>Larger than $x_b$</td>
<td>g</td>
</tr>
<tr>
<td>$y$</td>
<td>Reversible body mass</td>
<td>From $q_1 x_b$ to $y_{\text{max}} = q_1 x$</td>
<td>g</td>
</tr>
<tr>
<td>$\psi_i$</td>
<td>Degree of specialization of larvae, juveniles or adults ($i=$L, J, or A) on the secondary food source</td>
<td>From 0 - 1</td>
<td>-</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Extent of metamorphosis</td>
<td>From 0 - 1</td>
<td>-</td>
</tr>
<tr>
<td>$w_f$</td>
<td>Standardized body mass at metamorphosis</td>
<td>Larger than $w_b$</td>
<td>g</td>
</tr>
</tbody>
</table>
### Table 4.2: Model parameters and their default values from [Persson et al.](1998)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Default Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \delta )</td>
<td>Food-source turnover rate</td>
<td>0.1</td>
<td>day(^{-1} )</td>
</tr>
<tr>
<td>( X_{1,\text{max}} )</td>
<td>Maximum biomass density of primary food source</td>
<td>0.055</td>
<td>mg l(^{-1} )</td>
</tr>
<tr>
<td>( X_{2,\text{max}} )</td>
<td>Maximum biomass density of secondary food source</td>
<td>Variable</td>
<td>mg l(^{-1} )</td>
</tr>
<tr>
<td>( x_b )</td>
<td>Irreversible body mass of newborns</td>
<td>0.000804</td>
<td>g</td>
</tr>
<tr>
<td>( w_A )</td>
<td>Standardized body mass at maturation</td>
<td>8.71</td>
<td>g</td>
</tr>
<tr>
<td>( w_0 )</td>
<td>Standardized body mass at which maximum attack rate is attained on primary resource</td>
<td>17.42</td>
<td>g</td>
</tr>
<tr>
<td>( \alpha )</td>
<td>Size scaling exponent of the attack functions</td>
<td>0.6</td>
<td>-</td>
</tr>
<tr>
<td>( \zeta_1 )</td>
<td>Constant in handling-time function</td>
<td>0.00036(^*)</td>
<td>day mg(^{-1} )</td>
</tr>
<tr>
<td>( \zeta_2 )</td>
<td>Constant in handling-time function</td>
<td>0.00745(^*)</td>
<td>day mg(^{-1} ) g(^{\zeta_3} )</td>
</tr>
<tr>
<td>( \zeta_3 )</td>
<td>Slope of decrease in handling time at small consumer sizes</td>
<td>0.68</td>
<td>-</td>
</tr>
<tr>
<td>( \zeta_4 )</td>
<td>Slope of increase in handling time at large consumer sizes</td>
<td>1.15 (10^{-3} )</td>
<td>g(^{-1} )</td>
</tr>
<tr>
<td>( p_1 )</td>
<td>Metabolic constant</td>
<td>0.033</td>
<td>g(^{-1-p_2} ) day(^{-1} )</td>
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<tr>
<td>( p_2 )</td>
<td>Metabolic exponent</td>
<td>0.77</td>
<td>-</td>
</tr>
<tr>
<td>( k_e )</td>
<td>Metabolic conversion factor</td>
<td>0.00061(^*)</td>
<td>-</td>
</tr>
<tr>
<td>( q_1 )</td>
<td>Constant determining maximum reversible body mass</td>
<td>0.742</td>
<td>-</td>
</tr>
<tr>
<td>( q_A )</td>
<td>Constant in adult energy-allocation function</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>( \eta )</td>
<td>Gonad-offspring conversion</td>
<td>0.5</td>
<td>-</td>
</tr>
<tr>
<td>( \mu )</td>
<td>Background mortality rate</td>
<td>0.01</td>
<td>day(^{-1} )</td>
</tr>
</tbody>
</table>

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\(^{-1} \) instead of individuals l\(^{-1} \).
### Table 4.3: Model parameters and their default values related to specialization and metamorphosis

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Default Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{\text{max}}$</td>
<td>Maximum value of the attack-rate constants $A_1$ and $A_2$</td>
<td>$10^5$</td>
<td>1 day $^{-1}$</td>
</tr>
<tr>
<td>$A_{\text{min}}$</td>
<td>Minimum value of the attack-rate constants $A_1$ and $A_2$</td>
<td>$10^4$</td>
<td>1 day $^{-1}$</td>
</tr>
<tr>
<td>$w_{\text{min}}$</td>
<td>Standardized body mass at which the secondary food source becomes available</td>
<td>1.742</td>
<td>g</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Constant in habitat-switching rate</td>
<td>10</td>
<td>day g $^{-1}$</td>
</tr>
<tr>
<td>$q_s$</td>
<td>Ratio of reversible to irreversible body mass immediately after full metamorphosis</td>
<td>0.2</td>
<td>–</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Probability of dying during full metamorphosis</td>
<td>0.5</td>
<td>-</td>
</tr>
</tbody>
</table>
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 \( w > w_{\text{min}} \) 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: $\delta X_{2,\text{max}} = 0.0011$ (light green), 0.0022 (orange), 0.0066 (dark pink), 0.011 (purple), or 0.022 (dark blue) mg l$^{-1}$ 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.
4. The evolutionary ecology of metamorphosis

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 ($\psi_L=\psi_A = 1$). 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-
4.3 Results

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 (l 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: $\delta_X_{2,\text{max}} = 0.011$ (B), or $0.0022$ (C) mg l$^{-1}$ day$^{-1}$. The body mass at metamorphosis is $w_{\text{min}} = 1.742$ 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.
4. The evolutionary ecology of metamorphosis

cus on the conditions under which metamorphosis evolves when individuals are ini-
tially specialized on the primary food source (figure 4.3B). In appendix 4.B we ana-
logously 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 juve-
niles 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 $w_I$ at metamorphosis.

Figure 4.4A shows that metamorphosis originates abruptly when the supply rate
of the secondary food source becomes sufficiently high. Surprisingly, however, meta-
morphosis is not lost when the supply of the secondary food source decreases, which
results in population extinction through evolutionary trapping when this supply be-
comes 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 metamor-
phosis, specialization on the secondary food source is not possible; therefore, individ-
uals 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 individu-
als 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 effi-
ciency 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: metamor-
phosis 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 (mg l\(^{-1}\) 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.
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

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 (mg l$^{-1}$ 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 (mg l$^{-1}$ day$^{-1}$). Parameter values are as shown in tables 4.2 and 4.3.
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

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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.A).

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.A), demonstrating that metamorphosis evolves approximately when the initial value of $\psi$ exceeds the value of the evolutionary repeller in figure 4.A, and in particular, when it equals the value of the positive CSS in figure 4.A. The initial value of $\psi_J$ 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 $\delta X_{2,\text{max}}$ 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 $\delta X_{2,\text{max}}$ 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 $\delta X_{2,\text{max}}$ 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: $\delta X_{2,\text{max}} = 0.0011$ (A), 0.0031 (B), or 0.0044 (C) mg l$^{-1}$ 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 $\delta X_{1,\text{max}}$ is high and $\delta X_{2,\text{max}}$ 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 $w > w_{\text{min}}$) 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 $w_0 + w_{\text{min}}$, 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 (mg l$^{-1}$ 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 (†). Parameters: $X_{1_{\text{max}}} = 0.022$ (A, C) or 0.11 (B, D) 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 (mg l$^{-1}$ 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: $w_{\text{min}} = 0.88$ (A, C) or 6 (B, D). Other parameter values are as shown in tables 4.2 and 4.3.
4.D Robustness of results

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 (mg l$^{-1}$ 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: $q_s = 0.742 = q_J$, 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 (mg l$^{-1}$ 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 (†).