Evolution of complex life cycles

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CHAPTER 6

GENERAL DISCUSSION

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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 (*Salvenilus 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 (chapter 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.