Ontogenesis

Eco-evolutionary perspective on life history complexity

Hin, V.

Publication date
2017
Document Version
Other version
License
Other

[Link to publication](#)

Citation for published version (APA):
Hin, V. (2017). *Ontogenesis: Eco-evolutionary perspective on life history complexity* . [Thesis, fully internal, Universiteit van Amsterdam].

General Discussion

Vincent Hin

7.1 – ONTOGENETIC ASYMMETRY

Ecological theory based on structured population models has revealed an important role of ontogenetic development for the dynamics of populations and communities (De Roos and Persson 2013). Ontogenetic development of organisms includes processes such as individual body size growth (ontogenetic growth) and development of maturity. Ontogenetic development is a major life-history process in many, if not all species, and can substantially affect the type and the strength of the interaction between an individual organism and its environment. Examples of such changes in ecological interactions during ontogeny are: diet changes of individuals during ontogeny, differences in predation rates between newborn and fully grown individuals, or the ability of large individuals to better withstand resource scarcity than small individuals. Most of the changes in ecological interactions that arise from ontogenetic development have consequences for population and community dynamics (reviewed in De Roos and Persson 2013).

However, there are conditions under which ontogenetic development, through its impact on ecological interactions of individual organisms, does *not* affect population and community dynamics. These are the conditions referred to as *ontogenetic symmetry*. In case of ontogenetic symmetry, *i*) the mass-specific rate of resource ingestion, *ii*) the mass-specific rate of biomass production (MBP) and *iii*) the individual mortality rate do not change during ontogenetic development (De Roos et al. 2013). The resource ingestion rate determines an individual's impact on the environment. The rate of biomass production describes the productivity of an individual that can be used for either growth (in juveniles), or reproduction (in adults), and is therefore an important component of fitness. Any deviation from the above three conditions leads to *ontogenetic asymmetry*. In the event of ontogenetic asymmetry, ontogenetic development will lead to a change in the interaction between an organism and its environment in a way that affects population and community dynamics (De Roos et al. 2013).

Most likely, ontogenetic asymmetry plays an important role in all populations. The predominance of ontogenetic asymmetry can be derived from both individual-level observations and inferred from dynamics of natural and experimental systems. On the individual level, ontogenetic asymmetry arises from the non-linear relationships of resource ingestion and maintenance metabolism with body size. Maintenance metabolism tends to be proportional to body mass, while resource ingestion rates increase sub-linearly with size (Kooijman 2010). Consequently, adults (or large individuals) are less productive on a mass-specific basis, compared to juveniles (or small individuals). In population dynamical equilibrium, ontogenetic asymmetry in terms of low productivity for adult individuals creates an energetic bottleneck in the adult life stage (De Roos et al. 2007). Any increase in mortality then relaxes competition

among adults more than among juveniles and this leads to a disproportional increase in the productivity of adult individuals, with a concomitant increase in reproduction rate. As a result, recruitment to the juvenile stage increases and leads to an increase in juvenile biomass. The positive response of juvenile biomass to increasing mortality is a type of biomass overcompensation (De Roos et al. 2007). The phenomenon of biomass overcompensation has been observed in experimental and natural systems and is indicative of ontogenetic asymmetry in the energetics of individuals. Next to biomass overcompensation, another population-level expression of ontogenetic asymmetry are cyclic population dynamics. That many natural populations appear to show such oscillatory dynamics is an indication that ontogenetic asymmetry is likely driving the dynamics of these populations.

Overall, ontogenetic asymmetry appears to be common in natural populations (Schröder et al. 2014) and there is a good understanding about the connection between ontogenetic asymmetry and the dynamics of populations and communities (De Roos and Persson 2013). This thesis takes a next step and studies the eco-evolutionary implications of ontogenetic asymmetry. The general question is whether and how natural selection can explain the occurrence of ontogenetic asymmetry. Also, what are the evolutionary consequences of ontogenetic asymmetry for the long-term persistence of species? The previous chapters contribute in various ways to answering these questions. In this final chapter, I will summarize these results and discuss them in the context of the evolutionary origin and consequences of ontogenetic asymmetry.

7.2 – The origins of ontogenetic asymmetry

Competitive asymmetry

Chapter 2 and 3 study whether evolution can lead to ontogenetic asymmetry in consumer individuals that compete for a single food resource. The consumer energetics are described by a net-production Dynamic Energy Budget (DEB) model, with body-mass scaling exponents for energy supply (represented by maximum ingestion rate of the functional response) and energy expenditure (represented by maintenance metabolic rate). These scaling exponents determine the strength and direction of ontogenetic asymmetry. Furthermore, because all individuals feed on a shared resource, if ontogenetic asymmetry occurs, it translates into competitive asymmetry between consumer individuals of different sizes. A competitive difference between two differently-sized individuals can mean two things (illustrated in figure 7.1). Firstly, it can mean that a superior competitor can eat more per unit of body mass (it has a higher mass-specific resource ingestion rate) and, in addition, spends only little energy on maintenance (it has a lower mass-specific maintenance rate), compared to an inferior competitor. As a consequence, the superior competitor produces more biomass per unit of body mass

(it has a higher mass-specific biomass production (MBP) rate), and also requires less resources to cover its maintenance metabolism (it has a lower maintenance resource density; MRD), in relation to the inferior competitor (left panels figure 7.1). Secondly, a competitive difference can also exist when the superior competitor can eat more per unit of body mass, but also spends more energy on maintenance, than the inferior competitor. In this case, the superior competitor still produces more biomass per unit of body mass compared to the inferior competitor (has a higher MBP), but the dependence on resources for maintenance is identical to that of the inferior competitor (equal MRD; right panels figure 7.1).

Evolution of competitive asymmetry

Chapter 2 shows that evolution of ontogenetic asymmetry will only lead to the second type of competitive asymmetry (right panels figure 7.1). Therefore, the evolved outcome of ontogenetic asymmetry implies that the maintenance resource density (MRD) does not change with consumer body size. Competitive asymmetry only arises through differences in the mass-specific biomass production (MBP). Both an increase in juvenile mortality and an increase in the extent of pre-maturation growth, favor evolution towards a higher juvenile mass-specific biomass production. This adaptive response increases juvenile growth rates. Conversely, an increase in adult mortality and an increase in the extent of post-maturation growth, favor evolution towards a higher adult mass-specific biomass production. This increases growth and reproduction of adults. With this evolved form of ontogenetic asymmetry, population cycles, that are readily induced by changes in the maintenance resource density with body size (Persson et al. 1998), do not occur. Biomass overcompensation only occurs when the scaling exponents respond adaptively to increasing mortality. There is no biomass overcompensation for equal and fixed scaling exponents (chapter 2).

The evolved form of ontogenetic asymmetry (size-independent MRD and size-dependent MBP; right panels figure 7.1) is robust to the incorporation of an additional scaling exponent of energy supply (chapter 3). In chapter 3, the body-mass scaling of energy supply is controlled by two processes that can scale with body mass: the maximum ingestion rate (that was also considered in chapter 2) and the attack rate. Attack rates and maximum ingestion rates represent different processes that both control resource ingestion rates by altering the shape of the functional response. It is therefore important to consider the effect of both these processes on the evolution of ontogenetic asymmetry. With a total of three scaling exponents, the maintenance resource density and the mass-specific biomass production rate can change in more diverse ways with body size than with only two exponents. Nonetheless, the same type of competitive asymmetry evolves. Also with three scaling exponents, selection
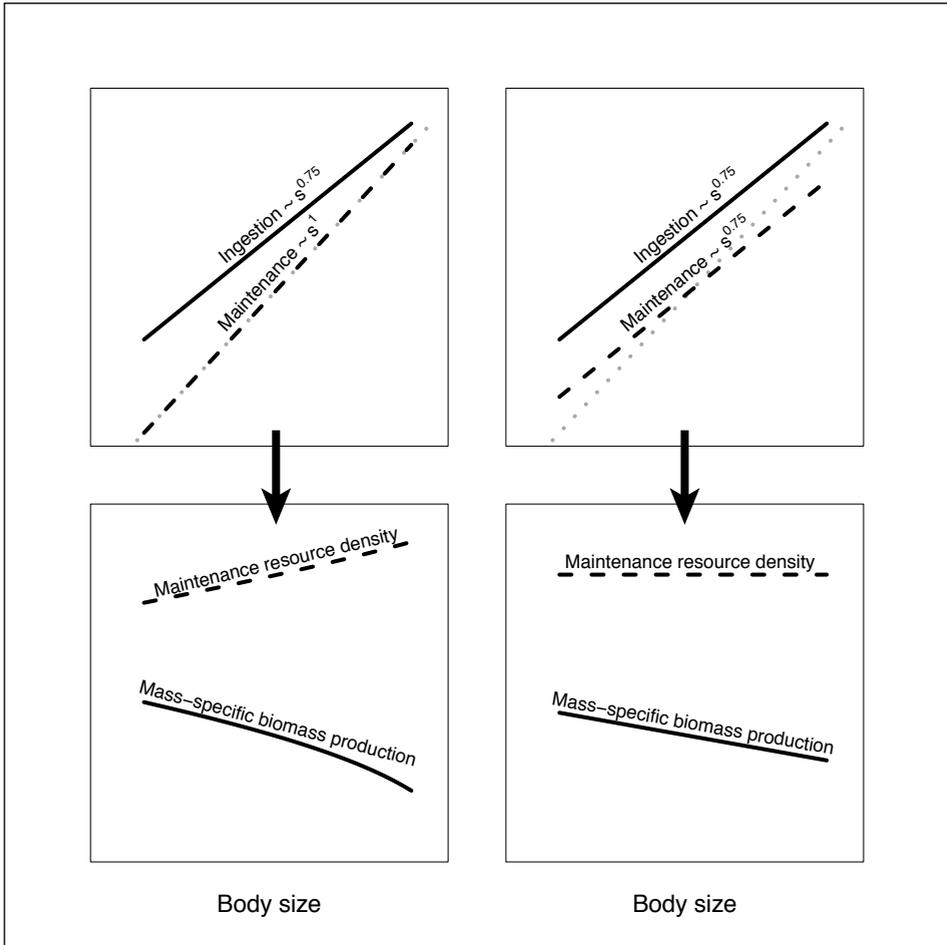
FIGURE 7.1 – The body-mass scalings of resource ingestion and maintenance rate (top panels) determine the body-mass scalings of the mass-specific biomass production (MBP) and the maintenance resource density (MRD). Biomass production is used for growth and reproduction and is therefore an important component of fitness. The MRD is the resource level required to cover the costs of maintenance metabolism. For resource levels below the MRD, individuals face increased mortality due to starvation. A steeper scaling of maintenance compared to ingestion (top left; as occurs in theories for ontogenetic growth Kooijman 2010; West et al. 2001), causes the mass-specific biomass production to decrease with body size, while the maintenance resource density increases with size (bottom left). In such a setting, small individuals are competitively superior compared to larger individuals, both through a lower MRD and a higher MBP. Selection leads to equal body-mass scalings of maintenance and ingestion rates (top right). This causes a decrease in the mass-specific biomass production when the scaling exponents are below one (0.75 in this case), but a constant maintenance resource density (bottom right). In this case, small individuals are only competitively superior because they have a higher MBP. Dotted gray lines in top panels indicate linear scaling (scaling exponent equals one).

leads to a size-independent maintenance resource density and a size-dependent mass-specific biomass production rate (figure 7.1; right panels).

The evolved type of ontogenetic asymmetry (figure 7.1; right panels) only comes about when all the size-dependent metabolic processes (*i.e.* maximum ingestion rate, attack rate and maintenance rate) scale in an identical, but non-linear way with body mass. The size-dependent changes in the mass-specific biomass production can explain variation in the ontogenetic scaling of metabolic rate between different species of teleost fish (chapter 2), possibly through changes in life-history processes that contribute to metabolic rate, such as growth rates. However, the evolved size independency of the maintenance resource density does not match very well with observations (chapter 2). The maintenance resource density seems to be an increasing function of body mass for at least some populations of fish (Byström and Andersson 2005; Hjelm and Persson 2001; Lefébure et al. 2014; Persson and De Roos 2006). In Daphnia, ingestion scales with a lower exponent than maintenance requirement (Gurney et al. 1990; McCauley et al. 1990). This leads to an increase in the maintenance resource density with body size. Also, the lack of biomass overcompensation from the evolved type of ontogenetic asymmetry (chapter 2), is at odds with empirical observations that biomass overcompensation does occur (Cameron and Benton 2004; Ohlberger et al. 2011; Reichstein et al. 2015; Schröder et al. 2009*b*, 2014, 2015). Summarizing, the approach adopted in chapters 2 and 3 does not contain a full story on how ontogenetic asymmetry as observed in nature evolves. It does provide a useful baseline for exploring how different types of trade-offs and more ecological complexity can lead to the evolution of the type of ontogenetic asymmetry that is readily observed in nature.

Trade-offs

Trade-offs are an insurmountable aspect of life and crucial for the outcome of evolutionary processes (Roff 1992; Zera and Harshman 2001). Simultaneously, it is notoriously hard to discover which trade-off constrains evolutionary processes most. Therefore, in many cases a certain trade-off is assumed, with limited prior knowledge about the importance of this trade-off in living systems. In chapters 2 and 3 this is not any different. It was assumed that a juvenile-adult trade-off constrains the evolution of ontogenetic asymmetry, by parameterizing the scaling constant on the body size at maturation. An increase in the scaling exponent of a metabolic process (*i.e.* maintenance rate or maximum ingestion rate), then leads to an increase in the rate of this process for adult individuals, and to a concomitant decrease for juveniles. The empirical evidence of a juvenile-adult trade-off is limited. However, such a trade-off can still be of use for studying selection on metabolic scaling. Studying the evolution of

metabolic scaling under a juvenile-adult trade-off translates into studying the relative importance of these different life stages, and their associated life-history processes (growth vs. reproduction), in determining the evolutionary process.

The use of multiple trade-offs helps to get an idea about the robustness of the obtained results. Besides the juvenile-adult trade-off, evolutionary dynamics of metabolic scaling were also studied with an energetic trade-off (chapter 3). Under this trade-off, increasing the processes related to energy supply (maximum ingestion rate and attack rate) also leads to increasing metabolic costs. Furthermore, the energetic trade-off does not constrain evolution of the maintenance rate exponent, which is therefore assumed to be fixed. Evolution of both scaling constants and scaling exponents under the energetic trade-off, reveals that the processes related to energy supply evolve towards the same scaling with body mass (chapter 3). Therefore, the energetic trade-off confirms the result that was already obtained under the juvenile-adult trade-off; optimally, attack rate and maximum ingestion rate should scale in the same way with body mass. Any evolved ontogenetic asymmetry cannot be expected to occur from scaling differences of these processes. However, the energetic trade-off allows evolution in only a single scaling exponent related to energy supply (either the maximum ingestion rate exponent or the attack rate exponent). If these processes evolve simultaneously, this leads to run-away selection towards ever increasing rates of resource ingestion (chapter 3). Therefore, the energetic trade-off cannot address the question whether evolution leads to ontogenetic asymmetry that is derived from a difference between energy supply (maximum ingestion and attack rate) and energy expenditure (maintenance metabolism).

The juvenile-adult trade-off and the energetic trade-off each have their applications and limitations. An interesting step for further research would be to combine these two trade-offs. This will allow one to separate selection that operates on the scaling exponents, from the selection that operates on the scaling constants (through the energetic trade-off). It furthermore permits the simultaneous evolution of one scaling exponent of energy supply with the scaling exponent of maintenance. Potentially, such an exercise could explain to which extent the evolution of a size-dependent mass-specific biomass production rate under a juvenile-adult trade-off, is driven by selection on the size-independent consequences that are part of changes in these scaling exponents. Because both trade-offs separately show evolution towards ontogenetic symmetry, although each within the restrictions of the parameters that can evolve, combining these trade-offs is unlikely to lead to the evolution of ontogenetic asymmetry.

Box 7.1

Increasing ecological complexity has the potential to lead to ontogenetic asymmetry when the scaling of maintenance rate is fixed at one. The model as studied in chapter 2 is adapted to include size-dependent cannibalism and size-dependent interference competition. Cannibalistic voracity of adults (β) increases mortality rates for juveniles, which becomes:

$$\mu_c + \mu_j + M \left(\frac{s}{s_r} \right)^Q \frac{\beta A}{R + \beta J + H} \tag{7.1}$$

Cannibalism furthermore increases adult resource intake, $I_A (R, J)$, which becomes:

$$I_A (R, J) = M \left(\frac{s}{s_r} \right)^Q \frac{R + \beta J}{R + \beta J + H}$$

Interference of adults negatively affects juvenile resource intake. This is modeled by an interference scalar ε. Juvenile resource ingestion becomes:

$$I_J (R, A) = M \left(\frac{s}{s_r} \right)^Q \frac{R}{R + \varepsilon A + H}$$

These size-dependent ecological interactions lead to a decrease in the evolutionary equilibrium (CSS) of the maximum ingestion scaling exponent (Q), when the maintenance exponent is constraint at one ($P = 1$). In figure 7.2, the effect of cannibalistic mortality (last term in equation 7.1), is compared with the effect of increasing juvenile mortality μ_j. Comparing left and right panels in figure 7.2, it can be concluded that the effect of interference is less pronounced than the effect of mortality.
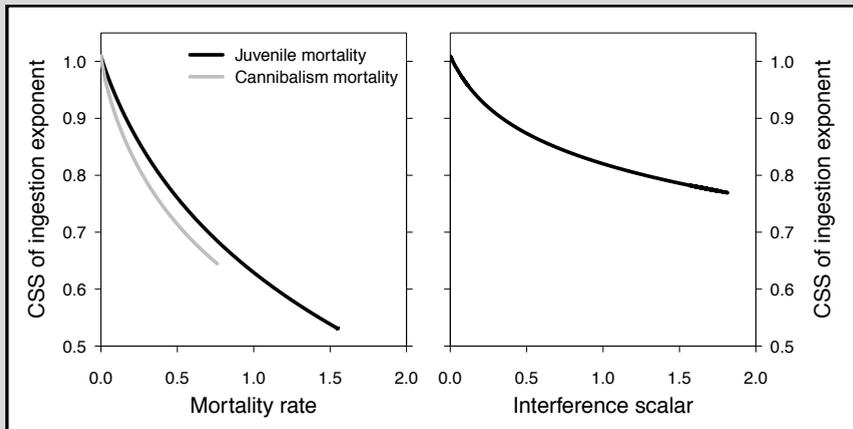

FIGURE 7.2 – The effect of cannibalism and interference on the evolution of the maximum ingestion exponent. Model is adapted from the model in chapter 2 (see table 2.1)

Conclusions and perspectives

Concluding, ontogenetic asymmetry in the basic ecological setting of chapters 2 and 3 probably arises from constraints on metabolic processes. Of the three different scaling processes that are explored in chapters 2 and 3 (attack rate, maximum ingestion rate and maintenance metabolism), the maintenance rate scaling is probably most constraint. A constant mass-specific maintenance rate is used in both DEB and the Metabolic Theory of Ecology (MTE) and arises from the idea that each cell (in MTE), or unit of structure (in DEB theory), requires a fixed amount of energy for maintenance (Hou et al. 2008; Kooijman 2010; West et al. 2001).

The results of chapters 2 and 3 show that when the maintenance is fixed at one, the scaling of energy supply (maximum ingestion rate and attack rate) evolves to closely match this linear maintenance scaling. This close match represents only a slight deviation from ontogenetic symmetry. Further research could study the factors that lead to an increase of this deviation. Examples are increasing juvenile mortality, size-dependent cannibalism or interference competition. In combination with a fixed maintenance scaling, such asymmetries through size-dependent ecological conditions could lead to asymmetries in the metabolic scaling processes of organisms. Preliminary explorations show that these factors can give rise to ontogenetic asymmetry in terms of a size-dependent maintenance resource density (box 7.1). In such a way, ontogenetic asymmetry evolves as a consequence of more complex ecological interactions.

7.3 – Eco-evolutionary dynamics of ontogenetic asymmetry in more complex communities

Ontogenetic asymmetry and intraguild predation

Ontogenetic asymmetry in intraguild predation (IGP) systems can arise through different ecological processes. In intraguild predation systems, an intraguild predator and an intraguild prey (or intermediate consumer) also compete for a basal resource (Polis et al. 1989). In many IGP systems, intraguild predation results from an ontogenetic diet change in the intraguild predator. The intraguild predator switches from feeding on the resource as a juvenile, to preying on consumers and, potentially, juvenile predators (cannibalism) as an adult. This interaction is referred to as life-history intraguild predation (LHIGP; Hin et al. 2011; Pimm and Rice 1987; Van de Wolfshaar et al. 2006). Competition between predators and prey is therefore restricted to the juvenile life stage of the intraguild predator. Both the ontogenetic diet change and cannibalism induce ontogenetic asymmetry in the intraguild predator. The ontogenetic diet change leads to ontogenetic asymmetry through a shift in the mass-specific resource ingestion rate at maturation. This shifts also affects the mass-specific biomass production rate. Cannibalism induces ontogenetic asymmetry because it leads to higher resource inges-

tion and production rates for adult predators and increased mortality rates of juvenile predators.

Ontogenetic asymmetry from different sources (*e.g.* cannibalism or ontogenetic diet shifts) manifests itself either as a maturation bottleneck or as a reproduction bottleneck. In population dynamical equilibrium, ontogenetic asymmetry in the intraguild predator leads to asymmetry in the productivity of the different predator life stages (De Roos and Persson 2013; De Roos et al. 2007). A high density of consumers, or high rates of cannibalism, lead to a net source of biomass in the adult stage and a net sink of biomass in the juvenile stage. Consequently, in such a population, biomass turn-over rate is regulated most by maturation (maturation bottleneck). Alternatively, low consumer density and high resource density lead to a net source of biomass in the juvenile stage, and a net loss of biomass in the adult stage. Hence, biomass turn-over in such a population is regulated most by reproduction (reproduction bottleneck; De Roos et al. 2007). The type of bottleneck largely determines the size distribution. High juvenile/adult biomass ratio is indicative of a maturation bottleneck and low juvenile/adult ratio points to a reproduction bottleneck (De Roos et al. 2007).

In fact, in absence of cannibalism there are only two possibilities for ontogenetic symmetry to occur in this system. In population dynamical equilibrium, ontogenetic symmetry occurs when there is no energetic bottleneck in the life history of the intraguild predator. For this to happen, the population maturation rate in biomass must equal the population reproduction rate in biomass (De Roos et al. 2007), which implies that both resource ingestion rates and mortality rates are equal for juveniles and adults. The first possibility for this, is when consumer and resource biomass densities are equal. This possibility for ontogenetic symmetry represents an exceptional case that cannot be predetermined, but depends on how resource and consumer densities equilibrate. The second possibility is when adult predators can still feed on the resource, because they undergo a partial diet shift (diet broadening), instead of a complete diet shift. With a diet broadening, ontogenetic symmetry arises when consumers are absent from the population dynamical equilibrium. Furthermore, adult and juvenile predators must feed with equal efficiency on the resource. This possibility only exists in the model of chapter 5, when juvenile and adult attack rates on the resource are equal.

Persistence of life history intraguild predators depends on ontogenetic asymmetry

Theoretical work on LHIGP systems shows that intraguild predators generally only persist in a reproduction regulated state, because the maturation bottleneck leads to predator exclusion (Hin et al. 2011; Van de Wolfshaar et al. 2006; Van Leeuwen et al. 2013). An ontogenetic diet shift in the intraguild predator generally leads to

two types of stable community equilibria. Predators only persist in one of these two stable states and in this state, predator biomass turn-over is generally regulated by reproduction. Due to a strong maturation bottleneck, predators cannot invade the alternative community state.

Chapter 4 shows that cannibalism in LHIGP is detrimental for the persistence of the predator, because it changes the reproduction bottleneck into a maturation bottleneck. Cannibalism in the intraguild predator has two effects: it increases biomass production in the adult stage and it increases mortality in the juvenile stage. Both these effects increase the maturation bottleneck. This results in the disappearance of the stable ecological equilibrium in which predators can persist (figure 4.3). The increased juvenile mortality is the main effect of cannibalism that disrupts predator persistence (chapter 4).

In cannibalistic LHIGP systems, intraguild predators can only persist when they can overcome the maturation bottleneck. This is for example the case when juvenile predators are superior in resource competition compared to consumers. In such a situation, cannibalism even promotes coexistence between intraguild predators and prey, because it diminishes the competitive effects of predators on consumers (chapter 4). These results show the importance of the strength and direction of ontogenetic asymmetry for the persistence of species in complex ecological communities.

Evolution of ontogenetic asymmetry in intraguild predators
Selection on resource specialization can alter the degree and direction of ontogenetic asymmetry. As argued in chapter 5, ontogenetic omnivores often face an ontogenetic trade-off in resource specialization, due to genetic constraints between different life stages. As a consequence, increased juvenile specialization on the resource leads to adults being less adapted to inter- and intraspecific predation. Vice versa, increased adult predation rates diminish foraging efficiency of juveniles on the resource. In terms of ontogenetic asymmetry, increasing juvenile specialization increases mass-specific ingestion and biomass production rates of juveniles and decreases mass-specific ingestion and biomass production rates of adults. This reinforces the reproduction bottleneck. Alternatively, increasing adult specialization strengthens the maturation bottleneck, through an increase in adult mass-specific ingestion and biomass production, and a concomitant decrease of those rates for juveniles. But does selection lead to more or less ontogenetic asymmetry in life-history intraguild predators?

If selection tends to decrease ontogenetic asymmetry, adult specialization should evolve when intraguild predators persist in a reproduction-regulated population. Conversely, juvenile specialization should evolve when intraguild predators persist in a maturation-regulated population. Because the opportunity for persistence in a maturation-regulated population is limited, we mainly expect to see evolving adult

specialization. In non-cannibalistic predators, this indeed occurs for the diet shift scenario, where intraguild predators coexist with consumers and are reproduction regulated (low juvenile/adult biomass ratio; chapter 5). However, in the diet broadening scenario, consumers are excluded from the stable community equilibrium. In absence of cannibalism, adults only feed on the resource. Therefore, there are no benefits of increasing adult specialization on consumers and no costs of increasing juvenile specialization on the resource. The community dynamics hence determine the effectiveness of the ontogenetic trade-off in constraining evolutionary change. Consequently, selection favors juvenile specialization.

Due to eco-evolutionary feedbacks, the processes that drive selection are not necessarily equal to what selection ends up achieving. Evolution can select for more ontogenetic *symmetry*, but when the ecological feedback loop changes fast enough, selection can result in more ontogenetic *asymmetry*. This happens because the indirect effect through the ecological feedback loop is opposite to the direct effect of selection (Richard 2014; Richard et al. 2015). In the diet shift scenario, selection increases adult specialization, which potentially releases the reproduction bottleneck. However, the community equilibrium responds by a decrease in consumer biomass and an increase in resource biomass. This response increases the reproduction bottleneck and counters the direct effect of selection. The combined result of the direct effect of selection (the decrease in juvenile attack rate on the resource and a concomitant increase in adult attack rate for predation) and the indirect effect of selection (decreasing consumer biomass and increasing resource biomass), is a relatively small change in ontogenetic asymmetry (juvenile/adult biomass ratio stays approximately constant). Ultimately, selection towards increasing adult specialization results in evolutionary suicide of the intraguild predator. Evolutionary suicide is probably the most convincing example of how the outcome of evolution is disconnected from the processes that drive evolutionary change (Ferrière and Legendre 2013).

To answer the question whether selection leads to more or less ontogenetic asymmetry in non-cannibalistic LHIGP systems hinges on two contingencies. First, the ontogenetic trade-off must be fully operational. In the diet broadening scenario when consumers are absent, stabilizing selection against poor adult feeding ability is missing. In the diet shift scenario, the ontogenetic trade-off is functional. In this case, selection is directed towards less ontogenetic asymmetry. However, the ecological feedback loop prevents selection from decreasing the level of ontogenetic asymmetry.

Although the direction of selection coincides with a decrease in the reproduction bottleneck, we cannot conclude that ontogenetic asymmetry is the main determinant of the strength and direction of selection on the ontogenetic trade-off. Moreover, the cannibalistic case provides an example where selection is disconnected from the type of ontogenetic asymmetry. Cannibalism changes the reproduction bottleneck to a
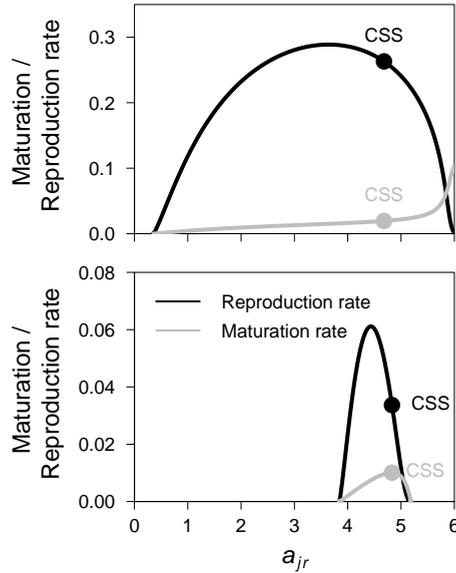
FIGURE 7.3 – Population-level biomass maturation and reproduction rates as a function of resource specialization (a_{jr}) of juvenile intraguild predators, as studied in chapter 5. Top panels are for the diet broadening scenario ($a_{ar} = 3$) and bottom panel for the diet shift scenario ($a_{ar} = 0$). All parameters as in table 5.2, in addition to $\beta = 1$. The dot indicates the position of the continuously stable strategy (CSS) for the resource specialization trade-off (equation 5.1). Each panel only shows the stable equilibrium in which the predator persists.

maturation bottleneck (chapter 4) and stabilizes selection on the ontogenetic trade-off (chapter 5). If selection on the ontogenetic trade-off corresponds directly to the type of ontogenetic asymmetry, the evolutionary equilibrium would correspond to the transition between maturation versus reproduction regulation. Figure 7.3 shows that this is not the case. Instead, selection is stabilized in a maturation regulated population. Possibly, evolution towards maturation regulation occurs because of the high benefits of cannibalism in a maturation regulated population, which is characterized by a high juvenile/adult biomass ratio.

Conclusions and perspective

Concluding, compared to the basic ecological setting as studied in chapters 2 and 3, ontogenetic asymmetry more readily evolves in the more complex ecological community of life-history intraguild predation (chapters 4 and 5). The direction of ontogenetic asymmetry has a considerable impact on persistence of intraguild predators and coexistence with intraguild prey. Ontogenetic asymmetry can drive evolutionary dynamics, but evolution does not necessarily act to minimize the extent of ontogenetic asymme-

try. This is because the indirect response of selection through the ecological feedback loop can counter the evolution of ontogenetic symmetry and because more (complex) ecological interactions (such as cannibalism) can induce evolution towards ontogenetic asymmetry. Therefore, a certain amount of ecological complexity (as in the nature and number of ecological feedbacks) seems a prerequisite for the evolution of ontogenetic asymmetry.

The evolution of cannibalism establishes a novel ecological interaction and, as such, provides a route to increased ecological complexity in simple communities. Cannibalism is an inherently size-dependent interaction (Claessen et al. 2004; Polis 1981) and therefore a good candidate to lead to the evolution of ontogenetic asymmetry in simple ecological communities (box 7.1). Furthermore, cannibalism can inhibit persistence of intraguild predators on ecological timescales (chapter 4), but also stabilize evolutionary dynamics and prevent evolutionary suicide (chapter 5). Cannibalism readily evolves in ecological models if there are not explicit disadvantages to cannibalistic feeding (Getto et al. 2005). Chapter 6 shows that cannibalism also evolves when cannibalistic feeding brings associated costs through increased mortality rates. Moreover, mortality from other sources, such as fisheries-induced mortality, promotes the evolution of cannibalism, by discounting the expected remaining lifetime of cannibals.

7.4 – Remaining questions and future directions

The above discussion shows that different levels of ecological complexity can result in different outcomes for the evolution of ontogenetic asymmetry. In a simple ecological system ontogenetic symmetry evolves, but more ecological complexity (multiple feedbacks in the ecological dynamics) can lead to the evolution of ontogenetic asymmetry. However, the influence of the nature and number of ecological feedbacks on the evolution of ontogenetic asymmetry is still very implicit. Future research can contribute to a more thorough understanding about the level of ecological complexity that is needed for ontogenetic asymmetry to evolve. Another aim is to get a more complete understanding of the conditions, under which selection leads to an increase or a decrease in ontogenetic asymmetry. Furthermore, if ontogenetic asymmetry evolves in response to increased ecological complexity, the obvious question arises how ecological complexity originates.

The most important prerequisite for studying the above questions, is a good understanding of the trade-offs and constraints that mark the boundaries of the evolutionary process. Currently, there is a focus on the variation in metabolic scaling with body mass and the possible adaptive consequences of this variation (Glazier 2005; Hirst et al. 2014). Unfortunately, there is little knowledge of the limits of this variation or about which trade-offs are most important. This knowledge will be helpful for making

further progress in understanding eco-evolutionary effects of ontogenetic asymmetry on populations and communities.

With more detailed information on the constraints and trade-offs that limit the evolution of ontogenetic asymmetry, the approach adopted in this thesis is promising for making further progress. In this thesis, complex ecological interactions are combined with evolutionary processes that shape individual-level dynamic energy budgets. This combination has not been used often (see *e.g.* Kooi and Van der Meer 2010; Troost et al. 2005), but has the potential to connect the evolution of metabolic organization and life histories to the complexities of ecological reality.

Box 7.1 shows that cannibalism can induce an evolutionary response in the scaling of ingestion rate with body mass. In turn, cannibalism readily evolves in ecological models (Getto et al. 2005), even if there are associated costs to cannibalistic feeding (chapter 6). An interesting avenue for future research is to study the coevolution between cannibalism and ontogenetic asymmetry. Is cannibalism evolution dependent on levels of ontogenetic asymmetry? And how is cannibalism influencing the selection on ontogenetic asymmetry?

Complexity does not only occur in ecological interactions. The metabolic organization of individuals is also highly complex. Although the DEB models used in this thesis are based on mass and energy conservation, they are simplified versions of metabolic organization, because they only consider a single metabolic compound (biomass). According to DEB theory (Kooijman 2010), heterotrophic organisms have at least two types of compounds, namely structural volume and energy reserves. However, the effect of adding explicit reserve dynamics only matters when considering variable food supply, as the reserve density equilibrates under constant food supply. The assumption of a constant food environment holds for most results in this thesis, with the exception of the adult-driven cohort cycles in chapter 2 (figure 2.1). Under variable food environments, periods of resource scarcity and starvation events become important. These events can be expected to considerably impact the evolution of the scaling of maintenance and ingestion with body size. Therefore, a full understanding of the origins of ontogenetic asymmetry is not complete without studying the effects of variable food supply on DEB models with explicit reserve dynamics.

Ultimately, the complexity of ecological systems with multiple feedbacks, should be integrated with the complexity of metabolic organization with multiple metabolic compounds, to answer questions about how complex life forms and ecosystems have coevolved, and how they are maintained.