Ontogenetic bottlenecks
Effects on intraguild predation systems and ecosystem efficiency

Birte Reichstein

"Experiments are needed to disentangle the roles of IGP and resource competition in determining realized guild structure"

(Polis et al. 1989)

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List of papers

This thesis is a summary and discussion of the following papers, referred to in the text by Roman numbers.

I. **Reichstein, B.**, Schröder, A., Persson, L., and De Roos, A.M. **2013.** Habitat complexity does not promote coexistence in a size-structured intraguild predation system. *Journal of Animal Ecology*. 82(1):55-62

II. **Reichstein, B**., Persson, L., and De Roos, A.M. Predator life-history affects persistence times in predators and consumers in a size-structured intraguild predation system. *Submitted manuscript.*

III. **Reichstein, B.**, Persson, L., and De Roos, A.M. Exclusive juvenile predator resource promotes coexistence in a size-structured intraguild predation system. *In review.*

IV. **Reichstein, B.**, Persson, L., and De Roos, A.M. Coexistence in size-structured intraguild predation system – promoted by ontogenetic diet shift in the consumer. *Manuscript.*

V. **Reichstein, B.**, Persson, L., and De Roos, A.M. **2015**. Ontogenetic asymmetry modulates population biomass production and response to harvest. *Nature Communications*. 6:6441.

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Other papers:

Schröder, A., Nilsson, K.A., Persson, L., van Kooten, T., and **Reichstein, B. 2009**. Invasion success depends on invader body size in a size-structured mixed predation-competition community. *Journal of Animal Ecology*. 78(6):1152-62.

Author contributions

Paper I
BR and AS conceived the study. BR carried out the experiment, analysed the data, and wrote the first draft of the paper. AS, AMdR, and LP contributed with comments to the final version of the paper.

Paper II
BR and LP conceived the study. BR carried out the experiment, analysed the data, and wrote the first draft of the paper. AMdR and LP contributed with comments to the final version of the paper.

Paper III
BR conceived the study, ran the model, carried out the experiment, analysed the data, and wrote the first draft of the paper. AMdR validated model results. AMdR and LP contributed with comments to the final version of the paper.

Paper IV
BR conceived the study, analysed the model, and wrote the first draft of the paper. AMdR validated model results and provided publication figure data. AMdR and LP contributed with comments to the final version of the paper.

Paper V
BR and LP conceived the study. BR carried out the experiment, analysed the data, and wrote the first draft of the paper. AMdR and LP contributed with comments to the final version of the paper.

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Abstract

Size-dependent differences between individuals in size-structured organisms have fundamental effect on population and community dynamics. Intraguild predation (IGP) is one specifically interesting constellation that often arises when two size-structured populations interact. Ontogenetic bottlenecks that determine population size-structure are affected by both population intrinsic as well as population extrinsic factors, and are therefore context-dependent. Surprisingly, size-structured IGP systems have mainly been investigated theoretically and especially long-term empirical studies are widely lacking. In this thesis I investigate empirically how habitat complexity, interaction strength, and stage-specific resource availabilities affect population processes and their effects on the dynamics of a size-structured IGP system. I conducted multi-generation experiments in a size-structured IGP system, with the Least Killifish (*Heterandria formosa*) as IG prey and the Common Guppy (*Poecilia reticulata*) as IG predator. With no alternative resource next to the shared resource, IG predator and IG prey could not coexist. Weak interactions only increased IG prey and IG predator persistence times and observed exclusion patterns depended on habitat complexity. An alternative resource for either the juvenile IG predator or the juvenile IG prey on the other hand promoted coexistence. However, this coexistence was context-dependent. Ontogenetic bottlenecks played a central role in the dynamics of the size-structured IGP system in general. In the final study I show that an ontogenetic bottleneck can, through changes in stage-specific resource availabilities, be affected in a way that leads to increased trophic transfer efficiency with potential effects on higher trophic levels.

Overall, the results emphasize importance of the broader context in which size-structured communities are embedded. Especially, when managing natural communities it is important to account for the combined effects of size-structure, stage-specific resource availabilities, and habitat structure. Specifically, when managing species that connect habitats or ecosystems all life-stages' environmental conditions must be consider in order to ensure strong predictive power of tools used for ecosystem management planning.
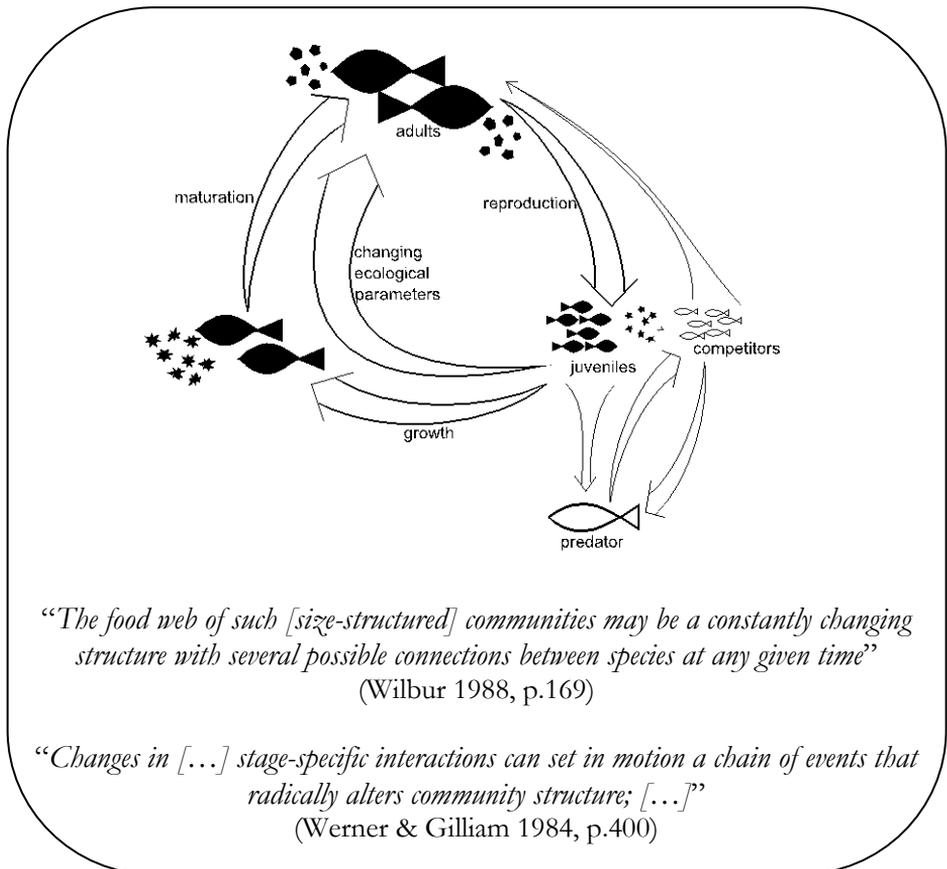
Introduction

Individuality

In natural systems many species are embedded in complex food webs, where they interact with each other. In order to facilitate our understanding of species interactions, traditionally we try to categorize species by their ecological role (predator, competitor …) and trophic level (producer, consumer, detrivor …). Nature, however, often evades this simple classification and species cannot be easily categorized. For example omnivory, which takes place when a species feeds on more than one trophic level, is a very common phenomenon in nature. However, a label 'omnivore' which we put on such species does not often sufficiently describe them, and even when looking at a single species pair one label is not enough. An omnivore may be the predator of a species that it also shares a resource with. This particular species pair would still require two labels: "predator-prey" and "competitors". Polis et al. (1989) provided us with the label "intraguild predation" (IGP) for such species pairs that involve in both predator-prey and competitive interactions. The authors also acknowledged that various types of IGP arise from different constellations: omnivorous IGP from size selective feeding, coincidental IGP from ingesting food with inhabitants, miscellaneous IGP from "accidental" feeding, asymmetric IGP when only one preys on the other, and symmetric IGP when both prey on each other. The authors further highlighted that size/stage-structure and diet changes over time play an important role for the occurrence of IGP. For example, a predator may prey on the juvenile stage and compete with the adult stage of a consumer, or a large predator species may include an earlier competitor in its diet at a later (larger) stage.

The majority of animal taxa are characterized by size-structured populations with individuals that exhibit ontogenetic niche shifts - qualitative and/or quantitative diet changes throughout their life cycle (Werner and Gilliam 1984). An individual's ecological role and trophic level in size-structured populations is rather determined by its body size (life stage) than by species identity. Similar sized individuals of different species may show more ecological similarities than differently sized individuals of the same species (Neill 1988). Consequently, in many cases categorization according to individual body size or life stage is more useful than categorization according to species identity.

Populations consisting of differently sized individuals come about by continuous growth over the main part of the individual's life cycle.

Continuous individual growth results in constantly changing size relationships and changes in individual size-dependent parameters e.g. resource use efficiency, metabolic demands, fecundity, and mortality (Peters 1983; Werner and Gilliam 1984; Wilbur 1988). Hence, as an individual grows the way it interacts with its environment changes over time:

"The food web of such [size-structured] communities may be a constantly changing structure with several possible connections between species at any given time"
(Wilbur 1988, p.169)

"Changes in […] stage-specific interactions can set in motion a chain of events that radically alters community structure; […]"
(Werner & Gilliam 1984, p.400)

This complexity should not be ignored when we study population and community ecology. Community structure is determined by the way species interact and how strong these interactions are. Species interactions are context-dependent and change with the number of species involved, relative body size, life history stage, and other biotic and abiotic factors (Wilbur 1988). To understand the processes that structure ecological communities and drive their dynamics, it is fundamental to understand how individuals interact and how interactions change with time.

Ontogenetic bottlenecks

Using a species-centric approach assumes that all individuals can be represented by the population mean and that population changes over time can be described accounting only for mortality rate (deaths) and reproduction rate (births) (Fig. 1A).

However, food-dependent individual growth and size-dependent differences fundamentally affect population dynamics and structure (as summarized in: Persson and De Roos 2013). Thus, to appropriately describe population changes of size-structured populations we need to account for each stage (e.g. non-reproducing juveniles and reproducing adults) separately (Fig.1B). For instance, in one possible scenario of a stage-structured species, juveniles are produced when adults reproduce. Juveniles then grow until they at a certain size become adults themselves (maturation). Hence, juveniles become fewer not only through stage-specific mortality but also through maturation. Adults become more when juveniles mature. Adults do not grow but produce new juveniles (reproduction), and become less through stage-specific mortality. Maturation and reproduction – two food-dependent processes – couple the juvenile and the adult stage dynamically.
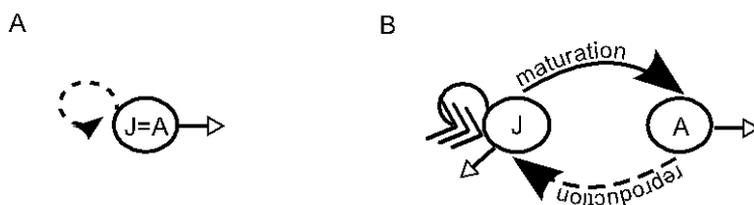

Figure 1: Population processes affecting population changes. (**A**) The species-centric approach. (**B**) The size-/stage-structured approach. A population consists of juveniles (J) and adults (A)**.** Dashed arrows represent reproduction. The circular arrow represents growth. The bended solid arrow represents maturation. Straight arrows represent mortality.

Individual growth rates determine the time it takes individuals to grow through different stages and reach maturity, and thereby the rate of the inflow of new individuals to the adult stage. Reproduction rate determines the inflow rate of new individuals to the juvenile stage. Because these processes are food-dependent, their relative importance strongly rests on food availability. When juveniles and adults share the same resource, the resource is negatively affected by the stage-specific

feeding rates. Accordingly, the stages affect each other's resource supply and therefore are (intraspecific) competitors. How strong the intraspecific competition is, depends on stage-specific resource use efficiencies. Size-dependent differences in ecological parameters often lead to a situation in which stages differ in resource use efficiency with one stage being an inferior competitor. The term ontogenetic asymmetry was coined by Persson and De Roos (2013) to describe the phenomenon of size/stage-dependent differences in resource use efficiency within a population. In an ontogenetically symmetric population individuals do not differ in resource use efficiency.

The structure of populations with ontogenetic asymmetry is fundamentally affected by ontogenetic bottlenecks that impede population processes (maturation and reproduction) (Fig.2). For example, when the juvenile stage is the weaker competitor, the population is likely to experience a bottleneck in maturation rate (maturation limitation, (De Roos et al. 2007)). A population that is regulated through maturation limitation is characterized by low juvenile growth and maturation while adult reproduction is high and juvenile biomass accumulates. The opposite applies to a population that is regulated through reproduction limitation; here low reproduction and fast maturation result in adult biomass accumulation (De Roos et al. 2007).
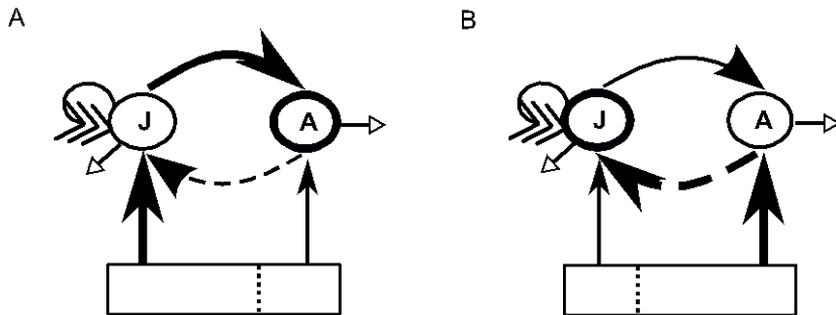

Figure 2: Ontogenetic bottlenecks in a stage-structured population. (**A**) Reproduction limitation when the juvenile stage is the more efficient resource user. (**B**) Maturation limitation when the adult stage is the more efficient resource user. The rectangular box represents the resource that either is used with different efficiencies (vertical arrows) or differs in stage-specific availability (separation with dotted line).

A fundamental consequence of ontogenetic asymmetry is that a population may respond with stage-specific biomass increase when subjected to increased mortality (e.g. harvest or predation). Increased mortality can relax the intraspecific competition which causes an ontogenetic bottleneck by increasing *per capita* resource availability, and thereby leading to an increase in the inflow to the non-limited stage which then increases in biomass (De Roos et al. 2007; Schröder et al. 2009b). This effect is strong when the stage that experiences the bottleneck is subjected to increased mortality but occurs also when both stages or only the non-limited stage is affected (De Roos et al. 2007; Schröder et al. 2009b).

Ecological parameters of growing organisms change over time and, in order to achieve optimal growth rates, ontogenetic niche shifts - changes in resource and/or habitat use with increasing size from birth to maximum size - are common in nature (Werner and Gilliam 1984). When stages feed on different resources the population regulating processes (maturation and reproduction) are not only determined by stage-specific resource use efficiencies but also by relative productivities of stage-specific resources. Also, the type of ontogenetic niche shift - discrete and complete, or continuous and incomplete - will affect population structure (Werner and Gilliam 1984). Discrete habitat shifts, like in species with complex life-cycles (e.g. amphibians), create a connection across ecosystems or habitats because juvenile and adult stages are spatially separated but dynamically coupled via reproduction and maturation (Schreiber and Rudolf 2008; Guill 2009; de Roos and Persson 2013). In such systems, the abundance/biomass of one stage in its habitat is not only determined by the productivity in its own habitat. For example, at identical environmental conditions, the juvenile stage may be very abundant (more productive adult habitat: maturation limitation) or not (less productive adult habitat: reproduction limitation). Similarly, also when environmental conditions (e.g. productivity) are constant across habitats, population structure can either be juvenile-dominated or adult-dominated depending on habitat-specific productivity levels. The occurrence of different population structures, or community structures, at identical environmental conditions is described with the term alternative stable states (ASS). Consequently, environmental changes in one habitat may simultaneously affect another habitat due to changes in the population structure of a species with a discrete ontogenetic habitat shift and may, hence lead to regime shifts across habitat boundaries (Schreiber and Rudolf 2008).

Species interactions

Species are embedded in communities in which they interact in complex ways with other species. Complexity increases even further because population structure is not only determined by intraspecific interactions but also by interspecific interactions that all change as individuals grow. Which stages are most abundant in a population will determine the type of interaction that drives community dynamics and community structure (Rudolf 2011).

In a community context bottlenecks in the juvenile stage become especially important because they can determine how long it takes for an individual to grow through a predation window, to be able to use a more profitable resource, or to become a predator. Ontogenetic changes in resource use can be connected to trade-offs in resource use efficiency (Werner and Gilliam 1984; Mittelbach and Persson 1998). For example, morphological trade-offs may occur for herbivorous juveniles of an as adult carnivorous species (life-history omnivory). Consequently, small specialized species may dominate a resource that they share with the juveniles of an omnivorous species, thereby imposing a maturation bottleneck on the latter (Werner and Gilliam 1984; Neill 1988; Walters and Kitchell 2001). However, adult omnivores may have a positive effect on the juvenile stage by reducing competition when preying on their juveniles' competitor (Walters and Kitchell 2001). This positive effect however depends on the adult stage being sufficiently abundant and a severe depletion of the adult stage may lead to a collapse of the predator population (Walters and Kitchell 2001). This exemplifies the occurrence of two ASS, a predator-prey state where the predator is adult-dominated and the prey abundance is low, and a prey-only state where the prey abundance is high.

Further, ASS can occur when a predator has a positive effect on its own food supply because it feeds on the juveniles of a reproduction limited prey population and causes biomass overcompensation in the juvenile prey stage (emergent Allee effect, (De Roos and Persson 2002; Roos et al. 2003)). Here the predator-prey state requires sufficient predator abundance to sustain the positive feedback that leads to a juvenile-dominated prey population. When at too low abundance the predator collapses and the prey persists alone in an adult-dominated stage. Alternatively, a stage-specific predator may through biomass overcompensation in a prey population facilitate the invasion of a predator that specializes on the other prey stage (emergent facilitation, De Roos et al. 2008a). Also here, depending on initial population

structures different ASS occur: a two-predators-one-prey state, a one-predator (feeding on the limited stage)-prey state, and a prey-only state. These examples show how dramatically community dynamics and community structure depend on population structural changes.

Intraguild predation

Intraguild predation (IGP) is widespread in nature and describes the phenomenon of two species involved in a predator-prey interaction and competition for a common resource (Polis & Holt 1989, Arim & Marquet 2004). IGP systems received a lot of attention, because theoretical predictions suggested that IG predator and IG prey coexistence should only occur at intermediate resource productivities (Polis and Holt 1992; Holt and Polis 1997; Diehl and Feissel 2001). In contrast to a classic tri-trophic food chain (resource-prey-predator), the IG predator´s persistence is not solely dependent on the presence of its IG prey because the IG predator also feeds on the shared resource. Several consequences result from this additional feeding link (Diehl and Feissel 2000, Mylius et al. 2001, Borer et al. 2007): the IG predator can invade a system at lower resource levels in comparison to a tri-trophic food chain. At intermediate resource levels, depending on initial condition two alternative stable states (ASS) occur, either all three (IG predator, IG prey, and resource) can coexist or only resource and IG predator. At high resource levels the IG prey is excluded. A necessary condition for coexistence is a competition-predation trade-off in the IG predator, so that the IG prey is the superior resource competitor (Holt and Polis 1997; HilleRisLambers and Dieckmann 2003; Amarasekare 2007a; Verdy and Amarasekare 2010).

In contrast to theoretical predictions, empirical observations report coexistence even at high productivities. This discrepancy inspired the investigation of more complex IGP models. Cannibalism in the IG predator and alternative resources to the IG prey were shown to promote coexistence and relax the necessary condition that the IG prey has to be the more efficient resource user (Daugherty et al. 2007; Holt and Huxel 2007; Rudolf 2007a). A seasonal or temporal refuge in the IG prey was shown to facilitate coexistence over a broader range of productivities (Amarasekare 2008). Habitat complexity was suggested to promote the persistence of IGP through a positive effect on the IG prey by weakening intraguild predation (Janssen et al. 2007).

Although size-structure and individual growth were, early on, pointed out as important variables affecting IGP dynamics the above studies mostly neglect size-structure and/or individual growth.

> *"Most IGP occurs in systems with size-structured populations by generalist predators that are usually larger than their intraguild prey. […] Because size is critical, historical effects and factors that influence the rate and duration of growth are of paramount importance."*
> (Polis et al. 1989, pp 305-306)

But, IGP commonly arises from life-history omnivory, i.e. feeding on different trophic levels throughout ontogeny (Pimm and Rice 1987). Taking stage-structure but not food-dependent growth into account Mylius et al. (Mylius et al. 2001) showed that a non-predatory stage in the IG predator promotes coexistence between IG predator and IG prey. Including size-structure and food-dependent development in both the IG predator and the IG prey, van de Wolfshaar et al. (2006) demonstrated a positive feedback for the IG predator between a competition-dominated juvenile phase and a later predation-dominated phase - a detrimental effect on coexistence. Note, that here it was assumed that the IG predator can reproduce even when only feeding on the shared resource. On the other hand, it has recently been shown that when the IG predator's reproductive success strongly depends on the IG prey, coexistence is promoted in size-structured IGP systems (Hin et al. 2011; Schellekens and van Kooten 2012; Hartvig and Andersen 2013).

An extensive body of unstructured and size-structured IGP theory is currently developing fast, while thorough empirical testing of this theory is lagging behind. The majority of empirical IGP studies are short-term within generation studies and usually use, as model organisms, microbes or invertebrates. Long-term multi-generation IGP studies in general but specifically on vertebrates are scarce. Multi-generation studies are fundamental because short-term experiments may not be useful to predict the long-term dynamics of a community (Briggs and Borer 2005). Last but not least, short-term experiments investigating size-structured interactions neglect individuals' changes in size and the related dynamic changes in interaction strengths, interaction type, and trophic structure that all fundamentally affect community dynamics (Miller and Rudolf 2011; Rudolf and Lafferty 2011; Persson and De Roos 2013). At the departure point of this thesis I was aware of only two empirical multi-generation size-structured IGP studies. These demonstrated that the

size-structured IGP dynamics depend on initial conditions (Montserrat et al. 2008) like initially realized size-dependent interactions (Schröder et al. 2009a).

Ecosystem efficiency

Biomass production, trophic structure (food chain length), and community stability are determined by the efficiency of energy transfer between trophic levels (trophic transfer efficiency, TTE)(Hairston et al. 1960, Oksanen et al. 1981). Already Lindeman (Lindeman 1942) identified system productivity and trophic transfer efficiency as important factors determining patterns in biomass production. To increase biomass production either an increase in system productivity and/or an increase in TTE is necessary. Given constant system productivity, TTE is the crucial factor determining biomass production. TTE varies with metabolism, food quality, and species diversity, and differs therefore between and within trophic levels (Lindeman 1942; Neill 1975; Leibold and Wilbur 1992; Hairston and Hairston 1993; Shurin et al. 2002; Ernest et al. 2003; Borer et al. 2005; Shurin and Seabloom 2005; Shurin et al. 2006; Trussell et al. 2006; Barnes et al. 2010; Tanaka and Mano 2012; Smith et al. 2013). Studies on TTE are traditionally species-centric assuming no individual differences in ecological parameters within species. However, the majority of species grow substantially over their life-cycle and stage-dependent differences (ontogenetic asymmetry) in individuals' ecological parameters rather than ontogenetic symmetry have recently been suggested to be the rule in nature (Persson and De Roos 2013). Ontogenetic asymmetry may affect population level TTE. As described earlier, stage-dependent intraspecific differences in resource use efficiency and metabolic rates have been shown to affect population and community dynamics significantly (Barnes et al. 2010; Miller and Rudolf 2011; Persson and De Roos 2013). Within one population individuals of different stages very likely differ in transfer efficiency and therefore contribute differently to population-level energy transfer. Hence, population structure and stage-dependent resource availability may affect population level energy transfer and hence ecosystem efficiency.

Objectives

The overall objective of this thesis is to improve the understanding of how ontogenetic bottlenecks affect population biomass production, community dynamics, and ecosystem efficiency. A strong focus on communities with intraguild predation was chosen because, although rather extensively investigated theoretically, empirical tests and especially multigenerational studies on vertebrates are widely lacking.

The specific objectives of the five papers were to test:

I. How habitat complexity and its weakening effect on intraguild predation affects ontogenetic bottlenecks in and the dynamics of a size-structured IGP system.

II. How weaker intraguild predation *per se* affects ontogenetic bottlenecks in and the dynamics of a size-structured IGP system.

III. How an ontogenetic habitat shift in the IG predator and its effect on IG predator population regulation affects ontogenetic bottlenecks in and the dynamics of a size-structured IGP system, both in the presence and absence of habitat complexity.

IV. How an ontogenetic resource shift in the IG prey and its effects on IG prey population regulation affects ontogenetic bottlenecks in and the dynamics of a size-structured IGP system.

V. How stage-specific resource availability affects population regulation, population biomass production, and population responses to harvest.
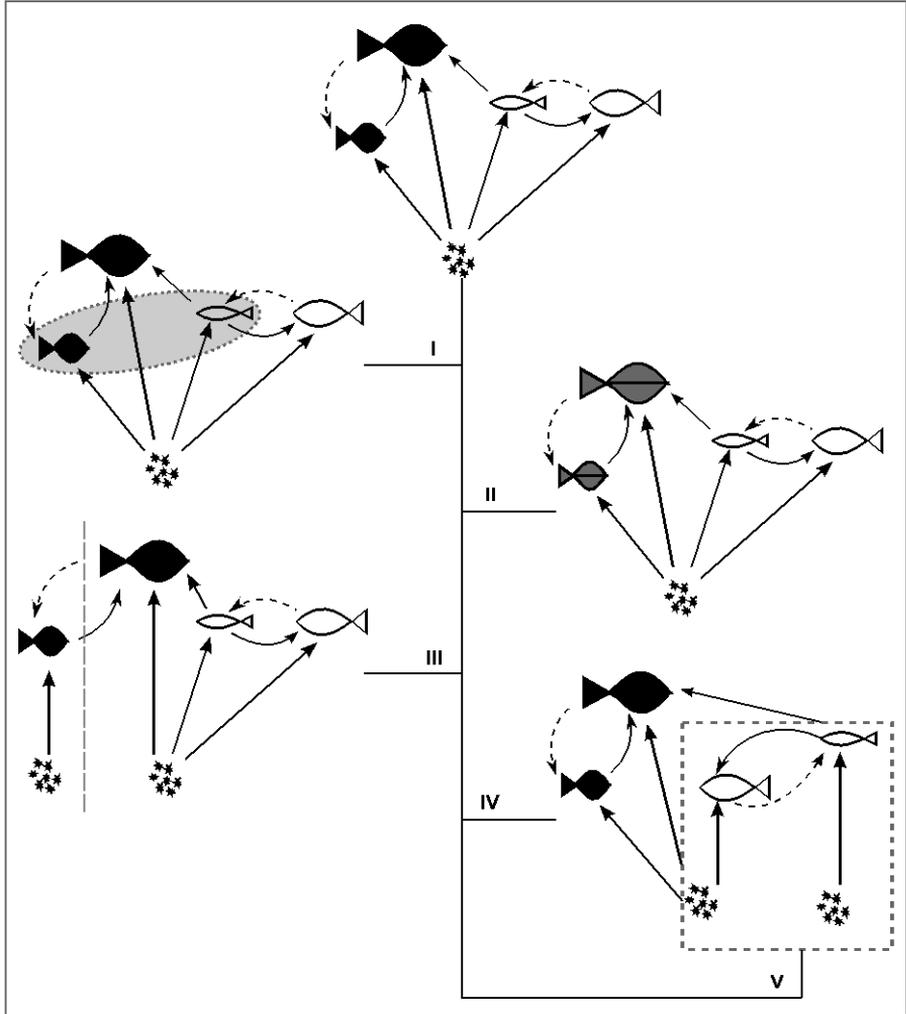
Visual summary of the work presented in this thesis. On top the departure point, the Common Guppy (black) – Least Killifish (white) IGP system. The first (**I**) modification was the addition of habitat structure (shaded ellipse) providing spatial refuge for small individuals. The second (**II**) modification was the use of a less voracious guppy population (grey). The third (**III**) manipulation was the introduction of an ontogenetic habitat shift in the Guppy (vertical dot-dash line = habitat boundary). Fourth (**IV**) the effect of an ontogenetic resource shift in the IG prey was theoretically investigated. Finally (**V**), the effect of stage-specific resource availability on population structure and response to harvest was investigated using Least Killifish populations. Solid and dashed bended arrows indicate maturation and reproduction, respectively. Straight solid arrows indicate energy flow from resource to consumer.

Study system and methods

To study the effects of ontogenetic bottlenecks in a size-structured IGP system and ecosystem efficiency I used both controlled experiments in the laboratory and a theoretical approach. In the experiments I used, as a model system, an artificially constructed IGP community consisting of two species of poecilliid viviparous fish that are easily bred and maintained in aquaria: the Common Guppy (*Poecilia reticulata*) and the Least Killifish (*Heterandria formosa*). All experiments were executed in accordance with the Swedish law for animal welfare.

Common Guppy – Least Killifish system

The Common Guppy occurs naturally in freshwater streams and ponds in the coastal regions of Northern Brazil, Venezuela, Guyana, Barbados and Trinidad. Males grow to a maximum length of 19 mm and females grow to a maximum length of 41 mm (Reznick and Miles 1989). Size at birth is 6-9 mm (Cheong et al. 1984; Reznick and Miles 1989) and the generation time is ten weeks. Depending on their origin populations of the Common Guppy show different life-history traits. I used two different populations, one that originated from a low predation site in the Quare River in Trinidad (LP-guppy, **paper II**) and one that originated from a high predation site in the Turure River (HP-guppy, **paper I & III**). LP-guppies have been shown to have a lower cannibalistic voracity (Nilsson and Persson 2013), grow slower, and reach smaller asymptotic body sizes (Reznick et al. 2001).

The smaller Least Killifish occurs naturally in freshwater streams and ponds in North-America in the coastal plains from North-Carolina to Florida. Males grow to a maximum length of 20 mm and females grow to a maximum length of 35 mm (Frank 1977). Size at birth is 5-8 mm and the generation time is seven weeks. All life-stages of the two species are easily distinguished visually.

When kept together with the Least Killifish the Common Guppy exhibits life history omnivory, large females (> 18 mm) feeding on juvenile Least Killifish (Schröder et al. 2009a) and the shared resource. Accordingly, in our system the Common Guppy was the IG predator and the Least Killifish was the IG prey.

Set - up

All experiments were performed in an aquaria system consisting of a total of 56 aquaria (each 80 L). The aquaria system was water-fed from a 600 L reservoir with a water exchange rate of 20 L per hour and equipped with air supply, thermostat and UV water sterilizer (Wiegandt HW 4000). Water salinity was kept at 900-1000 μS per cm to prevent infection with ectoparasites. Water temperature was kept at 25 °C. Aquaria were illuminated with 15 W neon lights in a 14 h light and 10 h dark regime and were equipped with computer controlled micro feeders. Every 28th day aquaria were fished empty and cleaned. Fish were sorted by gender and life-stage and were photographed. Photographs were used to count and measure fish on a computer screen. Measurements were then converted into biomass.

Experiments

The starting point for all IGP experiments were resident Least Killifish populations that then were subjected to invasion by the Common Guppy.

First, to investigate the effect of habitat complexity on the size-dependent invasion success of the Common Guppy (**paper I**), I introduced a range of HP-guppy invader size classes (XS, S, M, L, and XL) into resident Least Killifish populations in the presence and the absence of refuges. Additional short-term experiments on predator attack rate and juvenile competition were also performed.

Second, to investigate the effect of weaker intraguild predation as a result of the IG predator's life-history evolution contrasted to weaker intraguild predation as a result of habitat complexity (**paper II**), I used small (XS) and large (XL) invaders of the LP-guppy that is less voracious than the HP-guppy and recorded invasion success in the absence of refuges and compared the results to the invasion success of HP guppies in the presence and absence of refuges.

Third, to investigate the effect of an ontogenetic habitat shift in the HP-guppy on its invasion success and the potential for coexistence (**paper III**), I assigned two aquaria to each guppy population separating juveniles and adults and adjusted resource levels such that the population either was expected to be maturation or reproduction limited. New-born and matured guppies were moved between aquaria weekly and bi-weekly,

respectively. Initially only the juvenile aquaria were stocked with five juveniles and guppy invasion started when matured guppies were moved to the adult aquaria that initially were stocked with only the resident Least Killifish population.

Last but not least, to investigate the effect of stage-specific resource availability on population biomass production, population regulation, and response to harvest (**paper V**), I used populations of the Least Killifish. In order to control stage-specific resource availability each population was divided into two aquaria, one for juveniles and one for adults. New-born and matured individuals were moved between aquaria weekly and bi-weekly respectively. I applied two juvenile to adult resource ratio treatments with identical total resource input and three per capita mortality rates.

Stage-structured biomass model

In contrast to the effects of ontogenetic niche shifts in the IG predator, the effects of ontogenetic shifts in the IG prey have not been theoretically investigated for size-structured models. Therefore, to investigate how an ontogenetic resource shift in the IG prey affects ontogenetic bottlenecks in the IG prey population and the dynamics of a size-structured IGP system theoretically (**paper IV**) I used the stage-structured biomass modelling framework developed by De Roos et al. (2007, 2008). In the model both IG predator and IG prey exhibit ontogenetic niche shifts. The IG predator feeds as a juvenile on the shared resource and can as an adult feed on the shared resource and/or the juvenile IG prey. The IG prey feeds as a juvenile on the shared resource and/or an exclusive resource and as an adult on the shared resource. Both niche shifts indirectly affect interspecific competition, either juvenile IG prey and/or adult IG predators reduce their feeding on the shared resource. The model followed biomass dynamics and assumed that maximum ingestion and maintenance rates were mass-specific. Juvenile and adult stages were coupled through food-dependent maturation and reproduction.

I also used the stage-structured biomass modelling framework to estimate resource levels for **paper III** and to theoretically investigate community level consequences of the results reported in **paper V**.

Results and discussion

When I started the work on this thesis I was only aware of two empirical multigenerational studies investigating the dynamics of size-structured IGP systems. In a mite system Montserrat et al. (2008) showed that the outcome of IGP interactions depends on initial conditions. In a fish system Schröder et al. (2009a) showed that IG predator invasion success depends on invader body size - large predacious individuals succeeding and small competing individuals failing. In both studies the IG predator could persist on the shared resource alone and coexistence did not occur. IG predator or IG prey extinctions were caused by an ontogenetic bottleneck in the juvenile stage that was imposed by the IG prey or the IG predator, respectively. The Schröder et al. (2009a) study was the departure point for my thesis work.

Using a range of invader size-classes I showed that invasion success continuously increased with increasing invader size even when the initial interaction was competition (**paper I**). Initially, non-predacious invader size classes were exposed to a competitive bottleneck. The larger the invaders were the shorter the time they were exposed to this bottleneck was, and the better were their odds of reaching predacious size. Once invaders could predate on the IG prey they exposed the IG prey population to a detrimental bottleneck: removing juveniles from the IG prey population, while simultaneously reducing interspecific competition for juvenile IG predators. Coexistence did not occur because IG predator reproduction did not depend on the IG prey. Habitat complexity reduces the negative effect of the IG predator on the IG prey through weakening predation interaction and may promote coexistence (Persson and Eklöv 1995; Finke and Denno 2005; Janssen et al. 2007). I tested this hypothesis with invasion experiments similar to the above, providing green plastic thread to simulate filamentous macro algae (**paper I**). The presence of spatial refuges for small individuals reduced the strength of intraguild predation substantially. Large invader success was lower in the complex habitat than in the habitat without spatial refuges. Large IG predators were negatively affected in their ability to prey on the IG prey population and thereby reduce competition for their juveniles. An increased invasion success of small IG predator invaders reflected an effect of habitat complexity on competitive interactions. In complex habitats small and large individuals may differ in their spatial distribution (Werner and Hall 1988; Persson and Eklöv 1995). Juveniles of our IG predator have been shown to use spatial refuges 50 % of their

time when under predation risk (Nilsson et al. 2011), while juveniles of our IG prey use spatial refuges more rigorously. Depending on habitat use individual IG predators were positively (exploiting the refuge periphery) or negatively (staying in the refuge) affected. In the complex habitat the dynamics were driven by competition and all invader size-classes experienced a competitive bottleneck that determined survival and reproduction. Invasion success was 50 % and coexistence did not occur. When IG predators invaded successfully reproduction rates were high and a numerical dominance of IG predator juveniles may have reintroduced the juvenile bottleneck in the IG prey both directly through competition and indirectly through monopolizing the spatial refuges.

Habitat complexity reduced not only the strength of the predation interaction, but also affected the spatial distribution of large and small individuals and thereby the competitive landscape (**paper I**). I thereafter investigated the effect of weaker intraguild predation without changing the competitive landscape (**paper II**), using IG predator individuals from a population with a different evolutionary background, lower predation efficiency (Nilsson and Persson 2013) and smaller asymptotic size (Reznick et al. 2001). When large IG predators invaded IG prey populations always went extinct as was also the case when the more predacious IG predators invaded. IG prey extinction rates however were more similar to those experienced by IG prey populations in the presence of spatial refuges. Reduced IG prey extinction rates confirm the expected reduced predation impact of the IG predator. On the other hand, when small IG predators invaded, invasion success was similar to the invasion success of small more predacious IG predators (1 out of 4). Extinction rates of small IG predators however were lower than those of small more predacious IG predators and similar to small IG predators that invaded when spatial refuges were present. Lower small IG predator extinction rates reflect better competitive abilities. Accordingly, juveniles of the less predacious IG predator population are slightly larger and better adapted to competitive environments than those of the more predacious IG predator (Bashey 2008). Smaller asymptotic and larger offspring size affect not only the IG predator population's predacious and competitive abilities but limits also the scope for cannibalism. Lower predation and cannibalism capacity of the large IG predator resulted in stronger dependence on the shared resource and had positive effects on the competitively superior IG prey.

In summary, in size-structured IGP system with one resource weaker interactions did not promote coexistence because the manipulations of

the predator-prey interaction strength were coupled to indirect or direct changes of the competitive interactions. Nevertheless, weaker intraguild predation reduced extinction rates and prolonged IG predator and IG prey persistence times under stable environmental conditions. In temporarily or spatially variable systems, however, prolonged persistence times may be the key for the asymptotic persistence of IGP in natural systems (Amarasekare 2006; Amarasekare 2007a; Amarasekare 2007b).

With only one resource, none of the coexistence mechanisms suggested for unstructured IGP systems (habitat complexity and weak interactions) promoted coexistence in the size-structured IGP system. This result is in accordance with theoretical predictions for size-structured IGP systems with one resource and an IG predator that can persist on the shared resource alone (van de Wolfshaar et al. 2006; Hin et al. 2011). Adding an IG predator exclusive resource to a size-structured IGP system has been suggested to promote coexistence, when IG predator and IG prey are limited in resource overlap and the ratio between exclusive and shared resource is such that the IG predator is subjected to a maturation bottleneck (de Roos and Persson 2013). I tested the effect of an IG predator exclusive resource on coexistence (**paper III**), dividing my IG predator populations in two habitats (juvenile and adult habitat, manually moving matured and new born individuals) so that only adult IG predators shared resource and habitat with the IG prey. Effectively, I introduced an exclusive resource for only the juvenile IG predator stage. Adequate resource ratios I estimated by adjusting de Roos and Persson's (2013) model to my experimental setting and extracting resource ratios at which the IG predator population was maturation or reproduction limited.

I show that the juvenile IG predator exclusive resource indeed promoted coexistence. This positive effect however was context-dependent. With spatial refuges present, coexistence occurred always but only when the IG predator experienced a maturation bottleneck as was predicted by my model. In contrast, when the IG predator population experienced a reproduction bottleneck coexistence did not occur. But diverting from model predictions the IG predator did only exclude the IG prey in half of the replicates and was excluded by the IG prey in the other half. This discrepancy may be related to either that the model assumes only reproduction and no growth after maturation while our IG predator allocates energy to growth even after maturation, or to that the presence of spatial refuges affects the competitive landscape and leads to random invasion success as shown in **paper I**. Anyhow these treatments with

spatial refuges were expected to cohere best with the model predictions because the model did not account for cannibalism in the IG predator.

When no spatial refuges were present the IG predator almost always invaded successfully and coexistence occurred independent of resource ratio in 50 % of the replicates. Here the resource ratio effect was offset by direct and indirect positive cannibalism effects on adult and juvenile IG predators, respectively. As is characteristic for cannibalistic populations (Nilsson and Persson 2013), the IG predator populations had a small fraction of juvenile biomass and a larger fraction of large female (cannibal) biomass. Juvenile IG predators never experienced a maturation bottleneck, because they as well as the IG prey's numbers were kept low through predation. Because they were less dependent on the shared resource cannibalistic adult IG predators always reached large sizes.

In summary, these results suggest that potential positive effects of cannibalism (Rudolf 2007b; Ohlberger et al. 2012) and habitat complexity (Janssen et al. 2007) on coexistence are context dependent in size-structured IGP systems. The positive effect of habitat complexity required an IG predator exclusive resource and the right resource ratio while the positive effect of cannibalism required the IG predator exclusive resource only. Compared with the one resource system (**paper I** and **II**), I reduced interspecific competition when introducing the exclusive IG predator resource. Still, when interspecific competition was strong (low shared resource and refuges present) coexistence did not occur. Coexistence was highest when competition was intermediate (high shared resource and refuges present) and coexistence was intermediate when competition was weak (high shared resource and no refuges). Overall, the coexistence promoting effect was related reduced interspecific competition.

An IG prey exclusive resource also reduces interspecific competition and has also been suggested to promote coexistence in unstructured IGP systems (Daugherty et al. 2007; Holt and Huxel 2007). I investigated the effect of an IG prey juvenile exclusive resource on the dynamics of a size-structured IGP system (**Paper IV**) using a modelling approach. I show that an exclusive resource to the IG prey can promote coexistence. Coexistence extended to high productivities and was stable even when the IG predator was not energetically dependent on the IG prey. Coexistence also required that the juvenile IG prey depended strongly on the exclusive resource and a high shared to exclusive resource ratios. High shared to exclusive resource ratios imposed a maturation

bottleneck on the IG prey thereby reducing interspecific competition (low adult IG prey biomass). At high shared resource productivity coexistence was promoted when the IG predator was either strongly or weakly dependent on the IG prey. When IG predator reproduction depended on the IG prey predation driven coexistence occurred. When the IG predator did not depend on the IG prey competitive coexistence occurred. Overall, coexistence ar high productivities required a strong life-history separation in resource use in either the IG prey or the IG predator.

In general, IGP dynamics were fundamentally affected by ontogenetic bottlenecks that determine population structure, realized interactions and interactions strengths (**papers I-IV**). Ontogenetic bottlenecks arise from population intrinsic differences in stage-specific resource use efficiency or due to differences in stage-specific resource productivities. In the last study I investigated how stage-specific resource availability affects the occurrence of ontogenetic bottlenecks in a size-structured population without changing total resource input or resource quality (**Paper V**). I provide experimental evidence that stage-specific difference within species due to ontogenetic habitat shifts on its own strongly impacts vital ecosystem aspects such as standing biomass, biomass production, and response to harvest. Population biomass was 2 times higher when resource availability was biased towards the less efficient resource user. With equal stage-specific resource availability the population was subject to a reproduction bottleneck, because adults were the less efficient resource users. Channeling a larger fraction of the total resource input towards adults relaxed the bottleneck and the population was neither maturation nor reproduction limited. Changes in population regulating bottlenecks affected population responses to harvest. When no bottleneck was at play, all stages were negatively affected by harvest. When the reproduction bottleneck was at play, harvest led to juvenile biomass overcompensation. With this population level experiment I could show how easily ontogenetic bottlenecks can change when stage-specific resource availabilities change. This is important to realize because whether and what kind of ontogenetic bottleneck is at play has potentially far reaching implications for higher trophic levels, community structure and community stability (e.g. **papers III and IV**).

Concluding remarks

When model assumptions were met the empirical results reported here cohered rather well with the theoretical predictions of the stage-structured IGP biomass models. Accordingly it has recently been recognized that it is important to account for size/stage-structure when modelling ecological systems with the aim to make accurate predictions about how an ecological system response to harvest regimes or environmental changes.

Improving our understanding of the complexity of community interactions is critical for planning management strategies for exploited populations. Especially important is the development of methods to accurately predict population dynamics under different harvest regimes. The management of marine environments is of fundamental importance and size-structured communities are common in aquatic systems. Environmental conditions that determine ontogenetic bottlenecks (e.g. habitat structure, resource productivities, or predator presence) affect the outcome of size-structured community dynamics fundamentally (e.g. Claessen et al. 2009; Miller and Rudolf 2011; van de Wolfshaar et al. 2011; van Denderen and van Kooten 2013; Persson et al. 2014 and **papers I-IV**). The results reported in this thesis underpin the complexity and context-dependence of size-structured community dynamics. The outcome of the interaction between the same two species depended strongly on habitat structure, interaction strengths, population size-structure, and the presence and the relative productivities of alternative resources. Keeping this complexity in mind it is alarming that traditionally fisheries management strategies have been derived from single-species models not accounting for community interactions. When performing ontogenetic habitat shifts target species' interactions with other species may be sensitive to relative changes in habitat productivities and/or changes in habitat structure (**paper III**). Importantly, stage-specific biomass distributions determine whether a competitor or predator can coexist and the strength of competition or predation pressure other species are exposed to. The number of trophic levels present may differ between communities with different realized ontogenetic bottlenecks. Accordingly, I showed that population biomass production may change when stage-specific resource availabilities change (**paper V**). Not only the trophic structure but also the energy transfer efficiency within an ecosystem may change when community structure changes.

In summary, when managing natural systems it is of outmost importance to account for the combined effects of size-structure, stage-specific resource availability, and habitat structure on community dynamics. Especially, when managing species that connect habitats or ecosystems it is important to consider all life-stages' environmental conditions to be able to prevent catastrophic regime shifts.

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