Populations crossing habitat boundaries in the face of environmental change

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Discussion

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Predicting population and community responses to current environmental change presents a major challenge for ecologists. However, we have largely failed to generate accurate predictions and clear suggestions to reduce negative impacts (Dawson et al. 2011; Gilman et al. 2010; Grimm and Railsback 2012). In the introduction of this thesis, I argued that this failure stems from the fact that predictive studies of environmental change are not based on a strong theoretical foundation in which population and community dynamics emerge from interactions between individuals and their responses to the environment.

Individuals, rather than populations, respond to the environment and engage in the biotic interactions that shape community structure (Clark et al. 2011). Therefore, accurate predictions regarding population and community consequences of environmental change can only arise from explicit description of the multiple responses of the different individuals that make up the population. For instance, the majority of animal species have an ontogenetic habitat shift, where individuals change their habitat when they grow larger (Werner and Gilliam 1984). Because environmental change impact differs across habitats, individual responses are different among individuals of the same population using different habitats in different life stages.

By considering the effects of changing environmental conditions on individual life history and resource-consumer interactions, this thesis presents the ecological (chapter 2 and 3) and eco-evolutionary (chapter 4, 5 and 6) consequences of those changing conditions on populations with an ontogenetic habitat shift. In this chapter I summarize and discuss the main results presented in previous chapters.

7.1 – Ecological responses to a changing environment

Much of the literature on the biological impacts of environmental change has reported ecological effects including shifts in distributions and abundances of species as well as in their biotic interactions (Parmesan 2006; Sih et al. 2011; Walther 2010). Although most of these effects have been recorded at a population or species level, there is growing evidence that changes in life history traits and population dynamics in response to environmental change are intimately linked (Parmesan 2006). However, the mechanisms causing these joint responses remain largely unidentified. Chapter 2 contributes to fill this gap by identifying the mechanisms causing joint responses in life history traits and population dynamics of anadromous fish populations exposed to deteriorating environmental conditions. The main result of this chapter is that when stressors directly affect older individuals only, this causes a population decline that can lead to indirect positive effects in other life stages. This counterintuitive result can be explained as follows. Low survival and food abundance in the habitat used by older individuals as well as high cost of the migratory breeding travel negatively

impact the population birth rate by reducing the abundance, body size and energy reserves of reproducing individuals. As a consequence of low population birth rate, the density of individuals and hence competition for food resources in the breeding habitat is low, enabling a high body growth rate. This mechanism therefore explains the relation between negative impacts on individuals in later life stages and increased body growth rates in other life stages by taking into account population processes. In particular, the well supported fact that density-dependence is strong in the breeding habitat of salmon (Jonsson et al. 1998) and negatively affects individual body growth (Walters et al. 2013).

Characterizing mechanisms causing joint responses in life history traits and population dynamics exposed to environmental change may help to identify early warning signals of population declines and explosions. For instance, in the yellow-bellied marmot, larger body masses before hibernation correlate positively with population growth (Ozgul et al. 2010). The growing season of this mammal species has increased as a result of environmental change. This allows individuals to gain a large body mass before hibernation, resulting in lower winter mortality and an abrupt increase in population size. Likewise, the mechanism presented in chapter 2 reveals that an increased body growth rate of salmon individuals in the freshwater habitat may be a signal of population decline and the presence of negative impacts affecting individuals in the oceanic life stage.

Given that little information regarding the oceanic life stage of salmon is available, stressors affecting this life stage may be difficult to assess directly. Therefore, characterizing the indirect effects of these stressors on the better-known freshwater life stages may signal potential risks for the lesser-known oceanic life stages. By characterizing the indirect effects on freshwater life stages and population dynamics of deteriorating environmental conditions for individuals in the oceanic life stage, chapter 2 demonstrates that observations of increased growth rates in the freshwater habitat may be used as an early warning signal for deteriorating oceanic conditions, and therefore, provides managers with an additional tool to assess salmon populations in order to adopt conservation measures accordingly.

Populations are often exposed to multiple stressors simultaneously, especially in the current scenario of rapid environmental change that increases the diversity of stressors (Crain et al. 2008). Yet, most research addressing the consequences of environmental change has documented the individual effects of various stressors on populations and communities, while the cumulative and interactive effects of various stressors in combination are poorly studied (Crain et al. 2008). The cumulative effect of multiple interacting stressors is often not the result of a simple addition of the independent negative effects of these stressors. In fact, chapter 3 demonstrates that multiple stressors interact in a highly non-linear manner and thereby, counterintuitively, mitigate each

other's negative effect. On their own, both increased costs of the breeding migration and low marine food levels negatively affect anadromous fish populations, as shown in chapter 2. But, unexpectedly, low marine food levels benefit as opposed to threaten the ecological success of anadromous populations when these are negatively affected by high costs of the breeding migration.

The individual energy budget plays a key role in this counterintuitive effect. Individuals switching to higher food levels in the ocean reach larger sizes with concomitant larger migration costs but have lower energy densities. Biomass production is fueled by energy, but covering metabolic maintenance and the costly breeding migration also require energy; therefore, the processes whereby individuals acquire and utilize energy are causal mechanisms shaping population abundance and biomass. Previous population models of migratory fish lacked an explicit description of the individual life history in terms of the energetic processes described above. These models did therefore not account for the mechanism by which the two stressors interact and mitigate each other's negative effect.

Empirical evidence shows that mitigating interaction between multiple stressors may be common in nature. Crain et al. (2008) synthesized 171 studies manipulating multiple stressors in marine ecosystems and found found that in 38% of the studies stressors mitigate each other's negative effect, while in 36% they exacerbate each other's negative effect and only in 26% their effect is equal to the addition of the independent negative effects. This meta-analysis therefore showed that stressors mainly interact in a non–linear manner (antagonistic 38% and synergetic 36%). Predicting the ecological consequences of multiple stressors is therefore challenging and requires gaining further insight into the mechanisms causing these non-linear effects. Chapter 3 shows how such consequences can be investigated by integrating individual energetics and life history into population models.

7.2 – ECO-EVOLUTIONARY RESPONSES TO A CHANGING ENVIRONMENT

With environmental change come novel conditions that trigger ecological and evolutionary responses simultaneously. Although most studies have focused on the ecological effects of environmental change, there is growing evidence that rapid evolutionary change in response to the novel conditions is widespread in wild populations (Allendorf and Hard 2009; Olsen et al. 2004; Palkovacs et al. 2012; Singer et al. 1993; Woodward et al. 2007). The evolution of life history traits has received particular attention in this context of rapid environmental change (Sih et al. 2011). This is due to the fact that these traits determine individual fitness and thus individual viability, which in turn influence demographic processes and ultimately population persistence. Traditionally, research on life history evolution has been carried out through an ap-

proach in which the optimal life history traits are inferred by means of an optimization of individual fitness that ignores ecological interactions between individuals (Parker and Smith 1990). However, the fitness of an individual is the result of its interactions with competitors, resources, and natural enemies.

Chapter 4 demonstrates that considering ecological interactions in the evolution of life history traits can overturn the result of an optimal life history assessment based exclusively on individual optimization principles. This chapter shows that increasing size-dependent mortality in the adult habitat will decrease the body mass at which individuals switch from their natal habitat to the adult habitat. This result is in contrast with optimization theory, which would in this case predict the exact opposite, namely that they switch at a larger body size. These results are derived while keeping the life expectancy of the individuals in the adult habitat constant and hence express the effect of just the nature of the mortality source (size-dependent vs. size-independent) while eliminating the effect of the absolute magnitude of mortality.

This evolution to switching habitats at smaller body sizes when mortality is more size-dependent is the consequence of population processes. In particular, it results from the indirect effects that are mediated by changes in the strength of competition and the differential effects that size-dependent and size-independent mortality have on density dependence processes via population structure. Inferring optimal life history traits from maximizing individual fitness in isolation inevitably ignores density dependent feedbacks to and from the population. It is therefore not surprising that such an approach leads to a different evolutionary outcome.

Empirical evidence demonstrates that environmental change frequently alters population abundance (Ehrlén and Morris 2015) and structure (Allendorf and Hard 2009), which, in turn, affect density dependence processes. Chapter 4 demonstrates that those effects on density dependence processes shape the evolution of life history traits and therefore cannot be overlooked when investigating the eco-evolutionary consequences of a changing environment.

Abrupt and dramatic transitions in the composition and functioning of diverse ecosystems, including lakes, coral reefs, deserts, woodlands and oceans have been attributed to the existence of alternative ecosystem stable states (ASS) for the same set of conditions. Existing ecological theory on ecosystems with alternative stable states only considers catastrophic ecosystem regime shifts as a consequence of perturbations of abiotic conditions to values beyond a specific threshold value (Scheffer et al. 2001). However, the possibility that such regime shifts may result from phenotypic changes has up to now been overlooked. Furthermore, the idea that selection acts as a driver of phenotypic trait changes and thereby causes a regime shift to an alternative ecosystem state is equally novel and unexplored.

Habitats hosting different life stages of organisms with an ontogenetic habitat shift are indirectly connected through the flux of individuals between them. Schreiber and Rudolf (2008) showed that, as a consequence if this connection, multiple stable community states exist under a set of values of mortality risk or food resource productivity in these habitats. As a result, changes in mortality risk or food resource productivity in either habitat can cause dramatic ecological changes in the population and its food resources in both habitats simultaneously. Chapter 5 shows that these alternative ecological stable states (ASSs) exist under a set of values of the timing of the habitat shift as well. Consequently, natural selection can drive this trait to values beyond a critical value (tipping point), which causes an abrupt regime shift to a contrasting ASS. This evolutionary process can, in turn, cause gradual and abrupt ecological changes in the communities that host the different life stages.

The trait-based ASSs describe in chapter 5 suggest that altered selective pressures as a result of changes in environmental conditions (i.e. human-induced evolution), which are increasingly documented in wild populations (Allendorf and Hard 2009; Sih et al. 2011; Woodward et al. 2007), may be an important cause of regime shifts. Chapter 6 demonstrates that the evolutionary process initiated by altered selective pressures can drive trait values beyond the tipping point where a regime shift occurs. Therefore, changes in environmental conditions may not occur beyond a threshold and therefore do not immediately cause an abrupt regime shift, but it may trigger an evolutionary process that ultimately causes a delayed regime shift to a contrasting ASS.

Chapter 6 therefore contributes to the body of theory on ecosystems resilience by presenting a new mechanism whereby changes in environmental conditions cause delayed abrupt regime shifts in nature. Through this mechanism it is possible that regime shifts in ecosystems, which are observed in the present, are the consequence of perturbations that occurred in the distant past. The mechanism that is the ultimate cause of a documented regime shift may therefore be impossible to determine from a correlation between the time series of the ecosystem state and measured values of the abiotic environment, which is common praxis at present (Scheffer et al. 2001).

Although most research addressing the effects of environmental change has focused on a separate understanding of its ecological and evolutionary consequences, simultaneous ecological and evolutionary responses are common in nature (Urban et al. 2012). Moreover, rapid changes in phenotypic traits can have important effects on ecological processes (Palkovacs et al. 2012). Such joint responses should in fact be the rule because, as I mentioned above, environmental change frequently affects population abundance. In turn, changes in population abundance alter demographic dynamics that differentially affect the fitness of individuals with different phenotypes, thus triggering an evolutionary response. Chapters 4, 5 and 6 demonstrate that

considering both ecological and evolutionary responses to changing environmental conditions yields unexpected outcomes. Specifically, the result of chapter 4 contradicts classical theory on evolution of life history traits that is based only on individual optimization. The result of chapter 5 shows that phenotypic changes can affect the resilience of ecosystems with alternative stable states, in contrast to traditional theory in ecology that assume that only external conditions affect the resilience of these ecosystems. The result of chapter 6 expands the possible causes of regime shifts in ecosystems with alternative stable states after a perturbation. These results join recent research efforts that have documented the emergence of novel phenomena when both ecological and evolutionary processes are considered in concert (Bolchoun et al. 2017; Norberg et al. 2012; Palkovacs et al. 2012; Urban et al. 2012).

7.3 – ASPECTS TO CONSIDER IN THE FUTURE WHEN INVESTIGATING RESPONSES TO A CHANGING ENVIRONMENT

Up to this point I have argued for the integration of individual life history, ecological interactions, and eco-evolutionary dynamics in a theoretical foundation that serves as a framework of an explanatory and predictive ecological science. Some aspects of life history, ecological interactions, and eco-evolutionary dynamics have been considered in different chapters of this thesis. We should not forget that modeling approaches necessarily simplify the complexity of natural systems. In this section I discuss other aspects that should be considered in future research in this field.

Complex communities

In this thesis, I investigated the ecological and eco-evolutionary consequences of changing environmental conditions on populations with an ontogenetic habitat shift by considering the interplay between individual life history and ecological interactions. Throughout this thesis, I have considered intraspecific competition via resource-consumer interaction. Populations, however, inhabit more complex communities: besides their interaction with resources, they interact with competitors of other species and with natural enemies. Such interactions have large effect on the stability and structure of populations and communities.

de Roos and Persson (2013) demonstrate that two predator species that forage in different habitats on the juveniles and adults, respectively, of a prey species with a shift at maturation between these habitats reciprocally facilitate each other as a consequence of bistability (the same type of bistability as presented in chapters 5 and 6). Therefore, extinction of one of the predators results in extinction of the stage-specific predator in the other habitat for a wide range of resource productivities.

Chapters 4, 5 and 6 demonstrate that mortality, which may be caused by predation, affects the evolution of the timing of the habitat shift. Therefore, by foraging, the predators affect this life history trait in their prey population. Since the timing of the habitat shift determines the recruitment of prey from one habitat to the other, the predator populations influence the prey biomass in each habitat and thus their own food availability. This raises the questions: How do habitat-specialized predators affect the evolution of the timing of the habitat shift and their own persistence when this trait evolves? May the presence of one or both predators stabilize the eco-evolutionary cycles observed in chapter 5? How does this life history trait of the prey coevolve with diet preference traits of the two predators?

In this thesis I assumed a very simple food web with a structured consumer feeding on unstructured prey. However, in marine pelagic ecosystems the food web can consist of at least four trophic levels: the primary producers (phytoplankton), the zooplankton that forages on the phytoplankton, zooplanktivorous fish (forage fish) and piscivorous fish (top predators), in which ontogenetic shifts are common (de Roos and Persson 2013). In this system, species that dominate the zooplankton (copepods) increase in body size up to 2 orders of magnitude (Kiørboe and Sabatini 1994), while fishes grow up to 4 orders of magnitude in size (Werner and Gilliam 1984) throughout the life cycle. Therefore, marine food webs in their simplest representation include three trophic levels of consumers comprising at least one population with a pronounced size-structure.

The introduction of additional size-structured populations is likely to increase considerably the complexity of the ecological stage where the evolutionary play takes place. de Roos and Persson (2013) identified three alternative stable community states occurring under the same conditions of resource productivity when only two trophic levels (prey and predator) are size-structured and the predator has an ontogenetic niche shift. We currently can only guess at the ecological consequences of three size-structured populations operating at different trophic levels and supported by an unstructured producer population. This opens an enormous scope for future research to understand how life history traits coevolve in interacting size-structured populations with ontogenetic shifts and how a changing environment affects these coevolving populations.

Phenotypic plasticity

Faced with a changing environment, populations may respond by adapting. Adaptive phenotypic change can be mediated by phenotypic plasticity, which is the range of phenotypes that a single genotype can express as a function of environmental conditions, or by genetic evolution, in which existing genetic variants that are capable of

coping with the novel conditions are selected for. A meta-analysis suggests that in response to environmental change the contribution of phenotypic plasticity to adaptation is greater than that of genetic evolution in phenotypic traits (Hendry et al. 2008). However, given that phenotypic change does not guarantee increased population viability, a future avenue of research should investigate under which conditions phenotypic plasticity or genetic evolution or both increase population viability.

Most life history traits exhibit plasticity in response to environmental conditions (Caswell 1983) and this plasticity can alter demographic rates and ecological interactions (Miner et al. 2005). Phenotypic plasticity hence has the potential to influence stability and composition of population and communities. A first theoretical approach in a predator-prey system suggests that the source of phenotypic change, that is phenotypic plasticity or genetic evolution, differentially affects population dynamics (Cortez 2011). How do such differential effects influence the stability and composition of communities in response to a changing environment? Do the interaction of ecological and selective processes after a perturbation differ when phenotypic changes are mediated by phenotypic plasticity or genetic evolution? Elucidating the effects of phenotypic plasticity and genetic evolution on ecological processes and the feedback between them will contribute to characterize the role of evolutionary processes on ecosystem resilience.

7.4 – Conclusion

The results presented in this thesis contribute to an understanding of the mechanisms whereby changes in populations with an ontogenetic habitat shift occur as a result of a changing environment. Characterizing these mechanisms required the consideration of the multiple responses of individuals that make up the population, including the different individual responses throughout life history. Individual life history, ecological interactions, and eco-evolutionary dynamics prove to be necessary ingredients in a theoretical foundation that serves as a framework of an explanatory and predictive science. In this framework, the linkage that connects these components is individual energetics. An explicit description of how individuals acquire and utilize energy is essential to link individual life history and ecological interactions, which together determine individual fitness and thus evolutionary processes. In this way, energy connects individuals with their environment in a bidirectional manner: individuals depend on their environment and the environment is the product of the organisms that inhabit it. The consequences of a changing environment on populations, communities and ecosystems can only be understood in the context of the interaction between individuals and their environment.