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Fishing in a warmer sea – effects of warming and fishing on community dynamics and life history evolution in fish communities

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Front cover: Sun rises over Galtfjärden (Uppsala County) in the Baltic Sea. Photo: Viktor Thunell, SLU.

Abstract

Ecological interactions within and between species play an important role in evolutionary processes. Importantly since natural selection acts on the phenotypic variation among individuals that in turn depends on their different interactions with the environment. This is of particular importance in organisms with high variation in their phenotypic response to the environment and considerable variation in size and ecology throughout ontogeny, such as fish. In these size-structured communities, the individual response to environment, in e.g. growth and maturation, depends on ontogeny. This affects population level processes, which in turn affect the size structure of the population, and ultimately interactions within the community that shape natural selection.

Therefore, the feedbacks between individual, population and community structures should be a central aspect in research of life history evolution in fish communities. However, research of the main drivers of structural change in fish communities, such as warming and fishing, often overlooks this aspect. This renders much of the theory on evolutionary processes in size-structured communities incomplete. Furthermore, this presents a gap in knowledge for management of fish as a resource.

In this introductory essay, I review research on the ontogeny dependent ecological processes that transfer individual level effects of warming to the community to form a basis for future research on their role in life history evolution in exploited fish communities. A long history of scientific endeavour shows that the size- and temperature scaling of biological rates, such as metabolism and feeding rate, can be variable but generalizable. The importance of such scaling relationships in shaping population and community responses has only recently been explored, but highlights the importance of intraspecific individual scaling of biological rates for the effect of warming on community dynamics. Interspecific interactions in fish communities are generally size dependent and thus affected by how warming affects ontogeny in fish. These impacts of warming on the structure of populations can affect interactions as a source of natural selection. However, few studies has focused on the ontogeny dependence of biological rates as a source of indirect evolutionary responses in fish communities. Such plastic responses in phenotypic expression should be acknowledged together with direct sources of selection from fishing and warming to gain more comprehensive understanding of ecological processes in contemporary life history evolution in fish communities.

Keywords: Climate change, body size, temperature, ontogenetic development, eco-evolutionary dynamics, life history evolution, intraspecific interactions, interspecific interactions.

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1 Introduction

1.1 Contemporary Ecological and Evolutionary processes

All ecosystems on Earth are, or will be, affected by recent and future climate change (Parmesan 2006, IPCC 2014). Moreover, few systems can be considered pristine in the sense that they are unaffected by some form of exploitation, and many are heavily exploited (Halpern et al. 2008, Ellis 2011). Examples of studies of “natural” systems are therefore rare and our understanding of contemporary distribution and ecology of species and evolution is based on the effects of environmental change and exploitation. However, by studying responses to rapid environmental shifts such as climate change, and devastating perturbations through exploitation such as overfishing, our knowledge of ecological and evolutionary processes can increase substantially. Therefore, the study of effects of anthropogenic pressures on ecosystems is not only crucial for the development of proper methods of conservation and resource management but also provides a significant opportunity for science to increase the understanding of how ecology and evolution shape ecosystems.

Contemporary and future increases in water temperature, both in freshwater and marine systems, change the conditions that species depend on for their existence. Increases in mean temperature and frequency of extreme temperature variations such as heat waves are expected and raise questions on how species will respond, function and persist in a warmer climate (Parmesan 2006, IPCC 2014). However, climate warming reflects an unusually fast change in species’ environmental conditions on most evolutionary time scales (Visser 2008, IPCC 2014). Therefore, understanding whether a species or population can adapt (evolve through natural selection) or not, and what adaptations that will improve fitness in a warmer climate is important for our ability to understand both ecosystem responses and how species and communities evolve (Thompson 1998, Visser 2008). Most importantly, we need to understand how the ecology that mediate the effects of warming also mediate evolution, especially since species and population specific responses to temperature can be highly dependent on environmental context.

To understand evolutionary adaptive processes in response to warming, it is necessary to consider both the direct and indirect effects on organisms acting through different levels of biological organization. Importantly, indirect effects may occur through trade-offs, such that adaptations that may appear to increase fitness when viewed on one level of organization, actually could decrease fitness on another (Farkas et al. 2013). For example, a decrease in individual maturation size that increases population growth rate could expose individuals to increased predation risk from other species in the community (Audzijonyte and Kuparinen 2016). Possible

adaptation in a specific population to rapidly changing environments depends on factors such as the scale of environmental change in relation to the current environment, the evolutionary history of a species, the sensitivity and exposure of various life stages (Visser 2008, Hoffmann and Sgro 2011, Pankhurst and Munday 2011). However, the key factor determining adaptation in a population is the natural selection acting on the phenotypic variation of individuals. Therefore, focusing on the selective processes on an individual level that determine adaptation in a population to new environments is important for developing general theory that can be used to predict species evolutionary responses to, and persistence in, warmer environments. Warming acts as a direct selective force on individuals, but selection pressures also arise through interactions between individuals within populations and between species, and from human exploitation of these (Abrams and Rowe 1996, Gårdmark et al. 2003, Ohlberger 2013, Waples and Audzijonyte 2016). Thus, to resolve evolutionary responses of fish to warming, we need to account for both the exploitation on and interactions within fish communities.

1.2 Effects of warming on fished communities

Evolutionary processes are an important aspect for management of natural resources to account for in order to sustain the services and functions that ecosystems provide (Conover and Munch 2002, Jørgensen et al. 2007). Industrial scale fishing and climate change driven temperature increases have coincided on a global scale during the last century, posing a particularly precarious situation for our dependence on fish communities as a natural resource (Audzijonyte et al. 2016). Overfished populations are subject to strong selection in both size and behaviour, with adaptive responses in traits related to size, growth, and reproduction (i.e. life history) (Heino et al. 2015, Eikeset et al. 2016). The adaptive responses to overfishing is one of the factors that contribute to the commonly observed lack of recovery in overfished populations (Hutchings 2000, Audzijonyte and Kuparinen 2016). Furthermore, changes in size structure of fished populations may also be detrimental for the recovery of a population even in absence of evolutionary processes, by altering reproductive output and offspring survival, size-dependent trophic interactions between species and life stages inhibiting body growth (Persson et al. 2007, Gårdmark et al. 2015, Barneche et al. 2018). Changes in individual growth patterns may however, in turn, intensify or set the conditions for evolutionary processes, as species interactions are drivers of natural selection (Gårdmark et al. 2003, Gårdmark and Dieckmann 2006). This highlights the interaction between ecological and evolutionary processes. Importantly, warming can induce structuring responses in fish populations similar to the ones caused by fishing (Lindgren et al. 2013, Audzijonyte et

al. 2016). However, the consequence of warming for species interactions, community dynamics as well as their interaction for evolutionary processes in fish communities are largely unknown. Consequently, studies on the interactive effects of warming and fishing are also lacking, which calls for research on this to develop knowledge that can form a basis for proper fisheries management in a warmer climate (Audzijonyte et al. 2016).

At the core of understanding the overall effects of temperature on individual growth in fish communities is considering the direct size- and temperature dependence of growth (Atkinson 1994, Gillooly et al. 2001, Brown et al. 2004). Both metabolism, energetic requirements, and feeding rates in ectotherm animals are determined by temperature, which therefore governs growth through foraging and processing of food (Gillooly et al. 2001, Rall et al. 2012). However, metabolic costs and feeding rates also scale with the size of an individual; increasing in size increases costs of maintenance, which in turn affect energetic demands and feeding behavior throughout ontogeny (here defined as increase in size and/or progress in stage in a life cycle). The difference in ontogeny-dependent scaling of metabolism and feeding rate, referred to as ‘ontogenetic asymmetry’, has consequences for how the environment structures and constrains populations. Ontogenetic asymmetry has proven important to size-structured population and community ecology in general (de Roos and Persson 2013, Ryabov et al. 2017), but also has consequences for temperature and size dependent growth and thus for population and community responses to warming (Ohlberger et al. 2011, Lindmark et al. 2018a). Interestingly, much theory on the structuring effects of temperature through ontogenetic asymmetry and simple community interactions are lacking (but see Ohlberger et al. 2011, Lindmark et al. 2018a). Furthermore, the importance of ontogenetic asymmetry and species interactions for evolutionary theory has received even less scientific interest. Applying a size- and temperature dependent approach to individual growth in a community perspective to understand the effects of fishing in a warmer climate opens an important field of research attempting to gain better understanding of the ecological and evolutionary processes that shape present-day animal populations.

Aim of the essay

The aim of this essay is to answer the following questions:

- 1) How are the physiological effects of warming transferred from an individual level to the community by size-dependent processes?
- 2) What are the evolutionary consequences of warming on exploited fish communities?

I attempt to answer these questions by reviewing available knowledge of direct effects of warming on physiology, and its effects on ecology across different levels of organization in fished communities and ultimately evolution. First, I present a theory for the size dependent effects of warming on individual ontogeny. Then, I use an individual ontogenetic development point of view to consider how warming affects the feedback between the environment and the individual, determined by ontogenetic asymmetry and consequently population level regulation. Furthermore, I compare effects of warming and fishing on population- and community dynamics to identify knowledge gaps on the general effects of warming on fished communities. Finally, the essay evaluates warming, fishing and species interactions as sources of natural selection that can determine evolutionary processes in fished communities. This essay highlights the importance of size-dependence in ecological processes in fish communities and the importance of these for the interactive effects of warming, exploitation and species interactions on evolutionary processes.

2 Performance of ectotherms in a warming climate

2.1 Size- and temperature dependence of metabolism

The importance of temperature- and body size scaling of metabolism is a broad area of study that has encouraged research and debate for over 100 years (see e.g. Savage et al. 2004). This reflects both the importance and complexity of our understanding of the influence of temperature and body size in physiology and ecology respectively as well as their interactions. Nearly all biological rates scale with temperature, which acts directly on physiology, because increasing temperatures increases the rate of the biochemical cellular processes of metabolism (Gillooly et al. 2001, Rall et al. 2012, Kingsolver et al. 2015). Moreover, a larger body size increases metabolic demand in an organism and therefore also its resource dependence (Clarke and Johnston 1999, Gillooly et al. 2001). Both temperature and body size therefore indirectly determine an organisms' viability and development (Clarke and Johnston 1999, Gillooly et al. 2001, Brown et al. 2004). Metabolic rate further depends on other physiological and ecological factors, such as age, hormonal activity and food availability (Glazier 2015). However, size and temperature are the two most important axes that can be used to generally encompass environmental dependent metabolism for individual growth. These aspects of metabolism therefore provide a solid theoretical basis for size-structured animal community ecology (Brown et al. 2004).

Since temperature sets metabolic rate, the physiological activity in ectothermic animals is much more limited by the temperature of its surroundings in comparison to endothermic animals. This limitation in ectothermic animals involves a steep temperature-dependent increase in biological rates linked to metabolism, such as activity and growth rates (Karås and Thoreson 1992, Pörtner et al. 2017). An increase in metabolism also implies higher energy demand at high temperatures (Clarke and Johnston 1999). The temperature dependence of metabolic rate within a temperature range common for normal biological activity is often described using the Van't Hoff-Arrhenius equation (Gillooly et al. 2001, see Box 1). As this equation was developed to describe the rate of chemical reactions, it describes all the processes that metabolism consists of, including anabolic, catabolic and regulatory processes. Accordingly, this equation can describe whole body rates such as temperature dependent growth rate in ectotherms, and be used for comparing and modelling rates of ectotherm individuals or species in a certain environment (Fig. 1) (Brown et al.

2004). The temperature dependence of metabolic rate is thus a key factor when analysing an ectotherm organism's physiological performance, and its ability to persist in a warmer environment.

Box 1. The Van't Hoff-Arrhenius equation

The estimation of an organism's metabolic rate (B) can be given by Van't Hoff-Arrhenius equation (Gillooly et al. 2001):

$$B=e^{-E/kT}$$

where

E = the activation energy that is required for a potential reaction to occur,
k = Boltzmann's constant, which specifies the rate of reaction,
T = absolute temperature in Kelvin.

The allometry of biological characteristics, describing e.g. how physiological rates or behaviour depend on body size, is in a macro-ecological context often explained by an exponent of multiples of $\frac{1}{4}$ to organism mass (usually denoted 'b'). Studies suggest that this allometric relationship relates to the design of the hierarchical branching biological networks and their fluxes of which organisms are dependent on, e.g. vascular and lymphatic systems (Gillooly et al. 2001, Savage et al. 2004). According to Kleiber (1947), metabolic rate for a whole organism is best explained by $\frac{3}{4}$ to the power of body mass (e.g. Savage et al. 2004). This estimate has been widely used in physiological and ecological theory to relate body size dependent scaling of metabolic rate (Fig. 1) to body growth, and to gain knowledge on general population level processes (Yodzis and Innes 1992, Lindmark et al. 2018a). However, it is important to consider that deviations from this general pattern across taxa are common and explained by a range of factors including taxonomy, physiology and ecology of species, ontogeny and environmental conditions and most importantly temperature (e.g. Kozłowski and Konarzewski 2004, Killen et al. 2010, Glazier 2015). Considering the importance of metabolic rate in ecology (conceptualized as the "metabolic theory of ecology" by Brown et al. (2004)), the interactive effects of temperature, body size and developmental stage of ectotherms on metabolic rate can have large implications for growth and thus the ecology of populations (Ohlberger et al. 2012, Pörtner et al. 2017, Lindmark et al. 2018a).

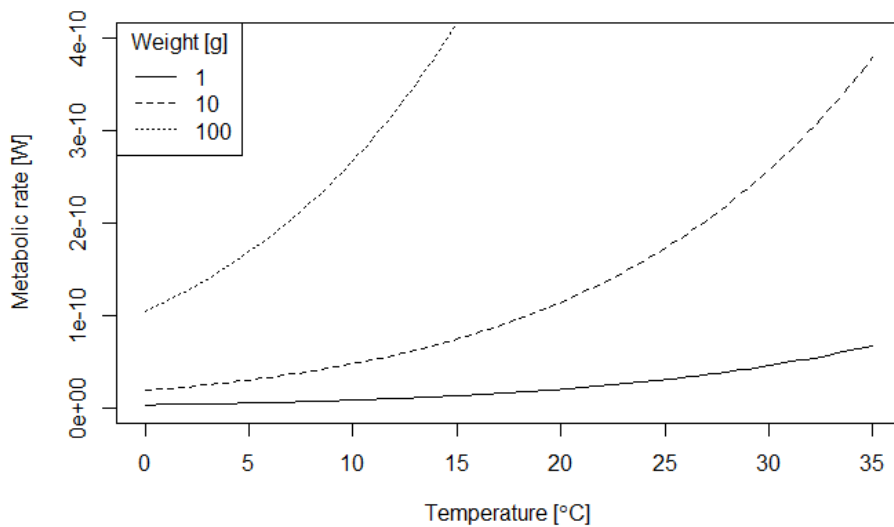


Figure 1. Size- and temperature dependence of metabolic rate (W) scaling across taxa in three different body weights as suggested by Gillooly et al. (2001). Metabolism scales with temperature (C°) with the Van't Hoff-Arrhenius equation ($E=0.62$) and scales $\frac{3}{4}$ to the power of body mass (Weight, g).

2.2 Temperature effects on individual growth

The general effect of temperature on the size of an individual, of a certain developmental stage, is a relatively fundamental and well-researched aspect of biology, especially in the case of ectotherms (Atkinson 1994). The temperature-size-rule has gained wide support in experimental studies (Atkinson 1994), and states that ectotherm individuals reared in elevated temperatures show an increased growth rates when young that trades off for a decrease in growth rate when old compared to individuals reared in lower temperatures. This results in a change in size-at-age. Though not universal, studies from a wide spectrum of taxa supports this rule by showing the negative effects of temperature on body size (Atkinson 1994, Thresher et al. 2007, Ohlberger 2013). Examples of reductions in size following increased temperature have also been observed in the field, e.g. in recent studies of sizes of fish species in both the North Sea and the Mediterranean (Baudron et al. 2014, van Rijn et al. 2017). However, the physiological mechanisms underlying the temperature-size-rule are still widely debated (Clark et al. 2013, Farrell 2013, Lefevre et al. 2017, Pauly and Cheung 2018).

The scaling relations discussed in the previous section provide an important tool for a more comprehensive understanding of how biological responses to environmental change occur, but does not give physiological explanation. Despite debate,

limitations in oxygen supply to support metabolic demand forms a basis of consensus for more detailed explanations of the effects of temperature on growth of aquatic ectotherms (Pörtner et al. 2017, Pauly and Cheung 2018). The temperature dependence of molecular and whole-animal oxygen demand in relation to oxygen supply has been described within the oxygen- and capacity-limited thermal tolerance concept (Pörtner et al. 2004). This relates organismal physiological constraints (e.g. the cardiovascular system and aerobic capacity of tissue and cells) to a temperature optimum (T_{opt}) for performance (i.e. the functioning of an individual in any aspect of ontogeny, e.g. foraging capacity, growth rate, mortality, reproductive output etc.) reflecting a species' preferred environmental conditions (Pörtner 2010). The oxygen- and capacity-limited thermal tolerance concept is based on the 'aerobic scope', which is the difference between resting metabolic rate (called standard metabolic rate) and maximum metabolic rate and reflects the metabolic capacity of an individual (Fig 2). Where standard metabolic rate reflects the energy demand required for maintenance of body functions, maximum metabolic rate describes the maximum capacity for e.g. foraging activity, growth or any other performance considered, at the whole organism level and is set by the maximum rate of oxygen consumption possible at a certain temperature. Maximum metabolic rate is limited by physiological capacity of an organism to deliver oxygen for oxidization of organic carbon for energy used in metabolic processes (Pörtner et al. 2017 and references therein). A larger aerobic scope means a larger possibility for change in metabolic rate, thus a higher performance, e.g. attack rate or growth (Rall et al. 2012). Because standard metabolic rate increases with temperature and maximum metabolic rate can decrease, warming can result in a smaller aerobic scope (Fig 2). In this framework, body growth links to temperature by individual performance described in terms of aerobic scope.

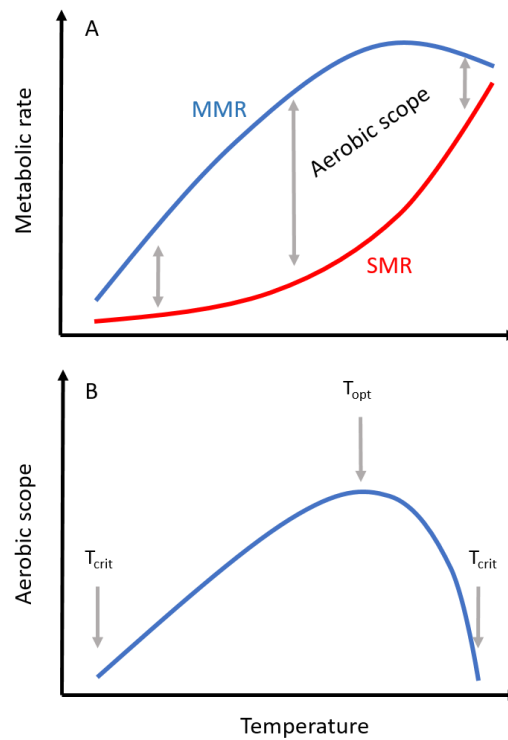


Figure 2. Conceptual drawing of the aerobic scope as a function of temperature. (A) Aerobic scope equals the difference between metabolic rate at maximum activity (maximum metabolic rate, MMR) and at rest (standard metabolic rate, SMR) which each respond differently to temperature. (B) The performance of an individual measured in terms of aerobic scope is generally constrained between high and low critical temperatures and has an optimum (T_{opt}). Redrawn from Verberk et al. (2016).

Because larger body size leads to higher standard metabolic rate, body size could affect the aerobic scope with consequences for larger individuals (Clarke and Johnston 1999, Pörtner and Knust 2007). An increase in metabolic demand also requires a higher amount of energy to cover increased costs (Werner and Gilliam 1984). This can be obtained by an increase in foraging capacity or in energy storage (i.e., fat reserves). If not met, these requirements may result in that larger individuals are energetically inferior (i.e. has less energy to allocate to growth) compared to smaller conspecifics. Thus, larger individuals are in warmer waters penalized twofold, as metabolic demand increases with both size and temperature (Gillooly et al. 2001). Both size- and temperature effects on individual performance and metabolism may thus underlie observed patterns such as the temperature-size-rule (Ohlberger et al. 2011, Ohlberger et al. 2012). However, whether such effects are realized depends also on population level processes, because individual performance is limited by intraspecific competition for shared resources. To understand effects of temperature on body growth and attained size, individuals therefore need to be put in the context

of their population and in their community (Brose et al. 2012, Lindmark et al. 2018a).

2.3 Temperature effects on maturation

Body size and growth of an individual also depend on maturation, as this involves a shift in allocation of acquired energy to reproductive organs and spawning instead of somatic growth. Maturation therefore involves an abrupt shift in the individual's growth trajectory. An interaction of physiology, individual ontogenetic characteristics and environmental conditions determines the onset of maturation in ectotherms. However, the probability of maturation increases as a heritable determined function of age and size, and this relationship is commonly used as a proxy to describe the likelihood of maturation in various environmental conditions (Stearns and Koella 1986, Heino et al. 2002). Even though temperature independently can affect the onset at maturation, increased growth rates following warming commonly lowers age at maturation (Atkinson 1994, Kuparinen et al. 2011, Ohlberger 2013). Responses in size at maturation to warming are more complex, as temperature affects both growth and developmental processes. Following the temperature-size-rule, maturation generally occurs at smaller sizes with increasing temperature (Atkinson 1994). However, these findings are based on controlled experimental environments. Field observations instead support maturation at both larger and smaller sizes in response to increasing temperatures (Audzijonyte et al. 2016). Other aspects of ontogeny, such as mortality play an important role in determining the size of maturation (Jennings et al. 1998, Gårdmark and Dieckmann 2006, Heino et al. 2015). As both growth and mortality depend on interactions with other individuals, so does maturation of an individual. Consequently, there is a feedback between population dynamics and ontogeny. Therefore, studying individual ontogeny accounting for the feedbacks from a population, or even community level, is required to understand the effect of temperature on size at maturation.

3 Warming and ontogeny in size-structured populations

3.1 An individual perspective on population processes

Changes in population size or population growth rate in response to environmental change consist of the sum of the relative contribution of each individual to the population. As obvious as this may seem, average growth, mortality and birth rates have in the past, and sometimes still are, viewed as sufficient to understand population responses in growth to changing environment (de Roos and Persson 2013). This approach ignores within-population individual variation in performance, and in sensitivity to environmental changes (affecting individual growth, reproduction and mortality) (Kirkpatrick 1984, de Roos et al. 2003a). Consequently, it ignores the importance of individual variation for the ecological feedback between the individuals in a population and the environment that can determine population dynamics. Therefore, studying populations from an individual point of view can reveal the underlying mechanisms behind responses in both individual and population level growth to environmental change (de Roos et al. 2003a).

Understanding the relative contribution of individuals to population level rates requires accounting for individual variation in the main factors that govern individual growth. Ectotherms have indeterminate body growth (i.e. growth continues throughout life) and growth is often directly dependent on the environment. Growth can therefore be highly variable in different environments and throughout ontogeny. An individual trait that reflects ontogeny (i.e. size or life stage) can, as opposed to age of an individual (which has been commonly used in ecological theory (e.g. Tschumy 1981, Polis 1984)), link both to physiological (e.g., size-dependent performance) and ecological characteristics (e.g., diet shifts and food consumption) relevant to individual rates (Kirkpatrick 1984, Werner and Gilliam 1984, Yodzis and Innes 1992).

Whereas separating individuals by size is suitable to explain the dependence and the effect of an individual on the environment through metabolic demand or feeding niche, life stages can separate e.g. maturation and ecological niche shifts that influence both individual growth and reproduction. Sizes or life stages of individuals in a population are therefore characteristics that can mechanistically link population level rates and regulation (i.e. structuring processes and flow of biomass and abundance between different sizes and stages of the population) to environmental change (de Roos and Persson 2013).

3.2 Food dependent growth and intraspecific competition in population regulation

The implications of two very basic insights of individual growth explain why ontogenetic asymmetry, ontogeny dependent shifts in diet, and energy allocation matter for the regulation of size-structured populations; (1) food availability and the process of turning that food into body mass governs the growth of an individual (food-dependent growth), and (2) competition from conspecific individuals within the population (intraspecific competition) limits food availability and thus food-dependent body growth (de Roos and Persson 2013).

As energy requirements, the ability to exploit a resource (e.g. ingestion rate, handling time) (Fig. 3A), and resource availability vary throughout ontogeny (e.g. due to diet-shifts), strength of intraspecific competition will also vary (Fig. 3B) (de Roos et al. 2003a). Food-dependent growth combined with variation in intraspecific competition results in a bottleneck among individuals in the part of the population that is the most energetically inferior. This bottleneck will determine both individual growth and the structure and size of the population (de Roos et al. 2007). For instance, competition-induced limitation in gonadal growth and thus reproduction among mature individuals, would lead to low production of juveniles and further accumulation of biomass of adult individuals since juveniles have sufficient energy to grow and mature, while adults are limited in their ability to spawn (Fig. 3C). Such a population is referred to as being reproduction-regulated, as opposed to maturation-regulated where the bottleneck is present among juveniles (de Roos et al. 2007). This structuring effect on a population level thus results from a feedback between the environment and the population, mediated by individual food-dependent body growth and intraspecific competition. Accounting for these mechanisms is central for understanding population level responses to environmental change (Persson et al. 2007, de Roos and Persson 2013, Ryabov et al. 2017).

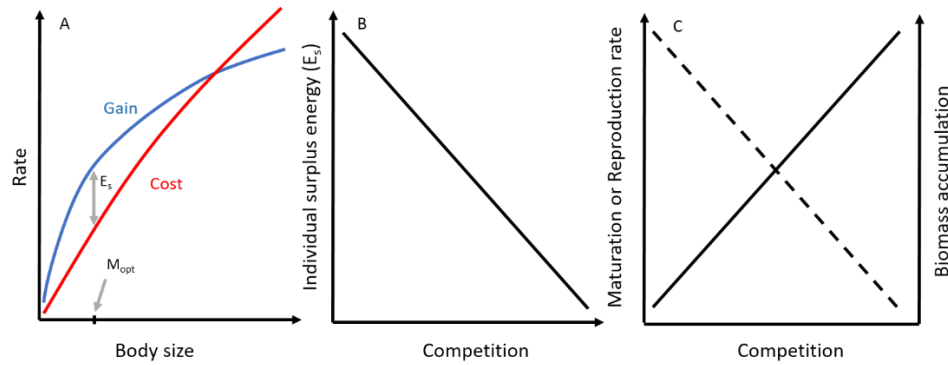


Figure 3. Conceptual drawings of the causes and consequences of food-dependent growth and intraspecific competition on individual energetics, intraspecific rates and biomass accumulation. (A) Metabolic costs (Cost) and foraging gains (Gain) vary throughout ontogeny, primarily as a direct consequence of body size or due to diets shifts resulting in variation in surplus energy (E_s), which is maximized at a certain size (M_{opt}). Redrawn from Werner & Gilliam (1984). (B) Surplus energy decreases due to competition for shared resources and this, in turn, (C) decreases maturation or reproduction rates (dashed line) and increases stage specific biomass accumulation (solid line).

Any change in the environment that reduces competition for available resources can produce overcompensatory changes in how biomass is distributed within the population. These rather unintuitive observed increases in biomass of size classes or life stages (or even total biomass) of populations, become comprehensible only when accounting for ontogenetic asymmetry between individuals (de Roos and Persson 2013). A size-structured model of juveniles and adults that incorporates differences in feeding rates and maintenance costs between life stages (juvenile and adults) showed the mechanisms of overcompensation (de Roos and Persson 2002, de Roos et al. 2007). In this model, differences in net biomass production between juveniles and adults result in that the life stage with lower resource competition acts as a source of biomass for the other stage, and the other (with higher competition) as a sink. A release in competition in the sink will increase biomass transfer to the source, making the source overcompensate in biomass as it can better utilize its resource (Fig. 4). For example, if mortality reduces competition in a reproduction-regulated population, adults will have more energy available per capita and can increase their reproduction, producing more juvenile biomass (Fig. 4A and C). Biomass overcompensation is most pronounced when the competition is released in the stage that regulates the population but can occur regardless of whether competition is released in a specific stage or across the whole population (Fig. 4) (de Roos et al. 2007). Therefore, overcompensatory mechanisms are necessary to account for when studying the effects of environmental change that may affect competition between individuals within the population (Persson et al. 2007, Lindmark et al. 2018a).

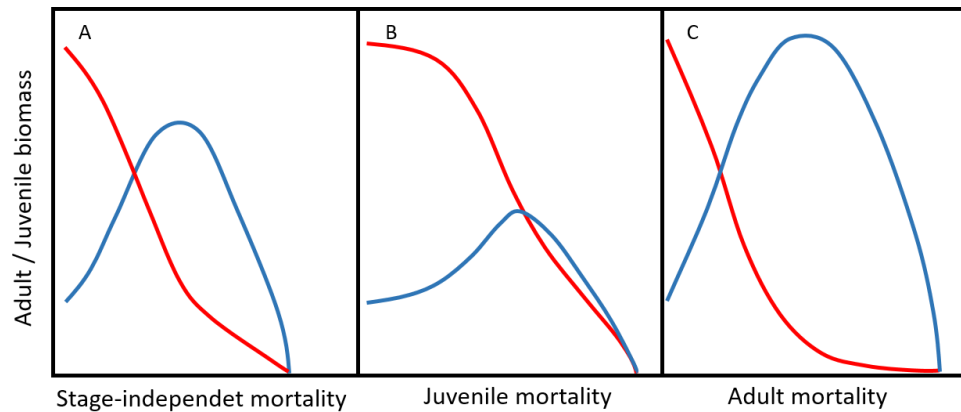


Figure 4. Biomass overcompensation in a reproduction regulated population in response to mortality. Equilibrium juvenile (blue) and adult biomass (red) in response to increasing (A) stage independent, (B) juvenile and (C) adult mortality. Redrawn from de Roos et al. (2007).

3.3 Effects of warming on consumer-resource dynamics

Field studies presenting observations of reduced mean size of individuals with warming have yet to provide the ecological mechanisms of such changes (Baudron et al. 2014). Only a few theoretical studies have considered the importance of ontogenetic asymmetry and food-dependent growth for responses to warming (Ohlberger et al. 2011, Lindmark et al. 2018). These have shown how these processes mediate temperature effects on population dynamics; models of size- or stage structured fish populations predict that size-specific individual responses to warming in performance shape both population size structure and regulation (Ohlberger et al. 2011, Lindmark et al. 2018a). For example, through the size dependent differences in feeding rates and metabolic demand, warming can increase the competitive advantage of juveniles (see section 2.2). This allows them to dominate the population, which shifts the size distribution towards juveniles. Such dominance of juveniles may shift the population from equilibrium dynamics to juvenile-driven cohort cycles (Ohlberger et al. 2011). Furthermore, the type and strength of regulation in a population may also be determined by how temperature effects on metabolism scales with body size (Lindmark et al. 2018a). With such interactions between size and temperature, warming directly affects ontogenetic asymmetry. Increasing temperatures can in such cases cause abrupt shifts in population regulation, by shifting competitive advantage between life stages (or size classes) (Lindmark et al. 2018a). Consequently, theory suggests that field observations of the temperature-size-rule may not only be driven by physiological constraints in oxygen supply, but that also population processes govern responses to warming (Ohlberger et al. 2011, Ohlberger 2013, van Rijn et al. 2017, Lindmark et al. 2018a).

The effects of temperature on resource density in relation to its consumer population is also important to resolve, in order to understand warming effects on populations. This has been studied theoretically in consumer-resource models of temperature effects based on both structured (Ohlberger et al. 2011, Lindmark et al. 2018a) and unstructured population dynamics (Vasseur and McCann 2005, Ohlberger et al. 2012, Lindmark et al. 2018a). As temperature can increase growth rates of ectotherms, it should have a positive effect on resource growth for fish (typically represented in these studies by an unstructured plankton community). However, despite positive effects on growth, resource densities typically decrease with temperature because of a higher temperature sensitivity in consumer feeding rates compared to resource production (Vasseur and McCann 2005, Ohlberger et al. 2012, Lindmark et al. 2018a). This indicates a strong effect of temperature on the strength of intraspecific competition among consumers, which, in turn, controls population regulation. The consumer population density may thus be more sensitive to warming than resource density. However, if there is an additional resource or cannibalism among consumers, such that inferior competitors can be released from competition, this reduces sensitivity to warming and can alter system regulation and stability (Vasseur and McCann 2005, Ohlberger et al. 2012, Lindmark et al. 2018a). Consequently, taking into account how resource use changes throughout ontogeny is important to understand effects of temperature on populations, but also displays the importance of community processes for population dynamics (van Leeuwen et al. 2014, Lindmark et al. 2018a).

4 Warming and ontogeny in size-structured communities

4.1 Predation and competition mediate effects of warming

Relative differences in body size generally determine the potential of predators to consume their prey. Typically, the gape size of a fish limits the potential maximum size of the ingested prey but body size also increases the handling and consumption capacity of prey (Hjelm and Persson 2001, Dörner and Wagner 2003). Thus, size affects the ability to exploit a resource and thus the shape and stability of a food-web (Warren and Lawton 1987). Larger prey are often more energetically profitable than small prey, resulting in that ontogenetic diet shifts commonly are associated with growth over ontogeny (Werner and Gilliam 1984). Since temperature dependent performance and the scaling of temperature-effects over size generally differ between species (Ohlberger et al. 2012, Lindmark et al. 2018a), relative differences in responses in individual growth to warming between interacting species should be common. Warming can thereby influence predator-prey interactions by offsetting or hindering size-dependent diet shifts (Brose et al. 2012). Furthermore, as predators generally are larger than their prey, growth in predators should be more sensitive to the effects of warming than in their prey. A larger relative decrease in size of a predator compared to its prey negatively affects the size-dependent predator-prey interaction they depend on for individual growth and consequently affects population size-structure. Similar truncation of predator size-structure has been observed in response to overfishing, which also affects the size-composition of the other species in the fish community (e.g. van Leeuwen et al. 2008, Svedäng and Hornborg 2017). Consequently, size-dependent ontogenetic diet shifts may be affected by both temperature- & fishing-induced changes in growth within and between species.

Competition between species are largely dependent on rates that are both size- and species dependent (e.g. feeding and maintenance rates), but also vary with temperature (Persson et al. 1998, Ohlberger et al. 2012, Rall et al. 2012). Consequently, the effect of warming will differ among competitors and affect community responses to temperature. Furthermore, many competitive interactions are ontogeny-dependent; ontogenetic diet shifts generally involves a trophic specialization, or a trade-off in morphological traits that optimizes feeding for different diets (Polis et al. 1989, Morin 1999). This implies going through a phase of being an inferior competitor, e.g. as in omnivorous species with planktivorous juvenile stages but an adult piscivore stage. Warming induced increases in interspecific competition can inten-

sify the competitive disadvantage of species with ontogenetic diet shifts or intraspecific competition may delay or affect the strength of predation. Changes in competition due to increasing temperatures could thereby shape species composition and stability of size structured communities (Holt and Polis 1997, Walters and Kitchell 2001, Huss et al. 2012).

4.2 Effects of warming on ontogeny dependent community processes

Warming induced changes in growth in predators could alter the structuring effect that predation can have on its prey population, with consequences for the community (Lindmark et al. 2018b). Predation-induced overcompensation in the prey population (resulting in e.g. improved condition or increased abundance) also benefits the predator population, as more prey or prey of better quality become available (de Roos et al. 2003b). This mechanism is called the “emergent Allee effect”, referring to that the positive effect of predation (through increasing predator density) on per capita growth in the predator emerges from the structural changes in the prey population that the predator induces (de Roos et al. 2003b). Such predation-induced overcompensation in the prey population may also increase the amount of suitably sized prey for other predator species (known as emergent facilitation) (de Roos and Persson 2013). Therefore, overcompensation can be a fundamental process for the structure and stability of whole communities (de Roos and Persson 2013). Accordingly, warming may not only affect the predators own persistence, but also community structure and stability.

Not much is known about how predation and competition can mediate the effects of warming on size-structured fish communities (but see Lindmark et al. 2018b). They have, however, been shown to mediate the response of overfishing (e.g. Persson et al. 2007, van Leeuwen et al. 2008). The top down control imposed by predation on the distribution of size, condition and abundance of a prey population can be lost when the predator is overfished. This weakens important structuring processes that facilitate stability in fish communities (Walters and Kitchell 2001). An intraguild predator-prey system, where adult predators predate on a prey but competition occurs between juvenile predators and that prey species, provides a suitable example for the stabilizing mechanisms of predation and competition (Polis et al. 1989, Hin et al. 2011). Loss of large predators decreases predation and promotes prey abundance. This increases competition from the prey on juvenile predators. This results in a juvenile bottleneck, which controls the growth of the predator population (Hin et al. 2011). The system is thereby stabilized through processes preventing predator recovery (Walters and Kitchell 2001). Another important result of loss of predators is its effect on the prey size-structure, and its consequences for

predator persistence. Loss of adult predators induce maturation regulation in the predator population, which increases the abundance of smaller predators. At the same time, it also affects the prey size distribution following the principles of emergent Allee effects, such that the abundance of suitably sized prey decreases (Walters and Kitchell 2001, de Roos et al. 2003b). This lack of prey for adult predators can thus also prevent the predator population from recovery (Persson et al. 2007). Field observations of changes in the spatial distribution and condition and body growth of predators have been correlated with lack of suitable sized prey and prey of poor condition, showing the effects of these structuring and stabilizing processes in marine fish communities (van Leeuwen et al. 2008, Golet et al. 2015, Gårdmark et al. 2015, Jacobson et al. 2018). Furthermore, a lake-scale field study has shown that selectively decreasing the number of prey individuals of certain sizes induced overcompensation in the prey (Persson et al. 2007). This increased the number of properly sized prey for a collapsed top predator population, which promoted predator growth and recovery (Persson et al. 2007). These fishing-induced effects on the community are determined by size-dependent intra- and interspecific interactions. As shown above (chapter 2-3) these processes can also be affected by temperature. The potential effects of warming on fish communities may therefore be similar to those of overfishing. This indicates the importance of considering both inter- and intraspecific size-dependent processes also when studying the effects of warming on fish communities but also the interactive effects of fishing and warming.

The implications of size-dependent community interactions have been acknowledged in fisheries ecology (May et al. 1979, Yodzis 1994, Persson et al. 2014, Golet et al. 2015, Jacobson et al. 2018). Similar studies are lacking on the effects of warming on exploited species that may emerge from temperature-dependent physiology, size-dependent interactions and intraspecific variation in size. Because both pressures affect growth and body size, there are potential interactive effects of fishing and warming on fish communities. These interactive effects may influence the potential for recovery of overfished fish populations in future climates, but are rarely considered in fisheries science. Thus, when studying the ecological consequences of warming, it is essential for our understanding of past, present and future exploitation of fish communities that we apply an individual level approach that considers how ontogenetic asymmetry in predator-prey interactions can depend on temperature.

5 Eco-evolutionary processes in response to warming in exploited fished populations

5.1 Life-history evolution in fish populations

Evolution in populations occurs among genotypes, predominantly by natural selection but also randomly by processes such as genetic drift. Natural selection generally causes evolutionary adaptation of genetic variation through shifts in the distribution of phenotypes in a population so that average fitness increases over an environmental gradient. Fitness is commonly measured as reproductive success (i.e. the total production of viable offspring throughout life) which, in turn is governed by traits related to individual ontogeny and reproduction such as fecundity, size at maturation, life span etc. Studying adaptive changes in such traits, or “life history evolution”, allows for a mechanistic understanding of evolutionary processes by the means of natural selection across environmental gradients.

Natural selection acts on phenotypic variation (but selects among genotypes), which is the individual response to heritability (the genotypes effect on phenotypic expression) and phenotypic plasticity (the environmental and random factors that affect phenotypic expression). The phenotypic environmental response can be substantial in organisms with highly plastic ontogeny such as fish. Therefore, changes in reproductive success over environmental gradients attributed to natural selection is not always due to evolutionary adaptation, as it can be plastic responses to the environment (Rijnsdorp 1993, Jennings et al. 1998). To separate such plastic responses from evolutionary adaptive responses, knowledge on heritability of a trait is required. Furthermore, heritability governs or constrains adaptive responses (Etterson and Shaw 2001, Visser 2008, Vindenes and Langanen 2015), and plasticity itself may be a variable and adaptive trait (Stearns and Koella 1986, Kingsolver et al. 2007). Consequently, studying adaptation in species with indeterminate growth such as fish are therefore particularly complex and strongly dependent on ecological processes (Ebenman and Persson 1988, Dunlop et al. 2009, Eikeset et al. 2016).

Both adaptive and plastic phenotypic responses in life history traits commonly involve trade-offs in optimal energy allocation due to negative correlations in allocation between growth, maintenance and reproduction, and between reproductive effort and survival (Stearns 1989, Audzijonyte and Richards 2018). Importantly, energy allocated to reproduction trades off for somatic growth throughout life and thus affects the timing of maturation (i.e. individual size or age) in relation to growth, survival or fecundity (Stearns 1989, Roff et al. 2006, Audzijonyte and Richards 2018). Therefore, trade-offs linked to individual age and size at maturation affect individual lifetime reproductive success and thus population growth and

productivity and ultimately natural selection (e.g. Jennings et al. 1998). Furthermore, life history trade-offs may also drive natural selection by affecting body size (via growth), and thus the ecological role of an individual in its community through size- and ontogeny dependent population and community processes such as ontogenetic asymmetry and size-dependent interactions (Fig. 5) (Ebenman and Persson 1988, Abrams and Rowe 1996, Gårdmark et al. 2003, de Roos et al. 2006, Farkas et al. 2013). Consequently, even if body size is a highly plastic trait in fish populations, it can also be a determinant of evolutionary adaptation because of its strong influence on the physiology and ecology of individuals, and thus both on fitness and selection pressures. Trade-offs are therefore a core aspect of life history in both ecological and evolutionary theory (Stearns 1976, Audzijonyte and Kuparinen 2016).

In summary, life history trade-offs closely links reproductive success to size and growth across levels of ecological organization and can affect the function or even persistence of a species in the community and are thus key in understanding adaptation in fish communities (Stearns 1989). Accounting for the environmental feedback across these levels that govern plastic responses but also affect genetic responses through natural selection (a concept referred to as eco-evolutionary dynamics, Fig. 5 (Pelletier et al. 2009)) is crucial to develop general theory on life history evolution in fish communities (Crozier et al. 2008, Farkas et al. 2013, Lion 2018). To understand how eco-evolutionary processes are driving contemporary changes in life history in fish communities requires knowledge on the origin of phenotypic expression and that present selection pressures – from warming, fishing and species interactions – are disentangled.

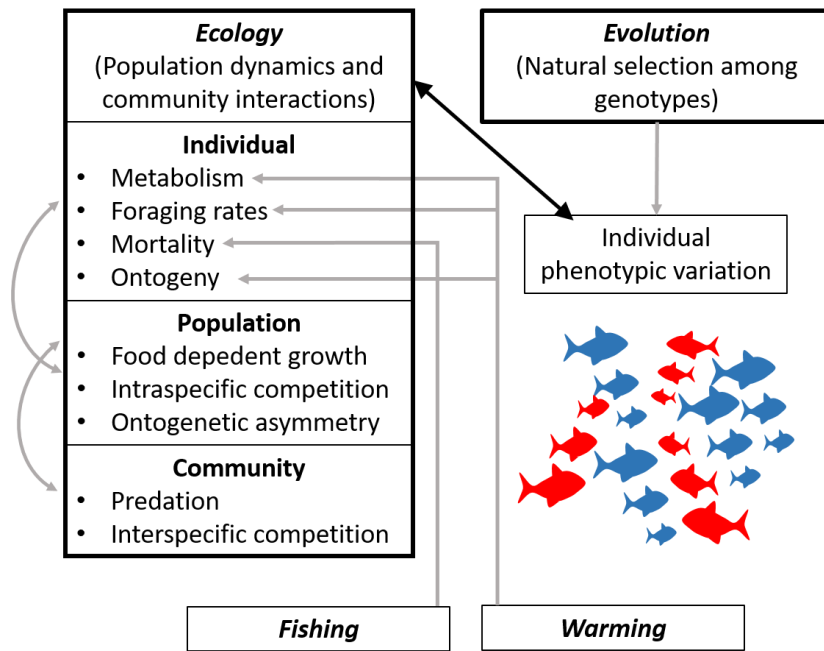


Figure 5. Ecological processes mediate the effect of the environment, such as warming and fishing, on evolution across levels of ecological organization. The feedback between ecology and evolution (or eco-evolutionary dynamics) is determined by individual phenotypic variation. Phenotypic variation depends on the feedback between the response of individuals to warming and fishing and the size dependent structure and dynamics of populations and communities.

5.2 Warming induced evolution in exploited fish communities

As temperature rapidly increases, warming could pose a strong selection pressure where the life history of a species may govern its ability to adapt (Hoffmann and Sgro 2011). Rapid evolution that occur over ecologically relevant time scales is common, and has been shown to play an important role in the adaptation of a species to fast environmental change (Thompson 1998, Araki et al. 2007). Still, the predicted rates of climate change may outpace, or at least affect the possibility of adaptation (Etterson and Shaw 2001). A fast directional change in the environment in relation to the generation time of individuals creates a delay in evolution of the optima of a trait, increases the selection pressure and thus reduces genetic variation and increases extinction risk (Hoffmann and Sgro 2011). Fast life histories and short generation times in a population that increases the rate of adaptation, should thus be favoured by warming. Direct plastic responses to temperature often has been shown to induce such faster life histories, including a shorter generation time through increased growth rate, decreased age at maturation and higher mortality (Bestion et al. 2015). This increases the rate of selection of genotypes across generations. However, despite observed rapid changes in genetic variation in response to temperature,

the means by which these adaptations can counteract the negative effects of temperature is often not known (Rodríguez-Trelles and Rodríguez 1998, Parmesan 2006).

Adaptation may be constrained by heritability and plastic responses can thus play an important role in maintaining reproductive success in warmer climates. The many observations of phenotypic changes (e.g. in size-at-age) in aquatic organisms correlated with temperature has yet to provide genetic evidence of adaptation (Daufresne et al. 2009, Baudron et al. 2014, van Rijn et al. 2017). Studies of fisheries induced evolution show that both plastic and adaptive responses can explain the many examples of changes in life history traits in response to fishing (Rijnsdorp 1993, Jennings et al. 1998, Bianchi 2000, Dunlop et al. 2009, Heino et al. 2015). Where similar studies are lacking for adaptation to warming in fish populations, studies of other animal taxa suggest the same response as to fishing (Parmesan 2006, Hoffmann and Sgro 2011). A study of non-fish taxa show that loss of genetic diversity suggests rapid evolution in response to warming (Rodríguez-Trelles and Rodríguez 1998). However, a review of the few related quantitative genetic studies suggests that adaptation explain less than plasticity, and warming is thus not considered a strong driver of selection (Hoffmann and Sgro 2011). In accordance with the latter, fishing is suggested to be the main driver of observed evolutionary changes and lack of recovery in fished populations (Audzijonyte et al. 2016, Brander 2018). However, the temporal scale of warming suggests that even if plastic, observed changes in body size and growth will affect population persistence and function in a community in the long term. Thus, it should affect adaptive processes through eco-evolutionary dynamics in fish communities (Werner and Gilliam 1984, Ebenman and Persson 1988, Farkas et al. 2013, Lion 2018).

Much knowledge exists on the link between the ecological effects of fishing and its role in evolution (e.g. de Roos et al. 2006, Dunlop et al. 2009, Eikeset et al. 2016) that can be used for comparison and understanding of adaptation in response to temperature (Waples and Audzijonyte 2016). For example, studies of fisheries induced evolution show that the adaptive change in a trait is not only dependent on the life history of the species and the strength of mortality (Jennings et al. 1998, de Roos et al. 2006, Gårdmark and Dieckmann 2006), but also depends on the selectivity of the fishery, i.e. what individual size or life stage that is targeted (Gårdmark and Dieckmann 2006, Matsumura et al. 2010, Heino et al. 2015). Similarly, the evolutionary effects of warming should depend not only on intensity of temperature change, but also on life history of a species and the ontogeny of an individual, particularly since the effects of warming depend on their body size. This, in turn, affects population dynamics. For example, warming induced changes in population regulation could affect selection in growth rates and size at maturation through intraspecific competition. Consequently, despite the suggested weak selection induced by

non-lethal warming, processes such as changes in species interactions and community dynamics induced by warming could alter the strength and direction of other selection forces such as fishing, competition and predation. Warming may induce loss of top down control, which should affect size structure in a consumer prey, which in turn could affect selection from fishing on that prey. All of these processes depend on individual characteristics, primarily ontogeny or body size, making size-dependent processes in life-history evolution important to account for (de Roos et al. 2006, Gårdmark and Dieckmann 2006).

An individual based perspective on the evolutionary effects of warming on exploited fish populations could open up for new insights of ecological processes in evolution arising from the link between individual physiological responses, ecology and adaptive processes (Lion et al. 2011, Vindenes and Langangen 2015, Lion 2018). However, the interaction between ecological and evolutionary processes are hard to separate in field or experimental research on contemporary evolution (Hendry 2013). Here, various eco-genetic modelling frameworks provide tools to investigate such interactions and disentangle causes of phenotypic variation from adaptation across environmental gradients (Dunlop et al. 2009, Dercole and Della Rossa 2017, Lion 2018). Furthermore, a broad general theory life history evolution and important trade-offs in size-structured population exists (e.g. Stearns 1976, Ebenman and Persson 1988, Stearns 1989, Roff et al. 2006, Audzijonyte and Richards 2018). This can be applied to theory of size dependent population and community processes that may govern evolutionary processes in response to warming (de Roos and Persson 2013, Ohlberger 2013, Eikeset et al. 2016, ten Brink and de Roos 2017). Such theoretical research on the role of ecological effects of physiological responses to warming and how that affects evolution in fish populations is scarce (Waples and Audzijonyte 2016, but see Crozier et al. 2008). Furthermore, studies accounting for the effects of ontogenetic asymmetry, diet shifts and food dependent growth on community interactions to study evolution are few in spite of their theoretical importance (but see ten Brink and de Roos 2017). Most importantly, to my knowledge, no studies to date have focused on the mediating role of size-dependent physiological and ecological processes in evolutionary responses of warming and exploitation in spite of their hypothesized interactive effects on fish as a resource globally.

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