# Climate-driven population responses of resident brown trout, *Salmo trutta*: Trends and future projections.

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# Preface

Doing a PhD sometimes feels as taking a rollercoaster ride with ups and downs, twists and turns, loops and….absolutely standstill. It might be super fun and motivating, but also highly nerve-wracking and scary. However, at the end of the ride you feel like running all the way to the end of the que again, to have another go. (Well, considering *real* rollercoaster rides: At least until you realize that you are getting older and are actually quite noxious after the first run). It is safe to say that my rollercoaster ride is one I would never have been without. It might have taken a bit longer than I originally planned it to, which sometimes have felt frustrating, but in the end I have learned a whole lot of stuff I didn't know before. Also, the added bonus time gave some new opportunities of trying out a completely different type of job, besides being a PhD-candidate.

I have had a lot of help building my rollercoaster, and have many to thank. First of all, I would like to thank my main supervisor Thrond Haugen. Even though it have sometimes be hard to get a hold of you, I have really appreciated being your PhD-student. At the end, I feel that you have guided me in all the right directions, and I have learned so much from it. Also, to come up with the main idea for this thesis is rather impressive. It is fun to work with somebody that has you level of expertise on so many things, and a good sense of humour. I am also very thankful for my two co-supervisor Peter Kiffney and Asbjørn Vøllestad. You have both been extremely nice to lean on when the ride have made me dizzy. Moreover, you have of course provided a well of knowledge, of which I have enjoyed some buckets. I hope to collaborate more with you all in the future!

I also want to thank Hedmark University College, campus Evenstad, which is where I have spent most of my time doing the last five years, and also who has financed my PhD. My time at Evenstad have given me so many good friends and colleges, so I will not mention them all. I rather say that the people, and Evenstad as a place, will bring back good memories for the rest of my life. I will however direct an extra thank you to Harry Andreassen, an extremely talented and successful person at so many levels, including being the dean during my time at Evenstad. Harry, you seem always optimistic and you see the opportunity in everything, even in me. Keep on the good work, and I hope we will keep in touch. I would also give an extra thank you to the people at Evenstad fish hatchery: Olav Berge, Kåre Sandklev and Frode Næstad. You were invaluable during the building process of my experimental set-up.

I have also been connected to CEES at the Department of Biosience, UiO. This has been extremely nice during my occasional loneliness at Evenstad, being at times the only member of "Evenstad fish group". Taking the rollercoaster-ride down to this excellent scientific community, with so many extremely talented researchers, have always helped me a lot and boosted my motivation to keep on riding. And, it was always nice to hear the fraise; "Jasså, er det bønder i by'n" when I showed up; which translates for you non-norwegian speakers: "Oh, bring us your wisdom and we will bask in your glory". Thank you for the kind words. I have enjoyed scientific and non-scientific talks with all of you, and especially some of you (I will not mention names here either, as 1) there are so many of you that I want to mention, if you know me, you're one of them, and 2) I'm in general terrible with names).

I also want to thank my new employer NINA, with my closest boss Jon Museth in particular. Believing in me, and giving me the opportunity to work even before handing in the PhD, have been a lifesaver. You have also given me the freedom to finish the PhD, while also including me in multiple exiting project. I'm very grateful. I really enjoy working at NINA Lillehammer, and hope I have the opportunity to do so for a long time still.

My family has always been very supportive, and it means a lot to know they will always be there for me, and help me with whatever they can. Basically, I couldn't have had it any better. So thanks a lot for being you!

And at the end, I am extremely grateful for my second rollercoaster ride in life: Annette, my big love and Torbjørn (including unnamed children), my everything. Being with you makes life easy, because when I know what is important in life everything else seems trivial.


Kim Magnus Bærum. Lillehammer, November 2015.

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**K. M. Bærum**, L. A. Vøllestad, P. Kiffney, A. Rémy & T. O. Haugen. 2015. Population-level variation in juvenile brown trout growth from different climatic regions of Norway to an experimental thermal gradient. *Submitted manuscript.*

Paper II

**K. M. Bærum**, T. O. Haugen, P. Kiffney, E. M. Olsen & L. A. Vøllestad. 2013. Interacting effects of temperature and density on individual growth performance in a wild population of brown trout. Freshwater Biology, **58**: 1329-1339. DOI: 10.1111/fwb.12130

Paper III

**K. M. Bærum**, A. G. Finstad & T.O. Haugen. 2015. Population consequences of climate change through trait-based effects on a freshwater ectotherm, *Salmo trutta*. *Submitted manuscript.*

Paper IV

T.O. Haugen, **K.M. Bærum**, L. A. Vøllestad, R. Borgstrøm, T. Qvenild, S. Rognerud & H. Sægrov. 2015. Spatial variation in alpine brown trout population responses to climate change: a glimpse into the glass sphere. *Manuscript.*

# Summary

The climate is changing at an alarming rate with consequences such as species and population extinctions, changes in species distribution and phenology. However, mechanisms underlying these global trends are not well understood, especially at a population level. Climate effects on demographic traits and population dynamics have recently received increasing attention as key importance for understanding the ecological impacts of climate change. The effects on demographic traits might vary across populations that are adapted to respective local environmental conditions. Hence, different populations within the same species might perform differently while subjected to the same climate scenario.

In this thesis, I focused on how environmental variability and its effects on key life history traits of freshwater resident brown trout, *Salmo trutta,* influence population dynamics. In particular, I explored effects of variations in temperature, precipitation and general winter conditions together with other ecological variables to elucidate how climate induced variations in demographics characteristics might result in altered population dynamics. I explored these matters mainly through statistical models based on climate variations in spatio-temporal environmental data, studying individual differences within and between-populations. Further, I included possible adaptive responses to climate change in the population projections to assess possible eco-evolutionary rescue scenarios.

I found evidence for local environmental adaptations in early growth of brown trout. I argue that higher growth rate associated with populations experiencing more precipitation and low temperatures, was an adaptation to short, harsh and unstable environments in streams during early life stages. Further, I found that density and temperature interacted in a non-additive and complex way as controlling agents of growth performance, where a general positive effect of warm temperature minimised an apparent negative effect of density.

Finally, by combining demographic parameters into population models I was able to infer mechanistic effects of climate change at the population level. In general, simulations including increasing and more variable temperatures in the next 100 years resulted in negative effects on the brown trout population growth rates. The effect on the population growth was, however, dependent on the population's spatial location and the spawning reaction norms in relation to altered individual growth rates. Simulated adaptations towards maturation at younger and smaller

fish countered a negative population effect of a changing climate in some situations, thus showing possible eco-evolutionary rescue scenarios.

It is clear that climate may induce phenotypic plasticity in life history traits. I hope that my thesis will contribute to illuminate why and how altered life history traits might affect an ectothermic species, such as the brown trout, at the population level in a changing climate. In addition, I have tried to explore an intersection between ecological and evolutionary responses to address how adaptive evolutionary scenarios might counteract the effects of a rapidly changing climate. I propose that the type of model framework used in this thesis should be a compelling applied tool for nature managers to infer future mitigation efforts at the population-level.

# Introduction

**Climate change – general biological consequences and directions**

Climate change can in a broad sense be defined as changes in the mean and variance in weather condition over a certain period and geographical area. Such changes have occurred multiple times and comprised long-term natural dynamic processes. Thus, climate change does not pose a new challenge to living organisms. In a biological perspective, variation in climate has played an essential role in defining the distribution range of species. Factors related to climate are well known arbitrators of evolutionary and ecological changes, where species have adapted (or perished) to changes in their ecological environment accordingly. However, contemporary climate change is of a very different magnitude compared to what has been observed in the past as global average temperatures will probably be 5 to 12 standard deviations above the Holocene temperature mean by 2100 (Marcott *et al.* 2013). The anthropogenic alteration of climate predicted within this century (IPCC 2007; IPCC 2013) raises big concerns for multiple species, as the environment is a key determinant of a species' ecology and survival. Accordingly, a large proportion of the scientific community focus on climate change and its effects on natural systems, resulting in a growing body of studies examining the ecological consequences of climate change (Walther *et al.* 2002; Parmesan 2006). As pointed out below, some general effects on the biota have been recognized in the literature, but there is still a long way to go before revealing the full picture of future ecological consequences.

*The knowledge base –General trends of climate change*
Current climate change has been attributed to the extinction of a number species (e.g., Deutsch *et al.* 2008; Sinervo *et al.* 2010), and more extinctions are expected as habitats are made uninhabitable (Thomas *et al.* 2004). One option to avoid extinction resulting from climate change is to disperse to more suitable environmental conditions. Indeed, this phenomena is already observed in terrestrial (Root *et al.* 2003; Chen *et al.* 2011) and marine (Perry *et al.* 2005) ecosystems, with a general trend of a poleward shift (Parmesan & Yohe 2003; but see VanDerWal *et al.* 2013). Shifts in a species' distribution are thus considered one the most widespread global responses to climate change.

Another option is to counter the changes through plastic (e.g., Przybylo, Sheldon & Merila 2000) and/or evolutionary (e.g., Bradshaw & Holzapfel 2006) responses. The latter adaptive mechanism

might be referred to as "evolutionary rescue" (Carlson, Cunningham & Westley 2014) as various populations avoid extinction by adaptive responses to changing climate. However, it is often not clear whether the response has an evolutionary component or not (Skelly & Freidenburg 2010; Merilä & Hendry 2014). Regardless, plastic or adaptive responses could range from behavioral alterations (Charmantier *et al.* 2008) to changes in phenology (Przybylo, Sheldon & Merila 2000). Especially advancement in phenology (i.e., the timing of seasonal activities such as breeding), seems to be another general trend observed across taxa (see e.g., Menzel *et al.* 2006; Wedekind & Küng 2010; Bartomeus *et al.* 2011; van Asch *et al.* 2013; Anderson & Gezon 2015).

Recent studies have also focused on how individual growth and size respond to climate change variables, as these traits are expected to be modified by factors such as temperature, and they are key predictors of a species population dynamics (Post *et al.* 1997; Parmesan & Yohe 2003; Daufresne, Lengfellner & Sommer 2009). The subsequent observed general negative trend of temperature warming on body size is proposed as the third main universal response to climate warming alongside changes in phenology and the distributions of species (Gardner *et al.* 2011). Effects of temperature on body size could be explain by temperature-body size rules (Atkinson 1994), where organisms exposed for warmer temperatures grow faster through ontogeny, but reach a smaller adult size (Berrigan & Charnov 1994). However, relationships between temperature and body size are probably not general and simple, but likely complex with proximate explanations that vary according to specific organisms (Angilletta & Dunham 2003). It is the effect on individual growth, and especially how variations in growth might alter the population dynamics that will be one of the main focuses throughout this thesis.

*Climate driven variations in individual growth –what to expect and how to address?*
Somatic growth and size are considered key life history traits across taxa as they are often directly linked to sexual maturity, survival, reproductive success and movement/migration (Peters 1983; Stearns 1992; Wootton 1998). Hence, growth and size are very important life history traits with the potential to shape the population dynamics and the ecological community (reviewed in Ohlberger 2013). The observed general negative trend in growth with increasing temperature (Gardner et al. 2011) is thus expected to affect the population dynamics of multiple taxa. However, the coupled effects of climate-induced variations in individual size and population effects are still largely unexplored in the wild. We thus know fairly little about how different natural populations will be affected in the future. Nonetheless, there are some compelling cases in the literature which point

out that the coupling of the climate effects on demographic traits and population growth indeed is relevant for understanding climate change effects (see e.g., Coulson et al. 2011; Salguero-Gomez et al. 2012). As the literature on these types of climate effects is relatively scares, it is difficult to extract general predictions. However, one expectation might be that the effect of climate on life history parameters will be especially prevalent in ectotherm species as temperature both has direct and indirect consequences on growth (see more details under "Climate change and brown trout - a contribution to the climate-change puzzle").

As computational and statistical tools have become more available the last decade, we can now produce models that are better in matching the dynamics of natural systems. However, interpreting the output produced by these new techniques is sometimes challenging as models become more complex with more variables. Thus, it is important to find study systems where one can investigate the ecological effects of climate change while isolating or minimizing confounding factors. One way to do this is to track populations that are restricted to specific and relatively small areas, thus reducing other potential environmental interactions due to e.g. long migrations. Further, by focusing on species where knowledge on different life history traits and their relations already is considerable, the potential to piece together realistic and informational population models increases. Then, by utilizing data from e.g. long time series or data collected from a climate gradient, it is possible to extract the effect of focused climate variables and thus extrapolate into the future.

Land –locked freshwater systems are intriguing in this perspective as the inhabiting populations typically are well defined and their biology relatively well-known. Additionally, one can find systems from sea level to high mountain regions, representing a clear environmental gradient that can be used to make predictions about how different populations might respond to climate change variables. Another important aspect related to the consequences of climate change on freshwater systems is the fact that inhabitants "adapt or perish" as their distribution is often physically restricted by migration barriers. Exploring the effects of environmental variability, e.g. temperature increment, on growth and the consequences for the population dynamics in such systems have therefore a large potential to increase our general understanding of climate change effects.

**Climate change and brown trout - a contribution to the climate-change puzzle**

Brown trout (*Salmo trutta*) is a well studied and ecologically important freshwater fish species native to Europe, but has also been introduced throughout the world for commercial and recreational purposes (Budy *et al.* 2013). It inhabits a tremendous range of habitats, from very small streams and lakes at a variety of altitudes, to large water bodies and even coastal habitats (i.e., as anadromous sea trout (Jonsson & Jonsson 2011)). The associated environmental properties encompass cold systems with a few weeks of ice-free conditions at high altitudes, to warm low-land systems without seasonal ice coverage. The large variability in habitats and variation in life history responses within this species (Elliott 1994), makes it ideal for exploring ecological consequences of a changing environment. The fact that this species is ecologically and economically important also makes it a model system for portraying effects of climate change to the general audience. Consequently, a large body of literature concerning the consequences of environmental variation on life history traits such as growth (Elliott 1976; Borgstrom 2001; Cucherousset *et al.* 2005), maturity (Jonsson & L'Abée-Lund 1993) and survival (Einum & Fleming 1999; Vøllestad & Olsen 2008) already exist. The potential to make inferences on the effects of climate change on these traits is thus considerable (see review of potential effects in Jonsson & Jonsson 2009).

In general, temperature can have both direct and indirect effects on individual growth for brown trout. The direct effect is linked to metabolism. As brown trout are ectotherms, growth rate will depend on metabolic rate, which in turn is dependent on ambient temperature. For brown trout, optimal temperature for growth (i.e. fastest growth rate) is expected to occur around 12-14 °C, whereas minimum and maximum temperature is around 3°C and 20°C, respectively, when fed maximum rations (Elliott 1975). These temperature thresholds will, however, vary with food abundance, individual size and acclimatisation time (see further details below in *"Thermal adaptations of growth –direct effect").* The indirect thermal effects are more complex and might involve variation in food and density effects (**Paper II**). Also, changes in seasonal temperature regimes may, in combination with winter precipitation, alter growth season length and thus growth prospects directly (**Paper III**, **Paper IV**) or indirectly via changed among-individuals interaction dynamics pertinent to under-the-ice-cover behaviour of the brown trout (Watz *et al.* 2015).

*Thermal adaptations of growth –direct effect*

In general, there are two main thermal adaptation hypotheses related to trout growth (Figure 1). The *local optima hypothesis* predicts that natural selection can shift the optimum, as well as the

minimum and maximum temperature for growth to match conditions the species experiences, as this will provide fitness benefits (Levinton & Monahan 1983). This specialisation in performance at one temperature regime is expected to lead to a trade-off against individual performance in another regime, i.e. specialist-generalist trade-offs (Angilletta *et al.* 2003). The *counter-gradient adaptation* hypothesis, on the other hand, predicts that populations from relatively harsh environments (low temperature, short season for growth and strong competition) grow faster than conspecifics from benign environments at all temperatures (Levins 1968; Conover & Present 1990). Consequently, no trade-offs concerning specialist-generalist are expected; however other types of trade-offs might be found, such as increased mortality due to behavioural differences (Biro *et al.* 2006) or reduces investment in immune defence (Niemelä *et al.* 2012).
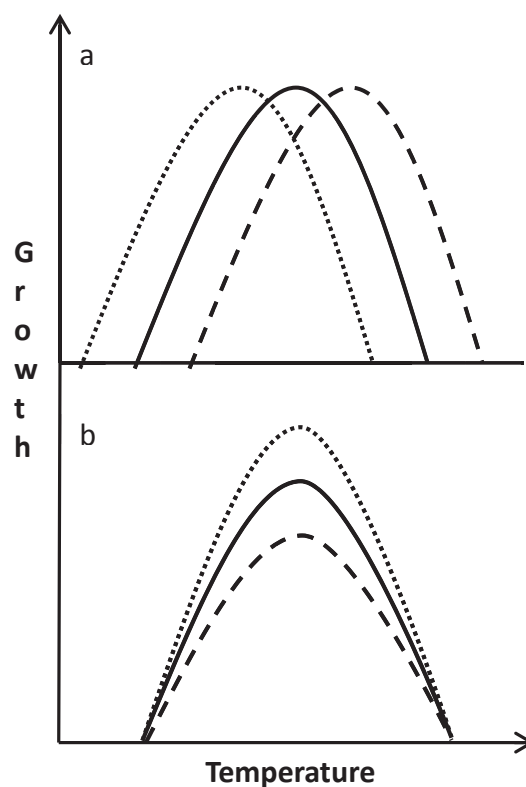


Figure 1: Theoretical thermal growth trajectories with a maximum, minimum and optimum temperature for growth for the local optima hypothesis (a) and the counter gradient hypothesis (b). Dotted (small) lines represent a cold environment and short growth season, solid line represent medium temperature and length of growth season while stippled line represent a warm environment and long growth season (**Paper I**).

Although several studies have addressed possible thermal adaptation for brown trout, the evidence for this seems ambivalent at best. The literature contains both support for a local optima hypothesis (Lobón-Cerviá & Rincón 1998; Jensen *et al.* 2008) and possibly the counter-gradient hypothesis (Jensen, Forseth & Johnsen 2000), but there is also support for no thermal adaptation

(Forseth *et al.* 2009). Establishing if and how adaptations to temperature occurs is important in many perspectives, but it is especially important concerning the use of established growth models (Elliott, Hurley & Fryer 1995), and also regarding entangling possible effects on the population dynamics. Many studies exploring possible thermal adaptations are centred around direct comparisons of experimental or natural growth rates to the growth rates predicted by a growth model originally developed for British brown trout (Elliott, Hurley & Fryer 1995). This type of modelling is potentially useful as a tool to account for the direct effect of temperature on growth. Specifically, one can predict the expected growth rate of a fish at any given temperature while feeding at maximum rations. Thus, by comparing the observed growth at a given temperature with the predicted growth at the same temperature, it is possible to infer the direct effect (metabolism) of temperature with more indirect effect of temperature (e.g. food abundance). However, the interpretation of these results will depend on the realism of the growth model at various temperatures and locations. Consequently, the original growth model for brown trout (Elliott, Hurley & Fryer 1995) has been modified and combined with other established growth models originally developed for bacteria (Ratkowsky *et al.* 1983), to produce area-specific growth curves (see e.g., Vøllestad, Olsen & Forseth 2002). The need to re-parameterize the model for various trout populations indicates that thermal growth trajectories differ among locations; which might not necessarily represent evolutionary adaptations but rather plastic responses according to acclimatisation time or other interacting environmental variables (Crozier & Hutchings 2014). Further research to address thermal adaptations of growth in brown trout is therefore necessary to account for the direct effect of temperature in natural systems and explore how this effect varies among populations. In the first manuscript (**Paper I**) included in this thesis, I have addressed the question of thermal adaptations through an experimental setup, to get better insight into how climate changes might affect different populations (see further description in material and methods).

*Temperature and interacting effects—direct and indirect effects*
Understanding the direct effect of temperature on brown trout growth across environments is an essential part of understanding effects of climate change at the individual level. However, to increase the realism of climate change predictions on growth, it is also crucial to include knowledge about how indirect and interacting effects of temperature affect growth in natural systems. Interacting factors have the potential to affect growth in non-additive ways.  Examples of such

interactions include: size-temperature (Imsland *et al.* 1996), photoperiod-temperature (Fiala & Oriol 1990), food-temperature (Brett, Shelbourn & Shoop 1969) and density-temperature (Crozier *et al.* 2010). For brown trout and many other fish species, information regarding temperature and how it interacts with other covariates to modify growth is essentially a missing piece of the climate change puzzle.

The density-temperature interactions should be of particular interest in a changing climate as density effects seems to have a large potential to modify temperature effects on growth of salmonids (Lobon-Cervia 2005; Crozier *et al.* 2010). Multiple studies have shown that, individually, temperature and density can have profound effects on brown trout growth (e.g., Elliott 1975; Jenkins *et al.* 1999; Ojanguren, Reyes-Gavilán & Braña 2001; Bohlin *et al.* 2002; Vøllestad, Olsen & Forseth 2002; Grant & Imre 2005; Lobon-Cervia 2007; Kaspersson & Höjesjö 2009). However, relatively few have explored the combined effects of these two controlling agents in natural systems. It is thus very interesting to look more closely on how these interacting effects jointly affect growth in the wild. Thus, in the second manuscript (**Paper II**) included in this thesis I have explored how temperature and density interacts to control individual growth in a wild population of brown trout.

*From separate effects on life histories to population dynamics*
Demographic frameworks like matrix models (Caswell 2001) represent a potent approach to disentangle mechanisms linking individual life histories and population-level responses (e.g., Crouse, Crowder & Caswell 1987; Hansen 2007). From matrix projection models it is possible to infer the relative contribution of each life stage (e.g, age) in the population processes. It is also possible to extract the long-term population growth rate (lambda). Long-term viability analysis including specific climate scenarios, could give good indications on future population responses. Further, elasticity and sensitivity analyses following the matrix model might identify key demographic parameters affecting the population dynamics. Additionally, during the model development process, gaps in the data- and knowledge bases could be pinpointed. However, the quantity of data needed to make reliable estimates of the various parameters included in a full age specific matrix model is large. This is especially true when including multiple environmental variables.

One way to achieve large data sets to explore climate effects on natural population is through long time series. However, as long and consistent time series often are difficult to obtain, piecing together the demography following both spatial and temporal scales might be one of our best chances to get insights in the effects of climate change on a population level. In Norway, trout populations inhabit natural climate gradients ranging from low to high altitudes, south-to-north (both to be considered as temperature gradient), and west-east gradient (precipitation gradient in Norway). The potential to explore how climate affects populations is accordingly large in Norway, as the different populations are exposed to a large variation in climate conditions (Figure 2).
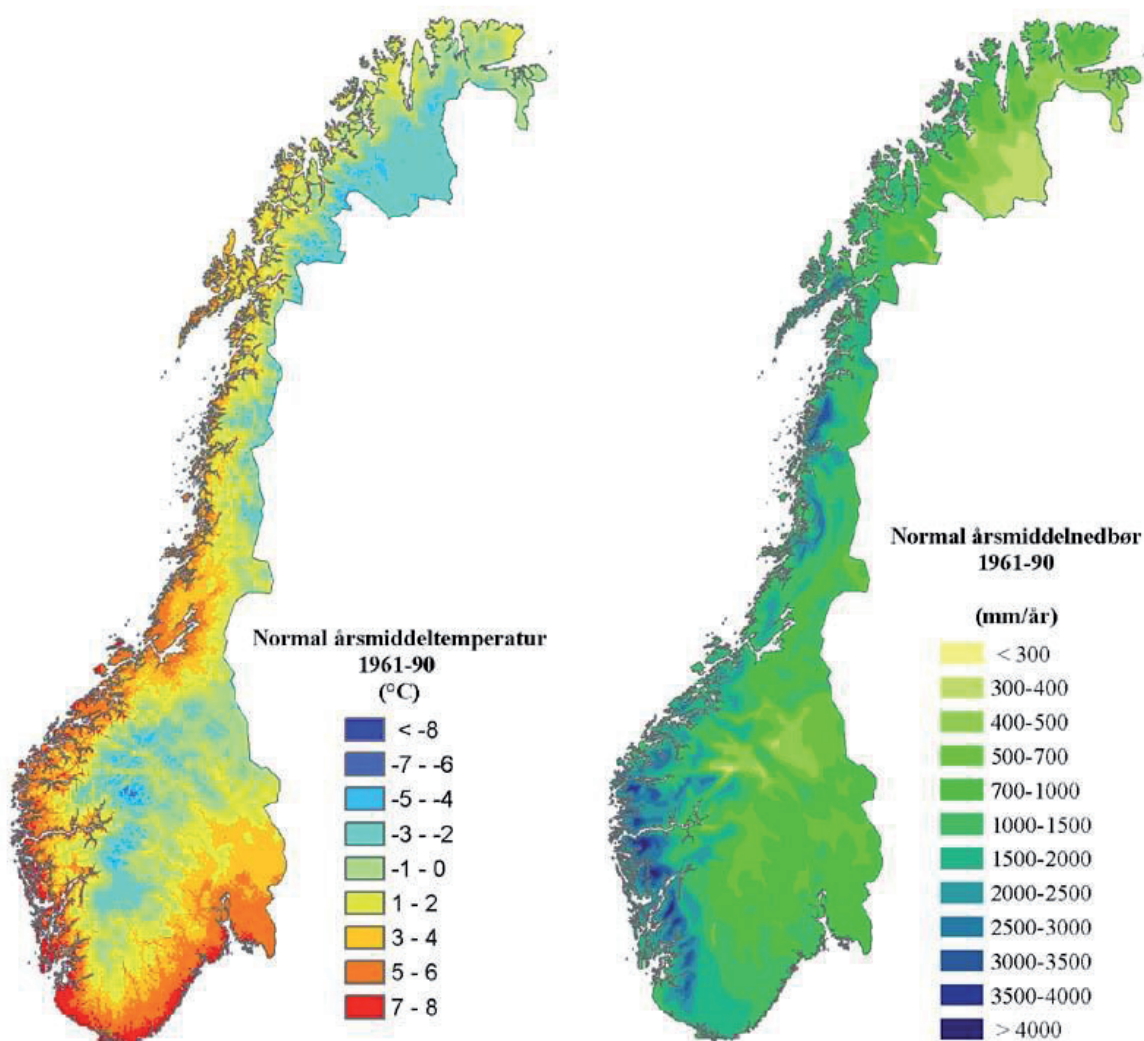


Figure 2: Annual mean air temperatures (left) and annual total precipitation (right) for year 1961-1990 (http://met.no/Klima/Klimastatistikk/Klimanormaler/).

Although there is an extensive literature base on the effects of the environment on life history elements, surprisingly few have focused on a population dynamic perspective of climate change (but see Sæther *et al.* 2000; Clark *et al.* 2003; Ozgul *et al.* 2010; Ohlberger *et al.* 2011; Vindenes *et al.* 2014). For brown trout there seems to be no attempt to build a functional matrix projection model that incorporates the effect of climate and potential modifying covariates. However, given the potential for such models in exploring population responses in life history traits to climate change, one should have good arguments not to pursue this approach. This is thus one of the main tasks of this thesis. Though, making realistic population projections as a function of climate change is challenging, and requires detailed knowledge on how populations respond to multiple potential interacting factors that vary across multiple scales. A more practical approach is exploring mechanistic effects of climate change variables on key life history traits on population viability. As temperature in general is expected to have a large effect on growth and growth is considered one of the most important life history trait across taxa (Peters 1983), exploring climate change effects on brown trout growth would not only reveal possible population specific responses but might be representative for a range of fish species and other ectotherms with similar life cycles. The third (**Paper III**) and fourth manuscript (**Paper IV**) in this thesis utilizes a demographic model framework and explores population responses through phenotypic changes in life history traits, following simulated climate change scenarios.

## Objectives

The overall objective of this thesis is to contribute to our understanding of climate change effects on biological systems, through environmental effects on brown trout. To achieve this, I constructed models based on temporal and spatial data to predict mechanistic effects on demographic parameters of particular variables related to climate change, such as precipitation and temperature. The demographic parameters were included in a matrix projection model to explore long-term effects on population growth.

The effects of climate, where I particularly focus on temperature, were explored utilizing inter-individual variation within a population, between-population at a regional scale and between populations at an inter-regional scale.

The above-mentioned topics were divided in four manuscripts. Specifically:

**Paper I**: Investigated potential thermal adaptations among populations of brown trout inhabiting different altitudes.

**Paper II**: Explored individual fish growth with the aim to understand how temperature might interact with other controlling agents, such as density, for growth in natural systems.

**Paper III**: Constructed a matrix projection model with the aim for a mechanistic understanding of population-level consequences of increasing temperatures at various altitudes and different adaptive responses at a regional scale.

**Paper IV**: Quantified climate effects on brown trout population life histories along a west-to-east gradient in southern Norway and forecasted population effects under different climate scenarios and different adaptation responses.

The following material and method chapter, as well as the results and discussion chapter, means to portray the larger and more general picture found in the above-mentioned manuscripts/papers. Detailed descriptions considering analysis, results and discussion are found in the respective manuscripts.

## Material and methods

The objectives in this thesis were achieved through three different main approaches:

- *A common garden experiment (**Paper I**)*, where fry from four different populations in Norway were reared in three different temperature regimes. The various populations were chosen from an altitudinal gradient from approximately 10 to 1060 meters above sea level. All fish populations were potamodromous, using inlet tributaries as spawning- and nursery habitat and lakes as feeding habitat. Mature male and female brown trout were collected during spawning and stripped for eggs and sperm, where the sperm and eggs were transported to a research facility. In order to test for the effects of temperature on growth, we build an experiment facility that included multiple small tanks with the possibility to individually control the temperature and water flow in each tank. The fertilized eggs was incubated in an experimental set up at similar temperatures and moved to the experimental temperature regimes at the start of external feeding. The specific temperature regimes were chosen to represent optimal (~13°C) and sub-optimal temperatures for growth below (~8 °C) and above (~15 °C) the defined optimal temperature for growth. Temperature was

recorded 5 times a day with temperature loggers and eggs and fry were monitored on a daily basis. All tanks were given a standard amount of commercial fish pellets four times a day during the experiment. Food was always observed in tanks from the preceding feeding event, indicating satiation. High-resolution digital photos were taken of the fry at the start and the end of the experiment, 14 days later. Fish lengths were measured on the photos (Figure 3). The difference between length at the start and length at the end of the experiment were treated as growth, and compared between populations. See a general description of statistical analysis under "*The general statistical approach*".
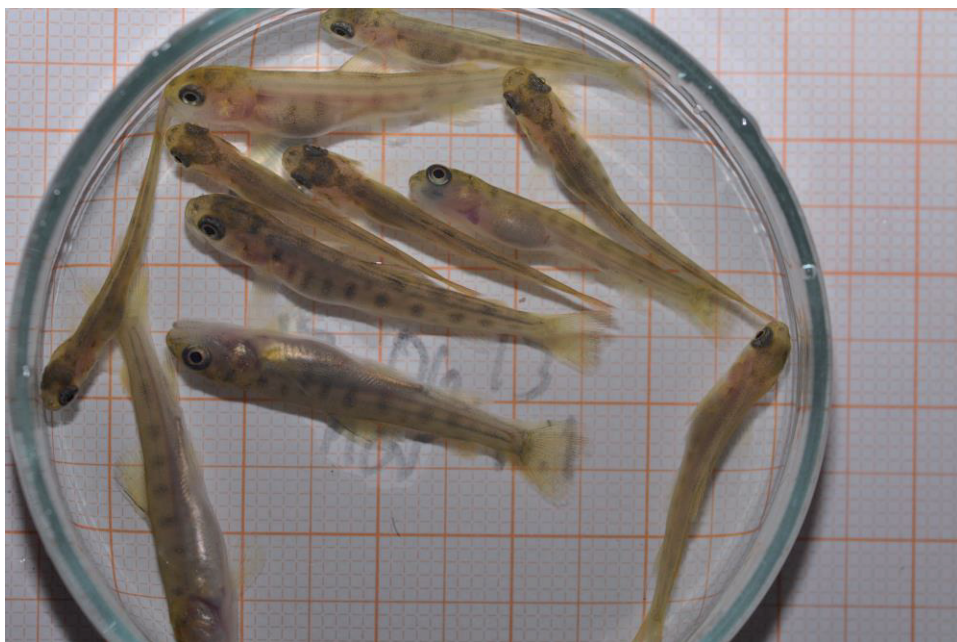


Figure 3: Example of photo used for length measurements of brown trout fry during the experiment in Paper III.

- *Detailed field study (**Paper II**)*, where we utilized an eight-year capture-mark-recapture data series on resident brown trout from a small stream system in Norway. The stream was organised into 25 contiguous stream sections, each ranging in length from 32 to 96 m. Temperatures were monitored at a daily basis by loggers throughout the growth season. The trout population was sampled with a backpack electrofisher during early summer and just prior to the spawning season in autumn. Trout abundance (excluding age-0 fish) at each site and sampling occasion was estimated using the Zippin multiple-pass removal method (Bohlin *et al.* 1989). Each fish (excluding age-0 fish) was tagged and length was meassured. As previous studies had shown very little between- sections-movement of individuals, we

were thus able to produce high-resolution (i.e., section-specific) density estimates. Observed growth rates were compared to maximum predicted growth rates at the same temperature from an already established growth model (Vøllestad, Olsen & Forseth 2002) to account for direct effect of temperature on growth. The variation between observed and predicted maximum growth was explored in a linear mixed effect model as a function of length, age, density, a spatial effect and average temperature during the growth period.

- *Population models based on temporal and spatial capture data of resident trout in lakes (**Paper III and Paper IV**)*, where environmental induced variations in growth, survival and maturation and their effects on the population dynamics were explored. Data were based on captures from gillnetting across multiple lake populations in Norway, with some time series extending decades back in time. These data were used to explore effect of environmental variation at a regional and an inter-regional scale within Norway. At the regional scale (Figure 4), we derived climate variables such as precipitation and temperature mainly from variations in altitude*longitude gradient (divided in three different climate zones), but also in time (variation between years). At the larger inter-regional scale (Figure 5), we focused on the variation in climate in a longitude gradient, including variation in time within the gradient. We then explored the effects of the derived climate variables on life history traits and population dynamics. Air temperatures and precipitation levels were estimated based on weather station recordings for the specific time and areas. We also included effects of a "weather package" (i.e., NAO-index) to explore spatial variation to large scale climate effects. The NAO-index (North Atlantic Oscillation-index) measures the anomalies in sea pressure between the Icelandic low pressure system and the Azores high pressure system. In Norway, a positive difference can is in general associated with more precipitation and warmer weather, while a negative difference is associated with drier and colder weather. At the inter-regional scale, we were able to better account for variation in density-effects utilizing a stock-recruitment model, compared to the smaller regional scale where variations in density only had a direct effect on growth in the population model. To project potential population effects under a changing climate, different 100-years climate scenarios were simulated to portray realistic future scenarios, downscaled from assessments from the Intergovernmental Panel on Climate Change (IPCC 2007; IPCC 2013). Possible effects of hypothetic evolutionary rescue scenarios (see Gonzalez *et al.* 2013; Carlson, Cunningham & Westley 2014) were also explored, following specific climate

scenarios at both the regional and inter-regional scale. Specifically, spawning ogives, as functions of age and size (Heino, Dieckmann & Godo 2002) was altered to mimic adaptive responses in maturation trends.



Figure 4: Study lake positions (filled dots) and names in the regional study system used in Paper III. Unfilled large circles represent the predefined climate zones with the respective number 1-3. Stars represent positions for representative weather stations (www.eklima.no). The dashed line constitute the national border between Norway and Sweden.
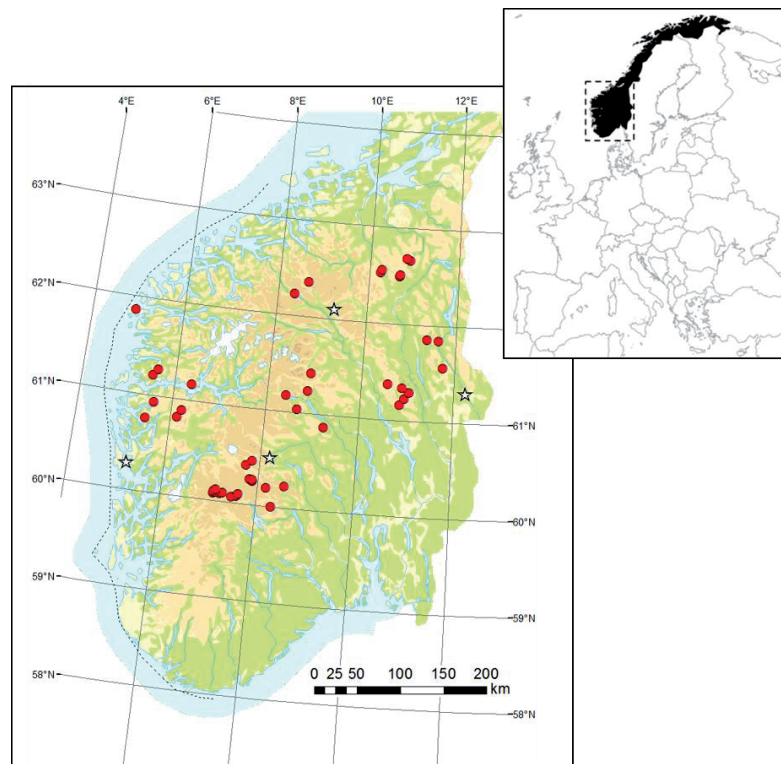


Figure 5: Study locations (red circles) in the inter-regional study system used in Paper IV. Weather stations (www.eklima.no) are shown as white stars. Non-green areas represent either agricultural (yellow) or alpine (brown) areas.

*The general statistical approach*

Throughout the thesis, I have mainly utilized statistical models such as generalized linear mixed models and linear mixed effects models to exploring biotic and abiotic effects on trout life history traits. I preferred mixed model approaches as they allow for inclusion of random and fixed effects and thus better address the lack of independence of repeated measurements (e.g., size measured at different time on the same fish) and allow for generalization of conclusion relating to effects such as time and place (Bolker *et al.* 2009). In general, the mixed models used can be defined as (in matrix notation):

$$y = X\beta + Zu + \epsilon$$

where $y$ is a vector of the focused observation, e.g. size at age, $\beta$ is a vector of unknown fixed effects and $u$ is an vector of unknown random effects, whereas $X$ and $Z$ represent known design matrices, chosen from biotic and abiotic factors in the environment, relating to $y$, $\beta$ and $u$. $\epsilon$ represent an unknown vector of random errors.

Further, I explored population viability based on projections from an age-structured matrix population model (Caswell, 2001), with focus on how temperature and other climate factors, through growth variations, affects the potential for population growth (Fig 2). Specifically, changes in age structure and trout abundance are modeled from:

$$
\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_{t+1} =
\begin{bmatrix}
f_1(E,Y_t)s_0(E,Y_{0,t}) & f_2(E,Y_t)s_0(E,Y_{0,t}) & \cdots & \cdots & f_{a_{max}}(E,Y_t)s_0(E,Y_{0,t}) \\
s_1(E,Y_t) & 0 & \cdots & \cdots & 0 \\
0 & s_2(E,Y_t) & \cdots & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 0 & 0 \quad s_{a_{max}-1}(E,Y_t) & 0
\end{bmatrix}
\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_t
$$

where $Y_t$ is the abundance of trout across all age classes $a=1,..., a_{max}$ at year $t$. Census time is chosen so that reproduction occurs at the beginning of each annual season. $f_a$ is the fecundity at age $a$ (i.e., the number of offspring produced per individual of age a during a year), $s_a$ is the survival probability of individuals from age $a$ to age $a + 1$, and $a_{max}$ is the maximum age considered in the model (may

vary between locations, depending on $E$). The vital rate $f_a$ differ from year to year depending on the age-specific growth rate $g_{a,t}$. The life history parameters $f_a$ and $s_a$ are also functions of the ecological environment $E$ and vary with location and time. Further, $f_a$ might also vary according to simulated evolutionary adaptations in maturation norms as a function of $E$. Accordingly, $K(E,Y)$, the Leslie matrix, is a function of $Y$ and $E$. In each time step, the survival of individuals in age class $a_{max}$ is 0, whereas individuals at all other ages spawn if mature and experience natural and recreational fishing mortality as defined below. From the Leslie matrix $K$, we can infer the population's long term rate of increase, λ, from the dominant eigenvector of the matrix. All statistical analysis was done in the statistical computing environment R (R core team 2013).

## Results and discussion

The complete set of analysis performed in this thesis show convincing results of climate effects of virtually all of the aspects explored. In an evolutionary perspective, **Paper I** demonstrates evidence for adaptations to both temperature and precipitation. Specifically, our models predicted higher early-life growth rates at all temperatures for populations living under conditions with high and unpredictable precipitation levels, as well as for high altitude populations. This is in line with a counter-gradient pattern, where populations living under harsh conditions often experiences short effective growing season and thus compensates with faster growth within the season (Conover 1990; Conover & Present 1990). Both temperature and precipitations is key elements in the present climate change predictions in Norway (CICERO 2009), and the results from **Paper I** thus suggest that populations from different rearing environments will vary in their response to predicted changes in climate. In particular, variation in precipitation seems to have a stronger selection potential for juvenile growth compared to direct temperature effects. As higher precipitation levels with more extreme weather is expected (IPCC 2007; CICERO 2009; IPCC 2013), populations in Norway might therefore experience selection towards increased growth rates during early life. This selection might be especially strong for western populations, where an already costal and wet environment might be even more pronounced. Adaptations in growth as a consequence of climate change might also result in trade-offs such as poorer swimming performance (Billerbeck, Lankford & Conover 2001) and reduced survival (Lankford, Billerbeck & Conover 2001). However, generalization of the results should be done with care as we only explored early-growth variations between four populations.

In **Paper II**, we showed how complex interactions between temperature and density act as controlling agents of growth in a natural stream-dwelling trout population. Here temperature had an indirect positive effect on growth, after controlling for the direct effect of temperature on metabolism. However, the positive effect of temperature was most prominent as density increased. At low densities, an increase in average water temperature of almost 4 °C had no to very little effect on growth rates, whereas the same temperature increase at higher densities almost doubled the estimated individual growth rates in the population. The positive indirect effect of temperature on brown trout growth at high density was likely an effect of variation in both food quality and quantity, although the empirical evidence for this was limited. Other studies focusing on interacting effects of growth and density found the opposite effect, where growth was reduced at warm temperatures and where this effect exacerbated at high densities (Crozier *et al.* 2010; Xu, Letcher & Nislow 2010). The discrepancy between results from **Paper II** and these other studies might result from multiple aspects. Yet, **Paper II** portrays a population living in an on average colder environment, where average daily temperatures is below the optimum temperature for brown trout growth (~12-13°C), compared to the warmer study systems of Crozier et al (2010), and Xu et al (2010). This suggests that the effect of the temperature–density interaction is reversed in systems where average summer temperatures are consistently lower than that optimum for growth. The results from **Paper II** and these other two studies should be compared with caution as our models controlled for a direct effect of temperature on growth (i.e. direct metabolic constraints of temperature), while the two other studies included the total effect of temperature in their models. Further, the temperature effect in **Paper II** was also very much dependent on age class, where young individuals showed the most pronounced response. Therefore, the results indicates that age structure and population density are highly important variables to include in population specific predictions when assessing climate change effects on resident salmonids.

In **Paper III**, we constructed an age structured matrix projection model including parameter estimates for multiple factors associated with the natural environment for trout and also multiple climate variables. This approach allowed us to produce area-specific population growth potential estimates (i.e., lambda) under different temperature simulations at a regional scale in Norway. Specifically, we found that an average summer temperature increase of 0.04 °C over 100 years produced a general positive effect on population growth in low altitude populations, but a negative

effect at increasing altitudes. Temperature simulations including more variable average summer temperatures over time had a general negative effect on lambda in all hypothetical populations. The negative effect on lambda seemed to mainly be governed by a reduction in fecundity due to reduced sizes at maturity, with the reduced size at maturity being an effect of the increased growth in early life, but with a small size at age for older individuals. Some of the results from **Paper III** are in direct contrast to a comparable study which found a *positive* effect of temperature and little effect of variable temperatures on population growth of pike, *Esox lucius,* in Windermere, United Kingdom (Vindenes *et al.* 2014). The dissimilarities in the results from **Paper III** compared to Vindnes *et al.* (2014) are likely a reflection of the difference in ecological interactions among the two study systems. One important difference between the trout populations used in our study and the Windermere pike populations is the dominantly piscivore diet of pike and dominantly invertebrate diet of the trout. A temperature increase might affect growth and fish condition differently according to food availability (see e.g. Winfield, James & Fletcher 2008, Paper II). Hence, variation in the response on climate change on the population dynamic in fresh water ectotherms might depend largely on possible ecological interactions (e.g. food availability vs density). We also explored the effects of possible adaptations in the spawning reaction norm by increasing probability of spawning at smaller sizes and thus decreasing size at maturity. This resulted in positive population growth across all populations under the simulated temperature increase. I will discuss more on these evolutionary rescue scenarios below.

In **Paper III**, we did some assumptions and simplifications (due to data limitations) resulting in that survival did not vary according to population density, but rather by age and climate zone. With this simplification, which probably is unjustified under natural conditions, we were able to explore mechanistic effects of temperature variation on the population dynamics of brown trout at a regional scale in Norway. In **Paper IV**, we relaxed the assumption and allowed survival to vary also with density. In addition, we had a stronger focus on inter-regional variation in climate variables along a longitudinal gradient. Thus, although the same model framework applied, the analysis and results from **Paper IV** varied somewhat compared to the results from **Paper III**. Specifically, the results from **Paper IV** demonstrated significant climate-longitude interactions in virtually all life-history traits explored. Hence, large-scale climate variation has yielded different trait values along the west-to-east gradient – despite the populations existing within the same climate zone (i.e., altitude interval). In particular, the winter NAO-effect is very different across this longitude-

20

gradient. Low NAO values generally means cold and dry conditions throughout the gradient, but high values will often result in large amount of snow in western areas and to far less degree so in the rain-shady eastern areas. The populations in **Paper IV** appeared in general more resilient (i.e., little variation in lambda) to the different simulated climate change scenarios compared to the results from **Paper III**. In **Paper IV**, we found a negative effect of increasing temperature variation for the population in the east and mid region of a longitude gradient in Norway, but a positive effect for the western population. Further, there was a small positive effect for populations in all regions following a climate scenario with an increase in mean temperature of 2.3°C within a 100-year time span. A combination of increased variation in yearly temperature and a general increase of 2.3°C seemed to have little effect on the population dynamics in all regions. The latter is a somewhat surprising difference from the **Paper III** results, where similar climate scenario produced the largest effect on the population dynamics. The disparity between **Paper III** and **Paper IV** could be a product of multiple aspects and it is not completely clear why these differentiated results occur. One reasonable explanation could be; at least some of the disparity is due simply to the notion that the temperature effect interact with other environmental components to produce a complex effect pattern across populations. This is evident in all four papers included in this thesis, as I observe phenotypic plasticity in thermal growth reaction norms **(Paper I)**, temperature effects dependent on density **(Paper II)** and temperature effects dependent on other climate components, such as precipitation, during summer and winter **(Paper III, Paper IV)**. Thus, variation in the effect pattern across regions and populations for similar climate simulations are expected rather than surprising. However, we also speculate that a density feedback system on survival, which is included in **Paper IV**, plays a key role in explaining the differences. As population density might be reduced with a changing climate, increased survival could be expected as survival often is density dependent in salmonids (e.g., Marschall & Crowder 1995; Einum & Nislow 2005). There are two other important differences related to the climate scenario and projection settings that may relate to the variation in results between the two studies:

- In **Paper III**, the climate scenarios were focused around a temperature increase of 4 °C, whereas the **Paper IV** most simulations had a more moderate temperature increase of 2.3 °C. This indicate that trout populations might be relatively well adapted to a moderate temperature increase with varying temperatures, but some populations might struggle in a climate scenario with more extreme temperature variations and increments. This hypothesis is strengthen by the negative effect imposed on the western populations in

**Paper IV**, under climate simulations including mean temperature increases of more than 3 °C.

- While the projections in **Paper III** represent mean population growth derived from multiple populations in the respective climate zone; **Paper IV** projections are done for one specific population, while moving it along the longitudinal gradient. However, the models behind the projections still based on multiple populations, and the chosen population represent an average population in the dataset. Large differences in projections due to this variation in settings between the two studies are thus not very likely.

**In Paper IV**, we also explored how phenotypic adaptations in maturation reaction norms would potentially affect the population projections. Specifically, increasing the probability to mature and spawn at smaller size and at younger age (i.e., shifting the spawning reaction norm, SRN, down left), produced a small positive effect on population growth under a non-changing temperature regime, and a temperature regime with increased annual variation. Interestingly, under a 4°C increase scenario western populations showed a more pronounced positive effect by shifting a negative population growth tendency based on the contemporary SRN, to a stabilizing (lambda=1) tendency by shifting the SRN down left. Forcing maturation and spawning to occur at larger sizes and for older individuals (i.e., shifting the SRN up right), produced a general negative to no effect under the different climate simulations.  All simulations compared to the climate specific projections without any adaptations in SRN.

In both **Paper III** and **Paper IV**, the hypothetical evolutionary rescue scenario (see clarification of evolutionary rescue in  Carlson, Cunningham & Westley 2014) are only to be considered as one possible type of adaptation, and we have little empirical support for this exact phenotypic change to happen. We know neither if this adaption can happen fast enough to cope with the rapid changes. Nonetheless, the plasticity observed, as in the case of brown trout, in maturation reaction norms (see e.g., Stearns & Koella 1986) may facilitate evolutionary changes (Price, Qvarnström & Irwin 2003). Also, fast adaptations in this trait might be possible, as age at maturation seems to be controlled by one major loci  in salmonids (Barson *et al.* 2015). Indeed, such rapid adaptations have been documented within another salmonid, the grayling (Haugen & Vøllestad 2001; Koskinen, Haugen & Primmer 2002).

The effect of the possible adaptations was pronounced in **Paper III**, counteracting the projected negative effects of climate change. Thus, these hypothetical adaptations could indeed act as an

evolutionary rescue for brown trout populations in a changing climate. The positive effect of reduced size at maturation seen in **Paper III** is an important notion for management decisions. As modern sport fishing regulations often are enforced to favor larger individuals (Gwinn *et al.* 2015), this might reduce the plasticity within a population and as a utter consequence oppose possible natural selection towards reduced size at maturity. Fishery induced evolution is in general well known concept in the literature, with the most common examples from large marine fisheries which are targeting large individuals and thus selects for early maturation (e.g., Olsen *et al.* 2005; Kuparinen & Merilä 2007).

## Limitations and caveats

I will start this section with a quote from the late renowned statistician George E.P. Box which goes something like "Essentially, all models are wrong, but some are useful". In the complex reality of biological interactions, this is probably an understated fact as giving true projections of natural processes and populations seem simply not possible. A more encouraging approach from Box is also: "Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful". Giving hope in that most models can in some way or the other be of use. This should always be kept in mind when interpreting models and their predictions. When trying to portray the real world as good as possible given the data, we have to do some simplifications and assumptions, which probably deviates from natural conditions. Thus, true projections or predictions will probably never occur. Nonetheless, if we have adequate and useful data to address specific questions, a lot could be learned.

As I constructed models based on temporal and spatial data to predict mechanistic effects of particular variables related to climate change, it is also important to stress that uncertainty will always be present. One of the main contributors to the uncertainty throughout this thesis, is the challenge to correctly entangle the effect in focus with other co-occurring variations in the biogeography as one move in space or time. The predictions of mechanistic temperature effects on growth potential should thus be regarded with this in mind. However, the type of model structures used in this thesis, as well as careful statistical assessment and biological reasoning behind the decision to include the various parameters, allows us to assess and deal with some of the uncertainty. Thus, we are able to produce estimates within reasonable limits.

As the main focus in this thesis is the effect of temperature, much of the predictions represent mechanical interpretations of the temperature effect. Consequently, many aspects of climate change are neglected in the models, although some main variables related to climate change such as precipitation and NAO-index are accounted for. Nevertheless, I believe the predictions are realistic within the biological frame sat by the model parameters.

# Conclusion

Within the four papers in this thesis, I have found that temperature has a complex effect pattern on individual growth for brown trout. Especially age, size and density are important confounding factors. Further, the thesis provides supporting evidence for a counter gradient adaptation in the growth reaction norm of trout. The papers included are also the first, to my knowledge, to analyze complex interaction patterns of climate variables on multiple life history traits of brown trout, and to combine these into a matrix population model. The novelty is especially found within the statistical description and interpretation of the interactions.

Because of all the interacting parameters, the consequences of global warming on the population dynamics will vary according to environmental settings in the natural habitat (e.g., according to density-, altitude- or longitude-gradients). In general, most populations used in our studies seem to cope relatively well with a moderate increase in temperature (i.e., <~2 °C) within the next 100-years. However, temperature increases towards as much as 4 °C might have detrimental consequences for some populations, especially for high altitude populations. The most pronounced effect on population growth was however seen in simulations including temperatures with increasing yearly variation around the mean. Although the direction of this effect varied somewhat between study systems, variation rather than steady increase in temperatures seems to affect the populations the most. An evolutionary rescue to some "doomed" populations might come in the form of an adaptive maturation reaction norm towards maturation at smaller size and younger age. This is a highly relevant aspect to consider for managers as selective harvest might counteract natural selection processes.

By increasing the knowledge base of this now inevitable change in climate, decision makers, managers, scientists and the general public can act on the base of factual understanding rather than assumptions. I hope that this will prevent and reduce further catastrophic events, lessens the

permanent negative fingerprint of climate change and awake increased awareness of the seriousness of the situation we are facing.

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